Failure of reproduction in ringed seals (*Phoca hispida*) in Amundsen Gulf, Northwest Territories in 1984–1987

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ABSTRACT

Ringed seals (*Phoca hispida*) in Thesiger Bay (about 71°45'N, 125°00'W), in northwestern Amundsen Gulf in the western Canadian Arctic, suffered a failure of pup production in the years before 1987, starting probably in 1984. Pups taken in the summer hunt in the years before 1987 were reported scarce, and in 1987 were only 2.8% of the total 4+ and older. This low reproduction was associated with poor body condition in females and with an age distribution of adults that was weighted toward older animals (the modal year class was the 8+ class). An unusually high proportion of adult females had never reproduced; the median age of first birth was estimated at 8.6 years. By the summer of 1988 the age distribution had changed toward younger animals (modal age 5+), in better condition (by 20%), which had almost all ovulated. Pups were more numerous in the catch. In 1989 pups were very numerous in the catch (142% of the 4+ adults) and the estimated mean age of first birth had decreased to 5.3 years; almost all 5-year-olds sampled had borne pups. A similar occurrence of low pup production had been documented in the early 1970s, and resumption of reproductive activity had then also been associated with an apparent turnover of the population, the mean age of adults decreasing from 16-17 years when reproduction was low to 10.9 years in the year before reproduction resumed. Long-term data on ringed seals in the western Canadian Arctic has shown an average age at first ovulation of about 5.55 years and first birth just before age 7, about 1 year older than seen in this sample in 1989. Our 1989 sample may have been able to mature earlier because food was temporarily more abundant, or breeding densities temporarily lower, than long-term average values.

INTRODUCTION

Optimal strategy for genetic survival indicates that organisms will forgo or defer reproduction in marginal conditions, rather than compromise survival by unsuccessful attempts to raise young. In female mammals, the start of the reproductive career, and subsequent successful pregnancy, depends on attaining a critical level of stored resources (Ramsay 1986), a phenomenon well documented for humans (Frisch 1984) and domestic animals (Sadleir 1969). In the variable environment of the Arctic, reproductive failure in females associated with low fat reserves has been demonstrated for the Peary caribou (*Rangifer tarandus*) (Thomas 1982) as well as for ringed seals (*Phoca hispida*) (e.g. Smith 1987:29 and his Table 31). Population modelling shows that when populations are stationary, adult survival is more important than age at first birth in determining population growth rate (Goodman 1984); it is when a population is increasing that early reproduction has its greatest effect. So the optimal strategy for an adult female should switch, emphasising survival in poor conditions, but early reproduction when conditions improve.

This article documents an occurrence of reproductive failure in the ringed seals of north-western Amundsen Gulf in the western Canadian Arctic (Fig. 1) in the mid- to late 1980s, and relates it to an apparent shift in the age distribution of the local population of adult seals as well as a change in an index of body condition. This short-term investigation-samples were taken from the hunt in 1987, 88 and 89 - was prompted by reports from Inuk hunters at Sachs Harbour, Northwest Territories (N.W.T.) in the mid-1980s that young seals were absent from the hunting areas and were taken in unusually low numbers. They were concerned about possible causes, including industrial development in the Beaufort Sea and other areas of the western Canadian Arctic, and feared a permanent drop in the productivity of ringed seals.

In Sachs Harbour, adult and sub-adult ringed seals are now seldom hunted for food (other than for dog-teams), but pups are still esteemed as food. There is no longer much market for ringed seal pelts in the general fur trade in Canada, but a few families still use seal skins for clothing and handicrafts, either to supplement their incomes or because some items (such as mittens) hand-made from sealskin are preferred to store-bought versions. For such use the pelts of pups of the year ("silver jars") are preferred, and a dearth of this age class is quickly noticed.

There is little baseline data for the waters off southwest Banks Island. Cumulative results of aerial surveys from 1974 to 1979 (Stirling *et al.* 1982) show that the area from Cape Parry north

