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Growth and population parameters of ringed seals (*Pusa hispida*) from Svalbard, Norway, 2002–2004

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Samples were collected in Svalbard, Norway, during April and May 2002–2004 from 272 ringed seals (*Pusa hispida*; 62.5% males, 37.5% females) to study growth and population parameters. The age of the animals ranged from 1 to 32 years. Asymptotic values for standard length and body mass were 127.7 ± 1.6 (s.e.) cm and 69.0 ± 2.7 kg for males (maxima: 144 cm and 92 kg) and 127.6 ± 2.3 cm and 68.9 ± 2.5 kg for females (maxima: 141 cm and 91 kg). All animals were sexually mature at an age ≥ 6 years and the ovulation rate was 0.86. Mean Age at Maturity (MAM) was 4.2 ± 0.2 years for males and 3.5 ± 0.3 years for females, values significantly lower than calculated for ringed seals from the same area 20 years ago. This change in MAM suggests that either the prey base for ringed seals in the area has increased or alternatively that the density of ringed seals has declined, such that more resources are available *per capita*. If the climate of the Arctic changes in the manner predicted by a host of climate-change scenarios, it is likely to have a strong impact on ringed seal populations in future, although there are no data to suggest that dramatic changes have taken place yet in fish and invertebrate populations in the Svalbard area. Although cause-and-effect cannot be firmly established, there is a possibility that the substantial increase in the number of polar bears (*Ursus maritimus*) over the past 20 years, since hunting the species in Svalbard ceased in 1973, may have played a role in the observed change in the ringed seal population.

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Introduction

Ringed seals inhabit the Arctic Ocean and adjacent waters of the Barents Sea, Bering Sea, and the Sea of Okhotsk, in addition to the Baltic Sea and the freshwater systems of Lakes Saimaa and Ladoga (Frost and Lowry, 1981). Based on distribution and morphometry, the species has been divided into several subspecies. *Pusa hispida hispida* inhabits the circumpolar Arctic Ocean, including the waters around Svalbard, Norway (Frost and Lowry, 1981). No research related to stock or population identity has been conducted within the huge distributional area for this subspecies, but it is assumed that such units exist (Reeves, 1998).

Information on growth and reproduction is vital for population assessment, and these data have been collected for ringed seals from many areas (Holst and Stirling, 2002). There is little sexual dimorphism within the subspecies *P. h. hispida*, and adults normally reach a length of 130 cm and attain an average body mass of about 65 kg (Smith, 1987; McLaren, 1993). Both males and females reach sexual maturity at an age of 5–7 years, with some variation between different geographic areas (McLaren, 1958; Nazarenko, 1965; Johnson *et al.*, 1966; Smith, 1973, 1987; Fedoseev, 1975; Holst and Stirling, 2002). Reproductive rates of female ringed seals usually vary between 0.45 and 0.86 (Reeves, 1998). Growth and population parameters of ringed seals from Svalbard have been studied previously, on the basis of a sample of 283 animals collected in 1981 and 1982 (April–July; Lydersen and Gjertz, 1987). In the early 1980s the mean standard length

of mature seals was 128.9 ± 10.0 cm for both sexes, and the mean body mass of adult females (61.4 ± 14.7 kg) was significantly heavier than that of adult males (53.5 ± 11.9 kg). At that time, males matured sexually between 5 and 8 years of age and females between ages 3 and 6; the ovulation rate for ringed seals was 0.91 for this sample.

Growth rates and population parameters are not static characteristics of populations. They change over time in response to changes in food availability, and are therefore influenced by intra- and interspecific population interactions, by human predation levels, and by physical changes to the environment that impact productivity (Eberhardt and Siniff, 1977; Bengtson and Siniff, 1981). Time-series that allow studies of trends in population parameters are therefore important in understanding the dynamics of the ecosystem inhabited by a given population. The purpose of the present study was to investigate current growth rates and population parameters of ringed seals from Svalbard in the years 2002−2004, and to compare these results with those from the same area measured 20 years ago (1981−1982; Lydersen and Gjertz, 1987).

