Arctic cod (*Boreogadus saida*) hatching season and growth rates in the Bering, Chukchi and Beaufort seas

Zane M. Chapman [1,] *, Franz J. Mueter[1], Brenda L. Norcross[2], Dion S. Oxman[3]

[1]University of Alaska Fairbanks, 17101 Point Lena Loop Rd. Juneau, AK 99801

[2]University of Alaska Fairbanks, PO Box 757220, Fairbanks, Alaska 9975-7220

[3]Alaska Department of Fish and Game, Division of Commercial Fisheries, Mark, Tag, and Age Laboratory, 10107 Bentwood Place, Juneau, AK 99801

*Corresponding author: zmchapman@alaska.edu

Abstract

Arctic cod is an important prey species in Arctic marine ecosystems that provides efficient energy transfer from producers to consumers in the food web. Arctic cod are locally abundant throughout the Arctic, though little is known about their early life stages in the Pacific Arctic, especially when and where they spawn and hatch. This study estimated hatch dates and growth rates of first year Arctic cod through analysis of otolith growth increments. First-year Arctic cod were captured in the northern Bering, Chukchi, and Beaufort seas during the spring or summer between 2012 and 2017. Estimated hatch dates ranged widely from November to June with peak hatching occurring from February through May, depending on the region of capture. Combined with large individual and regional variability in growth rates, this suggests a bet-hedging strategy to ensure some larvae encounter favorable growth conditions. In addition to regional differences, we identified a clear separation of hatch dates between spring- and summer-caught Arctic cod in the Chukchi Sea, suggesting different origins or strong size-dependent mortality. Finally, differences in hatch dates between pelagic and demersal juveniles indicate that older, larger juveniles begin to settle to the seafloor on deeper portions of the shelf in late summer. The results of this study set a benchmark for Arctic cod early life history in these regions and provide context for monitoring early life stages in a changing environment.

1. Introduction

Arctic cod (*Boreogadus saida*) was identified as a key species within Alaska's Arctic waters by the Fisheries Management Plan for Marine Resources in the Arctic (NPFMC, 2009) because it provides an important pathway for energy transfer from planktonic prey to larger animals. With large abundances, high energy content, and prey assimilation efficiency of around 80%, Arctic cod are ideal prey for many Arctic predators (Hop et al., 1997; Bluhm and Gradinger, 2008, Crawford et al., 2015). Many larger predators such as seals, whales, and seabirds depend on Arctic cod as a source of energy; in turn, polar bears and Alaska Native communities rely on some of these marine mammals for food (Welch et al., 1992). Arctic cod have also been targeted by commercial fisheries in the Barents Sea (Gjosaeter 1995) and by subsistence fisheries in northwest Alaska (Magdanz et al., 2010), among other regions.

Previous research on Arctic cod in many parts of the Arctic has described their general life history characteristics. Arctic cod reach sexual maturity at age 1+ with males maturing at a younger age than females (Nahrgang et al., 2015). They have a life span of 7 to 8 years (Hop and Gjosaeter, 2013), and reportedly spawn mostly between January and March in large groups underneath the ice (Craig et al., 1982; Bouchard and Fortier, 2011; Gallaway et al., 2017). Based on laboratory studies, Arctic cod eggs remain suspended at the surface of the water just under the sea ice and can tolerate sub-zero temperatures without affecting survival (Laurel et al., 2015). Hatch times have been estimated in the Canadian and European Arctic; however, they are currently unknown for US Arctic populations (Bouchard et al., 2017). Arctic cod early larval stages off Alaska have been found throughout the spring (Deary et al., 2021) and summer sampling seasons (Vestfals et al. 2019), suggesting a broad distribution of spawning and hatching in space and time. The Bongo nets used in these studies, however, under-sample larger larvae and juveniles in the summer. Large abundances of larvae and juveniles have been observed during multiple years over the northeast Chukchi Sea shelf (de Robertis et al., 2017; Levine et al. 2021), but their origins remain unknown. Large numbers of larval and juvenile Arctic cod have also been documented in the western Beaufort Sea (Parker-Stetter et al., 2011; Forster et al., 2020; Vestfals et al., 2019), but it is unclear if this population is connected to that found in the northern Chukchi Sea. Despite these recent observations; large gaps remain in the understanding of the reproductive biology and early life history of Arctic cod in the Pacific Arctic (Mueter et al., 2016; 2020).

The Arctic marine environment is changing rapidly and the impacts of these changes on the distribution, abundance, condition, and phenology of Arctic cod is of great interest to researchers and resource-dependent communities. The Alaskan Arctic specifically has seen significant reductions in sea ice, which decreases spring time surface albedo, thus increasing water temperatures during the spring and summer seasons. Sea ice melt and increases in water temperature are further accelerated by record increases in air temperature (Danielson et al., 2020; Baker et al., 2020a). These changes are reshaping the ecosystem, allowing southern, warmer-water species such as capelin (*Mallotus villosus*), saffron cod (*Eleginus gracilis*), and other gadids to move north and compete with Arctic cod for habitat and food resources (Hop and Gjøsæter, 2013, Marsh and Mueter, 2020, Baker, 2021, Mueter et al., 2021). Arctic cod have a lower thermal tolerance when compared to more southern gadid species and experience a high mortality occurring at 16°C and a peak growth rate at 7.3°C as juveniles (Laurel et al., 2015). The eggs of Arctic cod have a much narrower temperature tolerance and will not survive in temperatures exceeding 3.8°C (Drost et al., 2016). As the Arctic environment continues to change, the impact of these changes on Arctic cod will have ripple effects across the Arctic ecosystem.

Arctic cod growth and hatch timing have been examined in Canadian and European Arctic waters using daily otolith increment deposits. These analyses revealed two hatching patterns: a short hatch event that occurs concurrently with ice break-up and the beginning of increased biological production (May to June) as well as protracted hatching that can occur under the sea ice from the beginning of winter (January) extending into the summer (July) (Bouchard et al., 2011). Hatch timing may be an important determinant of subsequent growth and survival (Bouchard and Fortier, 2011).

Early hatching Arctic cod can attain a greater pre-winter size but experience higher cumulative mortality during the long larval phase. Later hatching Arctic cod have a smaller pre-winter size, but experience less larval mortality (Fortier et al., 2006; Bouchard and Fortier, 2008; Bouchard et al., 2017) and may experience higher overwinter mortality as a result. If hatch timing is linked to sea-ice retreat and impacts subsequent survival, reductions in sea ice and early ice melt may have contributed to the observed declines in the abundance of juvenile and adult Arctic cod at the southern end of their range such as in the Bering Sea (Marsh and Mueter, 2020).

The links between changing ice conditions, hatching, and the survival of larval Arctic cod in the Pacific Arctic are not currently understood. The timing and location of spawning and hatching, as well as the subsequent growth, movement and survival of eggs and larvae, is critical to identifying habitat requirements and the impacts of climate change on early life history stages of Arctic cod. This is especially true in areas of potential oil exploration, as Arctic cod are highly vulnerable to crude oil during their early life history (Gallaway et al., 2017; Laurel et al., 2019). Limited information is available on the distribution of eggs and early larval stages due to the challenges of sampling these life stages.

To better understand the early life history of Arctic cod and provide information to inform management, this study estimated and compared the distribution of hatch dates of larval and juvenile Arctic cod sampled during the spring and summer in the Chukchi and Beaufort seas. Specifically, we estimated age in days of Arctic cod larvae based on daily otolith growth increments and used age-at-length relationships to infer the distribution of hatch dates from observed length-frequencies. A second objective was to derive field-based estimates of average daily growth rates and to compare growth rates in the Pacific Arctic to laboratory-derived and other field-based estimates from the literature.

2. Methods

2.1 Study region

Arctic cod samples were obtained from the Bering, Chukchi and Beaufort seas and were assigned to five distinct regions based on differences in bathymetric and oceanographic characteristics within each of the seas (Figure 1). From south to north, these regions are northern Bering Sea (NBS), southern Chukchi Sea (SCS), northern Chukchi Sea (NCS), western Beaufort Sea (WBS), and eastern Beaufort Sea (EBS). The NBS has a broad shelf that encompasses Norton Sound and the Chirikov Basin between St. Lawrence Island, Alaska, and Bering Strait, with depths generally less than 50 m. It connects to the Chukchi Sea via the shallow (< 50 m) Bering Strait. The majority of the Chukchi Sea also has a shallow (40—60 m) continental shelf, which was split into a southern and northern region for our analyses due to differences in water masses. Alaska coastal water, Bering shelf water and Anadyr water from the Bering Sea converge in Bering Strait before entering the Chukchi Sea (Eisner et al., 2012; Danielson et al., 2017) and continuing to flow north. These water masses of recent Pacific origin cover a variable portion of the SCS shelf but are typically separated from distinct water masses in the NCS, referred to as winter water and recent melt water, by a semi-permanent front that extends from the surface to the sea floor (Weingartner 1997; Danielson et al., 2017a). The colder and more saline winter water extends as far south as 70°N (Pickart et al., 2010), therefore 70°N was used as the dividing line between the NCS and SCS for our analyses. In contrast to the Chukchi Sea, the Beaufort Sea has a narrow shelf that quickly drops into the Arctic Basin to depths exceeding 2,000 m. The Beaufort Sea shelf receives relatively nutrient-poor water via the Alaska Coastal Current entering from the west and is influenced by fresher waters from the Mackenzie River, as well as by deeper Atlantic waters from the basin (Carmack and Macdonald 2002, Pickart 2004). For this analysis, the Beaufort Sea was separated into an eastern (samples east of 147°W; EBS) and western region (153 °W to 147 °W; WBS) (Figure 1), with the EBS experiencing a stronger influence from the Mackenzie River than the WBS (MacDonald et al., 1987).

Because of the strong connectivity between the NCS and the westernmost portion of the Beaufort Sea (west of 153° W), we pooled samples from these regions and refer to them collectively as the NCS (Figure 1).

2.2 Sample processing and collection

Larval and juvenile Arctic cod were collected during five Arctic surveys conducted during the spring (June) and summer (August/September) seasons: the Arctic Shelf Growth, Advection, Respiration and Deposition (ASGARD) rate measurement survey in the NBS and SCS in the spring of 2017 (Danielson et al., 2017), the Arctic Marine Biodiversity Observation Network (AMBON) survey in the Chukchi Sea in the summer of 2017 (Iken et al., 2018), the Arctic Integrated Ecosystem Survey (Arctic IES II) in the Chukchi Sea and WBS in the summer of 2017 (Farley et al., 2017), and the summer Transboundary Surveys conducted in the WBS in 2012 (TB12) and in the EBS in 2013 (TB13) and 2014 (TB14) (Norcross et al., 2017; Table 1). Both the ASGARD and Arctic IES II initiatives were part of the North Pacific Research Board Arctic Integrated Ecosystem Research Program (Arctic IERP; Baker et al., 2020b, Baker et al., 2022).

Table 1: Season, cruise, region, and sampling year with the dates, gear type, number of stations and number of Arctic cod that were captured and their length range and mean length (mm). Regions are the northern Bering Sea (NBS), southern Chukchi Sea (SCS), northern Chukchi Sea (NCS), western Beaufort Sea (WBS) and eastern Beaufort Sea (EBS). Bongo, Isaacs-Kidd Midwater Trawl (IKMT), and Marinovich trawls sampled fish in the pelagic zone and bottom trawls sampled fish in the demersal zone. Cruises included the Arctic Shelf Growth, Advection, Respiration and Deposition (ASGARD) rate measurement survey, the Arctic Marine Biodiversity Observation Network (AMBON) survey, the Arctic Integrated Ecosystem Survey (Arctic IES II) and the Transboundary Surveys in 2012 (TB12) 2013 (TB13) and 2014 (TB14). See text for details.

Season	Cruise	Region	Year	Sampling Dates	Gear Type	# of Stations	Arctic cod Captured	length range (mm)	mean length (mm)
Spring	ASGARD	NBS	2017	Jun-10 — Jun-28	Bongo (pelagic)	7	19	6—19	12
Spring	ASGARD	SCS	2017	Jun-23 — Jun-28	Bongo (pelagic)	23	838	5—17	8
Summer	AMBON	SCS	2017	Aug-6 — Aug-21	IKMT	4	91	18—56	37

					(pelagic)				
Summer	AMBON	SCS	2017	Aug-6 — Aug-21	Bottom Trawl (demersal)	11	584	28—68	50
Summer	AMBON	NCS	2017	Aug-18 — Aug-22	IKMT (pelagic)	6	1076	21—51	29
Summer	AMBON	NCS	2017	Aug-9 — Aug-22	Bottom Trawl (demersal)	50	2841	11—73	38
Summer	Arctic IES	SCS	2017	Sep-13 — Sep-27	Marinovich (pelagic)	9	666	28—74	52
Summer	Arctic IES	SCS	2017	Sep-12 — Sep-27	Bottom Trawl (demersal)	14	190	34—74	52
Summer	Arctic IES	NCS	2017	Aug-13 — Sep-13	Marinovich (pelagic)	19	1256	25—71	42
Summer	Arctic IES	NCS	2017	Aug-10 — Sep-14	Bottom Trawl (demersal)	30	463	22—73	48
Summer	TB12	WBS	2012	Sep-21 — Sep-29	Bottom Trawl (demersal)	12	480	15—71	54
Summer	TB12	WBS	2012	Sep-22 — Sep-30	IKMT (pelagic)	13	254	22—71	46
Summer	TB13	EBS	2013	Sep-15 — Sep-30	Bottom Trawl (demersal)	11	15	30—42	35
Summer	TB13	EBS	2013	Aug-13 — Aug-30	IKMT (pelagic)	27	351	17—47	33
Summer	TB14	EBS	2014	Aug-19 — Aug-31	Bottom Trawl (demersal)	27	264	27—73	46

Four types of sampling methods were used: (1) an Isaacs-Kidd Midwater Trawl (IKMT, Methot 1986) with a 3-mm-mesh body and 1-mm-mesh cod-end liner was deployed obliquely to collect larval and juvenile pelagic fishes from near bottom to the surface during the AMBON, TB12, and TB13 surveys; (2) a modified Marinovich trawl with a 64-mm-mesh body which tapered to a 3-mm-mesh codend was used to target aggregations identified by acoustic backscatter as part of an acoustic-trawl survey during Arctic IES II (de Robertis et al., 2017; de Robertis et al., 2017b); (3) two types of bottom trawls were used to sample demersal fishes, including a 3-m modified Plumb Staff Beam Trawl (PSBTA, Abookire and Rose, 2005) with a 7-mm-mesh body and a 4-mm liner during the AMBON, Arctic IES II and Transboundary Surveys, and a Canadian Beam Trawl (CBT, Majewski et al., 2017) with a 10-mm-mesh body and a 6-mm-liner during the Transboundary Surveys; and (4) a 60-cm-diameter Bongo net with a 505-µm-mesh body was used to sample zooplankton and ichthyoplankton during ASGARD and Arctic IES II surveys.

Two sets of Arctic cod samples were used for analyses. The first sample consisted of all Arctic cod sampled in the field and was used to characterize the length-frequency distribution of the population and the second sample consisted of a length-stratified subset to remove otoliths for aging. Standard lengths of all larval and juvenile Arctic cod sampled in a given season, cruise, region, and vertical location (demersal or pelagic) were measured in the field or laboratory to the nearest mm (Table 1). Lengths of samples that were preserved in ethanol had a shrinkage correction model applied to them in order to estimate the true length at capture. The model was based on Bouchard et al. (2016), who compared standard lengths of fresh samples to standard lengths of the same fish after ethanol preservation, which produced the relationship: Standard Length = 1.073 * Standard Length preserved + 0.253 (Bouchard et al., 2016). No correction was applied to length measurements of frozen fish. Hereafter, "standard length" refers to the measured standard length of fresh or frozen fish or to the standard length of ethanol-preserved fish after correcting for shrinkage. Length-stratified subsamples for otolith aging were obtained from each region and season, except the WBS and 2012 EBS, to estimate region-specific relationships between length and age (Table 2) and to convert observed length-frequencies to estimated hatch date distributions using the approach described below.

Table 2: Number of age-0 Arctic cod aged by season and region with the range of standard lengths (mm) and estimated ages (days), and parameters of the length-at-age regressions with the slope representing estimated growth rates in mm d^{-1}.

Season	Region	Total aged	Length range (mm)	Age range (days)	Length-age regressions Slope	Intercept	R^2
Spring	N. Bering	14	5—22	17—161	0.124	3.553	0.943
Spring	S. Chukchi	29	6—19	10—104	0.146	4.218	0.688
Summer	S. Chukchi	15	21—61	109—302	0.215	-1.131	0.673
Summer	N. Chukchi	88	12—53	55—308	0.131	13.927	0.441
Summer	E. Beaufort	31**	24—50	76—241	0.081	22.364	0.241

** 27 fish were aged from 2013 survey and four were aged from 2014 survey

To summarize length-frequencies and hatch date distributions, samples from different seasons, regions, and vertical locations were aggregated into groups. We defined a total of 10 groups consisting of pelagic spring samples from the NBS (1 group), pelagic spring and pelagic and demersal summer samples from the SCS (3 groups), and pelagic and demersal summer samples from the NCS, WBS, and EBS (2 groups each).

