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Early life of an inshore population of West Greenlandic cod *Gadus morhua*: spatial and temporal aspects of growth and survival

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ABSTRACT: Understanding the processes that affect fish larval survival and recruitment is a fundamental tenant of fisheries science. Small, isolated fjords are ideal study systems for elucidating early life history processes, as population dynamics are well traced in these partially closed systems. We examined the distribution, growth and mortality of eggs and larvae of a fjord population of cod during a 5 mo field campaign in the fjord Kapisigdlit, West Greenland. Cod mainly spawned early in the season in the innermost shallow region of the fjord. Egg survival was generally high in the fjord. The high survival may have been driven by relatively high temperature and/or low predation in the inner region. Early in the season, the distribution of eggs and young larvae was mostly restricted to the spawning area. Later in the season, larger larvae had become more evenly distributed in the fjord. This shift in distribution was observed after the seasonal pulse in freshwater outflow following the ice break-up in Kapisigdlit River. There was a positive correlation between the amount of food in a larval stomach and growth, and larval growth was greater in the outer fjord where prey availability was higher. The timing between spawning and freshwater input may be essential for survival and recruitment, this ensuring low dispersal of eggs and younger stages and high dispersal of older, actively feeding stages. Therefore, cod in this area could be vulnerable to future climate change affecting the timing and magnitude of freshwater outflow, by changes in precipitation, temperature or prey availability.

KEY WORDS: Ichthyoplankton abundance · Otolith growth · Arctic · Annual egg production · Spawning stock biomass

INTRODUCTION

Reproductive strategies of fishes have evolved to ensure that spawning and progeny development takes place when and where conditions are favorable to larval growth, survival and ultimately recruitment (Cushing 1990). Unlimited dispersal of eggs and larvae challenges the population connectivity, and low-dispersive environments, such as fjords and embayments, may facilitate the maintenance of self-seeding populations through retention of early life stages (Hastings & Botsford 2006, Espeland et al. 2007, Bradbury et al. 2008). For instance, local populations of Atlantic cod *Gadus morhua* with inshore spawning grounds have been documented in Norway (Jakobsen 1987, Knutsen et al. 2007, Nordeide et al. 2011),

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Canada (Robichaud & Rose 2004, Wroblewski et al. 2005) and Greenland (Hansen 1949, Smidt 1979, Storr-Paulsen et al. 2004). Often the inshore areas have a shallow entrance to the spawning area (Knutsen et al. 2007), which might promote retention of the early pelagic life stages of fish by reducing water exchange between the fjord and the outer sea. Indeed, observed genetic differences among fjord populations of cod separated by small distances (e.g. 30 km) indicate very limited inter-fjord mixing between populations (Knutsen et al. 2003, Jorde et al. 2007). Despite the importance of local fjord populations in the meta-population structure of several important fish species, little is currently known about the reproductive strategies involved and the processes that affect egg and larval survival in these systems (Wroblewski et al. 2005, Knutsen et al. 2007).

West Greenlandic offshore populations of cod have shown large fluctuations during the 20th century and have now almost disappeared (Storr-Paulsen et al. 2004). Similarly, the Canadian offshore population of cod collapsed, and the decline was attributed to both high fishing pressure and climate variations (Rose et al. 2000, Buch et al. 2004, Stein & Borovkov 2004). Inshore populations of West Greenlandic cod have also experienced large fluctuations in population size, but they have managed to persist in the restricted areas of distribution (Buch et al. 1994, Engelstoft 1997, ICES 2013, Bonanomi et al. 2015). The inshore and coastal populations are relatively small in size, but they are more numerous than those spawning offshore. A recent study compiling more than 500 publications found that of the 174 Atlantic cod populations studied 57% were coastal or inshore and most (63%) displayed high spawning site fidelity (Robichaud & Rose 2004). Fjords may offer stable and predictable conditions for growth and survival of early life stages, such as optimal temperature and prey availability and a moderate drift due to the geographical restriction and weak currents.

Early studies on Atlantic cod egg distributions showed that the Godthåbsfjord system harbors the largest inshore population of Atlantic cod in West Greenland (Hansen 1949, Smidt 1979). These studies identified the fjord branch Kapisigdlit as a principal spawning site for cod, where the shallow, innermost section of the fjord contained the highest egg densities observed along the entire west coast. To improve our understanding of the processes that govern the survival of early life stages of fish in such Arctic fjords, and ultimately determine the size of the adult populations, we set up an investigation of the key characteristics of the early life of cod in this fjord. The overall goal was to clarify in what way the specific characteristics of the fjord are beneficial for cod larval feeding and growth, and hence provide comparative information for furthering our understanding of the population dynamics of the species. A set of questions guided our research: (1) How is the spatio-temporal distribution of cod eggs and larvae linked to the oceanography in the fjord? (2) Do physical dispersal characteristics impact egg development and larval growth, potentially leading to enhanced survival? and (3) To what extent do temperature and prey availability affect larval growth? To put this locally important inshore population into the overall context of cod populations, we also used our investigation to provide an estimate of the spawning stock biomass (SSB).

MATERIALS AND METHODS

Study site

Sampling was conducted from 24 March to 5 August 2010 in the fjord branch Kapisigdlit located in the inner part of the Godthåbsfjord system, West Greenland. The vessel 'Lille Masik' was used during all cruises, except on 17–18 June when sampling was done from RV 'Dana' (National Institute for Aquatic Resources, Denmark). A total of 15 cruises (of 1–2 d duration) 7–10 d apart were carried out along a transect of 6 stations, spanning the length of the 26-km-long fjord branch. Stn 1 was located at the mouth of the fjord branch and Stn 6 at the end of the fjord branch, in the middle of a shallower inner creek (Fig. 1, Table 1). Stns 1–4 covered deeper parts of the fjord (Table 1), and Stn 5 was located on the slope leading up to the shallow inner creek.

Hydrography

Vertical profiles of water temperature, salinity and water density were recorded by CTD casts (SBE 19 plus or 911 plus SeaCat, and a SBE 25 SM MicroCat) down to approximately 15 m above the sea floor. The CTDs were calibrated against each other and against salinity samples collected with a Niskin bottle at 1, 10, 20, 50, 75, 100, 150 and 250 m depth on 24 May and 6 July and analyzed on a Portosal salinometer. A ship-mounted 600 kHz acoustic Doppler current profiler (RD Instruments®) was used to assess vertical profiles of water currents during 3 tidal cycles between 17 and 19 June at Stn 4. Water flow rate was averaged for every 8 m strata at the surface and for every 16 m strata in the remaining water column.

