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Circum-arctic comparison of the hatching season of polar cod *Boreogadus saida*: A test of the freshwater winter refuge hypothesis

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ABSTRACT

The hypothesis that salt-related differences in winter sea surface temperature dictate regional differences in the hatching season of polar cod *Boreogadus saida* is tested by contrasting hatch-date frequency distributions among six oceanographic regions of the Arctic Ocean characterized by different freshwater input. Consistent with the hypothesis, hatching started as early as January and extended to July in seas receiving large river discharge (Laptev/East Siberian Seas, Hudson Bay, and Beaufort Sea). By contrast, hatching was restricted to April–July in regions with little freshwater input (Canadian Archipelago, North Baffin Bay, and Northeast Water). Length (weight) in late-summer (14 August) varied from <10 mm (<0.01 g) in July hatchers to 50 mm (0.91 g) in January hatchers. An earlier ice break-up, more frequent winter polynyas, a warmer surface layer, and increased river discharge linked to climate warming could enhance the survival of juvenile 0+ polar cod by enabling a larger fraction of the annual cohort to hatch earlier and reach a larger size before the fall migration to the deep overwintering grounds. A further test of the hypothesis would require the verification that the early winter hatching of polar cod actually occurs in the thermal refuge provided by under-ice river plumes.

1. Introduction

The polar cod *Boreogadus saida* plays a central role in the relatively simple pelagic food web of arctic seas by channeling a major fraction of the energy flow between plankton and vertebrates (Bradstreet et al., 1986; Welch et al., 1992). Polar cod spawn in late fall and early winter under the ice cover of arctic shelves, and fertilized eggs rise to the ice–water interface (Rass, 1968; Craig et al., 1982; Graham and Hop, 1995; Ponomarenko, 2000). Embryonic development may take as long as 60–90 d at the sub-zero temperatures prevailing under the ice (Altukhov, 1979; Ponomarenko, 2000). Length at hatch ranges from 4 to 8 mm (Rass, 1968; Aronovich et al., 1975; Graham and Hop, 1995; Michaud et al., 1996). Metamorphosis into pelagic juveniles occurs at 27–35 mm, and the migration from the surface layer to the deeper overwintering grounds begins at 30–35 mm (Baranenkova et al., 1966; Ponomarenko, 2000).

Starting in late-summer, polar cod fry are preyed upon by seabirds in the surface layer (Bradstreet, 1982; Karnovsky and Hunt, 2002) and then by their adult congeners as they migrate at depth to their overwintering grounds (Baranenkova et al., 1966).

A large size at the end of the short arctic summer should reduce the vulnerability of juveniles to avian predation, cannibalism, and winter starvation. Hence, selection pressures should push hatching to occur as early in winter or spring as environmental conditions will allow, so as to maximize the duration of the growth season and late-summer size (Fortier et al., 2006). We hypothesized that salinity-induced variations in sea surface temperatures dictate regional differences in the hatching season of polar cod (Bouchard and Fortier, 2008). In coastal seas influenced by large rivers, brackish conditions in under-ice river plumes would provide the larvae with temperature only slightly below 0 °C, accelerating embryonic development and allowing successful first-feeding and survival in winter. In regions with little freshwater input, the −1.8 °C temperature prevailing under the ice in winter would slow egg development and limit first-feeding and survival. In such regions, hatching would have to be delayed until the vernal warming of the surface layer for the larvae to survive.

In the present study, we test the prediction of the freshwater thermal refuge hypothesis that the hatching of polar cod starts in winter in regions of the Arctic Ocean influenced by freshwater, and is delayed until spring elsewhere. Based on new and published data, interannual variations and regional differences in the hatch-date frequency distribution (HFD) of polar cod are contrasted among six oceanographic regions of the Arctic Ocean ranging from inland and coastal seas heavily influenced by rivers to recurrent polynyas with little freshwater input.

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2. Materials and methods

2.1. Study areas

Previously published hatch-date frequency distributions (HFDs) and new HFDs based on the otolith aging of pelagic juveniles sampled in late-summer and early fall, were used as estimates of the hatching season of polar cod in six regions of the Arctic Ocean that differ widely in their surface salinity (Fig. 1). Depending on the availability of data, the hatching season of polar cod was estimated for one to three different years in each region.

The Laptev Sea covers a wide shallow continental shelf and part of the deep Nansen Basin. The Lena and other rivers inject a total annual freshwater input of 738 km^3 in the shallow sector (Gordeev, 2006). The resulting dilution of the surface layer extends far offshore (Fig. 1a). The Laptev Sea is typically covered with ice from October to June, with some sectors in the North and West remaining ice-covered throughout the year. Polynyas are important features of the Laptev Sea that form under certain wind conditions as an enlargement of the circumpolar flaw lead that separates the fixed landfast ice from the mobile central ice pack. Our sampling in this region extended to the fringe of the adjacent East Siberian Sea.

Hudson Bay is a shallow (average depth of 150 m) estuarine sub-arctic sea (Fig. 1b). Several large rivers and James Bay input an average annual freshwater volume of 714 km^3 in Hudson Bay (Déry et al., 2005). Together with Hudson Strait and Foxe Basin, it is often referred to as the Hudson Bay System. Seasonal ice is present in the bay from October to July with maximum thickness and extent in April. The general circulation is cyclonic and slow, with cold and salty water from Foxe Basin entering from the northwest, and warmer, fresher water exiting along the eastern coast (Saucier et al., 2004 and references therein).

Southeastern Beaufort Sea extends over the shallow and wide Mackenzie Shelf and the Amundsen Gulf (Fig. 1c). The surface layer of the Beaufort Sea is strongly diluted by the plume of the Mackenzie River, the third largest river discharging into the Arctic Ocean (330 km^3 year^{-1}; Macdonald et al., 1998). SE Beaufort Sea is typically covered with ice from October to June. In winter and spring, the circum-arctic flaw lead follows the 20-m isobath on the Shelf (Arrigo and van Dijken, 2004; Lukovich and Barber, 2005). Throughout winter, floe rafting at the edge of the landfast ice builds the stamukhi, a thick linear hummock that dams the Mackenzie River plume to form the seasonal brackish Lake Herlinveaux (70 km^3) under the ice cover of the inshore shelf (Macdonald et al., 1995). With ice break-up in June or July, the flaw lead widens to form the Cape Bathurst polynya that extends over the Shelf and the Amundsen Gulf (Arrigo and van Dijken, 2004). The break-up of the stamukhi in early summer releases the turbid and brackish waters of the seasonal lake in the top 5–10 m of the surface layer on the shelf. By August or September, the region is normally ice-free except for the permanent central ice pack over the northern sector.

The channels of the Northwest Passage in the Canadian Archipelago (Fig. 1d) are usually covered from October to July by a mixture of landfast ice and pack ice advected from the Canadian Basin of the Arctic Ocean (Melling, 2003). There is little direct river inflow in the region, but the easternmost reaches of the Mackenzie plume clearly affect surface salinity in the south-western region of the Archipelago (Fig. 1d).

Located between the Canadian Archipelago and Greenland, Baffin Bay is a large semi-enclosed sea with little freshwater input (Fig. 1e). It receives Arctic Ocean surface water through Nares Strait and Lancaster Sound, and Atlantic Water with the West Greenland current. Typically, most of Baffin Bay is covered with ice from October to July. Our sampling of polar cod juveniles was conducted primarily in the northern part of Baffin Bay which is

dominated by the North Water, the largest recurrent polynya in the arctic. The North Water starts to enlarge in spring, when the flux of arctic ice through Nares Strait is blocked by the formation of an ice bridge in Smith Sound, and northerly winds push the remaining ice south along the coast of Ellesmere Island. Open water expands in April and reaches over 70 000 km^2 by the end of July when the entire bay becomes ice-free (Mundy and Barber, 2001). Sometimes compared to an oasis, the North Water is a biological hotspot that supports large populations of seabirds and marine mammals (Deming et al., 2002).

