Do intraspecific life history patterns follow interspecific predictions? A test using latitudinal variation in ringed seals

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ORIGINAL ARTICLE

Do intraspecific life history patterns follow interspecific predictions? A test using latitudinal variation in ringed seals

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Abstract

Mammals adapted to unpredictable and low-energy environments often evolve a "bet-hedging" life history strategy characterized by less costly reproductive outputs over a longer and slower-growing life. In contrast, species adapted to more predictable (i.e., low variation) and higher energy environments may evolve greater fecundity over a shorter and faster-growing life. We tested whether this known interspecific pattern also occurs within a species. We compared life history traits of the ringed seal (*Pusa hispida*) in the Canadian High Arctic to those closer to the southern limit of the species' circumpolar distribution. We found that northern seals grew slower than southern seals (Brody growth coefficient), achieved a greater asymptotic body weight (82 and 69 kg vs. 74 and 54 kg female and male, respectively), reached sexual maturity later (6.1 years vs. 4.5 years), had lower fecundity (1.8 years vs. 1.3 years interbirth interval), longer average lifespan (5 years vs. 3 years median age), and greater movements (1,269 vs. 681 km). Mating systems also likely differed with northern seals showing morphological evidence of a promiscuous mating system with potential sperm competition as indicated by greater relative testes size. The northern region was also characterized by more unpredictable environmental timing of seasonal events, such as spring sea ice breakup. Life history variation between the intraspecific groups of seals appears to agree with interspecific patterns and provides a better understanding of how species' life history parameters shift in concert with environmental conditions.

KEYWORDS
age of maturity, body size, environmental predictability, latitude, mating system

1 | INTRODUCTION

Species inhabiting unpredictable (i.e., more variable) environments, such as high latitudes, may adopt a "slower" life-history that favors longer adult survival as a means of spreading reproductive risk over a lifetime and increasing the likelihood that some young will enter good environmental conditions (Morrison & Hero, 2003; Sæther & Bakke, 2000). In contrast, species living in highly productive and less seasonally variable environments, such as near the equator, may exhibit a "faster" life-history resulting in higher numbers of offspring that grow quickly, while adult

longevity is relatively shorter (Barclay, Harder, Kunz, & Fenton, 2003; Ferguson & Higdon, 2006; Ferguson & Higdon, 2013; Fisher, Owens, & Johnson, 2001; Roff, 2002; Sæther & Bakke, 2000). Similarly, mating systems show interspecific variation along a latitudinal cline whereby less breeding synchrony at low latitudes relates to smaller relative testis size suggesting a low level of sperm competition and extra-pair mates compared with temperate-zone species (Stutchbury, 1998).

However, few studies have tested whether those interspecific patterns hold for populations within a species' range (i.e., intraspecific). It has been hypothesized that a population at high latitude faces more unpredictable environments leading to later age of maturity, longer interbirth intervals and greater longevity (Ferguson, 2002; Giesel, 1976; Roff, 2002; Stearns, 1976) and less social mating systems (greater post- vs. precopulatory selection; Evans, Zane, Francescato, & Pilastro, 2003). In contrast, populations at lower latitudes and more stable environments may favor early maturation, short interbirth interval, shorter lifespan and more social mating behavior (e.g., territorial polygyny) (Searcy & Yasukawa, 1989; Table 1). Knowing how life-history and mating systems are shaped by environmental conditions would assist in understanding the distribution, abundance and conservation in our changing world (Perry, Low, Ellis, & Reynolds, 2005).

Life-history allometric theory predicts large body size and greater movements for high-latitude species contending with environmental unpredictability (McLoughlin & Ferguson, 2000). This pattern may be consistent with intraspecific variation in life history among populations across an environmental gradient (e.g., McLoughlin, Ferguson, & Messier, 2000; Nevoux, Forcada, Barbraud, Croxall, &

Weimerskirch, 2010). The variable distribution and relatively lower primary production at higher latitudes are related to greater body size (i.e., Bergmann's rule; Ashton, 2002). As such, allometric increases in movement rates are likely due to search and foraging behavior resulting in greater home range sizes and seasonal movements (Perry et al., 2005). This allometric migration hypothesis purports that mammals at high latitudes may show larger body sizes to enable long-distance movement from seasonally less productive and safe habitats to more productive and riskier habitats (Cox, 1985; Ferguson & Larivière, 2004; Lindstedt, Miller, & Buskirk, 1986; Stevick, McConnell, & Hammond, 2002).

