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Growth and population parameters of the world's northernmost harbour seals *Phoca vitulina* residing in Svalbard, Norway

Abstract The harbour seals (*Phoca vitulina*) in Svalbard are the northernmost population of this species. The population size is thought to be less than 1,000 individuals; these animals reside principally within a national park on Prins Karls Forland on the west coast of Spitsbergen, Svalbard, at about 78°20′N. The material presented in this study was collected from 367 live-captured animals, aged based on growth layers read from stained, decalcified incisor sections (except for pups of the year). Standard length ($F_{1,246} = 45.70$, $P < 0.0001$) and body mass ($F_{1,258} = 25.28$; $P < 0.0001$) were both significantly influenced by sex when age was taken into account. Adult males are both longer [152.9 ± 4.8 (SE) vs 140.1 ± 2.0 cm, standard length] and heavier (104.0 ± 5.0 vs 83.2 ± 2.7 kg, body mass) than adult females in this population. Age at sexual maturity was assessed based on analyses of sex hormones. Testosterone levels in males showed an abrupt increase at 6 years of age, while estradiol levels in females increased from age 4. The reproductive rate of adult females was 0.93. The longevity of Svalbard harbour seals was short compared to harbour-seal populations from other areas. However, these seals are not exposed to terrestrial predation; there is no known mortality due to fisheries or hunting and their pollution burdens are low. Extreme seasonality and perhaps other harsh environmental conditions at the northern edge of this species' distribution may exert long-term low levels of stress that result in short life span, or there are currently unknown acute sources of mortality in this population. To our knowledge, this is the first study of population parameters on a pinniped species using cross-sectional, non-terminal sampling.

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Introduction

The harbour seals *Phoca vitulina* in Svalbard constitute the northernmost population of this species in the world (Prestrud and Gjertz 1990). They reside primarily along the west coast of Prins Karls Forland at about 78°20′N, although harbour seals in this population have been recorded as far north as 80°50′N (Wiig 1989), and are sighted on islands in the northwest corner of Svalbard routinely each summer. The northern limits for the distribution of harbour seals are generally restricted by local sea-ice conditions across their range. The west coast of Svalbard is one of the northernmost areas in the Atlantic to be affected by the warm Norwegian Atlantic Current ("the Gulf Stream"); this area does not experience ice-cover outside the inner parts of the fjords during winter. A satellite tracking study of harbour seals on Svalbard showed that adult animals were more or less resident throughout the year in the immediate area of Prins Karls Forland (Gjertz et al. 2001). No recent data are available on population size, but surveys during the 1980s concluded that the population consisted of at least 500–600 animals (Prestrud and Gjertz 1990). The pupping period for harbour seals in Svalbard occurs in the second half of June (Gjertz and Børset 1992), which is similar to other European populations from latitudes as low as 50°N (Temte et al. 1991), and all pupping known to occur takes place in the vicinity of Prins Karls Forland. In addition to satellite tracking, studies of diet, levels of pollutants, haul-out behaviour, and pup-diving development have been conducted on the Svalbard harbour-seal population (Andersen 2001; Jørgensen et al. 2001; Reder et al. 2004; Wolkers et al. 2004).

Because this population is below the level that is generally thought to be "minimum viable population size" for a large mammal, its dynamics are intriguing from a population-biology perspective, and they are also important from a conservation perspective (e.g. Harcourt 2002; Reed et al. 2003). The purpose of the present

study was to investigate growth and population parameters from Svalbard's harbour seals. Traditionally vital population statistics from seal populations are retrieved from harvested specimens, but because of the small size and protected status of this population, this study is based on materials collected from live-captured animals.

