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ARTICLE

West Greenland ichthyoplankton and how melting glaciers could allow Arctic cod larvae to survive extreme summer temperatures

Caroline Bouchard, Agathe Charbogne, Fabienne Baumgartner, and Sarah M. Maes

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Abstract: Climate change is rapidly modifying marine fish assemblages in the Arctic. As fish eggs and larvae have a narrower thermal tolerance than nonreproductive adults, their response to increasing temperatures is likely one of the main drivers of these changes. In this study, we described ichthyoplankton assemblages in West Greenland between 62 and 73 °N, during summers 2017–2019, and investigated the relationship between sea surface temperature in the spring and summer and the survival of Arctic cod (*Boreogadus saida* (Lepechin, 1774)) early life stages over the hatching season. Warm years were associated with partial recruitment failures resulting from thermal stress to the eggs and larvae hatched late in the season. Using past environmental conditions, we forecasted an imminent decline in Arctic cod recruitment in the regions of Uummannaq and Disko Bay. Observations from fjords suggested that glacial meltwater could create a subsurface thermal refuge allowing Arctic cod larvae to survive despite very high summer sea surface temperature (ca. 10 °C). As the Greenland ice sheet is melting at an unprecedented speed, the mechanism underlying the "glacial meltwater summer refuge hypothesis" could curb some of the negative effects of ocean warming on the survival of young Arctic cod in West Greenland and other Arctic fjord systems.

Key words: early life stages, polar cod, *Boreogadus saida*, fjords, recruitment.

Résumé : Le changement climatique modifie rapidement les assemblages de poissons marins dans l'Arctique. Comme les œufs et les larves de poissons ont une tolérance thermique plus étroite que les adultes non reproducteurs, leur réaction à l'augmentation des températures est probablement l'un des principaux facteurs de ces changements. Dans cette étude, nous avons décrit des assemblages ichtyoplanctoniques dans l'ouest du Groenland entre 62° et 73° N, durant les étés 2017 à 2019, et nous avons étudié la relation entre la température de la surface de la mer au printemps et en été et la survie de la morue arctique (*Boreogadus saida* (Lepechin, 1774)). Les années chaudes ont été associées à des échecs de recrutement partiels résultant d'un stress thermique causé aux œufs et aux larves écloses tard en saison. En utilisant les conditions environnementales passées, nous prévoyons un déclin imminent du recrutement de la morue arctique dans les régions d'Uummannaq et de la baie de Disko. Les observations des fjords suggèrent que l'eau de fonte glaciaire pourrait créer un refuge thermique de sous-surface permettant aux larves de morues arctiques de survivre malgré une température estivale très élevée de surface de la mer (environ 10 °C). Comme l'inlandsis du Groenland fond à une vitesse sans précédent, le mécanisme

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sous-jacent à l'hypothèse de refuge estival des eaux de fonte glaciaire pourrait atténuer certains des effets négatifs du réchauffement océanique sur la survie des jeunes morues arctiques dans l'ouest du Groenland et dans d'autres systèmes de fjord de l'Arctique. [Traduit par la Rédaction]

Mots-clés : premiers stades de la vie, morue polaire, *Boreogadus saida*, fjords, recrutement.

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Introduction

The borealization of fish communities has been documented in many regions around the Arctic, especially in transition zones between the Arctic and the subarctic such as West Greenland. In some cases, the evidence came from direct observations (e.g., Ingvaldsen and Gjøsæter 2013; Fossheim et al. 2015), and in other cases from changes in the diet of seabirds (e.g., Gaston et al. 2003; Vihtakari et al. 2018) or marine mammals (e.g., Chambellant et al. 2013; Loseto et al. 2018). Larval fish surveys can also allow scientists to detect the introduction of new species in Arctic ecosystems, and have been used notably in documenting the arrival and successful reproduction of Pacific sand lance (*Ammodytes hexapterus* Pallas, 1814) in the Beaufort Sea and the Canadian Arctic Archipelago (Suzuki et al. 2015; Falardeau et al. 2017). Arctic cod (*Boreogadus saida* (Lepechin, 1774)) is a key species in Arctic marine food webs. Its replacement by boreal forage fish such as the capelin (*Mallotus villosus* (Müller, 1776)) and the sand lance (*Ammodytes* spp.) has been observed in the Barents Sea and Hudson Bay (Gaston et al. 2003; Hop and Gjøsæter 2013) and is anticipated for other seas (e.g., Berge et al. 2015; Wisz et al. 2015; Haug et al. 2017). Such replacements often have negative effects on Arctic predators. For example in marine mammals and seabirds consuming primarily Arctic cod, a shift to boreal forage fish has been linked to decreased body condition (Harwood et al. 2015). In West Greenland, many species preying on Arctic cod are culturally or economically important, and a decline in Arctic cod populations could have important socio-economic implications.

Arctic cod is highly adapted to the extreme conditions of Arctic seas. Documented adaptations include the production of antifreeze proteins (Osuga and Feeney 1978; Enevoldsen et al. 2003), spiny bony plates protecting the skin from sharp ice edges (Evseenko and Bolshakova 2020) and euryhaline larvae able to tolerate important salinity fluctuations associated with ice melt and freshwater discharge (Doroshev and Aronovich 1974; Spencer et al. 2020). The species' long hatching season (up to 7 months) is seen as an adaptation to maximize annual recruitment in an environment characterized by high interannual variations in the timing of sea-ice breakup, microalgal blooms, and secondary production (Fortier et al. 2006; Bouchard and Fortier 2008, 2011). Despite being an Arctic hyper-specialist, cold waters, long sea-ice seasons, and low zooplankton densities in the northernmost parts of its range often limit larval feeding success, growth, and survival (Fortier et al. 2006; Bouchard and Fortier 2008, 2011; Bouchard et al. 2017; LeBlanc et al. 2020). In the Canadian Arctic, warmer sea surface temperature (SST), earlier ice breakup, and their positive effects on zooplankton densities, have been linked with higher Arctic cod recruitment (Bouchard et al. 2017; LeBlanc et al. 2020). Hence, in High Arctic seas, Arctic cod populations could benefit from climate change in the short and medium term (Bouchard et al. 2017; Steiner et al. 2019; LeBlanc et al. 2020). However, in Low Arctic and subarctic seas, Arctic cod recruitment and abundance are declining or expected to decline in the near future mainly in response to increasing temperatures (Drost et al. 2016; CAFF 2017; Huserbråten et al. 2019; Marsh and Mueter 2020).

In addition to the direct effect of temperature, many factors could contribute to declining feeding success, growth, and survival of Arctic cod early life stages in the future. Arctic cod spawn in the winter; hence, the positively buoyant eggs generally develop under

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the sea ice (Aronovich et al. 1975; Spencer et al. 2020). With current and future sea-ice cover declines, exposure to UV radiation could damage the highly sunlight-sensitive, unpigmented Arctic cod eggs floating at the sea surface (Altukhov 1981; Christiansen 2017; Spencer et al. 2020). Very early sea-ice breakup could decrease the quantity of zooplankton prey available for Arctic cod larvae (Leu et al. 2011; LeBlanc et al. 2020). Furthermore, the quality of the food available to the larvae could decrease, both in terms of taxonomic and lipid composition (Bouchard and Fortier 2020; Copeman et al. 2020). In High Arctic seas, the large, lipid-rich copepod *Calanus glacialis* Jaschnov, 1955 is the preferred prey and main source of carbon for larval and juvenile Arctic cod (Bouchard and Fortier 2020). However in many regions, *C. glacialis* is being replaced by *Calanus finmarchicus* (Gunner, 1765), a small, relatively lipid-poor North Atlantic species (Aarflot et al. 2017; Møller and Nielsen 2020). Whether young Arctic cod can shift their diet from *C. glacialis* to *C. finmarchicus* without impairing the accumulation of sufficient lipids before the winter, a key determinant of the overwinter survival of age-0 Arctic cod (L. Copeman, Oregon State University, unpublished data, 2020), remains to be assessed, but the switch is expected to be detrimental (Bouchard and Fortier 2020).

Eastern Baffin Bay and the coastal waters of West Greenland are changing rapidly. On the West Greenland shelf, mean SST increased by 0.73 °C between 1982 and 2006 (Belkin 2009). In Disko Bay, increased inflow of North Atlantic water propagating along the coast from the south resulted in a sudden change in bottom temperature in 1997, with the long-term average increasing from 1.30 °C to 2.25 °C (Hansen et al. 2012). In recent decades, the region experienced an important decrease in sea-ice cover (Canadian Ice Service 2020) and an increase in glacier discharge with diverse effects on primary production and other ecosystem components (e.g., Ji et al. 2013; Hopwood et al. 2020). These climate-driven changes are certainly affecting, and will continue to affect West Greenland fish populations, especially spawning adults and eggs, the stages most vulnerable to climate change (Dahlke et al. 2020). Understanding and forecasting the response of fish populations to these different changes is crucial for the national economy of Greenland, which depends, aside from the Danish block grant, almost exclusively on fisheries (Greenland Economic Council 2019).

