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Geographic variation in ringed seal (*Pusa hispida*) growth rate and body size

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Abstract: We summarize geographical patterns in ringed seal (*Pusa hispida* (Schreber, 1775)) body length and girth growth using 3012 samples collected by Inuit hunters in the eastern Canadian Arctic from 1990 to 2016. Spatial structure was detected using cluster analysis of environmental variables separating a northern region in the eastern Canadian High Arctic and a southern region in Hudson Bay. The north was characterized by more fast ice, multiyear ice, greater snow depth, colder temperatures, and greater sea-ice concentration in the spring seal breeding season. Hierarchical Bayesian models described length and axillary girth growth of northern seals as slower than in the south, reaching asymptotic size 5–7 years later. Northern females were larger than males (asymptotic length of 149 versus 140 cm, respectively) and both were larger than southern seals (males and females 126 cm). We conclude that environmental variation was best represented by regions rather than latitude, regional body size differences were driven by differential growth rates, and northern ringed seals may be characterized by reverse sexual size dimorphism.

Key words: asymptotic body size, Brody growth rate, Nunavut, phocids, pinnipeds, *Pusa hispida*, ringed seal, sea ice, sexual size dimorphism, snow, temperature.

Résumé : Nous décrivons les motifs de répartition géographique de la croissance de la longueur du corps et du périmètre thoracique de phoques annelés (*Pusa hispida* (Schreber, 1775)) en utilisant 3012 spécimens prélevés par des chasseurs inuits dans l'est de l'Arctique canadien de 1990 à 2016. Une structure spatiale est décelée en utilisant l'analyse typologique de variables environnementales, qui distingue une région septentrionale dans l'est de l'Extrême-Arctique canadien d'une région méridionale dans la baie d'Hudson. Le Nord est caractérisé plus de glace fixée et de glace pluriannuelle, de plus grandes épaisseurs de neige, des températures plus froides et une plus grande concentration de glace marine durant la période de reproduction printanière des phoques. Des modèles bayésiens hiérarchiques décrivent la croissance de la longueur et du périmètre axillaire des phoques du Nord comme étant plus lente que celles des phoques du Sud, atteignant des valeurs asymptotiques 5 à 7 ans plus tard. Les femelles du Nord sont plus grandes que les mâles du Nord (longueur asymptotique de 149 cm contre 140 cm, respectivement), les deux étant plus grands que les phoques du Sud (126 cm pour les mâles et les femelles). Nous en concluons que les régions reflètent mieux les variations environnementales que la latitude, que les différences régionales sur le plan de la taille du corps sont le fait de taux de croissance différents et que les phoques annelés du nord pourraient présenter un dimorphisme sexuel inversé de la taille. [Traduit par la Rédaction]

Mots-clés : taille asymptotique du corps, taux de croissance de Brody, Nunavut, phocidés, pinnipèdes, *Pusa hispida*, phoque annelé, glace marine, dimorphisme sexuel de la taille, neige, température.

Introduction

Body size is strongly associated with all other life-history traits (Stearns 1983; Calder 1984). Interspecific variation in body size is thought to be due to selection pressure from environmental gradients and latitudinal patterns (Gaston 2000). Efforts to understand this pattern have been more successful at the species level (Kozłowski and Weiner 1997), whereas the intraspecific mechanism explaining body size variation has escaped a common description (Blackburn and Gaston 1994). Biotic and abiotic factors such as predation, competition, climate, and habitat heterogeneity have provided explanations of intraspecific patterns (Lindstedt and Boyce 1985). Latitudinal patterns are less common in marine environments, where regional patterns in body size such as nearshore–offshore ecotype differences are more typical (Blackburn et al. 1999; Best 2001; Pitman and Ensor 2003). Marine mammals in the Arctic tend not to display a strong latitudinal gradient in intraspecific body size, although there is a general trend for individuals from populations in the north to be larger (e.g., beluga whales (*Delphinapterus leucas* (Pallas, 1776)); Luque and Ferguson 2010).

Ringed seals (*Pusa hispida* (Schreber, 1775)) are the most successful pinniped in Arctic waters based on their circumpolar distribution, relatively high abundance, and generalist foraging and habitat selection (Reeves 1998). Knowing geographic and environ-

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mental patterns in key life-history traits, such as body growth, would assist conservation efforts related to predictions of distribution changes associated with climate warming and loss of sea ice (Ferguson and Higdon 2006; Laidre et al. 2015). Ringed seals in Hudson Bay have been shown to be smaller both in length and in mass than found in other areas, supporting both regional groupings and the hypothesis of latitudinal size differences (McLaren 1993; Holst and Stirling 2002; Krafft et al. 2006; Chambellant 2010). Dietary differences support the existence of a latitudinal gradient in ringed seal feeding habits, based on preference and (or) availability of fish (McLaren 1958; Siegstad et al. 1998; Chambellant 2010; Young and Ferguson 2014; Yurkowski et al. 2016*a*, 2016*b*).

The transitions from landfast sea ice (also known as shorefast ice) to open water in spring and vice-versa in autumn represent crucial separations of the Arctic seasonal cycle (Fay 1974; Kovacs et al. 2011). As a high-latitude marine mammal, ringed seals are adapted to strong seasonality transitioning from positive energy balance during the open-water season to a negative during the sea-ice season (Young and Ferguson 2013). It is during the ice-covered season that territories are defended, pups are born and nursed, and mating occurs (Chambellant et al. 2012). Key life-history events also occur in the spring when sea ice is melting (Smith 1980). At this time 5- to 7-week-old pups achieve independence (Smith et al. 1991; Lydersen 1998) and polar bears (*Ursus maritimus* Phipps, 1774) focus predation efforts on this relatively naïve food source (Stirling and McEwan 1975; Smith 1980). Thus, the spring season appears to be the vulnerable link in the ringed seal seasonal life history (Ferguson et al. 2005; Luque et al. 2014) because seals are at their lowest fat and energy reserves during April–June when seals moult while resting on the sea ice (Ryg et al. 1990; Young and Ferguson 2013). With a progressively earlier spring breakup, the moult may be interrupted due to a lack of access to a stable ice surface and can result in compromised body condition and disease (Ferguson et al. 2017).

