



Documenting growth parameters and age in Arctic fish species in the Chukchi and Beaufort seas

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ABSTRACT

Basic life history parameters of Arctic fishes have not been well characterized for many species in the Chukchi and Beaufort seas. Increasing environmental and anthropogenic changes in the Arctic may impact the biology of Arctic fishes and can best be evaluated if a benchmark is available against which to evaluate future changes in the biology of Arctic fishes. We used data from over 45,000 individual fishes to determine the length and weight relationships of 28 species, and further determined ages of 17 species of Arctic fishes. Specimens that we captured in the Pacific Arctic tended to be small in size, often less than 300 mm, and generally showed positive allometric growth. Despite their small sizes, individuals of some species, especially in Agonidae, Zoarcidae and Stichaeidae, were long-lived, reaching ages of up to 26 years. In the Chukchi Sea, individuals were shorter-lived and tended to be larger and longer-at-age. In contrast, the species that lived longer than a decade reached their maximum ages in the Beaufort Sea. While these long-lived species were smaller at age in the Beaufort Sea, they ultimately reached a greater maximum age than their Chukchi Sea conspecifics. Growth variation can have a large effect on management reference points, and understanding species-specific parameters would be required before any management action is considered, as mandated in the 2009 U.S. Arctic Fisheries Management Plan.

1. Introduction

There is a lack of information on the basic life history parameters, distribution, and life history strategies of Arctic fishes in the Chukchi and Beaufort seas. The remote, ice-covered environment where these Arctic species reside has historically impeded sampling during much of the year. In recent years, the combination of warmer waters, longer open-ice periods, and the existence of commercial fisheries in portions of the Atlantic Arctic have provided opportunities for consistent sampling of Arctic fishes in the Arctic region (Norcross et al., 2013; Logerwell et al., 2017). This has resulted in a larger body of knowledge about fishes in this area (Olsen et al., 2009; Johannesen et al., 2012), and presents an opportunity to better understand the life history parameters of these species.

In a preemptive move, the North Pacific Fisheries Management Council, the managing body for fisheries off the coast of Alaska, U.S., approved the Arctic Fisheries Management Plan (FMP) in 2009. The FMP provides a unique opportunity for precautionary management of Arctic fish resources (NPFMC, 2009) because it closed the U.S. Arctic to commercial fishing. Stock assessments are rarely conducted on U.S.

Arctic fishes, in part due to the commercial fishery closure, and also because basic information such as length, weight, and age, is not available for this region. Species-specific biological data are fundamental to establishing parameters that are incorporated into fisheries stock assessments. Basic stock assessment techniques such as virtual population analysis (VPA) require length, weight, and age, which makes the determination of these parameters for Arctic fish species essential for future management actions (Gulland, 1965; Maunder and Punt, 2013). Furthermore, modern stock assessments are moving beyond single species analysis and are increasingly incorporating multi-species interactions (Plagányi et al., 2014). Therefore, the length, weight, and age information assembled in this study for both potentially target and non-target species is vital to stock assessment efforts in the Arctic.

Analysis of fish length, weight, and age can be used to infer attributes of Arctic fish life history and provide insight into the susceptibility of a species to environmental change. The relationship between fish length and weight is one way to characterize growth patterns through the calculation of the allometric growth coefficient (Huxley, 1950; Froese, 2006). Growth patterns include isometric, negative allometric, and positive allometric, and indicate whether fish body length increases at

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the same relative rate as weight, growing long and thin, or short and stout, respectively. This allometry coefficient can be used to compare geographic variation in growth for a species across regions (Mendes et al., 2004). Fish age and maximum life expectancy have not been established for most Pacific Arctic fishes, with a few exceptions (Rand and Logerwell, 2011; Helser et al., 2017). The von Bertalanffy growth model is the most widely used growth curve in age-structured fisheries stock assessments and can be parameterized to the relationship between length and age (Quinn and Deriso, 1999). Both the overall lifespan of a species as well as the relative frequency of ages in a population permits assessment of a species' vulnerability to environmental disturbances (Berkeley et al., 2004). The difficulty of obtaining direct observation of Arctic fish biology renders indirect inference via length, weight, and age relationships especially useful.

Within the Pacific Arctic, the Chukchi and Beaufort seas form two habitats with distinct environmental conditions as a result of their widely differing physical oceanography. The Chukchi Sea has a wide and shallow shelf and receives an inflow of water from three primary water masses: Alaska Coastal Water, Bering Shelf Water and Anadyr Water (Weingartner, 1997; Weingartner et al., 2013). Nutrient-rich water originating from the Bering Sea creates areas of high production and rich benthic habitats on the Chukchi shelf (Dunton et al., 2005). In contrast, the Beaufort Sea has a narrow shelf that quickly drops off into deeper water. The Beaufort gyre, freshwater input from the Mackenzie River, and input from Atlantic Ocean water influence oceanographic processes in the Beaufort Sea, reducing the influence of nutrient-rich waters from the Pacific Ocean. Without these nutrient subsidies from richer sub-Arctic waters, production in the Beaufort Sea is much lower than in the Chukchi (Dunton et al., 2005).

It is understood that the Arctic is changing rapidly as a result of climate change (IPCC, 2018). Therefore, establishing a benchmark is necessary against which to evaluate the impacts of those changes on Arctic fish biology. With reduced sea ice, there is increasing interest in the Arctic for oil and gas exploration, shipping, and commercial fishing opportunities, which could significantly disturb the ecosystem (Gautier et al., 2009; Smith and Stephenson, 2013; Frey et al., 2015). In the absence of a formal stock assessment, knowledge of basic life history parameters of length, weight, and age is essential. In conjunction with growth type analysis, these parameters can provide a metric to evaluate the impact of these environmental changes. To determine these foundational life history parameters for Arctic fish species, this study analyzed more than a decade of length, weight, and age data collected from 28 species across the Pacific Arctic in the Chukchi and Beaufort seas (Table 1). Fishes collected spanned pelagic and benthic habitats and included ecologically critical species, such as Arctic Cod (*Boreogadus saida*), as well as species which are relatively undescribed (Table 2). Length, weight, and age were compared among species and across seas. By determining life history parameters of Arctic fish species, we have established a metric for future comparison in the data-poor region of the Pacific Arctic marine ecosystem.

2. Methods

Research cruises were conducted 2007–2015 in the Chukchi and Beaufort seas from July to October (Table 1). In the Chukchi Sea, sample locations spanned U.S. and Russian waters from approximately 174°E, to Point Barrow, 156°W, and extended from the Bering Strait at 66°N to approximately 76°N. In the Beaufort Sea, station locations covered the Alaskan coast from Point Barrow into Canadian waters past the Mackenzie River, 137°W, and extended northward to approximately 72°N (Fig. 1). The Chukchi Sea has a wide and shallow shelf, while the Beaufort Sea is characterized by a narrow shelf and a steep slope; thus, samples collected along the shelf and slope extend farther offshore in the Chukchi Sea, when compared to the Beaufort Sea. A variety of demersal and pelagic trawl gears, as well as beach seines were deployed to collect fish. Not all gear types were deployed on every cruise or at every sample

Table 1

List of sampling events by year, date range, ship, cruise designator, and sea.

Year	Start Date	End Date	Ship	Cruise	Region
2007	4-Sep	16-Sep	R/V Oscar Dyson	OD0710	Chukchi
2008	7-Jul	13-Jul	T/S Oshoro-Marū IV	OS190	Chukchi
2009	27-Jul	11-Aug	R/V Alpha Helix	COMIDA_2009	Chukchi
2009	4-Sep	29-Sep	R/V Professor Khromov	RUSALCA_2009	Chukchi
2009	13-Aug	29-Aug	F/V Westward Wind	WWW0902	Chukchi
2009	26-Sep	7-Oct	F/V Westward Wind	WWW0904	Chukchi
2010	21-Aug	4-Sep	R/V Norseman II	AKCH10	Chukchi
2010	1-Sep	18-Sep	F/V Westward Wind	WWW1003	Chukchi
2011	4-Sep	17-Sep	R/V Norseman II	AKCH11	Chukchi
2012	9-Aug	24-Sep	F/V Alaska Knight	Arctic Eis_2012	Chukchi
2012	27-Aug	16-Sep	R/V Professor Khromov	RUSALCA_2012	Chukchi
2016	2-Jul	10-Aug	USCGC Healy	HLY1601	Chukchi
2010	22-Sep	28-Sep	F/V Westward Wind	WWW1004	Beaufort
2011	15-Aug	4-Sep	R/V Norseman II	BOEM_2011	Beaufort
2012	20-Sep	1-Oct	R/V Norseman II	TB_2012	Beaufort
2013	12-Aug	2-Sep	R/V Norseman II	TB_2013	Beaufort
2014	14-Jul	2-Sep	R/V Norseman II	TB_2014	Beaufort
2013	14-Jul	25-Aug	Nearshore Beach Seine	ACES-2013	Chukchi, Beaufort
2014	15-Jul	27-Aug	Nearshore Beach Seine	ACES-2014	Chukchi, Beaufort
2014	15-Jul	28-Jul	R/V Launch 1273	ACES-2014	Chukchi, Beaufort
2015	14-Jul	15-Sep	Nearshore Beach Seine	AFF-2015	Chukchi, Beaufort

Table 2

List of taxa included in analysis.

