ECOGRAPHY

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# Comparing temporal patterns in body condition of ringed seals living within their core geographic range with those living at the edge

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**Ecography**
**43: 1–15, 2020**
doi: 10.1111/ecog.04988

Subject Editor:
Jean-Michel Gaillard
Editor-in-Chief: Miguel Araújo
Accepted 29 May 2020

Ecological theory suggests that demographic responses by populations to environmental change vary depending on whether individuals inhabit central or peripheral regions within the species' geographic range. Here, we tested this prediction by comparing a population of ringed seals *Pusa hispida* located at high latitudes as part of their core range (core) with a population located at the southern extremity of their range (peripheral). First, we compared the two regions' environmental trends in timing of sea-ice breakup and freeze-up, open-water duration and the North Atlantic Oscillation (NAO). We found that the core region shifted to progressively warmer conditions in the early 1990s; whereas, in the peripheral region, the warming trend shifted in 1999 to one with no warming trend but high inter-annual variability. Next, we examined how body condition, inferred from blubber depth, responded to temporal changes in sea-ice and climatic variables – variables that have been shown to influence ringed seal demography. Core seals displayed minimal seasonal changes in body condition; whereas peripheral seals displayed a 20–60% amplitude seasonal change in body condition with a phase shift to earlier initiation of fat accumulation and loss. Finally, we tested for interannual differences and found that both core and peripheral seals responded similarly with decreased body condition following more positive NAO. Environmental variables influenced body condition in opposite directions between the two regions with core seals declining in body condition with later spring breakup and shorter open-water duration, whereas peripheral seals showed opposite relationships. Seals living at the core likely benefit from an evolved match between adaptation and environmental variation resulting in dampened seasonal and interannual fluctuations in body condition. Knowledge of how different populations respond to environmental change depending on geographic location within a species range can assist in anticipating population specific responses to climate warming.

Keywords: blubber depth, Nunavut Canada, *Pusa hispida*, sea ice, sine wave, spring breakup

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## Introduction

Natural selection results in organism adaptations to local environmental conditions (Mayr 1956, Savolainen et al. 2013); however, local conditions vary spatially and temporally. Theory predicts a gradient in relative tolerance limits of populations located from the core to peripheral regions of a species' geographic range, with the expectation that individuals cannot tolerate environmental conditions beyond a periphery boundary resulting in species range limits (Gaston 2003, Sexton et al. 2009, Carroll et al. 2014). How species adaptations vary along environmental gradients defines range limits and these patterns influence range expansions and contractions (Hargreaves and Eckert 2014). For example, a species' longitudinal range can encircle the Earth, particularly at high latitudes, and within a latitudinal range band, populations are variably adapted to local conditions (Hewitt 2003). At the highest latitude, populations may be limited by density-independent factors such as extremes in food and temperature (Stevens 1989, Ferguson and Larivière 2004). At low latitudes, populations may be limited by density-dependent factors such as predation, competition, and disease (MacArthur and Wilson 1963). Core areas of a species' range have populations that are generally regulated by density-dependent factors whereby abundance is limited by biological controls, such as intraspecific competition. Understanding the ecological and evolutionary processes that shape species' geographic ranges is a fundamental goal of ecology and increasingly important for conservation.

Individual responses to environmental variation is typically observed as changes in body condition which is an important individual fitness metric affecting both survival and reproductive success. These responses are observed over various time scales, such as seasonal, annual, and decadal time periods. Thus, in peripheral regions, we would predict density-independent limitation to be manifested as greater variation in body condition, such as fat stores. In the case of a particular species that is distributed across a wide geographic region, predictions are that populations at the core of their range will be better matched to environmental conditions; whereas those near the periphery of the species' range will show acute responses to changes in the environment as they are less adapted to track variation (Jackson and Overpeck 2000, Holland and Zaffos 2011, Willis and MacDonald 2011). In addition, different life stages of an organism respond differently to environmental variation and thus, we predict that at the extremes of a species' range, young, smaller individuals (i.e. juveniles) will respond more than older, larger individuals (i.e. reproductive adults) to seasonal, annual, and decadal patterns. At the core of species' range, we might expect less variation in body condition for different life stages as they will be able to ameliorate their responses to environmental variation due to their superior adaptation.

The ringed seal *Pusa hispida* is a small (50–70 kg) pinniped with a circumpolar distribution and, as the most successful pinniped in Arctic waters, they display relatively high abundance and generalist foraging and habitat selection (McLaren 1958, Reeves 1998). Ringed seals have a southern limit that varies around the Holarctic; thereby providing a good model to test biogeographic predictions. In the eastern Canadian Arctic, ringed seals live within a wide latitudinal range (55 to 90° latitude) where seasonal and interannual variation in body condition has been observed (Ferguson et al. 2019). Ringed seals at the southern limit of their range in Hudson Bay have been shown to be smaller, both in length and mass, than seals found in core areas of the central Arctic, supporting both regional and latitudinal size differences (McLaren 1993, Holst and Stirling 2002, Krafft et al. 2006, Chambellant 2010, Ferguson et al. 2018). 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. 2016a, b, c). Understanding geographic and environmental patterns in the cycle of body fat deposition of ringed seals would assist conservation efforts related to predictions of distribution changes with climate warming and loss of sea-ice (Ferguson and Higdon 2006, Laidre et al. 2008).

Blubber depth in phocids has been shown to be highly variable, and thus, a good measure of body condition (Gales and Renouf 1994). Ringed seals undergo considerable fluctuations in fat stores seasonally, including female ringed seals losing approximately 27% of their body mass during the brief 5–7 week lactation period (Smith et al. 1991). The transitions from landfast sea ice (also known as shorefast ice) to open water in spring and vice-versa in autumn represent crucial divisions 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 energy balance 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 adults breed and moult (Smith and Stirling 1975, Chambellant et al. 2012). Key life history events also occur in the spring when sea ice is melting (Smith 1980). At this time pups are weaned (Smith et al. 1991, Lydersen 1998) and polar bears *Ursus maritimus* focus predation efforts on these relatively naïve prey (Stirling and McEwan 1975, Smith 1980). Thus, the spring season appears to be a vulnerable life-history stage (Luque et al. 2014) as seals are at their lowest energy reserves during April–June when seals moult and fast while resting on the sea-ice (Ryg et al. 1990, Young and Ferguson 2013).

Ringed seals are the focus of this study due to the species' relatively high abundance, availability of tissue samples collected at large temporal and spatial scales through Inuit subsistence hunting (Luque et al. 2014), and their association with sea-ice habitat that varies with geography (Hamilton et al. 2015). Unfortunately, comparisons of density among ringed seal populations are unavailable (with the possible exception of western Hudson Bay; Young et al. 2015) and therefore comparisons are made with respect to

temporal trends. We compared ringed seals in two habitat regions, a core region from Pangnirtung to Grise Fiord, Nunavut in northern Canada where some of the largest ringed seals have been harvested, and a southern peripheral population located in the Hudson Bay region characterized by smaller seals (Ferguson et al. 2018). Seals at the southern limit of their distribution in Hudson Bay have also shown dramatic fluctuations in numbers over 25 yr (Young et al. 2015, Ferguson et al. 2017). In contrast, less is known about the more northerly core ringed seal habitat region. However, researchers have agreed that based on seal habitat selection, this High Arctic region is likely where environmental conditions more closely match ringed seal life-history adaptations (Kingsley et al. 1985, Hobson and Welch 1992).

