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Quantifying Some of the Major Sources of Uncertainty Associated with Estimates of Harp Seal Prey Consumption. Part II: Uncertainty in the Estimates of Harp Seal Population Size

by

William G. Warren, Peter A. Shelton, and Garry B. Stenson

Science Branch, Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre
P. O. Box 5667, St. John's, Newfoundland, Canada A1C 5X1

SUMMARY

An effort is made to quantify some of the major sources of uncertainty associated with estimates of harp seal prey consumption. Part I focuses on the uncertainty in estimates of population size. A population dynamics model is use, the inputs for which are the annual catches at age and pregnancy rates. Two parameters, instantaneous mortality rate, m and s, representing hunting selection on the pups for years prior to the availability of pregnancy data, are estimated by nonlinear least squares via available survey estimates of pup production. The uncertainty in estimates of population size is estimated by Monte Carlo methods from the estimates of sampling error in the pregnancy rates and in the survey estimates of pup production, with the catches at age assumed to be known. It turns out that the uncertainty in the population estimates is dominated by the uncertainty in the survey estimates.

Introduction

The harp seal population in the Northwest Atlantic *Phoca groenlandica* is estimated to number 4.8 million and to be increasing at about 5% per year (Shelton et al. 1995). There is considerable interest in what impact this might have on fish populations. Prey consumption depends not simply on the size of the population but also, *inter alia*, on the seasonal and spatial distribution of these marine mammals, on their energy requirements, on the calorific content of the various prey species, and on the proportion of these species in the diet. There is uncertainty in our knowledge of all these components which, of course, carries through to uncertainty in any estimate of prey consumption. Our information on these ingredients ranges from sample estimates, sometimes with conventional measures of precision (standard errors) to guesses based on unquantified observation. This paper represents an attempt at quantifing the effect of these various sources of uncertainty on the estimate of annual prey consumption, in particular, the amounts of Atlantic cod, Arctic cod and capelin in NAFO Divisions 2J3KL, and to determine which of the components contributes most to this uncertainty.

Part I will consider the accuracy of estimates of the size of the harp seal population through estimates of pup production. In Part II (Shelton et al., this symposium), this will be linked to the uncertainty in what can be called the diet component.

A Population Dynamics Model

Our starting point is the population dynamics model given in Cadigan and Shelton (1993) which is based on an earlier model presented by Roff and Bowen (1983). Specifically, the population number at age a in year t, $n_{a,t}$ is given by

$$n_{a,t} = (n_{a-1,t-1}e^{-m/2} - c_{a-1,t-1})e^{-m/2}, \ 0 < a < A$$

$$n_{0,t} = \sum_{i} n_{i,t} f_{i,t}$$

where $c_{a,t}$ is the number at age a caught in year t; $f_{a,t}$ is the per capita pregnancy (fecundity) rate of age a parents in year t assuming a 1:1 sex ratio and m is the instantaneous mortality rate, assumed to be constant, i.e. independent of t, etc. A plus age class, A, i.e. ages A and greater is included in the model so that

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

where $A - 1$ is to be read as all ages $A - 1$ and greater.

To accomodate numbers at age for years prior to the first year for which pregnancy data are available, some modifications to the model are required. Let t_0 denote the first year for which pregnancy data are available. Further, assume that seals do not live longer than A_m years, thus obviating the need for a plus age class. Under the assumption that pup production prior to t_0 is equal to a hunting selection parameter, s, times the pup production, where as with the mortality rate, m, s is taken to be constant, we have

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

To transform the above to a "statistical" model Cadigan and Shelton introduce the following:

$$\mathbf{P} = \begin{bmatrix} 0_{1 \times A} & 0 \\ I_{A \times A} & 0_{A \times 1} \end{bmatrix}$$

$$\mathbf{F}_t = \begin{bmatrix} \mathbf{f}' \\ 0_{A \times A+1} \end{bmatrix}$$

where

$$\mathbf{f}_t = [f_{0,t}, f_{1,t}, ..., f_{A,t}]$$

$$\mathbf{D} = \begin{bmatrix} 0_{1 \times (A_m-1)} & 0 \\ I_{(A_m-1) \times (A_m-1)} & 0_{(A_m-1) \times 1} \end{bmatrix}$$

$$\mathbf{D}_1 = \begin{bmatrix} 1 & 0_{1 \times (A_m-1)} \\ 0_{(A_m-1) \times 1} & 0_{(A_m-1) \times (A_m-1)} \end{bmatrix}$$

$$\Lambda_t = (I_{(A+1) \times (A+1)} + \mathbf{F}_t)\mathbf{P}$$

since here $f_{0,t} = 0$, all t.

$$\mathbf{B} = \begin{bmatrix} I_{A \times A} & 0_{A \times (A_m-A)} \\ 0_{1 \times A} & 1_{1 \times (A_m-A)} \end{bmatrix}$$

$$\mathbf{u}_t^i = [\prod_{k=0}^{t} \Lambda_{t-k}]\mathbf{B}\mathbf{D}^i\mathbf{c}_{t_0-i-1}^*$$

$$\mathbf{w}_t^i = [\prod_{k=0}^{t} \Lambda_{t-k}]\mathbf{B}\mathbf{D}^{i-1}\mathbf{D}_1\mathbf{c}_{t_0-i}^*$$

$$\mathbf{v}_t^i = [\prod_{j=i}^{t} \Lambda_{t-i+j}]\mathbf{c}_{i-1}$$

where

$$\mathbf{c}_t' = [c_{0,t}, c_{1,t}, ..., c_{A,t}]$$

and likewise $\mathbf{c}_t^*$ but without the plus age class; thus $\mathbf{c}_t^*$ is a $A_m \times 1$ vector.

