

Variation in Reproduction and Body Condition of the Ringed Seal (*Phoca hispida*) in Western Prince Albert Sound, NT, Canada, as Assessed Through a Harvest-based Sampling Program

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ABSTRACT. Between 1992 and 1998, 869 ringed seals taken in the subsistence harvest in western Prince Albert Sound were sampled by two Inuvialuit seal monitors from Holman, Northwest Territories. Considering the 1992–98 data along with data from 1971–78, we found that the mean body-mass index (BMI) values for females (≥ 7 yr) were significantly lower in 1974 than in all other years examined. At the same time, ovulation rates fell from 100% in 1971 and 1972 to lows of 42.9% (1974) and 64.3% (1975), with a return to 93.8% in 1976. Mature females that had ovulated had significantly higher BMI values than those that had not ovulated. In eastern Amundsen Gulf, 1974 was the most severe ice year on recent record, with the latest date of clearing of the landfast ice (6 September), the earliest date of new ice formation (4 October), and the fewest number of open water days (28 days). There were no years between 1992 and 1998 that compared to 1974 in reduced ovulation rates, reduced body condition, or severity of ice conditions. Between 1992 and 1998, mean BMI values for adult females and males were lowest in 1994 and highest in 1998, and all annual mean BMI values were between the extremes of the 1970s. This variation in condition in the 1990s did not coincide with a reduction in ovulation rates of mature females, which remained high (93.5–100%) from 1992 to 1998. In 1998, the landfast ice cleared 43 days earlier than the average clearing date for the 1990–98 period, apparently interrupting the lactation period for seal pups located at the periphery of the core breeding habitat. The apparent effects on growth and condition of unweaned pups came at a time when marine food appeared to be abundant and available to all age classes of ringed seals.

Key words: Amundsen Gulf, body condition, ice, ovulation, Prince Albert Sound, ringed seal

RÉSUMÉ. Entre 1992 et 1998, 869 phoques annelés pris dans le cadre de la récolte de subsistance de l'ouest de la baie Prince-Albert ont fait l'objet d'échantillonnages par deux moniteurs inuvialuits de Holman (T. N.-O.), chargés de la surveillance des phoques. En tenant compte des données de 1992 à 1998 jointes à celles de 1971 à 1978, on a trouvé que la valeur moyenne de l'index de masse corporelle (IMC) pour les femelles (≥ 7 ans) était sensiblement inférieure en 1974 par rapport à toutes les autres années de l'étude. En même temps, les taux d'ovulation ont chuté, de 100 p. cent qu'ils étaient en 1971 et 1972 à 42,9 p. cent en 1974 et à 64,3 p. cent en 1975, opérant une remontée à 93,8 p. cent en 1976. L'IMC des femelles adultes qui avaient ovulé était sensiblement plus élevé que celui des femelles adultes qui n'avaient pas ovulé. Dans l'est du golfe Amundsen, l'année 1974 fut celle qui connut la plus intense formation de glace enregistrée récemment, avec la date la plus tardive pour la disparition de la glace de rive (6 septembre), la date la plus précoce pour la formation de la nouvelle glace (4 octobre) et le plus petit nombre de jours de mer libre (28 jours). Entre 1992 et 1998, aucune année n'était comparable à 1974 en ce qui a trait à la réduction des taux d'ovulation, la réduction de l'état corporel ou l'intensité de la glace. Entre 1992 et 1998, les moyennes de l'IMC pour les femelles et pour les mâles adultes étaient les plus basses en 1994 et les plus élevées en 1998, et toutes les moyennes annuelles de l'IMC se situaient entre les extrêmes des années 1970. Cette variation dans l'état corporel durant les années 1990 n'a pas coïncidé avec une réduction du taux d'ovulation des femelles adultes, qui est resté élevé (de 93,5 à 100 p. cent) de 1992 à 1998. En 1998, la glace de rive a disparu 43 jours plus tôt que la date de dégagement moyenne pour la période se situant entre 1990 et 1998, ce qui semble avoir interrompu la période de lactation pour les bébés phoques qui se trouvaient à la périphérie de l'habitat de reproduction principal. Les effets apparents sur la croissance et l'état des bébés phoques se sont produits à un moment où le réseau trophique marin était abondant et à la portée de toutes les classes d'âge des phoques annelés.

Mots clés: golfe Amundsen, état corporel, glace, ovulation, baie Prince-Albert, phoque annelé

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INTRODUCTION

The ringed seal (*Phoca hispida*), abundant throughout the circumpolar Arctic, is an important element of arctic marine ecosystems. The ringed seal is the main prey of the polar bear (*Ursus maritimus*). Ringed seals themselves feed at several trophic levels, showing seasonal and age-related differences in prey selection (Dunbar, 1941; Lowry et al., 1978, 1980; Smith, 1987). Ringed seal stocks have yet to be defined, but evidence suggests that at least some individuals undertake large-scale movements (1000s of km), probably in response to food availability (Smith, 1987).

The large bays of Amundsen Gulf, including Prince Albert Sound, are particularly important to the ringed seal in the western Arctic. During ice-covered periods, the seals establish and maintain territories, the ice providing a substrate for pupping, lactation, haul-out, and protection from weather and predators (Smith and Stirling, 1975, 1978; Stirling et al., 1982; Smith, 1987).

The ringed seal is an important species in the subsistence economy of the Inuvialuit, the Inuit of Canada's western Arctic. Seal harvests between 1988 and 1996 averaged 1050 per year (Fabijan, 1995a, b, 1997), which is approximately 20–30% of harvest levels in the 1960s and 1970s (Inuvialuit Regional Corporation, 1989). Most of the Inuvialuit harvest of seals (75.7% between 1988 and 1996) is taken by the residents of Holman. Both the harvests of the 1960s–70s and present-day harvests are a small proportion (0.6% and 0.1% respectively) of the estimated 0.65 million seals in the Beaufort Sea and Amundsen Gulf (Stirling and Oritsland, 1995).

The relationship between nutrition and reproduction in female mammals has been well documented for a number of species, including humans (Frisch, 1990), caribou (*Rangifer tarandus*, Thomas, 1982; Ouellet et al., 1997), muskoxen (*Ovibos moschatus*, White et al., 1997), mule deer (*Odocoileus hemionus*, Taylor, 1996), fin whales (*Balaenoptera physalus*, Lockyer, 1986), polar bears (*Ursus maritimus*, Stirling et al., 1976) and the South African fur seal (*Arctocephalus pusillus*, Guinet et al., 1998). Changes documented in the seal population of the western Arctic have included reductions in ovulation rates among mature females, the percentage of pups in the harvest (Smith, 1987), and the number of birth lairs (Smith and Stirling, 1978); a possible shift in the age of sexual maturity (Kingsley and Byers, 1998); and changes in relative abundance during both ice-covered (Stirling et al., 1977) and open water (Harwood and Stirling, 1992) periods.

