Greenland halibut (*Reinhardtius hippoglossoides* Walbaum, 1792) early stage distribution in the Gulf of St. Lawrence

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Abstract

Combining information from ichthyoplankton and bottom trawl surveys conducted since the mid 2000s, we present the first report on the distribution and development of early stages of Greenland halibut in the Gulf of St. Lawrence. Forty Greenland halibut larvae were captured during the early surveys (end of April, early May), especially south and north of Anticosti Island. Only 10 larvae were captured during the June surveys, few south of Anticosti Island and most were still found near the southeast end and north of the island over the deep Anticosti Channel. In August, newly settled postlarvae were found mainly north of Anticosti Island but also at deep stations in the Laurentian Channel and westward up to the Lower St. Lawrence Estuary. From the combined distribution of larva and newly settled postlarva standard lengths over sampling dates, it was estimated that the larvae would have hatched in late March or early April. Taken together, data on the distribution of Greenland halibut larvae and postlarvae support the conclusion of late-winter spawning in the Gulf of St. Lawrence, possibly over an area located in the deep Laurentian Channel southwest of Newfoundland.

Keywords: Greenland halibut, Gulf of St. Lawrence, larvae distribution

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Introduction

In the late 1980s and early 1990s, a combination of unfavourable environmental conditions for growth and reproduction along with overfishing caused a major collapse in the Atlantic cod (Gadus morhua) population in the northern Gulf of St. Lawrence (Lambert and Dutil, 1997; Savenkoff et al., 2004). In parallel with the decline in Atlantic cod biomass, an increase in the biomass of crustacean decapod species such as northern shrimp (Pandalus borealis) and snow crab (Chionoecetes opillio) was observed. Large Atlantic cod were the main top predator in this system before the 1990s, and the collapse of the population had important consequences for the entire ecosystem (Savenkoff et al., 2004). Recently, results from ichthyoplankton surveys have suggested that the abundance of small-bodied demersal forage species increased in the northern Gulf relative to the pre-1990 period, reflecting the impact of removing Atlantic cod predation on the fish community (Bui et al., 2010).

Although the relationship with the collapse of the Atlantic cod population is not clear, the Greenland halibut

(*Reinhardtius hippoglossoides*) population in the Gulf of St. Lawrence has also undergone a strong increase in abundance since the late 1990s and early 2000s (DFO, 2010). Greenland halibut now represents one of the most important fish species of the northern Gulf fisheries. However, despite its importance, very little is known of the biology and ecology of Greenland halibut in the Gulf of St. Lawrence ecosystem, especially concerning the main locations of egg and larva production and the conditions for development, growth, and survival of the early stages.

Between 2005 and 2009, ichthyoplankton surveys were conducted in spring (May and June) in the northern Gulf of St. Lawrence around Anticosti Island with the objective of documenting the ichthyoplankton community in that sector (Bui *et al.*, 2010). On those occasions, for the first time pelagic Greenland halibut larvae were regularly captured north, northeast, and south of Anticosti Island. In addition, newly settled Greenland halibut postlarvae are captured during the annual summer (August) bottom trawl research survey conducted by the Department of Fisheries and Oceans (DFO), Canada, in the northern Gulf of St. Lawrence. Using information from these ichthyoplankton and bottom trawl surveys, this study presents the first description of Greenland halibut larval development and distribution for the Gulf of St. Lawrence. Such information will be of great interest to those concerned with conservation of the Greenland halibut population, managers of the fishery as well as those interested in the ichthyofauna of the Gulf. Results from this study will serve as a basis for further investigations on the early life history stages of Greenland halibut in the Gulf of St. Lawrence.

Materials and Methods

Sampling

The sampling protocol for the ichthyoplankton surveys is described in detail in Bui et al. (2010). Briefly, ichthyoplankton samples were collected in May and June from 2005 to 2009 (see Table 1) using a 61 cm diameter bongo net with 333 µm mesh and flow meters at the mouth of each net to calculate the volume filtered. A double-oblique tow was carried out between the surface and 150 m when possible; at shallower stations (less than 150 m) the double-oblique tow sampled between about 10 m off-bottom and the surface. An additional doubleoblique tow was done in the upper layer (surface down to about 50 m). Samples were immediately preserved in a 4% buffered formaldehyde and seawater solution or pure ethanol (one side of the bongo in 2007 and 2008). All samples, from both bongo nets and both tows, were sorted for ichthyoplankton. When Greenland halibut larvae were found in both nets of the bongo sampler, paired sample *t*-test were used to verify the effect of the preservative agent (formaldehyde or pure ethanol) on larval measurements.