Materials and methods

This study is based on material collected from animals during three field periods on the west coast of Prins Karls Forland (78°20′N, 11°30′E), which is the westernmost island of the Svalbard Archipelago, Norway. Ninety-eight animals were captured in the period 3–11 September 1998, 130 animals in the period 17 June–7 July 1999, and 139 animals in the period 17 June–7 July 2000. The seals were caught using nets set from shore near haulout sites, hoop-nets from Zodiacs or they were captured directly on land using hand-held nets. After capture, seals were transferred into individual restraint-nets and weighed (Salter spring scales ±0.5 kg). All seals except pups of the year were immobilised with an intramuscular injection of Telazol (1 mg/kg body mass for sub-adults of both sexes and adult females; 0.75 mg/kg body mass for adult males) before extraction of one of the lower incisors for age determination. Standard lengths and girths (American Society of Mammalogists 1967) were measured to the nearest centimetre while the seals were drugged and thus in a relaxed position, and a 50-ml blood sample was taken from the epidural vein for hormone analyses. Standard lengths, girths, and blood samples were also taken from a sub-sample of the pups, depending on the conditions surrounding the capture. All seals were tagged with a Rototag in each hind flipper before being released. Blood samples were collected in heparinised blood tubes, centrifuged for 10 min and then the plasma was removed using pipettes and subsequently frozen at −20°C until analyses. Ages were determined by counting cementum growth layers in decalcified, stained longitudinal sections of the incisors (Bernt et al. 1996).

Growth was described using von Bertalanffy growth curves (Bertalanffy 1957; Schnute 1981):

$$L_x = L_\infty[1 - e^{-a(x-x_0)}]^b$$

$$M_x = M_\infty[1 - e^{-a(x-x_0)}]^b,$$

where L_x is the length (cm), and M_x is mass (kg) at time x, x is the age of the animal (years), x_0 is an estimated constant for prenatal growth (McLaren 1993), L_∞ and M_∞ are the asymptotic length and mass respectively, a and b are constants that are fitted to the data by regression where a describes the rate of approach to the asymptote and b describes the curvelinearity of this approach (McLaren 1993). The value 0.64 was chosen for x_0 (the time before birth at which the embryo starts growing after delayed implantation) based on data summarised in McLaren (1993). Growth curves were fitted using STATISTICA 6.0 (Statsoft, Tulsa, Okla.). Length data were available from 120 males (including 4 newborn pups), and from 129 females (including 3 newborn pups), while mass data were available from 127 males (including 11 newborn pups) and 134 females (including 8 newborn pups). Pup growth will be dealt with in detail elsewhere (Kovacs et al., unpublished data).

Age at sexual maturity was assessed using the age at which testosterone in males and estradiol in females increased markedly during the breeding season. Only animals sampled during the breeding period (1999 and 2000) were included in these analyses. Concentrations of testosterone and estradiol in blood-plasma samples of the seals were determined in duplicate samples using commercially available radioimmunoassay kits (testosterone: Coat-A-Count Total Testosterone; Diagnostic Products, Los Angeles,; estradiol Estradiol [125]I Sensitive Coated Tube Radioimmunoassay, Orion Diagnostica, Espoo, Finland). A gamma counter (Cobra Auto-Gamma, Packard Instrument, Dowers Grove, Ill.) was used for determination of radioactivity levels. Analyses were performed according to the instructions for each assay kit. Validation tests showed that serial dilutions of seal plasma with high steroid concentrations produced a dose-response curve parallel to the standard curve. The detection limits for testosterone and estradiol were defined as the concentration two standard deviations below the counts at maximum binding, which were 0.1 nmol/l and 2.5 pmol/l, respectively. Concentrations of estradiol were below the detection limit in nine females while concentrations of testosterone were below the detection limit in three males. The concentrations in these samples were set to 50% of the detection limit. The inter-assay CVs for control-samples (seal plasma) for testosterone and estradiol were 5.6 and 13.1%, respectively.

All animal handling was approved by the Norwegian Animal Research Authority and permission to do fieldwork was granted by the Environmental Branch of the office of the Governor of Svalbard, Norway.

Results

A total of 367 animals were captured during the 3 field seasons. Approximately one-third of these animals (121) were nursing pups captured during the breeding seasons of 1999 and 2000. The sample consisted of 178 males and 189 females. The age of the animals ranged from 0 to 22 years for females and 0 to 17 years for males. Excluding nursing pups from the analyses, the mean age of sampled animals did not differ significantly between the two summer and autumn samples (ANOVA) for either males ($F_{1,29}$, $P=0.24$) or females ($F_{1,65}$, $P=0.14$), indicating no seasonal bias with regard to the capture of particular groups.

