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Model Estimates of Harp Seal Numbers-at-age for the Northwest Atlantic

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Abstract

Survey estimates of pup production by the harp seal (*Phoca groenlandica*) population in the Northwest Atlantic, estimates of annual pregnancy rates, and annual catch-at-age data are used to fit a two parameter age structured population model which describes trajectories of numbers at age for the period 1955 to 1994. Two formulations are considered – one in which the pup mortality rate is equal to that of the 1+ population and another in which the pup mortality rate is 3 times the 1+ mortality rate. The uncertainty associated with the population trajectory from the first formulation and related quantities including replacement harvest, are explored by randomly resampling from the joint probability distribution of the estimated model parameters. The total population is estimated to be about 4.8 million in 1994 and to be growing at about 5% per year. The estimated replacement harvest at current population size is about 286 700 animals, exceeding the current TAC of 186 000 animals.

Key words: Harp seals, population model, population size, replacement harvest

Introduction

Various approaches to estimating the size of the harp seal (*Phoca groenlandica*) 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), 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 was viewed as a Poisson-distributed random variable. By taking into account selectivity and cumulative survival to age, he developed a multinominal 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.

The VPA method (more correctly the Pope (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 was therefore more similar to the approach of Cooke *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 is 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 here applied to six well-documented independent survey (mark-recapture and aerial) estimates of pup production. Two formulations were considered, Formulation 1 in which the natural mortality rate on pups was the same as that on the 1+ population, and Formulation 2 in which the natural mortality on the pups was 3 times the mortality on the 1+ population. Estimates of replacement harvest were 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 were 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 were available, it was assumed that the annual pup catch was 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 were 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 was 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 was 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 were obtained using PROC NLIN in SAS applying the Newton iterative method. Following the statistical model given above, the survey estimates of pup production were 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 1 000 random samples of pairs of parameter values. This provided 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, was available at the time of the analysis). 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.* (MS 1992). The pregnancy-at-age sample data are given in Table 2.

The pregnancy-rate data (Table 2) was 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 were 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 started by forming the 2 times 2 contingency table:

$$\begin{array}{ccc|c} x_1 & n_1 & -x_1 & n_1 \\ x_1 & n_1 & -x_1 & n_1 \\ \hline x & n & -x & n_1 \end{array}$$

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:

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

where $x_{..} = x+x_3$, etc. This procedure was continued as long as 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 1979–94. For consistency with ages 4 and 5, it seemed preferable to place 1978 with 1979–94. Also, although not significant, there was a drop in the rate after 1988 which was 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

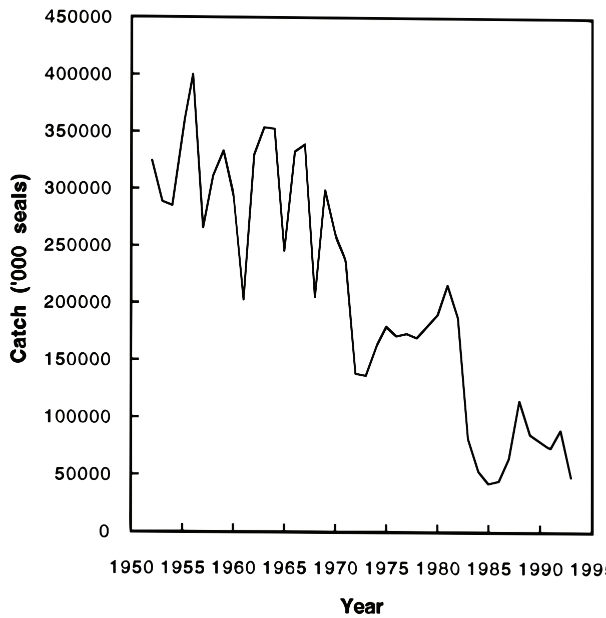

Fig. 1. Total annual catch in numbers for the period 1952 to 1994.

ratio for 1988 seemed more consistent with the ratios of the following years. Further, placing the break between 1987 and 1988 resulted in a slightly greater likelihood value for all data combined.

iii) For age 5, the procedure indicated a drop in rate for 1993 followed in 1994 by a return to more or less the rate prior to 1993. There was a reluctance to have different rates for isolated individual years, and since the sample size in 1993 was only 4, it seemed reasonable to combine 1993 with 1985–92 and 1994.

iv) For the same reason, for age 6, 1986 was included in the set 1967–89. The increase in rate between 1966 and 1967 appeared genuine.

v) For age 7+, the ratios in 1989 and 1994 were 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 departed from the sequential procedure as described, the overall likelihood for this grouping was slightly greater.

TABLE 1. Catch-at-age for the Northwest Atlantic harp seal.

