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TRENDS IN GROWTH AND REPRODUCTIVE PARAMETERS OF BARENTS SEA HARP SEALS

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ABSTRACT

Data from reproductive organs of Barents Sea harp seals Phoca groenlandica with corresponding age determinations have been analysed in combined samples collected during three periods: 1963-1972, 1976-1985 and 1990-1993.

A Gompertz growth model, fitted to the age and standard length (available only from the first and last sampling periods) data, suggest a trend of decreasing growth rates and reduced maximum lengths for both sexes in the most recent period.

Testes weights indicate that males attained sexual maturity in age groups 6-9 years during 1990-1993. This is confirmed by testes volumes which also suggest an apparent increase in age at sexual maturity for males from age groups 4-7 years in the combined 1963-1972 sample.

Cumulative maturity frequencies, based on ages at first ovulations as indicated by corpora lutea and albicantia formed within the last two years prior to the year of capture, show that the apparent mean age of maturity for females increased significantly from 5.5 years in the 1963-1972 sample to 6.7 years in 1976-1985 and 8.1 years in 1990-1993.

A limited number of mature females sampled after implantation in September-October 1990-1993 indicate a rate of early pregnancies of about 0.84. Temporal changes in fertility may be revealed by future analyses of data from ovaries in the samples.

The changes demonstrated in growth and reproductive parameters may presumably be explained as density-dependent responses to population growth in relation to a decreasing availability of staple food in the Barents Sea area.

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INTRODUCTION

Animal populations often exhibit changes in life history parameters following marked changes in population size, size in competing populations or in availability of prey species. Density dependent changes in parameters such as growth, age at maturity and fertility rate, are known to occur in several species of marine mammals including harp seals Phoca groenlandica (Bowen et al. 1981, Sergeant 1991).

The Barents Sea harp seal population was heavily exploited after World War Two, and was probably reduced from a level of 1.25-1.5 million individuals by the early 1950s to less than 500.000 in the mid 1960s when management actions were taken (Bowen et al. 1981). Norwegian estimates suggest that in 1978 the total stock size had increased to c. 800.000 animals which produced 170.000 pups annually and increased at an annual rate of about 5% (Benjaminsen 1979). In 1980, Soviet aerial surveys confirmed a pup production comparable to the Norwegian 1978 estimates, whereas later surveys indicate that a reduction in recruitment may have occurred after 1985 (Anon. 1992). A severe deficiency of recruits is also indicated by age compositions in samples from Norwegian catches of moulting harp seals in the East Ice (the southeastern Barents Sea) since the mid 1980s. The year-classes 1986, 1987 and 1988 are particularly weak, and recruitment of one year old seals did not improve significantly until 1992 (T. Øritsland, unpublished data).

In addition to the recent changes in harp seal exploitation pressure with subsequent changes in recruitment rate, other changes have occurred in the marine ecosystem in Norwegian waters including the Barents Sea between the late 1960s and today. Certainly, the most conspicuous change is the collapse of the two stocks of major pelagic shoaling fish species, the Atlanto Scandian herring Clupea harengus and the Barents Sea capelin Mallotus villosus (Anon. 1993). Both species are known to be

consumed by Barents Sea harp seals (Haug et al. 1991, Nilssen et al. 1992).

The recent changes in harp seal recruitment and population size, possibly related to a change in food availability, may have caused changes in density dependent life history parameters. Therefore, a study of possible plasticity in growth and reproduction parameters of Barents Sea harp seals was initiated. These parameters are also important to the management of the population, and updated information has been requested by the "Joint ICES/NAFO Working Group on Harp and Hooded Seals" (Anon. 1992).

This paper present preliminary results from analyses of growth and reproduction data collected during commercial and scientific sealing in 1990-1993. In addition to this documentation of present status, historical data collected during the period 1963-1985 by the Institute of Marine Research, Bergen, Norway, are included in the analyses for comparative purposes.

MATERIAL AND METHODS

Sampling

Material and data for this study were collected during three separate periods: 1963-1972, 1976-1985, and 1990-1993 (Table 1).

In the first two periods, all material was collected from seals taken during Norwegian commercial sealing in the East Ice in March-April (Fig. 1). Collection of material from females was given the highest priority. Thus, in 1976-1985 only females (155) were sampled, while in 1963-1972 material was obtained from 252 females and 95 males.

The most recent material (1990-1993) was collected in different seasons and in different parts of the area of Barents Sea harp

seal distribution (Table 1, Fig. 1). In addition to collections performed by scientific personnel during Norwegian commercial sealing in the East Ice in March-April, material was also secured from harp seals taken for scientific purposes during dedicated harp seal research expeditions in the Barents Sea, particularly designed to study the ecology of the species (Nilssen et al. 1991, 1992, 1993, Nilssen & Haug 1993). Material was also collected from harp seals taken as bycatches in gill net fisheries in Finnmark, North Norway (Nilssen et al. 1993). No sexual priority was given during sampling, and the material from this last period include 392 females and 276 males.

