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Recent Trends in the Population of Northwest Atlantic Harp Seals, *Phoca groenlandica*

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Abstract

Trends in the abundance of Northwest Atlantic harp seals *(Phoca groenlandica)* for the period 1960 to 1998 were estimated using survey estimates of pup production, and annual estimates of pregnancy rates and age structure of the catch. These data were fit to a two parameter age structured population model under two different assumptions of pup mortality. In one model formulation pup mortality was assumed to be equal to that of seals one year of age and older (1+) while in the second pup mortality rate was assumed to be 3 times the 1+ mortality rate. The uncertainty associated with the population trajectory from the first formulation was estimated by randomly resampling from within the sampling error of the available pup production estimates. Replacement and sustainable yields were estimated using both model formulations under differing assumptions of the age structure of the harvest. The impact of assuming different levels of unreported mortality on population trends was also examined.

Based upon the first model formulation, the total population was estimated to be approximately 5.5 million (95% C. I. 4.3 - 6.7) in 1998 while assuming higher pup mortality results in a slightly lower estimate of 5.3 million. Under both models, the population was estimated to have increased from the early 1970s until 1996. Since then the population has been relatively stable, growing at less than 0.5% per year. Using the current age structure of the harvest, the estimated 1999 replacement harvest was estimated to be approximately 407,000 animals under the assumption of constant mortality and 402,000 under the assumption of higher pup mortality. The estimates of population size and instantaneous mortality are reduced slightly if unreported mortality is added. Assuming low or moderate levels of additional unreported mortality result in slightly declining (0.2 – 0.8%) populations. Assuming a high level of unreported mortality resulted in an estimated 2% decline in the population in 1998, but the level of loss for young seals in Atlantic Canada used for this run is greater than the current data supports. Given the uncertainty associated with the model estimates the differences among the various model runs rates are not significant.

Introduction

Various approaches have been used to estimate the size of the harp seal *(Phoca groenlandica)* population in the Northwest Atlantic (see Roff and Bowen 1983 or Shelton *et al*. 1996 for reviews of the different methods). Earlier estimates, based primarily on interpreting age composition data, used either the survival index approach (for examples see Sergeant 1971; Winters 1978; Cooke 1985) or virtual population analysis (VPA, e.g. Lett and Benjaminsen 1977; Winters 1978). More recent efforts have focused upon fitting various forms of a two parameter population model (variation of a Leslie model) to independent field estimates of pup production for several years (termed the population model approach, e. g. Roff and Bowen 1983, 1986; Shelton *et al*.1992, 1996).

The most recent attempt to estimate the abundance of Northwest Atlantic harp seals was carried out by Shelton et al. (1996). Their model, described in Cadigan and Shelton (1993), involved fitting a population model to independent estimates of pup production. With the exception of the methods used to obtain initial pup production and parameter estimation, the model used by Shelton *et al*. (1996) was very similar to that of Roff and Bowen (1983). Two formulations were considered, Formulation 1 in which the natural mortality rate on pups was the same as that of seals one year of age and older (1+), and Formulation 2 in which the natural mortality on the pups was assumed to be 3 times the mortality on the 1+ population.

Using annual estimates of age-specific reproductive rates and catch-at-age up to 1993, Shelton et al. (1996) applied their model to six independent survey (mark-recapture and aerial) estimates of pup production (1978, 1979, 1980, 1983,1990 and 1994). The total population of Northwest Atlantic harp seals in 1994 was estimated to be 4.8 million (95% C. I. 4.1 – 5.5 million; Warren *et al*. 1997) under the first model formulation and 4.5 million using the second. The population was estimated to be growing at 5% per year in both formulations. The number of seals that could be taken in 1996 and result in the same total population as in 1995 (i.e. replacement yield) was estimated at 287,000 and 275,000 for model formulations 1 and 2, respectively (Shelton *et al*. 1996).

No new estimates of pup production are available since 1994. However, additional information has become available on catches in Greenland that indicates the level of harvest used in the previous runs of the model for the period 1975-1994 (Shelton *et al.* 1996) was underestimated (Anon 1998). Also, catches in both Canada and Greenland have increased significantly since 1996, to a level near or at the estimated replacement yields (Anon 1999). In addition, a review of the potential level of unreported mortality associated with seals that are killed but not recovered during the harvest (Lavigne, in press) has raised concerns about the status of this population.

In light of these new data on catches and concerns about the impact of unreported catches, we have attempted to estimate the current status of Northwest Atlantic harp seals using the population model described in Shelton *et al*. (1996). Updated data on the harvest levels, age frequencies and age-specific reproductive rates have been incorporated into the model in order to estimate the 1998 population and replacement yields in 1999. In addition, the impact of assuming different levels of unreported mortality on population trends was also examined.

Methods

Model Structure

The population model used to estimate numbers-at-age for harp seals in the Northwest Atlantic from 1960 to 1998 is described in Shelton *et al*. (1996) and Cadigan and Shelton (1993). The model consists of two components, the first is a population dynamics model while the second involves a statistical model. This brief description of the model is taken from Shelton *et al.* (1996).

The basic formulation of the population dynamics model is:

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

For 0 < a < A,

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

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 $n_{a,1}$ = 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=(l/exploitation rate)). Thus, for years prior to the first year for which pregnancy data were available (t_o)

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

for a = 1 to A, where A 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 component of the model is

$$N_{0,tj} \sim N(n_{0,tj},\tilde{o}^2_{tj})$$

where $N_{0,tj}$ is the ith survey estimate of $n_{0,tj}$ and $\tilde{o}^2_{tj}$ is its estimated variance.

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 was estimated by resampling the pup productions as describe in Warren *et al*. (1997). Each estimate of pup production was assumed to represent a normal distribution based upon the reported standard errors. A 1000 realizations were carried out to estimate the range of potential population trajectories, and mean and 95% confidence intervals of the 1998 population size determined.

A second formulation of the model was used to investigate the impact of assuming that the mortality of age class 0 (m_0) was equal to that of older seals (m_{1+}). (Roff and Bowen (1983) present arguments in favour of assuming that the mortality rate of pups is higher than that of older seals.) In this formulation, m_0 was assumed to be a constant multiplier of m_{1+}. To be consistent with previous studies (e.g. Roff and Bowen 1983, 1986; Shelton *et al.* 1996) and the assumed mortality rates for other harp seal populations (e.g. see Anon. 1999), we have assumed pup mortality is three times that of 1+ animals.