Material and methods

This study is based on data from 272 ringed seals from Spitsbergen, Svalbard, Norway (Figure 1) collected during spring (April and May) of 2002−2004 (2002, $n = 69$; 2003, $n = 92$; 2004, $n = 111$). Standard length (± 1 cm; Scheffer, 1967), body mass (Salter scale: 100 ± 0.5 kg), sex, and information on time and place of collection were documented for each seal. Reproductive organs were removed and stored frozen ($-20°$C) for later evaluation of reproductive status. The lower jaw was collected in the field, and a canine tooth was later extracted in the laboratory from each seal for age determination, by counting cementum layers in decalcified, stained longitudinal sections, following the methods of Lydersen and Gjertz (1987). The teeth were read serially, by multiple readers, and significant differences in age were explored further until consensus was reached (similar to the 1981−1982 collection).

The generalized von Bertalanffy functions (von Bertalanffy, 1957; Schnute, 1981) were used to describe growth:

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

$$M_x = M_\infty \left[1 - e^{-a(x-x_0)}\right]^b, \tag{2}$$

where L_x is the standard length (cm) and M_x is body mass (kg) at a given age x (years), x_0 (years) is an estimated value representing prenatal growth, which was set to be -0.61 on the basis of the assumption made for the ringed seal population at Svalbard by McLaren (1993). Parameter a determines the rate of approach to the asymptote (L_∞ or M_∞) and b determines the curvilinearity of this approach (McLaren, 1993). To fit the curves, a non-linear, user-specified
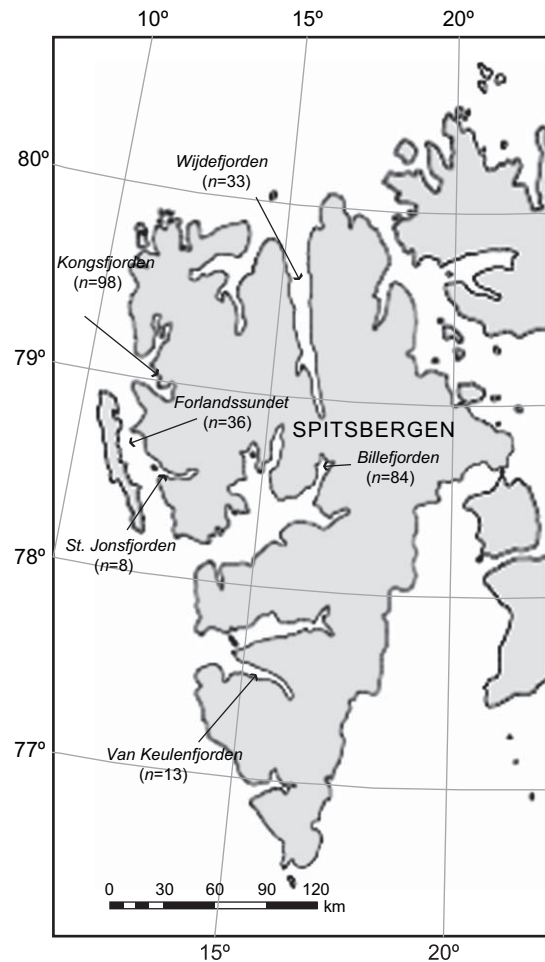

Figure 1. Map of the study area showing the numbers of ringed seals collected at different locations on Svalbard, 2002−2004.

regression was used without weightings (Statistica version 6.1 for Windows® StatSoft. Inc., Tulsa, OK, USA). The default loss function was set to least squares using a Quasi-Newton estimation method. In the ringed seal study based on the 1981−1982 data set (Lydersen and Gjertz, 1987), growth was described using a Gompertz curve, so to compare the results of the earlier study with those of the current study, von Bertalanffy functions were also applied to the older data set. Potential differences in growth rate and final body size between time periods were examined by exploring length and weight, by sex, for sub-adults (age classes up to and including the first group at which 100% of the animals are mature) and adults (age classes beyond the first group at which 100% of the animals are mature) in generalized linear models (GLMs; Statistica version 6.1 for Windows).