Standard body length (straight line from tip of snout to tip of tail) was recorded for all seals except the 1976-1985 sample. Lower jaws were secured and salted for later use in age determinations, and pairs of ovaries or testes were removed intact and fixed and stored in 4% formalin for later laboratory analyses.

Age determinations

Lower canine teeth were extracted from the jaws after boiling in water for about one hour. A thin (0.15 mm) transverse section of each tooth was prepared, washed in 70% alcohol and mounted on a glass slide. The ages of individual seals were determined by counting incremental growth layers in the dentine of the transverse sections, using a microprojector and transmitted light (Bowen et al. 1983). The 1990-1993 subsample include animals caught at different times of the year, but all ages are given in whole years corresponding to the age attained at the breeding season (March) in the year of capture.

Growth analysis

Body growth of postweaning seals was described using a Gompertz growth model:

$$SL = L_{\infty}(\exp(-b*\exp(-k*x)))$$

where SL is standard length, L_{∞} asymptotic length, x age in years, and b and k are constants to be fitted. The growth curves are fitted by regression analyses using size and growth rate as variables. Males and femals were analysed separately.

The two first sampling periods include only material collected in April-March. For comparability, therefore, only the winter and spring data from the 1990-1993 sampling period were applied in the growth analyses (subsamples collected from February to June when food intake and growth rate is assumed to be low, Nilssen *et al.* 1992, 1993).

Examination of reproductive organs

The weight and measurements of length and largest diameter were recorded for one or both fixed testes from each male. The size of the testes was described as the volume (V) of an idealized ellipsoid body, using the formula:

$$V = 4/3 * \pi * d^2 * l$$

where l is half the maximum length, and d is half the maximum diameter of the testes.

The fixed ovaries were cut in 1.0-2.5 mm thick sections and corpora lutea and albicantia were measured and recorded. The age at maturity (first ovulation) was determined for individual females by deduction from the age at last ovulation and the number of corpora in the ovaries. Accumulated maturity frequencies were then calculated from the distribution on age at maturity of all 2-11 years old females which had reached maturity within the three most recent breeding seasons (Øritsland 1964, 1971, Bowen *et al.* 1981, Sergeant 1991).

The mean age of first time ovulators (AFO) and its confidence interval was calculated using the formula of DeMaster (1984):

$$\text{AFO} = \frac{\sum (\text{no. of first-time ovulators per age group}) * \text{age}}{\text{total no. of first-time ovulators in sample}}$$

where the summation is over all age groups which include first time ovulators. Confidence intervals were constructed from the standard formula for the variance of a mean. Possible differences in AFOs between sampling periods were tested using t-tests.

Pregnancy rates

The delayed implantation of the blastocyst in seals makes it impossible to detect the foetus in the reproductive tract of pregnant harp seal females during spring and early summer (Sergeant 1991). However, embryos were easily detected in the 1990-1993 material collected in September and October, and the ratio of pregnant vs. not pregnant sexually mature females could be calculated. The 1993 February material, collected just prior to whelping, was excluded from the calculation since these seals were caught in the Barents Sea outside the main breeding area in the White Sea (Sivertsen 1941, Yakovenko & Nazarenko 1967) and therefore believed not to be representative of mature females in the population.

RESULTS

Growth rates

Data describing the relationship between body length and age by a Gompertz growth model are available for the sampling periods 1963-1972 and 1990-1993 (Table 2). The Gompertz growth curve non linear regressions fitted to these data revealed significance ($p < 0.05$) in both sexes for both periods. The asymptotic values (L_{∞}) for males were 174.1 cm and 165.8 cm in 1963-1972 and 1990-1993, respectively. The corresponding values for females were 172.5 cm and 168.4 cm. Also, the growth constants (k) were larger for the 1963-1972 data than for the 1990-1993 data. However, overlaps in 95% confidence intervals indicate that the observed trends of reduced growth rates and maximum body lengths from 1963-1972 to 1990-1993 are not statistically significant.

The observed length-age values and growth curves for the two sexes and periods are illustrated in Figs 2 and 3.

Sexual maturity in males

Testes have not been examined histologically. However, testes weights and volumes have been analysed to provide indirect evidence for male reproductive status. Weights are available only for the 1990-1993 period. From Fig. 4 it is evident that a significant increase in testes weight occurs through the age-groups 6-9 years. The same pattern is evident in the testes volume for this period, while the increase in testes volume appears within the age-groups 4-7 years in the 1963-1972 sample (Fig. 5). Testes volume data are not available for the 1976-1985 period.

