

Temporal variations in Hudson Bay ringed seal (*Phoca hispida*) life-history parameters in relation to environment

MAGALY CHAMBELLANT,* IAN STIRLING, WILLIAM A. GOUGH, AND STEVEN H. FERGUSON

Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada (MC, SHF)
Wildlife Research Division, Science and Technology Branch, Environment Canada, 5320-122 Street, Edmonton, Alberta T6H 3S5, Canada (IS)

Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada (IS)

Department of Physical and Environmental Sciences, University of Toronto at Scarborough, 1265 Military Trail, Scarborough, Ontario M1C 1A4, Canada (WAG)

Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada (SHF)

* Correspondent: mchambellant@yahoo.fr

We related temporal variation in the environment to demographic parameters and body condition of ringed seals (*Phoca hispida*) in Hudson Bay, near the southern limit of the species' geographic range. Ringed seals harvested by Inuit hunters for subsistence purposes in Arviat, Nunavut, Canada, from 1991 to 2006 were measured and sampled. Ringed seal ovulation rate did not change over time, but pregnancy rate and percent pups in the fall harvest increased in the 2000s, compared to the 1990s. Ringed seals grew faster and attained sexual maturity earlier in life, and the population age structure shifted to younger age classes in the 2000s compared to the 1990s. Ringed seal demographic parameters were characteristic of a population in decline in the 1990s and a growing population in the 2000s. A quadratic polynomial regression best described the relationship between percent pups in the harvest and snow depth, and between pup and adult female body condition index and date of spring breakup, suggesting that ringed seals have evolved to do best within a relatively limited range of environmental conditions. We propose that the decline of ringed seal reproductive parameters and pup survival in the 1990s could have been triggered by unusually cold winters and heavy ice conditions that prevailed in Hudson Bay in the early 1990s, through nutritional stress and increased predation pressure. The recovery in the 2000s may have been augmented by immigration of pups, juveniles, and young adult ringed seals into the study area. We discuss the possibility of a decadal-scale biological cycle that reflects fluctuations in climatic variables, and particularly in the sea ice regime.

Key words: age at maturity, body condition, decadal cycle, fetus, immigration, pregnancy rate, pup survival, reproduction, snow depth, spring sea ice breakup

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Climatic changes can have a strong influence on interannual variations in life-history parameters of both terrestrial and marine long-lived vertebrate species (e.g., Barbraud and Weimerskirch 2001; Forchhammer et al. 2001; Stenseth et al. 2002). Over the last 4 decades, Hudson Bay, a large Canadian inland sea that is ice-covered from November to June (Markham 1986; Saucier et al. 2004), has experienced significant reductions in sea ice extent and snow depth, while air and water temperatures increased, leading to earlier dates of spring sea ice breakup and lengthening of the open-water season (Ferguson et al. 2005; Gagnon and Gough 2005b; Galbraith and Larouche 2011; Parkinson and Cavalieri 2008; Skinner et al. 1998; Stirling and Parkinson 2006). General circulation models

for Hudson Bay under different climate change scenarios predict that the observed trends will continue, with dramatic consequences for the annual cryogenic cycle (Gagnon and Gough 2005a; Gough and Wolfe 2001; Joly et al. 2011). Arctic species dependent on the sea ice for most of their life cycle, such as polar bears (*Ursus maritimus*) and seals, are expected to be impacted by sea ice habitat loss, likely resulting in changes of distribution, nutrition, reproduction, and ultimately survival and abundance of these species (Laidre et al. 2008; Tynan and



DeMaster 1997). Such changes have already been documented for some ice-associated species in the Hudson Bay ecosystem. An earlier laying date and a decrease in chick growth rate and adult body mass were described for thick-billed murres (*Uria lomvia*) in northern Hudson Bay at the end of the 1990s (Gaston et al. 2005). Polar bear abundance, body condition, reproductive rate, and cub survival all have declined in the western Hudson Bay population since the 1980s, and the progressively earlier dates of ice breakup in the spring were suggested to be responsible for the observed patterns (Regehr et al. 2007; Stirling et al. 1999).

Ringed seals (*Phoca hispida*) have a northern circumpolar distribution and are the most numerous of arctic pinnipeds (Frost and Lowry 1981; Mansfield 1967). They also are among the smallest phocids (McLaren 1993), can live up to 40+ years of age, and mature around the age of 6 years (Holst and Stirling 2002; Lydersen and Gjertz 1987). After a gestation of 10–11 months, including a period of suspended development of 2–3 months, a single pup is born in early spring inside a subnivean lair built by adult females in drifted snow that forms over their self-maintained breathing holes in areas of stable ice (Hammill and Smith 1989; McLaren 1958; Smith 1987). The degree of protection from cold and predators, such as polar bears, arctic foxes (*Vulpes lagopus*), and humans, is directly related to the thickness and strength of the snow roofs over the birth lairs (Furgal et al. 1996; Hammill and Smith 1991). Pups are weaned before the spring sea ice breakup, after a 6-week lactation period (Hammill et al. 1991) during which mothers rely on both fat reserves and feeding (Kelly and Wartzok 1996; Lydersen 1995). Like other phocids (Bowen 1991), after weaning ringed seal pups use the sea ice as a platform to rest between diving bouts (Stirling 2005). Mating occurs underwater around the time pups are weaned (Lydersen 1995; Smith 1987) and precedes the annual molt in June, when ringed seals haul out on ice to bask in the sun (McLaren 1958; Smith 1973). Following the reproductive and molting periods, ringed seals feed intensely during the open-water season in order to replenish their fat reserves (McLaren 1958; Ryg and Oritsland 1991; Smith 1987). At freeze-up, adult ringed seals move toward prime breeding habitats in areas where the ice will be most stable through the winter and establish territories. Younger age classes of seals are excluded from the prime breeding habitat and most will spend the winter at the ice edge or in leads and polynyas (Krafft et al. 2007; McLaren 1958; Stirling et al. 1981). The ringed seal is only slightly sexually size-dimorphic (Chambellant 2010; McLaren 1993) and is thought to have a weakly polygynous, resource-defense mating system (Krafft et al. 2007; Smith and Hammill 1981; Yurkowski et al. 2011; but see Kelly et al. 2010). During the winter and spring months, some adult ringed seals have been shown to demonstrate signs of site fidelity (Kelly et al. 2010; Kelly and Quakenbush 1990; Krafft et al. 2007; McLaren 1958; Smith and Hammill 1981).

Considering their dependence on sufficient snow depth and a stable ice platform in the spring, and abundant food in summer and fall, ringed seal reproductive success and survival

may be particularly vulnerable to variations in the sea ice habitat that are predicted to occur as a result of climate warming. A decrease in the relative abundance of ringed seals during warming or light ice periods has been reported by archaeological and historical studies (Harington 2008; Vibe 1967; Woollett et al. 2000). More recently, early or late ice breakup, light or heavy ice conditions (Harwood et al. 2000; Kingsley and Byers 1998; Smith 1987; Smith and Harwood 2001; Stirling et al. 1982), unusual warm or rain events in the spring (Stirling and Smith 2004), and insufficient snow depth (Ferguson et al. 2005; Hammill and Smith 1991) have all been shown to negatively affect body condition, reproduction, and survival of ringed seals. Because of its highly specialized adaptations for exploitation of sea ice habitat for reproduction and survival, the ringed seal represents a good model to explore the possible effects of ecosystem changes on life-history traits, and ultimately population dynamics of ice-breeding seals. Because western Hudson Bay is near the southern limit of the species range (Frost and Lowry 1981; Mansfield 1967), such changes in life-history traits may occur there before they are seen in areas farther north.

In this study, we evaluated ringed seal life-history traits and body condition in western Hudson Bay over 9 sampling years spanning 1991–2006, in relation to temporal trends and variability in their sea ice environment. We predicted that ringed seals in Hudson Bay would respond in a nonlinear fashion to environmental changes, and indicate a negative response to the occurrence of environmental conditions outside of their optimal range. Our goals were to assess changes in ringed seal body condition, reproduction, and survival from 1991 to 2006 in western Hudson Bay; to evaluate the correlation between ringed seal demographic responses and environmental changes; and to propose testable hypotheses to explain the population-level responses of ringed seals to ongoing and predicted climate change.