Temperature data of the water column were collected during all surveys. Temperatures were measured using a Sea-Bird SBE19 CTD profiler in 2007, 2008, and 2009 and with a temperature and depth data logger (Minilog, Vemco) in 2005 and 2006. Mean temperatures of the upper layer (3 to 50 m) were calculated for each survey. The first few upper metres were not included in the mean temperature calculation to reduce variability caused by wind, tidal mixing, and solar heating.

Each year, DFO–Québec region conducts a summer (August) bottom trawl research survey to assess the abundance and distribution of groundfish species and northern shrimp (*Pandalus borealis*) in the northern Gulf of St. Lawrence (see Table 2). A complete description of the sampling protocol, which involves the depth-stratified random sampling of ~200 stations over the entire northern Gulf, can be found in Bourdages *et al.* (2010). The fishing gear used is a four-sided *Campelen* 1 800 shrimp trawl equipped with a 12.7 mm codend. The tows must last between 10 and 20 minutes (standard is 15 minutes) at three knots, starting from the time the trawl touches the sea floor. Catches are sorted by taxonomic groups and the number of individuals per group is recorded along with the total weight. Temperature data during the tows are recorded by a Sea-Bird SBE19 CTD profiler fixed to the top of the trawl; however, due to the rough towing conditions, data are often of poor quality or missing.

Data analysis

For the 2005 to 2009 ichthyoplankton samples, the volume of water filtered was used to standardize larval abundances, which are presented as the number of individuals per 10 m². However, it was rare that more than one postlarva was observed in the bottom trawl for a given tow, and no standardization for the duration (which varies little) or the sampled area of the tow was applied. Data were assembled by sampling period (larvae: May and June; postlarvae: August), and data for individual years were cumulatively plotted to present composite images of the seasonal distributions of early stages of Greenland halibut. The representations follow the proportional symbol mapping protocol recommended for the visualization of spatial data (Tanimura et al., 2006). Maps were produced using the PBS Mapping package (Schnute et al., 2008) available in R (R Development Core Team, 2010).

Distributions of Greenland halibut larvae collected from 2005 to 2009 were compared to available historical information for the region. De Lafontaine (1980) reported the observation of a single larva specimen of Greenland halibut caught with a 61 cm bongo net in May 1977 in the Lower St. Lawrence Estuary. In the mid-1980s, systematic sampling with similar bongo nets in May and June over most of the northern Gulf (see Ouellet et al., 1994) caught only three Greenland halibut larvae, all in June 1986. Therefore, prior to this study most data on Greenland halibut larva abundance and distribution in the Gulf of St. Lawrence come from ichthyoplankton surveys conducted in the 1960s and 1970s in the southern Gulf (e.g., Kohler et al., 1976; 1977). According to the cruise or time of the year, the sampling gears used in those surveys included neuston and conical plankton nets, a Miller high-speed sampler, bongo nets, and a ~ 2 m opening Isaacs-Kidd mid-water trawl. Greenland halibut larvae were caught on few occasions between 1971 and 1974 and almost exclusively in May (from 11 to 24 May) using the Miller high-speed sampler (between the surface and ~15 m in depth) and the Isaacs-Kidd (stepped oblique tows from

Year	Period	Sampling dates DoY	Nb of stations	Mean (Median) T°C Min.; Max.	Nb of larvae
2005	May	09/05–12/05 130.5	29	0.629 (0.634) 0.113; 1.449	6
	June	08/06–16/06 163.0	29	2.780 (2.706) 1.893; 4.088	4
2006	May	11/05–14/05 132.5	24	2.024 (1.999) 1.116; 2.950	5
	June	06/06–08/06 158.0	23	3.614 (3.484) 2.664; 5.042	1
2007	May	15/05–18/05 136.5	28	0.623 (0.694) -0.225; 1.029	2
	June	12/06 163.0	4	no data	1
2008	April	29/04–02/05 121.0	12	0.146 (-0.12) -0.424; -0.885	9
	May	13/05–17/05 136.0	34	1.074 (1.12) -0.469; 2.301	10
	June	11/06–15/06 165.0	24	2.666 (2.743) 0.916; 4.863	4
2009	May	11/05–13/05 132.0	23	0.800 (0.677) 0.300; 1.936	8
TOTAL					50