Family	Scientific Name	Common Name
Osmeridae	<i>Mallotus catervarius</i>	Capelin
Gadidae	<i>Boreogadus saida</i>	Arctic cod
	<i>Eleginus gracilis</i>	saffron cod
Cottidae	<i>Arctiellus scaber</i>	Hamecon
	<i>Gymnocanthus tricuspis</i>	Arctic staghorn sculpin
	<i>Icelus bicornis</i>	twohorn sculpin
	<i>Icelus spatula</i>	spatulate sculpin
	<i>Myoxocephalus scorpius</i>	shorthorn sculpin
	<i>Triglops pingelii</i>	ribbed sculpin
Hemirhamphidae	<i>Nautichthys pribilovius</i>	eyeshade sculpin
Agonidae	<i>Aspidophoroides olrikii</i>	Arctic alligatorfish
	<i>Podothecus veterinus</i>	veteran poacher
Liparidae	<i>Liparis fabricii</i>	gelatinous seasnail
	<i>Liparis gibbus</i>	variegated snailfish
	<i>Liparis tunicatus</i>	kelp snailfish
Zoarcidae	<i>Gymnelus hemifasciatus</i>	halfbarred pout
	<i>Lycodes adolfi</i>	Adolf's eelpout
	<i>Lycodes polaris</i>	Canadian eelpout
	<i>Lycodes ravidens</i>	Marbled eelpout
	<i>Lycodes sagittarius</i>	archer eelpout
	<i>Lycodes seminudus</i>	longear eelpout
Stichaeidae	<i>Anisarchus medius</i>	stout eelblenny
	<i>Lumpenus fabricii</i>	slender eelblenny
	<i>Stichaeus punctatus</i>	Arctic shanny
Ammodytidae	<i>Ammodytes hexapterus</i>	Pacific sand lance
Pleuronectidae	<i>Hippoglossoides robustus</i>	Bering flounder
	<i>Limanda aspera</i>	Yellowfin sole
	<i>Limanda proboscidea</i>	longhead dab

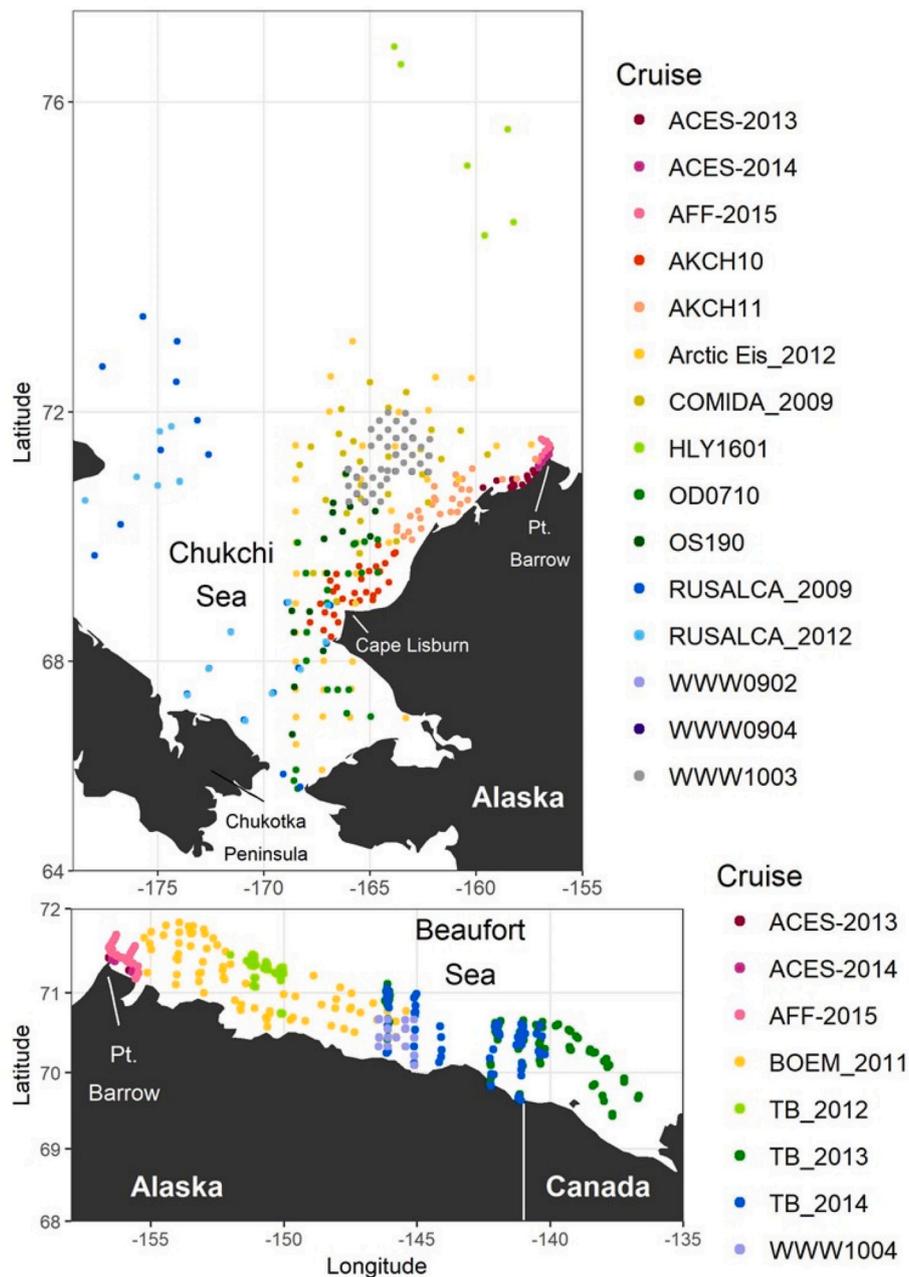


Fig. 1. Stations sampled in the Chukchi and Beaufort seas, 2007–2015. Colors correspond with cruise identity. Division between Chukchi and Beaufort seas occurs at Pt. Barrow. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

location. Codend mesh sizes ranged from 3 mm to 38 mm. By deploying a variety of gear types and mesh sizes, catches represented a wide range of sizes of the species we considered.

Fish were frozen in the field and sent to the Fisheries Oceanography Lab in Fairbanks, Alaska, U.S., for analysis. In the lab, field identification of fish specimens was confirmed using Mecklenburg et al., (2002); measurements were taken of total fish length (mm) with a fish measuring board and wet weight (g) with a top-loading balance. A size-based selection process was used to establish a subset of individuals for age estimation. Twenty individuals from each 10 mm size bin were randomly selected for aging from each cruise for each species if sufficient specimens were available. Sagittal otoliths were mounted on glass slides using Crystalbond™ (Ted Pella, Inc., Redding, CA, U.S.) thermoplastic glue and transversely sectioned under continuous water flow using a Buehler (Reno, NV, U.S.) rotating wheel with 1200 grit sandpaper. Once sectioned, the otolith was reheated, flipped onto the

flattened edge, remounted, and sanded to ~200–400 μm . Transverse cross sections of otoliths were photographed under transmitted light using a Leica DFC295 digital camera mounted on a Leica M165 C microscope at 5x magnification (Leica Biosystems DM1000, Wetzlar, Germany). Otoliths were aged from photographs by two independent readers (Helsler et al., 2017); a full year of growth consisted of one translucent ring of slower growth and one opaque ring of faster growth (Matta and Kimura, 2012). For the <5% of otoliths when readers disagreed on an age, the otolith in question was re-aged by both readers; most disagreements were rectified at this stage. If the disagreement persisted, readers worked together to agree on the best age for each fish; therefore, a statistical approach to reader agreement was not used here. Using this protocol, 100% of ages were checked.

Length and weight relationships were established using the standard fisheries allometric growth equation:

$$W = a * L^b$$

where W is fish weight, a is the y-intercept, L is total fish length, and b is the allometric growth coefficient (Huxley, 1950; Froese, 2006). The parameters a and b were estimated by log-transforming weight (W) and length (L) data and conducting a linear regression analysis. The fishes were generally small and lengths were measured in mm instead of cm, with the resulting a parameter expressed as 10^{-5} . Length-weight relationships were calculated for species where 50 or more individuals were collected in at least one sea. Approximately 99.7% of all measurements are expected to fall within \pm three standard deviations for a normal distribution; measurements outside that threshold could have been due to measurement or identification error. As a QA/QC procedure, following the methods outlined by (Giacalone et al., 2010), scatter plots of weight-at-length and age-at-length were visually examined for each fish species. Using the standardized residuals obtained from the initial weight-at-length regressions, we examined points >3 standard deviations from the mean. We inspected raw field data sheets and compared to lab data sheets to check for transposed numbers, lines, and handwriting interpretations. Errors were corrected when possible. Final length-weight regressions were refit after the removal of outliers, of which there were only $<1.0\%$.

For each species, growth type was compared between the Chukchi Sea and the Beaufort Sea using the following criteria. Growth was characterized using three criteria: if the growth coefficient, i.e., slope b , was 3 ± 0.1 growth was considered isometric, $b < 2.9$ was negative allometric growth, and $b > 3.1$ was positive allometric growth (Froese, 2006). To test for differences in growth between the Chukchi and Beaufort seas, a Student's t -test ($p < 0.05$) was performed comparing the growth coefficient b between seas.

Maximum ages were reported by region, when available, for all species for which a length-weight relationship was established. Species were selected for additional length-at-age and regional age analysis if more than 50 individuals had been collected in both the Beaufort and Chukchi seas (100 total). Eight species met these requirements (*Boreogadus saida*, *Eleginus gracilis*, *Gymnocanthus tricuspis*, *Myoxocephalus scorpius*, *Aspidophoroides olrikii*, *Lycodes polaris*, *Anisarchus medius*, *Lumpenus fabricii*). For each of these eight species, average length-at-age was calculated by region. We followed the same QA/QC protocol as for length-weight relationship, i.e., checking raw data. For the remaining ages >3 standard deviations outside of the mean, otoliths were examined again by two readers. Ages that could not be corrected ($<0.75\%$) were considered outliers and excluded from analysis. Because few data exist for these Arctic species, we use the term "outlier" without certainty that these data were necessarily incorrect.

Data for these eight species were fit to growth curves and compared to determine whether growth differed among the Chukchi and Beaufort fishes. The von Bertalanffy growth curve was selected because it is commonly used to describe fish growth and provides parameter estimates that are used in other relationships, (e.g., Beverton-Holt yield model, Beverton, 1954; Ricker, 1975). Data were fit in R using the R package *fishmethods* (<http://derekogle.com/fishR/>). When the von Bertalanffy relationship did not fit the data, the logistic growth model was chosen as an alternative (Quinn and Deriso, 1999).