MATERIALS AND METHODS

Seal collection.—Ringed seals were sampled from the Inuit subsistence fall harvest in the western Hudson Bay community of Arviat, Nunavut, Canada, by the Canadian Wildlife Service in 1991, 1992, and 1998–2000, and Fisheries and Oceans Canada from 2003 to 2006 (Fig. 1). Ringed seals were hunted nonselectively by Inuit hunters from September into early November. Seals of all age and sex classes occur together in the open water prior to freeze-up, and thus provide the best opportunity of the year to obtain a representative sample of the overall population in a particular area (Smith 1973). Inuit hunters were asked to provide basic information (species, sex, date, and location of kill), measurements (standard length, axillary girth, and fat depth at sternum [Committee on Marine Mammals 1967]), the mandible, and reproductive organs for all seals. Samples were frozen in the field at -20°C in community freezers and sent to Canadian Wildlife Service in Edmonton, Alberta, or Fisheries and Oceans Canada in Winnipeg, Manitoba, for analysis.

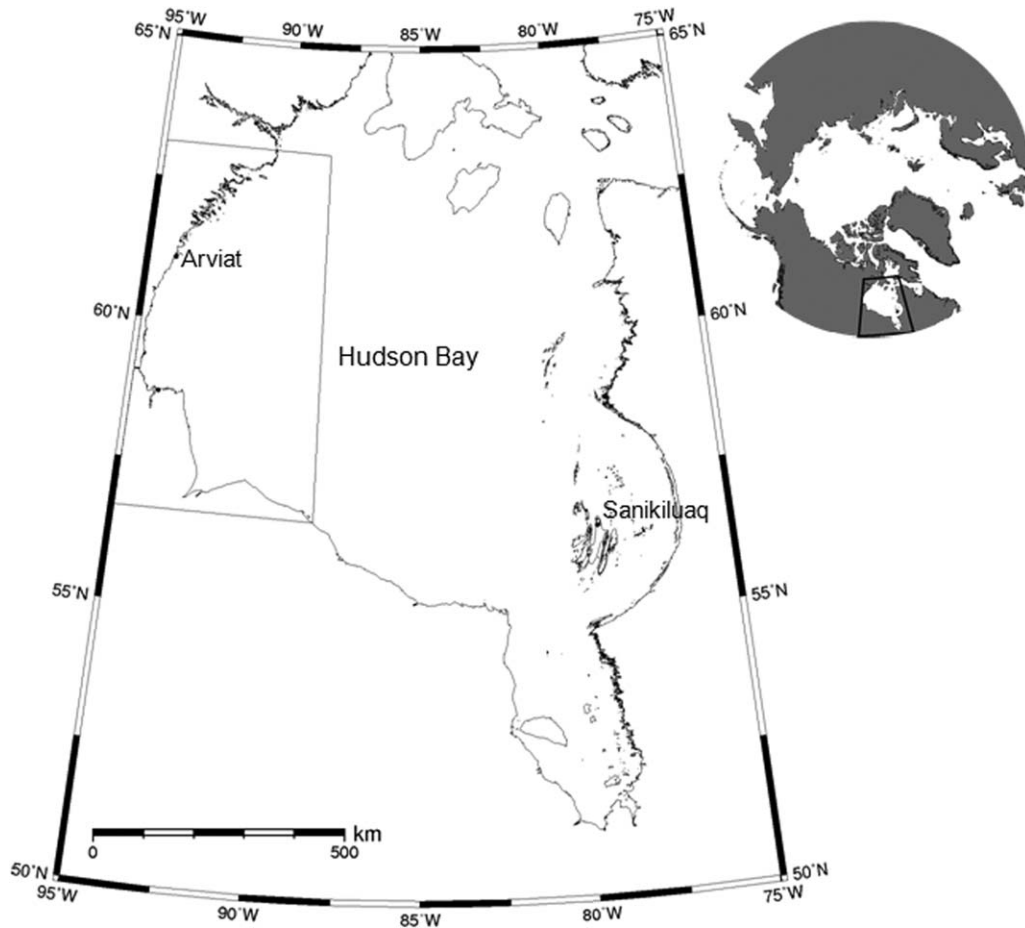


FIG. 1.—Study site was located within a marine region surrounding the Inuit community of Arviat, Nunavut, in the western Hudson Bay area (rectangle), Canada.

Age determination.—Ringed seal mandibles were simmered in hot water for 2–3 h and right canine teeth were extracted and preserved in 70% ethanol. When the right canine tooth was not available, another tooth was extracted in the order of preference as follows: the left canine tooth, the right or left 1st postcanine tooth, or a postcanine double-rooted tooth (Chambellant and Ferguson 2009). The periodontal ligament was not cleaned from teeth to prevent potential damage to the most recently deposited annual growth layer group. Ages were determined by interpreting and counting the growth layer groups in the cementum of decalcified, stained, longitudinal, thin tooth sections (Bernt et al. 1996; Stewart et al. 1996; Stirling et al. 1977). Growth layer groups were counted in 2 or 3 blind replicates for each tooth, and final ages were estimated using 2 identical readings or the median of 3 different readings.

Animals born in the spring and harvested in the fall of the same year were referred to as pups. Seals from 1 to 5 years of age were considered juveniles and seals of 6 years of age and older were categorized as adults (Holst et al. 1999).

Reproduction.—We examined 230 ringed seal female reproductive tracts but complete tracts (uterus and ovaries) were not always provided. When the uterus was available, we recorded the presence of an embryo or fetus, horn measurements, and the

parity status (nulliparous, primiparous, or multiparous) based on the size and aspect of uterine horns. Ovaries were detached from oviducts, measured, and weighed fresh before being soaked in 10% buffered formalin for 2 weeks. Ovaries were then sectioned at 2- to 3-mm intervals using a razor blade and examined macroscopically for the presence and number of follicles, corpora lutea, and corpora albicantia.

We defined pregnancy in adult female ringed seals as the presence of a fetus. Ovulation in adult females was determined by the presence of a corpus luteum in 1 of the ovaries or by the presence of a fetus in cases where ovaries were not provided. The average age of sexual maturity (1st ovulation) and 1st parturition were computed from the data collected in the 1990s and in the 2000s (the year 2000 was excluded from the calculation because only the adult reproductive tracts were examined) by bootstrapping 1,000 times with replacement following the algorithm of DeMaster (1981). However, contrary to DeMaster (1981), we chose not to assume that females ovulate every year after sexual maturity, nor that a female that did not ovulate at age x had never ovulated before and used the same algorithm for both age at maturity and at 1st parturition. Our choice was motivated by the fact that, of the 136 adult females for which an ovulation status was assessed, 8 aged 6–17 years did not ovulate in the year they were

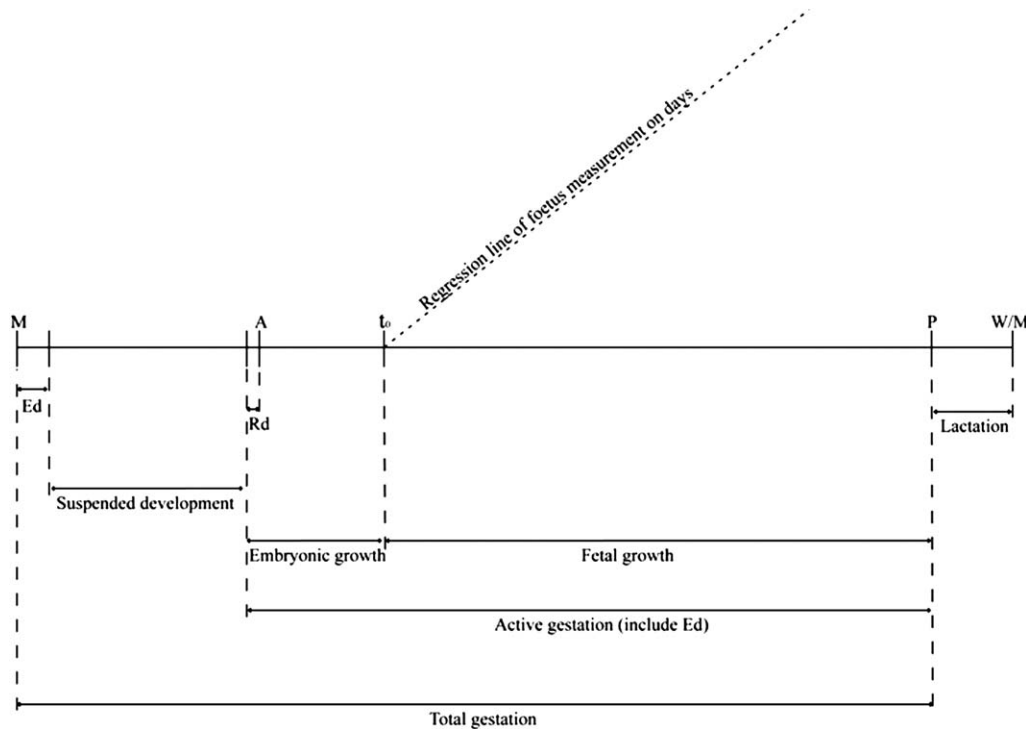


FIG. 2.—Schematic representation of a ringed seal (*Phoca hispida*) female life cycle from mating (M) to weaning (W). After mating, the fertilized egg develops into a blastocyst for approximately 7 days during the early development phase (Ed). Blastocyst development is arrested at this stage for several weeks (suspended development). Recommencement of development (Rd) follows and lasts about 4 days, after which the blastocyst attaches (A) to the uterine wall. The embryo grows for about 40 days (embryonic growth) before being termed a fetus (t_0), after which the growth rate is relatively constant during the remaining gestation period (fetal growth). The total gestation length is calculated from mating to parturition and includes the suspended development period. The active gestation refers only to the periods of development of the blastocyst, embryo, and fetus. Adapted from Hewer and Backhouse (1968).

sampled although 4 of them exhibited signs of previous gestations as confirmed by the presence of a corpus albicans or because of being classified as multiparous following examination of the uterine horns.

