

Contrasting the early life histories of sympatric Arctic gadids *Boreogadus saida* and *Arctogadus glacialis* in the Canadian Beaufort Sea

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Abstract The early life stages of *Boreogadus saida* and *Arctogadus glacialis* are morphologically similar, making it difficult to assess differences in their ecological niche. The present study documented for the first time the early life stage ecology of *A. glacialis*, compared it to that of *B. saida*, and identified the factors separating the niches of the two sympatric species. The 10,565 larval gadids collected in the Beaufort Sea from April to August of 2004 and 2008 were identified to species either directly by genetics and/or otolith nucleus size, or indirectly with a redistribution procedure. Between 8.0 and 8.7 % of all gadids were assigned to *A. glacialis*. Larvae of *A. glacialis* were longer at hatch and experienced lower mortality rates than those of *B. saida*. The two species shared similar spatiotemporal and vertical distributions, hatching season, and growth rate. Under the ice, feeding incidence of *B.*

saida was low (14 %) relative to *A. glacialis* (88 %). At lengths <15 mm, both species specialized on different prey. The diet of fish >15 mm overlapped (Schoener's index = 0.7), with *Calanus glacialis* and *C. hyperboreus* providing >50 % of the carbon intake of both species. The higher mortality in *B. saida* may be explained by the smaller size at age from hatching to metamorphosis and a lower under-ice feeding incidence. The early larval stage appears to be the key period of niche divergence between the two species.

Keywords Hatching season · Distribution · Diet overlap · Growth · Mortality · Resource partitioning

Introduction

The abundant *Boreogadus saida* (polar cod or Arctic cod) and the less common *Arctogadus glacialis* (polar cod, Arctic cod, or ice cod) co-occur in Arctic seas. Known interactions between the two gadids include predation on *B. saida* by *A. glacialis* (Coad et al. 1995) and possible interspecific competition for resources among adult stages (Christiansen et al. 2012). Despite its low abundance relative to *B. saida*, *A. glacialis* can be disproportionately important in the diet of marine mammals at specific times and locations. In years of low *B. saida* abundance, *A. glacialis* can become an alternative prey for narwhals (*Monodon monoceros*) summering near Pond Inlet in the Canadian Archipelago (Finley and Gibb 1982). In summer 1998, *A. glacialis* accounted for 82 % of the biomass in the stomach contents of adult ringed seals (*Pusa hispida*) from Grise Fiord (Holst et al. 2001).

Boreogadus saida, the most ubiquitous Arctic fish, is found in diverse arctic and subarctic habitats ranging from

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brackish to fully marine waters, from coastal to offshore waters and from surface waters to great depths (e.g. Scott and Scott 1988). Given its importance in the Arctic marine food web (Bradstreet et al. 1986), the reproductive strategy and early life history of *B. saida* are relatively well documented. *B. saida* spawn in late fall and early winter (e.g. Baranenkova et al. 1966; Craig et al. 1982), near shore (Craig et al. 1982; Fevolden and Christiansen 1997) and probably also in deeper water (Benoit et al. 2008; Geoffroy et al. 2011). The buoyant eggs rise to the ice–water interface (Graham and Hop 1995) and hatch after an incubation time that depends on temperature but differs among studies: 26–35 days at 0 °C (Aronovich et al. 1975) and 58 days at 1.5 °C (Graham and Hop 1995). Rass (1968) suggested an incubation time between 45 and 90 days at temperatures typical of Arctic waters (ca. 1 °C). Documented lengths at hatch range from 3.5 to 6.5 mm (Baranenkova et al. 1966; Aronovich et al. 1975; Michaud et al. 1996; Ponomarenko 2000). In the laboratory at 1.5 °C, exogenous feeding began at age 12–14 days, and the large yolk sac was completely absorbed 18–20 days post hatch (Aronovich et al. 1975). Average growth rates range from 0.18 to 0.24 mm day⁻¹ in different Arctic seas (Bouchard and Fortier 2011), but an individual-based model of the early growth of larvae sampled in two polynyas around Greenland suggests rates varying from 0.12 to 0.36 mm day⁻¹ (Thanassekos et al. 2012). Metamorphosis from planktonic larvae to pelagic juveniles with improved swimming ability occurs from 16 to 32 mm in the coastal Canadian Beaufort Sea (Walkusz et al. 2011). Depending on their hatch date and region of origin, the larvae and juveniles range in size from 7 to 57 mm in August (Bouchard and Fortier 2011) at the onset of the migration of juveniles from the surface layer to their deep overwintering habitat (Graham and Hop 1995).

Arctogadus glacialis is now considered to include the synonymized *Arctogadus borisovi*, making *Arctogadus* a monotypic genus (Møller et al. 2002; Jordan et al. 2003). *A. glacialis* is found mainly on Arctic continental shelves, often in coastal habitats, and sometimes in brackish waters (Nielsen and Jensen 1967; Aschan et al. 2009). The species is believed to spawn in winter (e.g. Süfke et al. 1998), but contradictory observations point to summer spawning (Jordan et al. 2003; Aschan et al. 2009). While the adults *A. glacialis* and *B. saida* are clearly distinct morphologically and ecologically, the larval and early juvenile stages of both species are morphologically similar and often confounded (Madsen et al. 2009; Bouchard and Fortier 2011; Bouchard et al. 2013). As a result, the early life of *A. glacialis* remains poorly documented. The eggs and newly hatched larvae remain undescribed, although the eggs have been reported to be demersal (Fahay 2007). Cannibalism can be intense with

juveniles and young adults making over 90 % of the gut content of adults in summer in Cambridge Bay (Boulva 1970).

In the present study, molecular genetics and a recently developed otolithometric method are used to discriminate *B. saida* and *A. glacialis* in a subset of the larvae and juveniles sampled in the south-eastern Beaufort Sea in 2004 and 2008. Based on the standard length in the month of capture, all remaining gadids are assigned to one of the species. The early life histories of the two species, including spatiotemporal and vertical distributions, hatching season, length at hatch, diet, growth, and mortality, are compared with the underlying hypothesis that some of these traits diverge enough to create the niche separation needed for the two similar species to live sympatrically in the plankton.

Materials and methods

Study area

The south-eastern Beaufort Sea is characterized by the deep Canada Basin to the north-west, the shallow Mackenzie Shelf influenced by the freshwater plume of the Mackenzie River to the south, the Continental Slope separating the Basin and the Shelf, the Amundsen Gulf that connects the Beaufort Sea to the Canadian Archipelago to the southeast, and the shelf of Banks Island to the northeast (Fig. 1). Typically, ice formation starts in October at the coastal margins of Amundsen Gulf, and ice consolidation over the entire region takes place in December with the connection of landfast ice to the perennial Beaufort Sea ice pack west of Banks Island (Galley et al. 2008). In winter, the circum-Arctic flaw lead separates the landfast ice and the mobile central ice pack (Arrigo and van Dijken 2004; Lukovich and Barber 2005). On average since 1979, sea ice has started to retreat in early June as the flaw lead enlarges to form the Cape Bathurst Polynya complex (Barber and Hanesiak 2004). Generally, the region becomes ice-free by August or September (except for the northern sector), and landfast ice starts forming again in October on the shallow shelf, reaching its maximum thickness in March. The extent and persistence of open water vary considerably from year to year (Arrigo and van Dijken 2004).

Weekly percent ice cover in 2004 and 2008 was obtained from the Canadian Ice Service IceGraph 2.0.5 application for the Mackenzie Shelf, Banks Island and western Amundsen Gulf areas. Per cent ice cover for the overall 194,350 km² sampling region was calculated as a weighted average taking into account the relative surface of the three areas (61, 21 and 18 %, respectively).

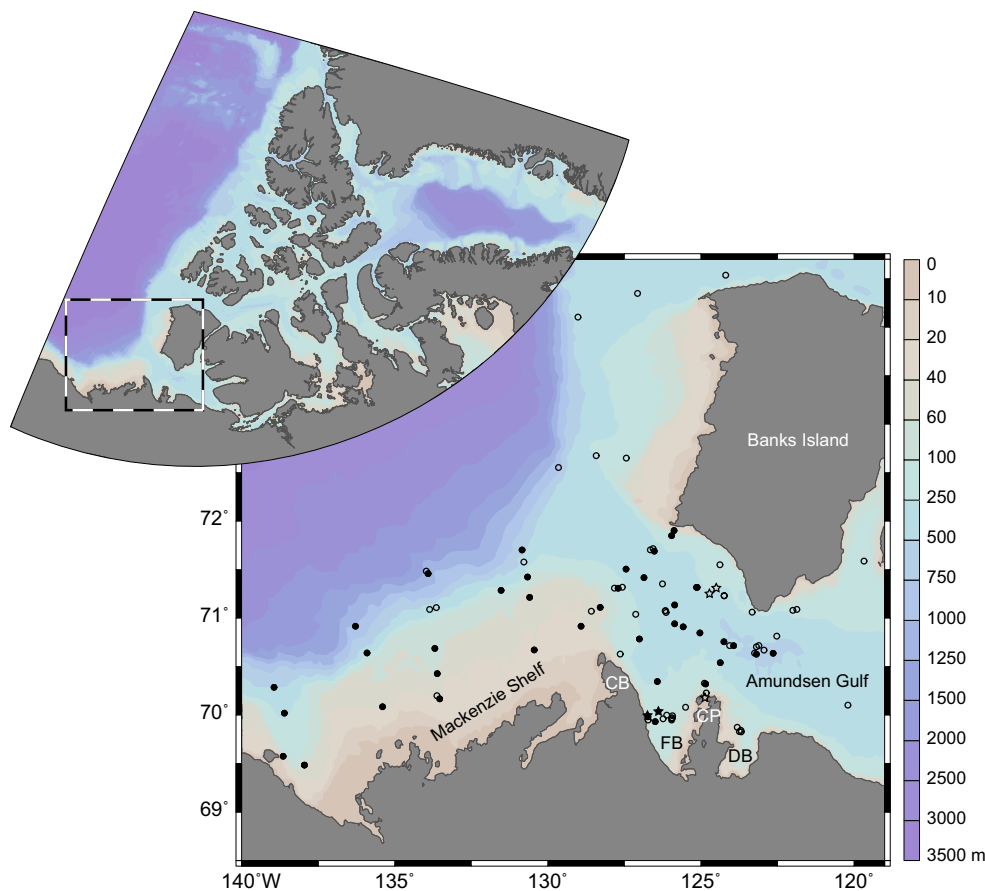


Fig. 1 Bathymetric map of the south-east Beaufort Sea with sampling locations in 2004 (closed symbols) and 2008 (open symbols). Circles indicate sampling conducted from the ship; stars

indicate sampling conducted from sea ice. CB: Cape Bathurst, FB: Franklin Bay, CP: Cape Parry, DB: Darnley Bay