The purpose of the paper is to quantify the difference in seal growth patterns between two regions and discuss the possible explanations for these patterns. First, we tested whether environmental variation in spring conditions is best represented by a latitudinal gradient or by regional groupings that relate to phenotypic plasticity in ringed seal body growth. Next, using an unprecedented data set from Inuit-harvested seals collected over a 27-year period (from 1990 to 2016), we applied Bayesian statistics to model selection and multimodel inference (MMI) based on deviance information using eight candidate models of standard length and axillary girth. The information–theoretic approach guided selection of a subgroup of robust but parsimonious models to examine the growth parameters of asymptotic size and growth rate and assess whether ringed seals grow differently according to environmental patterns.

Materials and methods

The study area covered the majority of the eastern Canadian Arctic from southern Hudson Bay (Sanikiluaq: 55.28°N) to northern Ellesmere Island (Grise Fiord: 76.4°N) and from the east coast of Baffin Island (Pangnirtung, 65.71°W) to the Canadian Arctic Archipelago in the west (Resolute Bay: 94.97°W; Fig. 1). Fisheries and Oceans Canada and Environment and Climate Change Canada (Northern Contaminants Program) have been working with Nunavut community Hunters and Trappers Organizations and the Nunavut Wildlife Management Board more or less consistently since 1980 to collect samples from harvested ringed seals.

Environmental variables

We collected environmental data from the month of May, as this period represents a key time in ringed seal life history (Smith and Stirling 1975). Few changes in sea-ice condition occur from February to April and most spring sea-ice dynamics occur during the June to July transition from ice to open water depending on latitude and geographic location in the Arctic (Comiso et al. 2008). Also, the choice of environmental variables was considered the ones that relate to ringed seal habitat requirements including stable landfast ice (Smith 1980), predictable spatial availability of ice (Ainley et al. 2003), availability of food (Gjertz and Lydersen 1986), and snow cover over the ice (Iacozza and Ferguson 2014).

We selected nine communities (Arviat, Chesterfield Inlet, Sanikiluaq, Naujaat (Repulse Bay), Kugaaruk, Pangnirtung, Arctic Bay, and Resolute Bay) that were best represented by biological sample size (>60) (Fig. 1). In addition, we added Grise Fiord ($n = 33$ samples) to represent the High Arctic. We measured the availability of landfast ice as prime ringed seal breeding habitat using Canadian Ice Services (CIS) Archived ice charts (available from http://iceweb1.cis.ec.gc.ca/Archive/; select "Weekly Regional Ice Charts - Black and White", from 1980 to 2016) for Hudson Bay and the Eastern Arctic in May. Extent of landfast ice in proximity to where hunters would take seals in spring was measured for each year. We used Google Earth™ calculator to estimate the distance from shoreline to the nearest ice edge as identified by moving ice <100% concentration obtained from CIS ice maps for the end of May.

Total sea-ice concentration and multiyear ice concentration were obtained from May CIS Ice Graphs (for region associated with each community see Table 1). North and South regions were also compared using CIS historical ice coverage summaries for the week of 19 June, from 1981 to 2017 (Hudson Bay - WIS54CT versus Eastern Arctic - WIS55CT).

Weather variables were obtained from historical data from the nine Nunavut communities (available from http://climate.weather.gc.ca/historical_data/search_historic_data_e.html) in May for snow depth (cm) (end of month total in cm) and average spring temperature (°C). Monthly summaries were not available for all years and therefore the weather data was not complete (29% of community × year data missing).

Morphological variables

The majority of seals were measured in the field by Inuit hunters. Date, time, location, sex, and condition were noted. Standard length and axillary girth were measured to the nearest 0.5 cm with flexible measuring tapes. Assigned sample collectors, for example, four in Sanikiluaq, were trained to collect measurements following the protocols of the American Society of Mammalogists' Committee on Marine Mammals (1967); however, considerable variation likely occurred depending on the skill and experience of individual hunters. Age was determined by counting dentinal annuli from a cross-sectioned portion of the lower right canine tooth (Bernt et al. 1996) both in the Fisheries and Oceans Freshwater Institute in Winnipeg, Canada (Stewart et al. 1996), from 1990 to 2002, and by Matson's Laboratory in Montana, USA, from 2003 to 2016. To assess possible differences in sampling methods between communities and regions, we compared age structure (ages 0 to 43 years). Most (71%) hunting occurred during the open-water season (June–December) using a rifle from a distance, often shooting the seal in the water with only the head showing. As a result, hunters are generally not able to be selective of size and age structure of the harvest is considered representative of the population (Ferguson et al. 2017).

Statistical analyses

All statistical analyses and modeling was done using R version 3.2.3 (R Core Team 2015). For environmental patterns, we tested for latitudinal variation in environmental variables using linear regression with latitude as the independent variable. No interactions were included within the fixed effects. We used median and coefficient of variation (predictability: Lindstedt and Boyce 1985) for the time series of environmental variables by community to test for a latitudinal pattern. To test for clumped patterning, we

Fig. 1. Community locations in northeastern Canadian Arctic where ringed seal (*Pusa hispida*) samples were collected and sample sizes, from 1990 to 2016. Black square represents north and black circle represents south.