Table 1 Calculated parameter estimates for von Bertalanffy's growth curves for harbour seals in Svalbard. L_∞ and M_∞ are the asymptotic length (cm) and mass (kg) respectively; a determines the rate of approach to the asymptote and b determines the curvelinearity of this approach in the model: L_x (or M_x) = L_∞ (or M_∞)$[1 - e^{-a(x-x_0)}]^b$. Values are given with SE

Growth parameter	n	Parameter estimate			r^2
		L_∞ or M_∞	a	b	
Male mass	127	104.0 ± 5.0	0.22 ± 0.05	0.96 ± 0.13	0.88
Female mass	134	83.2 ± 2.7	0.29 ± 0.06	1.02 ± 0.17	0.85
Male length	120	152.9 ± 4.8	0.21 ± 0.04	0.30 ± 0.03	0.90
Female length	129	140.1 ± 2.0	0.26 ± 0.06	0.31 ± 0.04	0.86

Growth

The growth curves show sexual dimorphism in the Svalbard harbour seals, with asymptotic values for both standard length and body mass being greater for males (Table 1, Fig. 1). Multiple regressions showed that these differences were highly significant when age was accounted for (Standard length—$F_{1,246} = 45.70$, $P < 0.0001$; Body mass—$F_{1,2} = 25.28$; $P < 0.0001$). Maximum recorded values for standard lengths and masses were 156 cm and 122 kg for males and 147 cm and 111 kg for females. The heaviest female was pregnant; the heaviest non-pregnant female recorded was 101 kg. A total of 14 males were heavier than 100 kg.

Body mass (BM) was highly correlated with both standard length (SL) and axillary girth (AG) for both sexes. These allometric relationships were best described by power the following functions: Males—$BM = 0.0002 \times SL^{2.573}$, $r^2 = 0.92$; $BM = 0.0004 \times AG^{2.579}$, $r^2 = 0.95$; and females—$BM = 0.0001 \times SL^{2.732}$, $r^2 = 0.90$; $BM = 0.0002 \times AG^{2.707}$, $r^2 = 0.93$.

Age at sexual maturity

Testosterone levels in males showed an abrupt increase when the males reached the age of 6 years (Fig. 2). For this age group and older males, mean testosterone levels remained above 6 nmol/l. Estradiol levels in females increased abruptly from age 4 (Fig. 3). For this and older age groups, average estradiol levels were above 20 pmol/l. Females were more variable than males in when their hormones began to rise: one of three (33.3%) 3-year olds, three of four (75%) 4-year olds, one of three (33.3%) 5-year olds and all older females had estradiol levels higher than 20 pmol/l.
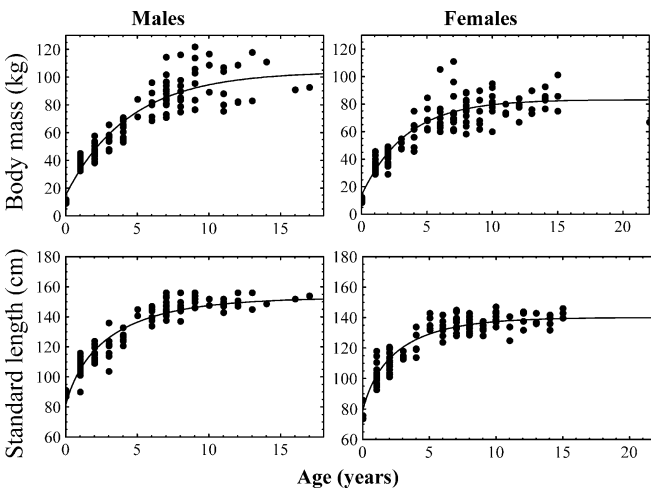
Reproductive rates and age distribution

A total of 54 females were either captured with their pup, were lactating or were heavily pregnant. Four females that were older than 8 years of age were not pregnant, lactating or captured with a pup. Thus, reproductive rate defined as the proportion of adult females producing a pup ($n = 54$) in relation to the total

Fig. 1 Von Bertalanffy growth curves fitted to standard body length (males $n = 120$, females $n = 129$) and body mass (males $n = 127$, females $n = 134$) data from harbour seals from Svalbard, Norway

