



# Spatial patterns, environmental correlates, and potential seasonal migration triangle of polar cod (*Boreogadus saida*) distribution in the Chukchi and Beaufort seas

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## Abstract

Polar cod (*Boreogadus saida*) is a key forage fish in the Arctic marine ecosystem and provides an energetic link between lower and upper trophic levels. Despite its ecological importance, spatially explicit studies synthesizing polar cod distributions across research efforts have not previously been conducted in its Pacific range. We used spatial generalized additive models to map the distribution of polar cod by size class and relative to environmental variables. We compiled demersal trawl data from 21 cruises conducted during 2004–2017 in the Chukchi and Beaufort seas, and investigated size-specific patterns in distribution to infer movement ecology of polar cod as it develops from juvenile to adult life stages. High abundances of juvenile polar cod ( $\leq 70$  mm) in the northeastern Chukchi Sea and western Beaufort Sea were separated from another region of high abundance in the eastern Beaufort Sea, near the US and Canadian border, suggesting possible population structure in the Pacific Arctic. Relating environmental correlates to polar cod abundance demonstrated that temperature and salinity were related to juvenile distribution patterns, while depth was the primary correlate of adult distribution. A comparison of seasonal 2017 abundances of polar cod in the southern Chukchi Sea found low demersal abundance in the spring when compared to the summer. Seasonal differences in polar cod abundance suggest that polar cod migration may follow a classical ‘migration triangle’ route between nursery grounds as juveniles, feeding grounds as subadults, and spawning grounds as adults, in relation to ice cover and seasonal production in the Chukchi Sea.

**Keywords** Polar cod · Pacific arctic · Chukchi sea · Beaufort sea · Harden jones migration triangle

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## Introduction

Currently, understanding of the basic life history of many marine organisms in the Arctic, including polar cod (*Boreogadus saida*), is based on intermittent “snapshots” of species’ presence, abundance, and distribution. While the distribution and movement of polar cod has been investigated in Atlantic Arctic regions such as the East Greenland shelf (Astthorsson 2015), and the Barents, Laptev, and East Siberian seas (Ponomarenko 1968; Lønne and Gulliksen 1989), a comprehensive study synthesizing multiple research efforts to describe the distribution of polar cod is yet to be completed for its range in the Chukchi and Beaufort seas (Mueter et al. 2016).

Polar cod is an abundant, circumpolar forage fish species and is a critical trophic link in the Arctic marine ecosystem (Lowry and Frost 1981; Mecklenburg et al. 2011; Hop and Gjosaeter 2013). This small-bodied species spawns under sea ice in the late fall and early winter and has buoyant eggs

that float to the ice–water interface (Graham and Hop 1995; Bouchard and Fortier 2011). Its diet is composed primarily of zooplankton such as copepods, hyperiid amphipods, and euphausiids in the summer, open water season (Rand et al. 2013; Gray et al. 2016), and ice amphipods and *Calanus* copepods in the winter, ice-covered season (Kohlbach et al. 2017). In the Pacific Arctic, polar cod is found in high salinity and intermediate water temperatures of the Chukchi Sea shelf (Norcross et al. 2010; Logerwell et al. 2017; De Robertis et al. 2017b). In the Beaufort Sea, polar cod is ubiquitous, present at all depths both on the shelf and the extending seaward down the slope (Benoit et al. 2008; Geoffroy et al. 2011; Norcross et al. 2017).

Body size and ontogeny influence the ability of fishes to exploit available resources and may affect their distribution with respect to these resources. As fish size increases, individuals become stronger swimmers and can exploit larger and more energetically valuable prey (Werner and Hall 1974; Christensen 1996; Clark et al. 2005), while increasing gape size widens the size range of exploitable resources (Scharf et al. 2000; Gray et al. 2017). In the Chukchi and Beaufort seas, body size influences the composition of prey in polar cod diets (Walkusz et al. 2013; Gray et al. 2016). Smaller polar cod are restricted to consuming small-bodied prey (i.e., calanoid and cyclopoid copepods), while larger individuals can also consume large-bodied zooplankton (i.e., hyperiid amphipods and euphausiids) (Gray et al. 2016; Norcross et al. 2017). Therefore, as ontogenetic increases in body size also improve prey resource accessibility, polar cod distribution is likely impacted by size-specific resource distribution.

Differential distribution in fish size with respect to resources can influence species-level life history strategies, including both ontogenetic and seasonal migration patterns. In classic ‘migration triangle’ theory, species migrate from nursery grounds to feeding grounds and finally to spawning grounds throughout the course of a life cycle (Harden Jones 1968; Secor 2002). Many species in the North Pacific exhibit this life history strategy, including close relatives of polar cod, Pacific cod (*Gadus macrocephalus*), and walleye pollock (*Gadus chalcogrammus*) (Shimada and Kimura 1994; Kotwicki et al. 2005). Seasonal migrations are also common for fish species in the highly seasonal North Pacific ecosystem. Pacific herring (*Clupea pallasii*) and yellowfin sole (*Limanda aspera*), for example, exploit abundant food resources as they migrate between summer feeding grounds and offshore overwintering grounds (Nichol 1998; Tojo et al. 2007). Both the ontogenetic and seasonal migration patterns of polar cod in the Pacific Arctic are not well established and could be improved with additional sampling beyond the August and September open water sampling season.

Global attention has recently shifted to the Arctic, creating a unique opportunity for national and international

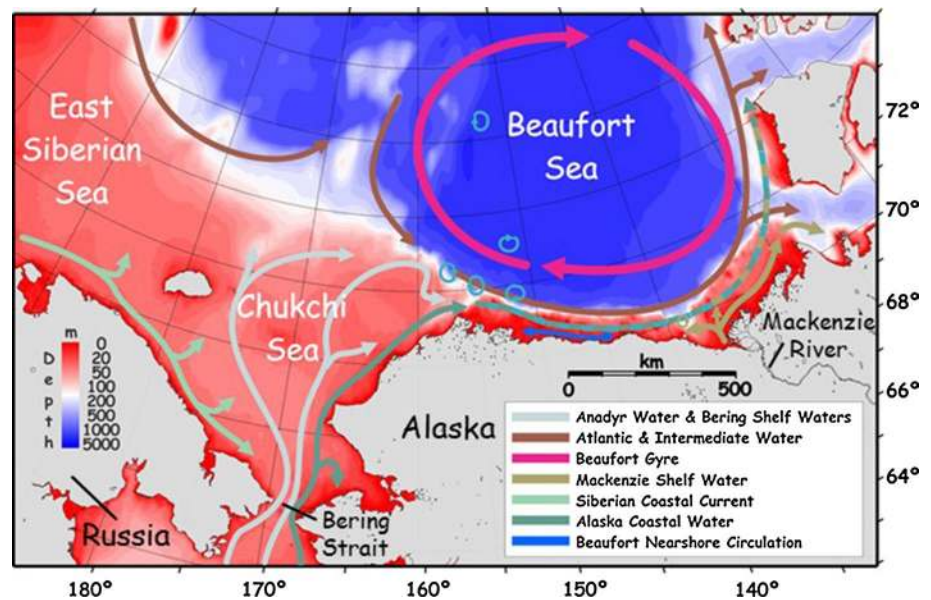
fisheries management organizations to incorporate precautionary management strategies from the outset. In 2009 the North Pacific Fisheries Management Council (NPFMC) closed US Arctic waters to commercial fishing until sufficient information becomes available to sustainably manage a fishery (NPFMC 2009). Polar cod is listed as one of only two finfish species with commercial potential within the NPFMC Arctic Fisheries Management Plan, and any fishery development would require a review of the life history of the potential target species, as well as an evaluation of the impacts to essential fish habitat. While a number of recent pelagic and demersal trawl surveys conducted by both the National Marine Fisheries Service and academic researchers (Rand and Logerwell 2011; Norcross et al. 2013; De Robertis et al. 2017b) have described broad patterns in polar cod distribution and overall abundance (Logerwell et al. 2015), a study specifically investigating polar cod distribution patterns across multiple years and many cruises is yet to be completed. Accordingly, we generated a comprehensive understanding of polar cod distribution in the Chukchi and Beaufort seas, investigating patterns with respect to size class, environmental covariates, and seasonal data in the southern Chukchi Sea to inform a hypothesis about a polar cod migration triangle.

## Methods

### Study region

Within US waters, polar cod is abundant in the Chukchi and Beaufort seas, two waterbodies with differing physical and biological conditions. The Chukchi Sea has a wide and shallow shelf with average depths ranging from 40 to 60 m. This sea benefits from an inflow from three primary water masses, nutrient poor Alaska Coastal Water (ACW), nutrient-rich Bering Shelf Water (BSW), and nutrient-rich Anadyr Water (AW) (Fig. 1; Weingartner 1997; Weingartner et al. 2013; Danielson et al. 2017b). There is considerable mixing between the BSW and AW, creating a water mass that has been termed Bering Chukchi Summer Water (BCSW) (Danielson et al. 2017b). The ACW, BSW, and AW originate in the Bering Sea and travel northward through Bering Strait, transporting nutrients and creating areas of high primary production and rich benthic habitats in portions of the Chukchi Sea (Dunton et al. 2005; Grebmeier et al. 2006). The high levels of Chukchi Sea shelf productivity are influenced to a greater extent by nutrient input from BCSW, than by ACW (Grebmeier et al. 1988). In contrast to the Chukchi Sea, the Beaufort Sea has a much narrower shelf with a slope that drops off steeply to the Arctic Basin. In addition to nutrient-rich waters flowing eastward from the Chukchi Sea, oceanographic processes in the Beaufort

**Fig. 1** Schematic of oceanic current flow in the Chukchi and Beaufort seas. After S. Danielson, personal communication



Sea are influenced by water from the Atlantic Ocean, the Beaufort Gyre, and freshwater input from the Mackenzie River (Carmack and Macdonald 2002). Water masses in the Beaufort Sea include a continuation of the eastward flowing ACW from the Chukchi Sea, Summer Shelf Water (SSW) influenced by both sub-Arctic and Arctic currents, and deep Atlantic Water (AtlW) transported west from the Atlantic Ocean (Carmack et al. 1989; Lansard et al. 2012; Norcross et al. 2018). Without nutrient subsidies from richer sub-Arctic waters, production in the Beaufort Sea is much lower than in the Chukchi Sea (Dunton et al. 2005). Regional differences in production create an unequal availability of resources between the Chukchi and Beaufort seas, which may drive both broad-scale patterns of polar cod distribution between the two seas, as well as more fine-scale patterns of polar cod distribution by size class in each respective sea.