Table 1.Summary of the sampling effort, temperature conditions in the upper layer (0–50 m) of the
water column, and the number of Greenland halibut larvae captured in the northern Gulf of
St. Lawrence from 2005 to 2009. DoY = Day of the Year (median of sampling dates).

bottom to surface) (Kohler *et al.*, 1977). Unfortunately, no demographic data (*e.g.*, standard length) are available on the specimens, and the volumes of water filtered were not recorded for those gears. Therefore, the total number of larvae caught at the stations was plotted to illustrate the distribution. Finally, two Greenland halibut larvae as reported in May 1982 from a series of zooplankton samples collected in Baie des Chaleurs (Quebec, Canada) were also included (Lanteigne, MS 1985).

Single-factor ANOVAs or non-parametric Kruskal-Wallis tests when there was heterogeneity of variances among groups (years) were used to test for significant difference in mean larvae or postlarvae standard length between years.

Results

Larva and postlarva distribution

The ichthyoplankton surveys were conducted in spring, with the earliest starting on 29 April 2008 and the latest ending on 16 June 2005 (Table 1). The June 2007 survey was stopped early because of mechanical problems with the ship. More Greenland halibut larvae were observed during the late April and May surveys (Table 1). Despite the low number of stations visited due to bad weather, nine larvae were captured along the south coast of Anticosti Island during the earliest survey conducted at the end of April 2008 (Table 1). During the May surveys, Greenland halibut larvae were observed at

Year	Sampling dates	Nb of	Nb of	Postlarvae standard length	
	DoY	stations	postlarvae	Mean ± 1SD (mm)	Min. – Max. (mm)
2004	03/08–01/09 236.7	142	4	60.7 ± 5.1	56.0-68.0
2005	29/07–30/08 237.0	204	1	66.0	_
2006	01/08–31/08 232.8	220	8	65.2 ± 15.7	30.0-78.0
2007	01/08–31/08 231.4	206	10	60.6 ± 13.2	33.0-76.0
2008	23/07–26/08 223.8	239	8	67.0 ± 8.9	56.0-79.0
2009	30/07–02/09 231.3	203	10	64.2 ± 5.1	54.0-71.0
2010	01/08–05/09 239.4	198	5	69.0 ± 4.0	64.0-74.0
Total			46		

Table 2. Summary of data on Greenland halibut postlarvae from the August bottom trawl research surveys in the northern Gulf of St. Lawrence. DoY = median day of the year.

the easternmost stations south and north of Anticosti Island (Fig. 1a). During the June surveys, the fewest Greenland halibut larvae were captured south of Anticosti Island, but were still observed near the southeast end and also north of the island, over the Anticosti Channel (Fig. 1a).

Although the surveys were conducted at about the same time each year, there were marked differences in mean water temperature among years. Spring 2006 was very warm relative to other years, with the mean near-surface water temperature in May 2006 being nearly a full degree Celsius warmer than the second warmest year (2008; Table 1). Near-surface water temperatures were much colder in May 2005 and 2007 (Table 1).

Despite an almost constant sampling effort each year, the number of newly settled postlarvae found in August in the bottom trawl from 2004 to 2010 varied among years; from a single specimen in 2005 to a maximum of 10 in 2007 and 2009 (Table 2). Most postlarvae were captured north of Anticosti Island. Interestingly, many of the larger postlarvae were found westward of Anticosti Island and in the deep stations of the Laurentian Channel (Fig. 1b).

Larva size and growth

On some occasions (one station in 2006 and two stations in 2008), Greenland halibut larvae were found in

both nets of the bongo sampler. The paired sample *t*-test detected a significant difference (t = 3.646, df = 3, p = 0.036) with larvae in ethanol being larger (mean difference = +2.026 mm) relative to larvae in formaldehyde. However, given that most larvae through the years were preserved in formaldehyde (n = 35; ethanol, n = 14) and the low number of larvae for the test, it may be premature to conclude that significant shrinkage occurs in larvae



Fig. 1a. Composite distribution of Greenland halibut larvae in the northern Gulf of St. Lawrence obtained from ichthyoplankton surveys conducted in May and June between 2005 and 2009.