	Age													
Year	0	1	2	3	4	5	6	7	8	9	10	11	12	13
1952	207 800	7 939	12 105	8 279	6 321	7 143	12 212	8 400	8 177	5 910	6 770	6 457	1 743	1 638
1953	207 712	23 415	7 530	6 418	4 396	3 960	3 235	2 855	2 915	2 766	2 358	3 539	1 617	1 211
1954	186 253	35 151	14 146	5 539	6 033	3 529	4 080	3 440	3 377	2 125	3 121	2 211	2 619	2 479
1955	261 471	23 964	9 134	6 327	4 948	4 070	3 956	3 377	3 510	3 020	3 292	3 503	2 206	1 707
1956	347 879	13 991	5 305	3 777	3 024	2 393	2 303	2 020	2 027	1 736	1 928	2 246	1 284	1 057
1957	173 121	23 875	8 853	6 680	5 888	4 793	4 679	3 658	3 737	3 109	3 468	3 620	2 276	1 871
1958	150 916	27 050	10 962	11 685	11 365	9 828	6 378	6 086	4 999	4 887	9 733	6 376	6 958	4 001
1959	244 112	23 615	9 549	7 664	5 052	4 176	4 223	3 439	3 256	2 781	3 198	3 167	2 124	1 670
1960	165 659	35 044	13 243	9 350	7 714	5 882	5 860	4 887	4 801	4 191	4 693	4 763	3 133	2 522
1961	175 893	7 092	2 641	2 370	2 632	1 622	1 137	1 252	971	789	1 127	1 224	323	355
1962	212 095	31 029	34 823	10 145	8 941	6 208	3 092	2 461	2 565	2 554	1 233	1 762	1 959	958
1963	276 283	10 361	8 751	7 326	4 274	3 489	3 869	3 873	3 590	3 277	3 769	4 191	2 615	2 855
1964	271 745	6 500	5 836	6 067	7 317	4 912	6 995	3 765	3 075	2 742	4 172	2 770	2 174	1 710
1965	188 184	12 952	6 501	5 317	5 139	6 248	5 921	2 471	984	867	1 435	1 131	1 612	193
1966	255 874	14 385	11 278	5 189	4 849	5 206	5 133	4 934	3 384	1 783	1 987	2 793	1 745	1 505
1967	280 257	14 683	6 826	2 992	2 452	2 931	3 784	3 232	2 438	1 553	1 465	2 108	1 334	1 002
1968	160 595	7 530	4 865	3 590	2 371	2 225	1 766	2 576	2 566	1 818	1 874	1 898	1 025	1 001
1969	237 103	21 346	3 905	3 422	2 722	3 099	2 200	2 241	2 980	2 397	2 117	2 107	1 181	1 286
1970	221 075	9 399	7 603	2 865	2 345	2 204	1 352	1 394	1 309	1 074	1 566	1 392	994	716
1971	212 854	8 281	3 098	2 068	1 328	1 011	745	608	485	648	648	897	521	315
1972	120 263	4 862	2 798	1 745	1 475	746	657	664	417	364	402	814	457	329
1973	103 435	7 060	4 875	3 264	2 575	3 583	1 845	1 129	1 460	782	819	1 306	574	570
1974	119 413	13 192	7 783	3 370	2 556	2 407	2 771	1 358	1 051	1 002	755	881	680	700
1975	144 449	14 183	6 247	3 276	1 886	1 371	1 282	1 104	674	580	925	558	456	375
1976	136 974	15 565	7 691	4 166	2 563	743	395	410	419	182	159	400	232	124
1977	134 893	9 222	6 831	6 580	5 066	3 075	1 702	1 081	681	407	507	537	291	233
1978	121 058	18 409	11 010	5 958	3 938	2 532	1 846	663	823	290	815	224	243	279
1979	139 200	16 161	7 580	4 345	2 691	2 009	1 459	1 058	729	515	796	268	260	179
1980	136 182	18 205	9 770	6 269	4 249	3 305	2 243	1 690	1 117	756	410	665	699	470
1981	184 593	9 164	5 038	3 830	2 409	1 887	1 748	1 027	845	482	417	575	398	269
1982	153 096	14 996	7 195	3 444	1 727	1 307	715	733	425	351	346	302	227	166
1983	58 544	7 608	4 576	2 714	1 416	1 150	943	679	535	350	409	289	295	164
1984	31 850	5 906	5 315	2 806	1 729	921	722	582	420	336	386	264	256	145
1985	21 690	6 725	4 913	2 517	1 222	747	591	536	388	281	341	213	215	147
1986	28 240	4 747	3 366	2 412	1 210	662	562	419	328	263	310	226	229	136
1987	40 951	5 686	4 139	3 369	2 234	1 171	1 012	806	591	536	479	441	308	240
1988	74 244	10 722	9 602	5 489	3 500	1 937	1 689	805	776	534	390	308	342	382
1989	61 173	6 759	5 129	3 377	2 167	1 514	1 068	481	352	286	389	307	295	205
1990	40 482	8 905	5 952	5 141	4 128	3 515	1 849	1 060	432	644	581	844	695	675
1991	49 673	6 005	3 395	2 740	2 527	1 994	1 251	642	452	386	461	537	485	395
1992	51 155	10 763	7 125	4 024	3 173	2 257	2 040	1 549	819	1 033	676	526	370	270
1993	23 695	7 095	4 659	2 673	1 833	1 250	1 116	867	513	572	459	348	273	183