One testicle and one epididymis from each male aged 1−10 years ($n = 100$) were weighed (± 0.1 g) and measured (length and width, ± 0.1 mm). A volume index [testis (length + width) $\times 0.5$ ($\pm$s.d.)] was calculated (Lydersen

and Gjertz, 1987). A cross-sectional tissue slice about 2 mm thick was taken from the mid-portion of both the testis and the epididymis and fixed in 4% phosphate-buffered formaldehyde. The sections were infiltrated with paraffin, and slices 2−3 μm thick were made using a microtome. These thin slices were then mounted on microscope slides and stained with hematoxylin and eosin. Males were defined as sexually mature on the basis of either the presence of spermatozoa in the epididymides or the presence of spermatogenesis in the seminiferous tubules.

Ovaries from all females were weighed (±0.1 g), and measured (length and width, ±0.1 mm). Longitudinal sections about 2 mm thick were made through each ovary using a scalpel, and analysed macroscopically for the occurrence of mature follicles (≥6 mm), corpora lutea or corpora albicantia, which were used as indicators of sexual maturity. To determine the rate of ovulation, the number of females with follicles ≥6 mm in diameter or a healthy corpus luteum was compared with the number of females that were sexually mature (Lydersen and Gjertz, 1987).

Mean Age at Maturity (MAM) was estimated with the procedures outlined in Frie et al. (2003), using ringed seal male and female reproductive data for all animals between 1 and 10 years old:

$$\text{MAM} = w + 1 - \sum_{x=1}^{x=w} \hat{P}(x), \tag{3}$$

where w is the oldest age group in the sample and $\hat{P}$ is the estimated proportion of mature seals at age x. If $\hat{P}(w) = 1$, this expression is equivalent to the DeMaster (1978) formula for MAM. If $\hat{P}(w) < 1$, Equation (3) is based on the assumption that all seals will be mature at age $w + 1$. The equation is based on Richards curves (Richards, 1959) and was fitted with maximum likelihood optimization to observed age-specific proportions of mature seals in each age group. The fitting of the Richards curves was based on the parameter options presented by Sugden et al. (1981):

$$\hat{P}(x) = \hat{P}_\infty \left\{ 1 - [1-m] \exp[-k(x-M)/m^{m/(1-m)}] \right\}^{1/(1-m)}, \tag{4}$$

where the asymptote $\hat{P}_\infty$ was set to 1, assuming that all animals would eventually reach sexual maturity, M is the point of inflection (age in years), k the slope at the point of inflection (the maximum proportion of mature seals per year), and m is the shape parameter related to $\hat{P}$ at the point of inflection, as $\hat{P}_{\text{inf}} = \left\{ m^{[1/(1-m)]} \right\}$. Richards curves were fitted by optimizing M, k, and m to maximize the binominal likelihood function $L = \prod_x \hat{P}(x)^{n_x P_x} \left[1 - \hat{P}(x) \right]^{n_x(1-P_x)}$, where L is the likelihood value, $\hat{P}(x)$ the estimated proportion of seals of age x (of a sample size n_x) that has reached maturity, and P_x is the observed proportion at age x from the sampled animals that have reached maturity. Two independent models were fitted to the data sets for males and females,

respectively. For each sex, unconstrained curves fitted to the data sets from 1981−1982 and 2002−2004 constituted the full models for maturity-at-age. Differences in the Richards parameters and MAM between sampling periods were subsequently tested by imposing constraints on the full model, and evaluating the significance of the change in likelihood using likelihood ratio (LR) tests. For each sex, shape parameter fits were examined to see whether a common shape parameter could be fitted to both sampling periods before proceeding to test for differences in MAM. Maximum likelihood equivalents of univariate standard errors for MAM and Richards parameters were estimated as the half-width of the interval resulting from maximizing and minimizing a given parameter, by re-estimating the Richards parameters under the constraints of the chosen model without decreasing the original log-likelihood value by more than 0.5 (for detail, see Frie et al., 2003).

The Richards curves were fitted with the "solver function" in an Excel® XP2000 (Microsoft Corp.) spreadsheet. The growth curves and other statistical analyses were done with Statistica (version 6.1 for Windows® StatSoft. Inc.). Mean values are presented ±standard error (s.e.), except where otherwise noted (s.d.).