To obtain representative length-frequency distributions for larval and juvenile Arctic cod for each group, the length of fish from different gear types and cruises were used (Table 1). Length-frequency distributions during spring were quantified using Bongo net samples because larval fish are generally small (< 20 mm) at that time. Although the Bongo net may select against some of the larger larvae in the water column, because of its small mesh size Bongo net samples were considered to be most representative of the size distribution of larval Arctic cod in the sampling area during spring. This assumption was supported by opportunistic IKMT samples catching larvae that were generally less than 20 mm in June. During the summer sampling period the Bongo net was not used for Arctic cod collection because age-0 fish were generally larger than 20 mm and were distributed throughout the water column or had settled to the bottom. We used fish collected by either the Marinovich trawl or the IKMT (when Marinovich trawl was unavailable) to quantify length-frequencies of pelagic juveniles, whereas samples from the bottom trawls (PSBTA or CBT) were used to characterize lengths of demersal fish. The Marinovich trawl has little size selectivity over the size range of interest (de Robertis et al., 2017; A. de Robertis, NOAA, Seattle, pers. comm.). Similarly, the PSBTA has been estimated to retain all or most age-0 Arctic cod in late summer (Marsh et al., 2020). We focused primarily on the pelagic fish for comparisons among regions because they are assumed to be age-0 fish, whereas the bottom trawl catches may include some small Arctic cod (< 75 mm) that could be age-1 or older as there is considerable overlap in sizes among ages (Helser et al., 2017). Length data for the Transboundary Surveys from both the PSBTA and CBT were combined to characterize the length-frequency distribution of Arctic cod in the eastern Beaufort Sea because there was no evidence that the size composition of the catches differed significantly between these gear types (Norcross et al., 2017). The combined gear type will be referred to hereafter as bottom trawl. In summary, pelagic fish in spring were represented by Bongo samples, whereas in the summer Marinovich and IKMT samples were used to represent pelagic samples, and bottom trawls were used to represent demersal fish.

To assess length frequency distributions of age-0 fish, as well as for aging age-0 fish, we included only individuals equal to or less than 75 mm in the Bering Sea, Chukchi Sea and WBS and up to 60 mm in the EBS. The upper limits were estimated to be the maximum size of age-0 Arctic cod in late summer based on the length-frequency distribution of all Arctic cod sampled in a given region (Supplement 1: Fig. S.1). The estimated cutoff of 75 mm for the southern regions was consistent with that used for age-0 fish sampled in the Chukchi Sea in late summer 2012 and 2013 (Marsh et al., 2020). In the EBS, a cutoff of 60 mm was used as larger fish were clearly separated from a dominant mode of smaller, age-0 fish and were continuous with a mode of larger, presumably age-1 or older fish (Fig. S.1). This cutoff is consistent with previous studies in the Beaufort Sea (Norcross et al. 2017).

Representative age-0 Arctic cod for otolith aging were sampled over the full range of sizes of larval Arctic cod observed in the spring (< 20 mm) and young-of-year Arctic cod observed in late summer within each sampling region (<75mm). We collected size-stratified random subsamples of specimens collected across much of the study region (Figure 1). Lengths were stratified into thirds to form small, medium, and large groups for each region to ensure that a broad range of lengths was represented for aging. Subsamples of larval and juvenile gadids for otolith analyses were frozen or stored in 95% ethanol and shipped to the University of Alaska Fairbanks in Juneau, Alaska, where they were identified and processed for further analysis. Samples of archived otoliths from the Transboundary Surveys in the Beaufort Sea and the corresponding standard lengths were obtained from the Fisheries Oceanography Lab at the University of Alaska Fairbanks (UAF). Of the smaller specimens (< 15 mm) used in this study, about 60% were examined by a larval fish taxonomist to confirm species identification. Because larger fish are difficult to identify in the field, IDs of fish greater than 20 mm captured during the Arctic IES II survey were verified by sequencing the mitochondrial cytochrome oxidase c, subunit 1, and aligning them with known gadid sequences at the National Oceanic and Atmosphere Administration (NOAA) Ted Stevens Marine Research Institute in Juneau, Alaska (Sharon Wildes, NOAA, Seattle, pers. comm.). All samples were processed and analyzed at UAF's Lena Point Fisheries Facility and at the Alaska Department of Fish and Game Mark, Age and Tagging laboratory in Juneau, Alaska.

2.3 Otolith aging

To estimate ages of juvenile Arctic cod, sagittal otoliths were examined for daily growth increments. After measuring standard lengths, the otoliths were removed under a dissecting microscope with fine-tipped forceps. The left otolith was extracted, rinsed with 95% ethanol to remove organic matter, and mounted to a glass slide using clear, thermal plastic cement. The right otolith was removed, cleaned, and stored dry to be used if the left otolith was damaged or unusable. The mounted otoliths were polished on the distal plane with various grades of lapping film to expose the daily growth increments within the otolith. Due to their uneven shape, some otoliths required polishing on both sides.

To estimate hatch dates, daily growth increments were counted on the sagittal otolith. The presence of daily growth increments on lapillar otoliths from Arctic cod have been previously confirmed by Bouchard and Fortier (2011). In other gadid species such as Atlantic Cod (*Gadus morhua*) and Pacific Cod (*Gadus macrocephalus*) the sagittal and lapillar otolith were both similar in increment counts and both produced reliable age estimates (Narimatus et al., 2007; Hüssy et al., 2003; Campana and Hurley, 1989). In the current study, five lab raised Arctic cod from the Hatfield Marine Science Center in Newport, Oregon, were aged to test whether daily increments are deposited on sagittal otoliths. Lab-reared fish hatched over the course of a week and were approximately 33 days old when sampled for aging. Increment counts were within 6 increments of the approximate age, providing additional support to using sagittal otoliths for daily aging. Hatch marks were also identified using otoliths of lab-reared, known-age Arctic cod from the Hatfield Marine Science Center in Newport, Oregon, as reference specimens (Benjamin Laurel, NOAA Alaska Fisheries Science Center, pers. comm.; Figure 2 C). Using the known age and hatch date of the fish, the location of the hatch mark was identified and confirmed to further improve age determinations. This method of hatch mark identification is similar to other studies that determined the hatch mark by examining otoliths shortly after the fish hatched (Eckmann and Rey 1987). Otolith images were captured on the distal plane using Image Pro Plus© (Media Cybernetics) at 40X and 100X depending on the size of the otolith, and these images were used to enumerate daily rings. Each visible ring, a light band followed by a dark band in the otolith matrix was assumed to represent one day of growth (Figure 2 A). These daily growth increments were counted from the hatch mark to the edge of the otolith (Figure 2 B).

To ensure consistency of otolith aging, all otoliths were aged at least twice and a third time if the first two ages were not within a 5% coefficient of variation (CV). The second and third ages used the same otolith image and were done on different dates from the previous read to minimize potential bias. If the first two ages fell within a 5% CV of each other, the second age was used. In the event the first two ages had a greater than 5% CV the otoliths was aged a third time and the final age was used if it was within 5% of either the first or second age. If the third read had a CV greater than 5% the ages were not used for analysis. This occurred on some otoliths that became damaged from over-polishing. Although there are other methods for validating age determinations, the CV is statistically more rigorous and flexible (Chang, 1982; Campana 2001). A subsample of the aged otoliths (n = 15) was examined by a second otolith aging expert to confirm that the image quality was adequate and that increment measurements and ages were consistent between readers.

Growth increments in the center of some otoliths were unreadable (n=38 of 177 sampled) because too much material had been removed during polishing. Therefore, the saved otolith was used for aging, but for some of the larger fish (20—54mm), the center again became over-polished. In these cases, daily ages were counted using the otolith with the most amount of visible increments starting at the first readable growth increment. The number of increments that were unreadable was estimated based on a regression approach using completely aged otoliths from the same region (Supplement 2).

2.4 Length-frequency distributions

Length-frequency distributions for the entire sample of captured larval or juvenile Arctic cod were visually examined by season and region, and separately for pelagic and demersal sampling gear. In addition, the mean lengths of demersal and pelagic larvae and juveniles were plotted for each station to visualize spatial patterns in mean size. These distributions, combined with age-at-length regressions for a given region, provided the basis for determining the hatch date distribution.

2.5 Hatch date estimation

To estimate the distribution of hatch dates for Arctic cod in each group we first estimated age-at-length relationships and their uncertainty for a subsample of fish using linear regressions. The resulting relationships were then used to convert all observed lengths in a group to estimated ages. Finally, the estimated ages were subtracted from the dates of capture to obtain an estimated hatch-date distribution. We assumed a linear relationship between age and length based on a previous study of larval Arctic cod (Bouchard and Fortier, 2011) and visual examinations of age-at-length. Therefore, counts of daily growth increments (hereafter 'age') within each season were modeled as a linear function of length and region with an interaction term to allow for possible differences in age-at-length by region(*r*):

Eq. 1 $$age_{r,i} = \alpha_r + \beta_r \cdot length_{r,i} + \varepsilon_{r,i} \quad \varepsilon_{r,i} \sim N(0, \sigma_\varepsilon^2)$$

where $age_{r,i}$ and $length_{r,i}$ are the estimated age and the measured length of the i^{th} specimen in region r, α_r and β_r are the intercept and slope for region r, and the $\varepsilon_{r,i}$ are residuals that are assumed to be normally distributed with mean 0 and variance σ_{ε}^2. Region-specific coefficients (α_r, β_r) were only estimated if the interaction term was significant ($p < 0.05$), otherwise a single regression line was estimated across the sampled regions (α, β). Preliminary analyses indicated that the standard deviation in estimated ages increased linearly with the predicted mean ages, therefore the residual standard deviation was modeled as a linear function of age. All models were fit using a weighted least squares approach as implemented in the 'nlme' package in R (Pinheiro et al., 2020). Residual diagnostics did not suggest any violations of the linearity or normality assumptions.

To estimate age distributions within each region, we used the best age-at-length model for each region to predict ages from observed lengths. Age data were not available for the WBS so the age-at-length model for the NCS was applied to this region because it is contiguous with and immediately downstream of the NCS. Juveniles from the NCS are likely advected into the western Beaufort Sea (Levine et al. 2021). To reflect variability in age-at-length arising from individual variations in growth, we randomly simulated up to 10 ages for each observed length based on the estimated mean age and its standard deviation at a given length. Occasionally, the age of a simulated fish exceeded one year due to the large estimated variance in the age of larger fish; those fish were removed from the simulated age distribution. The number of simulated ages per measured individual was arbitrarily chosen to generate at least 10,000 ages for obtaining a smooth age distribution for plotting and this choice did not affect results. Simulated ages were subtracted from the corresponding capture dates to obtain estimated hatch date distributions. Regression models to predict ages from lengths for the SCS were fit separately to data from spring and summer surveys due to large differences in the observed length ranges of fish between spring and summer. The SCS was the only region where data from both seasons were available.

2.6 Hatch date comparisons

The estimated hatch date distributions were visually compared among groups using density plots. To statistically compare these distributions, we calculated the mean hatch dates for each group of Arctic cod and used a bootstrap approach to construct confidence intervals for the means. Bootstrap samples were generated for each group by randomly re-sampling with replacement both the observed length-frequencies for a given group and the age-length samples used for estimating age-at-length for that group. For each set of bootstrap samples, a hatch date distribution was simulated following the same series of steps used in estimating the hatch date distribution from the original samples and the mean hatch date of the simulated distribution was calculated. This was repeated for each of 10,000 sets of bootstrap samples to construct 95% confidence intervals for the mean hatch date of each group, as well as for pairwise differences between groups. If the confidence interval for a pairwise difference did not include zero, mean hatch dates between groups were considered statistically different. In addition, p-values for all pairwise comparisons were computed based on the proportions of simulated differences that were less than and larger than zero. The smaller of these proportions was multiplied by 2 for a two-sided test of the null hypothesis that the difference is zero. The proportion was multiplied by two for a two-sided test because we did not specify *a priori* hypotheses about which groups had earlier or later hatch dates.

Initial comparisons among regions showed no difference in mean hatch dates between Arctic cod captured in the most western portion of the Beaufort Sea and the Northern Chukchi Sea from the 2017 Arctic IES survey. This was true for both the pelagic and demersal captured fish with p-values of 0.647 and 0.952, respectively. Along with the lack of significant difference, there were relatively few samples from this survey collected from the western Beaufort Sea (n = 68 pelagic and 77 demersal Arctic cod), therefore these two regions were pooled and will be referred to as NCS hereafter (Figure 1). The similarity between the two regions was not surprising given their close proximity and oceanographic connectivity, and the assumption that most northern Chukchi and western Beaufort Sea Arctic cod are advected into those regions from southern hatching locations (Levine et al., 2021).

In the Chukchi Sea during summer, data for both pelagic and demersal Arctic cod were available from two overlapping surveys and were analyzed separately. Mean hatch dates for pelagic Arctic cod collected during the transect-based AMBON survey (IKMT) and those collected during the grid-based Arctic IES II survey (Marinovich) (Table 1.1) were quantified separately as the surveys covered different areas. For comparing hatch dates of fish among regions, we present results for Arctic IES II samples collected in the SCS and NCS using the Marinovich trawl (pelagic fish) or bottom trawl (demersal fish) because the Arctic IES II survey sampled a systematic grid and covered a larger geographical area within each region, providing more representative length-frequency distributions.

2.7 Growth rates

To obtain in situ estimates of age-0 growth rates for Arctic cod we fit linear regressions of length on age by region and season. A simple linear regression of length as a function of age was used, where the slope (mm d^{-1}) represents the estimated average growth rate of the sampled population in a given region and season. Growth rates were estimated separately by region to account for differences in temperature, prey availability among regions, and potential genetic differences among regions, all of which can affect the rate of growth (Laurel et al., 2015; Helser et al., 2017; Laurel et al., 2018). Growth rates were also estimated by season to account for potential differences between the growth of early larval and juvenile stages and the apparent growth of the surviving age-0 fish sampled later in the summer, whose average growth may differ due to size selective mortality or seasonal changes in temperature or prey availability.

3. Results

3.1 Otolith-based ages

A total of 177 Arctic cod otoliths were examined, with ages ranging from 10 to 161 days for Arctic cod sampled in the spring, and from 55 to 308 days for those collected during summer (Table 1.2). The age range was greater for samples from the Chukchi Sea (55—308 days) than the Beaufort Sea (76—241 days), (Table 1.2). The mean CV between first and second age assessments was 0.020 (range from 0.000 to 0.050), indicating age estimates were reproducible.

3.2 Length comparisons among seasons, regions and vertical locations

Length-frequency distributions of age-0 Arctic cod differed by season, region and vertical location in the water column. Arctic cod captured in the spring were on average 80.5% smaller than those captured in the summer (Table 1). In the SCS, where Arctic cod were sampled in both seasons, pelagic spring-caught fish (Bongo) had a mean length of 8 mm (range: 5 — 17 mm) whereas those caught in summer (beam trawl) had a mean length of 52 mm (range: 28 — 74 mm). Within seasons, differences in length frequency distribution were observed among regions (Figure 3). The WBS had the largest mean length of age-0 Arctic cod followed closely by the SCS (Table 1). Within regions, demersal-caught fish were up to 36% larger on average than fish caught in pelagic nets (Table 1). Spatial patterns in mean length across the study region suggest a gradient from larger fish in the south to smaller fish in the north during both spring and summer in the Chukchi Sea (Figure 4). During summer, the smallest average length of fish was observed in the EBS, whereas WBS fish had an average length similar to the NCS fish. These spatial differences are confounded with differences in the timing of sampling as the SCS and WBS were sampled later in the year than the NCS and EBS (Table 1).

3.3 Age-at-length regressions

The best age-at-length model included a significant interaction between length and region for spring-caught samples (F = 323.900, p = 0.001, R^2 = 0.969), indicating that slopes differed between the NBS (β_{NBS} = 7.652, se = 0.504) and SCS (β_{SCS} = 5.112, se = 0.501; Table 3). In contrast, there was no interaction between length and region in the summer (F=24.470, p = 0.001), indicating that age increased at the same rate with length across sampling regions (β = 2.541, se = 0.309, R^2 = 0.346; Table 3). However, intercepts differed among regions (F = 4.837, p = 0.009) and fish at a given length were on average 17 days older in the NCS compared to the EBS and 10 days older in the SCS than in the NCS (Table 3).

Table 3: Model coefficients, their estimates and standard errors, and Wald's t-test results for regressions of age in days on standard length (mm) by season. Region-specific intercepts (α) and slopes (β) were estimated in the spring; a common slope was estimated in the summer. Subscript for regions are Northern Bering Sea (NBS), southern (SCS) and northern Chukchi Sea (NCS) and eastern Beaufort Sea (EBS).

Season	Region	Coefficient	Estimate	Std. Error	t-value	P value
Spring	NBS	α_{NBS}	-23.903	6.263	-3.817	0.001
	NBS	β_{NBS}	7.652	0.504	15.185	0.001
	SCS	α_{SCS}	-12.776	5.489	-2.327	0.025
	SCS	β_{SCS}	5.112	0.501	10.197	0.001
Summer	SCS	α_{SCS}	82.971	15.114	5.483	0.001
	NCS	α_{NCS}	72.819	10.430	6.975	0.001
	EBS	α_{EBS}	55.634	11.949	4.656	0.001
	All	Β	2.541	0.309	8.217	0.001

3.4 Hatch timing

Hatching occurred over a protracted period ranging from November through June with peak hatching from late January to May (Figure 5). The estimated distribution of hatch dates differed between Arctic cod sampled in the spring and in the summer, between Arctic cod from different regions and between pelagic and demersal age-0 Arctic cod (Figure 5). Within the SCS, spring-captured pelagic fish had a mean hatch date that was 43 days later than summer-captured pelagic fish (Table 4; Figure 6). Arctic cod hatch dates of summer-caught fish also differed significantly among regions ($p<0.05$) except for pelagic fish caught in the NCS and WBS ($p=0.547$, 7-day difference), demersal fish from the WBS and EBS ($p=0.982$, 0-day difference), and demersal fish from the NCS and WBS/EBS ($p=0.581$, 11-day difference for both comparisons; Table 5; Figure 6).

