NOT TO BE CITED WITHOUT PRIOR
REFERENCE TO THE AUTHOR(S)

Northwest Atlantic Fisheries Organization

Serial No. N012 NAFO/SCR Doc. 79/XI/1

SPECIAL MEETING OF SCIENTIFIC COUNCIL - NOVEMBER 1979

Changes in harp seal reproductive parameters: another look

by

W. D. Bowen
Northwest Atlantic Fisheries Center
Department of Fisheries and Oceans
St. John's, Newfoundland

Animal populations often exhibit changes in reproductive parameters following marked fluctuations in population size. Two of these parameters, fertility rate and mean age of sexual maturity are of particular interest with respect to the management of Northwest Atlantic harp seals, *Pagophilus groenlandicus*.

A period of heavy commercial exploitation reduced 1+ population size of harp seals in the Northwest Atlantic from about 2.4 x 10^6 individuals in 1952 to an estimated 1.1 x 10^6 individuals in the early 1970's (Lett *et al*., 1978; Winters 1978). These same analyses suggest that since the introduction of quotas in 1972, population size has stabilized and may be slowly increasing. Thus, over a period of 20 years, population size was reduced by 50% or more. Fortunately, biological sampling of female harp seal reproductive tracts began in 1951 and has continued to the present. Thus it is possible to follow changes in reproductive parameters as the population has declined in numbers.

Sergeant (1978, 1976, 1973, 1966) concluded that mean age of whelping of female harp seals has declined currently with population size, but that fertility rate of older (age 8+) females has not changed. Lett and Benjaminsen (1977) and Lett *et al*. (1978) have argued that both of these parameters have changed with changing density. Winters (1978) agreed with Sergeant claiming that mean age of whelping alone was density dependent. Both authors argued (pers. comm.) that the Lett analysis was an artifact resulting from the indiscriminate combination of early- and late-pregnancy rates. This introduces a bias since early-term pregnancy rates are always equal to or greater than late-term pregnancy rates.

On reviewing the literature, I found sufficient confusion and misinterpretation of the data to warrant a more critical analysis. I conclude that both mean age of sexual maturity and fertility rate have changed significantly over the period 1950-79, but that the data are insufficient to enable us to determine the exact pattern of change over time. Further, both parameters have changed concurrently with a decline in population size and although it is likely that density-dependent mechanisms are responsible for these changes, empirical data are lacking.

Materials and Methods

The analysis is based on female reproductive tracts and jaws collected during the spring (late March-April) or winter period (January-February) at various times from 1951 to 1979. These samples, their origin and author source are given in Appendices A and B. Excepting the 1979 winter and spring samples which I collected and analyzed, data used in the analyses are those presented by Sergeant and Fisher (see Appendices A and B) and Øritsland (1971).

In all samples, age is determined to the nearest year by the method of counting dentine annuli described by Fisher (1954). For samples taken in April this is actual age less one month, whereas for January-February samples this is actual age plus 1 or 2 months.

Reproductive condition of females is assessed based on examination of serially sectioned ovaries and where possible of the uterus. Immature females have small ovaries containing only small inactive follicles and no corpus luteum or corpus albicans. The ovaries of mature females samples in April contain an incompletely-luteinized corpus luteum or at least one corpus albicans in which case the female would be mature but not pregnant. In January samples, the corpus luteum will be larger and fully luteinized if the female is pregnant or will have begun to degenerate if pregnancy was missed or the fetus aborted.

I define fertility rate as the percentage of mature females that are pregnant at the time of the sample. Because the female harp seal delays implantation of the blastocyst for approximately three months, this parameter is easily measured only after implantation has occurred; that is in winter samples. April samples will estimate ovulation rate as the percentage of mature females that have ovulated at the time of the sample. Thus, January and April samples should not be directly compared.

Mean age of sexual maturity was determined using the algorithm of DeMaster (1978) as follows:

$$f(x) = t(x)/n(x) \qquad (1)$$

where x = age of female, f(x) = estimated probability of ovulating at or before age x, t(x) = number of females of age x in sample which have ovulated, and n(x) = number of females age x in sample. Thus estimated probability of first ovulating at age x is

$$P(x) = f(x) - f(x-1) \qquad (2)$$

The average age of sexual maturity is then

$$\bar{x} = \sum_{x=1}^{w} (x)\, P(x) \qquad (3)$$

where $\bar{x}$ = average age of sexual maturity and w = maximum age in sample. The estimated variance for $\bar{x}$ is

$$v(\bar{x}) = \sum_{x=1}^{w-1} \frac{f(x)(1-f(x))}{n_x - 1} + \frac{w^2 f(w)(1-f(w))}{f(w)-1} \qquad (4)$$

This estimate assumes that all of the f(x)'s are independent of each other. The 95% confidence intervals can be approximated by

$$95\%\ CI = \bar{x} \pm 1.96(v(\bar{x}))^{\frac{1}{2}} \qquad (5)$$

To obtain mean age of whelping, one year must be added to the values in Fig. 1 and 3 and Appendix C.