Fig. 1b. Composite distribution of Greenland halibut postlarvae in the northern Gulf of St. Lawrence from 2004 to 2010 by 10 mm size (standard length) group. The postlarvae were captured during the August bottom trawl research surveys over the entire area (station sampled during the 2010 survey are shown as an example).

preserved in the formaldehyde–sea water solution. Thus, the difference was not considered further in the analysis. Combining the results for all years, Greenland halibut larva size (standard length) during the May surveys ranged from 14.43 to 24.48 mm with a mode at 20.30 mm (Fig. 2). Fewer larvae were captured during the June surveys, and standard lengths ranged from 25.47 to 31.87 mm (Fig. 2). Postlarva standard lengths in August varied from 30.0 to 79.0 mm, with a modal length of 62.5 mm (Fig. 2).

Considering each year individually, there was interannual variability in larval size between years. Although this was not statistically significant (Kruskal-Wallis non-parametric test: $\chi^2 = 8.49$, p = 0.075, df = 4), the larger Greenland halibut larvae were found in May 2006 and 2008, the two warmest years (Fig. 3). In comparison, smaller larvae were observed in the colder period of May 2005 and 2009 (Fig. 3). Likewise, mean standard lengths of postlarvae were smaller in 2004 and 2007 compared to 2006, 2008, and 2010 (Table 2). However, there was a wide range of postlarval sizes each year and again these differences were not statistically significant (ANOVA, F = 0.521, p = 0.789, df = 6).

All larvae caught with bongo nets during the ichthyoplankton surveys were bilaterally symmetrical and showed no indications of the shape changes (*e.g.*, eye migration) associated with metamorphosis (Fig. 4a–d), thus we assumed that all were still fully pelagic. The majority, 68% (34 out of 50), were found in the 0 to 50 m bongo tows.



Fig. 2. Frequency distribution of Greenland halibut larvae and postlarvae captured in the northern Gulf of St. Lawrence between 2005 and 2009 (2004 and 2010 for postlarvae samples). In May and June, larvae were captured by a bongo sampler during ichthyoplankton surveys. In August, specimens were captured in bottom trawl tows.



Fig. 3. Greenland halibut larva size (each circle represents one larva) for each ichthyoplankton survey between 2005 and 2009 and mean water temperature in the upper 50 m of the water column for each survey (stars).

Distribution of larvae and postlarvae standard lengths over sampling dates suggest a linear increasing trend in size between larvae caught in May and June and the few small postlarvae caught in August (Fig. 5). Assuming a standard length at hatching of ~10 mm (Fahay, 2007) those larvae would have hatched in late March or early April (Fig. 5). However, the size of most postlarvae captured in



August would indicate that hatching principally occurred earlier, or that those specimens grew faster than suggested when comparing the larvae captured in May and June (Fig. 5). More sampling throughout the season would be required to solve those questions.

Historically, only four Greenland halibut larvae were captured in the northern Gulf, including the Lower Estuary; one in May 1977 in the Estuary and three in June 1986, two larvae were located near Quebec's North Shore northeast of Anticosti Island and one larva was located in the center of the north-western Gulf (Fig. 6). During the 1970s, systematic ichthyoplankton surveys were conducted seasonally in the southern Gulf. Greenland halibut larvae were rarely captured, and almost all were from May surveys and at the northeast limit of the sampling grid, over the deep Laurentian Channel southwest of Newfoundland (Fig. 6).

Discussion

Larva hatching time and growth

Our study presents the first detailed information to date on the distribution and development until settlement

of Greenland halibut larvae and postlarvae in the Gulf of St. Lawrence. Historically, Greenland halibut larvae have rarely been reported in the northern Gulf of St. Lawrence. In contrast, young Greenland halibut larvae were regularly found in our recent ichthyoplankton surveys (2005 to 2009), possibly reflecting the increase in abundance of the Gulf population observed since the late 1990s (DFO, 2010). In addition, the observations of smaller (younger) larvae along the southern margin of Anticosti Island in spring (May), the persistent presence of older larvae (June), and the relative abundance of postlarvae north of the Anticosti Island in August as well as the apparent displacement of postlarvae westward in the Laurentian Channel (see Fig. 1a, b) are consistent with late winter spawning in the deep Laurentian Channel, southwest of Newfoundland, and a transport of the eggs upstream with the residual deep current or of the larvae after rising to the upper layer of the water column in the northern Gulf.

