A Model to Assess the Effect of Predation by Sawbill Ducks on the Salmon Stock of the River North Esk

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Abstract

Two species of sawbill duck, the goosander and the red-breasted merganser, prey on smolts of the Atlantic salmon during the smolt run. A simple steady state model has been developed which considers the effect of the predation by sawbill ducks on the number of adult salmon returning to the river North Esk in Scotland. The model can be used to examine the effect of controlling the predation by sawbills on the number of returning salmon.

Introduction

Sawbill ducks have been identified as one of the predators of smolts of the Atlantic salmon, *Salmo salar* L. In view of the importance of the salmon fishery it is of some interest to evaluate the possible impact that this predation may have on salmon populations. This paper presents a simple model which examines the effects of predation on salmon smolts by sawbill ducks on the population of adult Atlantic salmon returning to the river North Esk in north-eastern Scotland. Predation at different levels is examined. Two species of sawbill are considered, the goosander, *Mergus merganser merganser* L., and the red-breasted merganser, *Mergus serrator serrator* L. For simplicity the red-breasted merganser will be referred to as the merganser.

The Model

A simple way to begin is to consider the sawbill-salmon interaction to be in a steady state, ie for a given level of predation by sawbills, the same number of adults return to river and the same number of smolts are produced each year. We are, therefore, interested in a new steady state when the level of predation by sawbills is changed. In particular, we are interested in determining how the number of adults returning to the river is affected. Since we are concerned with the change from one state to another, we need only consider the proportionate change. Thus if the number of adults returning to the river is A_r and the number returning when sawbill-inflicted mortality is reduced is A_r', then the proportionate change, P, in returning adults is given by:

$$P = (A_r' - A_r)/A_r \qquad (1)$$

It can be shown (see Appendix I) that when sawbill predation is reduced by an amount d for a particular population of smolts, N_s, entering the sea, then:

$$P = \exp\,[dk_1 + u(N_s) - u\,(N_s \exp\,(dk_1))] - 1 \qquad (2)$$

where k_1 = mortality due to sawbill ducks

d = the proportionate reduction in k_1

u = the density dependent function relating marine mortality to the smolt population entering the sea.

We can, therefore, investigate how P changes as d is increased; that is how the proportionate change in returning adults responds to a reduction in sawbill mortality k_1.

It is worth noting that in the absence of density dependence, when $u(N_s) = 0$, equation (2) reduces to;

$$P = \exp[dk_1] - 1 \tag{3}$$

When dk_1 is small this can in turn be approximated by,

$$P = dk_1 \tag{4}$$

This means that for small changes in the mortality due to sawbills the proportionate increase in the number of adults returning is equal to the reduction in mortality.

Estimation of Model Parameters

The purpose of formulating the model is to investigate how the proportion of adults returning to the river is affected by reducing sawbill predation on smolts ie how P responds to increases in d. In order to evaluate P, it is necessary to;

a. estimate the smolt population entering the sea, N_s

b. define the density dependent function, u

c. estimate the prevailing value of k_1.

Smolt Production

The annual smolt production of the North Esk is estimated using a mark-recapture technique in which known numbers of smolts are marked at Kinnaber Mill Trap, a sampling site in a lade off the lower reaches of the North Esk, and released again upstream. Table I shows the number of smolts entering the sea estimated in this way taken from Shearer (1984). Since we are primarily interested in the change to the system in a steady state, a simple arithmetic mean of these values (172,000) was used for N_s.