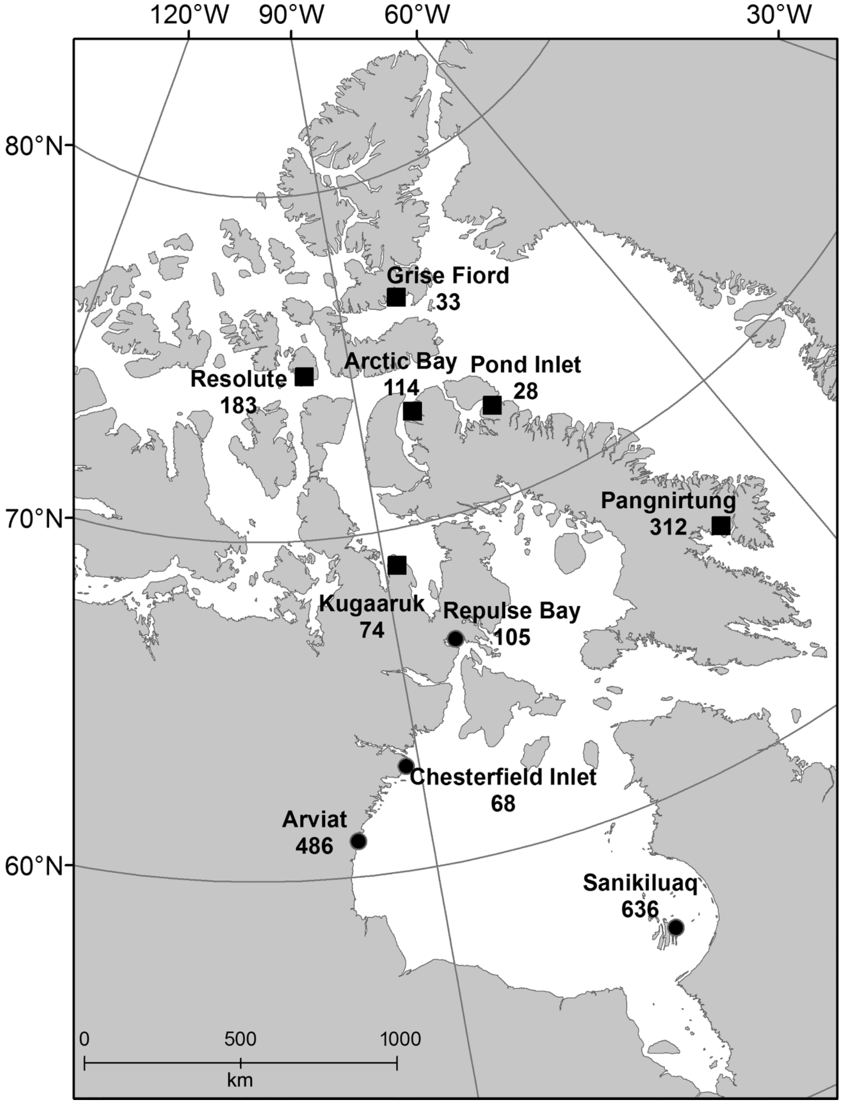

Table 1. Summary information for the nine major Nunavut, Canada, communities that provided the bulk of ringed seal (*Pusa hispida*) samples used in the study (median ± SD).

Community	Latitude (°N)	Longitude (°W)	Canadian Ice Service region	Fast-ice distance (km)	Multiyear ice concentration (%)	Total ice concentration (%)	May average temperature (°C)	Snow depth (cm)
Arviat	61.10	94.07	Northwestern Hudson Bay	7.70±0.126	0.0±0.001	79.10±0.126	–4.35±2.35	0.0±9.64
Sanikiluaq	55.28	77.75	Eastern Hudson Bay	43.20±0.147	0.0±0.000	71.10±0.147	1.30±2.64	0.0±0.0
Naujaat	66.52	86.22	Foxe Basin	37.70±0.079	0.0±0.002	87.40±0.079	–6.95±2.19	7.0±16.49
Chesterfield Inlet	63.35	90.73	Northwestern Hudson Bay	22.6±0.121	0.0±0.001	75.9±0.121	–6.54±2.08	5.0±7.14
Kugaaruk	68.54	89.80	Prince Regent–Boothia	99.00±0.202	8.53±0.10	28.00±0.202	–7.50±2.16	17.0±22.1
Pangnirtung	66.15	65.71	Davis Strait	40.90±0.084	1.66±0.028	43.00±0.0787	–2.80±2.13	10.0±13.2
Arctic Bay	72.98	84.62	Lancaster Mouth	84.90±0.079	0.38±0.280	73.40±0.224	–10.00±2.49	17.0±20.54
Resolute Bay	74.72	94.97	Lancaster Eastern Barrow	145.60±0.181	1.04±0.042	78.20±0.181	–9.80±2.20	16.0±9.79
Grise Fiord	76.42	82.90	Jones Sound	44.90±0.086	3.44±0.084	97.20±0.086	–7.70±2.07	18.0±16.94

used hierarchical cluster analysis with Euclidean distance as the distance measure. Variables were measured on different scales and therefore we standardized the data using *z* scores. Two sample Kolmogorov–Smirnov tests were used to compare age structure between the two regions using "stats" in R.

For body growth modeling, we first identified outliers using dot plots to examine extreme values of biological measurements. Missing values of standard length and girth were calculated using bivariate regression of a power function of age versus length or girth from existing measurements. Seal samples with no associated age data were excluded from analyses. A total of 3012 ringed seals were sampled through 1990–2016. Among these, 101 outliers were detected and missing values occurred and included no measurements of girth (e.g., 213 seals in the north) and no age data

Table 2. Characteristics of somatic growth models used for quantifying body length growth relationships of ringed seals (*Pusa hispida*).

Model	Number of parameters	Shape
Standard von Bertalanffy growth model (SVB; von Bertalanffy 1938) $L_t = L_\infty[1 - e^{-K_1(t-t_1)}]$	7	Concave
Generalized von Bertalanffy growth model (GVB; Schnute 1981) $L_t = L_\infty[1 - e^{-K_2(t-t_2)}]^P$	8	Sigmoidal
Standard logistic growth model (SLM; Karkach 2006) $L_t = \dfrac{L_\infty}{1 + \beta e^{-K_3(t-t_3)}}$	8	Sigmoidal
Gompertz growth model (GPM; Quinn and Deriso 1999) $L_t = L_\infty e^{-\alpha[e^{-K_4(t-t_4)}]}$	8	Sigmoidal
Log logistic growth model (LLM; Bennett 1983) $L_t = \dfrac{L_\infty}{1 + \beta e^{[-K_5 \times \ln(t-t_5)]}}$	8	Sigmoidal
Schnute–Richards growth model (SRM; Schnute and Richards 1990) $L_t = L_\infty\{1 + \beta e^{[-K_6(t - t_6)^{\delta}]}\}^{\frac{1}{m}}$	10	Sigmoidal
Stannard growth model (STM; Panik 2014) $L_t = L_\infty\left\{1 + e^{\left[-\frac{\beta+K_7(t-t_7)}{m}\right]}\right\}^{-m}$	9	Sigmoidal
Weibull growth model (WBM; Panik 2014) $L_t = L_\infty - \beta e^{-[K_8(t - t_8)^{m}]}$	9	Sigmoidal

Note: Model parameter L_∞ is asymptotic length; K_i and t_i are Brody growth rate and age, respectively, at which an individual would have been of length 0 in model set i. Other model parameters (P, β, δ, and m) are dimensionless factors. Numbers of model parameters included hierarchical model parameters and standard deviation.

(e.g., 366 seals in the south). The power function estimated the missing morphological values. We excluded young of the year from further analyses. Consequently, sample sizes of 808 (343 female and 465 male seals) in the north and 1313 (579 female and 734 male seals) in the south were included for the following analyses.