Length-at-age data were first fit to a general model, with a separate parameter for each sea (Chukchi, Beaufort) for each of the three parameters in the von Bertalanffy model (L_{inf} , K , and t_0). The general model was the most complex, and was examined to ensure that residuals were normally distributed and randomly dispersed around the horizontal axis (Appendix Fig. A1). If this was true for the general model, it also applied to other subset models. A subset of seven simpler models were fit to the data for each species, with hierarchically fewer parameters, and an analysis of variance (ANOVA) was employed to examine whether a more parsimonious model could provide an equally good fit to the data. The seven simpler models were as follows: three "one-

parameter models" models which combined L_{inf} , K , or t_0 among the Beaufort and Chukchi samples; three "two-parameter" models with separate parameters for L_{inf} , K , or t_0 and combined parameters for the other two; and one combined model with all parameters combined for the Beaufort and Chukchi data. As each one parameter model was simpler than the general model, a one-parameter model that was not significantly different ($\alpha = 0.05$) from the general model was considered more parsimonious and a better model. If two or three one-parameter models were better than the general model, then the model with the smallest residual sum of squared was selected. The Akaike Information Criteria (AIC) was also used to compare models, as the same data were used in each nested model.

3. Results

We examined 28 common Arctic fish species from 10 families (Table 2) and more than 45,000 individuals for analysis of length-weight relationships (Table 3). The sizes of fishes collected in the Pacific Arctic were small, often no larger than 300 mm. Sizes of individuals ranged from 13 mm (*Limanda proboscidea*) to 465 mm (*Lycodes sagittarius*). Of the 16 species caught in both seas, individuals of 11 species grew to a larger maximum size in the Chukchi Sea, though the size difference was minimal for *Liparis tunicatus* (Table 3). Only two species, *Triglops pingelii* and *Gymnelus hemifasciatus*, had isometric growth, both in the Beaufort Sea. Negative allometric growth types were found for *Podothecus veterinus* and *Anisarchus medius*; in contrast to isometric growth, negative allometric growth was only detected in the Chukchi Sea. Positive allometric growth was the most common pattern and was found in 24 species in both the Chukchi and Beaufort seas (Table 3). Significant inter-sea differences of the parameter b were found for six species (Student's t -test, $p < 0.05$). The growth parameter b was larger in the Chukchi Sea in four species: *Boreogadus saida* ($3.24 > 3.12$), *Icelus spatula* ($3.35 > 3.15$), *Myoxocephalus scorpius* ($3.30 > 3.13$), *Gymnelus hemifasciatus* ($3.16 > 2.92$). The b parameter was significantly larger in the Beaufort Sea for *Lycodes polaris* ($3.32 > 3.22$) and *Anisarchus medius* ($3.31 > 2.88$).

The range of estimated ages of fish was 0–26 (Table 4). Of the 17 species for which ages were estimated ($n = 7585$), six species, one Agonidae, all four Zoarcidae, and one Stichaeidae, lived to a maximum age of more than a decade; the oldest were all in the Beaufort Sea. The remaining 11 species had maximum ages in the single digits.

Fish species with the greatest maximum ages were not necessarily the largest fish. Although the two oldest species, *Lycodes sagittarius* (age-26, max size 427 mm) and *L. seminudus* (age-24, max size 465 mm) also displayed the greatest maximum total length, the next two oldest species, *Anisarchus medius* (age-19, max size 158 mm) and *Aspidophoroides olrikii* (age-15, max size 80 mm) were less than a third as long (Table 3). In comparison, *Eleginus gracilis* grew to a length of 112 mm by age-1.

Patterns in species' mean length-at-age differed between the Chukchi and Beaufort seas for some of the eight species for which sufficient data were available (Table 5). Growth curves and length frequency data indicate that most species grew more quickly in the Chukchi sea (*Eleginus gracilis*, *Gymnocanthus tricuspis*, *Myoxocephalus scorpius*, *Anisarchus medius*, *Lumpenus fabricii*, *Aspidophoroides olrikii*, and *Lycodes polaris*). *Boreogadus saida* was the exception; it appeared to grow more quickly in the Beaufort Sea (Fig. 2, Table 5). There were no instances where a species' size-at-age was more frequently larger in the Beaufort Sea than in the Chukchi Sea (Table 5). Three species reached a maximum age, as estimated in the current study, in the Chukchi Sea (*Eleginus gracilis*, *Myoxocephalus scorpius*, *Lumpenus fabricii*). For the species *Eleginus gracilis* and *Myoxocephalus scorpius*, the largest individuals were not retained and aged; however, these large individuals were only caught in the Chukchi Sea and were much larger than conspecifics caught in the Beaufort (Table 3), which is consistent with the oldest individuals being found in the Chukchi Sea. Four species obtained a maximum age in the Beaufort Sea (*Gymnocanthus tricuspis*, *Aspidophoroides olrikii*, *Lycodes*

Table 3

Length-weight relationships for 28 species, calculated individually for the Beaufort and Chukchi seas. n = number of individuals analyzed, a = intercept, b = allometry parameter, r² = correlation coefficient. Growth type determined as allometric positive (b > 3.1), isometric (b = 3.0 ± 0.1), or allometric negative (b < 2.9). * indicates significant differences in growth (b) between the Chukchi and Beaufort seas, p < 0.05

Family	Species	Sea	n	Length Range (mm)	Weight Range (g)	a	b	r ²	Growth Type
Osmeridae	<i>Mallotus catervarius</i>	Chukchi	341	37–147	0.082–15.991	−7.214	3.909	0.9814	positive
Gadidae	<i>Boreogadus saida</i>	Chukchi	6538	11–252	0.008–98.680	−5.698	3.237*	0.983	positive
		Beaufort	6288	14–240	0.011–106.130	−5.444	3.119*	0.977	positive
	<i>Eleginus gracilis</i>	Chukchi	560	15–268	0.022–189.580	−5.828	3.341	0.966	positive
		Beaufort	95	20–62	0.028–1.590	−5.883	3.453	0.922	positive
Cottidae	<i>Artediellus scaber</i>	Chukchi	1157	17–113	0.040–25.800	−5.074	3.186	0.9472	positive
		Beaufort	420	14–95	0.030–13.630	−5.167	3.223	0.9762	positive
	<i>Gymnocanthus tricuspis</i>	Chukchi	5856	22–167	0.078–88.270	−5.578	3.360	0.976	positive
		Beaufort	1901	21–117	0.110–27.100	−5.493	3.323	0.928	positive
	<i>Icelus bicornis</i>	Beaufort	105	29–87	0.230–10.940	−5.462	3.304	0.9745	positive
	<i>Icelus spatula</i>	Chukchi	72	25–98	0.090–12.610	−5.605	3.345*	0.9593	positive
		Beaufort	838	23–111	0.090–19.830	−5.191	3.150*	0.9273	positive
	<i>Myoxocephalus scorpius</i>	Chukchi	4911	20–250	0.072–138.470	−5.471	3.302*	0.9684	positive
		Beaufort	275	31–141	0.220–36.300	−5.092	3.128*	0.8714	positive
	<i>Triglops pingelii</i>	Chukchi	198	33–161	0.200–26.920	−5.899	3.364	0.9688	positive
		Beaufort	543	26–151	0.150–27.690	−5.210	3.041	0.9807	isometric
Hemipteridae	<i>Nautichthys pribilovius</i>	Chukchi	87	24–85	0.159–9.400	−5.419	3.313	0.964	positive
Agonidae	<i>Aspidophoroides olrikii</i>	Chukchi	446	15–75	0.013–3.696	−6.247	3.596	0.921	positive
		Beaufort	826	22–80	0.040–3.690	−6.402	3.715	0.959	positive
	<i>Podothecus veterus</i>	Chukchi	90	30–133	0.130–11.180	−5.052	2.862	0.8919	negative
Liparidae	<i>Liparis fabricii</i>	Beaufort	319	15–212	0.040–112.530	−5.279	3.118	0.9775	positive
	<i>Liparis gibbus</i>	Beaufort	154	24–211	0.180–159.500	−5.350	3.246	0.9789	positive
	<i>Liparis tunicatus</i>	Chukchi	191	25–133	0.080–40.590	−5.474	3.294	0.9809	positive
		Beaufort	383	19–134	0.090–28.150	−5.455	3.261	0.9231	positive
Zoarcidae	<i>Gymnelus hemifasciatus</i>	Chukchi	158	33–131	0.100–8.060	−5.773	3.164*	0.9551	positive
		Beaufort	116	43–139	0.200–12.150	−5.293	2.922*	0.9392	isometric
	<i>Lycodes adolfi</i>	Beaufort	234	38–205	0.190–29.320	−5.730	3.104	0.9811	positive
	<i>Lycodes polaris</i>	Chukchi	371	32–229	0.100–65.010	−5.811	3.219*	0.9815	positive
		Beaufort	231	39–271	0.170–121.400	−5.948	3.318*	0.9632	positive
	<i>Lycodes raridens</i>	Chukchi	134	27–372	0.070–445.600	−5.849	3.264	0.9845	positive
		Beaufort	81	41–294	0.330–176.300	−5.528	3.148	0.9871	positive
	<i>Lycodes sagittarius</i>	Beaufort	187	44–427	0.330–347.600	−5.666	3.119	0.9896	positive
	<i>Lycodes seminudus</i>	Beaufort	176	41–465	0.300–535.990	−5.696	3.170	0.9918	positive
Stichaeidae	<i>Anisarchus medius</i>	Chukchi	1163	38–158	0.100–9.880	−5.301	2.877*	0.932	negative
		Beaufort	311	43–145	0.100–9.780	−6.124	3.308*	0.957	positive
	<i>Lumpenus fabricii</i>	Chukchi	4790	21–243	0.019–31.660	−5.931	3.205	0.960	positive
		Beaufort	507	26–164	0.030–11.680	−5.886	3.199	0.950	positive
	<i>Stichaeus punctatus</i>	Chukchi	486	15–122	0.0143–15.340	−6.000	3.444	0.9654	positive
		Beaufort	171	17–67	0.0128–2.400	−5.931	3.378	0.8381	positive
Ammodytidae	<i>Ammodytes hexapterus</i>	Chukchi	2031	19–167	0.016–17.190	−6.380	3.418	0.9618	positive
		Beaufort	615	24–146	0.022–9.280	−6.818	3.683	0.9461	positive
Pleuronectidae	<i>Hippoglossoides robustus</i>	Chukchi	577	15–226	0.017–104.800	−5.728	3.312	0.9693	positive
	<i>Limanda aspera</i>	Chukchi	395	14–217	0.034–131.230	−5.507	3.292	0.9842	positive
	<i>Limanda proboscidea</i>	Chukchi	156	13–171	0.014–70.910	−5.403	3.214	0.9783	positive

Table 4

Maximum age (years) for 17 species in the Chukchi Sea and Beaufort Sea. n = number of individuals aged species, - indicates no fish available.