Sexual maturity in females

The data from analyses of the ovaries, including the distribution on age at capture, age at sexual maturity or first ovulation and the calculated maturity frequencies for the maturing age groups, show that female harp seals examined matured in age groups from 2 to 11 years (Tables 3-5, Fig. 6). Maturity at ages below 4 years was observed only in the 1963-1972 sample where all 9 year old and older females were mature.

Cumulative maturity frequencies (Fig. 6) indicate a shift towards higher ages at maturity for the harp seal females from 1963-1972 to 1990-1993. The mean age of maturity (AFO, with 95% confidence intervals in parentheses) was found to be 5.5 (5.1-5.9), 6.7 (6.4-7.0) and 8.1 (7.6-8.6) years in 1963-1972, 1976-1985 and 1990-1993, respectively. The observed differences proved statistically significant between all three periods (t-tests, $p < 0.05$).

Fertility

A total of 27 (84%) of the 32 mature females examined in September-October were pregnant (Table 6). All females older than 15 years were pregnant.

DISCUSSION

Previous investigations on harp seal growth have revealed that length as a function of age gives the most precise measure of body size, and that the best fit to the length at age data has been obtained with a Gompertz growth model (Innes et al. 1981). Consistent with previous observations (Khuzin 1963), the present growth data indicate that Barents sea harp seal males generally attain sizes in excess of the females. Both growth rates and the asymptotic body length values were higher for both sexes in the period 1963-1972 than in 1990-1993. However, the growth curve model failed to reveal any statistical significant difference between the two periods, and these results should therefore only be interpreted as indicative of a possible trend.

In studies of Barents Sea harp seals in the period 1958-1964, Yakovenko & Nazarenko (1967) found fully developed testes with sperm in the epididymis in the great majority of 4 years old and all older males. Our data from the 1963-1972 material, with a significant testes volume increase from the age of 4 years on, suggest a similar situation in this period. The testes volume data from 1990-1993, however, suggest a delay in sexual maturity age groups 6-9 years in males. This difference is also apparent in testes weights.

The methods used for determination of female sexual maturity are based on the assumptions that sexually mature female harp seals have a regular one year reproductive cycle, that only one ovum is released and only one corpus luteum is formed at conception every year, and that corpora persist as recognizable scar tissue

or corpora albicantia for at least three years after they are formed. Fairly strong evidence exist that these assumptions are met in case of harp seal females (Fisher 1954, Yakovenko & Nazarenko 1967, Øritsland 1971). The present observations for the period 1963-1972 is in relatively good agreement with previous studies, made in 1958-1964 by Yakovenko & Nazarenko (1967), who concluded that Barents Sea harp seal females attained maturity at ages between 3 and 7 years, usually at 4-5 years of age. The data from the two more recent periods indicate that age at maturity must have increased in females during the past 20 years. At present maturity is attained at ages between 4 and 11 years with a mean age of maturity of 8.1 years.

According to Laws (1956, 1959), most phocid seals attain sexual maturity at a rather constant proportion of adult body length. The present data, which suggest a declining trend in growth rate concurrent with an increase in age at maturity during the past 30 years, imply that Barents Sea harp seals follow these general patterns for phocid seals. The known increase in population size (Benjaminson 1979) and depletion of potential prey organisms (Anon. 1993) may have increased the competition for food and reduced the per capita food availability to such an extent that subsequent density dependent reactions have occurred in this population. The present data confirm that the slightly increasing trend in median age at maturity observed for Barents Sea harp seals in the early 1970s (Nazarenko 1975) and during the first half of the 1980s (Yablokov & Nazarenko 1986) has prevailed. In Northwest Atlantic harp seals, Bowen *et al.* (1981) observed density dependent reactions in age at maturity going in the opposite direction in that a reduction in population size were followed by a reduction in age at maturity. They concluded that an implication of the rather rapid change in median age at maturity could be that this parameter provide a useful indicator of harp seal population change. The present results seems to support this view.

In their studies of the declining Northwest Atlantic harp seal

population, Bowen et al. (1981) observed an increase in fertility rate from 1952 (85%) to 1979 (94%). Unfortunately, the present material include data on pregnancy rates only from the last period (1990-1993) when the overall rate of pregnancies observed in September and October, i.e. after the implantation has occurred, was 84%. However, the available material is quite restricted, and a larger sample, particularly of younger females, is necessary to document lowered pregnancy rates in females up to 15 years old. Observations made of potential near term females in February revealed that only 3 of 9 mature females (33%) carried a foetus. However, all seals available from February were taken in the East Ice, outside the main whelping grounds in the White Sea. This implies an overrepresentation of nonpregnant females which may have cancelled their annual visit to the White Sea breeding grounds simply because they were not pregnant. It is worth notice that some of these nonpregnant mature females appeared to have aborted some time before they were captured. A relatively low frequency of pregnancies in mature females has also been observed in harp seals invading the coast of North Norway in January-February in 1988-1990 (P. Aspholm, University of Oslo, Norway, pers. comm.). Information on temporal changes in fertility may presumably be obtained from future analyses of missing corpora as indicators of missed pregnancies (Øritsland 1971) in the samples presented in this study.