Here, we test for differences in seal body condition patterns over time between two geographic regions and assess relative support for the theory explaining these patterns (Kirkpatrick and Barton 1997). Using an unprecedented data set from Inuit-harvested seals collected over a 26-yr period, 1990–2015, we compare environmental data and body condition (blubber depth) from core and peripheral populations to test whether 1) environmental variation in sea-ice condition has shifted over time and varies between regions; 2) seasonal cycles in body condition varied with the prediction of greater amplitude in peripheral seals; and 3) interannual variation in seal body condition is greater in peripheral populations than core populations in association with environmental factors such as sea-ice seasonal cycles and major climatic indices (North Atlantic Oscillation). Understanding local adaptations to interannual and conditions will be key to understanding and predicting demographic responses of ringed seals to a changing Arctic environment.

## Material and methods

The study area covered a large latitudinal and longitudinal swath of the eastern Canadian Arctic from southern Hudson Bay (Sanikiluaq, 55.28°N) to northern Ellesmere Island (Eureka, 80.0°N) and from the east coast of Baffin Island (Pangnirtung, 65.71°W) to the western Canadian Arctic Archipelago (Resolute Bay, 94.97°W) and encompasses core and southern peripheral ringed seal habitat (Fig. 1). To describe environmental differences between the core (High Arctic) and peripheral (Hudson Bay) regions, we summarize results from Table 1 in Ferguson et al. (2018).

### Environmental variables

Spring breakup and its associated measurements (duration of open water and timing of autumn freeze-up) have been consistently reported as key environmental drivers for ringed seal demography (Stirling et al. 2008, Ferguson et al. 2017). We used archived weekly sea-ice data from the Canadian Ice

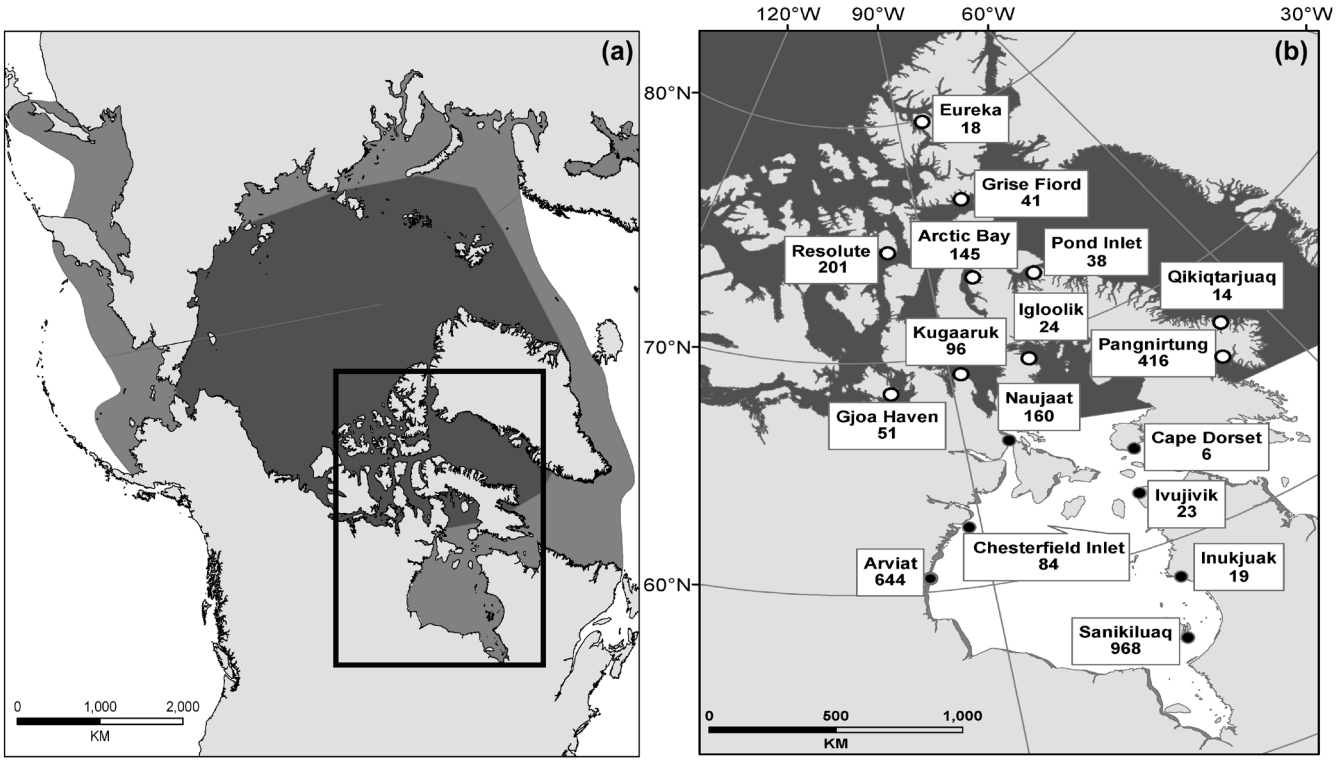


Figure 1. Graphical representation of geographic range model depicting (a) core ringed seal habitat in black and southern peripheral range as grey within ringed seal Holarctic regional distribution and (b) study area in northern Canada (box from a) where ringed seal samples were collected from Inuit hunts in Nunavut and Nunavik communities with sample sizes, 1990–2015.

Table 1. Summary of previously published environmental and biological differences between the core and southern peripheral regions of the Canadian Arctic where ringed seal samples were collected, 1980–2016.

| Region | Multi-year ice concentration (%) | Landfast ice width (km) | Total ice concentration (%) | Spring average temp-erature (°C) | Snow depth (cm) | Adult length (cm)[b] | Adult weight (kg)[b] | Average age (yr)[b] | Age of sexual maturity (yr)[c] |
|---|---|---|---|---|---|---|---|---|---|
| Core | 3.0 | 83.1 | 65.0 | −7.6 | 15.6 | 124.2 | 49.8 | 11.3 | 6.1 |
| Peripheral | 0.0 | 29.5 | 50.0 | −3.3 | 2.3 | 119.2 | 47.6 | 9.1 | 4.5 |
| ANOVA[a] | $F_{1,259}=106.2$ | $F_{1,259}=204.1$ | $F_{1,259}=42.2$ | $F_{1,259}=314.1$ | $F_{1,259}=46.1$ | $F_{18,1822}=18.9$ | $F_{14,1165}=30.2$ | $F_{19,1903}=9.5$ | |
| Test p value | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | – |

[a]All ANOVAs test regional differences while controlling for community and year.
[b]Average age of adult seals older than 10 yr to minimize bias associated with hunter selection.
[c]Age of sexual maturity was determined following the methods of Demaster (1978). See Ferguson et al. (2019) for details of statistical calculation method.

Services (<http://iceweb1.cis.ec.gc.ca/archive>) to calculate sea-ice breakup date as the day when total ice concentration for the regions (Canadian Eastern Arctic for core habitat and Hudson Bay for peripheral habitat) decreased and remained below 50%. Freeze-up date was the day on which the total ice concentration increased and remained above 50%. Duration of open-water season was the number of days between the sea-ice breakup and the freeze-up.