With time standardized so that $t_0 = 0$, it then follows (for details see Cadigan and Shelton 1993) that for pups

$$n_{0,t} = \sum_{i=1}^{A_m} [se^{-m(t+i-1)}\mathbf{w}_t^i(1) - e^{-m(t+i-1/2)}\mathbf{u}_t^i(1)] - \sum_{i=1}^{t} e^{-m(t-i+1/2)}\mathbf{v}_t^i(1)$$

and for total population numbers

$$n_{.,t} = \sum_{i=1}^{A_m} [se^{-m(t+i-1)}\mathbf{w}_t^i(.) - e^{-m(t+i-1/2)}\mathbf{u}_t^i(.)] - \sum_{i=1}^{t} e^{-m(t-i+1/2)}\mathbf{v}_t^i(.)$$

where $\mathbf{w}_t^i(1)$ is the first, i.e. age zero, element in the vector $\mathbf{w}_t^i$, etc. and (.) denotes the sum over all ages. Note that the $\mathbf{u}_t^i$, $\mathbf{v}_t^i$ and $\mathbf{w}_t^i$ are functions solely of quantities assumed to be known, namely catch numbers and pregnancy rates. Thus, the expression for $n_{0,t}$ has the form $sg_1(m) - g_2(m)$, where $g_1(m)$ and $g_2(m)$ involve m but not s.

Let $\hat{n}_{0,t_i}$ be an estimate of n_{0,t_i} for those years, t_i in which a survey estimate of pup production is available, and let $\hat{\sigma}_{t_i}^2$ be an estimate of its variance. Cadigan and Shelton then assume that $\hat{n}_{0,t_i} \sim N(n_{0,t_i}, \hat{\sigma}_{t_i}^2)$ thus enabling s and m to be estimated by weighted non-linear least squares in a relatively straightforward manner.

Survey Estimates of Pup Production

Of the relatively few survey estimates of pup production that are available for the Northwest Atlantic harp seal, six have been chosen to be used for parameter estimation, namely the mark-recapture estimates of 1978-80 and 1983 (Bowen and Sergeant 1983, 1985; Roff and Bowen 1986) and the aerial survey estimates of 1990 and 1994 (Stenson et al. 1993, 1995). The mark-recapture estimates were critically reviewed by Warren (1991), who also took into account Cooke et al.'s (1985) review of harp-seal population dynamics. What appear to be the more viable estimates are given in Table 1, along with their estimated standard errors.

The aerial surveys were accomplished by regularly spaced photographic and visual belt transects over the whelping patches. Because sampling was systematic, the sampling error was estimated from the serial differences. Additional components of variance were incorporated to take into account possible errors in the adjustment made for pups not on the ice at the time of the survey (either not yet born or already weaned) and, in the case of the photographic surveys, corrections made to the counts because of reader bias. Details are given in Stenson et al. (1993, 1995). The resulting estimates, with their estimated standard errors, are included in Table 1.

Table 1.
Survey Estimate of Pup Production
Standard Errors in Brackets

Year	Method	Estimate	(S.E.)
1978	Mk-Recapt	497000	(34000)
1979	Mk-Recapt	478000	(35000)
1980	Mk-Recapt	475000	(47000)
1983	Mk-Recapt	534000	(33000)
1990	Aerial Srvy	577900	(38800)
1994	Aerial Srvy	702900	(63600)

Pregnancy Rates

Pregnancy-rate data (number of female seals examined, number of these pregnant) are available by age (3, 4, 5, 6, and 7+) for 1954, 1965-70, 1978-1982, 1985-1994 (see Sjare et al., this symposium). Sample sizes in the 1980's are small (usually less than 10 for combinations of year and age, and not much greater in the 1990's. Indeed, in the 1980's there are two years where one age class is not represented and some combinations of year and age when only one seal was examined. From 1965 to 1970 and in 1978, sample sizes are noticeably greater, although it should be noted than no sampling was undertaken from 1971 to 1977, nor in 1983 and 1984.

In addition to the question of what to do for those years for which pregnancy data are missing, it would seem precarious to use the small-sample data as they stand. For example, with only one seal examined the pregnancy rate would be estimated as either 0 or 100%, neither of which is realistic. With sample sizes of 5 or less, which make up about half the data of the 1980's, there would seem to be an unacceptably high probability of having individual estimates appreciably different from the true rate. Our strategy has been, therefore, to determine, with certain provisos, the most parsimonious representation of pregnancy rates that is consistent with the data.

For a given age class, let N_i be the number of seals examined in year i and let X_i denote the number of these that are pregnant. Let p_i be the (unknown) pregnancy rate in year i. Then the *likelihood* of the observations is

$$\prod_i \frac{N_i!}{X_i!(N_i - X_i)} p_i^{X_i} (1 - p_i)^{N_i - X_i}$$

It is more convenient to work with the logarithm of the likelihood which, with the terms not involving the p_i omitted, is

$$\sum_i [X_i \log(p_i) + (N_i - X_i) \log(1 - p_i)]$$

This is maximized by taking the $p_i = X_i/N_i$, which are the maximum likelihood estimates, m.l.e.