Here we examine two parameters of seal reproduction: ovulation rate and the percentage of pups in the harvest. These parameters were selected because (1) they varied with changes in the seal population during work in this same area in the 1970s, and (2) it was possible and practical to monitor these aspects over the long term through a harvest-based study in the community of Holman, NT (Fig. 1). Data we collected from 1992 through 1998 are presented here along with data from adult female ringed

seals collected in the same manner and from the same location during 1971–78 (Smith, 1987). To more fully elucidate the factors that may be involved in changes in seal reproduction, we examine our results in relation to seal body condition and in the context of annual regional ice conditions.

METHODS

Between 1992 and 1998, two Inuvialuit seal hunters (here called 'seal monitors') from Holman, NT, sampled and measured 869 ringed seals taken in their own seal hunting camps and by hunters in neighbouring camps. Eighty-six percent of the samples were taken during the months of June and July, from western Prince Albert Sound (Fig. 1).

All aspects of the field sampling and laboratory work in 1992–98 involved the same people and procedures that Smith (1987) used in this same area in 1971–78. One of the two seal monitors, J. Memogana, worked closely with T.G. Smith in the 1971–78 collections and was a seal monitor in this study in 1992 and 1993. The second monitor, J. Alikamik, was trained by Smith in 1992 and was a seal monitor from 1992 through 1998. This consistency in monitors, and the retraining/refreshing that was conducted each year by the project authority or designate, ensured that the data were collected as consistently as possible.

Each year, a random sample of 100 seals was sought from each monitor, with the following information collected from each seal: sex, date, location of kill, and the monitor's assessment of relative age. The monitors worked for ten weeks per year during the peak of the seal hunting activity. They were instructed to sample approximately ten seals per week (from their own catch and that of neighbouring camps) and to choose those ten seals randomly (i.e., without preference for size, sex, or relative age). Each seal monitor kept his own records of 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 hunting area by small boat).

Seals were laid on their backs on a smooth, flat surface, and standard length (nose to tail, ± 1.25 cm) was measured using a steel tape measure (American Society of Mammalogists, 1967). Body weight was measured to the nearest 0.5 kg using a spring dial scale suspended from a tripod. No corrections were made for blood loss. The monitors also measured blubber thickness at the sternum and at the hip, axillary girth, and hip girth (L. Harwood, unpubl. data).

The lower mandible was removed from as many of the sampled seals as possible, as were entire reproductive tracts from as many of the females in the sample as possible (Smith, 1973). These specimens were labelled and preserved in the field in 10% buffered formalin.

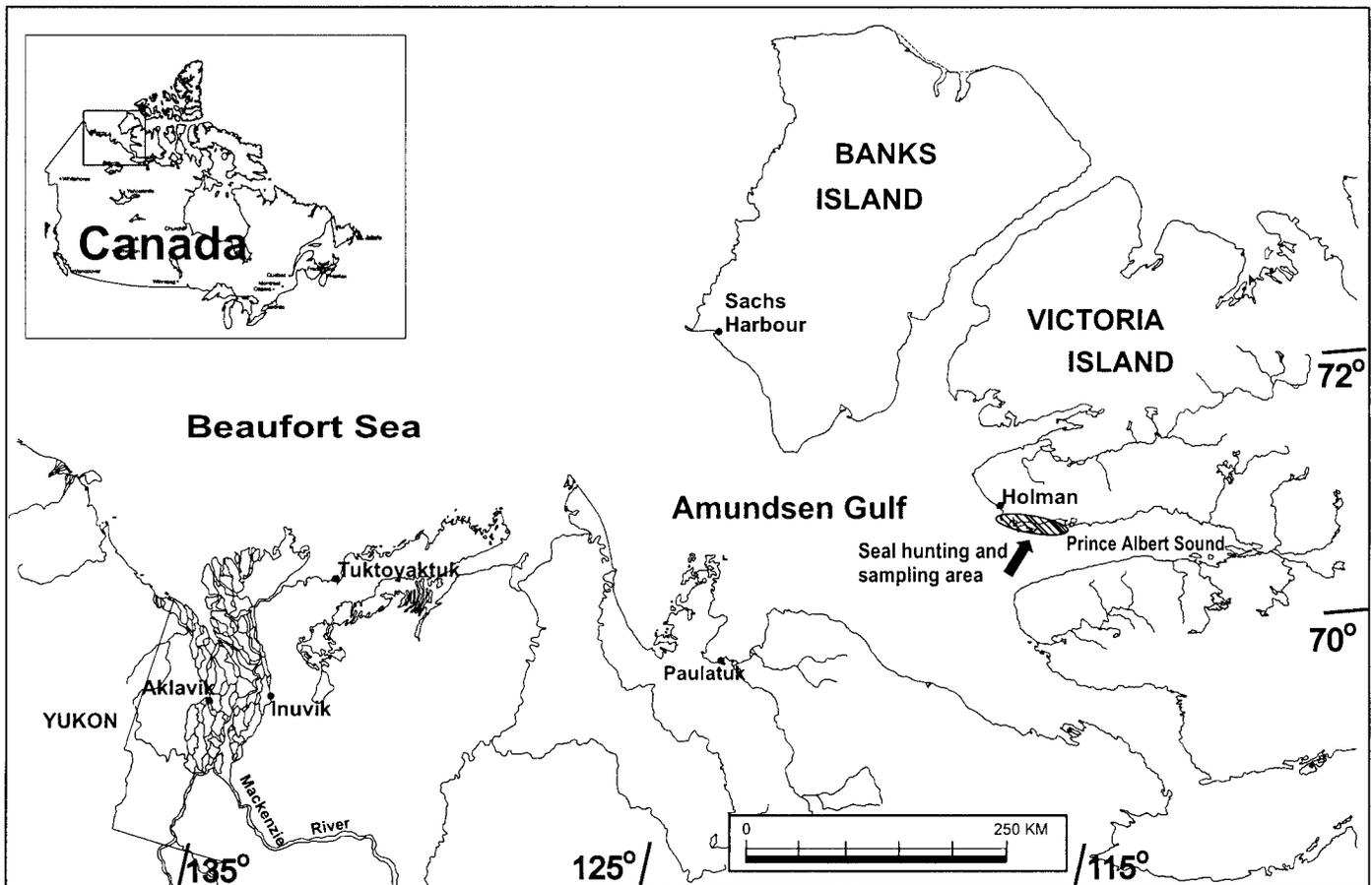


FIG. 1. Location of Holman, Northwest Territories, and the main seal hunting and sampling area on western Prince Albert Sound.

In the laboratory, the lower jaws were boiled, lower canines were extracted, and one was cut in cross section. Age determinations were made by reading the dentinal annuli of cross sections under transmitted light (Smith, 1973). Duplicate readings by the same reader were made for each tooth, with the second reading done separately. If the first two readings did not agree, a third reading was done. A decision on the age was based on recounts 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.