The Northeast Water is a large recurrent polynya that extends over the East Greenland Shelf (Fig. 1f). It is bounded by the Arctic Ocean to the north and by the polar front of the Greenland Sea to the east and south (Smith et al., 1990). The Northeast Water usually opens in April or May, reaches its maximum extent of ca. 44,000 km^2 in July–August, and closes around September (Wadhams, 1981; Smith et al., 1990; Barber and Massom, 2007). Bathymetry ranges between 100 and 500 m and features two shallow banks (Ob and Belgica). No large river drains the area and surface salinity is mainly dictated by ice formation and melting. With the recent collapse of the landfast ice shelves that helped form the polynya by deflecting the arctic flux of ice, the Northeast Water has formed irregularly in recent years (Barber and Massom, 2007).

2.2. Sampling of fish larvae and juveniles

Fish larvae and juveniles were collected in the Canadian Arctic during the ArcticNet annual mission of the CCGS *Amundsen* from 14 August to 2 October 2005 and from 4 September to 29 October 2006 (Table 1). Young fish were sampled with four different samplers: (1) a Double Square Net (DSN) consisting of a rectangular frame carrying two 6-m long, 1-m^2 mouth aperture, square-conical 500-µm mesh nets; (2) a 8-m^2 effective aperture, 1.6-mm mesh Rectangular Midwater Trawl (RMT); (3) a large Pelagic Trawl (PT) with mesh size decreasing from the mouth (5 mm) to the end of the net (1.6 mm); and (4) a 1-m^2 aperture multi-layer sampler equipped with nine 6-m long, 333-µm mesh nets (EZNet®). All four samplers were towed obliquely from the side of the ship at a speed of 1 m s^{-1} (two knots) to a maximum depth of 90 m (DSN, RMT and EZNet®) or 150–200 m (PT). The nets of all samplers were fitted with rigid cod-ends to minimize the deterioration of fish larvae and zooplankton. TSK flow meters were mounted on all samplers to record filtered volumes.

In the Siberian Arctic, fish larvae and juveniles were collected during the Nansen and Amundsen Basins Observational System (NABOS) annual missions of the icebreaker *Kapitan Dranitsyn* in 2003 and 2005 (Bouchard and Fortier, 2008), and the research vessel *Victor Buynitskiy* in 2007 (Table 1). Young fish were sampled with a DSN as described above.

At sea, the indistinguishable larvae and juveniles of *Boreogadus saida* and *Arctogadus glacialis* were sorted from the zooplankton samples and measured fresh (standard length, SL) before preservation in 95% ethanol. Up to 25 cod per sample were randomly selected and measured fresh. In the laboratory, all preserved fish were measured again and the fresh standard length of fish not measured fresh at sea was estimated from the preserved-length on fresh-length regression for the region of origin. The number of young cod captured, measured fresh, and aged by otolith analysis for each region is given in Table 2.

2.3. Discriminating Boreogadus saida and Arctogadus glacialis larvae and juveniles

The larvae and juveniles of *Boreogadus saida* and *Arctogadus glacialis* are almost impossible to discriminate morphologically.
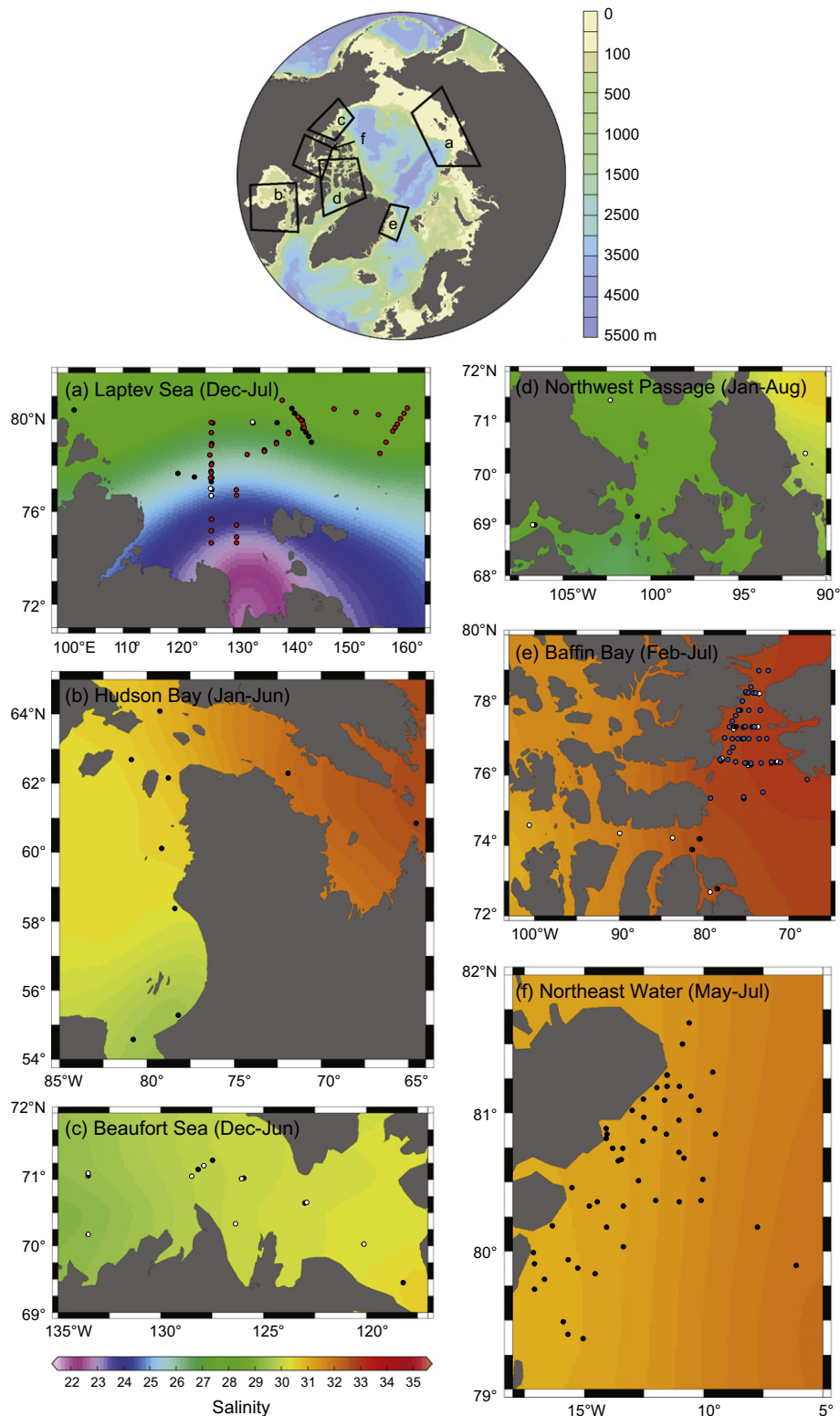
Fig. 1. Bathymetric map of the Arctic Ocean indicating the six regions studied (top). Panels a–f present the long-term average surface salinity during the hatching season of polar cod (months given) for regions characterized by strong (a–c) or weak river discharge (d–f). Surface salinities were extracted from the World Ocean Atlas. Symbols give the location and year of sampling of polar cod larvae and juveniles in each region: black: 1993, 2005; white: 2003, 2006; blue: 1998; and red: 2007.