Table 4: Mean and range of hatch dates (HD) by season, region and vertical location in water column. Dates marked with * are from the previous year. Regions are Northern Bering Sea (NBS), southern (SCS) and northern Chukchi Sea (NCS) and western (WBS) and eastern Beaufort Sea (EBS).

Season and region	Vertical location	Mean HD	Earliest	Latest
Spring				
NBS	Pelagic	Apr—14	Mar—01	Jun—09
SCS	Pelagic	May—26	Mar—08	Jun—22
Summer				
SCS	Pelagic	Jan—30	Sep—27*	Jul—15
SCS	Demersal	Jan—22	Sep—27*	Jul—31
NCS	Pelagic	Mar—12	Sep—28*	Aug—29
NCS	Demersal	Mar—07	Sep—30*	Aug—11
WBS	Pelagic	Mar—11	Sep—30*	Sep—01
WBS	Demersal	Mar—01	Sep—29*	Aug—29
EBS	Pelagic	Apr—08	Oct—10*	Aug—12
EBS	Demersal	Mar—01	Dec—17*	Jul—17

Table 5: Pairwise comparisons of mean hatch dates among regions by season and vertical location in the water column with bootstrap-based p-values and estimated difference in mean hatch dates. Negative differences in mean HD imply that the first region had an earlier hatch date than the second region.

Regional comparisons	Season	Vertical Location	P-value	Difference in Mean HD
Spring				
NBS — SCS	Spring	Pelagic	0.005	- 36
Summer				
SCS — NCS	Summer	Pelagic	0.001	- 43
SCS — WBS	Summer	Pelagic	0.003	- 50
SCS — EBS	Summer	Pelagic	0.001	- 69
NCS — WBS	Summer	Pelagic	0.547	- 7
NCS — EBS	Summer	Pelagic	0.006	- 26
WBS — EBS	Summer	Pelagic	0.065	- 19
SCS — NCS	Summer	Demersal	0.001	- 47
SCS — WBS	Summer	Demersal	0.001	- 36
SCS — EBS	Summer	Demersal	0.001	- 37
NCS — WBS	Summer	Demersal	0.588	-11
NCS — EBS	Summer	Demersal	0.581	11
WBS — EBS	Summer	Demersal	0.982	0

Demersal SCS fish sampled during the summer had the earliest mean hatch date (January 22) and pelagic EBS fish had the latest mean hatch date (April 14, Table 4). Summer-caught pelagic fish in the SCS hatched on average 43 days earlier than those in the NCS, 50 days earlier than those in the WBS, and 69 days earlier than EBS pelagic fish (Table 5). Pelagic fish in the EBS had mean hatch dates significantly later in the year (were significantly younger) than demersal fish.

3.5 Growth rates

Estimated growth rates differed among regions (Table 2). Growth rates of spring-caught Arctic cod larvae were 18% slower in the NBS (0.124 mm d^{-1}) than in the SCS (0.146 mm d^{-1}) (Table 2; Figure 7A). Growth rates of Arctic cod captured in the summer season similarly differed significantly among regions (F=3.14, p=0.047), ranging from 0.081 mm d^{-1} in the EBS to 0.215 mm d^{-1} in the SCS (Table 2; Figure 7B).

4. Discussion

Arctic cod from all regions hatched over a protracted period between November and June, with peak hatch dates ranging from January through May depending on the season, region, and vertical location of capture. This variability among groups and locations likely reflects gradients in the timing of sea ice retreat and different transport pathways from hatching to sampling locations.

Estimated hatch dates ranged from as early as late September through August of the following year but the vast majority ranged between November and June. This protracted hatching pattern is consistent with previous studies (Bouchard and Fortier, 2011) and maximizes the chances that a least some offspring will hatch during favorable conditions. This bet-hedging strategy helps mitigate against annual variability in environmental conditions (Shama, 2015), which at high latitudes can impact the timing and magnitude of the spring algal bloom and thereby the timing and abundance of prey for Arctic cod (LeBlanc et al., 2020). Because of these highly variable conditions, a bet-hedging strategy can impart some resilience to Arctic cod in a changing environment if some portion of a given year class encounters conditions within an acceptable range. The protracted hatching period can be a result of differences in incubation time, differences in spawn timing among regions or a combination of both. The large sizes (>50 mm) of some fish in our samples produced hatch dates that indicate spawning occurred outside of published literature dates (November—March) and prior to ice formation. At least two factors may have contributed to these results. First, early hatch dates could be an artifact of simulating ages based on lengths that exceeded the maximum length in our aging samples. Out of the 10,400 Arctic cod lengths used, 709 were greater than the maximum length of the aged fish but still within the age 1 cutoff. The variance in the age distribution at a given length increased in the age-at-length model, which could have produced unrealistic ages when extrapolating beyond the maximum length used in the age-at-length regression. The length range used to estimate the age-at-length relationship was narrower than the observed length range due to the challenges associated with aging larger larvae. Second, some of the

Arctic cod in our length samples may have been age-1 fish. The oldest estimated ages and earliest mean hatch dates were associated with fish sampled in the SCS for both demersal and pelagic samples. Within this region, length varied considerably and fish in demersal samples may have included some age-1 individuals. Previous studies have reported age-1 Arctic cod below the age-0 cutoff lengths used for this study (Norcross et al., 2017). Both the presence of age-1 fish and the assumed large variances for the age of larger juveniles are likely causes of the seemingly unrealistic early hatch dates.

4.1 Seasonal differences in hatch dates

Arctic cod captured during the spring and summer had different mean hatch dates, with the spring-caught fish hatching much later in the year. This was unexpected and suggests that spring-caught and summer-caught fish in the same region originated from at least two separate hatch events. Two separate hatch patterns among regions have been documented, specifically a short hatching event associated with ice break up and a protracted event extending from January to July (Bouchard and Fortier, 2008; Leblanc et al., 2020). The protracted dates were associated with regions like the Chukchi Sea and western Beaufort Sea which lack a significant freshwater influence (Bouchard and Fortier, 2006). Larval fish captured in the SCS in June had a narrow hatch date distribution with a mean hatch date in mid-May, suggesting that they originated relatively close to their sampling locations. Within the SCS, Kotzebue Sound has been hypothesized to be a hatching location for Arctic cod due to the large number of larval fish captured in the outer Sound during the 2017 Arctic IES survey (Deary et al., 2021). In contrast, the summer-captured pelagic fish in the SCS had a mean hatch date of mid-February, ranging from January to June. The age of the summer SCS fish and prevailing currents in the region indicates that they were likely advected from the northern Bering Sea as suggested by biophysical transport models (Deary et al., 2021; Vestfals et al., 2021).

Arctic cod hatching locations in the Pacific Arctic are largely unknown, but hatching may occur in several areas in the Bering Strait region, including the waters south of St. Lawrence Island, the Gulf of

Anadyr, Kotzebue Sound, and areas along the Russian coast both south and north of the Bering Strait (Craig et al., 1982; Christiansen and Fevolden, 2000; Kono et al., 2016; A. Whiting, Native Village of Kotzebue, personal communication). In 2017, sea ice melt in the NBS began during late April and was complete by late May and 99% of estimated hatch dates occurred prior to May 25 with the mean hatch date occurring on April 6th. This suggests that Arctic cod in the NBS hatched prior to and during sea ice retreat. Spring-captured fish in the SCS had the latest mean hatch dates of all the regions in this study, possibly reflecting later ice melt in their hatching region. Two hatching sites have been proposed within the SCS; Kotzebue Sound in Alaska and the region along the Chukotka Peninsula in Russia (Deary et al., 2021). Both of these locations had later sea ice recession than the proposed hatching locations in the NBS. The delayed sea ice recession in these potential source regions could explain why the spring SCS fish had a later mean hatch date than those caught in the NBS, which originated from more southern source regions.

The length distribution of Arctic cod sampled in spring 2017 was similar to lengths observed during 2008 and 2013 in the NBS and SCS regions (Kono et al., 2016). In all three years, lower numbers of larger Arctic cod were observed in the NBS compared to high abundances of smaller fish in the SCS. For example, the mean catch per unit effort in summer 2017 was 73 times higher in the SCS than in the NBS (this study). Although Kono et al. (2016) did not estimate hatch dates, the observed differences in size and relative abundance of Arctic cod between the two regions suggest that earlier ice retreat, coupled with warmer waters in the NBS, is associated with earlier hatching (Kono et al., 2016). The earlier hatching larvae experienced a longer period of natural mortality, which can explain their lower abundances in the NBS. Additionally, larvae hatched in the NBS may have been advected into the SCS prior to sampling, where they mix with more recently hatched larvae originating from spawning locations in the Chukchi Sea.

In contrast to spring-captured fish, the mean simulated hatch date for all summer-captured fish occurred 87 days earlier, which suggests that they originated from a different spawning population than those caught in the spring. Summer-caught fish in the SCS displayed a wide range of hatch dates from January to May (Figure 5). The protracted range of hatch dates in the SCS and lack of a single peak hatch date from the summer captured fish may be an indication of multiple spawning events occurring at different times in different areas of the Bering and Chukchi sea. By the time of summer sampling, fish from multiple hatching events may have been advected into the Chukchi Sea, explaining the wide range of hatch dates observed. The earlier hatch dates of summer-captured fish indicate that they likely hatched south of Bering Strait when sea ice was still present in the region, before being advected with the prevailing northward currents through the Bering Strait into the Chukchi Sea (Berline et al., 2008; Vestfals et al., 2021). Simulations with an individual based particle tracking model also suggest that age-0 Arctic cod in the Chukchi Sea must have originated in more southern, warmer waters to grow to the sizes observed during the summer surveys (Vestfals et al., 2021).

Alternatively, spawning could have occurred at similar times, but differences in development rates driven by environmental influences could have contributed to differences in hatch dates. For example, earlier hatching has been hypothesized to be associated with areas that receive an influx of fresh water such as the Mackenzie River (Bouchard and Fortier, 2008). This could warm the area enough to accelerate egg development and larval growth under the ice, giving juvenile Arctic cod a physiological advantage over juveniles in colder waters because their increased size likely leads to increased feeding success and predator avoidance (Bouchard and Fortier, 2011; Laurel et al., 2015; Kent et al., 2016).

Spawning and hatching of Chukchi Sea Arctic cod may also occur in association with northern polynyas, such as the recurring polynyas in the eastern Chukchi Sea between Cape Lisburne and Icy Cape, Alaska. However, this polynya is characterized by high salinity and low but stable temperatures, despite reduced sea ice (Ladd et al., 2016). This contrasts with polynyas in the Beaufort Sea, which provide more favorable conditions for EBS Arctic cod because of warmer temperatures (Bouchard and Fortier, 2011). Moreover, simulations suggest that larvae hatched in the northeast Chukchi Sea would be advected out of the region by early summer (Vestfals et al., 2021). Therefore, we conclude that the observed hatch date distributions in the NBS and Chukchi Sea are most consistent with spawning and hatching occurring in the Bering Strait region or south of Bering Strait, with some contributions from Kotzebue Sound or other coastal areas in the Chukchi Sea. After hatching, larvae are advected northward but may aggregate and be retained for extended periods over the northeast Chukchi Sea shelf due to wind and flow patterns that favor retention in the summer, before being advected northward off the shelf (Levine et al., 2021).

Bias could have been introduced in length frequencies and estimated hatch date distributions because multiple gear types with different size selectivity were used to sample fish. Specifically, the Bongo net may not have adequately sampled larger larvae in the spring (Shima and Bailey, 1994) and the Marinovich trawl and IKMT may have excluded some small larvae in the summer (de Robertis et al., 2017). This could have generated a bias towards later hatch dates in the spring because the Bongo net retains larvae that are smaller and younger on average than those in the water column. In contrast, summer samples could have been biased towards earlier hatch dates because the midwater trawls target larger and older larvae. Although these differences may partially explain the difference in hatch dates between the spring-and summer-caught Arctic cod, they were unlikely to account for the large difference in mean hatch dates. Although the Bongo net may have selected against larger larvae, larvae over 20 mm were absent from IKMT hauls during ASGARD. The similar size composition between the IKMT and Bongo samples supports our assumption that the Bongo samples provided an adequate representation of the larval Arctic cod present in the region during spring.

In addition to gear selectivity, natural mortality can also be size selective as smaller fish are typically more likely to be preyed upon then larger ones (Houde, 1987). Natural mortality of larval Arctic cod is likely high (Marsh et al., 2020) and size dependent. Feeding success and survival typically increase with size, thus faster growing larvae tend to have greater survival rates and may be overrepresented in the summer samples (Pepin et al., 2015). The selection against smaller Arctic cod due to both natural mortality and gear selectivity may have caused our hatch date estimates to be biased towards earlier hatching, as well as faster growth rate estimates for summer-captured fish. On the other hand, our estimated hatch date distributions could also be biased towards later hatching because early hatching larvae have experienced a longer period of natural mortality and are therefore under-represented in the length samples. The lack of reliable natural mortality estimates and its size dependence precludes correcting for these potential biases.

4.2 Regional differences in hatch dates

Differences in hatch dates among regions may be partially explained by the timing of sea ice recession, as well as other oceanographic differences among regions. Although sea ice formation may affect spawn times (Craig et al., 1982), we focus on the timing of hatch, which is influenced by ice coverage, water temperature (Kent et al., 2016), and possibly genetic differences. Sea ice retreat generally proceeds in a northerly direction, which is consistent with fish from the southern regions hatching earlier in the season relative to their counterparts in the north. Both pelagic and demersal age-0 Arctic cod captured during summer had significantly earlier mean hatch dates in the SCS than in the NCS, possibly indicating that they originated from different spawning populations, although there was considerable overlap in hatch date distributions between the two regions. Similarly, pelagic and demersal age-0 fish in the WBS on average hatched earlier compared to those from the EBS. It is important to note that while the differences were significant, the two Beaufort Sea regions were sampled in different years, so these differences could also be the result of interannual variability.

Similar hatch dates for pelagic captured fish in the NCS and WBS are consistent with oceanographic connections between the two regions. The NCS and WBS are connected via the Alaska Coastal Current, which flows along the coast of Alaska from the Gulf of Alaska to the Beaufort Sea (Pickart et al., 2005) and has been hypothesized to transport larval and juvenile Arctic cod from southern hatching locations into the WBS (Forster et al., 2020; Levine et al., 2021). Arctic cod in the NCS and WBS appeared to be distinct from those in the EBS based on a gap in the spatial distribution of age-0 fish (Forster et al., 2020), genetic differences (Wilson et al., 2017a, 2019b; Nelson et al., 2020), and different elemental compositions of age-0 otoliths (Frothingham 2020; Z. Chapman, unpublished data). The differences in observed hatch dates provide additional evidence that juvenile Arctic cod in the WBS and EBS may originate from two separate spawning populations. However, as noted above, these differences could also arise from interannual differences in hatch timing because the regions were sampled in different years.

4.3 Differences in hatch dates between demersal and pelagic juveniles

Hatch date distributions differed significantly between demersal and pelagic age-0 Arctic cod in the EBS (Figure 6). Demersal fish were typically older on average than pelagic fish across regions, consistent with the general ontogenetic movements of age-0 fish from the surface into deeper waters or settlement to the bottom in late summer (Houde et al., 2002; Geoffroy et al., 2016). Arctic cod in the Chukchi Sea descend out of the epipelagic layer and into deeper waters when they reach lengths > 30 mm (Levine et al., 2021). In the Beaufort Sea, they descend to depths >100 m and are completely out of the epipelagic zone by October (Geoffroy et al., 2011; Bouchard et al., 2015). Differences in hatch dates between demersal and pelagic fish were more pronounced in the Beaufort Sea, where the average station depth was 283 m deeper than in the Chukchi Sea with maximum sampling depths of 200 m for the IKMT and 1,000 m for bottom trawls. Deeper stations in the Beaufort Sea allowed for greater stratification of size classes between demersal and mid-water habitats. By contrast, in the NCS region the difference in mean hatch dates between pelagic and demersal fish were much smaller and not significant as demersal captured fish had a mean hatch date slightly later than pelagic captured fish. This is likely due to the shallow depth (< 50 m) of the Chukchi Sea shelf, which is less than the depth ranges over which age-0 Arctic cod are distributed in late summer in the Beaufort Sea (Geoffroy et al., 2016). Thus, daily vertical migrations of juvenile Arctic cod on the Chukchi shelf are likely to extend to the bottom, limiting the vertical separation by size class.