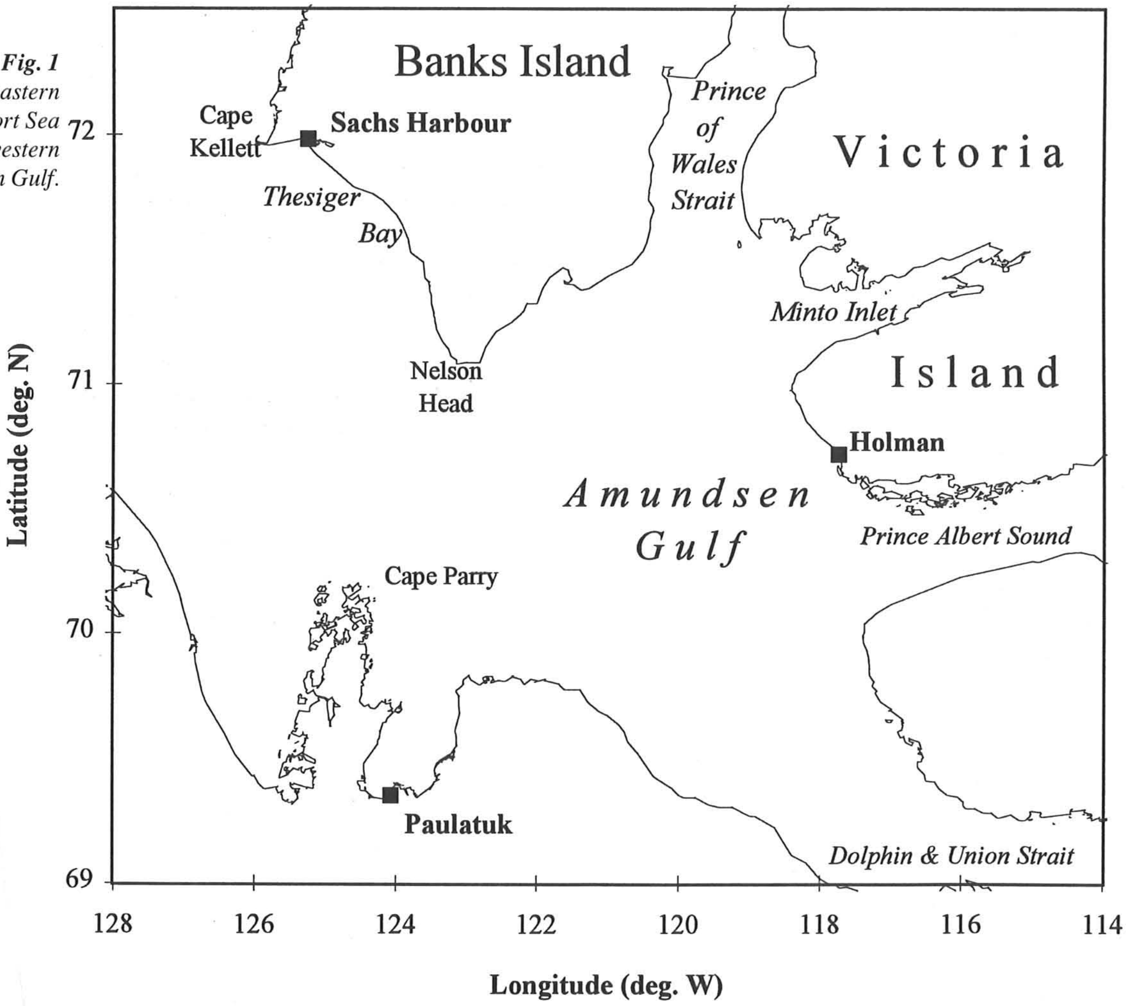

Fig. 1
The southeastern Beaufort Sea and western Amundsen Gulf.

to Banks Island had the highest concentration of ringed seals in the eastern Beaufort Sea; mean densities in Thesiger Bay, south of Cape Kellet and west of Nelson Head (Fig. 1), ranged from 0.161 to 0.6/km^2 (Stirling *et al.* 1982, aerial survey detailed data). Further east, the fast ice of Amundsen Gulf had high densities of ringed seals, up to 3/km^2, in four years of aerial surveys from 1981 through 1984 (Kingsley 1984, 1986).

MATERIAL AND METHODS

A total of 394 ringed seals were collected by Inuk hunters on ice and in open water hunts in the summers of 1987-1989 (Table 1). The Sachs Harbour people hunt seals mostly in Thesiger Bay, as far west as C. Kellett (Usher 1966:45, map 8). Seals brought in to Sachs Harbour by the hunters were processed according to standard gross necropsy procedures for pinnipeds (Fay *et al.* 1979). Comprehensive measurements, weights, and tissue samples were obtained, of which the following are relevant to the analyses presented here:

- straight-line total body length (standard length) to the nearest half centimetre;
- total body mass and sculp mass to the nearest pound, later converted to kilograms;
- sternal blubber thickness in millimetres
- reproductive organs, preserved in formalin;
- lower jaws, detached and frozen for subsequent age determination by extraction and sectioning of canine teeth.

Seals were aged by the methods of Smith (1973). The jaws were boiled to loosen the teeth, and a canine was pulled out. Cross sections about 0.1mm thick were sawn, cleared in a mixture of water, alcohol and glycerine, and examined under transmitted light. Annual layers in the dentine of each section were counted three to five times in blind replicate readings by one experienced reader. Recent results have shown that reading cementum layers in thin section of decalcified teeth give greater mean ages and layer counts that are more repeatable and complete, especially for older animals (Stewart *et al.* 1996).

The ratio of total mass to standard length (kg/m) was calculated as an index of body condition, and an adjusted total mass, based on the mass-length trend line, was calculated as:

$$\text{Adjusted Total Mass (kg)} = \text{Mass (kg)} + 50 - 69 \times \text{Length (m)}.$$

Sculp mass was subtracted from total mass to give a crude lean mass, and a blubber volume index (approximately litres) based on Ryg *et al.* (1990) was calculated as:

$$\text{Blubber Volume Index} = \text{Blubber Thickness} \times (\text{Total Mass} \times \text{Total Length})^{1/2}$$

using measurements in dm and mass in kg. Body condition indices were averaged over the collection season for each year, without correction for the fall-off in body condition associated with early summer moult in ringed seals (McLaren 1958), which in our samples was small. Product-moment correlation coefficients were calculated between pairs of condition indices for seals at least 2 years old for all three years pooled, and their approximate standard errors were calculated as:

$$SE = (1-r^2) / (n-3)^{1/2}$$

Reproductive history of females was determined from the condition of the uterus. Females that had carried more than one embryo were identified by both uterine horns' being stretched or swollen; primiparae by stretching of only one horn. Ovaries were examined for enlarged

Table 1. Ages of ringed seals collected at Sachs Harbour in the summers of 1987–1989