The most parsimonious representation possible is for all the p_i to be equal. Under this hypothesis, the (log) likelihood becomes

$$\log(p) \sum_i X_i + \log(1 - p) \sum_i (N_i - X_i)$$

and the m.l.e. $p = \sum_i X_i / \sum_i N_i$. Asymptotically, under the hypothesis, twice the negative of the difference between the log likelihoods would be distributed as χ^2 on, here 21 degrees of freedom, d.f. (Since there are 22 years and, under the hypothesis, one parameter is being estimated in the place of 22, i.e. the difference in the number of parameters being estimated is 21). It turns out that, for all age classes, the hypothesis of a single pregnancy rate has to be rejected.

It would seem reasonable to suppose that pregnancy rates in successive years would be similar. The following strategy was therefore adopted. Begin by forming a 2 × 2 contingency table from the data of the first two years, namely

$$\begin{array}{cc|c} X_1 & N_1 - X_1 & N_1 \\ X_2 & N_2 - X_2 & N_2 \\ \hline X_. & N_. - X_. & N_. \end{array}$$

where $X_. = X_1 + X_2$, etc. The conventional χ^2 statistic 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 × 2 table formed by including the next year's data, namely

$$\begin{array}{cc|c} X_. & N_. - X_. & N_. \\ X_3 & N_3 - X_3 & N_3 \\ \hline X_{..} & N_{..} - X_{..} & N_{..} \end{array}$$

where $X_{..} = X_{.} + X_3$, etc. This procedure was continued as long as the successive χ^2 values remained non significant (5% level). When a significant χ^2 value was encountered, the sequence was terminated and a new sequence begun, starting with the year for which a (significant) change in pregnancy rate was encountered. (Since the χ^2 test is asymptotic and may be unreliable for the smaller sample sizes, it was replaced by Fisher's (1935) exact test, which, with modern computing facilities, can be readily computed for relatively large sample sizes).

The sequential χ^2 tests have been described as moving forward in time. While this seems logical, from a purely statistical viewpoint they might equally well be carried out moving backward in time from 1994. This was done and yielded essentially the same result. Sometimes in moving forward, a change in pregnancy rate would be indicated between 1987 and 1988, say, whereas, in moving backward, the change would be placed between 1987 and 1986. Such cases were resolved by computing the log likelihood for the two possibilities and the one with the (slightly) greater likelihood selected.

One of the provisos was not to have single isolated years with rates different from the neighbouring years. There were only 3 such instances. Finally, on viewing the overall estimates, it was found that the estimates for age 5 would be more consistent with those for the other ages if initial groupings of 1978-82 and 1985-94 were taken as 1978-88 and 1989-94. Although this departs from the sequential procedure as described, the overall likelihood was again improved, albeit slightly.

For ages 6 and 7+, the pregnancy rates appear to be the same prior to and after the gap in the data from 1971 to 1977. However, for the younger ages, there was a marked increase between 1970 and 1978. For these years the rate was taken as the average of the rates before and after the break. With the amendment of the age 5 estimates, there was no indication of a change in rate between 1982 and 1985. The resulting estimates are given in Table 2.

Table 2
Estimated Pregnancy Rates

Year	3	4	5	6	7+
			Age		
1954-1967	0.0172	0.1818	0.5435	0.7321	0.8648
1968-1970	0.0172	0.1818	0.5435	0.8684	0.8648
1971-1977	0.0570	0.3662	0.7162	0.8684	0.8648
1978-1987	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
1990-1994	0.0615	0.1467	0.4048	0.6154	0.6341

There is strong evidence for a decline in pregnancy rates in recent years, starting with the younger seals in the late 1980's. Whether the drop is as sharp as indicated in Table 2 is debatable, however various approaches at smoothing the transition resulted in inconsequential differences in the estimates of pup production or total population size. The lack of sensitivity to reasonable changes in the pregnancy rates will be demonstrated further in what follows.

Catch Data

Catch at age data from 1952 to 1993, compiled by Sjare and Stenson, are given in Shelton et al. (1995). Although there is the possibility of under-reporting, of incorrect aging and the misapportioning to individual years those captures reported by broader age classes, these data are, for the purpose of this study, taken at face value.

Results Based on Asymptotic Properties

Shelton et al. (1995) apply the model to these data to obtain, *inter alia*, estimates of pup production and total population size in 1994. They consider two formulations, one in which the mortality rate of pups is assumed to be the same at that for all other ages and one in which it is assumed to be three times that of the other ages. The differences in the estimates turn out to be inconsequential; the results presented below are based on the first-mentioned and more parsimonious assumption.

The pup production is estimated as 714,525, slightly greater than the survey estimate, and the total population size as 4,759,984. These follow from estimates of s and m of 2.912801 and 0.107364, respectively, i.e. a mortality rate of about 11% and an exploitation rate on pups of $1/2.912801 \approx 34\%$.

The asymptotic standard errors of the estimates of s and m are 0.084319 and 0.003188, respectively, with correlation 0.999677. High correlation between parameter estimates is common in growth models.