Table I

Estimated number of smolts entering the sea each year and the corresponding number of adults returning over subsequent years from each smolt year

Smolt year	Smolt production	Number of adults returning
1964	275,000	61,700
1965	183,000	62,200
1966	172,000	56,000
1967	98,000	43,000
1968	227,000	60,100
1971	167,000	50,700
1972	260,000	68,400
1973	165,000	55,800
1974	106,000	49,100
1975	173,000	36,100
1976	93,000	38,600
1980	132,000	21,300
1981	195,000	33,100
1982	160,000	22,200

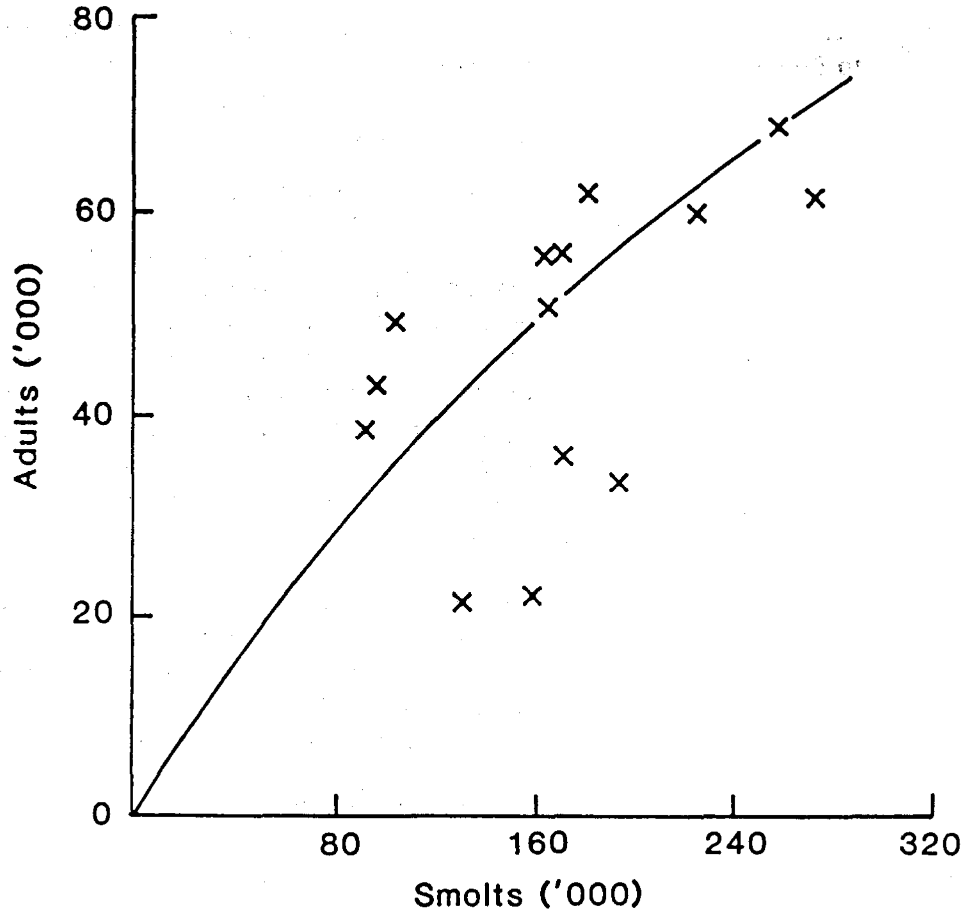

Figure 1. **A plot of the number of returning adult salmon from a given smolt year. The line is the fitted Beverton-Holt curve whose parameter values are given in Table II.**

Density Dependence

Shearer (1984) gives estimates of the number of returning adults from each smolt year. These numbers, now updated, are shown in Table I and they are plotted against the smolt population in Figure I. If the survival of the returning fish was density dependent then the points in Figure I would lie on a curve whose shape is convex upward. The scatter of points is too great to determine such a curve but in order to accommodate the possibility of density dependence it is both conventional and convenient for purely descriptive reasons to fit the Beverton-Holt curve;

$$A_r = aN_s/(1 + bN_s) \qquad (5)$$

to the data, where a and b are constants. This curve implies that the density dependent function is:

$$u(N_s) = \log(1 + bN_s) + a' \text{ where } a' = -\log(a) \qquad (6)$$

Estimates of a and b obtained from a least squares fit of equation (5) to Figure 1 are given in Table II. The coefficient of density dependence b is clearly not significantly different from zero so the case for density dependence is not proven. However, although density dependence is uncertain, it may have an important effect on the number of returning adults, and it has been included in examples of model output given below. These examples use the estimate of b in Table II.