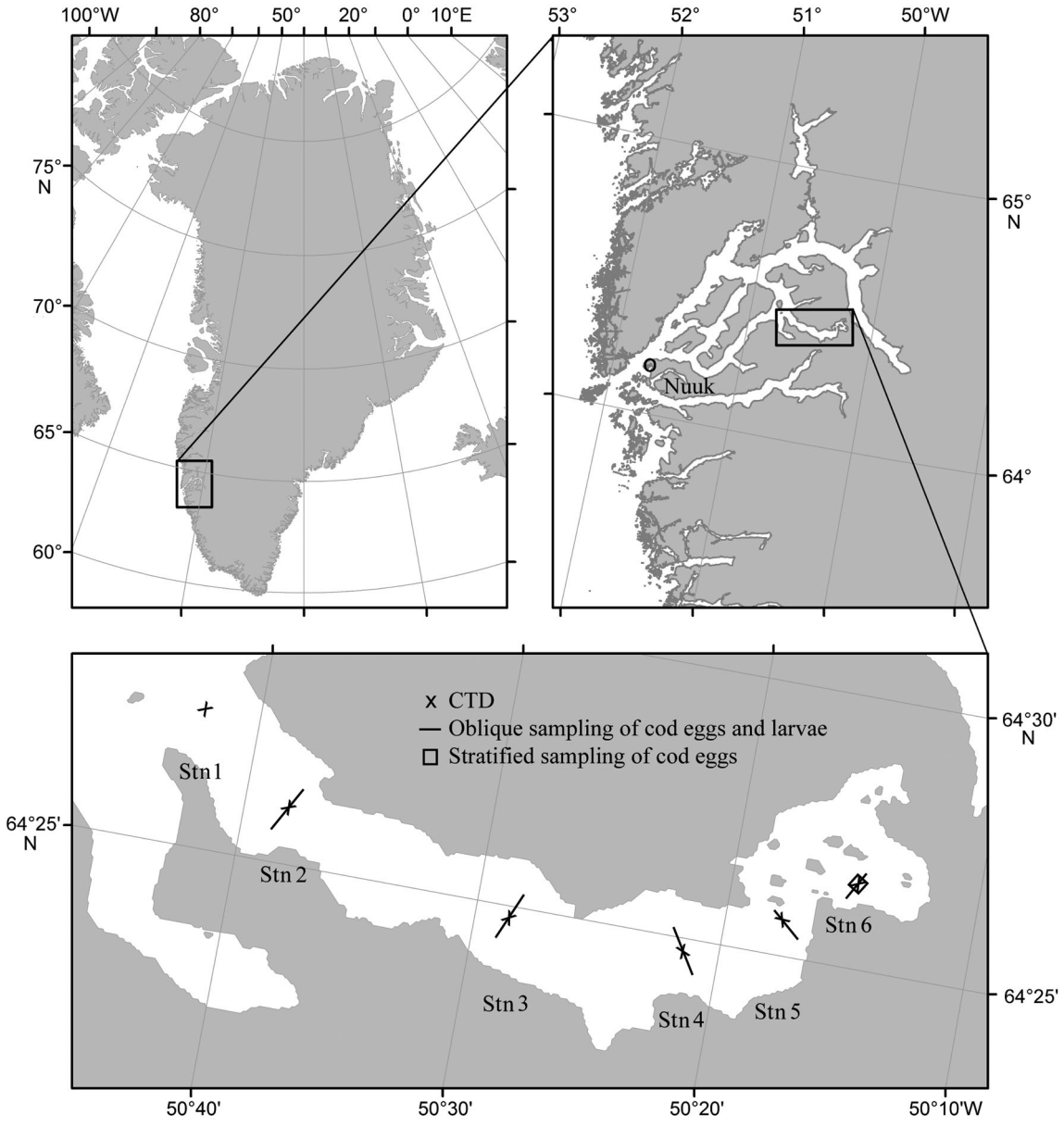

Fig. 1. Locations of sampling stations on the transect covering the length of the fjord branch Kapisigdlit

Fish eggs and larvae

Fish eggs and larvae were collected from Stns 2–6 using a Bongo net (2 circular rings of 60 cm diameter with mounted open nets of 300 and 500 µm mesh size, 135–1150 m^3 sample volume) from 24 March to 5 July. Subsequent sampling was carried out with a MIK ring net (ring of 2 m diameter and a 14 m long white open net of 600 µm mesh size, 2027–20 240 m^3 sample volume). Both net types were fitted with a flow meter and a CTD (MicroCat SBE 25 SM) to record the flow of water into the net and haul profiles. Oblique net tows were conducted at a ship speed of 1.6 knots from the surface down to 100 m depth at most stations, but to 35–50 m above the sea floor at the 2 innermost stations due to shallow depths and uneven bathymetry (Table 1). Sampling at Stn 6 on 18 June was done with a vertical towed WP-2 net (200 µm mesh size, 14 m^3 sample volume) and the larvae were preserved in ethanol (95% final conc.). Bongo net samples were preserved in buffered formalin (the 300 µm net, 4% final conc.) and in ethanol (the 500 µm net, min. 50% final conc.). MIK net samples were split in 2 subsamples, one preserved in formalin and one in ethanol. Occasionally, MIK net samples were too large to preserve in full,

Table 1. Station, distance from the fjord opening, locations, depths and location names. NS = no samples

Stn no.	Distance (km)	Area name	Latitude, Longitude	Station depth (m)	Net sampling depth (m)
1	0	Outer fjord	64° 27′ N, 50° 42′ W	212	NS
2	4.1	Outer fjord	64° 26′ N, 50° 39′ W	194	100
3	13.1	Outer fjord	64° 25′ N, 50° 29′ W	230	100
4	17.9	Outer fjord	64° 25′ N, 50° 22′ W	251	100
5	21.2	Slope	64° 25′ N, 50° 18′ W	125	75
6	24.1	Inner creek	64° 26′ N, 50° 15′ W	85	50

in which case a subsample was preserved and the remaining part kept cold (~5°C) and inspected for fish larvae within 48 h of sampling. All fish larvae found in the refrigerated part were then preserved in 95% ethanol. A specific study of the vertical distribution of fish eggs was carried out on 10 and 24 May and 3 June at Stn 6 in 5 depth strata (0–10, 10–20, 20–30, 30–40, 40–50 m) using a MultiNet (50 µm mesh size, Hydrobios mini) hauled vertically at 0.2–0.3 m s^{-1}. Samples were immediately preserved in buffered formalin (4% final conc.).

Fish eggs from all samples preserved in formalin were counted and the diameter of a maximum of 100 eggs per sample was measured and corrected for shrinkage due to formalin preservation (7%, Hiemstra 1962). In 16 samples with high egg densities, a subsample (between 1/2 and 1/128) was taken using a Folsom plankton splitter. Egg development stages were determined for the measured eggs following the descriptions by Thompson & Riely (1981). Only a few stage 1A eggs (visible cellular mass) were positively identified and these were therefore grouped together with stage 1B eggs (visible blastodisc). Eggs in the size range 1.15 to 1.73 mm (Ouellet et al. 2001) were assumed to be Atlantic cod *Gadus morhua*, as this species was the only one present with pelagic eggs within this size range, and Atlantic cod larvae emerged at the time when these eggs disappeared from the water column. Furthermore, this assumption was supported by examination of stage 5 eggs in this size range, in which the embryos had pigmentation characteristic of cod. In total, 7439 eggs were counted in the sample aliquots that were sorted, and out of the 3140 measured, 1510 were identified as Atlantic cod eggs.

All fish larvae were sorted and identified to genus or species level under a dissecting microscope. Standard lengths of Atlantic cod larvae (up to 40 per sample) were measured to the nearest 0.2 mm. In total, 705 out of the 1257 sorted larvae were measured. Before measurement, cod larvae were soaked in freshwater for approximately 2 min to minimize larval bending due to preservation. Standard lengths were corrected for shrinkage due to handling and preservation following Theilacker (1980):

$$\ln(L) = \ln X_1 + 0.289e^{-0.434X_1 \cdot X_2^{-0.68}} \quad (1)$$

where L is the standard length (mm) prior to handling and preservation, X_1 is the standard length of the preserved larvae (mm) and X_2 is the time from death to fixation (which was set at 20 min).

Due to differences in sampling depth between stations (Table 1), abundances of eggs and larvae were calculated per m^2 based on net area, water flow and depth of the haul. Total abundances of cod eggs and larvae were calculated for the 5 sample stations. Egg abundances were extrapolated to 5 different geographical areas with the sampling stations at the center. The border between areas was defined as the halfway point between stations. Stn 2 was also assumed to represent half the area between that and Stn 1, and Stn 6 was assumed to represent the entire inner creek area. As the major part of the inner creek is shallower than Stn 6, we assumed that 3.1 km^2 is ≥50 m deep, 8.15 km^2 is approximately 30 m deep and 7.65 km^2 is approximately 10 m deep. The 10- and 30-m-deep areas were then assumed to contain 20 and 60% of the eggs and larvae, respectively, compared with Stn 6. As no bathymetric maps exist, the areas were calculated based on topographic observations by L. Heilmann, Greenland Institute of Natural Resources (pers. comm.). Calculations of the number of spawning females or spawning stock biomass (SSB) were based on unpublished data by R. Hedeholm, who in Kapisigdlit in 2007–2011 found the average female and male weight to be 1.65 kg (n = 319) and 1.64 kg (n = 672), respectively, and fecundity to be 817 200 eggs $female^{-1}$. The average percentage of females was 32% (n = 991, R. Hedeholm unpubl. data).

Egg development, production and mortality

The average cod egg development time was calculated following Thompson & Riely (1981):

$$\ln(D) = A \cdot T + B \quad (2)$$

where D is the development time (d) from fertilization to the end of stage 5, T is the temperature (°C), and A

and B are regression coefficients of −0.1 and 3.46, respectively. Mean development time was calculated using the average temperature from the main spawning period between 30 April to 3 June within the upper 30 m of the water column. The daily egg production (EP) was calculated as:

$$EP = A_{Stage1}/D_{Stage1B} \quad (3)$$

where A_{Stage1} is the abundance of stage 1A + 1B eggs on the day of sampling and $D_{Stage1B}$ is the development time (d) from fertilization to the end of stage 1B calculated from the average temperature within the upper 30 m on the day of sampling. We assumed no mortality during this period. Coefficients A and B for stage 1B were −0.11 and 1.96, respectively (Thompson & Riely 1981). The annual egg production (AEP) was calculated following Armstrong et al. (2001) by integrating EP over the study period at intervals of 4–18 d depending on the time between cruises.