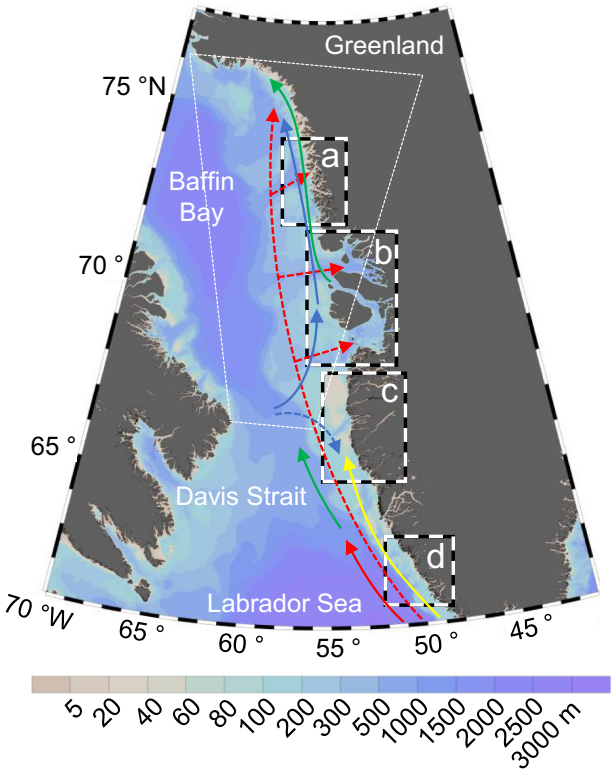
In the present study, we first document the composition and distribution of larval fish assemblages in West Greenland during the summers of 2017 to 2019 across a >11° latitudinal range. We then use monthly mean SST in region-years with Arctic cod catches to estimate hatch parameters from published temperature-dependent regression models, and to depict how SST may have affected the eggs and larvae over the hatching season. We also use past environmental conditions (SST and sea-ice breakup date) in three regions to speculate on the future of Arctic cod recruitment in Northwest Greenland. Lastly, we describe a mechanism (the glacial meltwater summer refuge hypothesis) occurring in some stratified fjord environments where Arctic cod early-stage larvae are neutrally buoyant in subsurface waters, hence benefitting from a thermal refuge against the extreme temperatures attained in the surface layer in the summer.

Materials and Methods

Study area

The waters off West Greenland consist of the deep basins of Baffin Bay, Davis Strait, and the Labrador Sea, a 40–250 km wide continental shelf characterized by a number of shallow banks intersected by deep channels and numerous fjord systems receiving glacial meltwater from the Greenland ice sheet (Fig. 1). Three major water masses characterize the region (Rysgaard et al. 2020): (1) the Baffin Bay Polar Water, a cold water occurring on the continental slope north of Davis Strait, with a diluted version occurring on the

Fig. 1. Bathymetric map of West Greenland indicating the regions studied in Upernavik (*a*), Uummannaq and Disko Bay (*b*), Central Greenland (*c*), and South Greenland (*d*). The white trapezoid shape indicates the Canadian Ice Service (2020) defined area in East Baffin Bay used to document remotely sensed sea-ice concentration. The arrows represent the distribution of water masses and circulation system described by Rysgaard et al. (2020), showing the warm upper Subpolar Mode Water (uSPMW, red line) associated with the West Greenland Current; the deep Subpolar Mode Water (dSPMW, dotted red line); the cold Baffin Bay Polar Water (BBPW, blue lines); the southward transport of BBPW (broken blue line); the Southwest Greenland Coastal Water (CW, yellow line); and the "diluted water" (green lines). The map was created using Ocean Data View software version 4.7.10 (Schlitzer 2020).



continental shelf, and a potential branch flowing southward; (2) the Southwest Greenland Coastal Water, a thick layer of cold and fresh water overlain by a seasonally heated surface layer, and flowing northward along the southern coast as part of the Greenland Coastal Current, up to Davis Strait, where its progression is blocked by the colder, more saline Baffin Bay Polar Water; and (3) the Subpolar Mode Water, originating from the Atlantic and part of the West Greenland Current flowing over the continental slope. Only the deep component of the Subpolar Mode Water (dSPMW), continues northward passed Davis Strait. From there, the dSPMW enters the coast via deep troughs such as the Upernavik Icefjord, the Uummannaq Fjord, and Disko Bay (Fig. 1; Rysgaard et al. 2020 and references therein). Around Upernavik Icefjord, in the Uummannaq Fjord system and in Disko Bay, the runoff from large glaciers and the melting of sea ice create a 20–30 m deep, low-salinity surface layer during the summer. The resulting high stratification combined with solar heating causes these surface waters to warm considerably over the summer season.

The northern part (>68 °N) of the West Greenland shelf typically freezes up between November and December. The ice breakup starts in early spring in the south, and

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progresses northward during the summer until the entire area becomes ice-free by late July–August. The southern part of the shelf (<68 °N) typically remains ice-free all year round.

Field sampling

Physical and biological sampling was conducted in West Greenland in July and August in 2017 and 2018 on board the RV *Sanna*, and on board the SV *ATKA* and the CCGS *Amundsen* in 2019. The sampling took place in Disko Bay and the Uummannaq Fjord system (hereafter referred to as Uummannaq), in 2017 and 2018 respectively, and in coastal waters and fjords covering a latitudinal gradient from ~73 °N to ~62 °N, including a region around the town of Upernavik (hereafter referred to as Upernavik), Disko Bay, and Uummannaq, in 2019 (Fig. 1). Vertical profiles of temperature and salinity were obtained with a Seabird SBE19plus CTD on board the *Sanna*, a Seabird SBE911plus CTD on board the *Amundsen*, and a RBR Concerto® CTD on board the *ATKA*. Zooplankton and ichthyoplankton were sampled using bongo nets (two 0.6 m diameter frames equipped with one 335 μm and one 500 μm mesh nets) on board the *Sanna* and *ATKA* and a double square net (two 1 m^2 frames equipped with one 500 μm and one 750 μm mesh net) on board the *Amundsen*. The samplers were equipped with General Oceanics (2017) or KC Denmark (2018–2019) flowmeters. The sampler was towed obliquely from the surface to a maximum sampling depth of ca. 100 m depth at a ship speed of 1–3 knots. In 2017 and 2018, the sampler was equipped with a Scanmar real-time depth sensor, allowing the net to reach a maximum sampling depth of 100 m precisely. In 2019, the target depth of 100 m was estimated and adjusted during each deployment using the cable length and its angle relative to the horizon, and a Star-Oddi mini-CTD attached to the sampler provided the real depth reached a posteriori.

On board the *Sanna* and *Amundsen*, all fish larvae and juveniles were enumerated and identified to the lowest taxonomic level possible, and up to 25 individuals per station and species were measured for fresh standard length (SL_f) and body depth at the anus (BD_f), and preserved individually in 96% ethanol. The remaining zooplankton samples were preserved in 4% buffered formaldehyde seawater solution. On board the *ATKA*, whole samples containing zooplankton and ichthyoplankton were preserved in 96% ethanol. Due to limited storage space on board the sailboat, some samples were split using a cylindrical zooplankton splitter and only half (or a quarter) of the sample was kept. For other logistical reasons (time constraints, limited expertise on board, and unstable platform) the larvae were not sorted from the zooplankton samples before splitting. These splits were considered in the calculation of the number of larvae collected and larval fish abundances. Back in the laboratory, all fish larvae and juveniles were sorted from the samples, enumerated and identified to the lowest taxonomic level possible, and up to 25 individuals per station and species were measured for preserved standard length (SL_p) and body depth at the anus (BD_p), and preserved individually in 96% ethanol. Larval fish abundances were calculated for each taxon by dividing the number of larvae collected in a net by the volume of water filtered during the deployment (data from the flowmeter), and averaged between the two nets for each station.

Sea-ice concentration and SST time-series

To insert our data into a longer temporal context, two independent time-series of sea-ice concentration in the study area were constructed. Satellite remote sensing of sea-ice concentration (weekly averages) from the Canadian Ice Service (2020) were used to determine the annual ice breakup week in East Baffin Bay between 1979 and 2019. Daily visual observation of sea-ice concentration from the Copenhagen University's Arctic Station in Qeqertarsuaq on the southern shore of Disko Island, averaged over 7 day periods, were used

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to determine the annual ice breakup week in Disko Bay since 1991. For both data sets, the ice breakup week was defined as the week during which ice concentration fell below 50% for the rest of the season.