The two species co-occur in arctic seas, and some limited (<1%) contamination of *B. saida* collections by *A. glacialis* has been reported (Sekerak, 1982). Recently, a simple genotyping method based on the microsatellite marker Gmo8, has been developed to distinguish the two species with >95% certainty (Madsen et al., 2009). To assess the contribution of *A. glacialis* to the assemblage of young cod, sub-sets of larvae and juveniles from five of the six regions (Laptev Sea, Hudson Bay, Beaufort Sea, Baffin Bay, and Northwest Passage) were analyzed with this method. In addition, assuming a daily deposition of increments in the otolith of *A. gla-*

Table 1
Details of juvenile cod sampling by region and year, and sources of primary data.

Region	Program	Research ship	Year	Sampling dates	Number of stations	Number of cod	References
Laptev Sea	NABOS	I/B *Kapitan Dranitsyn*	2003	3–11 September	3	170	Bouchard and Fortier, 2008
	NABOS	I/B *Kapitan Dranitsyn*	2005	13–21 September	24	427	Bouchard and Fortier, 2008
	NABOS	RV *Victor Buynitskiy*	2007	18–30 September	36	169	This study
Hudson Bay	ArcticNet	CCGS *Amundsen*	2005	26 September –2 October	9	47	This study
Beaufort Sea	ArcticNet	CCGS *Amundsen*	2005	2–14 September	6	54	This study
	ArcticNet	CCGS *Amundsen*	2006	29 September –17 October	8	66	This study
Baffin Bay	NOW	CCGS *Pierre Radisson*	1998	30 April–20 July	44	1087	Ringuette et al., unpubl. data
	ArcticNet	CCGS *Amundsen*	2005	14 August –19 September	10	292	This study
	ArcticNet	CCGS *Amundsen*	2006	4–23 September	11	342	This study
Northwest Passage	ArcticNet	CCGS *Amundsen*	2005	27–30 August	2	30	This study
	ArcticNet	CCGS *Amundsen*	2006	25 September –23 October	3	21	This study
Northeast Water	NEW	RV *Polarstern*	1993	23 May–2 August	52	823	Fortier et al., 2006

cialis, the age and hatch-date of 55 fish positively identified as *A. glacialis* collected in the Beaufort Sea in 2004 were determined (see Section 2.5 for methodology).

2.4. Validation of the aging of young polar cod

The daily nature of increment deposition in the otolith of polar cod was verified using a chemical marking technique (Geffen, 1992). Live juveniles collected in the 0–30 m surface layer of the North Water from 10 September to 5 October 1999 were delicately transferred to individual jars containing seawater at 0 °C (representative of *in situ* temperature) and kept in an incubator on board the ship. The fish were fed once daily with fresh zooplankton. The light regime in the incubator was set at 12 h of darkness and 12 h of light to simulate the photoperiod prevailing at the time in the region. Light intensity in the jars (21.2 µmol photon m^2 s^{-1}) was representative of daytime irradiance at depths of 30–60 m. After ca. 24 h of acclimation, juveniles were transferred for 12 h in a 400 mg/L oxytetracycline hydrochloride (OTC) seawater solution with pH re-adjusted to original value of seawater with TRIS buffer. The surviving fish were transferred back to clean seawater and normal rearing conditions resumed. Eleven polar cod juveniles survived the marking procedure. Following death or sacrifice after variable periods of rearing, these fish were measured and preserved in 95% ethanol. The lapilli were dissected from each fish and embedded in thermoplastic glue (Crystal Bond®). After polishing, the left lapillus of each fish was examined under a microscope equipped with a fluorescent light source (380 nm) to locate the OTC mark which appeared as a clear green ring. Once the OTC mark was located, the number of increments between the mark and the edge of the otolith was counted under normal transmitted light.

In some species, the increments deposited in the first days of life are sometime too narrow to be resolved under the light microscope, resulting in the underestimation of age (e.g. Campana et al., 1987). In particular, narrow initial increments linked to slow growth may occur in low-temperature environments. To verify that the initial increments in the otolith of polar cod are resolved accurately by light microscopy, counts were compared for a subset of lapilli analyzed both under light microscopy and scanning electron microscopy (e.g. Jones and Brothers, 1987). The left lapilli of 13 polar cod of varying age collected in 2005 in Baffin Bay and in 2008 in the Beaufort Sea were analyzed under the light microscope in 2006 and 2009 respectively. The same otoliths were re-analyzed in scanning electron microscopy (SEM) independently by the same operator in 2010. The operator could not remember the light microscopy count when interpreting the SEM image of the otolith. In preparation for SEM, the polished lapilli were etched by immersion in a 5% EDTA solution (KOH-buffered to pH 7.5) for 30 s to 2 min, then rinsed in distilled water, air dried for 24 h, and coated with gold.

2.5. Regional hatch-date frequency distribution (HFD) of polar cod

Based on the aging of larvae and juveniles collected in late-summer, new unpublished HFD of polar cod are presented for five regions: Beaufort Sea, Laptev Sea, Baffin Bay, Northwest Passage, and Hudson Bay. In each region, between 51% and 96% of the fish collected were aged by otolith analysis (Table 2). A sub-set of polar cod stratified by length and region was selected for otolith aging. The two lapilli of each fish selected were dissected and mounted separately on microscope slides in Crystal Bond® thermoplastic glue. Each otolith was ground on its medial side on a 3-µm aluminum grit paper. The increments of one of the two lapilli (preferentially the left) were enumerated and measured by a first reader under a light microscope (1000× magnification) coupled to a camera and image analyzer system (Image Pro Plus®). To estimate aging precision (Campana, 2001), an independent reading by a second reader was made on 200 otoliths from the different regions, yielding a mean coefficient of variation of 2.8%. The counts of the first reader were retained in subsequent analyses. The number of increments was strongly and linearly correlated to the radius of the otolith over the range of increments (20–284) and radii (31–305 µm) analyzed (number = 0.906 radius – 0.881, $r^2 = 0.938$, $n = 1047$, $p < 0.0001$).

The age of the remaining fish was estimated from their standard length using a region-specific redistribution procedure in which fish in a given 1 mm length class are randomly assigned an age according to the known age probability function for that 1 mm length class (Kimura, 1977). The hatch-date of an individual fish was determined by subtracting its age (in days) from its date of capture. The hatch-date frequency distribution (HFD) was built by tallying the number of fish hatched in the same 7-d hatch-date bin.

Two additional HFDs based on the collections of polar cod larvae in spring and early summer in the Northeast Water Polynya in 1993 (Fortier et al., 2006) and in the North Water Polynya in 1998 (M. Ringuette, Université Laval, unpublished data) respectively, were included in the present analysis (Table 1). Polar cod larvae were sampled with a DSN and a RMT in the Northeast Water (Fortier et al., 2006) and with a DSN in the North Water (M. Ringuette et al., unpublished data). In both studies, small larvae collected in 4-m^2 aperture zooplankton nets towed vertically were included in the reconstruction of the HFD. Fish not aged by otolith analyses were aged with the redistribution method described above and the HFDs were built by classifying fish in 7-d hatch-date bins.

When HFDs from adjacent regions did not differ statistically, the data were pooled and a new HFD was calculated. This was the case for the HFDs from the Laptev and East Siberian Seas (Kolmogorov–Smirnov, $p = 0.087$) and the HFDs from the Lancaster Sound, Baffin Bay and North Water regions (Kolmogorov–Smirnov, $p = 0.312$). Henceforth, these pooled regions are referred to as

Table 2
Number of young polar cod captured, measured fresh, and aged by otolith analysis, as well as parameters of the regression of length on age by region. The slope of the length-age regression is an estimate of growth in mm d^{-1}.

