Canadian Atlantic Fisheries
Scientific Advisory Committee

CAFSAC RES. DOC. 77/24
(Revised)

CRITICAL ANALYSIS OF TWO HARP SEAL POPULATION MODELS

R.K. Mohn

Fisheries Systems and Data Processing Group

Department of Fisheries and Environment
Marine Fish Division
Bedford Institute of Oceanography
Dartmouth, Nova Scotia

Fisheries Systems and Data Processing Group Contribution No. 2

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Introduction

Two models have recently been published which produce divergent results as to the stability of the population under current harvest quotas. The one model is reported in Capstick et al. (1976) Model 3 and for convenience will be called the Guelph model. The other model is reported in Lett and Benjaminsin (1977) and in this work will be denoted as the L-B model. In order to locate sources of divergence and form an estimate of parameter performacne a sensitivity analysis was carried out on both models. Both simulations were carried out using starting values as similar as possible. The analyses were performed over long (20 year) and short (4 year) periods. The long period was used to ensure long term effects of given parameter sets would be present. The short period was introduced as management policies are not usually formed over a large time scale.

The actual programs used were coded by the author. The Guelph model was based on a listing provided by C. Capstick, September 1977. The L-B model is a Fortran version of the APL listing given in Lett & Benjaminsin (1977).

We proceed with a brief description of each model with emphasis on differences; next a description of the sensitivity methods employed is given. Results and a discussion are then developed.

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11 The Guelph Model

The Guelph model has evolved from Allen's (1975) work which has been in use since 1972. It offers a major feature which was not evaluated in this work, the use of a Leslie Matrix to produce a stable age distribution from an initial number of pups. The maximum age for an animal in this model is 30 years. The population data used as a starting point for all simulations was the Lett and Benjaminsin 1977 figure with 5 data appended for the ages 26 - 30 (See Table 1). The annual cycle for this model is outlined as:

i Scale harvest over population by age group

ii Prepare output of population

iii Subtract harvest

iv Evaluate herd size of 1^{+} animals (THERD)

v Calculate whelping rate (Egn. 1 + 2 below)

vi Find pups born to 30 year olds

vii Apply natural mortality and age population

viii Find pup production or remaining of adults

End of loop

The whelping rate (FEC) is either held constant at specified values or determined from the herd size by:

$$C\ mean = 3.9967 + .845 \times 10^{-6}\ THERD \quad (1)$$

$$FEC = Gauss\ (Age - C\ mean)/1.118 \quad (2)$$

Where Gauss is the probability function P (X) and FEC, THERD etc. are variable names used in the supplied program. Equation (1) is the result of a linear regression through three points and the ogive

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follows the probability function. See Figure 1.

The pup production for this model is significantly less than that of the L-B model, approximately 44,000 animals for the population given. See Table 1. Approximately 4% of this difference is due to the different ogives when applied to the population given., 3.5% is due to the 50:50 sex ratio and another 1% due to the pregnancy rate. Furthermore, the L-B figure is increased by 6% to account for breeding animals over 25 years of age. These four factors all work in concert to give this difference in pup production.

One of the options available in this program is to run simulations without density dependent feedback control. For this study internal data were used corresponding to Sergeant's 1976 estimates when density dependence was not desired.

Catch quotas were scaled over bedlamers (age classes 2 - 6) and adults, (classes 7 - 30) proportionally to the population relative to the total. In all cases it was assumed that the two quotas were in a 2 to 1 ratio.

111 The L-B Model

This model is more complex than the above. The two principle differences are the incorporation of sex ratio data and the ability to undertake stochastic simulation. Stochastic is used in the sense that certain catch quotas and the natural mortality are drawn from distributions whose means and standard deviation are specified in the model.

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The annual cycle in this model differs from the Guelph model with respect to phase and is principally:

i Split population into sexes

ii Determine adult catch by sex

iii Evaluate herd size N

iv Calcualte maturity and pregnancy rates (Egn's 3 + 4 below)

v Find pup production

vi Harvest adults and pups

vii Apply natural mortality adult + pups

viii Update population

End of loop

An important difference when compared to the Guelph model is the mechanism of the feedback control. Instead of a probability function a sinusoid whose argument is constrained to the first quadrant was used to produce a maturity ogive (in L-B notation). See Figure 1.

$$E_t = \sin (15.522A - 2.245 \times 10^{-5} N_t - 16.017) \quad 3)$$

Also if the population falls beneath a given level 1.002 million (incorrectly stated as 1.2 million in caption Figure 4 L+B 1977) the ogive ceases to translate. A second feedback control is contained in this model, the pregnancy rate. This rate is linear with population size.

$$\text{Preg.} = 1.048 - 9.746 \times 10^{-8} N_2 \quad 4)$$

These two mechanisms, working in series, greatly stabilise the model.