Ichthyoplankton sampling

In 2004 and 2008, zooplankton and fish larvae were sampled in the south-eastern Beaufort Sea as part of two overwintering expeditions of the research icebreaker CCGS *Amundsen*, which was intentionally ice-locked in Franklin Bay before the ice break-up in 2004, but remained mobile in the sampling area in 2008 (Fig. 1). In order to capture all early life stages, including the larvae hatching under the ice cover and subsequently the larvae and juveniles of various sizes occurring in open waters during an extended growth period, different sampling methods were used.

Sampling under the ice cover

In winter and spring 2004, sampling was conducted under the ice at two stations near the icebreaker fixed position (70°N, 126°W) in the landfast ice of Franklin Bay. The first ice station (225 m bottom depth) was located 450 m east of the icebreaker position and the second station (110 m bottom depth) 18 km to the WSW of the ship (Fig. 1). The under-ice sampler consisted of a rectangular metal frame

carrying two 6-m long, 1-m² mouth aperture, square-conical nets with 750- μ m mesh side-by-side. This double square net (DSN) was towed at ca. 1 m s⁻¹ between two holes in the ice separated by a distance of 300 m, using a Bombardier BR180[®] tractor (Drolet et al. 1991), either horizontally by maintaining the sampler at the ice-water interface (0.5- to 1.5-m depth interval) with two free-wheeling spherical buoys mounted on the frame, or obliquely by lowering the sampler without buoys to a depth of 40 m and towing it towards the surface at the second hole.

In 2008, 1-m-diameter ringnets were deployed vertically through a hole in drifting ice floes in the Amundsen Gulf or at the edge of the landfast ice near Cape Parry.

Integrated sampling from the vessel

After the fast ice break-up in 2004, sampling was conducted from the *Amundsen* over a series of stations covering the study area (Fig. 1). Three different samplers were used in ice concentrations ranging from 0 to 80 %. The DSN was equipped with one 750- μ m mesh net throughout the sampling period while the mesh of the other net

Table 1 Number of gadids collected by different sampling methods in 2004 and 2008, with standard length SL (mean \pm 1 standard deviation, SD)

Year	Sampling gear	Deployment	Conditions	Maximum sampled depth (m)	<i>n</i> casts	<i>n</i> gadids	SL \pm SD (mm)
2004	DSN	Horizontal	Under ice	1.5	8	48	8.8 \pm 2.3
	DSN	Oblique	Under ice	40	24	3,538	6.6 \pm 0.9
	DSN	Oblique	Open water	25–400	59	2,263	12.5 \pm 4.1
	RMT	Oblique	Open water	25–530	9	111	16.8 \pm 3.7
	EZ-Net	Oblique	Open water	20–500	25	457	13.7 \pm 3.2
	Other	Vertical	Open water	85–375	12	61	6.9 \pm 2.3
2008	DSN	Oblique	Open water	25–163	37	3,202	8.1 \pm 4.2
	RMT	Oblique	Open water	60–92	12	369	13.8 \pm 3.7
	Other	Vertical	Under ice or open water	10–1,080	58	516	7.2 \pm 1.8

The category ‘‘Other’’ includes ringnets deployed through the ice, square–conical nets deployed from the vessel and Hydrobios® multinet sampler

increased from 200 μ m in June to 500 μ m in July and August. The sampler was deployed in a single oblique tow down to depths of ca. 80 m, with a ship speed of ca. 1 m s⁻¹ and a cable angle of 60° on the horizon.

In summer 2004, a 8-m² effective aperture, 1,600- μ m mesh rectangular midwater trawl (RMT) was deployed at some stations, in shallow double oblique tows (maximum depths from 25 to 90 m according to respective station depth) or in deep single oblique tows (maximum depths from 100 to 500 m depths).

From April to August 2008, sampling in partially ice-covered and open waters was conducted over a series of stations using a 500- μ m mesh DSN and a 1,600- μ m mesh RMT both deployed in single oblique tows to depths of ca. 80 m (Table 1).

For both years, fish larvae collected by other zooplankton nets towed vertically (1-m² square–conical nets and 0.5-m² aperture Hydrobios® multinet sampler) were included in the present analysis (Table 1).

The number of individuals per unit volume of water was estimated for the DSN collections in June–August 2004 and May–August 2008. The volume of water filtered through the net was estimated from the product of the mouth area of the net opening area (2 m²), ship speed (1 m s⁻¹), and tow duration.

Stratified sampling from the vessel

At some stations in 2004, a 1-m² aperture EZNet® multi-layer sampler equipped with nine 6-m long, 200- μ m mesh nets (333 μ m in August) was deployed in a single oblique tow down to depths ranging from 20 to 500 m depending on the station. The nets were opened and closed sequentially starting at maximum cast depth. The nine sampling layers were tailored according to maximum cast depth and varied in thickness from as little as 1 m for shallow casts and up to 60 m for deep casts. To reconstruct the vertical distribution, each fish was attributed a capture depth equal to the mean depth of the sampling layer in which it was captured.

Use of the different samplers in data analysis

With the exception of the monthly abundances estimated quantitatively from the DSN open water sampling, and the vertical distribution documented with the EZNet sampling, the results and analyses presented hereafter combined the gadids collected with all gear types. This grouping allowed us to document the early life ecology of *B. saida* and *A. glacialis* over two entire growing seasons, under the ice as well as in open waters. However, as the samplers may have different size selectivity, some bias may have been introduced by this pooling but would be difficult to detect and quantify. For example, the larger individuals collected by the RMT compared to the DSN could result from size selectivity but most likely reflect the different time periods each sampler was deployed (later for the RMT, Table 1).

Morphometric measurements

At sea, all fish larvae and juveniles were sorted from zooplankton samples. For each sample, fresh standard length (SL) and body height at the anus (*H*) of up to a maximum of 50 haphazardly selected gadids from different lengths spanning the entire length range were measured to the nearest 0.1 mm before individual preservation of the fish in 95 % ethanol in separate vials. Non-measured fish were preserved in 95 % ethanol as well. Back in the laboratory, standard length (SL_P) and body height at the anus (*H*_P) of preserved fish were measured on the fish measured fresh at sea, as well as on all intact preserved fish >ca. 20 mm and on a maximum of 50 fish <ca. 20 mm per sample, for a total of 3,697 gadids in 2004 and 1,284 in 2008. Standard length and body height of preserved fish were corrected for shrinkage using the relationships SL = 1.073 SL_P + 0.253, (*r*² = 0.995, *n* = 663) and *H* = 1.048 *H*_P + 0.085, (*r*² = 0.966, *n* = 321).

Table 2 Total number of gadids collected, number and percentage of gadids identified to species by genetics and/or otolithometry, by sampling month in 2004 and 2008

Year	Month	<i>n</i> total	<i>n</i> identified	% identified
2004	Apr	36	30	83
	May	3,600	530	15
	June	834	169	20
	July	1,839	516	28
	Aug	169	150	89
2008	Apr	5	2	40
	May	2,326	207	9
	June	1,017	260	26
	July	707	232	33
	Aug	32	30	94

Identification uncertainty (percentage of identification divergence among the fish analysed by both methods) of 6 %

Species determination

The early stages of *B. saida* and *A. glacialis* can be distinguished by genotyping the *Gmo8* microsatellite locus (Madsen et al. 2009) or by measuring the nucleus of the lapillar otolith (Bouchard et al. 2013). A subset of 2,155 gadids (1,412 in 2004 and 743 in 2008), chosen randomly from all months, all sampling stations, and all 1-mm standard length classes, was identified to species by *Gmo8* and/or lapillus analysis (see Bouchard et al. 2013 for details). In summary, 802 gadids (494 in 2004 and 308 in 2008) were identified by genotyping the microsatellite locus *Gmo8* (Madsen et al. 2009). Bouchard et al. (2013) estimated an overall misclassification error of 3.4 % for larval gadids from the Beaufort Sea based on *Gmo8*. In addition, the lapillar otolith of 1,806 gadids (1,116 in 2004 and 690 in 2008, including 453 of the fish genotyped for *Gmo8*) was measured, and individuals with a product of the shortest and longest diameters of the nucleus $SN \times LN \geq 653 \mu\text{m}^2$ were assigned to *A. glacialis* (Bouchard et al. 2013). The analysis of 453 gadids by both methods (198 in 2004 and 255 in 2008) yielded the same identification in 94 % of cases. The 29 ambiguous fish for which identification differed between methods were assigned to species by redistribution (see redistribution section). Eighty-eight per cent of the few fish sampled in April and August were identified to species by either method, as opposed to 33 % of the thousands of fish sampled from May to July (Table 2).