In addition, the North Atlantic Oscillation (NAO) has been reported as a key climatic index due to its relationship with winter (December through March) snowfall and ice (Frei and Robinson 1999) that are key features for ringed seal life history, including pup survival in subnivean dens (Chambellant et al. 2012). NAO (<https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>) is measured over the Northern Hemisphere as relative differences in surface sea-level pressure between the Arctic and the subtropical Atlantic. Swings in NAO phase can produce large changes in surface air temperature, winds, and precipitation over the Atlantic as well as the adjacent North American continent (Ottersen et al. 2001), thereby relating to the structure and functioning of marine ecosystems (Hurrell 1995, Hurrell and Deser 2010).

## Biological variables

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 consistently since 1980 to collect samples from harvested ringed seals. The majority of seals were measured in the field by Inuit hunters who recorded date of kill, sex and blubber depth at sternum (0.5 cm). Age was determined by counting cementum annuli from a cross-sectioned portion of the lower right canine tooth (Bernt et al. 1996). Age determination was done in the Fisheries and Oceans Freshwater Institute in Winnipeg, Canada (Stewart et al. 1996: 1990–2002 samples), or by Matson's Laboratory in Montana, USA (2003–2016 samples). Ringed seals were divided into three age classes: young-of-year (YOY also known as pups; < 1 yr old), juveniles (1–5 yr old), and adults (≥ 6 yr old; McLaren 1958, Young et al. 2010). YOY are generally born from March to April (Smith and Stirling 1975) and therefore, we started the seasonal growth models in March and ended them the following year in February. For juveniles and adults, we started the seasonal models in January and ended in December to relate to the calendar year used by most published studies. To describe seal population differences between the core (High Arctic) and peripheral (Hudson Bay) populations, we summarize average adult (> 10 yr) length (cm), weight (kg), and age (yr). In addition, we provide the estimate of female age of sexual maturity as an informative life-history variable that assists in comparing the two populations (Ferguson et al. 2019).

### Statistical analyses

All statistical analyses were performed using R ver. 3.4.4 (R Core Team). Comparison of environmental variables between regions was done using ANOVA while controlling for community (five in the core and four in the peripheral regions) and year (1980–2017).

Environmental patterns were assessed with broken stick regression (package 'segmented') to demarcate changes in temporal trends for all four environmental variables: timing of spring breakup, fall freeze-up, duration of open-water season, and NAO.

To compare seasonal variation between the two regions, we modeled time cycles as recurring oscillations that can be portrayed with sine curves that repeat annually (Cary and Keith 1979). For an annual cycle, amplitude measures the extent of a seasonal cycle (height of a peak) and phase describes the positional relationship allowing comparison between two cycles (Ferguson et al. 2000). We developed sine models to fit temporal patterns of ringed seal blubber deposition and metabolism (depth). A simple sine curve was fit to blubber depth as amplitude × sin ($x$ + phase) and can be written in linear form as $\alpha \times \sin(x) + b \times \cos(x)$. Using ($\alpha$, $\beta$) as a vector and writing in polar coordinates ($r$, $\varphi$) yields:

$$\alpha\sin(x)+\beta\cos(x) = r\cos(\phi)\sin(x) + r\sin(\phi)\cos(x) = r\sin(x+\phi) \quad (1)$$

With error structure $\epsilon_i$ assumed to be independent and identically distributed $\epsilon_i \sim N(0, \sigma^2)$

where $r$ is the amplitude and $\varphi$ is the phase. We then fit a linear model for core and peripheral seals and for each of the three age classes to assess significance of coefficients that represented amplitude and phase.

To compare interannual temporal patterns in body condition between core and peripheral seal populations, we modeled blubber depth of seals as a function of environmental (spring breakup, open-water duration, NAO) and biological (region, year, month, age group, sex) covariates. Working with multivariate variables, we conducted data exploration by examining outliers, collinearity, and auto-correlation (Zuur et al. 2010). A gamma general linear model (GLM) with a log link function was used (Eq. 2). The log link function ensures positive fitted values, and the Gamma distribution is typically used for continuous positive data (Zuur and Leno 2016). Explanatory variables included sex (categorical with two levels), age class (categorical with three levels: YOY, juveniles, adults), and region (categorical core and peripheral), spring breakup (continuous), autumn freeze-up (continuous), duration of open water (continuous), and NAO (continuous) and year. Due to the detection of autocorrelation, we introduced 1-yr lagged environmental covariates to the model selection suite. Interaction terms were only included for age and environmental variables since our focus was on whether temporal effects dominated core or peripheral populations of ringed seals.

$$F_{ij} \sim \text{Gamma}\left(\mu_{ij}\right)$$

$$E\left(\text{Growth}_{ij}\right) = \mu_{ij}$$

$$\begin{aligned}\text{Log}(\mu_{ij}) = {} & \text{Sex}_{ij} + \text{AgeClass}_{ij} + \text{Region}_{ij} + \text{Spring}_{ij} + \text{Fall}_{ij} \\ & + \text{Open}_{ij} + \text{NAO}_{ij} + \text{Spring}(t-1)_{ij} + \text{Fall}(t-1)_{ij} \\ & + \text{Open}(t-1)_{ij} + \text{NAO}(t-1)_{ij}\end{aligned} \quad (2)$$

Where $F_{ij}$ is blubber depth (cm) at sternum measured on $\text{seal}_I$ on $\text{date}_J$. We model the mean $\mu_{ij}$ and variance $\sigma^2{}_{ij}$. We assessed temporal lags by first testing for autocorrelation using a Durban–Watson test.

We used the Akaike information criterion (AIC) as an estimator of relative quality of statistical models. AIC provided the means for model selection using information theory (Burnham and Anderson 2002). The information theory approach to model selection allows for a trade-off between the goodness of fit of the model and the model's parsimony; thereby dealing with both the risk of overfitting and of underfitting. Covariation among variables was assessed using variance inflation factors (VIF). For models with variables having VIF > 2, we removed the variable with the highest VIF and re-ran the model. Successive iterations of removing highly correlated covariates resulted in a GLM model testing a smaller sub-set of explanatory variables. Using the information-theoretic approach, we then selected the top four models based on Delta (ΔAICc; Burnham and Anderson 2002). Model diagnostics were assessed by checking plots of residuals versus fitted values and q–q plots of theoretical quantiles (Zuur and Leno 2016).

## Results

### Environmental variation

Relative to the peripheral region, the core region had more multi-year ice, total ice, landfast ice, colder temperatures, and greater snow depth in spring (Table 1).

For the core region, all four environmental measures displayed temporal shifts (breakpoints from regression analysis) to warmer conditions since the early 1990s: sea-ice breakup (1993), duration of open water (1993), timing of fall freeze-up (1992), and NAO (1993) (Table 2). In contrast, for the peripheral region, all environmental variables shifted from warming to no trend after 1999 (Fig. 2). Since temporal shifts occurred around the time collections began in each region: 1990 in the core and 1999 in the peripheral region, we did not consider time periods in subsequent tests of seasonal and annual variation.

