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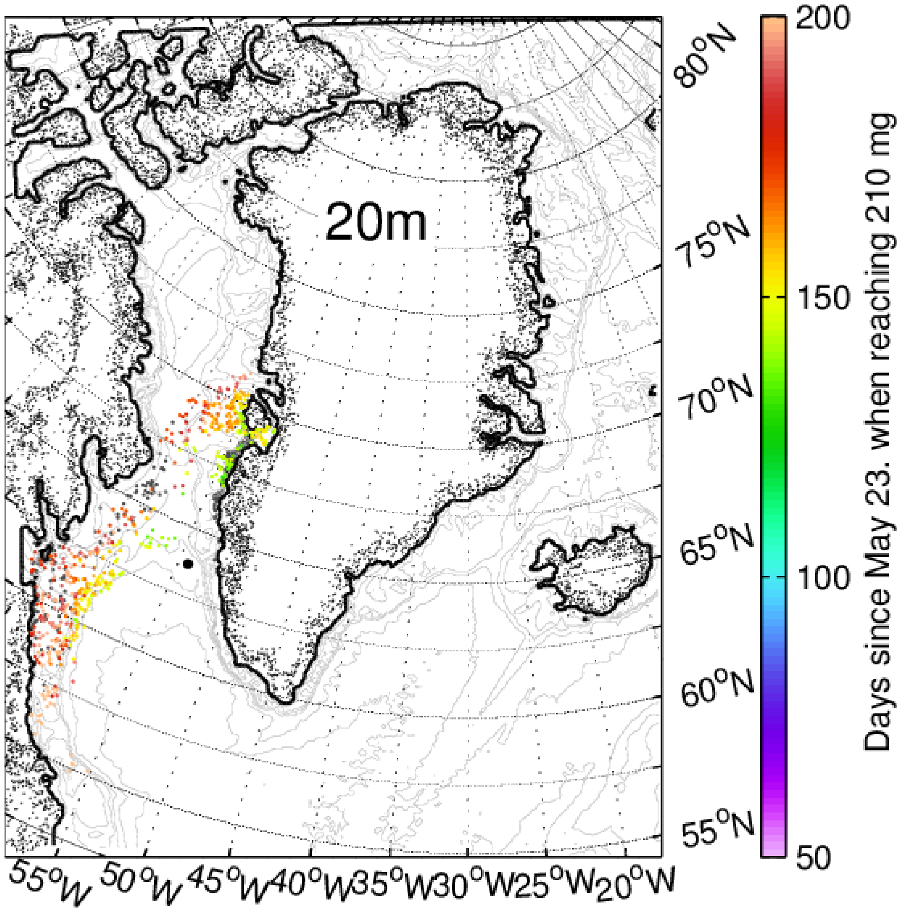

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Preface

The present article is a slightly modified version of a manuscript published for the first time as an appendix (Paper IV) within a Ph.D. thesis by Claus Stenberg:

> Stenberg, C., 2007. Recruitment processes in West Greenland waters: With special focus on Greenland halibut (*Reinhardtius hippoglossoides, W.*). Ph.D. thesis. University of Bergen.

The article is here re-issued as a DMI report, because there has been an interest for getting a copy of the article and to be able to referee to it. There has been no attempt to update the ocean model configuration or the drift simulations, which was "state-of-the-art" at that time, but which has improved since. Similar, the scientific knowledge on halibut biology gained since then has not been updated.

Thereby, the report is simply a slightly modified version based on the recommendations given by the opponents in relation to the Ph.D. defense.

Larval drift and settling of Greenland halibut (*R. hippoglossoides* Walbaum) in Northwest Atlantic with special focus on Greenlandic waters.

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Abstract

Early life history of Greenland halibut, *Reinhardtius hippoglossoides*, Walbaum, was tracked by drift and growth models in waters around Greenland. Model simulations were initiated from known and suggested spawning areas and were run from egg stage to larvae reached settling size. Research trawl surveys were carried out off West Greenland in July, August and September 2002 to validate the models and to examine time and spatial distribution of newly settled and juvenile Greenland halibut in two sub-areas of Hellefisk Bank. Drift model simulations revealed that egg and larvae had a total drift phase between 5 to 11 months. Analyses of spatial distribution of settling larvae showed that larvae from geographical separate spawning areas could intermix. The most important settling areas in West Greenland were found at Hellefisk Bank, Disko Bank and Disko Bay. Survey results validated that larvae were settling at Hellefisk Bank and that abundance of older juveniles were very high in all of the areas. However, the spatial distribution of newly settled and older juvenile Greenland halibut differed significantly. Settling was observed in both sub-areas of Hellefisk Bank while the older juveniles only occurred in one of the sub-areas. Either, the settled fish migrates away or there is a higher mortality rate in certain settling areas. Consequently the successful nursery areas must have a lesser extent than the settling areas. Concentrating of juveniles to more specific nursery areas implies that recruitment dynamics in Greenland halibut may be controlled by density dependent mechanism.

Introduction

Eggs and larvae of Greenland halibut (Gr. halibut) (*Reinhardtius hippoglossoides*, Walbaum) drift in the water masses for more than half a year before they settle to the bottom (Jensen, 1935; Smidt, 1969). Their drift route and location when reaching the size when they metamorphose and settle the bottom is primarily determined by the location of spawning site; the vertical distribution of egg and larvae and the duration of the egg and larval stages. Present knowledge in each of these stages for Gr. halibut can be summarized as:

Locations of the spawning areas in the NW Atlantic are not known in detail. Observations of ripe female Gr. halibut and drifting eggs suggest that spawning areas exist in four main areas: In the Davis Strait off the Greenland /Canadian shelf (Simonsen and Gundersen, 2005; Jensen, 1935; Smidt, 1969; Gundersen *et al.*, 2004; Templeman, 1973); West of Iceland along the shelf to the Irminger Sea (Sigurdsson, 1977; Magnusson, 1977); in East Greenland close to Kap Bille (Gundersen *et al.*, 2001) and in Baffin Bay (Gundersen *et al.*, 2004). Spawning probably takes place demersal and depths of 800 to 1200 m (Albert, 2003; Bowering and Nedreaas, 2000; Morgan *et al.*, 2003).

Egg are dispersed and transported passively by currents from the spawning areas. Egg buoyancy determined the vertical distribution and hence indirectly the drift route. In Davis Strait, the vertical distribution is estimated to be between 240 to 640 m based on observations by Smidt (1969) using a ratio between wire length and fishing depth on 0.4 (Stenberg unpublished results). At larval hatching the density changes as the chorion is lost (Bagenal and Braum, 1978). Hence, the larvae must get a hydraulic lift and rises further up in the water column. When larvae reach first feeding they must be in be in the same depths layers as their plankton prey. For Gr. halibut this is at 13−40m depth (Simonsen *et al.*, 2006).

Ontogenetic development rate determine the duration of egg and larval stages. In the egg stage the rate is determined by temperature and development time can thus be estimated from the degree-days (Hamel *et al.*, 1996). For Gr. halibut a pilot study showed that fertilization to hatching took around 115 degree-days (5 days at 4°C and subsequent 48 days at 2°C) (Stene *et al.*, 1998). In the larval stage a combination of food and temperature determine the development rate. Temperature is probably the parameters that acts most significantly (Otterlei *et al.*, 1999; Houde, 1989; Neuheimer and Taggart, 2007). The closing of the pelagic larval stage, and thus the drift phase, take place when the Gr. halibut larvae reaches a length of 65−70 mm and settle to the bottom (Jensen, 1935; Smidt, 1969). In West Greenland settling is believed to occur in the autumn (Jensen, 1935; Smidt, 1969) .

The aim of this study is to describe and analyze the overall drift pattern and growth of Gr. halibut eggs and larvae from geographically-separated spawning areas around Greenland by combining drift modelling and individual based egg and larval temperature-dependent growth models. The focus will be the spatio-temporal distribution of first feeding and settling larvae, and larval connectivity patterns. Model results from West Greenland waters will be validated by a trawl surveys targeting newly settled and juvenile Gr. halibut.

Materials and Methods

The ocean circulation model

The ocean circulation model used is the Hybrid Coordinate Ocean Model (HYCOM) (Bleck, 2002). HYCOM is a primitive equation ocean general circulation model which solves the three-dimensional prognostic equations for horizontal velocity, continuity (giving elevation and layer thickness), salinity and temperature. We used the hybrid configuration where the vertical coordinate is isopycnal in the open, stratified ocean, but smoothly reverts to a terrain-following coordinate in shallow coastal regions, and to z-level coordinates in the mixed layer and/or unstratified seas. Tidal forcing is included as a body tidal potential (Ribergaard *et al.*, 2006). The model includes a thermodynamic representation of sea ice, whereas sea ice momentum is not included.

The model covers the Atlantic Ocean from about 20°S and the entire Arctic Ocean with an approximately 50 km horizontal resolution and 29 vertical levels. For the drift simulations we used a one-way nesting of about 10 km resolution and 26 vertical levels covering the Greenland Waters. The atmospheric forcing was taken from the Danish Meteorological Institute (DMI) numerical weather prediction model DMI-HIRLAM-T (Yang *et al.*, 2005) covering a large part of the northern hemisphere with a 0.15 degree resolution. Freshwater input outside Greenland was applied as mean monthly climatological discharges from the 115 largest river discharge stations of the Global Runoff Data Centre (GRDC, Federal Institute of Hydrology (BfG), Am Mainzer Tor 1, 56068 Koblenz, Germany, http://grdc.bafg.de) and scaled as in Dai & Trenberth (2002). In Greenland pseudo monthly climatologies was made for 5 fjords using discharges taken from an ice-cap model (Box *et al.*, 2004). Surface temperature and salinity was relaxed towards (1/4°) climatological temperature and salinity fields by Boyer *et al.* (2005). A detailed description of the ocean model setup is found in Ribergaard *et al.* (2006) including a preliminary validation of the model performance.