Age determination

All intact gadids >24 mm in length were aged by otolith analysis. For larvae <24 mm, a subset of larvae including individuals in each 1-mm interval and representing all stations and capture months were selected for otolith age

determination. The lapillar otoliths of selected fish were extracted, mounted on microscope slides with thermoplastic polymer, and polished from one or both sides on a 0.5- μm metallurgical lapping film. Daily increments of the left lapillus were enumerated and measured under a microscope coupled to a camera and image analysing system (Image Pro Plus[®]). A first reading was made on 380 lapilli from 2004 and 327 lapilli from 2008 (both species included). Ageing precision (Campana 2001) was estimated by comparing the first reading with a second independent reading (different reader) made on 73 otoliths from 2004 and 48 otoliths from 2008, resulting in a mean coefficient of variation of 4.3 % for 2004 and 4.0 % for 2008. The first counts were retained in subsequent analyses.

Redistribution of length, species, and age

To obtain unbiased size frequency distributions and estimates of species occurrence, all larval gadids sampled in 2004 and 2008 were assigned morphometric measurements (standard length and body height), age, and species identification, either directly as previously detailed or from the following redistribution procedures.

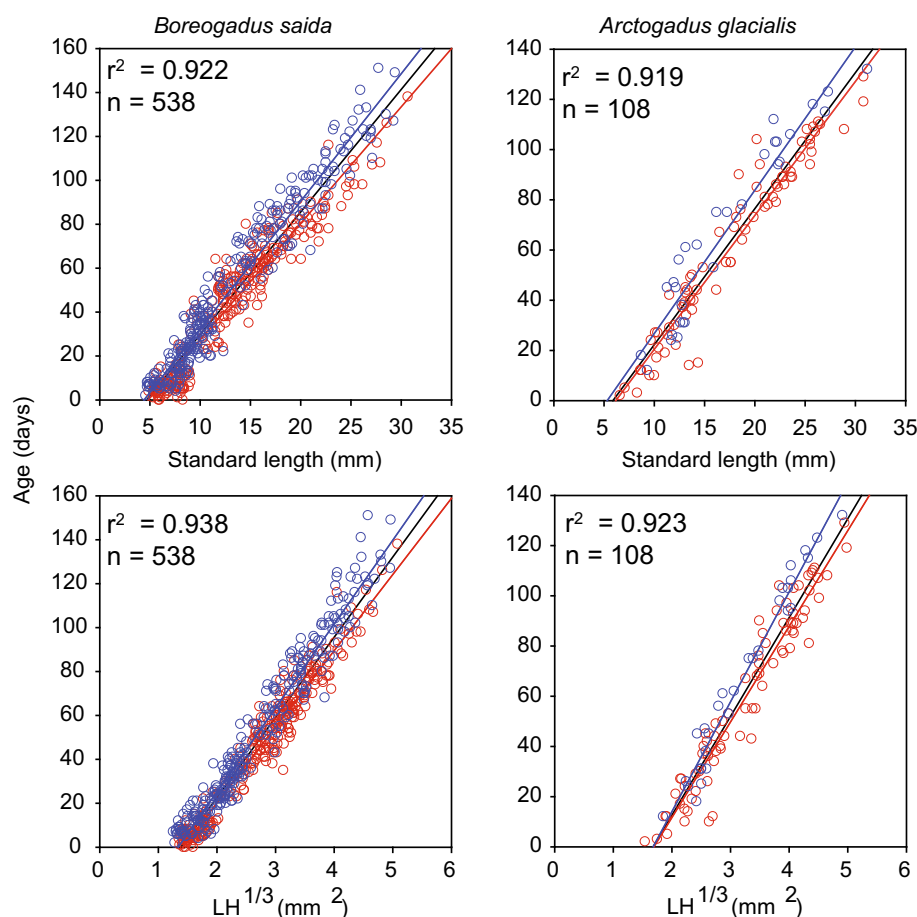
Standard length and body height redistribution

For samples containing over 50 larvae <20 mm, each non-measured gadid was assigned randomly a fresh standard length (SL) and body height (*H*) *pro rata* of the frequency distribution of SL and *H* for the 50 fish <20 mm actually measured in that sample. Overall, SL and *H* of 2,782 gadids <20 mm in 2004 (43 % of the total number of fish of all sizes) and 2,824 in 2008 (69 %) were reassigned following this procedure.

Age redistribution

The ages of the larvae that were measured but not aged by otolith analysis ($n = 3,317$ in 2004 and 957 in 2008) were estimated from their size. The age of identified and measured fish was strongly correlated with standard length, but for *A. glacialis*, the residuals of the linear regression were unevenly distributed in the 5- to 15-mm length interval (Fig. 2). The residuals of the regression of age on the cubic root of the product of standard length by body height ($LH^{1/3}$) were more evenly distributed around the line than the residuals of the regression of age on standard length (Fig. 2). Therefore, age was estimated from $LH^{1/3}$, with fish in a given $0.5 \text{ mm}^{2/3}$ $LH^{1/3}$ class being attributed an age in proportion to the known age probability function for that $LH^{1/3}$ class in each sampling year. The unmeasured small (<20 mm) larvae ($n = 2,782$ in 2004 and 2,824 in 2008) were attributed an age randomly in proportion to the frequency distribution of the ages of measured larvae in the sample they came from. Note

Fig. 2 Linear regression of age against standard length (*top*) and the cubic root of the product of standard length by body height at the anus ($LH^{1/3}$, *bottom*) for *Boreogadus saida* and *Arctogadus glacialis* aged by otolith analysis and identified to species by genetic and/or otolith nucleus size in 2004 (*red*) and 2008 (*blue*) and for pooled years (*black line*)



that the vast majority of the unmeasured larvae <20 mm were actually small recently hatched fish.

Species redistribution

Among the 2,126 gadids identified to species by molecular genetics and/or otolith analyses, the *A. glacialis* sampled on a given date were generally larger than the *B. saida* sampled on the same date (Fig. 3). For a given sampling month, unidentified gadids in a given 1-mm SL class were assigned to species based on the per cent occurrence of *A. glacialis* in this SL class. The overlap in SL between the two species, and hence the risk of misidentification, was relatively small in spring, in particular in May and June when large numbers of small larvae were sampled (Fig. 3; Table 2). The size overlap and hence the ambiguity in species attribution were maximum for the large fish sampled in July and August, 29 and 90 % of which, respectively, were identified by genetics and/or lapillar nucleus size (Fig. 3; Table 2).

Hatch date frequency distributions

The hatch date of an individual fish was determined by subtracting its estimated age (in days) from its date of

capture. An uncorrected hatch date frequency distribution (HFD) of the young fish captured in a given month was determined by tallying the number of fish hatched in each 3-day bin. In uncorrected HFDs, a hatch day bin comprising older larvae that have experienced mortality and dispersion for a longer period will be under-represented relative to a bin comprising young larvae (Yoklavich and Bailey 1990; Campana and Jones 1992; Fortier and Quiñonez-Velazquez 1998). Mortality–dispersion rates were estimated from the slope of the descending limb of the catch-at-age curve (e.g. Fortier et al. 2006). Based on these rates, the HFDs were corrected by calculating for each hatch date bin the initial number of fish needed to account for the observed number given losses by mortality–dispersion during the interval between hatching and the average age in that bin.

Gut content analysis

The gut contents of 209 *B. saida* and 67 *A. glacialis*, identified to species by genetics and/or otolithometry and chosen to represent all length classes, were examined under a stereomicroscope at magnifications of $50\times$ to $80\times$. Each prey was identified to the lowest taxonomic level possible

