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Model Estimates of Harp Seal Numbers at Age for the Northwest Atlantic

by

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Introduction

Various approaches to estimating the size of the harp seal population in the northwest Atlantic have been explored in the past. Those methods based primarily on interpreting age composition data fall into two categories - the survival index approach (SI) and virtual population analysis (VPA). Alternative methods have depended on fitting various forms of a two parameter population model (variation of a Leslie model) to independent field estimates of pup production for several years - here termed the population model (PM) approach.

The SI method was originally formulated by Sergeant (1971) and then applied by Sergeant (1975), Benjaminsen and Øritsland (1975) and Winters (1978) with minor variations. It provides a single estimate of pup production for a period of years for which pup production is assumed to be constant. Cooke (1985) reviewed the method and concluded that it was unreliable because of its poor mathematical formulation. He provided a modified SI formulation in which the age sample is viewed as a Poisson distributed random variable. By taking into account selectivity-cum-cumulative survival to age he developed a multinomial for the age composition for which parameters could be estimated by maximum likelihood. The method performed well on simulated data. He applied the method to the pup kill and age composition sample data for 2 to 8 year old animals taken in the large vessel hunt, tabled in Bowen (1982), to get pup production estimates for two 10 year periods for which pup production was assumed to be constant (1958-67 and 1968-77). However, in order to obtain a trajectory of population size, the assumption of constant pup production must be replaced with a model in which pup production is linked to the mature population via pregnancy rates. This approach was applied to the northwest Atlantic harp seal population by Cooke et al. (1985) using assumed pregnancy rates.

VPA (more correctly Pope's (1972) approximation to VPA, called cohort analysis) has been applied to harp seal catch-at-age data up to the mid to late 1970s by Lett and Benjaminsen (1977) and Winters (1978). Both VPAs provided very similar trajectories (Stenson et al. 1993), despite the fact that their methods for obtaining terminal fishing mortality differed. Although illustrative of the general relative trends of populations at the time, these applications predate the development of "calibrated" VPAs and therefore are unscaled with respect to absolute population size.

The PM approach involving fitting a population model to independent estimates of pup production was first applied to the northwest Atlantic harp seal population by Roff and Bowen (1983). They suggested that their approach was similar to that of Beddington and Williams (1980). However, Beddington and Williams (1980) fit their population model to catch-at-age data and is therefore more similar to the approach of Cook et al. (1985), whereas Roff and Bowen (1983) fit their model to survey estimates of pup production, using age composition data only in the estimation of initial pup production and in subsequent updating of numbers at age from one year and age to the next.

The PM approach adopted by Cadigan and Shelton (1993) and used here to estimate the trajectory of the number of pups and total population size in each year up to 1994 is very similar to that of Roff and Bowen (1983), but benefits from a more objective method for obtaining initial pup production and an improved method for parameter estimation. The model is applied to six well-documented independent survey (mark-recapture and aerial) estimates of pup production. Two formulations are considered, Formulation 1 in which the natural mortality rate on pups is the same as that on the 1+ population, and Formulation 2 in which the natural mortality on the pups is 3 times the mortality on the 1+ population. Estimates of replacement harvest are made for both formulations. For formulation 1 the probability distribution of total population size, population growth rate, replacement harvest, replacement population size and replacement exploitation rate are calculated, taking into account only the uncertainty in the population model parameter estimates.

Methods

The model developed by Cadigan and Shelton (1993) consists of a population dynamics model and a statistical model.

The population dynamics model is

$$n_{a,t} = (n_{a-1,t-1} e^{-\frac{m}{2}} - c_{a-1,t-1}) e^{-\frac{m}{2}}$$

for $0 < a < A$,

$$n_{A,t} = (n_{A-1,t-1} e^{-\frac{m}{2}} - c_{A-1,t-1}) e^{-\frac{m}{2}}$$

for $a = A$, where A-1 is taken as ages A-1 and greater, and

$$n_{a,t} = \sum_{a=1}^{A} n_{a,t} p_{a,t}$$

for $a = 0$;

where $n_{a,t}$ = population numbers at age a in year t,

$c_{a,t}$ = the numbers caught at age a in year t,

$p_{a,t}$ = per capita pregnancy rate of age a parents in year t, assuming a 1:1 sex ratio

m = instantaneous rate of natural mortality.

A = the "plus" age class (i.e. older ages are lumped into this age class and not dealt with separately, taken as age 12 in this analysis).

In order to estimate numbers at age for years prior to the first year for which continuous pregnancy data are available, it was assumed that the annual pup catch is a constant proportion s of the number of pups born (s=(1/exploitation rate)). Thus, for years prior to the first year for which pregnancy data are available (t_0)

$$n_{a,t_0-1} = se^{-ma} c_{0,t_0-a-1} - \sum_{i=1}^{a} e^{-m(i-\frac{1}{2})} c_{a-i,t_0-i-1}$$

for a = 1 to Å, where Å is a terminal (rather than a plus) age (=25 years in the formulations that follow). This equation is applied iteratively to go back in time and fill in the numbers-at-age matrix. The numbers at age for the initial years do not have a large influence on model estimates beyond the mid-1970s but do influence perceptions about the decline and recovery of the population.

The statistical model is

$$\tilde{n}_{0,t_i} \sim N(n_{0,t_i}, \tilde{\sigma}^2_{t_i}),$$

where $\tilde{n}_{0,t_i}$ is the ith survey estimate of n_{0,t_i} and $\tilde{\sigma}^2_{t_i}$ is its estimated variance.

The model is rewritten in matrix notation and transformed into a standard nonlinear regression model (Cadigan and Shelton 1993). Maximum likelihood (or equivalently least-squares) estimates of the parameters m and s are obtained using PROC NLIN in SAS applying the Newton iterative method. Following the statistical model given above, the survey estimates of pup production are given weights that are inversely proportional to their variance.

The uncertainty in the population trajectory for Formulation 1 is illustrated by randomly sampling 50 pairs of parameter values (s and m) from a bivariate normal distribution defined by the parameter estimates, their standard errors and the correlation between the parameter estimates, and plotting the corresponding population trajectories. While perhaps useful for illustration purposes, many more samples are required to provide an adequate representation of the uncertainty associated with the parameter estimates. The frequency distribution and cumulative probability distribution of estimates of, population size in 1994, population growth rate (total 1994 population divided by total 1993 population), replacement harvest, replacement population size and replacement exploitation rate was estimated from 1000 random samples of pairs of parameter values. This provides only a partial exploration of the uncertainty associated with the estimates. It is conditional on assumptions that the pregnancy rates and catch-at-age estimates are known precisely and that the model structure is correct (e.g. catches taken in the middle of the year, pup mortality is equal to the mortality on the 1+ population, and for replacement calculations, that the age composition of the catch and the pregnancy rates remain unchanged from recent estimated values). The uncertainty is therefore underestimated in this analysis.

To calculate replacement harvest, the estimated numbers at age up until 1994 were projected to year

2064 using the 1994 estimates of pregnancy-at-age (see below). Catch was removed by applying the 1993 estimated proportions at age in the catch (only the total catch for 1994, i.e. aggregated by age, is presently available). A constant annual total catch for the period 1995 to 2064 was varied until a constant population size was attained.

The total annual catch-at-age up to 1993 (Sjare and Stenson, unpublished data) is given in Table 1 and illustrated in Fig. 1. The data up to 1990 are described in Shelton et al. (1992). The pregnancy-at-age sample data are given in Table 2.

The pregnancy-rate data is characterized by highly variable sample sizes; for example, for the 7+ age class, the sample size ranges from 1 in 1985 to 164 in 1969. The data are also suggestive of changes in pregnancy rates over time. Rather than use the overall average (by age) or the individual-year estimates, many of which are subject to relatively large sampling error, our objective was to find the most parsimonious representation of pregnancy rates consistent with the data.

"Harmonising" the pregnancy data was accomplished as follows. For a given age class, let n_i denote the number of seals examined in year i and let x_i denote the number of these determined to be pregnant. We start by forming the 2 times 2 contingency table

$$\begin{array}{ccc} x_1 & n_1 - x_1 & | \; n_1 \\ x_2 & n_2 - x_2 & | \; n_2 \\ \hline x_. & n_. - x_. & | \; n_. \end{array}$$

where $x_i = x_1 + x_2$, etc. The conventional χ^2 statistic, on 1 d.f., was calculated for this table and if the null hypothesis (of common pregnancy rate) was accepted (at the 5% level), these data were pooled and a new 2 times 2 table formed by including the next year's data, namely

$$\begin{array}{ccc} x_. & n_. - x_. & | \; n_. \\ x_3 & n_3 - x_3 & | \; n_3 \\ \hline x_{..} & n_{..} - x_{..} & | \; n_{..} \end{array}$$

where $x_{..} = x_. + x_3$, etc. This procedure was continued as long the the successive χ^2 values remained non significant. When a significant χ^2 was encountered, the sequence was terminated, and a new sequence begun, starting with the year for which a (significant) change in pregnancy rate was indicated.