4.4 Interannual variability in hatch dates

Samples in the EBS were collected over two years in 2013 and 2014, allowing for comparisons of hatch dates and growth rates among years as well as with previous studies. Previous estimates are available from Bouchard and Fortier (2011), who sampled pelagic age-0 Arctic cod in 2005 and 2006 approximately 285 km east of our EBS sampling region and from Gallaway et al. (2017) who sampled the WBS and the EBS in 2011. These comparisons suggest some notable differences that may be due to annual differences in sea ice conditions, sea surface temperatures (SST), or salinity, all of which have been hypothesized to play a large role in Arctic cod early life history (Doroshev and Arnovich, 1974; Graham and Hop, 1995; Geoffroy et al., 2011). Peak hatching in 2011 occurred in late April (Gallaway et al., 2017), similar to 2005. The range of hatch dates was also similar among the four years, beginning in mid- to late-December and extending through mid-July. There were, however, some differences among years in the peak hatch dates. Specifically, the hatch date distributions in 2005 and 2006 were bimodal with one peak occurring in early April and the other in mid-May (Figure 6 in Bouchard and Fortier, 2011). These peaks were more pronounced in 2005, whereas the 2006 hatch dates were more broadly distributed around these peak dates. In contrast, the hatch date distributions in 2011 (Gallaway et al., 2017)) and 2013 (Figure 5) showed a single, broad peak in late April. Differences in hatch timing could be due to interannual differences in environmental conditions such as sea ice coverage and freshwater influences. Mean hatch dates of samples from 2006 and 2013 were similar, differing by only one day, possibly because timing of sea ice retreat (Figure 8) was similar during those years.

Alternatively, hatch timing in the EBS may be explained by differences in freshwater discharge. The mean Mackenzie River discharge rate in March, which coincides with the incubation period just prior to hatching, was 25% higher in 2006 (4938 $m^3 s^{-1}$) than in 2005 (3672$m^3 s^{-1}$; extracted from https://wateroffice.ec.gc.ca/mainmenu/historical_data_index_e.html on 10/1/2020) and was associated with earlier hatching in 2006. This is consistent with the hypothesis that increased freshwater discharge is associated with earlier hatching due to accelerated egg development in a freshwater lens that has slightly elevated temperatures compared to the surrounding seawater (Bouchard and Fortier, 2011). Thus, differences in freshwater discharge may be more important than the timing of sea ice retreat for determining the timing of hatching of Arctic cod in areas near major river systems, whereas the timing of sea ice retreat may determine hatch timing in areas without strong freshwater influences such as the Chukchi Sea.

Mean hatch dates for demersal Arctic cod in 2013 were 26 days earlier than those from 2014. These differences are consistent with the freshwater discharge hypothesis as the Mackenzie River discharge was considerably higher in 2014 (4655 $m^3 s^{-1}$) compared to 2013 (4022 $m^3 s^{-1}$). These differences were also consistent with the hypothesis that hatch timing is determined by the timing of sea ice retreat. In 2013, sea ice began to decrease in early June and some ice was still present in mid-August in the EBS, whereas ice began to recede in early May and was completely gone by the end of June in 2014 (Figure 8). Therefore, the observed differences in hatch timing between 2013 and 2014 could be explained by either differences in freshwater discharge, differences in the timing of ice retreat or both.

4.5 Arctic cod growth rates

Regional differences in growth rates may reflect differences in temperatures, food availability, or genetic composition. Arctic cod growth rates range from 0.18 to 0.54 mm d^{-1} for field-based estimates (Bouchard and Fortier, 2011; Deary et al., 2021; Levine et al., 2021; Vestfals et al., 2019), whereas laboratory estimates are generally lower, ranging from 0.11 to 0.19 mm d^{-1} (Laurel et al., 2015; Koenker et al., 2018). The growth rates from our study fall within the range reported by Bouchard and Fortier (2011) for the Beaufort Sea, with the exception of the spring NBS and summer EBS samples, which were lower (Table 2). Estimates in the latter regions were based on small sample sizes and should be interpreted with caution, particularly in the NBS (n=14). The low r^2 values associated with the growth rates of Arctic cod in the NCS and EBS may be a result of uncertainty in ages arising from the difficulty associated with counting increments of larger otoliths and should similarly be interpreted with caution. Samples from the EBS were comprised of two different years and were combined to increase sample size, but this may have resulted in higher variability in length-at-age and larger uncertainty in the growth rate estimate due to interannual differences in growth. In general, growth rates of Arctic cod are positively correlated with SST across multiple Arctic seas (Bouchard and Fortier, 2011), consistent with the decrease in growth rates from south (not including the NBS) to north (EBS) observed in this study.

Estimates of Arctic cod growth rates could also be affected by methodological differences. Growth estimates can be affected by size-selective mortality, gear selectivity, and sampling design. Size-selective mortality favors faster growing individuals; thus, in situ growth rates based on the survivors may overestimate the population growth rate (Bailey and Houde, 1989; Litvak and Leggett, 1992) and likely contributed to the higher estimated growth rates for summer-captured larvae in the SCS. While gear selectivity may also bias growth rate estimates by selecting against larger fish, the lack of Arctic cod captured in the IKMT during the spring indicate larger fish were not present at that time. In contrast, pelagic Arctic cod in the summer were sampled with a Marinovich trawl that may have selected against smaller larvae due to its large mesh size. These gear-related biases could have contributed to the apparent differences in growth rates between the spring and summer-caught Arctic cod in this study.

Additionally, the sampling design can result in biased growth rate estimates. Many studies (e.g., Deary et al., 2021; Levine et al., 2021 for Arctic cod) have estimated growth rates based on increases in mean length between successive surveys, making the strong assumption that the same population was sampled across surveys. This assumption may be justified if estimates are made over a relatively short time period (as in Levine et al., 2021), but are more difficult to justify when sampling is separated by several months in a highly advective environment (as in Deary et al., 2021). Our approach is based on data from single surveys and requires age and length samples that are representative of the population of interest. Samples from two different surveys in the SCS and NCS in 2017 (AMBON and Arctic IES II) had similar lengths and hatch dates, despite differences in sampling locations and gear type (Marinovich vs. IKMT). Age samples were collected over a wide range of stations to minimize geographical biases but the extent to which they were representative of the populations in the study region is unclear as the population structure and the spatial distribution of different populations is largely unknown.

4.7 Management considerations

Arctic cod are recognized as a critically important forage species in the Arctic and in the US are managed and protected under the Arctic Fishery Management Plan (FMP) (NPFMC, 2009). The FMP requires periodic mapping of essential fish habitat, including potential spawning areas and nursery grounds that were largely unknown at the time the Arctic FMP was written (NPFMC, 2009). After more than a decade of research on Arctic cod in the Pacific Arctic, much has been learned (Mueter et al., 2020), but direct observations of spawning or eggs are still lacking. Our hatch date estimates can provide essential information for biophysical transport models to refine estimates of likely hatching locations (Deary et al., 2021; Vestfals et al., 2021). The results from this study have created a benchmark for hatch timing as well as growth rates for multiple Alaskan Arctic regions. More broadly, this study increases our understanding of the population dynamics of Arctic cod to help predict how their life history and abundance will change under changing Arctic conditions. Important subsistence resources such as ringed seals and beluga whales rely on Arctic cod as a lipid dense food source and changes in Arctic cod distribution and abundance will impact the Indigenous people that depend on them (Magdanz et al., 2010; Crawford et al., 2015).

5. Conclusions

The wide range of estimated hatch dates provides strong evidence that Arctic cod use a bet-hedging strategy that distributes offspring over a wide range of environmental conditions by spawning over a protracted time period across multiple locations in the Pacific Arctic. Our results align with previous findings from other regions and indicate that regional and interannual variation in hatch dates and growth rates are associated with the timing of sea ice retreat and freshwater discharge, highlighting the sensitivity of Arctic cod to changing environmental conditions in the Pacific Arctic. Earlier sea ice retreat and increased freshwater discharge under climate warming suggest that Arctic cod will hatch earlier in the future, with unknown consequences for their early growth and survival. Any impacts of climate change on Arctic cod have the potential to negatively affect upper trophic level species that rely on them or their consumers as food, including humans. Regional and seasonal differences in Arctic cod hatch dates documented here also provide evidence for the existence of multiple spawning populations in the Pacific Arctic. Although our results provide an initial assessment, additional genetic and biological information is required to help differentiate putative populations or sub-populations. Finally, the improved understanding of hatch timing and spawning dynamics can inform the development of measures to protect Arctic cod during their early life history. Continued monitoring and additional research on Arctic cod will be required to fully understand how climate change will impact their distribution and abundance and the consequences of these changes for the Arctic ecosystem.

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References

Abookire, A.A., Rose, C.S., 2005. Modifications to a plumb staff beam trawl for sampling uneven, complex habitats. Fish. Res. 71 (2), 247—254. https://doi.org/10.1016/j.fishres.2004.06.006

Agersted, M., Møller, E., Gustason, K., 2018. Bioaccumulation of oil compounds in the high-Arctic copepod *Calanus hyperboreus*. Aquat. Toxicol. 195, 8—14. https://doi.org/10.1016/j.aquatox.2017.12.001.

Aronovich, T., Doroshev, S., Spectorova, L., Makhotin, V., 1975. Egg incubation and larval rearing of navaga (*Eleginus navaga* pall.), polar cod (*Boreogadus saida lepechin*) and arctic flounder (*Liopsetta glacialis pall*.) in the laboratory. Aquac. 6 (3), 233—242. https://doi.org/10.1016/0044-8486(75)90043-5

Bailey, K.M., Houde, E.D., 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. 25, 1—83. https://doi.org/10.1016/S0065-2881(08)60187-X

Baker, M.R., 2021. Contrast of warm and cold phases in the Bering Sea to understand spatial distribution of Arctic and sub-Arctic gadids. Pol. Biol. 44(6), 1083 – 1105; https://doi.org.10.1007/s00300-021-02856-x

Baker, M.R., Kivva, K.K., Pisareva, M.N., Watson, J.T., Selivanova, J., 2020a. Shifts in the physical environment in the Pacific Arctic and implications for ecological timing and conditions. Deep-Sea Res. II 177, 104802. https://doi.org/10.1016/j.dsr2.2020.104802

Baker, M.R., Farley, E.V., Ladd, C., Danielson, S.L., Stafford, K.M., Huntington, H.P., Dickson, D.M., 2020b. Integrated ecosystem research in the Pacific Arctic—understanding ecosystem processes timing and change. Deep-Sea Res. II 177, 104850. https://doi.org/10.1016/j.dsr2.2020.104850

Baker, M.R., Farley, E.V., Danielson, S.L., Mordy, C., Stafford, K.M., Dickson, D.M.S., 2022. Integrated research in the Arctic—ecosystem linkages and shifts in the northern Bering Sea and eastern and western Chukchi Sea. Deep-Sea Res. II

Bender, M.L., Giebichenstein, J., Teisrud, R.N., Laurent, J., Frantzen, M., Meador, J.P., Sørensen, L., Hansen, B.H., Reinardy, H.C., Laurel, B., Nahrang, J., 2021. Combined effects of crude oil exposure and warming on eggs and larvae of an arctic forage fish. Sci. Rep. 11, 8410. https://doi.org/10.1038/s41598-021-87932-2

Berline, L., Spitz, Y.H., Ashjian, C.J., Campbell, R.G., Maslowski, W., Moore, S.E., 2008. Euphausiid transport in the Western Arctic Ocean. Mar. Ecol. Prog. Ser. 360, 163—178. https://doi.org/10.3354/meps07387

Bluhm, B., Gradinger, R., 2008. Regional variability in food availability for arctic marine mammals. Ecol. Appl. 18 (2), 77—96. https://doi.org/10.1890/06-0562.1

Bouchard, C., Fortier, L., 2008. Effects of polynyas on the hatching season, early growth and survival of Arctic cod *Boreogadus saida* in the Laptev Sea. Mar. Ecol. Prog. Ser. 355, 247—256 https://doi.org/10.3354/meps07335

Bouchard, C., Fortier, L., 2011. Circum-arctic comparison of the hatching season of Arctic cod *Boreogadus saida*: A test of the freshwater winter refuge hypothesis. Prog. Oceanogr. 90, 105—116. https://doi.org/10.1016/j.pocean.2011.02.008

Bouchard, C., Thorrold, S., Fortier, L., 2015. Spatial segregation, dispersion and migration in early stages of Arctic cod *Boreogadus saida* revealed by otolith chemistry. Mar. Biol. 162, 855—868. https://doi.org/10.1007/s00227-015-2629-5

Bouchard, C., Mollard, S., Suzuki, K., Robert, D., Fortier, L., 2016. Contrasting the early life histories of sympatric Arctic gadids *Boreogadus saida* and *Arctogadus glacialis* in the Canadian Beaufort Sea. Polar Biol. 39, 1005—1022. https://doi.org/10.1007/s00300-014-1617-4

Buchheister, A., Wilson, M.T., 2005. Shrinkage correction and length conversion equations for *Theragra chalcogramma*, *Mallotus villosus* and *Thaleichthys pacificus*. J. Fish Biol. 67(2), 541—548. https://doi.org/10.1111/j.0022-1112.2005.00741.x

Campana, S.E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. 59 (2), 197—242. https://doi.org/10.1111/j.1095-8649.2001.tb00127.x

Campana, S.E., Hurley, P.C., 1989. An age- and temperature-mediated growth model for Cod (*Gadus morhua*) and Haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine. Can. J. Fish. Aquat. Sci. 46, 603—613 https://doi.org/10.1139/f89-077

Carmack, E.C., Macdonald, R.W., 2002. Oceanography of the Canadian shelf of the Beaufort Sea: A setting for marine life. Arctic. 55 (5), 29—45. https://doi.org/10.14430/arctic733

Chang, W.Y.B., 1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 39 (8), 1208—1210. https://doi.org/10.1139/f82-158

Christiansen, J.S., Fevolden, S.E., 2000. The Arctic Cod of Porsangerfjorden, Norway; revisited. Sarsia. 85 (3), 189—193. https://doi.org/10.1080/00364827.2000.10414571

Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichefet, T., Friedlingstein, P., Gao, X., Gutowski, W.J., Johns, T., Krinner, G., Shongwe, M., Tebaldi, C., Weaver, A.J., Wehner, M., 2013. Long-term climate change: projections, commitments and irreversibility. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, United Kingdom and New York, NY, USA.

Cowan, J.H., Houde, E.D., Rose, K.A., 1996. Size-dependent vulnerability of marine fish larvae to predation: an individual-based numerical experiment. ICES. J. Mar. Sci. 53, 23—37. https://doi.org/10.1006/jmsc.1996.0003

Craig, P., Griffiths, W., Haldorson, L., McElderry, H., 1982. Ecological studies of Arctic Cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. Can. J. Fish. Aquat. Sci. 39 (3), 395—406. https://doi.org/10.1139/f82-057

Crawford, J.A., Quakenbush, L.T., Citta, J.J., 2015. A comparison of ringed and bearded seal diet, condition and productivity between historical (1975—1984) and recent (2003—2012) periods in the Alaskan Bering and Chukchi seas. Prog. Oceanogr. 136, 133—150. https://doi.org/10.1016/j.pocean.2015.05.011

Danielson, S.L., Eisner, L., Ladd, C., Mordy, C., Sousa, L., Weingartner, T.J., 2017a. A comparison between late summer 2012 and 2013 water masses, macronutrients, and phytoplankton standing crops in the northern Bering and Chukchi Seas. Deep Sea Res Part II. 135, 7—26. https://doi.org/10.1016/j.dsr2.2016.05.024

Danielson, S., Ahkinga, O., Edenfield, L., Eisner, L., Forster, C., Hardy, S., Hartz, S., Holladay, B., Hopcroft, R., Jones, B., Krause, J., Kuletz, K., Lekanoff, R., Lomas, M., Lu, K., Norcross, B., O'Daly, S., Pretty, J., Pham, C., Poje, A., Roth, E., Seabrook, S., Shipton, P., Smith, B., Smoot, C., Stafford, K., Stockwell, D., Yamaguchi, A., Zinkann, A., 2017b. Arctic Shelf Growth, Advection, Respiration and Deposition (ASGARD) rate measurements project. Anchorage AK: North Pacific Research Board. SKQ201709S Cruise Report to the Arctic Integrated Research Program.