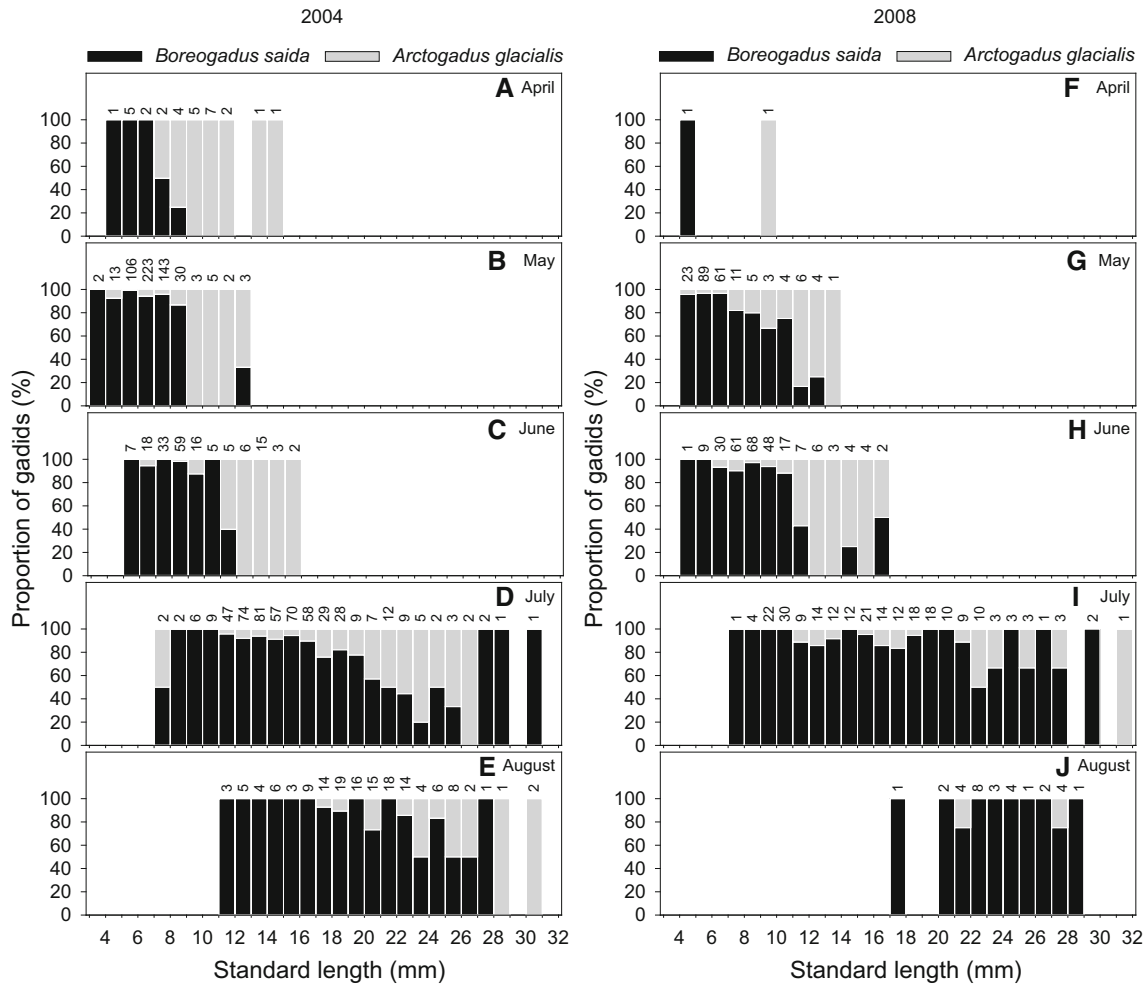


Fig. 3 Monthly proportion of *Boreogadus saida* (black) and *Arctogadus glacialis* (grey) by 1-mm standard length class in 2004 and 2008. Number above each bar indicates the number of gadids

and measured (prosome length for copepods and total length for other taxa). The carbon content of each prey was estimated using published length–weight and carbon–weight relationships (Table 3). Specific relationships were used when available. Otherwise, carbon content was estimated with generic or more general equations for closely related taxa. The overlap in the diet of the two species was measured with Schoener’s index (Schoener 1970).

Results

Comparison of occurrence, length, and growth of *B. saida* and *A. glacialis*

Gadidae represented 93 and 89 % of the ichthyoplankton sampled in the Beaufort Sea in 2004 and 2008, respectively. The 6,478 larval and juvenile gadids sampled from April to August 2004 ranged from 3.3 to 30.8 mm in length

identified to species by genetic and/or otolith nucleus size in the corresponding standard length class

and from 0 to 138 days of age. The 4,087 young gadids collected from April to August 2008 ranged from 4.1 to 31.2 mm in length and from 2 to 151 days of age. Among the 2,126 gadids collected in 2004 and 2008 and identified to species by genetics and/or otolith nucleus size, 155 (7.3 %) were *A. glacialis*. Of all the gadids identified visually or by genetics, no evidence of species other than *B. saida* or *A. glacialis* was found.

Mean length of individuals identified to species was significantly larger in *A. glacialis* than in *B. saida* for all months in 2004 and for May, June and July in 2008 (*t* tests, *p* < 0.01, Table 4). In both years, the size distribution of these species showed relatively little overlap for April, May and June, intermediate overlap for July and maximum overlap for August (Fig. 3). After redistribution based on length at date, *A. glacialis* represented 8.0 % of all gadids sampled in 2004 and 8.7 % in 2008.

Somatic growth estimated from the slope of the length–age regression for individuals identified to species was

Table 3 Summary of references on relationships between carbon content (C , in mg), prosome (PL, in mm) or total length (L , in mm) for the main prey of *Boreogadus saida* and *Arctogadus glacialis* early life stages

Gut contents taxa	Equation taxa	Equations	References
<i>Acartia</i> spp.	<i>Acartia longiremis</i>	$C = 1.023 \times 10^{-8} \times (\text{PL} \times 1,000)^{2.906}$	Hansen et al. (1999), Fig. 9
<i>Calanus glacialis</i>	<i>Calanus glacialis</i>	$C = 4.742 \times \text{PL}^{3.452}$	Forest et al. (2011), Fig. 4b (summer)
<i>Calanus hyperboreus</i>	<i>Calanus hyperboreus</i>	$C = 7.263 \times \text{PL}^{3.106}$	Forest et al. (2011), Fig. 4a (summer)
<i>Calanus</i> spp. nauplii	<i>Calanus finmarchicus</i> nauplii	$C = 4.29 \times 10^{-6} \times (L \times 1,000)^{2.05}$	Hygum et al. (2000), Fig. 4 (high food resources)
Cyclopoid nauplii	<i>Oithona similis</i> nauplii	$C = 5.545 \times 10^{-8} \times (\text{PL} \times 1,000)^{2.71}$	Sabatini and Kiørboe (1994), Fig. 1
<i>Eurytemora</i> spp.	<i>Eurytemora herdmani</i>	$C = (10^{2.96 \times \log(\text{PL} \times 1,000) - 7.604}) \times 0.447$	Middlebrook and Roff (1986), Eq. 8, (1)
Harpacticoida	<i>Macrosetella gracilis</i> and <i>Macrosetella</i> spp.	$C = e^{1.03 \times \ln(L \times 1,000) - 7.07}$	Satapoomin (1999), Table 2
<i>Limnocalanus</i> spp.	Copepoda	$C = 10^{3.07 \times \log(\text{PL} \times 1,000) - 8.37}$	Uye (1982), Table 1
<i>Metridia longa</i>	<i>Metridia longa</i>	$C = 7.498 \times \text{PL}^{3.225}$	Forest et al. (2011), Fig. 4c (summer)
<i>Metridia</i> spp. nauplii	<i>Acartia tonsa</i> nauplii	$C = 3.18 \times 10^{-9} \times (\text{PL} \times 1,000)^{3.31}$	Berggreen et al. (1988), Fig. 3
<i>Microcalanus</i> spp.	Copepoda	$C = 10^{3.07 \times \log(\text{PL} \times 1,000) - 8.37}$	Uye (1982), Table 1
<i>Microcalanus</i> spp. nauplii	<i>Pseudocalanus newmani</i> nauplii	$C = (10^{2.515 \times \log L + 0.975}) \times 0.447$	Lee et al. (2003), Fig. 3, (1)
<i>Oithona similis</i>	<i>Oithona similis</i>	$C = 9.4676 \times 10^{-7} \times (\text{PL} \times 1,000)^{2.16}$	Sabatini and Kiørboe (1994), Fig. 1
<i>Oncaea parva</i>	<i>Oithona similis</i>	$C = 9.4676 \times 10^{-7} \times (\text{PL} \times 1,000)^{2.16}$	Sabatini and Kiørboe (1994), Fig. 1
<i>Paraeuchaeta glacialis</i>	<i>Paraeuchaeta</i> spp.	$C = (0.0075 \text{ PL}^{3.274} + (0.07 \times 0.0075 \times \text{PL}^{3.274})) \times 0.447 \times 1,000$	Mumm (1991) Appendix C (1)
<i>Pseudocalanus</i> spp.	<i>Pseudocalanus</i> spp.	$C = (10^{2.85 \times \log(\text{PL} \times 1,000) - 7.62}) \times 0.447$	Liu and Hopcroft (2008), Fig. 1, (1)
<i>Pseudocalanus</i> spp. nauplii	<i>Pseudocalanus newmani</i> nauplii	$C = (10^{2.515 \times \log L + 0.975}) \times 0.447$	Lee et al. (2003), Fig. 3, (1)
<i>Triconia borealis</i>	<i>Oithona similis</i>	$C = 9.4676 \times 10^{-7} \times (\text{PL} \times 1,000)^{2.16}$	Sabatini and Kiørboe (1994), Fig. 1
Unidentified copepod	Copepoda	$C = 10^{3.07 \times \log(\text{PL} \times 1,000) - 8.37}$	Uye (1982), Table 1
Unidentified copepod nauplii	<i>Pseudocalanus newmani</i> nauplii	$C = (10^{2.515 \times \log L + 0.975}) \times 0.447$	Lee et al. (2003), Fig. 3, (1)
Unidentified cyclopoid	<i>Oithona similis</i>	$C = 9.4676 \times 10^{-7} \times (\text{PL} \times 1,000)^{2.16}$	Sabatini and Kiørboe (1994), Fig. 1
Amphipoda	<i>Scina crassicornis</i> , <i>Phrosina semilunata</i> , <i>Phronima sedentaria</i>	$C = 10^{(\log L - 0.063)/0.277} \times 0.285$	Gorsky et al. (1988), Tables 1 and 2
Appendicularia	<i>Oikopleura rufescens</i> (synonym: <i>Oikopleura vanhoeffeni</i>)	$C = 8.20 \times 10^{-8} \times (L_{\text{TR}} \times 1,000)^{2.70}$ (where L_{TR} = trunk length)	Sato et al. (2003), Eq. 7
Bivalvia	<i>Mytilus edulis</i>	$C = 3.06 \times 10^{-8} \times (L \times 1,000)^{2.88}$	Fotel et al. (1999), Sect. 3.4
Chaetognatha	<i>Sagitta crassa</i>	$C = 10^{3.16 \times \log L - 1.29}$	Uye (1982), Table 1
Cirripeda	<i>Mytilus edulis</i>	$C = 3.06 \times 10^{-8} \times (L \times 1,000)^{2.88}$	Fotel et al. (1999), Sect. 3.4
Cnidaria		$C = 0$	
Eggs	7 copepod species (<i>Calanus finmarchicus</i> , <i>C. hyperboreus</i> , <i>Temora longicornis</i> , <i>Acartia longiremis</i> , <i>A. tonsa</i> , <i>Centropages hamatus</i> and <i>Pseudocalanus</i> spp.)	$C = 0.14 \times 10^{-6} \times (4/3\pi(L \times 1,000/2)^3)$	Kiørboe (1985)