To calculate replacement harvest, the estimated numbers-at-age up until 1998 were projected to year 1999 using the 1998 estimates of pregnancy-at-age (see below). Catch was removed assuming differing proportions-at-age in the catch (Table 1). The average proportion of age-class 0 in the catch from 1994-97 (the years for which age structures are available, see Stenson *et al*. 1999) was 65%. In order to illustrate the impact of differing age structures, replacement yields were also estimated assuming 50% (average age composition from 1984-94) and 80% pups (age composition of the current catch in southern Canadian areas). The age structure of the harvest of seals 1 year of age and older was assumed to be equal to the 1994-97 average of total catches. The 1999 total catch was varied until the total population in 2000 equalled that of 1999 (i.e. catch removes excess production).

The sustainable catch was also estimated by projecting the 1998 numbers-at-age forward to year 2050. Pregnancy rates and age structure of the catch (described above) were assumed to be constant. A constant annual catch (i.e sustainable yield) for the period 1999 to 2050 was varied until a constant population size (‘sustainable population’) was attained.

Data Inputs

Pregnancy-at-age data up to 1993 were presented in Sjare *et al*. (1996). The pregnancy-rate data used in this model (Table 2) was obtained from Sjare *et al*. (unpublished data). These data are based upon samples collected up to 1996 and a reanalysis of earlier data. Due to the highly variable nature of annual estimates of age-specific pregnancy rates, the data was 'harmonized' to find the most parsimonious representation of pregnancy rates consistent with the data. The methods used to harmonize the pregnancy data are described in Shelton *et al*. (1996)

and Warren *et al.* (1997). Reproductive rates in 1997 and 1998 were assumed to be the same as in 1996.

The total annual catch-at-age up to 1998, taken from Stenson *et al*. (1999), are given in Table 3 and illustrated in Fig. 1. This table includes the revised estimates of Greenland catches since 1975 (Anon. 1999).

As in Shelton *et al*. (1996), the models were fitted to the mark-recapture estimates for 1978, 1979, 1980 and 1983 and the aerial survey estimates for 1990 and 1994 (Table 4). The mark-recapture experiments were described in Bowen and Sergeant (1983, 1985) and the 1978-80 results revised in Roff and Bowen (1986). All of these estimates were critically reviewed by Warren (1991), who also took into account the Cooke *et a*l. (1985) review of harp seal population dynamics. Bowen and Sergeant (1983) also presented the results of a mark-recapture experiment based on the 1977 marking of seals in the Gulf only, but this was not included in our analysis since Bowen and Sergeant (1983) concluded the estimates based on Gulf tags only were likely to be negatively biased.

The aerial survey estimates were taken from Stenson *et al*. (1993, 1996). Stenson *et al.* (1993) presents three estimates of pup production at the Front in 1990. However, one of the photographic estimates was known to be incomplete while the other was based on a series of flights made over two weeks and required a variety of assumptions to estimate ice drift over this period. Therefore, we have used a 1990 pup production estimate of 577,900 (SE=38,000) based upon the visual surveys at the Front and photographic surveys in the Gulf (Stenson *et al*. 1993).

Although other pup production estimates are available, many of these (e.g. Sergeant 1975; Lett and Benjaminsen 1977; Winters 1978; Cooke 1985) are based upon models that make assumptions about population dynamic processes and so do not provide independent estimates of pup production. Additional aerial surveys were also carried out (e.g. Fisher 1955; Sergeant and Fisher 1960; Lavigne 1976; Lavigne *et al.* 1980, 1982; Myers and Bowen 1989), but unfortunately they did not cover all of the whelping concentrations in a single year.

The model was applied to estimated pregnancy rates back to 1960 and the catch-at-age data back to 1952. Thus the pup exploitation rate parameter was estimated from pup harvests for the eight-year period 1952 to 1959. Ages 12 and older were lumped into a 'plus' age class in the analysis.

Unreported Catches

In order to investigate the influence of unreported catches on model population trajectories and yields, model runs were made assuming differing levels of additional mortality (Table 5). Three levels of mortality were assumed. One represents a low range of possibilities while the high represents the high end of ranges suggested by Lavigne (in press). The moderate level is based upon estimates of struck and lost provided by Sjare and Stenson (1999). In all scenarios it was assumed that the loss rate of age 0 seals in the Front and Gulf region prior to 1983 was low (1%). This is likely since the vast majority of the catches during this period consisted of pups taken on the whelping patch.

Results and Discussion

Estimates of total population size and pup production for the two formulations are given in Table 6 and illustrated in Figs. 2 and 3. Parameter estimates, and estimates of population growth rate (defined as the ratio of 1998/1997 population) are given in Table 7. Approximate replacement harvest, sustainable yield and sustainable population size under differing assumption of the age structure of the catch are given in Table 8. The 1000 population trajectories for Formulation 1 ($m_0 = m_{1+}$) are illustrated in Fig. 4 and the frequency distribution of the estimated population size in 1998 in Fig. 5.

As in previous studies (Roff and Bowen 1983, 1986; Shelton *et al*. 1996), the trajectories for total population estimated from the two formulations were very similar (Fig. 2). The 1998 population was estimated to be approximately 5.5 million (95% C. I. 4.3 - 6.7) using the first model formulation while assuming higher pup mortality (model formulation 2) resulted in a slightly lower estimate of 5.3 million. Under both models, the steady growth in the population observed since the early 1970s has not continued. The population appears to be relatively stable since 1996, growing at less than 0.5% per year (Table 7).

Estimates of total population up to 1994 from the Shelton et al. (1996) are also plotted in Fig. 2 for comparison. As expected, the overall trend in the estimates are similar although the total populations estimated by this study are slightly lower in the earlier period and higher in recent years. This difference may be a result of incorporating higher catches reported in Greenland since 1975 (Anon 1998, 1999). It may also be a result of correcting the manner in which the reproductive data were incorporated into the model in Shelton *et al*. (1996).

The estimates of pup production obtained from the two model formulations were virtually identical (Table 6, Fig 3). Although the general pattern of the pup production trajectories since the mid 1970s were similar to those estimated by Shelton *et al*. (1996), current estimates are lower for the earlier period (Fig. 3). The lower estimates observed at the beginning of the 1960s may have been affected by the longer period over which the selectivity parameter was estimated. In this study it was based on an eight-year period while in Shelton *et al*. (1996) there were only three years between the start of the catch data and the beginning of the model estimates. Although the current estimates suggest that pup production was less than 400,000 in the early 1970s, they are still higher than those estimated by Winters (1978), Roff and Bowen (1983) and Cooke *et al.* (1985).

