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Ringed Seals and Sea Ice in Canada's Western Arctic: Harvest-Based Monitoring 1992–2011

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ABSTRACT. We examined the relationship between ringed seal body condition and reproduction and spring sea ice conditions in prime ringed seal habitat in Canada's western Arctic during 1992–2011. Since 1970, ice conditions in east Amundsen Gulf and west Prince Albert Sound have shown only a slight trend toward earlier ice clearance (breakup) in spring (3–7 days per decade) ($p < 0.10$) and no trend toward later freeze-up or increased variability in timing of spring ice clearance. A subsistence harvest–based sample of 2281 ringed seals was obtained during 1992–2011 from Masoyak, a traditional hunting camp located on the northwest shore of west Prince Albert Sound and less than 5 km from east Amundsen Gulf. The results revealed a statistically significant trend of decreasing mean annual body condition of ringed seals (using an index of length-mass-blubber depth [LMD]: adults, 0.14 $m^{1.5}/kg^{0.5}/y$; subadults, 0.24 $m^{1.5}/kg^{0.5}/y$) over the past two decades. A parallel result was that mean annual body condition of adults and subadults was correlated with the timing of fast ice clearance in spring (later ice clearance = worse condition). This correlation was most obvious in the extreme ice years in all sex/age groupings and was statistically significant for subadults. In mature females sampled since 1992, annual ovulation rates averaged 92.4 ± 16.3% (SD) and were greater than 80%, and mostly at 100%, in all years but two. Failure to ovulate was obvious in 2005, the most extreme late ice clearance year in our series, when only 30.0% of the mature adult females sampled ovulated. At the same time, values for seal body condition indices (adult females, LMD = 11.3; adult males, LMD = 12.4) and percent pups in the harvest (3.3%) were among the lowest recorded, and spring ice clearance was 38 d later than the 1992–2011 average. While this and previous studies indicate that the seal population in this core habitat has recovered from natural and extreme-year sea ice fluctuations over the past four decades, the potentially magnified effect of several consecutive extreme ice years, compounded by the concurrent decline in seal body condition that we have now detected over the past 20 years, is of particular concern.

Key words: ringed seal, *Phoca hispida*, ovulation, reproductive failure, body condition, Amundsen Gulf, Prince Albert Sound, sea ice, subsistence harvest, ice clearance

RÉSUMÉ. Nous avons examiné le lien qui existe entre l'état corporel du phoque annelé, l'état de reproduction de ce phoque et l'état de la glace de mer printanière dans son habitat d'élection de l'ouest de l'Arctique canadien et ce, entre 1992 et 2011. Depuis 1970, l'état de la glace dans l'est du golfe Amundsen et dans l'ouest du détroit de Prince-Albert n'a affiché qu'une petite tendance vers une débâcle printanière plus hâtive (de 3 à 7 jours par décennie) ($p < 0,10$) et aucune tendance vers un englacement plus tardif ou une variabilité accrue caractérisant la période de la débâcle du printemps. Un échantillon recueilli à partir de 2 281 phoques annelés ayant fait l'objet d'une récolte de subsistance a été obtenu entre 1992 et 2011 à Masoyak, un camp de chasse traditionnel situé sur la côte nord-ouest de l'ouest du détroit de Prince-Albert et à moins de cinq kilomètres de l'est du golfe Amundsen. Les résultats ont permis de constater une tendance statistiquement significative sur le plan de la décroissance de l'état corporel annuel moyen des phoques annelés (en fonction d'un indice de la profondeur et de la longueur de la masse du petit lard [LMD] : reproducteurs, 0,14 $m^{1,5}/kg^{0,5}/a$; préreproducteurs, 0,24 $m^{1,5}/kg^{0,5}/a$) au cours des deux dernières décennies. Un résultat parallèle a permis de corréler l'état corporel annuel moyen des reproducteurs et des préreproducteurs à la période d'une débâcle printanière rapide (débâcle tardive = pire état). Cette corrélation était plus évidente au cours des années où la glace était extrême chez tous les groupements en fonction du sexe ou de l'âge, et elle était statistiquement significative chez les préreproducteurs. Parmi les femelles matures échantillonnées depuis 1992, les taux d'ovulation annuels atteignaient 92,4 ± 16,3 % (DS) en moyenne, et étaient plus grands que 80 %, et à près de 100 % au cours de toutes les années, sauf deux. L'anovulation était évidente en 2005, ce qui correspondait à l'année de notre série où la débâcle a été la plus tardive, lorsque seulement 30,0 % des femelles adultes et matures qui avaient été échantillonnées ont ovulé. En même temps, les valeurs relatives aux indices de l'état corporel des phoques (femelles adultes, LMD = 11,3; mâles adultes, LMD =

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12,4) et au pourcentage de petits faisant partie de la récolte (3,3 %) figuraient parmi les valeurs les plus basses à n'avoir jamais été enregistrées, et la débâcle printanière était plus tardive de 38 jours par rapport à la moyenne de 1992-2011. Bien que cette étude et des études antérieures laissent croire que la population de phoques de cet habitat important a réussi à se remettre des fluctuations naturelles et extrêmes des conditions de glace des quatre dernières décennies, l'effet potentiellement grossissant de plusieurs années consécutives de glace extrême, allié au déclin concurrent de l'état corporel des phoques que nous avons décelé au cours des 20 dernières années, présente une source d'inquiétude particulière.

Mots clés : phoque annelé, *Phoca hispida*, ovulation, échec de reproduction, état corporel, golfe Amundsen, détroit de Prince-Albert, glace de mer, récolte de subsistance, débâcle

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INTRODUCTION

The ringed seal (*Phoca hispida*), which has a circumpolar distribution, is the most abundant and widespread marine mammal in the Canadian Arctic. The species is important in the subsistence economy of the Inuvialuit (IRC, 1989; Joint Secretariat, 2003) and the main prey of the polar bear (*Ursus maritimus*) (Stirling, 2002). Ringed seal survival and reproductive success are closely linked to the extent, persistence, and characteristics of sea ice (Smith, 1987; Stirling, 2002; Laidre et al., 2008), and changes to the annual sea ice regime are expected to have direct effects on ringed seals, although relationships are complex and difficult to predict (Tynan and DeMaster, 1997; Kovacs et al., 2010). Ringed seals are vulnerable to sea ice changes because they depend on sea ice for reproduction during spring (Smith, 1987; Ferguson et al., 2005).

Females give birth to a single pup in a subnivean lair on the sea ice between late March and early April (Smith and Stirling, 1975). To construct lairs, they need stable ice that has sufficient snow cover and remains intact for several months as a site for lactation, protection from predators and weather, and basking (Smith and Stirling, 1975, 1978; Smith, 1976, 1987; Hammill and Smith, 1989; Kelly and Quakenbush, 1990; Lydersen and Hammill, 1993; Ferguson et al., 2005; Kovacs et al., 2010).

The quality and quantity of prey available during fall and winter, about which we know very little, are believed to be particularly important in determining whether females are able to reproduce successfully (Smith, 1987). Ringed seals are vulnerable to ecosystem shifts, and prime ringed seal breeding habitat must also be located near readily available food (Smith, 1987). The ringed seals' main prey is arctic cod, *Boreogadus saida* (Johnson et al., 1966; Lowry et al., 1978, 1980; Bradstreet et al., 1986; Crawford and Jorgenson, 1993; Crawford et al., 2011), and invertebrates also form a main part of their diet in certain areas and years, particularly for subadults. Adult female ringed seals forage for food while actively tending their pups (Smith and Hammill, 1981; Hammill et al., 1991; Smith et al., 1991; Kelly and Wartzok, 1996). The open water period that follows pupping and basking is a time of extensive feeding and foraging (Harwood and Stirling, 1992), during which the seals regain condition in preparation for the winter and next breeding season (McLaren, 1958; Smith, 1973).