Although the method is as objective as possible, given the data, some minimal amount of subjectivity was nevertheless required:

(i) For Age 3, the procedure grouped 1978 with 1954-70 for an estimate of 0.0192, and an estimate of 0.1017 for 1979-1994. For consistency with Ages 4 and 5, it seems preferable to place 1978 with 1979-94. Also, although not significant, there is a drop in the rate after 1988 which is incorporated in the above table for greater consistency with the estimates for the remaining ages.

(ii) For Age 4, the procedure indicated the break to be between 1988 and 1989 rather than between 1987 and 1988. However the sample ratio for 1988 seems more consistent with the ratios of the following years. Further, placing the break between 1987 and 1988 results in a slightly greater likelihood value for all data combined.

(iii) For Age 5, the procedure indicates a drop in rate for 1993, followed, in 1994, by a return to more or less the rate prior to 1993. There is a reluctance to have different rates for isolated individual years and, since the sample size in 1993 is only 4, it seems reasonable to combine 1993 with 1985-92 and 1994.

(iv) For the same reason, for Age 6, 1986 is included in the set 1967-89. The increase in rate between 1966 and 1967 appears genuine.

(v) For Age 7+, the ratios in 1989 and 1994 are high in relation to their neighbouring years. Again to avoid having different rates for individual isolated years and to obtain the most consistency, 1989 has been included with 1954-58 and 1994 with 1990-93.

(vi) On viewing the overall estimates given above, it was found that the estimates for Age 5 would be more compatible with those for the other ages if the second and third groups were taken as 1978-88 and 1989-94 with estimates 0.8043 and 0.4048, respectively. Although this departs from the sequential procedure as described, the overall likelihood for this grouping is slightly greater.

(vii) The test statistics used are asymptotic and may be suspect for small sample sizes. Exact tests can be performed. However, since the transitions in the data show up as relatively sharp, it seems unlikely that exact tests will result in any consequential changes.

(viii) The sequential χ^2 tests have been carried out moving forwards in time. While this seems logical, from the purely statistical viewpoint, they might equally well have been carried out moving backwards in time from 1994. Again, because the transitions in the data show up as relatively sharp, moving backwards should give essentially the same outcome.

For years with missing data, the gap was filled by averaging the value within an age class for the year before and after the gap and assuming this average value pertained to the entire period for which no data are available. Alternative methods, such as linear interpolation could have been applied but would have been equally arbitrary.

In the model fits reported here, mark-recapture estimates for 1978, 1979, 1980 and 1980, and the aerial survey estimates for 1990 and 1994 are used. The mark-recapture estimates are critically reviewed in Warren (1991) and all but the 1994 estimate are discussed in Stenson et al. (1993). The 1994 estimate is given in Stenson et al. (1995). The model was applied to estimated pregnancy rates back to 1955 and the catch-at-age data back to 1952. Thus the pup exploitation rate parameter s was estimated from pup harvests for the three year period 1952 to 1954. Ages 12 and older were lumped into a "plus" age class in the analysis.

Results and Discussion

The estimates of pregnancy-at-age are given in Table 3 and illustrated in Fig. 2. The estimates suggest that the proportion of pregnant females aged 3 to 7+ increased in the early 1970s and then decreased abruptly in the late 1980s. These changes are, to some extent, consistent with a density dependent response by the population, if the estimated population trajectory (see below) is accurate. However, because the population trajectory estimated here depends on the pregnancy rates, caution must be used in following this line of reasoning.

Estimates of pup production and total population size for the two formulations are given in Table 4 and illustrated in Figs. 3 and 4. Parameter estimates, estimates of population growth rate, replacement population size, replacement harvest and replacement exploitation rate for both formulations are given in Table 5. A random sample of 50 population trajectories for Formulation 1 is illustrated in Fig. 5. The frequency distribution and cumulative probability plots of estimates of population size in 1994, population growth rate, replacement harvest, replacement population size and replacement exploitation rate estimated from 1000 random samples from the joint probability distribution of the model parameters are given in Figs 6-10.

Pup production trajectories estimated from the two formulations are very similar (Fig. 3). Estimates of pup production from the Winters' (1978) VPA are also plotted for comparison. The overall trend in the VPA and PM estimates are similar, however the VPA pup production in the late 1970s is substantially lower (by about 100,000 pups) than the mark-recapture estimates of the late 1970s and early 1980s. The drop in pup production in 1990 coincides with the abrupt decline in pregnancy rates.

Total population size trajectories for the two formulations are also similar. The VPA estimates at the start of the period are close to those from the PM, but diverge by as much as 500,000 animals in the 1970s (Fig. 4). Overall, the model illustrates a declining population over the 1960s, reaching a minimum in the early 1970s, and then rapidly increasing to the present. The rate at which the population is growing is estimated to have slowed slightly in recent years as a consequence of the decline in the pregnancy rate.

The trajectories of pup production and total population size estimated here are not substantially different from those estimated up to 1980 by Roff and Bowen (1983). Cooke et al. (1985) provide several different trajectories based on using different subsets of the catch data. The pup production trajectory based on the "large vessel" age samples, as an example, is not very different from the trajectory estimated here. However, pup production trajectories in Winters (1978), Roff and Bowen (1983) and Cooke et al. (1985) all gave numbers below 400,000 for the trough in pup production in the 1970s, whereas the present estimates are just above.

As indicated above, parameter estimates for the two formulations are similar (Table 5). In Formulation 1, the instantaneous rate of natural mortality (all ages), m, is 0.107, corresponding to an annual survival rate as a result of natural causes of about 90%. Lett and Benjaminsen (1977) and Winters (1978) estimated m from age composition samples from the molting patch to be 0.114 and between 0.08 and 0.109 respectively. The VPA estimates illustrated in Figs. 3 and 4 are for m = 0.1. In Formulation 2 m0 = 0.2695 and m1+ = 0.0898. Roff and Bowen (1983) estimated m = 0.075 and for their separable m formulation, m0 = 0.2175 and m1+ = 0.0725. The estimates of m for Formulations 1 and 2 are somewhat higher than those of Roff and Bowen (1983) but the Formulation 1 estimate is similar to those by Lett and Benjaminsen (1977) and Winters (1978). Note that the separable m formulation (Formulation 2) gives a very similar outcome to the age-independent m formulation (Formulation 1), confirming the finding of Roff and Bowen (1983) that models of this form are relatively insensitive to this assumption.

Calculations of replacement harvests and equivalent equilibrium population size for the two formulations are quite similar (Table 5). It is noteworthy that, assuming the 1993 age composition of the catch, population growth rate is halted at a relatively low exploitation rate (6%), although, given current population size, the equilibrium harvest (286,700) is substantially higher than the current TAC of 186,000 animals. Although harvests in the 1950s were as high as 400,000 and averaged about 300,000 over the 1960s (Table 1) the population was declining over this period.

The frequency distributions and cumulative probability plots for the population trajectory and related quantities, including replacement harvest, are underestimates of the uncertainty - they only include the variance in the model parameter estimates and are conditional on all the associated assumptions that have been made. As indicated by the 50 randomly sampled trajectories illustrated in Fig. 5, but shown more clearly in the 1000 realizations in Fig. 6, there is a range of feasible population trajectories. Ignoring the limitations of this analysis it could be considered unlikely that the present population size is below 3.5 million or above 5.1 million. Current population growth rate estimates range from 3.4% to 5% (Fig. 7). Growth rate was somewhat higher (± 8.5%) before the recent drop in pregnancy rates. Although replacement harvest may be as low as 170,000 animals, the present analysis suggests that it is around 280,000 but not higher than 300,000 animals, given the assumptions that have been made (Fig. 8). Replacement population size ranges from 3.4 million to 5.0 million (Fig. 9). Replacement exploitation rate is estimated to be about 6% but may be as low as 4.6% or has high as 7.2% (Fig. 10). It is important to note that the replacement harvest and associated exploitation rate will be quite sensitive to any changes in pregnancy rate from the assumed (1994) values.

In the two formulations considered in this working paper, only six mark-recapture and aerial survey estimates are used for fitting the model. Stenson et al. (1993) provide a composite of pup production estimates which includes estimates from VPA (Lett and Benjaminsen 1977, Winters 1978) and modified SI estimates (Cooke 1985). There are also other SI estimates available (e.g Sergeant 1975). Should all these estimates be used to fit the harp seal model? In VPA the instantaneous rate of natural mortality must be provided in order to estimate numbers at age (including pup production) from catch-at-age data and in the SI approaches a quantity or vector of quantities related to mortality are estimated. We maintain that to use estimates of pup production derived from VPA or SI methods in a model in which the natural mortality rate is estimated would be circular and illogical.