Egg mortality was expressed as the percentage of the AEP that did not survive until egg stage 4+5. Stages 4 and 5 eggs were pooled to improve the estimate as very few were found at the outer Stns 2, 3 and 4. Egg mortalitywas calculated as:

$$Mortality = 100 - (AEP_{Stage4+5}/(AEP_{Stage1} \cdot 100)) \quad (4)$$

where AEP_{Stage1} is the annual egg production calculated from stage 1 eggs as described above, and $AEP_{Stage4+5}$ is calculated from stage 4+5 eggs using Eq. (3), where $D_{Stage4+5}$ is the development time from the end of stage 3 to the end of stage 5 calculated from the average temperature within the upper 30 m on the day of sampling. The daily egg mortality (Z) was then calculated as:

$$Z = \frac{\ln(AEP_{Stage4+5}/AEP_{Stage1})}{-t} \quad (5)$$

where t is the average development time (d) during the main spawning period between stage 1 and stage 4+5, assuming that eggs are on average halfway through their respective development stage and thus calculated as (Eq. 6):

$$t = D_{Stage5} - (D_{Stage1B} + D_{Stage5} - D_{Stage3})/2 \quad (6)$$

Coefficients A and B for stage 3 were −0.11 and 2.97, respectively (Thompson & Riely 1981).

Otolith analysis

Otoliths from a maximum of 15 ethanol-preserved cod larvae from each station on each date where cod larvae were caught were included in the analysis (161 larvae in total). Each otolith was removed using fine needles under a stereo microscope and deposited in thermoplastic resin on a glass slide. Lapilli were used as a better alternative to the commonly used sagittae because of their more regular pattern of increment deposition and relatively larger size in the early larval stage. There is strong correlation between the width of individual lapilli growth increments and cod larval somatic growth (Bergstad 1984, Dale 1984, Geffen 1995). Both lapilli from each larva were polished with 1 µm lapping film. Lapilli >50 µm in diameter were polished on both sides, while smaller otolith were only polished on one side due to high risk of damage or overgrinding. Otolith photos were taken with a Qimaging (FAST 1394) camera mounted on a microscope using 20× to 63× magnification objective lenses and analyzed with Image-Pro v. 6.3 software. Growth increment width was measured on the longest axis from the core to the edge of each otolith to the nearest 0.15 µm. Most otoliths did not have a clear hatch mark. Previous studies indicated that hatch marks are located at a radius of approximately 8–13 µm (Bolz & Lough 1983, Campana 1989, Otterlei et al. 2002). Therefore, it was assumed that the first D-zone (discontinuous zone, dark band within the growth increment) at a minimum distance of 8 µm from the central core was the hatch mark ring.

Lapillus growth was expressed as the average width of each growth increment. Curvature at the edge of the lapilli resulted in an underestimation of the width of the outermost 3 growth increments. The 3 outer increments were therefore excluded from further analysis. In the lapillus growth trajectory analysis, only growth increments from a minimum of 3 replicate larvae within each specified group of larvae were included. Recent lapillus growth was calculated as the average increment width of the outermost increment numbers 4, 5 and 6 in the 2 lapilli. Only larvae with a minimum of 3 lapillus growth increments were included.

Statistics

To test for differences in larval growth between areas in the fjord, we analyzed lapillus growth trajectories by a linear mixed model in the R statistical software (R Core Team 2014) using the nlme package (Pinheiro et al. 2014). The model was fitted to the data, where otolith increment width was set as the dependent variable and area as independent. The analysis

used otolith increment number, area and their interaction as fixed effects. Increment number (grouped by individual otoliths, left and right) were nested by individual larvae and included as a random effect. The random effects were applied to both model intercepts and slopes. As the data contained multiple repeated measurements on otoliths, data were potentially autocorrelated and non-independent (Chambers & Miller 1995, Campana 1996). To correct for this, the model was refitted with an autocorrelation structure with increment number as a continuous time covariate (grouped for each otolith in each individual larva) using the corCAR1 function (Fox & Weisberg 2015). Growth increment widths were log transformed. Because the design was unbalanced (i.e. of the 161 larvae analyzed, 30 only had one usable otolith and the number of growth rings differed between otoliths), we used the maximum likelihood to estimate slopes and model significance (Plant 2012).

We next sought to test whether larval growth was affected by environment (water temperature) and prey availability, measured indirectly as *in situ* prey biomass within the larval prey size spectra, and directly as number of prey items and amount of carbon in a larval gut (as presented in Swalethorp et al. 2014). Estimates of larval growth were based on otolith increment width. We averaged otolith increment widths across the fourth to sixth increments from the otolith edge (approximately days 4 to 6) to link potential growth effects to environmental conditions around the time of capture. As otolith increment width becomes wider with age and older, larger larvae can fit more food in their stomachs simply because of their size, we needed to correct for age effects prior to constructing the models. We explored several methods (linear regression, quadratic regression, kernel-density regression and Generalized Additive Models [GAMs]) to model mean increment number, as a proxy for age, over approximately days 4 to 6 prior to larval capture against (1) increment width averaged across the fourth to sixth increments closest to the otolith edge, (2) number of prey items in a stomach and (3) amount of prey carbon in a stomach, and ultimately settled on GAMS because these provided the best and smoothest fit. The GAMs used thin plate regression splines to fit the data with a penalized likelihood approach to avoid overfitting. Evaluation of residuals indicated that a Gaussian distribution with an identity link was appropriate to model this data. GAM analyses were carried out using the mgcv package in R (Wood 2006). We used the residuals of these 3 models (henceforth referred to as 'age-corrected' and denoted as ~age) for further analysis.

To evaluate the effect of temperature, *in situ* prey biomass, and age-corrected number of prey items and carbon in stomachs on mean, age-corrected otolith increment width across the fourth to sixth increments from the otolith edge, we established a set of 14 candidate linear, additive multiple regression models relating these independent and dependent variables. To provide direct comparison of slopes among the independent variables, all variables were standardized to zero mean and unit variance using the R vegan package (Oksanen et al. 2012). Because samples were collected from 5 locations at 10 time points, it was possible that these random effects could affect the model results. However, comparison of models with and without time and location as random effects (the R package lme4 [Bates et al. 2015] was used to build the mixed models) demonstrated that there was no benefit to including the random effects into the models. Relative model plausibility was evaluated using Akaike's information criteria scores adjusted for small sample size (AICc), and model-averaged slopes and 95% confidence intervals were calculated from model selection results using the R package AICcmodavg (Mazerolle 2013).

Capture effects where stressed larvae evacuate all food items from their stomachs while in fishing nets have the potential to bias gut content–growth relationships. While there is no perfect way to deal with this largely unknown bias, we conducted analyses first using all larvae and second using only those that had at least one prey item in their gut.

RESULTS

Hydrography

The hydrography changed during the study period and differed between stations within the fjord. In March and early April, the water column was completely mixed in the upper 100 m, and this layer was cold, saline and nutrient rich (data not shown, see Riisgaard et al. 2014). By the end of April, warming of the upper 30 m in the inner half of the fjord branch Kapisigdlit had begun, but no stratification of salinity was apparent (Fig. 2a,b). Temperature increased from the entrance towards the head of the fjord branch. Such a pattern in temperature profiles was apparent at the beginning of June when a thermocline had formed at 20 m depth. The temperature gradually increased with distance from 4.5°C at Stn 1 to 7.8°C at Stn 6 (Fig. 2c). During May, melt water from land formed a weak halocline at 20 m depth