### Biological variation

Over 1000 seals were collected from hunts in the core region from 1990 to 2015 (Arctic Bay (145), Qikiqtarjuaq (14),

Table 2. Breakpoint regression analysis of environmental data to determine when a shift in slope occurred and the direction of change for core and peripheral regions of the Canadian Arctic. Note earlier breakup and later freeze-up in the core region after the 1990s whereas in the peripheral region sea-ice conditions were not trending following a 1999 event.

| Environmental variable | Region | Model | Year of change (inflection point ± SE) | Slope before (mean ± SE) | Slope after (mean ± SE) |
|---|---|---|---|---|---|
| Freeze-up | Core | $F_{1,33} = 10.38$, $p = 0.0029$ | 1991.9 ± 8.2 | −0.169 ± 0.860 | **+0.573 ± 0.217*** |
| | Peripheral | $F_{1,33} = 19.4$, $p < 0.001$ | 1999.0 ± 4.1 | **+1.097 ± 0.310** | −0.0304 ± 0.338 |
| Breakup | Core | $F_{1,33} = 49.0$, $p < 0.001$ | 1993.1 ± 4.4 | −0.0204 ± 0.474 | **−0.912 ± 0.178** |
| | Peripheral | $F_{1,33} = 10.7$, $p = 0.002$ | 1999.0 ± 5.2 | **−0.868 ± 0.326** | +0.063 ± 0.355 |
| Duration of open water | Core | $F_{1,33} = 31.5$, $p < 0.001$ | 1992.7 ± 5.4 | −0.114 ± 1.101 | **+1.489 ± 0.340** |
| | Peripheral | $F_{1,33} = 21.2$, $p < 0.001$ | 1998.9 ± 3.7 | **+1.971 ± 0.557** | −0.0846 ± 0.511 |
| North Atlantic Oscillation | Arctic | $F_{1,33} = 1.205$, $p = 0.28$ | 2010.6 ± 3.1 | −0.0879 ± 0.0489 | **+0.541 ± 0.526** |

*Bold indicates significant slope coefficients from regression analysis ($p < 0.05$).

Eureka (18), Grise Fiord (41), Gjoa Haven (51), Igloolik (24), Kugaaruk (96), Pangnirtung (416), Pond Inlet (38), Resolute (201)), whereas almost 2000 were collected from the peripheral region (Arviat (644), Cape Dorset (6), Chesterfield Inlet (84), Hudson Bay (14), Inukjuak (19), Ivujivik (23), Naujaat (160), Sanikiluaq (968)) from 1999 to 2016. The majority of seals collected were adults but the peripheral region had more YOY relative to the core region (30 versus 21%). The season when most seals were collected shifted from May to September in the core region to June–January in the peripheral region (see Supplementary material Appendix Table A1 in Ferguson et al. 2019). For both regions, more males than females were harvested (58% in core and 56% in peripheral; Chi-square test p-value = 0.90). Seals in the core region were generally larger with older age of sexual maturity (Table 1).

To assess seasonal variation, we fit a sine wave to the monthly samples of seals for three age classes (YOY, juveniles, and adults) and compared core and peripheral regions. For both regions, the model was not significant for YOY (Table 3). The lack of a fit for YOY was not surprising as we predicted the seals would grow over their first year of life and add fat throughout the year (i.e. limited cycle); whereas juveniles and adults would show a seasonal cycle. In the peripheral region, amplitude was significantly greater compared to the core region for all three age classes (Supplementary material Appendix 1 Fig. A1). The peripheral seals also differed in the seasonal period when fat accumulated with the summer open-water season (April to September) resulting in large blubber deposits whereas in the core region, an increase in seal blubber depth started and ended later (June–October; Fig. 3b). Next, we compared the two regions separately to assess how blubber depth varied interannually with environmental variables while controlling for sex and age class.

Interannual variation of seal blubber depth differed significantly between the two regions while controlling for body length with peripheral seals being in better condition (greater depth; $F_{2,2761} = 67.15$; $p < 0.001$; Tukey HSD between stocks $p < 0.001$) although biologically, the differences were small (core 4.20 ± 0.039 cm versus peripheral 4.28 ± 0.036). To test for temporal patterns, we ran models separately for the two regions. Autocorrelation was significant with a 1-yr lag (Durban Watson = 1.563, $p < 0.001$). Therefore, we used 1-yr lagged covariates for timing of spring breakup and open-water duration since seals were collected during all seasons of the year. For NAO, we used the values generated from December to March to compare with the same year seals were collected.

Our aim was to assess differences in interannual variation between the regions while controlling for confounding biological variables using the information-theoretic approach. First, we removed correlated variables in order of greatest VIF, re-ran the GLM model, and continued the process until VIF for all variables indicated appropriate model performance. The best interaction term was age class × lag spring breakup; however with a VIF = 8.8. The model performed better (lower AICc) using the two variables, age and lag spring breakup separately. All environmental variables had high VIF and although lag spring and lag open water were correlated, they were both kept as their biological significance to body condition likely differed and VIF was minimal (5.9). For the core region, the final subset of variables, once correlated variables were removed, included age class, month (season), NAO, lag spring, and lag open water duration (Table 4; Supplementary material Appendix 1 Table A1). For the top models, seal blubber depths varied with age class (older seals had greater fat), month (nonlinear), NAO (more positive NAO resulted in greater fat; Fig. 4c), spring breakup in the previous year and duration of open-water during the previous year (Table 5). Blubber depth decreased with later spring breakup or shorter open-water duration the previous year (Fig. 4a–b).

For the peripheral region, all environmental variables and interaction terms had high VIF and although lag spring and lag open were correlated (VIF 4.4), we kept both variables since their correlation was lower than the other environmental variables (VIFs > 8.0). The final subset of variables included age class, year, month, NAO, lag spring, and lag open water duration (Table 4). For the top model, the final subset of variables indicated that seal blubber depth varied with age class, year, month, NAO, lag open-water duration, and lag spring breakup (Supplementary material Appendix 1 Table A1). For the peripheral region, condition decreased over years (2003–2016) and increased over months with poorer condition in winter and better condition in autumn, Table 5. More positive NAO resulted in greater blubber depth similar as for