There are essentially three kinds of information that relate to estimating the population size of harp seals in the northwest Atlantic: (i) age composition samples (from commercial harvests, research on molting patches and research on pregnant females); (ii) samples of pregnancy at age; and (iii) survey estimates of pup production. Future research into combining these sources of information in a single estimation procedure needs to be considered. The best approach may be an extension of the methods of Cooke (1985) and Cooke et al. (1985) in that likelihood equations are developed to describe the combined probability of all sampled values for different estimates of a few parameters that, when used in a population model, describe the trajectory of the population. In using the age composition of the catch, the variability in the selectivities of 1-year old and 2-year old animals (Roff and Bowen 1985, Cook et al. 1985), problems with respect to missing catch data and the very low overall selectivity on 1+ animals (Shelton et al. 1992) will be important considerations. Research samples of the age composition of seals on the molting patch for the period 1967 to 1983 (Roff and Bowen 1986) and 1992/95 (Stenson and Sjare, unpublished data) have a broader age composition than the commercial hunt data and are likely to be of most value, despite the bias in these kinds of samples documented by Roff and Bowen (1986).

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Year	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13	Age 14	Age 15	Age 16	Age 17	Age 18	Age 19	Age 20	Age 21	Age 22	Age 23	Age 24	Age 25	Total
1952	207800	7939	12105	8279	6321	7143	12212	8400	8177	5910	6770	6457	1743	1638	2411	4205	1544	2349	1892	988	5363	992	74	487	1336	1873	324408
1953	207712	23415	7530	6418	4396	3960	3235	2855	2915	2766	2358	3539	1617	1211	972	1901	1899	1380	880	656	2789	1627	915	642	467	374	288429
1954	186253	35151	14146	5539	6033	3529	4080	3440	3377	2125	3121	2211	2619	2479	1300	1736	2245	1019	340	1124	626	323	309	707	152	1102	285086
1955	261471	23964	9134	6327	4948	4070	3956	3377	3510	3020	3292	3503	2206	1707	1378	2357	2278	1491	910	932	2570	1317	808	669	589	857	350641
1956	347879	13991	5305	3777	3024	2393	2303	2020	2027	1736	1928	2246	1284	1057	855	1407	1307	864	497	518	1420	753	475	357	323	524	400270
1957	173121	23875	8853	6680	5888	4793	4679	3658	3737	3109	3468	3620	2276	1871	1391	2377	2180	1471	804	838	2475	1306	796	671	582	1033	265552
1958	150916	27050	10962	11685	11365	9828	6378	6086	4999	4887	9733	6376	6958	4001	3104	8904	5905	2998	545	1530	5377	2921	2430	994	1940	3420	311292
1959	244112	23615	9549	7664	5052	4176	4223	3439	3256	2781	3198	3167	2124	1670	1273	2339	2209	1429	769	803	2467	1321	801	634	544	813	333428
1960	165659	35044	13243	9350	7714	5882	5860	4887	4801	4191	4693	4763	3133	2522	1801	3486	3220	2082	1101	1175	3640	1946	1163	951	806	1250	294363
1961	175893	7092	2641	2370	2632	1622	1137	1252	971	789	1127	1224	323	355	433	435	381	294	218	201	243	44	179	85	40	195	202176
1962	212095	31029	34823	10145	8941	6208	3092	2461	2565	2554	1233	1762	1959	958	1418	1856	734	1747	757	651	1338	223	617	98	195	714	330173
1963	276283	10361	8751	7326	4274	3489	3869	3873	3590	3277	3769	4191	2615	2855	2802	2103	2635	1807	1179	961	930	850	606	463	397	589	353845
1964	271745	6500	5836	6067	7317	4912	6995	3765	3075	2742	4172	2770	2174	1710	1639	2658	2092	2520	3892	2035	88	1979	989	983	1471	2477	352603
1965	188184	12952	6501	5317	5139	6248	5921	2471	984	867	1435	1131	1612	193	1208	1046	622	336	658	699	287	455	259	33	18	728	245304
1966	255874	14385	11278	5189	4849	5206	5133	4934	3384	1783	1987	2793	1745	1505	1745	1484	1382	1021	1613	996	1088	787	317	638	402	1050	332568
1967	280257	14683	6826	2992	2452	2931	3784	3232	2438	1553	1465	2108	1334	1002	1438	1541	1064	1307	1362	1405	906	585	462	504	283	943	338857
1968	160595	7530	4865	3590	2371	2225	1766	2576	2566	1818	1874	1898	1025	1001	1201	1092	980	818	1151	982	738	464	567	316	245	567	204821
1969	237103	21346	3905	3422	2722	3099	2200	2241	2980	2397	2117	2107	1181	1286	1300	1419	944	1402	911	1055	958	605	394	475	243	829	298641
1970	221075	9399	7603	2865	2345	2204	1352	1394	1309	1074	1566	1392	994	716	630	721	810	399	453	444	383	305	231	172	111	203	260150
1971	212854	8281	3098	2068	1328	1011	745	608	485	648	648	897	521	315	268	281	218	184	225	172	231	152	131	90	51	305	235815
1972	120263	4862	2798	1745	1475	746	657	664	417	364	402	814	457	329	313	352	276	190	165	103	151	63	176	16	18	44	137860
1973	103435	7060	4875	3264	2575	3583	1845	1129	1460	782	819	1306	574	570	400	481	452	285	179	222	225	103	85	71	54	271	136105
1974	119413	13192	7783	3370	2556	2407	2771	1358	1051	1002	755	881	680	700	524	421	382	316	307	193	116	85	94	79	130	432	160998
1975	144449	14183	6247	3276	1886	1371	1282	1104	674	580	925	558	456	375	265	389	301	259	161	218	158	114	92	94	96	87	179600
1976	136974	15565	7691	4166	2563	743	395	410	419	182	159	400	232	124	172	144	118	79	75	49	78	34	47	48	33	35	170935
1977	134893	9222	6831	6580	5066	3075	1702	1081	681	407	507	537	291	233	448	463	271	120	81	83	84	45	36	41	38	98	172914
1978	121058	18409	11010	5958	3938	2532	1846	663	823	290	815	224	243	279	122	286	107	143	182	98	152	123	118	47	41	93	169600
1979	139200	16161	7580	4345	2691	2009	1459	1058	729	515	796	268	260	179	294	391	208	195	72	84	200	120	110	44	47	625	179640
1980	136182	18205	9770	6269	4249	3305	2243	1690	1117	756	410	665	699	470	576	656	393	413	184	255	295	135	108	100	104	152	189401
1981	184593	9164	5038	3830	2409	1887	1748	1027	845	482	417	575	398	269	282	382	304	407	266	245	207	238	221	113	91	249	215687
1982	153096	14996	7195	3444	1727	1307	715	733	425	351	346	302	227	166	173	336	155	234	115	182	233	124	87	108	74	193	187044
1983	58544	7608	4576	2714	1416	1150	943	679	535	350	409	289	295	164	216	375	182	217	177	156	212	111	76	101	95	169	81759
1984	31850	5906	5315	2806	1729	921	722	582	420	336	386	264	256	145	155	275	130	175	114	124	180	84	100	64	71	105	53215
1985	21690	6725	4913	2517	1222	747	591	536	388	281	341	213	215	147	226	359	166	171	144	152	189	85	71	82	71	119	42361
1986	28240	4747	3366	2412	1210	662	562	419	328	263	310	226	229	136	168	264	131	161	121	122	182	104	78	75	82	149	44747
1987	40951	5686	4139	3369	2234	1171	1012	806	591	536	479	441	308	240	244	377	238	249	177	173	282	161	95	155	161	694	64969
1988	74244	10722	9602	5489	3500	1937	1689	805	776	534	390	308	342	382	310	443	380	304	363	456	500	171	116	154	293	770	114980
1989	61173	6759	5129	3377	2167	1514	1068	481	352	286	389	307	295	205	163	309	203	157	245	135	236	142	275	153	159	329	86008
1990	40482	8905	5952	5141	4128	3515	1849	1060	432	644	581	844	695	675	342	639	255	406	308	106	498	84	211	275	73	1056	79156
1991	49673	6005	3395	2740	2527	1994	1251	642	452	386	461	537	485	395	252	421	157	246	218	186	190	84	152	67	152	431	73499
1992	51155	10763	7125	4024	3173	2257	2040	1549	819	1033	676	526	370	270	289	305	414	487	318	539	224	157	79	210	147	594	89543
1993	23695	7095	4659	2673	1833	1250	1116	867	513	572	459	348	273	183	196	253	242	283	192	293	180	116	73	129	103	341	47937

Table 1. Catch at age for the northwest Atlantic harp seal.