The particle tracking model

Particles were tracked using the model described in Ribergaard *et al* (2004). This drift model solve the advection-diffusion equation for a passive tracer C given by

$$\frac{\partial C}{\partial t} + \vec{\nabla} \bullet (\vec{u} C) - \vec{\nabla} \bullet \left(k \vec{\nabla} C\right) = 0 \qquad (1)$$

where t denotes time, k horizontal diffusion and $\vec{u} = (u, v)$ is the horizontal advection velocity.

For the turbulent diffusion a random walk model is used. The basic idea is that the ensemble mean of the square of the particle displacement $\vec{x} = (x, y)$ satisfies

$$\frac{d < \vec{x}^2 >}{dt} = 2k \qquad (2)$$

For each particle the solution of equation 2 at time step n+1 is of the form

$$\vec{x}_{n+1} = \vec{x}_n + R_n \sqrt{\frac{2k\Delta t}{r}} \qquad (3)$$

where R_n is a random number with mean $< R >= 0$ and standard deviation $< R^2 >= r$. We choose R as uniformly distributed between -1 and +1, in which case r=1/3.

Following Visser (1997) and Spagnol *et al.* (2002), the solution of equation 1 is

$$\vec{x}_{n+1} = \vec{x}_n + \vec{u}\Delta t + \nabla k_{\vec{x}_n}\Delta t + R_n\sqrt{\frac{2k_{\left(\vec{x}_n + \frac{1}{2}\nabla k_{\vec{x}_n}\Delta t\right)}\Delta t}{r}} \qquad (4)$$

where the diffusion, k, is allowed to vary in space.

The two first terms on the right hand are the solution for pure advection with no diffusion. The fourth term is the random walk diffusion similar to equation 3 but as the diffusion varies in space, the diffusion is estimated at a distance $\frac{1}{2}\nabla k_{\vec{x}_n}\Delta t$ offset $\vec{x}_n$. The third term is an additional advective term that tends to transport particles towards regions of increasing diffusivity. Without this term, the particles will concentrate at regions of low diffusion which is obviously incorrect (e.g. Visser, 1997). The drift model was run with a time step of 5 minutes and the horizontal diffusion coefficient was set constant to 60 m^2/s as in Ribergaard *et al.* (2004)

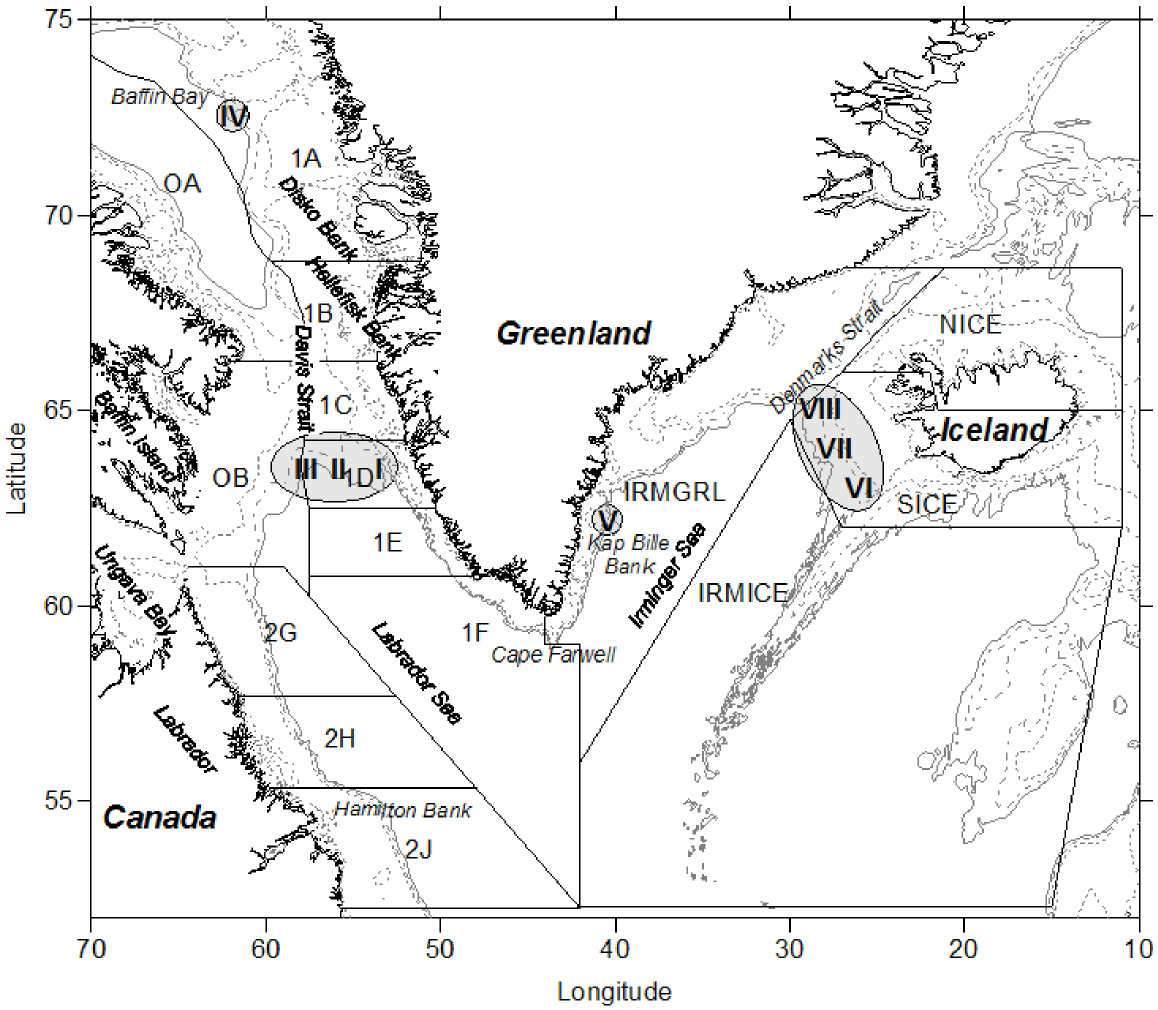


Figure 1. *Map of study area. "Spawning areas" where mature ripe female and/or eggs have been reported is shown by shaded grey areas. Numbers I to VIII refers to release points listed in table 1. Depth contours shown for 100, 500, 1000 and 1500 m. Area delimitations and their label are sketched.*

Drift simulations

The vertical distribution and biology of the egg and larval stages are different in Gr. halibut. Consequently, a two step model approach was taken. In the first step the period from the egg was spawned to the larvae began to feed (end of yolk sac stage) was modelled. The information on distribution pattern from step one was used in the second step to continue the modelling of the pelagic larvae until they reached metamorphosis. The ontogeny of the simulated egg and larvae was tracked daily by applying temperature dependent growth models using the temperature information from the ocean circulation and particle tracking models.

Egg and yolk sac larvae drift model simulation

Particles where released in four areas with observations of Gr. halibut eggs, yolk sac larvae or ripe females (cf. introduction). A total of eight spawning sites were chosen within these four areas (Figure 1; Table 1). A thousand particles was released within a normal distributed time window ($f=a*\exp(-.5*((x-x0)/b)^2)$). Based on a study of Gr. halibut female maturity development in Davis Strait (Gundersen *et al.*, 2004), spawning was assessed to take place from mid-February. The normal distribution coefficients was found by a Gaussian, 3 parameter fitting of larval size distribution in May (Simonsen *et al.*, 2006). The coefficient were determined to; a= 0.4; b=8.1; x0=31. The bathypelagic eggs and yolk sac larvae were assumed to be distributed just below the halocline, which in West Greenland waters is found as the upper part of the Irminger water component, and in Southeast Greenland waters in upper ~200 m. In the isopycnal hydrodynamic ocean model these depths correspond to the density (Sigma-theta) 27.63 kg m^{-3}. The temperature-dependent growth model was a simple cumulative number of degree days using the temperature information from the ocean circulation and particle tracking models. In order to ensure growth also at temperatures around zero degrees, a minimum increase in degrees-days was set to 0.1 per day. The degree-days to complete the egg and yolk sac larvae were, based on information on the well-studied Atlantic halibut (*H. hippoglossus*) (Pittman *et al.*, 1990), assumed to be 300 degree-days. At this point the simulated larvae were first feeding and pelagic larvae (FF larvae).

Pelagic larvae to settling drift model simulation

A thousand particles were released each of the respective areas of highest modelled FF larvae concentration. The release followed the same procedures described earlier. Starting date was set to the average calendar day for reaching the 300 degree-days. Vertical distribution was constant at 20 or 40 m. A temperature-dependent growth model was applied from an initial larval length of 12 mm length (0.34 mg DW) (smallest pelagic larval size observed in the upper water masses (Jensen, 1935)), to a terminal length of 65 mm (210 mg DW) (largest pelagic larvae and smallest newly settled observed (Jensen, 1935; this study). The daily temperature-dependent growth increase is calculated as:

$$W_i = W_{i-1} * \exp(G + (0.014 * (T_{mod} - T_{mid}))) \quad (5)$$

where W_i is dry weight in mg of the specific day; W_{i-1} is dry weight in mg the day before; T_{mid} is in situ midpoint temperature; T_{mod} is temperature for the drift particle in the model; G is weight-specific growth rate. G was found the increase in larval weight from May, June and July (Simonsen *et al.*, 2006):

$$G=(\ln W_2 - \ln W_1)/(d_2-d_1) \quad (6)$$

where W_2 and W_1 are dry weights in mg at the calendar days d_2 and d_1, respectively.