Results

The sample of 272 ringed seals collected in this study included 170 (62.5%) males and 102 (37.5%) females. Ages ranged from 1 to 30 years for males and from 1 to 32 years for females (Figure 2). The asymptotic body masses were 69.0 ± 2.7 kg for males and 68.9 ± 2.5 kg for females (Table 1), and the corresponding values for length were 127.7 ± 1.6 cm for males and 127.6 ± 2.3 cm for females. The maximum recorded values for body mass and standard length for ringed seals collected 2002−2004 were 92 kg and 144 cm for males and 91 kg and 141 cm for females, respectively. The models for the growth curves for the complete samples explained 54.0% of the variance for male mass, 47.6% for female mass, 60.6% for male length, and 56.8% for female length for the ringed seals collected 2002−2004. For the ringed seals collected in 1981−1982, the model explained 35.1% of the variance for male mass, 45.1% for female mass, 49.8% for male length, and 55.6% for female length.

Lengths of adult seals did not differ according to sex or time period of sampling (1981−1982 vs. 2002−2004; $F = 1.96$, $p = 0.16$). However, mass of adult animals was influenced by both sex and time period ($F = 16.27$, $p \leq 0.01$), seals being significantly heavier in 2002−2004 than in the early 1980s, with the most notable differences between males (Figure 2). Similarly, no differences were detected in growth according to sex or period for lengths of sub-adults ($F = 0.05$, $p = 0.83$), but body masses were greater in the period 2002−2004 than in the early 1980s ($F = 11.36$, $p \leq 0.01$).
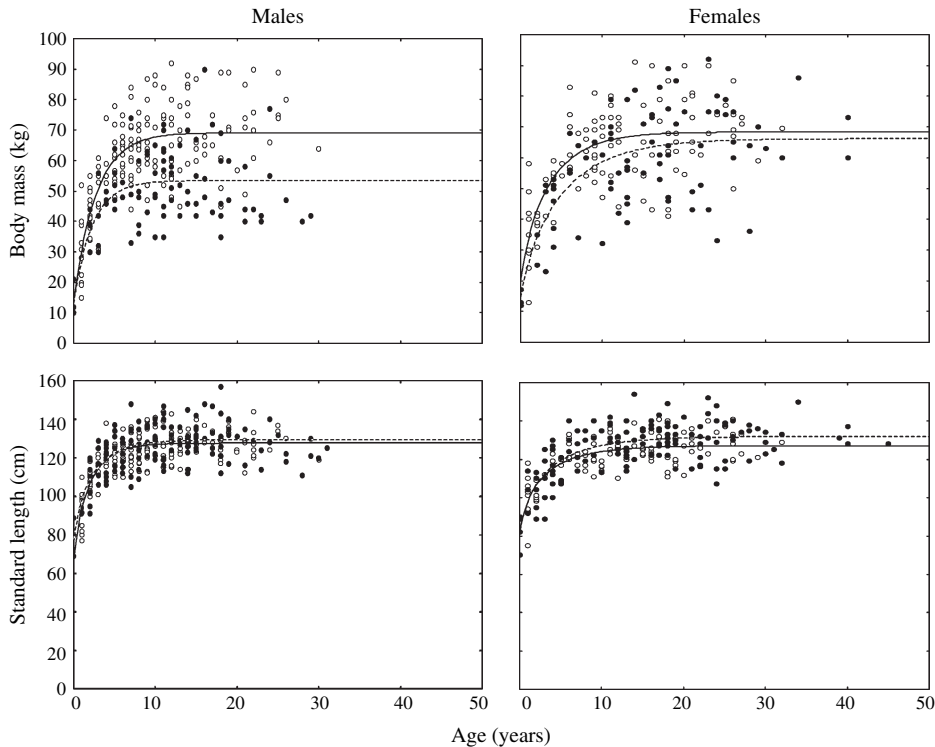
Figure 2. Von Bertalanffy growth curves fitted to body mass and standard body length of ringed seals from Svalbard, with data from animals collected in 1981−1982 (filled circles, dashed line) and 2002−2004 (open circles, continuous line).

Microscopic analysis of male reproductive organs revealed that they started to become sexually mature at an age of 3 (25% of 3-year-old males), and that all were mature by 6 years of age (Table 2). Macroscopic investigation of female reproductive organs showed that they also began to mature at age 3 (50% of 3-year-old females), and that all were sexually mature at an age of 4 (Table 2). In all, 143 (84%) of the males and 90 (88%) of the females

in the 2002−2004 sample were sexually mature. Changes in the morphometrics of ovaries and testes and epididymi- des with age all supported the findings from the micro- and macroscopic analyses of these organs (Figures 3 and 4).