It could be considered that 50 Greenland halibut larvae captured in the northern Gulf of St. Lawrence is too low a number on which to infer reliable ecological information; however, these numbers are comparable to concentrations observed in various tows (mid-water trawls or bongos)



Fig. 5. Suggestion of Greenland halibut hatching time from the distribution of larva and postlarva standard length on sampling dates (DoY). For the postlarvae, only data from the years when the larvae were sampled (2005 to 2009) are included.

from other regions (Haug et al., 1989; Simonsen et al., 2006; Sohn et al., 2010). Sohn et al. (2010) also reported that smaller larvae occupy the deeper regions of the water column, whereas our deeper bongo tows were limited to 150 m. Thus, although most larvae were observed in the upper-layer tows, it is possible that a portion of the larval population was not sampled by the bongos. Nonetheless, the larvae caught in our study varied in standard length from 14 to ~31 mm and all were bilaterally symmetrical. The larvae and postlarvae were caught in May, June, and August each year. Combining all years, larval mean standard length was 19.92 ± 2.36 and 28.85 ± 1.85 mm for May and June samples, respectively; these values are slightly larger but comparable to the mean standard length of Greenland halibut larvae caught at similar periods of the year west of Greenland (Simonsen et al., 2006). The distribution of standard length over time suggest that hatching occurred in March or early April from eggs most likely spawned in February or early March. Unfortunately, our data are insufficient to determine if the larval growth rate varies during early development or following metamorphosis and settlement to deep water. Moreover, this increase in length was accompanied by notable development of the ventral or abdominal region (see Fig. 4a-e), hence an increase in body height. Future studies investigating development and growth performance should take into account the continuous shape change of larvae during development. Finally, our data also indicate that water temperature conditions in the upper 50 m of the water column may influence larval growth. Interannual fluctuations in water temperature could therefore have a



Fig. 6. Historical observations of Greenland halibut larvae in the Gulf of St. Lawrence. Larvae in the northern Gulf in June 1986 are from Ouellet *et al.*, 1994, and one larva was recorded in the Lower St. Lawrence Estuary in May 1977 (De Lafontaine, 1980). Data for the May surveys in the southern Gulf of St. Lawrence are from Kohler *et al.* (1976, 1977), and Lanteigne (MS 1985).

significant impact on the duration of the pelagic phase of Greenland halibut, on the timing of metamorphosis, and, potentially, on recruitment success.

Possible spawning area of Greenland halibut

Earlier investigations of Greenland halibut distribution concluded that the population assembles in relatively warm deep waters for spawning in winter (Smidt, 1969; Templeman, 1973). Since small yolk-sac larvae, from 10 to 15 mm, were caught mostly in deep waters whereas larvae larger than ca. 16 mm were more frequent in the upper layers, the earlier reports also refer to the newly hatched larvae as being bathypelagic (Jensen, 1935; Smidt, 1969; Bulatov, 1983). However, Simonsen et al. (2006) reported larvae as small as 12.5 mm with gut content; in addition, most larvae between 12 and 16 mm had little yolk sac remains and were feeding (presumably in the upper layer of the water column). Similarly, in our study, the smallest larvae were about 14 mm with no yolk sacs and the majority of the specimens were caught in the surface (0-50 m) tows.

Historically, adult Greenland halibut were captured in abundance in January in the deep region southwest of Newfoundland (Castonguay and Valois, MS 2007). Late-winter spawning and egg development in the deep waters of the southern Laurentian Channel would be compatible with the spring distribution of young pelagic larvae reported in the earlier studies (1970s) and with the spatial pattern observed in May and June in our study. In May, the distribution of young larvae south of Anticosti Island and north over the slope of the Anticosti Channel could represent local hatching from eggs spawned and transported westward in the deep channels (the Laurentian Channel divides in two minor branches northwest of the proposed spawning area: the Anticosti and the Esquiman channels). Greenland halibut eggs have been reported to be bathypelagic. The reported specific gravity of newly spawned Greenland halibut eggs of ca. 1.0279 g m-3 (Stene et al., 1999; P. Ouellet, unpubl. data) corresponds to the density (sigma-t) normally recorded near the bottom in that region of the Gulf (Petrie et al., 1996). However, the residual near-bottom westward current was estimated at 0.025 to 0.05 cm s⁻¹ for that region (Saucier *et al.*, 2003; Sourisseau et al., 2006). This circulation implies a limited displacement of the eggs (from 20 to 40 km over 30 days) during incubation (assuming an incubation period of 28 days at 5°C; Yvan Lambert, DFO, Maurice Lamontagne Institute, pers. comm.), hence larval hatching should occur relatively near the spawning ground.