The choice of growth models can influence the ability to assess differences in growth patterns (Roemmich et al. 1997; Ozgul et al. 2010). Therefore, we compared eight growth models that analyzed age-specific standard length (cm) and girth (cm) of seals using hierarchical Bayesian methods (Table 2). Parameter number is dependent on the specific models used, varying from 3 to 6. Standard growth model (G1: SVB), von Bertalanffy model (von Bertalanffy 1938), has been generally used for a wide variety of animals, including ringed seals (Auttila et al. 2016). Several alternative growth models have also been used for ringed seals including a generalized von Bertalanffy growth model (G2: GVB; Schnute 1981) by Krafft et al. (2006), GVB model (McLaren 1993), standard logistic model (G3: SLM; Chambellant et al. 2012), and Gompertz (G4: GPM; McLaren 1993; Chambellant 2010). In addition, we examined a log-logistic model (G5: LLM; Bennett 1983; Panik 2014), Schnute–Richards model (G6: SRM; Schnute and Richards 1990), Stannard growth model (G7: STM; Panik 2014), and Weibull growth model (G8: WBM; Panik 2014).

Three model parameters are asymptotic length (L_∞), Brody growth rate (k), and assumed age when length approaches zero (t_0). Parameter t_0 is an age-scale correction and is negative when birth is age 0. We cited a priori value of $t_0 = -0.61$ based on the assumption that embryos begin growth after a delay in implantation (McLaren 1993). Time of initiation of embryonic growth is treated as a constant t_0. Among all structured candidate models (i.e., G1–G8), there also are four additional parameters (P, β, δ, and m), which are positive dimensionless factors (Karkach 2006; Panik 2014).

We employed hierarchical Bayesian statistical modeling approaches to parameterize candidate growth models for ringed seals greater than or equal to one year of age (see Supplementary material).[1]

Multimodel inference (MMI)

Model selection and the estimation of model selection uncertainty were based on the deviance information criterion (DIC) with a priori parsimonious predictive Bayesian statistics to evaluate the relative goodness of fit of the structural models that profiled the complexity and instability that resulted from a particular parameterization (Carlin and Louis 1997; Burnham and Anderson 2003; Spiegelhalter et al. 2002). As a generalization of Akaike's information criterion that is based on the posterior distribution of the deviance statistic, DIC can be expressed as

$$D(\boldsymbol{\theta}) = -2\log f(\mathbf{y}|\boldsymbol{\theta}) + 2\log h(\mathbf{y})$$

$$\mathrm{DIC} = \hat{D} + 2\mathrm{pD} \text{ or } \mathrm{DIC} = \overline{D} + \mathrm{pD}$$

where $f(\mathbf{y}|\boldsymbol{\theta})$ is the likelihood function for the observed data vector $\mathbf{y}$ given the parameter vector $\boldsymbol{\theta}$, and $h(\mathbf{y})$ is a standardization function of the data alone (Carlin and Louis 1997). $\hat{D}$, $\overline{D}$, and pD are the deviance of the posterior mean, the posterior mean of the deviance as a measure of fit, and the effective number of parameters as a measure of complexity in the Bayesian model, respectively (Lunn et al. 2009). A small-sample, bias-corrected form (i.e., $\mathrm{DIC_c}$) is calculated by the following:

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[1] Supplementary material and Supplementary Tables S1–S4 are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0213.

$$\mathrm{DIC_c} = \mathrm{DIC} + \frac{2k(k+1)}{n-k-1}$$

where k and n are numbers of model parameters including precisions and observations. Its difference between individual and minimum $\mathrm{DIC_c}$ (i.e., Δ_i) was suggested by Spiegelhalter et al. (2002) as

$$\Delta_i = \mathrm{DIC}_{ci} - \mathrm{DIC}_{\mathrm{cmin}}$$

where DIC_{ci} and $\mathrm{DIC}_{\mathrm{cmin}}$ are $\mathrm{DIC_c}$ in model i and minimum, respectively. The model with the smallest $\mathrm{DIC_c}$ value was selected as the "best" among the candidate models tested. According to Burnham and Anderson (2003), if two models differ by only one or two $\mathrm{DIC_c}$ units, then one cannot distinguish between the two models and both are supported. If models differ by three to seven $\mathrm{DIC_c}$ units, then there is some support for the second model, but the first model is clearly better. When the $\mathrm{DIC_c}$ difference is greater than 10, there is no support for the second model. Therefore, $\mathrm{DIC_c}$ offers a straightforward means of comparing different models when using the same observed data.

For each fitted estimation model, the $\mathrm{DIC_c}$ weight (w_i) was calculated as (Burnham and Anderson 2003)

$$w_i = e^{-\frac{1}{2}\Delta_i} \Big/ \sum_{i=1}^{R} e^{-\frac{1}{2}\Delta_i}$$

Multimodel inference is a way to average a model parameter set, using w_i for the comparative model parameters:

$$\beta_{\mathrm{DIC}} = \sum_{i=1}^{R} \beta_i w_i$$

In terms of Kullback–Leibler (K–L) best model criteria (Burnham and Anderson 2003), a confidence set on model is selected if the information–theoretic importance of respective model alternatively meets one of those: (1) the smallest $\mathrm{DIC_c}$, (2) $\mathrm{DIC_c}$ difference $\Delta_i \leq 2.0$, (3) the sum of $w_i \geq 90\%$, and (4) cut-off value $\exp(-0.5\Delta_i) \geq 0.125$.

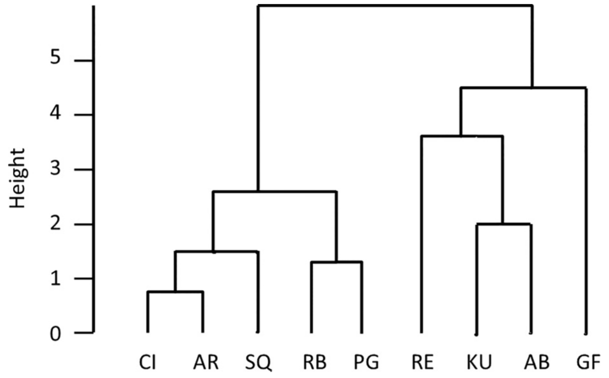
Results

Environment

We summarized environmental information from the nine communities with the majority (97%) of seal sample collections: Arviat, Chesterfield Inlet, Sanikiluaq, Naujaat (Repulse Bay), Kugaaruk, Pangnirtung, Arctic Bay, Resolute Bay, and Grise Fiord (Table 1). Although the trend was for more ice and colder temperatures at higher latitudes, the linear regression was only significant for snow depth among the five environmental variables (adjusted $r^2 = 0.91$, $F_{[5,3]} = 16.37$, $p = 0.02$; fast ice: $p = 0.71$; multiyear ice: $p = 0.67$; total sea ice: $p = 0.32$; temperature: $p = 0.38$; snow depth: $p = 0.03$). Similarly, coefficient of variation as a measure of environmental predictability was not correlated with latitude among the nine communities (adjusted $r^2 = 0.63$, $F_{[5,3]} = 3.38$, $p = 0.24$).