Fetal growth rate was estimated by regressing the mass^{1/3} and the standard length of fetuses on the Julian day of collection. Four fetuses collected in Sanikiluaq, Nunavut, Canada, an Inuit community located on the Belcher Islands in southeastern Hudson Bay (Fig. 1), in September ($n = 2$), November ($n = 1$), and January ($n = 1$) 2006 were added to the Arviat collection ($n = 95$) to augment sample sizes. Using a birth mass of 5.4 ± 0.3 kg ($\bar{X} \pm SE$) and standard length of 63.4 ± 1.3 cm (Hammill et al. 1991), we extrapolated the regression line to determine a date of parturition for ringed seals in Hudson Bay. We then calculated a weaning date by adding the 39 days of lactation (Hammill et al. 1991) to the parturition date. We assumed ovulation and mating to be concurrent with weaning date (Lydersen 1995; Smith 1987). Duration of total gestation (G_T) was determined as the time between mating and parturition (Fig. 2). Duration of active gestation (G_A), suspended development or embryonic diapause (D), and date of attachment (A) of the blastocyst to the uterine wall were determined following a modified method of Huggett and Widdas (1951) and Hewer and Backhouse (1968; Fig. 2). We did not use the regression of days of collection on fetus mass^{1/3} and standard length to calculate t_0 (intercept of

the regression line on the date of collection axis) as suggested in Huggett and Widdas (1951) and Hewer and Backhouse (1968), but used the regression of fetus mass^{1/3} and standard length on days of collection instead and applied the inverse prediction algorithm to calculate the 95% confidence interval (95% CI) of the x-intercept (Laws et al. 2003; Sokal and Rohlf 1995). The spread of the different reproductive cycle events (parturition, weaning, and attachment) was estimated by using the highest (upper point) and lowest (lower point) residual, to compute 2 regression lines of similar slopes than the main regression line but with different intercepts (McLaren 1958).

Growth.—We described changes in female length with age during the 1990s and the 2000s using a sigmoid curve with 3 parameters of the form:

$$y = \frac{a}{1 + e^{-\left(\frac{x-x_0}{b}\right)}}$$

where a is the asymptote, x_0 is the inflection point, and b is the slope.

Body condition.—Ringed seal body condition was estimated using the general prolate spheroid model described in Goodyear (1999). Briefly, ringed seal body shape was approximated by 2 prolate spheroids: one for the total body shape (total body volume, TBV) and one for the skeletal-muscular inner core. The fat volume (FV) was then estimated by a 2-step algorithm:

$$\text{TBV} = \frac{4}{3} \times \pi \times \frac{1}{2}L \times \left(\frac{G}{2\pi}\right)^2,$$

where L is the standard length in centimeters and G is the axillary girth in centimeters, and

$$\text{FV} = \text{TBV} - \frac{4}{3} \times \pi \times \frac{1}{2}L \times \left(\frac{G}{2\pi} - F\right)^2,$$

where F is the fat depth at sternum in centimeters. The body condition index (BCI) was then computed by dividing the fat volume by L^3 .

Environmental variables.—Daily temperatures, snow depth, and rain in Arviat were obtained from the airport weather station through Environment Canada (http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html). Temperatures were averaged for each year of the study period (1991–2006) per season as follows: winter: 1 January–31 March; spring: 1 April–30 June; summer: 1 July–30 September; and fall: 1 October–31 December. The mean of each season for all years available (1973–1975 and 1985–2007) also was computed. We calculated the maximum snow depth for the period February–May for each study year, as well as the average maximum snow depth for all years available (1985–2007). The sum of rainfall for the months April, May, and June was computed from the daily values for each study year, and averaged over all years available (1973–1975 and 1985–2007). The percentages of ice cover of northwestern Hudson Bay for 21 May, 28 May, and 4 June (Canadian Ice Service; <http://ice-glaces.ec.gc.ca/>) were averaged to provide a mean ice cover for the period from the end of May to the beginning of June for each study year and for all years available (1971–2008).

Breakup and freeze-up dates in western Hudson Bay were calculated for each study year, and averaged for all years available (1990–2007), following the method described in Gagnon and Gough (2005b). The western Hudson Bay region (as defined in Stirling et al. 1999; Fig. 1) was divided into a grid 0.5° latitude \times 1.5° longitude. Weekly ice concentration maps of Hudson Bay were retrieved from the Canadian Ice Service and used to obtain the ice concentration at the 42 center points defined by the grid. The breakup date (± 1 week) at each point was then defined as the earliest date with an ice concentration of 50% or less for 2 weeks. Freeze-up dates were defined as when the ice concentration at each point reached 50% over the period October–December, and maintained this condition for 2 weeks. Breakup and freeze-up dates for the entire western Hudson Bay region were then computed by taking the median of the 42 center points of the grid.

The sea-surface chlorophyll-*a* concentration (mg/m^3) in the western Hudson Bay region during the open-water seasons (June–October) of 1998–2006 was obtained from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) Level 3 monthly composite images at 9-km resolution, distributed by the Ocean Color Group at the National Aeronautics and Space Administration (Feldman and McClain 2009). A new composite was created for the time period available (1998–2006) using

SEADAS software (Baith et al. 2001). The mean chlorophyll-*a* concentration of the 11,658 cells of the western Hudson Bay region was used as an index of primary productivity.

Statistical analyses.—Normality was assessed using the Anderson–Darling test and used to determine whether parametric or nonparametric tests were employed. The sex ratio was assessed for unity departure using a *G*-test goodness-of-fit with Williams' correction (Sokal and Rohlf 1995). Percent of pups in the harvest, ovulation, and pregnancy rates in the 1990s and 2000s were compared using a *G*-test of independence with Williams' correction (Sokal and Rohlf 1995). The mean age at maturity and 1st parturition, the mean BCI, the mean length of open-water period, sum of rainfall, spring temperatures, and percent ice cover between 1990s and 2000s were compared using a *t*-test with a Welch correction to account for different standard deviations (Zar 1996), when necessary. The median age and adult female length, and the median date of spring breakup and maximum snow depth between the 2 decades were compared using a Mann–Whitney test corrected for ties and large samples because normality of residuals was not reached. Correlations between percent pups in the harvest, ovulation and pregnancy rates, and BCI were investigated using Spearman rank order correlation (r_s). Correlations between environmental variables were explored using Pearson product moment correlation analyses (r_p). To remove the year effect in the analyses, residuals of the linear regression of ringed seal demographic and body condition parameters over years were used to explore the relationship (linear or polynomial) with environmental variables.

Statistical analyses were performed using SYSTAT 12 (SYSTAT Software Inc., Chicago, Illinois), SygmaPlot 11 (SYSTAT Software Inc., 2008) and the GNU R system (R Foundation Core Team 2009). Unless otherwise stated, results are provided as mean \pm *SD* or median (1st–3rd quartile). All tests were 2-tailed and differences considered significant at $P < 0.05$.

RESULTS

A total of 672 ringed seals were sampled through the study period. Median dates of collection were fairly constant over the years (mid- to late October), with the exception of 2006 when 69% (33 of 48) of the sample was collected in early November (Table 1).

The sex ratio of adults pooled over all years did not differ from 1:1 (46% females; $G_1 = 2.66$, $P > 0.1$, $n = 338$), but was significantly male biased in 2000 ($G_1 = 10.95$, $P < 0.001$, $n = 54$) and female biased in 2005 ($G_1 = 4.61$, $P < 0.05$, $n = 22$; Table 1). The adult sex ratio was similar in the 1990s and 2000s ($G_1 = 0.004$, $P > 0.9$, $n = 338$; Table 1).