Surveys

Three trawl surveys were conducted off West Greenland to validate the drift simulations. The first survey was carried out from 3 July-7 August 2002 (July survey) and covered depths from 70-600 m from Cape Farvell (60°N) to the Uummannaq peninsular (71°N). Sampling was undertaken at 186 stations. The survey covers depths from 70-600 m. The second and third surveys were carried out in two areas of the Hellefisk Bank in NAFO 1B from 25−27 August 2002 (August survey) and 27−29 September 2002 (September survey). AREA 1 was at N 68°15−68°54 to W 56°−57° and AREA 2 at N 67°30−67°54 to W 57°−58°. Six stations in each area were revisited in the August and September survey. The trawl gear was a Skjervøy 3000/20 trawl with bobbin gear and double bag. Mesh size in the codend was 20 mm. The 20 mm mesh size will give a full selectivity on Greenland halibut from sizes of about 9 cm assuming a selection factor of 3.1 (Huse *et al.*, 1999). Trawl doors were Greenland Perfect size 370*270 cm and wing spread was set as 19.0 m. The tow speed was 2.5 knots and duration was 15 or 30 minutes. All trawl hauls were carried out during daytime. Greenland halibut catch was length measured (total length to the cm below), counted and the total weighs recorded (to 0.1 kg). In larger catches a sub-samples was taken. All catches were standardized to one hour trawling. In order to homogenize variance abundance was transformed by the natural logarithm to n+1 prior to statistical analysis.

Gr. halibut were separated on ages 0, 1 and 2+ by their length distribution (Bowering and Nedreaas, 2001; Lear and Pitt, 1975). A “Bhattacharya” modal progression analysis was carried out in the software FiSAT II version 1.2 (Gayanilo *et al.*, 2005; Bhattacharya, 1967). The separation resulted in different cohorts with a mean length and standard derivation to the mean. Mean length +/- 1.96 *standard derivation was used to define 95% confidence intervals for the age cohorts (Sokal and Rohlf, 1995).

On the September survey the seabed was classified into 6 different classes based on acoustic data obtained from a Furuno FCV-161 dual frequency echo sounder operating at 28 KHz, a 3.0 ms pulse length and using a transducer beam width of 22 degrees. The acoustic data were sampled by the QTC-V acquisition system (Quester Tangent Corporation, Suite 201 - 9865 West Saanich Road, Sidney, BC, Canada, V8L 5Y8) and processed in the QTC IMPACTTM software from Quester Tangent. This processing approach has proven to be an effective technique for bottom mapping (Hamilton *et al.*, 1999). To ground truth the classification results, 13 sediment box cores were collected during the survey.

All statistical analyses were performed in the SAS/STAT software Version 9 of the SAS System for PC, SAS Institute Inc., Cary, NC, USA. The following abbreviations were used for statistical tests; ANOVA: analyse of variance; ANCOVA: analysis of covariance; GLM: general linear models. ANOVA, ANCOVA and GLM analyses were carried out by the GLM procedure which accommodate unequal balance designs.

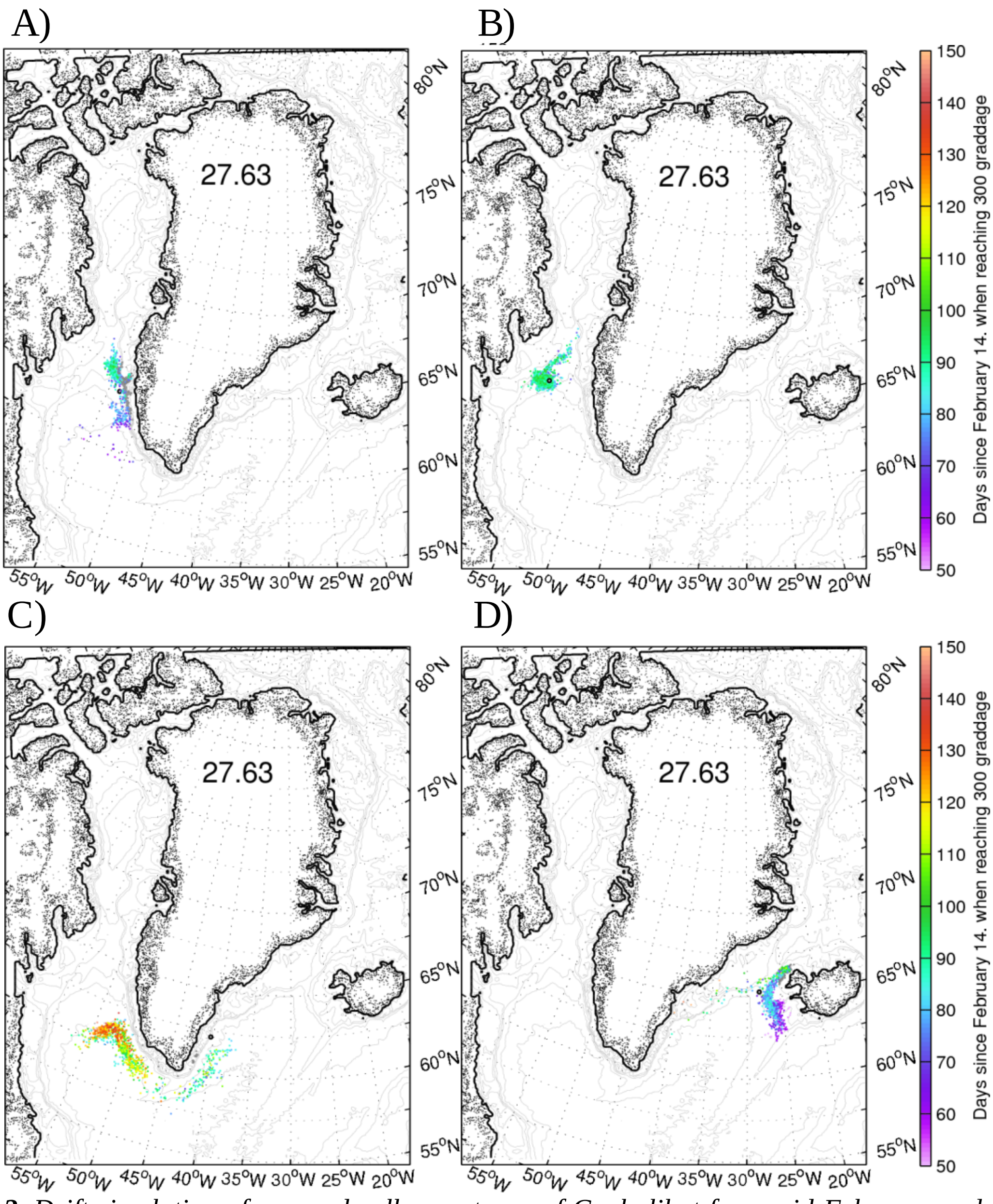


Figure 2. *Drift simulation of egg and yolk-sac stages of Gr. halibut from mid-February and for 300 degree-days at density interval* σ_θ *=27.63. A) release I; B) release III; C) release V; D) release VIII. Release point shown by black circle.*

Results

In the following, the distribution of simulated halibut larvae were divided into areas as follows: West of Greenland the Northwest Atlantic Fisheries Organization (NAFO) fishery management area was used, while East of Greenland four areas were defined: North Iceland waters (NICE); South Iceland waters (SICE); “Greenlandic part of” Irminger Sea (IRMGRL) and “Icelandic part of” Irminger Sea (IRMICE); (Figure 1).

Modelling of egg and yolk sac larvae stages

A marked difference was observed in the distribution pattern for the Davis Strait releases I to III. In release I and II FF-larvae were distributed parallel to the shelf break both north and south of the release point with the majority in areas NAFO 1C (55-56%) and 1D (21-43%) (Figure 2a, Table 3). FF larvae from release III were distributed more west (W) with the far majority in NAFO 0B (89%) (Figure 2b, Table 3). Vertically, they were situated in water masses about 300 to 700 m, deepest for the particles closest to Greenland (data on vertical distribution not shown). The development from egg to FF larvae in the Davis Strait releases took 80 to 110 days (Figure 2a,b). There was a tendency to longer development time for larvae distributed toward W. On average the FF stage was reached on May 23, 24 and 27 respectively for the releases 1-III.

In Baffin Bay release IV the development time was prolonged in the cold water masses. In August the mean degree-days was only about 60 and the maximum observed was 128 degree-days. The simulated egg and yolk sac larvae were thus not even half way through their 300 degree-days ontogenesis to FF larvae. Due to the cumulative mortality effect, the long time span must result in few, if any, hatched FF larvae (Pepin, 1991). Furthermore, even if larvae succeeded they would be off phase with the plankton bloom resulting in starvation of the first feeding larvae (Smidt, 1979; Bagenal, 1971). Larvae in Baffin Bay were therefore not included in the further analyses.

In the East Greenland release V the FF larvae were distributed offshore around Cape Farewell into Labrador Sea in NAFO 1E (27%), 1F (60%) and 2G (1%) but some remained in the Irminger Sea in ICES IRMGRL (12%) (Figure 2c, Table 3). Vertically the model showed a deeper distribution in Labrador Sea, 600–700 m, compared to 400–500 m in the Irminger Sea. Development time varied between 80 and 140 days, longest in the Labrador Sea. On average the 300 degree-days was reached at June 20.

In the Iceland releases VI to VIII the drift resulted in different distribution of FF larvae. From release VIII FF larvae were mainly distributed along the Icelandic shelf from Southwest Iceland (SICE 88%) and across the Denmark Strait to North Iceland (ICES NICE 9%) (Figure 2d, Table 3). Releases VI and VII FF larvae remained at the Southwest Iceland shelf (SICE 59 and 71%) and into the Irminger Sea (IRMICE 41 and 29%) (Table 3). Vertically there was also considerable difference in distribution. In Southwest Iceland the simulated larvae were distributed around 600–700 m but only at 100–200 m in Northwest Iceland. Development time for the Icelandic releases was only 50 to 90 days (Figure 2d). Fastest growth was seen for the particles distributed Southwest of Iceland. On average the 300 degree-days was reached at May 3, 4 and 15 for release VI, VII and VIII respectively.