Monthly SST for April, May, June, and July between 1979 and 2019 were obtained from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC) (2020) extended reconstructed global sea surface temperature database version 5 for the regions of Upernavik (72–74 °N, 54–58 °W), Uummannaq (70–72 °N, 50–56 °W) and Disko Bay (68–70 °N, 50–56 °W). These SSTs were used to construct time-series and to estimate Arctic cod hatch parameters for the region-years larvae were collected.

Genetic identification of Gadidae

The early life stages of four species of Gadidae co-occur in the study area (Andersen et al. 1994 and references therein): Arctic cod (*B. saida*), ice cod (*Arctogadus glacialis* (Peters, 1872)), Greenland cod (*Gadus ogac* Richardson, 1836), and Atlantic cod (*Gadus morhua* Linnaeus, 1758). The early life stages of *B. saida* and *A. glacialis* are virtually impossible to distinguish using external morphology and accurate species identification relies on either otolith microstructure or genetics (e.g., Madsen et al. 2009; Bouchard et al. 2013; 2016; Bouchard and Fortier 2011; Nelson et al. 2020). Furthermore, larval *B. saida*, *G. ogac* and *G. morhua* can be difficult to differentiate morphologically (Andersen et al. 1994). To distinguish between *B. saida* and *A. glacialis*, and to confirm (or rebut) our taxonomic identification of other Gadidae, 72 Gadidae collected from the *ATKA* in 2019, 28 Gadidae collected from the *Sanna* in Uummannaq in 2018 and 14 Gadidae collected from the *Amundsen* in Uummannaq and Disko Bay in 2019, and representing the range of stations and standard length, were selected for species identification by genetics using a fragment of the cytochrome C oxidase subunit I (COI) gene in the mitochondrial genome (DNA barcoding). A small piece of tissue was cut from each selected individual, put in ethanol 97%, and sent to the Laboratory of Biodiversity and Evolutionary Genomics of the KU Leuven, Belgium. There, DNA was extracted from the samples using the NucleoSpin Tissue kit following the standard protocol for human or animal tissue and cultured cell purification according to manufacturer's instructions (Macherey-Nagel, Germany). The PCR mix for COI amplification contained 12.5 μL MyTaq HS 2X Mix (Bioline), 10.5 μL nuclease-free H_2O (Sigma-Aldrich), 1 μL primermix (20 μM of each primer) and 1 μL template DNA. The following primers were used: FishCOILBC-TCAACYAATCAYAAAGATATYGGCAC and FishCOIHBC-deg-ACTTCYGGGTGRCCRAARAATCA (Handy et al. 2011). PCR conditions consisted of 1 min initial denaturation at 95 °C, followed by 35 cycles of 15 s at 95 °C, 15 s at 55 °C, 10 s at 72 °C, and a final elongation of 5 min at 72 °C. Negative controls were included in all PCR runs to detect cross-contamination. PCR amplicons were purified with CleanPCR magnetic beads (CleanNA, GC Biotech B.V.) using a 0.8 beads to PCR product ratio. Purified amplicons were prepared for Sanger sequencing using the BigDye Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific). The sequencing reaction mix included 1.5 μL BigDye 5X Sequencing Buffer, 1 μL BigDye Terminator v3.1 Ready Reaction Mix, 1 μL primermix (3.2 μM primer FishCOIHBC-deg-ACTTCYGGGTGRCCRAARAATCA), 4.5 μL H_2O, and 2 μL purified PCR amplicon. PCR conditions consisted of 1 min initial denaturation at 95 °C, followed by 25 cycles of 10 s at 95 °C, 5 s at 50 °C, and 4 min final elongation at 60 °C. PCR products were purified using CleanDTR magnetic beads (CleanNA, GC Biotech B.V.). Sequencing took place on 3500 Genetic Analyzer (Applied Biosystems) at the Genomics Core, UZ – KU Leuven, Belgium. The sequences were edited manually using Geneious Prime 2019.1.3 (http://www.geneious.com, Kearse et al. 2012). Terminal regions with ambiguous base pair calls were deleted. The sequences were submitted to the BOLD

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Identification System for COI and the BLAST search tool in GenBank for species-level identification (Altschul et al. 1990; Ratnasingham and Hebert 2007). Sequences have been deposited in GenBank (accession numbers MT933069-MT933177).

Estimation of Arctic cod depth

For each station, the depth of Arctic cod larvae in the water column were estimated from CTD profiles, assuming a specific density of 1.024 $g \cdot cm^{-3}$, as measured from larvae aged 0–14 days in the laboratory (Spencer et al. 2020), and assuming no directional swimming behavior modified significantly the vertical position of the larvae in the water column. Stations with surface (0–5 m) density (σ_t) > 1.024 $g \cdot cm^{-3}$ were described as having low influence of freshwater (LF), whereas stations with surface $\sigma_t < 1.024$ $g \cdot cm^{-3}$ were identified as highly influenced by freshwater (HF). At LF stations, the larvae were considered to be at the surface (0 m), whereas at HF stations, the larvae were considered to be at the depth where $\sigma_t = 1.024$ $g \cdot cm^{-3}$.

Estimation of Arctic cod hatch date frequency distributions

To account for shrinkage after ethanol preservation in 2019, SL_f of each Arctic cod larvae was back-calculated from its SL_p using a regression calculated from larval Arctic cod collected in the Beaufort Sea in 2008 ($SL_f = 1.025SL_p + 1.097$; $n = 290$, $r^2 = 0.957$ for SL between 5 and 20 mm). Age and hatch date of individual Arctic cod were estimated from their length and capture date, assuming a size-at-hatch of 5.0 mm and a growth rate of 0.22 $mm \cdot day^{-1}$ (Bouchard and Fortier 2011; Bouchard et al. 2016). For each region-year with Arctic cod catches (except Upernavik 2019, as only one individual was caught), uncorrected hatch date frequency distributions (HFDs) were determined by tallying the number of fish hatched in each 7 day bin. In uncorrected HFDs, older larvae are under-represented relative to younger larvae as they have experienced mortality and dispersion for a longer period (Yoklavich and Bailey 1990; Campana and Jones 1992; Fortier and Quiñonez-Velazquez 1998). A mortality rate was estimated from the slope of the descending limb of the catch-at-estimated-age curve (e.g., Fortier et al. 2006), using the data from Uummannaq 2019, the only region-year with a sufficient number of individuals to obtain a reliable mortality rate. Based on this rate, 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. Different HFDs were built for LF and HF stations.

Results

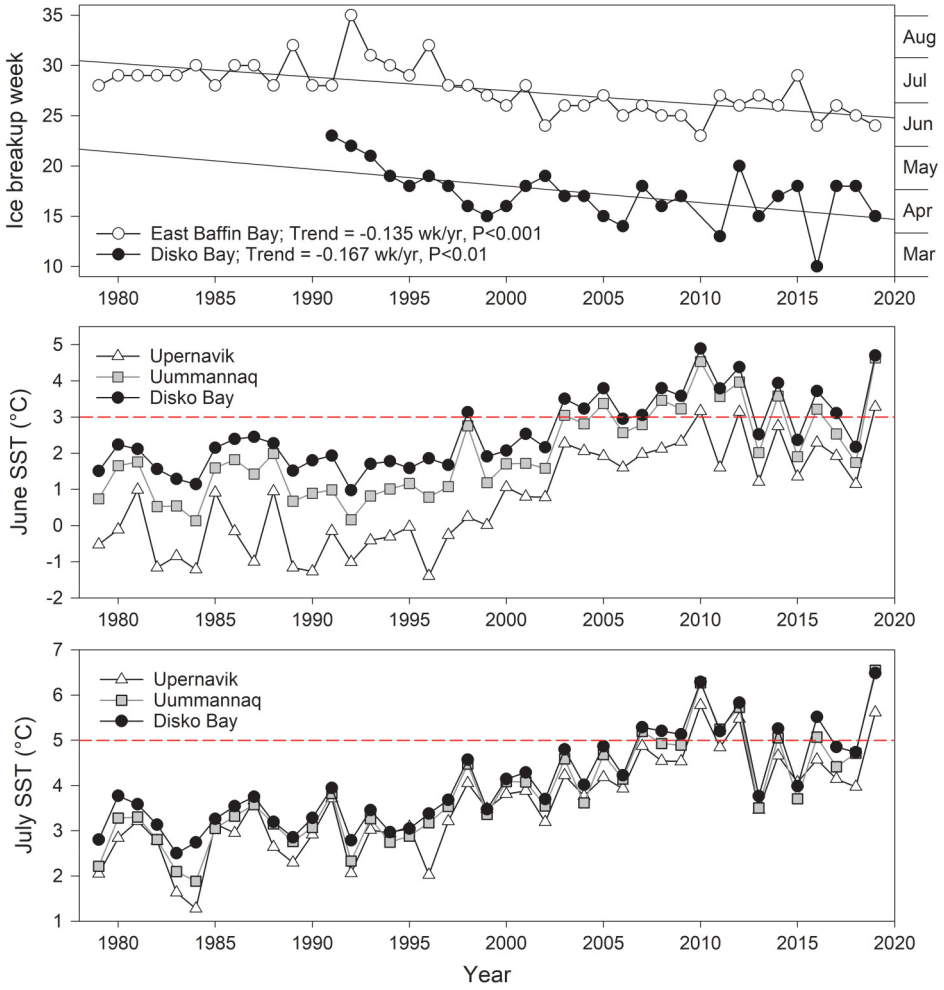
Timing of sea-ice breakup and summer SST