Collection year	Number collected	Pups of the year (%)	1–3+ yrs old (%)	Older than 4 yrs (%)	84–87 cohort total (%)
1987	75	2 (2.7)	2 (2.7)	71 (94.7)	4 (5.3)
1988	122	35 (28.7)	11 (9.0)	76 (62.3)	19 (15.6)
1989	197	97 (49.2)	32 (16.2)	68 (34.5)	28 (14.2)

follicles. Both non-parametric (DeMaster 1978) and curve-fitting methods have been proposed and used to analyse data on age at maturity (DeMaster 1984). We used a parametric method based on fitting sigmoidal curves, by maximum-likelihood methods, to age-specific data on whether females had previously been pregnant (and by supposition borne a pup). The curves tried were the logistic, which is symmetrical, and the Gompertz, which is not. The Gompertz curve fitted better overall (cf. York 1983, Hårding and Härkönen 1995), so only those results are reported. The Gompertz curve was defined by:

$$F(x)=exp(-exp(-e \cdot k \cdot (x-m+0.5)-B))$$

where $F(x)$ is the proportion of females having born a pup at or before age x, m is the mean age of females at first birth, and k is the population maximum rate of becoming mature (see Appendix). The constant B was determined numerically to be 0.5772. Long-term data on reproduction and maturity from the Holman area (Smith 1987:his Table 11) were analysed in the same way.

Growth was analysed by fitting a standard von Bertalanffy (1938) curve to data on length at age. Growth curves were fitted to the large-sample data in Smith (1987:his Table 18), and to data from the three years' collections at Sachs Harbour. For all data sets, age class was used as age with no correction for the difference between birth date (nominal mean about 15 April) and collection date. The curve was defined by the parameters asymptotic length, length at age zero, and growth rate at age zero.

Information on the formation and break-up of sea ice was obtained by observation in the field, from local residents and hunters, and from regular ice cover maps produced by the Canadian Ice Survey.

RESULTS

Ice chronology

In 1987, Thesiger Bay was clear of consolidated ice by 9 July, there being only a 2/10 cover of floating pan ice. By 30 July, Amundsen Gulf was relatively ice-free except for a wide belt of fast ice along the coast of Victoria Island and 2-6/10 ice cover at the western mouth of the Gulf. By the first week of June in 1988, the west coast of Banks Island to about 70-100km offshore, Thesiger Bay, and Amundsen Gulf were clear of ice save for a few large floes of thick first-year ice. Fast ice remained on the west coast of Banks Island until the third week of June, and in the large inlets of Victoria Island until the third week of July. In 1989, break-up started in Amundsen Gulf about 14 June. By the first week of July all of Amundsen Gulf and most of Thesiger Bay were clear of pack ice, but floating pack stayed in sight from Sachs Harbour all summer. Freeze-up, i.e. the approximate date of 9/10 ice cover, was at the end of October in 1987 and 1988 and in about the third week of October in 1989.

Age structure of the harvest

Presence of young of the year

The number of adult seals (defined here as 4 years old or more, although most population studies have shown that ringed seals usually bear their first pups older than this) taken in the three years varied little, from a minimum of 68 to a maximum of 76. The sampling was as complete as possible, but may not have been quite 100% of the catch. However, the number of young of the year taken varied between years; in 1987 there were only 2; in 1988 there were 35, forming over 25% of the catch, and 46% of the seals 4 years and older; and in 1989, young of the year numbered 97 and were almost 50% of the catch and 142% of the number of 4+ seals (Table 1).

Presence of older juveniles

The absence of the 1987 cohort is evident in the collections made in the two following years. Yearlings are only 3% of the collection in 1988, and 2-year-olds are 3% in 1989. The 1986 cohort is also small. Yearling seals from the 1988 cohort are evident in the catch from 1989, but there are few yearlings in the 1987 catch, indicating that the 1986 cohort was probably also missing. This confirms the hunters' reports that production had been low.

The 1987 collection also lacks the cohorts from 1985 and 1984, which would have been the 2+ and 3+ classes in that year. However, in 1988, and even more in 1989, these cohorts (3+ and 4+ in 1988, and 4+ and 5+ in 1989) are present in the sample; in 1989 the 1984 cohort is the second most numerous class older than yearling.

Age of adults

There is a marked variation in the age distribution of adults in the collections. In 1987, the mean age of adults (i.e. those over 4 years old) was 7.5 years, and the mode was 8. In 1988, the mean was 6.3 and the mode 5; in 1989 they were 6.5 and 6 years. The 1988 and 1989 samples had similar age distributions ($\chi^2_9 = 10.4$, $p>0.05$), but between 1987 and the 1988–89 pooled samples χ^2_9 was 31.5 ($p<0.01$). The difference was due to a long tail of older animals in the 1987 collection, and a relative absence of 5- and 6-year-olds (Fig. 2). In the two later years the large proportion of 7- to 9-year-olds was replaced by a preponderance of 5- to 7-year-olds. The 1989 sample resembled that of 1988 more closely in age-class distribution ($\chi^2_{10} = 10.4$, $p>0.05$) than in cohort distribution ($\chi^2_{10} = 17.3$, $p>0.05$) (Fig. 2).

Fertility of adult females

In adult age distribution, 1988 and 1989 were similar, but differed from 1987. But as regards evidence of previous pregnancy, the 1987 and 1988 samples had similar low frequencies, while in the 1989 sample it was more frequent. Gompertz curves were fitted to the data on previous pregnancy, and tested for similarity using likelihood ratios tested as χ^2. The three years had significantly different maturity curves ($\chi^2_4 = 37.0$, $p<0.01$). Only 10% of this statistic was due to a difference between 1987 and 1988 ($\chi^2_2 = 3.6$) (but comparing rates in these two years may be affected by their different age distributions); the other 90% was due to the difference between 1989 and 1987–88 combined ($\chi^2_2=33.4$, $p<0.01$). The best model to relate birth-rate to age fitted a single curve to the pooled data for 87 and 88, with a mean age at first birth of 8.02 years (SE 0.52), and a separate curve for 1989, with mean age at first birth 5.37 years (SE 0.23) (Table 2, Fig. 3). However, in 1988 most nulliparous females in the collection (5 of 6 aged over 6 years, all those aged 5–6 years, 3 of 4 aged 4–5 years and all those aged 3–4 years) had ovulated; in that respect, 1988 was similar to 1989 and different from 1987.