The population trajectories (Fig 4) and frequency distribution of the 1998 population (Fig 5) indicate that the total population in 1998 was unlikely to be below 4.3 million or above 6.7 million (Table 7). However, this is likely an underestimate of the total uncertainty since Warren *et al.* (1997) found that including the uncertainty associated with the estimates of pregnancy rates increased the confidence limits slightly. Also, the model assumes that there are no errors in the catch-at-age data. Future versions of this model should incorporate uncertainty in these parameters, possibly through the use of a maximum likelihood formulation (Anon 1997).

Estimates of replacement and sustainable yields for the two formulations were similar for a given age structure of the catch (Table 8). Generally, yields were higher under catches consisting of a greater proportion of pups. Replacement yields were lower than sustainable yields if the proportion of pups in the catch was high. However, if the catch was assumed to consist of 50% pups, the replacement yield was higher than the estimated sustainable harvest. This is likely due to the large number of juveniles taken under the age structure assumed. Reducing these year classes results in a declining population once they enter the reproductively active age classes.

The estimates of natural mortality (or more correctly, unreported mortality) for the two formulations are similar (Table 7). In Formulation 1, the instantaneous rate of natural mortality (all ages), m, was 0.085, corresponding to an annual survival rate of about 91.5%. In Formulation 2 m_{l+} was estimated to be 0.073, resulting in an m_O of 0.219 ($3m_{l+}$). These estimates are lower than those of Shelton et al. (1996; 0.107, 0.0898 and 0.269, respectively), but very similar to those of Roff and Bowen (1983) who estimated m = 0.075 for the constant mortality model, and m_{l+} = 0.0725 and m_O = 0.2175 for their formulation assuming $m_0=3m_{1+}$. As observed by Shelton *et al*. (1996) and Roff and Bowen (1983), the similarity of the results from the two formulations indicate that the model is relatively insensitive to the assumption of pup mortality and as such, the data does not indicate that pup mortality is significantly higher than that of older animals.

The current data on catches are based upon reports of the number of seals landed in Greenland, the Canadian Arctic and the Front and Gulf regions (Stenson *et al*. 1999). However, additional mortality occurs from a variety of sources such as animals that are killed, but not landed (struck and lost), and unreported hunting. Based on potential rates of struck and lost provided by Lavigne (in press) and Sjare and Stenson (1999), we estimated the impact of unreported mortality on the population trajectory of harp seals and estimates of current population (Table 9). Generally, the population trajectories assuming reported and differing levels of unreported catches were similar until 1995, but diverge in recent years due to the increased catch levels. To illustrate this, the population trajectories using model formulation 1 are shown in Fig. 6. Adding unreported catches resulted in slightly lower population estimates (Table 9). Low and moderate levels of unreported catches reduced the 1998 estimates from 5.5 million to 5.4 and 5.3 million, respectively, using model formulation 1 and from 5.3 million to 5.2 and 5.1 million, respectively, using formulation 2. In both models the population declined slightly (0.2% - 0.8%) between 1997 and 1998. Assuming a high level of struck and lost, the 1998 population was estimated to be approximately 5.2 and 5 million (model formulations 1 and 2, respectively) and to have declined approximately 2% in the last year. The latter runs were based upon Lavigne’s (in press) estimate that the loss rate for young of the year seals in Canadian waters could be as high as 25% (Table 5). However, available data (Rowsell 1977; Sjare and Stenson 1999) suggests that this level is much lower (<5%) and that loss rates in the Canadian hunt are closer to those used in the moderate runs. Given the slight differences observed and the uncertainty associated with these estimates, the difference among the various model runs are not significant.

Identifying the additional component of mortality reduced the mortality estimated in both models with higher additional catches resulting in lower estimates of instantaneous mortality. These lower estimates of mortality resulted in higher estimates of replacement and sustainable yields than those seen using reported catches only (Table 9). However, it must be remembered that these yields no longer refer to landed catch, but instead refer to total mortality due to hunting and include the assumed level of struck and lost. Therefore, if these estimates are used to set quotas, the allowable catches (TAC) must be adjusted to account for the level of unreported mortality assumed. Given the limited amount of data available on struck and lost, it is important that additional studies be carried out in order to properly quantified the level of unreported mortality that occurs in all components of the hunt.

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Table 1. Assumed age structure of the catches used to estimate replacement and sustainable yields.

Age Class	Percentage of pups		
	50%	65%	80%
0	0.500	0.650	0.800
1	0.090	0.063	0.036
2	0.075	0.053	0.030
3	0.065	0.046	0.026
4	0.050	0.035	0.020
5	0.040	0.028	0.016
6	0.030	0.021	0.012
7	0.025	0.018	0.010
8	0.020	0.014	0.008
9	0.010	0.007	0.004
10	0.010	0.007	0.004
11	0.005	0.004	0.002
12+	0.080	0.056	0.032

Table 2. Proportion of females pregnant-at-age, 1960-98 (from Sjare *et al*. unpublished data).