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from previous samples (project no. 4001-701.252).

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Table. 1. Summary of Barents Sea harp seal samples collected for reproductive studies in three periods between 1963 and 1993. For the 1990-1993 period each year of sampling is given in brackets for the separate sampling seasons. CS = commercial sealing; SE = scientific expedition; GN = gill net bycatches.

PERIOD	SEASON	AREA	SAMPLING TYPE	NUMBER OF	
				FEMALES	MALES
1963-1972	Mar-Apr	East Ice	CS	252	95
1976-1985	Mar-Apr	East Ice	CS	155	0
1990-1993	Feb(93)	East Ice	SE	50	52
	Mar-Apr(91)	East Ice	CS	58	62
	Mar-Apr(92)	East Ice	CS	79	37
	Mar-Apr(92)	Varangerfjord	GN	22	3
	Jun(91)	SE of Hopen	SE	131	64
	Sep(90)	E of Svalbard	SE	9	12
	Sep(91)	E of Svalbard	SE	17	23
	Oct(92)	E of Svalbard	SE	26	23
Total				799	371

Table 2. Asymptotic lengths (L_{∞}) and growth constants (b, k) obtained by a Gompertz growth model fitted to the Barents Sea harp seal length and age data from 1963-1972 and 1990-1993. r^2 are constants from regressions, and numbers in brackets indicate 95% confidence intervals.

L_{∞}	b	k	r^2
Males			
<u>1963-1972</u>			
174.1 (167.7-180.4)	0.40 (0.29-0.50)	0.28 (0.14-0.41)	0.92
<u>1990-1993</u>			
165.8 (156.4-175.1)	0.39 (0.26-0.51)	0.20 (0.05-0.35)	0.82
Females			
<u>1963-1972</u>			
172.5 (162.7-182.4)	0.37 (0.24-0.51)	0.24 (0.06-0.43)	0.84
<u>1990-1993</u>			
168.4 (162.7-173.9)	0.46 (0.38-0.54)	0.20 (0.13-0.27)	0.94

Tables 3-5. The distribution on age at sexual maturity (first ovulation) of female Barents Sea harp seals in combined samples collected in March-April in 1963-1972 and 1976-1985, and at different times of the year in 1990-1993.

Tab. 3 1963-72

Age at capture	No.	No. ovulating first time at age												Mature	
		1	2	3	4	5	6	7	8	9	10	11	12		
1	48														0
2	19														0
3	40		1												1
4	22			1											1
5	24			4	4										9
6	20			5	5	5									17
7	25			4	3	15	1								25
8	10			5	4										10
9	14			5	4		1	1							14
10	9			1	1	1	2	1							9
11	6			1	1	1	1								6
12	2														0
Sum total: 239															92
Sum first ov.			1	5	9	9	25	6	3	1					
Per cent			2	8	15	15	42	10	5	2					
Accum. per cent			2	10	25	41	83	93	98	100					

Tab. 4 1976-85

Age at capture	No.	No. ovulating first time at age												Mature	
		1	2	3	4	5	6	7	8	9	10	11	12		
1	10														0
2	4														0
3	4														0
4	5														0
5	8				1										1
6	12				2	4	1								7
7	20			1	1	3	14	1							20
8	29			1	2	12	11	2							28
9	18			2	2	4	6	5							17
10	8			1	1	1	4								6
11	6			1	1	1	1	2			1				6
12	3									2					2
Sum total: 127															87
Sum first ov.					3	7	27	18	11	2	2	1			
Per cent					4	10	38	25	15	3	3	1			
Accum. per cent					4	14	52	77	93	96	99	100			

Tab. 5 1990-93

Age at capture	No.	No. ovulating first time at age												Mature	
		1	2	3	4	5	6	7	8	9	10	11	12		
1	30														0
2	18														0
3	16														0
4	4														0
5	4														0
6	15				1										2
7	12				3	1									6
8	14				2	2									8
9	23				1	7	5								18
10	30				1	8	5	3							23
11	31				1	8	9	2	5						28
12	21									4	3				21
Sum total: 218															106
Sum first ov.					1	3	3	9	10	5	9	3			
Per cent					2	7	7	21	23	12	21	7			
Accum. per cent					2	9	16	37	60	72	93	100			

Table 6. Age specific pregnancy rates of female harp seals caught in the Barents Sea in September and October 1990-1992.