Modelling of pelagic larvae to settling stages

Drift simulations of the FF larvae to settling larvae (SE larvae) from Davis Strait showed that more than half (58% for the 20 m; 72% for 40 m) of the SE larvae from release I were distributed in Canadian waters (in NAFO OB, 2G-H-J) while for release II and III it was almost all (>89%) (Table 4). The Canadian distribution covered an extended area from NAFO 0B to 2J and the 40 m drift simulation resulted in a more southerly distribution compared to the

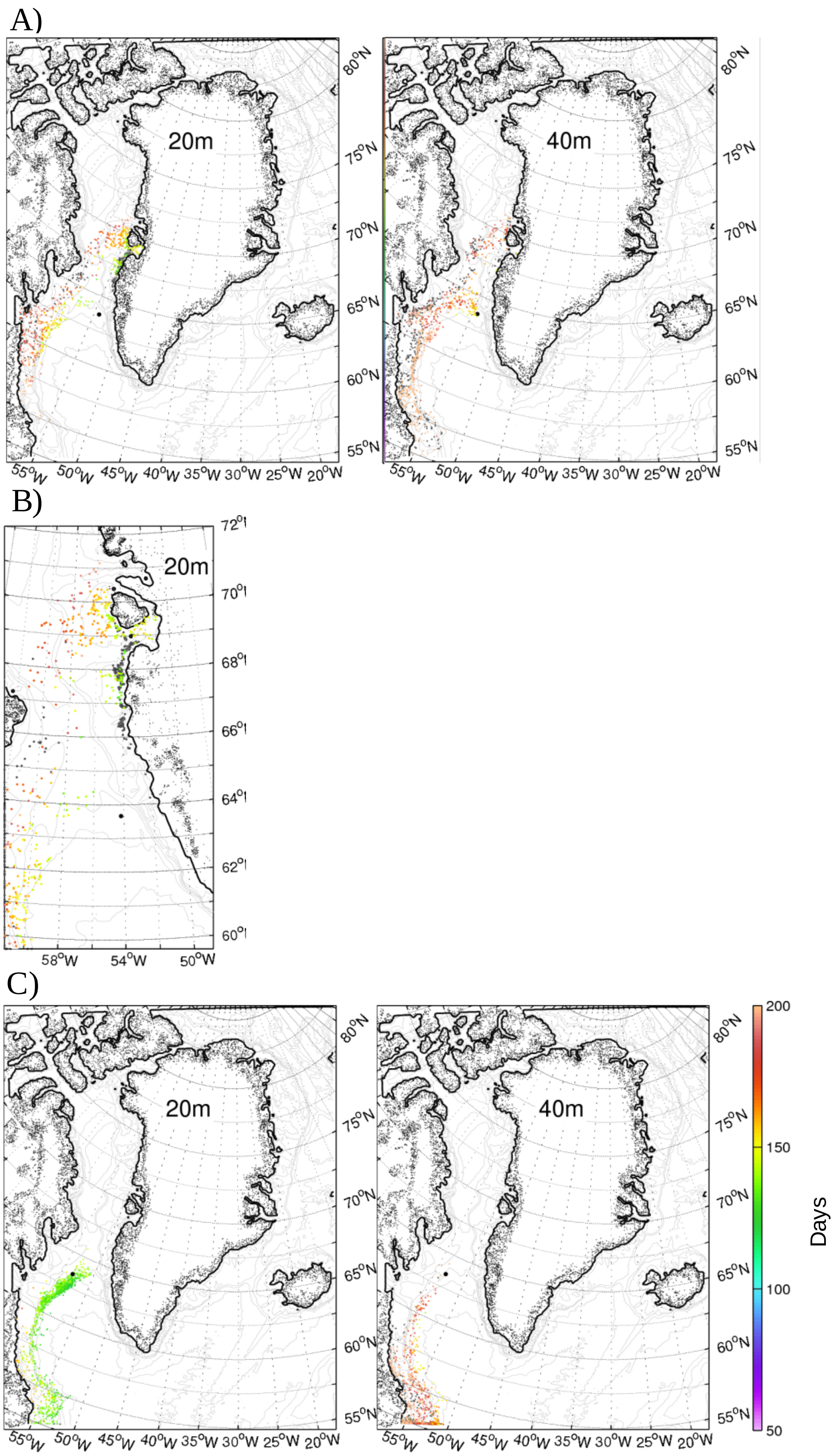


Figure 3. *Drift simulation of Gr. halibut pelagic larvae from Davis Strait from first feeding (DW 0.3 mg) to settling size (DW 210 mg). A) release I; B) close up of release I 20 m; C) release III. Start position (black circle) of drift simulation in release I is 63°40N, 54°12W; release III 63°29N, 58°21W.*

simulations (Figure 3c). Some SE larvae were observed to hit the models southern boundary. High SE larval concentrations were especially seen over deep waters in NAFO 0B and at more shallow depths over the shelf and Hamilton bank in NAFO 2 J (Figure 3a, c). In West Greenland SE larvae were, especially for the 20 m drift simulation, distributed over northern part of Hellefisk Bank, Disko Bank and inside Disko Bay in NAFO 1A (Figure 3b).

In East Greenland, larvae from release V was mostly transported to West Greenland waters, but some drifted to Canadian waters as well (Table 4). In West Greenland SE larvae from the 20 m simulation had a more northern distribution which included the bank areas in NAFO 1B-C but highest concentrations were seen in NAFO 1E-D over deep waters (Figure 4). For the 40 m simulation highest SE larval concentration was seen in the southern part of NAFO 1F over deep waters. The larvae that were transported to Canadian waters were mainly seen in the deep waters in NAFO 2G.

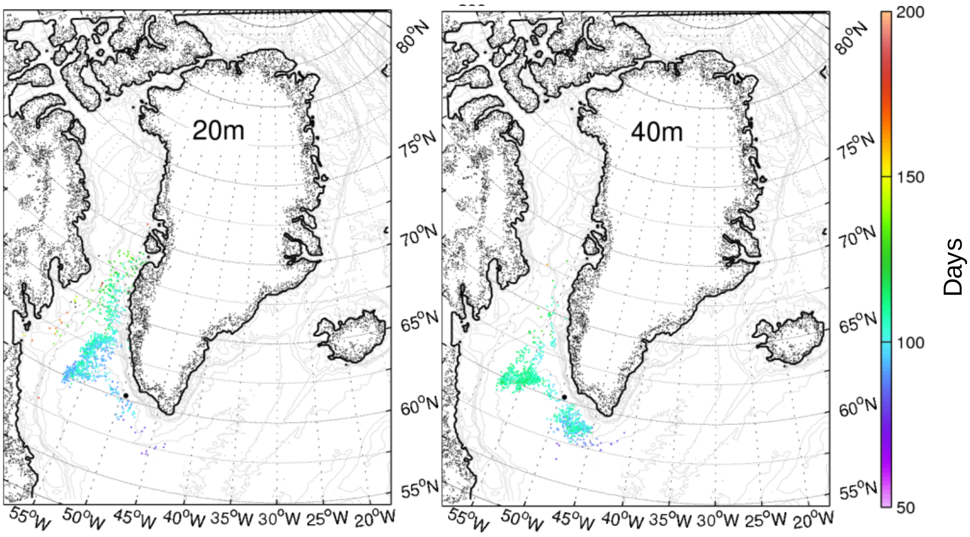


Figure 4. *Drift simulation of Gr. halibut pelagic larvae from first feeding (DW 0.3 mg) to settling size (DW 210 mg) in East Greenland release V at 20 and 40 m depth. Start position (black circle) of drift simulation is 60°13 N, 49°29W.*

In Iceland, larval drift was simulated from three positions in Southwest, West and Northwest Icelandic shelf as they were well represented by the general distribution pattern from the three Icelandic spawning releases. This approach was taken because there was no well-defined centre of mass for the FF larvae distribution and because initial simulations showed a great variability in drift route for the FF larvae depending on choice of release position within only 20-30 km distance. The Southwest position was the area with high FF larvae density from spawning release VII, while the West and Northwest positions were from the spawning release VIII (referred to as VIIIA VIIIB). Almost all larvae from Southwest (>98%) remained in Icelandic waters (Table 4) and were transported from South Icelandic waters to the shelf area (Figure 5a). From West larvae were retained in the same area until they reached settling size (Figure 5b). However, a prolongation of the drift model showed that larvae began to drift to East Greenland a few weeks later (mid-August) and one month later almost all had drifted to the East Greenland shelf and followed the same drift route as many of the Northwest larvae. Most larvae from Northwest drifted toward East Greenland and were, similar with larvae from Southeast, distributed with about 50% in East Greenland waters, mainly at the shelf from 60 to 65°N

A)

B)

C)