Amundsen Gulf, which is somewhat protected from offshore storm influences and has many large, sheltered bays and sounds with persistent fast ice in winter and spring, provides prime ringed seal habitat in Canada's Western Arctic (e.g., Prince Albert Sound, Minto Inlet, others, Fig. 1). The large bays have stable fast ice for many months, which is critical to breeding ringed seals because it offers a stable platform that allows fixed territories (Kelly et al., 2010) and favourable habitat for pupping, lactation, basking, and protection from cold and predators (Smith and Stirling, 1975, 1978; Smith, 1976, 1987; Stirling et al., 1977, 1982; Hammill and Smith, 1989). The subadult (immature) animals tend to disperse away from the core habitats, as they are excluded during winter by competition from the more aggressive adults (Smith, 1987; Harwood et al., 2012).

In the Beaufort Sea and Amundsen Gulf, long-term observation has revealed considerable variation in ice presence and thickness between years (Melling and Riedel 2004; Melling et al., 2005), but has not shown the significant statistical trends to thinner ice, earlier ice clearance, and longer ice-free seasons that have been observed in other parts of the Arctic (Comiso and Parkinson, 2004; Serreze et al., 2007; Walsh, 2008).

In Canada's Western Arctic, scientific surveys of breeding habitat and sampling of specimens were initiated in the early 1970s (Stirling et al., 1977, 1982; Smith, 1987), and this work continued during the 1980s (Kingsley and Byers, 1998) and 1990s (Harwood et al., 2000). Inuvialuit harvesters and scientists have worked together throughout this long period, bringing a wealth of local field expertise and shared knowledge of the ringed seal into our collective understanding (Stirling et al., 1982; Smith, 1987; Kingsley and Byers, 1998; Harwood et al., 2000).

These studies have revealed decadal-scale fluctuations in ovulation rate, percentage of pups in the harvest (Stirling et al., 1977; Smith, 1987; Kingsley and Byers, 1998; Harwood et al., 2000), density of birth lairs (Smith and Stirling, 1978; Smith, 1987), and seal abundance (Stirling et al., 1977, 1982; Smith, 1987; Harwood and Stirling, 1992) in this region. Researchers suggested that changes in ringed seal abundance and reproductive performance were somehow related to variations in environmental conditions, particularly changes in the sea ice regime (Stirling et al., 1977; Smith, 1987; Stirling, 2002). Changes in seal productivity were also reflected in the body condition and reproductive

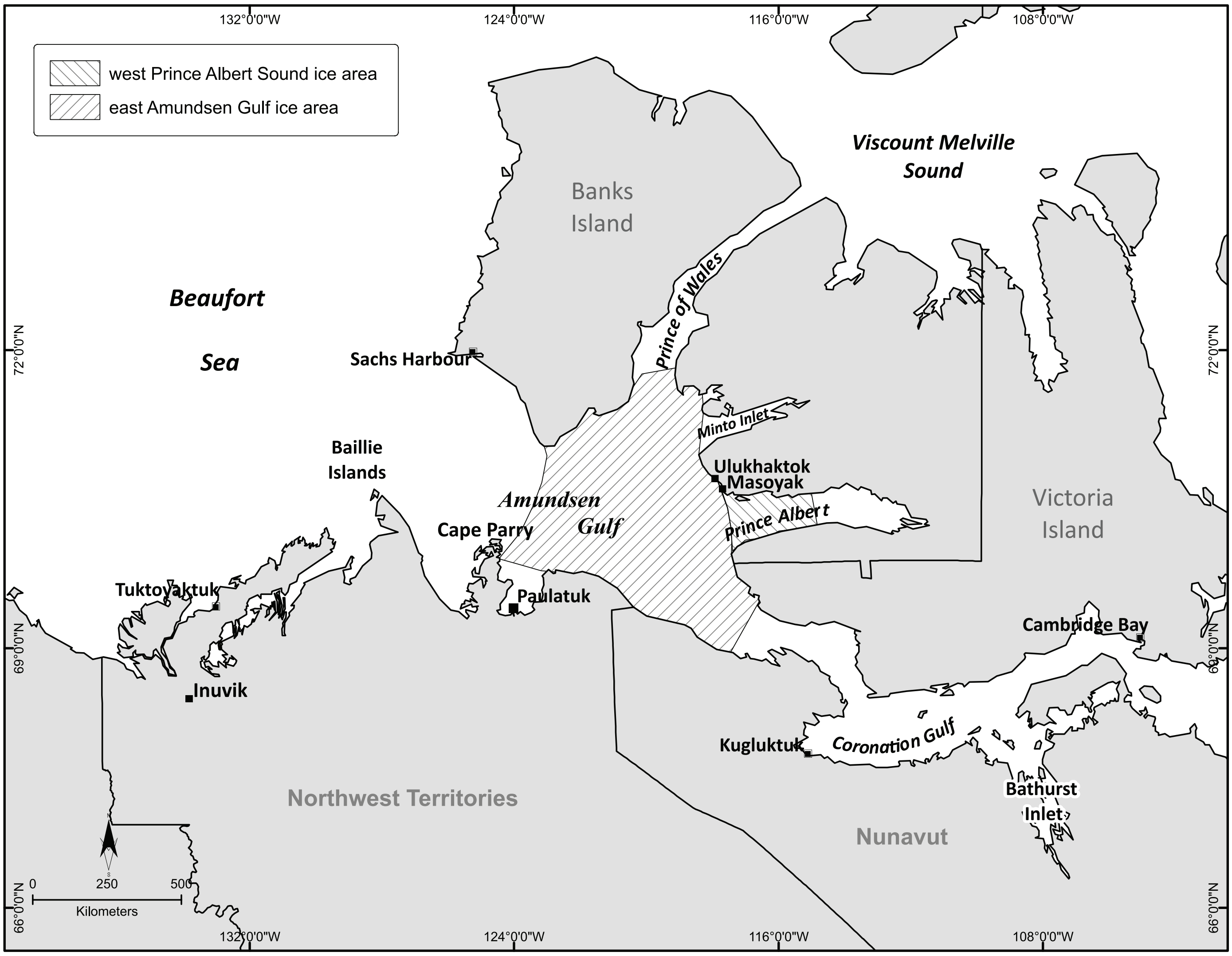

FIG. 1. Location of sampling site, East Amundsen Gulf and west Prince Albert Sound ice area boundaries, and place names mentioned in the text.

output of polar bears in the 1970s (Kingsley, 1979; Stirling, 2002) and are thought to have contributed to nutritional stress in polar bears in the Beaufort during 2004–06 (Stirling et al., 2008).

We extend an existing time-series of ringed seal sampling in west Prince Albert Sound and east Amundsen Gulf (Fig. 1) by 13 years, building on work initiated at the same location in the 1970s by Smith (1987) and continued in the 1990s (Harwood et al., 2000). Samples were obtained during a regular subsistence harvest by hunters from Ulukhaktok, Northwest Territories, formerly known as Holman. This seal harvest is the largest and most predictable in the western Canadian Arctic and provides the best opportunity to obtain adequate sample sizes on a reliable, long-term basis. The relationships between body condition, reproduction (ovulation rate, percent pups in harvest), and sea ice are examined in a 20 yr time series from 1992 to 2011. By studying the population response to natural environmental variation during this period, including a wide range of natural variation in both the seal population (Smith, 1987) and ice conditions (Melling and Riedel, 2004; Melling et al., 2005), we attempt to assess the effects of environmental change on the local ringed seal population.

