Grey seal (*Halichoerus grypus*) from the Northwest Atlantic: female reproductive rates, age at first birth, and age of maturity in males

M.O. Hammill and J.F. Gosselin

Abstract: Mean age at first birth and reproductive rates were examined in a sample of 526 female grey seal (*Halichoerus grypus*) reproductive tracts collected between 1968 and 1992. Age of first birth determined from reproductive tracts with a fetus was 5.5 ± 0.12 yr (mean ± SD). No trend over time was observed in mean age at first birth or in pregnancy rates. Pregnancy rates determined from reproductive tracts containing a fetus were 0.18, 0.86, and 0.88 for animals aged 4+, 5+, and >6+ yr, respectively. Pregnancy rates calculated from the presence of a corpus luteum were 0.01, 0.45, 0.9, and 1 for ages 3+, 4+, 5+, and >6+, respectively. Mean age of sexual maturity of males was 5.6 yr as estimated from changes in testes mass in a sample of 89 seals collected during August–September 1992. A marked increase in testes mass was observed among animals aged 3+ yr. By age 7+ yr, virtually all males had attained sexual maturity.

Résumé : L'âge moyen à la première parturition et les taux de gestation furent examinés pour un échantillon de 526 systèmes reproducteurs de femelles de phoque gris (*Halichoerus grypus*) ramassées entre 1968 et 1992. L'âge moyen de première parturition, déterminé par la présence d'un foetus dans l'utérus, était de 5,5 ± 0,12 ans (moyenne ± écart-type). Aucune tendance de l'âge moyen à la première parturition ou des taux de gestation n'a été observée avec le temps. Les taux de gestation, déterminés par les systèmes reproducteurs contenant un foetus, étaient respectivement de 0,18, 0,86 et 0,88 pour les animaux de 4+, 5+ et de plus de 6 ans. Les taux de gestation, calculés à partir de la présence d'un corpus luteum, étaient respectivement de 0,01, 0,45, 0,9 et 1 pour les âges 3+, 4+, 5+ et plus de 6 ans. L'âge moyen de maturité sexuelle de 5,6 ans fut déterminé à partir des changements de poids des testicules pour un échantillon de 89 mâles ramassés pendant août et septembre 1992. Un accroissement marqué des poids des testicules fut observé chez les animaux de 3+ ans, et à partir de 7+ ans, pratiquement tous les mâles avaient atteint la maturité sexuelle.

Introduction

Mammalian populations often exhibit changes in reproductive parameters following marked changes in population size (e.g., Bowen et al. 1981). These changes often manifested as changes in mean age of sexual maturity and age-specific reproductive rates are thought to reflect density-dependent changes in response to the availability of resources.

Grey seals (*Halichoerus grypus*) are found along the Atlantic coasts of Canada and northeastern United States. Although apparently abundant prior to the mid-1800s, extensive hunting reduced their numbers in the Gulf of St. Lawrence and along the Nova Scotia coast (Lavigueur and Hammill 1993). Little is known concerning their numbers early in the century but during the 1960s the population was estimated to be around 19 000 animals (Zwanenburg and Bowen 1990). From 1978 to 1990, a bounty was paid to licensed fishermen who submitted lower jaws from grey seals along with information on date and location of capture. In addition, between 1967 and 1984, seals in the Gulf of St. Lawrence and along the eastern shore of Nova Scotia were subject to a government-sponsored cull during the December–February breeding season (Zwanenburg and Bowen 1990). Despite this hunting pressure the grey seal population in Atlantic Canada increased to around 143 000 in 1993 (Mohn and Bowen 1994). This rapid population growth has been accompanied by concerns that grey seals may be having a negative impact on the commercial fishing industry (Malouf 1986).

In Canada, two major groups of grey seals are recognized. The largest group whelps on Sable Island located in the Atlantic Ocean 160 km east of Nova Scotia, while the second whelps on the pack ice in the Gulf of St. Lawrence. Smaller rookeries are located along the eastern shore of Nova Scotia, and on Deadman Island and Amet Island in the Gulf of St. Lawrence. Although seals from both groups mix extensively

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M.O. Hammill and J.F. Gosselin. Maurice Lamontagne Institute, Department of Fisheries and Oceans, P.O. Box 1000, Mont-Joli, QC G5H 3Z4, Canada.