For the 2002−2004 sample, MAM for males was 4.2 ± 0.2 years and females matured at 3.5 ± 0.3 years (Table 3). The corresponding MAM for the early 1980s was 5.8 ± 0.3 years for males and 4.4 ± 0.3 years for females (Table 3). Both

Table 1. Calculated parameter estimates for von Bertalanffy growth curves based on data from ringed seals from Svalbard during the years 1981−1982, and 2002−2004. L_∞ and M_∞ are the asymptotic length (cm) and body mass (kg), respectively, a determines the rate of the approach to the asymptote, and b determines the curvilinearity of this approach in the model: $L_x(\text{or } M_x) = L_x(\text{or } M_x)\left[1 - e^{-a(x-x_0)}\right]^b$. Values are given $\pm$s.e.

Growth parameter	n	L_∞ or M_∞	a	b
		Parameter estimate		
Male mass 1981−1982	86	53.4 ± 1.6	0.43 ± 0.20	0.96 ± 0.55
Male mass 2002−2004	170	69.0 ± 2.7	0.37 ± 0.24	0.92 ± 0.70
Female mass 1981−1982	82	66.2 ± 3.7	0.17 ± 0.11	0.64 ± 0.33
Female mass 2002−2004	102	68.9 ± 2.5	0.22 ± 0.13	0.53 ± 0.25
Male length 1981−1982	131	129.5 ± 1.2	0.34 ± 0.08	0.31 ± 0.07
Male length 2002−2004	170	127.7 ± 1.6	0.43 ± 0.22	0.42 ± 0.24
Female length 1981−1982	144	130.0 ± 1.6	0.17 ± 0.06	0.21 ± 0.04
Female length 2002−2004	102	127.6 ± 2.3	0.18 ± 0.11	0.18 ± 0.07

Table 2. Number and percentage of mature ringed seal males and females 1−10 years old collected in Svalbard, Norway, 2002−2004.

Age (years)	Males			Females		
	Number in sample	Number mature	% Mature	Number in sample	Number mature	% Mature
1	8	0	0	7	0	0
2	8	0	0	4	0	0
3	8	2	25	2	1	50
4	8	4	50	4	4	100
5	10	9	90	2	2	100
6	18	18	100	5	5	100
7	12	12	100	2	2	100
8	10	10	100	5	5	100
9	12	12	100	9	9	100
10	6	6	100	4	4	100

males and females from the 2002−2004 sample became sexually mature significantly younger than those in the 1981−1982 sample (Table 4). Of the 90 females that were sexually mature, 77 had at least one follicle ≥6 mm in diameter or a healthy corpus luteum, resulting in an ovulation rate of 0.86.

Discussion

Ringed seals in Svalbard fall within the normal size range of the subspecies, and the condition of animals in the population appears to be good; they are fat, mature young, and rates of ovulation are high. The current age at sexual maturity is significantly lower than it was in the same area in the early 1980s; the female MAM reported here is the lowest on record for ringed seals. Ringed seals were also heavier in the period 2002−2004 than they were in the 1980s.

Young age groups were under-represented in both sampling periods because hunting was largely in areas where densities of ringed seals were highest. Such areas are used for breeding earlier in spring, and young animals are generally excluded by older animals, so remain in more broken, unstable ice areas where it is more difficult to hunt. The longer sampling season during the early 1980s than in the recent study period likely contributed to some of the weight differences observed between the two sets of samples, because there is a general seasonal decline in phocid seal condition in spring as the moult approaches (Ryg *et al.*, 1990). Following an energy-demanding breeding period, ringed seals commence their annual moult, which peaks in early June in Svalbard (Carlens *et al.*, 2006). During this latter period food intake is minimal, resulting in a continued decline in body mass following the breeding season.

