# Long-term, Harvest-based Monitoring of Ringed Seal Body Condition and Reproduction in Canada's Western Arctic: An Update through 2019

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ABSTRACT. The circumpolar Arctic ringed seal (*Pusa hispida*) occupies its fast-ice breeding habitat for four to five months during winter and the pack ice or open water of adjacent areas for the rest of the year. From 1971–78 and 1992–2019, we sampled approximately 100 ringed seals annually from western Prince Albert Sound (WPAS), the prime ringed seal fast-ice breeding habitat in Canada's Western Arctic, adjacent to primary overwinter foraging habitat in eastern Amundsen Gulf (EAG). As our metric of body condition, we measured ventral blubber depth corrected for body size. As our metrics of reproduction, we measured the annual ovulation rate of multiparous females and percent pups in the open-water harvest. We examined these biological parameters in relation to the winter Arctic Oscillation Index (winAOI) and the timing of sea ice clearance in EAG in spring. There were no significant effects of age or sample month (June or July) on adult blubber depth, but significant sex and year effects and, in females, ovulation status effects. Across the series, as we have observed previously through 2011, there was a sustained temporal declining trend in blubber depth in adults of both sexes. There was no temporal trend in residual blubber depth, no correlation between blubber depth and sea ice clearance date in EAG, and a quasi-cyclic pattern in blubber depth that tracked some of the phases of the winAOI. Annual ovulation rates were mainly in the 80%–100% range and correlated with percent pups in the open-water harvest in the same year. Three (1974, 2005, 2012) of the 36 y had reproductive failures, when $\geq 50\%$ of the multiparous females failed to ovulate. In each case, ovulation rates returned to normal within 1–3 y. Low annual ovulation rates were correlated with late sea ice clearance in EAG in spring, with two ovulation failure events taking place in years when spring sea ice clearance was delayed by five to six weeks. The most recent ovulation failure (2012) differed in that it came in an average ice year but at the end of a six-year sequence of negative residual mean blubber depths. Earlier spring sea ice clearance in WPAS, based on the observed rate of 3.8 d per decade, would on average not result in the physical loss of sea ice for pupping in this core habitat before 2140. The mechanisms involved in the sustained declining temporal trend in body condition, linkage with some phases of the winAOI, and the temporary but episodic failures of ovulation are complex and not fully explained by either the timing of sea ice clearance or the winAOI. Until the complex mix of factors, pressures and responses are understood, our ability to predict the impacts of a changing climate on ringed seals will remain limited.

Key words: ringed seal; sea ice; ovulation; ovulation failure; body condition; blubber depth; percent pups; Amundsen Gulf; Prince Albert Sound; sea ice clearance date; winter Arctic Oscillation Index

RÉSUMÉ. Le phoque annelé de l'Arctique circumpolaire (*Pusa hispida*) occupe son habitat de reproduction sur glace rapide pendant quatre à cinq mois de l'hiver, et la banquise ou les eaux libres adjacentes pendant le reste de l'année. Entre 1971 et 1978 puis entre 1992 et 2019, nous avons échantillonné environ 100 phoques annelés par année dans l'ouest du détroit de Prince-Albert, le principal habitat de reproduction sur glace rapide du phoque annelé dans l'ouest de l'Arctique canadien, adjacent au principal habitat d'alimentation hivernal de l'est du golfe Amundsen. Comme paramètre de mesure de la condition corporelle, nous avons mesuré l'épaisseur du lard ventral du phoque, pour laquelle nous avons appliqué une correction en fonction de la taille du corps. Comme paramètre de reproduction, nous avons mesuré le taux annuel d'ovulation des femelles multipares et le pourcentage de veaux récoltés en eaux libres. Nous avons examiné ces paramètres biologiques par rapport à l'indice d'oscillation arctique hivernal et par rapport au moment du dégagement des glaces de mer dans l'est du golfe Amundsen au printemps. Nous n'avons pas remarqué d'effets importants en ce qui a trait à l'âge ou au mois d'échantillonnage (juin ou juillet)

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sur l'épaisseur du lard de l'adulte, mais nous avons constaté des effets importants en ce qui a trait au sexe et à l'année, et, chez les femelles, des effets en matière d'ovulation. Entre les séries, comme nous l'avions déjà observé jusqu'en 2011, il y avait une importante tendance temporelle à la baisse sur le plan de l'épaisseur du lard chez les adultes des deux sexes. Il n'y avait pas de tendance temporelle du point de vue de l'épaisseur résiduelle du lard, aucune corrélation entre l'épaisseur du lard et la date du dégagement des glaces de mer dans l'est du golfe Amundsen, et un modèle quasi cyclique du point de vue de l'épaisseur du lard par rapport à certaines phases de l'indice d'oscillation arctique hivernal. Les taux d'ovulation annuels se situaient principalement dans la gamme du 80 % à 100 %, en corrélation avec le pourcentage de veaux de la récolte en eaux libres pendant la même année. Trois des 36 années (1974, 2005, 2012) ont enregistré des échecs de reproduction, lorsque 50 % des femelles multipares n'ont pas ovulé. Dans chaque cas, les taux d'ovulation sont retournés à la normale en un à trois ans. Les faibles taux d'ovulation annuels ont été corrélés avec le dégagement tardif des glaces de mer dans l'est du golfe Amundsen au printemps, deux des grands échecs d'ovulation ayant eu lieu pendant les années où le dégagement printanier des glaces de mer a été retardé de cinq à six semaines. L'échec d'ovulation le plus récent (2012) était différent en ce sens qu'il s'est produit pendant une année moyenne de dégagement des glaces, mais à la fin d'une séquence de six ans d'épaisseurs moyennes résiduelles négatives du lard. Dans le détroit de Prince-Albert, le dégagement plus hâtif des glaces de mer au printemps, d'après un taux observé de 3,8 jours par décennie, ne se traduirait pas, en moyenne, par la perte physique de glaces de mer pour la mise bas des veaux dans cet habitat important avant 2140. Les mécanismes liés à la tendance temporelle soutenue à la baisse de la condition corporelle, le lien avec certaines phases de l'indice d'oscillation arctique hivernal, et les échecs d'ovulation temporaires, mais épisodiques sont complexes et ne s'expliquent pas entièrement par le moment du dégagement des glaces de mer ou par l'indice d'oscillation arctique hivernal. Tant que le mélange complexe de facteurs, de pressions et de réponses ne sera pas compris, notre capacité à prévoir les incidences du changement climatique sur le phoque annelé sera restreinte.

Mots clés : phoque annelé; glace de mer; ovulation; échec d'ovulation; condition corporelle; épaisseur du lard; pourcentage de veaux; golfe Amundsen; détroit de Prince-Albert; date du dégagement des glaces de mer; indice d'oscillation arctique hivernal

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## INTRODUCTION

The ringed seal (*Pusa hispida*) is the most abundant and widespread marine mammal in the circumpolar Arctic. Its distribution, survival, and reproductive success are closely linked to the extent, persistence, and characteristics of sea ice (Smith, 1987; Smith and Stirling, 1978; Stirling 2002; Laidre et al., 2008). The ice provides a substrate for pupping, nursing, and haul-out, while the snow cover over the birth lair provides protection from weather and predators (Smith and Stirling, 1975, 1978; Stirling et al., 1982; Smith, 1987; Kelly and Quakenbush, 1990).

Ringed seals are tractable links to oceanography, productivity, and sea ice through their responses in body condition and reproduction to environmental variation (Smith and Stirling, 1978; Smith, 1987; Stirling, 2002; Arrigo et al., 2008; Chambellant et al., 2012; Harwood et al., 2012a; Moore et al., 2014; Hamilton et al., 2015; Ferguson et al., 2017). Fast-ice breeding habitats that are stable through the winter and spring until breakup, in combination with sufficient winter prey and adequate snow cover for construction of birth lairs, are key requirements for ringed seal breeding success (Smith and Stirling, 1978; Smith, 1987).