Hierarchical cluster analysis grouped the communities based on the environmental covariates into two groups: one that was more southerly, which included Arviat, Chesterfield Inlet, Sanikiluaq, Naujaat, and Pangnirtung, and a second group located at higher latitudes, which included Arctic Bay, Grise Fiord, Resolute Bay, and Kugaaruk (Fig. 2). We incorporated Pangnirtung within the northern group based on geographic proximity to the other northern communities and to create a more balanced (four versus five) sample size between regions for statistical comparative purposes. In addition, we compared adult body size among communities and found that southern Hudson Bay locations were different from others (ANOVA: $F_{[6,584]} = 28.0$, $p < 0.001$ while controlling for sex), with Pangnirtung seals larger than either Arviat seals ($t = -6.89$, $p < 0.001$) or Sanikiluaq seals ($t = -4.21$, $p < 0.01$). Biological reasons for why seals harvested in Pangnirtung were grouped with the north region are presented in the Discussion.

Fig. 2. Cluster analysis dendrogram of environmental variables (fast ice, multiyear ice, total ice, temperature, snow depth) for nine Nunavut communities where ringed seals (*Pusa hispida*) were collected. CI, Chesterfield Inlet; GF, Grise Fiord; RE, Resolute Bay; AB, Arctic Bay; KU, Kugaaruk; PG, Pangnirtung; AR, Arviat; RB, Naujaat; SQ, Sanikiluaq.



The northern region was characterized by more fast ice (83.1 versus 29.5 km), more sea-ice concentration (65.0% versus 50.0%), more multiyear ice (3% versus 0%), colder temperatures (–7.6 versus –3.3 °C), and more snow depth (15.6 versus 2.3 cm) during the spring seal breeding season. Coefficient of variation was greater in the south region for total sea-ice concentration, temperature, and snow depth, whereas fast ice and multiyear ice were more unpredictable in the north region. However, differences between the two regions were not significant ($p > 0.09$).

Body length growth

Using seal morphometric data grouped by region (Table 3), candidate models evaluated growth patterns (Supplementary Table S1).[1] Age structure differed between the two regions (Kolmogorov–Smirnov test; females: $D = 0.118$, $p = 0.0007$; males: $D = 0.107$, $p = 0.0004$), with a slightly younger age structure in the south. However, mean age and oldest age of females and males were similar (north: female mean 7.24 years (max. 43 years) and male mean 6.06 years (max. 38 years); south: female mean 7.21 years (max. 40 years) and male mean 6.99 years (max. 40 years)). Overall, results indicate that WBM (Supplementary Table S2)[1] was the best supported model for the body length growth of ringed seals (Supplementary Table S1).[1] Two commonly used growth models (SVB and SRM) were not considered reasonable models describing length growth of the ringed seals according to their $\Delta_i > 100$ and $w_i = 0$. Northern female seals had 18% greater asymptotic length and 19% slower growth rate than southern female seals (Table 4; Figs. 3*a*, 3*b*). Similarly, northern male seals had 11% greater asymptotic length and 93% slower growth rate than southern populations (Figs. 3*c*, 3*d*).

As WBM was selected for all combinations (sex and region), we compared two kernel growth model parameters (i.e., asymptotic size (L_∞) and Brody growth rate (K)) using 95% levels derived from this model. Age of 95% asymptotic length of southern female seals was 38% earlier than in the north. For male seals, the age approaching 95% asymptotic size in the south occurred 49% earlier than those in the north (Table 4).

Axillary girth growth

Almost identical patterns were observed for girth as was observed for length (Supplementary Table S3).[1] The posterior esti-

Table 3. Summary of ringed seal (*Pusa hispida*) harvest information for the communities used in growth models to compare north and south regions.

	Age (year)			Month												Sex			
Community	0	1–5	>5	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	F	M	U	Sum
North total	221	397	426	56	57	34	35	137	173	102	84	266	66	33	1	431	585	28	1044
Arctic Bay	31	32	82				9	26	36	3	35	35	1			59	83	3	145
Qikiqtarjuaq		9	5									14				4	10		14
Eureka	4	2	12					6	12							10	8		18
Grise Fiord	8	22	11									39	2			14	27		41
Gjoa Haven	15	20	16					2	4	12	1	8	24			25	25	1	51
Igloolik	9	4	11						3	15	2	4				8	15	1	24
Kugaaruk	22	20	54					20	2	14	12	44	3	1		48	42	6	96
Pangnirtung	104	196	116	56	57	34	11	60	18	53	18	68	14	26	1	179	226	11	416
Pond Inlet	10	14	14								2	26	10			15	22	1	38
Resolute	18	78	105				15	23	98	5	14	28	12	6		69	127	5	201
South total	589	569	810	203	103	87	61	55	270	98	67	104	578	246	96	825	1045	98	1968
Arviat	158	172	314				1	2	110	6		13	425	87		309	280	55	644
Cape Dorset	4	0	2					1		2	3						4	2	6
Chesterfield Inlet	16	13	55	5	1				25	26	8	3	7	1	8	36	43	5	84
Hudson Bay	4	2	8						1	4	8	1				9	5		14
Kimmirut		0	50						50							21	29		50
Inukjuak	9	5	5					10	8				1			4	14	1	19
Ivujivik	11	11	1		6	16	1									8	15		23
Repulse Bay	55	42	63	3	1			1	18	22	10	39	58	7	1	62	88	10	160
Sanikiluaq	332	324	312	195	95	71	59	41	58	38	38	48	87	151	87	376	567	25	968
Total	810	966	1236	259	160	121	96	192	443	200	151	370	644	279	97	1256	1630	126	3012

Note: F, female; M, male; U, unidentified.

Table 4. Summary of key growth parameters from multimodel inference, as well as estimates of sizes and ages when the growth approaches the 95% asymptote sizes.