Table 3 continued

Gut contents taxa	Equation taxa	Equations	References
Gastropoda	<i>Spiratella retroversa</i>	$C = 10^{3.102 \log D + 1.469}$ (where $D = \text{diameter}$)	Conover and Lalli (1974), Fig. 1
Ostracoda	<i>Conchoecia pseudodiscophora</i>	$C = 0.346 \times e^{3.868 \times L} \times 0.4$	Ikeda (1990), Table 2. (2)
Polychaeta	<i>Neanthes succinea</i>	$1.42 \times 10^{-4} \times (L \times 1,000)^{1.47}$	Hansen (1999), Table 1
Digested material	Digested material	$C = (109.08 \times (\pi \times (W/2)^2 \times L)^{0.9591})$ $\times 0.4$ (where $W = \text{width}$)	Sirois (1999), (2)
(1)	Copepoda	$C = 44.7 \% \text{ DW}$ (where DW = dry weight)	Mauchline (1998)
(2)	Zooplankton	$C = 40 \% \text{ DW}$ (where DW = dry weight)	Legendre and Michaud (1998)

Table 4 Number and standard length SL (mean \pm 1 standard deviation, SD) of *Boreogadus saida* and *Arctogadus glacialis* collected by sampling month in 2004 and 2008

Year	Month	<i>Boreogadus saida</i>		<i>Arctogadus glacialis</i>	
		<i>n</i>	SL \pm SD (mm)	<i>n</i>	SL \pm SD (mm)
2004	Apr	10	6.3 \pm 1.0	26	10.5 \pm 1.6
	May	3,396	6.5 \pm 0.8	204	7.4 \pm 1.6
	Jun	749	8.1 \pm 1.0	85	12.0 \pm 2.4
	Jul	1,659	14.0 \pm 2.6	180	16.4 \pm 3.8
	Aug	146	19.2 \pm 3.4	23	23.6 \pm 3.7
2008	Apr	1	4.6	4	9.8 \pm 0.4
	May	2,188	5.8 \pm 0.9	138	8.0 \pm 2.9
	Jun	869	8.8 \pm 1.5	148	11.2 \pm 2.5
	Jul	642	15.4 \pm 3.7	65	17.2 \pm 4.4
	Aug	30	23.6 \pm 2.5	2	24.5 \pm 3.6

higher in 2004 than in 2008 (Table 5), significantly so for *B. saida* (ANCOVA, $F_{1,534} = 6.62$, $p < 0.05$) but not for *A. glacialis* (ANCOVA, $F_{1,104} = 2.18$, $p > 0.05$). In a given year, somatic growth did not differ significantly between the two species (ANCOVA, 2004: $F_{1,345} = 0.233$, $p > 0.05$; 2008: $F_{1,293} = 0.027$, $p > 0.05$). In both years, intercepts indicated a significantly smaller length at hatch in *B. saida* than in *A. glacialis* (ANCOVA, 2004: $p < 0.0001$; 2008: $p < 0.0001$).

Vertical distribution in ice-free waters

When summed across 14 EZNet casts performed at different dates from early June to early August, the vertical distributions of the two species were similar with 59 % of *B. saida* and 51 % of *A. glacialis* occurring within 10 m of the surface (Fig. 4). The remainder of the larvae and juveniles distributed primarily between 10 and 40 m, except for a few *B. saida* sampled between 40 and 160 m. In both species, most young fishes concentrated in the 5–10 m layer in daytime (06h00–18h00 local time) and in the 0–5 m layer at night (Fig. 4).

Table 5 Size at hatch and somatic growth rate of *Boreogadus saida* and *Arctogadus glacialis* collected in 2004 and 2008 as estimated, respectively, by the intercept and the slope of the regression of standard length against age for fish aged by otolithometry and identified to the species by genetics and/or otolithometry

Species	Year	Number of otoliths analysed	Size at hatch (mm)	Growth rate (mm day ⁻¹)
<i>Boreogadus saida</i>	2004	271	5.53	0.173
	2008	267	4.90	0.163
<i>Arctogadus glacialis</i>	2004	78	6.86	0.176
	2008	30	6.25	0.161

Monthly distribution of *B. saida* and *A. glacialis* in the partially ice-covered south-east Beaufort Sea

The monthly spatial distribution of the two species differed little within the partially ice-covered or ice-free areas sampled from June to August 2004 and May to August 2008 (Fig. 5). Among the 96 stations sampled with DSN oblique tows, only one (1 %) yielded no young gadids while both species were collected at 74 stations (77 %). In a given month, *B. saida* was usually one order of magnitude more abundant than *A. glacialis*. In May 2008, both species were recorded at stations sampled in the flaw lead west and north of Banks Island. In that month, *B. saida* was relatively abundant in the Amundsen Gulf with a large number of small larvae collected near the fast ice edge off Cape Parry (Fig. 5). In June 2004 and 2008, high densities of *B. saida* (up to 388 ind. 1,000 m⁻³) and *A. glacialis* (up to 83 ind. 1,000 m⁻³) were found in Franklin Bay, Darnley Bay and the Amundsen Gulf (Fig. 5). *B. saida* tended to be less abundant at the few stations sampled on and at the edge of the Mackenzie Shelf than in Amundsen Gulf. High densities were also recorded in July 2004 and 2008, with maximum values of 996 and 104 ind. 1,000 m⁻³ for *B. saida* and *A. glacialis*, respectively. In July, the highest densities of both species were found in the west part of the sampled area (Fig. 5). Sampling was limited to the

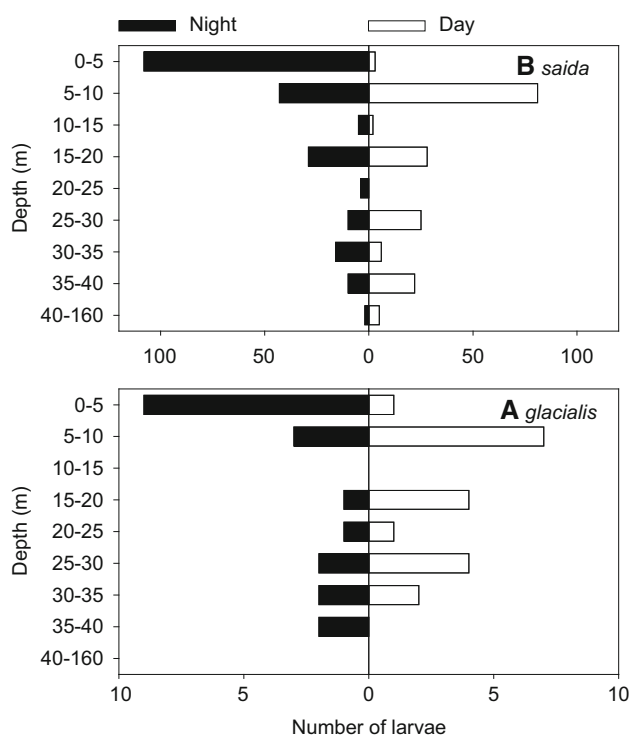


Fig. 4 Vertical distribution of larval and juvenile *Boreogadus saida* and *Arctogadus glacialis* collected by day (open bars) and by night (filled bars) with the EZNet multilayer sampler, over 14 dates from early June to early August 2004 in south-east Beaufort Sea

Amundsen Gulf in August, where relatively low densities of juveniles (maximum values of 102 and 5 ind. $1,000\text{ m}^{-3}$ for *B. saida* and *A. glacialis*, respectively) were recorded.

Hatch date frequency distributions of *B. saida* and *A. glacialis*

For *B. saida*, the uncorrected HFD of the young fish identified to species and aged, spanned from early March to late June in both 2004 and 2008 (Fig. 6). For *A. glacialis*, the uncorrected HFDs of 2004 and 2008 both began in late March, but ended at different periods: in early July in 2004 and in mid-May in 2008 (Fig. 6). In both years, the HFD of *B. saida* was shifted to the left when recalculated for all fish after the redistribution of ages. The centre of mass (or mean hatch date) of the HFD of *A. glacialis* was little affected by the redistribution process, but its seasonal extent increased as fish hatched in February–March of both years and May–June 2008 were included (Fig. 6).

The mortality rate of each species was assessed from catch-at-age curves (Fig. 7). Estimated mortality rates differed significantly between *B. saida* ($4.6\% \text{ day}^{-1}$) and *A. glacialis* ($2.4\% \text{ day}^{-1}$) in 2004 (ANCOVA, $F_{1,46} = 13.3$, $p < 0.001$), but not in 2008 (3.7 and $3.1\% \text{ day}^{-1}$ for *B. saida* and *A. glacialis*, respectively, ANCOVA, $F_{1,49} = 1.33$, $p > 0.5$). For each species, the estimated

Fig. 5 Monthly abundance (no. $1,000\text{ m}^{-3}$) of *Boreogadus saida* and *Arctogadus glacialis* larvae and juveniles collected by oblique DSN tows in summer 2004 (red) and summer 2008 (blue)

mortality rate was not significantly different between 2004 and 2008 (ANCOVA, *B. saida*: $F_{1,61} = 3.84$, $p > 0.05$; *A. glacialis*: $F_{1,34} = 0.822$, $p > 0.05$).

After correction for mortality–dispersion using the mortality rates presented in Fig. 7, the HFDs were shifted to the left as increased numerical weight was given in retrospect to older larvae that had suffered mortality for longer than young larvae (Fig. 8). In 2004, the hatching of *B. saida* started in early March and was most intense from mid-April to late May and was nearly completed by the end of June with little hatching in July. In 2008, hatching started in the second half of February, increased progressively until a peak in late April, and then declined until the end of June. In 2004, the protracted hatching of *A. glacialis* started in early February, peaked from mid-April to early May, and then declined progressively until early July (Fig. 8). In 2008, *A. glacialis* hatching season started in mid-February, peaked from early to late April, and declined until the end of June.