Recent studies have indicated that aging of ringed seals from counts of dentinal layers tends to underestimate the age compared to the method of reading of cementum layers, particularly in seals more than 10 years old. For seals over 10 years of age, a statistically significant correlation has been reported for ages obtained using the two methods (Stewart et al., 1996). In our study, we used the same aging method (dentinal) that was used in our 1970s data set, to ensure the data sets were comparable. For our analysis of condition, we pooled our data into three age-class categories, with seals 7 years of age and older in one grouping.

In 1996, lower jaws from seals judged to be young-of-the-year were not collected, so ages are not available for

those nine seals. However, the mean length of these nine seals (85.5 cm, SD 7.2) was less than the mean length of eight seals aged as neonates from the same monitor's 1994 sample (87.7 cm, SD 8.6), which he had also identified as young-of-the-year. We have thus assumed that the nine unaged seals in the 1996 sample designated by the monitor as young-of-the-year were indeed correctly classified.

Following the methods described by Smith (1973), we sectioned both left and right ovaries, counted the number of follicles larger than 5 mm, and measured the corpora lutea. The mean date of ovulation for ringed seals is 25 May (Smith, 1987), but the long delay between conception and implantation sometimes retards foetal development until September (Smith, 1973, 1987). Thus, since most of our sampling was done in June and July, we could not ascertain pregnancy from the presence of a foetus. We classified a female as mature on the basis of the presence of large follicles or corpora lutea in her ovary, plus either presence of a corpus albicans or evidence of past parturition from examination of her uterine cornua. The presence of a large, recently erupted follicle or a corpus luteum was taken as evidence of recent ovulation in adult females sampled during the months of June and July.

Data Analysis

Data on seals sampled by the monitors between 1992 and 1998 were included in our basic data set, as were those on females aged 6 and older sampled by Smith (1987) between 1971 and 1978. Data were entered onto a Lotus 123 spreadsheet, and statistical analyses were conducted using SAS version 6.11 (SAS, 1990) according to Sokal and Rohlf (1981).

The proportion of mature females that were ovulating in any given year was calculated for both 1971–78 and 1992–98. In our sample, females aged 6–9 years were poorly represented ($n = 26$ for June and July 1992–98) and our analysis of the reproductive aspects in our data set was limited to a basic tabulation of age-specific ovulation rates.

Our only direct measure of recruitment was the percentage of pups in the harvest. To minimize biases associated with these data, and to standardize the time at which our pup percentage data were collected, we used only seals taken during the times that hunters designated as “open water hunting.” We did not use data collected from periods of ice cover for this analysis because during those times adults predominate, subadults tend to be excluded, and pups are usually inaccessible to hunters (Smith, 1987).

The age-frequency distributions for the catches for 1992 to 1998 were compared pairwise between years, using a Kolmogorov-Smirnov two-sample test. The relationship between the ovulation rate in year x and the percentage of pups in the harvest in year $x+1$ was examined separately for the 1971–78 and 1992–98 data sets, using a Spearman’s ranked correlation. The relationship between the percentage of birth lairs in spring of year x (possible only for the 1971–78 data set) and the percentage of pups in the open water harvest in year x was also examined using a correlation analysis.

Condition indices specific to our data set were calculated according to the method described by Hammill et al. (1995). Body weight was related to standard length according to the formula: $\text{weight} = 10^a \text{length}^b$ (Innes et al., 1981, cited in Hammill et al., 1995). Age and sex differences among seals in our sample were tested by first fitting a curve to the pooled data, and then fitting separate curves for subsets (e.g., pups vs. 1–6 year olds; females ≥ 7 yr. vs. males ≥ 7 yr.). Standard variance-ratio tests were used to examine the change in the sum of squares about the fitted model (Hammill et al., 1995).

Our index of condition, referred to here as the body-mass index (BMI), was obtained using the relationship: $\text{BMI} = \text{weight (kg)} \times 10\,000 / \text{standard length (cm)}^{\text{exp}}$, where the exponent was the parameter b from the nonlinear regression of weight against length. The BMI is a measure of thinness and thus body fat, essentially independent of body length (Waterlow, 1997). Mean condition indices were calculated and tabulated for the months of June and July for each year examined, for pups (age 0+), subadults (age 1–6 yr), and adults of both sexes (age ≥ 7 yr).

Analysis of variance using PROC GLM (General Linear Models) was used to examine differences in seal body condition between years, accounting for time of year by using biweekly periods. A Duncan’s Multiple Range Test was used to examine the relationship between the mean BMI values for the years tested. These tests were done separately for our three groupings: pups and subadults pooled, females ≥ 7 yr, and males ≥ 7 yr.

Homogeneity of variances was examined using an F-test, followed by a T-test to compare mean BMI values of pups between June and July 1998, and pairwise comparison (multiple T-tests in PROC ANOVA) of mean BMI values for the month of July among years (for seals ≥ 7 yr, by sex). To examine the relationship between condition and ovulation rates, we compared the mean BMI values for ovulating and non-ovulating mature females, also using a T-test. The small sample of mature non-ovulating females necessitated pooling the mature females for all years.

To compare the severity of ice conditions among years, we obtained weekly ice charts from the Canadian Ice Service and examined the data for west Prince Albert Sound (where the seals were sampled), the adjacent east Amundsen Gulf, and the southeast Beaufort Sea (Fig. 1), extracting the dates of ice clearing and new ice formation for each year. The date of ice clearing was defined as the first day when a lead, opening, or otherwise ice-free area was large enough (ca. 10 km wide) to be noticed on the satellite image by the ice analyst. The date of new ice formation was designated as the day when new ice was first charted for a given area. Length of the open water period was calculated as the number of days between the date of ice clearing and the date of new ice formation. Since the ice charts are produced weekly, the dates of clearing and new ice cover may be late by as much as one week. A correlation analysis was used to examine the relationship between these parameters in west Prince Albert Sound, east Amundsen Gulf, and the southeast Beaufort Sea.

RESULTS

During 1992–98, a total of 869 ringed seals (45.3% females) were sampled from west Prince Albert Sound harvests during May–October (May 3.9%, June 30.6%, July 56.1%, August 7.9%, September 1.3%, October 0.1%). For the west Prince Albert Sound area, the proportion of Holman’s annual seal harvest that was sampled during June and July 1992–98 averaged 29.0%, and ranged from 12.8% (1996) to 42.8% (1992).

Seal Reproduction

A total of 167 reproductive tracts from females 6 yr or older were obtained for June and July of 1992–98. A total of 199 reproductive tracts from females 6 yr or older were examined for June and July 1971–78 (Smith, 1987).