Danielson, S.L., Ahkinga, O., Ashjian, C., Basyuk, E., Cooper, L.W., Eisner, L., Farley, E., Iken, K.B., Grebmeier, J.M., Juranek, L., Khen, G., Jayne, S.R., Kikuchi, T., Ladd, C., Lu, K., McCabe, R.M., Moore, G.W.K., Nishino, S., Weingartner, T.J., 2020. Manifestation and consequences of warming and altered heat fluxes over the Bering and Chukchi Sea continental shelves. Deep Sea Res Part II. 177, 104781. https://doi.org/10.1016/j.dsr2.2020.104781

Deary, A.L., Vestfals, C.D., Mueter, F.J., Logerwell, E.A., Goldstein, E.D., Stabeno, P.J., Danielson, S.L., Hopcroft, R.R., Duffy-Anderson, J.T., 2021. Seasonal abundance, distribution, and growth of the early life stages of polar cod (*Boreogadus saida*) and saffron cod (*Eleginus gracilis*) in the US Arctic. Polar Biol. 44, 2055—2076. https://doi.org/10.1007/s00300-021-02940-2

De Robertis, A., Taylor, K., Wilson, C.D., Farley, E.V., 2017. Abundance and distribution of Arctic cod (*Boreogadus saida*) and other pelagic fishes over the U.S. continental shelf of the northern Bering and Chukchi seas. Deep Sea Res., Part II. 135, 51—65. https://doi.org/10.1016/j.dsr2.2016.03.002

De Robertis, A., Taylor, K., Williams, K. and Wilson, C.D., 2017b. Species and size selectivity of two midwater trawls used in an acoustic survey of the Alaska Arctic. Deep Sea Research Part II: Topical Studies in Oceanography, 135, pp.40-50 https://doi.org/10.1016/j.dsr2.2015.11.014

Doroshev, S., Aronovich, T., 1974. The effects of salinity on embryonic and larval development of *Eleginus navga* (Pallas), *Boreogadus saida* (Lepechin) and *Liopsetta glacialis* (Pallas). Aquaculture 4, 353—362. https://doi.org/10.1016/0044-8486(74)90064-7

Drost, H., Lo, M., Carmack, E., Farrell, A., 2016. Acclimation potential of Arctic Cod (*Boreogadus saida*) from the rapidly warming Artic Ocean. J. Exp. Biol. 219, 3114—3125. https://doi.org/10.1242/jeb.140194

Eckmann, R., Rey, P., 1987. Daily increments on the otoliths of larval and juvenile *Coregonus* spp., and their modifications by environmental factors. Hydrobioligia 148, 137—143. https://doi.org/10.1007/BF00008399

Eisner, L., Hillgruber, N., Martinson, E., Maselko, J., 2012. Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi seas. Polar Biol. 36, 87—113. https://doi.org/10.1007/s00300-012-1241-0

Farley, E., Cieciel, K., Vollenweider, J., Ladd, L., Duffy-Anderson, J., Eisner, L., Kimmel, D., Lomas, M., McCabe, R., Mordy, C., Stabeno, P., Copeman, L., De Robertis, A., Levine, R., Guyon, J., Kulets, K., Logerwell, L., Mueter, F., Wilson, C., Vestals, C., Lebon, G., Berchok, C., Ferm, N., Wayner H., Reedy, M., Salo, S., Andrews, A., Grigorov, I., Baer, S., Cooper, D., Johnson G., Somoff, A., Kuznetsova, N., Flores, A., Goldstein, E., Wisegarver, E., Spear, A., Doyle, T., Pohlen, Z., 2017. Arctic integrated ecosystem survey. Anchorage AK: North Pacific Research Board. Cruise Report to the Arctic Integrated Research Program.

Forster, C., Norcross, B., Mueter, F., Logerwell, E., Seitz, A.C., 2020. Spatial patterns, environmental correlates, and potential seasonal migration triangle of Arctic Cod (*Boreogadus saida*) distribution in the Chukchi and Beaufort seas. Polar Biol. 43, 1073—1094. https://doi.org/10.1007/s00300-020-02631-4

Fortier, L., Sirois, P., Michaud, J., Barber, D., 2006. Survival of Arctic Cod larvae (*Boreogadus saida*) in relation to sea ice and temperature in the Northeast Water Polyna (Greenland Sea) Can. J. Fish. Aquat. Sci. 63 (7), 1608—1616. https://doi.org/10.1139/f06-064

Frothingham A., 2020. Age, growth, and movement dynamics of Arctic Cod (*Boreogadus saida*) in the Chukchi and Beaufort Seas. Master's thesis, College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, Alaska

Gallaway, B.J., Konkel, W.J., Norcross, B.L., 2017. Some thoughts on estimating change to Arctic Cod populations from hypothetical oil spills in the eastern Alaska Beaufort Sea. Arct. Sci. 3 (4), 716—129. https://doi.org/10.1139/as-2016-0056

Geoffroy, M., Robert, D., Darnis, G., Fortier, L., 2011. The aggregation of Arctic Cod (*Boreogadus saida*) in the deep Atlantic layer of ice-covered Amudsen Gulf (Beaufort Sea) in winter. Polar Biol. 34, 1959—1971. https://doi.org/10.1007/s00300-011-1019-9

Geoffroy, M., Majewski, A., LeBlanc, M., Gauthier, S., Walkusz, W., Reist, J., Fortier, L., 2016. Vertical segregation of age-0 and age-1+ polar cod (*Boreogadus saida*) over the annual cycle in the Canadian Beaufort Sea. Polar Biol. 39, 1023—1037. https://doi.org/10.1007/s00300-015-1811-z

Gjøsæter, H., 1995. Pelagic fish and the ecological impact of the modern fishing industry in the Barents Sea. Arctic. 48 (3), 267—279. https://www.jstor.org/stable/40511661

Graham, M., Hop, H., 1995. Aspects of reproduction and larval biology of Arctic Cod (*Boreogadus saida*). Arctic. 48 (2), 130—135. https://www.jstor.org/stable/40511636

Helser, T.E., Colman, J.R., Anderl, D.M., Kastelle, C.R., 2017. Growth dynamics of saffron cod (*Eleginus gracilis*) and Arctic Cod (*Boreogadus saida*) in the Northern Bering and Chukchi Seas. Deep Sea Res., Part II. 135, 66—77. https://doi.org/10.1016/j.dsr2.2015.12.009

Hop, H., Tonn, W.M., Welch, H.E., 1997. Bioenergetics of Arctic Cod (*Boreogadus saida*) at low temperatures. Can. J. Fish. Aquat. Sci. 54 (8), 1772—1784. https://doi.org/10.1139/f97-086

Hop, H., Gjøsæter, H., 2013. Arctic Cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. Mar. Biol. Res. 9 (9), 878—894. https://doi.org/10.1080/17451000.2013.775458

Houde, E., 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2, 17—29.

Houde, S., Albert, O., Nilssen, E., 2002. Spatial, seasonal and otogenetic variation in diet of Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*). J. Mar. Sci. 59 (2), 421—437. https://doi.org/10.1006/jmsc.2002.1171

Hüssy, K., Mosegaard, H., Hinrichsen, H.-H., Böttcher, U., 2003. Using otolith microstruction to analyse growth of juvenile Baltic cod *Gadus morhua.* Mar. Ecol. Prog. Ser. 258, 233—241 doi:10.3354/meps258233

Iken, K., Mueter, F., Grebmeier, J.M., Cooper, L.W., Danielson, S.L., Bluhm, B.A., 2018. Developing an observational design for epibenthos and fish assemblages in the Chukchi Sea. Deep Sea Res., Part II. 162, 180—190. https://doi.org/10.1016/j.dsr2.2018.11.005

Ivanova, S., Kessel, S., Espinoza, M., McLean, M., O'Neill, C., Landry, J., Hussey, N., Williams, R., Vagel, S., Fish, A., 2020. Shipping alters the movement and behavior of Arctic Cod (*Boreogadus saida*), a keystone fish in Arctic marine ecosystems. Ecol. Appl. 30 (3), e02050. https://doi.org/10.1002/eap.2050

Kent, D., Drost, H., Fisher, J., Oyama, T., Farrell, A., 2016. Laboratory rearing of wild Arctic Cod *Boreogadus saida* from egg to adulthood. J. Fish Biol. 88 (3), 1241—1248. https://doi.org/10.1111/jfb.12893

Koenker, B., Laurel, B., Copeman, L., Ciannelli, L., 2018. Effects of temperature and food availability on the survival and growth of larval Arctic Cod (*Boreogadus saida*) and walleye pollock (*Gadus chalcogrammus*). ICES J. Mar. Sci. 75 (7), 2386—2402. https://doi.org/10.1093/icesjms/fsy062

Kono, Y., Sasaki, H., Kurihara, Y., Fujiwara, A., Yamamoto, J., Sakurai, Y., 2016. Distribution pattern of Arctic Cod (*Boreogadus saida*) larvae and larval fish assemblages in relation to oceanographic parameters in the northern Bering Sea and Chukchi Sea. Polar Biol. 39, 1039—1048. https://doi.org/10.1007/s00300-016-1961-7

Ladd, C., Mordy, C.W., Salo, S.A., Stabeno P.J., 2016. Winter water properties and the Chukchi polynya. J. Geophys. Res.: Oceans. 121, 5516—5534. https://doi.org/10.1002/2016JC011918.

Laurel, B., Spencer, M., Iseri, P., Copeman, L., 2015. Temperature-dependent growth and behavior of juvenile Arctic Cod (*Boreogadus saida*) and co-occurring North Pacific gadids. Polar Biol. 39, 1127—1135. https://doi.org/10.1007/s00300-015-1761-5

Laurel, B., Copeman, L., Spencer, M., Iseri, P., 2018. Comparative effects of temperature on rates of development and survival of eggs and yolk-sac larvae of Arctic Cod (*Boreogadus saida*) and walleye Pollock (*Gadus chalcogrammus*). ICES J. Mar. Sci. 75, 2403—2412. https://doi.org/10.1093/icesjms/fsy042

Laurel, B., Copeman, L., Iseri, P., Spencer, M., Hutchinson, G., Nordtug, T., Donald, C., Meier, S., Allan, S., Boyd, D., Ylitalo, G., Cameron, J., French, B., Linbo, T., Scholz, N., Incardona, J., 2019. Embryonic crude oil exposure impairs growth and lipid allocation in a keystone arctic forage fish. iScience 19: 1101—1113. https://doi.org/10.1016/j.isci.2019.08.051

LeBlanc, M., Geoffroy, M., Bouchard, C., Gauthier, S., Majewski, A., Reist, J., Fortier, L., 2020. Pelagic production and recruitment of juvenile Arctic Cod (*Boreogadus saida*) in Canadian Arctic seas. Polar Biol. 43, 1043—1054. https://doi.org/10.1007/s00300-019-02565-6

Levine, R.M., De Robertis, A., Grünbaum, D., Woodgate, R., Mordy, C.W., Mueter, F., Cokelet, E., Lawrence-Slavas, N., Tabisola, H., 2021. Autonomous vehicle surveys indicate that flow reversals retain juvenile fishes in a highly advective high-latitude ecosystem. Limnol. Oceanogr. 9999, 1—6. https://doi.org/10.1002/lno.11671

Litvak, M.K., Leggett, W.C., 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. Mar. Ecol. Prog. Ser. 81, 13—24. www.jstor.org/stable/24827347.
MacDonald, R., Wong, C., 1987. The distribution of nutrients in the southeastern Beaufort Sea: Implications for water circulation and primary production. J. Geophys. Res., 92, 2939—2952. https://doi.org/10.1029/JC092iC03p02939

Magdanz, J.S., Braem, N.S., Robbins, B.C., Koster, D.S., 2010. Subsistence harvests in Northwest Alaska, Kivalina and Noatak, 2007. Alaska Department of Fish and Game Division of Subsistence Technical Paper No. 354, Kotzebue.

Majewski, A.R., Atchison, S., MacPhee, S., Eert, J., Niemi, A., Michel, C., Reist, J.D., 2017. Marine fish community structure and habitat associations on the Canadian Beaufort shelf and slope. Deep Sea Res., Part I. 121, 169—182. https://doi.org/10.1016/j.dsr.2017.01.009

Marsh, J.M., Mueter, F.J., Quinn II, T.J. 2020a. Environmental and biological influences on the distribution and population dynamics of Arctic Cod (*Boreogadus saida*) in the US Chukchi Sea. Polar Biol. 43 (8), 1055—1072. https://doi.org/10.1007/s00300-019-02561-w

Marsh, J.M., Mueter, F.J., 2020. Influences of temperature, predators, and competitors on Arctic Cod (*Boreogadus saida*) at the southern margin of their distribution. Polar Biol. 43, 995—1014. https://doi.org/10.1007/s00300-019-02575-4

Marsh, J.M., Mueter, F.J., Thorson, J.T., Britt, L., Zador, S., 2020b. Shifting fish distributions in the Bering Sea. In: State of the Climate 2019. Bull. Amer. Meteor. Soc. 101 (8), S254—S256. https://doi.org/10.1175/BAMS-D-20-0086.1

Meier, W.N., Stewart, J.S., Liu, Y., Key, J., Miller, J.A., 2017. Operational implementation of sea ice concentration estimates from the AMSR2 sensor. IEEE J Sel Top Appl Earth Obs Remote Sens. 10 (9), 3904—3911 https://doi.org/10.1109/JSTARS.2017.2693120.

Methot R.D., 1986. Frame trawl for sampling pelagic juvenile fish. CALCOFI Rep. 27, 267—278.

Mueter, F., Bouchard, C., Hop, H., Laurel, B., Norcross, B., 2020. Arctic gadids in a rapidly changing environment. Polar Biol. 43 (8), 945—950. https://doi.org/10.1007/s00300-020-02696-1

Mueter, F.J., Nahrgang, J., John Nelson, R., Berge, J., 2016. The ecology of gadid fishes in the circumpolar Arctic with a special emphasis on the Arctic Cod (*Boreogadus saida*). Polar Biol. 39 (6), 961—967. https://doi.org/10.1007/s00300-016-1965-3

Mueter, F.J., Planque, B., Hunt Jr, G.l., Alabia, I.D., Hirawake, T., Eisner, L, Dalpadado, P., Chierici, M., Drinkwater, K.F., Harada, N., Arneberg, p., 2021. Possible future scenarios in the gatways to the Arctic for Subarctic and Artic marine systems: II. Prey resources, food webs, fish, and fisheries. ICES J. Mar. Sci. 78(9), 3017 – 3045. https://doi.org/10.1093/icesijms/fsab122

Nahrgang J., Storhaug E., Murzina S.A., Delmas O., Nemova N.N., Berge J., 2015. Aspects of reproductive biology of wild-caught polar cod (*Boreogadus saida*) from Svalbard waters. Polar Biol. 39, 155—1164. https://doi.org/10.1007/s00300-015-1837-2

Narimatsu, Y., Hattori, T., Ueda, Y., Matsuzaka, H., Shiogaki, M., 2007. Somatic growth and otolith microstructure of larval and juvenile Pacific cod *Gadus macrocephalus*. Fish. Sci. 73, 1257—1264 https://doi.org/10.1111/j.1444-2906.2007.01463.x

Nelson, R.J., Bouchard, C., Fortier, L., Majewski, A.R., Reist, J.D., Præbel, K., Madsen, M.L., *et al.,* 2020. Circumpolar genetic population structure of Arctic Cod, *Boreogadus saida*. Polar Biol. 43, 951—961. https://doi.org/10.1007/s00300-020-02660-z.

Norcross, B.L., Apsens, S.J., Bell, L.E., Bluhm, B.A., Dissen, J.N., Edenfield, L.E., Frothingham, A., Gray, B.P., Hardy, S.M., Holladay, B.A., Hopcroft, R.R., Iken, K.B., Smoot, C.A., Walker, K.L., Wood, E.D., 2017. US-Canada transboundary fish and lower trophic communities: abundance, distribution, habitat and community analysis. US Dept. of the Interior, Bureau of Ocean Energy Management, Alaska OCS Region. Final Report Number for BOEM Agreement Number M12AC00011

NPFMC, 2009. Fishery management plan for fish resources of the Arctic management area. North Pacific Fishery Management Council, 605 W. 4th Ave., Suite 306, Anchorage, AK 99501, Anchorage.

Parker-Stetter, S., Horne, J., Weingartner, T., 2011. Distribution of Arctic Cod and age-0 fish in the U.S. Beaufort Sea. Polar Biol. 34, 1543—1557. https://doi.org/10.1007/s00300-011-1014-1

Peng G., Meier, W.N., Scott, D., Savoie, M., 2013. A long-term and reproducible passive microwave sea ice concentration data record for climate studies and monitoring. Earth Syst. Sci. Data. 5, 311—318. https://doi.org/10.5194/essd-5-311-2013

Pepin, P., Robert, D., Bouchard, C., Dower, J.F., Falardeau, M., Fortier, L., Jenkins, G.P., et al., 2015. Once upon a larva: revisiting the relationship between feeding success and growth in fish larvae. ICES J. Mar. Sci. 72 (2), 359—373. https://doi.org/10.1093/icesjms/fsu201

Pickart, R., 2004. Shelfbreak circulation in the Alaskan Beaufort Sea: Mean structure and variability. J. Geophys. Res., 109, C04024. https://doi.org/10.1029/2003JC001912

Pickart, R.S., Weingartner, T.J., Pratt, L.J., Zimmermann, S., Torres, D.J., 2005. Flow of winter-transformed Pacific water into the Western Arctic. Deep Sea Res., Part II. 52, 3175—3198. https://doi.org/10.1016/j.dsr2.2005.10.009

Pickart, R.S., Lawrence, P.J., Torres, D.J., Whitledge, T.E., Proshutinsky, A.Y., Aagaard, K., Agnew, T.A., Moore, G.W.K., Dail, D.J., 2010. Evolution and dynamics of the flow through Herald Canyon in the western Chukchi Sea. Deep Sea Res., Part II. 57 (1—2), 5—26. https://doi.org/10.1016/j.dsr2.2009.08.002

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team (2020). _nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-147, <URL: https://CRAN.R-project.org/package=nlme>.

Shama, L., 2015. Bet hedging in a warming ocean: predictability of maternal environment shapes offspring size variation in marine sticklebacks. Glob. Change Biol. 21 (12), 4387—4400. https://doi.org/10.1111/gcb.13041

Shima, M., Bailey, K.M., 1994. Comparative analysis of ichthyoplankton sampling gear for early life stages of walleye pollock (*Theragra chalcogramma*). Fish. Oceanogr. 3, 50—59. https://doi.org/10.1111/j.1365-2419.1994.tb00047.x

Thoman, R., Richter-Menge, J., Druckenmiller, M., Eds, 2020. Arctic Report Card 2020, https://doi.org/10.25923/mn5p-t549

Vestfals, C., Mueter, F., Duff-Anderson, J., Busby, M., De Robertis, A., 2019. Spatio-temporal distribution of Arctic Cod (*Boreogadus saida*) and saffron cod (*Eleginus gracilis*) early life stages in the Pacific Arctic. Polar Biol. 42, 969—990. https://doi.org/10.1007/s00300-019-02494-4

Vestfals, C.D., Mueter, F.J., Hedstrom, K.S., Laurel, B.J., Petrik, C.M., Duffy-Anderson, J.T., Danielson, S.L., 2021. Modeling the dispersal of polar cod (*Boreogadus saida*) and saffron cod (*Eleginus gracilis*) early life stages in the Pacific Arctic using a biophysical transport model. Prog. Oceanogr., 196:102571, https://doi.org/10.1016/j.pocean.2021.102571

Weingartner, T.J., 1997. A review of the physical oceanography of the northeastern Chukchi Sea. In: Fish ecology in Arctic North America. Am. Fish. Soc. Sym. 19, 40—59, Bethesda, Maryland.