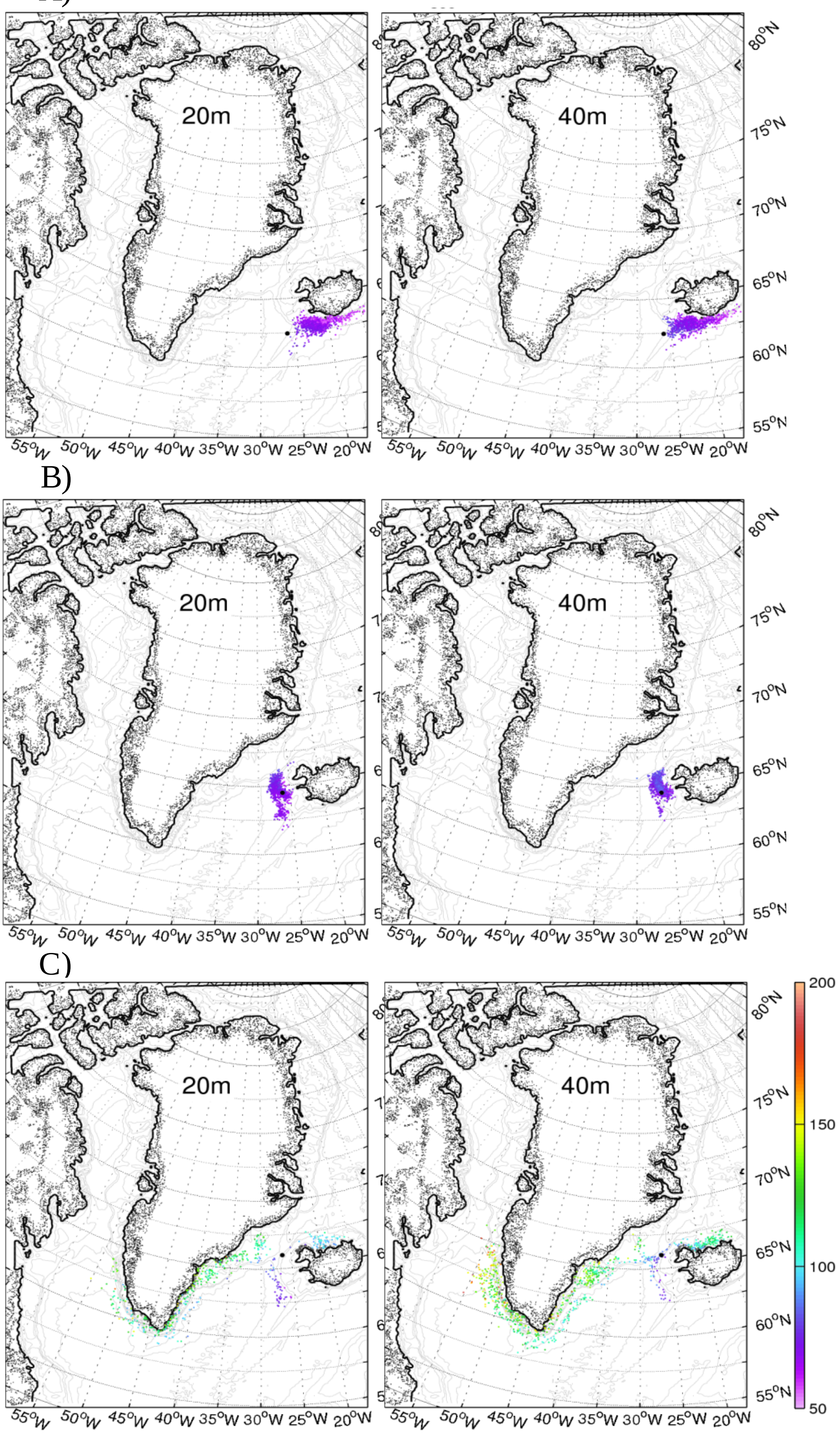


Figure 5. *Drift simulation of Gr. halibut pelagic larvae from Iceland from first feeding (DW 0.3 mg) to settling size (DW 210 mg). A) release VII; B and C) release VIII. Start position (black circle) of drift simulation is A) 62°26N, 26°08 W B) 64°29N, 26°13 W C) 66°00N, 26°30W.*

(in IMRGRL 45% to 53%), 20% to 30% rounded Cape Farewell into West Greenland waters (in NAFO 1F-E-D-E and 1B 19 to 34%) and a smaller number, about 15% of the larvae that did not drift toward East Greenland, were transported to the shelf North of Iceland (in NICE 15 to 16%) (Figure 5c, Table 4).

Larval growth simulations for the different releases showed differences between the settling date for the 20 and 40 m drift depth scenarios within the same area. In Canadian waters larvae in 40 m settled about 1½ to 2 months later compared to the 20 m scenario (Table 5). In the ICES areas, the difference between the 20 and 40 m simulations was less than 1 week. The earliest settling period was seen for the Icelandic spawning releases. Here settling was estimated to have its peak as early as July for larvae South of Iceland (Table 5) while larvae that drifted to East Greenland (in ICES IRMGRL) had their maximum settling period around September. The latest settling period was seen in Davis Strait spawning releases (I-III) that drifted to Canadian waters (in NAFO 0B and 2HGJ). Here settling had its maximum in October–January, latest for the 40 m drift scenario.
In West Greenland waters the Davis Strait (I) releases that drifted to NAFO 1AB settled over a relative long time span starting in August and ending in January with a peak around November for the 20 m and around December for the 40 m simulation. The East Greenland spawning release (V) had its maximum settling in NAFO 1CDEF in October (Table 5).

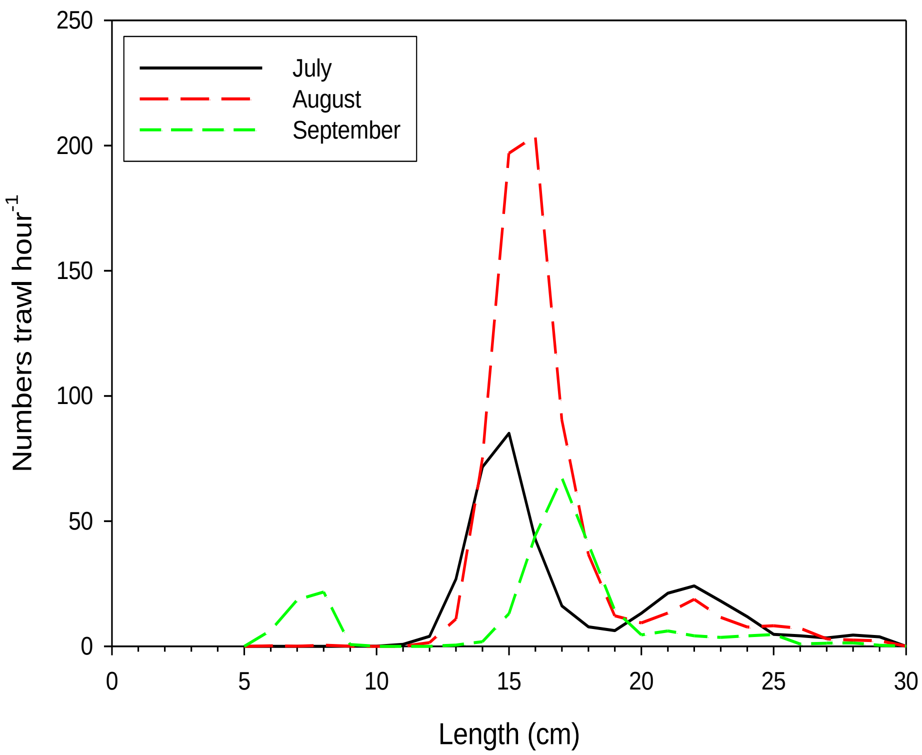


Figure 6. *Number of Gr. halibut (standardized to one trawl hour) in each 1 cm length group on the July (black solid line), August (red dashed line) and September survey (green dashed line).*

Fish size and age classes in West Greenland from surveys

The Gr. halibut size distribution showed distinct cohorts (Figure 6). The separation on age classes by the Bhattacharya method separated the age 0 and 1 with good precision and no overlaps in size distributions while it was more difficult to identify older age class cohorts

(Table 6). Hence, they were pooled into a 2+ age group. All fish above the minimum length (see Table 6) for age 2 was thus classified into this group. Age 0 was not observed before the August survey and had highest numbers on the September survey (Figure 6). For age 1 there was a progressive increase in mean length between the three surveys from 14.8 cm in July to 17.2 cm in September.

Spatial distribution of settled Gr. halibut in West Greenland from surveys

The July survey covered the West Greenland shelf area from 60 to 71°N but was conducted too early to catch the 0-group. Age 1 Gr. halibut was observed in the entire survey area, but they were clearly more abundant at 68° to 70°N at the slopes of Hellefisk Bank and Disko Bank and inside Disko Bay at 200 to 400 m depth (Figure 7). Average concentration for stations north of 68°N was 93 specimens per hour (SD=160 n=92) while south of 68°N concentration was 5 specimen per hour (SD=13 n=77). Age 2+ were also most abundant between 68° to 70°N but the centre of distribution were in the central parts of Disko Bay at 300 to 500 m depth (Figure 7). Average concentration for stations north of 68° N was 17 specimen per hour (SD=32 n=92) while south of 68°N 1 specimen per hour (SD=2 n=77). A significant correlation between fish size and depth (GLM, P<0.0001) indicated a general migration toward greater depths as the fish grew.