As ringed seals are long-lived and wide-ranging predators, trends in their reproduction and body condition can facilitate detection and interpretation of changes in the food web, sea ice, and ecosystem structure (Tynan and DeMaster, 1997; Laidre et al., 2008, 2015; Moore, 2008; Kovacs et al., 2011; Moore et al., 2014; Frey et al., 2015). For example, long-term, multiyear declines in body condition might indicate seals are experiencing fluctuations in their prey base, which

eventually translates to reduced reproduction and survival (Noren et al., 2015) and potentially increased susceptibility to disease agents (Beldomenico and Begon, 2010; Moore and Gulland, 2014). In this paper, we present data to examine years prior to and during the ~2007 emergence of significant environmental changes in the Pacific sector of the Arctic (Jeffries et al., 2013; Frey et al., 2015; Moore and Stabeno, 2015; Wood et al., 2015).

The suitability and productivity of seal habitats vary across regions and latitudes, reflecting differing environmental conditions dependent upon regional circumstances (Hamilton et al., 2015, 2017, 2018; Yurkowski et al., 2016a, b). These relationships are complex, and there is considerable regional variation in observed responses (e.g., Ferguson et al., 2005, 2017; Crawford et al., 2012; Harwood et al., 2012a; Hamilton et al., 2015, 2017, 2018; Yurkowski et al., 2016a, b). The large bays of Amundsen Gulf, which are covered with stable annual ice through the winter, are particularly important to breeding ringed seals in the western Canadian Arctic (Smith, 1987). The stable fast ice in western Prince Albert Sound (WPAS) is particularly critical for the establishment, maintenance, and quality of lairs and territories during winter and spring (Smith, 1987), as it provides a substrate for pupping, nursing, and haul-out, while the snow cover over the birth lair provides protection from weather and predators (Smith and Stirling, 1975, 1978; Stirling et al., 1982; Smith, 1987). Eastern Amundsen Gulf (EAG) also provides winter and breeding habitat as well as serving as an important wintertime foraging area for seals that move between EAG and WPAS when ice conditions allow (Harwood et al., 2015; Halliday et al., 2019).

Blubber, a layer of lipid-rich tissue between the epidermis and the underlying musculature, serves many functions in marine mammals including insulation and thermoregulation, storage of metabolic energy, and buoyancy and streamlining (Scholander et al., 1950; Pond, 1978; Ryg et al., 1988). The level of fat reserves, which in marine mammals are stored principally in blubber, is an important indicator of body condition (Ryg et al., 1990; Beck et al., 1993). Body condition in seals has been assessed using various indices of fat stores including body weight, sculp weight (weight of blubber layer, skin, and fur), axillary girth, and blubber depth (Beck et al., 1993).

Our objective is to track ringed seal reproduction and body condition over time, using a long-term, standardized, and harvest-based sampling approach, designed to control for location, season, and method. The present paper is an update from previous publications 1971–78 (Smith, 1987) and 1992–2011 (Harwood et al., 2000, 2012b), and incorporates data from these publications and new data through 2019.

We used blubber depth as our metric of body condition in adult ringed seals. The reproduction parameters monitored were ovulation rate of multiparous females and the proportion of pups in the open-water harvest. These two parameters were selected because (1) they have previously exhibited significant changes over time in seals in this area and the adjacent Beaufort Sea (Stirling et al., 1977; Smith, 1987; Kingsley and Byers, 1998) in response to environmental fluctuations, and (2) it is practical to reliably obtain adequate, long-term and consistent sample sizes over time because of the location and timing of the harvest from which we obtain our samples.

The Arctic is influenced by natural climatic oscillations that can alter the marine ecosystem and sea ice (Rigor et al., 2002), coincidentally with climate warming (Moore and Stabeno, 2015). Thus, our challenge is to measure, interpret, and unravel the responses of biota to these coincident influences. Here we explore and evaluate linkages in our biological variables with two explanatory environmental variables, sea ice clearance date and the winter Arctic Oscillation Index (winAOI). These variables were selected because (1) each reflects a suite of environmental variables and influences, and (2) the timing and location of their influence are relevant to the time and areas where we obtain our annual seal sample, which follows the winter period when seals are "confined" to their breeding territories (Smith, 1987; Harwood et al., 2007; Kelly et al., 2010). Linkages of these variables with seal body condition have been demonstrated previously in this and in other regions (Ferguson et al., 2017; Nguyen et al., 2017).

## METHODS

### Seal Sampling

Ringed seal specimens harvested by subsistence hunters from the Inuvialuit community of Ulukhaktok, Northwest Territories (70° 45′ 46″ N, 117° 48′ 22″ W) were obtained from the Masoyak area (Fig. 1), a traditional hunting camp located on the northwest shore of WPAS, adjacent to EAG from 1992 through 2019. All field methods for sampling and measuring seals and subsequent age determination (Smith, 1973) and laboratory analyses are as previously described in Smith (1987) for 1971–78 and Harwood et al. (2000, 2012b) for 1992–2011. Reliance on the same methods and samplers, and regular communication with the project authority before and during the season have facilitated optimal internal and across-year consistency in our season-specific, single-site data collection. The harvested seals remained the property of the harvester for his or her subsistence use, following sampling and measuring.

Each year a sample of approximately 100 harvested seals was obtained, with the following information collected from each seal: sex, date, and location of kill. Seals were laid on their backs on a smooth, flat surface to measure standard length (nose to tail) (± 1.25 cm) with a steel tape measure (Committee on Marine Mammals (1966–67), American Society of Mammalogists, 1967). Blubber depth (± 0.5 cm) was measured using a plastic ruler on the ventral line at the sternum and at the hip (60% of distance from nose to tail). The monitor worked for 10 weeks per year during the peak of the seal hunting activity, mainly in the months of June and July, to sample approximately 10 seals per week (from his own and nearest neighbours' catch) and to choose those 10 seals non-selectively (i.e., without preference for size, sex, or relative age).

The seal monitor also recorded ice conditions and travel mode used for each day's hunting as either "from the ice" (travel to and within the local hunting area by snow machine) or "from the open-water" (travel to and within the local hunting area by 18-foot open boat). There was usually a break of about a week between the ice and open-water hunting periods, when it was not practical to hunt from either snow machine or boat. We used this hunter-identified break in the collection period as our reference point for the start of open-water sampling. Only seals taken during open-water hunts were used for the percent pup calculation because that is when seals of all age and sex classes in the area are most evenly mixed and thus similarly available to be sampled non-selectively in the hunting area (Smith, 1987).