TABLE 1. Continued.

	Age												
Year	14	15	16	17	18	19	20	21	22	23	24	25	Total
1952	2 411	4 205	1 544	2 349	1 892	988	5 363	992	74	487	1 336	1 873	324 408
1953	972	1 901	1 899	1 380	880	656	2 789	1 627	915	642	467	374	288 429
1954	1 300	1 736	2 245	1 019	340	1 124	626	323	309	707	152	1 102	285 086
1955	1 378	2 357	2 278	1 491	910	932	2 570	1 317	808	669	589	857	350 641
1956	855	1 407	1 307	864	497	518	1 420	753	475	357	323	524	400 270
1957	1 391	2 377	2 180	1 471	804	838	2 475	1 306	796	671	582	1 033	265 552
1958	3 104	8 904	5 905	2 998	545	1 530	5 377	2 921	2 430	994	1 940	3 420	311 292
1959	1 273	2 339	2 209	1 429	769	803	2 467	1 321	801	634	544	813	333 428
1960	1 801	3 486	3 220	2 082	1 101	1 175	3 640	1 946	1 163	951	806	1 250	294 363
1961	433	435	381	294	218	201	243	44	179	85	40	195	202 176
1962	1 418	1 856	734	1 747	757	651	1 338	223	617	98	195	714	330 173
1963	2 802	2 103	2 635	1 807	1 179	961	930	850	606	463	397	589	353 845
1964	1 639	2 658	2 092	2 520	3 892	2 035	88	1 979	989	983	1 471	2 477	352 603
1965	1 208	1 046	622	336	658	699	287	455	259	33	18	728	245 304
1966	1 745	1 484	1 382	1 021	1 613	996	1 088	787	317	638	402	1 050	332 568
1967	1 438	1 541	1 064	1 307	1 362	1 405	906	585	462	504	283	943	338 857
1968	1 201	1 092	980	818	1 151	982	738	464	567	316	245	567	204 821
1969	1 300	1 419	944	1 402	911	1 055	958	605	394	475	243	829	298 641
1970	630	721	810	399	453	444	383	305	231	172	111	203	260 150
1971	268	281	218	184	225	172	231	152	131	90	51	305	235 815
1972	313	352	276	190	165	103	151	63	176	16	18	44	137 860
1973	400	481	452	285	179	222	225	103	85	71	54	271	136 105
1974	524	421	382	316	307	193	116	85	94	79	130	432	160 998
1975	265	389	301	259	161	218	158	114	92	94	96	87	179 600
1976	172	144	118	79	75	49	78	34	47	48	33	35	170 935
1977	448	463	271	120	81	83	84	45	36	41	38	98	172 914
1978	122	286	107	143	182	98	152	123	118	47	41	93	169 600
1979	294	391	208	195	72	84	200	120	110	44	47	625	179 640
1980	576	656	393	413	184	255	295	135	108	100	104	152	189 401
1981	282	382	304	407	266	245	207	238	221	113	91	249	215 687
1982	173	336	155	234	115	182	233	124	87	108	74	193	187 044
1983	216	375	182	217	177	156	212	111	76	101	95	169	81 759
1984	155	275	130	175	114	124	180	84	100	64	71	105	53 215
1985	226	359	166	171	144	152	189	85	71	82	71	119	42 361
1986	168	264	131	161	121	122	182	104	78	75	82	149	44 747
1987	244	377	238	249	177	173	282	161	95	155	161	694	64 969
1988	310	443	380	304	363	456	500	171	116	154	293	770	114 980
1989	163	309	203	157	245	135	236	142	275	153	159	329	86 008
1990	342	639	255	406	308	106	498	84	211	275	73	1 056	79 156
1991	252	421	157	246	218	186	190	84	152	67	152	431	73 499
1992	289	305	414	487	318	539	224	157	79	210	147	594	89 543
1993	196	253	242	283	192	293	180	116	73	129	103	341	47 937

vii) The test statistics used were asymptotic and may have been suspect for small sample sizes. Exact tests can be performed, however, since the transitions in the data showed up as relatively sharp, it seemed 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 seemed 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 showed 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 were 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 and 1980, and the aerial

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

	Age 3		Age 4		Age 5		Age 6		Age 7+	
Year	Proportion	Number	Proportion	Number	Proportion	Number	Proportion	Number	Proportion	Number
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

survey estimates for 1990 and 1994 were used. The mark-recapture estimates were critically reviewed in Warren (MS 1991) and all but the 1994 estimate were discussed in Stenson *et al*. (1993). The 1994 estimate was given in Stenson *et al*. (MS 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 parameters 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

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

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 Fig. 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 1 000 random samples from the joint probability distribution of the model parameters are given in Fig. 6–10.