Welch, H., Crawford, R., Hop, H., 1993. Occurrence of Arctic Cod (*Boreogadus saida*) schools and their vulnerability to predation in the Canadian High Arctic. Arctic46 (4), 331—339. https://doi.org/10.14430/arctic1361

Wilson, R.E., Sage, G.K., Sonsthagen, S.A., Gravely, M.C., Menning, D.M., Talbot, S.L., 2017. Genomics of Arctic Cod. Anchorage, AK: US Dept. of the Interior, Bureau of Ocean Energy Management, Alaska OCS Region. Report for BOEM OSC Study 2017—066

Wilson, R., Sage, G., Wedemeyer, K., Sonsthagen, S., Menning, D., Gravley, M., Sexson, M., Nelson, R., Talbot, S., 2019. Micro-geographic population genetic structure within Arctic Cod (*Boreogadus saida*) in Beaufort Sea of Alaska. ICES J. Mar. Sci. 76, 1713—1721.

Word, J., Stoekel, D., Greer, C., Coelho, G., Clark, J., Staves, J., Essex, L., et al., 2014. Environmental impacts of Arctic oil spills and Arctic spill response technologies. Arctic oil spill response technology joint industry programme. Available at https://neba.arcticresponsetechnology.org/assets/files/Environmental%20Impacts%20of%20Arctic%20Oil%20Spills%20-%20report.pdf [Accessed 23 February, 2021]

Word, J., Word, L., Gardiner, W., Word, J., McFarlin, K., Perkins, R., 2011. Joint industry program to evaluate biodegradation and toxicity of dispersed oil in cold water environments of the Beaufort and Chukchi Seas. Phase 1 and Phase 2 final report. University of Alaska Fairbanks. Available at https://neba.arcticresponsetechnology.org/media/1109/jip-ph-1-2-final-report-12-04-11.pdf [Accessed 23 February 2021]

Figures:

Figure 1: Locations where Arctic cod for aging were captured. Color change from dark to light represents the number of specimens captured at a station, where N=7 denotes 7 or more specimens. Study regions are the northern Bering Sea (NBS), southern (SCS) and northern Chukchi Sea (NCS) and western (WBS) and eastern Beaufort Sea (EBS). No samples for aging were obtained from the WBS.

Figure 2: (A) Polished sagittal otolith at 40x magnification with daily growth increments marked at every 5th increment. (B) Cropped image of the same otolith showing the hatch mark. **(**C) Sagittal otolith at 100X magnification from a lab raised Arctic cod with the hatch mark outlined.

Figure 3: Length frequency distributions (x-axis, in mm) of age-0 Arctic cod sampled in each region by season and vertical location in the water column. The number of individuals measured in each region is indicated (N).

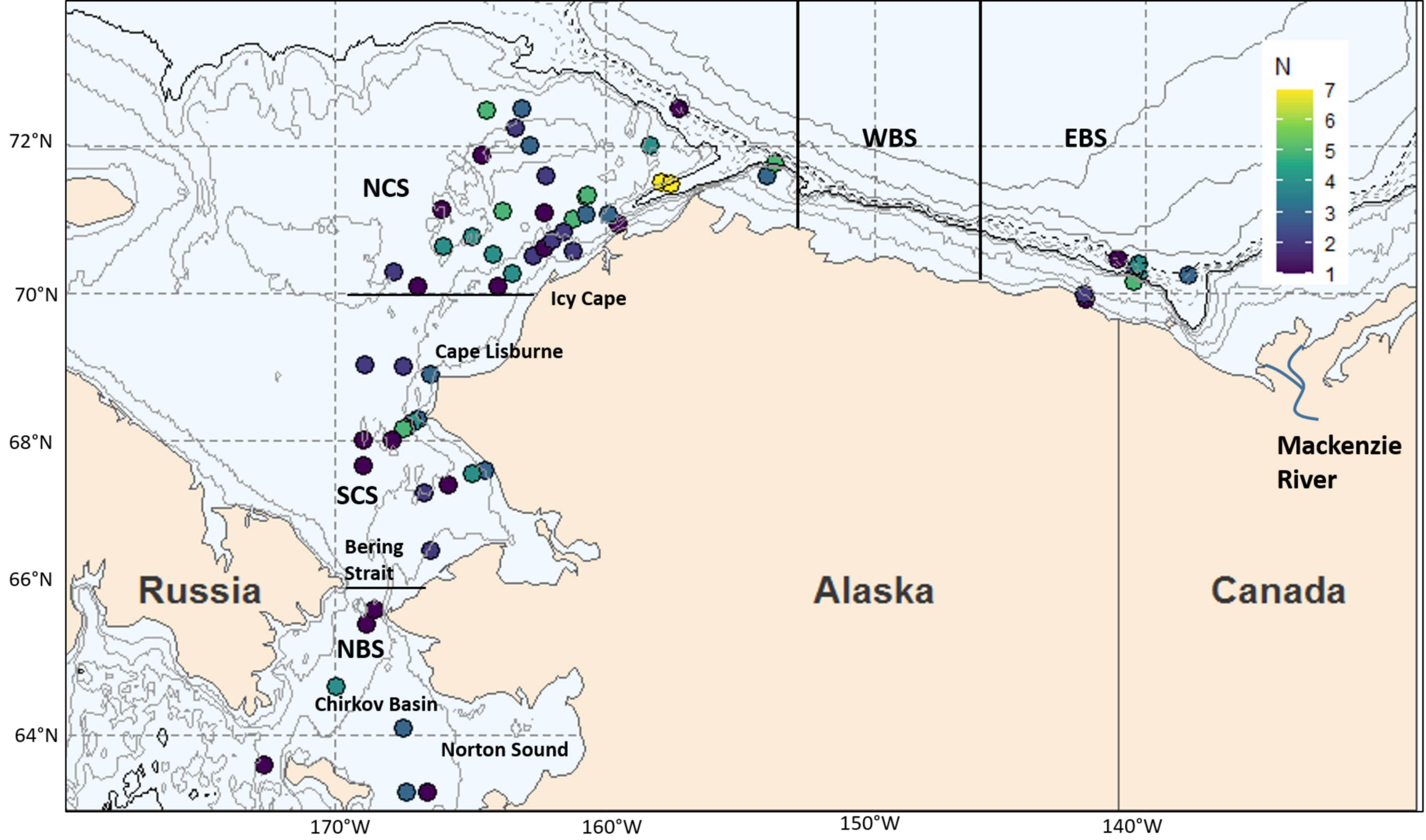
Figure 4: Stations with length data for Arctic cod. Shading denotes average length (mm) by station for Arctic cod captured during the spring survey in the water column (Bongo nets, BA) and during the summer survey in the water column (pelagic trawl, B) and on the bottom (demersal trawl, C).

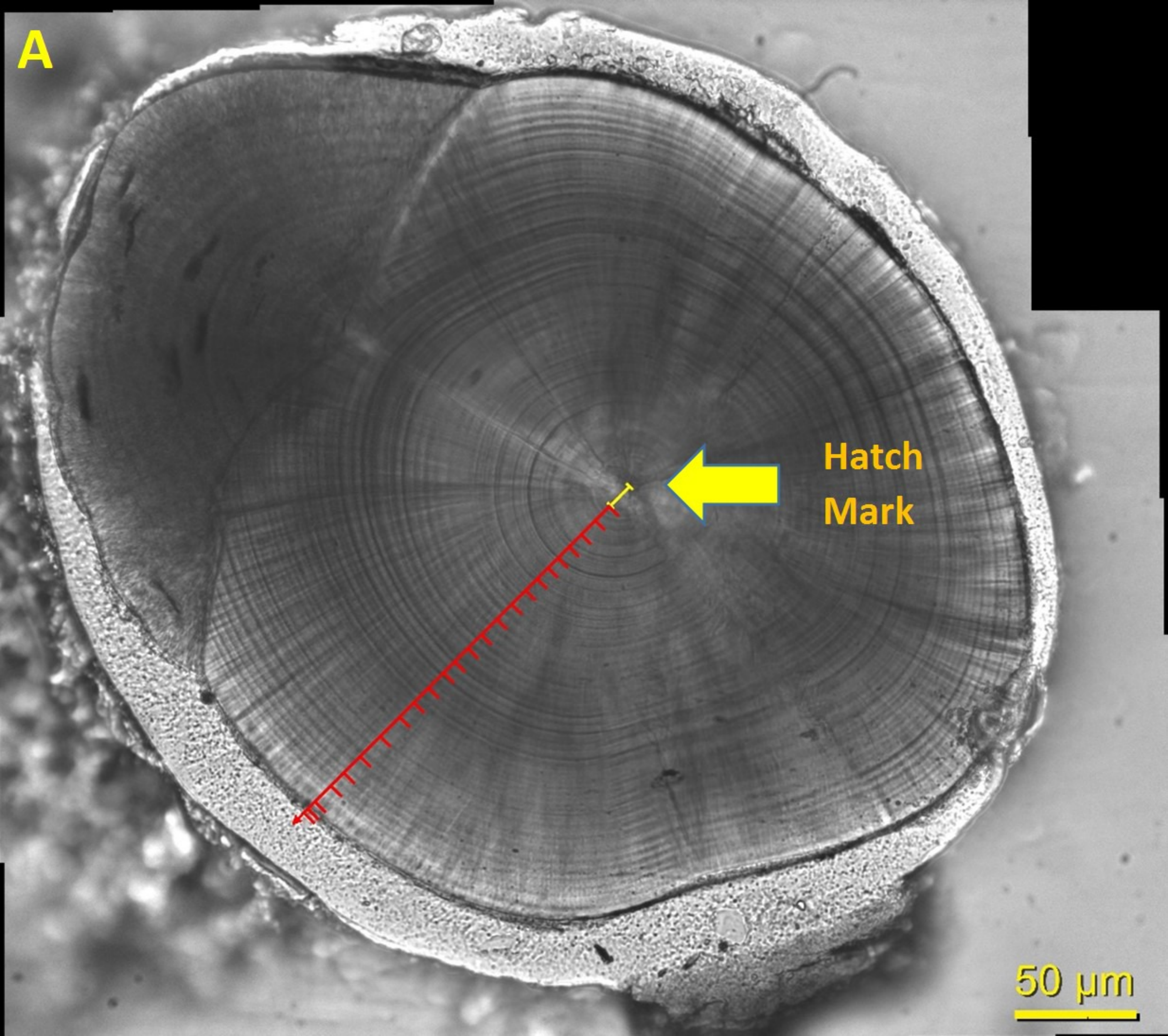
Figure 5: Estimated hatch date distributions by location in the water column for each region: northern Bering Sea (NBS), southern Chukchi Sea (SCS), northern Chukchi Sea (NCS), western Beaufort Sea (WBS), and eastern Beaufort Sea (EBS). Smoothed density plots were generated using 10,000 simulated hatch dates as explained in the methods.

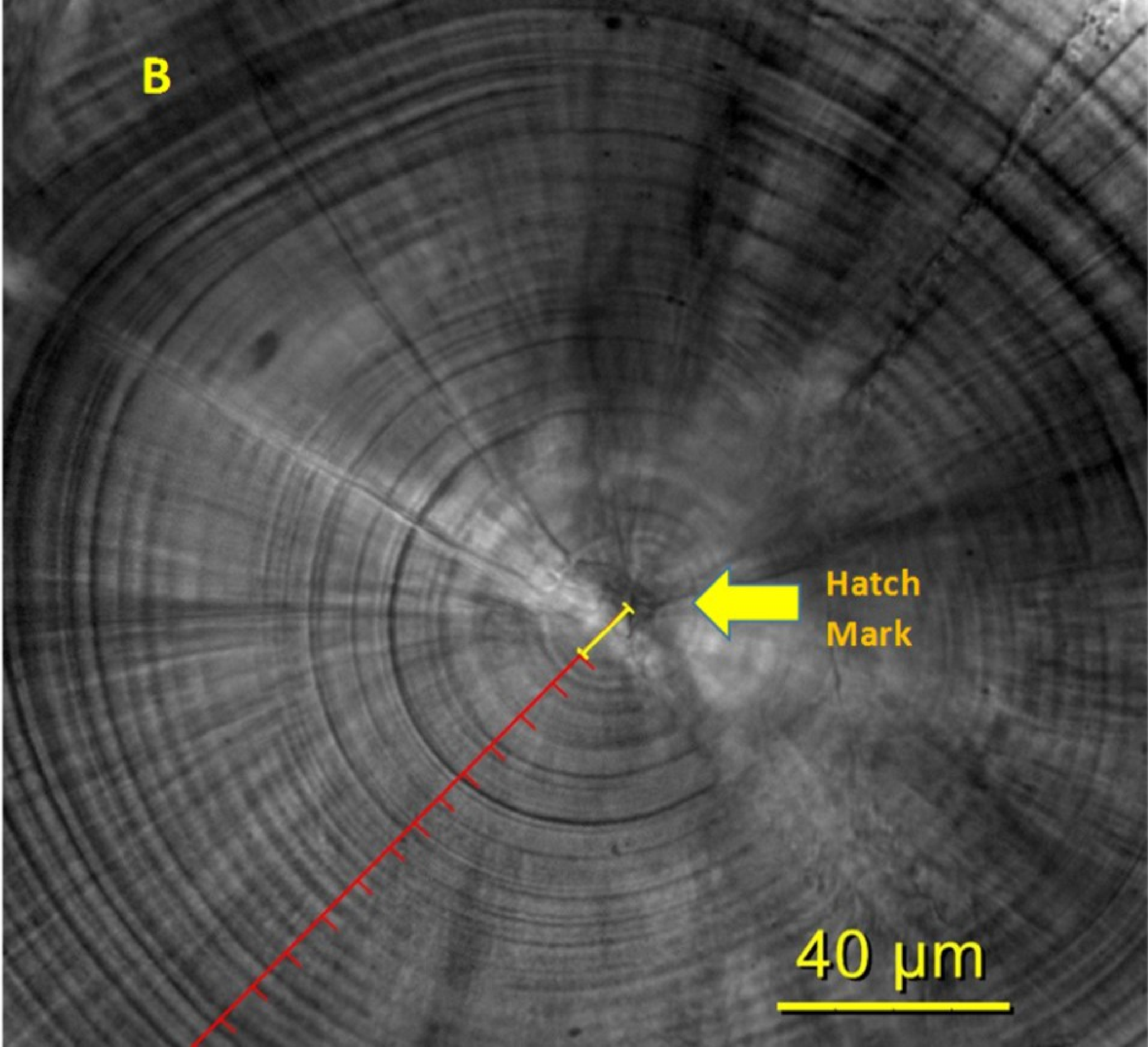
Figure 6: Estimated mean hatch dates with 95% confidence limits for each region (northern Bering Sea (NBS), southern Chukchi Sea (SCS), northern Chukchi Sea (NCS), western Beaufort Sea (WBS), and eastern Beaufort Sea (EBS)) and vertical location (pelagic or demersal). Tick marks on the y-axis refer to the first day of the month.