### Data collection

Data were compiled from 21 research surveys that were conducted during the open water season in the Chukchi and Beaufort seas beginning in 2004 and extending through 2017. Data were available from 16 cruises in the Chukchi Sea and five cruises in the Beaufort Sea (Table 1). In the Chukchi Sea, station locations ranged from approximately 170° W to Point Barrow, 156° W, and from the Bering Strait, 66.4° N, to approximately 73° N. Because the Chukchi Sea is relatively shallow, sampled depths were commonly between 40 and 60 m, with a maximum depth of 90 m. Station locations in the Beaufort Sea extended along the Alaskan coast from Point Barrow and into Canadian waters past the Mackenzie River to 137° W, and offshore to approximately 72° N (Fig. 2). Sampled depths reached nearly 1000 m in the

Beaufort Sea. Cruises were divided into two seasons, spring and summer, based on temporal proximity of sampling to sea ice retreat and spring bloom conditions, which has a median date of approximately 20–21 June, based on data collected from 1997–2009 (Kahru et al. 2011). A cruise conducted from 9 to 29 June 2017 in the Chukchi Sea (ASGARD, Table 1), produced some of the earliest seasonal sampling events to ever take place in this region and was categorized as a spring season cruise because sampling occurred at the same time as the spring bloom (Danielson et al. 2017a). The remaining 20 cruises, conducted from 7 July to 10 October, occurred after the initial pulse of spring production from the spring bloom, and were thus categorized as summer season cruises. Because sampling in the spring occurred much earlier than during other cruises, data from this season were excluded from a spatial analysis of the summer distribution of polar cod. Further description of sensitivity analyses regarding seasonal divisions are discussed below.

All polar cod were captured in one of two configurations of a 3-m plumb staff beam trawl (PSBT), either standard (Gunderson and Ellis 1986) or modified with rollers (Abookire and Rose 2005), which were deployed for 1–10 min and towed at a speed over ground of 1.5–2.0 knots. A rigid 3.05 m beam held the net open for an effective swath of 2.26 m; net mesh size was 7 mm in the body with a 4 mm codend liner. In a gear comparison study, neither catch per unit effort (CPUE) of all fishes nor size classes of polar cod were significantly different between these two gear types (Norcross et al. 2018), therefore, abundance data from both gear types were pooled for analysis. Fishing effort for each haul was defined as the total seafloor area swept by the net. Catches were standardized to an area of 1000 m<sup>2</sup> (catch per unit effort or CPUE in no. of fish per 1000 m<sup>2</sup>).

**Table 1** Cruise information for all surveys used in this study listed by cruise designator, vessel used, year, beginning date of sampling, ending date of sampling, and number of hauls collected

Region	Cruise designator	Vessel	Year	Begin date	End date	No. of hauls
Chukchi	RUSALCA_2004	R/V Professor Khromov	2004	10-Aug	22-Aug	5
Chukchi	OD0710	R/V Oscar Dyson	2007	4-Sep	15-Sep	21
Chukchi	OS180	T/S Oshoro-Marv IV	2007	6-Aug	10-Aug	9
Chukchi	OS190	T/S Oshoro-Marv IV	2008	7-Jul	13-Jul	15
Chukchi	COMIDA_2009	R/V Alpha Helix	2009	27-Jul	11-Aug	30
Chukchi	RUSALCA_2009	R/V Professor Khromov	2009	4-Sep	29-Sep	7
Chukchi	WWW0902	R/V Westward Wind	2009	14-Aug	29-Aug	25
Chukchi	WWW0904	R/V Westward Wind	2009	29-Sep	10-Oct	26
Chukchi	AKCH10	R/V Norseman II	2010	21-Aug	4-Sep	30
Chukchi	WWW1003	R/V Westward Wind	2010	1-Sep	18-Sep	40
Chukchi	AKCH11	R/V Norseman II	2011	4-Sep	17-Sep	28
Chukchi	Arctic EIS_2012	F/V Alaska Knight	2012	14-Aug	18-Sep	40
Chukchi	RUSALCA_2012	R/V Professor Khromov	2012	27-Aug	16-Sep	5
Chukchi	AMBON_2015	R/V Norseman II	2015	11-Aug	3-Sep	68
Chukchi	Arctic IES_2017	R/V Ocean Starr	2017	1-Aug	28-Sep	59
Chukchi	ASGARD_2017	R/V Sikuliaq	2017	9-Jun	29-Jun	8
Beaufort	BOEM_2011	R/V Norseman II	2011	15-Aug	4-Sep	81
Beaufort	TB_2013	R/V Norseman II	2013	12-Aug	2-Sep	90
Beaufort	ANIMIDA_2014	R/V Norseman II	2014	29-Jul	10-Aug	29
Beaufort	TB_2014	R/V Norseman II	2014	14-Aug	2-Sep	68
Beaufort	ANIMIDA_2015	R/V Norseman II	2015	31-Jul	8-Aug	18
Total no. of hauls						697

Due to difference in sampling seasons, ASGARD\_2017 cruise excluded from spatial analysis

In addition, at each haul location a Seabird conductivity-temperature-depth (CTD) recorder was deployed from the vessel separately and used to measure depth (m), bottom water temperature (°C), and bottom water salinity (PSU), hereafter referred to as depth, temperature, and salinity. Fish specimens were measured for total length.

### Data analysis

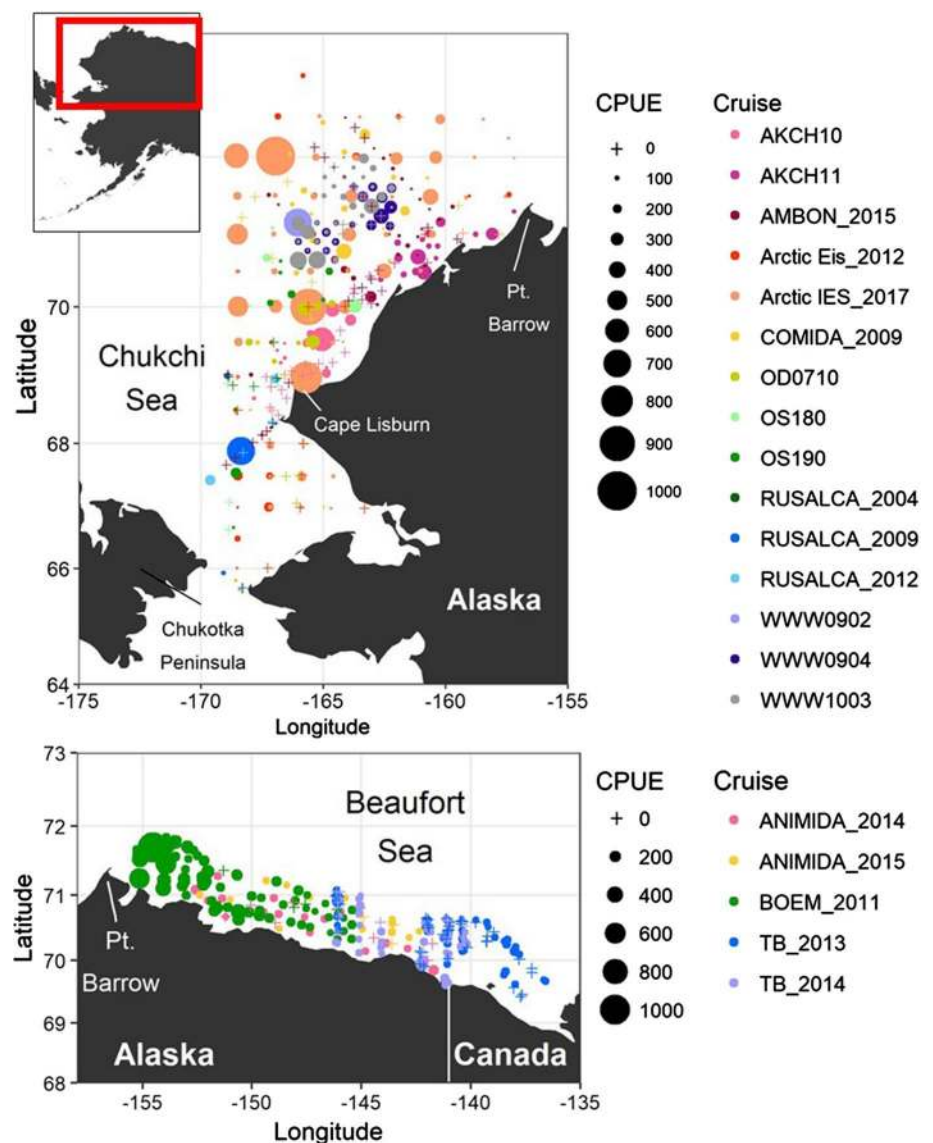
Patterns in polar cod abundance and total length were plotted and inspected prior to statistical analysis. Length frequencies of 6519 and 2752 fish in the Chukchi and Beaufort seas, respectively, were plotted by 10 mm increments (1–10 mm, 11–20 mm, etc.) and examined to inform selection of size classes for analysis (Fig. 3). Visual inspection suggested the presence of three modes, therefore size classes were identified using an expectation–maximization (EM) algorithm to fit a mixture of three Gaussian distributions to the length-frequency data (Benaglia et al. 2009). Based on the results, abundances of polar cod were separated by total length into small ( $\leq 70$  mm), medium (71–130 mm), and large ( $> 130$  mm) size classes. Size classes approximately correspond with age 0, 1, and 2+ polar cod, respectively, based on previously published work (Helser et al. 2017). However,

given considerable overlap in length-at-age distributions, the medium size class likely contains a mixture of age-1 and age-2 individuals.

Generalized additive modeling (GAM) was used to relate CPUE of polar cod to spatial and environmental predictor variables. A GAM is a regression technique that uses non-parametric smoothers to allow non-linear relationships between dependent and independent variables (Hastie and Tibshirani 1986; Wood 2006). The GAM approach was chosen to accommodate non-linear relationships between abundance and both spatial (latitude, longitude) and environmental (depth, temperature, salinity) predictors. All models were fit using the ‘mgcv’ package version 1.8–17 (Wood 2006) in R version 3.4.1 (R Core Team 2017). Analysis may be found in Online Resource 1.