AGE GROUP	NO. OF FEMALES	IMMATURE	MATURE NONPREGNANT	MATURE PREGNANT	FRACTION(%) PREGNANT AMONG MATURE FEMALES
0	10	10			
1	2	2			
2	0				
3	0				
4	1	1			
5	0				
6	3	3			
7	1		1		0
8	0				
9	1		1		0
10	5		1	4	80
11	4			4	100
12	3			3	100
13	6			6	100
14	4		1	3	75
15	2		1	1	50
15+	6			6	100
Total	48	16	5	27	84

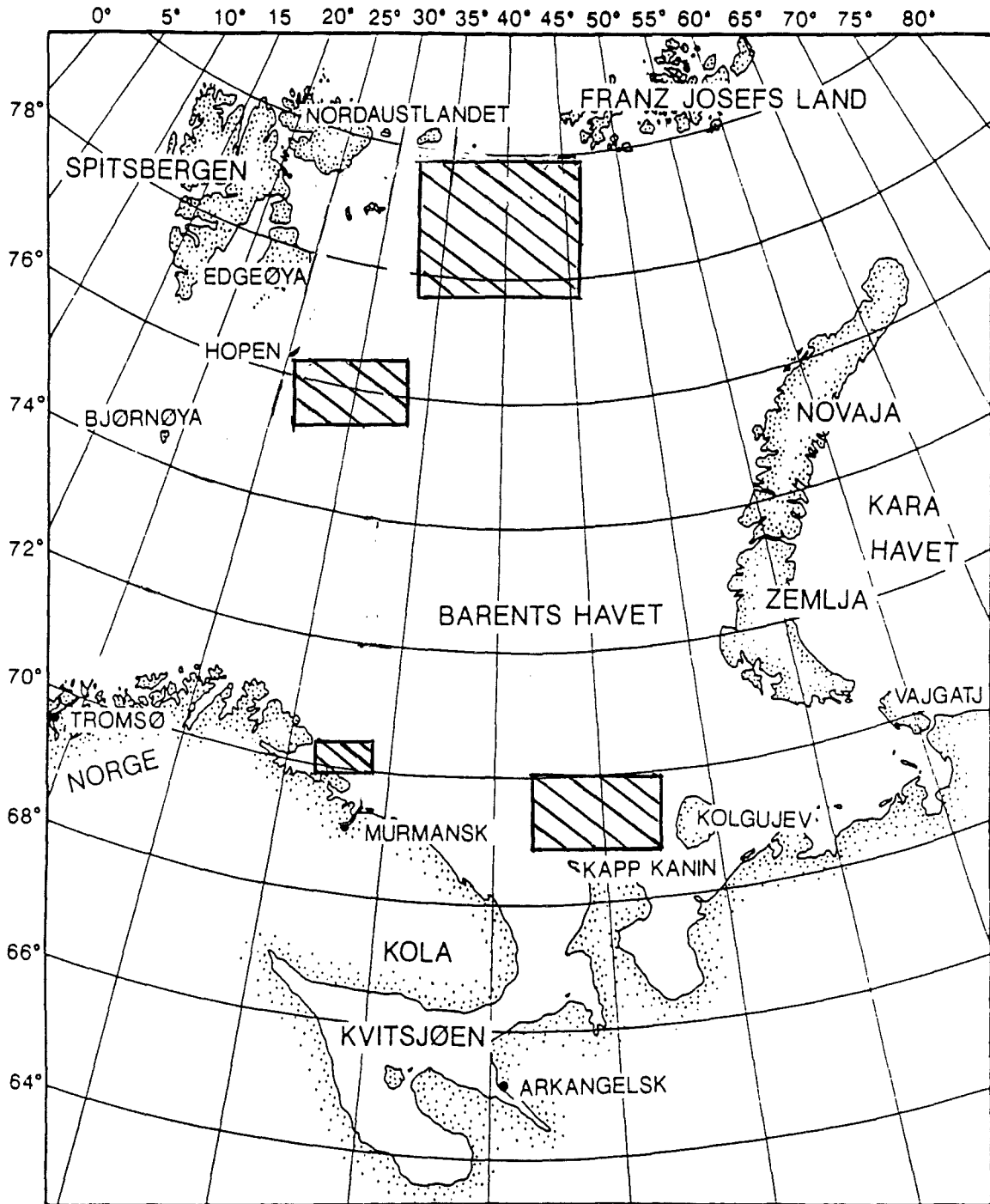


Fig. 1. Sampling sites where data were collected from harp seals in the Barents Sea, in the East Ice and on the coast of North Norway.