Family	Species	Chukchi		Beaufort	
		Max Age	n	Max Age	n
Osmeridae	<i>Mallotus catervarius</i>	3	100	1	9
Gadidae	<i>Boreogadus saida</i>	5	1514	5	1230
	<i>Eleginus gracilis</i>	1	115	0	59
Cottidae	<i>Gymnocanthus tricuspis</i>	6	759	7	395
	<i>Icelus spatula</i>	–	–	6	70
	<i>Myoxocephalus scorpius</i>	5	260	3	69
Agonidae	<i>Aspidophoroides olrikii</i>	9	83	15	258
Liparidae	<i>Liparis fabricii</i>	–	–	5	125
Zoarcidae	<i>Lycodes adolfi</i>	–	–	12	178
	<i>Lycodes polaris</i>	9	215	11	162
	<i>Lycodes sagittarius</i>	–	–	26	116
	<i>Lycodes seminudus</i>	–	–	24	114
Stichaeidae	<i>Anisarchus medius</i>	12	281	19	214
	<i>Lumpenus fabricii</i>	7	726	5	234
Pleuronectidae	<i>Hippoglossoides robustus</i>	8	247	11	16
	<i>Limanda aspera</i>	4	36	–	–
	<i>Limanda proboscidea</i>	3	4	–	–

polaris, *Anisarchus medius*), and *Boreogadus saida* reached age-5 in both seas (Table 5). For the three oldest species (*Aspidophoroides olrikii*, *Lycodes polaris*, and *Anisarchus medius*), the maximum age occurred in the Beaufort Sea.

Growth data for all species presented unbiased and normally distributed residuals, with the exception of *Anisarchus medius*, which presented slightly skewed residuals (Appendix Fig. A1). Length-at-age data for this species indicated either high variability at older ages (5 and higher) or two distinct groups with different growth patterns (Fig. 2). *Myoxocephalus scorpius* data included a single age-3 individual from the Beaufort Sea. This age-3 individual was 141 cm, which was 54.4 cm larger than the mean size of the eight age-2 individuals in the dataset from the Beaufort Sea. The model did not converge when the age-3 individual was included because the length of the age-3 individual was so much larger than the length of the mean age-2 year old; therefore the age-3 individual was not included in the growth fitting. Overall the model indicated that *M. scorpius* from the Chukchi grew faster than from the Beaufort, and the data confirmed this result even without the anomalously large 3 year old from the Beaufort Sea; the mean length of age-2 *M. scorpius* from the Beaufort was 86.6 cm and the mean length from the Chukchi was 108.5 cm. The only species that could not be fit to the von Bertalanffy data was *Lycodes polaris*, likely because the length

Table 5

Length-at-age for eight species collected in both the Chukchi Sea (CS) and Beaufort Sea (BS). Rows include sample size (n), average length-at-age (mm), minimum length-at-age (mm) and maximum length-at-age (mm). If no min or max is shown, only one fish was measured.

Estimated Age (yrs)		<i>Boreogadus saida</i>		<i>Eleginus gracilis</i>		<i>Gymnocanthus tricuspis</i>		<i>Myoxocephalus scorpius</i>		<i>Aspidophoroides olrikii</i>		<i>Lycodes polaris</i>		<i>Anisarchus medius</i>		<i>Lumpenus fabricii</i>	
		CS	BS	CS	BS	CS	BS	CS	BS	CS	BS	CS	BS	CS	BS	CS	BS
0	N	516	489	103	59	259	128	104	48	26	24	41	37	27	51	149	95
	Avg	55	49	59	37	38	35	46	47	38	38	41	47	73	59	61	59
	Min	20	15	18	24	25	24	34	31	34	28	31	39	61	49	46	46
	Max	92	103	95	62	57	47	69	56	45	44	45	60	87	69	93	80
1	N	496	397	12	-	151	81	121	12	23	45	15	25	27	22	168	59
	Avg	99	98	97	-	57	52	77	73	46	43	66	57	76	70	90	76
	Min	54	48	85	-	39	38	36	51	41	32	39	39	63	54	64	51
	Max	151	163	112	-	75	75	113	89	51	58	92	74	95	85	136	106
2	N	370	273	-	-	174	99	30	8	9	25	48	18	34	29	239	33
	Avg	127	135	-	-	77	64	103	87	52	50	77	75	97	87	120	104
	Min	62	71	-	-	60	41	60	60	43	44	56	62	64	72	87	47
	Max	197	194	-	-	101	90	156	126	58	60	131	99	130	108	175	148
3	N	100	52	-	-	109	66	4	1	6	39	45	29	42	25	84	41
	Avg	143	163	-	-	94	81	136	141	57	57	91	77	98	94	149	123
	Min	76	117	-	-	66	61	121	141	53	45	68	66	71	77	73	83
	Max	229	213	-	-	129	110	155	141	62	64	146	104	139	104	218	173
4	N	31	15	-	-	50	11	-	-	10	35	17	20	55	10	53	3
	Avg	141	197	-	-	116	103	-	-	61	59	102	99	102	107	155	128
	Min	80	175	-	-	80	70	-	-	54	48	71	69	81	91	112	87
	Max	212	231	-	-	167	127	-	-	66	69	133	145	131	127	209	162
5	N	1	4	-	-	9	5	1	-	5	39	24	13	35	24	23	3
	Avg	230	206	-	-	126	105	130	-	60	59	116	103	113	107	176	134
	Min	-	163	-	-	94	98	130	-	54	50	81	76	89	60	137	96
	Max	-	240	-	-	148	115	130	-	63	69	150	160	152	128	243	203
6	n	-	-	-	-	7	3	-	-	1	26	10	11	21	13	7	-
	Avg	-	-	-	-	138	103	-	-	63	62	142	128	114	110	181	-
	Min	-	-	-	-	108	89	-	-	-	52	108	89	55	68	132	-
	Max	-	-	-	-	156	113	-	-	-	71	168	205	134	127	223	-
7	n	-	-	-	-	-	2	-	-	1	9	10	3	24	16	3	-
	Avg	-	-	-	-	-	124	-	-	65	66	168	138	122	103	164	-
	Min	-	-	-	-	-	101	-	-	-	58	139	109	108	64	135	-
	Max	-	-	-	-	-	147	-	-	-	72	200	183	146	135	195	-
8	n	-	-	-	-	-	-	-	-	1	3	2	2	8	6	-	-
	Avg	-	-	-	-	-	-	-	-	68	73	149	191	127	106	-	-
	Min	-	-	-	-	-	-	-	-	-	68	132	176	120	73	-	-
	Max	-	-	-	-	-	-	-	-	-	76	165	205	139	139	-	-
9	n	-	-	-	-	-	-	-	-	1	1	3	1	2	5	-	-
	Avg	-	-	-	-	-	-	-	-	69	68	178	177	127	109	-	-
	Min	-	-	-	-	-	-	-	-	-	-	162	-	123	94	-	-
	Max	-	-	-	-	-	-	-	-	-	-	196	-	131	123	-	-
10	n	-	-	-	-	-	-	-	-	-	2	-	2	4	2	-	-
	Avg	-	-	-	-	-	-	-	-	-	68	-	130	131	118	-	-
	Min	-	-	-	-	-	-	-	-	-	66	-	117	123	105	-	-
	Max	-	-	-	-	-	-	-	-	-	70	-	142	136	130	-	-
11	n	-	-	-	-	-	-	-	-	-	4	-	1	1	2	-	-
	Avg	-	-	-	-	-	-	-	-	-	71	-	271	140	123	-	-
	Min	-	-	-	-	-	-	-	-	-	65	-	-	-	116	-	-
	Max	-	-	-	-	-	-	-	-	-	74	-	-	-	130	-	-
12	n	-	-	-	-	-	-	-	-	-	3	-	-	1	4	-	-
	Avg	-	-	-	-	-	-	-	-	-	71	-	-	128	120	-	-
	Min	-	-	-	-	-	-	-	-	-	66	-	-	-	94	-	-
	Max	-	-	-	-	-	-	-	-	-	75	-	-	-	145	-	-
14	n	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-
	Avg	-	-	-	-	-	-	-	-	-	73	-	-	-	135	-	-
	Min	-	-	-	-	-	-	-	-	-	66	-	-	-	-	-	-
	Max	-	-	-	-	-	-	-	-	-	80	-	-	-	-	-	-
15	n	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-
	Avg	-	-	-	-	-	-	-	-	-	75	-	-	-	145	-	-
16	n	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
	Avg	-	-	-	-	-	-	-	-	-	-	-	-	-	130	-	-
17	n	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
	Avg	-	-	-	-	-	-	-	-	-	-	-	-	-	107	-	-
19	n	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
	Avg	-	-	-	-	-	-	-	-	-	-	-	-	-	131	-	-

data did not asymptote at older ages. The logistic function provided a better fit for this species (Quinn and Deriso, 1999). A second species, *Eleginus gracilis* was excluded from growth modeling because there were insufficient ages in the dataset (only age-0 in Beaufort and ages 0 and 1 from the Chukchi).