METHODS

We examined ringed seal specimens harvested by subsistence hunters from the Inuvialuit community of Ulukhaktok, NT (70˚45′46″ N, 117˚48′22″ W). Most specimens (96%) were harvested within 20 km of the Masoyak area, a traditional hunting camp located on the northwest shore of Prince Albert Sound, approximately 5 km from the community. The balance of the sample was harvested from within 160 km of Masoyak, in east Prince Albert Sound (Fig. 1).

Ice conditions were examined for eastern Amundsen Gulf and western Prince Albert Sound, areas selected because they were the preferred (77%) year-round habitats used by seven ringed seals instrumented with satellite-linked transmitters deployed 17 km from Masoyak (www.

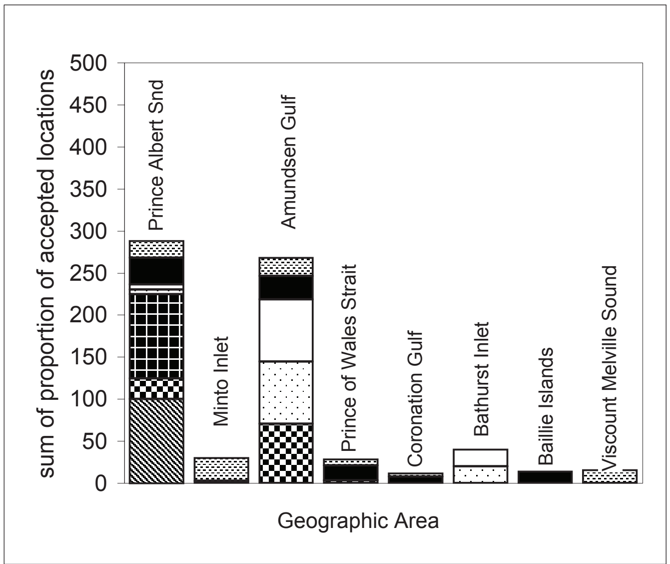

FIG. 2. Proportion of time spent by seven ringed seals tagged near Masoyak and tracked with satellite telemetry in various surrounding habitats, 1999–2000 (n = 5507 accepted locations by the filtering process); adapted from www.beaufortseals.com.

beaufortseals.com; Fig. 2). Satellite-tagged seals did travel outside these areas (e.g., to Minto Inlet, Viscount Melville Sound, Baillie Islands, Beaufort Sea, or Bathurst Inlet), but fewer than 5% of the accepted locations from any one of the tagged seals were in any one of these more remote areas (Fig. 2). Local ice conditions in east Amundsen Gulf are particularly relevant during the late spring, summer, and fall foraging periods, while ice conditions in west Prince Albert Sound are particularly important during winter and spring for establishment of lairs and territories in stable fast ice areas.

A sample of 100 or more ringed seals (totaling 2281 specimens) was collected from the Masoyak area subsistence harvest each year from 1992 to 2011. Eighty-nine percent of these samples were taken during the months of June and July, and these formed our basic data set. All aspects of the field sampling and laboratory work in 1992–2011 involved the same people and procedures that were used in 1971 to 1978 (Smith, 1987). Reliance on the same methods and samplers, and annual training by the project authority or designate, maintained optimal internal consistency in the data collected.

The normal seasonal decrease in blubber during May and June makes carcasses less buoyant (McLaren, 1958; Smith, 1973). To ensure we did not bias the seal body condition sample, we paid particular attention to avoiding the usual loss from sinking of seals shot in early summer. Except for pups of the year [see below], harvested seals brought to the camp were selected for sampling without preference for size, sex, or age. Sampling was done over a period of nine weeks each year, during the peak of the seal-hunting season. Approximately half of the sample was collected while fast ice was still intact, and the remainder, during open water after ice clearance.

Seals in poor condition were not lost from the harvest or sample, even if they sank after being shot. During the open water period, seals shot in the channel adjacent to Masoyak base camp are easily retrieved even if they sink because the waters in this area are clear, shallow, and sheltered. When favourable weather did permit hunting in deeper offshore areas, hunters shot only pups (i.e., young of the year, 2–4 months old), which are almost never lost by sinking because they are easily approached, readily retrieved, and usually buoyant. Thus sinking losses are not expected to have introduced significant bias to the data we have used to document seal body condition of subadults and adults.

We kept records of local ice conditions, describing each day's hunting as either "from the ice" (travel to and within the hunting area by snow machine) or "from the open water" (travel to and within the hunting area by small boat), the date, location of kill, sex, and age for each kill. Using his knowledge and experience, the seal monitor assessed the age of the harvested animal at the time of sampling, by identifying it as a pup, subadult, or adult. The harvested and then sampled seals remained the property of the harvester, for his or her subsistence use.

Harvested seals were laid on their backs on a smooth, flat surface, and a steel tape measure was used to determine standard nose-to-tail length (± 1.25 cm), axillary girth, and hip girth (American Society of Mammalogists, 1967). Body weight to the nearest half kilogram was measured using a spring dial scale suspended from a tripod. No corrections were made for blood loss. Blubber thickness (± 0.5 cm) was measured on the ventral line at the sternum and at the hip (60% of distance from nose to tail).

The lower 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 was cut in cross-section so that age could be determined by reading the dentinal annuli under transmitted light. Duplicate, independent readings of each tooth were done by the same reader, and a third reading was done 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. Ringed seal ages determined from counts of dentinal layers tend to be lower than ages derived by reading of cementum layers, particularly for seals older than 10 years. For younger seals, however, ages obtained using the two methods were well correlated (Stewart et al., 1996). In this study, we used the same ageing method and readers that were used in the 1970s series in order to maintain consistency in the full data set.

Left and right ovaries were sectioned following the methods described by Smith (1973), and the presence of corpora lutea was recorded. Pregnancy could not be detected directly from the presence of a foetus during our

TABLE 1. Age-specific status of reproductive tracts and occurrence of ovulation in female ringed seals, 20 yr and younger, 1992–2011.

		Reproductive Tract State			Ovulation	
Age	n	Nulliparous	Primiparous	Multiparous	No. ovulated	Proportion
0	157	157			0	0.0
1	22	22			0	0.0
2	12	12			0	0.0
3	10	9		1	2	20.0
4	15	15			0	0.0
5	17	16		1	2	11.8
6	20	18		2	1	5.0
7	37	30	1	6	18	48.6
8	25	14	1	10	16	64.0
9	27	12	1	14	19	70.4
10	31	9	1	21	23	74.2
11	29	7	1	21	21	72.4
12	30	6		24	25	83.3
13	27	1	5	21	25	92.6
14	48			48	44	91.7
15	39		1	38	34	87.2
16	41	2	1	38	39	95.1
17	40	1		39	40	100.0
18	39			39	38	97.4
19	27			27	24	88.9
20	21	1		20	19	90.5

June–July sampling, since implantation and foetal development do not take place until September (Smith 1973, 1987). The mean date of ovulation in eastern Amundsen Gulf is 25 May (Smith, 1987), prior to the start of our sampling efforts. We classified a female as mature if there was a corpus luteum in an ovary, or if examination of the uterus provided evidence of at least one previous pregnancy. We considered a large, recently erupted corpus luteum to be evidence of recent ovulation in females that were sampled in June or July. Ovaries of immature females lacked any follicular structures and evidence of previous pregnancy in the uterine cornua and were classified as nulliparous.

Data Analysis

We analyzed data on 2281 ringed seals sampled between 1992 and 2011, using Excel and SAS (1990). The mean age of maturity (equivalent to first ovulation) and mean age at first pregnancy (females with evidence of at least one previous birth) were calculated according to DeMaster (1981), using age-specific ovulation and reproductive tract data for 1992–2011 (Table 1). The proportion of mature females that ovulated in a given year was tabulated for females 20 years and younger in which uterine condition indicated at least one previous pregnancy.