Populations living along a latitudinal cline may also follow interspecific patterns in mating system (Stutchbury, 1998). A less social mating system such as females accepting multiple males with postcopulatory selection (e.g., sperm competition) likely occurs at high latitudes as an adaptation to unpredictable environments and lower population density (Ferguson & Larivière, 2008; Orians, 1969). With fewer mating opportunities at higher latitudes, females are more likely to mate with multiple males (Ferguson & Larivière, 2004). In order to increase their postcopulatory opportunities, reproductive morphology that is advantageous to sperm competition, such as a longer baculum, may be favored for males (Ferguson, Virgl, & Larivière, 1996). In contrast, low-latitude populations living at higher densities may have more social mating systems, such as territorial polygyny, that favors males monopolizing females for mating, and postcopulatory mechanisms may be less important. Thus, at low latitudes, the overall population may have smaller individuals. However, within the population there would be selection for greater male body size relative to

TABLE 1 Summary of ringed seal life history predictions based on the climate hypothesis describing environmental differences between high- and low-latitude regions. For each life history trait, the columns indicate the direction of change for northern and southern ringed seal populations and the variables used to test the hypothesis

| Life history trait	North (bet-hedgers)	South (reproducers)	Test	Variable(s)
Female sexual maturity	Later	Earlier	Reproductive tract assessment	Age at pregnancy
Male sexual maturity	Later	Earlier	Reproductive morphology	Inflection point in bacular and testicular growth
Physical maturity	Later	Earlier	Asymptotic length	Body mass and growth rate
Interbirth interval	Longer	Shorter	Pregnancy rate	Inverse of pregnancy rate
Longevity	Longer	Shorter	Age structure	Median age of harvest
Dispersal	Higher	Lower	Telemetry movement distance	Distance traveled and rate of movement
Mating system	Less social	More social	Relative testes and baculum size	Control for body size
Environment	Less predictable	More predictable	Coefficient of variation	Timing of sea ice breakup, freeze-up and duration

females for harem defense (Steyaert, Endrestøl, Hacklaender, Swenson, & Zedrosser, 2012).

The ringed seal (*Pusa hispida*) is a marine mammal with a circumpolar Arctic distribution. Their large spatial range allows us to test hypotheses on intraspecific life-history variation along latitudinal gradients. Ringed seals are panmictic breeders with low genetic substructure (Davis, Stirling, Strobeck, & Coltman, 2008), making it unlikely that seals have evolved life-history differences. However, ringed seals display considerable phenotypic plasticity that might account for latitudinal differences in life-history (Martinez-Bakker, Sell, Swanson, Kelly, & Tallmon, 2013). We tested latitudinal differences in body size and growth, reproduction, mobility and mating behavior using a large sample collection (>3,000 seals) from Inuit subsistence hunts (1980 to 2015) and telemetry database (*n* = 50) from the High Arctic to southern Hudson Bay in eastern North America. We predicted that in the north relative to the south, ringed seals would experience: (a) greater environmental unpredictability (variability in timing of sea ice breakup, freeze-up and duration), (b) greater body weight and slower body growth, (c) greater travel distances and movement rates, (d) delayed female sexual maturity, (e) delayed male sexual maturity, (f) longer interbirth intervals (i.e., lower pregnancy rate), (g) longer life and (h) a more promiscuous mating system. Using ringed seals, we provide the first intraspecific evidence of the relationship between environmental predictability and life history traits in aquatic mammals.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area covered most of the eastern Canadian Arctic from southern Hudson Bay (55°N) to northern Ellesmere Island (76°N) and from Baffin Island (66°W) to the Canadian Arctic Archipelago (95°W; Figure 1). Seals were collected by Inuit hunters for Fisheries and Oceans Canada and Environment and Climate Change Canada (Northern Contaminants Program) since 1980 as part of community-based monitoring projects working in collaboration with Hunters and Trappers Organizations, Nunavut Wildlife Management Board and the Government of Nunavut (Table S1). During the spring (May) ringed seal breeding season, the environment of the High Arctic (north) region compared to Hudson Bay (south) is characterized by more landfast ice (83.1 km from land to lead versus 29.5 km from land to lead), higher sea ice concentration (65.0% vs. 50.0%), more multiyear ice (3% vs. 0%), colder temperatures (−7.6°C vs. −3.3°C) and greater snow depth (15.6 cm vs. 2.3 cm) (Ferguson et al., 2018).
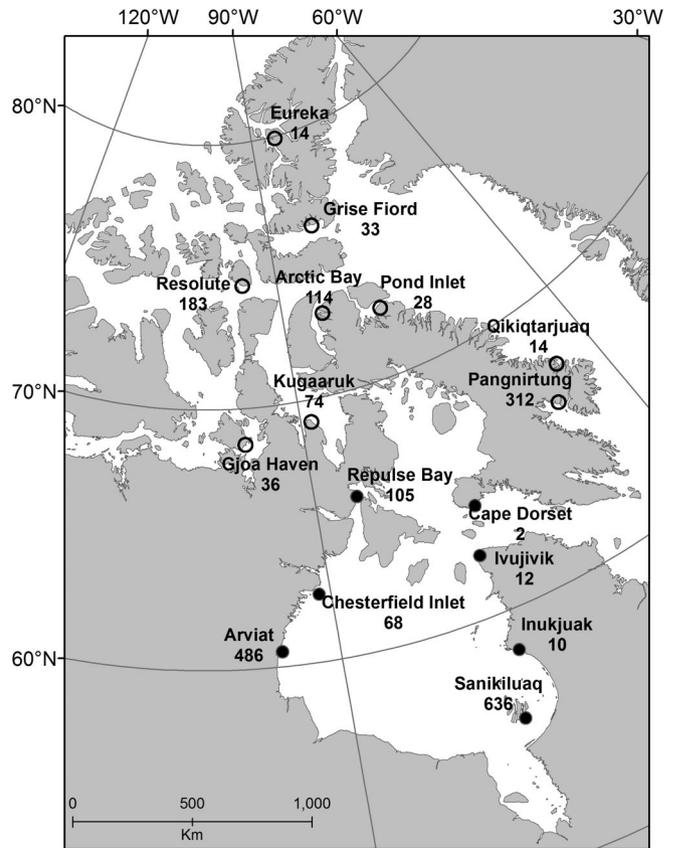
FIGURE 1 Community locations where ringed seal samples were collected in northeastern Canadian Arctic, 1990–2015. Open and solid circles represent north and south communities, respectively. The acronym names for sampling locations are in Table S1, and numbers under the location acronyms are sample sizes of all seals >1 year old (i.e., excludes 0)