	Age								
Year	0	1	2	3	4	5	6	7	8+
1960	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1961	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1962	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1963	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1964	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1965	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1966	0	0	0	0	0.0192	0.1818	0.5435	0.7231	0.874
1967	0	0	0	0	0.0192	0.1818	0.5435	0.9512	0.874
1968	0	0	0	0	0.0192	0.1818	0.5435	0.9512	0.874
1969	0	0	0	0	0.0192	0.1818	0.5435	0.8143	0.874
1970	0	0	0	0	0.0192	0.1818	0.5435	0.8143	0.874
1971	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1972	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1973	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1974	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1975	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1976	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1977	0	0	0	0	0.0192	0.3834	0.7162	0.8143	0.874
1978	0	0	0	0	0.0192	0.5849	0.8889	0.8143	0.874
1979	0	0	0	0	0.1395	0.5849	0.8889	0.8143	0.874
1980	0	0	0	0	0.1395	0.5849	0.8889	0.8143	0.874
1981	0	0	0	0	0.1395	0.5849	0.8889	0.8143	0.874
1982	0	0	0	0	0.1395	0.2054	0.8889	0.8143	0.7763
1983	0	0	0	0	0.1395	0.2054	0.7172	0.8143	0.7763
1984	0	0	0	0	0.1395	0.2054	0.7172	0.8143	0.7763
1985	0	0	0	0	0.1395	0.2054	0.5455	0.8143	0.7763
1986	0	0	0	0	0.1395	0.2054	0.5455	0.8143	0.7763
1987	0	0	0	0	0.1395	0.2054	0.5455	0.8143	0.7763
1988	0	0	0	0	0.1395	0.2054	0.5455	0.6866	0.7763
1989	0	0	0	0	0.1395	0.2054	0.5455	0.5588	0.7763
1990	0	0	0	0	0.1395	0.2054	0.5455	0.5588	0.6456
1991	0	0	0	0	0.1395	0.2054	0.5455	0.5588	0.6456
1992	0	0	0	0	0.1395	0.2054	0.5455	0.5588	0.6456
1993	0	0	0	0	0.0377	0.2054	0.3103	0.5588	0.6456
1994	0	0	0	0	0.0377	0.2054	0.3103	0.5588	0.6456
1995	0	0	0	0	0.0377	0.2054	0.3103	0.5588	0.6456
1996	0	0	0	0	0.0377	0.2054	0.3103	0.5588	0.6456
1997	0	0	0	0	0.0377	0.2054	0.3103	0.5588	0.6456
1998	0	0	0	0	0.0377	0.2054	0.3103	0.5588	0.6456

Table 3. Catch-at-age of harp seals in the Northwest Atlantic, based on reported catches 1952-98 (from Stenson et al. 1999)

	Age Class																										
YEAR	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25+**	**TOTAL**
1952	207799	8081	12790	8671	6646	7279	12060	8345	8145	5967	6821	5758	1930	1565	2284	4277	1508	2330	1869	1061	5508	929	47	476	1352	1794	325292
1953	207711	23343	7362	6645	4396	4460	3638	3082	3113	2990	2573	2991	1888	1457	1124	2009	2076	1505	977	750	2658	1720	983	665	499	455	291070
1954	186393	34826	13757	4951	6360	3412	4179	3614	3295	2252	3179	1405	2783	2629	1428	2037	2292	1124	416	1205	960	369	335	763	193	1198	285350
1955	261522	24402	9487	6858	4947	4395	4050	3361	3493	2802	3176	2754	2176	1639	1262	2402	2164	1458	808	842	2488	1357	823	655	559	805	350687
1956	347931	13941	5556	3974	3118	2508	2433	2112	2218	1907	2027	1699	1431	1067	929	1480	1390	947	635	632	1599	784	496	422	383	549	402167
1957	173100	23834	8838	6081	4822	3939	3809	3290	3324	2862	3198	2884	2206	1788	1405	2471	2246	1506	842	893	2520	1349	835	646	575	885	260148
1958	151018	27147	10873	12222	12522	10525	7014	6325	5328	5031	9918	5888	7236	4257	3252	9003	5934	3086	633	1576	5493	2956	2473	1049	2013	3686	316455
1959	244160	23427	8843	6051	4667	4062	4007	3414	3403	2968	3278	2796	2159	1716	1354	2482	2212	1492	793	874	2496	1340	806	663	559	825	330846
1960	165759	35256	13692	10402	7184	5979	5981	4886	4734	4071	4645	4035	3149	2481	1885	3523	3250	2142	1155	1221	3684	1980	1200	956	824	1216	295288
1961	175957	7071	2789	2667	2919	1145	1341	1222	804	755	1108	659	432	386	391	310	321	270	159	184	244	47	118	93	47	208	201646
1962	212163	30980	34513	9987	9139	6438	2934	2666	2720	2668	1247	1341	1975	1027	1421	2043	721	1732	813	632	1374	199	636	58	184	661	330273
1963	276343	10247	9022	7255	4305	3412	3730	3705	3528	3246	3767	3579	2679	2830	2864	2316	2704	1883	1241	994	1052	899	670	530	454	679	353937
1964	271780	6814	6109	6303	6997	4704	6782	3652	2948	2776	4277	2264	2258	1718	1718	2653	2089	2586	3919	2077	164	2002	1027	1018	1478	2535	352650
1965	188206	12849	6244	5229	5340	6342	5810	2373	1129	784	1403	512	1771	339	1284	1192	622	395	733	782	349	513	268	56	69	736	245326
1966	255288	14421	11358	5419	5163	5294	5248	4798	3229	1750	1856	2330	1716	1521	1708	1511	1442	1040	1565	991	1089	767	334	662	386	1095	331980
1967	280270	14704	6857	2958	2491	3339	4128	3600	2515	1658	1522	1876	1334	1037	1534	1601	1018	1289	1388	1432	970	618	454	507	319	961	340382
1968	160645	6647	4904	3321	2026	1779	1733	2365	2369	1644	1679	1256	1024	920	1193	1092	951	830	1154	1008	766	460	608	330	254	637	201596
1969	237134	21942	3478	3353	2706	2948	2179	2483	2947	2169	1875	1634	1119	1225	1257	1364	847	1335	861	969	842	589	369	441	224	744	297034
1970	220801	9284	7849	3167	2790	2709	1600	1620	1768	1636	2042	1388	1236	964	813	939	971	579	566	579	630	422	331	268	201	392	265548
1971	214141	8350	3035	2710	1342	1206	795	640	545	817	839	615	612	409	304	331	232	209	211	168	136	114	124	62	27	351	238322
1972	120301	4953	2960	1786	1737	838	724	594	403	208	322	321	352	185	260	272	152	168	202	121	259	148	108	79	69	142	137661
1973	103486	7021	4861	3345	2547	3437	1195	1047	1158	696	728	814	696	655	478	512	449	295	221	239	272	85	186	57	59	290	134828
1974	119482	11880	6495	2420	2003	1931	2829	914	1005	1108	785	583	743	699	532	480	497	433	282	264	173	147	170	104	144	463	156564
1975	144863	14449	6864	3495	1931	1691	1524	1494	876	666	905	582	610	520	408	346	331	253	242	220	154	149	81	84	89	72	182899
1976	139354	17362	8394	4604	2966	1013	680	623	641	276	433	370	345	206	249	322	186	173	95	89	110	70	43	57	41	43	178742
1977	136941	9080	6421	5609	4077	2058	1163	877	551	255	327	317	254	234	400	458	229	94	66	42	76	51	52	53	40	69	169793
1978	123242	20933	12099	7418	5003	3376	2408	795	1070	452	728	320	349	319	241	330	187	168	171	106	166	136	119	71	42	240	180490
1979	141421	17458	8407	4198	2420	1679	1205	765	493	404	284	210	232	169	279	326	166	196	137	151	152	129	117	93	85	531	181706
1980	136657	19804	9643	6660	3767	2669	2099	1547	1173	810	598	708	664	468	538	653	474	397	143	252	359	191	169	105	106	476	191131
1981	184608	13855	7131	5696	4105	3177	2217	1441	1099	544	707	705	532	389	347	485	343	372	280	298	244	272	264	153	124	427	229815
1982	153718	15557	9118	5399	2867	2294	1268	1357	815	1045	728	649	333	381	208	421	226	302	199	270	314	281	139	188	93	375	198547
1983	56982	10313	5150	3812	2694	1433	1303	1084	547	565	573	399	373	199	202	374	252	251	182	196	196	110	52	69	63	180	87555
1984	27690	6245	6796	5481	3431	2135	1609	1328	1037	547	603	503	321	339	254	483	343	326	312	287	365	265	256	216	187	269	61627
1985	16465	5964	5517	4378	2456	1630	1239	1092	850	420	490	385	248	295	290	506	325	274	297	276	325	216	191	192	153	228	44701
1986	25777	6015	5380	5340	3008	1928	1505	1180	971	493	541	474	301	339	268	480	349	324	327	293	374	281	240	222	195	309	56914
1987	39224	8528	7627	7881	4954	3078	2437	1940	1554	894	821	798	423	548	408	737	568	535	486	432	586	421	330	366	325	875	86775
1988	72588	13651	13164	10073	6261	3872	3135	1956	1753	897	738	670	459	695	476	808	715	594	676	719	808	434	355	369	460	955	137280
1989	60026	10321	9225	8483	5225	3654	2670	1749	1430	692	778	710	428	549	347	710	571	476	589	425	575	432	538	390	344	540	111875