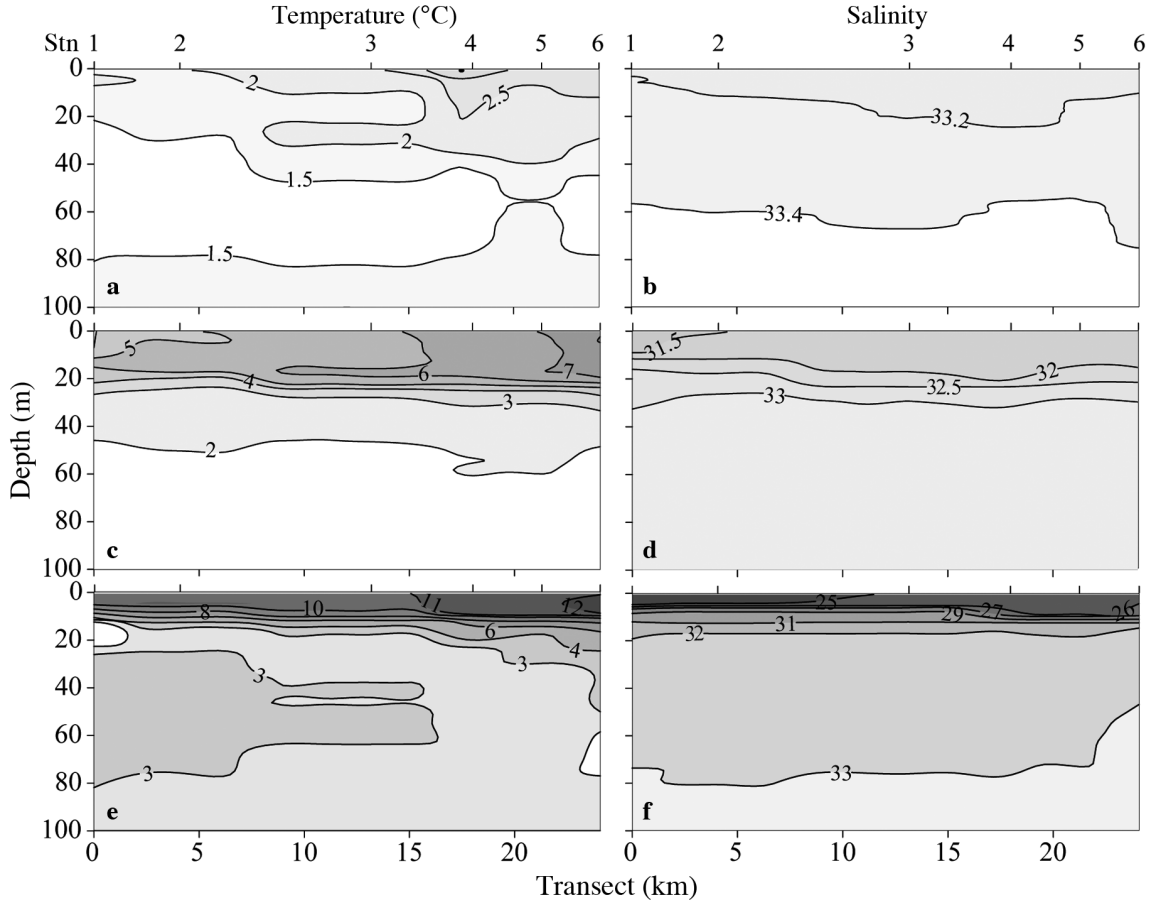

Fig. 2. Vertical sections of temperature (°C) and salinity at the 6 stations along the transect (km). Measured on: (a,b) 30 April, (c,d) 3 June and (e,f) 6 July

(Fig. 2d). The halocline strengthened after the break-up of ice around 20 June in Kapisigdlit River, which is located at the head of the fjord branch (Fig. 2f). By early July, temperatures below the pycnocline (10–50 m depth) gradually increased with distance from 2.8°C at Stn 1 to 4.4°C at Stn 6 (Fig. 2e). At the end of the study period (5 August, data not shown), salinities down to 16 were recorded near the surface. The average temperature below the pycnocline further increased by 0.8°C within the inner creek, while it decreased or remained the same at the other stations.

We found an estuarine circulation pattern within Kapisigdlit. Between 17 and 19 June, 3 semi-diurnal tidal cycles were recorded by the acoustic Doppler current profiler measurements at Stn 4. Generally, we found the same flow pattern in the top layer of the water column during all 3 cycles (Fig. 3a). Within the upper 80 m, there was net water outflow (calculated from 2 full semi-diurnal tidal cycles) from Kapisigdlit in the top 30 m and inflow within the 50 m layer below (Fig. 3b). There was also evidence of outward-flowing water between 80 and 160 m and inward flow >160 m. The outward flow in the top layer likely increased following the ice break-up in Kapisigdlit River. We acknowledge that this study only covered these 3 days of measurements as they represent the conditions during an important phase in the larval life, but flow characteristics would be expected to change during the season.

Atlantic cod distribution

Cod spawning mainly took place within the inner creek at the head of the fjord. Spawning was initiated between 3 April (Stn 5) and 30 April 30 (Stns 2 and 3) when the average temperature in the upper 30 m of the water column was between 0.8 and 2.1°C, respectively. Peak egg abundances were recorded on 10 May within the inner creek, on 24 May at Stn 5 and on 18 May at the 3 outer stations (Fig. 4a), when the average temperature was 3.2 to 4.2°C in the upper 30 m. Peak egg abundance within the inner creek (5185 egg m^{-2}) was almost 5–6 times higher

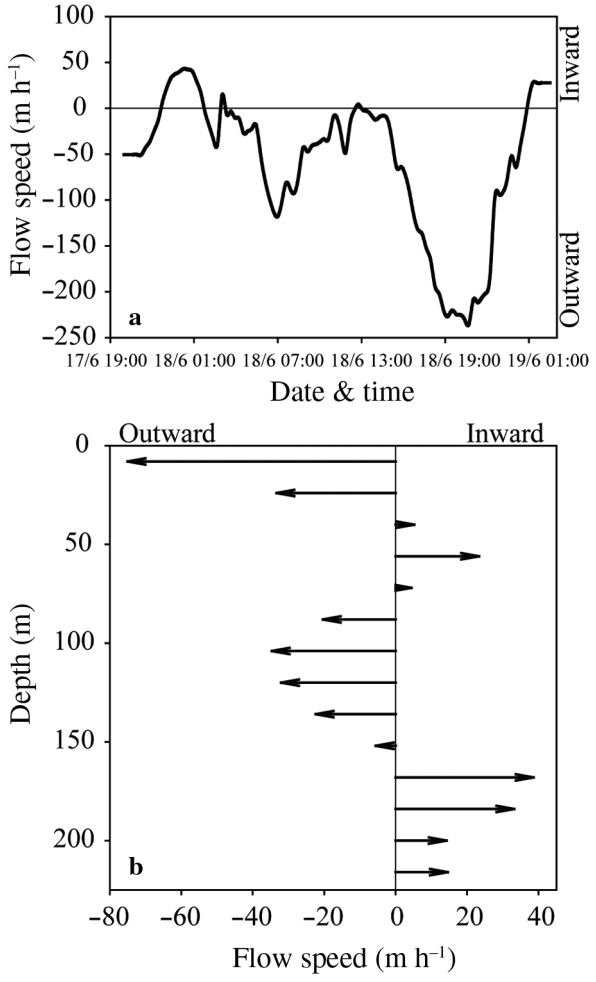

Fig. 3. Water flow inwards and outwards measured at Stn 4 on 17–19 June. (a) Flow (m h^{-1}) averaged in the depth stratum 8–16 m during 3 tidal cycles; (b) flow (m h^{-1}) averaged within each 16 m depth stratum during a 24 h period covering 2 tidal cycles

than at Stn 4 (893 egg m^{-2}) and Stn 5 (1079 egg m^{-2}) and around 2–3 orders of magnitude higher than the outer Stns 2 (3 egg m^{-2}) and 3 (103 egg m^{-2}). By 3 June, egg abundances had decreased to less than 5% of the peak values at all stations, but eggs were found until 18 July in the inner part of Kapisigdlit. Although the inner creek accounted for only a small part of the total study area, it encompassed 71% of the areal integrated egg abundance (Table 2).