Region	Total number captured	Number measured fresh	Number aged	Standard length range (mm)	Age range (days)	Length-age regressions		
						Slope	Intercept	r^2
Laptev Sea	766	766	535	14.4–67.3	59–284	0.196	4.357	0.855
Hudson Bay	47	47	45	25.5–61.8	104–266	0.235	1.437	0.871
Beaufort Sea	120	120	102	21.0–60.0	81–278	0.182	9.353	0.803
Northwest Passage	51	51	43	8.4–61.5	22–239	0.223	2.957	0.967
Baffin Bay[a]	634	506	322	9.0–47.4	20–212	0.215	3.020	0.865

[a] For 2005–2006.

Laptev Sea and Baffin Bay. To make them comparable, all HFDs were expressed in percent frequencies. The number of fish hatched in a given 7-d hatch-date bin was divided by the total number of fish collected in the region in a given year and multiplied by 100. When data from several years were available for a given region, the average regional HFD was calculated by averaging the frequencies over years.

To illustrate the differences in the pre-winter size of juveniles resulting from regional differences in the hatching season, the length frequency distribution of polar cod on 14 August was contrasted among the five regions sampled in late-summer (Northwest Passage, Baffin Bay, Laptev Sea, Beaufort Sea, and Hudson Bay). Standard length was linearly correlated to otolith radius (length = 1.547 + 0.201 radius, $r^2 = 0.930$, $n = 1047$, $p < 0.0001$),

Table 3
Number and percentage of *Arctogadus glacialis* in sub-sets of the young cod collected in different regions and years, based on the analysis of the microsatellite marker Gmo8 (Madsen et al., 2009). The number of fish analyzed and the number successfully amplified are given for each sub-set. All other fish in the sub-sets were positively identified as *Boreogadus saida*.

Region	Year	Number analyzed	Number amplified	*Arctogadus glacialis*	
				Number	Percentage
Laptev Sea	2003	32	26	0	0
Laptev Sea	2005	48	45	5	11
Hudson Bay	2005	38	38	0	0
Beaufort Sea	2006	48	47	3	6
Baffin Bay	2006	144	143	1	<1
Northwest Passage	2006	14	14	0	0

Fig. 3. (a) Composite photograph comparing the left lapillus of an 98-d old juvenile polar cod seen in scanning electron microscopy (left, taken at 400×) and the right lapillus of the same fish in light microscopy (right, taken at 400×). (b) Composite photograph comparing the nuclear region of the left lapillus of a 206-d old juvenile polar cod seen in scanning electron microscopy (left, taken at 1000×) and the right lapillus of the same fish in light microscopy (right, taken at 1000×).
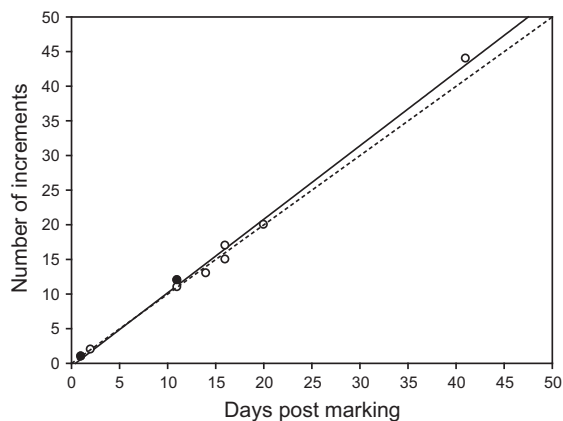

Fig. 2. Regression of the number of increments counted between the oxytetracycline hydrochloride mark and the edge of the otolith against the number of days of life after the marking of the otolith (increments = 1.062 d – 0.445, $r^2 = 0.995$, $n = 11$, $p < 0.0001$), for polar cod larvae and juveniles collected in the North Water and reared on board in 1999. The dashed line is the 1:1 line. Filled circles indicate two identical data points.
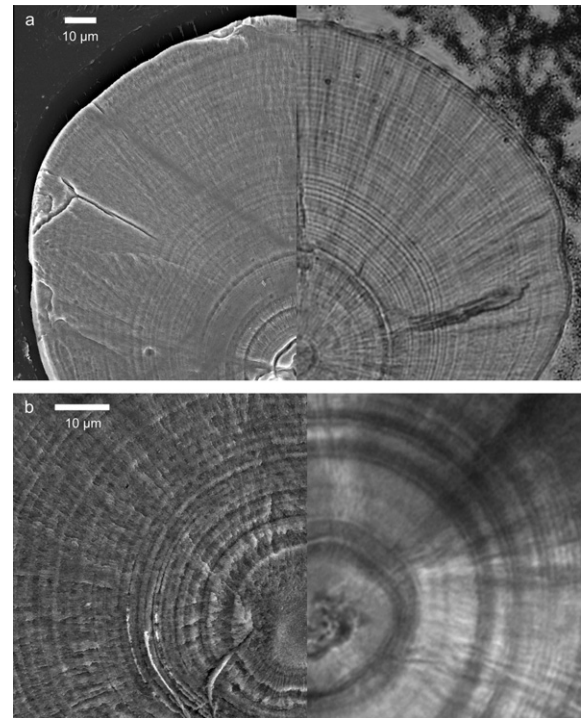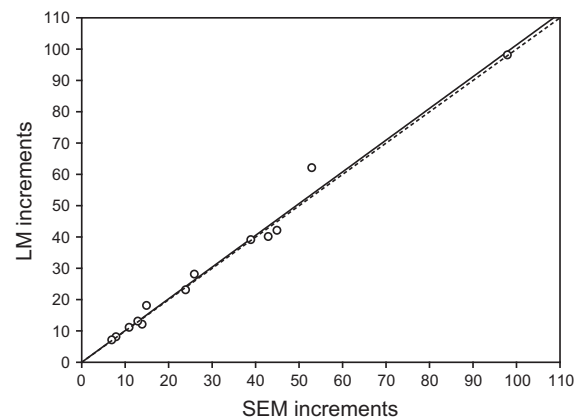

Fig. 4. Relationship between increment counts in the lapilli of polar cod analyzed under the light microscope (LM) in 2006 and 2009 and re-analyzed under the scanning electron microscope (SEM) in 2010 by the same operator (LM = 1.014 SEM – 0.027, $r^2 = 0.986$, $n = 13$, $p < 0.0001$). The dashed line is the 1:1 line.

enabling us to back-calculate the length of individual fish from the radius of the otolith on 14 August (the earliest capture date among the four regions) using the biological intercept method (Campana and Jones, 1992) and a length at hatch of 5.5 mm. The estimated length of juvenile polar cod on 14 August (mm) was converted into weight (mg) using the relationship ln weight = 3.095 ln length − 5.3 (after Ponomarenko, 2000).

2.6. Regional long-term average surface salinity and temperature

Our objective was to relate regional differences in the hatching season of polar cod (an evolutionary trait expected to be adapted to long-term average ocean climate) to differences in the long-term average surface salinity and temperature of different oceanic regions. The World Ocean Atlas of the National Oceanographic Data
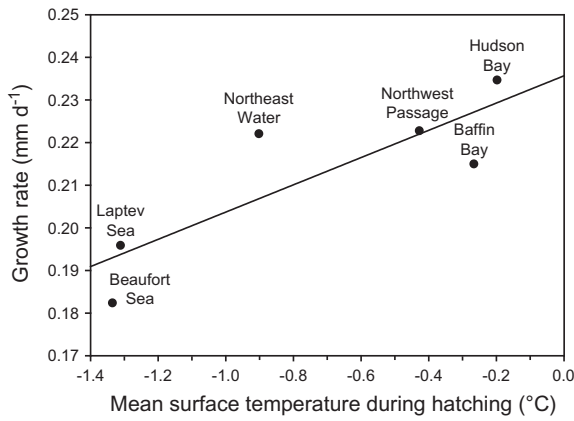

Fig. 5. Regression of young polar cod growth rate and long-term average surface temperature during the hatching season in a given region (growth = 0.032 temperature + 0.236, r^2 = 0.720, p = 0.033, n = 6). Surface temperatures were extracted from the World Ocean Atlas) for the months of polar cod hatching.