The percentage of pups in the subsistence harvest provides a measure of recruitment. This value was calculated only from the harvest in the open water season, when all age classes are present, which most closely represents the age structure of the population (Smith, 1973). For this aspect, we did not use data collected during periods of ice cover, when adults predominate, subadults tend to be excluded from core harvesting areas by competition with adults, and pups are usually in lairs and thus inaccessible to hunters (Smith, 1987).

Asymptotic lengths for males and females for 1992–2011 were estimated using PROC NLIN in SAS without weighting. Body condition was calculated using a length-mass-blubber depth (LMD) index (Ryg et al., 1990):

$$LMD = \sqrt{L/M} \times d \times 100,$$

where L = standard length (m), M = body weight (kg), and d = blubber depth (m) at the hip.

LMD for 1263 adults (age 7 yr or more) and 102 subadults (age 1–6 yr) sampled at Masoyak in June or July during 1992–2010 was analyzed using additive components-of-variance models. General linear models were fitted by least squares with PROC GLM in SAS, and components-of-variance models were fitted by Bayesian methods using WinBUGS and by maximum likelihood using Excel Solver. Sex, year, and month were considered as possible effects.

We investigated year-to-year variation in LMD in relation to the timing of spring clearance (breakup) of fast ice in east Amundsen Gulf and west Prince Albert Sound (Fig. 1). Navigational ice charts prepared by the Canadian Ice Service over the last four decades 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 (http://ice-glaces.ec.gc.ca). The date of ice clearing was taken as the earliest date when a largely ice-free area was charted in the domain of interest. According to the practice of the Canadian Ice Service, a lead (or generally ice-free area) would need to be persistent and at least 10 km wide to be charted. In early summer, the floe edge spans the mouth of Prince Albert Sound from north to south, so that the first area for clearance is east Amundsen Gulf. As the pack ice in the gulf is blown to the west under prevailing winds, a flaw lead forms seaward of the floe edge. Clearance of ice from west Prince Albert Sound occurs days or weeks later, when a curved line of fracture extending into the sound frees a slab of fast ice. Winds then move this slab westward to create ice-free conditions in the west Prince Albert Sound area.

The date of ice formation was the earliest date in the autumn when a complete cover of new ice was indicated on the ice chart. The duration of the open water season each year was calculated as the number of days between the date of ice clearance and that of ice formation. Least-squares linear regression was used to estimate trends in these variables from 1970 to 2011.

To examine variability in the annual dates of ice clearing, we tabulated ice clearing dates, by year, for west Prince Albert Sound and east Amundsen Gulf, and then subtracted the linear trend to yield a time series of residuals. Mean and standard deviation of the residuals were calculated separately and compared for two 20-year intervals, 1970–90 and 1991–2011. Confidence limits on the variance were estimated using a chi-square distribution.

For our analysis of year-to-year variation in LMD in relation to the timing of spring ice clearance, we focused on east Amundsen Gulf because it is the main location where the seals forage at this time of year. Marginal and partial correlations of LMD were done on year and on ice clearance date, as well as a principal components analysis of the multiple correlations of the three variables, LMD, year, and ice clearance date. These analyses were done separately for adults and subadults, by sex.

We compared the mean LMD value for ovulating mature females to that for non-ovulating mature females, using PROC GLM and a Duncan's multiple range test (SAS, 1990). We attempted to estimate a threshold of body condition at which ovulation failure would be expected, using a kernel smoothing of the proportion ovulating plotted against LMD. To investigate the power of LMD to discriminate, we fitted normal distributions to the LMD data for mature adult females with and without evidence of ovulation.

RESULTS

Sea Ice

Over the 40-year record from 1970 to 2010, there was a trend toward earlier ice clearance in spring, 7.4 days per decade in east Amundsen Gulf and 3.1 days per decade in west Prince Albert Sound. Both values were statistically significant at the 90% level (Fig. 3). Trends towards later freeze-up were not apparent.

There was no evidence of increased variability in the annual timing of ice clearance in recent years in either west Prince Albert Sound or east Amundsen Gulf. For west Prince Albert Sound, the earliest clearing was 29 June (in 1998) and the latest 2 September (in 1986), a span of 9.3 weeks; the median was 25 July. The sample standard deviations for the 1970–90 and 1991–2011 intervals were similar, 12.9 and 13.1 days. The 90% confidence bound on the true values of sigma spans much greater ranges (7.4 and 7.5 days) than this 0.2-day difference in the sample standard deviation, which is therefore judged insignificant at a 90% confidence level. This result indicates that there has not been a trend toward increased variation in time of ice clearance in west Prince Albert Sound in recent years.

For east Amundsen Gulf, the median ice clearing date was 26 July (mean = 11 July) and the median freeze-up was 24 Oct (mean = 23 Oct). The sample standard deviation in ice-clearing date for east Amundsen Gulf was 2.5 times that for west Prince Albert Sound (32.3 versus 12.8 days) during 1970–2010. Small increases in the variability of clearing date occurred between 1970–90 and 1991–2010; the larger increase, from 28.4 to 36.3 days, was observed in eastern Amundsen Gulf. However, neither increase was statistically significant at the 90% level. Again, the 90% confidence bounds on the true values of sigma span much greater ranges (16.4 and 20.9 days) than the difference between the sigma values for the first and second halves of the 40-year record (7.9 days). This result again provides no evidence for significantly (at the 90% confidence level) increased variability in ice clearance date in recent years in east Amundsen Gulf, although there was more variability there than in west Prince Albert Sound.

Ringed Seals

Ringed seal sampling took place annually between 1992 and 2011, and on average, our annual sample size was equivalent to approximately 28% of the mean annual harvest estimated for the community of Ulukhaktok from 1987 to 1997 (Joint Secretariat, 2003). Of 2281 seals sampled, 2034 (89.2%) were harvested during the months of June and July, and 1953 (85%) were sampled by the same hunter (JA). The other seals in the sample were measured by three other hunters, all with extensive, previous experience measuring and sampling seals in this area. Females made up 42.4% of the overall sample. Of the total, 34% of seals (n = 777) were shot on the ice and 65.9% (n = 1504) in the open water.

The mean age in the 1992–2011 sample was 10.6 yr (SD = 8.1, n = 928) for females and 10.71 yr (SD = 8.1, n = 1273) for males. Although seals from all ages were represented (Fig. 4), the sample consisted mostly of adults (age 7 and older, 65.6%, n = 1464) and pups (20.5%, n = 457), with relatively few subadults (1–6 yr; 14.0%, n = 314). Asymptotic lengths were 122.4 cm (SE = 0.67, n = 918) for females and 128.5 cm (SE = 0.57, n = 1270) for males. Calculated from values in Table 1, age of maturity was 6.32 yr (SE = 0.60) and age of first pregnancy was 7.08 yr (SE = 0.61).