Of the six species fit to the von Bertalanffy growth function, *Gymnocanthus tricuspis* and *Anisarchus medius* fit the general model (Table A1). The best model for *Boreogadus saida*, *Myoxocephalus scorpius*, and *Aspidophoroides olrikii* used a combined parameter for Beaufort and Chukchi seas for t_0 . *Lumpenus fabricii* was the only model fit to a von

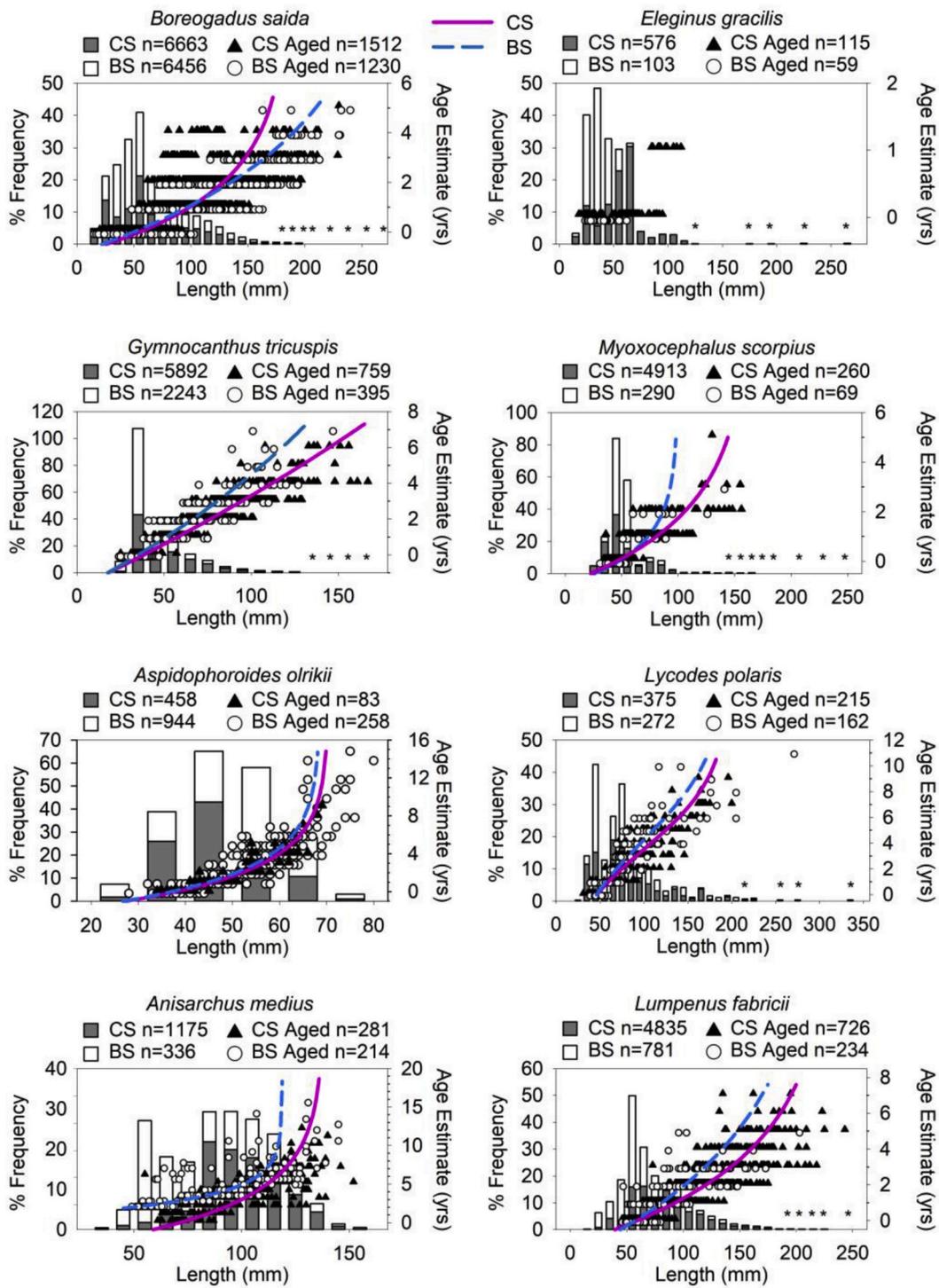


Fig. 2. Percent frequency for eight fish species of length (mm) partitioned by Chukchi Sea (CS) and Beaufort Sea (BS). Frequencies sum to 100 percent for each sea. Estimated fish age (years) are displayed on right y-axis; axes are not the same for each plot. Asterisks * above a size class indicate frequencies less than 0.4%; blanks indicate no individuals captured of that size. Lines represent growth curves (Table A1) calculated for each species in each sea, pink is CS, blue is BS. Growth curves were von Bertalanffy with the exception of *Lycodes polaris*, which used the logistic growth function, and were not generated for *Eleginus gracilis*, due to insufficient data. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Bertalanffy with a single parameter for L_{inf} . The *Lycodes polaris* model with the best fit was the logistic growth function with a single L_{inf} parameter.

Growth curves showed that there were significant differences in growth ($p < 0.05$) in at least one of the three growth parameters estimated in the six species fit to von Bertalanffy and logistic growth curves among collections from the Chukchi and Beaufort Seas (Appendix

Fig. A1; Table A1). The asymptotic average length differed among the Chukchi and Beaufort sea collections for *Boreogadus saida*, *Gymnocanthus tricuspis*, *Myoxocephalus scorpius*, *Aspidophoroides olrikii*, and *Anisarchus medius*; the growth rate differed for *Boreogadus saida*, *Gymnocanthus tricuspis*, *Myoxocephalus scorpius*, *Anisarchus medius*, *Lumpenus fabricii*, and *Lycodes polaris* (Appendix Table A1).

4. Discussion

New information on the length-weight relationships of 28 Arctic fish species indicates positive allometric growth, and age data show longevity over a decade despite relatively small size of some species. The knowledge gained in this study will be essential for fisheries science and stock assessment efforts in the Pacific Arctic, which may become necessary as global interest from industrial sectors, such as petroleum extraction, shipping, and potential commercial fisheries, increase in the region (Christiansen et al., 2014). Given the lack of current fisheries assessments in this region, the knowledge generated in this work provides a needed metric for comparison of future changes in the biology of Arctic fishes. Significant regional differences in growth type were detected for six species (Table 3), but neither the Chukchi nor the Beaufort seas were consistently superior for all intraspecific growth. Within the same species, differences in allometry may indicate that physical and oceanographic factors affect growth in separate geographic areas (Froese, 2006; Wund et al., 2012). Intraspecific differences in growth suggest that the environmental conditions may impact fish growth patterns, and future work should include genetic analysis to determine whether there is a genetic component to observed differences. Optimum environmental conditions for Arctic fishes vary from species to species; therefore, the impact of changes in environmental conditions in the Arctic will likely have a mosaic of species-specific effects on Arctic fish biology.

Several limitations should be considered when evaluating the results presented in this study. First, the collection of samples was not evenly distributed across gear types, years, or sampling locations. The data presented here are an opportunistic aggregation of available data. While this may introduce biases in the sizes and ages of fishes presented in this study, our goal was to present broad and foundational knowledge to support future work in the Arctic. Second, when aging otolith samples, we assumed that a dark band coupled with a light band reflect seasonal differences in growth rates and together are one year of growth as is standard practice (Campana and Stevenson, 1992). It would be good to verify this assumption by conducting age validation experiments for each species. The Arctic environment exhibits extreme seasonality, with dark, sea-ice covered winters and 24-hr daylight, open-water summers, making seasonal differences in growth more pronounced than they are for lower latitude fish species (Berge et al., 2015), thus supporting the validity of this assumption.

The size of many Arctic fish species is generally small compared to more southerly seas (Stevenson and Lauth, 2012) and is a factor that determines their ecological role in the Arctic marine ecosystem. Arctic fishes are important prey items, despite their small size, notably *Boreogadus saida*, for other marine vertebrates such as birds, seals, and beluga whales (Bluhm and Gradinger, 2008; Harter et al., 2013). In the Arctic, therefore, these small fish species play a role in the flow of energy through the ecosystem. The small sizes reported here are likely not an artifact of sampling effort failing to catch larger individuals, as a range of gear types and mesh sizes were employed to collect these specimens, and fishes as large as 525 mm were caught on the Beaufort Sea slope in a bottom trawl with 3 mm mesh (Norcross et al., 2017). Independent sampling efforts with larger nets in the Pacific Arctic also reported fish lengths similar to the values presented here (Frost and Lowry, 1983; Rand and Logerwell, 2011). Cool water temperatures generally constrain growth rates (Pörtner et al., 2001). Water temperatures in the Chukchi and Beaufort seas are cold, commonly -2 – -7 °C, though temperatures as warm as 13 °C have been detected (Pickart et al., 2005; Crawford et al., 2012), which potentially limits the maximum size achieved by Arctic fish species.

For six of the 28 species in this study, there are known lengths and allometry patterns from other northern collections. The size of *Mallotus catervarius* in the Chukchi Sea is equivalent to previous measurements in the Beaufort and Chukchi seas (Fechhelm et al., 1985; Wiswar and Frue, 2006), but 60 mm smaller than in the North Pacific (Hart, 1973),

and the growth parameter is similar to the Barents Sea (Gjosæter, 1998) but less than the more southern population in the Gulf of Alaska ($b = 4.23$, Brown, 2002). Though the maximum length of *Boreogadus saida* in both seas is like other collections in the Chukchi Sea (Mecklenburg et al., 2016; Helser et al., 2017), it is 70–200 mm smaller than at lower or comparable latitudes in Iceland (Astthorsson, 2016) and the Barents Sea (Wienerroither et al., 2011). Although there was no reason to question that *B. saida* had a positive growth type in both seas in this study, that differed from isometric growth in the Chukchi Sea (Helser et al., 2017) and in the Beaufort Sea (Rand and Logerwell, 2011). The differences in the same species in the same areas over the same times could be attributable to the larger-mesh nets collecting longer, thinner fish than did the small bottom nets and beach seines we used. The largest *Lycodes raridens* in our study was less than half the size found on the Asian side of the Pacific Arctic (Balanov et al., 2006; Kulik and Gerasimov, 2016); however, the growth parameters are the same. The flatfishes *H. robustus* and *Limanda aspera* were smaller in our collections than in the Chukchi Sea (Pruter and Alverson, 1962) or northeast Pacific (Kramer and Josey, 1995). In the current study both were shorter and fatter compared to previous efforts, but while *L. aspera* displayed positive allometry (Black et al., 2013) in both studies, *H. robustus* in our study had positive growth but had been reported as negative in the Chukchi Sea earlier (Smith et al., 1997b). The differences in our findings and those of others could be due to geography.