Center (http://www.nodc.noaa.gov/OC5/WOA05/pubwoa05.html) provides objectively analyzed climatological monthly averages of oceanographic variables based on all available measurements between 1800 and 2005 (Boyer et al., 2006). Monthly values of salinity and temperature within each 1° latitude × 1° longitude area of each region studied were extracted from the latest version of the World Ocean Atlas (Antonov et al., 2006; Locarnini et al., 2006). For each region, monthly surface salinities in each 1° × 1° area were averaged over the months corresponding to the hatching season of polar cod (based on the HFDs) and were mapped with the Ocean Data View software (Schlitzer, 2009, http://odv.awi.de). Monthly surface temperatures and salinities in the 0–10 m layer were averaged over all 1° × 1° areas in each region. To take into account that hatching does not start and end precisely with the month, mean regional temperatures over the hatching season of polar cod were calculated by attributing its monthly value to each weekly bin and then averaging the weekly values.

3. Results

3.1. Boreogadus saida versus Arctogadus glacialis

The percentage of *Arctogadus glacialis* in the collections of larval and juvenile cod varied from 0% in 2003 to 11% in 2005 in the Laptev Sea. It ranged from 0% to 6% among different regions of the Canadian Arctic (Table 3). *A. glacialis* was not detected in the Northwest Passage and in sub-arctic Hudson Bay, and was rare in Baffin Bay. The hatching date of 55 *A. glacialis* sampled in the Beaufort Sea in 2004 ranged from 21 March to 24 May.

3.2. Validation of the daily deposition of increments in the otoliths of polar cod

Juvenile polar cod died or were sacrificed from 1 to 41 d after the otolith marking procedure. Standard length at death ranged
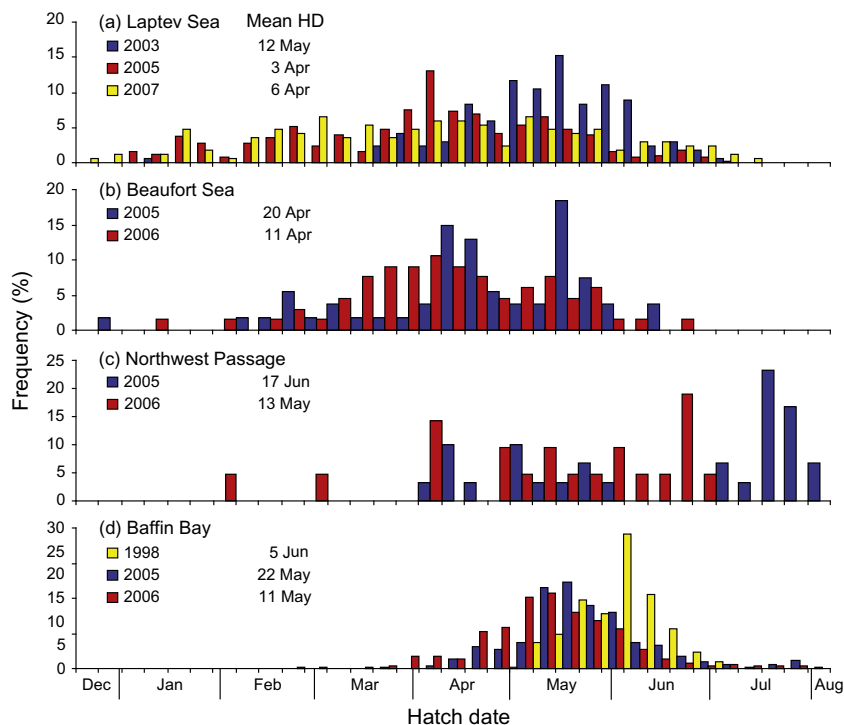

Fig. 6. Hatch-date frequency distributions and mean hatch-dates (HD) of polar cod in four regions of the Arctic Ocean for which multiple years of data are available. The number of fish hatched in the same 7-d calendar interval in a given year is expressed as a percentage of the total number of fish sampled in that year.

from 29 to 62 mm. There was no significant difference (paired *t*-test, $t = 1.027$, $n = 11$, $p = 0.329$) between the number of increments counted from the mark to the edge of the otolith and the number of days elapsed between marking and death (Fig. 2).

Light microscopy (LM) and scanning electron microscopy (SEM) revealed the same patterns in the microstructure of the lapillus, including a clear hatch mark (typical diameter around 21–23 μm) and equally-spaced growth increments (typically 1 μm wide) from the hatch mark to the edge (Fig. 3a). We found no evidence of small concatenated increments in the nucleus region of polar cod lapilli under SEM (Fig. 3b). There was no significant difference (paired *t*-test, $t = 0.448$, $n = 13$, $p = 0.662$) between increment counts from LM and SEM over the 7–98 d range of estimated ages of the polar cod analyzed (Fig. 4).

3.3. Length-age relationships and growth rates

The length of polar cod larvae and juveniles sampled in late-summer and early fall was linearly correlated to age (Table 2). Growth rate, as estimated by the slope of the regression, ranged from 0.182 mm d^{-1} in the Beaufort Sea to 0.235 mm d^{-1} in Hudson Bay. Growth was positively correlated to the average surface temperature in the region during the hatching season (Fig. 5).

3.4. Interannual variability in regional hatch-date frequency distributions

Interannual comparisons of polar cod HFDs were possible for four of the six regions studied (Fig. 6). With a few exceptions, the HFD in a given region was relatively consistent among years. In the Laptev Sea, the duration and shape of the prolonged hatching season (December–July) were similar in 2005 and 2007 (Fig. 6a). By contrast, except for one fish hatched in January, most of the polar cod sampled in 2003 were hatched between late March and early July. In the Beaufort Sea, a few fish hatched in December and January, but the main hatching started in mid February and ended in late June in both 2005 and 2006 (Fig. 6b). Based on the relatively few fish sampled in the Northwest Passage, the hatching season was earlier in 2006 (February to June) than in 2005 (April to early August) (Fig. 6c). In Baffin Bay, the hatching season in 1998 started in mid-April and ended in mid-July, but the sampling of polar cod in early fall 2005 and 2006 indicated an earlier onset with some larvae hatching as early as late February and hatching well under way in early April (Fig. 6d). For comparison, only 14% of the larvae were hatched before 22 May in 1998, whereas 55% and 70% hatched before that date in 2005 and 2006 respectively.