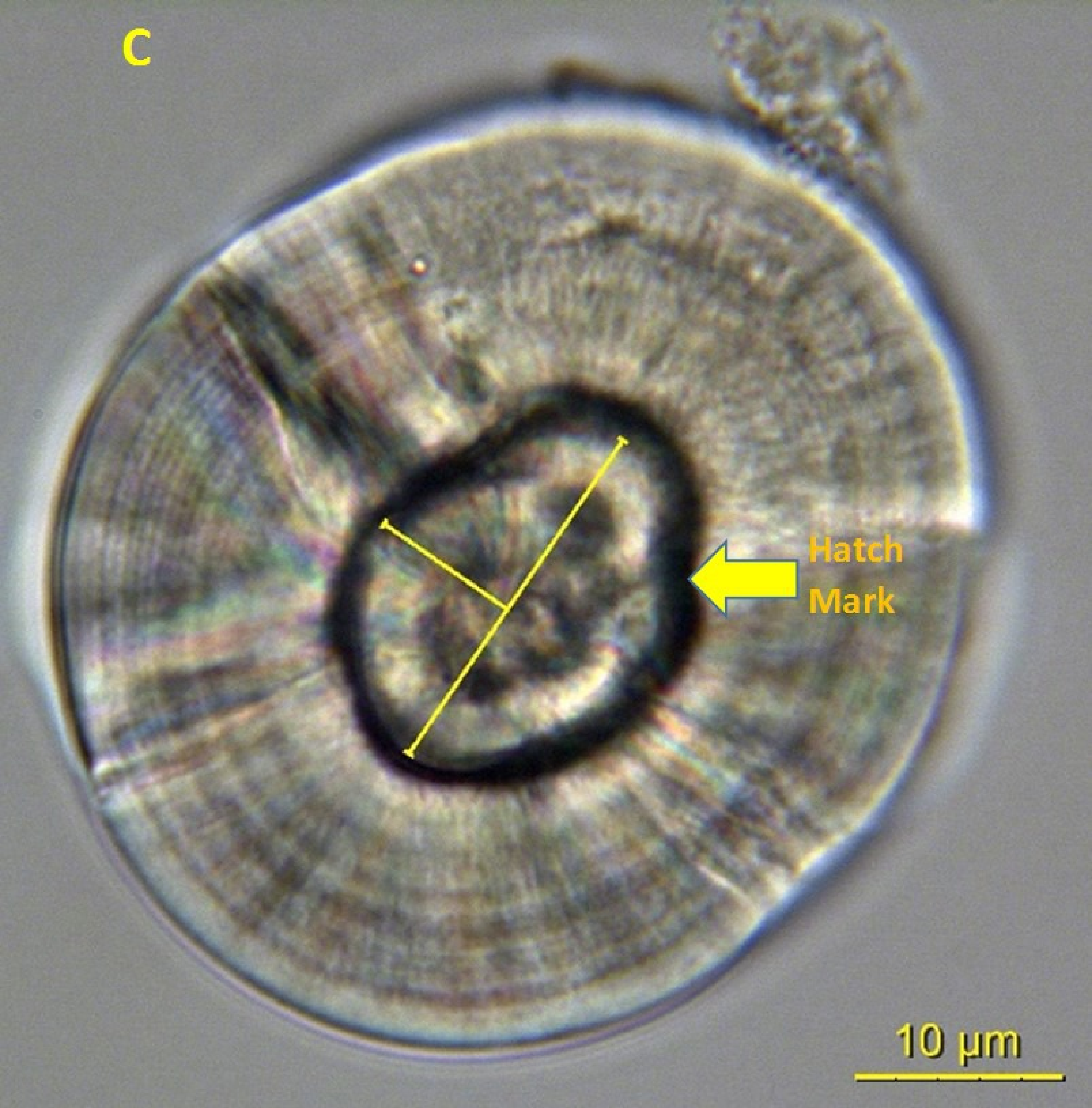
Figure 7: Regressions of length on age to estimate growth rates for spring (A) and summer (B) captured age-0 Arctic cod.

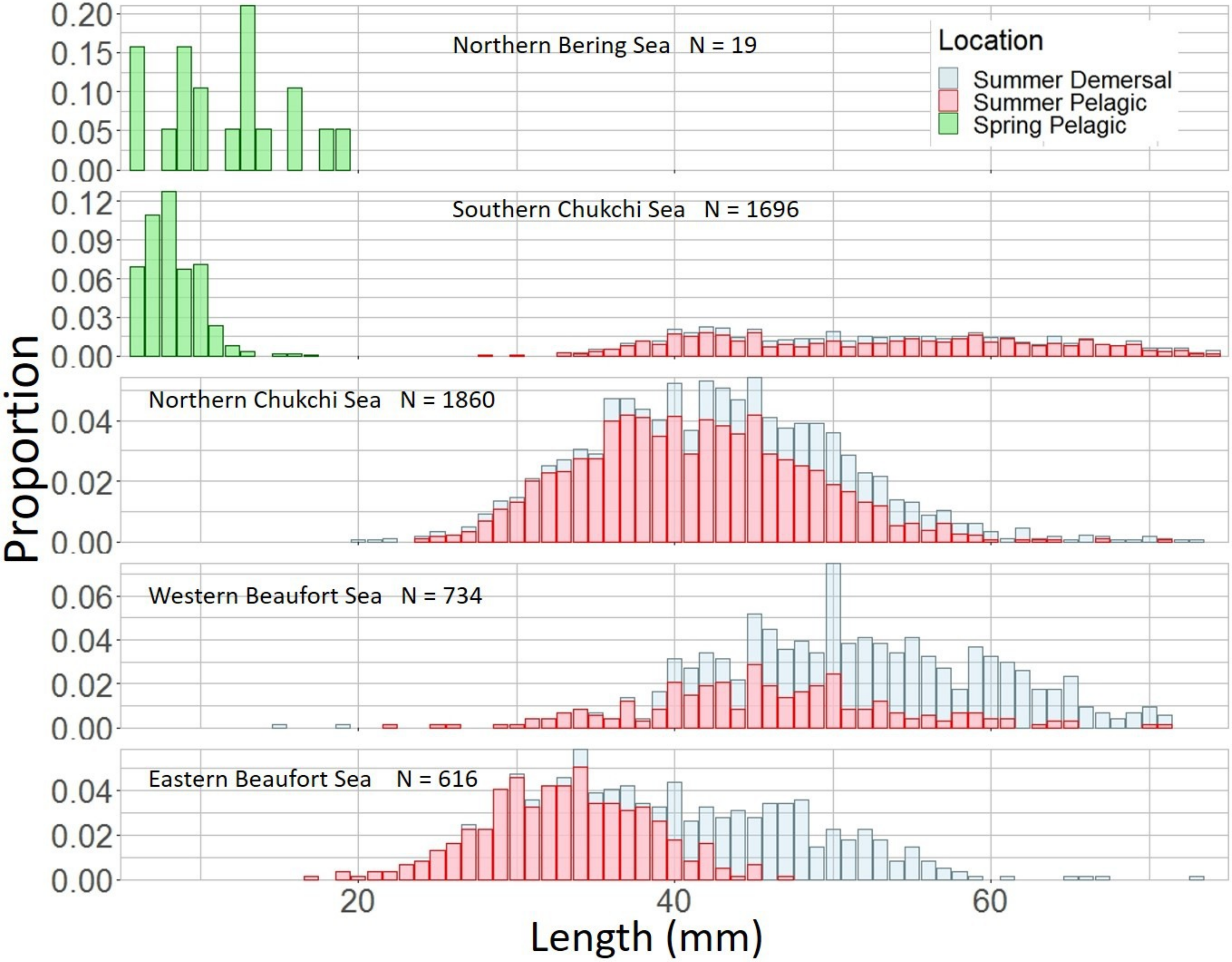
Figure 8: Seasonal trends in sea ice concentration (fraction of area with > 15% sea ice) for the eastern Beaufort Sea sampling region for five selected years with hatch date information. Sea ice concentrations are the fraction of the maximum daily extent of sea ice observed on the eastern Beaufort Sea shelf between 69.6 and 79.1°N and between 138°W and 134°W. Data from the NOAA National Snow and Ice Data Center (Peng et al., 2013; Meier et al., 2017).

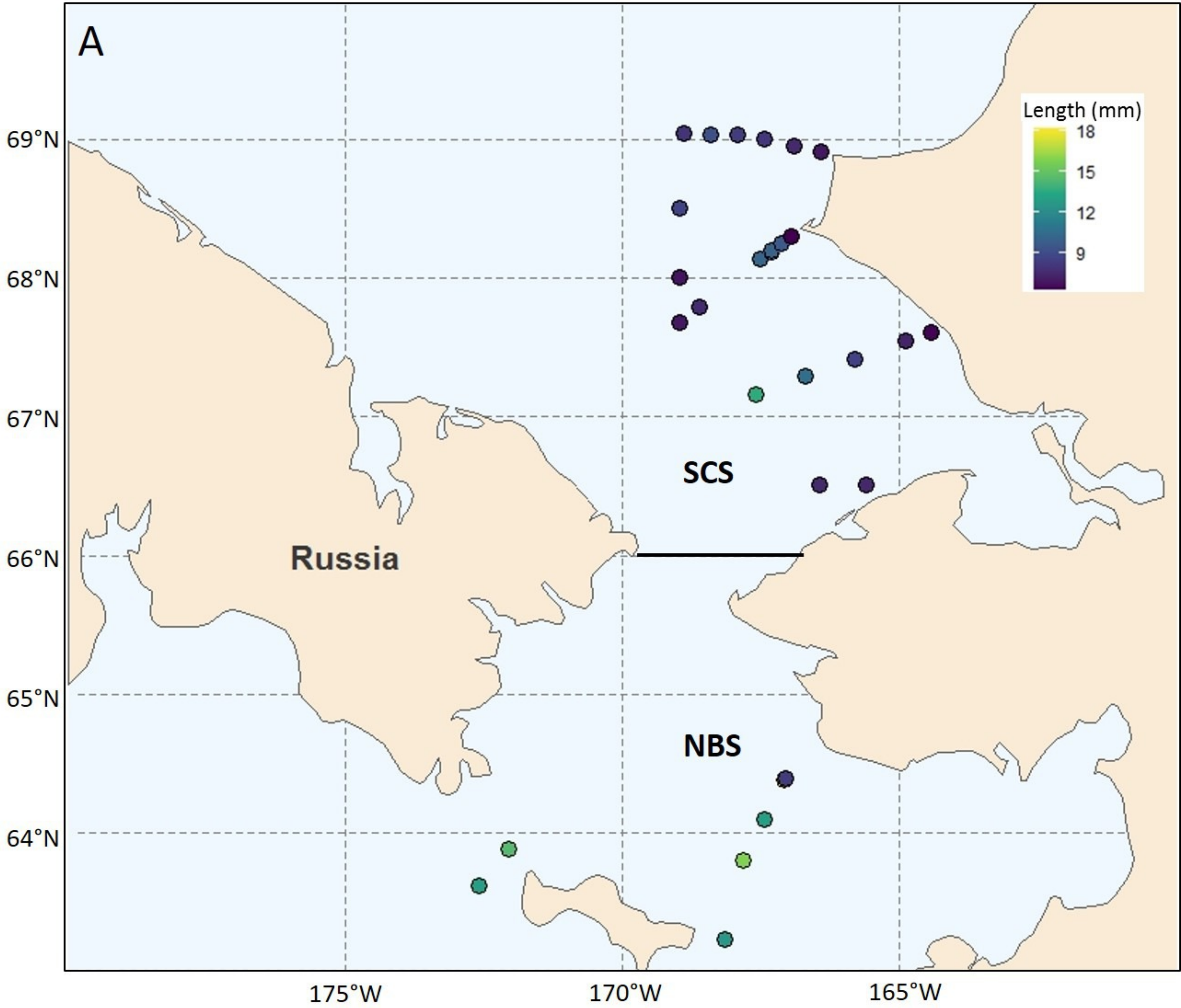

N
7
6
5
4
3
2
1
WBS
EBS
NCS
Icy Cape
Cape Lisburne
SCS
Bering Strait
NBS
Chirkov Basin
Norton Sound
Russia
Alaska
Canada
Mackenzie River
72°N
70°N
68°N
66°N
64°N
170°W
160°W
150°W
140°W