The maximum sizes for seven of the 28 species in this study either surpass the previously recorded maximum size for the Pacific Arctic or add new knowledge as the first length measurement record for the Pacific Arctic. The 113 mm *Arteidiellus scaber* in our study is the largest specimen recorded in the Chukchi Sea (Thorsteinson and Love, 2016). The 212 mm specimen of *Liparis fabricii* captured in the Beaufort Sea surpasses the previous record in this sea (Mecklenburg et al., 2014), and is equal to the maximum size in the Barents Sea (Wienerroither et al., 2011). In the same Liparidae family, *L. tunicatus* is similar in maximum size to the previous record in the northern Bering Sea (Mecklenburg et al., 2016). In the Zoarcid family, many maximum lengths are reported from the Atlantic Arctic. For *Lycodes adolfi*, maximum lengths reported from east Greenland (Mecklenburg et al., 2014) and north of Spitzbergen (Byrkjedal et al., 2011) are similar to that in the Beaufort Sea from the current study. While the largest *L. seminudus* in the Beaufort Sea adds new information, it was over 100 mm smaller than the maximum reported from West Greenland (Møller and Jørgensen, 2000). In family Stichaeidae, information on *Anisarchus medius* maximum lengths fills in gaps between studies in the Western Pacific (Mecklenburg et al., 2018) and the Barents Sea (Wienerroither et al., 2011). Differential growth for *Anisarchus medius* among the Chukchi and Beaufort Seas may be a topic for future research in this species. The maximum sizes of *Stichaeus punctatus* in the current study are smaller than maximum length recorded in the North Pacific (Eschmeyer and Herald, 1983), but provide information from Arctic locations. By documenting maximum fish size, we are able to corroborate and update basic life history information for these Pacific Arctic species.

We characterized the fishes in the U.S. Chukchi and Beaufort seas as “short-lived” (<age-10) and “long-lived” (>age-10) (Tables 3 and 4). *Mallotus catervarius* may be categorized as short-lived, at a maximum of age-6 (Gjosæter, 1998). Our values of age-3 (Chukchi Sea) and age-1 (Beaufort Sea) fit within range of both sexes in all seasons in the Barents Sea (Gjosæter, 1998). *Boreogadus saida* is also short-lived, with maximum age-7 (Hop et al., 1997) or age-8 (Gillispie et al., 1997), and of age-5 found in this study, in the Chukchi and Bering seas (Helser et al., 2017), and in the Svalbard Archipelago (Nahrgang et al., 2016). Likewise, two of the three sculpins we found up to age-7 are short lived; this is corroborated by others finding age-9 *Gymnocanthus tricuspis* in the Chukchi Sea (Smith et al., 1997a) and age-7 *Icelus spatula* off the Kuril Islands (Tokranov and Orlov, 2005). For *Myoxocephalus scorpius*, though we only aged specimens as old as age-5, it can be found up to age-15 in Newfoundland waters (Ennis, 1970), thus it cannot be categorized as

short-lived with the other two sculpin species. *Liparis fabricii*, previously without age recorded in Pacific Arctic, now is documented as age-5, which is similar to the 6 years in the Barents Sea (Wienerroither et al., 2011).

The ages documented in this study, sometimes for the very first time in the Pacific Arctic, highlight the different life history traits of Arctic fish species. Four *Lycodes* species now have recorded ages in the Pacific Arctic, including *L. adolfi*, age-12, *L. polaris* age-11, and the two oldest species we aged, *L. sagittarius*, age-26, and *L. seminudus*, age-24. Only two of these had a previously recorded maximum ages, *L. polaris* age-5 (Frost and Lowry, 1983) and *L. seminudus* age-8 (Mecklenburg et al., 2018). One of the biggest surprises was finding that some small species were long-lived, such as *Aspidophoroides olrikii*, which are small in size (80 mm), but nevertheless long-lived, with a maximum age-15. Similarly, *Anisarchus medius*, is a long-lived (age-19) and small (134 mm) species. For both species, no other age records in the Pacific Arctic exist, highlighting the novel information gained in this study. Furthermore, the size-at-age documented here emphasizes that small body size is not necessarily an indicator of limited longevity.

Though nearly twice as many species grew to greater maximum lengths in the Chukchi Sea than the Beaufort Sea, patterns of maximum ages between the Chukchi and Beaufort seas are more nuanced than those characterizing fish maximum length and length-at-age. Species that lived longer than a decade (*Aspidophoroides olrikii*, *Lycodes polaris*, and *Anisarchus medius*), reached their maximum age in the Beaufort Sea. Although these long-lived species are smaller at age in the Beaufort Sea, they ultimately reach a greater maximum age than their Chukchi Sea conspecifics. Increased resource availability has a positive impact on fish growth (Jones, 1986; Rosenfeld et al., 2005), but rapid growth can lead to a reduction in overall lifespan (Metcalf and Monaghan, 2003). The importance of this trade-off between growth and longevity may depend on species-specific life history. In the biologically productive Chukchi Sea (Grebmeier et al., 2006), abundant resources can foster rapid growth; for short-lived species, the benefits of growing quickly may outweigh associated metabolic costs. In contrast, the impact of these metabolic costs may be more important for long-lived fishes, explaining why species such as *Lycodes polaris* lives to its maximum age in the colder Beaufort Sea, where scarce resources promote slow growth rates. Similarly, *Lycodes reticulatus* reached a maximum age of 35 years in the cold waters of northeastern Greenland and only 19 years in the warmer waters of the Barents Sea; low resource availability leads to slower growth rates in Greenland (Hildebrandt et al., 2011). Further research into the mechanisms driving differences in fish growth and maximum age in each region is necessary to explain the physiological processes driving these patterns.

Though a current stock assessment does not exist for the U.S. Arctic,

the NPFMC Arctic Fisheries Management Plan could require the development of such a plan in the future. International interest in high latitude fisheries resources may increase as other economic opportunities shift global attention towards the Arctic. A cooperative international agreement was recently reached among nine Arctic and sub-arctic nations and the European Union that prevents commercial fishing in the central Arctic Ocean (Hoag, 2017). Numerous specimens were collected and examined for this study, and we acknowledge they may already have been affected by climate change. Potential shortcomings of this research may include aging methodology and limited data on all life stages of each species. However, this work lays a solid foundation for understanding life history traits of Arctic fish species. These data will meet the increasing demand for information as both domestic and international regulatory decisions are made regarding Arctic resources. Independent of future Arctic fisheries management actions, the knowledge gained in this study establishes a benchmark of fundamental biological parameters for fishes in the Pacific Arctic.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

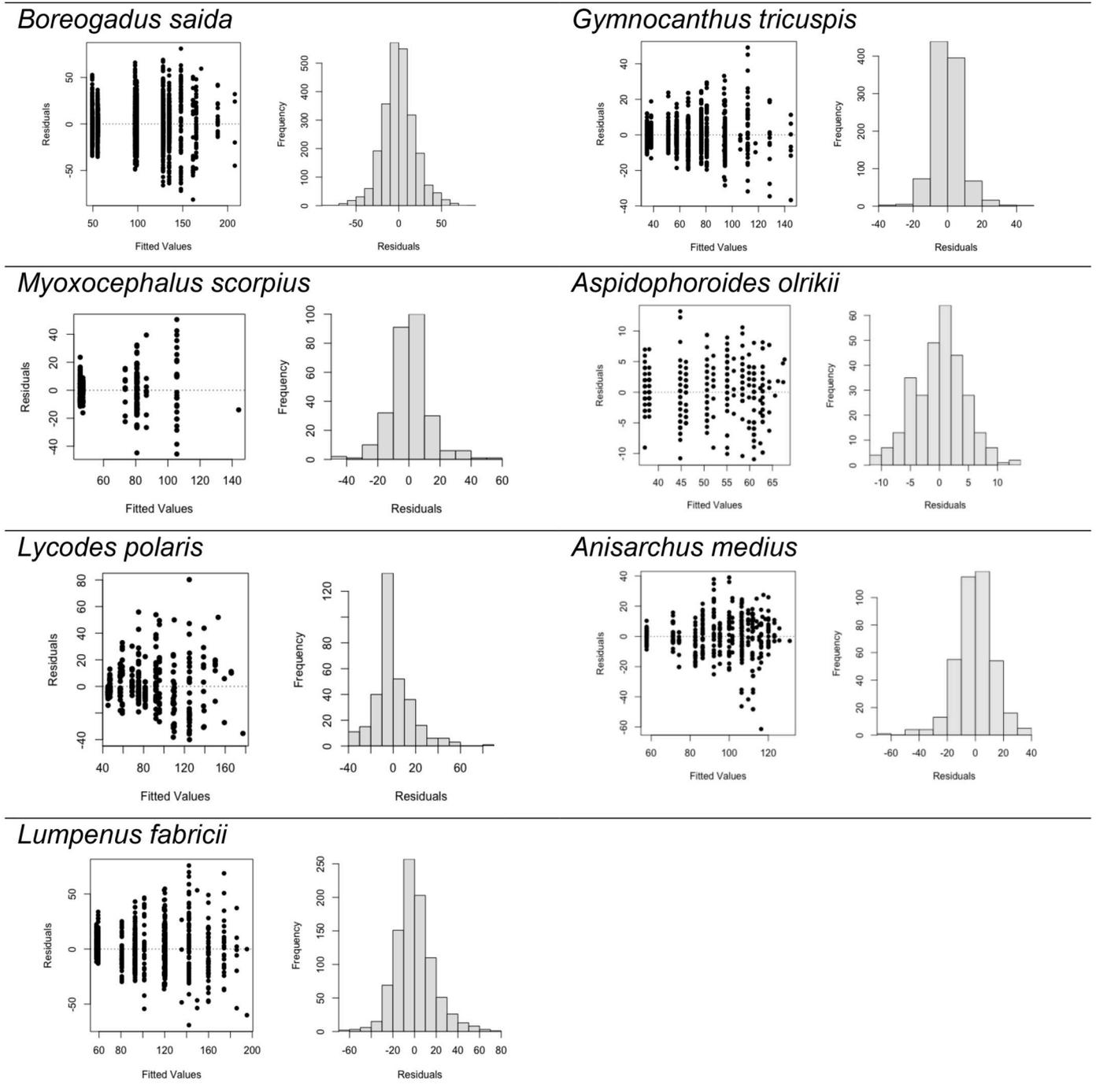


Fig. A1. Diagnostic plots for general growth models with separate parameters for the Chukchi and Beaufort Seas for seven selected species. Residual plots include data from both seas but are not differentiated. *Eleginus gracilis* was not included in the analysis because there were insufficient ages in the dataset (only age 0 in Beaufort and ages 0 and 1 from the Chukchi).