2.2 | Environmental predictability

We compared sea ice features between the High Arctic and Hudson Bay regions using archived weekly sea ice data from the Canadian Ice Services (http://iceweb1.cis.ec.gc.ca/archive). Sea ice breakup date was defined as the day of the year on which the total ice concentration for the region decreased and remained below 50%. Freeze-up date was the day on which the total ice concentration increased and remained above 50%. Through interpolation, weekly ice concentrations from before and after sea ice breakup and freeze-up were used to estimate the day of the year on which the sea ice breakup and the freeze-up occurred. Duration of open-water season was the number of days between the sea ice breakup and the freeze-up for each year.

2.3 | Body size and growth rate

Seals were measured in the field by Inuit hunters and tissue samples kept frozen at −20 to –30°C. Date, time, location,

sex and morphology were recorded. Standard length, axillary girth and body weight were measured to the nearest 0.5 cm with a flexible measuring tape and to the nearest 0.5 kg using a weigh scale and a tripod when available. Age was determined by counting cementum annuli from a cross-sectioned portion of the lower right canine tooth (Stewart, Stewart, Stirling, & Street, 1996).

Often direct measurement of body weight was not possible due to logistics (638 missing of 1,020 for north and 460 of 1,904 for south). For missing values of body weight, we used a regression power function of standard length and girth versus body weight data that were previously summarized (Ferguson et al., 2018). Ringed seal samples with no associated age data were excluded from analyses. We also excluded young-of-year ($n = 797$) resulting in a total of 2,924 ringed seals collected from 1990–2016 used for analyses.

2.4 | Movement

We used movement data from satellite telemetry of ringed seals across the study area to test the prediction that at higher latitudes, ringed seals disperse farther and move faster. A total of 50 ringed seals were captured in August and September from 2006 to 2017 (Table S2). Thirteen seals from the north and 37 from the south had satellite telemetry transmitters attached (see Luque, Ferguson, & Breed, 2014; Yurkowski et al., 2016 for specific details on capture, measuring and tagging procedures). The three locations of capture in the north included Resolute Bay ($n = 6$), Pond Inlet ($n = 2$) and Igloolik ($n = 5$). All southern seals were captured on the Belcher Islands near Sanikiluaq ($n = 37$). Calculation of rate of movement and distance traveled for the open-water season included data from the tagging date to October 31 and only included tagged seals that provided greater than 25 days with locations (range 26–91 days). Minimum age was estimated by counting light and dark annuli on the claws of live animals (Ferreira, Loseto, & Ferguson, 2011) to demarcate subadults (≤ 5 years) and adults (>5 years) (McLaren, 1958). Distance traveled and rate of movement were compared using a mixed model with age class (subadult and adult) and region (north and south) as factors.

2.5 | Sexual maturity

Age at sexual maturity was assessed as first ovulation using methods described by DeMaster (1978). Extracted whole reproductive tracts were labeled and shipped frozen to the Freshwater Institute in Winnipeg, Manitoba, Canada, where they were thawed and examined in the laboratory. Both excised left and right ovaries were preserved in 10%

buffered formalin, and later sectioned and read for number of follicles larger than 5 mm, and corpora lutea and albicantia (T. G. Smith, 1973). The mean date of ovulation for ringed seals is May 25 (Chambellant, Stirling, Gough, & Ferguson, 2012), but the period of embryonic diapause between conception and implantation delays foetal development until September (T. G. Smith, 1987). Thus, we estimated pregnancy from the presence of a foetus from ringed seals harvested from September to March. We classified a female as mature based on the presence of large follicles or corpora lutea in her ovary, plus either the presence of a corpus albicans or evidence of past parturition from examination of uterine cornua (Table S3). The presence of a large, recently erupted follicle or a corpus luteum was considered evidence of recent ovulation.

For males, measures of reproductive morphology included testes weight (without epididymis) and baculum length following protocols from Yurkowski, Chambellant, and Ferguson (2011). Male testes size and spermatogenetic activity peak when males are rutting from March to mid-May (Johnson, Fiscus, Ostenson, & Barbour, 1966; McLaren, 1958). Thus, we compared testes samples collected in June–December to minimize size due to the mating season. To compare growth differences in reproductive morphology between north and south male seals, we controlled for body size by dividing testes weight and baculum length by total body weight or length. We assumed that the inflection point for the growth of male reproductive organs (testes weight or baculum length) provided an estimate of the age when seals begin accelerated reproductive development associated with mating competition (Pereira & Leigh, 2003). We graphically compared testes weight and baculum length between the two regions to assess whether male seals showed positive allometric growth indicative of post-copulatory competition (Tasikas, Fairn, Laurence, & Schulte-Hostedde, 2009).