	North		South	
	Females	Males	Females	Males
Asymptote length (L_∞, cm)	148.77±5.50	140.07±1.48	125.64±3.85	125.80±0.75
Brody growth rate (K, per year)	0.2026±0.0518	0.0170±0.0088	0.2512±0.0846	0.2380±0.0688
95% Asymptote length (cm)	135.44	133.06	116.07	119.26
Age at 95% asymptote length (year)	11.0	9.0	4.2	4.4
Asymptote girth (G_∞, cm)	133.94±11.92	110.22±1.93	121.70±17.22	100.23±0.65
Brody growth rate (K, per year)	0.2552±0.0647	0.2389±0.0461	0.2900±0.1065	0.2107±0.0662
95% Asymptote girth (cm)	109.42	103.30	95.66	95.05
Age at 95% asymptote growth (year)	17.9	6.6	7.2	4.1

Note: Weibull growth model was used for estimates of 95% asymptote length for both sexes and male girth, whereas generalized von Bertalanffy growth model was used to estimate 95% asymptote girth for female ringed seal (*Pusa hispida*).

mates of asymptotic axillary girth (G_∞) and Brody growth rate (K) from hierarchical growth models estimated northern female seals as 10% greater than that of the southern female seals, whereas the K value of northern female seals was 12% less than that of the southern female seals (Table 4). For male seals in the north, the mean values of the posterior G_∞ and K were 10% greater and 13% less than those of male seals in the south, respectively (Supplementary Table S4).[1]

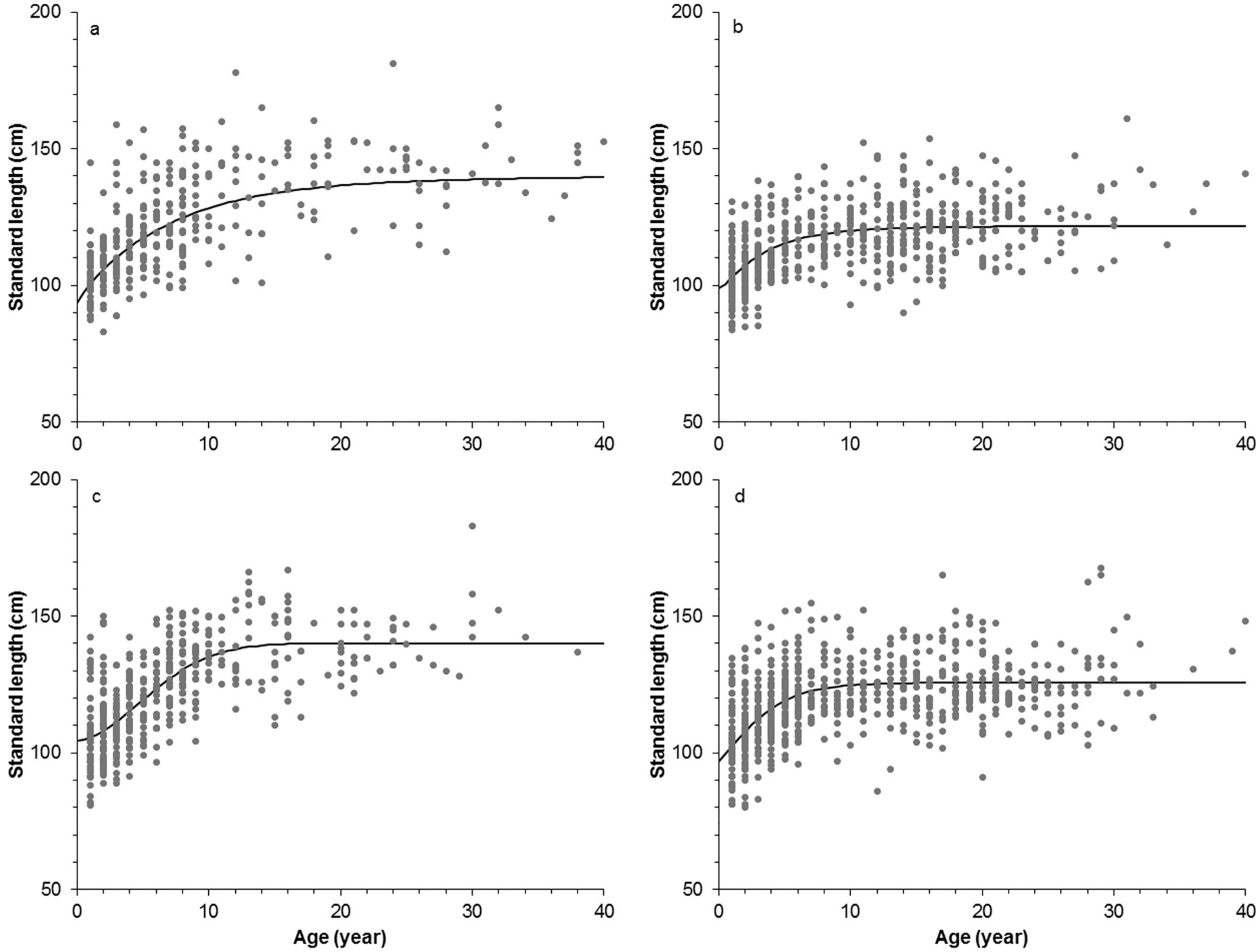
GVB for female seals and WBM for male seals estimated the 95% asymptotic axillary girth (Figs. 4*a*–4*d*) at 107.5 cm at the age of 12 for northern female seals and 97.5 cm at 7.7 years for southern female seals (Figs. 4*a*, 4*b*). Compared with the northern region, the axillary girth of southern female seals was smaller but asymptotic age was earlier than northern female seals. Similarly, for males, a smaller axillary girth occurred earlier in southern seals than that of northern seals (Table 4).

Discussion

Our results revealed significant spatial variability in the environmental conditions faced by ringed seals in the Canadian Arctic and corresponding patterns in ringed seal size and growth rates. Differences in growth and age at asymptotic size between northern and southern groups suggest that ringed seals in these two areas have adopted starkly different life-history strategies, with northern seals growing more slowly (0.20 versus 0.25 mm/year in females) to a large asymptotic size (ca. 15% longer and 10% greater girth) and southern seals growing relatively quickly (asymptote size reached 7 years earlier) to a smaller size. We suggest that these divergent life-history patterns have emerged in response to local environmental conditions and may have implications for the species in a changing Arctic environment.