Cod larvae generally hatched within the inner creek and later dispersed out into the fjord. Larvae emerged between 14 April (Stn 5) and 10 May (Stn 2, Fig. 4b). The first larvae were collected 10–16 d after eggs were first found (except for Stn 3 where eggs and larvae emerged at the same time). At Stn 6, peak larval values occurred 24 d after the highest egg abundances had been recorded, while at Stns 4 and

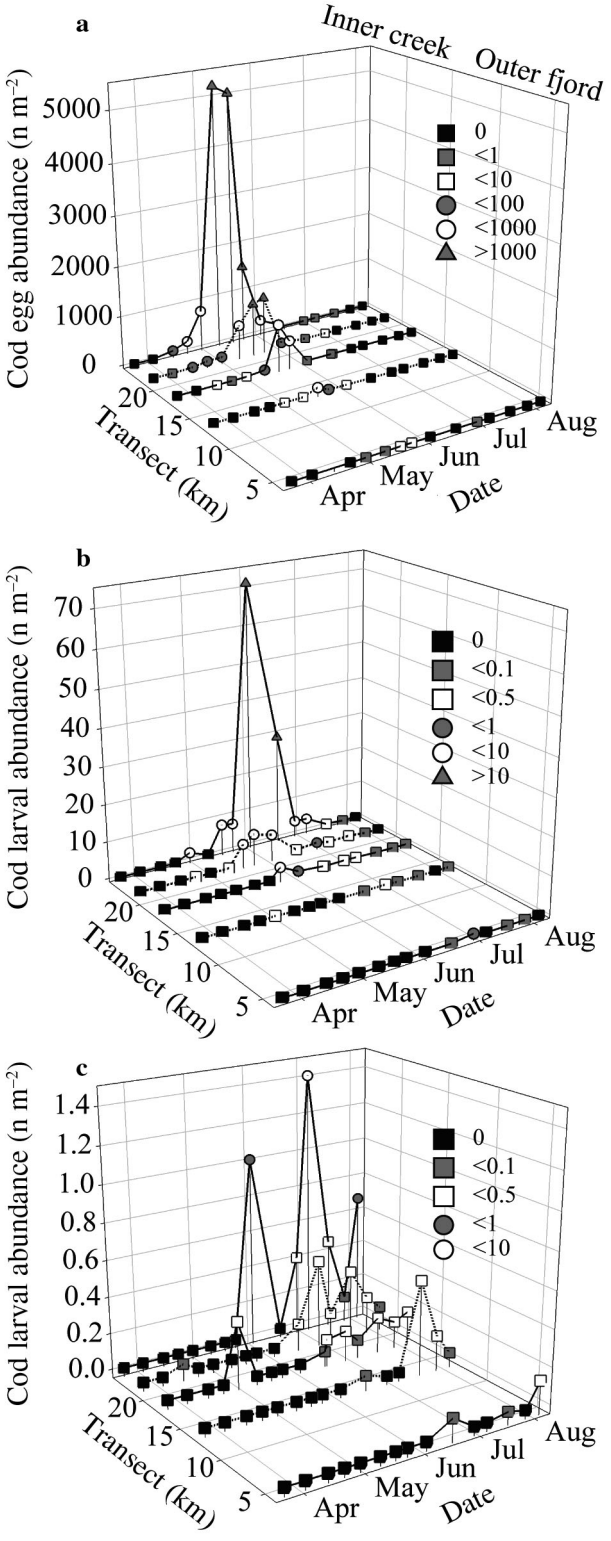

Fig. 4. Abundance of (a) Atlantic cod eggs, (b) larvae ≤10 mm and (c) larvae >10 mm in length at each station and sampling date. Different symbol shapes and shades for each abundance range. Note different scales on *z* axis

Table 2. Integrated egg and larval abundance and annual egg production within each area represented by each sampling station. The total number of eggs and larvae collected at each station is shown in brackets. Weighed egg development time from fertilization to hatch (weighed by egg abundance), and average mortality estimates along the fjord transect (between egg stage 1 and 4+5). Development time was calculated from average temperatures within the top 30 m during the main spawning period (30 April–3 June). SL = standard length

Station no.:	2	3	4	5	6	Fjord
Area size (km^2):	19	24.2	18.6	8.2	18.9	89
Integrated egg abundance ($n\ area^{-1}$)	1.07×10^9 (<1%, n = 467)	2.43×10^{10} (2%, n = 1480)	2.01×10^{11} (14%, n = 5024)	1.90×10^{11} (13%, n = 13503)	1.02×10^{12} (71%, n = 41169)	1.43×10^{12}
Egg development time (d)						21.4
Egg mortality (%)						90.3
Egg daily mortality						0.158
Integrated larval abundance ($n\ area^{-1}$)	2.26×10^8 (n = 18)	3.55×10^8 (n = 29)	6.74×10^8 (n = 98)	1.75×10^9 (n = 277)	1.46×10^{10} (n = 858)	1.76×10^{10}
Relative larval abundance at station						
≤10 mm SL	1%	1%	5%	12%	81%	
>10 mm SL	3%	21%	20%	12%	44%	
Annual egg production ($n\ m^{-2}$)	10	105	949	2202	14181	
Annual egg production ($n\ area^{-1}$)	1.91×10^8 (<1%)	2.53×10^9 (1%)	1.76×10^{10} (10%)	1.81×10^{10} (10%)	1.35×10^{11} (78%)	1.73×10^{11}

5, eggs and larvae peaked around the same time. Peak larval abundance within the inner creek (72 larvae m^{-2}) was almost 10 and 50 times higher compared with Stns 5 (7.7 larvae m^{-2}) and 4 (1.5 larvae m^{-2}), respectively, and 2 orders of magnitude higher than the outer Stns 2 (0.8 larvae m^{-2}) and 3 (0.5 larvae m^{-2}). While the smaller, younger larvae (≤10 mm length) were more concentrated at Stn 6, the larger, older larvae (>10 mm) were more evenly distributed along the fjord transect (Fig. 4b,c). When comparing the 5 areas, 83% of the integrated larval abundance was located within the inner creek (Table 2). For the smaller larvae, 81% were located in the inner creek compared with only 44% of the larger larvae.

The vertical distribution of cod eggs in the inner creek during the period between peak occurrence of eggs and larvae showed that 95% of the cod eggs were located in the upper 30 m of the water column (Fig. 5). Decreasing water salinity in the upper 20 m resulted in a higher fraction of the neutrally buoyant cod eggs sinking below the pycnocline (Fig. 5b,c). A few larvae were also caught on 24 May (2.5 larvae m^{-3}) and 3 June (3.3 larvae m^{-3}) in the 10–20 m and 20–30 m depth layers, respectively (data not shown).

Cod egg development and mortality

We found an overall daily egg mortality of 16% along the transect in Kapisigdlit (Table 2). It was assumed that the disappearance of eggs between development stages 1 to 4+5 was due to mortality. During the main spawning period, the average percentage of eggs in developmental stages 4+5 was 6, 4 and 14% in the outer fjord (Stns 2, 3 and 4), slope (Stn 5) and inner creek (Stn 6), respectively. At the inner creek, stage 4 and 5 eggs were only found in the top 30 m of the water column, and these first occurred on 10 May, 26 d after the first occurrence of stage 1 eggs.

Areal production

The average daily egg production within the inner creek was 134 eggs m^{-2} (maximum 685 eggs m^{-2} measured on 10 May) and substantially higher than the fjord average of 18 eggs m^{-2} (maximum 162 eggs m^{-2} measured on 10 May). The inner creek area contributed most of the AEP within Kapisigdlit (Table 2). The AEP for the entire Kapisigdlit fjord branch corresponded to 212000 spawning females and a spawing stock biomass (SSB) of 1090 tons.

Cod larval growth

There was a strong relationship between larval length and otolith size (Fig. S1a in the Supplement at www.int-res.com/articles/suppl/m555p185_supp.pdf). Linear mixed models demonstrated that larval otolith growth trajectories differed throughout the fjord.

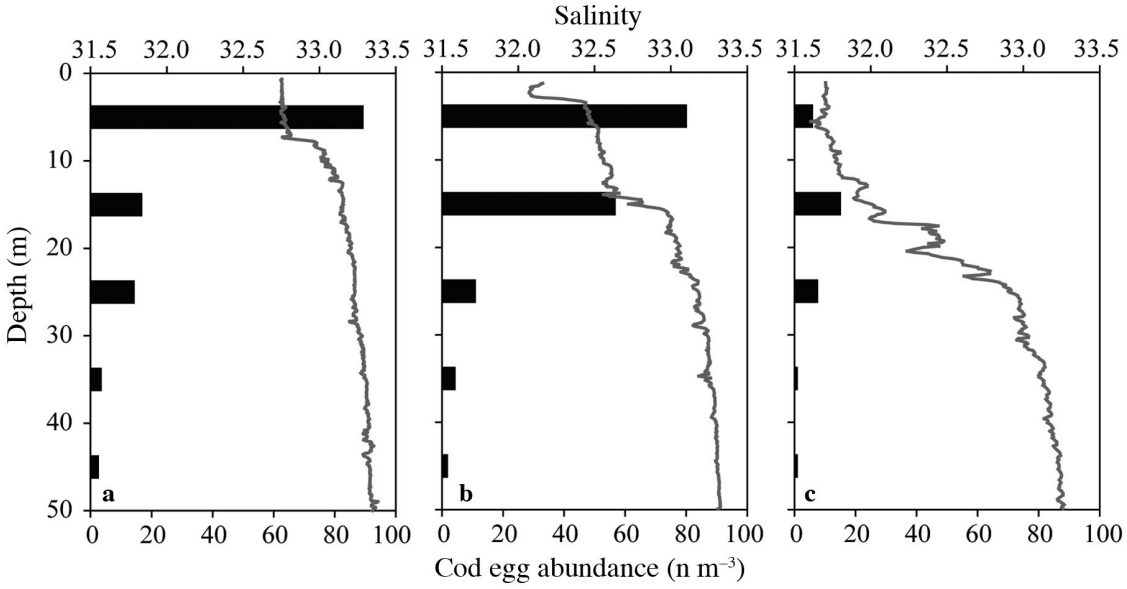

Fig. 5. Atlantic cod egg abundance (bars) within five 10-m depth strata on (a) 10 May, (b) 24 May and (c) 3 June at Stn 6. Gray lines illustrate water salinity profile at each sampling date