Table II

Parameters of the Beverton-Holt curve estimated by least squares

Parameter	Mean	Standard deviation
a	0.495	0.269
b	0.000005	0.000005

Estimates of Mortality due to Sawbill Predation

There is no satisfactory estimate of the mortality due to sawbill predation, k_1. However if an estimate of the number of smolts consumed by the population of sawbills on the North Esk, C, can be made then k_1 can be estimated by solving the well known catch equation;

$$C = k_1 N_s (\exp(k_1 + k_2) - 1)/(k_1 + k_2) \quad (7)$$

where k_2 is the mortality which is not due to sawbills. As the smolt estimation is made at a point in the river at the head of the tide, this equation assumes that the predation by sawbills on smolts has taken place before they reach Kinnaber Mill Trap. It also assumes that any reduction in sawbill numbers, perhaps as a result of control measures, is not accompanied by a concommitant local increase in the numbers of other predators; ie that k_1 and k_2 are independent. It further assumes that sawbills are not selectively feeding on weak and diseased smolts which would not reach the sea anyway.

An estimate of C can be obtained by considering the composition of the diet of sawbills, their food requirements and the population of ducks on the river. In particular, if an individual sawbill duck requires F weight of food per day and the mean weight of a smolt is S then the total number of smolts eaten by a population of ducks during the smolt run is given by;

$$C = R \sum_j \sum_i t(i)q(j)p(i,j)N(i) \quad (8)$$

where
- R = F/S
- $t(i)$ = number of days in month that smolts are at risk.
- $q(j)$ = proportion by weight of smolts in the diet of sawbill species j.
- $p(i, j)$ = proportion of total sawbills which are of species j in month i.
- $N(i)$ = total number of sawbills in month i.

There are a number of estimates of F, the daily food requirement of sawbills. On the basis that wild American megansers, *Mergus merganser americanus* L. consume 1/3 to 1/2 of their body weight each day and that the average weight of these birds is 1.153 kg (Sayler and Lagler, 1940), Elson (1962) estimated that the daily food requirement of an adult bird is approximately 0.45 kg. This value is supported by feeding experiments on captive birds (White, 1937, 1957) and by recent observations on captive sawbills by S. P. Carter and P. R. Evans (pers. comm.). However, Latta and Sharkey (1966) reported that American merganser adults require 18–27% of their body weight per day. This is equivalent to a daily intake of approximately 0.21–0.31 kg. Because of the wide range of published food requirements of sawbill ducks, an arbitrary value of F = 0.35 kg of food per day has been assumed. This is close to the midpoint of the published values.

Various estimates of the salmon component of a sawbill's diet (q(j)) have been reported. For the American merganser Anderson (1986) states a value of 0.73, Elson (1962) 0.42 and White (1936) 0.822. Mills (1962) reported that the salmon component of the diet of Scottish sawbills was 0.572 for the goosander and 0.425 for the merganser. Since Mills' estimate is more relevant to the North Esk and is comparable to the estimates for the American merganser his values have been used for the q(j)s.

S. P. Carter (pers. comm.) has provided data on the number of sawbills on the river North Esk during the smolt run. On the basis of his data the proportion of goosanders (p(i, goosander)) in each month are as follows;

April	0.352	(N(i)=51)
May	0.024	(N(i)=69)
June	0.042	(N(i)=42)

[NB: p(i, merganser) = 1 – p(i, goosander)]

In addition the following assumptions have been made;

1. a smolt weighs 0.021 kg = S
2. smolts are "at risk" to saw bill predation for the duration of the smolt run, which on the North Esk lasts some 70 days (all of April and May and the first nine days of June).
3. during smolt migration smolts represent the sole salmon component of the sawbills' diet.
4. the population of sawbills, N(i), lies between 50 and 100 birds each month.