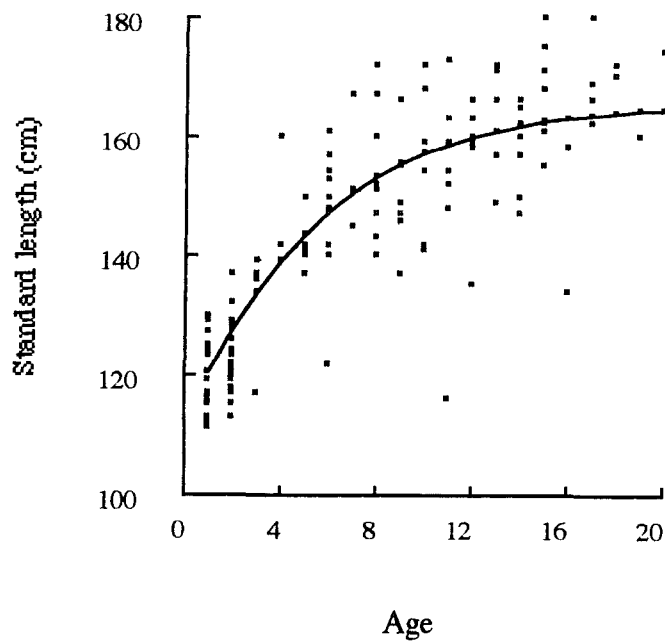
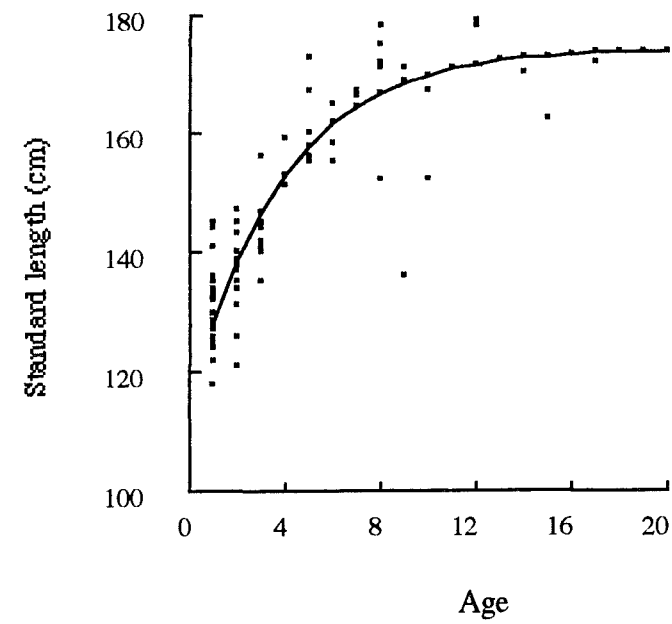


Fig. 2. Growth in length for male Barents Sea harp seals sampled during commercial sealing operations in 1963-1972 (above) and during commercial and scientific operations in 1990-1993 (below). The curves are fitted by a Gompertz growth model.

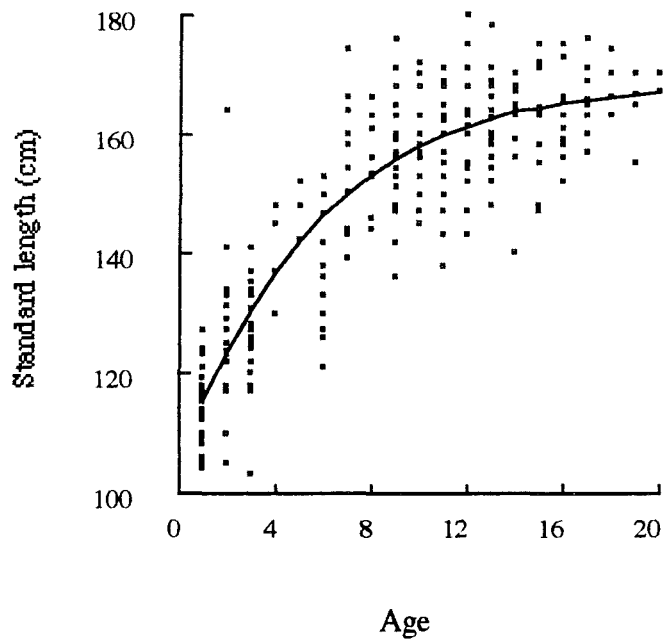
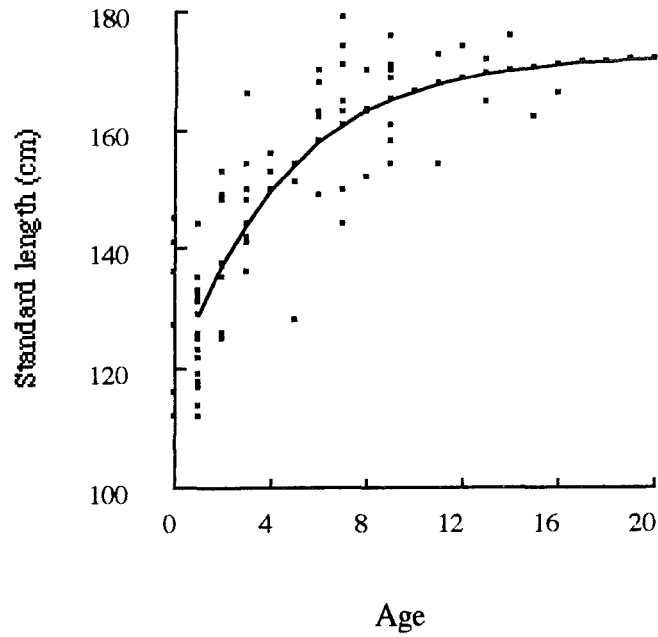