To compensate for a life span of 25 years the pup production is multiplied by a factor of 1.06. The pup production figures for 1977 are

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shown in table 1.

The principle effects observed when the simulations were averaged over 20 stochastic runs over a 20 year period were a slight decrease in population (1.36 as opposed to 1.42 million) and a slight variation in sensitivities. It is concluded that using this stochastic ability has little affect on relationship between the input parameters and the state variables.

Sensitivity Analysis

A sensitivity analysis was undertaken as a basis for comparison between the two models. This was done to reveal the dependence of the simulations on each parameter. As the action of each parameter is isolated in this analysis and as each model has corresponding parameters, it is a direct method for comparison.

We assume that the state of the system is defined by the total population, or in one instance by total breeding population. A reference value, TOTP ref, is determined from the unperterbed values shown in Tabes 2 & 3. The percentage change relative to this value is found when the ith parameter, Pi^{O}, is changed by an increment UiPi. In this work Ui was constrained to $\pm$ .01, a one percent change, and Ri is the relative sensitivity due to that change.

$$Di = TOTPi - TOTP\ ref/TOTP\ ref \times 100 \qquad (5)$$

where TOTPi resultant when $Pi = Pi^{O} (1 + Ui)$

An implicit assumption in sensitivity analysis is that the state variable at any time is completely determined by the input parameters. Also we assume that the parameters act in an independent and linear manner

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To demonstrate local linearity the sensitivities were determined using a positive and a negative incremental change in the parameters. The assumption of independence is obviously not fulfilled in a feedback control system. For example, increasing the adult harvest quota, decreases herd size, increases whelping rates, which tends to increase herd size, etc.

This assumption of a completely deterministic system would appear to contradict a stochastic model. But as a pseudo-random number generator was used to determine the stochastic draws, resetting the seed insures the same 'path' is followed. The seed was therefore treated as an unvarying initial condition. Had this not been done the variances in the parameters, particularly natural mortality, would have dominated the variance due to a 1% parameter change as well as violating one of our assumptions.

Results

Table 4 contains the relative sensitivities for the Guelph model. The main feature of this table is the dominance of R_7 which is the survivorship. As one would expect this term is largest when the density dependence is not in effect. A comparison of the 20 year runs with Ui positive and negative shows the model is locally linear with the exception of the survivorship and this is not surprising due to the magnitude of R_7.

The sensitivities for the L-B model are given in Table 5. This model does not yield a single dominant sensitivity although parameters 3, 4, and 7, respectively the natural mortality and the constants in the two feedback equations for density dependence are more important. The sensitivities of the breeding population show an interesting inter-dependence of the parameters. Parameters 2, 7 and 8 change sign between

4 and 20 years. An explanation will be given below.

Discussion

The two models have been given as similar initial conditions as possible and their performance compared. Starting from basically the same population, natural mortality and harvest quotas, the pup production was first checked for differences (Table 1). A surprisingly large discrepancy was observed. The L-B model had a larger output for three reasons: 1) the presumably erroneous shift in the fecundity in the Guelph model: 2) its incorporation of sex ratio data and the correction factor of 6% for contribution from animals over 25 years of age.

Before the sensitivity analysis was undertaken it was important that the models were operating under similar, stable conditions. Therefore, the pup quotas was dropped from 160,733 to 120,000 for the Guelph model. Had this not been done, the sensitivities would have been greatly biased. For example, R_7 in the first column of Table 4 would have been 59% instead of 36%. The main feature of the Guelph sensitivity is the magnitude of the effect due to a 1% change in the survivorship. A variance or an uncertainty in the final population is 50 times more strongly affected by an uncertainty in P_7 than any other variable. That is a 10% uncertainty in R_7 would contribute 50 times more to the uncertainty in the population size than a 10% uncertainty in the fecundity, for example. This is due to the weaker control exhibited by density dependent fecundity, as compared to the L-B model. For the sake of comparison, a constant survivorship was used. In Capstick et al. 1976, an age dependent table is given for natural mortality. Sensitivities were not estimated using this

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data but it seems unlikely that the results would differ significantly.

The L-B model does not display a clearly dominant sensitivity. The largest value, R_7, is the constant term in the regression for population size dependent pregnancy rate. The importance of R_7 and R_4, both constants in the feedback loop are best seen by making an analogy to a house thermostat. These constants are analogous to the setting of the thermostat and natural mortality analogous to heat loss. Thus in a strongly controlled system, with two density dependent terms acting in series, it is understandable that they should have large sensitivities.