TABLE 1. Proportion of female ringed seals ovulating, by maturity status and age, Prince Albert Sound, 1971–78 and 1992–98.

| Year | Proportion Ovulating | | | | | | | | | |
|------|--|------|------|------|----------|---|------|------|------|----------|
| | Females with no evidence of previous pregnancy (nulliparous) | | | | | Females with evidence of previous pregnancy | | | | |
| | 6 yr | 7 yr | 8 yr | 9 yr | 10–20 yr | 6 yr | 7 yr | 8 yr | 9 yr | 10–20 yr |
| 1971 | | | | | | | | 2/2 | 1/1 | 14/14 |
| 1972 | | 1/1 | | | | | | | | 8/8 |
| 1973 | | | | | | | | 0/1 | 1/1 | 3/4 |
| 1974 | | | | | | 0/1 | 1/2 | | 1/2 | 13/30 |
| 1975 | | 1/1 | | | | 1/1 | | 1/1 | | 6/11 |
| 1976 | 0/1 | | | | | | | 1/1 | 3/3 | 11/12 |
| 1977 | | 1/1 | | | | 1/2 | 3/3 | 7/7 | 8/8 | 24/24 |
| 1978 | | | | | | 2/2 | 2/2 | 6/6 | 2/2 | 44/44 |
| 1992 | 0/1 | 1/1 | | 0/1 | 1/1 | | | 1/1 | 2/2 | 24/26 |
| 1993 | | 2/2 | | | 1/1 | | | | 1/1 | 15/16 |
| 1994 | | | 1/1 | | | | 1/1 | | | 24/24 |
| 1995 | 0/1 | 1/2 | | 0/1 | | | | 1/1 | 2/2 | 13/13 |
| 1996 | | 0/1 | | | 4/4 | | | | 1/1 | 29/29 |
| 1997 | 0/1 | | 0/1 | | | | | 1/1 | 1/1 | 10/10 |
| 1998 | 0/1 | | | 1/1 | | | | | | 17/17 |

Our small sample of 26 females aged 6–9 yr precluded calculation of the age of sexual maturity or the age of first birth, as a minimum of 25 individuals per age class is recommended for this analysis (DeMaster, 1978). This fact obviates comparison with the values calculated by Smith (1987) or those available from other studies (i.e., Kingsley and Byers, 1998).

However, an examination of the age-specific reproductive status within the 1992–98 and 1971–78 data sets is still instructive (Table 1). In our small sample of adolescent females examined in 1992–98, all 6-year-olds were immature, and the majority (57%) of the 7-year-olds were ovulating for the first time; the majority of 8- and 9-year-olds were ovulating, and some had evidence of one or more previous births (60% and 70%, respectively).

In contrast, the corresponding data for 1971–78 (Table 1) show that most (6 of 7) of the 6-year-olds examined in that sample were mature. Of the 7-year-olds, three were ovulating for the first time, and seven showed evidence of previous births. All of the 8- and 9-year-olds in the sample were mature. These comparisons of reproductive status within the age classes suggest that the age of sexual maturity may have been higher in 1992–98 than in 1971–78.

All but three (132/135) of the females aged 10–20 years in the 1992–98 sample had ovulated in the year they were harvested. Ovulation rates were 93.5% in 1992, 95.0% in 1993, and 100% in 1994–98 (Table 2). Two of the three mature adult female seals that were not ovulating were 12 years old, and the third was 13 years old. There was no evidence in our 1992–98 sample that any of our 7-, 8-, or 9-year-old females had suppressed ovulation. These data suggest a period of relative stability with “normal” reproductive output for the years 1992–98. In contrast, ovulation rates for mature adult females in 1971–78 varied, reaching lows of 42.9% in 1974 and 64.3% in 1975 (Table 2).

Our monitors recorded their seals as being harvested during periods of ice cover (17.6%) or open water (82.4%). The latter group formed our basic data set for determining

the percentage of pups in the harvest. The age composition of this catch ranged from a low of 0% pups in 1993 to a high of 61.5% pups in 1998 (Table 3). The age-frequency distributions varied among years, with 1995 and 1998 being statistically different from each other ($KS = 1.86$, $n = 229$, $p < 0.0020$) and from all other years examined ($p < 0.0001$ for 1998 comparisons; $p < 0.0002$ for 1995 comparisons). Pairwise comparison showed that the age-frequency distribution for 1993, the year with no pups in the harvest, was not statistically different from the age-frequency distributions for 1994 (8.4% pups, $KS = 0.88$, $n = 81$, $p > 0.05$), 1996 (10.7% pups, $KS = 0.57$, $p > 0.05$, $n = 92$) or 1997 (6.2% pups, $KS = 1.18$, $n = 54$, $p > 0.05$). For the 1992–98 period, there was no statistical correlation between the ovulation rate in year x and the percentage of pups in the harvest in year $x+1$ (Spearman's ranked correlation, $r = 0.67612$, $p = 0.14$, $n = 6$).

Similar variation in the percentage of pups in the harvest was apparent in the 1971–78 data set, ranging from a low of 0.3% pups in 1974 to a high of 42.3% pups in 1972 (Table 2). Birth lair surveys, undertaken in 1972–74 and 1976–78, provide corroborating evidence of reduced productivity in those years (Table 2). Pup production in 1971–78 was well correlated with the percentage of birth lairs ($r = 0.900$, $p = 0.0374$, $n = 5$), but not with ovulation rate in the previous year ($r = 0.20520$, $p = 0.7406$, $n = 5$). The lowest ovulation rate in the series (1974) was well matched to the lowest proportion of pups harvested in the following year (1975), but the other years showed considerable variability.

Seal Body Condition

Since the length-weight curves for pups (age 0) and sub-adults (age 1–6 yr) were not statistically different ($F = 0.32$, $df = 2, 306$, $p > 0.20$), these age class categories were pooled to derive the BMI formula. The relationship between body weight and length for this grouping was

TABLE 2. Seal production and ice conditions in Prince Albert Sound, Amundsen Gulf, and the SE Beaufort Sea, 1970–78 and 1990–98.