Pup production trajectories estimated from the two formulations were 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 coincided 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

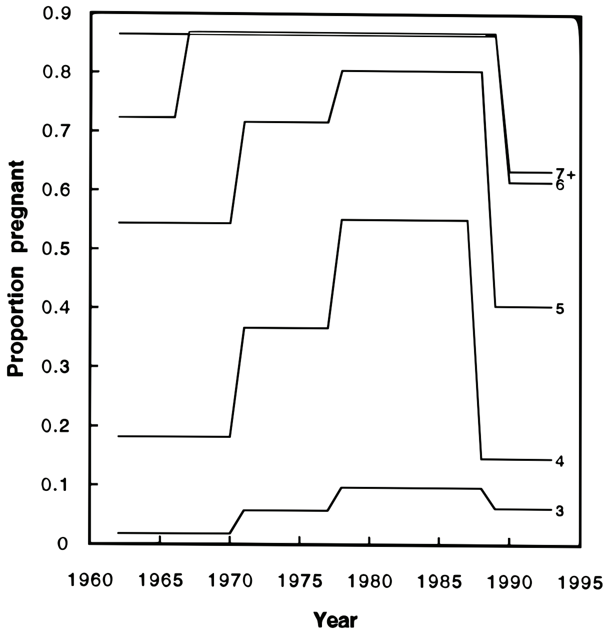

Fig. 2. Estimates of proportion of females pregnant-at-age used in the model.

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 was 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, was 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.

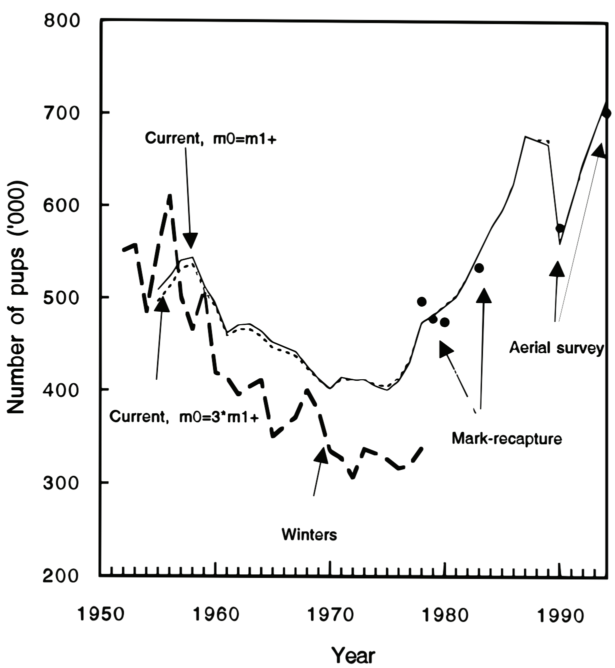

Fig. 3. Trajectories of pup production for the period 1955 to 1994 from the model fit to the 6 survey estimates of pup production. The trajectory from the VPA estimates by Winters (1978) is shown for comparison.

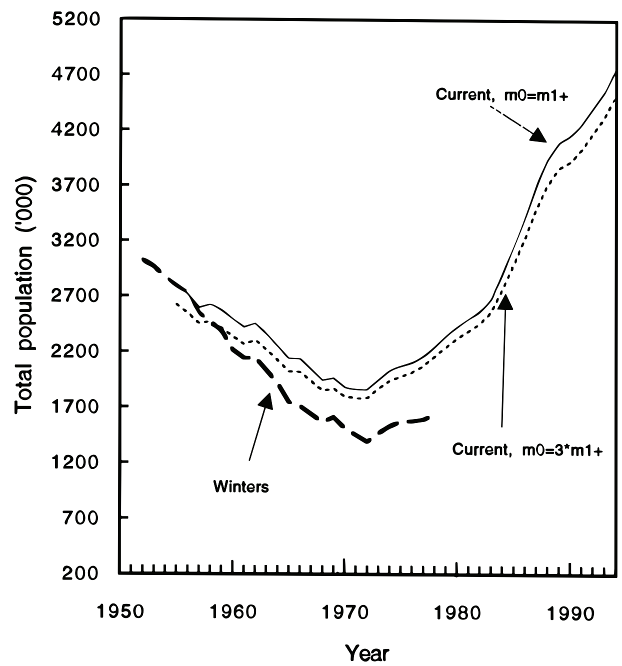

Fig. 4. Trajectories of total population size for the period 1955 to 1994 from the fit of the two formulations of the model to the survey estimates of pup production. The trajectory of total population size from the VPA by Winters (1978) is shown for comparison.

