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Population forecasts for Northwest Atlantic
harp seals, *Pagophilus groenlandicus*

by

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Introduction

Allen's (1975) model has been used since 1972 to provide population assessments and forecasts for northwest Atlantic harp seals (Anon., 1972; Ronald et al., 1973; Ronald and Capstick, 1975).

Flowcharts representing the basic operations of the model and the alternative choices of data input and operation have been described by Capstick and Ronald (1976).

Recently, other types of models using different assumptions have been presented. The question was then raised as to how these assumptions would effect forecasts of pup production and sustainable yield produced by the modified Allen model.

The present paper evaluates how various input assumptions effect forecasts of pup production and sustainable yield in the future. The model was initialized using an estimate of pup production for 1951 (Fisher, 1955) and published catch statistics from then until 1976. This approach is significantly different from the other models (Benjaminsen and Lett, 1976; Winters, 1976).

Model Parameters and Assumptions

Density Dependent Pupping Relationship

Since the original proposal (Capstick and Ronald, 1976) was made, Sergeant (1976) has provided data from a sample of Front

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seals collected in 1976 which indicate that the mean age at first maturity has now dropped to 3.8 years. These data have been added to those used to develop the previous relationship (Capstick and Ronald, 1976), to provide the complete data set shown in Table 1.

These three sets of values do not include precise or definitive estimates of herd size. As all historical estimates are approximations, these figures are rounded to the nearest million from information in the literature (Table 1). When fitted to a straight line, by linear regression, the relationship can be expressed as:

$$\text{Mean age at first maturity} = 2.9967 + .845 H$$

$$\text{Mean age at first whelping} = 3.9967 + .845 H$$

where H = herd size of 1+ seals in decimal millions.

The relationship is shown graphically in Figure 1. It is used, by substitution for μ in the original formula (1), as described in Capstick and Ronald (1976, page 4), to give a family of ogives describing the relationship between the percentage of female seals producing pups and the age of the female seals, for different herd sizes.

Age-Specific Natural Mortality

One of the most elusive parameters for western Atlantic Harp seals is natural mortality (Lett and Lavigne, 1975; Benjaminsen and Lett, 1976; Winters, 1976). At the present time, it is generally agreed that average annual natural mortality is about 0.11. The most recent detailed estimate of natural mortality (Benjaminsen and Lett, 1976) is 0.114 ± 0.0302 (SE), for 2+ seals.

As Benjaminsen and Lett (1976) and others have suggested, higher mortalities may be experienced by younger seals, although no data are available to support or refute this point. Mammals, in general, exhibit higher natural mortalities in the earlier age-classes, decreasing to some lower level as the animal matures. Natural mortality later increases as the animal approaches "old age" (Caughley, 1966). Such would appear to occur in the southern elephant seal, Mirounga leonina (see Laws, 1960), but was not found for the harbour seal, Phoca vitulina richardi (see Bigg, 1969).

We have been experimenting with the Allen model, and historical estimates of pup production to develop a hypothetical age-specific natural mortality curve for the harp seal (Table 2). The results of this exercise are not significantly different from estimates of natural mortality used in the other models. Therefore we have retained them in the present evaluation.

For example, a calculation of weighted average annual natural mortality over all ages for a 1975 age distribution produced in the present evaluation, resulted in a value of 0.114. Natural mortality for 2+ seals was 0.106. Included in our natural mortality estimates are all deaths resulting from all causes other than those reported in the catch statistics for the Front and Gulf of St. Lawrence each year. Thus, our natural mortality values, like other recent estimates (Benjaminsen and Lett, 1976; Winters, 1976), include sinkages and other deaths in the Newfoundland hunt. However, our estimates of natural mortality might be expected to be slightly higher than the others as we include the West Greenland and Canadian high arctic summer "fisheries", both of which are probably density-dependent, in natural mortality, rather than in the catch statistics.

Alternative Models

To carry out this evaluation it was necessary to develop a series of five models, each with a different set of parameters (Table 3). Each of these models is described briefly below:

Model 1

This model is basically Allen's original model and does not provide for density-dependent changes in any of the parameters. The sex-ratio of the population, and the hunt is assumed to be 50:50. Natural mortality is described in Table 2, and the pregnancy rate of mature female is held constant at 90%.

Model 2

This version is the same as model 1 but allows for an exponential density-dependent change in average age at maturity, and thus age of whelping (Capstick and Ronald, 1976).

Model 3

Model 3 differs from model 2 in that the density-dependent whelping relationship incorporates Sergeant's (1976) latest data. It provides for linear changes in average whelping age with population size (1+ seals) (Fig. 1). In addition, the bedlamer catch is distributed over ages 1-6 rather than ages 1-5 as in Allen's (1975) model.