To determine the most appropriate model framework for both the spatial and environmental GAM analyses, preliminary analyses and model diagnostics were conducted prior to selection of final models. Abundance of polar cod was non-normal, including a high proportion of zero-catch hauls, as well as a few hauls with very high abundance values. Exploratory analyses compared models using a Gaussian distribution with log-transformed polar cod CPUE and the identity link function, with negative binomial and tweedie

**Fig. 2** Catch per unit effort (CPUE, no. of fish per 1000 m<sup>2</sup>) of polar cod by haul in the Chukchi Sea (top panel) and Beaufort Sea (bottom panel). The + symbol denotes hauls where zero polar cod were caught. Colors correspond to separate cruises. Symbol size is proportional to CPUE. For details about each cruise, see Table 1



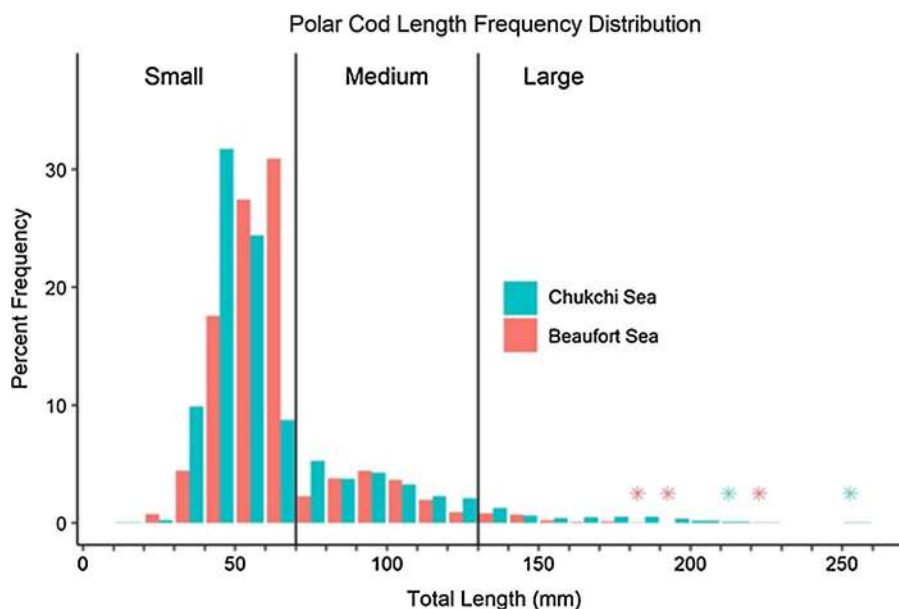
distributions using counts of polar cod and the log link function. The negative binomial distribution with a log link was selected as the top performing model based on residual diagnostics, deviance explained, and generalized cross validation scores. This model framework was thereafter used for all GAM analyses. The negative binomial distribution utilizes count data, and is commonly used for analyzing ecological data, as it can accommodate overdispersed observations, or observations with a high proportion of zeros (Zuur et al. 2007). Therefore, we used the count data with a log link and accounted for fishing effort by including the logarithm of area swept (m<sup>2</sup>) as an offset in the model.

GAM analyses were conducted on cruises conducted in the summer season, defined as open water and more than 30 days after the start of the spring bloom. Two cruises, T/S Oshoro-Marū IV 2008 (Table 1) and WWW0904 2009 were conducted early and late in the summer season (July

and October). To verify that it was appropriate to include these cruises in an analysis of polar cod summer distribution patterns, a sensitivity analysis both including and excluding these cruises was conducted. The results of all analyses were virtually identical; therefore, T/S Oshoro-Marū IV 2008 and WWW0904 2009 were included in summer season analyses. Due to considerable differences in oceanographic and bathymetric conditions and due to their spatial separation, analyses were conducted separately for the Chukchi and Beaufort seas.

To describe polar cod distribution patterns and the impact of environmental drivers on those patterns, two separate analyses were undertaken using GAM. The first analysis described the spatial distribution of polar cod abundance using latitude and longitude as covariates. Environmental conditions were strongly confounded with spatial location; for example, in the Beaufort Sea, depth increased with

**Fig. 3** Length-frequency distribution of polar cod captured in Chukchi Sea (blue) and Beaufort Sea (pink), weighted by station-specific catch per unit effort (CPUE, no. of fish per 1000 m<sup>2</sup>). Percent frequency is percent of total CPUE for that sea, and bars represent size class in between tick marks. Asterisks above a length bin indicate percentage < 0.1%, color corresponds to sea



latitude as sampling moved both northerly and offshore. Thus, we modeled spatial patterns separately from assessing the effects of environmental covariates. We compared the predicted values of the spatial and environmental models at each station to examine to what extent environmental covariates were able to account for estimated spatial patterns in polar cod distribution. Results of this analysis may be found in Online Resource 2. Spatial and environmental analyses were conducted for each of the three length classes of polar cod in the Chukchi and Beaufort seas. The spatial model was fit as follows:

$$\log(\text{count of polar cod}) \sim s(\text{latitude, longitude}) + \log(\text{area swept}), \quad (1)$$

where  $\log$  denotes the natural logarithm and  $s$  denotes a smooth function of latitude and longitude estimated using a thin-plate regression spline. The second analysis investigated the impact of environmental correlates by modeling polar cod abundance as a function of selected environmental covariates:

$$\begin{aligned} \log(\text{count of polar cod}) \sim & s_1(\text{depth}) \\ & + s_2(\text{temperature}) + s_3(\text{salinity}) \\ & + \log(\text{area swept}), \end{aligned} \quad (2)$$

where the  $s_i$  are smooth functions of the respective covariates estimated using thin-plate regression splines. For the environmental analysis, a model selection approach was used to select a best-fitting model. To evaluate the effect of each environmental covariate on polar cod abundance, a suite of seven models was developed for each size class and in each sea, where every combination of environmental variables was considered. Within a size class and a sea, models

were compared and the model with the lowest Akaike Information Criterion (AIC) was selected as the best performing model. Results from the best-fitting model for each size class were visually examined to describe the estimated relationships between polar cod abundance and the environmental predictors. When the best performing environmental model included both temperature and salinity, the temperature and salinity values were used to identify water masses and relate them to polar cod abundance. Literature values characterizing typical water mass temperature and salinity ranges in the Chukchi Sea (Danielson et al. 2017b) or Beaufort Sea (Norcross et al. 2018) were overlaid on relationships of polar cod abundance relative to those variables to determine patterns of polar cod abundance with respect to water mass.

Environmental model residuals suggested some degree of spatial autocorrelation among sites, where sites closer to each other were more similar than sites that were located farther apart. Both spatial and environmental models were tested for residual spatial autocorrelation by plotting the semivariance of model residuals as a function of distance between sampling points by year. Data for all length classes were combined to determine the spatial relationship between stations in each sea within a year. Comparison of AIC between the full model with spatial autocorrelation and the full model without spatial autocorrelation indicated slightly lower values in each sea (Chukchi Sea:  $\Delta\text{AIC} = 2$ ; Beaufort Sea:  $\Delta\text{AIC} = 10$ ) and thus a modest preference for the models that include a spatially autocorrelated error structure. Each environmental model, therefore, included an exponential decline in residual correlation with distance, as well as a nugget effect, conditioned on sampling year. Spatial correlation scale parameters (range and nugget) were estimated independently for each sea using the full model and were

included in all subsequent models. Due to statistical programming constraints caused by the inclusion of a spatially autocorrelated error structure, the dispersion parameter of the negative binomial distribution was estimated independently using the full model and fixed for each sea. After the incorporation of a spatially correlated error structure in the environmental model, both the spatial models and environmental models met assumptions of independence.

The completion of the spring cruise in the Chukchi Sea in June 2017 provided a seasonal comparison of offshore polar cod abundances. As these data were collected in spring rather than summer, they were not included in the previously described spatial analysis. However, the spring abundance data were directly compared to abundance from a cruise conducted during August and September 2017 in the southern Chukchi Sea. The two research efforts used the same gear and sampled from the Bering Strait (66.4° N) to Cape Lisburne (69.1° N). Due to the small number of sample stations within the area of overlap (spring  $n = 9$ , summer  $n = 14$ ), we were not able to develop a geostatistical model and instead compared abundance of polar cod between spring and summer using a non-parametric (rank-based) Wilcoxon two-sample test. The test assumes that sampling in each season resulted in independent random samples that were representative of the area of overlap. Several August hauls caught large numbers of fish  $\leq 70$  mm, a size that was not observed in June. These small fish presumably consist of young-of-the-year fish that were too small to be retained by the beam trawl in June. Therefore, instead of statistically comparing overall seasonal abundances for all sizes of polar cod, we only applied to Wilcoxon two-sample test to compare seasonal abundances for fish  $> 70$  mm, i.e., those fish that were available to be caught by the gear in both spring and summer. Mean values of depth, temperature, and salinity for each season are reported; however, environmental data were not available for two stations sampled in August 2017.