The mandible was removed from as many of the sampled seals as possible, and the entire reproductive tract was removed from as many of the females as possible (Smith, 1973). These specimens were labeled and preserved on site in 10% buffered formalin. In the laboratory, the lower jaws were boiled and lower canines extracted (Smith, 1973). One canine tooth was cut in cross-section so that age could be determined by reading the dentinal annuli under transmitted light. Independent readings of each tooth were done twice by the same reader; a third reading was done by the same reader if the first two did not agree. The determination of age was based on counts of the dentinal layers, a consideration of the clarity of the dentinal lines, the closure of the pulp cavity, and the number of layers in the cementum, if it was readable.
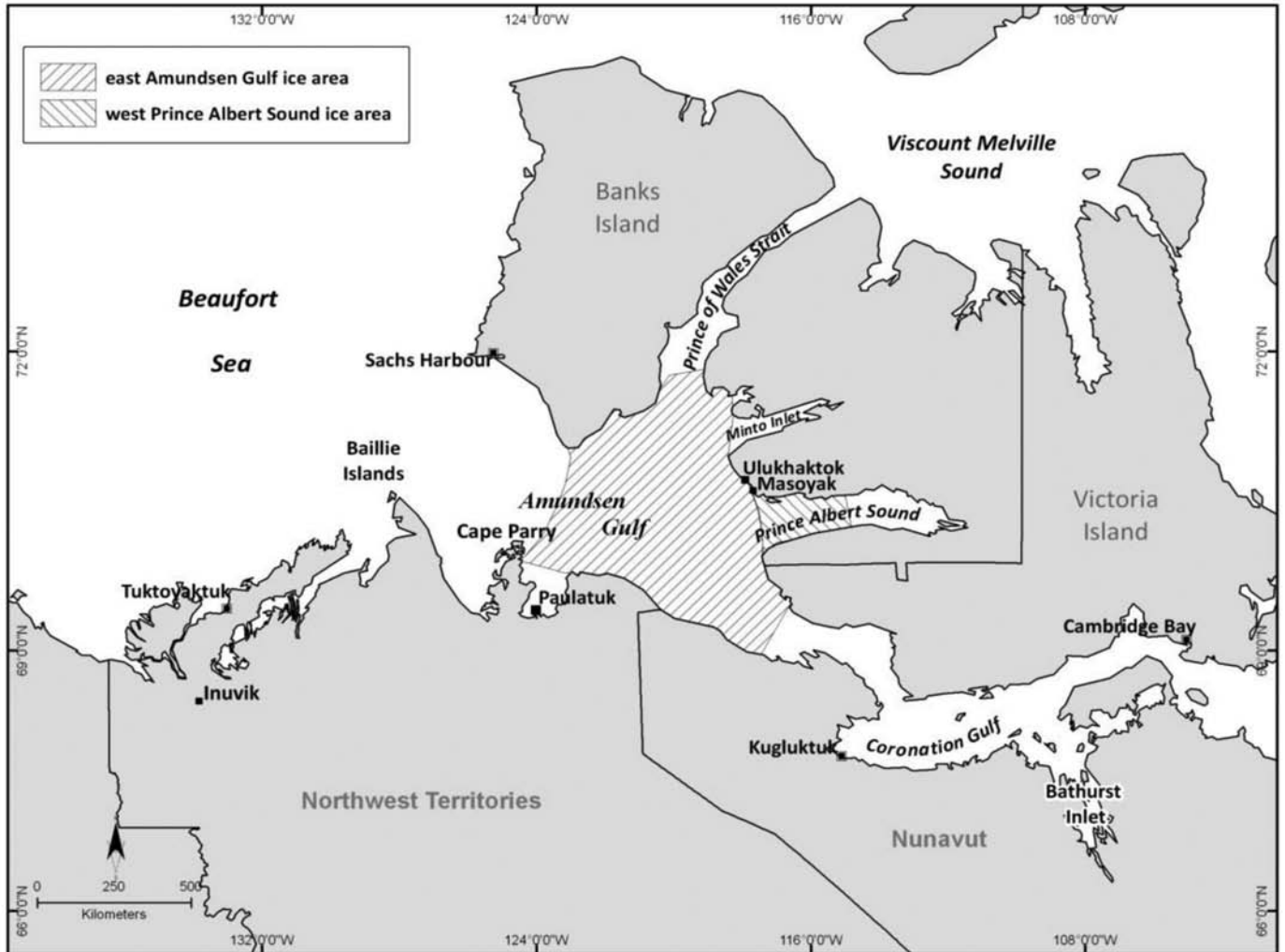
FIG. 1. Location of ringed seal subsistence harvesting and monitoring location in eastern Amundsen Gulf (EAG) and western Prince Albert Sound (WPAS).

Left and right ovaries were sectioned following the methods described by Smith (1973), and the presence or absence of corpora lutea was recorded. We considered a large, recently formed corpus luteum to be evidence of recent ovulation in females that were sampled in June or July. Ovulation peaks in mid to late May (Smith, 1987), but pregnancy cannot be confirmed by the presence of a foetus during June or July sampling, since implantation and foetal development do not begin until September (Smith, 1973, 1987).

The reproductive history of females was determined from the state of the uterus. Females that had given birth at least once (one or both uterine horns stretched or swollen) were classified as multiparous. Females with no evidence of having had a previous pregnancy were classified as nulliparous.

*Data Analysis*

We calculated mean age, modal age, and asymptotic length for males and females, including all aged seals sampled in all months. For body condition and reproduction

analyses, we excluded seals younger than 7 and older than 20 y, to control for maturing and senescent females. Asymptotic lengths were estimated for males and females using a non-linear regression fit by least squares in PROC NLIN in SAS V 8.0, using the Gauss-Newton iterative method of regressing residuals until iterations converged.

The mean age of sexual maturity (equivalent to first ovulation) and mean age at first pregnancy (females with evidence of at least one previous birth, i.e., multiparous) were calculated according to DeMaster (1981), using age-specific ovulation and age-specific reproductive tract data for all females 0–20 y sampled on or after 1 June.

The proportion of females that ovulated in a given year, the annual ovulation rate, was tabulated for females 7–20 y in which uterine condition indicated at least one previous pregnancy. The rate was calculated as the number of ovulating multiparous 7–20 y females sampled in June or July, divided by the total number of multiparous 7–20 y females in the annual sample in June or July. The percentage of pups in the subsistence harvest, our measure of recruitment, was calculated from the open-water hunt sample. We did not use data collected during periods of

ice cover for this variable because adults predominate, maturing subadults tend to be excluded from core harvesting areas due to competition with adults, and pups are usually in lairs and are thus inaccessible to hunters (Smith, 1987).

The annual proportion of pups in the open-water sample was calculated as number of pups (young of the year) divided by total number of seals sampled, during June and July open-water hunting, as defined by the monitor, in that year. For both ovulation rate and percent pup analyses, we included published data for 1971 – 78 from Smith (1987). We used Pearson correlations in XLStat to test if annual ovulation rates were correlated with percent pups in the open-water harvest in the sample year and in the following year.

We corrected ventral blubber depth (cm) for body size by dividing by standard length (cm) (Beck et al., 1993), then tested for collinearity between the hip and sternum sites. We used a General Linear Model (GLM) in SAS (1990) V8 to test for effects of month of collection (June versus July), sex, year, and age (7 – 20 y) on blubber depth in adults, and additionally, on ovulation status in multiparous females aged 7 – 20 y. We used a Duncan multiple range test in SAS to test for differences in mean ventral blubber depth of multiparous females that ovulated versus those that did not, all years pooled, and show annual mean blubber depth and sample sizes for ovulating and non-ovulating multiparous females on a scatterplot.

We evaluated autocorrelation in the annual mean blubber depth by autocorrelogram in XLStat and then used a least-squares linear regression in XLStat to test for a temporal trend in mean annual blubber depth, sexes separately. The regression included a Shapiro-Wilk test for normality and a Newey-West correction with a lag interval of 5 y (corrects for autocorrelation up to and including the specified value). The annual standardized residuals (the residual divided by its standard deviation), being the difference between mean annual blubber depth and the fitted regression line, were evaluated for temporal trend using a Mann Kendall test in XLStat, by sex.

*Environment*

Sea ice clearance date reflects a suite of oceanographic and meteorological conditions that prevailed during the winter months prior to when and where our seal sampling was conducted each spring. Ice charts dating back to 1970, which are prepared by the Canadian Ice Service (CIS) to support navigation (Weekly Regional Ice Charts), were used to determine the dates when winter ice cleared each spring, when new ice formed in autumn, and if and when fast ice was established in winter in each of WPAS and EAG (CIS, 2020). To track the timing and progress of sea ice clearance each spring, we used the earliest date when the analyst at the CIS first created a polygon to represent light ice cover adjacent to the floe edge in Prince Albert Sound, provided that this identified pack-ice "feature"

remained lightly ice covered in subsequent analyses. The concept of light ice cover embraces low ice concentration and dominance of new and young ice forms as defined by the World Meteorological Organization. We acknowledge the limitations of the various satellite sensors used for ice mapping over the years and the navigational client for ice charts, which means that such a "feature" (typically a flaw lead) would need to be persistent and at least 10 km wide to be consistently charted over the duration of our study. Since charts were prepared weekly, each date we used could lag behind the actual clearing event by as much as a week.

The date of ice formation (freeze-over) was the earliest date in the autumn when the weekly ice chart indicated new or older ice covering nine-tenths or more of the sea surface within a nominal 50 km of Prince Albert Sound. Estimates of the duration of the ice cover from the preceding winter were calculated as the number of days from fall freeze-over in the year preceding sampling to spring clearance in the year of sampling.

Pearson correlations were used to test for collinearity between EAG and WPAS ice clearance dates and between winter duration and spring clearance in EAG. A least-squares linear regression in Microsoft Excel was used to estimate temporal trends in the sea ice variables from 1970 to 2019.

The Arctic Oscillation Index (AOI) is a measure of the varying average monthly state of the atmosphere north of 20° N. It is a single number that represents the dominant contributor to the pattern of atmospheric pressure at the sea surface in the Northern Hemisphere and the pattern, direction, and strength of winds that result from it. It consists of a positive phase with below average air pressure over the Arctic, a negative phase in which the opposite is true, and impacts weather in the Arctic and beyond (Thompson, 2019). Data for the AOI were obtained from the National Weather Service, National Oceanic and Atmospheric Administration (NOAA NWS, 2020). The standardized seasonal mean AOI index for winter (winAOI) was calculated by averaging the monthly AOI for January, February, and March for 1970 – 2019 (NOAA NWS, 2020), as these months correspond to the relevant period prior to our seal sampling.