Model 4

Model 4 is essentially the same as model 3 except that the pregnancy rate is variable, being 85% from 1951-1960, 90% from 1961-1970, and 94% from 1971-1977. There is some evidence for such changes in pregnancy rate during the last 27 years (Benjaminsen and Lett, 1976), although the relationship is not entirely clear.

Model 5

Model 5 incorporates changes in the sex ratio of the catch described by Benjaminsen and Lett (1976) for the period 1965-1976. Benjaminsen and Lett (1976) began to change the sex ratio of the catch in 1961 in accordance with regulations governing closing dates for the hunt, which should reduce the number of females in the catch.

Varying sex ratios in the catch were initiated in 1965, the first year in which females were protected on whelping patches (Sergeant, in press). Both possibilities include the assumption that the sex ratio of the population was 50:50 in 1961 (Benjaminsen and Lett, 1976) or 1965 (this MS). Such data do not exist to our knowledge.

Catch Statistics

Catch statistics were obtained from a variety of sources (e.g. Department of Fisheries of Canada, 1968; Department of the Environment, 1975; Øritsland 1967, 1969, 1970, 1971a, 1972, 1973). Canadian statistics are reported as young of the year (pups and beaters), bedlamers, and adults. Norwegian catches are reported as young of the year, and older (1+) seals.

To accommodate the input format of the Allen model, the Norwegian 1+ catch was prorated into bedlamers and adults according to the Canadian ratio for the corresponding year. The catch statistics so derived and used in the present evaluation are shown in Table 4.

Since the model assumes that the sex ratio of the population and the catch is 50:50 it was necessary, in model 5, to adjust the catch according to sex ratio data provided by Benjaminsen and Lett (1976). For example, if a catch of 10,000 adults contains 60% males and 40% females, the catch can be adjusted to 8,000 to represent 4,000 females and 4,000 males but ignoring the additional 2,000 males. This 8,000 catch is then applied by the model, which then accurately represents the population dynamics of females. Under these circumstances it can be used only to assess the breeding population and pup production. Estimates of total 1+ animals and herd size are naturally invalid. Table 5 shows the sex ratios used and the conversion factors applied to the catch statistics given in Table 4, in order to use the model in this fashion.

In models 1 and 2 the bedlamer catch was distributed over ages 1-5 and in models 3 to 5 this catch was distributed over ages 1-6. There are some apparent shortcomings in this aspect of the Allen model, since pelt type is apparently not a precise indicator of age, especially in female seals (Potelov and Mikhnevich, 1969; Sergeant, 1976).

Results

The results of the present evaluation are given in Table 7. For the five models considered, pup production for 1977 varied from 193,000 to 321,000, suggesting a 1+ population size of between about 0.7 and 1.2 million animals. Estimates of a sustainable yield from the present population varied from 65,000 to 160,000 animals. These estimates assume that future catches are comprised of 82% pups, 12% bedlamers, and 6% adults, similar to the composition of catches in the last few years.

Discussion

The estimates of pup production for 1977 and the sustainable yield determinations (Table 7) may all be traced back to the basic assumption that pup production in 1951 was 645,000 seals (Fisher, 1955) (Fig.2). In reality, Fisher's estimate, based on aerial photography, may have been an underestimate of pup production (Fisher, 1955) in 1951.

Our historical reconstruction of pup production from 1951 to 1976 is shown in Fig. 2. All 5 models indicate a general decline in pup production during this period. Models 1 to 4 suggest that this decline is continuing; model 5 appears to be approaching stability in 1976. None of the models evaluated in this paper suggest any recovery in pup production during the 1972-1976 period.

In general, the 5 models all produced higher estimates of pup production than occur in the literature (Fig. 2). Perhaps a key checkpoint might be the 1970 estimate of pup production of 300,000 or less agreed upon by ICNAF (1971). ICNAF (1975) also considered that 359,000 was a reasonable estimate of pup production for 1967. The general trend of the published estimates of pup production is reasonably similar to the trends observed in the 5 models considered in this paper. There are reasons to believe that some of these earlier estimates are "minimum" estimates, especially those based on black and white aerial photography (Sergeant, 1975). The actual history of the pup production in the western Atlantic is impossible to verify.

Model 5 incorporates an increasing proportion of males in the catch since 1965. Although closing dates were first introduced in 1961, we chose to apply the varying sex ratios in the catch (Lett, 1976) beginning in 1965 when adult females on whelping patches were protected. Model 5, and Benjaminsen's and Lett's (1976) model, produced similar estimates of 1977 pup production and sustainable yield (Table 7).