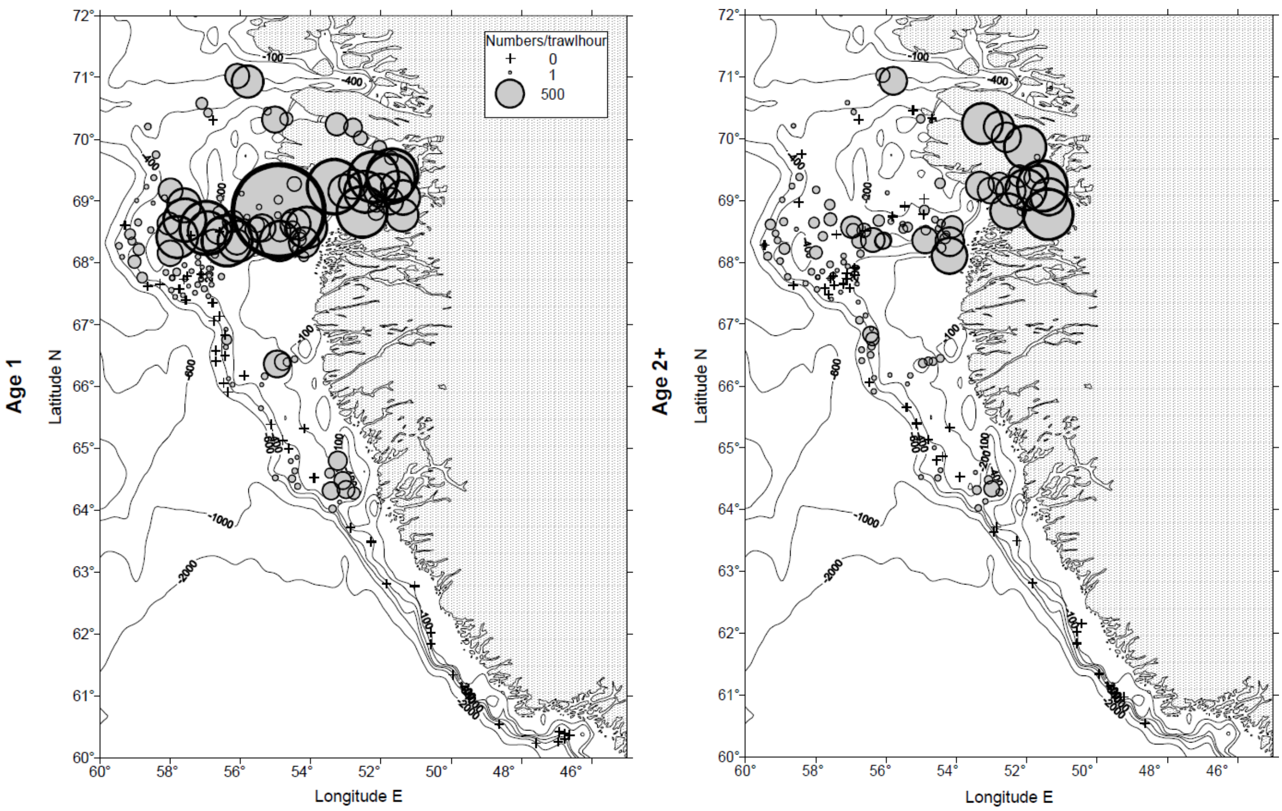


Figure 7. *Abundance of 1 year old Greenland halibut on July survey. Area of circle is showing abundance as numbers per trawl hour. Depth contours shown for 100, 200, 400, 1000 and 2000 m.*

The surveys in August and September at the slope of Store Hellefisk Bank in the two sub areas AREA 1 and AREA 2 showed considerable difference in the spatial distribution pattern of the 0-group and the older Gr. halibut (Figure 8). For the 0-group there was no difference in concentration between sub areas on both surveys (ANOVA, August P>0.7; September

P>0.3) (Figure 8), but for both age 1 and 2+ there was a highly significant difference in concentration between areas in both August and September (ANOVA, P<0.0001). The age 1 and 2+ fish was clearly associated to area AREA 1 (Figure 8).

As for the July survey, the August and September survey also show significant increase in Gr. halibut size (length) with fishing depth (GLM, P<0.0005).

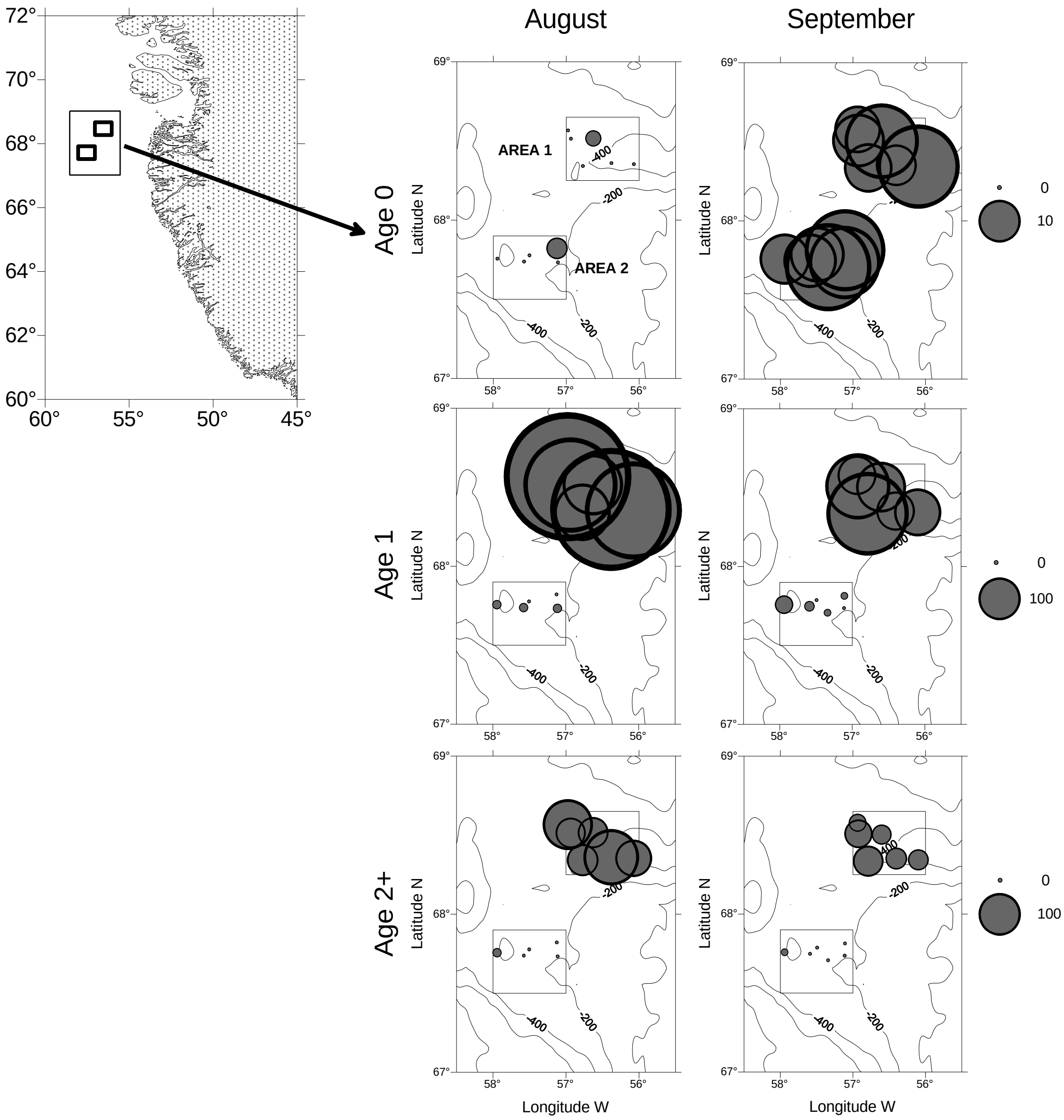
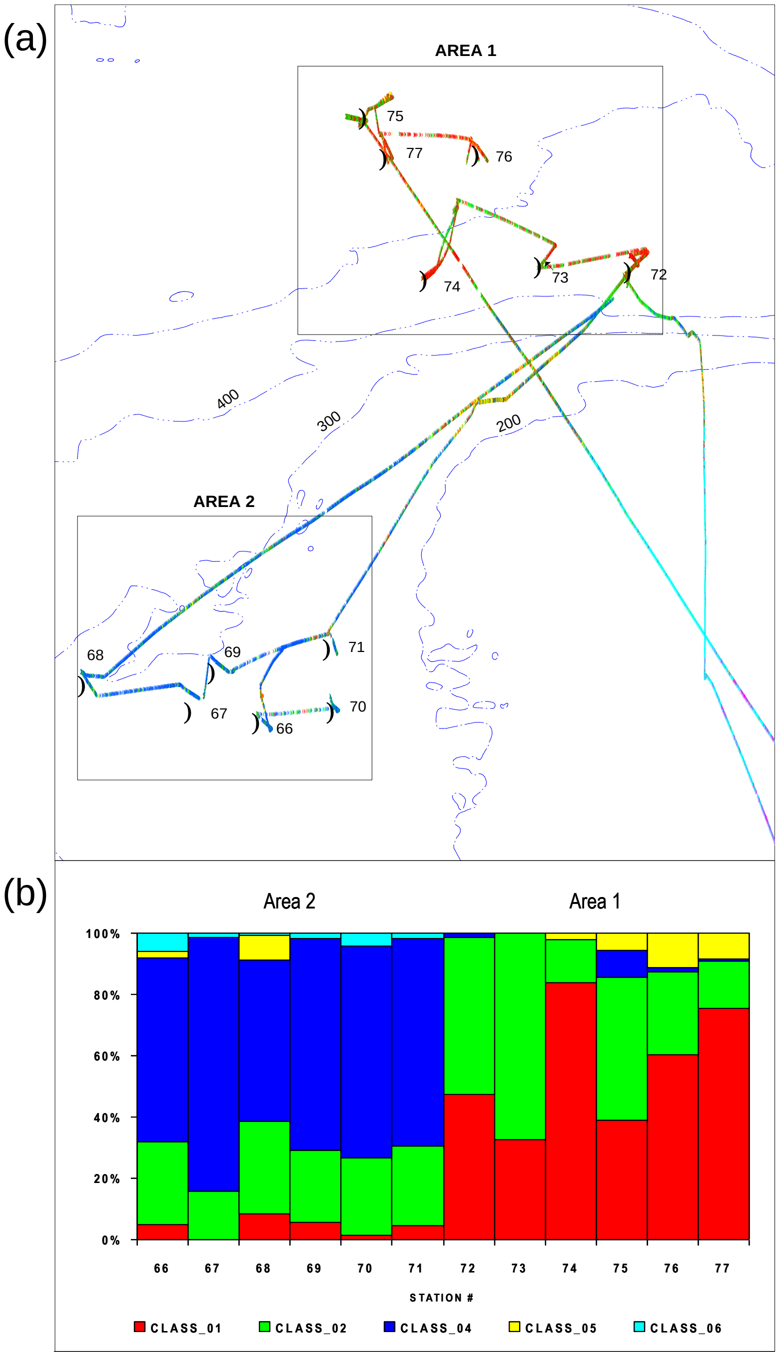


__Figure 8.__ Abundance of 0, 1 and 2+ year old Greenland halibut on August and September survey (number trawl hour^{-1}) in AREA 1 and AREA 2. Depth contours shown for 100, 200, 400, 1000 and 2000 m.

Sediment

Classification of the echo sounder data resulted in six acoustic classes as descriptors of seabed type; three types predominated in the studied areas at the slope of Hellefisk Bank (Figure 9). In AREA 1 the predominated classes where 1 and 2 while class 4 predominated in AREA 2 (Figure 9). Box cores showed that the class 1 and 2 was clay and silt w. shell or little organic material while class 4 was silty sand w. gravel, less clay and some shells.