Timing of sampling also influenced the sex ratios; in the 1981−1982 sample the sex ratio was 1:1, but in the present
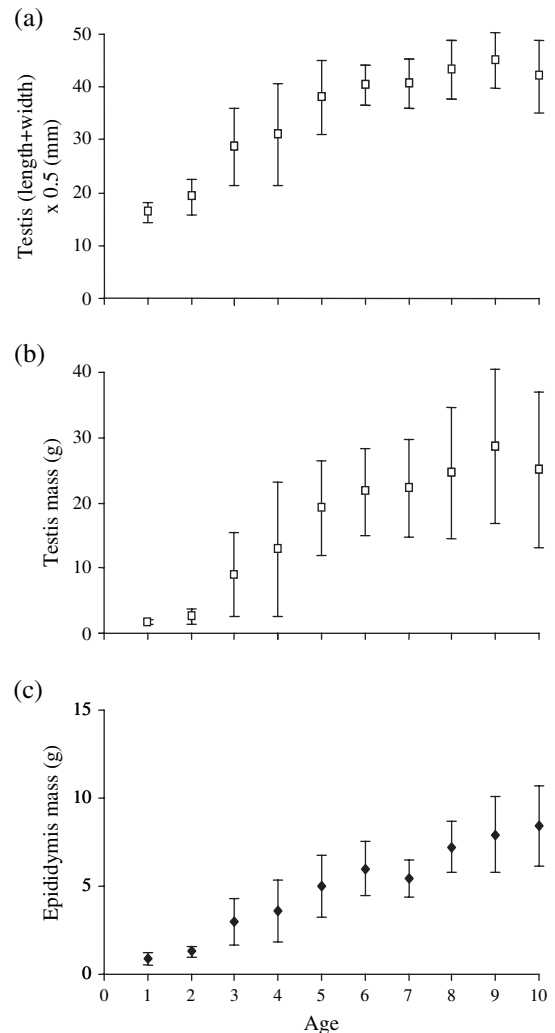

Figure 3. Changes in (a) testis (length + width) × 0.5 (±s.d.), (b) mass of testis (±s.d.), and (c) mass of epididymis (±s.d.) with increasing age for ringed seals from Svalbard, 2002−2004.

sample it was skewed towards males (62.5% males, 37.5% females). This is because adult females were not targeted prior to opening of the ringed seal hunting season on Svalbard (20 May) in the recent collection, in order to avoid the possibility of shooting mothers with dependent young. The 1981−1982 ringed seal sample was collected from March to July; there were no restrictions related to ringed seal hunting in the early 1980s, so a 1:1 sex ratio was achieved.

The most significant finding in the present study relates to a decline in the age at sexual maturity for ringed seals in Svalbard between the early 1980s and 2002−2004. In the early 1980s, males matured at 5−8 years of age, and the corresponding value for females was 3−6 years (Lydersen and Gjertz, 1987). The analysis of MAM conducted in the present study on the 1981−1982 data set
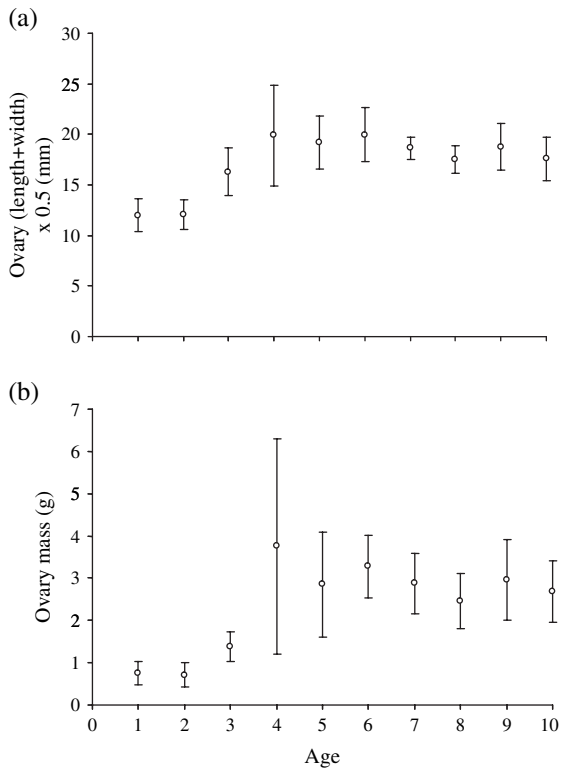
(a)

(b)

Figure 4. Changes in (a) ovary (length + width) × 0.5 (±s.d.) and (b) ovary mass (±s.d.) with increasing age for ringed seal females from Svalbard, 2002−2004.