The regressions of fetus mass^{1/3} and standard length on days were significant (fetus mass^{1/3} = $0.09\text{days} - 19.40$, $r^2 = 0.73$, $F_{1,48} = 130.24$, $P < 0.0001$, intercept_{lower} = -21.48 , intercept_{upper} = -17.79 , and fetus standard length = $0.31\text{days} - 72.11$, $r^2 = 0.64$, $F_{1,97} = 171.54$, $P < 0.0001$, intercept_{lower} = -79.32 , intercept_{upper} = -65.40). Dates of birth and weaning are presented in Table 2. Mean spread of the

TABLE 1.—Date of collection, sample size of collection, percent of adults, sex ratio, percent pups, and ovulation and pregnancy rates of ringed seals (*Phoca hispida*) sampled during the fall subsistence harvest in Arviat, Nunavut, Canada, from 1991 to 2006. An asterisk (*) denotes a statistical difference between the 1990s (1991–1999) and the 2000s (2000–2006) or a departure from unity, from *G*-tests. NS = not significant; *n* = sample size; *n_A* = number of adults; *n_{AF}* = number of adult females; *n_P* = number of pups; *n_O* = number of ovulating females; *n_{Pr}* = number of pregnant females.

Year	Median date (range)	<i>n</i>	Adult	Adult female	Pup	Ovulation rate	Pregnancy rate
			% (<i>n_A</i> / <i>n</i>)	% (<i>n_{AF}</i> / <i>n</i>)	% (<i>n_P</i> / <i>n</i>)	% (<i>n_O</i> / <i>n</i>)	% (<i>n_{Pr}</i> / <i>n</i>)
1991	19 October 1991 (2–21 October)	41	48.78 (20/41)	55.00 (11/20)	4.88 (2/41)	100 (11/11)	90.91 (10/11)
1992	24 October 1992 (17–29 October)	71	56.34 (40/71)	47.50 (19/40)	4.23 (3/71)	83.33 (15/18)	0 (0/18)
1998	12 October 1998 (21 September–12 October)	93	72.5 (58/80)	48.28 (28/58)	7.50 (6/80)	100 (25/25)	64.00 (16/25)
1999	12 October 1999 (4–14 October)	99	79.59 (78/98)	39.74 (31/78)	5.10 (5/98)	90.32 (28/31)	70.97 (22/31)
1990s total		304	67.59 (196/290)	45.41 (89/196)	5.52 (16/290)	92.94 (79/85)	56.47 (48/85)
			*	NS	*	NS	*
2000	25 October 2000 (13 October–2 November)	97	56.84 (54/95)	27.78 (15/54) *	22.11 (21/95)	86.67 (13/15)	46.67 (7/15)
2003	18 October 2003 (22 September–28 October)	101	52.08 (50/96)	54.00 (27/50)	13.54 (13/96)	100 (17/17)	100 (17/17)
2004	21 October 2004 (30 September–31 October)	31	16.13 (5/31)	— ^a	22.58 (7/31)	— ^a	— ^a
2005	20 October 2005 (12–23 October)	91	24.72 (22/89)	72.73 (16/22) *	14.61 (13/89)	100 (13/13)	100 (13/13)
2006	5 November 2006 (23 October–8 November)	48	35.42 (17/48)	43.75 (7/16)	20.83 (10/48)	100 (5/5)	100 (5/5)
2000s total		368	41.23 (148/359)	45.77 (65/142)	17.83 (64/359)	96.00 (48/50)	84.00 (42/50)

^a 2004 was excluded from the analyses because sex was recorded from only 2 adults.

breeding season was 44 days. The duration of total gestation for ringed seals was estimated at 326 days. The regression line of fetus mass^{1/3} and standard length on days intercepted the *x*-axis at *t*₀ = 222 (95% *CI* = 194–245) and at *t*₀ = 235 (95% *CI* = 212–255), respectively. Date of attachment, duration of active gestation, and suspended development extrapolated from *t*₀ are presented in Table 2.

The number of pups in the harvest and the pregnancy rate were significantly lower in the 1990s than in the 2000s (*G*₁ = 24.11, *P* < 0.001, *n* = 649 and *G*₁ = 11.32, *P* < 0.001, *n* = 135, respectively; Table 1). The ovulation rate, however, did not differ between the 2 periods (*G*₁ = 0.52, *P* > 0.1, *n* = 135; Table 1). Adult females up to 37 years of age showed signs of a recent ovulation (including pregnancy). Ovulation and pregnancy rates were correlated (*r*_s = 0.81, *n* = 8, *P* = 0.01) but the percent pups in the harvest was not correlated with the pregnancy rate the year before (*r*_s = 0.41, *n* = 5, *P* = 0.450). Because the percentage of pups in the fall harvest increased significantly over the years (*F*_{1,7} = 10.09, *P* = 0.016), we took the residuals of the linear regression to explore the correlation with the BCI, in order to control for the effect of the year. Residuals of the percentage of pups were not correlated with the pup BCI (*r*_s = 0.43, *n* = 9, *P* = 0.223) nor with the female BCI (*r*_s = 0.24, *n* = 8, *P* = 0.537) or the female BCI the year before (*r*_s = 0.00, *n* = 5, *P* = 1). Ovulation and pregnancy rates of adult females were not

correlated with their BCI (*r*_s = -0.44, *n* = 8, *P* = 0.260 and *r*_s = -0.37, *n* = 8, *P* = 0.353, respectively).

The age structure of ringed seals sampled in the 1990s was skewed toward older age classes with very few seals 2 years of age or younger (Fig. 3a). In the 2000s, however, the age structure was largely skewed toward younger age classes with animals younger than 6 years having the highest frequency of occurrence (Fig. 3b). The younger age structure in the 2000s was reflected in the percent of adults (*G*₁ = 45.32, *P* < 0.001, *n* = 649; Table 1) and the median age (1990: age = 9 [5–16] years, *n* = 290; 2000: age = 4 [1–11] years, *n* = 359; *U* = 70,722, *P* < 0.0001) of ringed seals that were higher in the 1990s than in the 2000s. The median age of adult females, however, stayed constant over the 2 periods (1990: age = 15 [10–20] years, *n* = 89; 2000: age = 16 [12–20] years, *n* = 66; *U* = 3,158.5, *P* = 0.424).

The average age at sexual maturity of ringed seals sampled in the 1990s (\bar{X} = 5.4 ± 0.3 years) was significantly older than for seals sampled in the 2000s (\bar{X} = 3.8 ± 0.2 years, *t*_{1,721} = 150.2, *P* < 0.0001). Similarly, the average age of 1st parturition of ringed seals in the 1990s (\bar{X} = 7.3 ± 0.6 years) was greater than in the 2000s (\bar{X} = 5.5 ± 0.5 years, *t*_{1,849} = 73.4, *P* < 0.001).

The median standard length of adult females was significantly lower in the 1990s (standard length = 113.5 [108.8–119.4] cm) than in the 2000s (standard length = 123 [115.8–

TABLE 2.—Date and length (in days) of different life-cycle events of ringed seals (*Phoca hispida*) sampled in Arviat and Sanikiluaq, Nunavut, Canada, from 1991 to 2006, determined by the regression of fetus standard length and fetus mass^{1/3} on time. Values are given as date (range) and length (95% confidence interval).