Results

Age of maturity

There is a significant linear regression ($F_{1,5} = 21.20$, $P < 0.01$) of mean age of sexual maturity of females sampled in April on time (Fig. 1a). Mean age of sexual maturity declined from approximately 6.0 years in the early 1950's to 4.5 years in 1979 (see Appendix C for estimates of variance and 95% CI of means). The trend in mean age of sexual maturity in January samples (Fig. 1b) agrees with the April data with the exception of the 1951-54 sample collected by Fisher (1954). I believe this point should be regarded as sampling error as there were only 6 individuals of ages 5 and 6 in the sample. These are critical ages in determining age of maturity; thus a change in the reproductive status of a single female would markedly alter the mean estimate. The uncertainty associated with the 1951-54 estimate is reflected by the wide confidence intervals. Note also that the approximation given by DeMaster (1978) appears to underestimate true confidence limits at small sample sizes.

Several authors have suggested that the change in mean age of maturity is density dependent (Sergeant, 1973, 1966; Lett and Benjaminsen, 1977; Winters, 1978). To investigate this, mean age of sexual maturity was plotted against 1+ population size lagged 5 years as suggested by Lett et al. (1978) (Fig. 2). I found a significant linear regression of mean age of sexual maturity, SM, on 1+ population size lagged 5 years ($F_{1,5} = 24.00$, $P < 0.005$)(Fig. 3a). The regression equation is

$$\bar{SM} = 3.65 + 0.86\ POP_{t-5} \qquad (6)$$

Population size $_{t-5}$ explained 82% of the variation in mean age of sexual maturity as estimated from April samples.

In January samples, a change in mean age of sexual maturity with decreasing population size is also evident (Fig. 3b). If we omit the 1951-54 point for reasons given above, there is a marked decrease in $\bar{SM}$ from the middle 1960's to the late 1970's. The decrease in $\bar{SM}$ during this period agrees with the pattern shown in April samples.

Ovulation and fertility rate

I calculated ovulation rates from April samples of moulting females. Yearly estimates are given in Appendix B. There is no relationship between ovulation rate and 2+ population size (Fig. 4a). Mean ovulation rate during the period 1952 to 1979 was 98.5 ± 1.59 ($\bar{x}$ ± s).

I estimated fertility rates from January-February samples of southward migrating females captured in nets along the north shore of Quebec and near St. Anthony, Newfoundland (Appendix A). I omitted the 1964 point of Sergeant (1966) from the analysis for two reasons. First, the estimate was based on a small sample (n = 33 mature females). Second, a larger sample (n = 104) taken by Øritsland (1971) in March 1964 on the Front provided an estimate of 91.6%. Given that the 1965 estimate of 92.6% (n = 161 mature females) is based on a large sample, it is more likely that the fertility rate in 1964 was 91.6% and not 81.8%. Prior to regressing fertility rate on 2+ population size in the previous year, I normalized the percentages with the angular transformation (Sokal and Rohlf, 1969). Using these transformed data, the regression of fertility rate on 2+ population size was significant ($F_{1,9}$ = 9.34, P < 0.025) (Fig. 4b). Fertility rate increased from about 85% in the early 1950's at a 2+ population size of 2.2 x 10^6 individuals to 97% in the late 1960's at a 2+ population size of 0.8 to 1.0 x 10^6 individuals (estimates from the regression line). From 1969 to 1979, mean fertility rate was 95.0 ± 1.24% ($\bar{x}$ ± s, n = 4).

Discussion

Age of maturity

Several authors have concluded that change in mean age of sexual maturity of female harp seals is density dependent (Winters, 1978; Lett et al., 1978; Lett and Benjaminsen, 1977; Sergeant, 1973, 1976). It is clear from the present analysis that mean age of sexual maturity has declined during the period 1950 to 1979. Moreover, there is a strong correlation of mean age of sexual maturity and 1+ population size lagged 5 years (Lett et al., 1978; this study). On theoretical grounds we expect changes in mean age or sexual maturity to be density dependent. Sexual maturity in the Phocidae is attained at a rather constant proportion of adult body size (≈ 87%) and reached earlier when growth is increased (Laws, 1956, 1959). Thus, if other conditions remain constant, a reduction in population size may lessen competition for food and allow females to grow more rapidly. However, the extent to which this has occurred in the harp seal population is still uncertain.