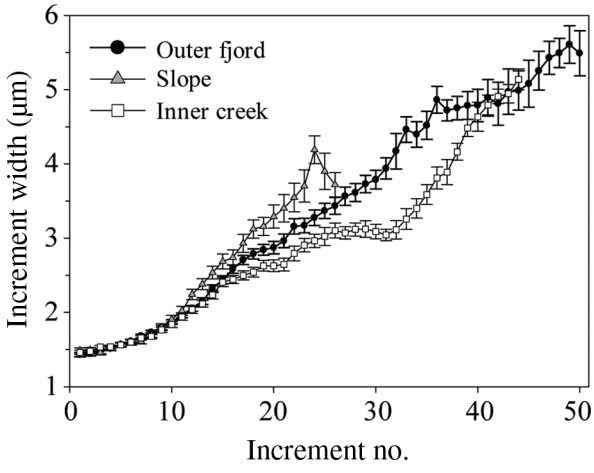

Fig. 6. Average growth increment width (±SE) per lapillus increment number in the outer fjord (Stns 2, 3 and 4), on the slope (Stn 5) and within the inner creek (Stn 6). Due to low numbers of larvae caught early in the season, larvae from Stns 2, 3 and 4 were pooled

Larvae located within the inner creek (Stn 6) grew slower than larvae on the slope (Stn 5) and outer fjord (Stns 4, 3 and 2, Fig. 6). This spatial difference in growth increment width was clear between increments 12–16 and 38. The interaction between geographical area and otolith growth increment number for the inner creek differed significantly from the slope and outer fjord, respectively (df = 4274, t = 2.371, p = 0.018, and df = 4274, t = 2.635, p = 0.008, respectively). There was no significant difference between the slope and outer fjord (df = 4274, t = –0.349, p = 0.727).

The GAMs revealed positive relationships between mean increment number, as a proxy for age, and mean otolith increment width across the fourth to sixth increments closest to the otolith edge (Fig. 7a, r^2 = 0.82, p < 0.00001, optimal number of knots (k′) = 9), number of prey items in a larval gut (Fig. 7b, r^2 = 0.37, p < 0.00001, k′ = 9), and amount of prey carbon in a larval gut (Fig. 7c, r^2 = 0.58, p < 0.00001, k′ = 9). Using residuals of these models, model selection demonstrated a strong, positive effect of age-corrected (~age) number of prey items in larval stomachs and growth during approximately days 4 to 6 prior to capture (Table 3). All of the top models included age-corrected number of prey items in stomachs, and the univariate model that included this variable alone explained 26% of the variation in otolith increment width and was indistinguishable from the most plausible model that also included age-corrected prey carbon in stomachs (Table 3, Fig. 8a). Model-averaged slopes indicated that age-corrected number of prey items in larval stomachs was the only independent variable that did not have 95% confidence intervals overlap with 0 (Table 4). There was not a strong indication that age-corrected otolith increment width was affected by temperature, *in situ* prey biomass or agecorrected stomach carbon, although

the univariate model that included stomach carbon and temperature explained 8% of the variance in age-corrected otolith increment width and had a p-value of 0.03 (Table 3, Fig. 8b–d). Qualitatively there was no difference in the results when including (n = 153) or excluding (n = 117) larvae with empty stomachs (Tables 3 & 4, and Tables S1 & S2 in the Supplement).

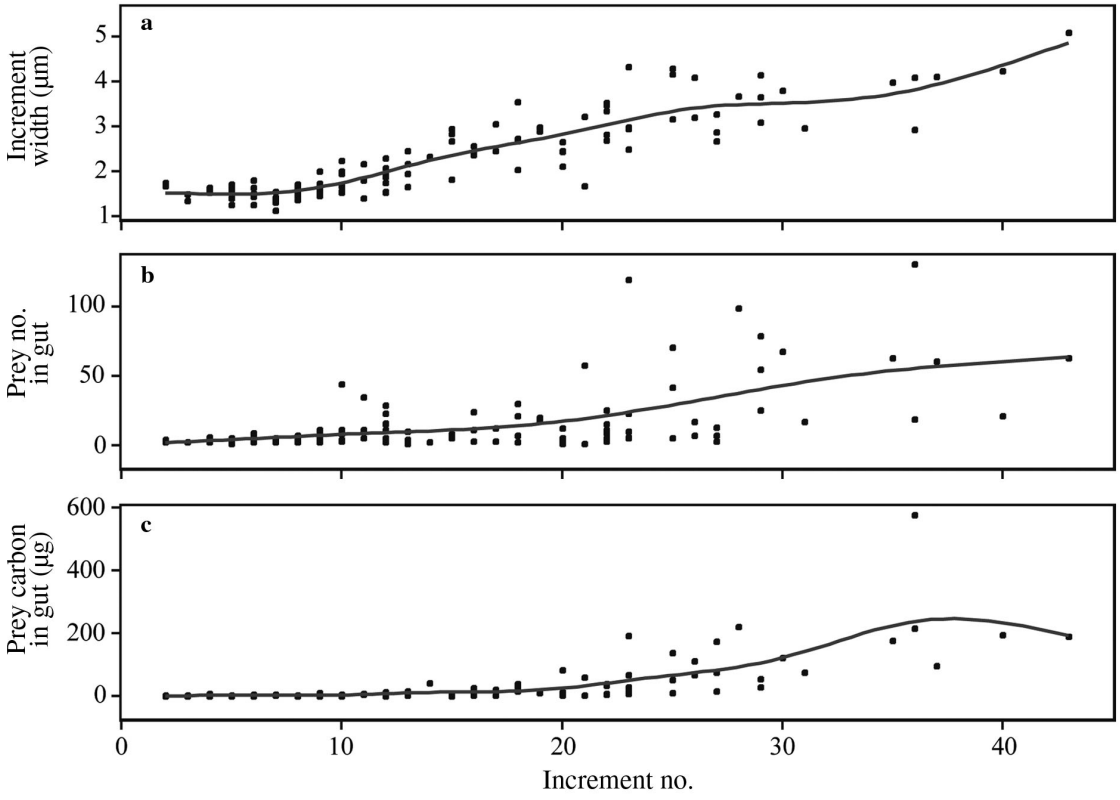

Fig. 7. Relationship between larval otolith growth increment number, as a proxy for age, and (a) mean width of increments 4 to 6 from the otolith edge, (b) number of prey items in a larval gut, and (c) amount of carbon in a larval gut. Curves are best fit estimates based on the Generalized Additive Model. This analysis included only larvae with at least one prey item in its gut

Table 3. Results of multiple regression models correlating residuals of otolith increment width~age, using otolith increment number as a proxy for age, against: residuals of prey carbon in a larval gut~age; residuals of prey number in a larval gut~age; *in situ* prey biomass from Swalethorp et al. (2014); and ocean temperature. K is the number of parameters and ΔAICc is the difference between a given model and the most plausible model, model weight is the weight of a given model, and cumulative weight is the weight of a given model plus all of the more plausible models. Only models within 10 AICc of the most plausible are shown. Only larvae with prey in their stomachs were used for this analysis. Results using all larvae are in the Supplement at www.int-res.com/articles/suppl/m555p185_supp.pdf

Independent variables correlated against otolith increment width~age	K	AICc	ΔAICc	Model weight	Cumul. weight	Multiple R^2	p
Prey carbon in gut~age + prey no. in gut~age	4	253.48	0	0.27	0.27	0.28	<0.0001
Prey no. in gut~age	3	253.6	0.12	0.25	0.52	0.26	<0.0001
Prey no. in gut~age + *in situ* prey biomass	4	254.96	1.48	0.13	0.65	0.27	<0.0001
Prey carbon in gut~age + prey no. in gut~age + *in situ* prey biomass	5	255.06	1.58	0.12	0.78	0.28	<0.0001
Prey no. in gut~age + temperature	4	255.27	1.78	0.11	0.89	0.26	<0.0001
Prey no. in gut~age + *in situ* prey biomass + temperature	5	256.26	2.78	0.07	0.95	0.27	<0.0001
Prey carbon in gut~age + prey no. in gut~age + *in situ* prey biomass + temperature	6	256.98	3.5	0.05	1	0.29	<0.0001