Gompertz curves fitted to maturity data from large collections made near Holman (Fig. 1) (Smith 1987:his Table 11) gave a mean age class of first ovulation 5.55 years (SE 0.15) and age at first birth 6.9 years (SE 0.15) (Fig. 3). When all three years' data from Sachs Harbour were pooled, the estimated mean age at first birth was 6.83 years (SE 0.33).

Body condition

Body condition indices were analysed for seals 2 years old and older (but 2- and 3-year-olds were few in all collections). For the three years' collections pooled, sculp mass had a correlation

Table 2. Mean age of first birth to female ringed seals from fitted Gompertz curves
$F(age) = \exp(-\exp(-e \cdot k \cdot (age - mean\ age + 0.5) - B))$ (where $B = 0.5772$).

Sample	k (SE) (%/yr)	mean age (SE) (yrs)	Test statistic[a]
Sachs Harbour 87	21 (8)	8.62 (0.65)	
Sachs Harbour 88	28 (11)	7.13 (0.61)	
Sachs Harbour 87–88 pooled	19 (5)	8.02 (0.52)	$\chi^2_2=3.6$ NS
Sachs Harbour 89	77 (39)	5.37 (0.23)	
Sachs Harbour 87–89 pooled	20 (5)	6.83 (0.33)	$\chi^2_2=33.4$***
Smith (1987, Table 11): ovulation	38 (5)	5.55 (0.15)	
Smith (*loc. cit.*): birth	38 (4)	6.94 (0.15)	

k is the population maximum rate of maturation (% per year), indicated by the maximum slope of the Gompertz curve fitted to population proportion mature.

[a] likelihood ratio test for similarity of the two preceding lines in this table; *** = significant at 0.1%.

Fig. 2
Age distribution of ringed seals in catches at Sachs Harbour, N.W.T. in 1987–1989.
a) by chronological age
b) by year of birth