Ovulation and fertility rates

Confusion regarding the density-dependent nature of fertility rates appears to have resulted for two reasons. Sergeant (1978, 1966) concluded that there has been no change in the fertility rate of older females (age 8+) from 1951 to the present. In fact, this is true. However, the true population fertility rate should include all mature females regardless of their age. When this is done, it is clearly evident that fertility rate has increased (Fig. 4b). The second source of confusion arose out of the indiscriminate combination of ovulation and fertility rates and the use of an incomplete data set by Lett et al. (1978). This resulted in a fortuitous relationship between fertility rate and population size. The conclusion of Winters (1978: p. 1258, Fig. 7) that there is no relationship between fertility rate and population size is also in error.

Whereas, fertility rate has increased with a reduction in population size, ovulation rate has not changed. The energetics of reproduction may explain this difference. It costs a female relatively little to produce a mature ovum and ovulate. However, once implantation of the blastocyst has occurred, the energetic demand of pregnancy will rapidly increase as the embryo increases in size. Thus the "decision" whether to bear young or not will probably be made at or shortly after implantation. As population size is reduced, females might be expected to be in better nutritional condition and therefore be less likely to abort the pregnancy. This would result in an increase in fertility.

The proposed density-dependent changes in mean age of sexual maturity and fertility rate rely heavily on the meagre data in the early 1950's. This is unfortunate for as Rivard (1978) has pointed out, our understanding of these relationships is unlikely to improve substantially until population size has once again reached a high level. Under the policy ensuring 5% annual increase in the 2+ population size this would not occur until the 1990-1999 period. Note that given our present knowledge of the population, a 5% increase would seem overly optimistic. Rivard's (1978) analysis clearly indicates that additional collections of reproductive samples in the near future will not reduce substantially the uncertainties associated with these density-dependent relationships. Thus I suggest that future sampling be carried out at three-year intervals until such time as significant changes are detected. This will allow more active pursuit of studies on growth patterns and the mechanisms responsible for changes in body growth (Lavigne et al., MS 1979). This research is particularly important given the close relationship between body size and age of maturity in harp and other seals (Laws, 1959, 1956.

Acknowledgements

I would like to thank Dr. D. E. Sergeant for allowing me access to unpublished data and for many informative conversations about harp seal reproduction. Dr. G. Winters provided the needed administrative and technical support during this our first year of operation. I am grateful to Messrs. Thomas Noel, Wayne Penney and Morris Clark for the collection and preparation of reproductive samples and teeth for analysis. Gary Somerton programmed the DeMaster algorithm which calculates mean age of sexual maturity.

Literature Cited

DeMaster, D. P. 1978. Calculation of the average age of sexual maturity in marine mammals. J. Fish. Res. Board Can., 35: 912-915.

Fisher, H. D. 1954. Studies on reproduction in the Harp Seal, Phoca groenlandica Erxleben in the Northwest Atlantic. Ph.D. Thesis, McGill Univ. 109 pp.

_____ 1952. Age determination and sexual maturity in the Harp Seal, Fish. Res. Board Can., Rep. Atl. Biol. Stn., Appl. No. 83, pp. 136-140.

Laws, R. M. 1959. Accelerated growth in seals, with special reference to the Phocidae. Norsk Hvalf.-Tid., 48: 425-452.

_____ 1956. Growth and sexual maturity in aquatic mammals. Nature 178: 193-194.

Lett, P. F., R. K. Mohn and D. F. Gray. 1978. Density-dependent processes and management strategy for the Northwestern Atlantic Harp Seal. ICNAF Res. Doc. 78/XI/84. 50 pp.

Lett, P. F. and T. Benjaminsen. 1977. A stochastic model for the management of the Northwestern Atlantic Harp Seal (Pagophilus groenlandicus) population. J. Fish. Res. Board Can., 34: 1155-1187.

Øritsland, T. 1971. Progress report on Norwegian studies of Harp Seals at Newfoundland. ICNAF Res. Doc. 71/8. 28 pp.

Rivard, D. 1978. Analysis of likely improvements in the estimation of density-dependent relationships for harp seal models. CAFSAC Working Paper 78/55. 12 pp.

Sergeant, D. E. 1979. Maturation rates of female harp seals, *Pagophilus groenlandicus*, Erxleben in the Northwest Atlantic, 1951-1978. Unpublished manuscript. 20 pp.