Shelton et al. (1995) used the these estimates (and their asymptotic normality) to construct a Monte Carlo estimate of the 95% confidence interval for the population size. The limits were estimated as approximately 4.1 - 5.0 million. It will be noticed that, although symmetric in probability, these limits are asymmetric. The Monte Carlo generated distribution of population size (Fig. 6 in Shelton et al.) exhibits strong negative skewness. These results are confirmed by an

independent simulation, based on 1000 Monte Carlo realizations, which yielded 95% limits of 4,049,584 - 4,936,532 and the distribution presented in Fig. 1. (There is a slight difference between Fig. 1 and Fig. 6 of Shelton et al. (1995); the groupings in Fig. 1 are centred on the 0.05 millions, i.e. ... 4.55, 4.65, 4.75, ... whereas in Shelton et al. they are centred on the 0.1 millions, i.e. ... 4.5, 4.6, 4.7, ...).

Results Based on a Non-Asymptotic Alternative Approach

With only six years of survey data from which to estimate the parameters, one may question the viability of the asymptotic variances (standard errors) of the estimates and their asymptotic normality. Monte Carlo simulation can, however, be moved back to an earlier stage in the estimation process. For example, we have the estimated standard errors for the survey estimates of pup production; indeed, it was assumed that $\hat{n}_{0,t} \sim n(n_{0,t}, \hat{\sigma}_t^2)$. For the purpose of determining how much the estimates of s and m, and thence the estimate of pup production and population size, would vary if the survey estimates departed from the obtained values, survey estimates may be simulated as $N(\hat{n}_{0,t}, \hat{\sigma}_t^2)$ random variables.

A similar approach may be applied to the pregnancy rates. The estimates are of the form X/N. Now $\arcsin \sqrt{(X/N)} = \theta$, say, in radians, is approximately normally distributed with standard deviation $\sqrt{821/N} \times \pi/180 = s_\theta$, say. Accordingly, simulated pregnancy rates, consistent with the data, may be constructed as $\sin^2(\theta + s_\theta z)$ where z is generated as a standard normal variable.

Simulations were performed by (1) varying the survey estimates of pup production with the pregnancy rates unchanged, and (2) varying both survey estimates of pup production and pregnancy rates.

These simulations, particularly (2), require considerably greater computational effort than those using the asymptotic variances of the estimates of s and m. For this reason, in contrast to 1000, only 100 realizations of each have been carried out. Nevertheless, the results clearly appear to differ from those based on the asymptotics.

We first look at the realized distributions of the estimates of s and m. Summary statistics are given in Table 3.

Parameter	Survey only	Survey & Pregnancy
Mean s	2.917856	2.937480
Mean m	0.107212	0.107532
Std. Dev. s	0.159921	0.196255
Std. Dev. m	0.006026	0.007291
Correlation	0.996480	0.988190

Table 3.

The means are in excellent agreement with the initial point estimates (2.923700 and 0.107786); the standard deviations, however, are approximately double the asymptotic estimates (0.084319 and 0.003188). That the standard deviations with both survey estimates and pregnancy rates varied should be greater than those with only the survey estimates varied is to be expected, as is the reduction in the correlation. What is, perhaps, surprising, is how small this increase is. Histograms of the generated s and m are given in Fig. 2.

Summary statistics for the population estimates for 1994 are given in Table 4.

Parameter	Survey only	Survey and Pregnancy
Mean n	4,745,856	4,751,650
Std. Dev. n	297,794	351,451
Corr. n,s	-0.800764	-0.835915
Corr. n,m	-0.813437	-0.850516

Table 4.

The is, again, excellent agreement between the means and the point estimate (4,759,985) and, as would be expected, the standard deviation is somewhat greater when both pregnancy rates and survey estimates are varied. What is, perhaps, surprising, are the somewhat stronger (negative) correlations with s and m. Histograms of the generated n are given in Fig. 3. These give no suggestion of the negative skewness. The 95% confidence limits would be placed at approximately 4.10 - 5.41 million with survey estimates varied, and 4.09 - 5.53 million with both survey estimates and pregnancy rates varied.

Pup production estimates for 1994 were likewise simulated. These were done independently of the population numbers although they could have been done simultaneously. The summary statistics are given in Table 5.

The mean n_0 are greater, but less than 1% greater, than the point estimate (714,525). The statistics for s and m should be the same as in Table 3 and again, given that these are based on only 100 Monte Carlo realizations, the differences are inconsequential. The histograms (Fig. 4) are comparable with those of Fig. 2. This, in effect, gives us 200 realizations for the distributions of s and m; the pooled histograms are given in Fig. 5. The one notable feature is the weaker (negative) correlations between n_0 and s or m when both survey estimates and pregnancy rates are varied.

Table 5.

Parameter	Survey only	Survey and Pregnancy
Mean n_0	719,961	720,743
Mean s	2.910435	2.896325
Mean m	0.106853	0.106228
Std. Dev. n_0	49,182	44,617
Std. Dev. s	0.173824	0.175254
Std. Dev. m	0.006428	0.007142
Corr. n_0, s	-0.827514	-0.674195
Corr. n_0, m	-0.848347	-0.687709
Corr. s,m	0.994853	0.985293

n_0 based on 200 realizations.

The histograms for the simulated pup production numbers are given in Fig. 6. These, as those for the total population (Fig. 3) appear reasonably symmetric. Approximate 95% confidence limits would be 633,000 - 819,000 when the survey estimates are varied, and 618,000 - 819,000 when both survey estimates and pregnancy rates are varied.