We used Pearson correlations in SAS and in XLStat to test for correlations between blubber depth, annual ovulation rate, and annual percent pups in the open-water harvest, with timing of sea ice clearance and the winAOI. We extrapolated the observed trend of earlier spring clearance in WPAS to estimate in what year early clearance might coincide with the end of the birth lair occupation period (mid-May, given mean date of ovulation is May 25; Smith, 1987) and thus result in the physical loss of pupping habitat.

## RESULTS

*Biological Parameters*

A total of 3028 harvested ringed seals were sampled between 1992 and 2019 (Table 1). As in the past, our

TABLE 1. Annual sample sizes of all seals and all months, and mean (SD) and residual annual mean ventral blubber depth (corrected for standard length) for 7–20 y male and multiparous female ringed seals sampled from subsistence harvest in June and July 1992–2019. Of the 576 females sampled, 93 nulliparous female seals were excluded from the analyses of body condition and ovulation rate.

| Year | Total # sampled | Males 7–20 y | | | | Multiparous females 7–20 y | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | n | Mean blubber depth (cm) | SD | Standardized residual | n | Mean blubber depth (cm) | SD | Standardized residual |
| 1992 | 195 | 48 | 2.54 | 0.50 | 0.70 | 31 | 2.92 | 0.73 | 1.14 |
| 1993 | 187 | 73 | 2.54 | 0.67 | 0.73 | 37 | 2.89 | 0.74 | 1.10 |
| 1994 | 112 | 39 | 2.31 | 0.40 | −0.61 | 25 | 2.37 | 0.53 | −0.93 |
| 1995 | 114 | 33 | 2.34 | 0.40 | −0.30 | 16 | 2.68 | 0.73 | 0.43 |
| 1996 | 96 | 23 | 2.19 | 0.36 | −1.17 | 33 | 2.18 | 0.56 | −1.50 |
| 1997 | 104 | 25 | 2.53 | 0.57 | 0.98 | 13 | 2.50 | 0.58 | −0.12 |
| 1998 | 151 | 14 | 2.39 | 0.40 | 0.23 | 12 | 2.59 | 0.81 | 0.32 |
| 1999 | 105 | 24 | 2.54 | 0.53 | 1.22 | 11 | 2.69 | 0.48 | 0.81 |
| 2000 | 106 | 26 | 2.30 | 0.53 | −0.20 | 10 | 2.70 | 0.93 | 0.94 |
| 2001 | 101 | 18 | 2.49 | 0.50 | 1.07 | 13 | 2.35 | 0.51 | −0.40 |
| 2002 | 102 | 29 | 2.42 | 0.43 | 0.72 | 6 | 2.36 | 0.52 | −0.24 |
| 2003 | 102 | 27 | 2.23 | 0.51 | −0.39 | 24 | 2.24 | 0.60 | −0.66 |
| 2004 | 102 | 41 | 2.15 | 0.48 | −0.80 | 20 | 2.60 | 0.54 | 0.91 |
| 2005 | 101 | 42 | 1.96 | 0.57 | −1.92 | 9 | 1.89 | 0.55 | −1.89 |
| 2006 | 100 | 17 | 2.33 | 0.56 | 0.44 | 9 | 2.75 | 0.37 | 1.67 |
| 2007 | 101 | 21 | 2.20 | 0.42 | −0.27 | 16 | 2.26 | 0.65 | −0.21 |
| 2008 | 100 | 29 | 2.20 | 0.48 | −0.18 | 17 | 2.15 | 0.53 | −0.58 |
| 2009 | 102 | 38 | 2.21 | 0.63 | −0.09 | 15 | 1.93 | 0.47 | −1.38 |
| 2010 | 100 | 18 | 1.73 | 0.42 | −2.97 | 11 | 1.81 | 0.44 | −1.78 |
| 2011 | 100 | 18 | 2.22 | 0.49 | 0.17 | 7 | 1.88 | 0.40 | −1.40 |
| 2012 | 100 | 27 | 2.01 | 0.60 | −1.10 | 24 | 2.15 | 0.47 | −0.22 |
| 2013 | 84 | 22 | 2.20 | 0.56 | 0.20 | 17 | 2.49 | 0.54 | 1.24 |
| 2014 | 98 | 34 | 2.19 | 0.55 | 0.19 | 23 | 2.27 | 0.71 | 0.42 |
| 2015 | 100 | 31 | 2.29 | 0.44 | 0.91 | 19 | 2.31 | 0.55 | 0.70 |
| 2016 | 80 | 17 | 2.41 | 0.46 | 1.69 | 20 | 2.25 | 0.66 | 0.51 |
| 2017 | 100 | 18 | 2.14 | 0.34 | 0.10 | 18 | 2.14 | 0.50 | 0.15 |
| 2018 | 97 | 26 | 2.21 | 0.39 | 0.61 | 16 | 2.10 | 0.60 | 0.10 |
| 2019 | 88 | 15 | 2.11 | 0.49 | 0.05 | 11 | 2.27 | 0.72 | 0.87 |
| Total | 3028 | 793 | | | | 483 | | | |

TABLE 2. Proportion and number of pups (young of year), subadults (1–6 y), and adults (≥ 7 y) in the June–July ice and open-water hunting samples from Masoyak, 1992–2019.

| Age class | Ice | | Open water | |
|---|---|---|---|---|
| | n | % | n | % |
| Young of year | 33 | 3.11 | 463 | 29.45 |
| 1 to 6 y | 123 | 11.58 | 216 | 13.74 |
| 7 to 20 y | 659 | 62.05 | 743 | 47.26 |
| > 20 y | 247 | 23.26 | 150 | 9.54 |
| Total | 1062 | | 1572 | |

harvest-based sample was biased to adults, with the age distribution during June-July hunting from the ice consisting of 85.3% seals 7 and older, and 56.8% 7 y and older during open-water hunting (Table 2). Including both ice and open-water hunting in June and July of the added years (2012–19), young of year, subadults 1–6 y, and adults 7 y and older accounted for 14.6% (n = 107), 10.1% (n = 74), and 75.3% (n = 553) respectively.

Our sample included 793 males (Table 1) and 576 females 7–20 y that were sampled in June–July. Of the 576 June–July females (Table S1), 48 were nulliparous and had inactive ovaries, and 45 were nulliparous but ovulating for the first time. These maturing animals are excluded from the body condition and ovulation rate analyses, so our June–July dataset consisted of 483 multiparous females

and 793 males; 148 of these females and 190 of the males were collected during the added years 2012–19 (Table 1). Most seals in our sample (90%) were measured by the same field monitor (J. Alikamik) and all were aged by the same reader (T.G. Smith).

On average, across all years 1992–2019, the annual June–July sample consisted of 17.3 multiparous females 7–20 y (range n = 6–37) (Table 1). Of the 1572 seals taken overall during June–July open-water hunting, 463 were pups (Table 2). Between the 1992–2011 and 2012–19 periods, mean and modal age for the June–July sample increased by 2.4 y and 2 y in females, and 1.7 and 1 y in males, respectively (Table 3). Asymptotic length showed a 2.8 cm increase (2.2%) in females and 0.7 cm increase (0.5%) in males between these two time periods (Table 3).

For 1992–2019, age of maturity (first ovulation) was 6.26 y (SE = 0.53, n = 944) and age of first pregnancy was 6.74 y (SE = 0.41, n = 944; Table S2). The small number of females in the maturing age classes in our sample precluded calculating these parameters for the subset of added years 2012–19 alone (DeMaster, 1978).