	Fetus standard length	Fetus mass ^{1/3}
Parturition	17 March (23 February–10 April)	26 February (8 February–22 March)
Weaning or mating	25 April (3 April–19 May)	6 April (19 March–30 April)
Attachment	13 July (21 June–6 August)	2 July (14 June–26 July)
Active gestation	258 (233–286)	250 (221–285)
Suspended development	69 (40–94)	76 (41–105)

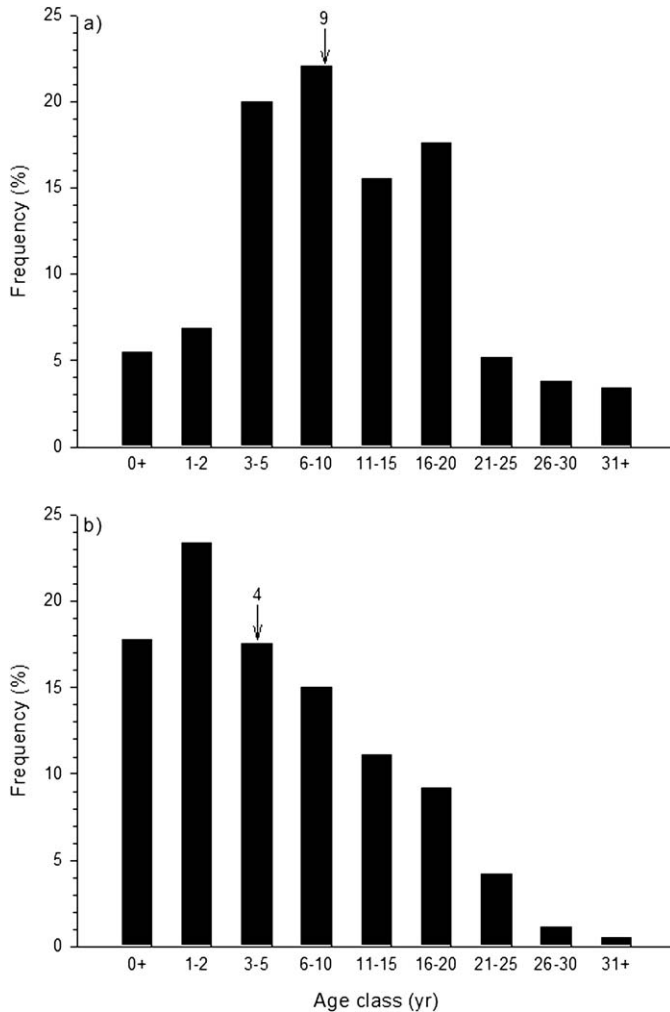


FIG. 3.—Age structure of ringed seals (*Phoca hispida*) sampled in Arviat, Nunavut, Canada, in the a) 1990s ($n = 290$) and b) 2000s ($n = 359$). Arrows indicate the median age of the sample. $n =$ sample size. 0+ = young-of-the-year (pups).

128.4] cm, $U = 4,222.5$, $n_1 = 89$, $n_2 = 64$, $P < 0.0001$). Ringed seal females sampled in the 2000s grew faster and were larger than females sampled in the 1990s (Fig. 4). The sigmoid model fit the 1990s data poorly, however, because of the small number of young age classes in the sample, particularly pups ($n = 5$) and yearlings ($n = 0$).

Adult female BCI tended to decrease over the study period ($\text{BCI} = -0.0003\text{year} + 0.68$, $r^2 = 0.50$, $F_{1,6} = 5.89$, $P = 0.051$), whereas juvenile and pup BCI did not change over the years (juveniles: $\text{BCI} = -0.0001\text{year} + 0.26$, $r^2 = 0.11$, $F_{1,7} = 0.86$, $P = 0.383$; pups: $\text{BCI} = 0.0002\text{year} - 0.42$, $r^2 = 0.20$, $F_{1,7} = 1.76$, $P = 0.226$). When the 2 decades were compared, adult females tended to be in better condition in the 1990s (1990: $\bar{X} = 0.0230 \pm 0.0059$, $n = 88$; 2000: $\bar{X} = 0.0210 \pm 0.0060$, $n = 62$; $t_{148} = 1.98$, $P = 0.049$), there was no difference in juvenile BCI (1990: $\bar{X} = 0.0211 \pm 0.0044$, $n = 74$; 2000: $\bar{X} = 0.0205 \pm 0.0057$, $n = 136$; $t_{192} = 0.83$, $P = 0.406$), and pups tended to be in better condition in the 2000s (1990: $\bar{X} = 0.0192 \pm 0.0034$, $n = 16$; 2000: $\bar{X} = 0.0213 \pm 0.0054$, $n = 57$; $t_{38} = 1.91$, $P = 0.064$). Only 2 and

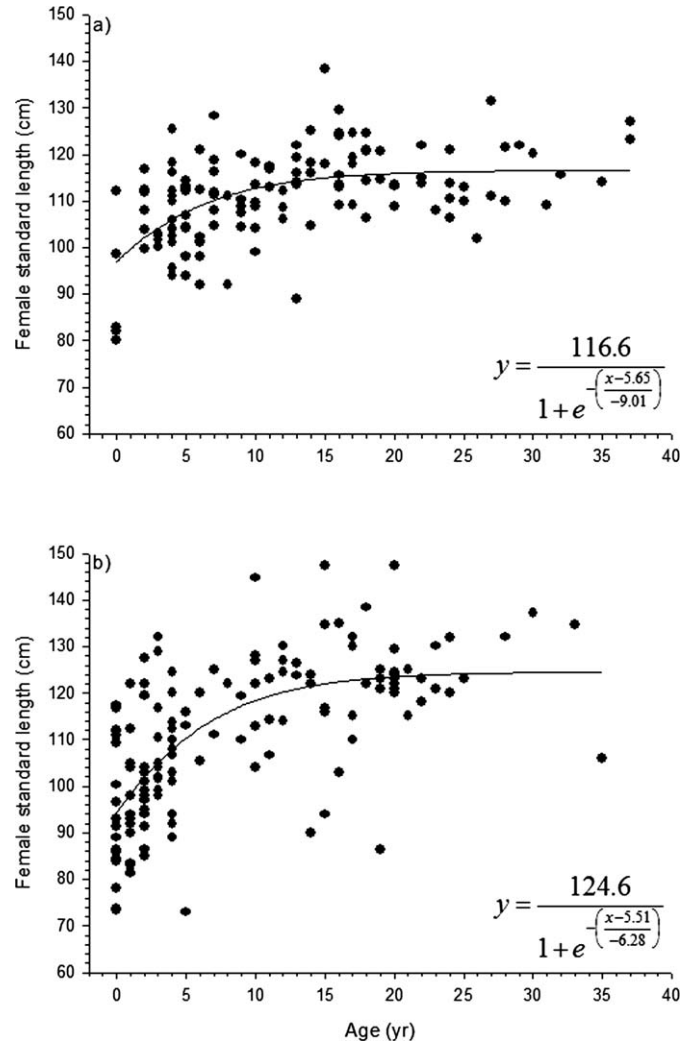


FIG. 4.—Growth of ringed seal (*Phoca hispida*) adult females sampled in Arviat, Nunavut, Canada, in the a) 1990s and b) 2000s, modeled by a sigmoid curve with 3 parameters. a) $r^2 = 0.29$, $n = 131$ and b) $r^2 = 0.45$, $n = 158$.

3 pups were sampled in 1991 and 1992, respectively, suggesting caution in interpreting pup BCI trend over the years. Pregnant females had a higher body condition than did nonpregnant females in the 1990s (pregnant: $\bar{X} = 0.0244 \pm 0.0061$; nonpregnant: $\bar{X} = 0.0209 \pm 0.0049$; analysis of covariance [ANCOVA] controlled for age and year: $F_{1,81} = 13.02$, $P = 0.0005$), but not in the 2000s (pregnant: $\bar{X} = 0.0209 \pm 0.0049$; nonpregnant: $\bar{X} = 0.0236 \pm 0.0044$; ANCOVA controlled for age and year: $F_{1,45} = 0.67$, $P = 0.420$).

Over our study period (1991–2006), the sum of rainfall from April to June presented a significant positive trend ($F_{1,14} = 8.83$, $P = 0.010$), the length of the open-water period was not significantly longer although a marginal increase was observed ($F_{1,14} = 4.52$, $P = 0.052$), and no trend was detected for the other variables (breakup date: $F_{1,14} = 2.03$, $P = 0.176$; maximum snow depth: $F_{1,13} = 0.18$, $P = 0.682$; spring temperatures: $F_{1,14} = 1.40$, $P = 0.257$; ice cover: $F_{1,14} = 0.09$, $P = 0.772$; chlorophyll-*a* concentration: $F_{1,7} = 1.49$, $P =$