1978. Research on harp seals in 1978. ICNAF Res. Doc. 78/XI/85. 11 pp.

1976. Studies on Harp Seals of the western North Atlantic population in 1976. ICNAF Res. Doc. 76/X/124. 32 pp.

1973. Environment and reproduction in seals. J. Reprod. Fert. Suppl. 19: 555-561.

1966. Reproductive rates of Harp Seals, *Pagophilus groenlandicus* (Erxleben). J. Fish. Res. Board Can., 23: 757-766.

Sokal, R. R. and R. J. Rohlf. 1969. Biometry. Freeman, San Franscisco. 776 pp.

Winters, G. H. 1978. Production, mortality, and sustainable yield of Northwest Atlantic Harp Seals (*Pagophilus groenlandicus*). J. Fish. Res. Board Can. 35: 1249-1261.

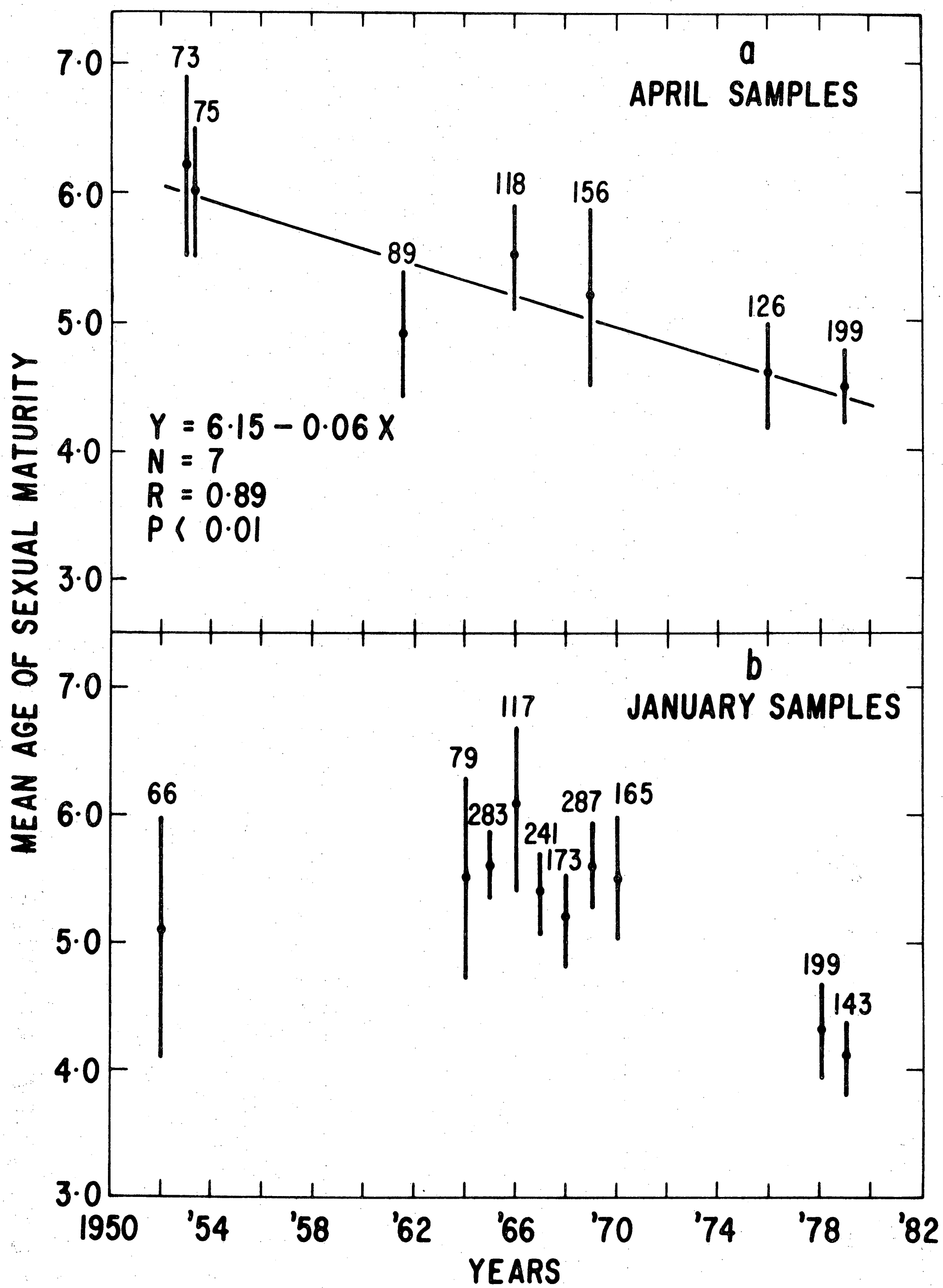

Fig. 1. Mean age of sexual maturity of female harp seals plotted against time for April samples (a) and January samples (b). Vertical lines indicate 95% confidence intervals of the mean. Numbers represent number of females in the sample.