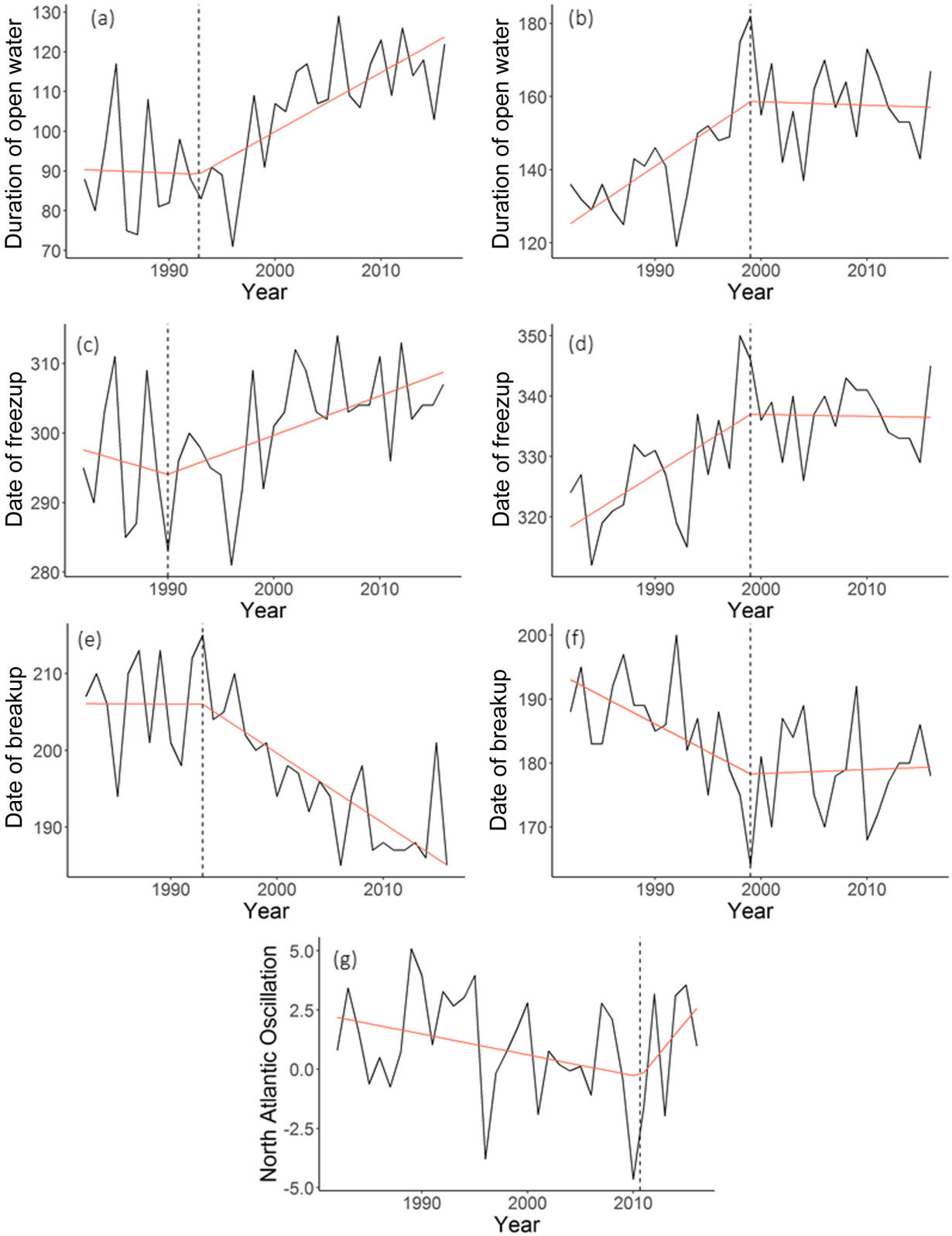


Figure 2. Environmental shifts demarcated using broken stick regression of duration of open water (a, b), timing of sea-ice freeze-up (c, d), breakup (e, f), and North Atlantic Oscillation (g) compared for the core (left column) and peripheral (right) regions as defined according to ringed seal geographic range in Arctic Canada, 1980–2016.

Table 3. Summary sine wave statistics for the seasonal changes in body condition (blubber depth) for three age classes (YOY, juveniles, and adults) of ringed seals. Seal measurements were taken from core and peripheral regions of the Canadian Arctic, 1980–2016. Note significant fit of model (i.e. strong seasonal cycle) to peripheral population for all age classes relative to core region.

| Age class | GLM results | Feature | n | Core | n | Peripheral |
|---|---|---|---|---|---|---|
| YOY | | 25–75th quantiles | 210 | 3.0–4.6 | 588 | **2.9–4.8** |
| | | Median, mean | | 3.8, 3.89 | | **3.8, 3.82** |
| Core | $F_{2,176}=0.785$, $p=0.46$ | Amplitude | | 0.175 | | **0.719**[a] |
| | | Phase | | 0.446 | | **−2.64**[b] |
| Peripheral | $F_{2,569}=33.7$, $p<0.001$ | Peak | | not. sig. | | **August–September** |
| | | Trough | | | | **January–February** |
| Juveniles | | 25–75th quantiles | 395 | 3.2–4.5 | 564 | **3.5–5.1** |
| | | Median, mean | | 4.0, 4.01 | | **4.0, 4.27** |
| Core | $F_{2,357}=3.12$, $p=0.045$ | Amplitude | | 0.202 | | **0.721** |
| | | Phase | | **2.491** | | **−2.822** |
| Peripheral | $F_{2,551}=35.66$, $p<0.001$ | Peak | | **November–December** | | **August–September** |
| | | Trough | | **April–May** | | **February–March** |
| Adults | | 25–75th quantiles | 415 | 3.8–5.1 | 752 | **3.0–6.0** |
| | | Median, mean | | 4.5, 4.54 | | **4.5, 4.64** |
| Core | $F_{2,569}=33.72$, $p<0.001$ | Amplitude | | 0.329 | | **1.432** |
| | | Phase | | **2.832** | | **−2.751** |
| Peripheral | $F_{2,728}=217.4$, $p<0.001$ | Peak | | **September–October** | | **August–September** |
| | | Trough | | **March–April** | | **February–March** |

[a]Bold indicates significant amplitude coefficients from general linear model (GLM; $p<0.05$).
[b]A negative phase is a shift is to the right of the typical position with the curve rising from 0 amplitude (January) to its peak (spring). Therefore, a negative shift indicates a later peak in blubber depth in the peripheral region and the positive value for the core region indicates an earlier seasonal peak. The seal blubber depth from core region shifts to the right due to a later peak in condition; whereas the peripheral seals shift to the left indicating an earlier peak in condition.

the core region (Fig. 4c). The length of open-water season the previous year affected body condition, with greater blubber depth following a shorter season (Fig. 4b). Similarly, later spring breakup the previous year resulted in greater blubber depth; the opposite of the core region (Fig. 4a).

## Discussion

Our results are the first to reveal significant differences in seasonal and long-term variability in body condition when comparing peripheral regions to core regions of a marine mammal's geographic range. Here, seals living at the southern extremity of their geographic range displayed remarkable variability in body condition between spring and fall with a 3× greater amplitude relative to core seals. Ringed seals near the periphery also exhibited stronger year-to-year variation. Differing responses to temporal patterns, both seasonal and decadal, have likely emerged due to the evolved limits of the species' plasticity in life history and habitat suitability (Piersma and Drent 2003). Ringed seals evolved to inhabit regions of the Arctic with consistent landfast ice for breeding and a more-or-less predictable pattern of an annual sea ice (Smith and Hammill 1981, Smith and Lydersen 1991, Kelly et al. 2010, Brown et al. 2014). They are less adapted and therefore less numerous in areas with greater multi-year ice at northern latitudes, areas with ice over deep water such as the Arctic basin, and sub-Arctic areas with unpredictable availability of late winter-spring annual ice for breeding and moulting such as the Gulf of St Lawrence (Stirling and Øritsland 1995). In addition to body condition, seals inhabiting the southern peripheral range with poorer quality environments would likely display greater temporal variability in demographic characteristics (Croxall 1992, Ferguson et al. 2017). Not considered here, are the seals located at the northern periphery of their geographic range. Future research is needed to assess whether they show similar body condition variation as seals in the southern periphery and what environmental conditions drive temporal variability.