3.5. Average hatching season in relation to regional river input

When contrasting the six regions, the average regional HFDs became shorter in duration and shifted from winter towards summer with decreasing regional freshwater input (Fig. 7, Table 4). Hatching started as early as December and January in the Laptev Sea, Hudson Bay and the Beaufort Sea where freshwater inputs are high and winter surface salinities are low (Fig. 7a–c). At the other end of the series, hatching was delayed until April or May in Baffin Bay and the Northeast Water where freshwater inputs are negligible and surface salinities are relatively high (Fig. 7e and f). In the Northwest Passage, the occasional early-hatching in February was at odds with the negligible local freshwater input. By comparison to the start of the hatching season, the end of the hatching season varied relatively little, hatching persisting until end of June to early August in all six regions (Fig. 7, Table 4).
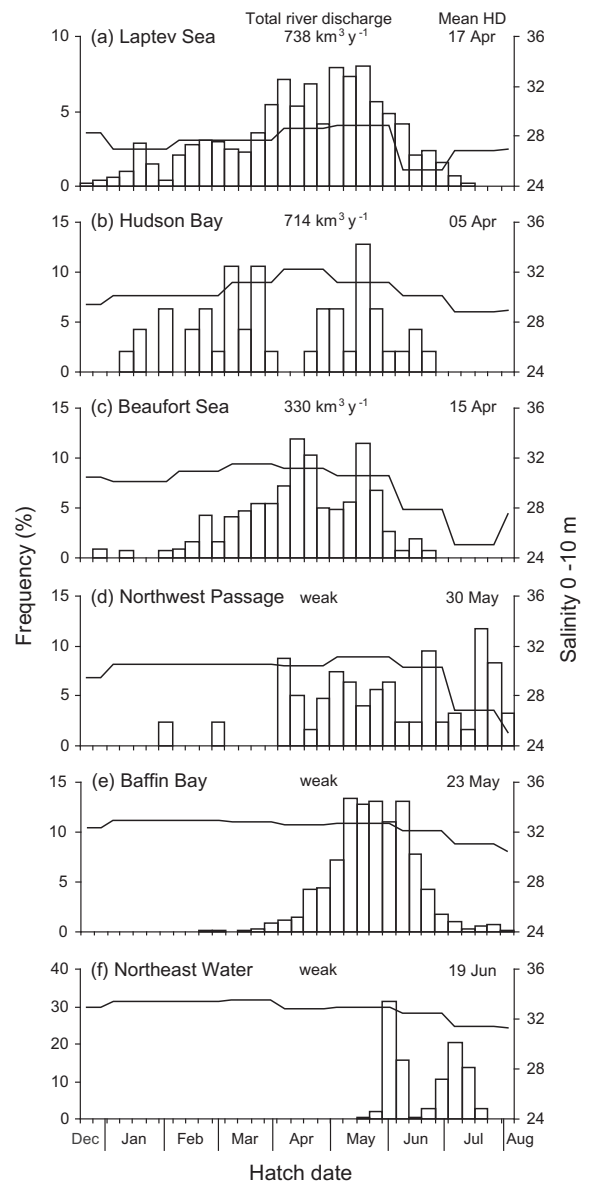

Fig. 7. Average hatch-date frequency distribution and mean hatch-date (HD) of polar cod in six regions of the Arctic Ocean ordered by decreasing freshwater input. The monthly salinities in the 0–10 m layer were extracted from the World Ocean Atlas. Total river discharge values are from Gordeev (2006) for the Laptev and Beaufort seas and from Déry et al. (2005) for Hudson Bay.

3.6. Pre-winter size

Hatch-date explained most of the variability (90%) in the length attained in late-summer by polar cod juveniles (Fig. 8). Estimated length on 14 August ranged from <10 mm (<0.01 g) in larvae hatched in July to as much as 50 mm (corresponding to 0.91 g) in juveniles hatched in December and January. The vast majority (97%) of polar cod that reached a length >35 mm on 14 August were collected in regions characterized by important freshwater input (Laptev Sea, Hudson Bay and Beaufort Sea). Among fish from the freshwater-influenced regions, 20.3% were larger than 35 mm on 14 August compared to 1.4% in the other regions.

The back-calculated length frequency distribution of polar cod juveniles on the common date of 14 August differed significantly among the five regions sampled in late fall (Fig. 9). As expected, length achieved in late-summer decreased with increasing lateness

Table 4
Statistics of the hatching season of polar cod by region and year. SD: standard deviation.

| Region	Year	Hatch-date				Hatching season duration (days)
		Mean	Min.	Max.	SD	
Laptev Sea	2003	12 May	10 January	4 July	24.4	175
	2005	3 April	2 January	20 July	40.2	199
	2007	6 April	20 December	10 July	46.8	202
Hudson Bay	2005	05 April	9 January	20 June	45.2	162
Beaufort Sea	2005	20 April	26 December	13 July	35.2	169
	2006	11 April	12 January	22 July	30.6	161
Baffin Bay	1998	5 June	14 April	11 July	12.6	88
	2005	22 May	26 March	31 July	20.9	127
	2006	11 May	21 February	27 July	21.7	156
Northwest Passage	2005	17 June	4 April	5 August	43.2	123
	2006	13 May	31 January	26 June	39.3	146
Northeast Water	1993	30 May	12 May	21 July	17.4	70
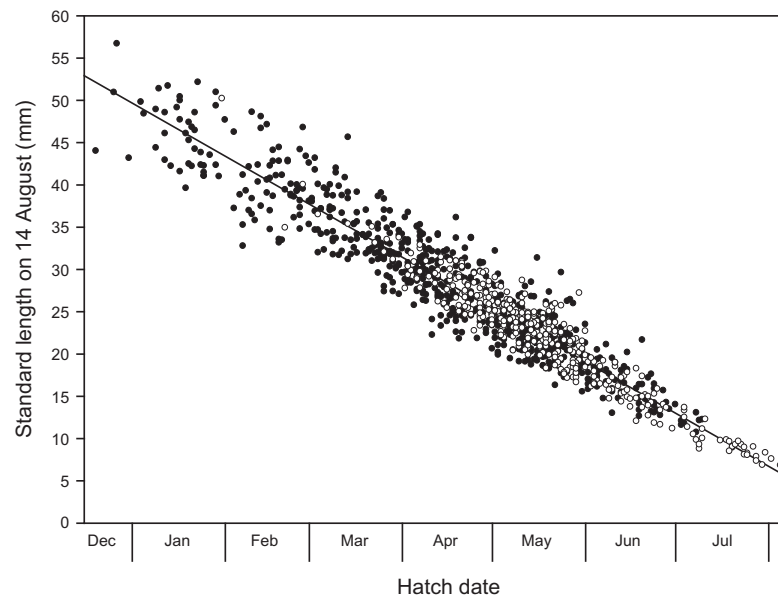
Fig. 8. Regression of standard length on 14 August (SL) on hatch-date (HD) for polar cod collected in late-summer and early fall in regions characterized by strong river discharge (full circles, Laptev Sea, Hudson Bay and Beaufort Sea) or weak river discharge (open circles, Northwest Passage and Baffin Bay). SL = 49.87–0.203 HD, r^2 = 0.906, n = 1075, p < 0.0001.

of the hatching season. At the two extremes of the series, the early-hatching population of Hudson Bay (January to June) averaged 33.1 mm on 14 August (Fig. 9a), compared to 19.2 mm for the late-hatching (April to August) population in the Northwest Passage (Fig. 9e). Differences in late-summer length were particularly marked between freshwater-influenced regions (27.0–33.1 mm) and regions with weak freshwater input (19.2–23.1 mm). Size in late-summer appeared unrelated or even inversely related to growth rate: the highest regional growth rate in Hudson Bay corresponded to the largest late-summer size, but size in late-summer was inversely related to growth for the four remaining regions (Fig. 9).

4. Discussion

4.1. The true age of the true polar cod

The overall contamination of *Boreogadus saida* samples by *Arctogadus glacialis* amounted to 9 out of 313 or 2.9%. While absent or rare in most regions, *A. glacialis* represented a sizable fraction of the cods in some regions (6% in the Beaufort Sea in 2006 and 11% in the Laptev Sea in 2005). However, the hatching dates of *A. glacialis* (21 March to 24 May) fell well inside the hatching season of polar cod (January to July). Hence, the few *A. glacialis* in our collections could affect the shape of the estimated HFDs of *B. saida* slightly by adding false counts in the early-spring bins of the distribution. But contamination by *A. glacialis* would have little impact on the estimated start and end of the hatching season of *Boreogadus saida*, which is the main focus of this study. Therefore, no correction was made to the HFDs to account for the occurrence of *A. glacialis* in our collections.