Fig. 2 Testosterone levels in male harbour seals from Svalbard with increasing age ($n = 53$). *Left panel* shows data presented as mean $\pm$ SD, while *right panel* shows the real data points for the age groups around attainment of sexual maturity
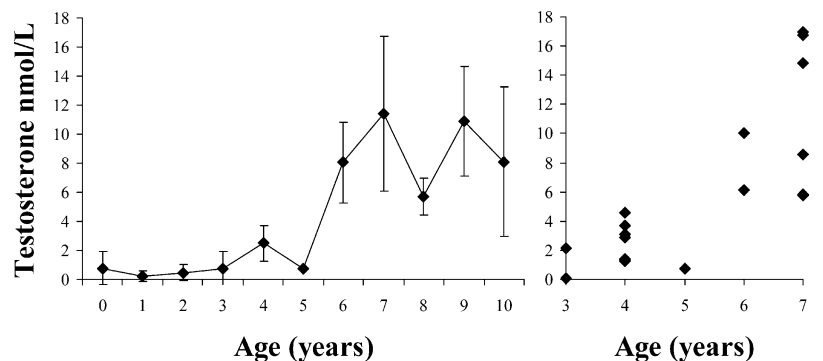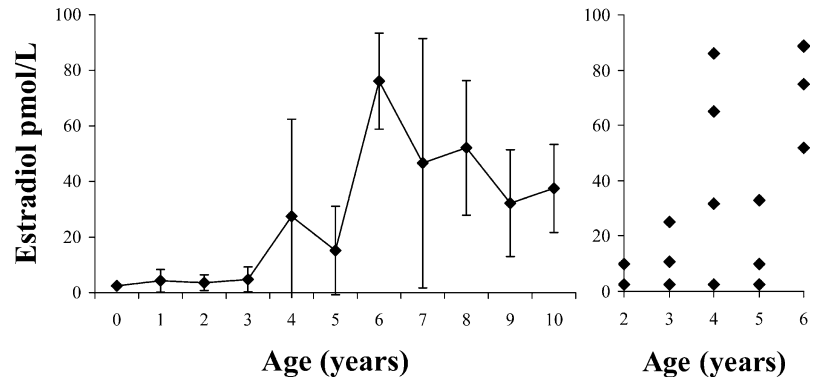
Fig. 3 Estradiol levels in female harbour seals from Svalbard with increasing age (*n* = 68). *Left panel* shows data presented as mean ± SD, while *right panel* shows the real data points for the age groups around attainment of sexual maturity

number of adult females (*n* = 58) is 0.93 for this sample of Svalbard harbour seals.

The age distribution of the captured harbour seals is illustrated in Fig. 4. Immature seals, other than pups of the year, are under-represented in the sample and there is a remarkable lack of older animals.

Discussion

The total population size of harbour seals on Svalbard is not currently known, but a minimum estimate of this population conducted in the early 1980s suggested that there were 500–600 animals (Prestrud and Gjertz 1990). The population might have undergone some change in the last decade, but the results of a recent study of haul-out behaviour that counted animals at most of the major sites used by this population suggest that numbers have not undergone dramatic change (Reder et al. 2004). If this assumption is correct, then the 367 animals in the present study represent a large fraction of the seals in this population. Our ability to capture such a large proportion of the population is at least in part due to the naïve behaviour these seals have towards humans and nets. The harbour seals in Svalbard are found along a very exposed arctic coastline with few human visitors; they are protected against hunting and the area is not

used by fisheries, except for occasional shrimp trawlers that operate offshore a significant distance away from the harbour-seal haul-out sites. The animals are curious and, at least initially in this study, were totally inexperienced with nets.

The asymptotic values for standard lengths for the harbour seals from Svalbard are somewhat smaller than those reported for other populations of this sub-species, *P. v. vitulina*. The value for Svalbard females was 140.1 cm, while the corresponding value for harbour-seal females in Denmark-Sweden was 146.0 cm (Härkönen and Heide-Jørgensen 1990), and from southern Norway this value is 147.2 cm (Markussen et al. 1989). Asymptotic length for harbour-seal males from Svalbard was 152.9 cm, and the corresponding value from Denmark to Sweden was 155.8 cm (Härkönen and Heide-Jørgensen 1990), and from southern Norway 155.5 cm (Markussen et al. 1989). Asymptotic values for body masses for the Svalbard harbour seals are higher for both sexes compared with data from these two other populations (females 83.2 vs 66.0 kg in Denmark-Sweden and 76.8 kg in southern Norway—males 104.0 vs 74.5 kg in Denmark-Sweden and 88.4 kg in southern Norway; Markussen et al. 1989; Härkönen and Heide-Jørgensen 1990).