Table 2. Proportion of females pregnant at age from samples together with sample sizes.

Year		Age 3		Age 4		Age 5		Age 6		Age 7+
	Prop	N	Prop	N	Prop	N	Prop	N	Prop	N
1954	0.00	4	0.33	3	0.67	3	0.75	16	0.88	33
1955										
1956										
1957										
1958										
1959										
1960										
1961										
1962										
1963										
1964										
1965	0.03	30	0.11	44	0.54	37	0.71	38	0.88	109
1966	0.00	7	0.11	9	0.35	17	0.73	11	0.88	49
1967	0.00	10	0.21	19	0.61	33	0.97	29	0.89	123
1968	0.00	27	0.32	19	0.70	20	0.92	12	0.87	55
1969	0.04	25	0.16	25	0.44	16	0.82	28	0.88	164
1970	0.00	13	0.23	13	0.50	12	0.90	10	0.86	107
1971										
1972										
1973										
1974										
1975										
1976										
1977										
1978	0.03	40	0.61	38	0.90	20	0.67	9	0.85	41
1979	0.33	9	0.67	9	1.00	3	1.00	4	0.91	11
1980	0.00	2	0.50	2	1.00	1			0.83	12
1981	0.20	5	0.50	4	0.50	2	0.86	7	0.78	18
1982	0.00	4	0.40	5	1.00	1	0.75	4	0.33	3
1983										
1984										
1985	0.00	4	0.33	3	0.40	5	1.00	3	1.00	1
1986	1.00	1			0.50	2	0.00	1	1.00	7
1987	0.17	12	0.38	8	0.78	9	1.00	4	0.63	24
1988	0.06	16	0.17	6	1.00	3			0.74	19
1989	0.00	8	0.00	9	0.33	6	0.67	3	0.95	22
1990	0.00	8	0.14	7	0.33	3	0.00	1	0.60	10
1991	0.09	11	0.18	11	0.57	7	0.33	3	0.61	28
1992	0.20	10	0.27	11	0.44	9	0.75	8	0.66	32
1993	0.00	8	0.12	17	0.00	4	0.75	8	0.39	23
1994	0.05	20	0.14	14	0.46	13	0.50	6	0.83	30

Table 3. Estimates of pregnancy at age (see text for method used).

Year	Age 3	Age 4	Age 5	Age 6	Age 7+
1955	0.0172	0.1818	0.5435	0.7231	0.8648
1956	0.0172	0.1818	0.5435	0.7231	0.8648
1957	0.0172	0.1818	0.5435	0.7231	0.8648
1958	0.0172	0.1818	0.5435	0.7231	0.8648
1959	0.0172	0.1818	0.5435	0.7231	0.8648
1960	0.0172	0.1818	0.5435	0.7231	0.8648
1961	0.0172	0.1818	0.5435	0.7231	0.8648
1962	0.0172	0.1818	0.5435	0.7231	0.8648
1963	0.0172	0.1818	0.5435	0.7231	0.8648
1964	0.0172	0.1818	0.5435	0.7231	0.8648
1965	0.0172	0.1818	0.5435	0.7231	0.8648
1966	0.0172	0.1818	0.5435	0.7231	0.8648
1967	0.0172	0.1818	0.5435	0.8684	0.8648
1968	0.0172	0.1818	0.5435	0.8684	0.8648
1969	0.0172	0.1818	0.5435	0.8684	0.8648
1970	0.0172	0.1818	0.5435	0.8684	0.8648
1971	0.057	0.36625	0.7162	0.8684	0.8648
1972	0.057	0.36625	0.7162	0.8684	0.8648
1973	0.057	0.36625	0.7162	0.8684	0.8648
1974	0.057	0.36625	0.7162	0.8684	0.8648
1975	0.057	0.36625	0.7162	0.8684	0.8648
1976	0.057	0.36625	0.7162	0.8684	0.8648
1977	0.057	0.36625	0.7162	0.8684	0.8648
1978	0.0968	0.5507	0.8043	0.8684	0.8648
1979	0.0968	0.5507	0.8043	0.8684	0.8648
1980	0.0968	0.5507	0.8043	0.8684	0.8648
1981	0.0968	0.5507	0.8043	0.8684	0.8648
1982	0.0968	0.5507	0.8043	0.8684	0.8648
1983	0.0968	0.5507	0.8043	0.8684	0.8648
1984	0.0968	0.5507	0.8043	0.8684	0.8648
1985	0.0968	0.5507	0.8043	0.8684	0.8648
1986	0.0968	0.5507	0.8043	0.8684	0.8648
1987	0.0968	0.5507	0.8043	0.8684	0.8648
1988	0.0968	0.1467	0.8043	0.8684	0.8648
1989	0.0615	0.1467	0.4048	0.8684	0.8648
1990	0.0615	0.1467	0.4048	0.6154	0.6341
1991	0.0615	0.1467	0.4048	0.6154	0.6341
1992	0.0615	0.1467	0.4048	0.6154	0.6341
1993	0.0615	0.1467	0.4048	0.6154	0.6341

Table 4. Pup production and total population size estimates for the period 1955 to 1995 for model Formulation 1 (mortality on pups = mortality on the 1+ population) and Formulation 2 (mortality on pups = 3 times the mortality on the 1+ population).

	Formulation 1		Formulation 2	
Year	Pups	Total population	Pups	Total population
1955	509184.23	2804495	496789.91	2624143.7
1956	522981.19	2709660.3	512220.12	2542104.8
1957	540463.69	2594927.3	531350.92	2450064.9
1958	543818.95	2622906.4	536528.73	2469549.5
1959	513605.73	2574474.6	508150.32	2410979.7
1960	493130.28	2489518.7	489250.1	2336302.3
1961	461990.88	2419095.3	458762.61	2265405.4
1962	470566.86	2451785.7	465879.22	2302048
1963	471671.04	2360945.4	465923.32	2217834.9
1964	464005.04	2249252	458021.85	2120411.2
1965	452062.83	2138164.1	446053.2	2021050.4
1966	447384.18	2135397.2	442061.05	2017477.7
1967	441952.23	2044777.1	436939.46	1936905.1
1968	426807.11	1942276.8	423722.2	1848629.4
1969	412931.79	1963366.3	411328.36	1866860.4
1970	401861.47	1882322.1	401038.57	1797432.3
1971	414091.75	1858237.9	411773.82	1780531
1972	411913.35	1857490.2	410647.66	1784314.6
1973	411835.09	1949575.5	411856.12	1868241.5
1974	405049.72	2027164.3	406954.57	1938906.3
1975	400543.91	2068756.7	403909.96	1979906
1976	410603.35	2098544.7	413904.83	2013988.6
1977	432298.38	2155207.3	434716.4	2071560.6
1978	473797.75	2245725.5	473145.45	2157266.9
1979	482037.37	2338409.1	482464.92	2240143.8
1980	490971	2421075.8	492490.61	2317779.2
1981	501574.76	2496679.8	503292.45	2388232.4
1982	523566.57	2561667	524187.58	2454386.2
1983	549680.56	2673298.2	549373.13	2559331.6
1984	575235.63	2898902.4	574748.72	2762639.9
1985	595699.88	3149056.2	595943.19	2988952.9
1986	625364.15	3413694.8	625345.33	3230817.9
1987	677094.89	3700862.3	674556.07	3495443
1988	672270.76	3934806.6	673714.78	3711758.4
1989	667203.48	4092470.6	672347.11	3865670.6
1990	560521.69	4154860.1	560154.43	3920017
1991	603707.33	4260577.8	602308.86	4032016.1
1992	647392.34	4404579.6	645462.53	4178062.4
1993	683227.17	4554551.2	681963.65	4326467.8
1994	714525.13	4759984.9	715017.01	4525148.4

Table 5. Comparison of estimates from model Formulations 1 and 2.