The change in sign of a few of the parameters observed when the breeding stock was used as the state variable, demonstrates the interdependence of the parameters. For example, the pup quota, P_2, over a short span increases the breeding population, but over a long term naturally causes a decrease. This is because the maturity ogive shifts immediately with the drop in population but the effects of the smaller production did not reach the breeding population for a few years.

With its lack of any dominant sensitivity, the L-B model is seen to offer a more precise estimate of the herd state in light of errors in the input parameters. But the question as to whether it is also more accurate cannot be answered by a sensitivity-type analysis. This must be done by independent observation of the herd. Its stability is the result of the two density dependent controls, and as they are both accepted effects their inclusion would be important. It is interesting to note that the effect of the pregnancy control is not obvious in a run from a given population, 328581 vs 327310 in Table 1, but is quite obvious in the sensitivities.

The pup productions shown in Capstick et al. 1976 are much higher than those reported here for a similar model. This could be the result of different starting populations or because the listing sent to the author was an older version.

In conclusion, we have investigated the differences and their causes between the Guelph and L-B models. The main differences are seen to be pup production and stability due to the inclusion of a density dependent pregnancy in one code and not the other. The difference in pup production is the summation of 4 effects; the 6% correction for older animals, 4% due to the ogives, 3.5% due to the sex ratio and 1% due to the pregnancy rate. The latter three depend upon the given population. The second feeback control, pregnancy, was seen to have a stabilizing effect in de-emphasizing the sensitivity to natural mortality.

It is hoped that by revealing underlying mechanisms that this work will lead to a common ground for agreement from which a model can be built of general acceptance.

Acknowledgements

The author thanks Dr. Capstick for the supplied programs and interesting discussion. Also acknowledges P. Lett and T. Benjaminsin for discussions during the investigation into these models.

Table 1 Starting Population and Pup Production

Age	Population	Pups (G)	Pups (L-B)	Age	Population	Pups (G)	Pups (L-B)
1	159765	0	0	16	21079	9486	11135
2	123409	0	0	17	15349	6907	8578
3	154244	2642	2895	18	14361	6463	7994
4	116366	10294	17492	19	10164	4574	5915
5	117449	28596	31101	20	12792	5756	6865
6	72145	29060	26029	21	6594	2967	3943
7	75410	33935	32476	22	5432	2444	3484
8	68885	30998	32414	23	3889	1750	2703
9	68093	30642	32722	24	4624	2081	3032
10	44124	19856	21100	25	2630	1184	2014
11	27682	12457	13440	26	2000	900	0
12	26119	11754	12854	27	1600	810	0
13	25511	11480	12558	20	1600	720	0
14	22891	10301	11410	29	1200	540	0
15	25003	11251	12620	30	1000	450	0
					TOTALS	290296	315772

Note: a) L-B total + 6% is 334718

b) L-B with .9 ceiling instead of PREG = .9443 as coefficient 312846

Table 2 Unperterbed parameter values Guelph Model.

Parameter #	Name	Unperterbed value Pi^{o}
1	Bedlamer harvest	18700
2	Adult harvest	9402
3	Pup harvest	120,000
4	Constant Egn. 1	3.9967
5	Coefficient of herd size Egn. 1	$.8450 \times 10^{-6}$
6	Max. fecundity	.90
7	Natural mortality	.114
8	Fecundity	As determined above or given as data
9	Divisor (S.D.) Egn. 2	1.118

Table 3 Unperterbed values L-B Model.