The ovulation rate of multiparous females 1971–78 and 1992–2019 (Table S2) was mainly in the 80%–100% range (mean 88.7%, S1 = 17.5, n = 36 y). Females that did not ovulate were not randomly distributed across the years of the series, with sequences of up to six consecutive years in which 100% of the multiparous females ovulated, and

TABLE 3. Mean age, modal age, and asymptotic length of male and female ringed seals sampled from the subsistence harvest, 1992 – 2011 and 2012 – 19.[1]

| Time period | Parameter | Females[2] | Males |
|---|---|---|---|
| 1992 – 2011[3] | Asymptotic length (cm)[4] | 122.4 cm (SE = 0.66, n = 918) | 128.5 cm (SE = 0.57, n = 1271) |
| | Mean age (y) | 10.6 yr (SD = 8.1, n = 928) | 10.70 yr (SD = 8.1, n = 1273) |
| | Modal age (y) | 11 | 11 |
| 2012 – 19 | Asymptotic length (cm) | 125.2 cm (SE = 1.40, n = 331) | 129.2 cm (SE = 1.23, n = 414) |
| | Mean age (y) | 13.0 (SD 8.1; n = 331) | 12.4 (SD = 8.6; n = 414) |
| | Modal age (y) | 13 | 12 |

[1] Incorporates all aged seals sampled in all months.
[2] Smith (1987) annual mean age for females varied from 10.0 y (1977) to 17.4 (in 1972 and 1973).
[3] Harwood et al., 2012b.
[4] Sample from years 1971 – 78 (Smith, 1987): asymptotic length 126.9 cm (SE 4.12) females and 131.2 cm (SE 3.53) males.

sequences of up to six years when there were occurrences of multiparous females that did not ovulate. Finally, there were three of 36 y in the series (1974, 2005, 2012) when $\geq 50\%$ of the multiparous females failed to ovulate; we define those as ovulation failure events (Table S1).

The percent pups in the open-water harvest from 1992 to 2019 was variable (range, 0% – 61%) (Table S1) and averaged 29.4%. Annual ovulation rates in multiparous females were correlated with percent pups in the annual harvest ($R^2 = 0.49$ $p = 0.003$, n = 36 y), but not with percent pups in the following year's harvest ($R^2 = 0.06$, $p = 0.76$, n = 35 y).

*Body Condition*

In 7 – 20 y males and multiparous females sampled in June – July, blubber depth was correlated at the ventral hip and at sternum sites (females, $R^2 = 0.94$, $p < 0.0001$; n = 483; males, $R^2 = 0.93$, $p < 0.0001$; n = 793), so only the one measurement (hip) could be used due to collinearity. We modelled the effects of sample month, sex, year, and age on ventral blubber depth from 1992 to 2019 ($F_{569, 1275} = 1.26$, $p < 0.002$). There were no effects of sample month (June vs July) ($F = 0.03$; df = 1, $p = 0.86$) or age (7 – 20 y) ($F = 1.42$; df = 13, $p = 0.15$), but year ($F = 7.05$, $p < 0.0001$, df = 27) and sex effects ($F = 5.96$, $p = 0.0015$, df = 1) were significant. Mean blubber depth of multiparous females 7 – 20 y (mean 2.38, n = 483) was significantly greater than that of males 7 – 20 y (mean 2.28, n = 792) ($p < 0.05$), which necessitated body condition analyses to be done separately for the sexes.

Mean annual blubber depth in both sexes was normally distributed (females: Shapiro-Wilk W = 0.957, $p = 0.30$; males: W = 0.94, $p = 0.09$). Linear regression, including a Newey-West correction with a lag of 5 y, showed annual mean blubber depth declining at 0.02 cm/y (SE 0.005) in females and 0.01 cm/y (SE 0.004) in males (Fig. 2) (females: $F_{1,27} = 14.001$, $p < 0.0001$, t = −4.148, $p < 0.0001$; males: $F_{1,27} = 10.596$, $p = 0.003$, t = −3.387, $p = 0.002$), with 35% and 29% of the variability in mean blubber depth explained by the variable year in females and males, respectively.
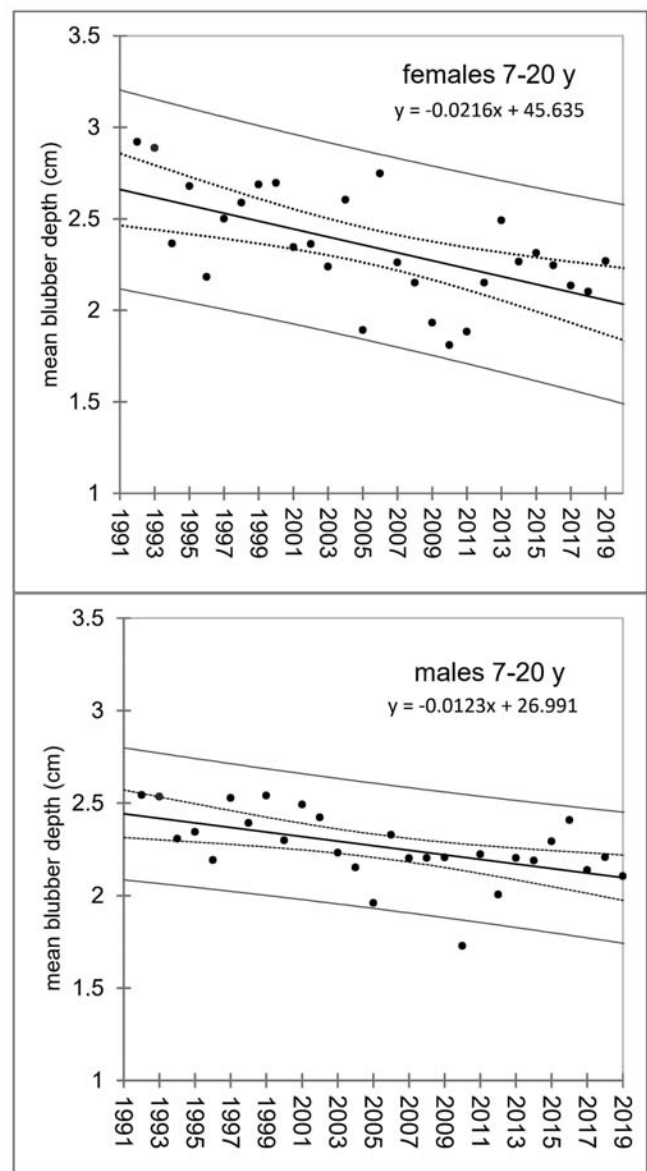


FIG. 2. Mean annual blubber depth of 483 multiparous female (upper) and 793 adult male (lower) ringed seals aged 7 – 20 y sampled from the subsistence harvest at Masoyak, June – July 1992 – 2019 (95% confidence interval of the model dashed lines; 95% confidence interval of observations, outer lines).
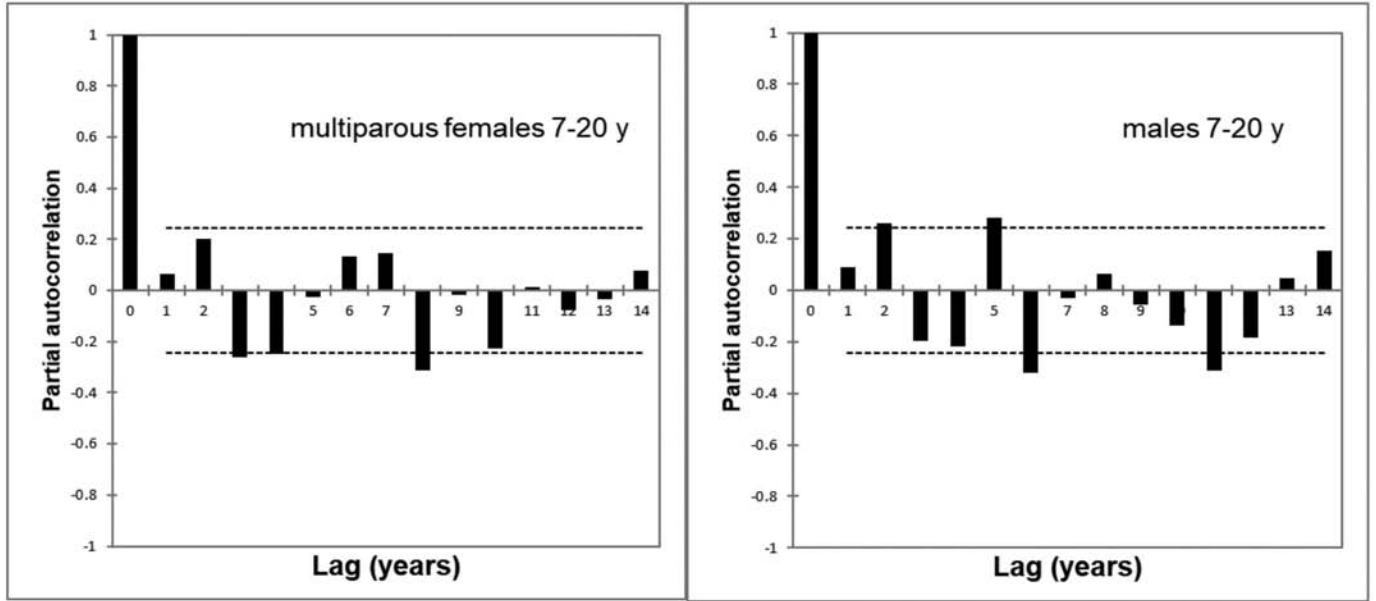
FIG. 3. Partial autocorrelogram of residual annual mean blubber depth in multiparous female (left) and male (right) ringed seals aged 7−20 y sampled from the subsistence harvest at Masoyak during June−July 1992−2019 (dotted line is significance at $p = 0.80$).