We incorporated Pangnirtung ringed seal data into the north region (Grise Fiord, Resolute Bay, Arctic Bay, Kugaaruk, and Pangnirtung) even though its environmental characteristics grouped with the Hudson Bay region (Arviat, Chesterfield Inlet, Naujaat, and Sanikiluaq). This decision was based on (*i*) geographic proximity and movement choke points (Fury and Hecla and Hudson Strait), (*ii*) a more balanced statistical sample design because Pangnirtung provided 36% of the samples collected in the north region, (*iii*) ringed seal telemetry movement results indicate a connection between Cumberland Sound (Pangnirtung) and the High Arctic but not with Hudson Bay (Yurkowski et al. 2016*c*), (*iv*) Cumberland Sound has more similar oceanographic and sea-ice features as the High Arctic (Tang et al. 2004, Brown et al. 2014;

Fig. 3. Comparison of multimodel inference selected model(s) estimated (solid line) versus observed (grey dots) body length growth for female ringed seals (*Pusa hispida*) in the north (*a*) and south (*b*), as well as male seals in the north (*c*) and south (*d*).

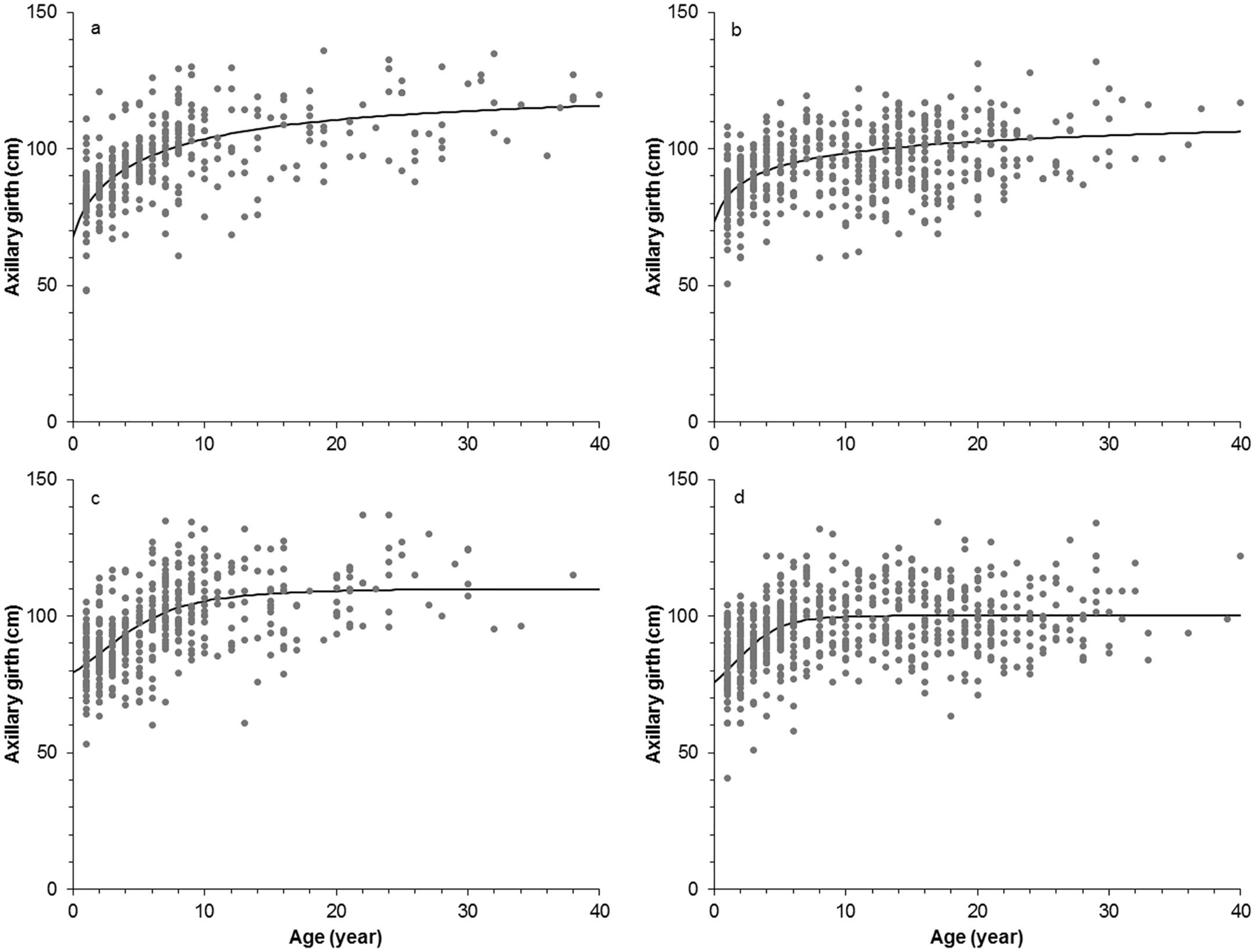


Hussey et al. 2017), and (*v*) Pangnirtung seals were larger than southern Hudson Bay seals. However, with climate warming, Pangnirtung may be becoming more representative of southerly regions like Hudson Bay. Future research should concentrate efforts on collections from High Arctic locations, which are generally under-represented in circumpolar data sets (Kovacs 2014).

Ringed seals show considerable variation in standard body length throughout their circumpolar range (McLaren 1958, 1993; Fedoseev 1965; Fedoseev and Nazarenko 1970; Smith 1973, 1987; Helle 1979; Frost and Lowry 1981; Finley et al. 1983; Lydersen and Gjertz 1987; Goodyear 1999; Holst et al. 1999; Holst and Stirling 2002; Chambellant 2010; Chambellant et al. 2012). Comparing our northern results (males 140.1 cm, females 150.8 cm) with reported values for other ringed seal populations suggests the northern seals are larger than those in other areas. Krafft et al. (2006) reported asymptotic values for standard length of 127.7 cm for Svalbard male ringed seals and 127.6 cm for females. Holst and Stirling (2002) reported ringed seals from Qaanaaq, Greenland (males 129.3 cm, females 125.6 cm), were significantly shorter ($p = 0.007$) than those from Grise Fiord, Nunavut (males 136.3 cm, females 136.0 cm). For Arviat in Hudson Bay, Chambellant (2010) reported similar seal lengths of 120.2 cm for males and 120.4 cm for females. Our Hudson Bay growth model used a larger data set (more communities and longer time frame) and indicated slightly larger ringed seals in Hudson Bay (males 125.8 cm, females 126.4 cm).