Body Condition

Only seals sampled during the months of June and July were included in the condition analyses. The month of sampling had no significant effect on LMD of adults, so month was excluded from the model. While there was a small

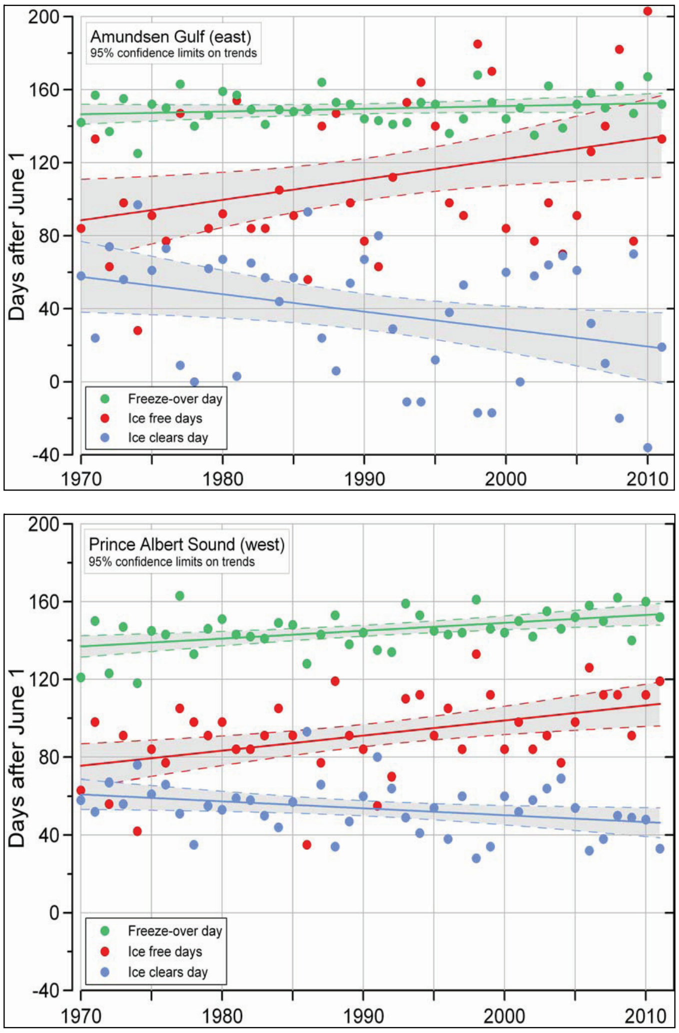

FIG. 3. Ice clearing date, number of open water days, and freeze-up date for east Amundsen Gulf and west Prince Albert Sound, 1970–2011.

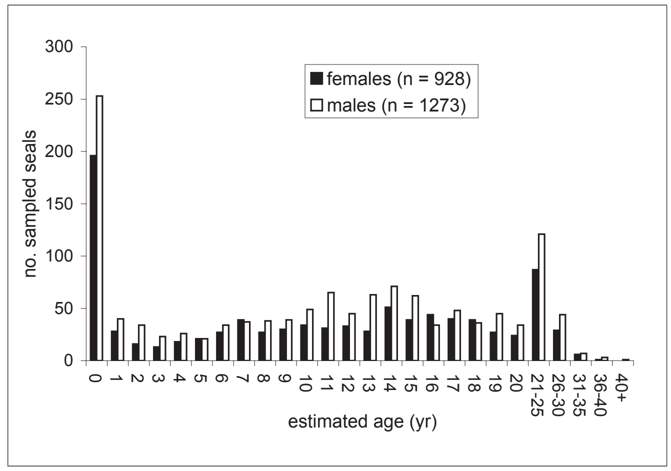

FIG. 4. Distribution of estimated ages of females and males in the Masoyak ringed seal harvest sample, 1992–2011.

month-year interaction, we did not consider it further in order to simplify the model. The sex-year interaction was not significant, with LMD of adult females and adult males varying in the same way from year to year. The resulting model had only sex and year effects, both of which were highly significant, as described below.

Mean LMD was 14.8 (SD = 3.67, n = 269) for adult females and 13.7 (SD = 2.97, n = 422) for adult males, with considerable year-to-year variation. The lowest mean annual adult LMD indices were recorded in 2005 and 2009, and the highest in 1992, 1993, 1994, and 1998. The variation among years was close to a normal distribution without evident skewness or outlying values.

There was a significant trend of decreasing mean annual LMD values in adults over the two decades of study. Overall, 57% of the between-year variance in annual mean condition of adults between 1992 and 2010 could be accounted for by a linear trend of LMD condition decreasing by about 0.144 $m^{1.5}/kg^{0.5}/y$ (SE = 0.029) (Fig. 5). The residual of condition after fitting the trend was, again, close to normal, with no outliers and no obvious skewness. The standard deviation of the residuals of LMD about the fitted relationship with year was 0.68.

The mean difference between the sexes was nearly constant from year to year (1.11, SE = 0.18). The uncorrected between-year standard deviation in LMD, for the period analyzed, was the same for the two sexes, with a maximum likelihood (ML) estimate of 1.040 (SE = 0.076). The variation between individuals induces uncertainty in the year effects, which inflates the simple estimate of between-year variance. An approximate corrected value for the between-year standard deviation for adults was 0.970.

The within-year standard deviation of LMD was significantly greater for females (ML estimate 3.26 with SE = 0.16) than for males (2.75, SE = 0.11). The foregoing analyses were carried out without regard for the reproductive state of adult female seals, which, however, when included, made little difference to the variance. The largest component of variation in this data set is that between individual seals of the same sex, within the same year. The variation between individuals was about three times as great as that between years or between the sexes.

Patterns were similar for subadults collected during the same sampling period. As for adults, there was a decreasing temporal trend in average condition over the sampling period (Fig. 6). The absolute value of the decrease was greater for subadults (0.24 $m^{1.5}/kg^{0.5}/y$, SD = 0.16) than for adults, but it accounted for only 10% of the much greater between-year variation observed in the subadults.

In subadults, the two sexes shared the same years of high and low condition, with females having on average slightly greater LMD values than males (n = 102, 16.2 vs 14.8; difference 1.39 with SE = 0.80). The between-year variation, however, was much greater for subadults than for adults: 4.03 (SE = 0.44). The variability between individuals was similar to that for adults and only slightly greater for females than for males (3.63, SE = 0.39 vs 3.59, SE = 0.37); this difference was not statistically significant for subadults.

The year effect for subadults did not follow a normal distribution as closely as that for adults, and there were

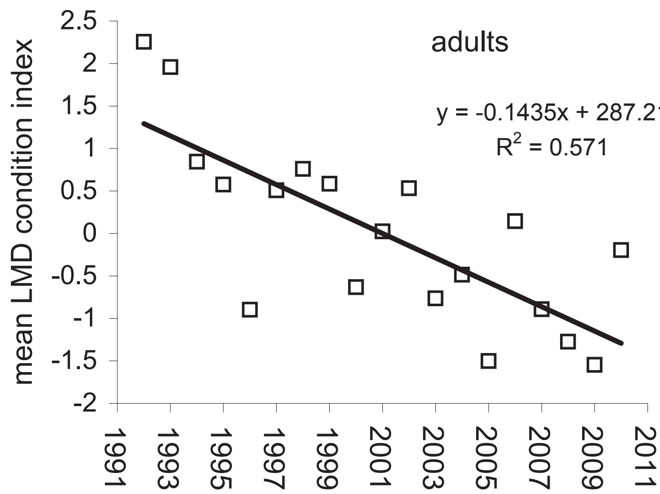

FIG. 5. Mean annual body condition indices of adult ringed seals sampled at Masoyak in June and July, 1992–2010.

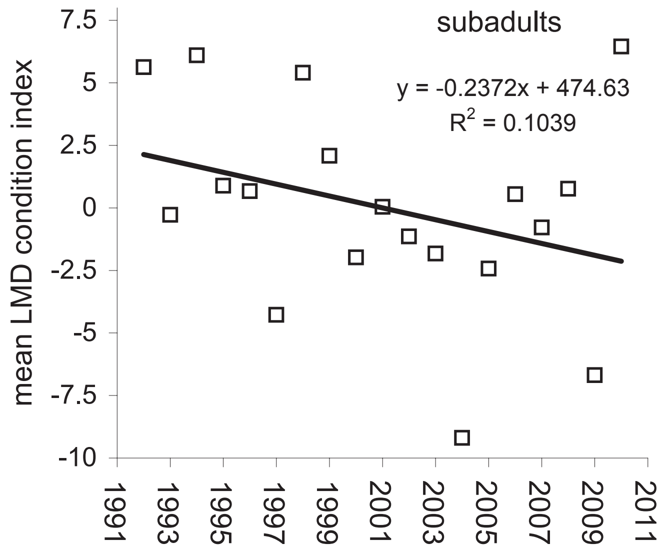

FIG. 6. Mean annual body condition indices of subadult ringed seals sampled in June and July, 1992–2010.

outlying groups. There were four high-condition years (1992, 1994, 1998, 2010) and two low-condition years (2004, 2009). In contrast to the adult pattern, the largest component of the variation for subadults was between years.