The present evaluation confirms that the output of models used for assessing harp seal stocks is largely dependent on the basic assumptions regarding input parameters. In the models

used here, and other models presently available, many assumptions are of necessity based on limited evidence, small sample sizes, and extrapolations beyond the available data base. These limitations must be recognized when considering the results of these models.

The principal value of modelling populations must not be overlooked. The many and recent attempts to model western Atlantic harp seals have been useful. All available data have been analyzed and reanalyzed. Deficiencies in the historical data and important priorities for future research have been recognized. As Dempster (1975) concluded:

"...only limited progress can be made in constructing realistic population models until there is a firmer basis of field data on which to build."

To this end, we agree with Benjaminsen and Lett (1976) that an ultra-violet aerial census of whelping harp seals in the western Atlantic, with adequate ground truthing, should be pursued until direct and precise estimates of pup production are obtained.

Acknowledgements

This paper was initiated as a result of a meeting of Canadian scientists and the Committee on Seals and Sealing in Guelph on 22 September, 1976. It investigates a number of alternative assumptions about the harp seal population arising either from our own work, or suggested by colleagues.

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TABLE 1. Relationship between mean age at first maturity and an estimate of herd size (1+ seals).

YEAR	Approx. Herd Size Millions of 1+ seals	Mean Age at First Maturity
1951/54	3.0 (Fisher, 1955)	5.49 (Sergeant, 1966)
1961/65	2.0 (Sergeant, 1966 & 1973)	4.77 (Sergeant, 1966)
1976	1.0 (Lavigne, 1976; Benjaminsen and Lett, 1976)	3.8 (Sergeant, 1976)

TABLE 2. Age specific natural mortality.

AGE	AVERAGE ANNUAL NATURAL MORTALITY* PER CENT
0	20.0
1	16.0
2	13.0
3	11.0
4	10.0
5	9.5
6	9.5
7	9.5
8	9.5
9	9.5
10	9.5
11	9.5
12	9.5
13	9.5
14	9.5
15	9.5
16	9.5
17	9.5
18	9.5
19	9.5
20	9.5
21	10.0
22	12.0
23	15.0
24	19.0
25	24.0
26	32.0
27	50.0
28	75.0
29	95.0

*includes West Greenland and Canadian high Arctic hunts.

TABLE 3. Alternative models evaluated.

MODEL NUMBER	DENSITY DEPENDENT PUPPING	PREGNANCY RATE	SEX RATIO IN CATCH
1	none	90%	50:50
2	exponential	90%	50:50
3	linear	90%	50:50
4	linear	85%-94%*	50:50
5	linear	85%-94%*	variable

*1951-1960, 85%

1961-1970, 90%

1971-1977, 94%

TABLE 4. Harp seal catch statistics.

YEAR	PUPS	BEDLAMERS	ADULTS	TOTAL
1951	318,626	89,023	47,936	455,585
1952	198,063	70,794	38,521	307,378
1953	197,975	48,634	26,277	272,886
1954	175,034	58,029	31,353	264,416
1955	252,297	52,634	28,438	333,369
1956	341,397	31,171	16,842	389,410
1957	165,498	51,965	28,077	245,540
1958	140,996	101,792	54,998	297,786
1959	238,823	52,783	28,519	320,125
1960	156,158	78,674	42,508	277,340
1961	160,319	10,438	5,664	176,466
1962	207,088	79,790	43,111	329,989
1963	259,819	42,020	22,703	324,542
1964	266,382	48,874	26,407	341,663
1965	182,758	33,432	18,063	234,253
1966	251,735	46,760	25,264	323,759
1967	277,750	36,901	19,705	334,356
1968	156,458	23,623	12,615	192,696
1969	233,340	36,162	19,310	288,812
1970	217,431	26,117	13,947	257,495
1971	210,579	13,290	7,097	230,966
1972	117,031	8,518	4,549	130,098
1973	98,325	16,621	8,876	123,822
1974	114,825	21,388	11,422	147,635
1975	140,629	21,796	11,639	174,064
1976	134,480	19,680	9,840	164,000

TABLE 5. Sex ratio* of the catch of harp seals and conversion factor.