## Results

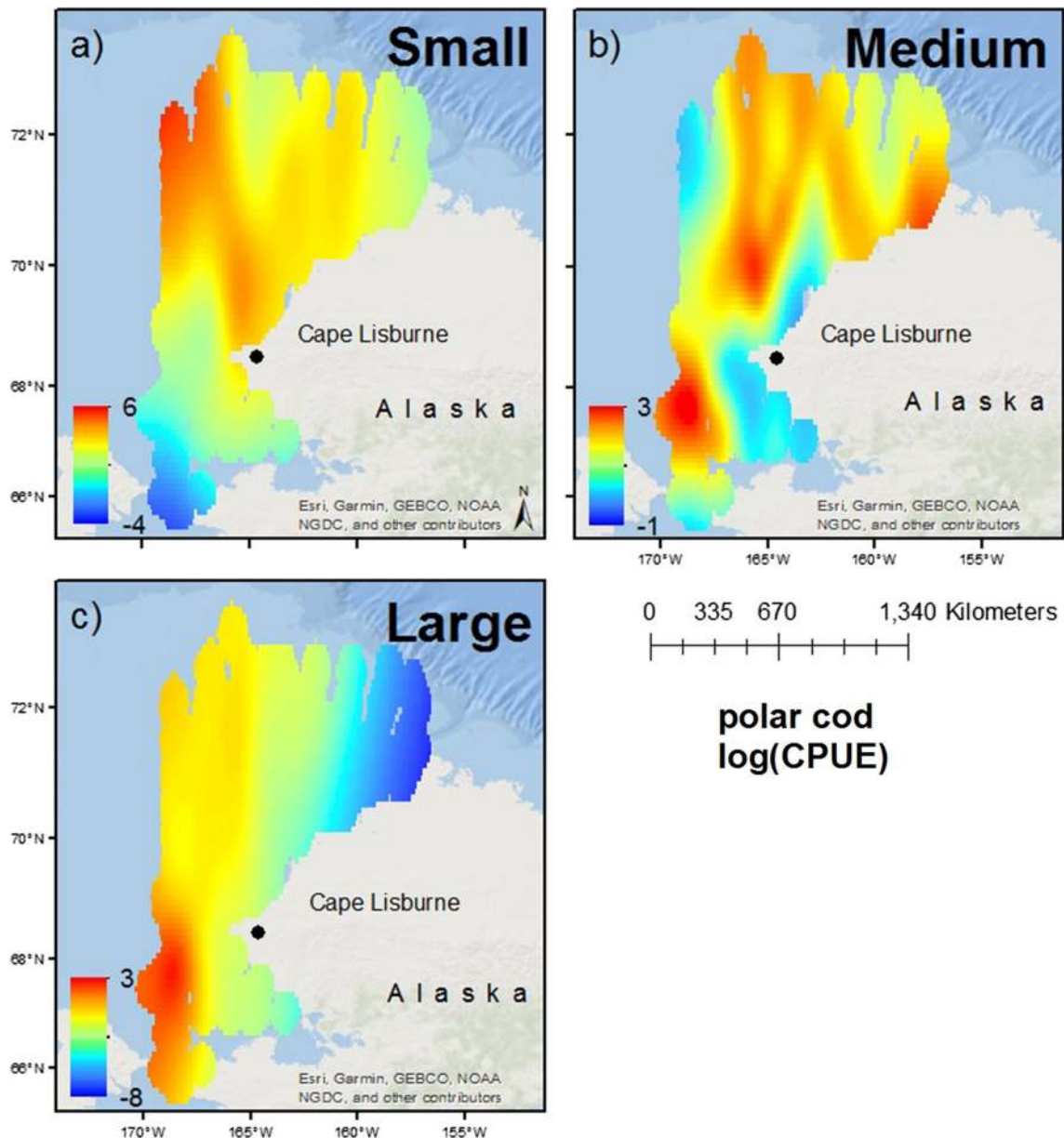
A total of 697 hauls from 21 cruises over 13 years were available for analysis (Table 1). The number of hauls conducted annually ranged from 5 to 88 in the Chukchi Sea and 18 to 97 in the Beaufort Sea. Sampling was conducted from 9 June to 10 October in the Chukchi Sea and from 29 July to 4 September in the Beaufort Sea. Bottom water in the Chukchi Sea ranged from  $-1.8$  to  $10.9$  °C, with salinities from 27.2 to 34.5 PSU. In comparison, conditions in the Beaufort Sea lacked the warmest and very coldest temperatures, with a range from  $-1.6$  to  $4.8$  °C, and had salinities from 29.2 to 34.9 PSU.

When pooling data across all years, polar cod showed latitudinal patterns in abundance in the Chukchi Sea and a strong longitudinal gradient in the Beaufort Sea. Generally, abundance of polar cod in the Chukchi Sea showed a south to north gradient, with the highest abundance values north of Cape Lisburne (Fig. 2). In the Beaufort Sea, polar cod abundance showed a predominantly west to east gradient, with the highest abundance west of 150° W (Fig. 2). Length frequencies of the catches were similar across both study regions; polar cod ranged from 11 to 260 mm in the Chukchi Sea and from 21 to 230 mm in the Beaufort Sea (Fig. 3).

## Spatial analysis

In the Chukchi Sea, GAM analysis of trawl catches revealed distinct patterns of polar cod distribution by size class. The small size class of polar cod was most abundant in the northern Chukchi Sea, north of approximately 68° N (Fig. 4), where the Bering Chukchi Summer Water mass is commonly present, while fewer small polar cod were found south of 68° N. The distribution of the medium size class was different when compared to the distribution of the small size class and did not show the same region of abundance in the NE Chukchi Sea. Medium-sized polar cod were present across the entire Chukchi Sea shelf and showed pockets of high abundance in both nearshore and offshore regions. However, the regions of high abundance for the medium size class were not the same as the regions of high abundance for the small size class offshore at 169° W and north of 70° N (Fig. 4). Finally, the large size class of polar cod was less abundant in the nearshore region and more abundant beginning ~80 km offshore and extending seaward, with an area of higher abundance south of Cape Lisburne (Fig. 4). Deviance explained for the small, medium, and large size class models was 24.4%, 20.2%, and 57.5%, respectively (Table 2).

Similar to the Chukchi Sea, the GAM spatial analysis in the Beaufort Sea also found distinct, size-based patterns of polar cod distribution. The small size class was distributed primarily along a west to east gradient, with an area of high abundance west of 150° W, and another smaller area of abundance nearshore and east of 144° W (Fig. 5). There was also a nearshore to offshore gradient, where small polar cod were distributed close to shore; however, the western aggregation was dispersed across the width of the entire Beaufort Sea shelf (to ~80 km), more than the eastern aggregation that was generally distributed closer to shore (within ~50 km). Abundance of the medium size class showed a less extreme longitudinal gradient than the small size class, and while abundance was highest west of 150° W, medium polar cod were diffuse across the entire Alaskan Beaufort Sea shelf. Unlike the small size class, medium-sized polar cod did not show a separate area of high abundance east of 144° W. The large size class of



**Fig. 4** Spatial distribution of polar cod catch per unit effort (CPUE, no. of fish per 1000 m<sup>2</sup>) in the Chukchi Sea for **a** small ( $\leq 70$  mm), **b** medium (71–130 mm), and **c** large (> 130 mm) size classes. Abun-

dances as predicted by generalized additive model (GAM) using a smooth function of latitude and longitude, shown on the log scale

polar cod was distributed offshore, beyond  $\sim 60$  km. The deviance explained for the small, medium, and large size class analysis was 62.7%, 22.9%, and 21.7%, respectively (Table 2).

### Environmental analysis

In the Chukchi Sea, the influence of the environmental variables on polar cod abundance depended on size class. For the small size class of polar cod, the top performing model included both temperature and salinity (Table 3). A

dome-shaped curve described the relationship between polar cod abundance and temperature with a peak at 4–5 °C, while abundances increased linearly with salinity to a maximum of 34.5 PSU (Fig. 6). For polar cod in the medium size class, the top performing model only included depth and abundance increased linearly with depth (Table 3, Fig. 6). The best-fitting model for the large size class of polar cod in the Chukchi Sea also only included depth as a covariate; there was a positive relationship between depth and abundance of large polar cod in the Chukchi Sea (Table 3, Fig. 6).



**Table 2** Results of generalized additive models (GAMs) for spatial distribution of polar cod, with latitude and longitude as explanatory variables (see Eq. 1)

Region	Size class	$\theta$	edf	$\chi^2$	<i>p</i> value	AIC	Deviance explained (%)
Chukchi	Small	0.19	19.5	99.3	<0.0001	1928.0	24.4
Chukchi	Medium	0.40	26.6	67.0	<0.0001	1642.0	20.2
Chukchi	Large	0.18	13.7	58.1	<0.0001	426.9	57.5
Beaufort	Small	0.38	13.4	300.2	<0.0001	1073.2	62.7
Beaufort	Medium	0.53	7.6	61.4	<0.0001	1051.0	22.9
Beaufort	Large	0.19	3.0	23.1	<0.0001	353.9	21.7

Separate models developed in each sea and for each size class.  $\theta$  parameter used for negative binomial parameterization, estimated degrees of freedom (edf), chi-square statistic, *p*-value denoting significance of latitude and longitude covariates, Akaike Information Criterion (AIC), and deviance explained

As in the Chukchi Sea, the relationships between environmental variables and abundance of polar cod in the Beaufort Sea were specific to size classes. The best-fitting model for the small size class in the Beaufort Sea included both temperature and salinity (Table 4). Abundance of small polar cod in the Beaufort Sea increased linearly to a maximum temperature of 4.8 °C, which was similar to the Chukchi Sea, and was highest at intermediate salinities; small polar cod were less abundant at the lowest (< 31 PSU) and highest (> 34 PSU) salinity values (Fig. 7). The top performing model for the medium size class in the Beaufort Sea included both depth and temperature (Table 4), unlike the analogous model in the Chukchi Sea, which only included depth. In the Beaufort Sea, abundance of medium polar cod increased with depth to approximately 300 m and then began to decline; medium polar cod abundance increased linearly with temperature (Fig. 7). As in the Chukchi Sea, the top performing model for the large size class included only depth as a covariate (Table 4). Notably, large polar cod abundance increased with depth in the Beaufort Sea to about 400 m, but as depth surpassed 400 m, abundance of polar cod decreased (Fig. 7). The shape of the relationship between depth and abundance was similar for both medium and large polar cod, but the medium size class was more abundant at shallow depths than the large size class of polar cod.