Table 4. Likelihood values for the tested Richards models for mean age at maturity. Values of p are derived from likelihood ratio tests comparing the model in a given line with the model in the row above. Models for males and females were fitted separately.

Model	Females		Males	
	ln L	p (d.f.)	ln L	p (d.f.)
No constraints	−13.41		−24.84	
Common m	−13.41	1.00(1)	−25.74	0.18 (1)
Common MAM	−15.83	0.03(1)	−33.32	0.00 (1)

Generally, variations in MAM over time can be explained by factors causing changes in food availability, either via overall changes in ecosystem productivity or through density-dependent responses (Laws, 1953; Carrick *et al.*, 1962; Gambell, 1976; Bengtson and Siniff, 1981; Bowen *et al.*, 1981; Capstick and Ronald, 1982; Lydersen and Gjertz, 1987; Kjellquist *et al.*, 1995; Sjare *et al.*, 1996). Reported average age at sexual maturity for female ringed seals varies in the literature from 4.4 to 7.1 for various areas and time periods (Holst and Stirling, 2002), with reports that females up to age 9 had not been pregnant in Amundsen Gulf, Northwest Territories, in the mid- to late 1980s when food was scarce there and animals were in poor condition (Kingsley and Byers, 1998). Ringed seals in the Svalbard area feed mainly on polar cod (*Boreogadus saida*), amphipods, and crustaceans (Gjertz and Lydersen, 1986a; Weslawski *et al.*, 1994), and the area is generally regarded as being highly productive (Gulliksen and Lønne, 1991; Hop *et al.*, 2002). The diet of ringed seals was documented in the early 1980s and simultaneously with the current study in the early 2000s, and it did not change notably between the two periods (Gjertz and Lydersen, 1986a; Labansen, 2005). Moreover, no data exist to suggest notable changes in prey availability for ringed seals during recent decades. Hop *et al.* (2002) suggested that climate change will likely result in rapid expansions by some typically temperate species into Svalbard, if the influence of Atlantic Water in Svalbard increases, and ACIA (2005) suggests that competition from southern species could

produced values of 5.8 ± 0.3 years and 4.4 ± 0.3 years for average age at maturity for males and females, respectively (Table 3). Analysis by Holst and Stirling (2002) of the ovulation rates by age for the same Svalbard data set from the early 1980s produced an identical average age at sexual maturity (4.4) for females, using the method of DeMaster (1978). In the recent sample, some members of both sexes were mature by age 3 and all animals were mature by age 6; average age at sexual maturity was 4.2 ± 0.2 years for males and 3.5 ± 0.3 years for females. MAM is a flexible characteristic of populations that can change rapidly.

Table 3. Mean Age at Maturity (MAM) estimates based on Richards maturity curves for male and female ringed seals sampled at Svalbard during 1981 and 1982, and 2002−2004. m is a shape parameter related to the estimated proportion of mature seals, M the point of inflection, and k the slope at the point of inflection. Values are given ±s.e.

Sex and sample years	m	M	k	MAM
Females 1981 and 1982	0.97 ± 1.69	3.43 ± 0.89	0.46 ± 0.39	4.41 ± 0.31
Females 2002−2004	0.97 ± 1.69	2.98 ± 0.43	9.36 ± x*	3.50 ± 0.31
Males 1981 and 1982	0.24 ± 0.53	4.30 ± 0.51	0.60 ± 0.35	5.80 ± 0.30
Males 2002−2004	0.24 ± 0.53	2.94 ± 0.46	0.72 ± 0.37	4.23 ± 0.23

*The point of inflection of the Richards curve is very poorly defined for this data set, because there is only one indeterminate age class (3-year-olds) containing just two individuals.

result in marked and rapid changes to the marine fauna of the Arctic. At least one change in the benthic community has been documented already: the re-establishment of blue mussels for the first time in 1000 years in Svalbard (Berge *et al.*, 2005). However, other changes in the marine community have not yet been documented, and the complexity of the system and the lack of appropriate time-series data will almost certainly lead to speculation preceding statistically documented change for quite some time, even if community changes have already commenced.