YEAR OF HUNT	AGE CLASS	RATIO ♂ : ♀ *	CONVERSION FACTOR
			FRACTION ♂'s ** x 2
1965	0	50:50	1.0
	1	50:50	1.0
	2	60:40	0.8
	3	60:40	0.8
	4-29	65:35	0.7
1966-68	0	50:50	1.0
	1	50:50	1.0
	2	53:47	0.94
	3	58:42	0.84
	4	65:35	0.70
	5	70:30	0.60
	6	75:25	0.50
6-29	75:25	0.50	
1969-77	0	50:50	1.00
	1	50:50	1.00
	2	53:47	0.94
	3	58:42	0.84
	4	65:35	0.70
	5	70:30	0.60
	6	75:25	0.50
	7	76:24	0.48
	8	78:22	0.44
	9	80:20	0.40
	10	82:18	0.36
	11	85:15	0.30
	12-29	86:14	0.28

*From Benjaminsen and Lett, 1976, Fig. 1.

**The pro-rated hunt in each age class is multiplied by the figures in this column to give "♂ only" hunt.

TABLE 6. Harp seal catch statistics adjusted to reflect reduced female catch.

YEAR	PUPS	BEDLAMERS (Ages 1-6)	ADULTS	ADJUSTED TOTAL	UNADJUSTED TOTAL (from Table 4)
1965	182,758	26,420	12,640	221,818	234,253
1966	251,735	36,808	13,632	301,175	232,759
1967	277,750	29,250	9,852	316,852	334,356
1968	156,458	18,633	6,307	181,398	192,696
1969	233,340	29,633	6,469	269,442	288,812
1970	217,431	21,724	4,606	243,761	257,495
1971	210,579	10,606	2,332	223,517	230,966
1972	117,031	6,825	1,492	125,348	130,098
1973	98,325	13,701	2,897	114,923	123,822
1974	114,825	17,750	3,694	136,269	147,635
1975	140,629	18,360	3,856	162,845	174,064
1976	134,480	16,206	3,005	153,691	164,000

TABLE 7. Estimates of 1977 pup production, population size, and sustainable yield generated by the 5 alternative models.

MODEL NUMBER (Table 2)	1977 PUP PRODUCTION	1977 1+ POPULATION	1977 TOTAL POPULATION	APPROX. SUSTAINABLE YIELD*
1.	193,000	714,000	907,000	65,000
2.	249,000	939,000	1,188,000	103,000
3.	313,000	1,240,000	1,553,000	130,000
4.	274,000	1,022,000	1,296,000	115,000
5.	321,000	-	-	160,000

* Future catches subdivided: 82% pups, 12% bedlamers, 6% adults.