Table 3. Con't.

	Age Class																										
YEAR	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25+**	**TOTAL**
1990	39880	13139	10616	10802	7502	5874	3616	2453	1617	1095	1013	1289	845	1053	545	1078	659	756	686	424	870	402	500	535	276	1295	108819
1991	49640	10950	8661	8988	6235	4584	3193	2167	1751	885	938	1028	653	808	475	901	598	629	631	534	596	432	468	352	375	700	107173
1992	51585	16283	12876	10746	7151	5033	4123	3181	2210	1571	1190	1053	552	712	528	817	886	896	759	912	658	530	418	515	387	887	126457
1993	24157	12655	10444	9429	5830	4039	3209	2506	1910	1112	975	878	456	627	436	768	716	694	635	667	616	490	413	436	344	636	85078
1994	33905	14206	12337	13911	10305	8228	6389	4791	3345	1948	1505	1559	1278	1600	1019	1906	1019	960	967	774	643	874	703	414	346	988	125919
1995	43715	14957	12969	14301	10231	8031	6224	4680	3345	1887	1502	1540	1198	1533	973	1832	1034	967	979	792	700	877	717	455	379	975	136792
1996	196285	26403	20053	14170	10216	8259	6883	6307	5629	2803	3579	2275	2481	1777	1489	2232	1819	1984	2003	1660	1549	1145	1576	780	688	2615	326660
1997	231848	23359	18112	13626	9394	7387	6077	5444	4829	2373	2968	1967	1994	1531	1244	1924	1572	1677	1696	1414	1364	1020	1331	717	626	2127	347619
1998	248010	24984	19350	14546	10027	7890	6489	5809	5156	2531	3161	2095	2122	1632	1324	2046	1676	1788	1810	1508	1451	1088	1421	764	666	2272	371616

Table 4. Survey estimates of pup production of harp seals in the Northwest Atlantic. Methods refer to either mark recapture (MR) or visual and/or photographic survey (AS) techniques.

Year	Method	Estimate	Standard Error	Reference
1978	MR	497 000	34 000	Roff and Bowen 1986
1979	MR	478 000	35 000	Roff and Bowen 1986
1980	MR	475 000	47 000	Roff and Bowen 1986
1983	MR	534 000	33 000	Bowen and Sergeant 1985
1990	AS	577 900	38 800	Stenson *et a*l. 1993
1994	AS	702 900	63 600	Stenson *et al*. 1996

Table 5. Assumed levels of unreported mortality (%). Prior to 1983 the level of unreported mortality among age class 0 in the Front and Gulf regions was assumed to be 1%.

Scenario	Harvest Area			
	Front and Gulf		Can. Arctic and Greenland	
	0	1+	0	1+
Reported Catch	0	0	0	0
Low	5	33	33	33
Moderate	5	40	50	50
High	25	50	50	50

Table 6. Pup production and total population size estimates for the period 1960 to 1998 for two model formulations.

	M_0-M_1		M_0=3M_{1+}	
Year	Pups	Total Population	Pups	Total population
1960	362,895	2,296,610	356,802	2,181,296
1961	380,206	2,206,961	374,232	2,094,780
1962	420,746	2,254,899	415,225	2,144,758
1963	432,903	2,187,811	429,048	2,080,586
1964	432,588	2,103,186	430,386	2,006,055
1965	424,420	2,018,511	423,202	1,930,035
1966	418,539	2,037,703	417,571	1,947,211
1967	414,117	1,967,860	411,738	1,883,240
1968	404,171	1,885,703	401,777	1,809,676
1969	391,434	1,930,513	390,508	1,849,494
1970	382,740	1,871,509	382,651	1,798,015
1971	398,974	1,863,719	397,803	1,794,518
1972	395,503	1,879,182	395,751	1,812,690
1973	401,552	1,995,916	402,118	1,921,058
1974	403,248	2,107,566	404,475	2,023,937
1975	400,499	2,186,550	403,047	2,099,010
1976	403,099	2,236,470	406,589	2,150,462
1977	419,898	2,303,109	423,327	2,217,890
1978	475,565	2,428,573	475,714	2,339,198
1979	507,356	2,565,371	506,101	2,463,715
1980	524,280	2,706,797	523,591	2,594,378
1981	537,170	2,840,577	537,388	2,717,783
1982	482,899	2,872,124	484,360	2,746,727
1983	490,208	2,938,386	492,398	2,814,478
1984	521,778	3,137,206	522,760	3,001,262
1985	536,193	3,359,118	537,522	3,207,097
1986	565,910	3,608,915	566,786	3,440,787
1987	596,273	3,857,051	597,022	3,674,108
1988	611,463	4,071,569	613,156	3,876,380
1989	637,311	4,246,076	639,224	4,044,171
1990	596,322	4,389,747	594,891	4,175,464
1991	635,034	4,563,372	632,733	4,341,301
1992	673,680	4,763,098	670,802	4,531,699
1993	656,434	4,910,845	657,815	4,672,646
1994	692,438	5,122,238	693,830	4,877,703
1995	719,707	5,304,558	721,411	5,053,339
1996	747,314	5,489,232	749,209	5,231,802
1997	768,531	5,498,119	770,426	5,252,277
1998	793,092	5,510,754	795,005	5,277,651

Table 7. Comparison of estimates from the two model formulations.