2.6 | Interbirth interval

Interbirth interval was measured as the number of years between a full-term pregnancy and the completion of the next pregnancy (Hill, 1993). Interbirth interval was calculated as the inverse of pregnancy rate (see Female sexual maturity) to estimate how often a female gave birth (e.g., annually or biannually) once they reached sexual maturity.

2.7 | Age structure

We were unable to measure maximum lifespan and instead used median age of seals harvested in autumn (August–December) as an index to compare age distribution of seals

in the north versus south. Previous research has indicated that the autumn hunt during the open-water season provides samples that are representative of the population age-sex distribution (Ferguson, Young, Yurkowski, Anderson, & Willing, 2017).

2.8 | Mating system

Mating system was inferred from male morphological measurements of testes and baculum size relative to adult body weight or length (R. L. Smith, 1984). Interspecific comparisons found that greater baculum length relative to mean body length indicated the degree of multimale mating (Ferguson & Larivière, 2004; Ramm, Parker, & Stockley, 2005). Similarly, greater testes weight relative to body weight has been used as an index of postcopulatory sperm competition (Møller, 1988). First, we compared adult testes and baculum size corrected for body size and next we used analysis of covariance (ANCOVA) to compare differences in slope (i.e., allometric growth rate).

2.9 | Statistical analysis

Analyses were run in R v. 3.3.2 (R Development Core Team, 2016) with growth modeling using JAGS v 4.2.0 (Plummer, 2003) and telemetry analysis using *bsam* v. 1.1.1 (Jonsen, 2016). Coefficient of variation (CV = the standard deviation divided by the mean) was used to assess predictability (Lindstedt & Boyce, 1985) for the time series of sea ice breakup, freeze-up and duration. For the telemetry data, we used hierarchical Bayesian state-space models at a 12-hr time step to reduce argos satellite-based location and data system (ARGOS) location error and estimate travel distances and movement rates (see Yurkowski et al., 2016 for more details on model fitting). We plotted baculum length/body length and testes weight/body weight against age and estimated the inflection point using the package "inflection" in R (Christopoulos, 2016). Since size structure data are non-parametric, we compared median age from all samples collected using a Mann–Whitney *U* test. Kolmogorov–Smirnov test (K–S) was used to compare age structure differences depending on season.

Body growth model methods used here for age-specific weight (kg) are as described in Ferguson et al. (2018) for age-specific length and girth (see Panik, 2014 for details about model and parameters). To compare the rate of growth, we used the Brody growth rate coefficient (units are per year), which is the K parameter of the "typical" von Bertalanffy Growth Model and measures the exponential rate of approach to the asymptotic size (Schnute & Fournier, 1980). We applied Bayesian statistics to model selection and multimodel inference (MMI) based on deviance information

criteria to evaluate the relative goodness of fit of the structural models (Burnham & Anderson, 2003).

3 | RESULTS

3.1 | Environmental predictability

Greater CVs were recorded for the northern region relative to the southern region for sea ice breakup (4.6 vs. 4.5), sea ice freeze-up (2.9 vs. 2.6) and duration of open water (15.7 vs. 10.1). Similar patterns were found in the range (36 vs. 30 for sea ice breakup; 38 vs. 37 for sea ice freeze-up; 69 vs. 64 for duration of open water) of environmental variables with greater values in the north.

3.2 | Body size and growth rate

We used Gompertz model for all four datasets because it is commonly used for seal growth studies and provided a comparison among regions and sex for the ages approaching 95% asymptotic weight. We defined the most parsimonious body weight-at-age growth model according to Akaike Information Criterion with correction for small sample size (AICc), separately for sex (female vs. male) and location (north vs. south). To assess possible bias due to using weights estimated from regression (38% of samples), we re-ran the growth models with only field weights and found no difference. However, to formulate the more robust regional and sex comparisons, we used the full data set.