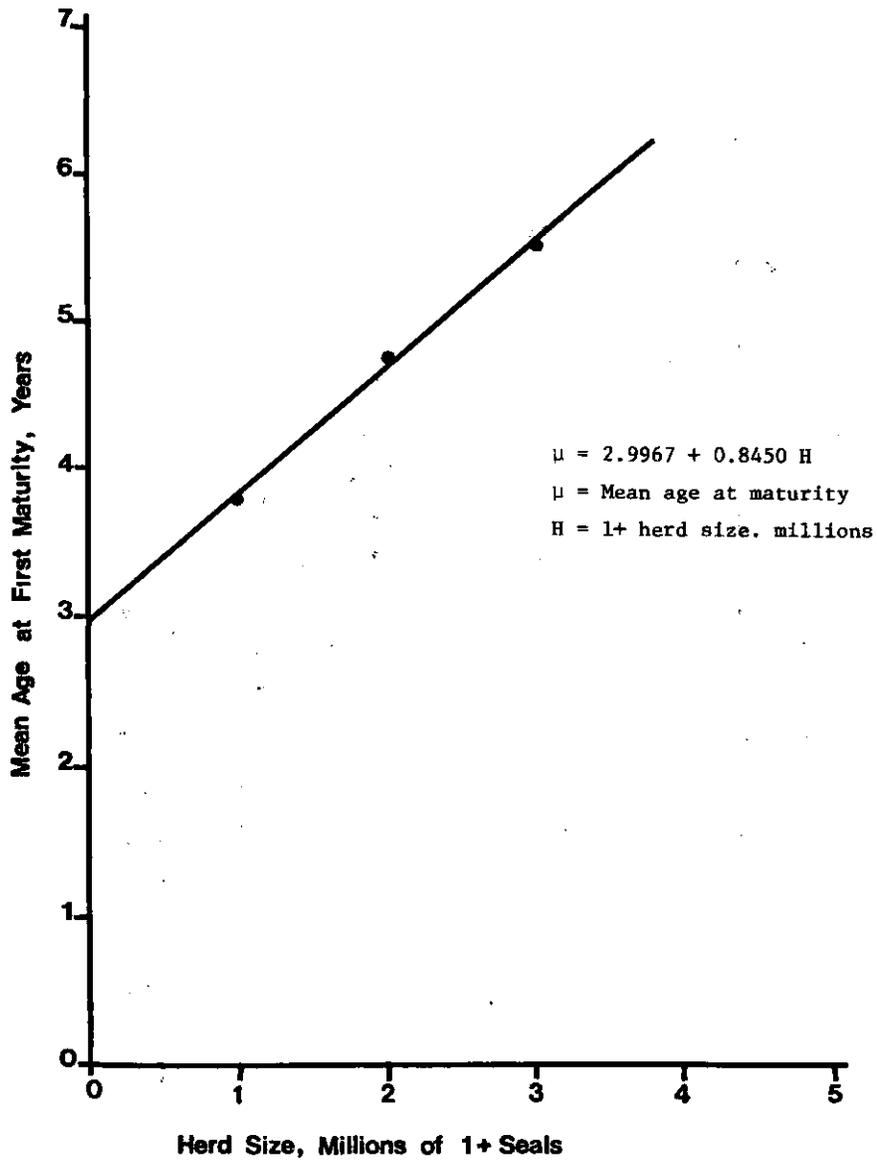


FIGURE 1. Regression between mean age at maturity and herd size for female harp seals.

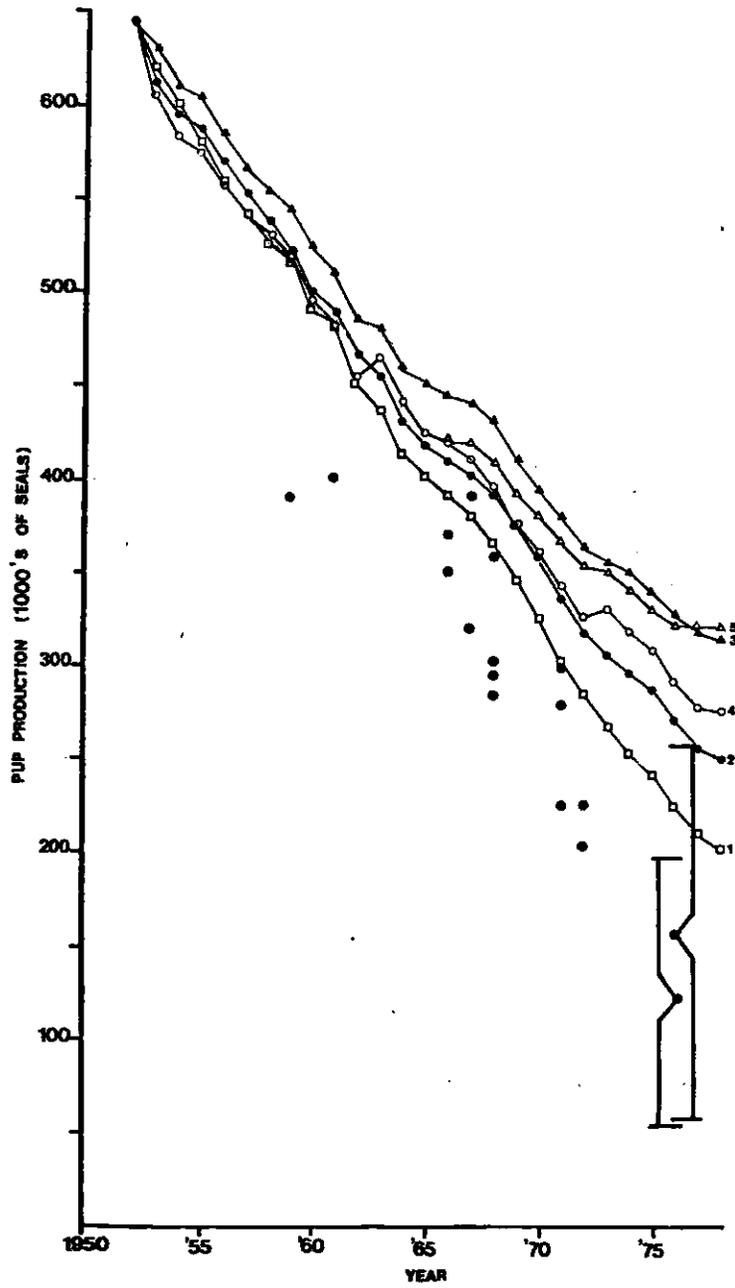


FIGURE 2. Pup production from 1951 to 1977 generated from models 1 to 5, and historical estimates (large dots) from the literature (Fisher, 1955; ICNAF, 1971, 1975; Sergeant, 1975; Benjaminsen and Øritsland, 1975; Ricker, 1975 and Lavigne *et al.*, 1975; Lavigne, 1976).