We observed geographic variability in decadal climatic patterns between the Central Arctic Archipelago and Hudson Bay ecosystems. Hudson Bay represents the southern extremity of Canadian geographic range of ringed seals. Here, we found support for an environmental regime shift occurring around 1999. Many biological parameters, including available forage fish and the abundance and growth of marine birds, also shifted at this time (Gilchrist and Robertson 2000, Gaston et al. 2003, 2012). Our trend analysis of environmental variables indicated a strong warming pattern prior to 1999. Following this decisive shift, the region has demonstrated no warming trend. Still, the 2000 to 2016 body conditions trend was negative suggesting an overall decline in ringed seal body fat over this period. Since the 2000s, there has been considerable year-to-year variation coincident with sea-ice loss (Gough et al. 2004, Tivy et al. 2011) and associated biological changes (Regehr et al. 2007, Gaston et al. 2012). In contrast, the core ringed seal region occurs at higher latitudes within the Canadian Arctic Archipelago, a series of islands separated by a complex set of channels over a continental shelf that includes polynyas of high biological

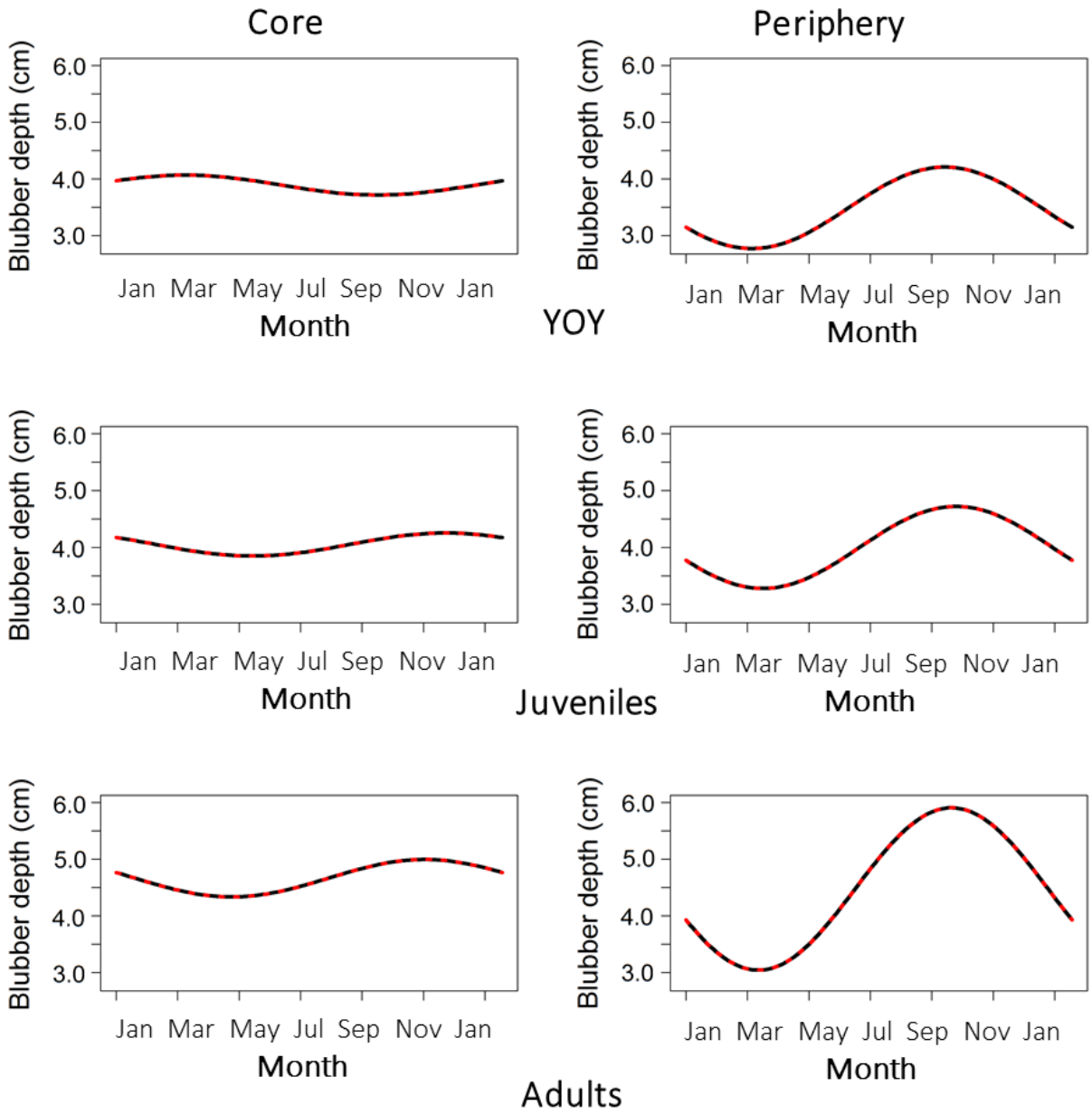


Figure 3. Modeled sine wave of ringed seal blubber depth over months of a year representing seasons compared by age class (YOY, juveniles and adults) for seals sampled from core (left) or peripheral (right) regions of their geographic range in Canada. See Supplementary material Appendix 1 Fig. A1 for results with mean ± SE by month.

productivity (Stirling 1997, Hannah et al. 2009). Here in the core region, the trend is towards a decrease in sea-ice condition since the early 1990s following the cooling from the eruption of Mount Pinatubo in 1991 (Soden et al. 2002). In support of this pattern, Tivy et al. (2011) estimated contrasting summer sea-ice changes with cover having decreased by 11.3% ± 2.6% in Hudson Bay versus 2.9% ± 1.2% in the Canadian Arctic Archipelago, 1968–2008. This dichotomous pattern with two adjacent regions is likely due to the geographic landscape and spatial pattern of landfast sea ice. Hudson Bay is a large inland sea with relatively flat topography, much pack ice and small amounts of landfast ice (Ferguson et al. 2010). In contrast, the Canadian Arctic Archipelago has a multitude of islands, fiords, inlets, and inter-island channels with acute topography, spatial variation, and considerable landfast ice (Melling 2002).

Ringed seals in the core and peripheral regions experienced very different patterns of temporal variation in body condition in response to environmental variation. However, blubber depths for ringed seals from both regions were related to climatic and sea-ice covariates. For the core region, both timing of spring sea-ice breakup and duration of open water were significant covariates while open water was important in the peripheral region. With climate warming, we would predict

Table 4. Summary of model selection of most parsimonious general linear model (Eq. 1) results for core and peripheral ringed seal populations of the Canadian Arctic. The top four ranked models are shown (see Table 5 for model statistical information). Included here in the table are number of estimated parameters (df), log-likelihood, Akaike's information criterion corrected for small sample sizes (AICc) values, ΔAICc (Delta), and AICc weights (Weight) for each model (see Supplementary material Appendix 1 Table A1 for complete results). Ringed seal blubber depth variation explained by age groups (age), years (year), season (month), and environmental variables: unlagged and lagged spring breakup date, open-water duration, fall freeze-up date, and interactions with age.

| Models | df | Log-likelihood | AICc | Delta | Weight |
|---|---|---|---|---|---|
| Core | | | | | |
| Int + age + seas + NAO + lag(spring) | 6 | −1414 | 2841 | 0.00 | 0.576 |
| Int + age + seas + NAO + lag(open) + lag(spring) | 7 | −1414 | 2842 | 1.75 | 0.240 |
| Int + age + seas + NAO + lag(open) | 6 | −1416 | 2845 | 3.96 | 0.079 |
| Int + age + NAO + lag(spring) | 5 | −1418 | 2845 | 4.62 | 0.057 |
| Peripheral: | | | | | |
| Int + age + seas + year + NAO + lag(spring) + lag(open) | 8 | −3246 | 6508 | 0.00 | 0.783 |
| Int + age + year + seas + NAO + lag(open) | 7 | −3249 | 6512 | 3.50 | 0.136 |
| Int + age + seas + NAO + lag(spring) + lag(open) | 7 | −3250 | 6514 | 5.07 | 0.062 |
| Int + age + seas + NAO + lag(open) | 6 | −3253 | 6517 | 8.67 | 0.010 |

a shifting spatial pattern along the ringed seal geographic range. For example, high latitude environments within coastal shelf areas would likely, at least initially, become more suitable for ringed seal habitat as multiyear ice is replaced by annual landfast ice and moving annual ice (Stirling and Derocher 2012).