On the basis of these assumptions the total number of smolts eaten by sawbills calculated from equation (8) lies in the range 20,000–60,000.

In order to solve equation (7) it is necessary also to know k_2 (the non-sawbill mortality). This is simply unknown. Table III therefore shows solutions to equation (7) for k_1 for a range of values of C and guesses of k_2. This gives estimates of k_1 lying between 0.05 and 0.3.

Table III

Estimates of sawbill-induced mortality k_1 for various values of k_2 and C. N_s = 172,000

k_2	C = 20000	C = 60000
0	0.110	0.299
0.1	0.105	0.286
0.2	0.100	0.273
0.5	0.086	0.236
1.0	0.065	0.182

Model Output

Our objective in formulating the model is to investigate the effect of reducing the mortality due to sawbills on the number of returning adult salmon; ie the effect of d on P. Unfortunately it is clear from the discussion above that there is large uncertainty in the estimates of the coefficient of density dependence, b, and in k_1. The uncertainty in k_1 arises through inadequate estimates or knowledge of k_2 and C. Thus we cannot simply vary d with all other parameters constant and examine P. Output from the model is therefore given in Figures 2 and 3 for a range of values of k_1 and two values of b.

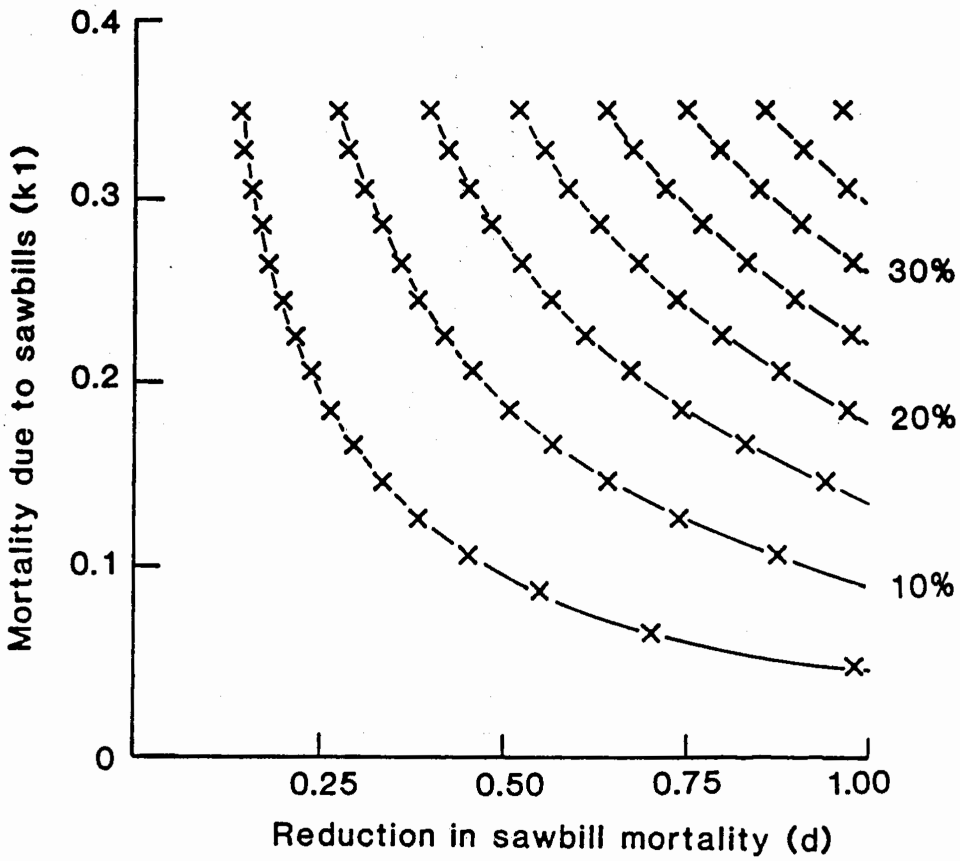

Figure 2. Contour plot showing lines of equal gain in the percentage of returning adult salmon for combinations of sawbill-induced mortality and the reduction in sawbill-induced mortality. No density dependence is assumed during the marine phase.