Long-term trends towards earlier sea-ice breakup were observed using satellite data in East Baffin Bay and shore-based observation in Disko Bay (Fig. 2). In East Baffin Bay, the ice breakup occurred between early June and the end of August (weeks 23–35) and declined at a rate of 0.9 day per year since 1979. In 2017, 2018, and 2019, the breakup in East Baffin Bay occurred in June, at week 26, 25, and 24, respectively. In Disko Bay, the breakup occurred between early March and early June (weeks 10–23) and declined at a rate of 1.3 day per year since 1991. In 2017 and 2018, the breakup in Disko Bay occurred in late April (week 15), whereas in 2019, it occurred in early April (week 18).

Between 1979 and 2019, April SST remained below 0 °C in the three regions studied, whereas May SST remained negative for Upernavik, varied between −1.58 °C and 1.62 °C in Uummannaq and between −1.26 °C and 2.13 °C in Disko Bay (data not shown). Before the mid-1990s, June SST averaged −0.38 °C in Upernavik, 1.05 °C in Uummannaq, and 1.79 °C in Disko Bay (averages 1979–1995; Fig. 2). Since then, increasing trends towards

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Fig. 2. Time-series of ice breakup week in East Baffin Bay and Disko Bay (top panel), and average sea surface temperature (SST) of three West Greenland regions in June (middle panel) and July (bottom panel). No data point exists for sea ice in Disko Bay in 2010 as ice concentration remained ≤10% the entire year. Dashed red lines indicate the temperature considered the upper thermal tolerance of Arctic cod during the egg (middle panel, 3 °C) and early larval stages (bottom panel, 5 °C).



warmer surface waters in June were observed in the three regions. June 2019 was particularly warm, with SST records attained in Upernavik (3.28 °C) and Uummannaq (4.63 °C), and a value of 4.70 °C reached in Disko Bay, the second-highest on record behind 2010 (4.89 °C; Fig. 2).

Over the period 1979–1995, July SST averaged 2.72 °C in Upernavik, 2.92 °C in Uummannaq, and 3.21 °C in Disko Bay (Fig. 2). Similar to the June SST, warming trends were observed for July in the three regions thereafter, with 2019 the warmest year on record for Uummannaq (6.54 °C) and Disko Bay (6.48 °C), and a temperature of 5.61 °C attained in Upernavik, close to the 5.77 °C record of 2010 (Fig. 2).

Genetic identification and spatial occurrence of Gadidae

DNA was successfully extracted from all selected samples, and the COI gene successfully amplified and sequenced for 112 of the 114 larvae. For fish larvae not identified genetically,

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the taxonomic identification was retained in further analyses, except for two larvae collected at a station in Upernavik where all nine specimens analysed had COI sequences corresponding to *G. morhua*; the two other Gadidae from this station were assumed to be *G. morhua*. Among the Gadidae collected in Upernavik, 7% were identified as *B. saida*, 20% as *A. glacialis*, and 73% as *G. morhua* (Fig. 3). The Upernavik Gadidae had different lengths and were segregated by station, with *B. saida* ($SL_p = 7.7$ mm, $n = 1$) found at a single station in the northern part of the region, *A. glacialis* ($SL_p = 17.0 \pm 2.1$ mm) at one relatively offshore station and one station in Eqalugaarsuit Sulluat (a fjord in the southern part of the region), and *G. morhua* (SL_p: 6.2 ± 1.1 mm) at one station in Eqalugaarsuit Sulluat (Fig. 3). All samples from Uummannaq and Disko Bay collected in 2018 and 2019 had COI sequences corresponding to *B. saida*. The only Gadidae collected from the Central and South regions was genetically identified as *G. morhua* (Fig. 3).

Ichthyoplankton composition and distribution

Larval fish assemblages varied over the latitudinal range covered. In the northernmost region of Upernavik, capelin (*M. villosus*) numerically dominated the assemblages with 77% of the catches (Table 1, Fig. 3). In the next region south, Uummannaq, Arctic cod dominated the assemblages with 39% and 51% of the catches in 2018 and 2019, respectively. In the adjacent Disko Bay, the assemblages were dominated by capelin in 2017 (40%) and sand lance (*Ammodytes* spp.) in 2019 (73%). Arctic cod represented 3% and 5% of Disko Bay catches in 2017 and 2019, respectively. In Central and South Greenland, capelin accounted for 98% of larval fish catches (Fig. 3). In total, fifteen species belonging to nine families were identified (Table 1). Arctic shanny (*Stichaeus punctatus* (Fabricius, 1780)) and daubed shanny (*Leptoclinus maculatus* (Fries, 1838)) were relatively abundant in Upernavik, Uummannaq, and Disko Bay, whereas sand lance was absent from Upernavik, relatively rare in Uummannaq, and abundant in Disko Bay (Table 1, Fig. 4).

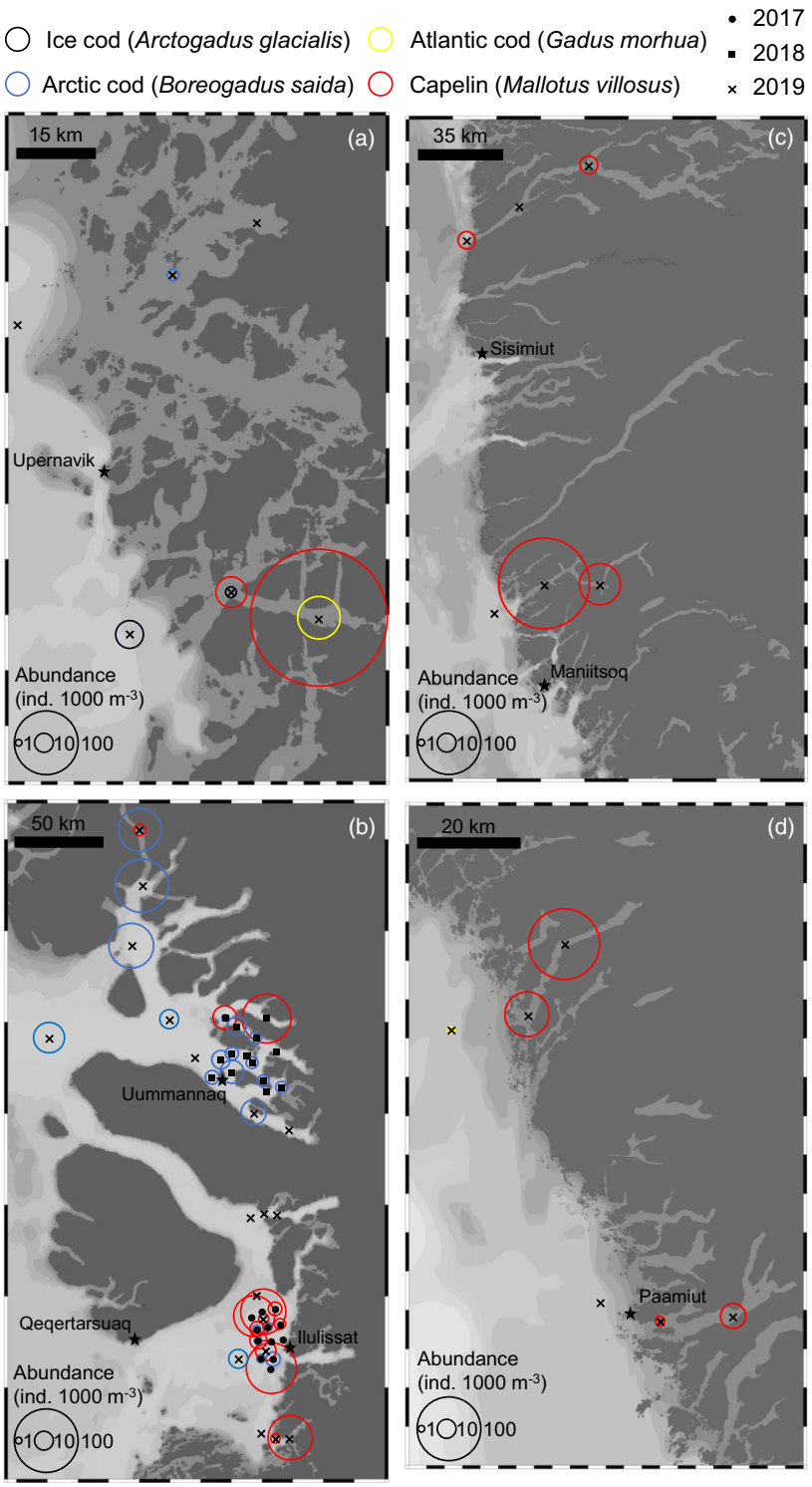
Vertical position of Arctic cod in stratified fjord environments