As an alternative explanation for the observed differences in ecological pattern between core and peripheral habitat,

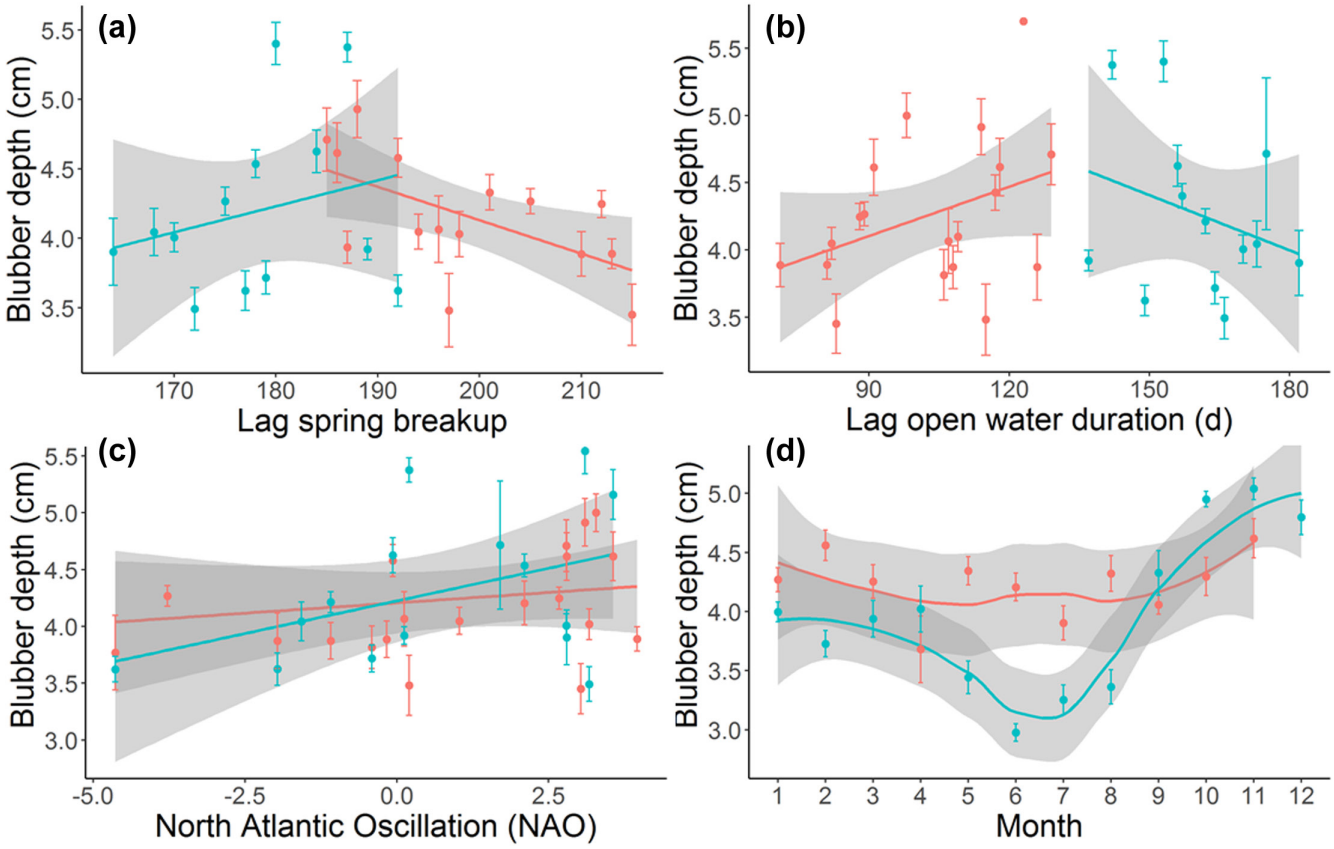


Figure 4. Graphical results describing ringed seal body condition (blubber depth) as explained by environmental covariates measured from core (red) and peripheral (green) regions of geographic distribution in the Canadian Arctic (Table 5). (a) Blubber depth versus timing of spring breakup the previous year. Note for the core region, poorer seal condition following a year with late spring breakup. (b) Blubber depth versus open-water duration the previous year. Note for peripheral region, poorer seal condition following a year with extensive open-water season. (c) Blubber depth and North Atlantic Oscillation (NAO: December–March) showing better seal condition with more positive NAO climatic signal. (d) Blubber depth by month for core and peripheral seal populations showing a strong seasonal cycle in peripheral region relative to core region.

Table 5. Best general linear model (gamma distribution, log-linked) parameters and standard errors estimated using information theory for core and peripheral ringed seal populations of the Canadian Arctic: ringed seal blubber depth was the dependent variable and variation was explained by biological (age class, sex, year, month) and environmental covariates (lagged and unlagged spring breakup date, autumn freeze-up date, duration of open water, North Atlantic Oscillation).

| Population parameter | Standardized coefficient (B) | Std. error | Z value | p-value |
|---|---|---|---|---|
| Core | | | | |
| Intercept | 2.436 | 0.6046 | 4.028 | < 0.001 |
| Age category | 0.0920 | 0.01269 | 7.028 | < 0.001 |
| Season | −0.0285 | 0.01173 | −2.433 | 0.015 |
| North Atlantic Oscillation | 0.0138 | 0.003829 | 3.602 | < 0.001 |
| Lag spring breakup | −0.004953 | 0.002352 | −2.106 | 0.035 |
| Peripheral | | | | |
| Intercept | 59.8 | 20.5 | 3.917 | 0.004 |
| Age category | 0.3757 | 0.04065 | 9.242 | < 0.001 |
| Year | −0.02338 | 0.01012 | −2.311 | 0.021 |
| Season | 0.1256 | 0.009733 | 12.90 | < 0.001 |
| North Atlantic Oscillation | 0.08833 | 0.02062 | 4.283 | < 0.001 |
| Lag open-water duration | −0.02793 | 0.008215 | −3.399 | < 0.001 |
| Lag spring breakup | −0.03136 | 0.01394 | −2.249 | 0.025 |

perhaps ringed seals are best adapted to the southern range areas (versus core) and have evolved the means to accommodate highly seasonal food availability through cyclic body fat stores. According to this alternative hypothesis, ringed seals would have evolved demographic means to accommodate this environmental variability (McNab 1980, Conover 1992) and adapt by means of higher densities than found at higher latitudes (Kingsley et al. 1985). Body growth is faster in Hudson Bay (Ferguson et al. 2018) and perhaps their life history is well matched to an environment with more food availability and high seasonal accessibility (Stirling 2005). However, mammals tend to have evolved the means to ameliorate environmental variation, such as seasonal cycles, in order to provide consistency and predictability in life-history processes (Bruno et al. 2003). Thus, we would expect high variability in ringed seal life history to indicate a lack of adaptability and a sign of possible demographic concern. In addition, we would hypothesize that the core population would display more density-dependent responses to environmental change in contrast to more dramatic density fluctuations in the peripheral population representing density independent or extreme responses to environmental fluctuations. Data is not currently available for the core region but our hypothesis fits the description of density responses found in the peripheral Hudson Bay population (Ferguson et al. 2017).