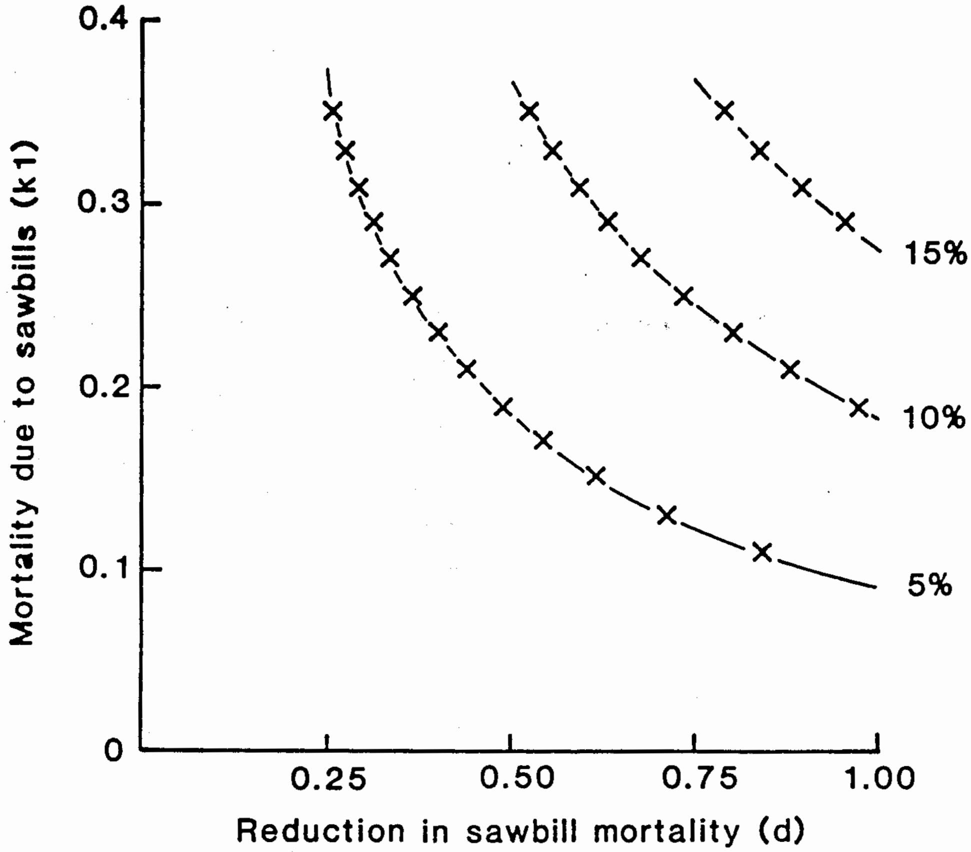

Figure 3. Contour plot showing lines of equal gain in the percentage of returning adult salmon for combinations of sawbill-induced mortality and the reduction in sawbill-induced mortality. The coefficient of density dependence during the marine phase is taken to be b = 0.000005.

Figure 2 shows the effect of reducing the mortality due to sawbills (ie by increasing d) on the proportion of returning salmon, P, in the absence of density dependence (b=0). The plotted contours (indifference curves) are loci of equal P. For example the curve labelled 10% in Figure 2 shows the possible combinations of d and k_1 which could give this value of P. The contours grade from low gain in the bottom left to high gain in the top right. Similarly, Figure 3 shows the output when density dependence is included (b = 0.000005). It has the effect of spacing the contours more widely and indicates that if density dependence is operating then a reduction in sawbill-induced mortality is compensated for by a higher marine mortality. The gain in returning adults is thus lower than anticipated.