Fig. 3. Growth in length for female Barents Sea harp seals sampled during commercial sealing operations in 1963-1972 (above) and during commercial and scientific operations in 1990-1993 (below). The curves are fitted by a Gompertz growth model.

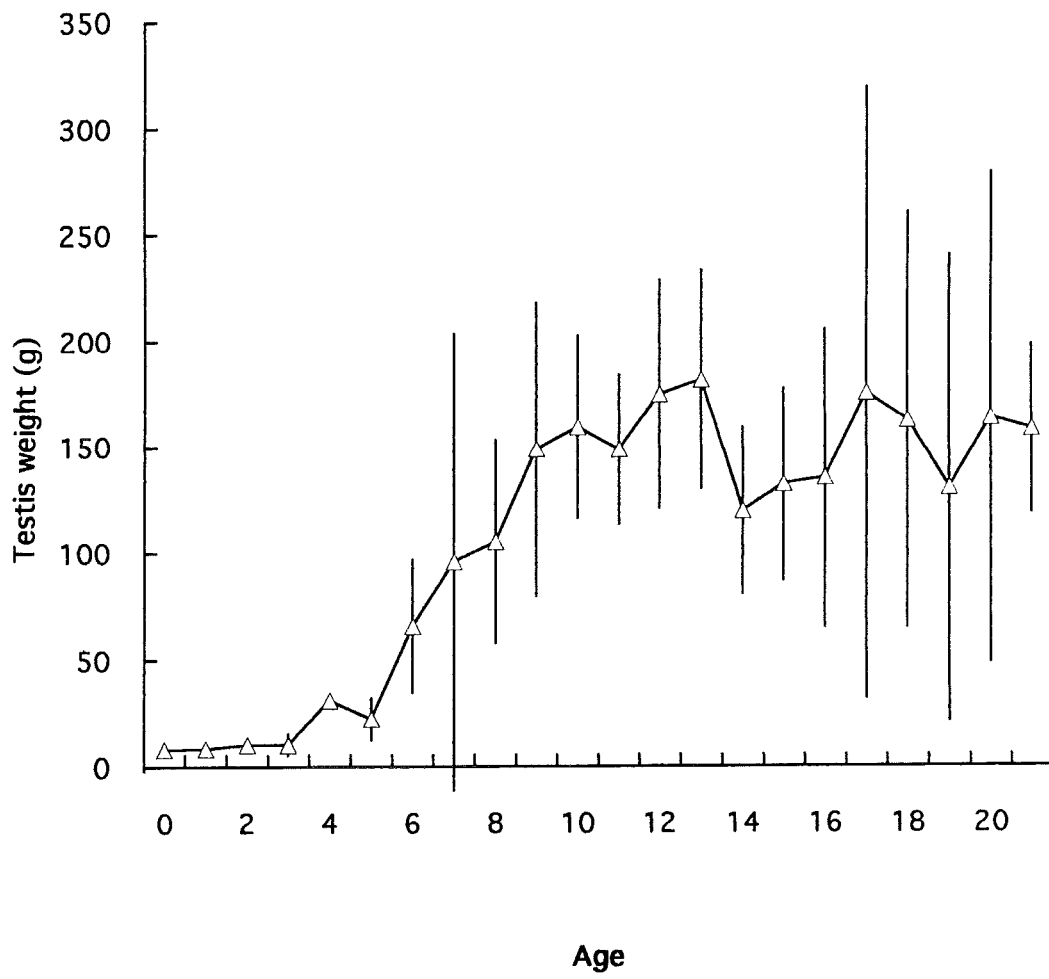


Fig. 4. Testes weights vs. age in male Barents Sea harp seals captured during commercial and scientific sealing operations in 1990-1993.

