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Comments to D. A. Roff and W. D. Bowen, 1981, "Population Dynamics of harp seals, 1967-1991", NAFO, SCR Doc. 81/XI/166

by

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1. The sections "Introduction", "The population" and "Age Structure of Catch", form a general introduction to the harp seal problem.

2. The section "Are Samples of Moulting Seals Really Random" shows that samples of moulting harp seals are not representative of the age structure of the population. In other words: different age groups have different vulnerabilities or catchabilities.

3. The section "The Survival Index Method" repeats the well known assumption and weaknesses underlying the Survival Index Method:

3.1. The fundamental assumptions are: that pup production is constant, and that vulnerabilities and the catchabilities of individual agegroups do not change with time.

3.2. The last three sentences on page 6 are contradictory: On the one hand they state "During the period 1950 to 1970 the pup kill fluctuated widely from 150 000 to 350 000, but did not show any trend. Thus while individual estimates may be over or under estimates due to these fluctuations there should be no consistent bias", while on the other hand they claim that "Because of the averaging over blocks of 5 years, we would expect the estimate to lay behind the correct value when the population is in a slow decline".

One source of error in their arguments about the properties of the survival index method for declining populations is that equation (4) rests on the assumption that $g(T-A) = g(T)$, i.e. the abundance does not change from time T-A to time T. This is a hidden equilibrium assumption, so conclusions based on equation (4) will always be doubtful.

3.3. However, I agree with the main conclusion of this section (page 7) that "Taking into account the uncertainties of this method, we may reasonably conclude from the analysis that between 1952 and 1972 pup production declined from 550 000 - 650 000 to between 325 000 to 425 000".

4. The section "Can we get from here?" shows that a population with Beddington and William's (1980) mortality rates would decline even in the absence of hunting and hence could not have achieved the population size of the pre 1950-ties. The section therefore correctly concludes that "There is something seriously wrong with the analysis of Beddington and Williams (1980)".

5. Roff and Bowen's model is explained on pages 8-14. Their approach may be outlined as follows:

(1) There are two unknowns: natural mortality and pup production in 1967.

(2) The age distribution in 1967 is estimated from a calculated set of selectivity factors which may be obtained by two procedures (p.12-14): the additive method and the multiplicative method. Both procedures assume that vulnerabilities and catchabilities are the same for all age groups 7+.

(3) Two independent distributions containing pup production estimate are required. One is obtained by a change in ratio method, the other by a markrecapture method. Natural mortality and pup production in 1967 are then estimated by maximization of the likelihood function (fig. 3b). This means that natural mortality and initial pup production are chosen so that the resulting population trajectory passes as

close as possible to the population estimates of the two preselected methods.

6. Unfortunately both step 2 and 3 above contain serious errors:

6.1. Underlying assumptions and definitions not explicitly given in the text on pages 9-10 and the text also contain many irritating misprints. I interpret these pages as follows:

Let

$N_{o,t}$ = Pup production in season t

$C_{o,t}$ = Kill of pups in season t

m = Natural mortality

q = Catch mortality

$n_{a,t}$ = Sample of a year old seals in season t

f_t = Effort of the collectors in season t

$\rho_{a,t}$ = Selectivity of age group a to the collectors in season t

Then

$$n_{a,t+a} = f_t \cdot \rho_{a,t} \cdot (N_{o,t} - C_{o,t})(1-m)\{(1-m)(1-q)\}^{a-1}$$

$$n_{a-1,t+a} = f_t \cdot \rho_{a-1,t} \cdot (N_{o,t+1} - C_{o,t+1})(1-m)\{(1-m)(1-q)\}^{a-2}$$

So

$$\frac{n_{a,t+a}}{n_{a-1,t+a}} = \frac{\rho_{a,t} \cdot (N_{o,t} - C_{o,t})(1-m)(1-q)}{\rho_{a-1,t} \cdot (N_{o,t+1}) - C_{o,t+1})}$$

In order to obtain equation (11) we therefore have to assume that all age groups have the same selectivities.

However, in addition equation (11) and equation (12) is wrong since e^{-M} must be replaced by $e^{-(M+F)}$ i.e. e^{-Z}.

To sum up, because the other cohort pairs are neglected the method proposed on pages 9-10 is nothing but a less powerful variant of the survival index method and in addition it is wrong.

6.2. The only way I can reproduce the suggested distribution on page 10 is as follows:

Consider only cohorts 1 and 2. Assume their sum is n while the total sample size is m. From the general formula P(A/B) = P(A∪B)/P(3). We get the following conditional distribution of the sampled number of seals from cohort 1:

$$p(X_1/n) = \frac{\frac{m!}{X_1!(n-X_1)!(m-n)!} p_1^{X_1} \cdot p_2^{n-X_1} (1-p_1-p_2)^{m-n}}{\frac{m!}{n!(m-n)!} (p_1+p_2)^n (1-p_1-p_2)^{m-n}}$$

$$= \frac{n!}{X_1!(n-X_1)!} \left(\frac{p_1}{p_1+p_2}\right)^{X_1} \left(1-\frac{p_1}{p_1+p_2}\right)^{n-X_1}$$

It is seen that X_1/n is a binomial variable with probability of success equal to $\frac{p_1}{p_1+p_2}$

Thus,

$$\frac{n_{a,t+a}}{n_{a-1,\,t+a} + n_{a,t+a}} = Z$$

have a normal distribution with mean Z and variance $\frac{Z(1-Z)}{n}$ where $n = n_{a-1,t+a} + n_{a,t+a}$

The formula $\frac{N_{t,t+i}}{N_{t+1+i,t+i} \cdot N_{t,t+i}} = Z$ on page 10 therefore must be full of errors, hopefully only misprints.