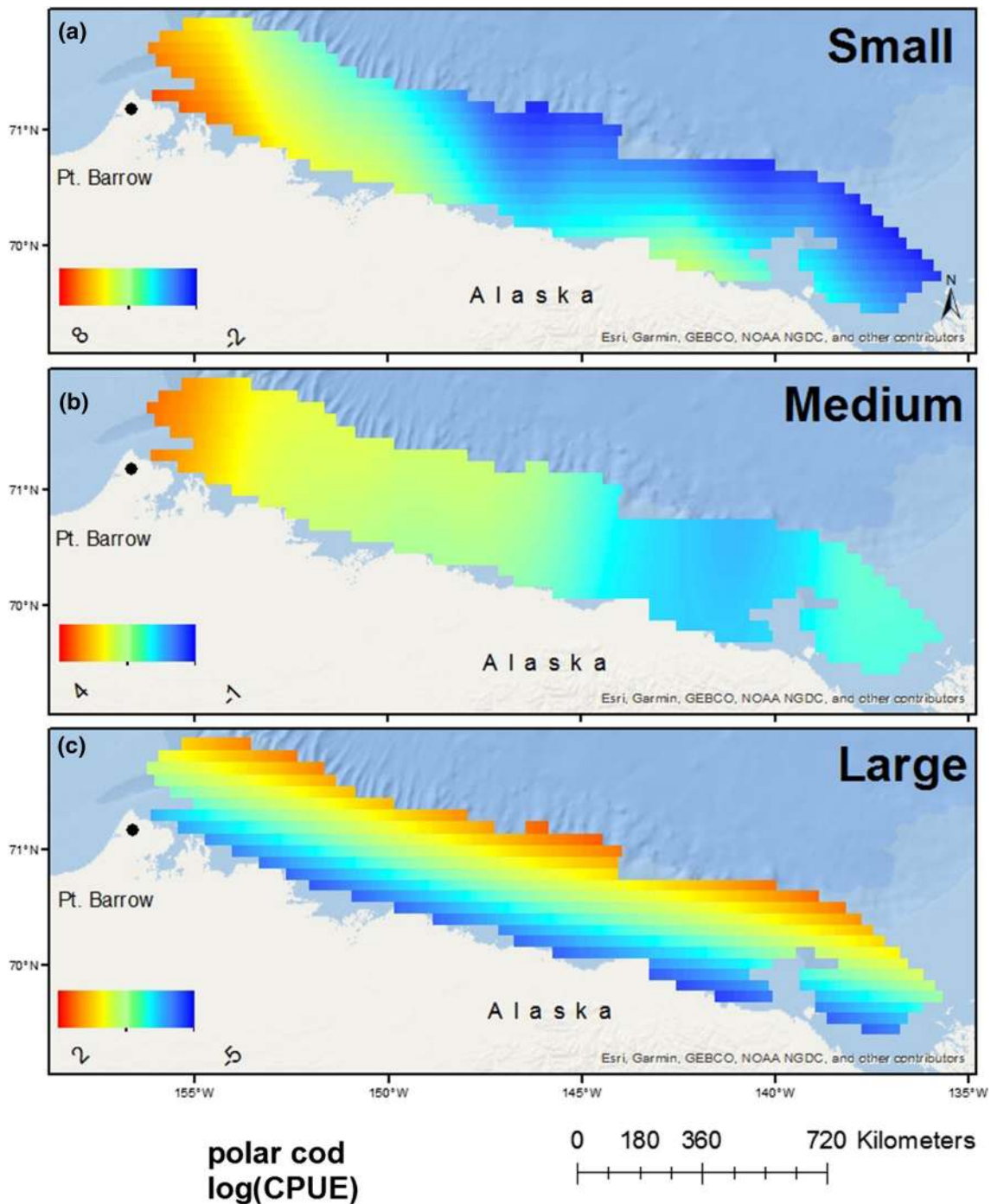
### Seasonal analysis

Comparison of polar cod catches between spring and summer in the southern Chukchi Sea revealed striking differences in fish abundance. Overall mean abundance of polar cod was much lower in June 2017 compared to August 2017 (Table 5). During the spring, polar cod was scarce in our nets; only four individuals were captured at three sampling locations (Fig. 8). In contrast, polar cod abundance

was higher at locations sampled in August 2017 (Table 5). There were summer hauls that captured high abundances of small-sized polar cod, including one station with an abundance of 832 fish per 1000 m<sup>2</sup>, with individuals ranging from 31 to 70 mm in length. Catch length-frequency composition in the summer contrasts with the polar cod caught in the spring, where only one fish < 70 mm was captured (Fig. 8). Polar cod 31 to 70 mm captured in August were likely young-of-the-year; these small fish were not available to the beam trawl in June due to both their pelagic distribution and small size before the summer growing season. Therefore, to verify that the observed seasonal differences in abundance were truly changes in abundance, and not the result of small fish growing in size and descending to the seafloor to become increasingly represented in the catch as the summer progressed, only spring and summer abundance of individuals > 70 mm were statistically compared. Seasonal differences in abundance were significant, using a Wilcoxon two-sample test, after the exclusion of small, highly abundant polar cod in August (Table 5, *p* = 0.02).

### Discussion

By visualizing the distribution patterns of small, medium, and large polar cod, understanding of ontogenetic shifts in distribution as well as possible migration patterns of this species in the Pacific Arctic has been improved. Furthermore, by relating patterns in distribution to environmental variables, we provide insight into potential mechanisms driving polar cod distribution. The importance of environmental covariates varies among the three size classes and suggests that the relative influence of external drivers on polar cod distribution influences life stages differently. A comparison of abundance between spring and summer in the southern Chukchi Sea revealed seasonal differences in polar



**Fig. 5** Spatial distribution of polar cod catch per unit effort (CPUE, no. of fish per 1000 m<sup>2</sup>) in the Beaufort Sea for **a** small ( $\leq 70$  mm), **b** medium (71–130 mm), and **c** large ( $> 130$  mm) size classes. Abun-

dances as predicted by generalized additive model (GAM) using a smooth function of latitude and longitude, shown on log scale

cod abundance. Finally, we hypothesize that both ontogenetic and seasonal movements of polar cod described in this study are evidence of a migration scenario that may be used to explain polar cod movement patterns in the Pacific Arctic.

There are several assumptions implicit in this analysis that could impact the interpretation of polar cod distribution patterns and potential environmental drivers of those patterns. First, we assume that our sampling gear is reasonably

**Table 3** Results of generalized additive models (GAMs) in the Chukchi Sea for environmental covariates, depth, temperature, and salinity (see Eq. 2)

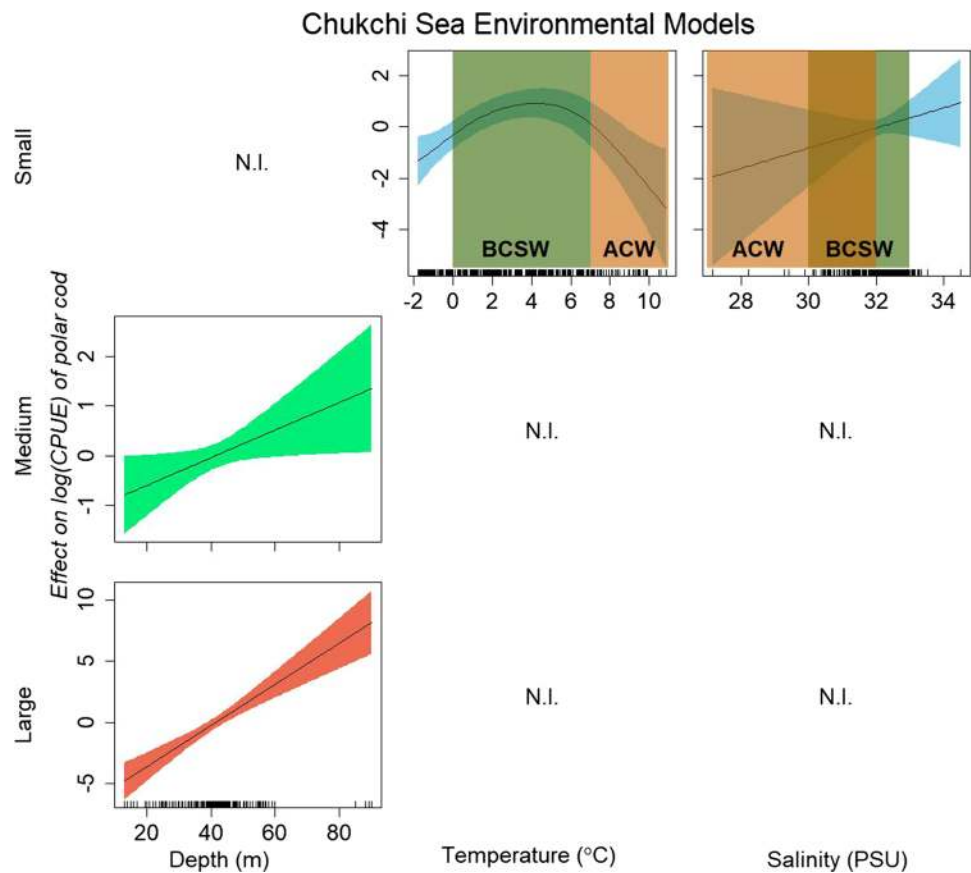
Size class	s (depth) (13–90 m)	s (bottom temperature) (–1.8 to 10.9 °C)	s (bottom salinity) (27.2–34.5 PSU)	– (logLikelihood)	AIC	ΔAIC	Model rank
Small		+	+	– 1011.1	2034.1	0.0	1
	+	+	+	– 1014.2	2044.3	10.2	2
		+		– 1032.7	2073.5	39.3	3
	+	+		– 1054.5	2121.1	86.9	4
			+	– 1075.7	2159.5	125.4	5
	+		+	– 1081.5	2174.9	140.8	6
	+			– 1115.9	2239.8	205.7	7
Medium	+			– 908.0	1824.0	0.0	1
			+	– 919.7	1847.3	23.4	2
	+		+	– 919.7	1851.3	27.3	3
		+	+	– 920.6	1853.1	29.1	4
	+	+	+	– 920.2	1856.5	32.5	5
	+	+		– 927.8	1867.6	43.6	6
		+		– 933.0	1874.0	50.0	7
Large	+			– 1224.2	2456.4	0.0	1
	+	+		– 1223.7	2459.5	3.1	2
	+		+	– 1247.0	2506.0	49.6	3
	+	+	+	– 1312.7	2641.4	185.0	4
			+	– 1477.5	2962.9	506.5	5
		+	+	– 1574.3	3160.6	704.2	6
		+		– 1595.1	3198.2	741.8	7

Suite of models developed for each polar cod size class, + denotes variables included in each model. The following statistics are reported: – log(likelihood), AIC, ΔAIC. Model performance ranked from best (1) to worst (7) using ΔAIC. ΔAIC calculated as the difference from the lowest AIC value for a size class and sea.  $\theta$  parameter estimated independently and fixed,  $\theta=0.345$ . Inclusion of a spatially autocorrelated error structure precludes the calculation of % deviance explained

effective at capturing all size classes of available polar cod. The 4 mm mesh codend liner ensures that this is an accurate assumption for individuals < 150 mm; however, a gear selectivity study indicates that the PSBT may not be the most effective sampling gear for polar cod > 150 mm (Kotwicki et al. 2017). Despite this selectivity, the results presented here nevertheless capture the bulk of the polar cod length distribution, as similar studies deploying a net with higher selectivity for large fish found that the majority of polar cod catch was < 150 mm in both the Chukchi Sea (Goddard et al. 2016) and the Beaufort Sea (Rand and Logerwell 2011). Second, we assume that the negative binomial distribution is effective at accommodating both the non-normal distribution of abundance and the high proportion of zero catches in the data. Sensitivity analysis comparing the performance of other distribution families (i.e., normal distribution with log-transformed response and tweedie distribution) showed that the top performing model used a negative binomial

distribution. Nevertheless, interpretation of analyses for the large size class should be undertaken cautiously, as there is a high proportion of zero-catch hauls for large fish. Patterns in abundance by size class (Online Resource 3) may be compared to GAM analysis output. Finally, by pooling data across years, we assume that the spatial patterns in average fish abundance are not biased by interannual variability in catches. In addition, the environmental analysis is limited in scope to local variables that were measured contemporaneously with at-sea sampling. Additional variables that may be correlated to polar cod distribution, such as mean sea ice coverage or mean distance to sea ice edge in the winter, were ultimately excluded, as we considered it inappropriate to relate the summer distribution of polar cod from multiple cruises conducted at different points in space and time to long-term means of winter sea ice conditions. However, it is important to consider that variable ice conditions during winter and spring likely also play a role in explaining

**Fig. 6** Estimated effects of three environmental variables on log(CPUE) of three size classes of polar cod in the Chukchi Sea based on generalized additive model (GAM) analysis; y-axis is magnitude of effect, rug along x-axis marks data values, colored envelopes are 95% confidence intervals. Results from the best model (Table 3) are displayed, and variables excluded from the best model are marked with N.I. (not included). Temperature and salinity measured at the seafloor. Characteristic water mass temperature and salinity values overlaid (BCSW Bering Chukchi Summer Water, ACW Alaska Coastal Water)



the distribution patterns of polar cod during the following summer.