Table 1. Total number (*N*) of female grey seals collected between 1968 and 1992 and numbers of those showing presence of a corpus luteum (CL) or a fetus.

Sampling period		Age (yr)									
		2	3	4	5	6	7	8	9	10	>11
1968–1970	*N*	20	12	7	9	6	6	4	4	2	20
	CL	0	7	7	9	6	6	4	4	2	20
	Fetus	0	3	5	9	6	6	4	4	1	14
1982	*N*	7	4	4	8	1	4	3	3	3	35
	CL	0	2	4	8	1	4	3	3	3	35
	Fetus	0	0	3	7	1	3	3	3	3	31
1986	*N*	16	4	2	4	7	4	3	4	0	23
	CL	0	2	2	4	7	4	3	4	0	23
	Fetus	0	0	2	3	6	4	3	3	0	22
1987	*N*	5	7	10	8	9	6	8	3	5	49
	CL	1	4	10	8	9	6	8	3	5	49
	Fetus	0	1	5	5	6	6	8	2	4	47
1988	*N*	3	4	10	9	3	2	3	1	3	38
	CL	0	4	8	9	3	2	3	1	3	38
	Fetus	0	2	7	8	2	2	2	1	3	35
1992	*N*	24	16	16	15	5	1	4	—	3	26
	CL	0	2	13	15	5	1	4	—	3	26
	Fetus	0	1	12	13	4	1	4	—	2	25

Note: —, data not available.

throughout most of the year, the amount of interchange during the breeding season is low (Stobo et al. 1990; Zwanenburg and Bowen 1990; Lavigueur and Hammill 1993).

Mansfield and Beck (1977) examined reproductive rates in a sample of female grey seals collected between 1968 and 1970 from the eastern shore of Nova Scotia. Given the changes that have occurred in the population since the 1970s, a re-examination of reproductive parameters is warranted. Here we examine age of first reproduction and age-specific reproductive rates in females, and age of sexual maturity of male grey seals collected mainly in the Gulf of St. Lawrence.

Materials and methods

Females

Reproductive tracts and lower jaws from females aged >1 yr were collected by trained hunters and fishers from the eastern shore of Nova Scotia, during May–November 1968–1970 (total number of females in sample (*N*) was 90). Some of this material was used by Mansfield and Beck (1977). Samples were also obtained from Anticosti Island during June–September 1982, 1986, 1987, 1988, and 1992 ($N = 436$). In the Northwest Atlantic population, implantation may occur as early as April, resulting in some recognizable embryos by early June (Mansfield 1978). For this analysis, all specimens obtained between the breeding season and late June, the period during which the presence or absence of embryos is difficult to determine, have been excluded. Samples collected during 1968–1970 are assumed to consist primarily of animals born on the eastern shore or on Sable Island. Because little marking of animals was undertaken at this time, it was not possible to verify an animal's origin. Between 1977 and 1990, all pups born on Sable Island were marked in the hind flipper with a uniquely coded tag (Stobo et al. 1990). In samples collected from Anticosti Island, the origin of some animals could be determined. Sable Island animals were recovered as follows: in 1982, $N = 3$; 1986, $N = 1$; 1987, $N = 7$; 1988, $N = 3$; 1992, $N = 4$. These animals have been included with the 1982–1992 samples. Animals without tags collected from Anticosti Island were assumed to consist primarily of animals of Gulf origin.

Female reproductive status was determined from whole reproductive tracts preserved in 10% formalin. In the 1968–1970 samples, the presence of an embryo or fetus was noted and only the ovaries were collected. Ovaries were cut into transverse slices 2–3 mm thick, and examined macroscopically for corpora lutea. Ovaries in which a corpus luteum was present were considered as evidence that females were pregnant. Pregnancy was also determined by the presence or absence of a fetus.

Males

In the 1992 sample from Anticosti Island, testes from male grey seals were collected and preserved in 10% formalin. Both testes were weighed without the epidydimides, and a mean testes mass was determined for each animal.

The age of individual seals was determined from longitudinal sections of a lower canine tooth (Mansfield 1991). Teeth were read at least twice. When disagreement occurred between two readings, the tooth was read a third time. If two of the three readings were the same, that age was assigned to the tooth. If ages did not agree, the mean of the three readings was taken.

Table 2. Proportion of pregnant females aged >4+ yr in samples collected from Anticosti Island in 1988 and 1992.