Sea ice declined more rapidly, and the ice break-up occurred 20 days earlier in 2008 than in 2004 (Fig. 8). Average ice concentration in the study area reached $<50\%$ in mid-June 2008 and at the end of June 2004. By the end of July, only 3% of the area was covered by ice in 2008, compared to 31% in 2004 (Fig. 8). *B. saida* began hatching approximately 3 weeks earlier in 2008 relative to 2004, while *A. glacialis* started to hatch within the same week in both years (Fig. 8). The end of the hatching season occurred earlier by ca. 6 days for *B. saida* and 15 days for *A. glacialis* in 2008 relative to 2004 (Fig. 8).

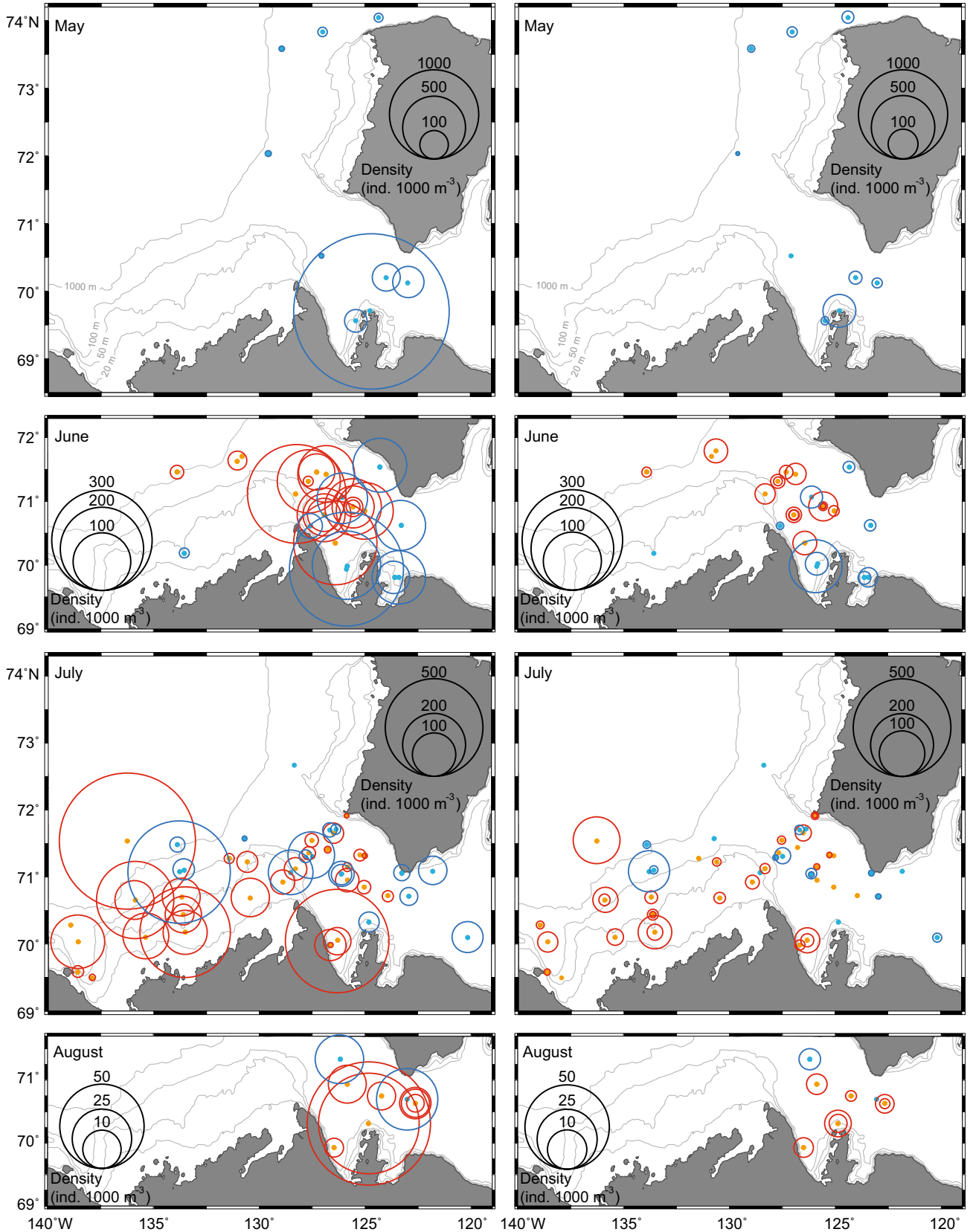
Prey and carbon intake

A majority of the *B. saida* larvae collected under the ice in April and May had empty guts (18 out of 21 larvae examined). The three feeding larvae contained *Pseudocalanus* copepodites, *Pseudocalanus* nauplii, and invertebrate eggs. In contrast, only two of the 16 *A. glacialis* larvae collected under the ice and selected for gut content analysis contained no prey. Under the ice, *A. glacialis* larvae preyed primarily on *Pseudocalanus* nauplii (38% of carbon intake), cyclopoid nauplii (28%), and *Calanus* nauplii (20%).

In open waters, the feeding incidence of both species was 100% . Pooling data for all sampling months (under ice and open waters combined), the diet of the two species by length classes, differed initially and then converged as the larvae metamorphosed into juveniles. Schoener's index of diet overlap was relatively low for the $<15\text{ mm}$ length class ($SI = 0.38$) and increased to 0.70 in fish $>15\text{ mm}$

Boreogadus saida

Arctogadus glacialis



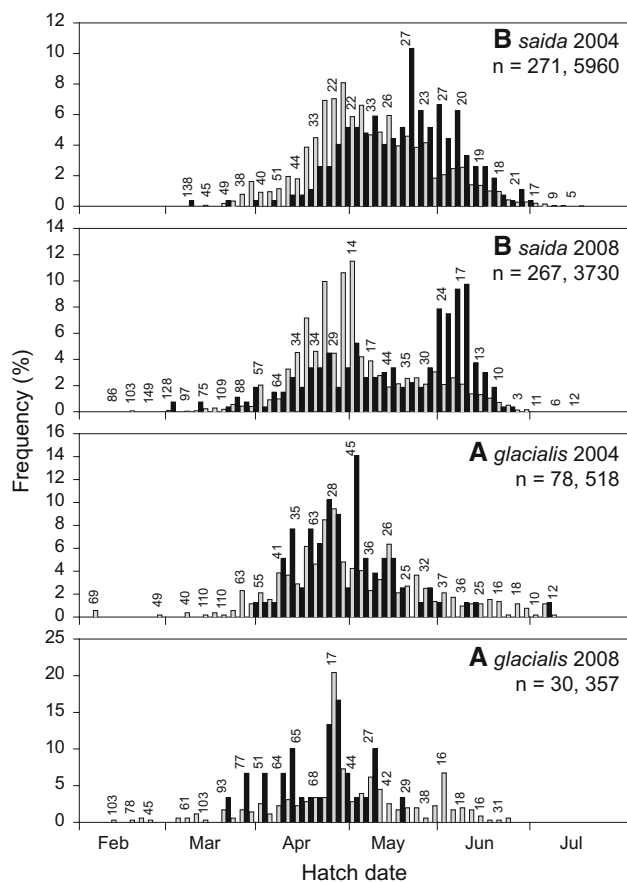


Fig. 6 Hatch date frequency distributions of *Boreogadus saida* and *Arctogadus glacialis* uncorrected for mortality in 2004 and 2008 for fish aged by otolith analysis and identified to species by genetic and/or otolith nucleus size (black) and for all fish after species and age redistribution (grey). Number above every second bar indicates mean age of the sub-cohort. *n* indicates the number of fish identified to species, the total number of fish assigned to the species

(Fig. 9). In larvae <15 mm, the most frequent prey of *B. saida* were *Pseudocalanus nauplii* (42 %) and *Calanus nauplii* (16 %), while *A. glacialis* preyed primarily (65 %) on cyclopoid nauplii (Fig. 9a). From 15 to 25 mm, the diet of the two species became more similar, with continued preference of *B. saida* for *Pseudocalanus* spp. nauplii and a shift of *A. glacialis* from nauplii to copepodites of *Oithona similis* and *Triconia borealis* (Fig. 9b). Beyond 25 mm in length, the diet of both species shifted from nauplii to larger copepodite prey, including *Calanus glacialis*, *Pseudocalanus* spp., *O. similis*, and to a lesser extent *T. borealis* (Fig. 9c).