Discussion

In the above above we have explored by simulation the uncertainty in the estimated pup production and total population. Since prey consumption will depend on the weight at age of a seal, numbers at age in the population will be required. These are, of course, also given by the population model. However, when the pregnancy rates are varied, each iteration requires a time consuming calculation to generate the set of non-linear equations from which s and m are estimated. This is followed by their actual estimation by weighted non-linear least squares, which, although not as time consuming as the generation of the set of equations, can take an appreciable amount of time. (The latter also applies when just the survey estimates of pup production are varied). The practicality of simulating population sizes in conjuction with simulation of all the other components necessary for examining consumption, [e.g. energy requirements, seasonal distribution, composition of diet,] is questionable.

However, once s amd m are known, the calculation of numbers and age, given the pregnancy rates, for all years of the study, is very rapid. This raises the question of whether one can, instead of generating variable pregnancy rates and survey estimates of pup production, generate s and m directly in such a way as to be equivalent to their generation by varying pregnancy rates and survey estimates? From the simulations, we have the realized values of s and m from which their joint distribution can be studied. Their means, variances and covariance (correlation), based on 100 realizations, have been presented. Recall that, although simulations were done separately for pup production and total population, for each of these the construction of s amd m is identical and we have, in effect, 200 realizations.

It would be convenient if the s and m followed a bivariate normal distribution. To test this the Anderson-Darling statistic has been used. Since the mean and variance have to be estimated from the data, the modification, A^*, has been calculated; 10%, 5%, 2.5% and 1% critical values are 0.631, 0.752, 0.873, 1.035 respectively (Stephens 1974, 1982). For s and m we obtain $A^* = 0.311$ and 0.330, respctively. Thus, with an estimated correlation of 0.9857, it would seem that the assumption of bivariate normality is justified.

The above result was obtained when both pregnancy rates and survey estimates were varied. Since it was of interest to determine how much of the variation in pup production and total population estimates was due to varying the pregnancy rates and how much to varying the survey estimates, results of varing only the latter as well as both have been given. Varying the pregnancy rates in addition to the survey estimates results in only a small, possibly inconsequential, increase in the variance of the pup production and total population estimates, and this applies also to the estimates of s and m. However, the modified Anderson-Darling statistics in the case of varying only the survey estimates turn out to be $A^* = 0.875$ and 0.251 for the generated distributions of s and m, respectively. The first value is significant at the 2.5% level whereas the second does not even approach significance. Given that the correlaton between the estimates of s and m is estimates as 0.9955, this inference, along with the difference between the two values, is surprising and puzzling.

To attempt to identify the cause of this paradoxical result, the realized values of s (as ordinate) were plotted against the realized values of m (as abscissa). This revealed a small but significant curvilinearity. The regression of s on m was calculated as

$$s = 3.1892 - 31.6322m + 270.6187m^2$$

It turns out that, because of the curvilinearity, the disposition of the larger values of s and m is such that when projected onto the m-axis the distribution is reasonably symmetric (normal) but is positively skew when projected onto the s-axis. The same characteristic can be found with the results from varying both pregnancy rates and survey estimates, although the disposition of the larger values of s and m is then such as to make it less obvious. Nevertheless, the quadratic regression of s on m,

$$s = 3.1219 - 30.3040m + 264.3880m^2$$

is a significant improvement over the linear fit ($F_{1,197} = 123.4$). (The relationship is, for practical

purposes, the same as obtained when only the survey estimates were varied). Accordingly, we are forced to reject the assumption that the estimates of s and m follow a bivariate normal distribution.

Notwithstanding, the normality assumption still seems viable for the estimates of m. Can the residuals of s about $3.1219 - 30.3040m + 264.3880m^2$ be regarded as being normally distributed? We again use th Anderson-Darling statistic, here without modification since the mean of the residuals is known to be zero. We obtain $A^2 = .867$ compared with a 10% ctitical value of 1.743 for this case (Stephens 1974). The normality assumption thus, appears to be viable. Accordingly, s and m may be simulated by first generating a value of m as normal with mean 0.106880 and standard deviation 0.007228, and then a value of s with mean $3.1219 - 30.3040m + 264.3880m^2$ and standard deviation 0.004073. A plot of points so generated is, from the interpretative point of view, indistinguishable from a plot of values calculated via varying pregnancy rates and survey estimates.

Nevertheless a problem still exists with regard to using values of s and m so generated in the calculation of numbers at age. Pregnancy rates are required and these should be consistent with the realization of s and m. The only way that this can be achieved is by generating pregnancy rates, fitting the nonlinear model (i.e. estimating s and m) and then using the same pregnancy rates to calculate the numbers at age. This, as noted, is computationally prohibitive. However, it has been demonstrated that level of uncertainty in the pregnancy rates contributes little additional uncertainty to the estimate of population size, given the uncertainty in the survey estimates of pup production. Accordingly, it would seem that it would not be in too much error if we were to generate s and m as above, but use fixed pregnancy rates in the calculation of numbers at age. A similar problem would exist if uncertainty in the catch-at-age data were to be incorporated.

Conclusions

Two major findings arise from the above.

1. The uncertainty in the model estimates of pup production and total population size stems primarily from the uncertainty in the survey estimates of pup production. The variability in the estimated caused by varying the survey estimates is only marginally inflated by varying the pregnancy rates. This does not imply that pregnancy rates can be ignored; they are essential to the model and some reasonable level in the precision of their estimation must needs be maintained. Changes in pregnancy rates, such as those observed in the late 1980's, have a profound effect on the population trajectory. Nevertheless, it would appear that the primary effort should go in to reducing the sampling error associated with the survey estimates of pup production.