### Spatial analysis

In the Chukchi Sea, visualizing the distribution of the small size class of polar cod suggests oceanic transport of the juvenile life stage of this species. Due to small body size and weak swimming ability, the distribution of small individuals, such as the  $\leq 70$  mm polar cod considered here, is largely influenced by the direction and speed of the prevailing oceanic currents and sea ice drift (Graham and Hop 1995; David et al. 2016). Because age-0 polar cod descend in the water column throughout their first summer (Geoffroy et al. 2016), the small polar cod captured in the demersal trawl had likely descended to the seafloor recently, after being subjected to movement by pelagic ocean currents. Pelagic acoustic surveys in the Chukchi Sea have also detected large numbers of small, 30–40 mm, age-0 polar cod in the water column in the northern Chukchi Sea (De Robertis et al. 2017a, b), which supports the idea that young-of-the-year polar cod hatch in the spring and are advected from hatch locations via ocean currents.

The primarily northward flow of water through the Bering Strait and across the Chukchi Sea (Weingartner et al.

2013) suggests that the abundance of age-0 polar cod found in the northeast Chukchi Sea in the late summer could have been transported from spawning locations in the southern Chukchi and northern Bering seas in Bering Shelf Water (BSW) and Anadyr Water (AW). Generally, polar cod hatch from buoyant eggs, occupy the water column as larvae, and descend to a demersal environment as they grow (Graham and Hop 1995; Ponomarenko 2000). Though still an area of active research, potential spawning grounds for polar cod in the Pacific Arctic have been proposed near St. Lawrence Island and east of the Chukotka peninsula, Russia (Ponomarenko 1968; Christiansen and Fevolden 2000; Vestfals et al. 2018), and could be the source of age-0 polar cod transported northward and captured in the northeast Chukchi Sea in late summer. However, the detection of larvae throughout the Canadian Arctic (Bouchard and Fortier 2011) indicates that spawning grounds in the Bering and Chukchi seas may be only a few of several spawning regions throughout the Pacific range of polar cod.

As a result of the orientation of the Alaskan coastline, the distribution patterns in the Beaufort Sea of small polar cod display a primarily west to east gradient, coupled secondarily with an inshore to offshore gradient. As in the Chukchi Sea, however, the distribution of small individuals in the Beaufort Sea is likely largely influenced by oceanic currents.

**Table 4** Results of generalized additive models (GAMs) in the Beaufort Sea for environmental covariates, depth, temperature, and salinity (see Eq. 2)

Size class	s (depth) (9–987 m)	s (bottom temperature) (– 1.6 to 4.8 °C)	s (bottom salinity) (29.2–34.9 PSU)	– (logLikelihood)	AIC	ΔAIC	Model rank
Small		+	+	– 620.5	1252.9	0.0	1
	+	+	+	– 594.8	1257.2	4.3	2
	+	+		– 700.6	1413.1	160.2	3
	+		+	– 754.5	1521.0	268.1	4
			+	– 756.7	1521.3	268.4	5
		+		– 767.4	1542.8	289.8	6
	+			– 780.7	1569.5	316.6	7
Medium	+	+		– 501.4	1014.7	0.0	1
	+	+	+	– 503.0	1022.0	7.3	2
		+		– 543.7	1095.5	80.7	3
		+	+	– 552.3	1116.6	101.8	4
	+			– 620.7	1249.3	234.6	5
			+	– 629.8	1267.6	252.9	6
	+		+	– 633.1	1278.2	263.5	7
Large	+			– 721.4	1450.9	0.0	1
	+	+		– 724.0	1460.0	9.1	2
		+		– 740.2	1488.4	37.5	3
	+		+	– 764.1	1540.3	89.4	4
			+	– 767.8	1543.6	92.7	5
	+	+	+	– 766.8	1549.5	98.6	6
		+	+	– 775.7	1563.4	112.5	7

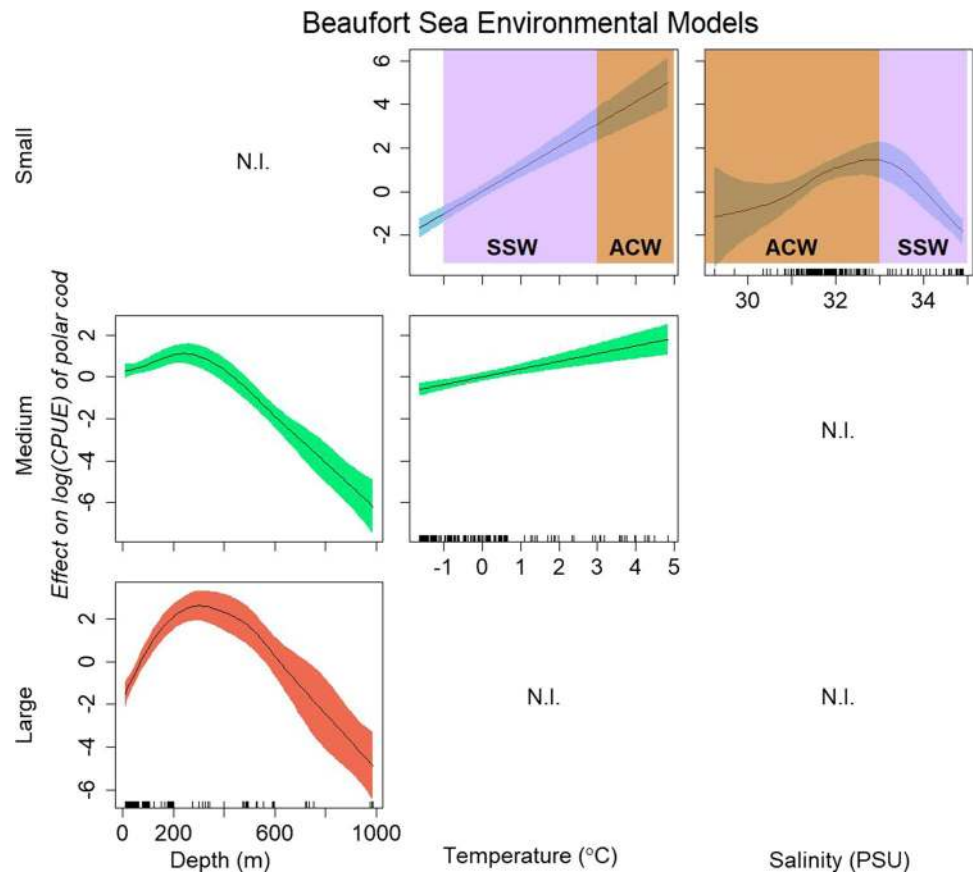
Suite of models developed for each polar cod size class, + denotes variables included in each model. The following statistics are reported: – log(likelihood), AIC, ΔAIC. Model performance ranked from best (1) to worst (7) using ΔAIC. ΔAIC calculated as the difference from the lowest AIC value for a size class and sea.  $\theta$  parameter estimated independently and fixed,  $\theta=0.878$ . Inclusion of a spatially autocorrelated error structure precludes the calculation of % deviance explained

A component of the Alaska Coastal Current (ACC), which may play a role in transporting polar cod northward in the Chukchi Sea, continues to flow along the Alaskan Coast, around Point Barrow, and into the Beaufort Sea (Okkonen et al. 2009). Barrow Canyon in the northern Chukchi Sea facilitates the movement of the ACC towards the Beaufort Sea (Pickart et al. 2005) and could effectively transport larval polar cod into the western Beaufort Sea as it does for zooplankton and other small particles (Ashjian et al. 2005; Berline et al. 2008). Further, small polar cod were also detected in the ACC in a plume extending 300 km eastward of Barrow Canyon (Crawford et al. 2012), demonstrating that small fish may be transported into the Beaufort Sea via eastward flowing currents.

Eastern and western aggregations of small polar cod in the Beaufort Sea, separated by a gap from 150° W to 144° W, suggests two separate groupings and perhaps distinct populations. Despite the prevailing eastward flow of water, the spatial separation indicates that polar cod in the eastern Beaufort Sea did not originate in the Chukchi Sea. Larval, juvenile, and adult polar cod are commonly captured in the

Canadian Beaufort Sea (Bouchard and Fortier 2011; Geoffrey et al. 2011; Walkusz et al. 2013) and could be a source of small polar cod in the eastern US Beaufort Sea. In 2011, pelagic, larval polar cod were most abundant in the eastern US Beaufort Sea when compared to the western US Beaufort Sea (Gallaway et al. 2017), suggesting that some polar cod in the US Beaufort Sea originate from Canadian sources. The distribution patterns are corroborated by a population genetic study which found that while polar cod comprises a single population, a significant difference in microsatellite alleles between polar cod from the southern Chukchi Sea and the central Beaufort Sea implies some degree of spatial genetic differentiation consistent with an isolation-by-distance pattern (Wilson et al. 2017, 2019). The low abundance of small polar cod between 150° W and 144° W is not an artifact of sparse sampling effort in the middle section, as the station sampling density is similar across the entire Beaufort Sea shelf; nor is it the result of a single year of low polar cod abundance, as this region was sampled over multiple years. Together, spatial and genetic information indicate that small polar cod across the Beaufort Sea shelf belong

**Fig. 7** Estimated effects of three environmental variables on log(CPUE) of three size classes of polar cod in the Beaufort Sea based on generalized additive model (GAM) analysis; y-axis is magnitude of effect, rug along x-axis mark location of data values, and colored envelopes are 95% confidence intervals. Results from the best model (Table 4) are displayed, and variables excluded from the best model are marked with N.I. (not included). Temperature and salinity measured at the seafloor. Characteristic water mass temperature and salinity values overlaid (SSW Summer Shelf Water, ACW Alaska Coastal Water)