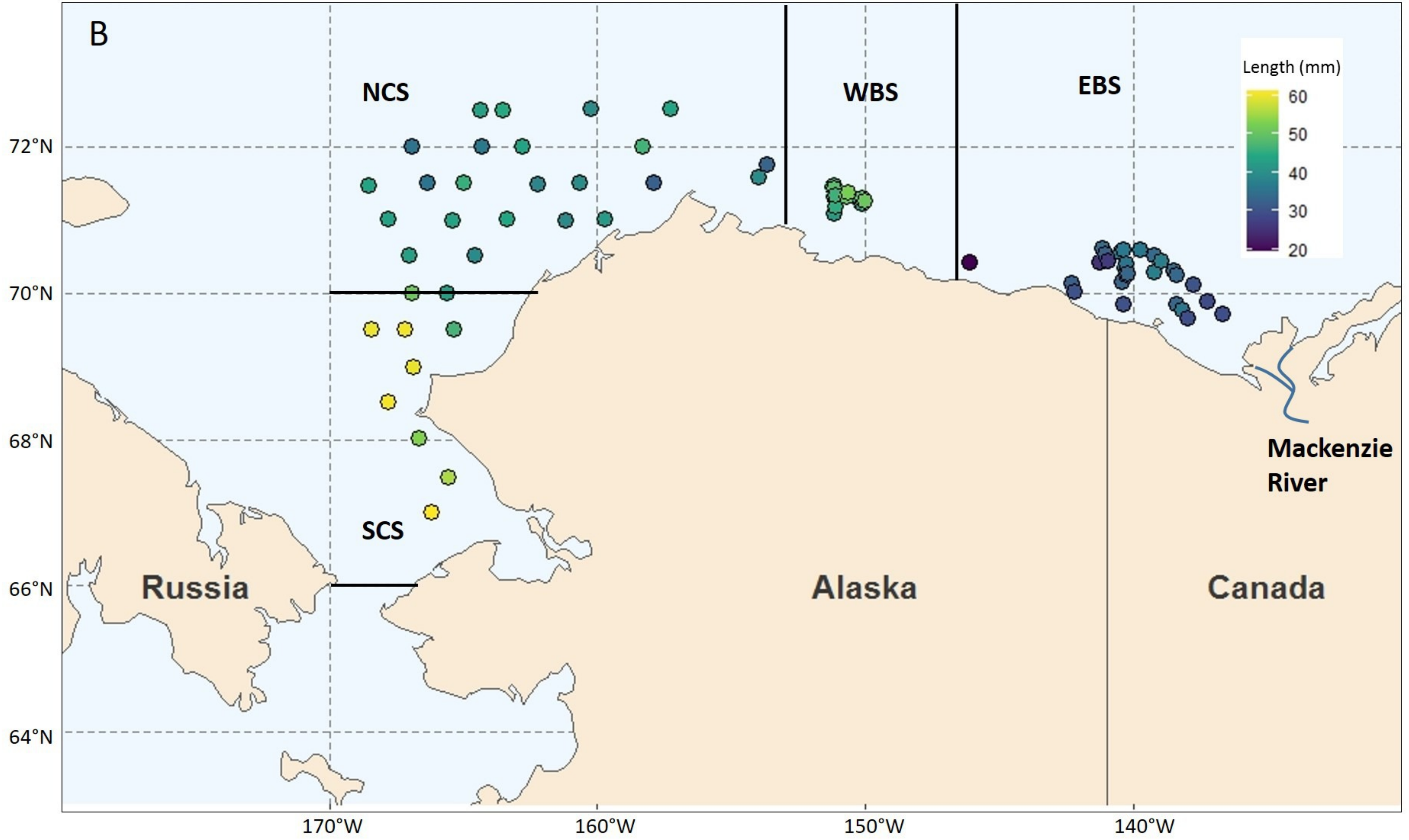

A
Hatch
Mark
50 µm

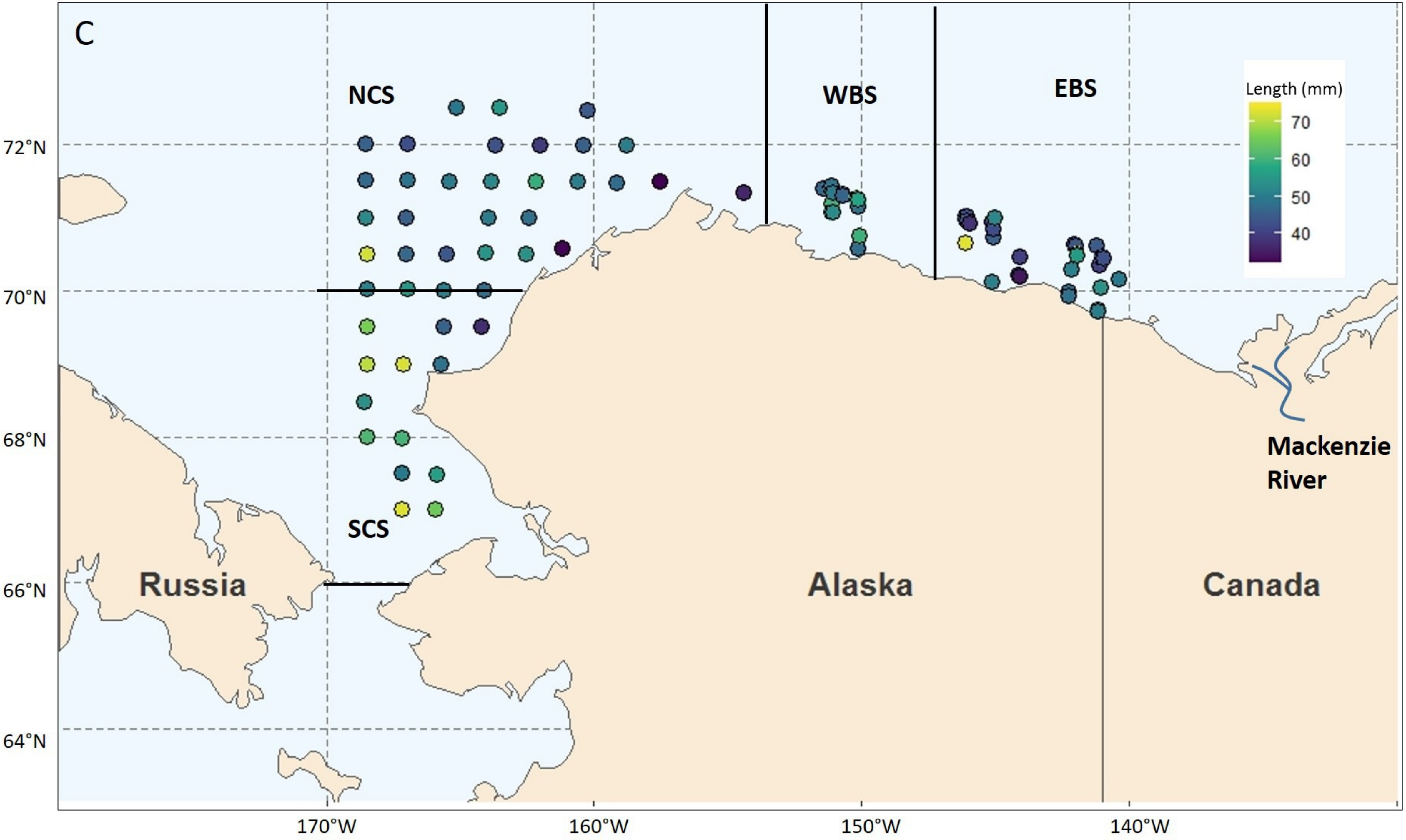

B
Hatch Mark
40 µm

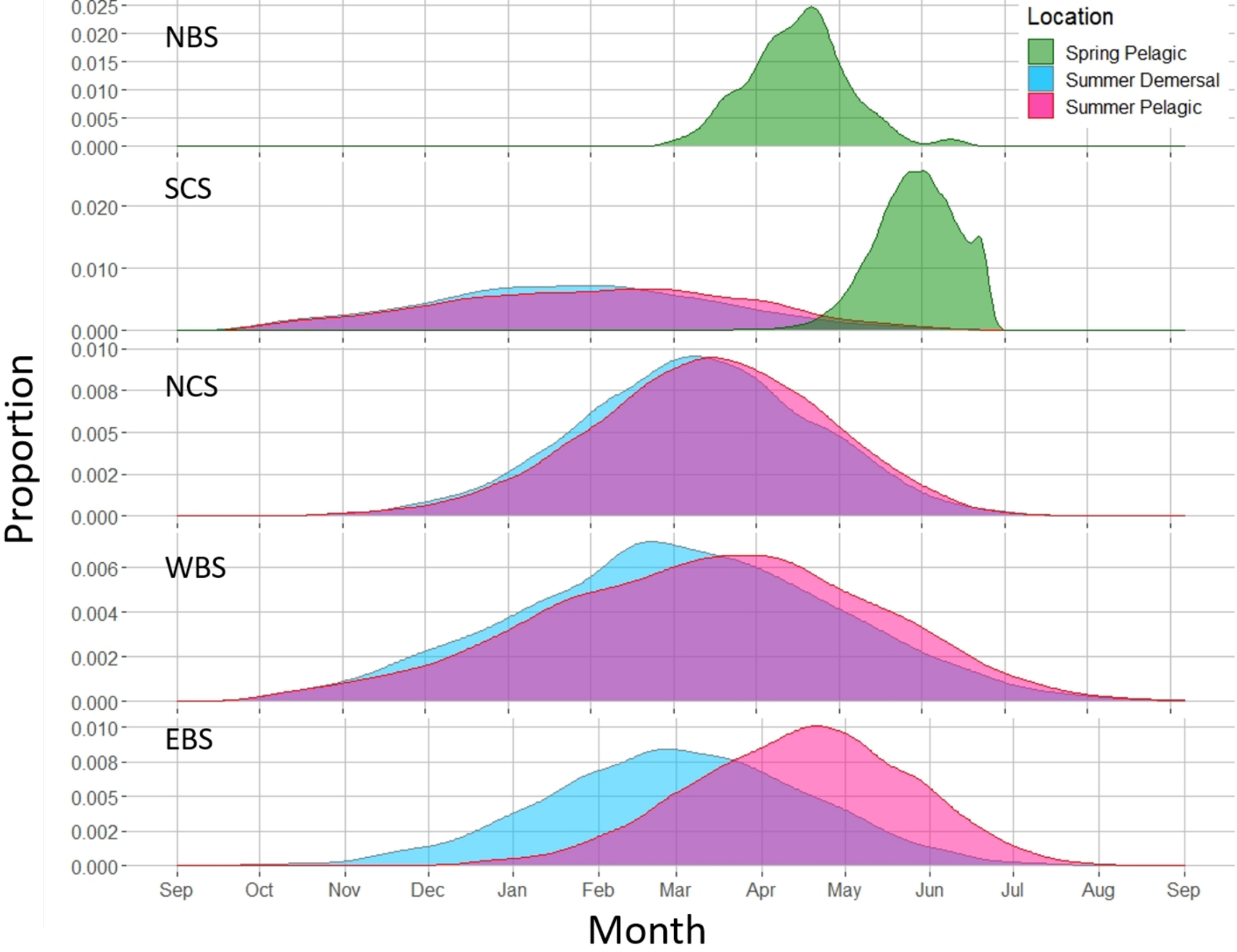

C
Hatch Mark
10 µm

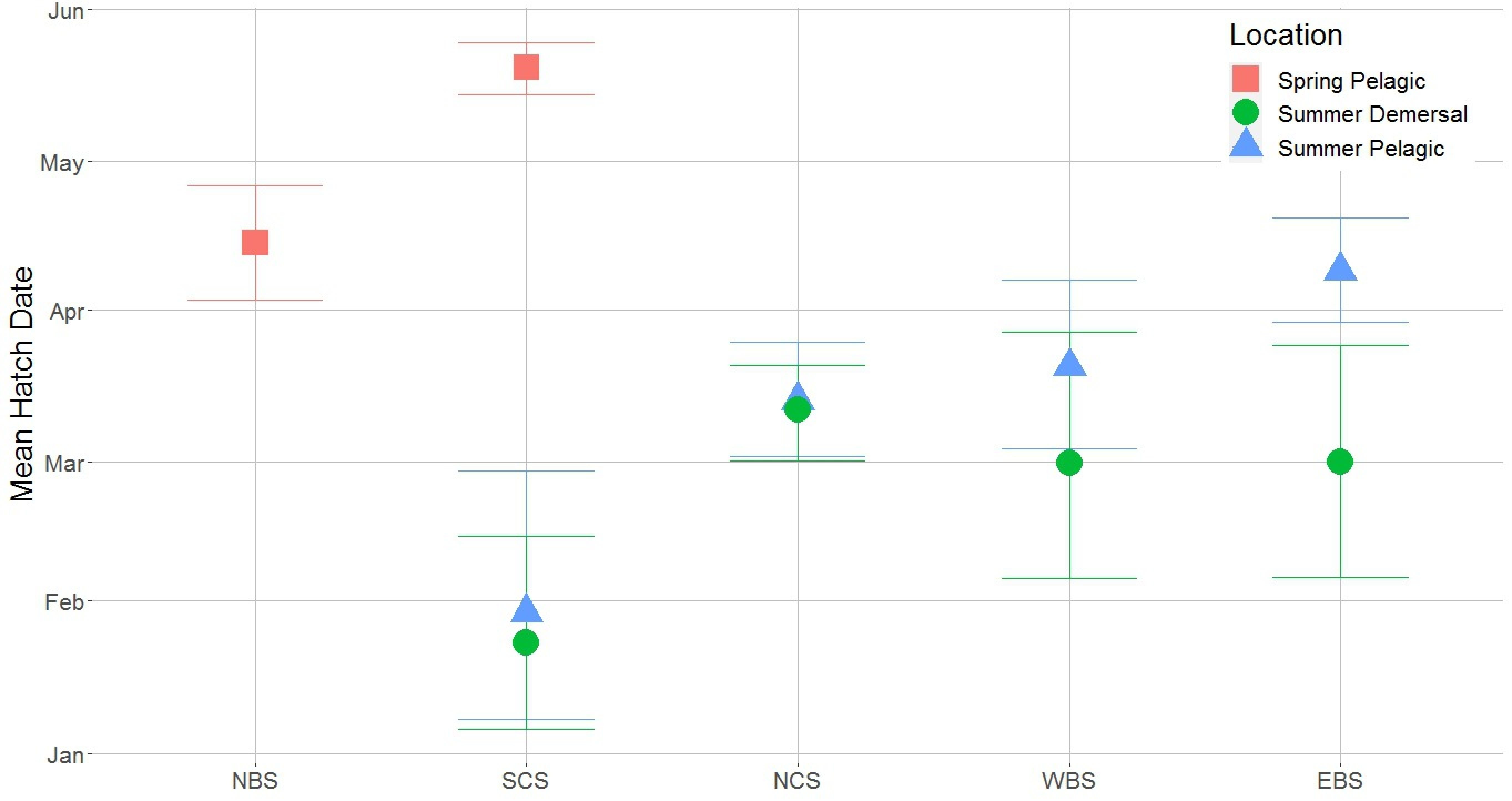

Northern Bering Sea N = 19
Southern Chukchi Sea N = 1696
Northern Chukchi Sea N = 1860
Western Beaufort Sea N = 734
Eastern Beaufort Sea N = 616
Location
Summer Demersal
Summer Pelagic
Spring Pelagic
Proportion
Length (mm)
0.20
0.15
0.10
0.05
0.00
0.12
0.09
0.06
0.03
0.00
0.04
0.02
0.00
0.06
0.04
0.02
0.00
0.04
0.02
0.00
20
40
60

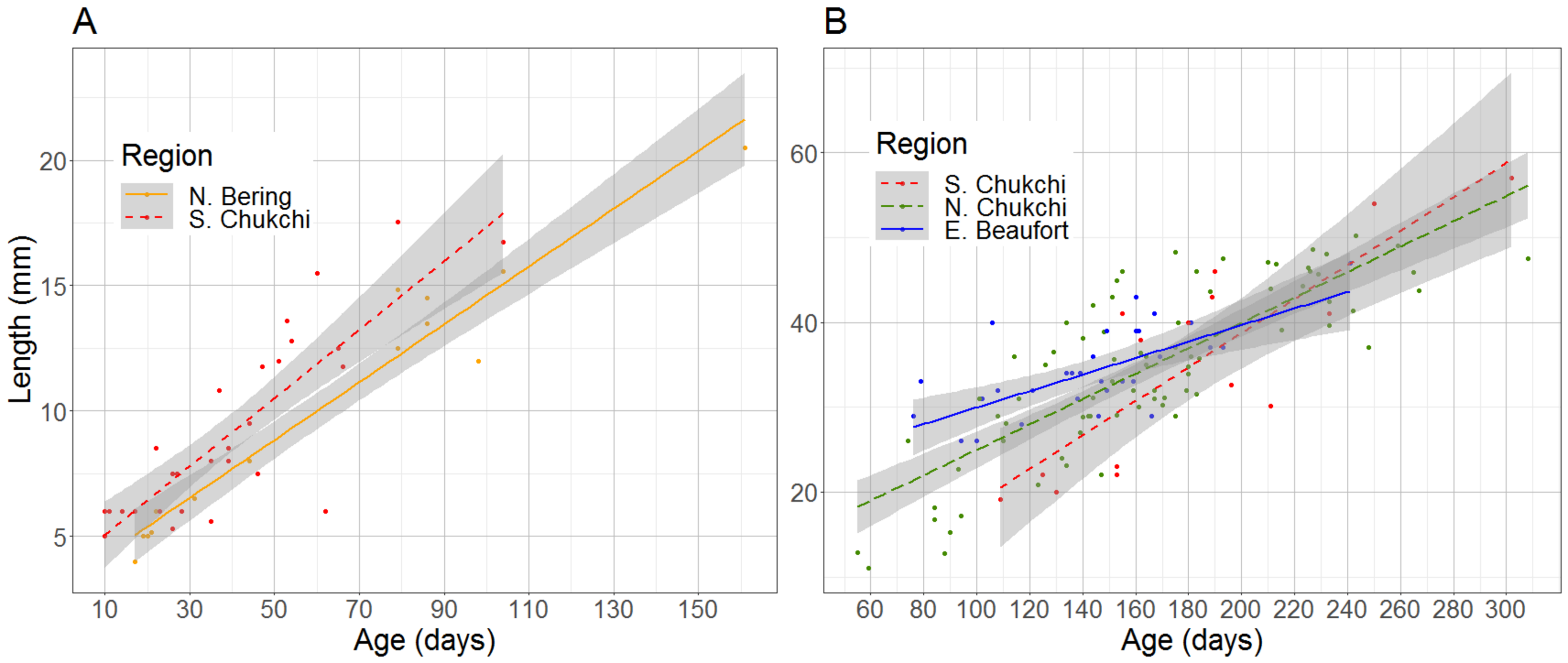

A
Length (mm)
18
15
12
9
Russia
SCS
NBS
69°N
68°N
67°N
66°N
65°N
64°N
175°W
170°W
165°W

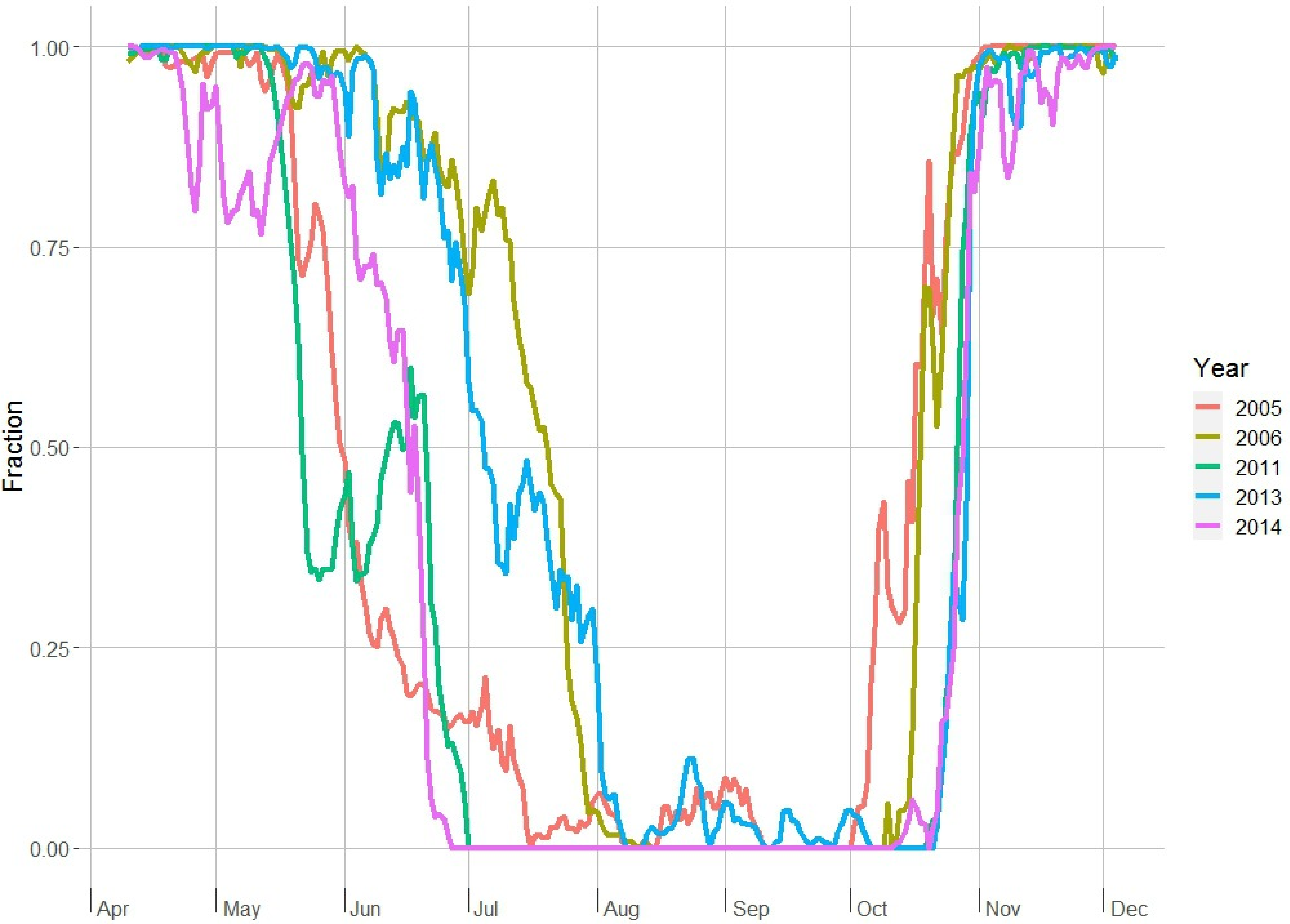

B
NCS
WBS
EBS
SCS
Length (mm)
60
50
40
30
20
72°N
70°N
68°N
66°N
64°N
170°W
160°W
150°W
140°W
Russia
Alaska
Canada
Mackenzie River


C
NCS
WBS
EBS
SCS
Length (mm)
70
60
50
40
72°N
70°N
68°N
66°N
64°N
170°W
160°W
150°W
140°W
Russia
Alaska
Canada
Mackenzie River


NBS
SCS
NCS
WBS
EBS
Location
Spring Pelagic
Summer Demersal
Summer Pelagic
Proportion
0.025
0.020
0.015
0.010
0.005
0.000
0.020
0.010
0.000
0.010
0.008
0.005
0.002
0.000
0.006
0.004
0.002
0.000
0.010
0.008
0.005
0.002
0.000
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Month


Location
Spring Pelagic
Summer Demersal
Summer Pelagic
Mean Hatch Date
Jun
May
Apr
Mar
Feb
Jan
NBS
SCS
NCS
WBS
EBS


A
Region
N. Bering
S. Chukchi
Length (mm)
20
15
10
5
10
30
50
70
90
110
130
150
Age (days)
B
Region
S. Chukchi
N. Chukchi
E. Beaufort
60
40
20
60
80
100
120
140
160
180
200
220
240
260
280
300
Age (days)


Fraction
1.00
0.75
0.50
0.25
0.00
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Year
2005
2006
2011
2013
2014