The comparison of morphometric data for these three populations suggests that the Svalbard harbour seals carry more blubber than animals from the populations further south. All phocid seals go through dramatic seasonal cycles in blubber mass as a consequence of extreme variation in energy intake and expenditure related to breeding and moulting, and perhaps also, availability of prey. However, the harbour seals from the three studies discussed above were all measured during the same period of the year, so the fact that the Svalbard seals generally are fatter is not due to seasonally biased sampling.

One possible reason for Svalbard harbour seals having thicker blubber could be that Svalbard's waters are colder than those in the southern areas where these other populations are found, and that the Svalbard harbour seals therefore need a thicker blubber layer in order to stay within their thermal neutral zone. The lower critical temperature for harbour seals in water has been estimated to be about 10°C (Irving and Hart 1957; Watts
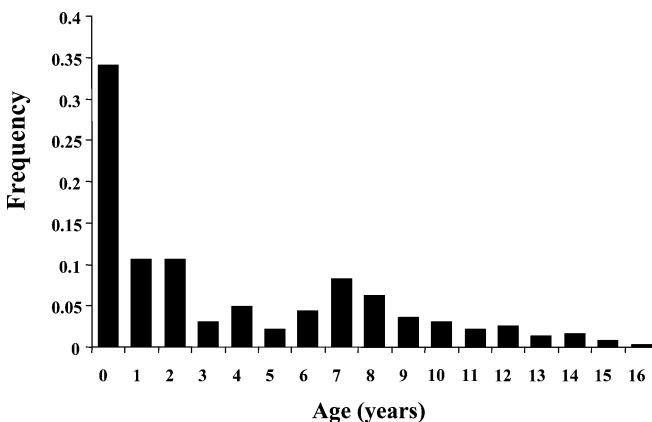
Fig. 4 Age distribution for harbour seals from Svalbard (*n* = 367)

et al. 1993). The animals used in these physiological studies were juveniles ranging from 26 to 50 kg. In Watts et al.'s (1993) study, a dorsal blubber thickness of 30–38 mm was reported, and the animals were described as being adapted to summer conditions in the Pacific, which has maximum water temperatures of about 18°C. Studies of thermoregulation in harbour-seal pups showed that they can stay in 5°C water for several hours without experiencing hypothermia (Miller and Irving 1975). Lower critical temperatures for harbour seals in air have been measured to be 3°C for pups (Miller and Irving 1975), −2.3°C for animals less than 1 year old (Hansen et al. 1995) and below −10°C for older animals (Irving and Hart 1957; Hansen and Lavigne 1997). Svalbard's average temperatures both in the air and the water are clearly challenging in relation to the thermoregulatory capacities for harbour seals measured in the studies discussed above. Air temperatures in Svalbard during the breeding and moulting periods are not likely to constitute any thermal challenge, and during cold periods in the winter, the harbour seals could avoid air-temperature problems by remaining in the water. However, surface water temperatures at the main breeding areas for the Svalbard harbour seals measured 1 July 1999–2002 ranged between 0 and 5°C (data from the Norwegian Meteorological Institute, Tromsø, Norway), which is well below measured lower critical temperatures in water for this species. One way of dealing with colder temperatures is, of course, to be better insulated and this may be why Svalbard's harbour seals are fatter than their southern counterparts. Another possible explanation could be that high interannual variation in food availability in arctic waters, or the long winter period, put a premium on having greater energy stores.