When present, Arctic cod larvae were more abundant at stations highly influenced by freshwater (HF, surface $\sigma_t < 1.024$ g·cm^{-3}) than at stations with no or little freshwater influence (LF, surface $\sigma_t > 1.024$ g·cm^{-3}; $median_{LF} = 3.5$ individuals (ind.) 1000 m^{-3}, $median_{HF} = 47.8$ ind. 1000 m^{-3}, Mann–Whitney $U = 1.0$, $n_{LF} = 17$, $n_{HF} = 4$, $p = 0.004$ two-tailed). Arctic cod larvae were found at stations with surface (0–5 m) temperature ranging from 3.1 to 10.3 °C and surface salinity ranging from 22.1 to 33.1. At most stations (17 of 21), the density of surface water exceeded the density of larval Arctic cod as determined in the laboratory for larvae aged 0–14 days (1.024 g·cm^{-3}, Spencer et al. 2020). Hence, at these stations, larval Arctic cod were most likely in the surface waters with SST ranging from 3.5 to 9.4 °C and surface salinity ranging from 30.6 to 33.1 (Fig. 5). Age-0 Arctic cod were in relatively low abundance at these stations (between 1 and 26 ind. m^{-3}; Fig. 5). At four stations influenced by freshwater discharge from the Greenland ice sheet (salinities 0–5 m = 22.1–29.5), Arctic cod larvae were most likely in water slightly below the surface, at a depth where the water density (σ_t) reached 1.024 g·cm^{-3} (2.4–10.3 m). The temperature at the depth where $\sigma_t = 1.024$ g·cm^{-3} for these stations, ranged from 2.6 to 6.5 °C (Fig. 5). The majority of age-0 Arctic cod were collected in these freshwater-influenced areas (maximum of 70 ind. m^{-3} at temperature of 4.1 °C), in Uummannaq in 2019 (Fig. 3).

Arctic cod hatch date frequency distributions

The standard length of the 169 Arctic cod collected ranged from 5.5 to 27.6 mm (Table 2). A mortality rate of 4.8%·day^{-1} was estimated from the 94 individuals collected in Uummannaq in 2019 (Fig. 6) and applied to the HFDs to correct for mortality-dispersion (Fig. 7). In Disko Bay in 2017 and 2019, two very warm years in the region, most fish collected

Fig. 3. Spatial occurrence of age-0 ice cod (*Arctogadus glacialis*, black), Arctic cod (*Boreogadus saida*, blue), Atlantic cod (*Gadus morhua*, yellow) and capelin (*Mallotus villosus*, red) in Upernavik area (*a*), Uummannaq Fjord system and Disko Bay (*b*), Central West Greenland (*c*) and South West Greenland (*d*), in 2017 (circles in Disko Bay), 2018 (squares in Uummannaq Fjord system) and 2019 (x-marks). The maps were created using Ocean Data View software version 4.7.10 (Schlitzer 2020).



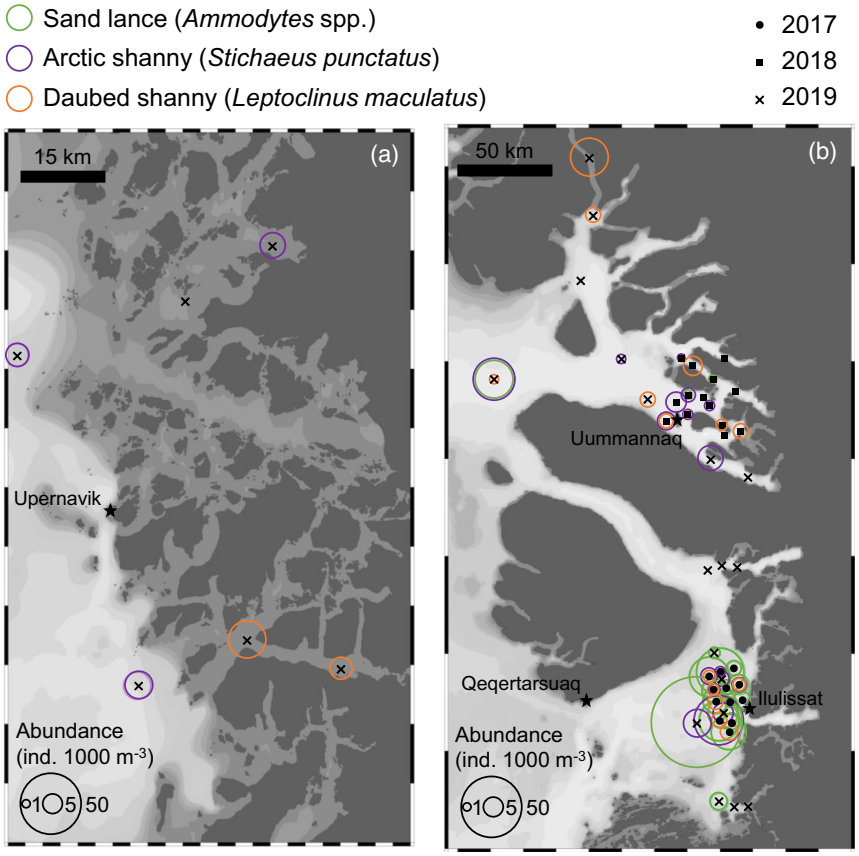
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Table 1. Summary of ichthyoplankton caught in five regions of West Greenland in July–August between 2017 and 2019. The numbers of individuals caught are the numbers estimated before the split of some samples in 2019.

Year	2017	2018	2019				
Dates	6–11 July	21 July–1 August	13–17 July	9–12 July	5–30 July	6–11 August	19–25 August
Region	Disko Bay	Uummannaq	Upernavik	Uummannaq	Disko Bay	Central	South
Number of tows	12	14	6	8	10	6	6
Number of individuals caught	210	155	244	204	223	196	130
Mean Density (ind. 1000 m^{-3})	31	12	110	43	23	56	42
Maximum Density (ind. 1000 m^{-3})							
Osmeridae							
Mallotus villosus	97	56	471	3	46	256	159
Gadidae							
Arctogadus glacialis	0	0	19	0	0	0	0
Boreogadus saida	6	14	4	70	0	0	0
Gadus morhua	0	0	49	0	0	0	2
Cottidae							
Myoxocephalus scorpius	0	2	8	6	0	0	0
Triglops nybelini	0	1	0	16	4	0	0
Cyclopteridae							
Cyclopterus lumpus	0	0	0	0	0	3	0
Liparidae							
Liparis fabricii	3	4	0	2	0	0	0
Liparis gibbus	0	0	0	0	0	0	2
Stichaeidae							
Leptoclinus maculatus	5	4	20	30	0	0	0
Lumpenus lampretaeformis	0	1	0	0	0	0	0
Stichaeus punctatus	35	6	10	26	12	0	0
Anarhichadidae							
Anarhichas sp.	0	0	0	0	1	0	0
Ammodytidae							
Ammodytes spp.	32	1	0	21	114	0	0
Pleuronectidae							
Hippoglossoides platessoides	3	0	20	0	0	4	0

Fig. 4. Spatial occurrence of age-0 sand lance (*Ammodytes* spp., green), Arctic shanny (*Stichaeus punctatus*, purple) and daubed shanny (*Leptoclinus maculatus*, orange) in Upernavik (*a*), Uummannaq and Disko Bay (*b*), in 2017 (circles in Disko Bay), 2018 (squares in Uummannaq Fjord system) and 2019 (x-marks). No individuals of these species were collected in Central and South Greenland. The maps were created using Ocean Data View software version 4.7.10 (Schlitzer 2020).



in July (the survivors of the cohort) hatched in April and May (Figs. 7*a*–7*b*). The small proportion of fish hatched in June–July 2017 suggests an extremely low survival rate among the summer hatchers that year, whereas their absence in June–July 2019 suggests null survival among summer hatchers that year (Fig. 7*a*–7*b*). In Uummannaq in 2018, a year with relatively normal SST in the region, the majority of the fish collected hatched in May–June, with some April hatching, suggesting both spring and summer hatchers composed the annual cohort (Fig. 7*c*). In Uummannaq in 2019, a very warm year in the region, the HFD of the fish collected at LF stations resembles the HFDs of Disko Bay in 2017 and 2019, with most survivors of the cohort hatched in May and an apparent low survival among June hatchers (Fig. 7*d*). The HFD of fish collected at HF stations in Uummannaq 2019 shows a peak of hatching in May, and a second peak in June (Fig. 7*d*), suggesting significant survival among both spring and summer hatchers.