In larvae <15 mm, *Calanus nauplii* (40 %) and invertebrate eggs (22 %) contributed the most to the carbon intake of *B. saida* (Fig. 9d). Cyclopoid nauplii (43 %) and *Calanus nauplii* (20 %) were the main sources of carbon for *A. glacialis*. In the 15–25 mm length class, *Calanus nauplii* represented 29 and 25 % of the energy intake of *B.*

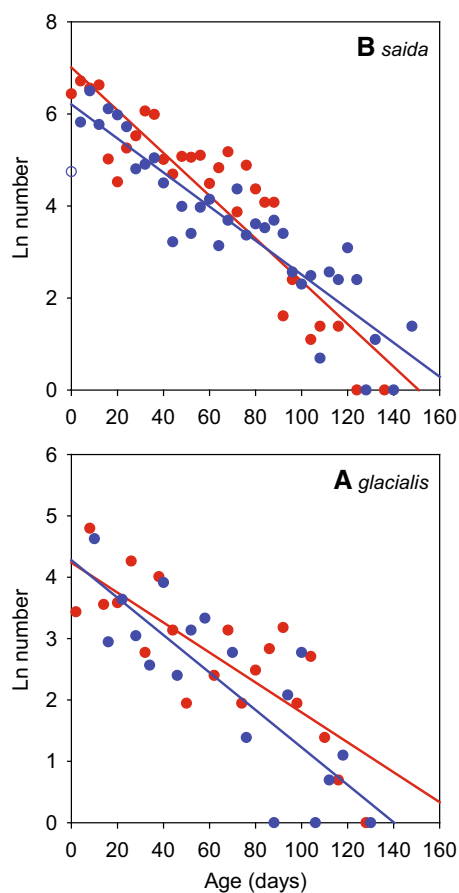


Fig. 7 Catch-at-age curves for *Boreogadus saida* (4-day age bins) and *Arctogadus glacialis* (6-day age bins) in 2004 (red) and 2008 (blue). The slopes of the regressions were used to estimate the mortality rate: *B. saida* 2004: Ln number = $7.010 - 0.046 \text{ age}$, $r^2 = 0.824$; *B. saida* 2008: Ln number = $6.207 - 0.037 \text{ age}$, $r^2 = 0.838$; *A. glacialis* 2004: Ln number = $4.237 - 0.024 \text{ age}$, $r^2 = 0.648$; *A. glacialis* 2008: Ln number = $4.277 - 0.031 \text{ age}$, $r^2 = 0.672$

saida and *A. glacialis*, respectively. The infrequent but large *C. glacialis* copepodite prey accounted for 24 % of the carbon intake of *B. saida* 15–25 mm (Fig. 9e). *Oithona similis* (16 %) and gastropod larvae (17 %) were important carbon sources for *A. glacialis* 15–25 mm. At lengths >25 mm, the large copepodites *C. glacialis* and *C. hyperboreus* contributed 90 % of the carbon intake of *B. saida*, while *C. glacialis* accounted for 63 % of the carbon intake of *A. glacialis* (Fig. 9f).

Discussion

Discriminating young *B. saida* and *A. glacialis* in large plankton collections

On the Mackenzie Shelf, larval fish assemblages comprise 34–60 % of Gadidae, mostly *B. saida* with rare occurrence of

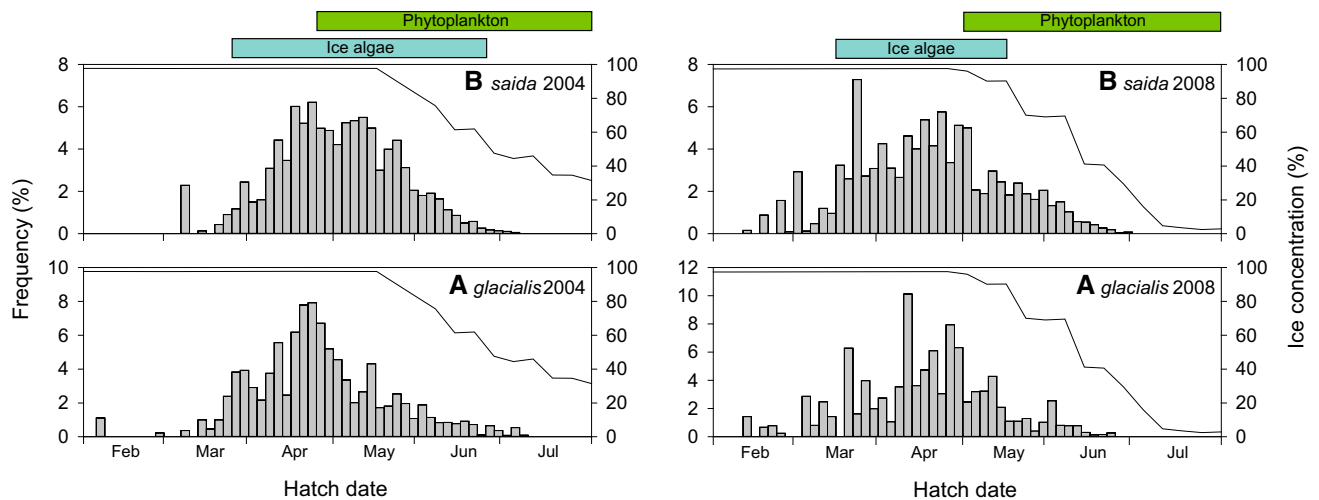


Fig. 8 Hatch date frequency distributions corrected for mortality for all *Boreogadus saida* and *Arctogadus glacialis* collected in the Beaufort Sea in 2004 and 2008 after species redistribution. The black

line indicates weekly ice concentration in the study area. The timing of ice algae and phytoplankton production in Franklin Bay (2004) and Amundsen Gulf (2008) are indicated above each panel

the genus *Arctogadus* and Saffron cod (*Eleginus gracilis*) found in very shallow (<13 m) waters highly influenced by the Mackenzie River plume (Paulic and Papst 2013; Wong et al. 2013). In an area with low freshwater influence including part of the Mackenzie Shelf, the Beaufort Slope, and the Amundsen Gulf, Gadidae, consisting of *B. saida* and *A. glacialis*, numerically accounted for >75 % of the ichthyoplankton in all summers between 2002 and 2011 (K. Suzuki, Kyoto University, unpublished data). Considering the area sampled for the present study, we assumed that all gadids collected were either *B. saida* or *A. glacialis*.

The morphological similarity of *B. saida* and *A. glacialis* during early life (Fahay 2007) has hindered the reliable discrimination of the two species in field collections. Recently, molecular (Madsen et al. 2009; Nelson et al. 2013) and otolithometric (Bouchard et al. 2013) identification methods were developed. These methods are relatively labour intensive, and the analysis of large numbers of fish often remains prohibitive (Bouchard et al. 2013). In the present study, 47 % of the young gadids collected were measured, 20 % were identified to species by genetics and/or otolithometry, and 6.1 % were aged. For these confirmed fish, the larger size at hatch of *A. glacialis*, its slightly earlier hatching in a given year, and very similar growth rates of the two species resulted in *A. glacialis* being consistently larger on a given date than *B. saida*, at least from April to June (Fig. 3). This size difference allowed the attribution of the newly hatched and small larvae collected in these months to either species with some confidence. By July, the size divergence between the two species had attenuated and, while our probabilistic extrapolation of the overall number of *A. glacialis* sampled in that month is probably correct, confidence in the

identification of a given gadid of a given size from a given station is low. This uncertainty in the statistical redistribution of species based on size prevails for August as well when the overlap in the size distribution of the two species was greatest. However, a larger fraction (90 %) of the relatively few fish sampled in that month were identified by genetics and/or their otolith nucleus.

The feeding and vertical distribution of *B. saida* and *A. glacialis* early life stages

The diet of the two species differed primarily during the early larval stage (<15 mm) when *A. glacialis* specialized on cyclopoid copepod nauplii and *B. saida* on calanoid copepod nauplii. As late larvae (15–25 mm), the diet of the two species converged, with the exception of a tendency for *A. glacialis* to prey on cyclopoid copepodites. During the juvenile stage (>25 mm), *B. saida* obtained most of its energy from *C. hyperboreus* and *C. glacialis*, and *A. glacialis* fed mainly on *C. glacialis*. At that time, the two gadid species occupied essentially the same niche in the plankton of the Beaufort Sea.

In spring and early summer, several copepod species dominated by *C. glacialis*, *Pseudocalanus* spp., *O. similis* and *C. hyperboreus* associate with a 0.3- to 0.5-m-thick meltwater layer under the landfast ice of the Beaufort Sea (Hop et al. 2011). In *C. glacialis*, *Pseudocalanus* spp. and likely *O. similis*, the early production of eggs and nauplii is fuelled by the production of ice algae before the phytoplankton bloom (e.g. Runge and Ingram 1991; Tourangeau and Runge 1991; Darnis 2013). The naupliar stages of these copepods were the primary carbon sources of *B. saida* and *A. glacialis* larvae under the ice. Thus, at least in