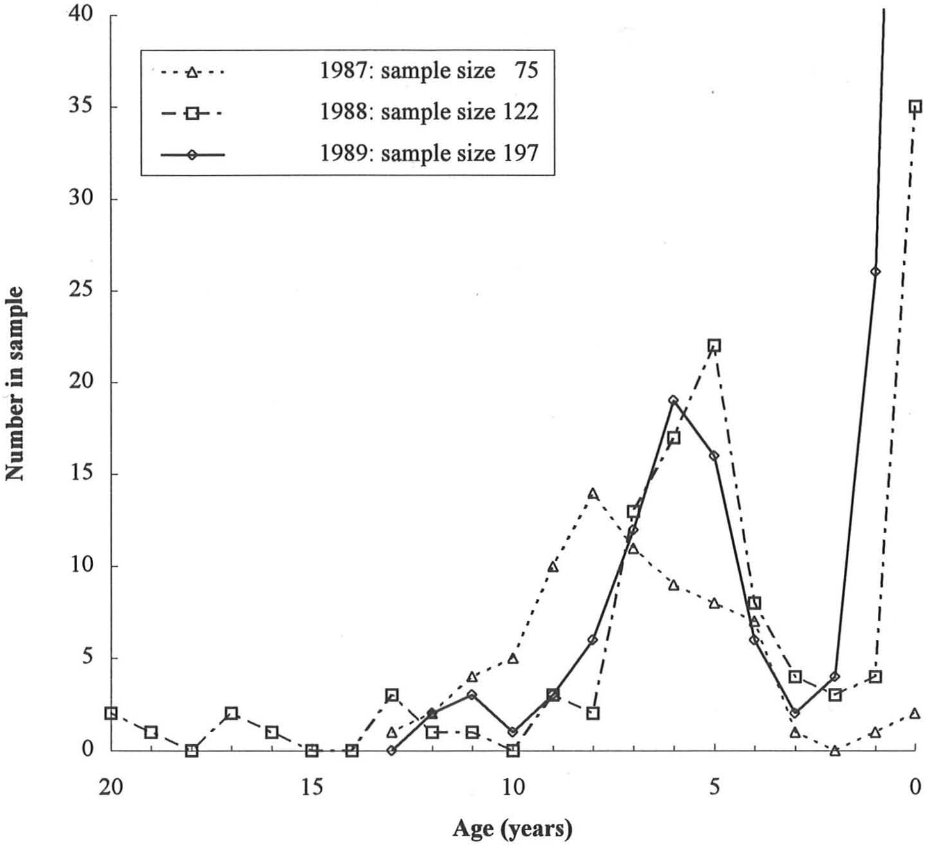

Fig. 2a

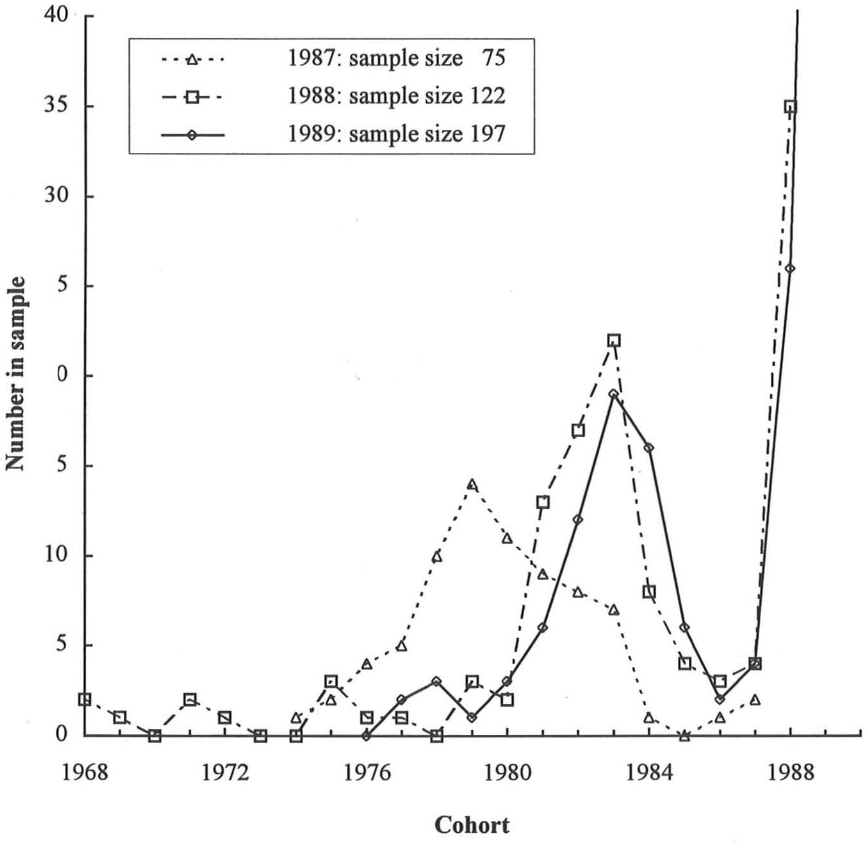

Fig. 2b

Table 3. Body condition of Sachs Harbour ringed seals during a pause in reproduction (1987) and on its resumption (1988 and 1989)

Year	Age (years) or Age Class	Sample size	Mean mass/length ratio (SE) (kg/m)	Mean of mass adjusted[1] for length (SE) (kg)
1987	at least 2	68	33.39 (0.68)	9.36 (0.67)
1988	at least 2	80	39.85 (0.72)	16.52 (0.76)
1989	at least 2	74	39.60 (0.80)	16.92 (0.86)
1989	Yearlings	24	26.26 (0.74)	9.69 (0.67)
1988	Young of the year	34	23.86 (0.49)	10.23 (0.42)
1989	Young of the year	97	22.23 (0.34)	9.89 (0.27)

[1] Mass was adjusted by adding 50kg and subtracting 69kg per m of total length.

coefficient of 79.4% (approx. SE 2.7%) with blubber volume index, and total mass had a correlation of 68.9% (SE 3.5%) with total length. However, sculp mass as a proportion either of total mass or of lean mass had correlations only of 17.6% (SE 7.1%) and 16.0% (SE 7.1%) with the ratio of total mass to total length, and lean mass was nearly as well correlated (r=66.0%, SE 4.1%) with adjusted total mass as sculp mass was (r=70.5%, SE 3.7%).

Seals collected in the summer of 1988 were on average in 19% better body condition (mean mass: length ratio 39.9kg/m) than those collected in 1987 (33.4kg/m) (Student's $t_{69} = 6.6$, $p<0.01$) (Table 3). The summer average of the condition index of 74 seals more than 2 years old remained about the same in 1989 at near 39.6kg/m (SD 7.6), but 24 yearlings (of which there had been only 1 in 1987 and 4 in 1988) had a mean index of only about 2/3 that value at