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

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 Fig. 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

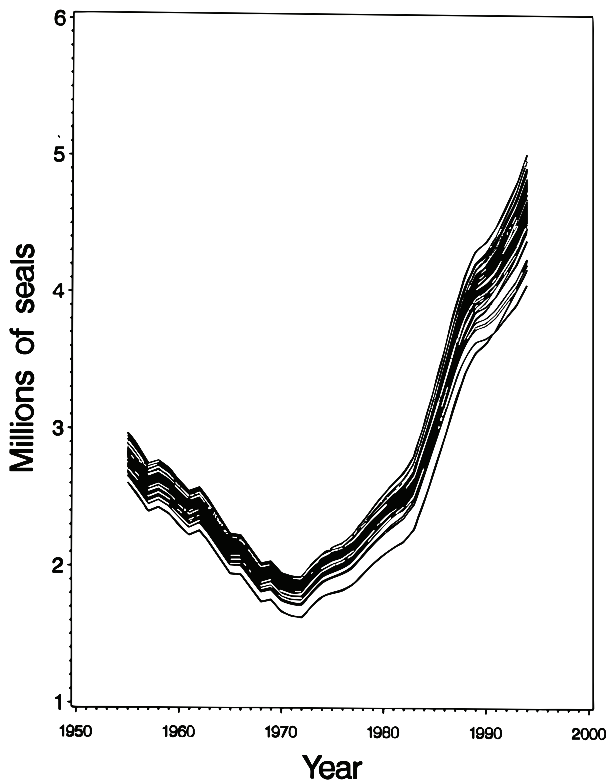

Fig. 5. A random sample of 50 trajectories of total population size from the joint probability distribution of the model parameters for Formulation 1 (pup mortality = mortality on the 1+ population).

formulations were quite similar (Table 5). It is noteworthy that, assuming the 1993 age composition of the catch, population growth rate was halted at a relatively low exploitation rate (6%), although, given current population size, the equilibrium harvest (286 700) was 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 1 000 realizations in Fig. 6, there is a range of feasible