Larvae residing in the upper layer of the water column will be subjected to the general circulation of the surface water masses. The larvae observed close to the southern shore of Anticosti Island would have been transported westward (Saucier et al., 2003); indeed, no older or larger larvae were caught there in June (although the bongo sampler is likely not very efficient for capturing the larger larvae). In contrast, the larger larvae caught in June were located over the shallow area southeast of Anticosti Island and north of the island over the Anticosti Channel, probably as a result of small-scale hydrodynamic features favourable to larval retention in those areas. Furthermore, the relative abundance of postlarvae north of Anticosti Island in August of each year confirms that pelagic Greenland halibut larvae are retained in that sector of the northern Gulf. Larger postlarvae tend also to be found farther west in the deep waters, which also agrees with a westward drift of larvae following hatching. Moreover, this scenario could explain why juvenile Greenland halibut are more abundant north of Anticosti and in the western sectors of the Gulf, including the Lower St Lawrence Estuary (Bourdages et al., 2010).

As stated by De Lafontaine (1980) more than 30 years ago, dedicated surveys with higher spatial resolution that include the deep waters of the Laurentian Channel will be necessary to detect the presence of eggs or newly hatched larvae early in spring, to validate and better define the limits of the suggested reproductive area, and to confirm the importance of that region of the Gulf of St. Lawrence for the Greenland halibut population.

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References

- BOURDAGES, H., D. ARCHAMBAULT, B. BERNIER, A. FRÉCHET, J. GAUTHIER, F. GRÉGOIRE, J. LAMBERT, and L. SAVARD. 2010. Preliminary results in the groundfish and shrimp multidisciplinary survey from August 2009 in the northern Gulf of St. Lawrence. *Can. Data Rep. Fish. Aquat. Sci.*, **1226**: xii +72 p.
- BUI, A. O. V., P. OUELLET, M. CASTONGUAY, and J.-C. BRÊTHES. 2010. Ichthyoplankton community structure in the Northwest Gulf of St. Lawrence (Canada): Past and present. *Mar. Ecol. Prog. Ser.*, **412**: 189–205. doi: 10.3354/meps08687
- BULATOV, O. A. 1983. Distribution of eggs and larvae of Greenland halibut, *Reinhardtius hippoglossoides* (Pleuronectidae), in the Eastern Bering Sea. J. Ichthyol. (Vopr. Ikhtiol. 1981), 23: 157–159.
- CASTONGUAY, M., and S. VALOIS. MS 2007. Ecologically and biologically significant areas for demersal fishes in the northern Gulf of St. Lawrence / Zones d'importance écologique et biologique pour les poissons démersaux dans le nord du Golfe du Saint-Laurent. Can. Sci. Adv. Sec., Res. Doc. 2007/014.
- DE LAFONTAINE, Y. 1980. First record of Greenland halibut larvae *Reinhardtius hippoglossoides* (Walbaum) in the lower St. Lawrence estuary. *Nat. Can.*, **107**: 285–287.
 DFO. 2010. Assessment of the Greenland Halibut Stock in the Gulf of St. Lawrence (4RST) in 2009. *DFO Can. Sci. Advis. Sec. Sci. Advis. Rep.* 2010/028.
- FAHAY, M. P. 2007. Early stages of fishes in the western North Atlantic Ocean (Davis Strait, southern Greenland and Flemish Cap to Cape Hatteras). Vol. 2, Scorpaeniformes through Tetraodontiformes. Northwest Atlantic Fisheries Organization. Dartmouth, N.S.
- HAUG, T., H. BJØRKE, and I.-B. FALK-PETERSEN.
 1989. The distribution, size composition, and feeding of larval Greenland halibut (*Reinhardtius hippoglossoides* Walbaum) in the eastern Norwegian and Barents Seas. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer.*, 191: 226–232.
- JENSEN, A. S. 1935. The Greenland halibut (*Reinhardtius hippoglossoides* (Walb.)). Its development and migrations. Mémoire de l'Académie Royale des Sciences et des Lettres de Danemark, Copenhague. Série 9, t. VI (4), 36 p.

KOHLER, A. C., D. J. FABER, and N. J MCFARLANE. 1976. Eggs, larvae and juveniles of fishes from plankton collections in the Gulf of St. Lawrence during 1970–1971. *Fish. Mar. Serv. Res. Tech. Rep.*, 645. 139p.