Model Estimates		$M_0 = M_{1+}$	$M_0 = 3M_{1+}$
Total Population Size	1998	5,510,754	5,277,651
	1997	5,498,119	5,252,277
StD of 1998 population		595,962	
Growth Rate (1998/1997)		1.0023	1.0048
Pup Production	1998	793,092	795,005
	1999	819,000	821,000
StD of 1998 pup production		79,864	
Instantaneous mortality rate		0.085	0.073
Pups			0.219
Proportion survival rate		0.915	0.927
Pups			0.781
Pup exploitation rate (1/S) 1952-59		0.4269	0.4132

Table 8. Approximate replacement and sustainable yields under differing assumptions of the age composition of the catch.

Model Estimates	% age class 0	$M_0 = M_{1+}$	$M_0 = 3M_{1+}$
Replacement yield			
	50	400,000	390,000
	65	407,000	402,000
	80	417,000	415,000
Sustainable yield			
	50	453,000	375,000
	65	482,000	406,000
	80	503,000	447,000
Sustainable Population Size (65%)		5,550,000	5,310,000

Table 9. Results of model runs assuming differing levels of unreported mortality. Estimates of replacement and sustainable yields were estimated assuming a catch consisting of 65% age class 0. The rates of additional mortality are given in Table 3.

	Assumed levels of unreported catch		
	Low	Moderate	High
Model 1 $M_0=M_{1+}$			
1998 Total Population	5,420,000	5,340,000	5,180,000
1998 Pup Production	785,000	778,000	770,000
Instantaneous mortality (M)	0.0762	0.0700	0.0671
Pup exploitations rate (1/s)	0.3912	0.3911	0.3702
Growth rate (1998/1997)	0.9962	0.9923	0.9808
Replacement Yield	453,000	482,000	503,000
Sustainable Yield	462,000	497,000	498,000
Model 2 $M_0=3M_{1+}$			
1998 Total Population	5,210,000	5,140,000	5,000,000
1998 Pup Production	786,000	779,000	772,000
Instantaneous mortality (M)			
1+	0.0649	0.0594	0.05688
Pup	0.1947	0.1783	0.1706
Pup exploitations rate (1/s)	0.3841	0.3842	0.3629
Growth rate (1998/1997)	0.9985	0.9942	0.9830
Replacement Yield	448,000	478,000	497,000
Sustainable Yield	457,000	491,000	494,000

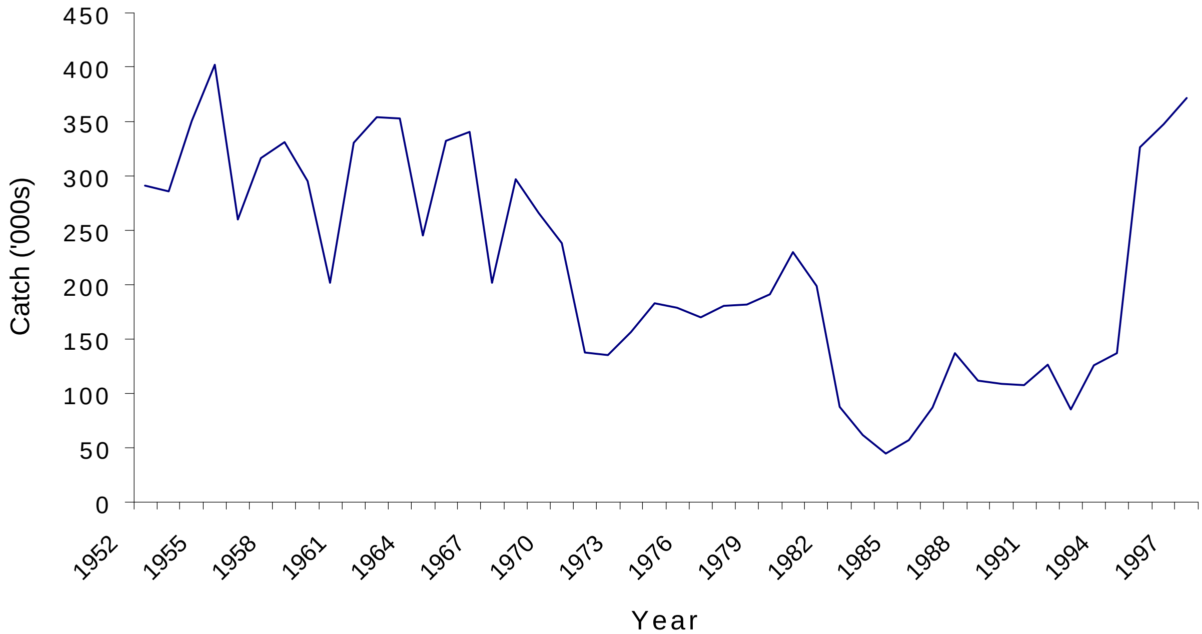

Figure 1. Total catches of harp seals in the Northwest Atlantic, 1952-98.