| Year | Seal Production | | | Ice Conditions (extremes for series in bold) | | | | | | | | |
|------|--|---------------------------------------|---|--|-------------------------|--------------------|------------------------|-------------------------|--------------------|------------------------|-------------------------|--------------------|
| | Percent of mature females ¹ with evidence of recent ovulation | Percent of pups in open water harvest | Percent of birth lairs among all lairs (from Smith, 1987) | West Prince Albert Sound | | | East Amundsen Gulf | | | Southeast Beaufort Sea | | |
| | | | | Date of Ice Clearing | Date of New Ice Forming | Days of Open Water | Date of Ice Clearing | Date of New Ice Forming | Days of Open Water | Date of Ice Clearing | Date of New Ice Forming | Days of Open Water |
| 1970 | nd | nd | nd | 29-Jul-70 | 30-Sep-70 | 63 | 29-Jul-70 | 21-Oct-70 | 84 | 15-Jul-70 | 7-Oct-70 | 84 |
| 1971 | 100 | 28.5 | nd | 23-Jul-71 | 29-Oct-71 | 98 | 25-Jun-71 ² | 05-Nov-71 ³ | 133 | 25-Jun-71 | 15-Oct-71 | 112 |
| 1972 | 100 | 42.3 | 60.5 | 7-Aug-72 | 2-Oct-72 | 56 | 14-Aug-72 | 16-Oct-72 | 63 | 26-Jun-72 | 23-Oct-72 | 119 |
| 1973 | 67.7 | nd | 48.3 | 27-Jul-73 | 26-Oct-73 | 91 | 27-Jul-73 | nd | nd | 29-Jun-73 | 19-Oct-73 | 112 |
| 1974 | 42.9 | nd | 21.9 | 16-Aug-74 | 27-Sep-74 | 42 | 6-Sep-74 | 4-Oct-74 | 28 | 4-Oct-74 | 4-Oct-74 | 0 |
| 1975 | 64.3 | 0.3 | 9.1 | 1-Aug-75 | 24-Oct-75 | 84 | 1-Aug-75 | 31-Oct-75 | 91 | 4-Jul-75 | 5-Sep-75 | 63 |
| 1976 | 93.8 | 14.1 | 14.3 | 6-Aug-76 | 22-Oct-76 | 77 | 13-Aug-76 | 29-Oct-76 | 77 | 30-Jul-76 | 15-Oct-76 | 77 |
| 1977 | 97.8 | 9.1 | 18.5 | 22-Jul-77 | nd | nd | 10-Jun-77 | nd | nd | 29-Jul-77 | 4-Nov-77 | 98 |
| 1978 | 100 | 30 | 38.8 | 6-Jul-78 | 12-Oct-78 | 98 | 1-Jun-78 | 19-Oct-78 | 140 | 13-Jul-78 | 5-Oct-78 | 84 |
| 1990 | nd | nd | nd | 31-Jul-90 | 23-Oct-90 | 84 | 7-Aug-90 | 23-Oct-90 | 77 | 19-Jun-90 | 16-Oct-90 | 119 |
| 1991 | nd | nd | nd | 20-Aug-91 | 14-Oct-91 | 55 | 20-Aug-91 | 22-Oct-91 | 63 | 4-Jun-91 | 15-Oct-91 | 133 |
| 1992 | 93.5 | 9.6 | nd | 4-Aug-92 | 13-Oct-92 | 70 | 30-Jun-92 | 20-Oct-92 | 112 | 21-Jul-92 | 29-Sep-92 | 70 |
| 1993 | 95.0 | 0 | nd | 20-Jul-93 | 7-Nov-93 | 110 | 21-May-93 | 21-Oct-93 | 153 | 15-Jun-93 | 1-Nov-93 | 139 |
| 1994 | 100 | 8.4 | nd | 12-Jul-94 | 1-Nov-94 | 112 | 21-May-94 | 1-Nov-94 | 164 | 9-Aug-94 | 25-Oct-94 | 77 |
| 1995 | 100 | 38.6 | nd | 25-Jul-95 | 24-Oct-95 | 91 | 13-Jun-95 | 31-Oct-95 | 140 | 21-May-95 | 31-Oct-95 | 163 |
| 1996 | 100 | 11.4 | nd | 9-Jul-96 | 22-Oct-96 | 105 | 9-Jul-96 | 15-Oct-96 | 98 | 6-Aug-96 | 10-Sep-96 | 35 |
| 1997 | 100 | 6.2 | nd | 31-Jul-97 | 23-Oct-97 | 84 | 24-Jul-97 | 23-Oct-97 | 91 | 15-Jun-97 | 16-Oct-97 | 123 |
| 1998 | 100 | 61.5 | nd | 29-Jun-98 | 9-Nov-98 | 133 | 15-May-98 | 16-Nov-98 | 185 | 1-Jun-98 | 16-Nov-98 | 168 |

nd = no data

¹ females with evidence of previous pregnancy based on status of uterine cornua.

² could be earlier, no chart.

³ no chart, date estimated.

weight = $10^{-3.68}$ (standard length^{2.56}), and the BMI = weight (kg) × 10 000/standard length (cm)^{2.56}.

The asymptotic lengths for our 1992–98 sample were 129.6 cm for males and 121.9 cm for females. Males were, on average, 6.3% longer than females. These differences were apparent in the length-weight curves. The growth equations for females ≥ 7 yr (weight = $10^{-4.07}$ × standard length^{2.76}) and males ≥ 7 yr (weight = $10^{-2.38}$ × standard length^{1.95}) were statistically different ($F = 11.42$, $df = 2$, 820 , $p < 0.001$). For this reason, the body-mass index formulas were calculated separately: for females, BMI = weight (kg) × 100 000/standard length (cm)^{2.76}; for males, BMI = weight (kg) × 10 000/standard length (cm)^{1.95}.

For our 1992–98 data set, the BMI values of the pup/subadult, females ≥ 7 yr and males ≥ 7 yr groupings all varied significantly between years (for adult females, $F = 2.42$, $df = 13$, 193 , $p > F = 0.0050$; for adult males, $F = 5.17$, $df = 13$, 250 , $p > F = 0.0001$; for the pup/subadult grouping, $F = 3.69$, $df = 13$, 287 , $p > F = 0.0001$). The multiple range tests revealed that the specific interannual differences tended to be the same across the three groupings. The year with the lowest BMI value, 1994, was the same for all three groupings. The differences were statistically significant for our pup/subadult and male ≥ 7 yr groups (Duncan's multiple range test, $df = 237$ for adult males, $df = 274$ for pups/subadults, $p < 0.05$). The years with the highest BMI values during the month of July were also the same for

females ≥ 7 yr and males ≥ 7 yr (in order, starting with the highest BMI values: 1998, 1992, 1997, 1995; Table 4).

July 1998 appears to have been particularly favourable for ringed seal feeding. BMI values were higher in July 1998 than in July 1992–97 (Table 4). The 1998 mean BMI values for pups, females ≥ 7 yr, and males ≥ 7 yr in 1994 were 11%, 13% and 12% lower, respectively, than BMI values for these same groups in July 1998 (Table 4).

We also compared the BMI values for our 1992–98 females ≥ 7 yr, with those from the 1970s data set. Body condition indices in the 1970s were more variable, ranging from a high of 92.4 (1977, $n = 40$), to a low of 69.0 (1974, $n = 41$). In 1974, the condition of females was lower than in all other years examined, while in 1977 and 1978, the mean BMI values were higher than in all other years examined (Duncan's multiple range test, $df = 295$, $p < 0.05$). All of the BMI values for the 1992–98 period fell between these extremes from the 1970s.