The MMI-based averaging Brody growth coefficient (K) and asymptotic body weight (W_∞) for northern female seals was 0.335 ± 0.057 per year and 82.4 ± 5.0 kg compared to 0.484 ± 0.121 per year and 73.8 ± 13.2 kg for southern female seals. Using a Gompertz model, the ages approaching 95% asymptote weight were estimated to be 18 years for northern females and 10 years for southern female seals (Figure 2). The 95% asymptote weight of northern females was 69.2 kg versus 49.6 kg for southern females. The MMI-based averaging Brody growth coefficient (K) and asymptotic body weight (W_∞) for northern males were 0.086 ± 0.023 per year and $69.4 \ 6 \pm 1.7$ kg, compared to 0.326 ± 0.079 per year and 53.9 ± 0.87 kg for southern males. The age at which northern males reached 95% asymptote weight was 17 years when the body weight was 68.9 kg. For southern male seals, the age was 9 years when the estimate of body weight was 51.3 kg. The difference in ages suggests that northern seals grow slower but reach a larger asymptotic size compared to southern seals. Males asymptote in weight at a younger age whereas females continue to grow well into their 20s resulting in an overall larger female: male adult body weight (reverse sexual dimorphism) in the north.
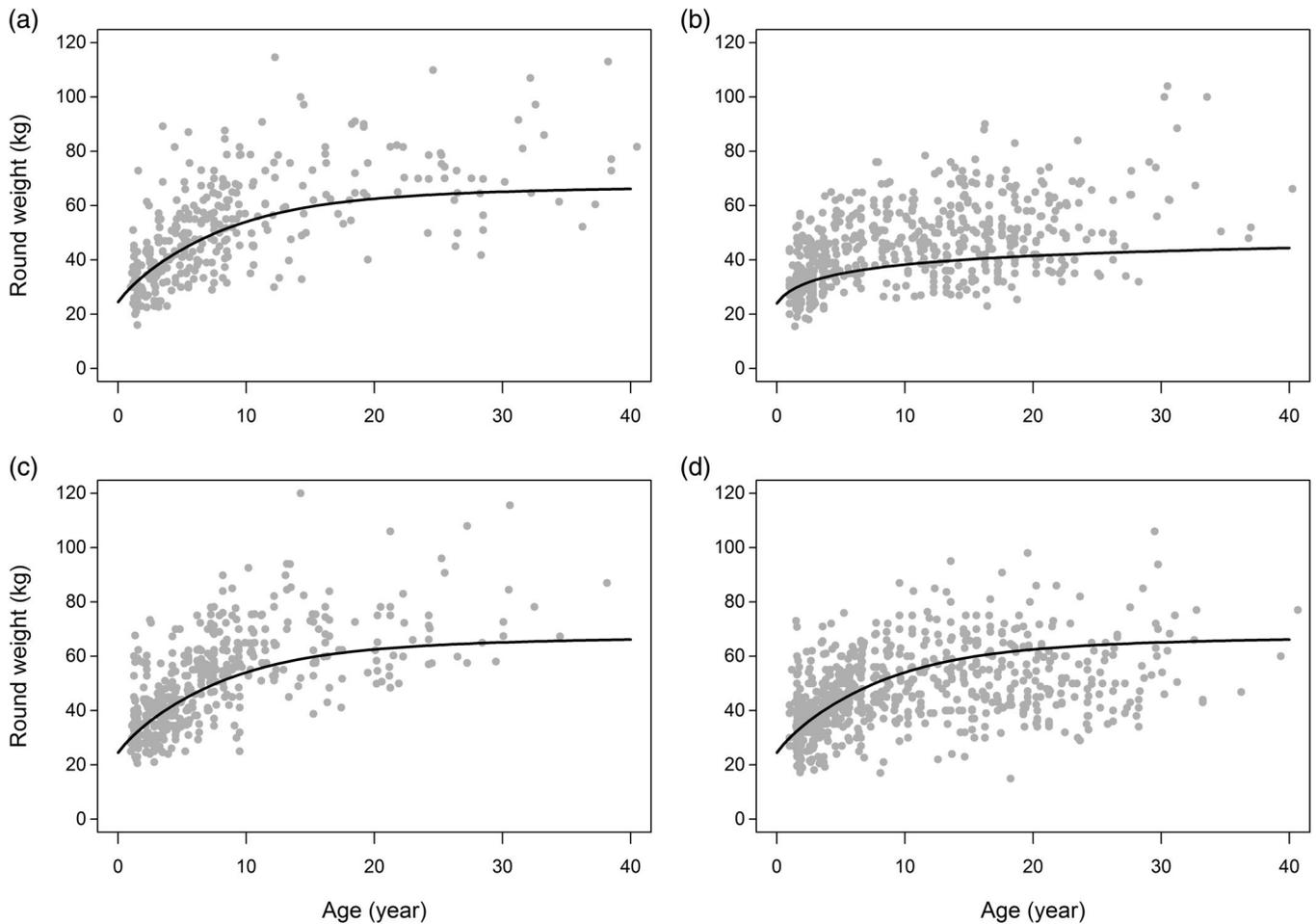
FIGURE 2 Ringed seal growth (solid line Gompertz model; gray dots observed) for body weight at age of female seals in the north (a) and south (b), and male seals in the north (c) and south (d) of the eastern Canadian Arctic

3.3 | Movement

Of the 50 tagged seals with >25 days transmitting, three adults and 10 subadults were from the northern region and 10 subadults and 27 adults were from the southern region (Table S2). There was no significant difference in distance traveled and movement rate between age classes (analysis of variance [ANOVA] $F_{1,48} = 1.04$, $p = .33$; Figure 3), although the test was limited to only three adult seals in the north. Distance traveled was significantly greater in the north ($1,269 \pm 844$ km) versus south (682 ± 228 km) as was rate of movement (19.1 ± 11.5 km/day vs. 11.3 ± 7.9 km/day, respectively; ANOVA $F_{1,48} = 11.27$, $p = .0016$; Figure 3).