2. Basing confidence intervals on the asymptotic properties of the estimates of s and m appears to be questionable. The Monte Carlo generated distribution of the population size, based on the asymptotic normality, and asymptotic variances and covariance of s and m, exhibits strong negative skewness. Moving the Monte Carlo simulation back the the survey estimates and pregnancy rates gives possibly symmetric (normal) distributions for the estimates of s and m, with means that correspond to their point estimates but standard deviations of the order of twice the asymptotic values (although their correlation remains of the order of 0.99). These in turn lead to reasonably symmetric distributions of the estimates of population size and, thus, roughly symmetric 95% confidence limits. While one should, perhaps, not be surprised that the asymptotic standard deviations be underestimates, it is not clear why this would translate into such a marked difference in the form of the distribution of population size. This, then, provides a subject for further research.

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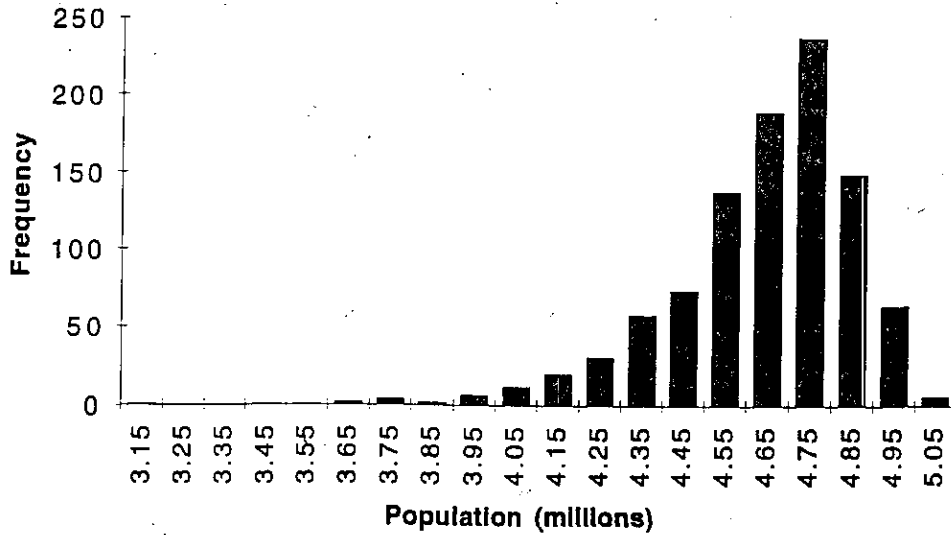
Fig. 1: Histogram of Monte Carlo generated population size based on the asymptotic normality and asymptotic variance-covariance of the estimates of s and m (1000 realizations).
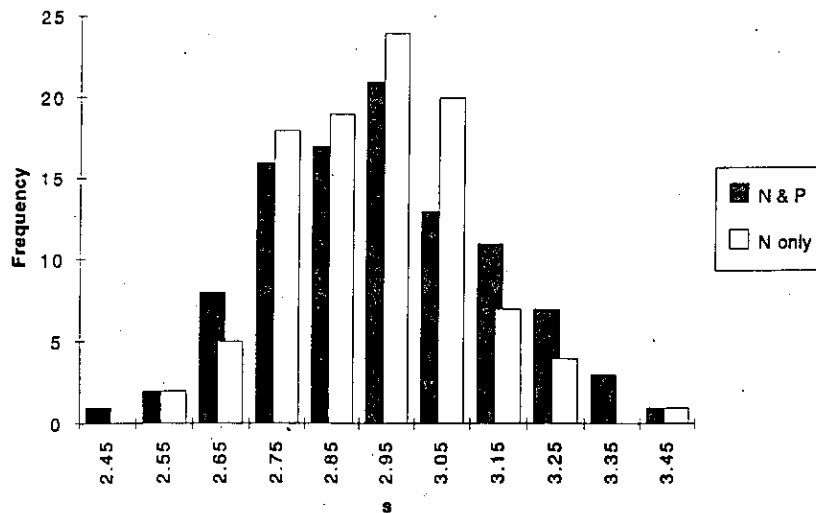
Fig. 2a: Histogram of Monte Carlo generated values of s obtained when generating total population size; N & P - both survey estimates and pregnancy rates varied, N only - only survey estimates varied (100 realizations).
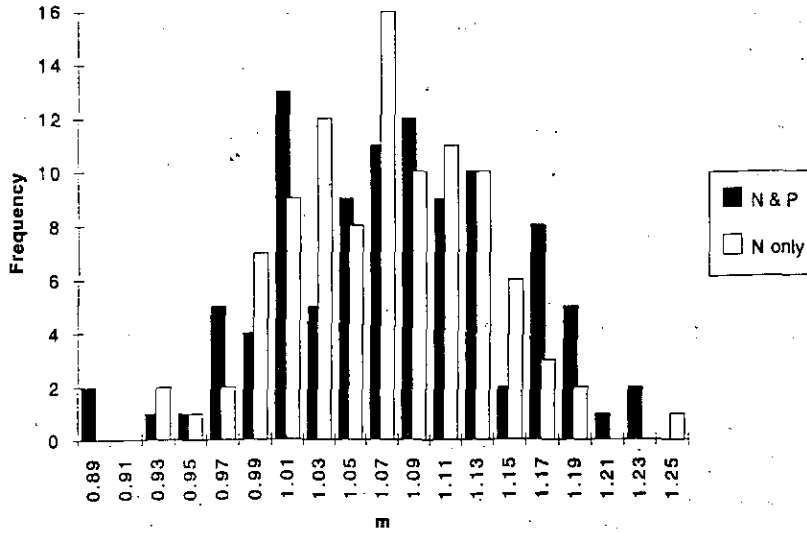
Fig. 2b: Histogram of Monte Carlo generated values of m obtained when generating total population size; N & P - both survey estimates and pregnancy rates varied, N only - only survey estimates varied (100 realizations).
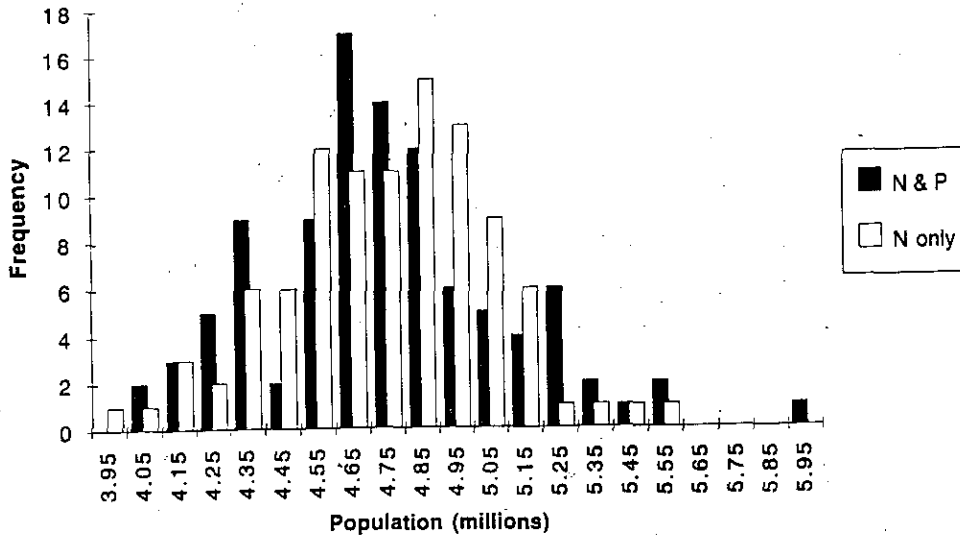