There was no temporal trend in the standardized residual annual mean blubber depth in females (Kendall's tau −0.016, $p = 0.92$) or in males (Kendall's tau 0.026, $p = 0.86$), and no autocorrelation at $p = 0.95$. However, at $p = 0.80$, years were autocorrelated at 3, 4, and 8 y in females, and 2, 5, 6, and 11 y in males (Fig. 3).

We modeled the effects of ovulation status and year on blubber depth of multiparous females aged 7−20 y ($F_{40, 482}$ = 3.85, $p < 0.0001$). There were significant effects of year (F = 4.142, df = 27, $p < 0.0001$) and ovulation status (F = 14.38, df = 1, $p = 0.0002$). On average, and using a pooled sample of all years, multiparous females that ovulated had greater blubber depth than those that did not ovulate (ovulated: n = 432, mean = 2.42 cm; did not ovulate: n = 51, mean = 2.07 cm, $p < 0.05$) (Fig. 4).

*Environment*

In EAG and WPAS, the two main areas used by seals in this region during winter, there was a trend toward earlier ice clearance in spring (9.0 days per decade in EAG ($p < 0.05$), and 3.8 days per decade in the core breeding habitats in WPAS ($p < 0.01$) (1970−2019). The accompanying trend toward later freeze-over, however, was less pronounced, 2.0 d/decade in EAG ($p < 0.05$) and 3.7 d/decade in WPAS ($p < 0.01$) (Fig. 5). In EAG, the date of ice clearance in spring was more variable than in WPAS. Clearance ranged from 26 April to 10 August 1992−2019 (mean = 22 June) in EAG, and 28 June to 9 August (mean = 17 July) for the same years in WPAS (Fig. 5).

Using the measured trend of 3.8 d/decade toward earlier breakup of fast ice in WPAS (Fig. 5), we calculated that early clearance of fast ice in the core pupping habitats
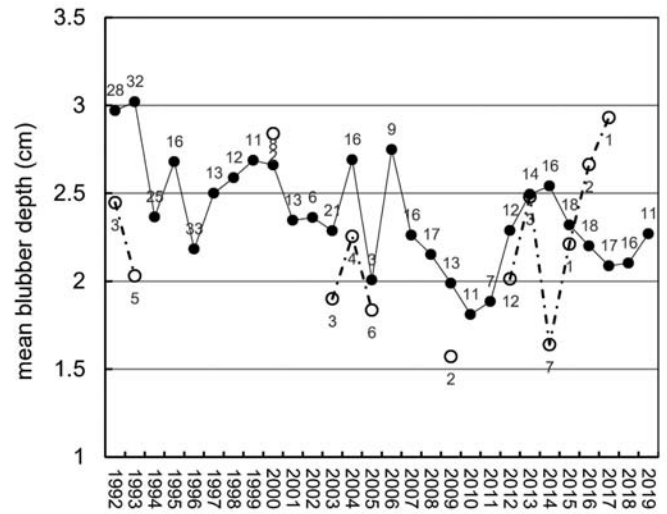


FIG. 4. Annual mean blubber depth of ovulating (solid lines/circles, n = 432) and not ovulating (short dash lines/open circles, n = 51) multiparous female ringed seals aged 7−20 y sampled from the subsistence harvest at Masoyak during June−July 1992−2019 (sample sizes indicated at each point).

would not result in physical loss of pupping habitat before 2140 and, in an extreme year, not before 2100 (Fig. 6).

Annual spring sea ice clearance dates in EAG and WPAS were significantly correlated ($R^2 = 0.380$, $p = 0.05$, n = 28 y), so in our comparisons with the biological data, we used only the more variable EAG as our sea ice metric because of collinearity. Annual spring sea ice clearance dates in EAG and duration of the previous winter were also significantly correlated ($R^2 = 0.95$, $p < 0.0001$, n = 28 y) so, again, we could not use winter duration because of collinearity.

Blubber depth was correlated with the winAOI in both sexes (females: $R^2 = 0.41$, $p < 0.0003$, n = 483; males: $R^2 =$
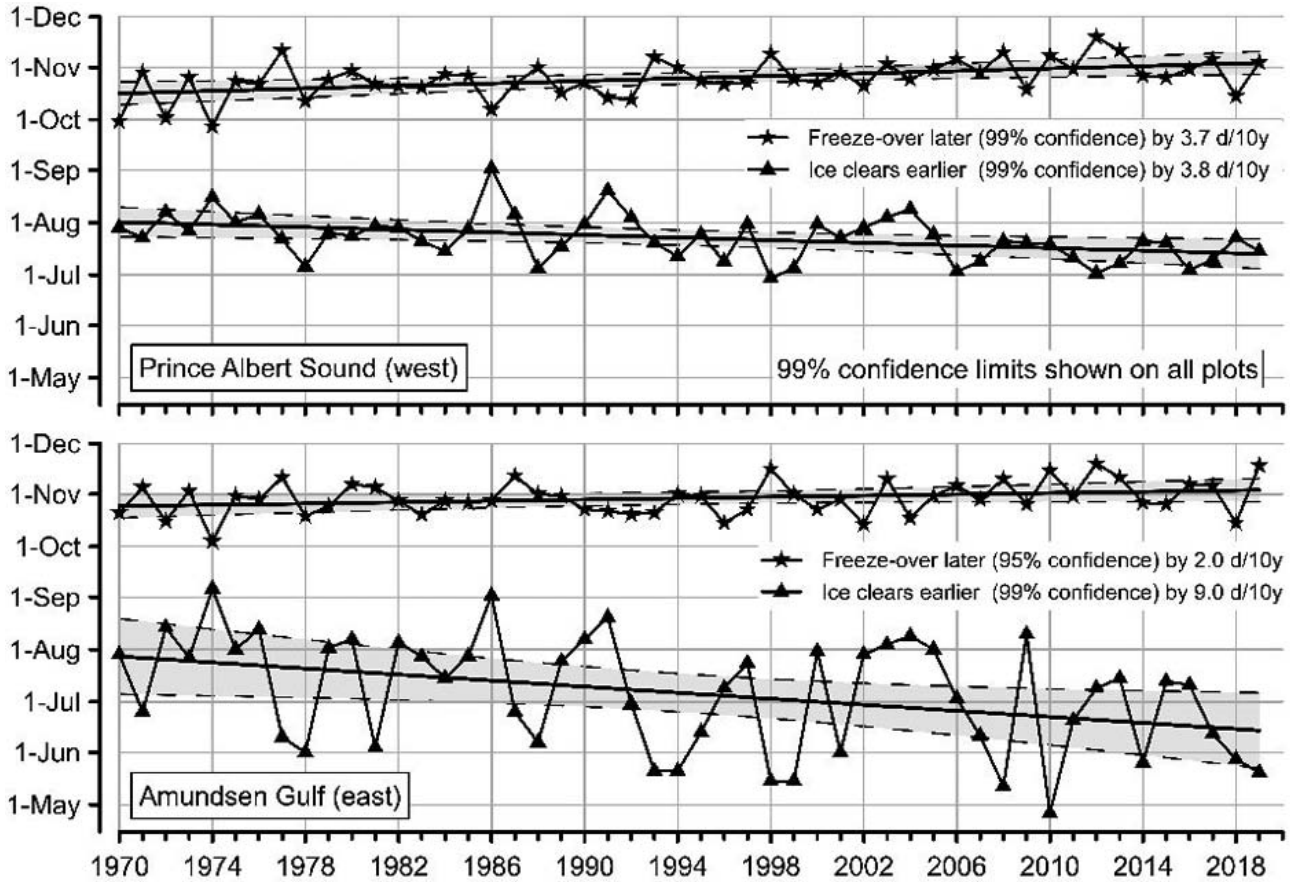
FIG. 5. Dates of freeze-over and ice clearance in western Prince Albert Sound and in the adjacent area of eastern Amundsen Gulf, 1970 through 2019. Trend lines and 99% confidence limits are plotted.
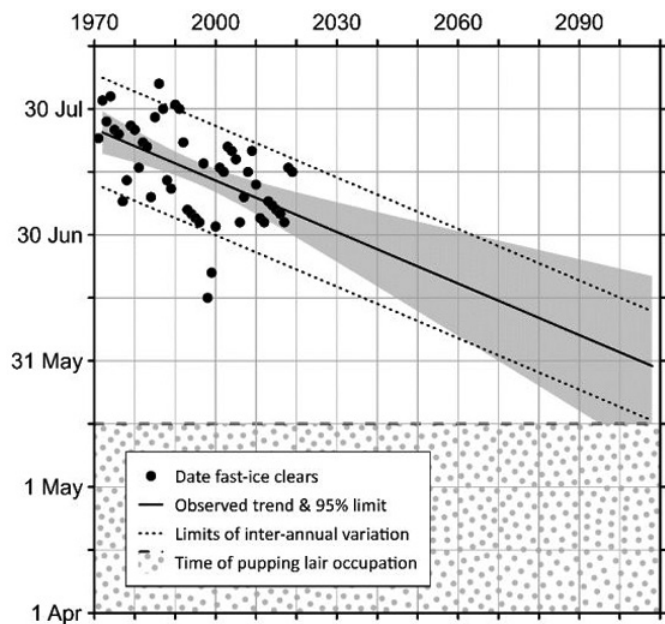