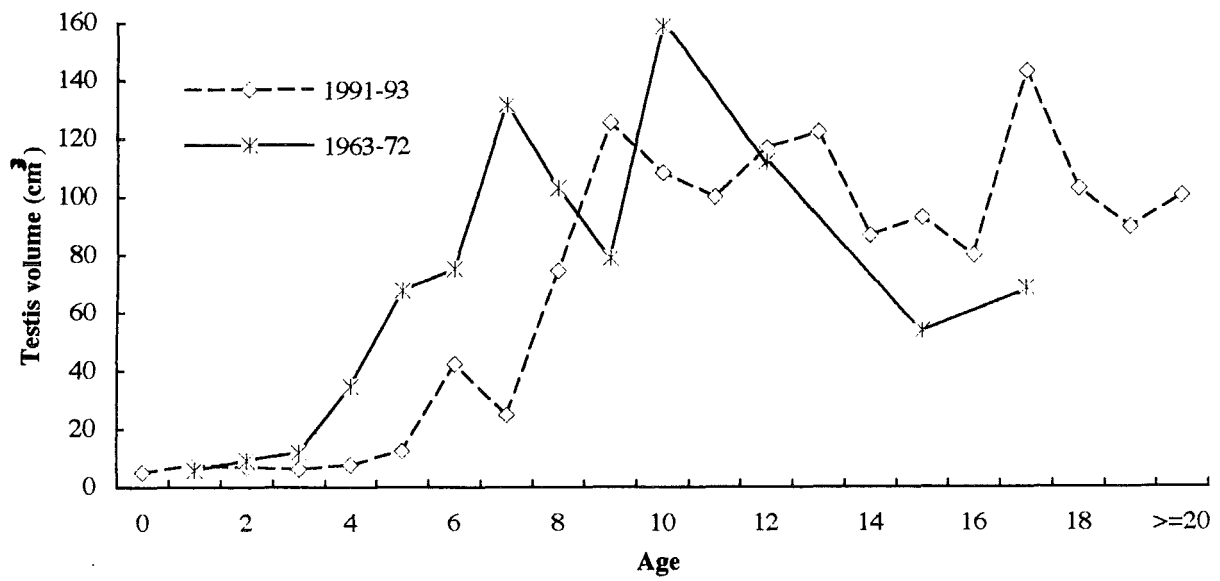


Fig. 5. Testes volumes vs. age in male Barents Sea harp seals captured during commercial sealing operations in 1963-1972 and during commercial and scientific sealing operations in 1990-1993.

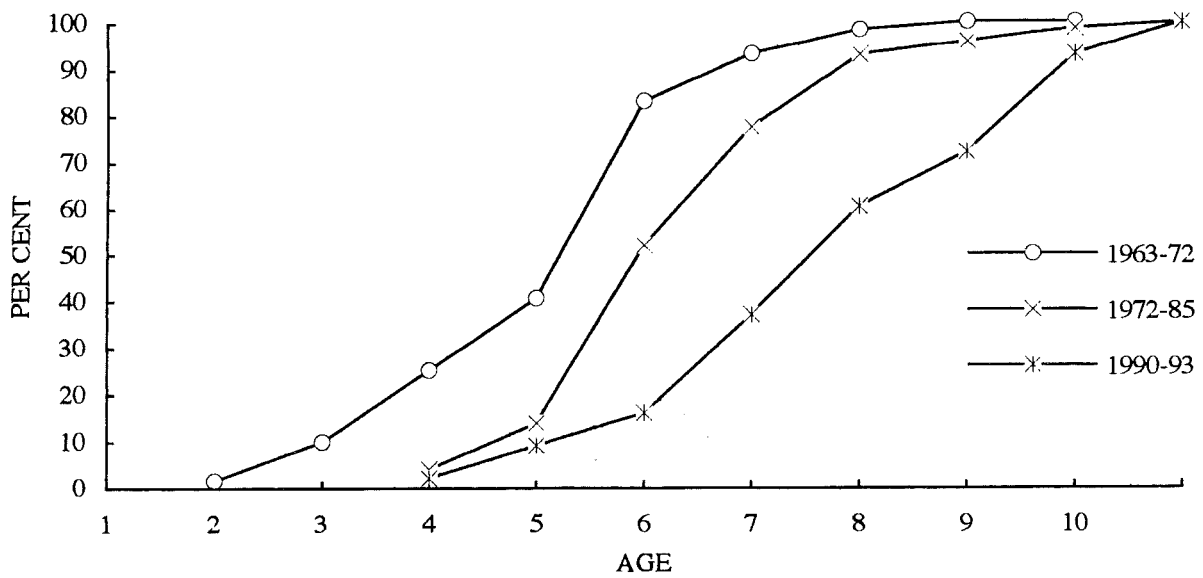


Fig. 6. Sexual maturity (age at first ovulation) of female Barents Sea harp seals. Accumulated frequencies are based on combined samples collected in 1963-1972, 1973-1985 and 1990-1993.