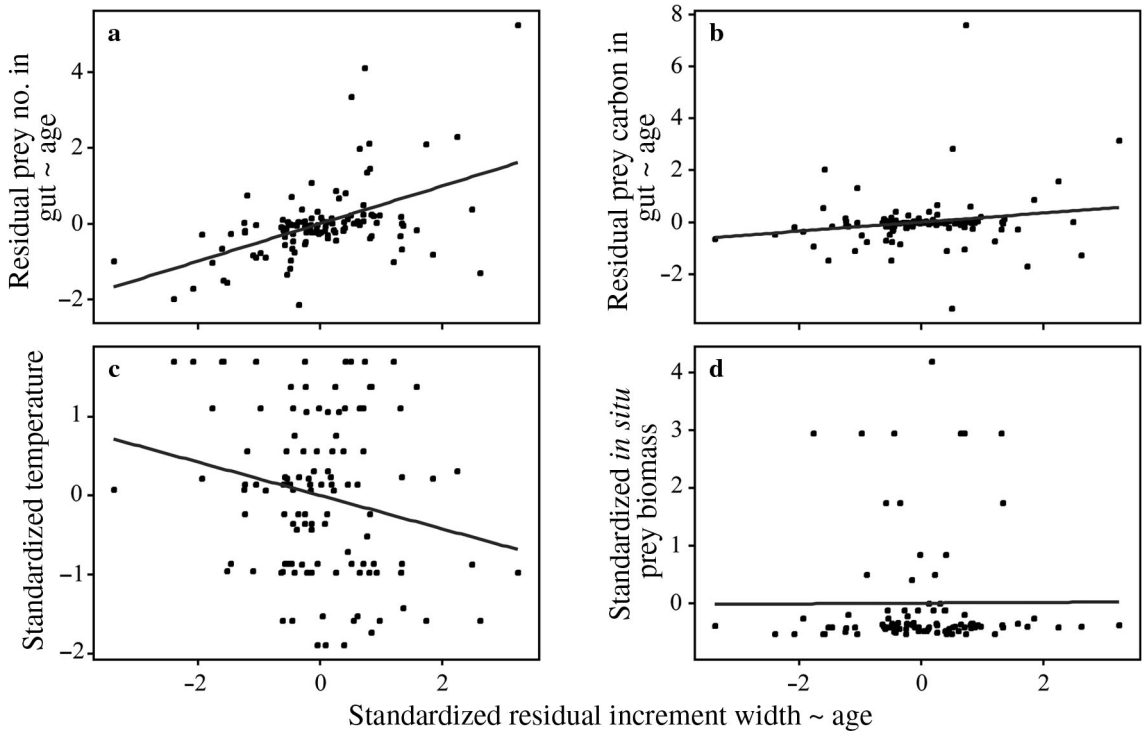

Fig. 8. Univariate relationships between residuals of Generalized Additive Models of mean otolith growth increment width~age (dependent variable), using otolith increment number, as a proxy for age, versus (a) residuals of number of prey items in a larval gut~age, (b) residuals of amount of prey carbon in a larval gut~age, (c) temperature and (d) *in situ* prey biomass. All variables were standardized to zero mean and unit variance

Table 4. Model-averaged estimates of the slopes (β) and 95% confidence limits (CL) of independent variables used in model-selection analysis

Variable	β	Lower 95% CL	Upper 95% CL
Stomach prey carbon	−0.15	−0.35	0.05
Stomach prey no.	0.52	0.32	0.73
In situ prey biomass	0.09	−0.10	0.27
Temperature	−0.07	−0.25	0.11

DISCUSSION

Cod spawning

Our results show that spawning of local fjord populations of cod can be strongly restricted, both spatially and temporally. In the population considered, a shallow, inshore locality was shown to be the important spawning ground, in agreement with past studies (Jensen & Hansen 1931, Hansen 1949, Smidt 1979). Accordingly, increasing egg densities towards the head of fjords has also been documented for cod populations in Canada and Norway (Knutsen et al. 2007, Knickle & Rose 2010). The timing of spawning in Atlantic cod has been shown to be closely related to water temperature (Kjesbu 1994). In our study, temperature increased from the mouth of Kapisigdlit to the inner creek, where spawning occurred earlier. Spawning was concentrated within 1 mo, but extended over 3.5 mo. Such prolonged spawning may be the result of adults being subjected to different thermal regimes (Knickle & Rose 2010) while migrating from different parts of the fjord (e.g. residing at greater depth for longer or shorter periods of time).

The average daily egg production at the principal spawning site at the head of the fjord was higher than those reported from high productive areas in the North Sea (up to 33 eggs m^{-2}, Fox et al. 2008), while the average daily egg production for the entire fjord was in the lower end of those reported from Georges Bank (up to 48 eggs m^{-2}, Mountain et al. 2008). Smidt (1979) found that egg abundance in Kapisigdlit fjord was even higher at a sampling station located further inside the shallow creek than our Stn 6, while his Stns 5 and 6 were comparable to our study. Because spawning cod are readily caught within the entire inner creek (R. Hedeholm pers.

comm.), it is likely that spawning occurs throughout the entire creek area. However, due to low numbers of eggs collected at the outer stations and a general lack of variance estimates, egg abundance and AEP should be interpreted with some caution.

The Godthåbsfjord system covers 2161 km^2. Considering that cod eggs and larvae are also found in other fjord branches (Smidt 1979, Engelstoft 1997, Storr-Paulsen et al. 2004, Swalethorp et al. 2015, P. Munk unpubl. data), and that there is no genetic differentiation between cod from these branches (Therkildsen et al. 2013), the estimated AEP and SSB would be a minimum estimate for the Godthåbsfjord system. The peak egg abundances within Kapisigdlit suggest that AEP and SSB were high compared with fjords in other areas, as egg abundances have not been reported higher than 36–536 eggs m^{-2} in 21 Norwegian fjords (Espeland et al. 2007, Knutsen et al. 2007) or 46 eggs m^{-2} from Smith Sound, Canada (Knickle & Rose 2010). Furthermore, our assumption of no egg mortality during the first development stage should make the AEP and SSB conservative estimates.

Egg and larval dispersal

Distributions of eggs and larvae changed markedly over the course of the study, likely driven by changes in water column structure and circulation. Initially, cod eggs and young larvae were mainly found within the inner part of the fjord, despite the presence of outward flow in the upper water column. Hansen (1949) and Smidt (1979) suggested that eggs and larvae are rapidly dispersed by currents, as they recorded large differences between egg and larvae caught within Kapisigdlit and outside the fjord branch. We measured a current of 1.8 km residual flow per day in the top layer at Stn 4 before the ice break-up in Kapisigdlit River. Therefore, during the main spawning season (30 April–3 June), eggs spawned within the inner creek could have drifted up to 40 km out before hatching. However, we found that the dispersal of eggs and young larvae was limited early in the season. The outward flow in the surface layer could be lower at the shallow inner Stn 6 compared with the centrally located Stn 4, and may on average be lower than what we measured over just 2 tidal cycles. Furthermore, a large proportion of the eggs were located below the top layer where the outward current was weaker. Rotational dynamics in water circulation that at high latitudes can exist in narrow fjords (Asplin et al. 1999, Cottier et al. 2010) could also have reduced egg and larval dispersal within Kapisigdlit. Changes in wind direction (Asplin et al. 1999), tidal advection (Fortier & Leggett 1982), and timing and magnitude of freshwater input (Myksvoll et al. 2011, 2014) can also greatly affect dispersal.