Our results for the northern region of the Canadian eastern Arctic indicated that females were longer and had wider girth than males (148.8 versus 140.1 cm length and 133.9 versus 110.2 cm girth), as well as weighing more than males (88.0 kg ($n = 734$) versus 69.3 kg ($n = 559$); data on file). Females were 8% longer and 24% more rotund in the north region, whereas females were similar in length as males but had 40% greater girth in the south. These results contrast with the southern region (Hudson Bay) and to other studies, including Smith (1973) who reported that in Davis Strait males were significantly larger than females; Goodyear (1999) found males from Baffin Bay reached greater asymptotic length than females; Johnson et al. (1966) found males in Point Hope, Alaska, were heavier than females from November to May; however, Lydersen and Gjertz (1987) reported that females collected between March and July in Svalbard were significantly heavier than males, which may be partly a result of reproduction (i.e., pregnancy) at that time of year. Sexual size dimorphism is common among phocids (14 of 20 species; Bininda-Emonds and Gittleman 2000) and is likely due to selection for larger male body size in species that form harems (Lindenfors et al. 2002). Reverse sexual size dimorphism occurs in six phocid species and only in species that do not form harems; ringed seals do not form harems (Yurkowski et al. 2011). Further research is needed to clarify regional disparities in sexual dimorphism for this species.

Fig. 4. Comparison of multimodel inference selected model(s) estimated (solid line) versus observed (grey dots) body girth growth for female ringed seals (*Pusa hispida*) in the north (*a*) and south (*b*), as well as male ringed seals in the north (*c*) and south (*d*).



We did not test whether our male to female ratio differed from unity (1:1) because our collections covered all seasons and a proper comparison of sex ratio should ideally use the same season (Holst et al. 1999). Generally, sex ratios of sampled ringed seals do not differ from unity, as has been a reported characteristic of populations throughout the Canadian Arctic (Smith 1973, 1987; Holst et al. 1999; Holst and Stirling 2002; Chambellant 2010), as well as other circumpolar locations (Fedoseev 1965; Helle 1979; Lydersen and Gjertz 1987).

Some uncertainties associated with our data can be outlined. We used the largest collection of ringed seals available to analyze body growth; however, the number of communities with reasonably large seal samples (eight communities with >100 seals) somewhat limited our ability to test for latitudinal patterns and regional groupings. We detected some temporal patterns in our data set despite having samples from different communities collected over different time periods. For example, most samples from Hudson Bay were collected from 2000 to 2015, whereas northern samples were more opportunistically collected back to 1980. Samples were collected throughout the year, although most (56%) southern samples were harvested in the autumn. For this analysis, we did not compare ringed seal body size patterns across seasons. Seals undergo considerable fluctuations in fat stores seasonally, including female ringed seals losing approximately 27% of their body mass during the brief 5- to 7-week lactation period (Smith et al. 1991). Future research will need to investigate whether differences in this seasonal cycle may help explain the diverging patterns in growth rate and asymptotic body size. Growth curve parameters can be influenced by age composition of the samples (Schnute 1981), which in the case of ringed seals varies with season of collection (Holst et al. 1999). The lack of data on implantation date can influence estimation of length at birth; however, asymptotic length tends to be robustly estimated (McLaren 1993).

What are the possible explanations of the observed north–south pattern? Specific proximate explanations that could relate to life-history traits such as body growth include (*i*) the amount of fast ice providing stable breeding habitat in spring for differential pup growth (McLaren 1958), (*ii*) density-dependent effects resulting from mortality (e.g., Inuit harvesting or polar bear predation; Goodyear 1999), and (*iii*) seasonal food availability and accessibility (Holst and Stirling 2002). The latter "resource availability hypothesis" purports that individuals living at higher latitudes deal more commonly with resource shortages and density-independent mortality, which favours selection of larger body size relative to individuals living at lower latitude that contend with resource competition requiring faster growth and earlier age of maturation (Perrin 1989; Ferguson and Larivière 2008). Additionally, ultimate mechanisms may include (*iv*) heat conservation (Bergmann's rule); (*v*) differences in migratory ability with higher latitudes requiring greater migrations and larger body size conferring energetic advantages for this activity; and (*vi*) starvation resistance whereby seals in the High Arctic endure longer periods of negative energy balance and having larger body size allows for greater relative fat storage (Blackburn et al. 1999).

Although heat conservation in the north is a possible explanation, whereby larger body size confers advantages in maintaining homoeothermic temperature (Angilletta et al. 2010), this seems unlikely in a seal with considerable body fat (Ryg et al. 1988). In fact, the physiological incapacity to offload excessive heat from the body has been proposed as an explanation for smaller body size at a species' southerly distribution limit (Gardner et al. 2011) and could be considered a reason for smaller seals in the south. Likely, explanations require consideration of differing selection pressures at a species' northern and southern distribution limits (e.g., Hersteinsson and Macdonald 1992).

Selection pressure from any of these variables may have resulted in genetic growth differences or an evolved plasticity for the species that allows for differing growth patterns with local environment. To date, very little genetic structure has been found among circumpolar ringed seal distribution (Davis et al. 2008) with evidence that ringed seals disperse on a pan-Arctic scale and both males and females may migrate long distances during the summer months when sea-ice extent is minimal (Martinez-Bakker et al. 2013). Thus, differences in asymptotic size and growth rate are likely the result of environmental factors operating on ecological timescales.

Predictability of stable ice for breeding has been suggested to be an explanation for differences in growth between larger seals using coastal landfast ice and smaller seals using offshore moving ice for nursing and mating (McLaren 1958; Pastukhov 1969; Fedoseev 1975; Finley et al. 1983). Here, the suggestion is either that pups born in more stable ice areas were nursed longer than those in less stable habitat (i.e., faster early growth rate) or the timing of ice breakup was early in some habitats at more southern latitudes resulting in abbreviated nursing (Smith 1973; Holst and Stirling 2002). We did observe less fast ice in the Hudson Bay region relative to the north and unpredictability (i.e., year-to-year availability) was greater in the north region. However, it is questionable whether ice conditions alone would cause significant differences in seal size or whether other factors work in conjunction to link sea ice to food availability (Goodyear 1999).

A more inclusive explanation links predation pressure from polar bears and Inuit hunters, as well as availability of food resources, which all may be related indirectly to ice conditions and ultimately affect seal growth patterns (Harwood et al. 2000, 2012; Pilfold et al. 2014). Food availability and prey quality have been considered the more likely cause of differences in growth among seal populations with better food conditions at higher latitudes (Laws 1953; Holst and Stirling 2002). However, even though ringed seals from some areas (e.g., Svalbard; McLaren 1993) had higher growth rates for young seals, we found that slower growing seals from the north attained higher asymptotic lengths. Thus, it does not seem that food availability alone explains observed patterns. More research is required; a circumpolar analysis of ringed seal growth characteristics would likely help to determine the mechanistic patterns in body growth related to the assemblage of environmental and geographical variation.

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