Comparing the condition of mature female seals, we found that ovulating females had statistically higher mean BMI values than mature females that were not ovulating ($F = 41.44$, $p > F = 0.0001$, $df = 3$, 369). The mean BMI of our pooled sample of ovulating females was 85.2 (SD 13.5, $n = 330$), while that of our pooled sample of non-ovulating mature females was 70.4 (SD 15.8, $n = 40$).

In 1998, 92 pups were sampled from Prince Albert Sound during the months of June ($n = 50$) and July ($n = 42$).

TABLE 3. Number of seals harvested during open water hunting in Prince Albert Sound in 1992–98, by age class categories.¹

| Year | Pups | Subadults | Adults | Total Seals | Percent Pups |
|------|------|-----------|--------|-------------|--------------|
| 1992 | 13 | 28 | 95 | 136 | 9.6 |
| 1993 | 0 | 7 | 42 | 49 | 0.0 |
| 1994 | 8 | 13 | 74 | 95 | 8.4 |
| 1995 | 32 | 6 | 45 | 83 | 38.6 |
| 1996 | 9 | 5 | 65 | 79 | 11.4 |
| 1997 | 5 | 25 | 51 | 81 | 6.2 |
| 1998 | 91 | 12 | 45 | 148 | 61.5 |

¹ Pups (age 0+); subadults (1–6 yr); adults (≥ 7 yr).

TABLE 4. Mean body condition indices (BMI) of ringed seals¹ in Prince Albert Sound harvests, June and July 1992–98.

| Pups | June | | | July | | |
|---------------------|------|------|----|------|------|----|
| | BMI | SD | n | BMI | SD | n |
| 1992 | 27.6 | | 1 | 23.3 | 3.3 | 8 |
| 1993 | | | | | | |
| 1994 | 18.1 | 5.5 | 5 | 19.5 | 2.0 | 3 |
| 1995 | | | | 21.0 | 2.4 | 32 |
| 1996 | | | | 18.6 | 2.6 | 6 |
| 1997 | | | | | | |
| 1998 | 20.2 | 2.7 | 44 | 22.0 | 2.1 | 39 |
| Females ≥ 7 yr | | | | | | |
| 1992 | 82.3 | 7.8 | 11 | 87.0 | 11.9 | 31 |
| 1993 | 82.9 | 7.8 | 11 | 80.0 | 10.8 | 11 |
| 1994 | 75.9 | 14.4 | 9 | 80.0 | 10.3 | 24 |
| 1995 | 90.9 | 13.7 | 13 | 82.0 | 18.3 | 11 |
| 1996 | 80.3 | 16.7 | 26 | 81.0 | 12.9 | 15 |
| 1997 | 75.1 | 5.1 | 2 | 83.0 | 10.3 | 17 |
| 1998 | 75.0 | 5.7 | 7 | 92.0 | 16.2 | 12 |
| Males ≥ 7 yr | | | | | | |
| 1992 | 38.5 | 6.5 | 5 | 43.7 | 8.3 | 43 |
| 1993 | 45.7 | 7.7 | 18 | 38.4 | 4.3 | 26 |
| 1994 | 36.9 | 5.0 | 16 | 38.4 | 4.0 | 28 |
| 1995 | 46.5 | 5.8 | 13 | 41.0 | 5.5 | 24 |
| 1996 | 42.8 | 8.7 | 12 | 39.8 | 5.6 | 15 |
| 1997 | 46.2 | 7.4 | 18 | 41.2 | 4.3 | 16 |
| 1998 | 43.8 | 6.1 | 6 | 43.7 | 5.2 | 11 |

¹ Seals aged 1–6 years were not included because the small sample sizes in most years did not allow meaningful interannual comparisons.

This group represents the largest sample of pups to date for the harvest area. In June 1998, the mean BMI of pups was 20.2 (SD 2.66, $n = 44$), and ranged from 13.8 to 27.7. By July 1998, mean BMI values had increased (22.0, $n = 39$), and the range of condition had narrowed (BMI ranged from 15.7 to 25.5). This lower condition of pups in June 1998 compared with July 1998 was statistically significant ($F = 1.67$, $df = 43, 38$; $p > F = 0.1092$; $T = 3.36$, $df = 81$, $p > T = 0.0012$).

This poor condition of pups during June 1998 was noted by the seal monitor, who reported six seal pups in the June sample as “skinny” and in “poor condition,” as well as reporting three seal pups washed up dead along the shore



FIG. 2. Range of size and condition of ringed seal pups harvested in western Prince Albert Sound on 23 June 1998 (left, female BMI = 23.6, standard length 86.4 cm; center, female BMI = 17.2, standard length 77.5 cm; right, male, BMI = 16.8, standard length 64.8 cm; mean BMI for all pups sampled in June 1998 for which BMI could be calculated = 20.2, $n = 44$).

near the sealing area. This was the first time the seal monitor had observed such a situation in his more than 30 years of experience as a seal hunter (J. Alikamik, pers. comm. 1998). Figure 2 illustrates the striking range of condition observed in three pups sampled on the same day in June 1998. Eleven of the 50 pups sampled in June 1998 were described as starvelings. By July 1998, starveling pups were no longer found in the harvest, and most pups in the sample ($n = 40/42$) had completely moulted their lanugo.

Females ≥ 7 yr showed the same trends as the pups in 1998: their condition was significantly lower in June (mean BMI = 75.0, SD 5.7, $n = 7$) than in July 1998 (mean BMI = 92.0, SD 16.2, $n = 12$), and it was higher in July 1998 than in July of all other years examined (Table 4). The same was true for males ≥ 7 yr: their mean BMI in July 1998 (mean BMI = 43.7, SD = 5.2, $n = 11$) was higher than in July of all other years examined except 1992, when the mean BMI was the same as in 1998 (1992, BMI = 43.7, SD = 8.3, $n = 43$; Table 4).

Ice Conditions

Dates of ice clearing and new ice formation and the length of the open water season for western Prince Albert Sound and eastern Amundsen Gulf were variable among years (Table 2). In western Prince Albert Sound, the average number of open water days for the 18 years examined was 85.5 days (SD 23), and the range was from 42 (1974) to 133 (1998). In eastern Amundsen Gulf, the length of the open water season showed the same trend, averaging 106.2 days (SD 42.7) and ranging from 28 days (1974) to 185 days (1998). The results from these two areas were correlated within years (for date of ice clearing, $r = 0.86012$, $p = 0.0001$, $n = 17$; for number of open water days, $r = 0.89668$, $p = 0.0001$, $n = 15$).

The earliest date of ice clearing among the years examined for Amundsen Gulf occurred in 1998 (15 May), while

the latest occurred in 1974 (6 September). The earliest date of new ice formation in eastern Amundsen Gulf in our series was also in 1974 (4 October), while the latest was also in 1998 (16 November). Clearly, of the years presented here, 1974 had the longest period of ice cover. At the other end of the spectrum, 1998 had the earliest clearing of ice and the longest period of open water (Table 2).