The growth of newly-hatched fish can be slowed by suboptimal feeding or temperatures in the low end of the temperature range of a species. Under such conditions, otolith increments may be deposited at intervals longer than daily, or may become too narrow to be resolved by light microscopy (e.g. Umezawa and Tsukamoto, 1991; Folkvord et al., 2004). The marking experiments confirmed the daily deposition of increments in polar cod juveniles >29 mm reared
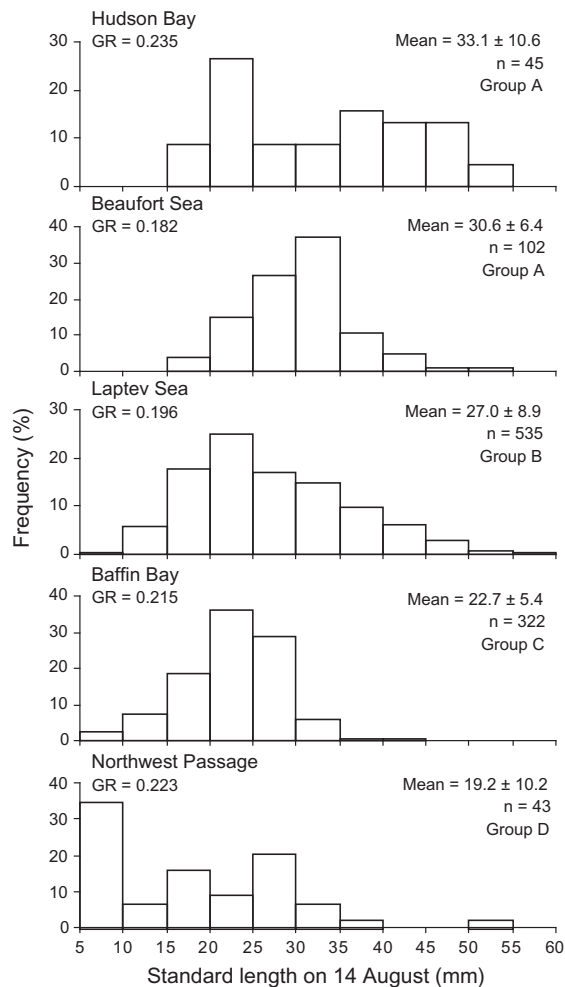
Fig. 9. The frequency distribution of standard length on 14 August for polar cod sampled in late-summer/early fall in different regions of the Arctic Ocean. Standard length on 14 August was back-calculated from otolith microstructure. Mean standard length on 14 August differed significantly among groups A–D (Tukey–Kramer test). The growth rate of polar cod (GR: in mm d^{-1}) in each region is also indicated.

at 0 °C. Furthermore, the examination of the core region of the otolith in scanning electron microscopy showed no evidence of thin increments that would not be resolved in light microscopy. These results are consistent with the observed daily deposition of increments in the otolith of larvae of the Antarctic fish *Nototheniops nudifrons* reared at sub-zero temperature from hatching to 38 d, and growing at 0.13 mm d^{-1} (Hourigan and Radtke, 1989). By comparison, polar cod larvae 0–70 d old grew at 0.234 mm d^{-1} in the Northeast Water (Fortier et al., 2006) and, in the present study, the growth of juveniles varied from 0.182–0.235 mm d^{-1} among the different regions. The typical width (1 μm) of the initial increments associated with such growth is resolved easily by conventional light microscopy. We conclude that the newly-hatched larvae of polar cod, a hyper specialist adapted to life at sub-zero temperatures, achieve initial growth rates that are sufficient for the daily deposition of clear increments on the otolith.

4.2. The winter thermal refuge hypothesis

A preliminary review of polar cod hatching season (Bouchard and Fortier, 2008) indicated two hatching patterns: a short spring hatching season (May–June) centered on the ice break-up and the onset of biological production in the Northern Baffin Bay and the

Greenland Sea (Sekerak, 1982; Fortier et al., 2006); and a protracted winter–spring–summer hatching season (January–June/July) in the Kara and Laptev Seas, where some larvae emerge under sea ice in winter well before the spring bloom (Baranenkova et al., 1966; Bouchard and Fortier, 2008). Fish larvae are visual predators that dwell in the surface photic layer. In arctic seas in winter and early-spring, temperature under the ice cover varies with salinity from 0 °C ($S = 0$) to ca. -1.8 °C ($S = 33$). The motility of Atlantic cod *Gadus morhua* larvae (Valerio et al., 1992) and the feeding success of recently hatched polar cod (Michaud et al., 1996) are drastically reduced at temperatures < -1 °C. Bouchard and Fortier (2008) proposed that salinity-induced differences in the sub-zero temperatures that prevail under the ice could explain the observed regional differences in the hatching season of polar cod. Brackish conditions in the under-ice plume of large rivers would provide relatively warm temperatures (0 to -1 °C), allowing more rapid egg development and the motility needed for successful first-feeding in winter. In regions lacking a river plume, the extreme sub-zero temperatures (ca. -1.8 °C) prevailing in winter would slow egg development and prevent successful first-feeding, leading to poor survival. In such regions hatching would be delayed until the ice break-up and the vernal warming of the surface layer.

Consistent with the winter thermal refuge hypothesis, the hatching of polar cod started in winter in regions strongly influenced by river discharge, and was delayed until spring in regions with weak freshwater input (Fig. 7). The hatching season was earliest in the Laptev Sea, Hudson Bay and the Beaufort Sea where freshwater influxes are large (738, 714 and 330 km^3 year^{-1}, respectively). Although the Beaufort Sea receives less than half the freshwater volume of the Laptev Sea and Hudson Bay, hatching there also started in early winter and the mean hatching date (15 April) was comparable to that in the Laptev Sea (17 April) and in Hudson Bay (5 April). This somewhat unexpected earliness of hatching in the Beaufort Sea may perhaps be linked to the presence of the stamukhi which, by damming the freshwater plume of the Mackenzie River, creates the brackish Lake Herlinveaux (Macdonald et al., 1995), an environment that could offer an early and particularly suitable winter thermal refuge for early hatchers. By contrast, with the exception of a few early hatchers in the Northwest Passage, hatching did not start until spring (April–May) in regions with little freshwater input (Northwest Passage, Baffin Bay, and the Northeast Water).

Diadromy in Gadidae is uncommon and is seen as a derived evolutionary state to exploit freshwater for reproduction (Dodson, 1997). In estuaries of the western North Atlantic, a fraction of the population of tomcod *Microgadus tomcod*, a facultative diadromous Gadidae, migrate from estuaries to rivers to spawn under the ice in winter (Scott and Scott, 1988). The polar cod, a Gadidae of similar size, share with the tomcod the challenges associated with a short season of biological production, seasonally ice-covered waters, and sub-zero temperatures in the surface layer in winter. Our study suggests that the polar cod may have developed some facultative partial diadromy that does not take the genitors into the rivers but nevertheless exploits the coastal under-ice plumes of rivers to hasten and lengthen the period of initial larval growth.