Model estimates	Model 1	Model 2
	M0=M1+	M0=3*M1+
Instantaneous mortality rate	0.107364154	0.089826031
Pups		0.269478093
Proportion survival rate	0.898198531	0.914090195
Pups		0.763778011
1/Exploitation rate on pups (1952-54)	2.912800865	2.92833602
Exploitation rate (pups)	0.343312175	0.341490865
Total population size		
1993	4554551.2	4326467.8
1994	4759984.9	4525148.4
Growth rate	1.045105147	1.045922126
Number of pups in 1994	714525.13	715017.01
Approximate replacement		
Replacement population size	5030000	4648000
Replacement harvest	286700	274450
Exploitation rate	0.06	0.06

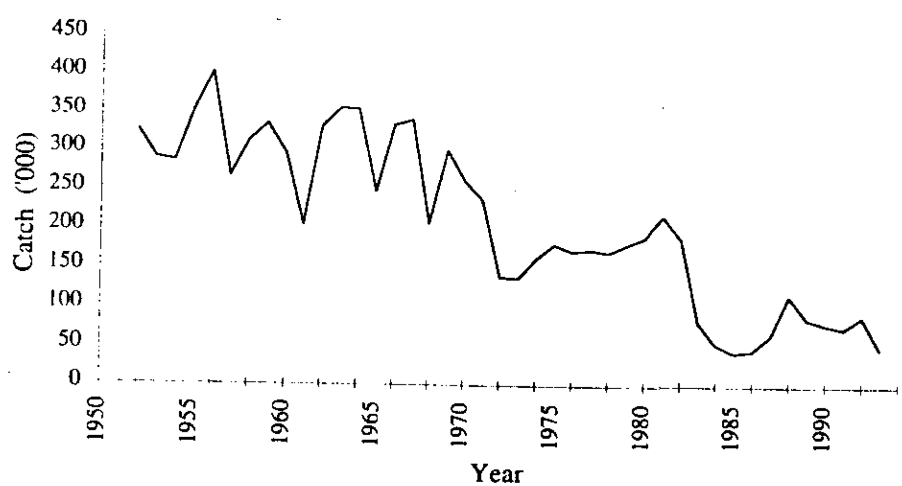

Fig. 1. Total annual catch for the period 1952 to 1994.

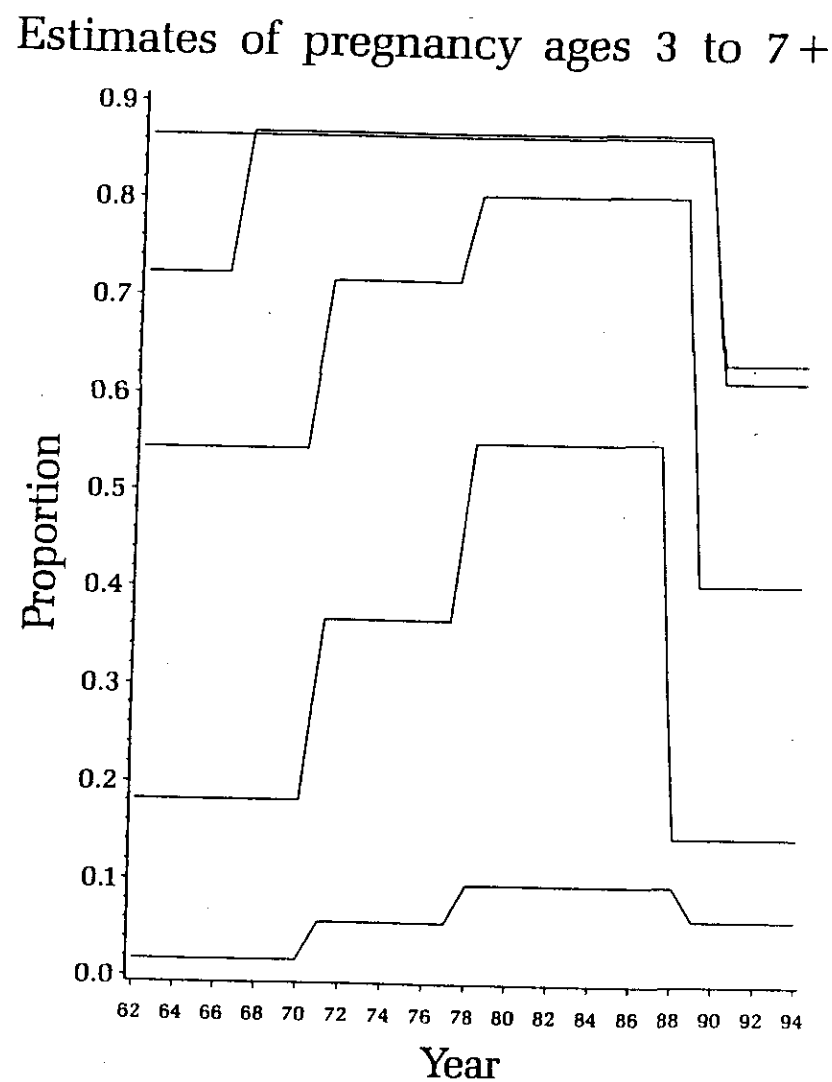

Fig. 2. Estimates of proportion of females pregnant-at-age used in the model.

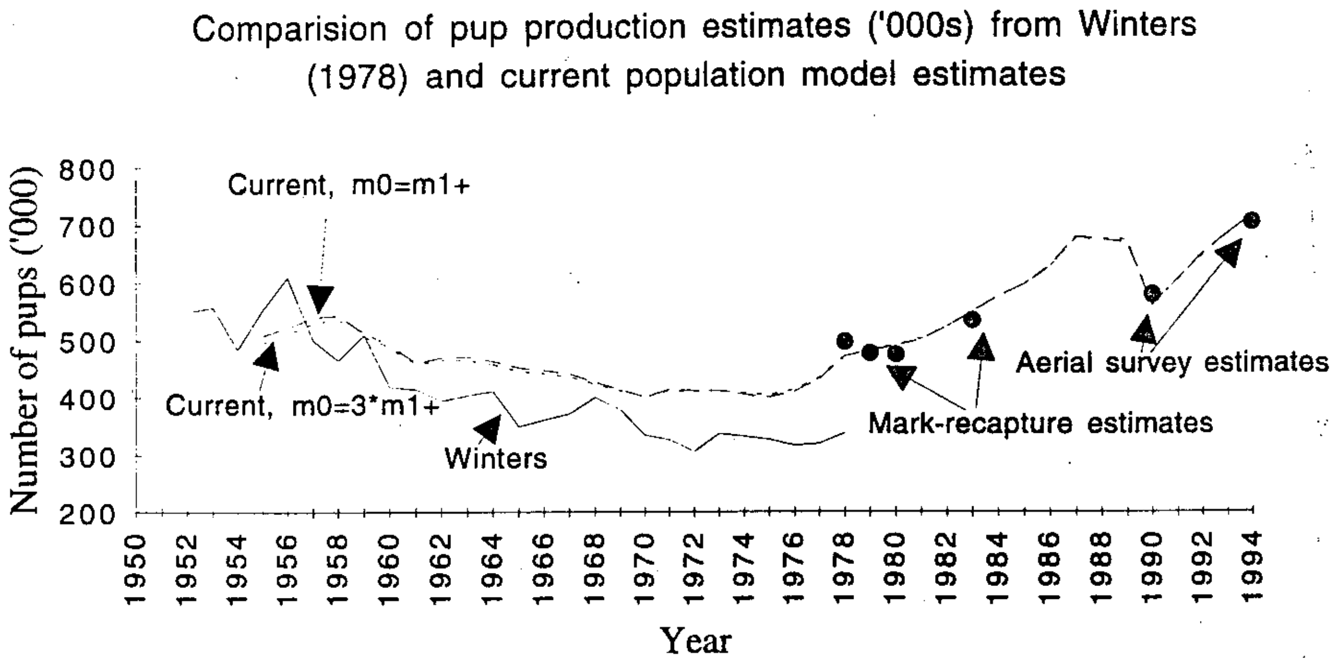

Fig. 3. Trajectories of pup production for the period 1955 to 1994 from the model fit to the 6 survey estimates of pup production. The trajectory from the VPA estimates by Winters (1978) is shown for comparison.