**Table 5** Polar cod mean CPUE in spring and summer 2017 in the southern Chukchi Sea

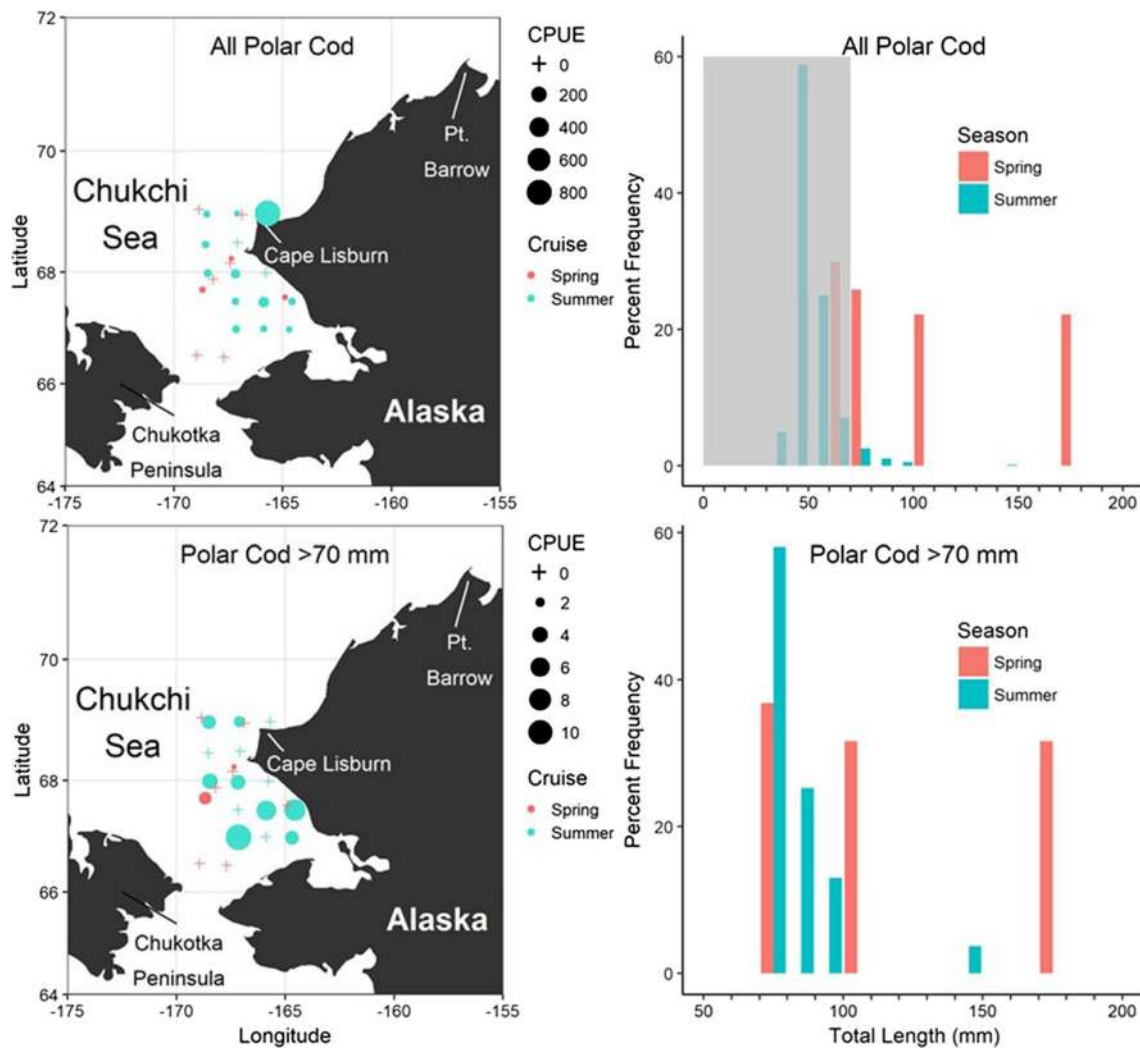
Season	Station ( <i>n</i> )	Depth	Temperature	Salinity	Size class	CPUE
Spring	9	43.1 (9.69)	1.69 (1.22)	32.42 (0.39)	All	0.71 (1.11)
					> 70 mm	0.50 (1.04)
Summer	14	39.1 (13)	4.18 (0.95)	32.26 (0.56)	All	70.31 (219.92)
					> 70 mm	3.02 (3.52)

Mean and (standard deviation) environmental conditions reported for depth (m), temperature (°C), salinity (PSU). Mean and (standard deviation) CPUE reported for all polar cod as well as only polar cod > 70 mm. CPUE significantly different ( $p < 0.05$ ) between spring and summer for polar cod > 70 mm

to two spatially segregated groups from different spawning locations.

In both the Chukchi and Beaufort seas, distribution patterns of medium and large polar cod suggest that larger fish actively disperse from areas occupied by the smallest fish. The small size class had a region of high abundance in the northeast Chukchi Sea that was not seen in the medium or large size classes. As fish develop, swimming ability improves (Webb 1994) and juveniles may disperse from nursery grounds to adult habitats (Gillanders et al. 2003). Improved dispersal capabilities gained with increasing body size could explain the spread of the medium size class beyond the confines of the areas occupied by small polar cod in the Chukchi and Beaufort seas. The large size class

showed further evidence of offshore ontogenetic movement in both the Chukchi and Beaufort seas, where large polar cod were most abundant beginning around 80 km in the Chukchi Sea and 60 km in the Beaufort Sea and extending seaward. Animals are often distributed with respect to resource availability to maximize fitness and reduce competition (Fretwell and Lucas 1969). The northeast Chukchi Sea and western Beaufort Sea, where there were regions of high abundance of the medium size class, are areas of high summer production (Walsh et al. 2005; Sigler et al. 2011). Therefore, mid-sized individuals may be maximizing growth by dispersing to productive feeding grounds. Offshore movement of large polar cod may be a component of adult spawning migrations. In the Chukchi Sea, several spawning grounds have been



**Fig. 8** Distribution and length-frequency of polar cod in the Chukchi Sea in spring and summer 2017. Length-frequency scaled by CPUE. Top two panels are all captured sizes of polar cod, total CPUE (fish per 1000 m<sup>2</sup>) spring=6.43, summer=984.40. Bottom two panels are

only polar cod > 70 mm, total CPUE spring=4.51, summer=42.29; gray box in top right shows small fish excluded from lower two plots. Note difference in scale between top left and bottom left plot

proposed in the northern Bering Sea and near the Chukotka peninsula (Ponomarenko 1968; Christiansen and Fevolden 2000; Vestfals et al. 2018). The abundance of the large size class of polar cod, both offshore and south of Cape Lisburne in the late summer, could reflect a movement towards these southern winter spawning locations.

**Environmental analysis**

Generally, both availability of food resources and temperature influence habitat selection of ectothermic species (Crowder and Magnuson 1983). Food resources are distributed unevenly among water masses (Eisner et al. 2013; Pinchuk and Eisner 2017; Smoot and Hopcroft 2017; Danielson et al. 2017b), which are identified by characteristic

temperature and salinity ranges in the Chukchi and Beaufort seas. Temperature also has a direct physiological effect on growth rates of juvenile polar cod (Laurel et al. 2017) and likely influences their distribution. Depth commonly influences distribution patterns and is associated with offshore migrations of other species such as Pacific cod and Pacific halibut (*Hippoglossus stenolepis*), in the neighboring Bering Sea (Shimada and Kimura 1994; Webster et al. 2013). In Alaskan waters, the addition of environmental information to species distribution maps has been identified as a recent research objective in the Alaska Essential Fish Habitat Research Plan, which is mandated by the Magnuson-Stevens Fishery Conservation and Management Act (Sigler et al. 2017). Characterizing the role of environmental conditions for polar cod at different life stages moves towards this

goal and identifies underlying processes influencing spatial patterns in distribution.

In the Chukchi Sea, small polar cod were associated with the intermediate temperature and salinity of the highly productive Bering Chukchi Summer Water (BCSW) mass. BCSW is a commonly detected water mass throughout the northeast Chukchi Sea during the open water season, with temperatures ranging from 0 to 7 °C and salinity from 30 to 33.5 PSU (Danielson et al. 2017b), which were the temperature and salinity ranges most commonly occupied by small polar cod (Fig. 6). Other water masses in the Chukchi Sea include the cooler Bering Chukchi Winter Water (BCWW) with temperatures from – 2 to 0 °C and salinity from 30 to 33 PSU, and the warmer Alaska Coastal Water (ACW) with temperatures from 7 to 12 °C and salinity from 27 to 32 PSU (Danielson et al. 2017b); however, small polar cod were less abundant in these water masses. BCSW is a nutrient-rich water mass with a characteristic zooplankton community of calanoid copepods and euphausiids (Eisner et al. 2013), which are prey for polar cod (Rand et al. 2013; Gray et al. 2016). In contrast, the BCWW and ACW are less nutrient rich, and have smaller-bodied zooplankton communities, including species such as *Oithona similis*, *Calanus abdominalis*, and *Pseudocalanus* spp. (Eisner et al. 2013), which are marginal resources when compared to lipid-rich *Calanus* copepods (Falk-Petersen et al. 2009). Maximizing energy intake as a result of consuming high-quality prey resources is beneficial to polar cod and results in increased growth rates and improved body condition (Hop et al. 1997). Therefore, distribution patterns of small polar cod in the Chukchi Sea are likely influenced by the abundance and composition of prey resources in different water masses.

In the Beaufort Sea, small polar cod were primarily associated with relatively warm and moderately fresh water found near the Alaskan coast. Environmental conditions in the Beaufort Sea are markedly different from those found in the Chukchi Sea; the warmest sampled Beaufort Sea temperature of 5 °C is comparable to the intermediate temperatures found in the Chukchi Sea. Yet in both the Chukchi and Beaufort seas (Figs. 6, 7), small polar cod were most abundant in water temperatures 4–5 °C. However, the relationship between small polar cod abundance and salinity differed between the Chukchi and Beaufort seas. Unlike in the Chukchi Sea where abundance increased linearly with salinity to a maximum of 34.5 PSU, small polar cod in the Beaufort Sea were less abundant at salinities > 34 PSU. Cold and saline water is associated with Summer Shelf Water (SSW), and our results suggest that the differing effect of salinity between seas is likely due to this association of small polar cod with distinct water masses, characterized by a signature combination of temperature and salinity (Danielson et al. 2017b).