There was no statistically significant correlation between the dates of ice clearing and length of the open water season for the southeastern Beaufort Sea and eastern Amundsen Gulf (for date of clearing, $r = 0.24233$, $p = 0.3487$, $n = 17$; for length of open water, $r = 0.3812$, $p = 0.2177$, $n = 15$), although the extreme years for the southeastern Beaufort Sea (1974 and 1998) matched those for eastern Amundsen Gulf and western Prince Albert Sound. In the southeastern Beaufort Sea, there was essentially no open water during the summer of 1974. The ice regime of the southeastern Beaufort Sea tends to differ from that of the first-year ice of Amundsen Gulf and Prince Albert Sound (Hammill, 1987), the Beaufort being more open and bounded to the north by multiyear pack-ice.

The years 1970–78 were a time of later ice clearing and earlier formation of new ice, compared with the period 1990–98. For eastern Amundsen Gulf, the mean date of ice clearing during 1970–78 was 25 July, and the mean number of open water days was 88.0 days (SD 38.9). Between 1990 and 1998, the mean date of ice clearing was approximately one month earlier (28 June), and the mean open water period was 32 days longer (mean = 120.3 days, SD 42.0).

DISCUSSION

Ovulation rates in the 1992–98 period remained above 90%, which is consistent with those of other pinniped populations (McLaren and Smith, 1985). These rates were prevalent among all of our mature females, regardless of age. Ovulation rates in the 1970s were lower and more variable than in the 1990s, particularly in 1974, the most severe ice year on recent record, and the following year, 1975. Body condition of females aged 7 or more years was significantly lower in 1974 than in the other 15 years examined here. Mature female seals that had ovulated had higher BMI values than mature female seals that had not ovulated. Ice conditions in 1974 appear to have led to a reduction in the food available to seals.

Seal body condition in 1998 contrasts with that of 1974: 1998 appears to have been a time when plentiful food was available to all age classes of ringed seals in Prince Albert Sound and adjacent areas (i.e., Amundsen Gulf). The ice cleared six weeks earlier than the mean date for the decade, and by July 1998, pups, adult females, and adult males were all in better condition than in July of other years between 1992 and 1998.

In our 1990 series, we found that seal condition was lowest in 1994, with BMI values 11–13% lower than in 1998. Although the differences in condition among years

were apparent, coincident among our three groupings, and statistically significant in two cases, the fluctuations in condition did not appear to be of a magnitude that would cause a change in the ovulation rate, which remained above 90% throughout 1992–98.

Skinner et al. (1998) show that for the month of June, air temperatures over Cape Bathurst, 300 km west of our study area, have been increasing at a faster rate than June temperatures elsewhere in Canada (0.7°C–0.8°C per decade since 1950). Tynan and DeMaster (1997) predict that ice-associated seals may be especially vulnerable to changes in the ice regime. Changes in condition of polar bears (Stirling et al., 1999) and geese (Skinner et al., 1998) have also been linked to changes in patterns of ice breakup.

In eastern Amundsen Gulf in 1998, the sea ice cleared on 15 May, 43 days earlier than the mean date of ice clearing for the 1990–98 period. We believe that the early breakup in 1998 led to an interruption of lactation for pups at the seaward portion of the core breeding habitat off Holman, which in turn affected the condition and growth of those unweaned pups. This happened at a time when marine food appeared to be abundant and available for the other age classes of ringed seals.

The percentage of pups in the annual harvest gave a more confusing measure of seal population status than did ovulation rate. In our 1992–98 series, the proportion of pups in the harvest fluctuated markedly and was not closely matched to ovulation rate in the previous year. This variation was also apparent in the 1971–78 data set, although the extreme low ovulation rate in 1974 was well matched to lower pup production in 1975. The percentage of pups as an index of seal production is closely tied to hunting effort, and thus has been particularly variable as hunting efforts by Inuvialuit have declined in recent years. Weather and ice conditions can greatly influence the availability of pups to Inuvialuit hunters, particularly just before ice breakup, when the largest harvests can be made (as was the case in 1998). Without other direct measurements of pup production, such as labour-intensive birth lair surveys (Smith and Stirling, 1975, 1978; Lydersen and Gjertz, 1986; Hammill and Smith, 1989; Kelly and Quakenbush, 1990; Furgal et al., 1996), the proportion of pups in a harvest may not be a particularly reliable measure with which to assess seal recruitment.

Measuring body condition along with ovulation rate provides a practical means of monitoring the ringed seal population in the Holman area, with the assistance of the local community hunters. Our study illustrates that a noticeable link exists between body condition and ovulation rates of ringed seals, even in years when no apparent climatic perturbations might have curtailed the production or availability of seal food. We have also documented the fact that a very local, small-scale, premature disruption of the landfast-ice breeding habitat can have a significant negative impact on the growth, the condition, and probably the survival of unweaned pups. Such an effect occurred in 1998, a year of apparent high production, when

seal food appeared to be abundant and available to all age classes of ringed seals. This brings home the lesson that any program attempting to monitor and understand factors in regional or large-scale change in ringed seal populations must take care in selecting the specific parameters used in making long-term assessments. It also underscores the need for careful documentation of changes in local ice, weather, and oceanographic conditions in the area where the samples have been gathered. Without such information, it would be difficult to differentiate between short-term or local effects and more significant, larger-scale, long-term changes in factors affecting the population.