There was some agreement between the rankings of years for adult and subadult LMD, with a rank correlation of 0.53. This correlation was not due to the decrease with time in the condition indices for both age groupings, as the partial correlation after removing the linear trend was nearly as high, 0.48.

Next we examined the relationship between annual LMD values and the corresponding spring dates for clearance of the sea ice in east Amundsen Gulf. For subadults of both sexes, the correlation of LMD with ice clearance date (later ice clearance = worse condition) was highly significant statistically, and this correlation increased when the effect of year was partialed out. For this age class, there was also a marginally significant trend of worsening condition with time (Table 2).

For adults, overall, there was a similar trend, but there was not a statistically significant correlation between condition and ice clearance date, regardless of whether the time effect was removed. The effect (slope of linear regression) of condition against ice clearance date was small, one-sixth the effect for subadults (Table 2). However, the effect of year, though only one-half the effect for subadults, was significant for adults. That is, the condition of adults has apparently worsened over the two decades examined, but not because of a progressive change in the date of ice clearance.

Reproduction and Body Condition

In total, 329 females aged 7 to 20 years, collected at Masoyak, were examined for the presence of a corpus luteum (CL). Of these, only 23 adult females had no CL (failed ovulation), and they were, on average, in poorer body condition (mean LMD = 13.5, n = 23) than adult females that had ovulated (mean LMD = 15.5, n = 312; Duncan's multiple range test, $p < 0.05$).

For females 20 yr and younger with evidence of previous pregnancy, the pooled ovulation rate was 92.4% (SD = 16.3). Annual ovulation rates varied, however, ranging from a low of 30% in 2005 to 76% in 2004 to 100% in each of 1994–98, 2001–02, and 2006–2011 (Fig. 7). The small sample of non-ovulating adult female seals was not randomly distributed between years (Fig. 8), with incidence of non-ovulating mature females occurring mainly in 2004 and 2005, and overall in only 7 of the 20 years sampled. The year 2005 provided the strongest signal in our 1992–2011 data, the lowest mean adult LMD value (Fig. 5), and particularly late clearance of the sea ice in spring. We also note that 2005 was preceded by three consecutive years of ice clearance dates that were 40 days later than the 1992–2011 average (Fig. 7), and that 7 of 10 mature adult females sampled in 2005 failed to ovulate. With one exception, the LMD values of all non-ovulating adult females sampled that year were lower than the median LMD for the entire sample (Fig. 8).

The annual proportion of pups in the open water harvest also varied between years from 0% to 61.5% (mean 29.8%) (Fig. 9). In 1992 to 2011, as with the ovulation rates, 2004 and 2005 were among the years with lowest percentage of pups in the harvest (6.4% and 3.3%, respectively), latest spring ice clearance dates, and lowest annual LMD values (subadults, 2004, Fig. 6; adults, 2005, Fig. 5).

To estimate a threshold of body condition at which failed ovulation might be expected, we did a kernel smoothing of the proportion of ovulating females against body condition. The kernel for LMD was normal, with SD = 1.6. A wide kernel was necessary because the data included only 23 adult female seals that did not ovulate. At LMD index values of about 18 and over, the smoothed proportion of ovulating females was just over 95% (Table 3). Seals in worse

TABLE 2. Mean annual LMD of ringed seals sampled during June 1992–2010 compared with ice clearance date in east Amundsen Gulf, 1992–2010.

	LMD–year (partial)[1]		LMD–ice clearance day (partial)	
	Correlation (%)	Slope/yr (×100)	Correlation (%)	Slope/d (×100)
Subadult females	-42 (-56*)[2]	-40 (-31)	-81*** (-85***)	-12 (-12)
Subadult males	-48 (-57*)	-33 (-28)	-70** (-74**)	-7.2 (-6.7)
Adult females	-58** (-58*)	-21 (-20)	-37 (-37)	-2.1 (-1.7)
Adult males	-71*** (-72***)	-18 (-17)	-34 (-38)	-1.3 (-1.0)

[1] A partial correlation (or regression) is the correlation (or regression) of residuals after removing the linear effect of the other variables from all the variables included in the analysis.

[2] * = $p < 0.05$, ** = $p < 0.001$, *** = $p < 0.0001$.

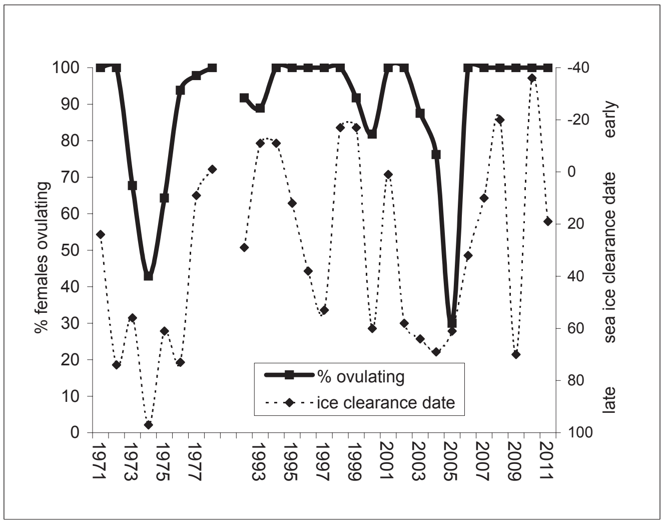

FIG. 7. Annual ovulation rate of mature adult females (n = 385) and annual date of ice clearance in East Amundsen Gulf in spring, 1971–78 (adapted from Smith, 1987) and 1992–2011.

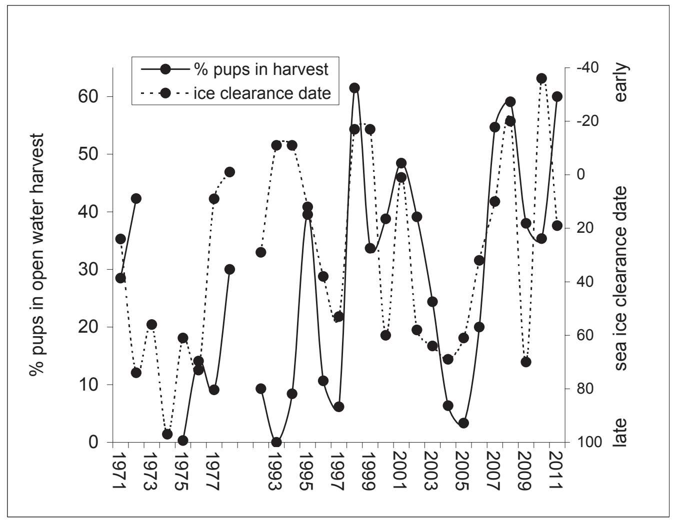

FIG. 9. Annual percent pups in the open water harvest and annual date of ice clearance in east Amundsen Gulf in spring, 1971–78 (adapted from Smith, 1987) and 1992–2011 (this study).