Sampling period	Number pregnant (n)	Total sample (N)	Percent pregnant
1–14 June	16	27	59
15–30 June	9	11	82
1–14 July	23	26	88
15–31 July	30	32	94
1–14 Aug.	17	19	89
15–31 Aug.	17	19	89
1–15 Sept.	14	15	93

Reproductive rate was defined as the percentage of mature females in each age-class that were pregnant. To estimate the age at first birth, age was increased to the age females would have at the time of the subsequent pupping period (January). Mean age at first birth was estimated as follows. The proportion (p) of females that were pregnant by age a in any given year t was $p_{a,t} = n_{a,t}/N_{a,t}$, where n is the number of females with a corpus luteum or a fetus. The probability of being pregnant for the first time at age a in year t is $f_{a,t} = p_{a,t} - p_{a-1,t}$, which was modified after Trites and York (1993), where $p_{a-1,t-1}$ was replaced by $p_{a-1,t}$. The average age at first birth and variance were then calculated by bootstrapping (Efron 1982) with replacement. For example, for each age-class having k_a pregnant and nonpregnant individuals, k draws with replacement were made at random from this pool and the mean age for the total sample collected in that year was then calculated as $x = \sum_{a=2}^{w} a(f_{a,t})/\sum_{a=2}^{w} f_{a,t}$, where w is the minimum age where $p(a) = 1.0$ (Trites and York 1993). The process was repeated 500 times, and the mean age at first birth and variance of x were estimated. Mean age of sexual maturity of males was estimated using the algorithm developed for marine mammal populations by DeMaster (1978). Differences between samples in reproductive rates were examined using a chi-square test for independence (Siegel 1956). Changes in mean age of first birth over time were examined using the SAS REG procedure (SAS Institute Inc. 1987). Changes in testes mass with age were described using a Gompertz curve (Hammill et al. 1995), fitted using the multivariate secant method in procedure NLIN (SAS Institute Inc. 1987).

Results

Females

Corpora lutea were first observed in animals aged 2+ yr, but there were no indications of pregnancy before age 3+ yr (January age 4 yr) (Table 1). Of 506 females examined, 344 were pregnant, of which 5 bore evidence of twin fetuses. In one female aged 40+ yr, the uterine horns were sclerotic suggesting that she was no longer fertile.

The percentage of females aged >4 yr with a corpus luteum and a fetus increased from 59% during the first 2-week period in June to 82% during the last 2-week period, but the differences were not statistically significant. During the remaining months (July–September) the fraction of reproductive tracts with both a corpus luteum and a fetus present remained constant between 88 and 94% (Table 2).

Table 3. Age at first birth in Northwest Atlantic grey seals.

Sampling period	Sample size	Mean age from corpora lutea	Mean age from fetus
1968–1970	90	4.42±0.14	5.03±0.22
1982	72	4.48±0.24	5.39±0.24
1986	67	4.49±0.24	5.40±0.25
1987	110	3.61±0.76	6.08±0.32
1988	76	4.19±0.12	5.22±0.42
1992	110	5.06±0.12	5.52±0.24

Note: Values are given as mean ± standard deviation.

The mean age of first birth, calculated using the presence of a corpus luteum to indicate pregnancy and using female age at the time of pupping during the subsequent January, ranged from 3.6 to 5.1 yr (Table 3). The regression of mean age of first birth against year was not significant ($P = 0.47$), indicating no change in mean age at first birth over time. Consequently, the data were pooled resulting in an age at first birth of 4.6 ± 0.10 yr (mean ± SD). The mean age of first birth calculated from reproductive tracts with a fetus varied between 5.0 and 6.1 yr (Table 3). The regression of mean age of first birth against year was not significant ($P = 0.32$) indicating no change in mean age at first birth over time. Consequently, the data were pooled, resulting in a mean age at first birth of 5.5 ± 0.12 yr.

No differences in pregnancy rates were observed between years ($\chi^2 > 0.05$). Similarly, a weighted linear least squares regression of adult pregnancy rates (January age >5 yr) against year, with weight inversely proportional to variance, did not show any linear trend over time in pregnancy rates ($P = 0.46$; Table 3). There was no indication that pregnancy rates declined with age (Fig. 1). Pregnancy rates appeared to be more variable in older animals (>20 yr), but this may also be a function of smaller sample sizes among older animals. Pooling of the data resulted in pregnancy rates, as indicated by the presence of a fetus, of 0.176, 0.861, and 0.875 for animals aged 4, 5, and >6 yr at the time of birth, respectively. Pregnancy rates calculated from the presence of a corpus luteum were 0.01, 0.447, 0.898, and 1 for ages 3, 4, 5, and >6 yr at the time of birth, respectively.