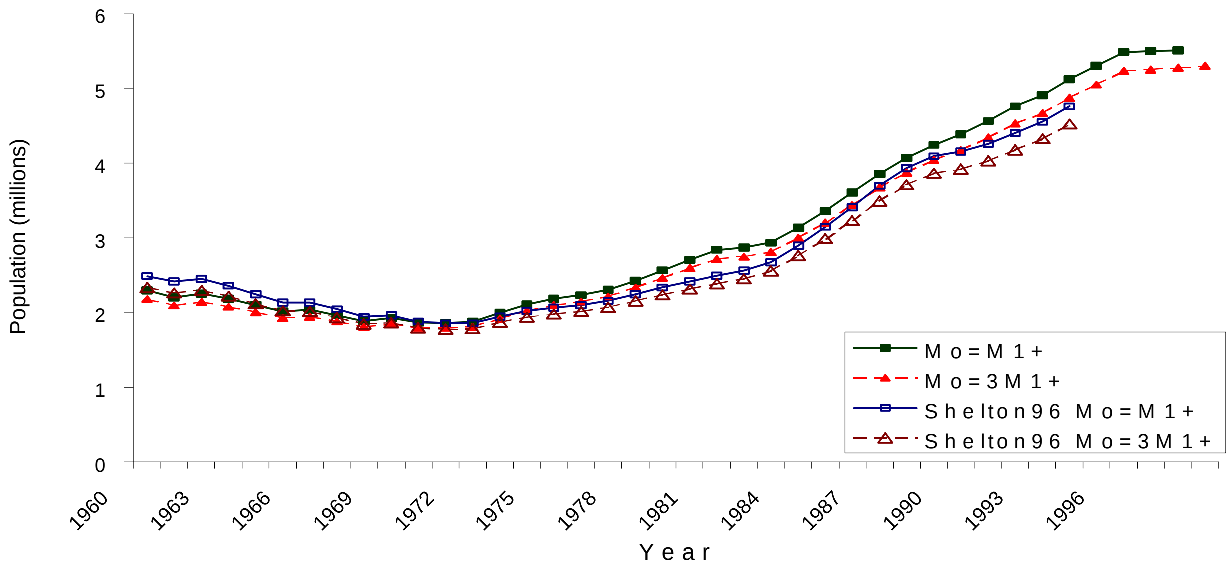

Figure 2. Trajectories of total population size, 1960-98. Estimates from Shelton *et al*. (1996) are shown for comparison.

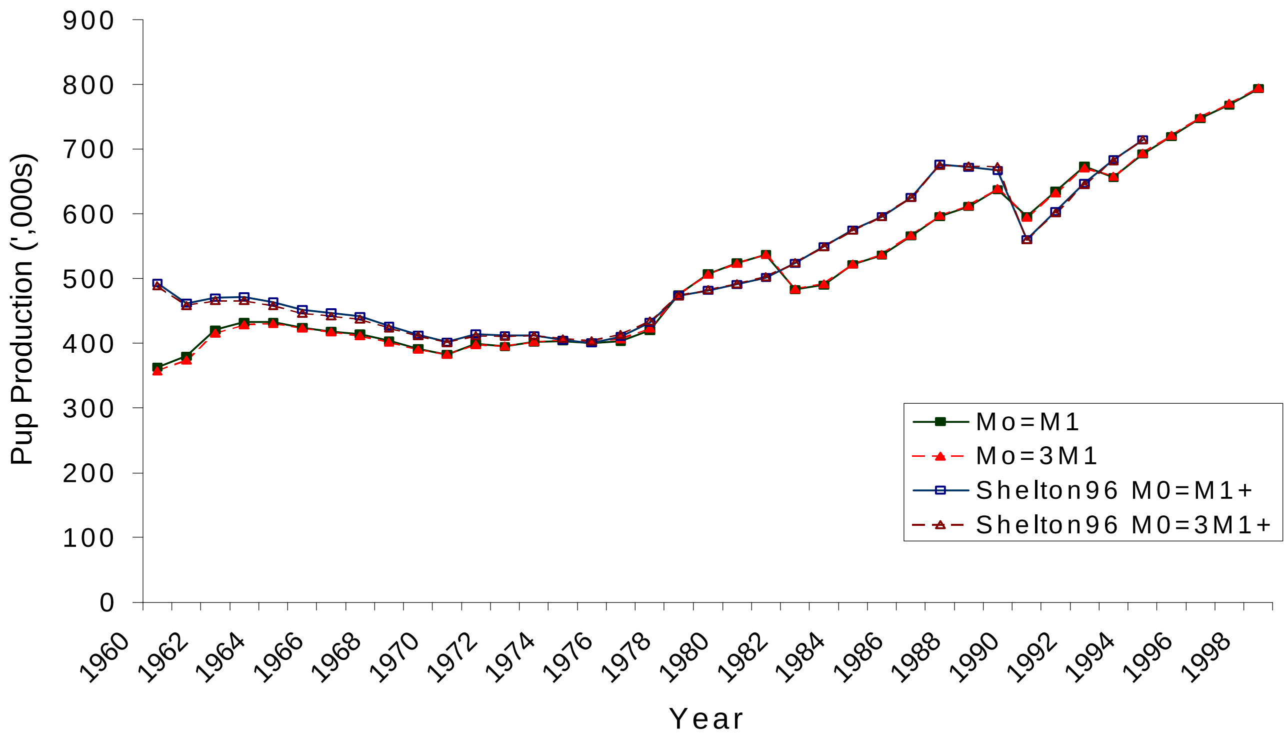

Figure 3. Estimated pup production, 1960-98. Estimates from Shelton *et al*. (1996) are shown for comparison.