Arctic cod hatch parameters

Temperature-dependent regression models based on incubation experiments (table 2 of Laurel et al. 2018), were used to depict how SST affected Arctic cod eggs and larvae over the hatching season for the four region-years with Arctic cod catches. Disko Bay 2019 was the

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Fig. 5. Abundance of age-0 Arctic cod in relation to temperature from CTD measurements at stations with Arctic cod catches. Solid symbols represent the temperature at the depth Arctic cod larvae were found according to their buoyancy determined in the laboratory (density = 1.024 g·cm^{-3}, Spencer et al. 2020): sea surface temperature (SST) for stations where surface seawater density (σ_t) exceeded 1.024 g·cm^{-3} (solid circles), and temperature at the depth where σ_t = 1.024 g·cm^{-3} for the other stations (other solid symbols, one shape per station, numbers below symbols indicate depth of σ_t = 1.024 g·cm^{-3}). Open symbols represent SST at the stations where Arctic cod larvae were below the surface waters (one shape per station, corresponding to solid symbols).

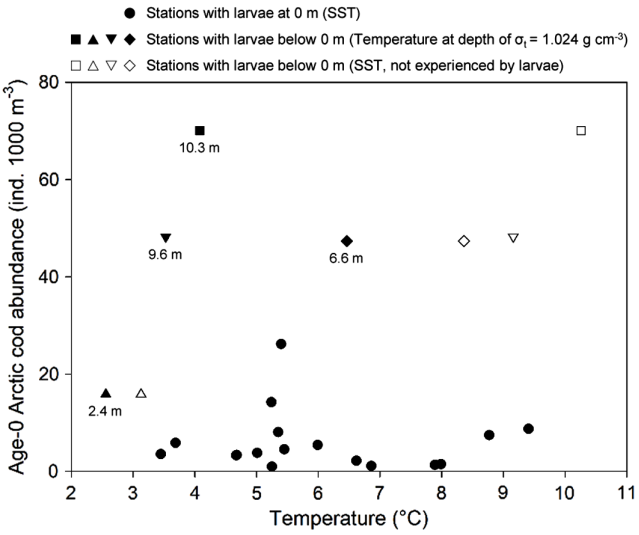


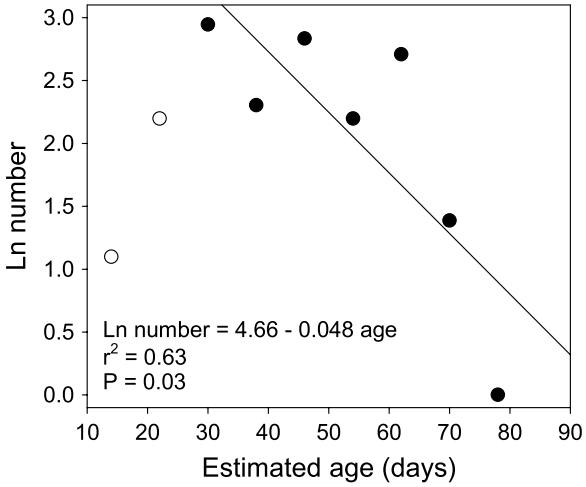
Table 2. Number of age-0 Arctic cod collected by different sampling platforms in Northwest Greenland between 2017 and 2019, and standard length (mean and range) before preservation in ethanol.

Year	Platform	Region	Number of Arctic cod collected	Number of Arctic cod measured	Standard length: mean (mm)	Standard length: range (mm)
2017	RV *Sanna*	Disko Bay	6	6	11.4	(5.5–18.9)
2018	RV *Sanna*	Uummannaq	58	58	14.4	(8.1–27.6)
2019	SV *ATKA*	Upernavik	1	1	9.0	—
		Uummannaq	58	58	13.3	(7.3–20.4)
	CCGS *Amundsen*	Disko Bay	10	10	19.1	(15.3–24.1)
		Uummannaq	36	29	16.8	(10.3–22.8)

most extreme case. At 2.13 °C, the mean SST of Disko Bay in May 2019 (Table 3), the hatching success of the eggs was 74%. According to the temperature-dependent models (Laurel et al. 2018), May hatchers were large at hatch (6.28 mm SL), and highly tolerant to starvation with 50% of the larvae dying within 40 days after hatching if not feeding (Table 3). However, very high SST in June 2019 (4.70 °C), resulted in the successful hatching of only 13% of the eggs that month (Table 3). The warm waters also resulted in the few larvae produced in June to be small at hatch (5.10 mm SL, but SST outside the temperature range modeled), and highly sensitive to starvation (time to 50% starvation: 14 days post hatch). April and May hatchers experienced a thermal history allowing them to stay below their upper thermal limit through ontogeny. By June, they had developed into early and late stage larvae and tolerated the ambient 4.70 °C; by July, many were at the juvenile stage, and able to tolerate 6.54 °C, Disko Bay SST at that time. However, June hatchers, already low in numbers after massive egg mortality, experienced the 6.54 °C of July 2019 as early larvae, a metabolically

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Fig. 6. Catch-at-estimated-age curve of age-0 Arctic cod in Uummannaq in 2019 (8 day age bins). Open circles were not used in the regressions. The slope of the regression was used to estimate the mortality rate (4.8%·day^{-1}).



challenging temperature for Arctic cod larvae at that stage, and we suspect very few survived. The HFD for that region-year matches this scenario: no June hatchers were found in Disko Bay in 2019, and the only survivors of the larval cohort were April and May hatchers (Fig. 7*a*).

In Disko Bay, May SST in 2017, and thus hatching parameters, were similar to 2019 (Table 3). June SST was warm (3.11 °C) but slightly lower than in 2019, resulting in a hatching success of 57%, larger hatch size, and larvae highly resistant to starvation (Table 3). July SST of 4.85 °C probably allowed sufficient survival among May hatchers and possible but limited survival among June hatchers. A HFD dominated by May hatchers, with a very low proportion of June and July hatchers, supports this scenario (Fig. 7*b*).

Summer SST in Northwest Greenland were relatively normal in 2018 compared to the extremely warm 2019 or the very warm 2017, hence the hatch parameters and HFD described for Uummannaq in 2018 could be seen as the normal situation for Arctic cod in the region (Table 3, Fig. 7*c*). In 2018, May hatchers had high hatching success, size-at-hatch, and were highly tolerant to starvation (Table 3). But contrary to the other region-years studied, June hatchers also had advantageous hatch parameters (hatching success: 79%, size-at-hatch: 6.42 mm SL, time to 50% starvation: 41 days post hatch) allowing high survival, and resulting in a HFD with more balanced proportions of April, May, and June hatchers (Fig. 7*c*).

The summer of 2019 was as warm in Uummannaq as in Disko Bay, and the hatch parameters were relatively similar (Table 3), concordant with the HFD for the region-year (excluding HF stations) skewed to the left and with a very low proportion of June hatchers (Fig. 7*d*). The HFD of the larvae collected at HF stations suggests that freshwater allowed a number of June hatchers to survive despite warm SST (Fig. 7*d*).

Discussion

West Greenland ichthyoplankton

The ichthyoplankton of West Greenland has been investigated very little after 1984, except in Nuup Kangerlua (Pedersen and Smidt 2000; Swalethorp et al. 2014, 2015; Topp-Jørgensen et al. 2017). To our knowledge, ichthyoplankton assemblages from

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Fig. 7. Estimated hatch date frequency distributions corrected for mortality, for Arctic cod collected in Disko Bay in 2017 (*a*) and 2019 (*b*) and in Uummannaq in 2018 (*c*) and 2019 (*d*) at stations without thermal refuge (grey) and with thermal refuge (black). The number of fish hatched in the same 7 day calendar interval in a given region-year is expressed as a percentage of the total number of fish sampled in that region-year.