FIG. 6. Extrapolation through 2110 of the measured trend of 3.8 d/decade from 1970 to 2019 in earlier fast-ice breakup in western Prince Albert Sound in relation to the period of lair occupation.

0.44, $p < 0.0001$, n = 793), with winAOI accounting for 41% and 44% of the variation in females and males, respectively. The mean annual blubber depth fluctuations tracked some of the negative and positive phases of the winAOI in both sexes (Fig. 7). Blubber depth was not correlated with annual sea ice clearance timing in EAG (females: $R^2 = 0.20$, $p = 0.40$, n = 483; males: $R^2 = 0.24$, $p = 0.11$, n = 793).

Annual ovulation rates in multiparous females were negatively correlated with sea ice clearance date in EAG ($R^2 = 0.464$, $p = 0.004$, n = 36 y), but not with winAOI ($R^2 = 0.012$, $p = 0.945$, n = 36 y). The percentage of pups was not correlated with sea ice clearance date in EAG ($R^2 = 0.260$, $p = 0.138$, n = 36 y) or with winAOI ($R^2 = 0.080$, $p = 0.65$, n = 36 y).

The ovulation failure events in 1974 and 2005 occurred in years when sea ice clearance was delayed by 5–6 weeks (Fig. 8), and the third failure (2012) occurred in the last of six consecutive years with negative residual annual blubber depths (Table 1).

## DISCUSSION

The inclusion of eight more years of monitoring data strengthened conclusions about the longer-term ecological trends described previously (Smith, 1987; Harwood et
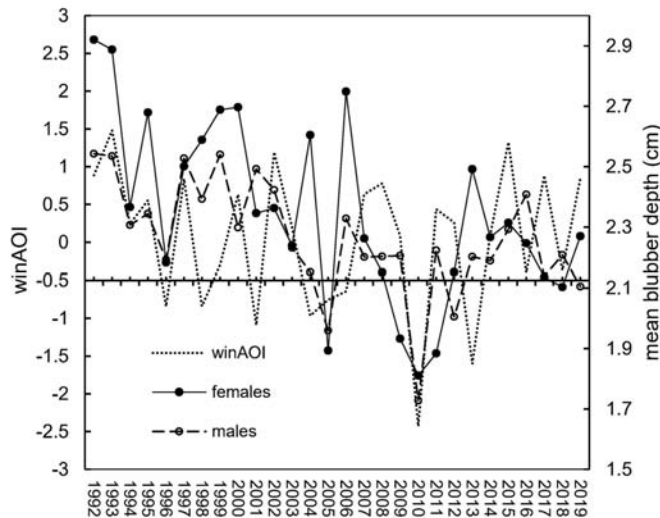
FIG. 7. Mean annual blubber depth in 7–20 y multiparous females sampled in June–July 1992–2019 (solid line, closed circles) and adult males (long dashed line, open circles), and the winter Arctic Oscillation Index (fine dotted line).



FIG. 8. Percent frequency of ovulating multiparous females 7–20 y in June–July 1992–2019 (n = 483) and 1971–78 (Smith, 1987), and the timing of spring sea ice clearance in eastern Amundsen Gulf.

al., 2000, 2012b) and revealed new linkages. The timing and location of our sample, independently determined by the timing of the peak subsistence seal harvest in this area, continues to be appropriate for studying adult body condition and ovulation rate in relation to environment.

The longer-term annual ovulation rates were again positively correlated with the percent pups in the harvest, indicating conditions favorable for ovulation also likely favour pup survival (and vice versa). In three of the 36 y in our series, there were ovulation failures, when ≥ 50% of the multiparous females failed to ovulate (1974, 2005, 2012). In each case, ovulation rates returned to normal within 1–3 y. Higher annual ovulation rates were correlated with earlier sea ice clearance dates in EAG in spring, and two ovulation failures took place in years when spring sea ice clearance was delayed by 5-6 weeks. The third failure of ovulation (2012) was similar in magnitude and duration to those documented previously in EAG/WPAS in 1974 and 2005 (Stirling et al., 1977; Smith, 1987; Harwood et al., 2012b), but occurred in an average ice year (Fig. 8).

Episodic failures of ovulation and consequent reductions in the proportion of ringed seal pups in the EAG/WPAS region have been detected in association with heavy winter and late spring ice conditions (Smith, 1987; Harwood et al., 2012b). In the adjacent eastern Beaufort Sea, major reductions in productivity of polar bears and ringed seals were correlated with heavy sea ice conditions and delayed breakup in the same years (Stirling and Archibald, 1977), as well as in 1985 and 1993 (Stirling et al., 1977; Stirling and Lunn, 1997; Kingsley and Byers, 1998; Stirling, 2002) and probably also in 1966 (Usher and Church, 1969).

During both the 1974 and 2005 ovulation failures, nutritional stress was apparent (Smith, 1987; Stirling and Lunn, 1997; Stirling, 2002; Harwood et al., 2012b; Nguyen et al., 2017); other marine mammals, such as the polar bear, also showed significant nutritional stress in these areas
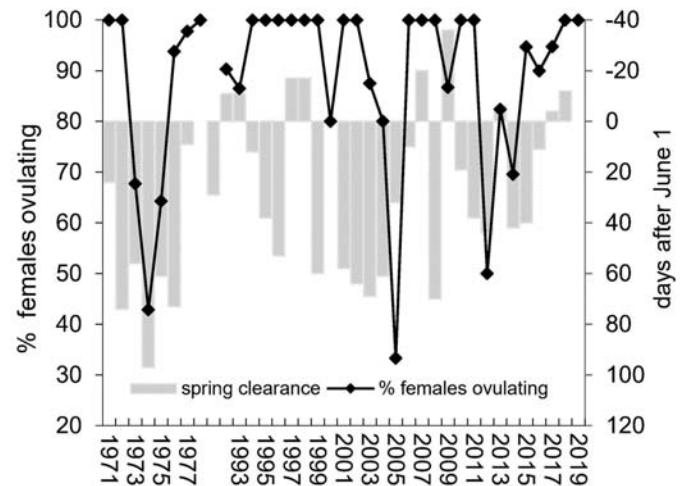
and years. Nutritional stress in the bears was linked with reduced numbers of ringed seal pups, which are critical to the diet of all bears, especially for pregnant females (Stirling and Øritsland, 1995; Stirling, 2002; Stirling et al., 2008; Rode et al., 2018).