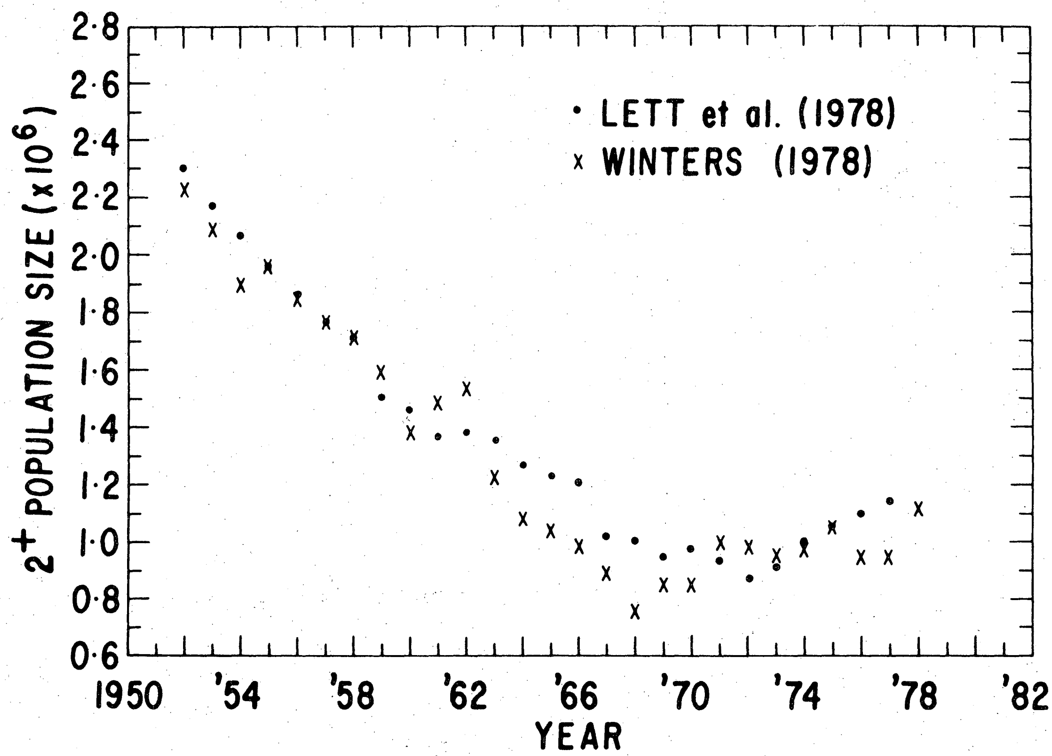

Fig. 2. Changes in 2+ population size over the period 1952 to 1978 from Lett et al. (1978) and Winters (1978).