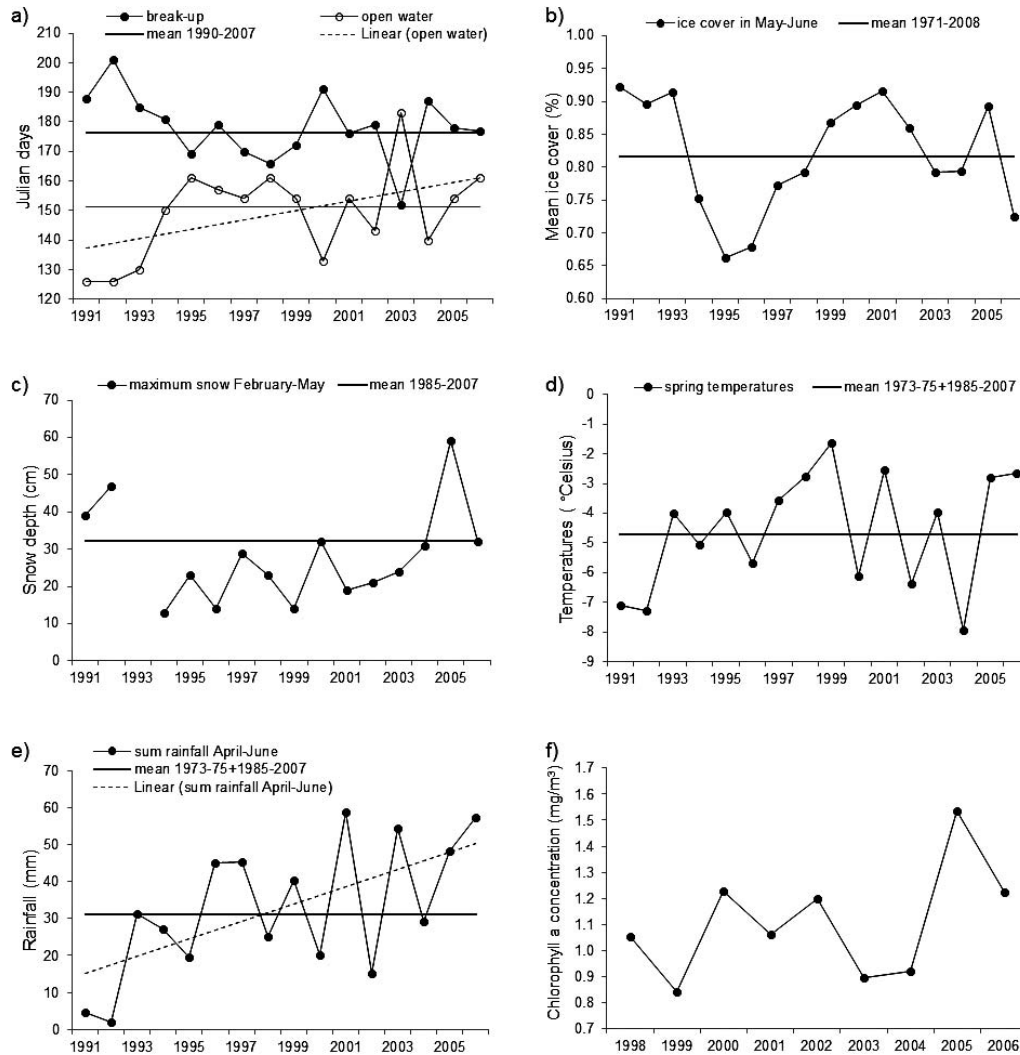


FIG. 5.—Trends in environmental variables over the study period 1991–2006 and comparison with long-term means. a) Breakup date (closed circle, bold line) and length of the open-water period (open circle, thin line). The dotted line represents the linear regression: length of open-water period = $1.60\text{year} - 3,039$, $r^2 = 0.24$, $n = 16$. b) Mean ice cover for the last 2 weeks of May and 1st week of June. c) Maximum snow depth from February to May. d) Spring temperatures. e) Sum of rainfall from April to June. The dotted line is the linear regression: sum of rainfall = $2.35\text{year} - 4,671$, $r^2 = 0.38$, $n = 16$. f) Chlorophyll-*a* concentration over 1998–2006.

0.261; Fig. 5). When the environmental variable means were compared between the 1990s and the 2000s, none of the differences observed was statistically significant (Table 3). The date of breakup was negatively correlated to the length of the open-water period, the spring temperatures, and the sum of rainfall in the spring, and was positively correlated to the ice cover in May–June (Table 4). The sum of rainfall in the spring increased with increasing winter and spring temperatures (Table 4). Spring temperatures were positively correlated to winter (Table 4), summer, and fall temperatures (summer: $r = 0.47$, $n = 22$, $P = 0.028$; fall: $r = 0.65$, $n = 22$, $P = 0.001$). Summer and fall temperatures were positively correlated to each other ($r = 0.61$, $n = 22$, $P = 0.003$) and to the length of the open-water period (summer temperatures: $r = 0.60$, $n = 18$, $P = 0.009$; fall temperatures: $r = 0.50$, $n = 18$, $P = 0.037$).

The residuals of the linear regression of percentage of pups in the harvest over years increased linearly as the spring

temperature decreased (Fig. 6b), but was related to the maximum snow depth in the spring by a quadratic polynomial relationship (Fig. 6a). A quadratic polynomial curve also was the best model to describe the relationship between residuals of pup and female BCI over years and date of spring breakup (Figs. 6c and 6d).

DISCUSSION

Ringed seal reproductive parameters and survival of pups were low in the 1990s and increased in the 2000s, indicating that conditions in western Hudson Bay were less favorable for the species in the 1990s than they were in the 2000s. The beginning of the 1990s was characterized by late dates of breakup (e.g., 21 July in 1992, 25 days later than average) and short open-water periods (126 days in 1991 and 1992), cold temperatures, and a high ice cover in late spring, suggesting

TABLE 3.—Comparison of environmental variables obtained for western Hudson Bay, Nunavut, Canada, between the 2 decades 1990s and 2000s. *P* = *P*-value from a 2-tailed *t*-test or a Mann–Whitney test; *SD* = standard deviation; *n* = sample size; *d.f.* = degrees of freedom.

	1990s				2000s				<i>t</i>	<i>d.f.</i>	<i>P</i>
	\bar{X}	<i>SD</i>	<i>n</i>	Range	\bar{X}	<i>SD</i>	<i>n</i>	Range			
Length of open-water period (days)	146.6	14.9	9	126–161	152.6	16.5	7	133–183	0.77	14	0.46
Sum of rainfall (mm)	26.7	16	9	1.8–45.4	40.5	18.5	7	15.2–58.8	1.6	14	0.13
Spring temperatures (°C)	−4.6	1.9	9	−7.3–−1.6	−4.6	2.2	7	−7.9–−2.5	0.06	14	0.95
Ice cover (%)	0.81	0.1	9	0.66–0.92	0.84	0.07	7	0.72–0.92	0.73	14	0.48
	Median	1st–3rd quartile	<i>n</i>	Range	Median	1st–3rd quartile	<i>n</i>	Range	<i>U</i>		<i>P</i>
Breakup date (Julian day)	179	170–185	9	166–201	178	176.5–183	7	152–191	31.5		0.96
Maximum snow depth (cm)	23	14.31.5	8	13–47	31	22.5–32	7	19–59	19		0.34

heavy ice conditions (Fig. 5). The combined effect of a strong positive phase of the North Atlantic Oscillation and a strong El Niño event in 1991–1992, and the eruption of Mount Pinatubo in June 1991, created colder than average conditions in the eastern Arctic, including Hudson Bay, in the early 1990s (Gough et al. 2004; Graf et al. 1993; McCormick et al. 1995; Mysak et al. 1996). In the western Arctic, heavy ice conditions in the mid-1970s and 1980s were proposed as the major cause of ringed seal reproductive failures and abundance decline,

although the mechanisms were not understood (Harwood et al. 2000; Kingsley and Byers 1998; Smith 1987; Stirling 2002; Stirling et al. 1982).

We believe the variation of ringed seal life-history traits over the years is not an artifact of our sampling program but that it reflects biologically significant events for ringed seals in western Hudson Bay. Stirling (2005) discussed this issue in a previous paper and concluded no support for sexual or age-class segregation that might bias the collection of

TABLE 4.—Pearson product moment correlation matrix for environmental variables obtained in western Hudson Bay, Nunavut, Canada. Boldface italic values indicate statistical significance. *r_P* = Pearson correlation coefficient; *P* = *P*-value; *n* = sample size. Open water = length of the open-water period; [Chl. *a*] = concentration of chlorophyll *a*; max. snow = maximum snow depth from February to May; sum of rain = total rainfall in April–June; temp. = temperatures; ice cover = ice cover in May–June.