Despite variation in the sampling time periods and duration of different studies, plus the geographic distribution and size and timing of various sample collections, the collective results from both indicator species (ringed seals and polar bears) suggest the trends and fluctuations observed in the EAG/WPAS area likely reflect broader-scale ecosystem change, which in some cases is fluctuating at decadal-scale time periods and at spatial scales beyond that of our local study area. The similarity of observations in both core and non-core seal habitat areas suggests that such effects occur at broader, regional scales, and likely at greater spatial scales than we are able to document at a single monitoring site in WPAS/EAG.

Increasingly earlier sea ice clearance at the present measured rate could eventually have a direct negative effect on the amount and quality of available fast-ice breeding habitat for ringed seals in WPAS and EAG (Smith and Harwood, 2001). However, the trends in sea ice clearance timing that we have observed in these areas since 1971 have been subtle (Melling and Riedel, 2004; Melling et al., 2005) and have taken several decades of monitoring to elucidate statistically significant relationships. These areas have not shown the same pronounced shift to earlier clearance as has been observed in some other areas of the Arctic, including the western Beaufort Sea (Serreze et al., 2007; Comiso et al., 2008; Walsh, 2008; Tivy et al., 2011; Stern and Laidre, 2016). The stable fast-ice of WPAS, now clearing at 3.8 d earlier per decade, is the main whelping area used by seals in our study area (Smith, 1987). At the observed rate, physical loss of sea ice pupping habitat during the lair occupation period would not occur, on average, before 2140. Physical loss of sea ice pupping habitat was observed

in the WPAS area during the pupping period in 1998, with an observed truncation of the nursing period and some pup mortality (Harwood et al., 2000; Smith and Harwood, 2001). However, these effects were localized and temporary.

The previously observed negative temporal trend in seal body condition was sustained with the additional years of data with this update, but has shown signs of reversal starting in 2013. We now see a quasi-cyclic pattern in blubber depth in adults of both sexes that tracked some of the negative and positive phases of the winAOI. The winAOI has alternated between positive and negative phases over most of the past century (NOAA NWS, 2020; Thompson, 2020). However, in the 1970s, and then again from the late 1980s to late 1990s, the index remained in a strong positive (warm) phase, with a record high in 1990. The current pattern, since about 2005, has been consistent with the more typical alternating pattern observed previously. The negative temporal trend described above may have been an artifact of seal monitoring through the atypically long positive phase of the AOI that peaked in 1990 and diminished through 1995 (NOAA NWS, 2020).

The AOI often shares phase with the North Atlantic Oscillation (NAO), a closely related variable that has also been used in similar types of analyses (e.g., Ferguson et al., 2017), especially in the Atlantic sector of the Arctic. It represents the same phenomenon of varying atmospheric pressure, wind, and temperature over a smaller region of the Northern Hemisphere. It is particularly well linked to air temperature and storm tracks across the North Atlantic (NCCO, 2020).

Ferguson et al. (2017) report declines in ringed seal body condition similar to what we observed in EAG/WPAS and over similar time periods in the more southerly seal habitats of Hudson Bay. Those authors note the patterns coincided with extremes in large-scale patterns of the AOI and the NAO, and also report on possible linkages in that location with the unidentified pinniped mortality event that emerged in November 2011 (Stimmelyr, 2013). However, a similar seal mortality event was not observed in our monitoring area, perhaps because EAG and WPAS are core stable habitats.

The most recent ovulation failure (2012) referred to above came at the end of six consecutive years during which residual annual blubber depths were negative, suggesting that in some cases, a reproductive failure may also result from the cumulative influence of a series of negative environmental effects over a sequence of years. In an independent analysis, Reimer et al. (2019) emphasized that, in some cases, a sequence of years in which environmental factors were unfavourable in some way, but not sufficient to trigger a negative response in a single year, might be capable of doing so after a series of years that capture the effect cumulatively. The ovulation failure in 2012 may be an example of such a phenomenon.

### Sources of Uncertainty

There are known but difficult to quantify additional factors besides the timing of sea ice clearance and winAOI that influence ringed seal body condition and reproductive outcomes from one year to the next, independently or in combination, and over sequences of years. In addition to our sea ice clearance variable, factors such as the location or quality and quantity of prey available throughout the winter, precipitation, strength and direction of winter winds during the period of sea ice formation, and sea ice surface deformation that influences the accumulation and drifting of snow necessary for construction of lairs, may individually or collectively affect ringed seal body condition and reproduction outcomes in spring (Smith, 1987). Year-to-year autocorrelation could result from several, annually variable factors, including reduced marine ecosystem productivity (which may also be cyclical) in the preceding fall, potentially compromising the nutritional status of seals before they even enter the winter period (Smith, 1987; Harwood and Stirling, 1992; Young and Ferguson, 2013). Also, because most snow in the Arctic falls in autumn, less snow may have accumulated on ice by spring if freeze-over is late. This lack of snow could have a detrimental impact on the establishment of birth lairs and overall quality of seal breeding habitat in the spring (Smith and Stirling, 1975, 1978; Ferguson et al., 2005; Iacozza and Ferguson, 2014). Similarly, negative influences in the same year could also result from early spring rainfall events that melt the protective snow cover of birth lairs (Stirling and Smith, 2004) or early sea ice clearance, which causes nursing substrates to deteriorate before the six-week nursing period is complete (Smith and Harwood, 2001; Ferguson et al., 2017).

### Study Strengths and Limitations

The size of our annual seal sample is directly related to the size of the subsistence harvest from the Masoyak area (Joint Secretariat, 2003). The size of the harvest is, in turn, dictated by local subsistence needs and by hunting effort and success. The latter may be influenced by access to hunting areas because of ice, suitable weather, equipment, and the availability of fuel for hunting. Thus, while our study lends itself to the study of ovulation rates, percent of pups in the open harvest, and body condition following winter and reproduction in spring, our ability to quantitatively examine demographic responses in timing of maturation, age at first pregnancy, or shifts in age structure is limited. This drawback is because the opportunities with our program to sample subadults and maturing females are limited, given the harvest in this area and season consists mostly of adults. Even with our sample consisting mainly of adults, the number of multiparous females in the annual sample has averaged only 17 per year. Still, with collaborations over the long-term, we have obtained adequate sample sizes relating to the EAG/WPAS area for our main variables and have been able to control for senescence, season, location, and sampler consistency.

Subadult seals tend to occur at the periphery of the prime fast-ice breeding habitat, as they are actively excluded

from the main breeding area by adults. Even after sea ice clearance, younger age classes (young of the year through 4 or 5 y) are not well represented in our sample because they disperse far to the west in autumn (Smith, 1987; Harwood et al., 2012a), and may not return to breed in their natal area in later years because of replacement by immigration from other areas. The likelihood of this pattern is indicated by the fact that ringed seals as a species lack the genetic structure exhibited by species in which the young have fidelity to their natal areas for subsequent reproduction (Davis et al., 2008).

*Outlook*

Understanding the linkages and mechanisms leading to the quasi-cyclic patterns in body condition and episodic failures of reproduction remains challenging. While our measurement of timing of sea ice clearance in spring has clear linkages to ovulation rate and will ultimately directly influence the breeding success of ringed seals because of the essential requirement for adequate pupping habitat (Laidre et al., 2008, 2015), delayed spring sea ice clearance did not provide a full explanation for the latest ovulation failure in 2012 and only for some of the patterns we observed in body condition. The timing of the 2012 ovulation failure suggests different mechanisms and pressures; it is possible that the cumulative influence of similar but lower intensity environmental pressures may have caused or contributed to that event. In the absence of empirical long-term data on marine productivity and prey availability in the ringed seals' winter foraging and overwintering areas, it is not possible to pinpoint the cause(s) or rule out that fluctuations in ocean productivity, for reasons not fully understood at present, might also have been a critical factor in previously documented reproductive failures in addition to the observed extremely heavy sea ice. Studies of ocean productivity and continuing quantitative long-term studies of the factors that influence the breeding success and body condition of ringed seals are needed to strengthen our ability to predict the impacts of a changing climate on ringed seals.

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