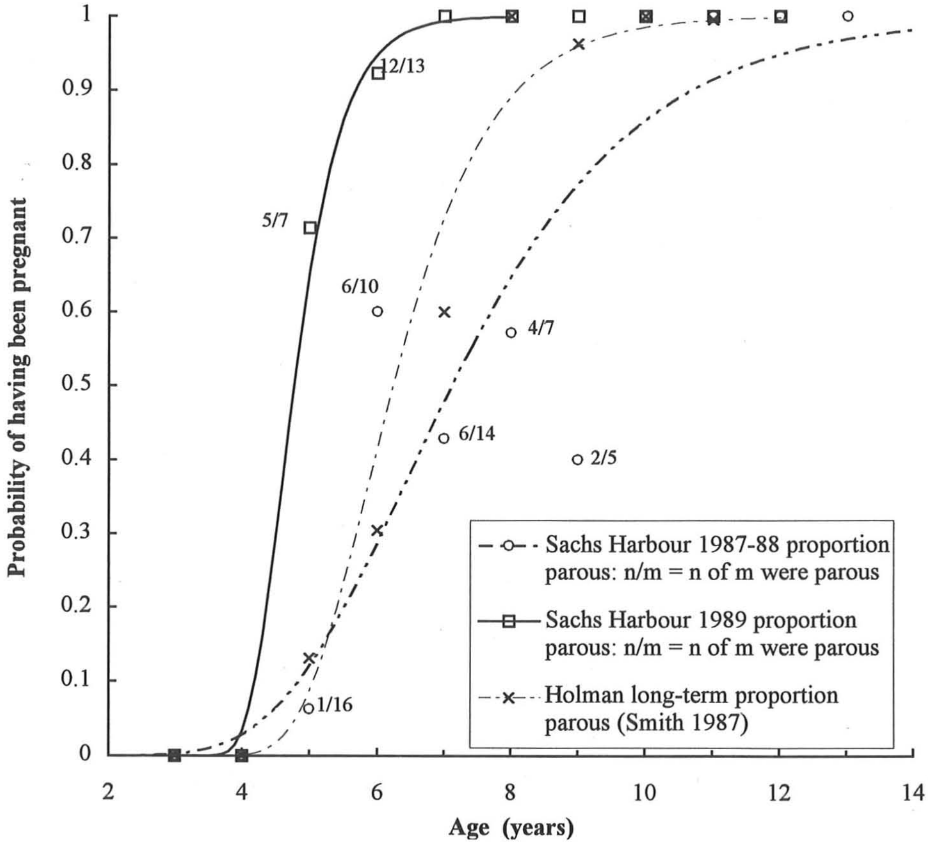

Fig. 3
Proportion of female ringed seals having been pregnant as a function of age in three sets of samples collected in the western Canadian Arctic, with fitted Gompertz maturity curves.

Table 4. Summer seasonal body condition indices of Thesiger Bay ringed seals at least 2 years old in 1987–1989.

Period	Mean condition index (kg/m) and (sample size)		
	1987	1988	1989
June 01-15	37.43 (10)	40.19 (24)	
June 16-30		39.76 (8)	
July 01-15	31.39 (4)	39.39 (16)	40.08 (34)
July 16-31	29.87 (11)	41.34 (6)	38.97 (17)
August 01-15	33.43 (43)	38.84 (8)	39.36 (16)
August 16-31		39.34 (18)	39.31 (7)
All summer	33.32 (68)	39.85 (80)	39.60 (74)

26.3kg/m (SD 3.7). The collections in the different years were not distributed over the summer exactly the same way, but the seasonal variation in body condition was small relative to the difference between years (Table 4).

Von Bertalanffy growth curves for length fitted to the age-class means for the 1987 collection at Sachs Harbour had asymptotic length of 129cm, length at zero age (l_0) of 85.2cm and growth rate at zero age (k_0) of 6.8cm/yr. For 1988 the values were 127cm, 86.9cm and 8.7cm/yr, and for 1989, 125cm, 85.3cm and 10.5cm/yr; i.e. in 1988 and even more in 1989, early growth seemed more rapid. A growth curve fitted to age-class means from Holman (Smith 1987: his Table 18) was defined by asymptotic length 127cm, l_0 85cm, and k_0 7.8cm/yr. The ages at 87% of asymptotic length were 5.03+ years for the Holman data, and 6.29+ for Sachs Harbour in 1987, but 4.05+ and 3.38+ years at Sachs Harbour in 1988 and 1989 (the input age data was year classes, not corrected for collection date).

Summary of results

In 1987 the adults collected in the summer were old, they were in poor condition, and females even as old as 8 (2 of 5) and 9 (3 of 4) years old had never been pregnant. The estimated mean age of first birth was well over 8 years. The young of the year were absent from the collections throughout the summer.

In 1988, the age distribution of adults changed significantly: the proportion of old adults (8-10 years old) was less and the proportion of young adults (5-6 years old) increased. Mean condition indices improved. The curve of first births shifted by 1.5 years younger (mean age 7.1 years). Almost all females over 3 years old showed evidence of previous pregnancy, or at least ovulation. Young of the year were present in the catch.

From 1988 to 1989, the age distribution of adults did not change. However, most of the young adult females that were represented in the sample in 1988 bore young in the spring of 1989, confirming high ovulation rates in 1988. The maturity curve shifted further down, the estimated mean age of first birth dropping to 5.4 years, and almost all females more than 6 years old had previously been pregnant.

DISCUSSION

Ages of ringed seals determined from counts of dentine layers in stained thin sections were found to vary more between readers than readings of cementum layers (Stewart *et al.* 1996). Ages estimated from dentine layers were also lower on average than those estimated from cementum layers; dentine readings seldom exceeded 15 years and for cementum ages over about 12 years dentine ages were between 5 and 15 and not closely correlated with cementum age. However, up to ages of 5-6 years, cementum and dentine ages agreed well (Stewart *et al.* 1996). Albright (1990) found that while in some samples, dentine was hard to read in stained thin sections of decalcified teeth and was then poorly correlated with cementum, dentine readings from sawn cross-sections had correlation coefficients of 60-70% with cementum readings of stained thin sections but averaged 1-2 years greater. From ages based on sawn sections, our analyses of the proportions of subadults and young adults were probably not much in error.

Several measures related to body condition were measured in the field, including maximum girth, sculp mass, total mass, and sternal blubber thickness. A detailed treatment of body condition indices was outside our objectives. Seals of a given length were heavier in the 1988–89 collections, but lean mass and sculp mass were both involved. The index suggested by Ryg *et al.* (1990) predicted sculp mass well, but it appeared that sculp mass alone, or its relationship to total or lean mass, was not the best index. So the relationships between length and total mass were retained as the leading indices of body condition; the Adjusted Total Mass was about as sensitive as the simple Mass:Length ratio in detecting differences between years.

The variation in the total number of seals collected was considerable, but was due to the increased number of young seals taken in 1988 and 1989. We did not measure hunting effort for the consecutive summers and have no catch:effort data by which to measure density. Collections made on fast ice in breeding areas may be biased towards breeding adults, but open water collections may be less biased (Smith 1987). Usher (1966) indicated that the area of Thesiger Bay within which seals were hunted in the open-water season was approximately the same as that of the winter area of breeding fast ice. In 1987, 87% of the collection was from summer hunting in open water, 92% in 1988 and 97% in 1989. The total number of adult seals caught per year was stable, which might indicate constant effort and density of adult seals, but might also indicate that the take of adult seals was matched to a constant demand (for dog food, for example). Seal pups of the year are esteemed, so hunters may hunt less if they do not think they have much chance of getting one.