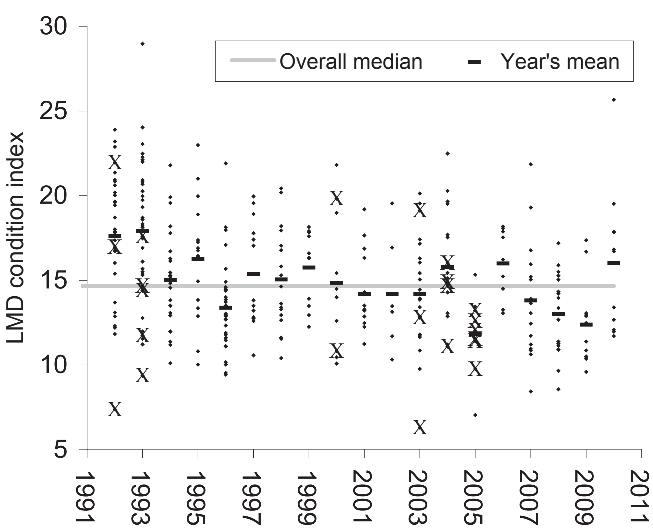

FIG. 8. Annual body condition indices of ovulating (•) and non-ovulating (X) mature female ringed seals, 1992–2011.

condition had progressively lower ovulation rates, and at LMD values below 10, the decline was markedly steeper. However, the lowest value reached with this smoothing was still greater than 80% at LMD 8, consistent with the small number of seals in the sample that did not ovulate.

Recognizing that the kernel smoothing would be expected to bias the estimated ovulation rates upwards at low LMD, owing to the increasingly sparse data in this region, we also fitted an increasing negative-exponential curve (von Bertalanffy curve) by likelihood methods. This curve was defined by the ovulation rates in Table 3. As expected, ovulation rate estimated by this method dropped further at low LMD values (e.g., 63% at LMD = 8), but again ovulation rates at low LMD values are uncertain, given the sparseness of data in this region. Although there was a difference in the distribution of LMD between adult females that ovulated and those that did not ovulate, the overlap in the distributions was large, and the power of LMD to discriminate ovulating females from non-ovulating females was weak with this particular core-habitat data set.

DISCUSSION

This long-term sample of harvested ringed seals from a core breeding habitat in Canada's Western Arctic revealed

TABLE 3. Ovulation rate and LMD estimated from data for 329 female ringed seals aged 7–20 years sampled from western Prince Albert Sound (von Bertalanffy curve fitted by maximum likelihood).

LMD condition	8	10	12	14	16	24
Est. ovulation rate (%)	63.1	86.0	92.5	94.4	95.0	95.2
SE (percentage points)[1]	18.9	8.0	3.4	2.0	2.3	2.8
Estimated CV for prop. not ovulating (%)	51	57	45	36	46	58

[1] Standard errors have been estimated from narrow likelihood-support intervals and are approximate.

a significant trend of decreasing mean annual body condition of adult and subadult ringed seals over the past two decades. The fact that the changes in body condition were well matched among years and sex/age groupings suggests that the trend may be linked to ecosystem changes in the seal's diet, possibly from shifts in fish species composition or availability. Mammals at or near the top of the food chain, like ringed seals, serve as effective indicators of significant changes that are occurring in the ecosystem, even if the mechanisms causing such changes are not understood. This temporal trend of declining seal body condition was also apparent in ringed seals in Hudson Bay during the same period (Chambellant, 2010).

A second main result of this study was that ringed seal body condition, particularly that of subadults, varied with changes in the timing of sea ice clearance in spring. Seals sampled in years of late ice clearing had, on average, lower body condition than those sampled in years of earlier ice clearing, particularly in the case of subadults. The situation was reversed in years of early spring sea ice clearance, such as 1998 (Smith and Harwood, 2001). This ice-related variation in seal condition has been documented previously during extreme ice years in the Beaufort/Amundsen region, and possibly as far back as the 1960s (Stirling et al., 1977; Smith, 1987; Kingsley and Byers, 1998; Harwood et al., 2000; Smith and Harwood, 2001; Stirling, 2002).

During the last four decades, the ovulation rate of mature female ringed seals in East Amundsen Gulf/Prince Albert Sound was generally high (80%–100%) and typical of the species (McLaren, 1958; Smith, 1973, 1987; Reeves, 1998; Krafft et al., 2006). Marked declines were seen in 1974 (Smith, 1987), in 1987 (Kingsley and Byers, 1998), and in 2005 (this study), all times when seals were in significantly poorer body condition. A corresponding lower percentage of pups in the harvest in the year following these instances of failed ovulation was also recorded in the 1970s (e.g., 0.3 % pups in 1975, Smith, 1987), in the 1980s (Kingsley and Byers, 1998), and in this study (2005). Signals were detected in the most extreme ice years (e.g., when fast ice breakup occurred 3–8 weeks later than the average since 1970) and were linked to the degree of severity of winters, as indicated by the annual ice regime. Similar linkages of late ice clearing and reduced seal recruitment have also been reported for ringed seals in Hudson Bay (Stirling, 2002, 2005; Ferguson et al., 2005; Chambellant et al., 2012).

Although spring ice clearance date is a crude measure of the specific ice conditions important to ringed seals, it represents a suite of prevailing conditions, including winds, currents, and air and water temperatures. It does not reveal specific factors such as the location or the quality and quantity of prey available throughout the ice-covered season, nor does it measure the precipitation, winds, and sea ice surface deformation that influence the suitability of snow depth for construction of lairs (Smith, 1987; Ferguson et. al, 2005). Late ice clearing does appear most likely to serve as an index of less favourable feeding conditions (as yet undefined). Such conditions might involve additional energy expenditures either in distance of travel to find food, or having to switch to prey that is lower in calories or more difficult to capture, and prolonged exposure to predation by polar bears. There are also some indications that oceanographic changes typical of heavy ice winters such as those of 1973–74 (Smith, 1987), 1987–88 (Kingsley and Byers, 1998), and 2004–05 (this study) could have affected seals by decreasing overall pelagic productivity (Forest et al., 2011), which in turn would reduce available prey for arctic cod, the main prey of ringed seals. The opposite appears to occur during years when ice retreat is early (e.g., 1998; Smith and Harwood, 2001; Wu et al., 2007), and early ice retreat, along with coastal upwelling, has been documented to contribute to exceptionally high primary productivity in the Beaufort Sea (Sallon et al., 2011).

When examining the association between seal condition and the annual sea ice regime, we must bear in mind that the variations and trends of climatic indicators (e.g., timing of sea ice clearance) depend upon the geographic scale and region in which the study is conducted. In the Beaufort/Amundsen region, for example, observations over the last 40 years have revealed large fluctuations in ice presence and thickness over intervals of years to decades, with so far only small trends toward earlier ice clearance and longer open water seasons (Melling and Riedel, 2004; Melling et al., 2005). The pan-Arctic perspective, in contrast, has revealed statistically significant trends toward thinner ice, earlier ice clearance, and longer ice-free seasons (Comiso and Parkinson, 2004; Serreze et al., 2007; Walsh, 2008). These trends are in large part linked to the decreasing presence of thick multi-year sea ice in the Arctic as a whole. They do not appear in our ice data and region of study because multi-year ice has never been common there.

The status of the polar bear population in the North Beaufort Sea (Stirling et al., 2011) corroborates the picture of changes in ecosystem productivity and sea ice in this region. Over the same time period as this study, this more northerly and easterly population of bears has remained relatively stable, with ice availability and conditions remaining suitable (or having not reached some lower threshold yet) for polar bears feeding largely on seals in summer and fall (Stirling et al., 2011). This was not the case for populations of bears in the South Beaufort or in Hudson Bay (Stirling et al., 1999, 2008), which have fluctuated or declined, respectively, likely as a result of reduced sea ice reductions and the concomitant lesser availability of seals. Specifically, Stirling et al. (2008), on the basis of cannibalized and starved bears in the southern Beaufort Sea, concluded that polar bears were nutritionally stressed from 2004 through 2006. One possible explanation was a decadal-scale downturn in seal productivity (Stirling et al., 2008), which was indeed apparent in our Masoyak seal data in those same years.