Fig. 3: Histogram of Monte Carlo generated population size; N & P - both survey estimates and pregnancy rates varied, N only - only survey estimates varied (100 realizations).
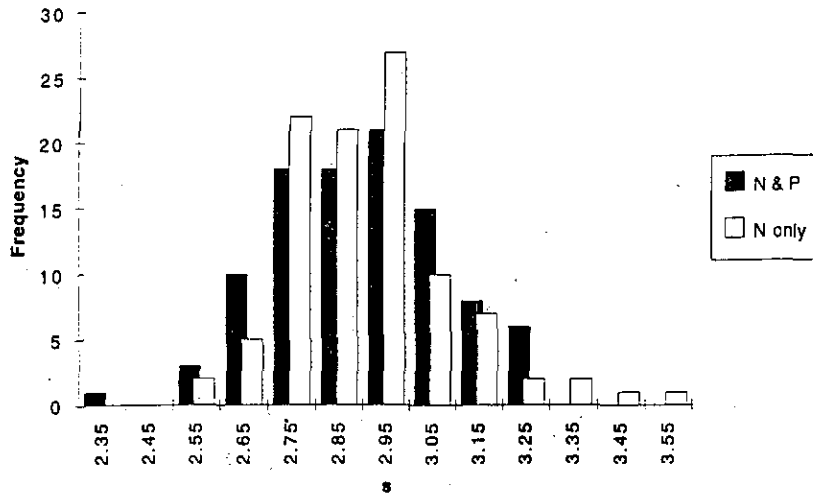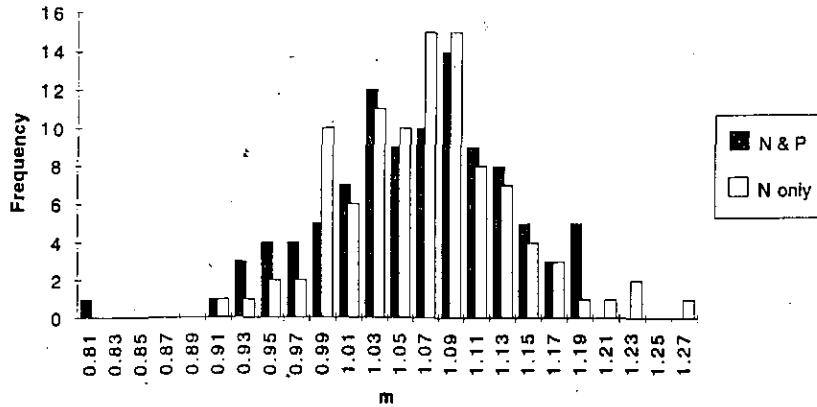
Fig. 4a: Histogram of Monte Carlo generated values of s
obtained when generating pup production; N & P - both
survey estimates and pregnancy rates varied, N only -
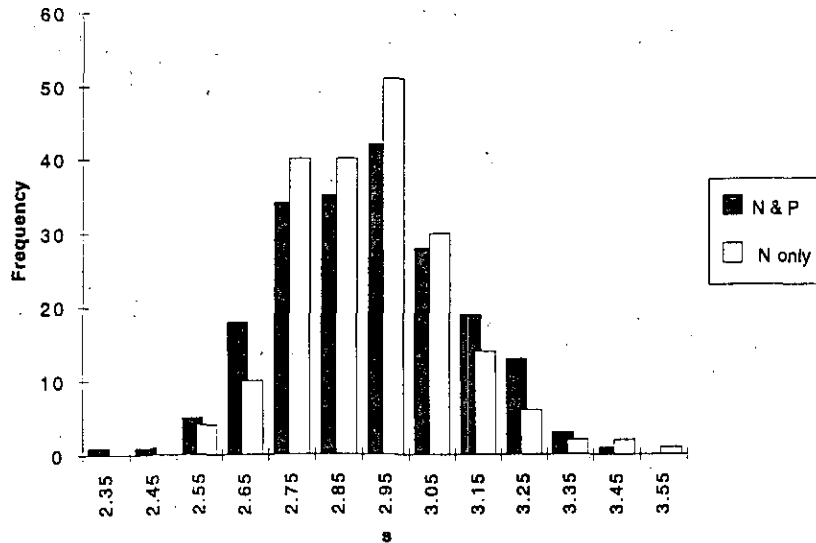only survey estimates varied (100 realizations).