Previous studies of ringed seals in the western Canadian Arctic showed that annual reproductive success and recruitment may fluctuate significantly from year to year (Stirling *et al.* 1977: their Table 9, Smith and Stirling 1978). Among the limiting factors suggested have been ice conditions, snow cover, or female body condition, ultimately due to variations in the weather (Hammill 1987b) and predation by the Arctic fox (*Alopex lagopus*) (Smith 1976, 1987, Stirling *et al.* 1977, 1982, Lydersen and Gjertz 1986, Smith and Stirling 1978). The collections made in 1987 and 1988 confirmed quantitatively the lack of reproduction in 1987. The collected adult seals were old, and a high proportion had never borne a pup; i.e. the reduced reproductive rate was associated with deferral of the reproductive career. The body condition of seals in summer of 1987 was below normal. This echoes a similar episode of reduced reproduction that occurred in the western Canadian Arctic in the early 1970s (Smith 1987), which was also associated with reduced values of condition indices, and with lower rates of ovulation.

The recovery of normal breeding was signalled by events in consecutive years, which may be reconstructed as follows. In 1987, the study area was inhabited by a rather old population of seals, on average in below-normal condition, many not reproducing and never having done so. Between the fall of 1987 and the spring of 1988, younger seals moved into the area. The absence of these cohorts from the collections in 1987 may reflect an age segregation of the ringed seal population, older sub-adults being absent from areas that in winter hold breeding seals; alternatively, the 3- and 4-year-old seals that appeared in the collections in 1988 could have been migrants from a long way away. In that case, local reproduction could have been low since 1984.

We do not know when the age distribution in the study area changed, perhaps at freeze-up in 1987, perhaps later in the winter. Nor do we know the social mechanism by which such a change in age distribution, possibly a turnover of the population, would occur. Studies in the central Canadian Arctic archipelago appeared to show that female seals establish territories in new fast ice as the ice edge progresses (Hammill 1987a), and a study in the eastern Canadian Arctic appeared to show that some adult seals stayed in the same breeding area from one year to another (Smith and Hammill 1981). One would predict for a species such as ringed seals that adults that had established a breeding territory would attempt to hold it from year to year, and to exclude non-breeders who would find it advantageous to make the best shift possible in areas unsuitable for breeding. New breeders should compete for entry into breeding territory only when in good enough body condition to make breeding success likely. If poor environmental conditions at maturity caused certain cohorts to defer the start of reproduction, and a subsequent return to good conditions allowed younger seals to mature early, turnover of the breeding population could occur simultaneously with improving environmental conditions as significant waves, involving simultaneous entry into the breeding population of more than one cohort, rather than a continuous process. Our results show an age distribution peaked on the 1979 cohort being replaced by a new wave centred on a 1983 cohort. The result was a different, younger age distribution in the collections in 1988. These seals, wherever they had been in the mating season of spring 1987, had generally not then been in reproductive condition: either they had been outside the breeding ice, in floe-edge and polynya areas inhabited by pre-breeding subadults (see Smith 1987: his Fig. 4), or they had been in breeding ice elsewhere but had not been in good enough condition to reproduce. Either way, they did not bear many pups in 1988.

But conditions in the autumn of 1987 and winter 1987-88 were good enough to bring these younger females into breeding condition–in summer 1988 the average condition index was 25% higher than in 1987 – and they almost all ovulated and conceived successfully in early summer of 1988, even at ages as low as 4 years. Although the number of pups was still low and the proportion of females that had previously been pregnant was also low, the evidence from ovarian examination was that ovulation rates had recovered: of 6 nulliparous females more than 6 years old, 5 had ovulated that year, and while all younger females were nulliparous, all the females between 5 and 6 years old, 3 of 4 from 4 through 5, and one of three females between 3 and 4 years old had also ovulated. So the birth rate soared in spring 1989, most females 5 or more years old bore pups, and large numbers of pups of the year were in the study area that summer and showed up in the hunters' catches.

From this reconstruction it is apparent that the chronology of such events is protracted: in this scenario, conditions improved in the winter of 1987-88 to cause pup production to be resumed in 1989. Equally, if the first missing cohort of pups was that of 1984 (as the Sachs Harbour hunters said), the key events might have taken place in winter 1982-83, or summer 1983. The Sachs Harbour hunters affirmed that pup production had been low as early as 1984. We could not confirm that from our data. Polar bears (*Ursus maritimus)* produced cubs at a normal rate in 1985. Although the 1984 cohort of ringed seals was absent from the sample in 1987, it appeared in 1988 and was the second most numerous in 1989, when it was 5 years old. We could not tell whether these were locally born seals that had spent their sub-adult years away from breeding areas, or seals born elsewhere that had moved in. However, the high proportion of seals 7, 8, and 9 years old in our 1987 collection that had never borne pups supports the idea that pup production in Thesiger Bay had been low for about 3 years before that.

After the reproductive failure in Amundsen Gulf in the early 1970s, a similar downward shift in the age distribution coincided with the recovery of reproduction. Ovulation rates were low in 1974 and 1975, and pups were still missing from collections at Holman in 1975, but were present in 1976. The mean age of females in the collections was 16.5–17.5 in 1972–1974, but dropped to 10.9 in 1975 (Smith 1987: his Table 12), i.e. one year before pup production resumed. That on both occasions there should have been a clear change in the age distribution of the collections when production was resumed indicates that more is going on than a simple response in fertility to changing conditions by a stable population of seals, but exactly what is difficult to be sure about. Sachs Harbour hunters considered that the smaller seals taken at the ice edge were a mobile stock, distinct from the larger seals taken in the fast ice in spring or in the corresponding open water area in summer (Usher 1966); they could be younger seals ready to move into breeding habitat.