Later in the season, we observed that especially larger larvae were more evenly distributed along the fjord transect (also see Swalethorp et al. 2014). This shift in distribution was seen after the ice broke in Kapisigdlit River, which significantly increased the freshwater outflow to the fjord. Myksvoll et al. (2011) defined a 'window of leakage' that occurs right at the start of melt water input and onset of estuarine circulation. This window lasts for approximately 1 mo, and transports low-density eggs residing in the top layer outward. Wind-driven currents can also disperse buoyant eggs before the water column becomes stratified, displacing the eggs to the deeper mixed layer (Knickle & Rose 2010) while trapping the wind-driven current near the surface layer (Svendsen & Thompson 1978). A 'window of leakage' seemed apparent in our study. The ice in Kapisigdlit River broke around 20 June, when 91% of the larvae had already hatched. After the ice break-up, larvae started drifting out as 81% of the ≤10- mm-long larvae were located within the inner creek area, compared with only 44% of the >10-mm-long larvae. Moreover, the peak in larval abundance at the outer stations (Stns 2 and 3) occurred very late in the season, 3 wk later than stage 4+5 eggs. Thus, cod larvae found at the 2 outer stations probably originated from the inner creek. The 'window of leakage' closes when a strong pycnocline is established (Myksvoll et al. 2011). At this time, many larvae were actively swimming and feeding around the top layer. Herring larvae have been found to actively modify their dispersal by migrating upward and crossing the pycnocline during tidal flooding (Fortier & Leggett 1982, 1983). Cod drift trajectories can also differ for larvae inhabiting different depths (Vikebø et al. 2005), and larvae have been found to aggregate close to or within the stratified layer (Lough & Potter 1993), performing vertical migrations and crossing strong haloclines (Grønkjær & Wieland 1997). Because currents within or just below the pycnocline may move in the same direction as the surface layer (Wiseman & Garvine 1995), cod larvae residing there were potentially dispersed out.

Egg mortality

The observed restriction of spawning to the innermost part of Kapisigdlit may have facilitated egg sur-

vival. Overall, our daily egg mortality estimate from the fjord was within the lower range of 10–32% daily mortality reported in other cod spawning areas (Campana et al. 1989, Köster & Möllmann 2000, Wieland et al. 2000, Armstrong et al. 2001, Mountain et al. 2003, Mountain et al. 2008). This low mortality might be due to sheltered conditions and specific hydrographical settings, such as temperature, occurring in such inshore areas (Wroblewski et al. 2005, Knutsen et al. 2007). The temperature was highest within the inner creek and could have reduced the development time by as much as 1.5 d compared with the outermost station (Stn 2) during the main spawning period (30 April–3 June). This would have left the passively drifting eggs less exposed to predation. The scarcity of potential egg predators within the main spawning area may also explain the lower mortality. Large krill (>2.5 cm) were abundant in the outer fjord (Agersted & Nielsen 2014), but only a few were caught on the slope or within the inner creek. Krill may be capable of consuming fish eggs considering they have been shown to consume large copepods (Falk-Petersen et al. 2000, Torgersen 2001) and northern anchovy larvae (Theilacker & Lasker 1974). Moreover, chaetognaths are voracious planktonic predators that eat early life stages of fish (Frank & Leggett 1985, and references therein) and their abundances were twice as high on the slope and in the outer fjord compared with the inner creek. Hence, the relatively lower abundances of potential predators around the main spawning site may have contributed to the low daily mortality.

Growth

Atlantic cod larval otoliths showed significant differences in growth trajectories in different areas of the fjord. These results are similar to those reported by Landaeta & Castro (2006) in Chile, where larger larval rockfish dispersed out from the inner fjords and attained faster growth. Interestingly, food, rather than temperature, appeared to be the main driver of growth in Kapisigdlit. Many studies have shown that larval fish growth is highly temperature dependent (Otterlei et al. 1999, Steinarsson & Björnsson 1999, Otterlei et al. 2002). The average temperature (top 30 m) was 0.8–2.4°C higher within the inner creek, so it is somewhat surprising that there was no correlation between temperature and growth. The background could be density dependence due to an increased competition for food within the inner creek area (Byström & Garcia-Berthou 1999, Swalethorp et al. 2014). The size composition and the potential nutritional quality of the prey differed considerably between the areas (Swalethorp et al. 2014). Although we did not find a direct relationship between growth and *in situ* prey biomass, there was a positive correlation between the amount of food in a larvae's stomach and growth. A possible reason for the lack of a relationship between *in situ* prey biomass and recent growth was the temporal mismatch between the 2 estimates, since larvae growth was estimated ≥4–6 d earlier than the *in situ* prey biomass and during which time the larvae could also have drifted from one area to another. Furthermore, larval prey perception is also affected by light (Huse 1994) and small-scale turbulence affects the prey encounter rate (MacKenzie & Kiørboe 2000). Although light intensities were always above 3.67×10^{-6} W m^{-2} in the top 50 m of the water column, at which cod larvae are capable of feeding (Vollset et al. 2011), and gut content was not affected by time of day (Swalethorp et al. 2014), small-scale turbulence generated by e.g. tidal flow and wind is likely to have differed both spatially and temporally.

We used ring increment number as a proxy for age, but patterns in increment width indicate that larvae did not deposit daily growth increments during the first part of their life. Compared with cod larvae from the Grand Banks and North Sea (Campana 1996, Nielsen & Munk 2004), lapillus increment widths were ~50% wider for the first 10 growth increments and became twice as wide thereafter. Although lapillus growth rates were comparable to some other studies (Suthers & Sundby 1993, Otterlei et al. 2002, Van der Meeren & Moksness 2003), comparison of length at increment number (age) with literature values also suggested that up until the size of metamorphosis (~12 mm length) growth increments in our study may only have been distinguished for approximately every second day (Fig. S1b, Bolz & Lough 1983, 1988, Campana & Hurley 1989, Meekan & Fortier 1996, Green et al. 2004, Nielsen & Munk 2004). Indistinguishable ring patterns are seen for larvae inhabiting temperatures of 6°C or less (Otterlei et al. 2002), a thermal regime that the present larvae experienced during their early life. However, considering that most young cod were located in the inner creek area, it is reasonable to assume that these were all subjected to the same environmental conditions during the early life and deposited otolith growth increments in a similar way, thus allowing us to ascertain relative differences and carrying out inter-regional comparisons using a linear mixed model. This model is ideal since it can deal with unbalanced datasets such as

most datasets of otolith growth trajectories from multiple field caught fish (i.e. different number of readable otoliths within larvae and number of increments within otoliths). Repeated measurements ANOVA, which is frequently used for this type of analysis, is not able to handle unbalanced datasets and consequently most data points have to be omitted when using this analysis. Lastly, when only part of the growth or feeding history is to be considered, GAMs are more appropriate than linear models as they do not assume linearity, but are adaptable to temporal changes in the relationships e.g. changes in the rate of readable otolith growth increment deposition.

CONCLUSIONS AND PERSPECTIVE

Our work on the early life history of a historically successful inshore population of Atlantic cod identified key features governing the success in early life and likely larval recruitment to the population. Spawning mainly occurred within a shallow and sheltered area at the head of the fjord. Initially, eggs and young larvae remained concentrated within this shallow area despite the presence of a moderate outflow of water in the surface layer. Egg daily mortality was low in the fjord, possibly due to the sheltered nature of the spawning area where temperatures were relatively high and abundances of potential predators low. Later in the season, most of the older actively feeding larvae had been transported into the main part of the Kapisigdlit fjord. This was observed after the seasonal peak in river runoff, which may have facilitated the larval dispersal, as has been demonstrated in other fjords (Myksvoll et al. 2011, 2014). Larval otolith growth trajectories showed that larvae that were transported into the main fjord, where prey availability was higher (Swalethorp et al. 2014), had a significantly faster growth rate, and that gut content rather than temperature influenced attainable growth rates. That fish spawn upstream from nursery grounds is well documented in oceanic migratory cod (Bergstad et al. 1987) reflecting an adaptive use of ocean hydrodynamics (Knutsen et al. 2007). Our study indicated an adaptive use of water flow in fjord populations, while timing between spawning and freshwater inflow may have been essential for retention of passive early stages and dispersal of older, actively feeding larvae, patterns which ultimately could determine survival chances.

Our results underscore the importance of phenology to survival chances of early life stages of Atlantic cod. Recent research on marine fish phenology suggests that the timing of spawning correlates with water temperature (Greve et al. 2005, Genner et al. 2010, Poloczanska et al. 2013) and that spawning has progressively arrived earlier in the year for many fishes over the past 60 yr (Asch 2015). Moreover, change in fish phenology does not necessarily correlate with phenology of the prey (e.g. zooplankton), thus potentially decoupling larval fish from their food source (Asch 2015). Chances of survival for eggs and larvae may thus change with potential future changes in freshwater outflow (see Myksvoll et al. 2011, 2014), changes in temperature or wind conditions, or changes in food resources.

The relatively high AEP and SSB estimated for the population in this fjord branch underline the significance of local populations, considering that over half of the known North Atlantic spawning groups of cod are such sedentary fjord populations (Robichaud & Rose 2004). Their importance to local communities, their potential role in rebuilding the offshore stocks (Wroblewski et al. 2005) and their genetic distinctness on small geographic scales (Jorde et al. 2007) calls for further investigations to enable fishery management on an individual population level.

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