	Open water	[Chl. <i>a</i>]	Max. snow	Sum of rain	Winter temp.	Spring temp.	Ice cover
Breakup date							
<i>r_P</i>	<i>−0.93</i>	0.37	0.34	<i>−0.51</i>	−0.07	<i>−0.56</i>	<i>0.48</i>
<i>P</i>	<i>0.00</i>	0.30	0.19	<i>0.03</i>	0.78	<i>0.02</i>	<i>0.05</i>
<i>n</i>	18	10	17	18	18	18	18
Open water							
<i>r_P</i>		−0.25	−0.33	<i>0.64</i>	0.16	<i>0.56</i>	<i>−0.60</i>
<i>P</i>		0.48	0.20	<i>0.00</i>	0.52	<i>0.02</i>	<i>0.01</i>
<i>n</i>		10	17	18	18	18	18
[Chl. <i>a</i>]							
<i>r_P</i>			<i>0.79</i>	−0.01	0.03	0.04	0.24
<i>P</i>			<i>0.01</i>	0.98	0.94	0.91	0.49
<i>n</i>			10	10	10	10	11
Max. snow							
<i>r_P</i>				−0.15	−0.12	−0.26	0.29
<i>P</i>				0.51	0.62	0.26	0.24
<i>n</i>				22	21	21	19
Sum of rain							
<i>r_P</i>					<i>0.43</i>	<i>0.56</i>	−0.23
<i>P</i>					<i>0.046</i>	<i>0.01</i>	0.32
<i>n</i>					22	22	20
Winter temp.							
<i>r_P</i>						<i>0.44</i>	0.02
<i>P</i>						<i>0.04</i>	0.93
<i>n</i>						22	20
Spring temp.							
<i>r_P</i>							−0.05
<i>P</i>							0.82
<i>n</i>							20

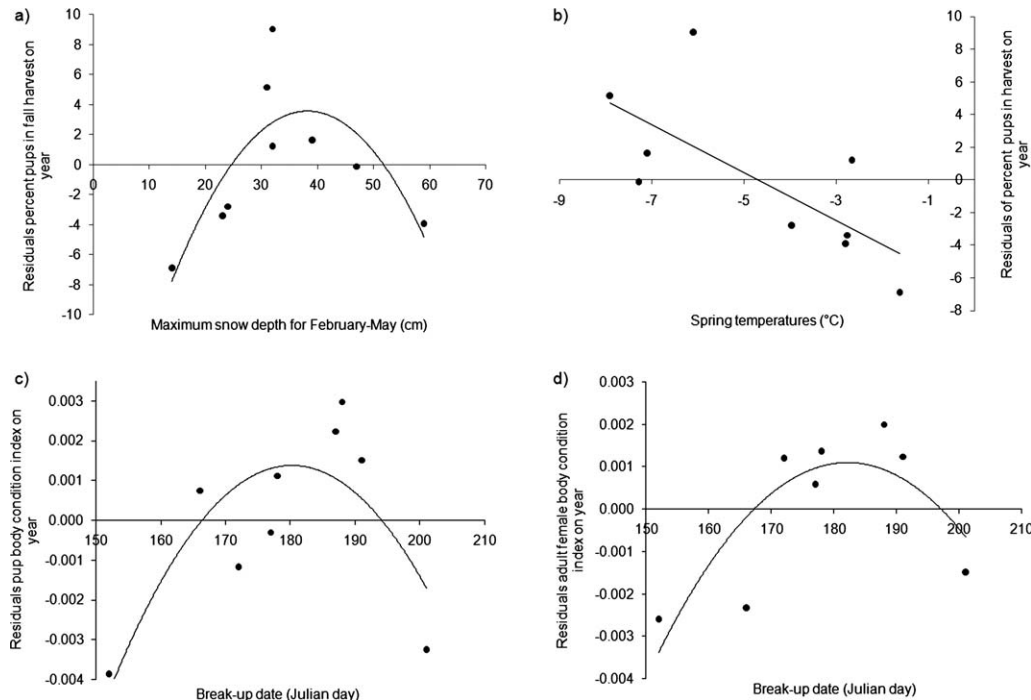


FIG. 6.—Relationship between a) residuals of the linear regression of percent pups in the harvest over years and maximum snow depth ($y = -0.019x^2 + 1.48x - 24.72$, $r^2 = 0.64$, $P = 0.047$, $n = 9$, $x_1 = 24.7$ and $x_2 = 51.6$); b) residuals of the linear regression of percent pups in the harvest over years and spring temperatures ($y = -1.46x - 6.84$, $r^2 = 0.51$, $P = 0.031$, $n = 9$); c) residuals of the linear regression of pup body condition index over years and date of breakup ($y = -7E-6x^2 + 0.0026x - 0.2306$, $r^2 = 0.63$, $P = 0.051$, $n = 9$, $x_1 = 166$ and $x_2 = 194$); and d) residuals of the linear regression of female body condition index over years and date of breakup ($y = -4.9E-6x^2 + 0.0018x - 0.162$, $r^2 = 0.66$, $P = 0.066$, $n = 9$, $x_1 = 167$ and $x_2 = 197$) of ringed seals (*Phoca hispida*) sampled in Arviat, Nunavut, Canada, from 1991 to 2006.

ringed seals sampled in Arviat during the fall harvest. In Arviat, the fall subsistence hunt is nonselective because hunters have no incentive to shoot ringed seals of a particular age class, and hunt them generally from long distances, thus precluding visual evaluation of the size of the animal prior to shooting. In fact, hunters throughout the Arctic do not discriminate on the basis of anything when hunting seals in open water. Successful killing is difficult and hunters get a limited number of opportunities, because of a rocking boat and a small target that offers itself, usually at considerable distance, for a very limited period of time. Thus, hunters cannot afford to waste any opportunity. Our experience suggests sampling in this manner provides as representative a sample of the population as it is possible to obtain at any time of the year.

In western Hudson Bay, the percentage of ringed seal pups in the fall harvest more than tripled in the 2000s compared to the 1990s, suggesting that conditions were less favorable for pups in the 1990s than in the 2000s. Even so, the proportion of pups in the fall harvest in western Hudson Bay in the 2000s (18%) was still a relatively low percentage compared to that reported from other locations around the Arctic with similar ovulation or pregnancy rates (20–100%—Kingsley and Byers 1998; Smith 1973, 1987; Teilmann and Kapel 1998).

Adult ringed seal ovulation rate was not different between the 2 decades and showed little variation, being 100% for 5 of the 8 years with data and never falling below 80%. This result

is similar to the range of rates previously reported in the literature for different locations across the Arctic (39–100%—Harwood et al. 2000; Holst and Stirling 2002; Krafft et al. 2006; Lydersen and Gjertz 1987; Smith 1973; Stirling et al. 1977, 1982). Pregnancy rate was significantly lower in the 1990s than in the 2000s, particularly in 1992 when none of the 18 adult females sampled was pregnant. No correlation between pregnancy rate and percentage of pups was found and the pregnancy rate in the 1990s was not sufficiently low to account for the low percent of pups in the harvest at the same period, suggesting that late intra uterine or newborn mortality occurred, that pups did not survive well through the summer, or that pups left the Arviat area before the fall harvest.

The age structure, the percentage of adults, and the median age of seals sampled in the 1990s and the 2000s indicated that ringed seals sampled in the latter decade were significantly younger. Considering the low pregnancy rates and percent pups in the harvest in the late 1990s, the high frequency of the age classes 0+, 1–2, and 3–5 in the 2000s suggested that not only pup production, survival (e.g., decrease predation pressure), and site fidelity (i.e., seals born in the Arviat area remained in this area until fall) increased, but that possibly pup and juvenile seals from other areas immigrated to the Arviat area. The low pregnancy rate in 1999 while the percent pups in the harvest in 2000 was the 2nd highest of the study period particularly supports the hypothesis of pup and juvenile immigration in the 2000s. Pups have been known to travel

large distances in the fall (e.g., Smith 1987). Despite a similar median age, adult females were longer and attained sexual maturity at a younger age in the 2000s than in the 1990s. These results, together with the growth curves (Fig. 4), indicate that females sampled in the 2000s grew faster (Laws 1956), possibly under conditions more favorable than may have prevailed in the Arviat area during the 1990s. Therefore, one possible explanation for the observed pattern is that not only pups and juveniles immigrated into the Arviat area in the 2000s, but possibly also some young adult females. The emigration of young animals to more productive and suitable areas during adverse environmental periods, and the subsequent recovery of population number and demographic parameters through the immigration of immature and young adult seals when favorable condition resumed, have already been suggested for ringed seals (Kingsley and Byers 1998; Smith and Stirling 1978; Stirling et al. 1982; Vibe 1967) and Weddell seals (*Leptonychotes weddellii*—Cameron and Siniff 2004; Testa and Siniff 1987). In Weddell seals, the ecological counterpart of ringed seals in the southern polar regions (Stirling 1969), Cameron et al. (2007) reported an increase in site fidelity with age up to 12 years, and an increased fidelity to sites where successful breeding events occurred. We suggest that in Hudson Bay ringed seals might follow a pattern similar to that of Weddell seals, moving among different sites at the beginning of their reproductive life.