We infer that ringed seals are capable of maturing, in good conditions, as early as 3 to 4 years of age and bearing at 5. As a rule, marine mammals mature sexually at about 87% of their physically mature length (Laws 1956), and in some species attainment of a critical length indicates maturity better than age does. Growth curve analyses showed variations in length-age relationships that were related to shifts in age at maturity. Analysis of long-term reproductive data from Holman by the methods used here gave 6.9 years for mean age at first birth, and growth analysis, using the 87% rule, estimated a mean age at potential maturity of 5+ years (approximately 5.25), with an implied mean age of first ovulation 5.75 years, and mean age at first birth at 6.6. From the long-term average growth pattern of ringed seals in Amundsen Gulf, maturity at 5 years, and first birth on average at about 6½ years, might be considered within the normal capacity of the species. The average age at first birth estimated from pooling all three years of this study was not very different at 6.8 years.

There is no readily apparent reason why recruitment of the 1987 and preceding year classes was low. It does not appear to have been due to poor pup survival, or to fox predation, because all the indicators are for poor reproductive performance by females. An earlier episode of low reproductive success in the 1970s might have been due to heavy ice cover in the winter of 1974-75 that stayed through much of the following summer. From contemporary reports, the Beaufort Sea cleared of ice late and slowly in 1985 and multi-year ice was farther south in the winter of 1985-86 than in the winter before or after (Stirling *et al.* 1988). Late break-up is often followed by early freeze-up, so primary productivity may be reduced at both ends of the summer (Hammill 1987b). No specific pathologies were noted that could have been associated with lowered birth-rates, and organochlorine contaminant analyses did not show burdens any higher than normal low Arctic levels (Kingsley and Byers 1990). Juvenile ringed seals appeared to have grown in length more slowly in 1987 than in 1989, and 1988 showed intermediate growth values. Similarly, lowered condition in Beaufort Sea polar bears in the early 1970s affected juveniles more than adults (Kingsley 1979).

This event of low ringed seal pup production, like others, had apparent consequences at the next trophic level: the natality rate of polar bears 6 or more years old in 1986 and 1987 averaged 2/3, and of 5-year-old bears less than 1/4, of the 1985 value. Also cubs born to bears of all ages were lighter (Stirling and Lunn 1997). It is not unusual that failure of a food source affects reproduction; nutritional effects on breeding success are a major factor in regulating populations. In the case of ringed seals and polar bears, the quick translation of this process through two steps in the trophic web has been documented. Newly weaned phocid seals have high fat content and young of the year have been estimated to furnish 48% of the annual energy that polar bears get from ringed seals (Stirling and Øritsland 1995). (This is different from most very young animals, which while numerous and vulnerable are often energy-poor.) The polar bear eats little else, so if ringed seal pups are scarce, its own reproduction is immediately affected. It might be predicted that variations in reproductive performance in other phocids would affect their next-level predators equally quickly, but for most phocid species, birth-rate variations are less well documented, dependent predators are less clearly identified, and predator population dynamics have been less closely followed.

CONCLUSIONS

Reduced pup production in Thesiger Bay in northwest Amundsen Gulf in 1987, and for at least two or perhaps three years before that, was due to low reproductive activity of females, not to post-natal mortality. The recovery of pup production was associated with a renewal of the population that took place in the winter of 1987-88 or spring of 1988, as the age structure changed in 1988 with a higher proportion of 5- and 6-year-old adults. Although many of these animals were nulliparous in 1988, reproductive activity recommenced as they ovulated and conceived in that year. This renewed population had a high pup production in 1989, estimated mean age at first birth being 5.37 years. All 3-year-old seals collected that year had ovulated. Growth of female ringed seals in the western Arctic, from long-term data, was consistent with attaining sexual maturity at about 5 years, but in 1989, the growth pattern was consistent with earlier maturity than that.

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Appendix: Estimation of mean age at first birth.

A parametric method was used to estimate mean age at first birth from cumulative proportions of females which had born pups in different age classes. A Gompertz sigmoidal curve was fitted to the cumulative proportions of parous females, following York (1983) and Hårding and Härkönen (1995), and because for most of our data it fitted better than a logistic, the other curve considered. The basic Gompertz curve is:

$$G(x) = \exp(-\exp(-e.k.(x-m)))$$

where k is the maximum slope of the curve and m is the abscissa at the point of inflection. Fitted to cumulative proportions mature, this curve represents potential maturity. Two adjustments were made: one for the fact that, the Gompertz curve being asymetrical, the mean age of becoming mature is not at the point of inflection; and the second to allow for the difference between potential maturity and its seasonally regulated expression: a seal has to wait on average 0.5 years between having the potential to bear a pup and having the seasonal opportunity to do so. The equation fitted was therefore:

$$P(x) = \exp(-\exp(-e.k.(x-M+K_2)-K_1))$$

where K_1, the allowance for the asymmetry of the Gompertz curve, was numerically determined to be 0.5772, and K_2 was set at 0.5. If P(x) is the proportion of females who have borne a pup at or before age x, M is then the estimated mean age of first birth, and k is a measure of how rapidly the population matures; it is the maximum rate of becoming mature within the population, per unit of time.