4.3. Winter hatching and the pre-winter size of polar cod juveniles

The winter thermal refuge hypothesis assumes that the evolutionary force driving hatching under the ice in winter is the need to maximize the pre-winter size of juveniles, so as to minimize mortality over the first fall and winter of juvenile life (Fortier et al., 2006; Bouchard and Fortier, 2008). Winter hatching resulted in spectacularly larger pre-winter size: by mid-August, January hatchers reach 0.9 g in weight and were typically 100–150 times heavier than July hatchers (<0.01 g). Regionally, differences in

length between freshwater-influenced regions (27.0–33.1 mm) and purely marine regions (19.2–23.1 mm) translated into fish that were on average three times heavier in regions influenced by freshwater (0.13–0.25 g versus 0.05–0.08 g). In juvenile fish, mortality is generally inversely related to size (see Sogard, 1997 for a review). A larger size provides a survival edge through enhanced predator avoidance, resistance to starvation, and physiological tolerance: three attributes that are particularly important in fending off winter mortality (Sogard, 1997). As the ice cover reaches a minimum in late-summer, polar cod fry in the surface layer become vulnerable to seabirds. These include the surface-feeder black-legged kittiwake *Rissa tridactyla* and several diving birds that can reach down to depths of 35–50 m, such as the dovekie *Alle alle*, Brünnich's guillemot *Uria lomvia* and the black guillemot *Cepphus grylle* (Bradstreet, 1982; Piatt and Nettleship, 1985; Barrett and Furness, 1990; Falk et al., 2000; Karnovsky and Hunt, 2002). Since the migration to the deep overwintering grounds starts at lengths of 30–35 mm (Ponomarenko, 2000), it can be expected that the larger the juveniles are at the end of summer, the earlier they will leave the surface layer and escape avian predation during the fall. As well, adult polar cod are likely the main predator of juvenile polar cod on the overwintering grounds (Baranenkova et al., 1966; Frost and Lowry, 1984), and a large size should provide the juveniles with enhanced capacity to avoid their cannibalistic congeners (e.g. Miller et al., 1988). A feasible but logistically demanding approach to verify the size-dependence of vulnerability to avian predation and cannibalism would be to estimate the size-distribution of juvenile polar cod prey from the otoliths recovered from the gizzard of seabirds and the digestive tract of adult polar cod, for comparison to the size-distribution of the population.

Maximizing pre-winter size can be achieved by maximizing growth, by maximizing the growth season, or by maximizing both. Hatch-date explained 90% of the variance in pre-winter size (Fig. 8), and polar cod obviously relied primarily on maximizing the duration of the first growth season to achieve a large pre-winter size. We found little evidence that fast growth also contributed to large pre-winter size. Regionally, with the exception of Hudson Bay where both growth and pre-winter size were highest, a larger pre-winter size was associated, somewhat paradoxically, with slower growth among the other four regions (Fig. 9). Hence, faster growth did not explain the larger pre-winter size in regions influenced by freshwater. Growth was rather dictated by the general surface temperature conditions prevailing in the sampling region during the hatching season and the early life of polar cod in the plankton (Fig. 2). This suggests that, in cold regions, the long growth season made possible by winter hatching in the thermal refuge provided by a river plume can actually overcompensate for slow early larval growth in producing large pre-winter sizes. Hudson Bay, where winter hatching combines with relatively warm surface temperatures during plankton drift, produced the largest pre-winter sizes.

4.4. The food of polar cod larvae under the ice in winter

A long standing tenet of the ecology of temperate and boreal fish is that the hatching of fish larvae coincides with the vernal production of their planktonic food to maximize food intake and early growth (see Leggett and Frank, 2008 for a recent review). Our circum-arctic census of the hatching season of polar cod confirms that, in all regions studied, a large fraction of the larval population emerge in spring and early summer (April/May to June/July) during the short season of production of calanoid copepod eggs and nauplii, its main prey. Obviously, however, wherever winter conditions allow, a fraction of the population will maximize the duration of the growth season by hatching as early as possible and well before the massive reproduction of calanoid copepods in

spring. Bouchard and Fortier (2008) speculated that polar cod hatching in winter feed on the nauplii of small omnivorous copepods that reproduce all year long and on the eggs of calanoid copepods that release their eggs in winter such as *Calanus hyperboreus* and *Metridia longa*. Another possibility is that winter-hatched polar cod larvae prey on organisms such as rotifers associated with the brackish waters of river plumes and/or the microbial food web that remains active in winter in temperate and ice-covered seas (Mousseau et al., 1998; Garneau et al., 2008).

4.5. Climate change and the hatching season of polar cod

Changes in the phenology of populations and in the structure of ecosystems have been linked to climate change (Walther et al., 2002; Parmesan and Yohe, 2003; Parmesan, 2006), in particular at sub-arctic and arctic latitudes where reproduction must be synchronized with the extreme seasonality in light, temperature, and food availability (e.g. Réale et al., 2003; Gaston et al., 2005; Perry et al., 2005; Grebmeier et al., 2006). To a large extent, the response of the entire arctic pelagic ecosystem to climate change could depend on perturbation in the phenology of a few key elements of the low-diversity trophic web such as the polar cod (e.g. Tynan and DeMaster, 1997).

On-going trends in arctic sea-ice cover (e.g. Bareiss and Gorgen, 2005; Stroeve et al., 2007), sea surface temperature (e.g. Belkin, 2009) and freshwater discharge (e.g. Peterson et al., 2006) all have the potential to alter the timing and success of the reproduction of polar cod. An earlier ice break-up, more frequent winter polynyas, a warmer surface layer, and increased river discharge would be expected to favor the feeding, growth and survival of winter hatchers (Fortier et al., 2006; Bouchard and Fortier, 2008; this study), therefore shifting the hatch-date frequency distribution (HFD) of survivors sampled in late-summer and fall to the left. The present review yielded limited but interesting information on the interannual and inter-decadal variability in polar cod HFD in response to climate variability and change. In the Laptev Sea, juveniles sampled in the fall were hatched from January to July in 2005 and 2007 (Fig. 3a), 2 years characterized by record spring/summer sea-ice regression over the Siberian Shelves. By contrast, juveniles surviving to the end of summer were hatched no earlier than March in 2003, a year of closer-to-normal ice conditions. In Baffin Bay, the HFDs in 2005 and 2006 were shifted earlier by at least a month relative to 1998 (Fig. 3d). This inter-decadal shift is consistent with an increase of sea surface temperature of 0.47 °C from 1982 to 2006, one of the most intense regional warming observed in the arctic (Belkin, 2009). Of course, although these shifts in the HFD are in the expected direction, any conclusion about the impact of climate change on the hatching season of polar cod will remain speculative until longer time series of observations are obtained in different regions of the Arctic Ocean.

5. Conclusion

Our review of hatching seasons of polar cod in relation to freshwater input generally supports the hypothesis that under-ice river plumes provide a thermal refuge that enables some polar cod to hatch, initiate first-feeding and grow in winter. In southeastern Hudson Bay in spring (late April to early June), newly-hatched polar cod larvae occur in the coastal zone influenced by the turbid freshwater plume of the Great Whale River that extends over the 0–5 m depth layer immediately under the ice cover (Drolet et al., 1991; Gilbert et al., 1992; Fortier et al., 1996). The seemingly euryhaline first-feeding larvae congregate in daytime in the brackish halocline ($S = 5$–25, $T = -0.3$ to -1.0 °C) between the plume and the underlying marine layer, where the product of prey density

by light intensity is maximum (Ponton and Fortier, 1992). These observations support our assumption that polar cod larvae associate with under-ice river plumes in winter as well. However, a definitive test of the winter thermal refuge hypothesis would entail the direct verification that polar cod hatch, feed successfully, and grow in the halocline of the under-ice plumes of rivers in arctic coastal seas in winter. The Laptev Sea, the area of the Beaufort Sea inside the stamukhi, and Hudson Bay would be particularly well suited to deploy the overwintering expeditions needed to sample polar cod larvae under sea ice in the extreme winter conditions of the Arctic Ocean.

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