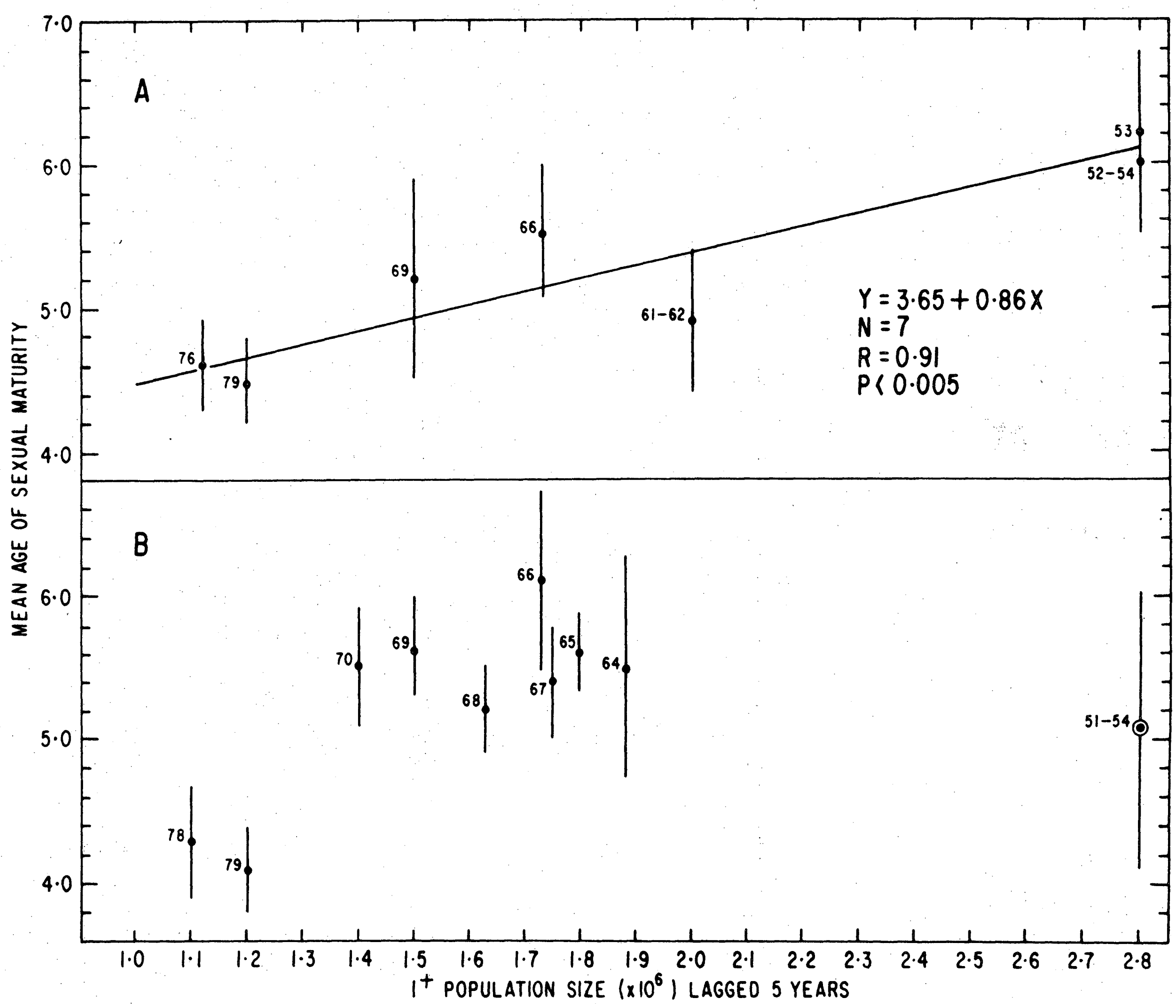

Fig. 3. Mean age of sexual maturity of female harp seals regressed against 2+ population size for samples collected in April (a) and January (b). The circled point in (b) was omitted from analysis (see text).