The warm and fresh water occupied by small polar cod in the Beaufort Sea is associated with nearshore coastal habitats and the eastward flowing ACW (Okkonen et al. 2009; Carmack et al. 2015), and could impact growth of individuals in the small size class. This warm coastal water is not nutrient rich (Dunton et al. 2005), but does provide a thermal habitat that is advantageous for polar cod. Though polar cod is a cold-adapted species and capable of surviving in sub-zero temperatures (Osuga and Feeney 1978), it is more commonly found at temperatures above 0 °C (Crawford et al. 2012). Small polar cod in the Beaufort Sea appear to be occupying the warmest available water to maximize growth. Higher growth rates are advantageous for the small, age-0, individuals (Helser et al. 2017). In harsh Arctic winters, survivorship increases dramatically when pre-winter size and body condition are good (Fortier et al. 2006; Heintz and Vollenweider 2010), while large gape size and increased swimming speeds enable better resource exploitation (Scharf et al. 2000). In the Beaufort Sea, the thermal advantages of warm, coastal water appear to be correlated with patterns of distribution of small polar cod. Though warm coastal water may be advantageous for growth in certain scenarios, the cost of occupying low nutrient and low production waters could result in a tradeoff with negative energetic consequences, including a scenario where accelerated growth outstrips resource availability, impacting polar cod growth and survival in the Beaufort Sea.

The positive relationship between depth and abundance (Figs. 6, 7) indicates that depth is a key environmental component correlated with the offshore shift in distribution of the medium and large size classes of polar cod in the Chukchi and Beaufort seas. In the Chukchi Sea, where sampled depths were 13–90 m, the increasing linear relationship with depth suggests that polar cod moves to offshore, somewhat deeper locations as they grow larger. In the Beaufort Sea, where sampled depths reached nearly 1000 m, medium and large polar cod were most abundant at 300 and 400 m, respectively, demonstrating that as individuals increase in size, they move offshore to a specific bottom depth range. A nearly identical pattern was identified in the Canadian Beaufort, where medium and large fish (~ 90+ mm) were encountered at deep, offshore stations and the highest abundances of those fish were found at depths between 350 and 500 m (Geoffroy et al. 2011; Benoit et al. 2014; Majewski et al. 2016). The distribution pattern of polar cod was attributed to distinctly layered water masses in the Canadian Beaufort Sea (Pickart 2004), with polar cod occupying a layer of Atlantic Water, which was warmer than 0 °C and detected from 350 to 500 m depth. In the present study area, Atlantic Water was observed in the US Beaufort Sea at depths > 250 m (Norcross et al. 2017; Smoot and Hopcroft 2017), and this was where large polar cod were most abundant (Fig. 7).



Therefore, polar cod occupies the Atlantic Water mass in both the US and Canadian Beaufort Sea.

### Seasonal analysis

Springtime demersal abundance of polar cod in the southern Chukchi Sea was strikingly low compared to late summer abundance. Low springtime abundance of demersal polar cod during 2017, when only four fish were captured, was corroborated the following year when a June 2018 research cruise captured only two polar cod at the same sampling locations (Danielson et al. 2018). While adult polar cod were not present in the demersal environment in the southern Chukchi Sea in the spring, small polar cod (< 20 mm) were captured in Bongo nets (R. Hopcroft, personal communication) concurrently sampled with the bottom trawl in June 2017 and 2018. The bottom trawl gear used in June 2017 and 2018 was identical to the gear used in the late summer collections that successfully captured demersal polar cod in the same region. Though there were approximately half the number of stations sampled in June when compared to August, the stations were distributed across the study area to maximize spatial sampling extent (Fig. 8). It is likely that growth of age-0 polar cod between June and August/September resulted in a higher catch of age-0 polar cod in the late summer. However, the complete lack of larger (> 70 mm), older (age 1+) individuals, which would be equally susceptible to the net in June and August/September suggests that the collections in June likely truly represent a lower abundance of subadult and adult polar cod near the sea floor in the southern Chukchi Sea in the spring.

Strong linkages between sea ice and polar cod life history suggest that the distribution of polar cod in the southern Chukchi Sea could be influenced by the distribution of sea ice. While polar cod occupies environments that are seasonally ice free, it is often characterized as a sympagic species for a portion of its life cycle (Craig et al. 1982; Lønne and Gulliksen 1989). Polar cod is thought to spawn under sea ice, and buoyant eggs float to the ice–water interface before hatching in early spring (Graham and Hop 1995; Bouchard and Fortier 2011). Sea ice also provides a platform for the growth of sea ice algae, which is not only an important source of primary productivity in the Arctic, but also has a distinct isotopic signature that can be traced throughout Arctic food webs (Iken et al. 2005; Gradinger 2009). Isotopic and fatty acid analyses have linked polar cod to sea-ice-derived carbon, demonstrating the significant influence that sea ice can have on the diet of polar cod (Kohlbach et al. 2017; Dissen et al. 2018). Finally, the seasonal melting of sea ice is a driver of springtime patterns of productivity in the Arctic, with ice-edge blooms typically following the retreat of sea ice, resulting in peak productivity ~ 20 days after ice retreat (Perrette et al. 2011). The spring bloom

stimulates and supports secondary productivity, ultimately resulting in planktonic food resources for polar cod (Sigler et al. 2011; Wassmann and Reigstad 2011).

Given the link between sea ice and polar cod life history, sea ice extent and retreat may influence the spring distribution of polar cod in the southern Chukchi Sea. It is possible that polar cod tracks the springtime ice retreat and the wave of productivity that follows. However, in the springs of both 2017 and 2018, when sampling occurred, the sea ice edge had already retreated far north of the sampling region (NASA 2018). If polar cod followed the ice edge in these years, then its distribution would be beyond the northernmost station sampled during the June cruises, explaining the extremely low abundances of subadult and adult polar cod observed in the southern Chukchi Sea. It is unlikely that the low abundances of subadult and adult polar cod in the southern Chukchi Sea can be explained by polar cod moving south into the northern Bering Sea. Though polar cod is found episodically in the northern Bering Sea in association with cold conditions and large ice extent (Wyllie-Echeverria and Wooster 1998; Cui et al. 2009), these conditions did not occur in 2017 or 2018. Furthermore, sampling in the northern Bering Sea from St. Lawrence Island to the Bering Strait caught few polar cod in 2017 and 2018 (Danielson et al. 2018), suggesting that polar cod did not move into the northern Bering Sea.

Movement inferred from size-based and seasonal patterns in distribution describes a plausible migration scenario. In classical fisheries science, the life history of a species that undertakes a migration triangle travels from nursery grounds as juveniles, to feeding grounds as subadults, to spawning grounds upon maturation. The triangle is complete when eggs and larvae are passively transported from the spawning grounds to the nursery grounds via oceanic currents and the cycle begins again (Harden Jones 1968; Secor 2002). Small, young polar cod are most abundant in the northeast Chukchi Sea, perhaps indicating that region functions as nursery grounds for juveniles. The northeast Chukchi Sea was also proposed as a nursery area by researchers analyzing the pelagic distribution of age-0 polar cod, though the suggestion remains untested (De Robertis et al. 2017b). The next step in a migration triangle is the movement of subadults to feeding grounds; in the current study, the distribution pattern of the medium size class was different from the small size class, indicating that medium polar cod move away from areas occupied by small fish and disperse across the productive northeast Chukchi Sea shelf (Grebmeier 2012) to take advantage of feeding opportunities. The final component of a classic migration triangle is movement to spawning grounds; the current study cannot address this directly as polar cod spawns in the late fall and early winter under sea ice (Ponomarenko 2000). Several locations in the northern Bering

Sea and near the Chukotka peninsula have been recognized for their potential as polar cod spawning grounds (Ponomarenko 1968; Christiansen and Fevolden 2000; Vestfals et al. 2018); and are geographically close to the late summer distribution of the large size class in this study, which contains the majority of the mature spawners (Nahrgang et al. 2016). Potential spawners in the southern Chukchi Sea in late summer would not have far to travel to proposed spawning grounds during the fall and winter seasons.

Completion of the proposed migration scenario could be achieved via advection of eggs and larvae by the north-bound currents traveling through Bering Strait and across the Chukchi Sea (Weingartner et al. 2005). Pelagic (De Robertis et al. 2017b) and demersal distributions are consistent with northward advection of eggs and larvae from southern spawning grounds. The spring absence of polar cod from the southern Chukchi Sea may be explained within the framework of the proposed migration triangle. In the spring, adult polar cod following the seasonal northward retreat of sea ice may be spawners seeking resources to replenish their depleted energy reserves. Spawning is energetically costly and these individuals would likely need to take advantage of the earliest available food resources (Hop et al. 1995). This possible movement scenario synthesizes both size-based and seasonal distribution patterns of polar cod and represents a new effort to characterize polar cod migration patterns in the Chukchi Sea.

The migration of a small-bodied, high-latitude fish species is not unprecedented, but there remains much uncertainty surrounding the migration patterns of polar cod in the Chukchi Sea. Other marine fish species, such as Pacific herring and walleye pollock in the Bering Sea, exhibit seasonal migrations between feeding grounds and spawning grounds (Kotwicki et al. 2005; Tojo et al. 2007). Additionally, telemetry studies in the Atlantic Arctic found that polar cod is physically capable of traveling over 100 km in response to rapidly evolving ice conditions (Kessel et al. 2015). The migration triangle proposed here is currently constrained by data collected during open water sampling efforts. Moored acoustics offer an opportunity to confirm and refine understanding of polar cod movement during the Arctic winter and are currently being deployed in the Chukchi and Beaufort seas (Kitamura et al. 2017; Hauri et al. 2018). Patterns in backscatter collected at moorings during the ice-covered season provide information on fish presence and abundance when net sampling is not possible (Kaartvedt et al. 2009). In addition to increased field sampling efforts, modeling studies using tools like ROMS will corroborate the direction and timing of transport of polar cod eggs and larvae in ocean currents, improving understanding of polar cod movement throughout their life cycle in the Chukchi Sea. The scale of

detail of the migration triangle proposed here is coarse and based on a small sample size, but nevertheless provides an initial framework against which new information may be tested to advance understanding of polar cod movement patterns in the Chukchi Sea.

## Conclusions

Advancing fisheries science in the remote and difficult to access Arctic ecosystem is a significant research challenge. The work presented here compiles a large number of disparate individual sampling efforts to develop a holistic picture describing polar cod summer distribution in the Chukchi and Beaufort seas. The size-based analysis demonstrates ontogenetic shifts in distribution, while consideration of environmental covariates provides insight into potential mechanisms driving these patterns. Though much work remains to be done in understanding polar cod distribution and migration, the comparison between spring and summer abundances shows that polar cod distribution in the Pacific Arctic varies by season and suggests that this species may undertake some form of seasonal migration. The mapping of polar cod distribution in the Chukchi and Beaufort seas improves understanding of one of the most abundant and critical trophic links in the Arctic ecosystem. As the Arctic experiences increased anthropogenic and climatological pressures, thorough knowledge of key components of this system, including species like polar cod, will inform responsible decision making in this dynamic and rapidly changing ecosystem.

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