Table A1

The preferred growth model for the following species: *Boreogadus saida* (BS), *Gymnancanthus tricuspis* (GT), *Myoxocephalus scorpius* (MS), *Aspidophoroides olrikii* (AO), *Lycodes polaris* (LP), *Anisarchus medius* (AM), *Lumpenus fabricii* (LF). Parameters that apply to the Beaufort (B) and Chukchi (C) Sea samples have no subscript (e.g. t_0), and a single value is presented. Parameters with separate values for the Beaufort and Chukchi Seas are given a subscript (e.g. $t_{0[\text{sea}]}$), where sea refers to Chukchi or Beaufort Seas. The von Bertalanffy growth function was used for all species, with the exception of *Lycodes polaris*, which was fit to the logistic growth function. The parameter t_t refers to total length. In the von Bertalanffy growth function, L_{inf} is the asymptotic average length, K is the Brody growth rate coefficient (units are in yr^{-1}), and t_0 represents the age when average length was zero. In the logistic growth function, L_{inf} and t_0 are as above, and G is the instantaneous growth rate at the origin of the curve

Species	Selected von Bertalanffy growth model	$L_{\text{inf}[\text{sea}=\text{B}]}$	$L_{\text{inf}[\text{sea}=\text{C}]}$	$K_{[\text{sea}=\text{B}]}$	$K_{[\text{sea}=\text{C}]}$	$t_{0[\text{sea}=\text{B}]}$	$t_{0[\text{sea}=\text{C}]}$
BS	$t_t \sim L_{\text{inf}[\text{sea}]} * (1 - \exp(-K_{[\text{sea}]} * (\text{age} - t_0)))$	290.7462	186.4611	0.2175	0.4067	-0.8603	
GT	$t_t \sim L_{\text{inf}[\text{sea}]} * (1 - \exp(-K_{[\text{sea}]} * (\text{age} - t_{0[\text{sea}]})$	282.5569	563.8271	0.0678	0.0378	-1.9496	-1.8555
MS	$t_t \sim L_{\text{inf}[\text{sea}]} * (1 - \exp(-K_{[\text{sea}]} * (\text{age} - t_0)))$	99.7263	164.6567	0.6945	0.3507	-0.9216	
AO	$t_t \sim L_{\text{inf}[\text{sea}]} * (1 - \exp(-K * (\text{age} - t_0)))$	68.5904	70.3428	0.2829		-2.7457	
AM	$t_t \sim L_{\text{inf}[\text{sea}]} * (1 - \exp(-K_{[\text{sea}]} * (\text{age} - t_{0[\text{sea}]})$	118.8974	138.0068	0.3164	0.1878	-2.0973	-3.8622
LF	$t_t \sim L_{\text{inf}} * (1 - \exp(-K_{[\text{sea}]} * (\text{age} - t_{0[\text{sea}]})$	234.8108		0.1429	0.2130	-1.9646	-1.3642

Species	Selected logistic growth model	L_{inf}	$G_{[\text{sea}=\text{B}]}$	$G_{[\text{sea}=\text{C}]}$	$t_{0[\text{sea}=\text{B}]}$	$t_{0[\text{sea}=\text{C}]}$
LP	$t_t \sim L_{\text{inf}} / (1 + \exp(-G_{[\text{sea}]} * (\text{age} - t_{0[\text{sea}]})$	198.6435	0.2858	0.3428	4.1995	3.4782

Appendix B. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr2.2020.104779>.

References

- Asthorsson, O.S., 2016. Distribution, abundance and biology of polar cod, *Boreogadus saida*, in Iceland–East Greenland waters. *Polar Biol.* 39, 995–1003.
- Balanov, A., Badaev, O., Napazakov, V., Chuchukalo, V., 2006. Distribution and some biological features of *Lycodes raridens* (Zoarcidae) in the western part of the Bering Sea. *J. Ichthyol.* 46, 148–155.
- Berge, J., Renaud, P.E., Darnis, G., Cottier, F., Last, K., Gabrielsen, T.M., Johnsen, G., Seuthe, L., Weslawski, J.M., Leu, E., 2015. In the dark: a review of ecosystem processes during the Arctic polar night. *Prog. Oceanogr.* 139, 258–271.
- Berkeley, S.A., Hixon, M.A., Larson, R.J., Love, M.S., 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 29, 23–32.
- Beverton, R., 1954. Notes on the Use of Theoretical Models in the Study of the Dynamics of Exploited Fish Populations (No. 2). US Fishery Laboratory.
- Black, B.A., Matta, M.E., Helsler, T.E., Wilderbuhr, T.K., 2013. Otolith biochronologies as multidecadal indicators of body size anomalies in yellowfin sole (*Limanda aspera*). *Fish. Oceanogr.* 22, 523–532.
- Bluhm, B.A., Gradinger, R., 2008. Regional variability in food availability for Arctic marine mammals. *Ecol. Appl.* 18, S77–S96.
- Brown, E.D., 2002. Life history, distribution, and size structure of Pacific capelin in Prince William Sound and the northern Gulf of Alaska. *ICES (Int. Coun. Explor. Sea) J. Mar. Sci.* 59, 983–996.
- Byrkjedal, I., Langhelle, G., de Lange Wenneck, T., Wienerroither, R., 2011. *Lycodes adolphi* nielsen and fosså, 1993 (teleostei: Zoarcidae) found in the Arctic Ocean. *Polar Biol.* 34, 465–467.
- Campana, S.E., Stevenson, D.K., 1992. Otolith Microstructure Examination and Analysis, vol. 117. Canadian Special Publication of Fisheries and Aquatic Sciences (Department of Fisheries and Oceans, Ottawa).
- Christiansen, J.S., Mecklenburg, C.W., Karamushko, O.V., 2014. Arctic marine fishes and their fisheries in light of global change. *Global Change Biol.* 20, 352–359. <https://doi.org/10.1111/gcb.12395>.
- Crawford, R.E., Vagle, S., Carmack, E.C., 2012. Water mass and bathymetric characteristics of polar cod habitat along the continental shelf and slope of the Beaufort and Chukchi seas. *Polar Biol.* 35, 179–190. <https://doi.org/10.1007/s00300-011-1051-9>.
- Dunton, K.H., Goodall, J.L., Schonberg, S.V., Grebmeier, J.M., Maidment, D.R., 2005. Multi-decadal synthesis of benthic–pelagic coupling in the western arctic: role of cross-shelf advective processes. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 52, 3462–3477. <https://doi.org/10.1016/j.dsr2.2005.09.007>.
- Ennis, G., 1970. Age, growth, and sexual maturity of the shorthorn sculpin, *Myoxocephalus scorpius*, in Newfoundland waters. *Journal of the Fisheries Board of Canada* 27, 2155–2158.
- Eschmeyer, W.N., Herald, E.S., 1983. A Field Guide to Pacific Coast Fishes. North America (Houghton Mifflin Harcourt, New York, NY).
- Fechhelm, R.G., Craig, P.C., Baker, J., Galloway, B.J., 1985. Fish Distribution and Use of Nearshore Waters in the Northeastern Chukchi Sea, vol. 32. US Department of Commerce, NOAA, and US Department of the Interior, Minerals Management Service, pp. 121–298. Outer Continental Shelf Environmental Assessment Program Final Report.
- Frey, K.E., Moore, G.W.K., Cooper, L.W., Grebmeier, J.M., 2015. Divergent patterns of recent sea ice cover across the bering, Chukchi, and Beaufort seas of the pacific arctic region. *Prog. Oceanogr.* 136, 32–49. <https://doi.org/10.1016/j.pcean.2015.05.009>.
- Froese, R., 2006. Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *J. Appl. Ichthyol.* 22, 241–253. <https://doi.org/10.1111/j.1439-0426.2006.00805.x>.
- Frost, K.J., Lowry, L.F., 1983. Demersal Fishes and Invertebrates Trawled in the Northeastern Chukchi and Western Beaufort Seas 1976–1977, vol. 764. US Department of Commerce, p. 22. NOAA Technical Report, NMFS-SSRF.
- Gautier, D.L., Bird, K.J., Charpentier, R.R., Grantz, A., Houseknecht, D.W., Klett, T.R., Moore, T.E., Pitman, J.K., Schenk, C.J., Schuenemeyer, J.H., Sorensen, K., Tennyson, M.E., Valin, Z.C., Wandrey, C.J., 2009. Assessment of undiscovered oil and gas in the Arctic. *Science* 324, 1175–1179. <https://doi.org/10.1126/science.1169467>.
- Giacalone, V., D'anna, G., Badalamenti, F., Pipitone, C., 2010. Weight-length relationships and condition factor trends for thirty-eight fish species in trawled and untrawled areas off the coast of northern Sicily (central Mediterranean Sea). *J. Appl. Ichthyol.* 26, 954–957.
- Gillispie, J., Smith, R., Barbour, E., Barber, W., 1997a. Distribution, abundance, and growth of Arctic cod in the northeastern Chukchi Sea. In: *Fish Ecology in Arctic North America*. American Fisheries Society Symposium, pp. 81–89.
- Gjosæter, H., 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. *Sarsia* 83, 453–496.
- Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006. Ecosystem dynamics of the pacific-influenced northern bering and Chukchi seas in the amerasian arctic. *Prog. Oceanogr.* 71, 331–361. <https://doi.org/10.1016/j.pcean.2006.10.001>.
- Gulland, J., 1965. Estimation of Mortality Rates. Annex to Arctic Fisheries Working Group Report. International Council for the Exploration of the Sea, CM.
- Hart, J., 1973. Pacific fishes of Canada. Ottawa: fisheries research board of Canada. Bulletin 180.
- Harter, B.B., Elliott, K.H., Divoky, G.J., Davoren, G.K., 2013. Arctic cod (*Boreogadus saida*) as prey: fish length–energetics relationships in the Beaufort Sea and Hudson Bay. *Arctic* 191–196.
- Helsler, T.E., Colman, J.R., Anderl, D.M., Kastle, 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 Top. Stud. Oceanogr.* 135, 66–77. <https://doi.org/10.1016/j.dsr2.2015.12.009>.
- Hildebrandt, N., Bergmann, M., Knust, R., 2011. Longevity and growth efficiency of two deep-dwelling Arctic zoarcids and comparison with eight other zoarcid species from different climatic regions. *Polar Biol.* 34, 1523–1533. <https://doi.org/10.1007/s00300-011-1011-4>.
- Hoag, H., 2017. Nations agree to ban fishing in Arctic Ocean for at least 16 years. *Science Magazine*. <http://www.sciencemag.org/news/2017/12/nations-agree-ban-fishing-arctic-ocean-least-16-years>.
- Hop, H., Tonn, W.M., Welch, H.E., 1997. Bioenergetics of Arctic cod (*Boreogadus saida*) at low temperatures. *Can. J. Fish. Aquat. Sci.* 54, 1772–1784.
- Huxley, J.S., 1950. Relative growth and form transformation. *Proc. Roy. Soc. Lond.* 137, 465–469.
- IPCC, 2018. Summary for policymakers. Global warming of 1.5°C. An IPCC special report on the impacts of Global Warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways. In: *The Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty*. World Meteorological Organization, Geneva, Switzerland.
- Johannesen, E., Hoines, A.S., Dolgov, A.V., Fosshem, M., 2012. Demersal fish assemblages and spatial diversity patterns in the Arctic-Atlantic transition zone in