The proximate explanation for variability in body condition would be food availability. Although the assumption of highly seasonal food resources has been made for the Hudson Bay region (Parks et al. 2006, Mallory et al. 2010, Ferguson et al. 2017) the casual linkages have not been thoroughly explored. For example, few forage fish abundance estimates exist for either region (Hoover 2010), largely because the fisheries have been deemed economically inviable. Instead, authors have speculated that the accessibility of quality food varies seasonally (Roth 2003, Chambellant et al. 2013) and interannually (Ferguson et al. 2005, Young and Ferguson 2014), largely as a result of sea-ice conditions. For example, adult ringed seals focus on polygynous reproductive activities over the winter by setting up mating territories, giving birth in subnivean dens, nursing, and mating (Yurkowski et al. 2011, Young and Ferguson 2013, Luque et al. 2014). During this reproductive period, adult seals lose body mass through fat loss which is likely due to selecting mating habitat over feeding habitat (Smith et al. 1991, Luque et al. 2014). Juvenile seals are not encumbered by the mating and reproductive cycle, and therefore can choose areas with greater food availability such as polynyas and floe edges which may explain why juveniles display a smaller seasonal cycle of fat mobilization and depletion relative to adults (Fig. 3).

Ringed seals are an important food for circumpolar Inuit (Furgal et al. 2002) and community-based collections that sample from these hunts have been successful in providing long-term information (Ferguson et al. 2012, Harwood et al. 2012). Studies on ringed seal seasonal and long-term variation in body condition are limited due to the logistical challenges associated with collecting large numbers of morphological measures and tissue samples (Harwood et al. 2000, Ferguson et al. 2005, Rosing-Asvid 2006). For example, very few studies have been able to collect samples from different months of the year to assess seasonal variation in body condition (Ryg et al. 1990, Young and Ferguson 2013). Other biological measures could be used to assess the predictions of greater variability associated with populations occupying peripheral range with suboptimal habitat. Movement studies, although challenging, have provided evidence of seasonal dive behavior (Gjertz et al. 2000, Crawford et al. 2019) and could be used to compare regions (Yurkowski et al. 2016b, Ferguson et al. 2019). In addition, analysis of seal tissues for dietary biomarkers (e.g. stable isotopes and fatty acids) can be used to test seasonal cycles and long-term variability in feeding habits (Lowry et al. 1980, Dehn et al. 2007, Thiemann et al. 2007, Young and Ferguson 2013, Yurkowski et al. 2016a). Results using foraging biomarkers have alluded to prey availability, such as forage fish versus zooplankton as key food items, driving latitudinal foraging variation (Yurkowski et al. 2016a, c). Ultimately, uncovering demographic responses

of seal populations living in peripheral regions that indicate increased mortality and decreased reproduction are required to complete a mechanistic model linking ringed seal demography to sea-ice habitat (Eberhardt 2002).

Our data cover an expansive temporal scale that accommodates modeling body condition variation over seasons and years. However, relative to the core area, the temporal scale for the southern peripheral region was shorter (16 versus 35 yr) and had greater sampling intesity (1968 versus 1044), making the comparison somewhat unbalanced. Seals were sampled throughout the year and therefore we made comparisons to the previous years' environmental data which did not allow testing for the effects of the current years' environmental conditions. Measuring blubber depth can be challenging and the hunters taking measurements changed over time, which could affect measurement accuracy. However, we did conduct extensive statistical testing for and removal of outliers (Ferguson et al. 2018) and inaccuracies in measurements would likely contribute to spurious variation that would reduce power to detect differences rather than result in directional bias (Gordon and Bradtmiller 1992). Other morphological measurements of body condition for ringed seals exist, each with their advantages and disadvantages. In addition to blubber depth (Ryg et al. 1990), researchers have used sculp weight (skin plus subdermal fat; Hammill et al. 1991), body girth (Usher and Church 1969), and other morphological measures (McLaren 1958). Physiological measures of body condition have also been used including blood chemistry (Geraci et al. 1979) and fatty acids (Young and Ferguson 2013). Future research on ringed seals should compare and assess the various indices to better evaluate strengths and weaknesses. It is not uncommon to observe a lag effect in body condition of mammals (Loison and Langyatn 1998, Wells et al. 2016). NAO has been implicated as a major climatic index in the Arctic (Møller 2002, Post and Forchhammer 2002) and although both ringed seal populations increased body condition with positive values, the peripheral region appeared to show a stronger relationship. For successful management of populations, we need quantitative measures of annual variation in a limiting resource (e.g. food) combined with measures of population density to assess the demographic processes such as productivity and survival to consider density-independent processes (Sinclair and Krebs 2002).

Most species are, or soon will be, affected by climate warming with consequent shifts in geographic distribution to accommodate shifting local abiotic conditions (Anderson et al. 2009, Pecl et al. 2017). The logical outcome of this transition is higher mortality of seals at the southern limits of their geographic range and possible range expansion poleward through improved demography at the northern extent. Knowledge of the drivers of distributional changes is required to manage and mitigate potential population declines. Here, we demonstrate that the location of populations within a species' geographic range provides important information necessary to predict response to climate change (Rebelo et al. 2010). While core populations will take longer to express demographic effects, peripheral populations will show extremes in body condition seasonal cycles that likely forecast reproductive difficulties and ultimately mortality. Managers can focus on understanding the limitations in phenotypic plasticity for a species and study seasonal cycles in body condition to provide early warning signs. Mitigation may reduce the severity of condition responses and avoid catastrophic results; however, changes in species' range distribution may be inevitable.

### Data availability statement

Data is available in Open Access web site Government of Canada.

*Acknowledgements* – We thank the Inuit hunters and the Hunters and Trappers Associations of Nunavut and Nunavik, Canada, for conducting community-based seal collections. We thank the anonymous reviewer and editors who provided substantive comments that assisted with improving our manuscript.
*Funding* – Funding received from Nunavut General Monitoring Plan, Nunavut Wildlife Management Board, Fisheries and Oceans Canada, Environment and Climate Change Canada, Northern Contaminants Program (Crown-Indigenous Relations and Northern Affairs Canada), ArcticNet Centre of Excellence, Natural Sciences and Engineering Research Council of Canada Discovery Grants, W. Garfield Weston Foundation, and the Molson Foundation.

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Supplementary material (available online as Appendix ecog-04988 at <www.ecography.org/appendix/ecog-04988>). Appendix 1.

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