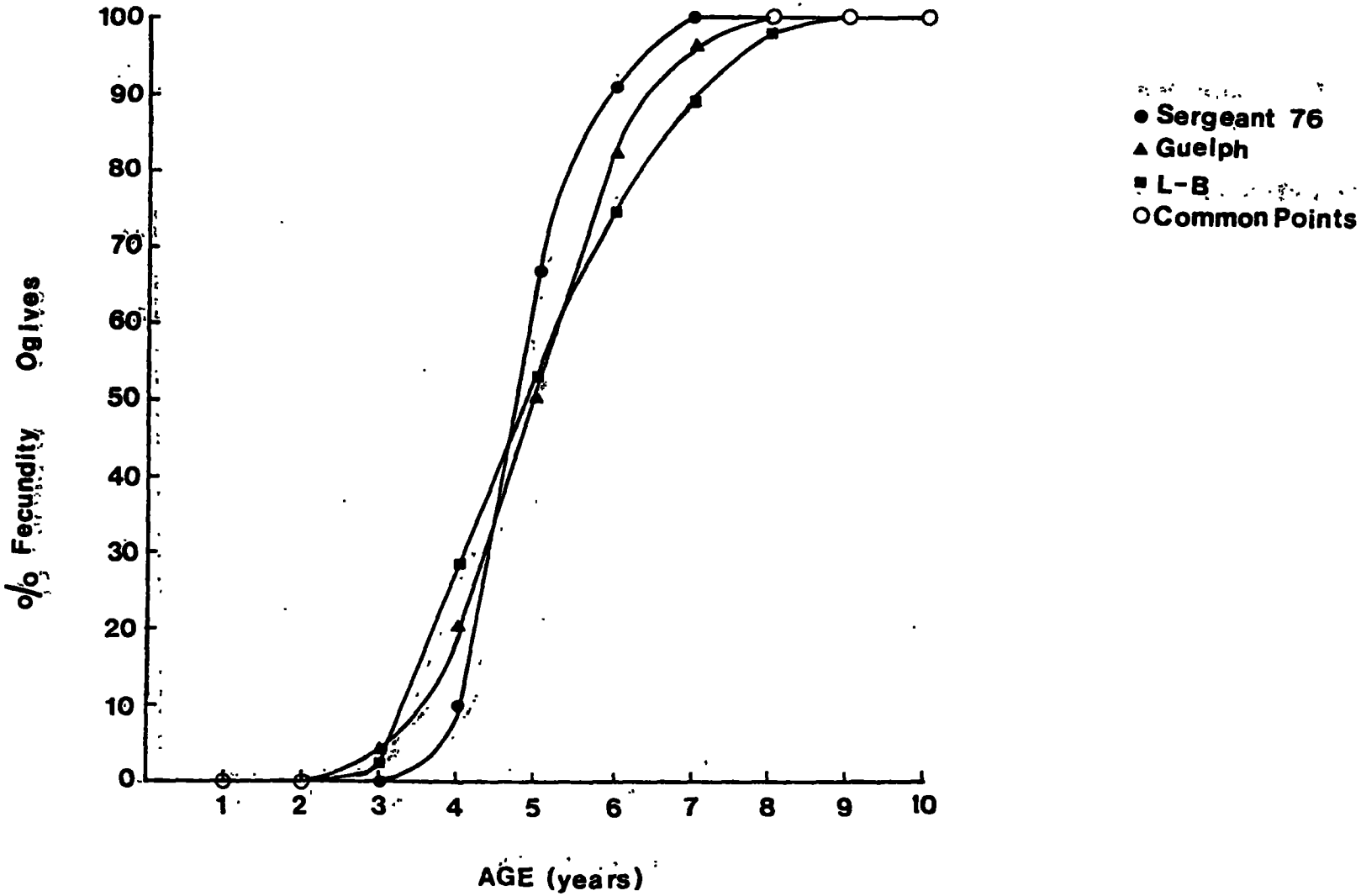
Parameter #	Name	Unperterbed value
1	Adult harvest	28102
2	Pup harvest	160733
3	Natural mortality	.114
4	Constant Egn. 3	15.5223
5	Coefficient of herd size Egn. 3	2.245
6	Coefficient of age	16.01743
7	Constant Egn. 4	1.048
8	Coefficient of herd size Egn. 4	9.7454×10^{-8}

Table 4 Relative Sensitivities Ri(%) Guelph Model.

Density Dep.	Yes	Yes	Yes	No
Period (Yrs.)	20	20	4	20
Ui	+1%	-1%	+1%	+1%
State Variable	TPOP	TPOP	TPOP	TPOP
Parameter #				
1	-.451	.450	-.043	-.514
2	-.284	.284	-.029	-.318
3	-1.709	1.700	-.197	-1.951
4	-2.313	2.360	-.345	0
5	-.580	.580	-.086	0
6	3.085	-3.074	.381	0
7	35.711	-30.882	3.283	42.686
8	4.021	- 3.999	.524	4.648
9	.152	-.151	.019	0
reference	1497381	1497381	1459552	1591987

Table 5 Relative Sensitivities Ri(%) L-B model

Stochastic	No	No	No	Yes	No	No
Period (yrs)	20	20	4	20	20	4
Ui	+1%	-1%	+1%	+1%	+1%	+1%
State variable	TOTP	TOTP	TOTP	TOTP	BREED	BREED
Parameter #						
1	-.413	.412	-.073	-.403	-.293	-.050
2	-1.476	1.473	-.315	-1.484	-.863	.039
3	-2.854	2.915	-.468	-2.843	-2.101	-.361
4	2.310	2.295	.562	2.395	2.007	.650
5	-.913	.942	-.232	-.948	-.790	-.274
6	-.483	.490	-.126	-.508	-.415	-.147
7	3.771	-3.727	.788	3.723	2.152	-.104
8	-.415	.417	-.084	-.392	-.239	.011
Reference	1424525	1424525	1341411	1364184	379292	368810


% Fecundity Ogives
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
AGE (years)
● Sergeant 76
▲ Guelph
■ L-B
○ Common Points

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