(c) Sediment types associated with acoustic seabed classes based on box cores

Seabed class	Sediment
1	Clay and silt, little organic material
2	Clay and silt w/ shells
3	Hard bottom, mussels
4	Silty sand w/ gravel, less clay, some shells
5	Sand gravel dunes
6	No information

Figure 9. *(a) Sediment classification on Hellfisk Bank with the same two sub-areas "Area 1" and "Area 2" as in Figure 8. (b) Relative cluster distribution in the sub-areas using 6 clusters of which 5 were present. (c) Box core sediment samples and the associated acoustic classification.*

Discussion

To our knowledge this study is the first that combine and validate a drift and growth model for Gr. halibut from egg to settling in the NW Atlantic. This approach have given new insight into the early life history of Gr. halibut on the linkage between spawning and nursery area, the time it takes to complete the pelagic egg and larval phase and larval dispersion patterns.

Drift from spawning to first feeding larvae

The offshore distribution of FF larvae in the drift simulations corresponded with observations from the Davis Strait made by Jensen (1935), Smidt (1969) and Simonsen *et al.* (2006). They found that small larvae (~10-22 mm length) primarily were distributed offshore in April−May. There are no reports on captures of yolk sac or small Gr. halibut larvae from the other areas. However, research surveys typically have no spatial overlap with the small larvae's believed distribution area why distribution patterns of FF larvae could not be validated.

Drift of pelagic larvae and the settling areas

The recruitment of juveniles to both Canadian and West Greenlandic waters from spawning in Davis Strait confirms earlier hypothesis made by Templeman (1973) and Smidt (1969). Templeman suggested that larvae from the spawning complex in Davis Strait are caught in the current off Baffin Island and drift south in the Labrador Current and settle on the banks off Labrador and eastern Newfoundland. On the other hand Smidt suggested that larvae spawned in Davis Strait were caught in the West Greenland Current and transported northward along West Greenland. Our drift simulations showed that the longitudinal position of the spawner is determining whether its offspring is recruited to the banks off Canada or off West Greenland. Satellite tracked drifting buoys with drogues at 15 m depth confirmed these drift patterns and also showed that advection towards Canada was especially high between 61 and 64 °N (Jakobsen *et al.*, 2003). This is the same latitude as both our FF and SE drift simulations were initiated. The three release points in the Davis Strait spawning area projected a ratio of eggs/larvae transported to Canada versus West Greenland waters to be respectively between 60/40 to 100/0 percent. This is a large difference and stress the importance of precise knowledge on location and extension of the spawning area and possible year to year variations when relating spawning stock and recruitment in fisheries management.

The southern distribution of SE larvae off the shelf and Hamilton Bank off Labrador in Canadian waters agrees with observation by Lear (1970) and Templeman (1973) who found large numbers of 8–16 cm Gr. halibut in trawl hauls and in cod stomachs in this area, especially at Hamilton bank off Labrador and at Ungava Bay. The northern distribution of SE larvae off Baffin Island in NAFO 0B corresponded at shallower depths (<400 m) with high abundance of juveniles, length mode at 12 cm, from trawl survey in September - October in NAFO 0B (Bowering, 1978). However, model results suggest that SE larvae also is distributed over greater depths in NAFO 0B and this is not verified from the trawl survey where juveniles virtually was absent in hauls deeper than 500 m.

Distribution of SE larvae in West Greenlandic waters, especially the 20 m drift scenario with high concentrations at Hellefisk Bank, Disko Bank and Disko Bay agreed with survey distribution of 1 and 2 year old Gr. halibut. Also older data from the “Tjalfe” expeditions in 1908-09 and the “Norwestlant” investigations in 1963, summarized in Smidt (1969), verify our models northern larval drift pattern. Smidt noted an increase in Gr. halibut larval length from 64 to 68°N and hypothesized that larvae were caught in the West Greenland Current and transported northward. Satellite tracked drifting buoys with drogues at 30 m were deployed in May 2000 at and off Fylla Bank (64°N) to simulate fish and shrimp larvae drift (Pedersen *et al.*, 2002). From May to September the drifters drifted northward along West Greenland following the bathymetry. In September to November, the period we estimated to be the main settling period (cf Table 5), they drifted along the slopes of Hellefisk Bank, northern part of Hellefisk Bank and across Disko Bank (cf fig. 7. Pedersen *et al.*, 2002). There where thus agreement between results from drift model, surveys and deployed drifters.

The larval drift scenarios from spawning areas in East Greenland and/or Iceland to West Greenland followed the major trends in the work by Ådlandsvik (2000) who simulated drift of Gr. halibut egg from Kap Bille in East Greenland. Ådlandsvik showed that after 120 days of drift most larvae were transported to West Greenland and were distributed up to NAFO 1 D. Our drift simulations also estimated that most larvae (up to 82%) would drift to West Greenland, but our simulation estimated a distribution as northerly as NAFO 1A. The more northern distribution could be explained by a much longer drift phase in the present study. This distribution of larvae in NAFO 1A and B implied that some larvae would settle in the same area as those from a Davis Strait spawning origin.

Riget and Boje (1988) hypothesized that larvae from an Icelandic spawning could be transported by the East Greenland Current from Denmark Strait to the East and Southwest Greenland areas. The present study validated the hypothesis as most of the pelagic larvae with a start position Northwest of Iceland in the drift simulations was transported to Greenland waters. However, the relative amount of larvae that drifted to Greenland seems to be extremely sensitive to their position in Denmark Strait. The area is characterized by sharp frontal activity between Polar and Irminger Water, and only a small spatial displacement results in a shift from one water mass to the other. Wind directions and the resulting Ekman transport must therefore be expected to be important for which water mass the larvae enter and thereby their drift direction to either East Greenland or North Iceland shelf.

The SE larvae distribution off East Greenland was concurrent with the general higher densities of Gr. halibut larvae at 61 to 65°N observed from 0-group surveys in 1970–97 by Iceland (Albert *et al.*, 2002). The presence of Gr. halibut larvae in East Greenland was also noted by Smidt (1969) but he emphasized that larval abundance here was much lower compared to the West Greenland area from 62°30 to 66°15N. The same conclusion was made by Boje and Hjörleifsson (2000) on juvenile Gr. halibut (<28 cm).

The distribution of SE larvae West and South Iceland on the shelf could not be validated from in situ observations. In spite of considerable survey effort, Gr. halibut larvae and juveniles (less than 45 cm) have only rarely, and always in very limited numbers, been reported from Icelandic waters (Albert *et al.*, 2002; Sigurdsson, 1980; Boje and Hjörleifsson, 2000). We compared the SE larval distribution patterns with the ones from Ådlandsvik (2000) and noted that he also had a considerable amount of particles distributed West and Southwest of Iceland. Deployed drifters have shown that a westward or southward transport is possible (Ribergaard, 2004). The drift scenario for the simulated Gr. halibut larvae to West or South Icelandic waters thus seems plausible. However, drift simulations showed that even small spatial displacements of the spawning area or the distribution of FF larvae would result in different SE larvae distributions. Furthermore, the background for the definition of the spawning area is sparse. It is based on few observations of mature Gr. halibut females from one scientific bottom trawl cruise and few observations of bathypelagic eggs (Sigurdsson, 1977; Magnusson, 1977). This emphasize a need for further investigations on where Gr. halibut spawn in Iceland waters before firm conclusions can be made on the drift and settling areas of larvae from this spawning area.

Development time and effect of temperature

Egg and larvae drifted in water masses with different temperatures, and according to the temperature-dependent growth models, different egg development time and larval growth rates between areas were expected. For development of the egg and yolk sac to FF larvae the difference was up to up to one month, earliest for West Iceland, latest for Southwest Greenland. There is only in situ data from Davis Strait in West Greenland to validate model results on FF larvae: Model results predicted FF occurrence around 23−27. May and surveys who found small larvae with remains of yolk in the end of April and beginning of May (Smidt, 1969; Jensen, 1935) and small feeding larvae in mid May (Simonsen *et al.*, 2006).

The estimated settling period in West Greenland in NAFO 1A in late October and November was partly confirmed by our survey results: The missing observations from July and increased abundance from August to September fitted the trends in the model. However, as surveys were not conducted later we were not able to validate a possible peak settling in late October. Other studies from the banks and Disko Bay in NAFO 1A have suggested a settling in autumn: Jensen (1935) and Smidt (1969) concluded that with a larval size of ~47 mm in August settling was likely to occur in September/October. Jørgensen (1997) observed many newly settled fish with a mode length around 75 mm in November. In Canada waters, in NAFO 2GHJ, there was no survey information to confirm the estimated settling period in November and December. However, there are reports of Gr. halibut with a length from 57 to 77 mm in cod stomachs caught in late October at Hamilton Bank (Lear and Pitt, 1975). Information is also missing from East Greenland. The Icelandic pelagic 0-group survey carried out in August found a modal larval length of 65 mm and a size distribution that was displaced to the left (p. 48 Albert *et al.*, 2002). The skewness was interpreted as the larger individuals had settled and was out of reach of the sampling gear. If so, it is validating our estimated settling period in early September.

Hellefisk Bank – a settling and nursery area

Our study clearly demonstrates that Hellefisk Banke is a settling area for Gr. halibut. The settling larvae are most likely to have origin in a David Strait spawning but can also stem from spawning as far away as East Greenland.