Males

Testes mass was obtained from 89 males collected during August–September 1992. Little difference was observed in weights between young of the year, yearlings, and animals aged 2+ yr (Fig. 2). A marked increase in testes mass compared with younger animals was observed among animals aged 3+ yr, with testes mass ranging from 11 to 71.8 g. The change in testes mass with age was described by fitting a Gompertz curve to the data. The coefficient of variation about the fitted line was 16%. Testes mass

Fig. 1. Age-specific pregnancy rates of female grey seals calculated using the presence of a fetus. Numbers above the columns represent the number of animals in the sample.

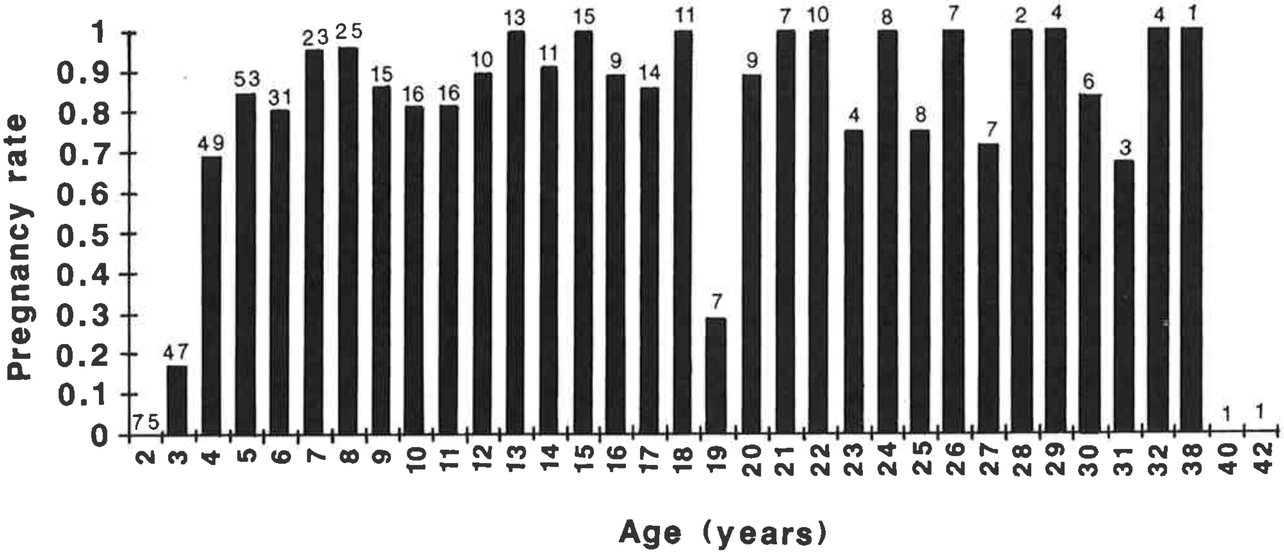
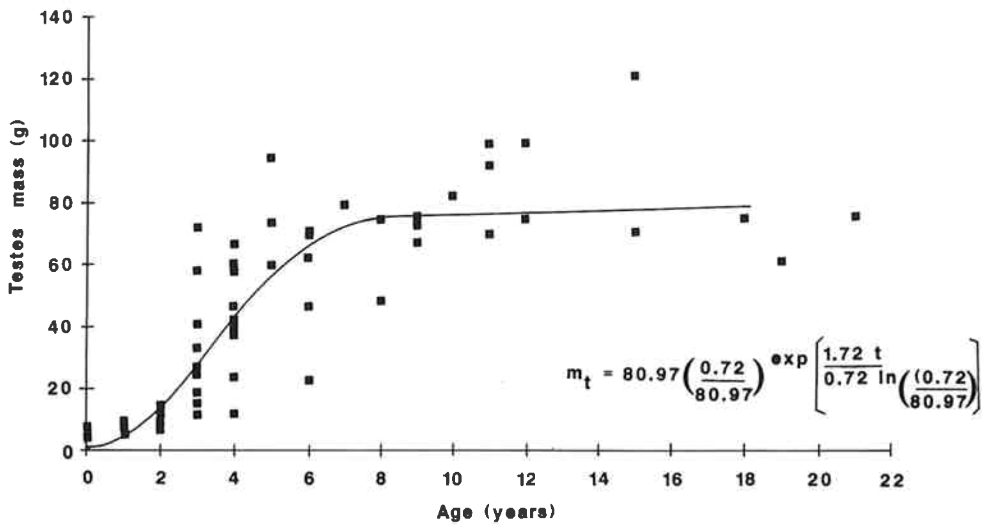