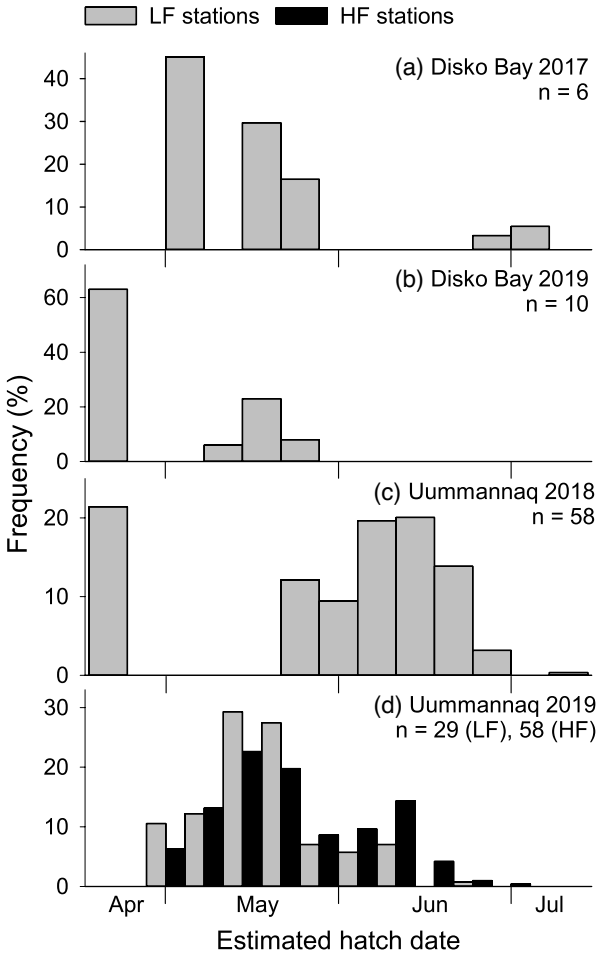


Table 3. Mean sea surface temperature (SST) in May and June for region-years with Arctic cod catches, and corresponding hatch characteristics estimated using temperature-dependent regression models based on incubation experiments (table 2 of Laurel et al. 2018).

		May				June			
Region	Year	SST (°C)	HS (%)	SH (mm)	TS (dph)	SST (°C)	HS (%)	SH (mm)	TS (dph)
Disko Bay	2017	0.38	88	6.79	45	3.11	57	5.90	35
	2019	2.13	74	6.28	40	4.70	13	*5.10*	14
Uummannaq	2018	0.24	88	6.82	46	1.74	79	6.42	41
	2019	1.62	80	6.46	41	4.63	15	*5.13*	15

Note: HS, hatching success (%); SH, size-at-hatch (mm standard length); TS, time to 50% starvation (dph, days post hatch). Numbers in italics were estimated using SST exceeding the temperature range of the model.

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Upernavik, Uummannaq, and the four fjords sampled in Central and South Greenland have not been described previously. Fish larvae, mostly capelin, were sampled from the coast near Qeqertarsuaq, Disko Island, in 2014 (Malanski et al. 2020), but the latest accounts of ichthyoplankton in central Disko Bay date from 1996 and 1997 (Munk et al. 2003, 2015).

Surprisingly, Atlantic cod dominated the Gadidae assemblages in Upernavik, the northernmost region studied, with densities 13 times higher than Arctic cod. Atlantic cod has occurred in Upernavik since at least 1920 (Jensen 1939; Drinkwater 2009) and spawning grounds have been localized in the area (Nordic Council of Ministers 2002). The presence of recently-hatched larvae (5.0–8.0 mm SL_p) confirms that the species is spawning locally. Ice cod larvae were also relatively abundant in Upernavik, and aged ca. 60–85 days, according to their size, and the mean growth rate and size-at-hatch of the species in the Beaufort Sea (Bouchard et al. 2016). Adult ice cod are often reported in Upernavik, in both summer and winter (Greenland Institute of Natural resources, unpublished data, 2020), suggesting a region potentially important for the spawning and larval retention of the species. Arctic cod larvae were present in low abundance at stations sampled in mid-July 2019. The co-occurrence of two arctic and one boreal Gadidae at the larval stage suggests that Upernavik could be an appropriate region to study competitive and predatory interactions among the three species.

The ichthyoplankton of Uummannaq in July 2018 and 2019 was composed mostly of Arctic cod and species typical of Arctic assemblages such as Arctic shanny and daubed shanny. Capelin were found mostly in the inner part of the fjords sampled, whereas sand lance were rare, except at the mouth of the Uummannaq Fjord in 2019. No Atlantic cod larvae were collected in Uummannaq, despite large numbers of adults reported in the region in July 2018 (Greenland Institute of Natural resources, unpublished data, 2020), suggesting either an absence of spawning in the region, or an advection of the larvae outside the system.

In Disko Bay, the ichthyoplankton assemblages in July 2017 and 2019 were dominated by boreal species (capelin and sand lance), whereas Arctic cod represented ≤5% of the catches. However, a direct comparison with the 1996 and 1997 ichthyoplankton assemblages reported by Munk et al. (2003; 2015) is difficult as sampling month, location, and equipment partially differed between both periods. In the June 1997 survey, Arctic cod larvae were widespread and very abundant (Munk et al. 2003). It was the most abundant of the fish larvae collected during the survey, performed with a 1 mm mesh net; hence, likely excluding potential newly hatched capelin larvae (Munk et al. 2003). The 1996 survey was performed in July, and overlapped partially with an area covered in 2017 and 2019 in front of Ilulissat (Munk et al. 2015). For this area, the larval fish assemblages were dominated by sand lance, Arctic shanny, and daubed shanny in both periods (mid-1990s vs. 2017–2019). Capelin were absent from the 1996 survey, and abundant in 2017 and 2019, but it is impossible to determine whether this difference is solely due to the different mesh sizes used (1 mm in 1996, ≤ 750 μm in 2017 and 2019). Arctic cod were collected at 100%, 42% and 10% of the stations sampled in Disko Bay in July 1996, 2017, and 2019, respectively, possibly indicating a rarefaction of the species in the region, although comparability issues preclude any clear conclusion from being drawn.

The vast majority of fish larvae collected in Central and South Greenland in August 2019 were capelin. This is consistent with the ichthyoplankton collected monthly at the mouth of Nuup Kangerlua since 2008 showing a predominance of capelin in the samples from July to October, and extremely rare catches of other species in August (Topp-Jørgensen et al. 2017; Greenland Institute of Natural Resources, unpublished data, 2020). Besides capelin, most fish larvae collected in Nuup Kangerlua in the summer and in Central and South Greenland in August 2019 belong to benthic families such as Cottidae, Liparidae,

Stichaeidae, Ammodytidae, and Pleuronectidae. A possible explanation for their absence and rarity in August catches is that all juvenile fish had already left the top 100 m of the water column during the settlement process. Another non-exclusive explanation is that some juvenile fish were present in the top 100 m in August, but not adequately sampled by bongo nets due to low abundances or swimming capability allowing them to escape the small-aperture net.

Survival of Arctic cod early life stages in a warming Northwest Greenland

Our results suggest that, except at stations highly influenced by freshwater, very few Arctic cod that hatched in June–July 2017 and 2019 in Disko Bay and Uummannaq, survived. June and July 2017 and 2019 were particularly warm in the region, and thermal stress to the eggs and early-stage larvae, resulting in null or extremely low hatching success and early survival rate among June–July hatchers, was probably the most important cause of these apparent mortalities. As shown by a meta-analysis including 694 fish species, eggs consistently have narrower thermal tolerance ranges than larvae and nonreproductive adults (Dahlke et al. 2020). Arctic cod is no exception to that rule. Under controlled laboratory conditions, Arctic cod eggs developed normally between −1.5 and 3.0 °C and their hatching success declines drastically above 3.0 °C (Sakurai et al. 1998; Laurel et al. 2018). Different rearing experiments suggest that the upper thermal limit of the early-stage larvae is around 5 °C. Sakurai et al. (1998) reported that newly hatched larvae survived longer at temperatures below 0.5 °C. Drost et al. (2016) found that above 3.3 °C, the hearts of the larvae can no longer adjust to temperature increases. Laboratories generally reared the larvae at 2.0–3.5°C to achieve high growth rate without impairing survival (e.g., Kent et al. 2016; Nahrgang et al. 2016; Koenker et al. 2018*a*, 2018*b*; B. Laurel, NOAA, personal communication, 2020). Koenker et al. (2018*b*) reported adequate growth and survival rates among early-stage larvae between −1 and 5 °C, and a sharp decline in survival at 9 °C, the next temperature treatment available for the experiment. The precise upper thermal limit is, thus, difficult to determine, but the high mortality observed among larvae reared slightly above 5 °C 4 (B. Laurel, NOAA, personal communication, 2020) suggests that 5 °C is a metabolically challenging temperature for early-stage larvae. The thermal tolerance of age-0 Arctic cod broadens considerably during ontogeny, and age-0 juveniles have been shown to tolerate temperatures up to 11 °C (Laurel et al. 2017).