3.4 | Sexual maturity

Female ringed seals matured at a later age in the north compared to the south. Age at sexual maturity was 6.08 ± 0.07 years (mean $\pm$ SE; $n = 41$ mature females) in the north and 4.52 ± 0.06 years ($n = 91$) in the south

(Table S3). Age at first reproduction was 8.61 ± 0.20 years (mean $\pm$ SE; $n = 41$) in the north versus 5.96 ± 0.20 years ($n = 91$) in the south. Using the age when greater than 50% of females were ovulating, the estimated age at sexual maturity was 6 years in the north and 4 years in the south. Similarly, using the age when greater than 50% of females were pregnant, the estimated age at first reproduction was 7 years in the north and 5 years in the south. Morphological maturity of males was later in the north with the inflection point in growth of testes weight and baculum length occurring at 5.8 and 4.8 years compared to 4.3 and 2.5 years in the south.

3.5 | Interbirth interval

In the north, ringed seal ovulation rate was high (98%) but pregnancy rate low (56%). In the south, both ringed seal ovulation rate and pregnancy rate were high (88% and 79%, respectively). As a result, northern ringed seals would have a pup born on average every 1.8 years (1/0.56), whereas in the south seals would pup every 1.3 years (1/0.79).
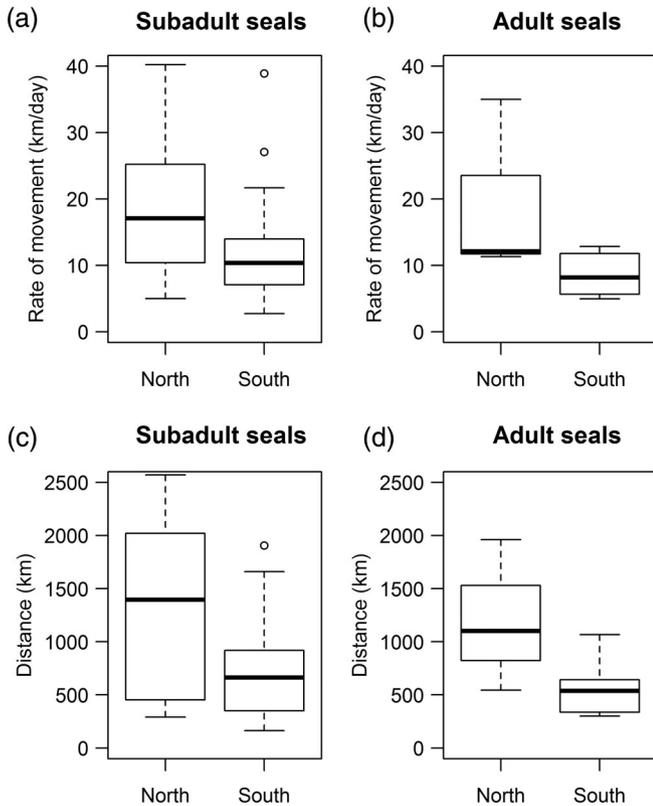
FIGURE 3 Rate of movement for subadult (a) and adult (b) ringed seals and distance traveled for subadult (c) and adult (d) ringed seals from telemetry studies in northern and southern regions of the eastern Canadian Arctic

3.6 | Age structure

Age structure of harvested seals differed between the two regions (Kolmogorov–Smirnov (K-S), $D = 0.44$; $p < .01$) with southern seals being younger (Mann–Whitney U test: $W = 6,968,300$, $p < .001$). The southern seals had a median age of 3 years for males and females compared to 4 and 5 years for males and females in the north. The age structure for the open-water seasons (August–December) was not significantly different between regions (K-S: $D = 0.10$, $p < .06$).

3.7 | Mating system

While controlling for body size (testes weight/body weight), adult males older than 5 years of age during the nonmating season (June–December; $n = 431$) had greater testes size in the north versus south (0.164 vs. 0.136, $t = 2.60$, $p = .013$; Figure 4). Using an ANCOVA of all aged seals (June–December; $n = 841$) to test for north–south differences in testes against body weight found no difference in intercept ($F = 0.906$, $p = .34$) indicating no relative size difference as juvenile seals. However, the regression slope differed ($F = 5.55$; $p = .0023$), indicating testes weight is relatively

greater for northern seals upon reaching sexual maturity (ca. 10 years of age). In contrast, we found no significant difference in length of baculum (controlling for body size; $p > .10$).