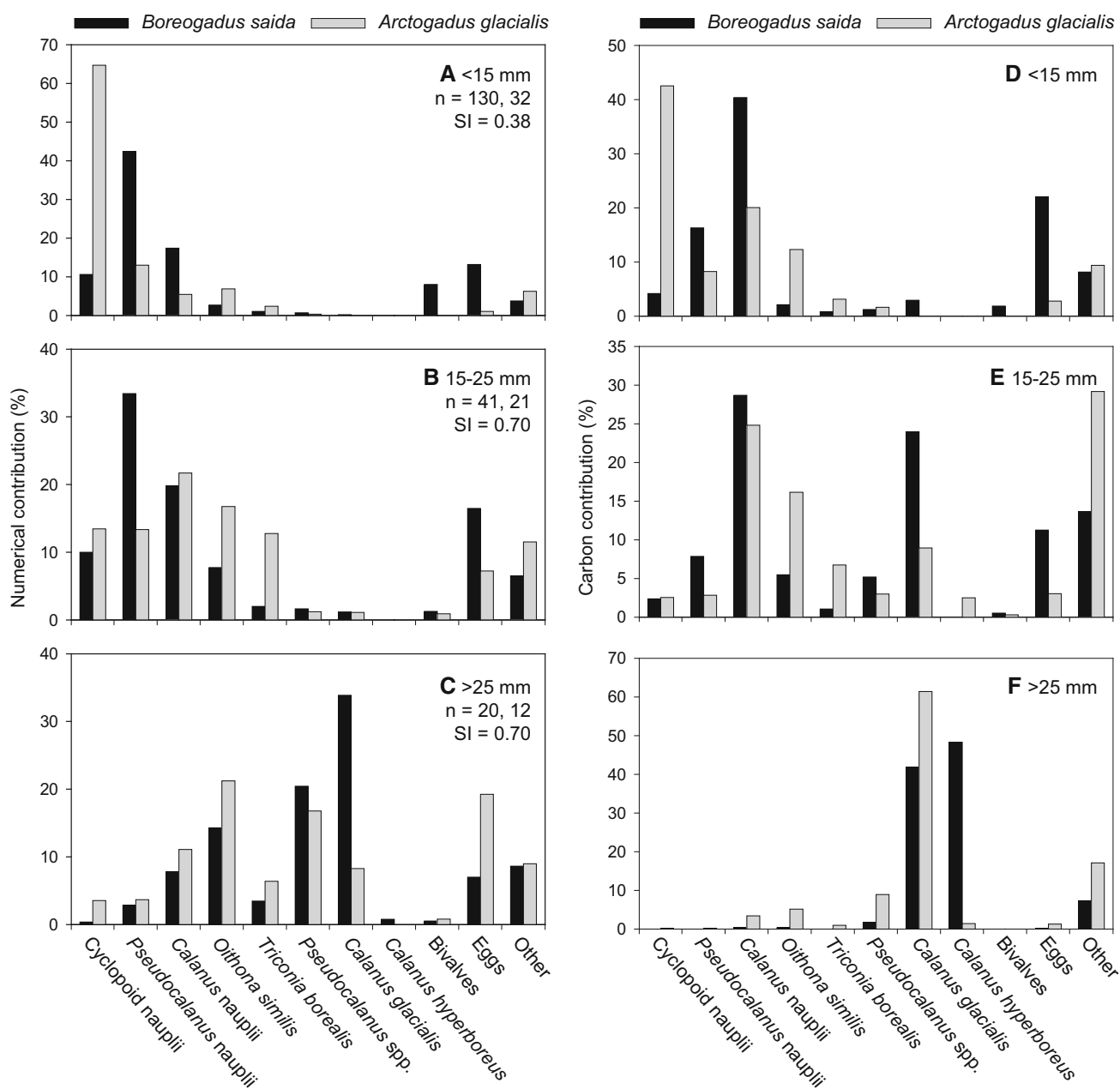


Fig. 9 Per cent diet composition by number (a–c) and carbon (d–f) for three length classes of *Boreogadus saida* and *Arctogadus glacialis* sampled in 2004 and identified to species by genetics and/or otolithometry. *n* indicates the number of *B. saida*, *A. glacialis* analysed. SI is Schoener’s index of diet overlap between the two species. The category “Other” includes *Acartia* spp., *Eurytemora*

spp., Harpacticoida, *Limnocalanus* spp., *Metridia longa*, *Metridia* nauplii, *Microcalanus* spp., *Microcalanus* nauplii, *Oncaea parila*, *Paraeuchaeta glacialis*, unidentified calanoid copepod, unidentified cyclopoïd copepod, unidentified copepod nauplii, Amphipoda, Appendicularia, Chaetognatha, Cirripedia, Cnidaria, Gastropoda, Ostracoda, Polychaeta and digested material

April and May, the first-feeding success and early growth of both species could depend on the early reproduction of copepods grazing on ice algae. The food of larvae hatched under the ice in February and March before the onset of microalgal production (Fig. 8) remains unknown, but the naupliar stages of small omnivorous copepods that reproduce year round and the floating eggs of *C. hyperboreus* laid in winter (Darnis 2013) are potential candidates.

In partially or fully open waters in summer, the late larval and early juvenile stages of the two species shared essentially the same vertical distribution. The possibility of a small-amplitude diel vertical migration (DVM) in which most larvae occupy the 0–5 m layer at night and the 5–10 m layer in daytime is suggested by a composite figure including all individuals collected with the multinet sampler from June to early August (Fig. 4). Such a DVM is

typical of situations in which greater food availability near the surface is offset by higher vulnerability to visual predators in daytime (Lampert 1989; Fortier et al. 2001). Assuming increased availability of prey near the surface, foraging larvae and juveniles may minimize predation mortality by remaining in the 5–10 m layer in daytime and invading the 0–5 m layer at night when the midnight sun is low enough on the horizon to hamper seabirds and other visual predators. Our study design did not allow an accurate assessment of circadian migration patterns, and the occurrence of DVM in Arctic gadid early life stages will remain speculative until further studies are undertaken.

Spatiotemporal sympatry of the planktonic stages of *B. saida* and *A. glacialis* in the south-east Beaufort Sea

Spatially, the early stages of the two species shared the same geographical distribution, occupying most of the region sampled in a given month. This is consistent with the ubiquity of juvenile gadids in the surface layer (0–100 m) of the south-eastern Beaufort Sea as detected by acoustic surveys (M. Geoffroy, Université Laval, personal communication). Adult *A. glacialis* are distributed in shallow coastal and estuarine habitats and on continental shelves (Nielsen and Jensen 1967; Aschan et al. 2009) while *B. saida*, at least in the Beaufort Sea, often congregate in deep embayments and on the slope of the continental shelf (Benoit et al. 2008, 2014; Geoffroy et al. 2011). We found no evidence for such a general inshore–offshore segregation of the two species during the larval and juvenile stages.

The planktonic stages of *B. saida* and *A. glacialis* not only co-occurred spatially but also coincided in time, the two species presenting a similar protracted hatching season from February to July. In subarctic seas, hatching is typically synchronized with the vernal onset of primary production and the maximum seasonal production of the zooplankton prey of the larvae (e.g. the match/mismatch hypothesis, Cushing 1990). In Arctic seas influenced by large rivers, the protracted hatching season of *B. saida* starts in winter when the abundance of suitable zooplankton prey is at a minimum and ends in early summer when prey availability peaks (Bouchard and Fortier 2011). Obviously, some constraint other than matching the emergence of the larvae with peak availability of their prey dictates the hatching season of *B. saida*. A large size at the end of the short Arctic summer should reduce the vulnerability of juvenile *B. saida* to avian predation, cannibalism and winter starvation (Fortier et al. 2006). Hence, the need to maximize the duration of the first growth season to achieve a minimum threshold size in August could explain the paradox of winter–spring hatching when food is relatively scarce under the sea-ice cover (Bouchard and Fortier 2008, 2011). In the Beaufort Sea, the hatching season of *A.*

glacialis was similar to that of *B. saida*, also extending from February to early July (Fig. 8). This suggests that the two species are equally constrained by this imperative of hatching early to achieve a threshold pre-winter size. Arctic shelves are unpredictable environments, and early-hatched cohorts of *B. saida* have been observed to vanish, leaving summer hatchers as the main survivors in a given year in a given region (Fortier et al. 2001; Bouchard and Fortier 2008). Hence, despite the resulting lower pre-winter size, summer hatching may be maintained as a way to avoid complete recruitment failure in years when under-ice conditions preclude the survival of the early hatchers. Therefore, the long hatching season of *B. saida* and *A. glacialis* from January to July may be seen as a bet-hedging strategy to minimize variation in fitness among years (Olafsson et al. 2009).

Ecological divergences and niche separation during life in the plankton

While adult *B. saida* and *A. glacialis* are morphologically and ecologically quite different, many aspects of the planktonic life of the two species proved remarkably similar. In addition to being almost indistinguishable morphologically, the young stages overlapped geographically, presented virtually the same hatching season, grew at the same average rate, and, as pre-juveniles and juveniles, were distributed in the same depth interval and shared essentially the same diet in open waters in summer. High dietary overlap has often been reported between early life stages of sympatric, closely related marine fish species and was often explained by non-limiting food resources (e.g. Rodrigues and Vieira 2010; Wasserman 2012). In the North Water polynya, the feeding success of newly hatched *B. saida* larvae was seldom limited by the abundance of their prey (Michaud et al. 1996). In the Canadian Beaufort Sea, *B. saida* and *A. glacialis* larger than 15 mm had a high index of diet overlap, suggesting an access to abundant prey may characterize this region as well. For larvae smaller than 15 mm, however, some niche-partitioning mechanisms (differences in micro-habitat or behaviour, for example) must play a role in reducing the inter-specific competition.

Three divergences in early life-history traits may reduce the competition between the two species and help explain the sympatric existence of the nearly identical larvae and juveniles in the plankton. First, *A. glacialis* was larger at hatch (6.2–6.9 mm) than *B. saida* (4.9–5.5 mm, see also Michaud et al. 1996; Ponomarenko 2000). This difference in initial size combined with a slightly earlier hatching season resulted in the modal length of *A. glacialis* being on average ca. 3 mm longer at a given date than that of *B. saida* from April to July. Second, the mortality rate estimated over the larval and juvenile stages was about 1.5

times higher in *B. saida* than in *A. glacialis*. Third, the first-feeding larvae of the two species specialized on different prey items and although the larvae analysed for gut content were of similar size (5.3–12.3 vs. 6.6–14.4 mm, respectively), the feeding incidence of *B. saida* sampled from 0 to 40 m under the ice was low (14 %) relative to *A. glacialis* (88 %). Finally, the scarcity of adult *A. glacialis* relative to *B. saida* in the study area (Cobb et al. 2008) was reflected in the relative abundance of their respective early life stages, with *B. saida* being approximately 12 times more frequent in our collections than *A. glacialis*.

Several hypotheses on the determinism of larval fish survival emphasize the advantage provided by fast growth and a large size (see Robert et al. 2013 for a recent review). Most other traits being equal in the morphologically similar early stages of the two species, a larger size at age and at date likely provided *A. glacialis* with some survival advantage over *B. saida* from hatching to metamorphosis. The lower mortality rate of *A. glacialis* compared to *B. saida* is consistent with this interpretation. As predicted by the r/K selection theory, a more stable and predictable food source (in the form of small cyclopoid nauplii) could be a key ingredient allowing *A. glacialis* to persist as a species by producing fewer and larger larvae than *B. saida*. The validation of this hypothesis awaits the high-resolution sampling of the vertical co-distribution of larval gadids and their microzooplankton prey under the ice in winter–spring (using, for example, the methodology of Ponton and Fortier 1992), and the analysis of their isotopic composition to assess the relative importance of ice algae and phytoplankton in the food of their main copepod prey (e.g. Hobson et al. 2002; Pineault et al. 2013).

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