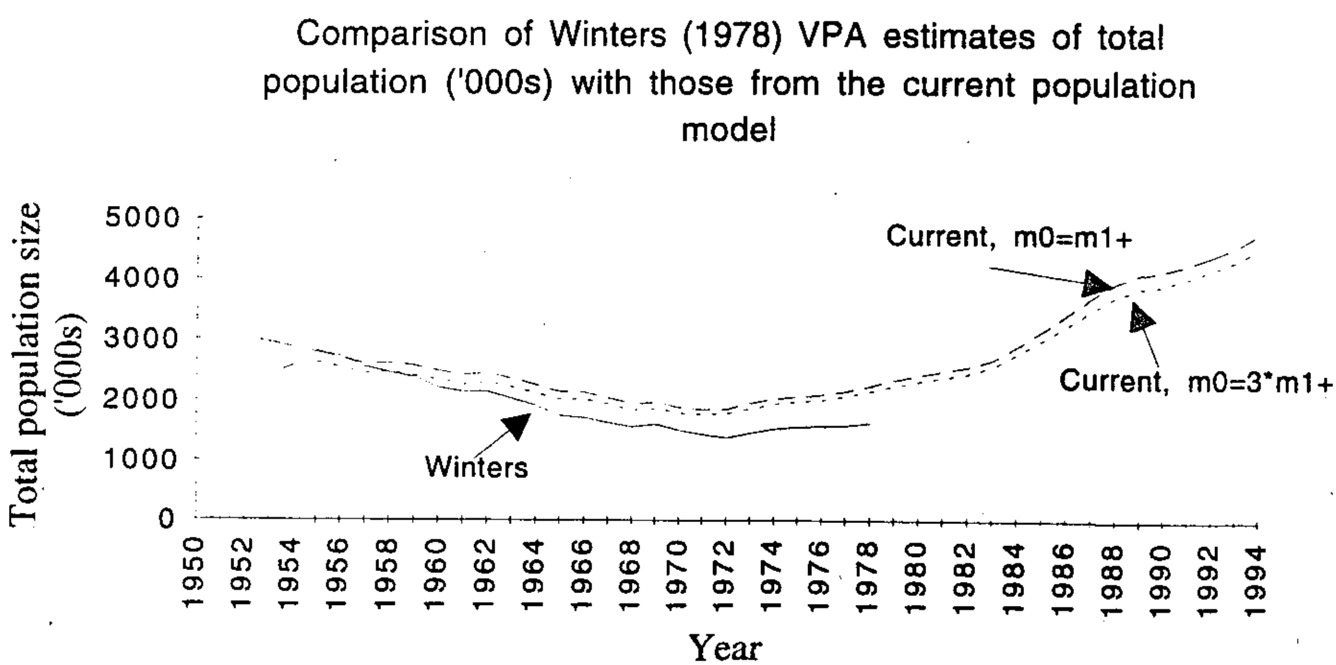

Fig. 4. Trajectories of total population size for the period 1955 to 1994 from the fit of the two formulations of the model to the survey estimates of pup production. The trajectory of total population size from the VPA by Winters (1978) is shown for comparison.

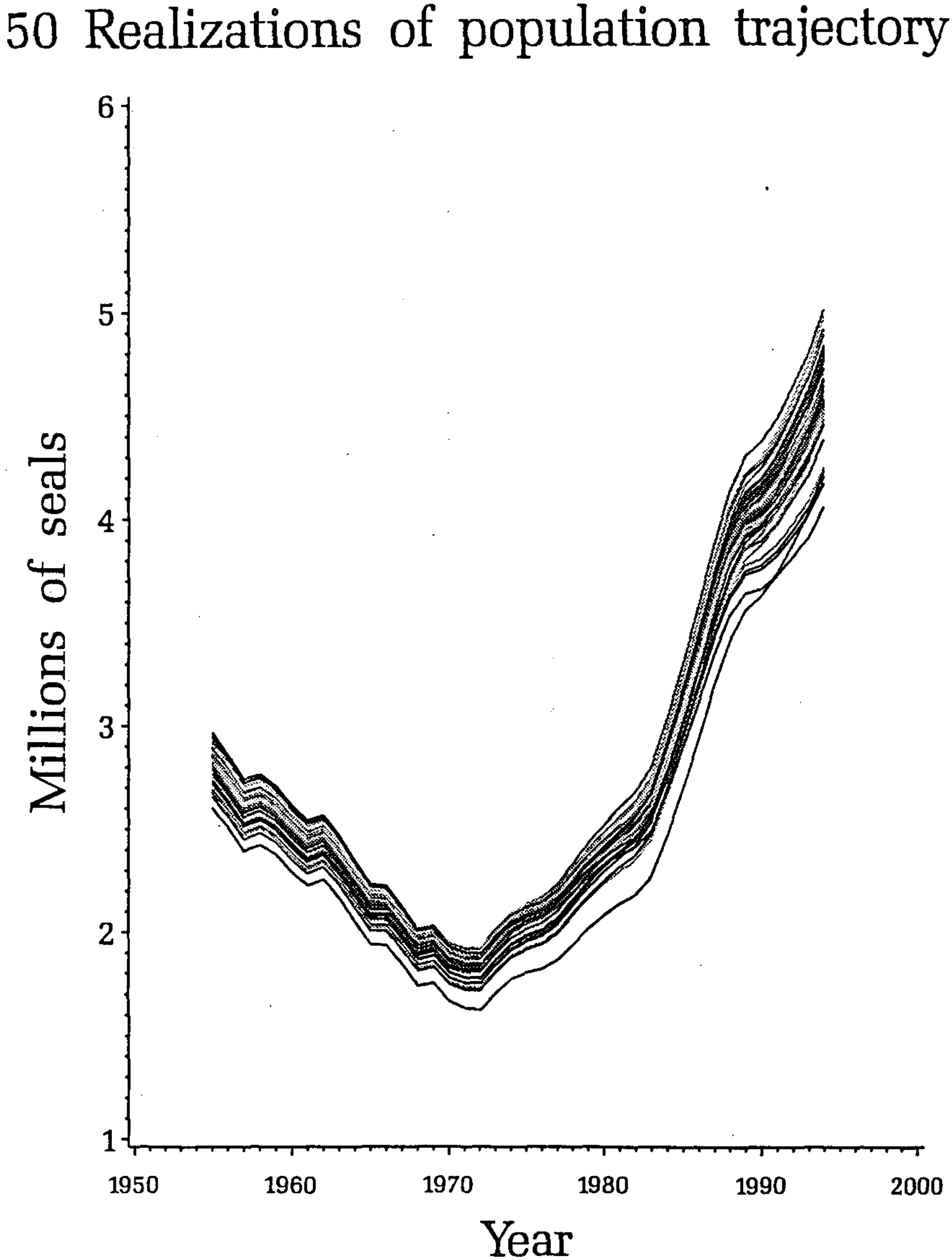

Fig. 5. A random sample of 50 trajectories of total population size from the joint probability distribution of the model parameters for Formulation 1 (pup mortality = mortality on the 1+ population).

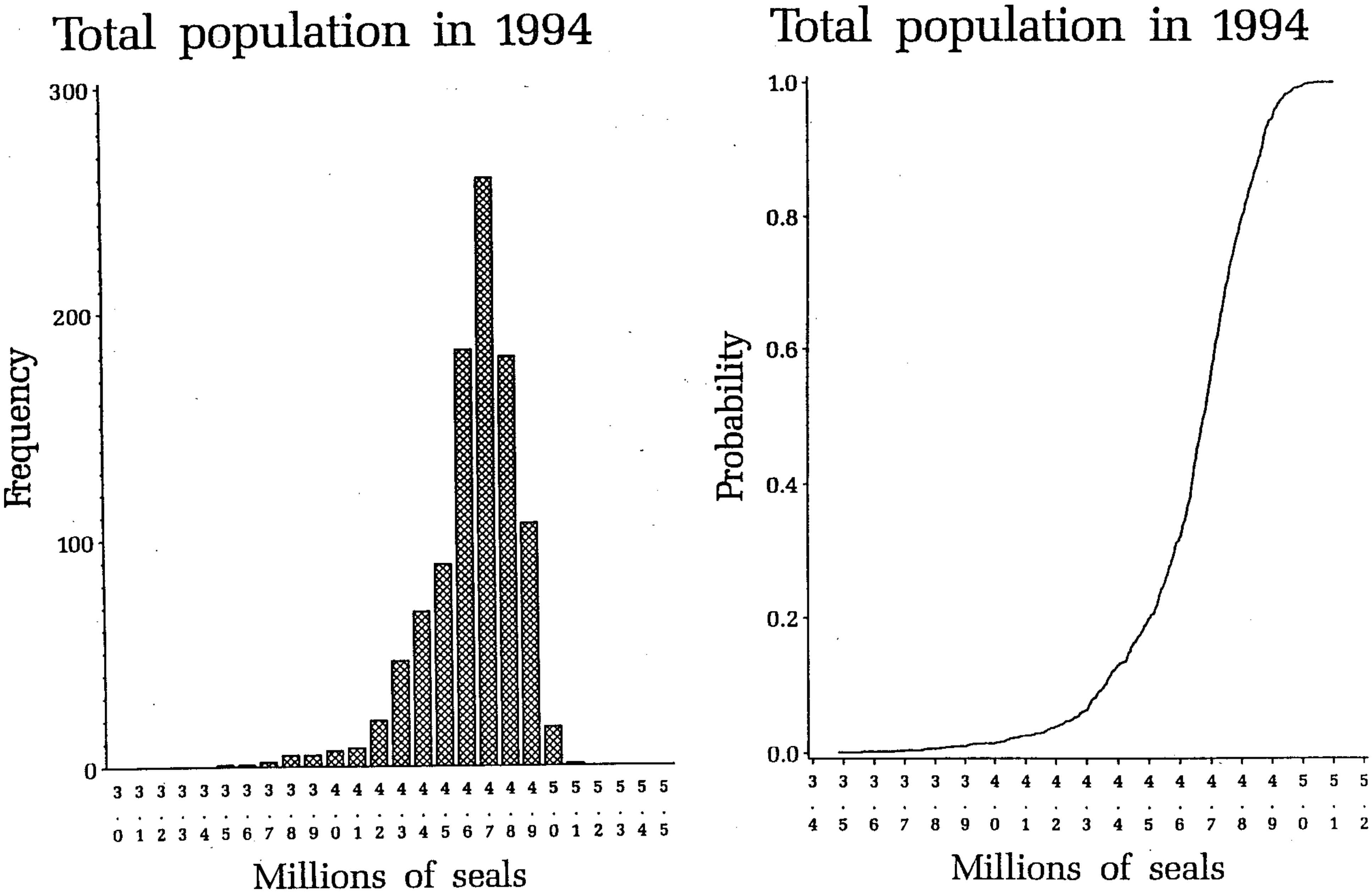

Fig. 6. Frequency and cumulative probability distribution plots for the total population size in 1994 obtained from 500 random samples from the joint probability distribution of the model parameters for Formulation 1.