Climate-change-induced alteration of the physical structure of the habitat is another factor that is expected to impact populations of ringed seals in future, through increased pup mortality attributable to poorer ice conditions causing an earlier break-up of fast-ice breeding habitat and separating mother/pup pairs, and through less snow cover on birth lairs resulting in less protection against predation and thermal stress (Stirling and Derocher, 1993; Stirling and Smith, 2004; Ferguson *et al.*, 2005; Stirling, 2005). However, although the IPCC (Intergovernmental Panel on Climate Change) has concluded that global warming is taking place, and will continue in the decades to come, and has said that the Arctic will experience twice the average rate of warming (IPCC, 2001; ACIA, 2005), spring ice conditions in Svalbard's fjords have not as yet changed beyond normal levels of interannual variation typical of recent decades.

Competition can of course have an influence on the availability of food to ringed seals, and the species does have an overlapping distribution with the other resident phocid seals in Svalbard, harbour (*Phoca vitulina*) and bearded seals (*Erignathus barbatus*), and the diets of these species overlap with ringed seals to some degree (Hjelset *et al.*, 1999; Andersen *et al.*, 2004). However, the harbour and bearded seal populations in the area are far less numerous than ringed seals, and are not thought to have changed significantly since the 1980s.

Human hunting of ringed seals can impact their density and indirectly the availability of their prey resources. However, in contrast to the situation in many other Arctic areas, ringed seals are not an important food source for the people of Svalbard. The Archipelago has no aboriginal people, so there is no subsistence hunting. Just a few hundred ringed seals are killed annually in the whole of the Archipelago for consumption by humans and polar dogs, the same situation as applied 20 years ago. Such a modest harvest is unlikely to have had an impact on this ringed seal population. Other potential human impacts include effects of pollution, but the ringed seals in Svalbard have relatively low levels of persistent organic pollutants (Wolkers *et al.*, 1998), and they are also generally healthy, with low levels of disease (Tryland *et al.*, 1999, in press; Krafft *et al.*, in press).

Ringed seals are important prey for polar bears (*Ursus maritimus*), and for part of the year also for Arctic foxes (*Alopex lagopus*; Lønø, 1970; Gjertz and Lydersen, 1986b; Lydersen and Gjertz, 1986; Derocher *et al.*, 2002). Glaucous gulls (*Larus hyperboreus*) take ringed seal pups

born outside lairs (Lydersen and Smith, 1989), and other predators of ringed seals present in the area include walruses (*Odobenus rosmarus*), killer whales (*Orcinus orca*), and Greenland sharks (*Somniosus microcephalus*). Limited information is available on status of most of these ringed seal predators. However, changes in age structure, reproductive rate, and body length all suggest that the size of the polar bear population increased continuously for almost 30 years after harvesting of the species stopped in 1973, with subsequent density-dependent changes perhaps coming into play recently (Derocher, 2005). The polar bear population had been reduced in the 1970s to the point where it was threatened, but the current size of the Barents Sea polar bear population, which includes Svalbard, is about 3000 animals (surveyed in 2004; J. Aars, pers. comm.). If these polar bears fed solely on ringed seals they would need to take about 120 000 seals per year (Stirling and Øritsland, 1995), but they also feed in the area on other seal species, including bearded and harp seals (*Pagophilus groenlandicus*), although ringed seals are the most numerous prey species taken (Derocher *et al.*, 2002). Although the precise size of the polar bear population is not known for the early 1980s, the ringed seal data collected in 1981−1982 reflect a population exposed to little predation pressure from bears. At that time, the bears had been protected for less than a decade, and long-lived, slow-reproducing mammal populations take a long time to recover from overharvesting. However, the present study was conducted 30+ years after polar bear hunting was stopped, so it is possible that the substantially increased polar bear population can have had some impact on the ringed seal population in the area.

The sample sizes in this study are small when the data are broken into year classes, or even into mature and immature groups, and the seasonal spread of sampling is not identical in the two sampling intervals (1981−1982 and 2002−2004). Therefore, any conclusions at a population level can only be tentative. The data suggest that MAM has dropped significantly over the past 20 years, and that ringed seals are generally in better condition (heavier), lending support to a change in age at maturity. These changes have taken place at the same time that the polar bear population has in all likelihood increased a lot, so the bears may have played some role in the changes observed in the ringed seal population. However, impacts of climate change on the ringed seal population through, *inter alia*, changed availability of prey cannot be ruled out, even if large ecosystem changes have not yet been documented for the region.

Acknowledgements

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