1977. Eggs, larvae and juveniles of fishes from plankton collections in the Gulf of St. Lawrence during 1972 to 1975. *Fish. Mar. Serv. Tech. Rep.* **747**, 180p.

- LAMBERT, Y., and J. -D. DUTIL. 1997. Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. *Can. J. Fish. Aquat. Sci.*, **54**: 2388–2400. doi.org/10.1139/ cjfas-54-10-2388
- LANTEIGNE, M. MS 1985. Distribution spatio-temporelle des larves de crabe appartenant aux genres Chionoecetes et Hyas dans la baie des Chaleurs, Canada. M.Sc. Thesis, Moncton Univ., N.B.
- OUELLET, P., J.-P. ALLARD, and J.-F. ST-PIERRE. 1994. Distribution des larves d'invertébrés décapodes (Pandalidae, Majidae) et des œufs et des larves de poissons dans le nord du golfe du Saint-Laurent en mai et juin de 1985 à 1987 et 1991–1992. *Rapp. tech. can. sci. halieut. aquat.*, **2019**: viii+60 p.
- PETRIE, B., K. DRINKWATER, A. SANDSTRÖM, R. PETTIPAS, D. GREGORY, D. GILBERT, and P. SEKHON. 1996. Temperature, salinity and sigma-t atlas for the Gulf of St. Lawrence. *Can. Tech. Rep. Hydrogr. Ocean Sci.*, **178**: v + 256 p.
- R Development Core Team. 2010. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <u>http://</u> www.R-project.org/.
- SAUCIER, F. J., F. ROY, and D. GILBERT. 2003. Modeling the formation and circulation processes of water masses and sea ice in the Gulf of St. Lawrence, Canada. J. Geophy. Res. 108 C8, 3269. doi:10.1029/2000JC000686
- SAVENKOFF, C., M. CASTONGUAY, A. F. VÉZINA, S.-P. DESPATIE, D. CHABOT, L. MORISSETTE, and M. O. HAMMILL. 2004. Inverse modelling of trophic

flows through an entire ecosystem: the northern Gulf of St. Lawrence in the mid-1980s. *Can. J. Fish. Aquat. Sci.*, **61**: 2194-2214. doi: 10.1139/F04-154

- SCHNUTE, J. T., N. M. BOERS, R. HAIGH, and A. COUTURE-BEIL. 2008. PBS Mapping 2.57: user's guide revised from *Can. Tech. Rep. of Fish. and Aquat. Sci.*, 2549: v1 + 118 p. Last update Jul 24, 2008.
- SIMONSEN, C. S., P. MUNK, A. FOLKVORD, and S. S. PEDERSEN. 2006. Feeding ecology of Greenland halibut and sandeel larvae off West Greenland. *Mar. Bio.*, 149: 937–952. doi: 10.1007/s00227-005-0172-5.
- SMIDT, E. L. B. 1969. The Greenland halibut, *Reinhardtius hippoglossoides* (Walb.), biology and exploitation in Greenland waters. *Meddelelser fra Danmarks Fiskeri-og Havundersøgelser*, 6: 70–148.
- SOHN, D., L. CIANNELLI, and J. T. DUFFY. 2010. Distribution and drift pathways of Greenland halibut (*Reinhardtius hippoglossoides*) during early life stages in the eastern Bering Sea and Aleutian Islands. *Fish. Oceanogr.*, 19: 339–353. doi: 10.1111/j.1365-2419.2010.00549.x
- SOURISSEAU, M., Y. SIMARD, and F. J. SAUCIER. 2006. Krill aggregation in the St. Lawrence system, and supply of krill to the whale feeding grounds in the estuary from the gulf. *Mar. Ecol. Prog. Ser.*, **314**: 257–270. doi.org/10.3354/ meps314257
- STENE, A., A. C. GUNDERSEN, T. O. ALBERT, K. H. NEDREAAS, and P. SOLEMDAL. 1999. Early development of Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*). J. Northw. Atl. Fish. Sci., 25: 171–177. doi.org/10.2960/J.v25.a16
- TANIMURA, S., C. KUROIWA, and T. MIZOTA. 2006. Proportional symbol mapping in R. J. Statis. *Software*, 15: 1–7.
- TEMPLEMAN, W. 1973. Distribution and abundance of the Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Northwest Atlantic. *ICNAF Res. Bull.*, **10**: 83–98.