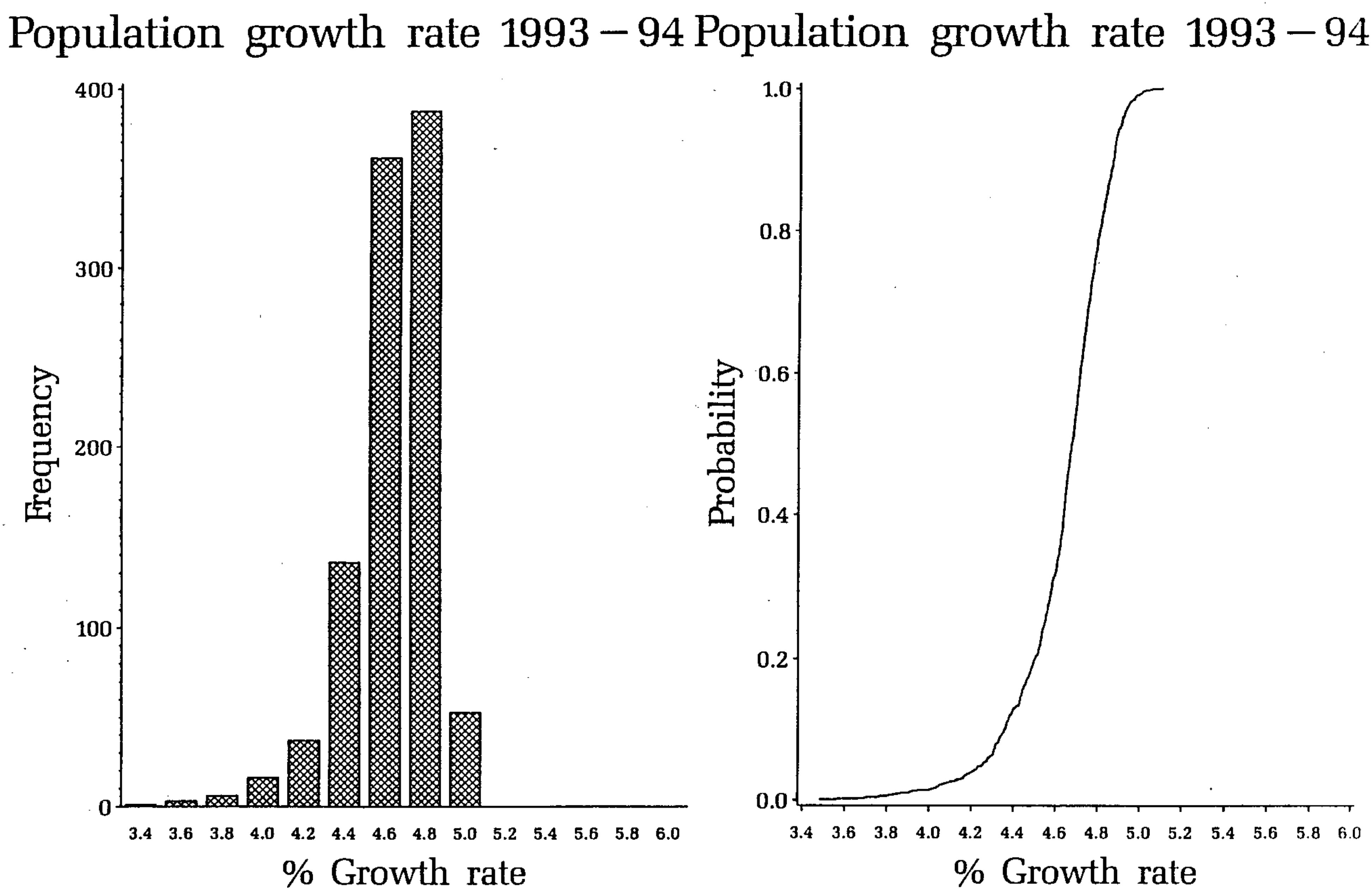

Fig. 7. Frequency and cumulative probability distribution plots for the total population percentage growth rate (1994 over 1993) obtained from 500 random samples from the joint probability distribution of the model parameters for Formulation 1

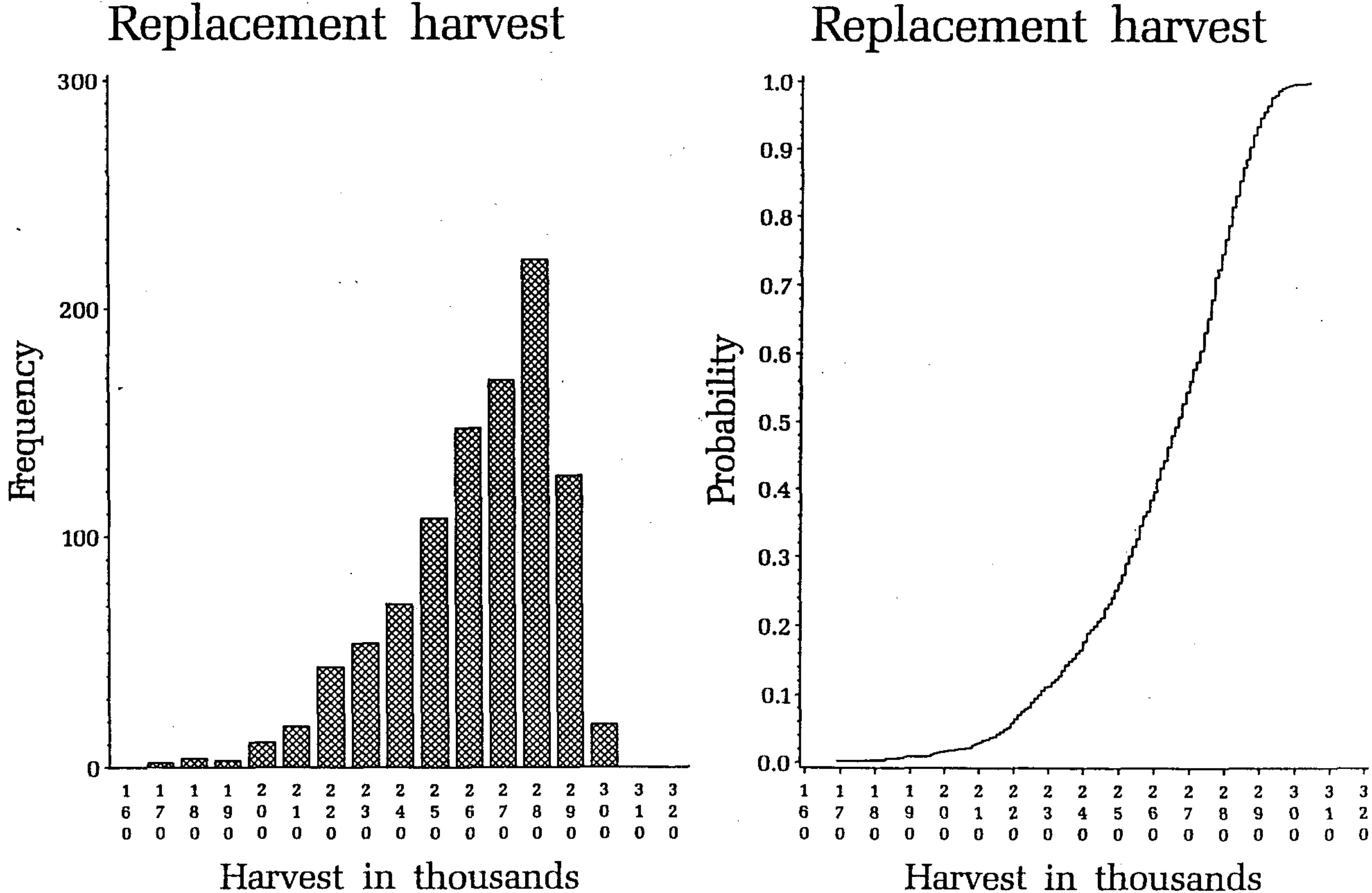

Fig. 8. Frequency and cumulative probability distribution plots for the replacement harvest obtained from 500 random samples from the joint probability distribution of the model parameters for Formulation 1.