4 | DISCUSSION

This study is the first to provide evidence of intraspecific variation in the life history of an Arctic marine mammal across a latitudinal gradient that is consistent with interspecific theory. We found that ringed seals showed differences in life history and mating traits between less predictable (variability) northern environments and more predictable southern environments of the Arctic. The northern seals grew slower, lived longer, matured later at a larger size, had longer interbirth intervals, and greater relative testes size. This pattern is characteristic of a bet-hedging strategy where reproductive bouts start later and occur less frequently over a longer adult life. As a result, progeny born in different years sample a variety of environmental conditions, and overall lifetime reproductive success is greater (Lake, Burton, Barker, & Hindell, 2008). This bet-hedging strategy would allow some females to have progeny born into good conditions, while minimizing reproductive investment (Nevoux et al., 2010). In contrast, southern seals invested more into offspring at an earlier age to take advantage of more productive environmental conditions (Stearns, 1992). In the south, seals cycled seasonally from high blubber storage (up to 60% of body mass) to very low body condition (30% blubber) that likely threatened their survival (Ferguson et al., 2017; Ferguson et al., 2018; Young & Ferguson, 2013). Progeny born into southern regions likely encountered good feeding conditions during the open-water season allowing for faster growth and earlier reproduction, with shorter longevity as a tradeoff. We suggest that environmental variability is likely a major factor in the life history variability reported here for different ringed seal populations of the same species. For ringed seals, the key life history traits, reproduction and survival, may display phenotypic plasticity within tolerance ranges that allow populations from different environments to be highly adapted without necessarily genetic modification (Caswell, 1983; Gaillard & Yoccoz, 2003; Stearns & Kawecki, 1994).

Theory predicts that greater seasonal and inter-annual variability in climatic conditions will favor larger-bodied mammals that are better able to survive poor food availability (Lindstedt & Boyce, 1985; Luque & Ferguson, 2010). This predicted pattern has been found interspecifically for fish and reptiles (Olalla-Tárraga, Rodríguez, & Hawkins, 2006; Pyron, 1999). We found that ringed seals inhabiting northern areas with greater unpredictability in the timing of sea ice breakup and freeze-up grew to a larger size than in
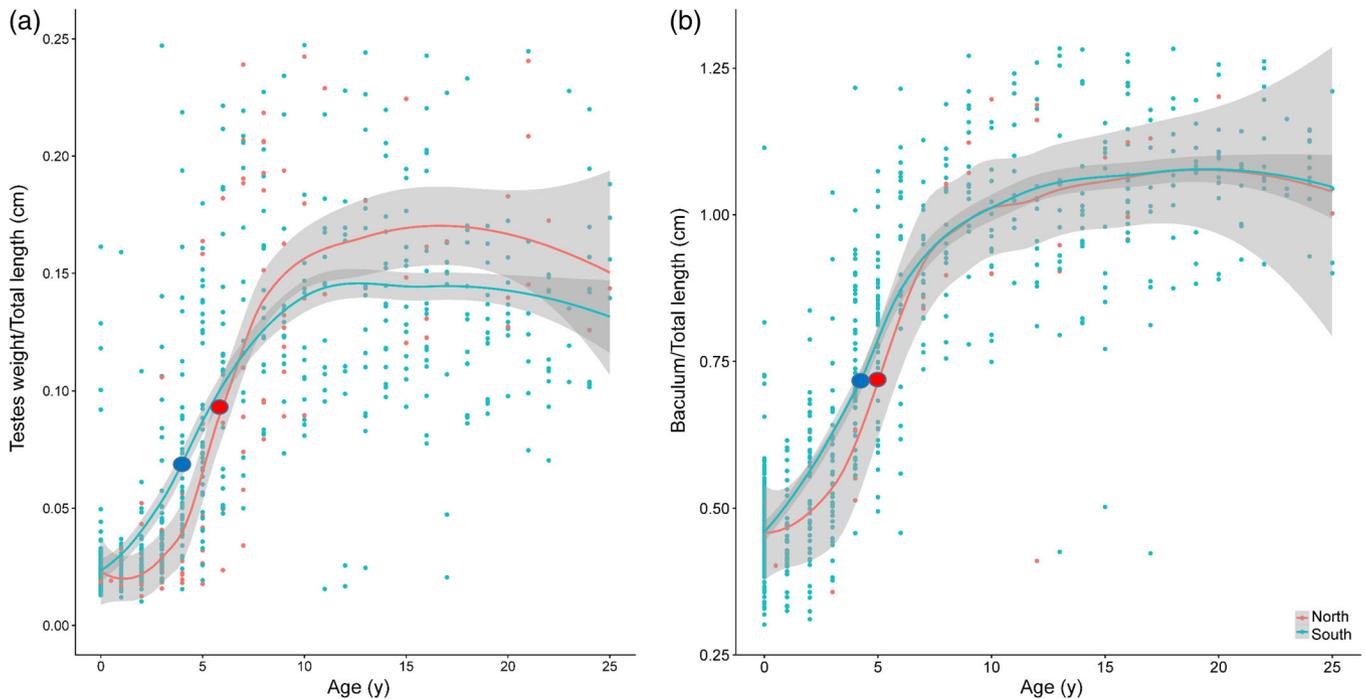
FIGURE 4 (a) Standardized testes weight (testes/body weight) and (b) bacula length (baculum/body length) with age for northern (red) and southern (blue) ringed seals collected from the eastern Canadian Arctic. Loess regression, a nonparametric least squares regression method, is performed to smooth the time series graphic. The gray area is the 95% confidence interval. Dots represent inflection points. Note, no significant difference in length of baculum (controlling for body size), whereas testes weight is greater for northern seals upon reaching sexual maturity (ca. 10 years of age)

the south. This pattern of slower growth to reach larger size follows the expected interspecific pattern when comparing high-latitude mammalian species (Sibly & Brown, 2007); a pattern that has been previously described as due to global climatic conditions (Ferguson & Messier, 1996; Stevens, 1989). In addition, the high-latitude adaptation of large size allows the ability to travel greater distances to find productive habitats as well as greater fat storage that assists in surviving periods of fasting when food is seasonally less available (Lindstedt et al., 1986; Owen-Smith, 1992).