Svalbard harbour seals are sexually dimorphic with respect to both body mass and standard length. McLaren's (1993) review of pinniped growth reported no sex differences in any harbour-seal populations from the Atlantic that had been studied at that time and the review was equivocal regarding whether sexual dimorphism was displayed in harbour-seal populations from the Pacific. Large body size in males of a species compared to females in pinnipeds, and in animals more generally, is thought to occur principally via selection imposed by large size accruing benefits to males during combat for females directly, or for resources that determine mating access to females (e.g. Bartholomew 1970; Emlen and Oring 1977; Clutton-Brock 1988). A low level of sexual dimorphism or monomorphy among aquatic-mating pinnipeds has been suggested to be the norm, because manoeuvrability may be more important in aquatic combat than large size (Stirling 1975, 1983). Harbour seals are aquatic breeders. Males use underwater displays including vocalisations to attract females and perhaps to repel competitors at sites along routes used by females between haul-out sites and foraging areas (e.g. VanParijs et al. 1997, 2000a, b). In areas where the water is quite cold, large body size is likely beneficial

to aquatic maters, because it would permit males to stay onsite at underwater display areas longer without suffering thermal stress. Comparative morphometric data from other harbour-seal populations from cold-water areas like Hudson Bay or Greenland would be of great interest to pursue this hypothesis further.

Age at sexual maturity in population studies of pinnipeds is normally determined by macroscopic investigations of ovaries and microscopic investigations of testes (e.g., Bigg 1969; Boulva and McLaren 1979; Härkönen and Heide-Jørgensen 1990). In the present study, we used the level of circulating sex hormones to estimate the time of the onset of sexual maturity. Sexual maturity in mammals begins when the hypothalamus increases secretion of gonadotrophin-releasing hormones. These hormones stimulate production of the gonadotrophic hormones, follicle stimulating hormone (FSH) and luteinising hormone (LH), by the anterior pituitary gland. FSH stimulates growth of ovarian follicles in females and the seminiferous tubules and early stages of sperm production in males. High concentrations of LH induce ovulation in a Graafian follicle that has been primed by FSH. In addition, FSH and LH stimulate production of testosterone in males and oestrogens in females, and these were the hormones measured in this study.

Testosterone levels in the plasma of adult male hooded *Cystophora cristata*, Hawaiian monk *Monachus schauinslandi*, Weddell *Leptonychotes weddellii* and harp *Phoca groenlandica* seals all show clear peaks in the periods corresponding to the breeding season for each respective species in the wild (Noonan et al. 1991; Atkinson and Gilmartin 1992; Bartsh et al. 1992; Serrano 2000). This was not found to be the case in a single study done on harbour seals by Gardiner et al. (1999). However, our testosterone versus age analysis seems to produce a meaningful pattern that fits with what would be expected for age at sexual maturity in males of this species. Plasma testosterone levels in male harbour seals from Svalbard suggest that some males become sexually mature as early as age 4 and that all males 6 years of age and older were mature. This is similar to the results of other investigations of age at sexual maturity in this species using traditional methods (Bigg 1969; Boulva and McLaren 1979; Härkönen and Heide-Jørgensen 1990; Bjørge 1992).

Studies on the ovaries and levels of estradiol in grey seals *Halichoerus grypus* indicate that a single wave of follicular growth starting about the time of parturition results in a single mature follicle being produced towards the end of lactation (Boyd 1983). This process coincides with high circulating levels of estradiol in the plasma of mature females. In pregnant harbour seals, estradiol gradually starts to increase at the time of implantation and it peaks about 3 weeks after parturition when the female enters oestrus (Reijnders 1990). Mature harbour-seal females without offspring follow a similar overall pattern, but their estradiol levels peak about 2 weeks earlier (Reijnders 1990). Based on levels of plasma

estradiol, Svalbard harbour-seal females start to mature at the age of 3 and all individuals 6 years of age and older were sexually mature. This is similar to the findings of investigations of age at sexual maturity for female harbour seal using traditional methods in other areas (e.g. Bigg 1969; Boulva and McLaren 1979; Burns and Goltsev 1984; Hayama et al. 1986; Härkönen and Heide-Jørgensen 1990; Bjørge 1992).

The reproductive rate calculated in this study for the Svalbard harbour seals is similar to those reported for harbour seals in other areas (Bigg 1969; Boulva and McLaren 1979; Hayama et al. 1986; Härkönen and Heide-Jørgensen 1990; Bjørge 1992) where more than 90% of adult females are typically pregnant. One exception is a study from the Aleutian and Pribilof Islands where the pregnancy rate was only 75% (Burns and Goltsev 1984).