- the Barents Sea. *PLoS One* 7, e34924. <https://doi.org/10.1371/journal.pone.0034924>.
- Jones, G., 1986. Food availability affects growth in a coral reef fish. *Oecologia* 70, 136–139.
- Kramer, D.E., Josey, T., 1995. Guide to northeast Pacific flatfishes: families bothidae, cynoglossidae and pleuronectidae. Sea Grant.
- Kulik, V., Gerasimov, N., 2016. Length–weight and length–length relationships of 11 fish species from the Sea of Okhotsk. *J. Appl. Ichthyol.* 32, 1326–1328.
- Logerwell, E., Rand, K., Danielson, S., Sousa, L., 2017. Environmental drivers of benthic fish distribution in and around Barrow Canyon in the northeastern Chukchi Sea and western Beaufort Sea. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 152, 170–181. <https://doi.org/10.1016/j.dsr2.2017.04.012>.
- Matta, M.E., Kimura, D.K., 2012. Age Determination Manual of the Alaska Fisheries Science Center Age and Growth Program. NOAA Professional Papers, pp. 1–97, 13.
- Maunder, M.N., Punt, A.E., 2013. A review of integrated analysis in fisheries stock assessment. *Fish. Res.* 142, 61–74. <https://doi.org/10.1016/j.fishres.2012.07.025>.
- Mecklenburg, C., Mecklenburg, T., Sheiko, B., Steinke, D., 2016. Pacific arctic marine fishes. Conservation of arctic flora and fauna. CAFF monitoring series report No. 23, akureyri, Iceland.
- Mecklenburg, C.W., Byrkjedal, I., Karamushko, O.V., Møller, P.R., 2014. Atlantic fishes in the Chukchi borderland. *Mar. Biodivers.* 44, 127–150.
- Mecklenburg, C.W., Lynghammer, A., Johannesen, E., Byrkjedal, I., Christiansen, J.S., Dolgov, A.V., Karamushko, O.V., Mecklenburg, T., Møller, P.R., Steinke, D., 2018. Marine fishes of the arctic region. Conservation of arctic flora and fauna, akureyri, Iceland.
- Mecklenburg, C.W., Mecklenburg, T.A., Thorsteinson, L.K., 2002. Fishes of Alaska. American Fisheries Society, Bethesda, Maryland.
- Mendes, B., Fonseca, P., Campos, A., 2004. Weight-length relationships for 46 fish species of the Portuguese west coast. *J. Appl. Ichthyol.* 20, 355–361. <https://doi.org/10.1111/j.1439-0426.2004.00559.x>.
- Metcalfe, N.B., Monaghan, P., 2003. Growth versus lifespan: perspectives from evolutionary ecology. *Exp. Gerontol.* 38, 935–940.
- Møller, P.R., Jørgensen, O.A., 2000. Distribution and abundance of eelpouts (pisces, Zoarcidae) off west Greenland. *Sarsia* 85, 23–48.
- Nahrgang, J., Storhaug, E., Murzina, S.A., Delmas, O., Nemova, N.N., Berge, J., 2016. Aspects of reproductive biology of wild-caught polar cod (*Boreogadus saida*) from Svalbard waters. *Polar Biol.* 39, 1155–1164. <https://doi.org/10.1007/s00300-015-1837-2>.
- 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, Fairbanks AK. Final Report for BOEM Agreement Number M12AC00011. 435 pp + appendices.
- Norcross, B.L., Raborn, S.W., Holladay, B.A., Gallaway, B.J., Crawford, S.T., Priest, J.T., Edenfield, L.E., Meyer, R., 2013. Northeastern Chukchi Sea demersal fishes and associated environmental characteristics, 2009–2010. *Continent. Shelf Res.* 67, 77–95. <https://doi.org/10.1016/j.csr.2013.05.010>.
- NPFMC, 2009. Fishery Management Plan for Fish Resources of the Arctic Management Area. North Pacific Fisheries Management Council, Anchorage AK.
- Olsen, E., Aanes, S., Mehl, S., Holst, J.C., Aglen, A., Gjosæter, H., 2009. Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. *ICES (Int. Counc. Explor. Sea) J. Mar. Sci.* 67, 87–101.
- 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 Top. Stud. Oceanogr.* 52, 3175–3198.
- Plagányi, É.E., Punt, A.E., Hillary, R., Morello, E.B., Thébaud, O., Hutton, T., Pillans, R. D., Thorson, J.T., Fulton, E.A., Smith, A.D., 2014. Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. *Fish. Fish.* 15, 1–22.
- Pörtner, H.-O., Bernal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., Giuliani, A., Johansen, T., Fischer, T., Knust, R., 2001. Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Continent. Shelf Res.* 21, 1975–1997.
- Pruter, A.T., Alverson, D.L., 1962. Abundance, distribution, and growth of flounders in the south-eastern Chukchi Sea. *ICES (Int. Counc. Explor. Sea) J. Mar. Sci.* 27, 81–99.
- Quinn, T.J., Deriso, R.B., 1999. Quantitative Fish Dynamics. Oxford University Press.
- Rand, K.M., Logerwell, E.A., 2011. The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. *Polar Biol.* 34, 475–488. <https://doi.org/10.1007/s00300-010-0900-2>.
- Ricker, W., 1975. Computation and Interpretation of Biological Statistics of Fish Populations, vol. 191. Department of the Environment, Fisheries and Marine Service, Ottawa, pp. 1–382.
- Rosenfeld, J.S., Leiter, T., Lindner, G., Rothman, L., 2005. Food abundance and fish density alters habitat selection, growth, and habitat suitability curves for juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 62, 1691–1701. <https://doi.org/10.1139/f05-072>.
- Smith, L.C., Stephenson, S.R., 2013. New Trans-Arctic shipping routes navigable by midcentury. *Proc. Natl. Acad. Sci. Unit. States Am.* 110, E1191–E1195. <https://doi.org/10.1073/pnas.1214212110>.
- Smith, R., Barber, W., Vallarino, M., Gillispie, J., 1997a. Ritchie A population biology of the arctic staghorn sculpin in the northeastern Chukchi sea. In: *Fish Ecology in Arctic North America*. American Fisheries Society Symposium, pp. 133–139.
- Smith, R., Vallarino, M., Barbour, E., Fitzpatrick, E., Barber, W., 1997b. Population biology of the bering flounder in the northeastern Chukchi sea. In: *Fish Ecology in Arctic North America*. American Fisheries Society Symposium, pp. 127–132.
- Stevenson, D.E., Lauth, R.R., 2012. Latitudinal trends and temporal shifts in the catch composition of bottom trawls conducted on the eastern Bering Sea shelf. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 65–70, 251–259. <https://doi.org/10.1016/j.dsr2.2012.02.021>.
- Thorsteinson, L.K., Love, M.S., 2016. Alaska Arctic Marine Fish Ecology Catalog. U.S. Geological Survey Scientific Investigations Report 2016-5038. OCS Study, BOEM 2016-048, p. 768.
- Tokranov, A., Orlov, A., 2005. Some features of the biology of *Icelus spatula* (cottidae) in pacific waters off the northern Kuril Islands. *J. Ichthyol.* 45, 229–236.
- Weingartner, T., 1997. A review of the physical oceanography of the northeastern Chukchi Sea. In: *Fish Ecology in Arctic North America*. American Fisheries Society Symposium, pp. 40–59, 1997.
- Weingartner, T., Dobbins, E., Danielson, S., Winsor, P., Potter, R., Statscewich, H., 2013. Hydrographic variability over the northeastern Chukchi Sea shelf in summer-fall 2008–2010. *Continent. Shelf Res.* 67, 5–22. <https://doi.org/10.1016/j.csr.2013.03.012>.
- Wienerroither, R., Johannesen, E., Dolgov, A., Byrkjedal, I., Bjelland, O., Drevetnyak, K., Eriksen, K., Høines, Å., Langhelle, G., Langoy, H., 2011. Atlas of the Barents Sea fishes. IMR/PINRO Joint Report Series 1, 1–272.
- Wiswar, D.W., Fruge, D.J., 2006. Fisheries Investigations in Western Camden Bay, Arctic National Wildlife Refuge, Alaska, 1987. US Fish and Wildlife Service, Fairbanks Fish and Wildlife Field Office.
- Wund, M.A., Valena, S., Wood, S., Baker, J.A., 2012. Ancestral plasticity and allometry in threespine stickleback reveal phenotypes associated with derived, freshwater ecotypes. *Biol. J. Linn. Soc.* 105, 573–583.