Fig. 4b: Histogram of Monte Carlo generated values of m
obtained when generating pup production; N & P - both
survey estimates and pregnancy rates varied, N only -
only survey estimates varied (100 realizations).

Fig. 5a: Histogram of Monte Carlo generated values of s
pooled from generating pup production and total population
size; N & P - both survey estimates and pregnancy rates varied,
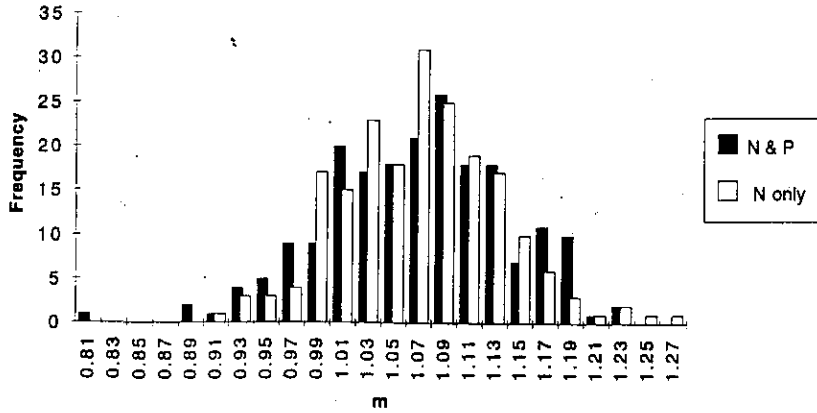N only - only survey estimates varied (200 realizations).

Fig. 5b: Histogram of Monte Carlo generated values of m
pooled from generating pup production and total population
size; N & P - both survey estimates and pregnancy rates varied,
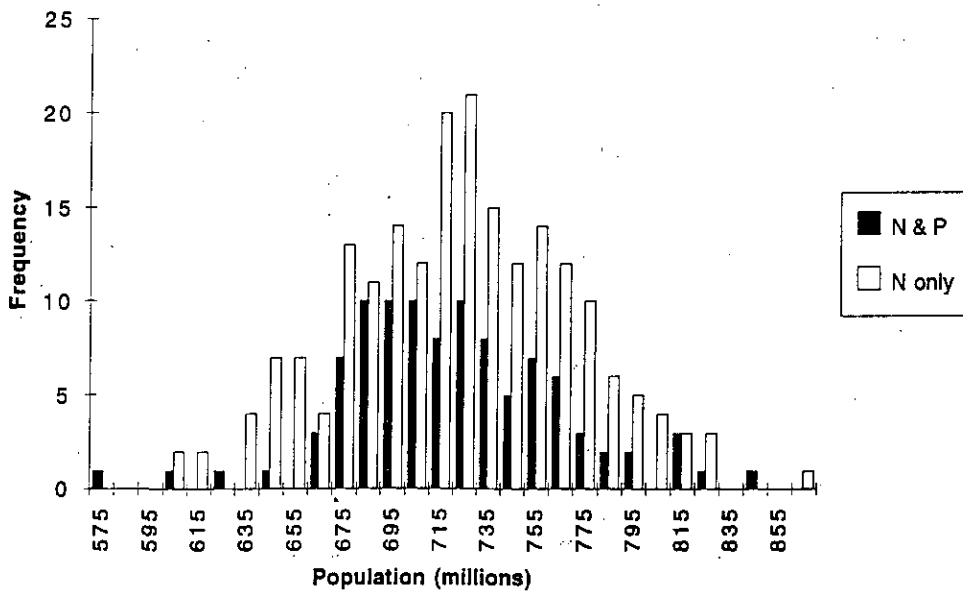N only - only survey estimates varied (100 realizations).

Fig. 6: Histogram of Monte Carlo generated pup production;
N & P - both survey estimates and pregnancy rates varied
(200 realizations), N only - only survey estimates varied
(100 realizations).