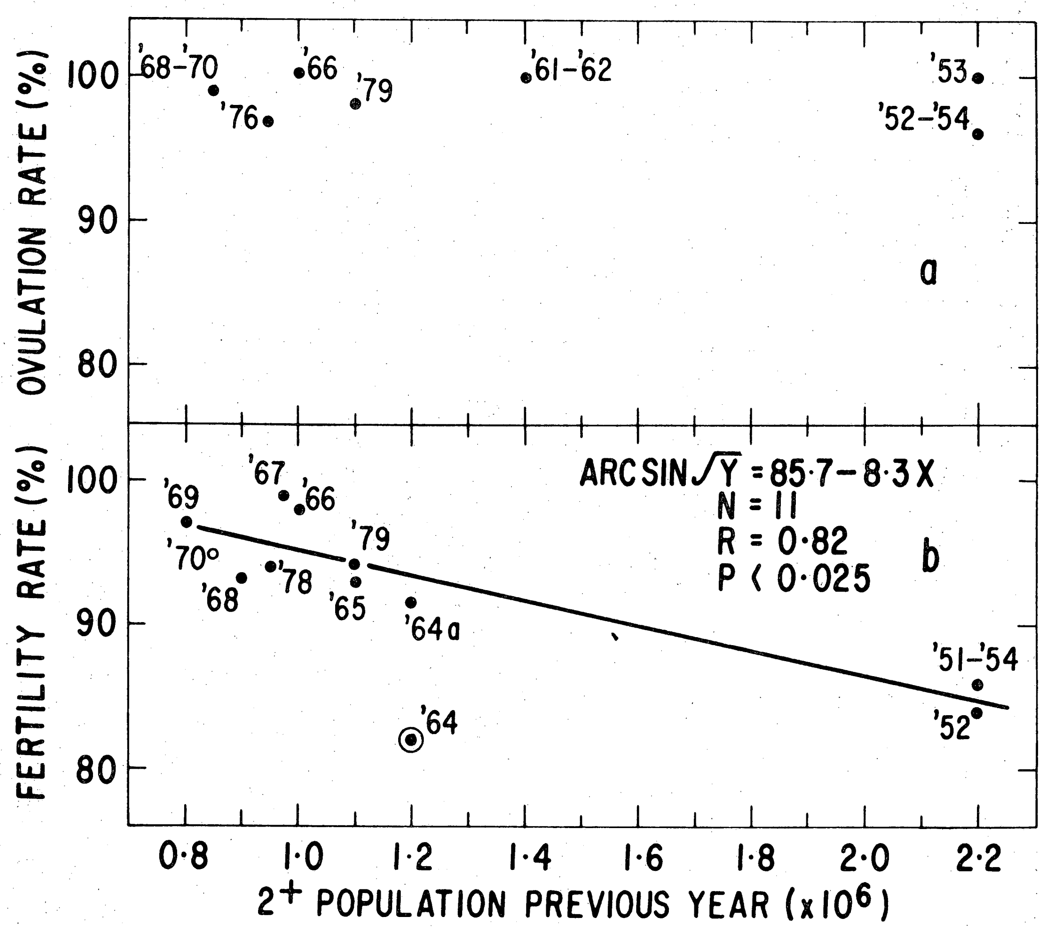

Fig. 4. Ovulation rate (a) and fertility rate (b) of female harp seals regressed against 2+ population size in the previous year. The circled point in (b) was omitted from the analysis (see text).

[a] Sample collected by Øritsland (1971).

Appendix A. Reproductive samples of harp seal females collected in January-February from the Gulf and Front.

	1951-54; Fisher (1954)				1964; Sergeant (1979)				1965; Sergeant (1979)			
Age in years	n	Imm.	Preg.	Mat. Non-Preg.	n	Imm.	Preg.	Mat. Non-Preg.	n	Imm.	Preg.	Mat. Non-Preg.
1					3	3						
2	1	1			8	8			7	7		
3	5	5			16	16			18	18		
4	4	4			11	11			30	29	1	
5	3	2	1		9	7	1	1	44	39	5	
6	3	1	2		2		1	1	37	16	20	1
7	16	1	12	3	4	1	3		38	11	27	
8	4		3	1	5		5		33	1	28	4
9	8		7	1	4		4		15	1	12	2
10	8		7	1	2		1	1	5		5	
11	4		4		1		1		5		5	
12	3		3		6		5	1	10		10	
13					1		1		7		5	2
14	2		2		1		1		8		8	
15+	4		3	1	6		4	2	26		23	3
TOTAL	65	14	44	7	79	46	27	6	283	122	149	12
FERTILITY RATE			86.3%				81.8%				92.6%	
			84.6% from Fisher (1952)[a]									

[a] No details provided, but n = 133.

	1966; Sergeant (1979)				1967; Sergeant (1979)				1968; Sergeant (1979)			
Age in years	n	Imm.	Preg.	Mat. Non-Preg.	n	Imm.	Preg.	Mat. Non-Preg.	n	Imm.	Preg.	Mat. Non-Preg.
1	3	3			6	6			4	4		
2	11	11			7	7			12	12		
3	10	10			14	14			24	24		
4	7	7			10	10			27	27		
5	9	8	1		19	15	4		19	13	6	
6	17	11	6		33	13	20		20	6	14	
7	11	3	8		29	1	28		12	1	11	
8	8	1	7		23	3	20		11	1	9	1
9	4	1	3		18	2	16		4		4	
10	5		5		18	4	14		5		5	
11	4		4		11	1	10		4		3	1
12	4		4		4		4		5		3	2
13	6	1	5		5		4	1	3		3	
14	2		2		12		12		6		6	
15+	16	2	13	1	32	2	29	1	17		15	2
TOTAL	117	58	58	1	241	78	161	2	173	88	79	6
FERTILITY RATE			98.0%				98.8%				92.9%	

Appendix A. continued.

Age in years	1969; Sergeant (1979) n	Imm.	Preg.	Mat. Non-Preg.	1970; Sergeant (1979) n	Imm.	Preg.	Mat. Non-Preg.	1978; Sergeant (1979) n	Imm.	Preg.	Mat. Non-Preg.
1	4	4							6	6		
2	5	5			4	4			13	13		
3	20	20			6	6			32	32		
4	25	24	1		13	13			40	39	1	
5	25	21	4		13	10	3		38	15	23	
6	16	9	7		12	6	6		20	2	18	
7	28	5	23		10	1	9		9	3	6	
8	29	2	27		19	1	18		10	1	7	2
9	22		21	1	21	1	18	2	9		8	1
10	17	1	16		12		12		7		7	
11	17	1	14	2	4		4		3		3	
12	9		9		8	2	6		1		1	
13	12	3	9		4	1	3		2		2	
14	11	1	10		6	1	4	1	2		2	
15+	47	5	40	3	33	3	27	3	7		5	2
TOTAL	287	101	180	6	165	49	110	6	199	111	83	5
FERTILITY RATE	96.8%				94.8%				94.3%			