In the Canadian High Arctic, early ice breakup and warmer SST from May to July increase age-0 Arctic cod biomass in August and September by allowing the survival of larvae hatched in winter and spring without impairing the survival of summer hatchers (Bouchard et al. 2017). In Northwest Greenland, earlier ice breakup and warmer SST from May to July may increase the survival of spring hatchers (which is impossible to determine with our data set), but can certainly create massive mortality among summer hatchers. The disappearance of the part of the larval cohort composed of summer hatchers in warm years likely results in lower abundance of age-0 Arctic cod at the end of the season. Such partial recruitment failures occurred in Disko Bay in 2017 and in Disko Bay and Uummannaq in 2019. All indications are that years with vernal conditions allowing a high recruitment composed of both spring (April–May) and summer (June) hatchers have become rare in Northwest Greenland (Fig. 2), and will become even rarer with climate change. Although Disko Bay SST in June exceeded the upper thermal tolerance of the eggs (3 °C) only once in the 24 years between 1979 and 2003 (in 1998), this threshold was surpassed 13 times in the following 17 years (Fig. 2). June SST in Uummannaq, albeit a little colder, has been following the same trend, exceeding 3 °C nine times in the last 17 years. July SST exceeding 5 °C, the temperature considered the upper thermal tolerance of early-stage larvae, began to appear in Disko Bay and Uummannaq in 2007, and in Upernavik in 2010, and was

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observed in eight, six, and two subsequent years in these respective regions (Fig. 2), suggesting that partial recruitment failures might occur frequently in Uummannaq and Disko Bay. In Upernavik, summer SST appears sufficiently low for Arctic cod recruitment, but other factors such as competitive or predatory interactions with other gadids may result in the area being a suboptimal nursery for the species.

The thermal tolerance of Arctic cod is the narrowest during the egg stage and also relatively narrow during the early larval stage (Sakurai et al. 1998; Drost et al. 2016; Laurel et al. 2018; Laurel et al. 2017; Koenker et al. 2018*a*, 2018*b*). We anticipate a decline in Arctic cod recruitment in Northwest Greenland as a response, primarily, to the lethal effect of water temperature above the upper tolerance limit of the eggs and, secondarily, to the thermal stress on the early-stage larvae. Earlier spawning in response to a warmer temperature could result in a smaller proportion of eggs experiencing high June SST, and thus counterbalance massive egg mortality in warm years. However, the temperature of the dSPMW, where we suspect Arctic cod to spawn (in relatively warm water of an Atlantic origin, as in the Beaufort Sea; Geoffroy et al. 2011), showed very low interannual variability (Rysgaard et al. 2020), suggesting that time of spawning remained stable in recent years. Faster embryonic development in response to a warmer temperature could result in an earlier hatching season and similarly counterbalance some of the mortality associated with warm summer SST experienced during the egg and early larval stages. April SST in Ummannanaq and Disko Bay between 2017 and 2019 (from −1.45 to −0.28 °C) would result (using the regression of Laurel et al. (2018) acknowledging that the lowest temperature is outside the range modelled), in incubation time between 64 and 80 days, making a relatively small difference in the hatching season.

Other contributing factors could however accelerate the decline in the recruitment of Arctic cod in Northwest Greenland. The scarcity of adequate prey may limit the feeding success of the larvae. In Disko Bay, the prey on which Arctic cod larvae depend the most, *C. glacialis* (Bouchard and Fortier 2020), has been gradually replaced by the smaller and less lipid-rich *C. finmarchicus* (Møller and Nielsen 2020). Additionally, an early ice breakup can trigger early algal bloom disconnecting herbivorous zooplankton from its prey, and leading to low abundance of *Calanus* copepods, as suggested for European Arctic shelf seas (Leu et al. 2011) and observed in the Canadian Arctic (LeBlanc et al. 2020) and in the Bering Sea (Hunt and Stabeno 2002). Arctic cod larvae <25 mm SL (the length of the vast majority of the individuals collected in the present study), prey preferentially on and source most of their carbon from *Calanus* spp. nauplii (Bouchard and Fortier 2020). The high abundance of *Calanus* spp. nauplii (up to 35 392 ind. m^{-2} in the top 100 m) and large size of the specimens (mean ± SD: 526 ± 79 μm carapace length) in Disko Bay in July 2017, estimated from stratified zooplankton samples collected on board the RV *Sanna* during the ichthyoplankton survey (K. Arendt, University of Copenhagen, unpublished data, 2020), suggest a sufficient quantity of adequate prey for Arctic cod larvae during a year of relatively late ice breakup (late April). Unfortunately, data are only available for this region-year and it is, therefore, impossible to verify whether low prey abundance and the dominance of lipid-poor species have limited the feeding success and survival of larval Arctic cod in the other region-years studied. The high metabolic rates of larval Arctic cod in warm waters (5 °C) make them highly sensitive (in terms of condition as measured by morphology or lipid storage) to low food availability (Koenker et al. 2018*a*), which could result in highly challenging conditions if early ice breakup and warm summer SST, in addition to directly impacting larval survival, decrease the abundance of prey available to the larvae. Finally, as suggested for other seas (Christiansen 2017; Spencer et al. 2020), a very early ice breakup could expose the buoyant and transparent Arctic cod eggs to damaging UV radiation.

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The glacial meltwater summer refuge hypothesis

Considering that June and July 2019 were as warm in Uummannaq as in Disko Bay, it is highly surprising that the highest Arctic cod abundances were found in Uummannaq that year. A possible explanation for this apparent contradiction comes from the fact that most Arctic cod larvae collected in Uummannaq in 2019 were found in Ukkusissat Fjord, a region highly influenced by freshwater. July SST in Ukkusissat Fjord was warmer (average temperature 0–5 m from CTD = 8.4–10.3 °C on 11–12 July) than the surrounding coastal waters (6.54 °C July average for Uummannaq region), but the lower salinity of the meltwater-influenced surface waters suggests that Arctic cod larvae were not found at the surface but in the colder waters slightly below it. Hence, instead of experiencing the life-threatening 8.4–10.3 °C of the surface waters, the larvae were at 7–10 m, in a thermal refuge formed of waters 3.5–6.5 °C (salinities = 30.0–30.5).

No glacial meltwater summer refuge suitable for Arctic cod were found in either Upernavik or Disko Bay. In Disko Bay, all stations had low influence of freshwater (salinities 0–5 m = 29.8–32.6; temperatures 0–5 m = 1.3–10.6 °C). In Upernavik, five of the stations had low influence of freshwater (salinities 0–5 m = 30.4–32.6; temperatures 0–5 m = 3.3–7.5 °C). One station, located in the inner part of Eqalugaarsuit Sulluat south of Upernavik, had high influence of freshwater (20.0) and hence could have represented a thermal refuge from the 9.5 °C of the surface water. However, the temperature at the depth where larval density equilibrates the seawater density ($\sigma_t = 1.024$ g·cm^{-3} = 4 m) was 8.0 °C, beyond the thermal tolerance of larval Arctic cod (Koenker et al. 2018*b*). These oceanographic conditions, unfavorable for Arctic cod, are optimal for Atlantic cod and capelin larvae (e.g., Otterlei et al. 1999; Nissling 2004; Malanski et al. 2020), and both species were collected in large numbers at that station.

In Arctic regions highly influenced by freshwater from large rivers, the hatching season of Arctic cod extends from January to July, whereas in regions with little freshwater input, no winter hatching seems to occur (Bouchard and Fortier 2011). To explain this pattern, the freshwater winter refuge hypothesis suggested that moderately fresher water near under-ice river plumes provides the larvae with temperatures slightly warmer than −1.8 °C, the temperature prevailing under the ice in winter in fully marine conditions, allowing first-feeding and survival in winter (Bouchard and Fortier 2011). Without such a thermal refuge protecting against extremely cold temperatures, the hatching of the larvae from the other regions have to be delayed until SST increase in the summer. Another type of thermal refuge provided by freshwater, this time provided by glacial meltwater, seems to help protect Arctic cod larvae against extremely warm temperature attained in the summer in some Arctic seas. The Greenland ice sheet and adjacent glaciers are melting at an unprecedented rate (Tedesco and Fettweis 2020). The associated increase in freshwater input into West Greenland fjords could curb, at least locally, some of the negative effects of current and future ocean warming on the survival and recruitment of young Arctic cod. However, a definitive test of the glacial meltwater summer refuge hypothesis would require a confirmation that in warm years, larval Arctic cod found in the subsurface layer of West Greenland fjords survive until the juvenile stage. Determining if the mechanism stipulated in the hypothesis also occurs in other fjords of the circumpolar Arctic, and whether freshwater from rivers could play a similar role, remain to be investigated, but would provide a further test of the hypothesis.

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