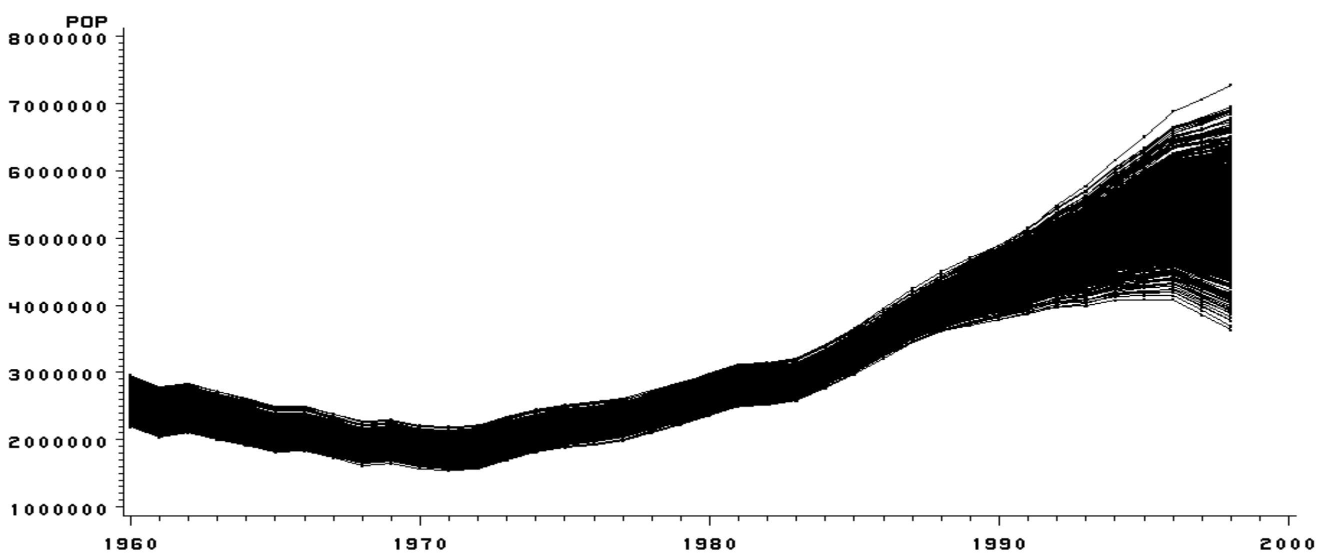

Figure 4. 1000 trajectories of total population size (m_0=m_{1+}) based upon resampling independent estimates of pup productions.

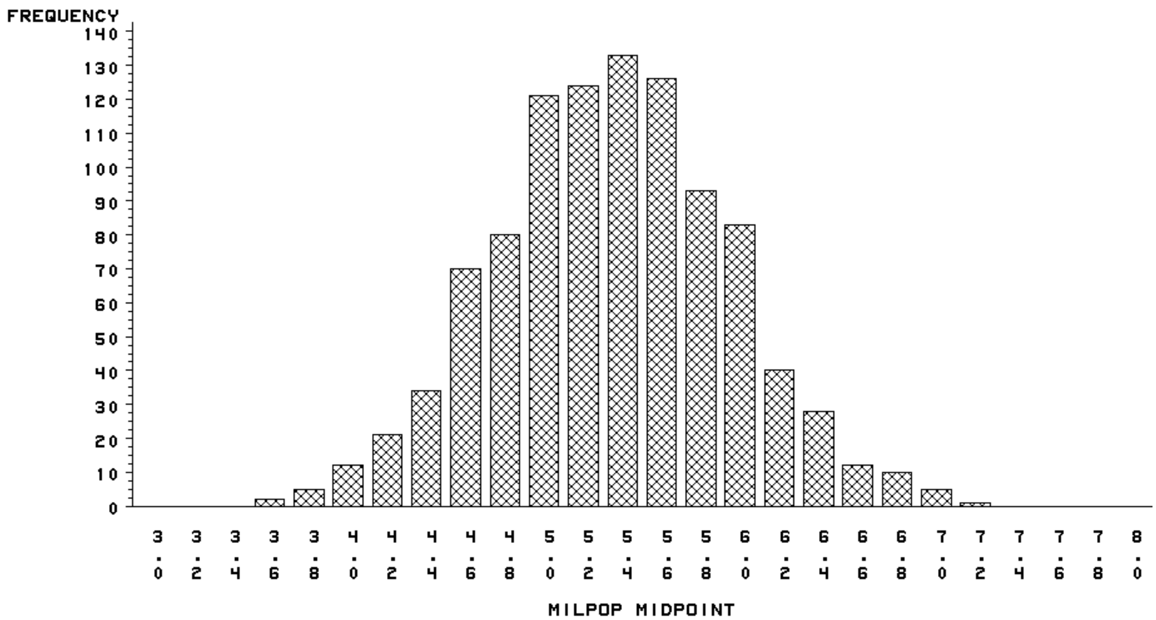

Figure 5. Frequency distribution of estimates for the total population size (m_0=m_{1+}) in 1998 obtained by resampling independent estimates of pup production (1000 realisations).

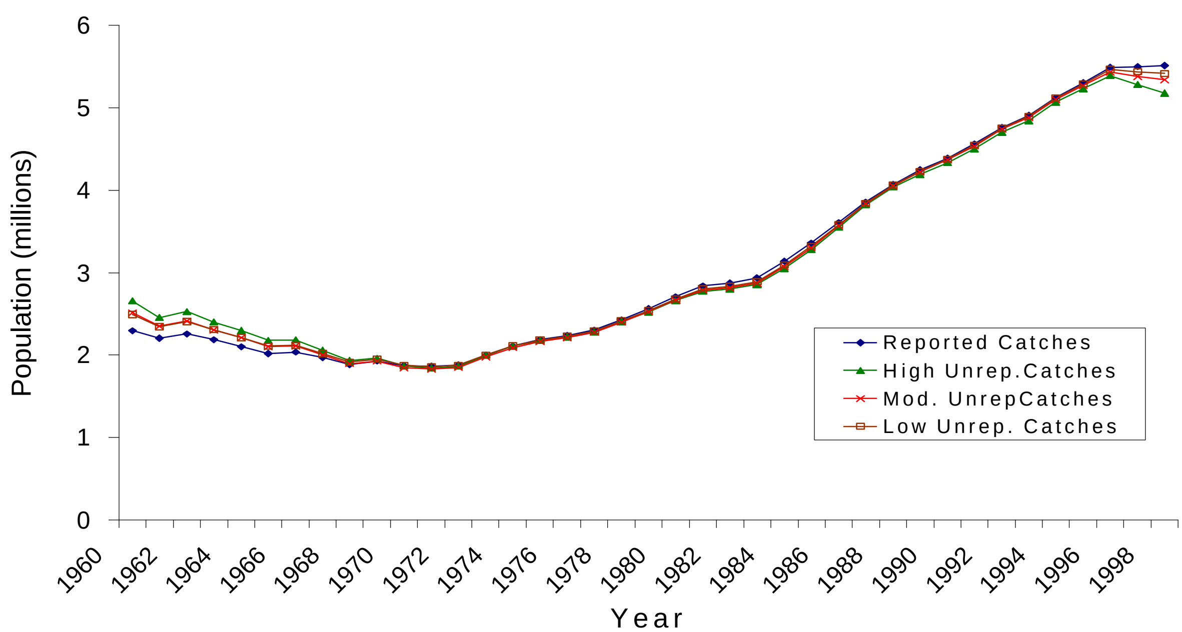

Figure 6. Trajectories of total population (m_0=m_{1+}) assuming reported catches and differing levels of unreported mortality. See Table 3 for definitions of unreported catch levels.