Age in years	St. Anthony 1979; this study n	Imm.	Preg.	Mat. Non-Preg.	Combined St. Anthony-St.Lawrence estuary (Sergeant, 1979) 1979 samples n	Imm.	Preg.	Mat. Non-preg.
1	7	7			12	12		
2	18	18			27	27		
3	18	16	2		33	31	2	
4	9	6	3		21	16	5	
5	9	3	5	1	15	6	8	1
6	3		3		5		5	
7	4		3	1	9		8	1
8	2		2		4		4	
9	1		1		3		3	
10	1		1		2		2	
11					1		1	
12	1		1		2		2	
13	1		1		1		1	
14	1		1		2		2	
15+	4		3	1	6		5	1
TOTAL	80	50	27	3	143	92	48	3
FERTILITY RATE	90%				94.1%			

Appendix B. Reproductive samples of harp seal females collected in April from moulting herds on the Front.*

	1953; Fisher (1954) (only April samples used)				1952-1954; Sergeant (1966)				1961-62, Sergeant & Khuzin combined; Sergeant (1966)			
Age in years	n	Imm.	Preg.	Mat. Non-Preg.	n	Imm.	Preg.	Mat. Non-Preg.	n	Imm.	Preg.	Non-preg.
1	4	4			3	3			15	15		
2	1	1			3	3			12	12		
3	12	12			6	6			8	7	1	
4	13	13			3	3			14	7	7	
5	17	11	6		6	4	2		10	4	6	
6	6	2	4		10	3	7		9	1	8	
7	4	1	3		8		8		11		11	
8	2		2		6		6					
9	3		3		8		8		2		2	
10	2		2		3		3					
11	1		1		6		6		1		1	
12	2		2		2		2					
13	2		2		3		3					
14					1		1		2		2	
15+	4		4		7		5	2	5		5	
TOTAL	73	44	29		75	22	51	2	89	46	43	
OVULATION RATE		100%					96.2%				100.0%	

	1966*; Sergeant (1979)				1968-70; Sergeant (1979)				1976; Sergeant (1976)				1979, this study				
Age in years	n	Imm.	Preg.	Mat. Non-Preg.	n	Imm.	Preg.	Mat. Non-Preg.	n	Imm.	Preg.	Mat. Non-Preg.	Age in years	n	Imm.	Preg.	Mat. Non-Preg.
1	9	9			20	20			36	36			1	69	69		
2	16	16			27	27			10	10			2	38	38		
3	10	10			15	15			10	9	1		3	16	16		
4	10	9	1		5	4	1		14	8	6		4	23	9	13	1
5	10	4	6		4	1	3		11	1	10		5	16	1	15	
6	14	3	11		7	1	6		5		5		6	8	1	7	
7	11		11		7		7		14		14		7	4		4	
8	4		4		7		7		7		7		8	6		6	
9	1		1		11		11		6		6		9	3		3	
10	3		3		9	1	8						10	3		3	
11	5		5		1		1		2		2		11	4		4	
12	4		4		6		6						12	2		2	
13	2		2		5		5		2		2		13	2		2	
14	2		2		5		5		1		1		14				
15+	17	2	15		27	2	23	1	8		6	2	15+	5		5	
TOTAL	118	53	65		156	71	84	1	126	64	60	2	TOTAL	199	134	64	1
OVULATION RATE			100.0%				98.8%				96.8%		OVULATION RATE			98.0%	

* 1966 sample taken in Gulf of St. Lawrence.

Appendix C. Mean age of sexual maturity ($\bar{x}$) of female harp seals, variance (s^2) of $\bar{x}$, and 95% C.I. of $\bar{x}$ for samples collected in January-February and April over the period 1951 to 1979.

January-February samples

Year	Mean Age Sexual Maturity ($\bar{x}$)	$s^2(\bar{x})$	95% C.I. of $\bar{x}$ Lower	Upper
1951-54	5.1	0.23	4.1	6.0
1964	5.5	0.17	4.7	6.3
1965	5.6	0.02	5.4	5.9
1966	6.1	0.10	5.4	6.7
1967	5.4	0.03	5.0	5.7
1968	5.2	0.04	4.8	5.5
1969	5.6	0.03	5.3	6.0
1970	5.5	0.05	5.0	5.9
1978	4.3	0.04	3.9	4.7
1979	4.1	0.03	3.8	4.4

April samples

1953	6.2	0.12	5.6	6.9
1952-54	6.0	0.07	5.5	6.5
1961-62	4.9	0.07	4.4	5.4
1966	5.5	0.05	5.1	6.0
1969	5.2	0.12	4.5	5.9
1976	4.6	0.04	4.2	4.9
1979	4.5	0.02	4.2	4.8