Among pinniped, some species have been characterized more as capital breeders (accumulate energy for future reproductive effort), whereas others are considered more of an income breeder (i.e., spend energy as it is collected) (Boyd, 2000). Among phocid seals, ringed seals are considered more "income breeders" having less energy reserves for reproduction than "capital breeders" such as gray seals (*Halichoerus grypus*), which depend more on maternal body stores for lactation (Hammill, 1987; T. G. Smith, Hammill, & Taugbøl, 1991; Wheatley, Bradshaw, Davis, Harcourt, & Hindell, 2006). This pattern appears to hold within the species where northern ringed seal populations tend to be more capital breeders and tend to terminate pregnancy and to thereby conserve energy during difficult periods of food shortage. Individual pregnant females may physiologically assess the probability of achieving viable weaning weight

for each pup based on maternal nutritional state (Chinn, Monson, Tinker, Staedler, & Crocker, 2018; Trites & Donnelly, 2003). In contrast, ringed seals living at low latitudes appear to be relatively more like income breeders by growing quickly and attaining maturity at smaller size. In the south, they regularly proceed with reproduction since greater food availability may provide them with a good chance of producing a viable pup.

As with other phocids, ringed seals generally display high ovulation and pregnancy rates (Boulva & McLaren, 1979; Oritsland, 1970; Sergeant, 1966) and most adult females giving birth annually (Chambellant, 2010). The percentage of ovulation in our study was high (88% south and 98% north) as noted previously for the same region (Stirling, 2005). Despite this high reproductive potential, ringed seals show remarkable year-to-year and geographic variation in reproductive rates (Chambellant et al., 2012; Fedoseev, 1975; Kingsley & Byers, 1998; T. G. Smith, 1973, 1987; Teilmann & Kapel, 1998). The nearly 2-year interbirth interval for adult females in the north found in our study is noteworthy. The northern populations had the low pregnancy rate (56%) that was temporally more-or-less constant over a 17-year period suggesting an adaptive life history pattern.

For male reproductive morphology, baculum length appeared to be invariant to geographic location and was strongly correlated with male body size in ringed seals. In

contrast, testes weight appeared to vary with geography as northern males tended to have larger testes relative to their body size compared to southern seals. This latter finding suggests a possible difference in mating system according to latitude. Northern ringed seals also showed reverse sexual dimorphism relative to southern ringed seals. Ringed seals may vary their mating system with environmental conditions in that they are more promiscuous at northern latitudes. There is limited evidence of the impact of climatic variation on sexual selection (Monteiro & Lyons, 2012) as it is undeniably a complex issue, but looking at intraspecific differences in mating system might help describe the spatial and temporal dynamics of sexual selection pressure. For example, acoustic telemetry under ice could potentially describe mating and territorial behavior by seals to test whether significant differences could explain the morphological patterns reported here.

Ringed seal body mass and growth rates have seldom been estimated, and due to variable use of growth models (e.g., McLaren, 1993), we were limited in our ability to make comparisons. Seals in our northern study area grew more slowly and to a larger size than seals in the south. Many animal taxa exhibit a positive correlation between sexual size dimorphism and sex differences in age at maturity (Kozłowski, 1989; Stamps & Krishnan, 1997). This pattern was evident in our data, where male ringed seals matured later (ca. 5–9 years for males vs. 3–6 years for females) and reached asymptotic body size later than females. The assumption is the ecological drivers (e.g., climatic uncertainty) that favor larger size of species at high latitudes (i.e., Bergmann's rule) would also favor greater body size of individuals in populations across a species' distribution.

Global conservation strategies typically consider uncertainty when prioritizing their protective activities (Wilson, Carwardine, & Possingham, 2009). Similarly, considering variation in life history traits across a species' distribution (Hughes, 2000; Parmesan, 2006; Root et al., 2003) can help focus conservation investment and allow for more adaptive conservations efforts. For example, populations at higher latitudes have broader environmental tolerance so that warming may even enhance their fitness (Deutsch et al., 2008). We have added evidence that less understood intraspecific patterns may follow better-known interspecific life history patterns. The caution is that this will not always be the case—for example, brown bears (Ursus arctos) in North America displayed opposite body-size scaling patterns among species (positive trend for Carnivora Mammalia) and within species (negative trend; McLoughlin & Ferguson, 2000). Still, managers and conservationists can assume bet-hedging characteristics are favored at high latitudes and faster life history favored at low latitudes for populations of the same species within their distributional range. Knowing

the area within a species' range where we may expect sensitivity to future human impact may help identify problems prior to significant impact (Cardillo, Mace, Gittleman, & Purvis, 2006). Incorporating life history variation patterns into conservation planning could help guard against future biodiversity loss by anticipating and preventing species declines before they begin.

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Additional supporting information may be found online in the Supporting Information section at the end of this article.