Finally, it is very hard to see from the text how $z = p_1/(p_1+p_2)$ is calculated. I see two alternatives

1) Z is calculated directly from a population projection, or

2) $Z = \frac{(B-C_{o,t})(1-m)}{(B-C_{o,t})(1-m)+(B-C_{o,t+1})}$

where

$B = N_{o,t} = N_{o,t+1}$ is the pup production in seasons t and t+1.

However, as explained in 6.1, this is a wrong formula. The correct version includes the average catch mortality of which there is no estimate (i.e. (1-m) must be replaced by (1-m)(1-q)).

In any case, both alternatives require that all age groups have the same catchabilities and vulnerabilities (Compare section 2 above).

6.3. The addivtive method (p. 12-13): We shall derive equation (17). (Roff and Bowen now change their symbols !):

let

$C_{a,t} = n_{a,t}$ = Sample of a year old seals in season t

$S_{a,t} = 1/\ _{a,t}$ = The inverse of the selectivity as defined in section 6.1.

It is assumed that age-groups 7+ are correctly represented in the sample:

$$\wp_{7,t} = \wp_{8,t} = \cdots = \wp_t$$

We then have

$$C(2,67) = f_{67}\wp_{2,67}(Age_{2,67})$$

$$C(7+,67) = f_{67}\wp_{67}(Age_{7,67} + Age_{8,67} + \cdots)$$

where

$Age_{a,t}$ = Number of a year old seals in the population in season t.

Hence

$$\frac{C(2,67)}{C(7+,67)} = \frac{\wp_{2,67}}{\wp_{67}} \cdot \frac{Age_{2,67}}{Age_{7,67} + \cdots}$$

We also have

$$Age_{7,72} = Age_{2,67}(1-f_{67}\wp_{2,67})(1-m)\ldots(1-f_{71}\wp_{6,71})(1-m)$$

and

$$Age_{12,72} + Age_{13,72} + \ldots = (Age_{7,67} + Age_{8,67} + \ldots)(1-f_{67}\wp_{67})(1-m)\ldots(1-f_{71}\wp_{71})(1-m)$$

so

$$\frac{C(7,72)}{C(12+,72)} = \frac{\mathcal{S}_{72}\ Age_{7,72}}{\mathcal{S}_{72}\ (Age_{12,72} + \ldots)} = \frac{Age_{2,67}}{Age_{7,67} + \ldots} \cdot \frac{(1-f_{67}\mathcal{S}_{2,67})\ldots}{(1-f_{67}\mathcal{S}_{67})\ldots}$$

$$= \frac{S(2,67)\ C(2,67)}{C(7+,67)} \cdot \frac{(1-f_{67}\mathcal{S}_{67})\ldots}{(1-f_{67}\mathcal{S}_{67})\ldots}$$

Eq (17), page 13, can therefore only be true if

$$(1-f_{67}\mathcal{S}_{2,67})\ldots(1-f_{71}\mathcal{S}_{6,71}) = (1-f_{67}\mathcal{S}_{67})\ldots(1-f_{71}\mathcal{S}_{71})$$

Since the effort varies independently of the selectivities this equality can only be generally satisfied for

$$\mathcal{S}_{2,67} = \mathcal{S}_{67}\ \mathcal{S}_{3,68} = \mathcal{S}_{68}\ \ldots,\mathcal{S}_{6,71} = \mathcal{S}_{71}$$

Hence, the only reasonable assumption needed for reproducing equation (17) is that all age groups have the same selectivities. The procedure which estimates the different values of the selectivities therefore rests on the assumption that they are all equal!

In addition the authors spend a whole section (see section 2 of these comments) to argue that selectivities vary with age!

Finally i emphasize that it is misleading and wrong to claim (page 13) that "The necessary condition of this method is that

$$\frac{C(7,72)}{C(12+,72)} = \frac{C(8,73}{C(13+,73)} = \ldots = \frac{C(11,76)}{C(16+,76)}\text{"}$$

6.4. The multiplicative method (p. 13-14): We shall derive equation (21):

As previously we have

$$\frac{C(2,67)}{C(7+,67)} = \frac{\mathcal{S}_{2,67}}{\mathcal{S}_{67}} \quad \frac{Age_{2,67}}{Age_{7,67} + \ldots}$$

and

$$\frac{C(3,68)}{C(8+,68)} = \frac{\mathcal{S}_{3,68}}{\mathcal{S}_{68}} \cdot \frac{Age_{3,68}}{Age_{8,68} + \ldots}$$

$$= \frac{\mathcal{S}_{3,68}}{\mathcal{S}_{68}} \cdot \frac{Age_{2,67}}{Age_{7,67} + \ldots} \cdot \frac{(1-f_{67}\mathcal{S}_{2,67})(1-m)}{(1-f_{67}\mathcal{S}_{67})(1-m)}$$

so Eq (21) can only be satisfied if $\mathcal{S}_{2,67} = \mathcal{S}_{67}$.

Continuing in this way we see that also the multiplicative method is based on the assumption that all age groups have the same selectivities.

7. In my opinion the authors should verify why their method of estimating the selectivities might be applied in spite of the critisisms mentioned in paragraph 6.

Some points which allow their approximations are:

1) A small catch mortality of age groups 2+ since 1967.

2) A small error in the estimated initial age structure does not influence their abundance estimates.