Mortality rates can, in principle, be calculated from age-distribution curves like that shown in Fig. 4. However, this technique assumes a stationary age distribution and equal catchability of all age groups, and if these assumptions are violated, the survival estimates will be unreliable (Gaillard et al. 1998). We have no information regarding stability of the age distribution, and Fig. 4 suggests that catchability is not the same for the various age groups, so no attempt is made in the present study to calculate age-specific survival.

The age distribution in our study, similar to many other samples from seal populations, clearly under-represents sub-adult age groups. This is common when most of the sampling occurs in the breeding period at active pupping sites, which are mainly occupied by adult animals and pups of the year. The lack of older animals in our sample is very different from other studies, where a much higher proportion of the populations are in the 15+ year age categories (Boulva and McLaren 1979; Burns and Goltsev 1984; Markussen et al. 1989; Härkönen and Heide-Jørgensen 1990; Hauksson 1992), with some individuals living to be older than 30 (Härkönen and Heide-Jørgensen 1990; Hauksson 1992). We are convinced that the short longevity measured in our study is not a sampling artifact due to older animals being harder to catch. Svalbard harbour seals are quite naïve, and we were able to enclose entire groups and get samples that were representative of group composition.

The short life-span in this population was surprising to us. This population is on Svalbard's Red List and hence hunting is prohibited. To our knowledge, there has been no acute source of mortality such as an epizootic outbreak in recent decades, such as those that have affected harbour seals along the coast of Europe (Heide-Jørgensen et al. 1992; Harding et al. 2002) that could explain the absence of older animals. There is little, if any, surface predation from polar bears (*Ursus maritimus*) or other terrestrial carnivores, and there is no reported mortality due to fisheries interactions. Pollution burdens measured thus far are low (Wolkers et al. 2004). Ringed seals from this area of Svalbard have similar levels of organochlorine pollutants to the har-

bour seals (Wolkers et al. 1998) and they are extremely long-lived, with some animals living to ages beyond 40 years (Lydersen and Gjertz 1987). It is reasonable to assume that ringed and harbour seals have similar abilities to deal with pollutants, so it seems unlikely that pollution levels are responsible for the observed short life-span in Svalbard harbour seals.

Another possible source of mortality for the harbour seals on Svalbard is marine predators like killer whales (*Orcinus orca*) and Greenland sharks (*Somniosus microcephalus*). In the western Atlantic at Sable Island, shark predation is responsible for 45% of harbour-seal pup mortality, and in a 5-year period 470 carcasses (241 adults, 23 juveniles and 206 pups) were found that had died due to shark attacks (Lucas and Stobo 2000). This is a minimum estimate of shark-inflicted mortality, since many seals are probably eaten entirely or at least their bodies do not wash up on shore. Lucas and Stobo (2000) concluded that shark-induced mortality has a significant impact on the Sable Island harbour-seal population, possibly to the extent that it has limited its growth and contributed to the recently observed declines (also see Bowen et al. 2003). In the first half of the 1900s, there was a large fishery for Greenland sharks in northern Norwegian waters, including the Greenland Sea, Svalbard and northern Barents Sea. Delivered quantities of oil from shark livers during the 1930s and 1940s correspond to a harvest of over 10,000 individuals annually (Anonymous 1949; Hoel 1949). These fisheries no longer exist and it is likely that the shark population has increased in recent decades following the cessation of the fishery. Thus, Greenland sharks may be a significant source of mortality for Svalbard's harbour seals. Based on sightings in recent decades and former whaling distribution records for killer whales, we also know that the distribution of this species (Øien 1988) overlaps with the Svalbard harbour seals, although we do not have any documentation of predation in the area of concern.

The short life-span of Svalbard's harbour seals might be related to extreme seasonality and other harsh environmental conditions that these animals experience at the northern edge of this species' distribution. Long-term, low levels of physiological stress may be induced in arctic populations of this normally temperate species that result in the short longevity observed in this population.

This study documents population parameters of the world's northernmost harbour seals and finds some morphological differences between this arctic group compared to populations of the same sub-species found further south, as well as a short longevity period. Local management of this population should include maintenance of the protected status of this population, and further research should be conducted on their distribution, foraging requirements through the year and, where possible, sources of mortality should be identified. This study also demonstrated that it is possible to perform traditional population studies of marine mammals without using terminal sampling; this approach will

undoubtedly be of value for conservation-oriented research performed on other threatened or endangered animal populations.

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