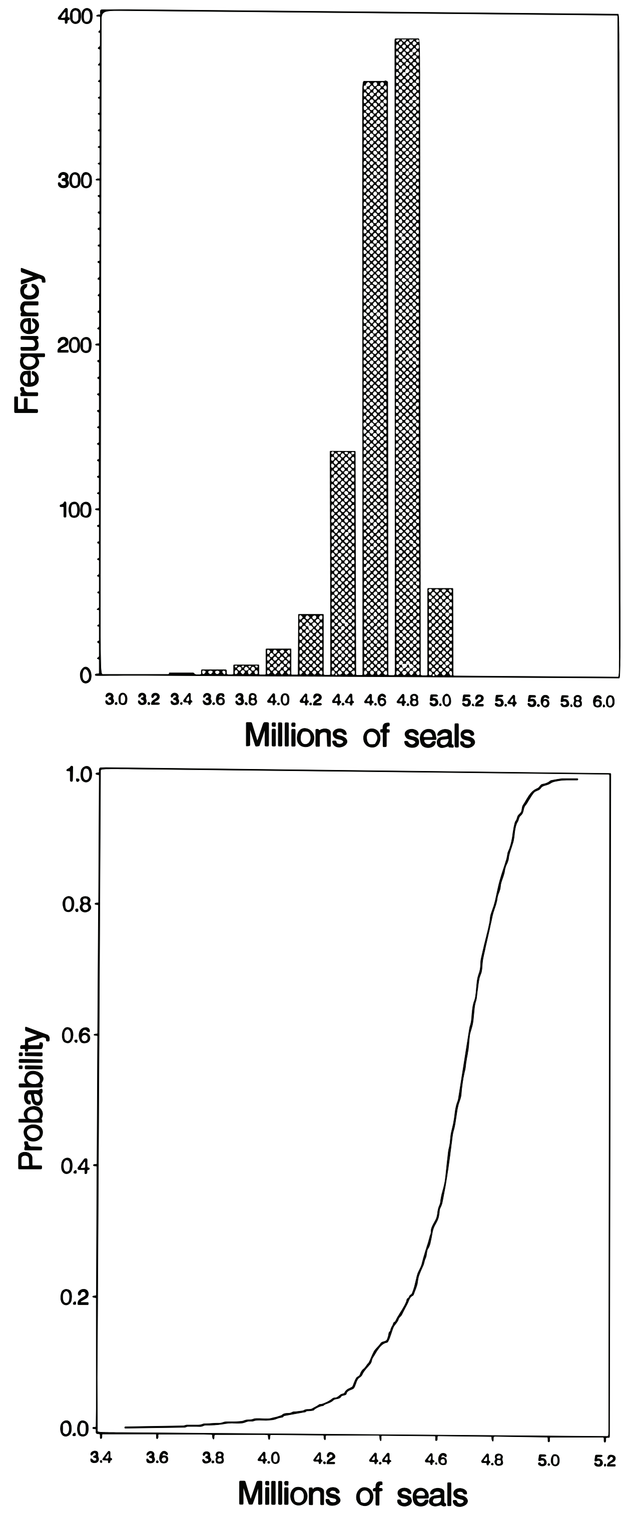

Fig. 6. Frequency and cumulative probability distribution plots for the total population size in 1994 obtained from 1 000 random samples from the joint probability distribution of the model parameters for Formulation 1.

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

Model estimates		Model 1 M0=M1+	Model 2 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

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 was 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 paper, only six mark-recapture and aerial survey estimates were used for fitting the model. Stenson *et al*. (1993) provided a composite of pup production estimates which included 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 as inputs 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, 1986, Cooke *et al*., 1985), problems with respect to missing catch data and the very low overall selectivity on 1+ animals (Shelton *et al*., MS 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).

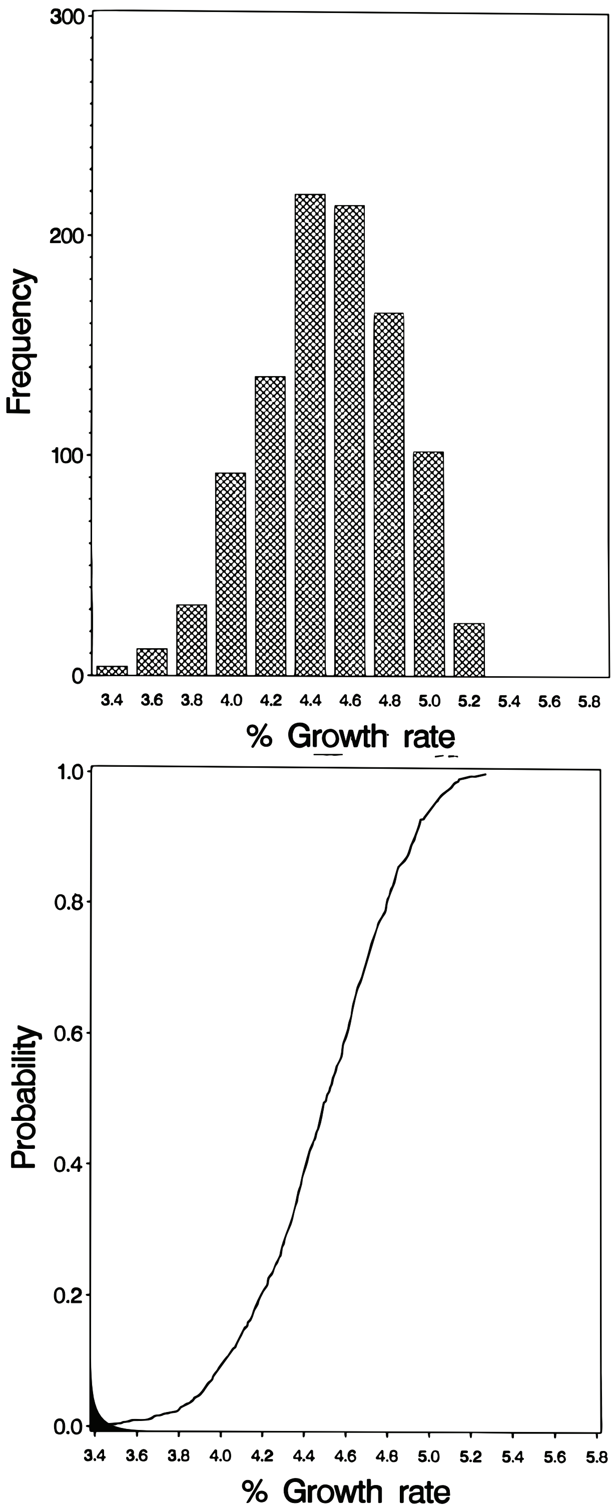

Fig. 7. Frequency and cumulative probability distribution plots for the total population percentage growth rate (1994 over 1993) obtained from 1 000 random samples from the joint probability distribution of the model parameters for Formulation 1.