As was the case in similar studies in Hudson Bay (Chambellant et al., 2012), the sample of non-ovulating seals taken from the Masoyak core breeding habitat was too small to permit us to predict with statistical confidence a level of lower body condition at which wide-spread ovulation failure would occur (Thomas, 1982). Nevertheless, the 23 non-ovulating females that we sampled were generally in poorer body condition than those that did ovulate (Fig. 8). In addition, the distribution of annual ovulation rates was strongly skewed, with only one low value from 1992–2011 (2005) and two consecutive low values (1973 and 1974) during the 1970s (Smith, 1987) (Fig. 7). This pattern is similar to that reported by Stirling (2005) and Chambellant et al. (2012) for Hudson Bay for the 1990s and 2000s. Collectively, results suggest that failed reproduction does occur periodically in ringed seal populations, but to date it has been detected only during extreme ice years (e.g., delayed ice retreat in spring) (Fig. 7). Populations in the Beaufort and Amundsen regions appear to recover from these failures within one or two seasons following the extreme year.

In mammals like ringed seals, with delayed implantation, it is normal for almost all adult females to ovulate, even when they are in relatively poor condition, simply because it does not cost much in energetic terms to do so. Later, after a period of feeding and improved or at least changed condition post-ovulation, the female can then continue, or not, with pregnancy, which probably depends on her body condition at the time. Because of this, when females do not even ovulate, especially such large proportions of them as was the case in 1974 or 2005 (Fig. 7), it strongly suggests that a consequential effect has occurred. The fact that we did detect a failure of ovulation from this core area indicates that there may have been larger-scale failed reproduction caused by widespread changes in resources on which regional ringed seal populations depend, even though we do not understand the mechanisms involved.

Seals also reside in non-core, less populated habitats (e.g., North Slope of Alaska, or offshore from the west coast of Banks Island). Such habitats may be more sensitive locations from which to detect wide-scale reproductive failure (e.g., Kingsley and Byers, 1998) and declines in seal body condition. We may have witnessed such failure in the sample of subadults for which reductions in condition were more closely linked with extreme ice years, while the effect was buffered in adults, who occupy the more stable core habitats. Subadults occupy a larger, peripheral, and less productive area because they are excluded by competition with adults from the prime habitats (Smith, 1987; www.beaufortseals.com), and this is likely the reason that they have shown more variation in body condition and have a greater response to changes in timing of sea ice clearance. It would be desirable to obtain a long-term sample of all age classes from a larger geographical area in order to monitor regional changes in annual productivity in the future. Unfortunately, obtaining a sufficient sample size using a harvest-based study from so large an area is usually not practical or is precluded by lack of secure long-term funding.

Pups would normally be expected to comprise approximately 20–30% of an open water harvest (Smith 1973, 1987), and our overall mean percentage of pups (26.3%) was within this range. In this study and others in the same region (Stirling et al., 1977; Smith, 1987; Kingsley and Byers, 1998), and also in Hudson Bay (Ferguson et al., 2005; Stirling, 2005; Chambellant et al., 2012), the proportion of ringed seal pups taken in the subsistence harvests has varied widely among years (0–61.5%). In the 1992–2011 sample, and as noted for the ovulation rate data, 2004 and 2005 were among the years with lowest percentages of pups in the harvest (6.4% and 3.3%, respectively). These low percentages further affirm that 2004–05 was likely a period of low seal productivity in east Amundsen Gulf and west Prince Albert Sound, which is also corroborated by nutritional stress noted in polar bears in those same years (Stirling et al., 2008).

It is important to note that while the annual percentage of pups in the harvest is used as an indicator of trends in seal population recruitment, these must be interpreted as broad trends and in the context of the local weather and ice conditions. Weather and ice can significantly affect the success of the annual seal hunt and the proportion of pups in the harvest, as we witnessed in the early breakup of pupping habitat in Prince Albert Sound in 1998 (Smith and Harwood, 2001). It would be preferable to use the percentage of pups as a recruitment measure from samples taken in August and later, since the hunting bias caused by the variability in pattern of ice breakup will have dissipated. A more direct and unambiguous measurement of pup production, such as intensive birth lair surveys (Smith and Stirling, 1975, 1978; Lydersen and Gjertz, 1987; Hammill and Smith, 1989; Kelly and Quakenbush, 1990; Furgal et al., 1996), would be especially informative in the assessment of trends in pup production and less subject to sampling (hunting) bias. Such surveys should be considered as an important periodic monitoring approach if long-term downward trends in ringed seal recruitment are suspected in areas of core ringed seal breeding habitats.

Our results point to the need for more detailed study of the causes for declining body condition, as part of the annual Masoyak seal monitoring study. While the seal population appears to have recovered from as many as four extreme-year fluctuations in reproduction during four decades of monitoring in the Beaufort/Amundsen region (Stirling et al., 1977; Smith, 1987; Kingsley and Byers, 1998; this study), the possible magnified effect of several consecutive extreme ice years, compounded by the nutritional stress presently manifest as a declining trend in seal body condition over the past two decades, is of obvious concern. Our results illustrate why long-term studies are necessary to reveal trends, particularly in ecologically important areas.

Identification of the types of food used by the seals is needed to elucidate changes in diet and thus point to the larger-scale environmental changes that are taking place. Future and archived tissue samples from this study are excellent candidates for dietary analysis studies using techniques such as fatty acid signatures (Thiemann et al., 2007, 2008) and stable isotopes (Kelly, 2000; Chambellant et al., 2012). Our sample of 100 seals per season from this core habitat location, arguably the most predictable and largest available harvest sample from the western Canadian Arctic, was sufficient to document clear temporal and ice-related trends in body condition of adult and subadult seals. A smaller sample would be inadequate given the large variation among seals of the same sex and age-class in the same year.

Our collective observations from 40 years of monitoring the ringed seal populations in the western Canadian Arctic have shown that significant changes are occurring in the marine ecosystem. This finding has been mirrored by the southern Beaufort polar bear population, which has shown similar effects at the population level. Unfortunately the lower trophic levels have not had the attention or the long-term studies needed to provide an explanation for the changes we have documented. We hope that our findings will provide some motivation for those in the fields of physical and biological oceanography to address these questions and contribute to the answers, which will be of great importance to the understanding of ecosystem processes and changes in the future.

From our perspective in considering future ringed seal studies, it would be productive to augment sea ice and seal body condition studies with other research approaches, to further unravel the factors that affect body condition and influence ringed seal reproduction. To date, limited sample sizes of tagged seals suggest that the winter distribution of seals varies widely between years (e.g., by a factor of 10) and is influenced by the severity of winter ice conditions (www.beaufortseals.com).

The opportunity to study the distribution of the formerly completely elusive winter distribution and abundance of arctic cod and other marine food species now exists with the satellite tagging of ringed seals. Marine mammals used as “educated” oceanographic sampling platforms (Smith, 2001; Lydersen et al., 2002, 2004; Fedak et al., 2011) could provide a key to understanding the proximate factors influencing cod distribution. Once a sufficient sample of seals has been tagged over several years, it should be possible to discern where and when they feed and assess the oceanographic conditions and ice characteristics at those locations. This information, along with data on body condition from the harvested seal specimens and the identification of their food species, would be directly pertinent to the study of the factors influencing the productivity of ringed seal populations.

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