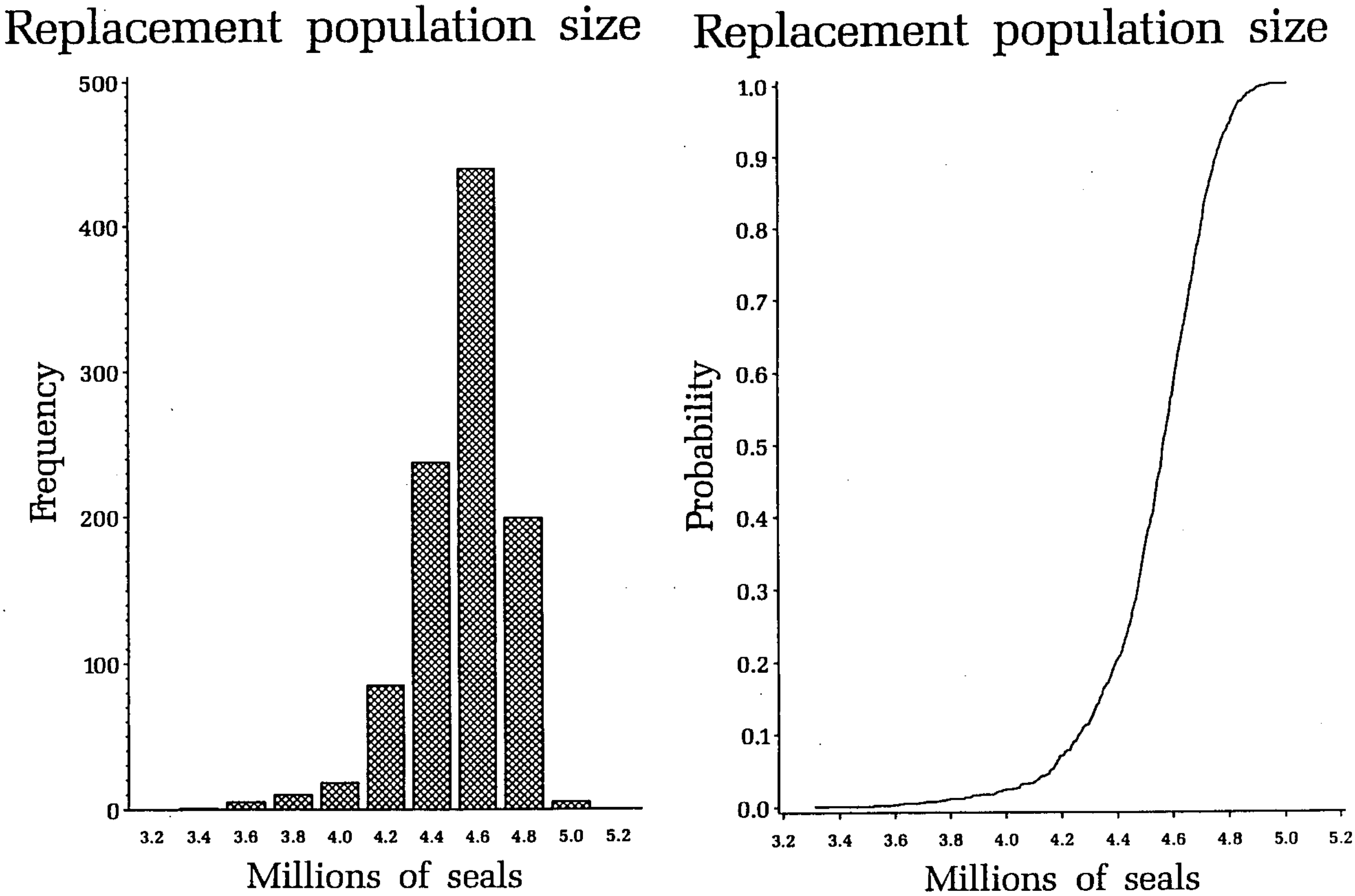

Fig. 9. Frequency and cumulative probability distribution plots for the population size at replacement from 500 random samples from the joint probability distribution of the model parameters for Formulation 1.

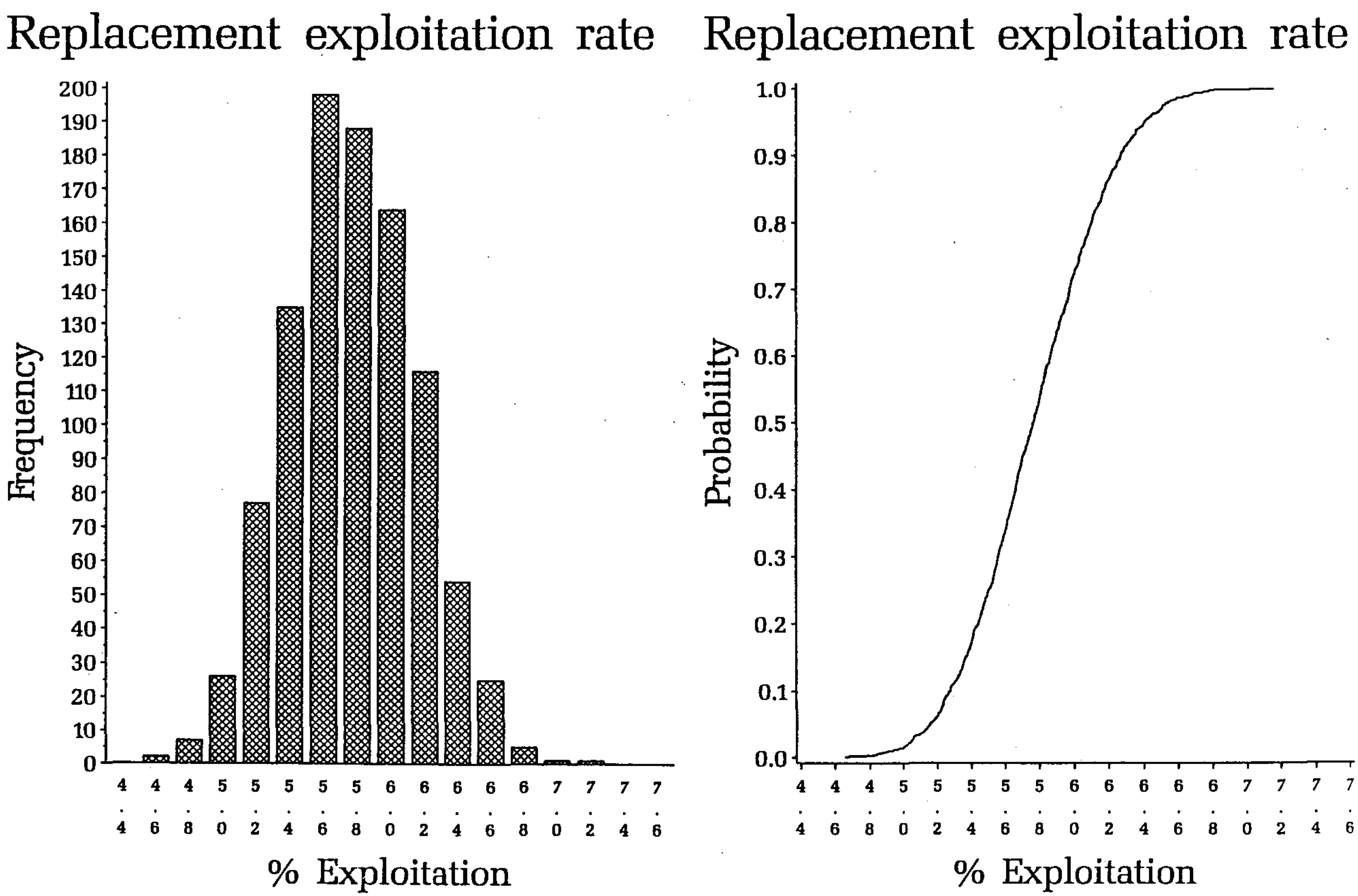

Fig. 10. Frequency and cumulative probability distribution plots for the replacement harvest exploitation rate (%) from 500 random samples from the joint probability distribution of the model parameters for Formulation 1.