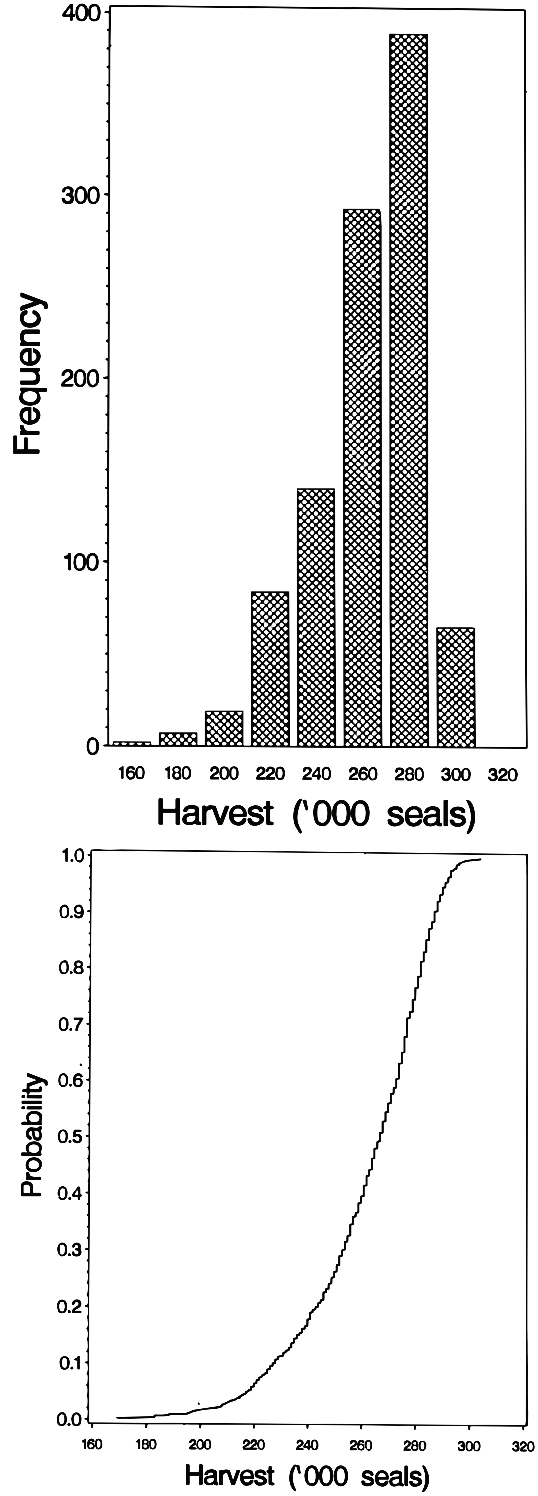

Fig. 8. Frequency and cumulative probability distribution plots for the replacement harvest obtained from 1 000 random samples from the joint probability distribution of the model parameters for Formulation 1.