Fig. 2. Gompertz growth curve fitted to testes mass (g) of grey seals.



reached an asymptotic mass of 80 g by age 7+ yr. Using a minimum testes mass of 60 g as an indication of sexual maturity (Hewer 1964), the average age of sexual maturity was estimated to be 5.6 yr. By age 7+ yr virtually all males had testes mass >60 g.

Discussion

With few exceptions, grey seals give birth to a single young. Pregnancies initially occur at age 3+ yr and continue at a high rate from age 5+ to 30+ yr. In this study, adult pregnancy rates for animals aged >5+ yr were 1.0 and 0.875 depending on whether estimates were obtained using the presence of a corpus luteum or a fetus to indicate pregnancy. Estimates based on the presence of a corpus luteum may overestimate pregnancy rates owing to early mortality of the embryo. Alternatively, our estimates using the fetus to indicate pregnancy may underestimate the true pregnancy rate, owing to the spread in implantation dates, which may extend into June (Mansfield 1978). However, our estimates of pregnancy rates are similar to high rates of 0.896 observed for a sample of female grey seals (aged >5+ yr) from the Hebrides and Farne Islands (Boyd 1985).

The Northwest Atlantic grey seal population has increased roughly sevenfold since the 1960s. In spite of this rapid population growth our data do not show any indication of changes in mean age at first birth or in reproductive rates that would be expected if density dependent changes in these parameters were occurring. In fact, recent surveys to estimate pup production on Sable Island indicate that this component of the population continues to increase at an annual rate of approximately 13% (W. Stobo, unpublished data; in Mohn and Bowen 1994).

Although there is much less certainty surrounding the Gulf component of the population, it appears to be increasing at a rate of approximately 9% per year (Mohn and

Bowen 1994). Reasons for the different trajectories between the two groups are unclear. In our samples, we did not observe any differences in mean age at first birth or pregnancy rates between a sample consisting largely of Sable Island animals collected between 1968 and 1970 and samples consisting largely of Gulf animals obtained from Anticosti Island (1982–1992). Because there is considerable overlap in distribution between the two groups outside of the January–February whelping period (Stobo et al. 1990; Lavigueur and Hammill 1993), it is possible that the differences in population trajectories result from higher first-year mortality rates of animals born on the unstable pack ice in the Gulf (Zwanenburg and Bowen 1990).

As in females, the male reproductive system also undergoes seasonal changes with a significant reduction in size of the testes occurring during the summer months, particularly in August (Mansfield 1978). Such changes limit comparisons to samples collected during a similar period in the reproductive cycle. Rapid changes in testes mass first occurred in males aged 3+ yr suggesting the onset of sexual maturity during the animal's fourth year and a mean age of sexual maturity of 5.6 yr. Hewer (1964) observed similar changes in testes mass and os penis mass/length ratios in a sample of male grey seals collected outside of the breeding season and suggested that the majority of males were sexually mature by age 5+ yr. In the Northwest Atlantic, there is no evidence of spermatogenesis in males aged 3+ yr collected during the breeding season from Sable Island (Mansfield 1978). In the same sample, active sperm production was observed in five of six males aged 4+ yr, and all animals aged >5+ yr were sexually mature. However, this sample may underestimate the age at which all males are sexually mature, as immature animals may be less likely to be present in the breeding colony. Although virtually all males may be sexually mature by 8+ yr, these animals appear to be limited to the periphery of the breeding colony (Hewer 1964), occasionally succeeding in copulating with females as transient males (Godsell 1991). On Sable Island, few animals are capable of maintaining tenure among whelping females before the age of 11 to 12 yr (Boness and James 1979; Godsell 1991).

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