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REFERENCES

- AMERICAN SOCIETY OF MAMMALOGISTS. 1967. Standard measurements of seals. *Journal of Mammalogy* 48:459–462.
- DeMASTER, D.P. 1978. Calculation of the average age of sexual maturity in marine mammals. *Journal of Fisheries Research Board Canada* 35:912–915.
- DUNBAR, M.J. 1941. On the food of ringed seals in the eastern Canadian Arctic. *Canadian Journal of Research* (19), Section D:150–155.
- FABIJAN, M. 1995a. Inuvialuit Harvest Study Data Report, January–December 1992. Available from the Joint Secretariat, Box 2120, Inuvik, Northwest Territories X0E 0T0, Canada. 70 p.
- . 1995b. Inuvialuit Harvest Study Data Report, January–December 1991. Available from the Joint Secretariat, Box 2120, Inuvik, Northwest Territories X0E 0T0, Canada. 73 p.
- . 1997. Inuvialuit Harvest Study Data Report, January–December 1996. Available: Michael Fabijan Consulting, Box 2318, Inuvik, Northwest Territories X0E 0T0, Canada. 44 p + app.
- FRISCH, R.E. 1990. The right weight: Body fat, menarche and ovulation. *Bailliere's Clinical Obstetrics and Gynaecology* 4(3):419–439.
- FURGAL, C.M., INNES, S., and KOVACS, K.M. 1996. Characteristics of ringed seal, *Phoca hispida*, subnivean structures and breeding habitat and their effects on predation. *Canadian Journal of Zoology* 74:858–874.
- GUINET, C., ROUX, J.P., BONNET, M., and MISON, V. 1998. Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. *Canadian Journal of Zoology* 76:1418–1424.
- HAMMILL, M.O. 1987. The effects of weather on ice conditions in the Amundsen Gulf, N.W.T. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* No. 1900. 10 p.
- HAMMILL, M.O., and SMITH, T.G. 1989. Growth affecting the distribution and abundance of ringed seal structures in Barrow Strait, Northwest Territories. *Canadian Journal of Zoology* 67:2212–2219.
- HAMMILL, M.O., KINGSLEY, M.C.S., BECK, G.G., and SMITH, T.G. 1995. Growth and condition in the Northwest Atlantic harp seal. *Canadian Journal of Fisheries and Aquatic Sciences* 52(3):478–488.
- HARWOOD, L.A., and STIRLING, I. 1992. Distribution of ringed seals in the southeastern Beaufort Sea during late summer. *Canadian Journal of Zoology* 70(5):891–900.
- INNES, S., STEWART, R.E.A., and LAVIGNE, D.M. 1981. Growth in Northwest Atlantic harp seals *Phoca groenlandica*. *Journal of Zoology* 194:1124.
- IRC (INUVIALUIT REGIONAL CORPORATION). 1989. The Inuvialuit sealing economy: Prospects for development. Ottawa: Inuit Tapirisat of Canada. Available from IRC, Box 2120, Inuvik, Northwest Territories X0E 0T0, Canada.
- KELLY, B.P., and QUAKENBUSH, L.T. 1990. Spatiotemporal use of lairs by ringed seal (*Phoca hispida*). *Canadian Journal of Zoology* 68:2503–2512.
- KINGSLEY, M., and BYERS, T. 1998. Failure of reproduction in ringed seals (*Phoca hispida*) in Amundsen Gulf, Northwest Territories, 1984–1987. In: Heide-Jorgensen, M.P., and Lydersen, C., eds. Ringed seals in the North Atlantic. NAMMCO Scientific Publication No. 1. Tromsø, Norway: The North Atlantic Marine Mammal Commission. 197–210.
- LOCKYER, C. 1986. Body fat condition in Northeast Atlantic fin whales, (*Balaenoptera physalus*), and its relationship with reproduction and food resource. *Canadian Journal of Fisheries and Aquatic Sciences* 43:142–147.
- LOWRY, L.F., FROST, K.J., and BURNS, J.J. 1978. Food of ringed seals and bowhead whales near Point Barrow, Alaska. *Canadian Field-Naturalist* 92(1):67–70.
- . 1980. Variability in the diet of ringed seals, (*Phoca hispida*), in Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 37:2254–2261.
- LYDERSEN, C., and GJERTZ, I. 1986. Studies of the ringed seal (*Phoca hispida*, Schreber 1775) in its breeding habitat in Kongsfyorden, Svalbard. *Polar Research* 4:57–63.

- McLAREN, I.A., and SMITH, T.G. 1985. Population ecology of seals: Retrospective and prospective views. *Marine Mammal Science* 1:54–83.
- OUELLET, J.P., HEARD, D.C., BOUTIN, S., and MULDER, R. 1997. A comparison of body condition and reproduction of caribou on two predator-free arctic islands. *Canadian Journal of Zoology* 75:11–17.
- SAS (STATISTICAL ANALYSIS SYSTEM). 1990. SAS Users guide: Statistics Version 6. Cary, North Carolina: SAS Institute Inc.
- SKINNER, W.R., JEFFERIES, R.L., CARLETON, T.J., ROCKWELL, R.F., and ABRAHAM, K.F. 1998. Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. *Global Change Biology* 4:3–16.
- SMITH, T.G. 1973. Population dynamics of the ringed seal in the Canadian Eastern Arctic. *Bulletin of the Fisheries Research Board of Canada* 181. 55 p.
- . 1987. The ringed seal, (*Phoca hispida*), of the Canadian western Arctic. *Canadian Bulletin of Fisheries and Aquatic Sciences* 216. 81 p.
- SMITH, T.G., and STIRLING, I. 1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. *Canadian Journal of Zoology* 53:1297–1305.
- . 1978. Variation in the density of ringed seal (*Phoca hispida*) birth lairs in the Amundsen Gulf, Northwest Territories. *Canadian Journal of Zoology* 56(5):1066–1071.
- SOKAL, R.R., and ROHLF, F.J. 1981. *Biometry*. 2nd ed. New York: W.H. Freeman and Company.
- STEWART, R.E.A., STEWART, B.E., STIRLING, I., and STREET, E. 1996. Counts of growth layer groups in cementum and dentine in ringed seals (*Phoca hispida*). *Marine Mammal Science* 12(3):383–401.
- STIRLING, I., and ORITSLAND, N.A. 1995. Relationships between estimates of ringed seal and polar bear populations in the Canadian Arctic. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2594–2612.
- STIRLING, I., PEARSON, A.M., and BUNNELL, F.L. 1976. Population ecology studies of polar and grizzly bears in northern Canada. *Transactions of the 41st North American Wildlife National Resources Conference*. Washington, D.C.: Wildlife Management Institute. 421–430.
- STIRLING, I., ARCHIBALD, W.R., and DeMASTER, D. 1977. Distribution and abundance of seals in the eastern Beaufort Sea. *Journal of the Fisheries Research Board of Canada* 34:976–988.
- STIRLING, I., KINGSLEY, M.C.S., and CALVERT, W. 1982. The distribution and abundance of seals in the eastern Beaufort Sea, 1974–79. *Canadian Wildlife Service Occasional Paper No.* 46. 25 p.
- STIRLING, I., LUNN, N.J., and IACOZZA, J. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52(3): 294–306.
- TAYLOR, T.J. 1996. Condition and reproductive performance of female mule deer in the Central Sierra Nevada. *California Fish and Game* 82 (3):122–132.
- THOMAS, D.C. 1982. The relationship between fertility and fat reserves of Peary caribou. *Canadian Journal of Zoology* 60: 597–602.
- TYNAN, C.T., and DeMASTER, D.P. 1997. Observations and predictions of arctic climate change: Potential effects on marine mammals. *Arctic* 50(4):308–322.
- WATERLOW, J.C. 1997. Protein-energy malnutrition: Nature and extent of the problem. *Clinical Nutrition* 16 (Suppl. 1):3–9.
- WHITE, R.G., ROWELL, J.E., and HAUER, W.E. 1997. The role of nutrition, body condition and lactation on calving success in muskoxen. *Journal of Zoology* 243:13–20.