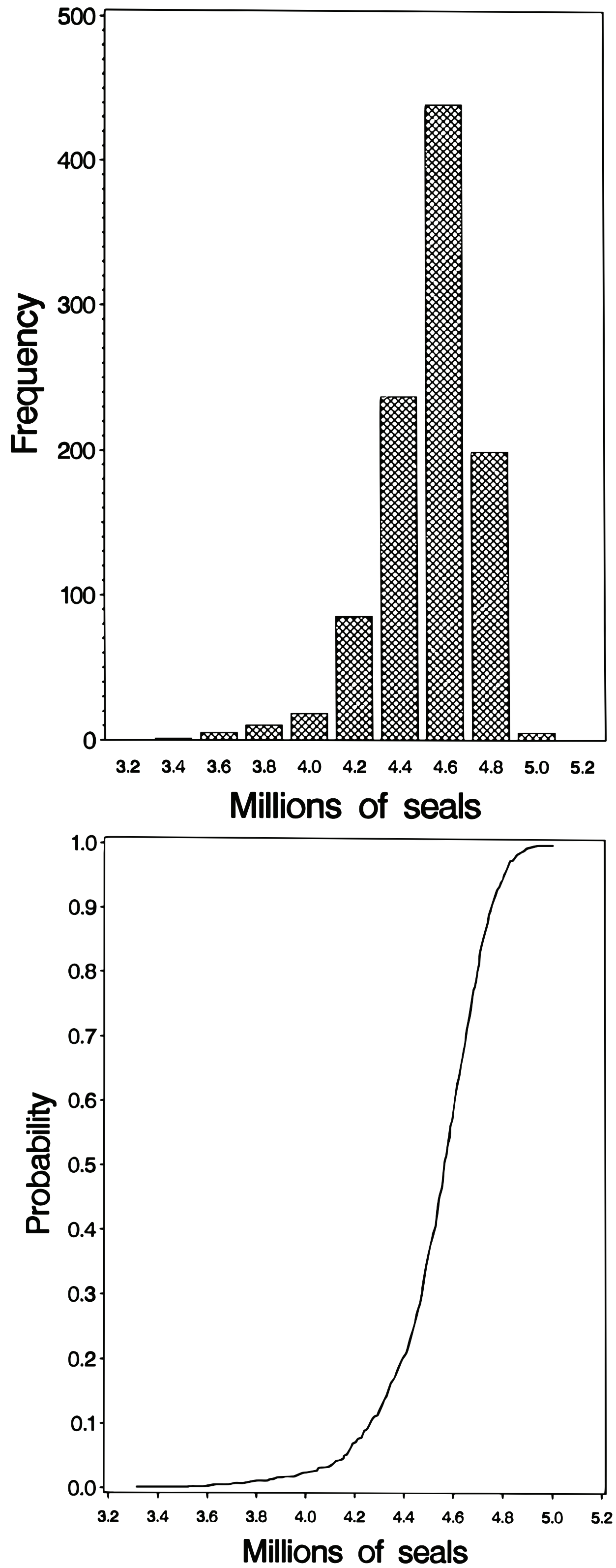

Fig. 9. Frequency and cumulative probability distribution plots for the population size at replacement from 1 000 random samples from the joint probability distribution of the model parameters for Formulation 1.

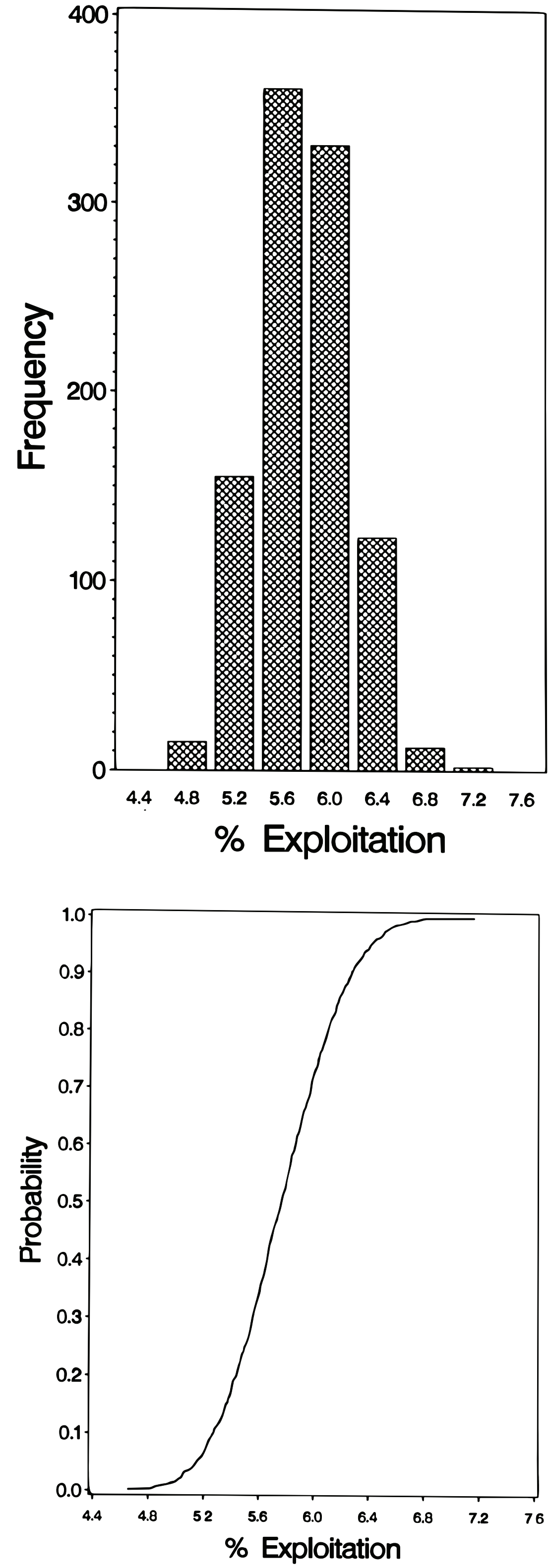

Fig. 10. Frequency and cumulative probability distribution plots for the replacement harvest exploitation rate (%) from 1 000 random samples from the joint probability distribution of the model parameters for Formulation 1.

Acknowledgements

The rewriting of the model into matrix notation and the transformation into the general form of a nonlinear regression model is the work of Noel Cadigan, Science Branch, Department of Fisheries and Oceans, St John's. This, and other aspects of the SAS code written by Noel has resulted in a potentially useful tool for harp seal assessments.

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