It was notable that settling took place equally in both subareas of Hellefisk Bank but that the older juveniles at age 1 and 2+ almost exclusively occurred in only one of the subareas. Processes in the first year after settling thus changed the distribution pattern - either the newly settled Gr. halibut experienced a different area specific mortality rate or they migrated away from or to specific areas. One difference between the two subareas was their sediment texture. The sediment in its self can of course have direct influence. Especially for flatfish that uses it for refuge from predators by burrowing (Gibson and Robb, 1992) or as a feeding chamber (Gibson *et al.*, 1998). Many flatfish species therefore show a preference for a fine grain size at settling and thereafter a progressively coarser sediment as they grow larger (e.g. Stoner and Abrokire, 2002: Hippoglosssus stenolepis; Moles and Norcross, 1995: Platichthys stellatus). Feeding ecology studies on Gr. halibut have shown that their diet is not benthivorous but rather dermersal and pelagic crustaceans such as *Parathemisto* sp., pandalid shrimps and small fish (Jørgensen, 1997; Godø and Haug, 1987). The role of the sediment for Gr. halibut therefore mores seems a refuge from predators than for feeding. However, in this discussion of the effect of sediment it must not be forgotten that sediment texture often is a proxy for the hydrographic situation in the specific area. Our data could thus indicate that current velocities could be different between areas. A difference in the hydrographic situations could lead to a number of other plausible explanations to the shift in distribution patterns from newly settled to older juveniles Gr. halibut. Regardless of the reasons behind the observed change in the distribution pattern, it underlines the importance of distinguishing between Gr. halibut settlement areas and nursery areas.

The nursery areas do not seems to be determined at settling but rather within the first year after settling. Such patterns where early juvenile after settlement concentrate into more specific nursery areas or habitats have been reported for other flatfish species (Gibson *et al.*, 2002; Kramer, 1991). The concentrating of juveniles to more specific nursery areas implies that there is an increased risk that juvenile densities may approach the nursery areas carrying capacity in years of high settlement. Such density dependent mortality effects is described for several flatfish species (Iles and Beverton, 2000; Nash and Geffen, 2000; Gibson, 1994). Density dependent mortality would dampen the annual variability in year class strength of Gr. halibut. This stresses that even though both our drift model and surveys showed that Gr. halibut settle over a wide range of areas and habitats, it is processes within the first year after settling that determine the actual nursery areas. Further knowledge on these processes therefore seems a prerequisite for a better understanding of overall recruitment dynamics for Gr. halibut.

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Tables

Table 1. *Release point of particles in egg and yolk sac larvae simulations. 1000 particles were released on each release position (I, II….VIII) following a normal distribution curve with peak spawning in mid-February and a spawning window of 40 days. Reference refers to publications that have defined the spawning area.*

Area	N	W	release	reference
Davis Strait	63 ° 30	53 ° 30	I	Gundersen *et al.* 2004; Simonsen and Gundersen 2005
	63 ° 30	55 ° 48	II	
	63 ° 30	57 ° 42	III	
Baffin Bay	72 ° 30	61 ° 48	IV	Gundersen *et al.* 2004
East Greenland	62 ° 09	40 ° 24	V	Gundersen *et al.* 2001
Iceland	63 ° 00	26 ° 00	VI	Magnusson 1977; Sigurdsson 1977
	64 ° 01	27 ° 24	VII	
	65 ° 02	28 ° 15	VIII	

Table 2. *Mean temperature and Gr. halibut larvae length and dry weight from surveys in May, June and July (from Simonsen et al 2006). September observations were from present study for 65 mm fish just metamorphosed. Weight specific growth rate G is derived using equation 5*

Cruise	Temperature (°C)		Larvae		G
Date	5-40m	midpoint T	length (mm)	dry weight (mg)	(exp mg / day)
15-May	0.13		17.6	1.28	
25-Jun	2.76	1.45	23.5	3.50	0.024
15-Jul	3.75	3.26	31.0	9.16	0.048
11-Sep	3.43	3.59	65.0	210.50	0.054

Table 3. *Relative distribution (in %) between areas of simulated egg and bathypelagic larvae from spawning releases I to VIII after 300 degree-days. N is the number out of the 1000 successful simulated egg bathypelagic larvae that did not hit land and reached 300 degree-days before August 1.*

Spawning	NAFO											ICES				N
Release	0A	0B	1A	1B	1C	1D	1E	1F	2G	2H	2J	NICE	SICE	IRMICE	IRMGRL	
I	-	-	-	-	56.2	21.0	19.8	2.6	0.4	-	-	-	-	-	-	505
II	-	1.8	-	0.1	55.1	43.0	-	-	-	-	-	-	-	-	-	975
III	-	88.7	-	0.5	4.6	6.2	-	-	-	-	-	-	-	-	-	999
IV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
V	-	-	-	-	-	-	26.9	60.3	0.5	-	-	-	-	-	12.3	964
VI	-	-	-	-	-	-	-	-	-	-	-	-	59.2	40.8	-	1000
VII	-	-	-	-	-	-	-	-	-	-	-	-	71.0	29.0	-	1000
VIII	-	-	-	-	-	-	-	-	-	-	-	8.6	88.3	0.4	2.6	917

Table 4. *Relative distribution (in %) between areas of simulated Gr. halibut larvae from spawning releases I, II, III, V, VII and VIII at settling size (210 mg). N is the number out of the 1000 successful simulated larvae that did not hit land and reached settling size before December 31.*

Spawning release	depth	NAFO 0A	0B	1A	1B	1C	1D	1E	1F	2G	2H	2J	ICES NICE	SICE	IRMICE	IRMGRL	N
I	20 m	2.3	27.9	30.9	9.1	0.7	0.5	-	-	23.8	4.1	0.7	-	-	-	-	563
II	20 m	0.4	43.3	1.5	0.1	2.2	8.8	-	-	34.4	8.0	1.2	-	-	-	-	849
III	20 m	-	55.0	-	-	0.5	3.8	-	-	12.7	8.6	19.4	-	-	-	-	996
V	20 m	0.3	6.7	1.3	6.1	9.8	20.5	27.5	15.7	12.1	-	-	-	-	-	-	972
VII	20 m	-	-	-	-	-	-	-	-	-	-	-	-	98.5	1.5	-	997
VIII A	20 m	-	-	-	-	-	-	-	-	-	-	-	0.7	98.5	0.3	0.5	1000
VIII B	20 m	-	-	-	-	-	1.8	4.8	11.8	-	-	-	13.9	10.0	0.7	57.0	440
I	40 m	1.7	32.6	10.8	2.5	4.0	6.9	-	-	17.0	17.5	7.1	-	-	-	-	595
II	40 m	-	19.7	-	-	7.8	1.2	-	-	21.5	19.5	30.3	-	-	-	-	498
III	40 m	-	3.2	-	-	-	-	-	-	8.0	18.8	70.0	-	-	-	-	654
V	40 m	0.1	1.3	-	0.3	2.0	3.7	12.9	65.3	14.2	-	-	-	-	-	0.2	1000
VII	40 m	-	-	-	-	-	-	-	-	-	-	-	-	99.1	0.9	-	999
VIII A	40 m	-	-	-	-	-	-	-	-	-	-	-	1.1	98.3	-	0.6	1000
VIII B	40 m	-	-	-	-	2.3	7.1	13.3	15.1	-	-	-	18.4	5.1	-	38.7	701

Table 5. *Mean estimated settling date for the different spawning releases in the different NAFO and ICES areas.*

Spawning release	depth	NAFO											ICES			
		0A	0B	1A	1B	1C	1D	1E	1F	2G	2H	2J	NICE	SICE	IRMICE	IRMGRL
I		Nov 12.	Nov 08.	Oct 30.	Oct 20.	Oct 21.	Oct 13.	-	-	Nov 23.	Dec 18.	Dec 27.	-	-	-	-
II		Nov 14.	Oct 28.	Nov 12.	Oct 28.	Oct 20.	Oct 21.	-	-	Nov 14.	Dec 06.	Dec 20.	-	-	-	-
III		-	Oct 07.	-	-	Oct 16.	Oct 11.	-	-	Oct 12.	Oct 16.	Oct 13.	-	-	-	-
V	20 m	Nov 08.	Oct 18.	Oct 30.	Oct 16.	Oct 06.	Sep 30.	Sep 27.	Sep 24.	Sep 24.	-	-	-	-	-	-
VII		-	-	-	-	-	-	-	-	-	-	-	-	Jul 08.	Jul 14.	-
VIII A		-	-	-	-	-	-	-	-	-	-	-	Aug 03.	Jul 24.	Jul 24.	Aug 03.
VIII B		-	-	-	-	-	Sep 25.	Sep 12.	Sep 07.	-	-	-	Aug 20.	Aug 01.	Jul 29.	Sep 08.
I		Nov 19.	Nov 30.	Nov 29.	Nov 18.	Nov 04.	Nov 02.	-	-	Dec 19.	Dec 22.	Dec 24.	-	-	-	-
II		-	Dec 22.	-	-	Dec 14.	Dec 17.	-	-	Dec 21.	Dec 22.	Dec 19.	-	-	-	-
III		-	Dec 02.	-	-	-	-	-	-	Nov 25.	Dec 04.	Dec 02.	-	-	-	-
V	40 m	Dec 01.	Oct 10.	-	Oct 19.	Oct 10.	Oct 07.	Oct 06.	Oct 01.	Oct 07.	-	-	-	-	-	Sep 12.
VII		-	-	-	-	-	-	-	-	-	-	-	-	Jul 11.	Jul 10.	-
VIII A		-	-	-	-	-	-	-	-	-	-	-	Aug 06.	Jul 29.	-	Aug 06.
VIII B		-	-	-	-	Oct 12.	Oct 06.	Sep 29.	Sep 15.	-	-	-	Aug 29.	Aug 05.	-	Sep 11.

Table 6. *Decomposition of composite Gr. halibut length distributions using Bhattacharya method (Bhattacharya 1967). Size interval for age class defined as mean TL +/- 1.96 S.D.*

Survey	age class	TL			
		mean (mm)	S.D.	min (mm)	max (mm)
July	1	14.82	1.25	12.37	17.27
	2	21.89	1.74	18.48	25.30
	3	25.33	0.54	24.27	26.39
August	1	16.01	1.29	13.48	18.54
	2	21.91	1.71	18.56	25.26
	3	25.79	0.94	23.95	27.63
September	0	7.09	0.7	5.72	8.46
	1	17.22	1.22	14.83	19.61
	2	23.07	1.41	20.31	25.83
	3	27.58	0.84	25.93	29.23

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