Ringed seal life-history traits varied between the 2 decades. Seals in the 2000s were younger, grew faster, matured earlier, and produced more pups that survived better than those in the 1990s. Such life-history traits in the 2000s are more suggestive of a growing population than in the 1990s (Hanks 1978; Oli and Dobson 1999; Stearns 1976). The change in life-history traits during the 2 study periods supports the hypothesis that ringed seal population dynamics in western Hudson Bay may follow a decadal cycle, as previously suggested for Hudson Bay (Ferguson et al. 2005) and the western Arctic (Stirling 2002; Stirling and Lunn 1997). In the Arctic, decadal fluctuations of the sea ice regime through atmospheric forcing (e.g., North Atlantic Oscillation) have been reported (Hurrell 1995; Mysak et al. 1996; Mysak and Manak 1989), and climatic variations have been linked to variations in life-history parameters of several arctic species (Ottersen et al. 2001; Regehr et al. 2007; Skinner et al. 1998).

We suggest that the poor ringed seal reproductive and survival performances in the 1990s could have been triggered by the cold and heavy ice conditions that prevailed in western Hudson Bay at the beginning of the decade, through 2 nonexclusive mechanisms. First, short open-water seasons and reduced number or extent of leads and polynyas in the winter resulting from cold and heavy ice conditions in the 1990s may have generated a decrease in the overall productivity of the area (Stirling 1997; Stirling et al. 1982; Stirling and Lunn 1997). The open-water period represents the most-productive phase of the Arctic Ocean annual cycle (Arrigo et al. 2008) and for ringed seals, represents a period of intense feeding, necessary to replenish their fat reserves in anticipation of the

coming winter. A decline in productivity could therefore be detrimental for ringed seals, especially for inexperienced pups. In 1992, when the breakup was delayed by 25 days compared to the 17-year average and the open-water season was the shortest recorded during the study period, ringed seal BCI declined for all age classes, suggesting a nutritional stress. The negative effects of nutritional stress on reproduction, survival, and growth of pinnipeds have been widely reported in the literature (Laws 1956; and see review by Trites and Donnelly 2003). Second, polar bear body condition and natality increased in western Hudson Bay in the early 1990s. This increase was associated with the delayed breakup dates in the early 1990s that created longer spring hunting seasons on the ice on ringed seals, and especially pups, for polar bears (Stirling and Derocher 1993; Stirling and Lunn 1997; Stirling et al. 1999). Roth (2003) found that arctic foxes increased their consumption of ringed seals during low lemming (*Lemmus trimucronatus* and *Dicrostonyx* spp.) years. In the Arviat area, lemming populations were in a trough in 1991 and 1992 (Krebs et al. 2002). These results suggest that, in addition to experiencing a possible nutritional stress, ringed seals, and particularly ringed seal pups, were under high predation pressure by both polar bears and arctic foxes at the beginning of the 1990s.

Pup survival, ovulation, and pregnancy rates were not affected by pup or female body condition, respectively. This is a surprising result because, as shown previously (e.g., Chambellant et al. 2003; Guinet et al. 1998; Harwood et al. 2000; see review by Trites and Donnelly 2003), we would expect the poor demographic and survival performances recorded in the 1990s to be affected by the poor environmental conditions partly through nutritional stress and consequently, poor BCI. Several nonexclusive hypotheses could be proposed to explain this result. First, our time series and sample sizes might not be sufficient to find a significant correlation between BCI and demographic parameters. Second, our BCI measure might not be sensitive enough to detect small but biologically significant changes in ringed seal nutritional conditions. The BCI of all age classes declined in 1992, a year with extreme climatic conditions, indicating that major stresses are reflected by our BCI but minor stresses might not be. Third, the fall might not be relevant to assess variations in female and pup BCI because females are the fattest at this period, and pups sampled in the fall are the ones that survived through the summer. Recording BCI in the spring may be more appropriate. Fourth, our pregnancy rates may be overestimated because abortion might have taken place later in gestation and would not be recorded. Fifth, the percentage of pups in the fall harvest may not be a good representation of pup survival because emigration and immigration, if they occur, are confounding factors. Sixth, adult ringed seals might have evolved behavioral or physiological responses to provide compensatory physiology to reoccurring high-variability stress of poor nutritional conditions (Trites and Donnelly 2003).

Ringed seal pupping in western Hudson Bay peaked at the beginning of March, a month earlier than previously described

in the literature from higher latitudes (Hammill et al. 1991; Lydersen 1995; McLaren 1958; Smith 1973, 1987). Our sample sizes of fetuses from early and late gestation stages were small, which might have biased the relationships and dates estimated, and thus reduce the strength of our interpretation. However, a March pupping date in Hudson Bay is corroborated by traditional knowledge (Cleator 2001; McDonald et al. 1997) and supports the hypothesis of a latitudinal gradient of pupping suggested by McLaren (1958) and Smith (1987). Our results indicated a relatively long breeding season (44 days), similar to previous studies and within the seasonal range of male spermatogenesis (Breton-Provencher 1979; McLaren 1958; Smith 1973, 1987). The estimated weaning date was around mid-April, with the latest weaning date on 19 May. Such an early date of pup independence is likely an adaptation of ringed seals living at lower latitudes where the spring breakup occurs earlier, and might be critical to pup survival by ensuring an uninterrupted lactation period. Indeed, a markedly earlier spring breakup in the southern Beaufort Sea was shown to negatively affect ringed seal pup survival by prematurely separating unweaned pups from their mothers (Harwood et al. 2000). In Hudson Bay, where the ice is now breaking up about 4 weeks earlier than in the 1970s, an early date of weaning could be particularly relevant and might temporarily shelter pups from the detrimental effects of climate warming.

Our results suggested that pup survival improves with cold conditions in the spring and possibly, by extension, later breakup dates and heavy ice years. Although colder springs might enhance pups' preweaning survival by ensuring the integrity of lairs and allowing completion of weaning, pups' postweaning survival might be compromised. More specifically, although a delayed breakup would provide a platform for pups to rest on and feed under for a longer time, it also would mean more-prolonged exposure to polar bear predation (Stirling and Derocher 1993), as well as a decrease in marine productivity resulting from a shorter open-water season. In fact, heavy ice years have been previously associated with reproductive failures in ringed seals (Kingsley and Byers 1998; Smith 1987; Stirling 2002). We propose that there is a range of spring temperatures and, thus, of breakup dates, that likely provides optimal conditions for pup pre- and postweaning survival, that is, breakup not too early to disrupt lactation, and not too late to increase mortality by predation and reducing feeding time by pups during their 1st summer. We found that the BCIs of ringed seal pups and, to a lesser extent, of adult females, were optimized when breakup occurred around the end of June (180 Julian days) and within a range of mid-June to mid-July (Fig. 6).

Our results also suggested a window of snow depths on the ground (25–52 cm; peak around 38 cm [Fig. 6]) that optimized pup survival. This is in agreement with the hypothesis that there is an optimal snow depth for ringed seal recruitment, as suggested by Ferguson et al. (2005). However, snow depth on sea ice is highly variable compared to that found near weather stations because of winds and ice deformations. Smooth ice

platforms will typically have less snow than highly deformed areas that constitute preferred birth lair sites for ringed seals (Hammill and Smith 1989; Lydersen and Gjertz 1986; McLaren 1958; Smith 1987; Smith and Stirling 1975). Consequently, snow depths reported at ringed seal lairs in the literature (Furgal et al. 1996; Hammill and Smith 1989; Lydersen and Gjertz 1986; Smith and Stirling 1975) are greater relative to the values reported in this study. The detrimental effect on pup survival of a snow layer deeper than 52 cm, and by extension a thicker lair snow roof, could include an altered air circulation inside the lair, forcing pups to leave lairs on regular basis to replenish the oxygen supply (Kelly and Quakenbush 1990).

In conclusion, our results support the paradigm described by Eberhardt (2002) by which early survival and age at parturition are the 1st life-history traits to be affected by a decrease in resources. We propose that ringed seal population dynamics follow a decadal cycle that relates to fluctuations in the environment and particularly in the sea ice regime, through changes in ocean productivity and predation pressure. At the low phase of the cycle, we suggest an important role of immigration of pups, juveniles, and young adult animals in the recovery of ringed seals in western Hudson Bay. Our results suggested that ringed seals are adapted to a specific but limited range of environmental variations (e.g., Gaden et al. 2009). However, if current trends continue in Hudson Bay, as projected (Gagnon and Gough 2005a; Gough and Wolfe 2001; Joly et al. 2011), environmental conditions may exceed ringed seal tolerance thresholds, and possibly trigger a long-term decline that could underlay or override the natural cycle. Further research exploring the mechanisms involved in the coupling of environmental variation and ringed seal demography, particularly the role of nutritional stress, would contribute to our understanding of the Hudson Bay ecosystem.

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