The basic problem in interpreting the model output is to decide where on the y axis in Figures 2 and 3 the true value of k_1 lies. The output has been generated for the range of values of k_1 calculated on the basis of the number of smolts eaten. An intermediate value of k_1 would therefore be about 0.15 and implies a gain of 15% if sawbill predation was eliminated (Fig. 2). The maximum benefit which might accrue is a 35% increase in returning adult salmon. This assumes that the existing mortality caused by sawbills, k_1, is high and would require the complete elimination of sawbill predation with no density dependent survival of adults (Fig. 2). At the other extreme, if the sawbill-induced mortality is actually small, and adult salmon survival is density dependent, then the maximum gain even if all predation was eliminated would be only a few percent (Fig. 3).

Discussion

On the basis of calculations performed here the greatest benefit that might be expected by controlling sawbill duck predation is a 35% increase in the number of adult salmon returning to the river. In reality the benefit is likely to be less than this if only because it is unlikely that all predation by sawbills could be eliminated.

The limitations of the model should be remembered. Firstly, the uncertainty in the values of the input parameters must be considered. This can to some extent be elucidated by sensitivity analysis (see Appendix II), which examines how sensitive the model output (ie P) is to uncertainty in the input parameters. This analysis suggests that provided the magnitude of the mortality not due to sawbills, k_2, is small (ie less than 0.3) then the model output is most sensitive to the estimate of the number of smolts, C, eaten by sawbills. It seems likely that k_2 is small, so that improving the estimate of C therefore seems worthwhile and a realistic possibility.

It should not be forgotten that the model developed here is a very simple steady state model. It does not consider annual fluctuations in smolt or sawbill populations, nor are patchy distributions of predator or prey accounted for. Mortality rates during the time of interaction are also assumed constant. No explicit consideration is given to the possibility that trout smolts may compete with salmon smolts in the diet of the birds at certain times. All these simplifications are made by necessity, not for biological realism. To evaluate these assumptions more research is required on the inter-relationships between sawbill ducks (and other avian and non-avian predators) and salmonid fishes. The following recommendations are made with this in mind;

(i) More reliable bird census data are required, including more detailed counts of sawbills by species, age and sex. To make the most efficient use of limited resources, the main initial effort should be concentrated on a single watershed where the bird population should be monitored throughout the year.

(ii) The behaviour of sawbill ducks should be investigated to determine such factors as their distribution in space and time, feeding range, prey preferences, territory size, inter- and intra-specific competition. The feeding behaviour of the large numbers of sawbills known to roost in estuaries, but which appear to spend much of the day upriver, should also be investigated.

(iii) Detailed investigations into the diet and energy requirements of sawbill ducks are required. These investigations should be conducted throughout the year and should include both species, both sexes and all age groups. It may be necessary to investigate methods to discriminate salmonid species and age groups in the diet.

(iv) More information is required on other causes of mortality of salmon throughout the juvenile phase.

Summary

Two species of sawbill duck, the goosander and the red-breasted merganser, prey on smolts of the Atlantic salmon during the smolt run. A simple steady state model has been developed which considers the effect of the predation by sawbill ducks on the number of adult salmon returning to the river North Esk in Scotland. The model can be used to examine the effect of controlling the predation by sawbills on the number of returning salmon.

The mortality rate of smolts due to predation by sawbill ducks is poorly estimated. This makes a precise prediction of the possible increase in the number of salmon returning to the river if sawbill duck populations were controlled very difficult. Simulations using apparently realistic values of this mortality rate suggest that the maximum benefit would be 35% increase in returning adult salmon. In practice the benefit is likely to be less than this.

Areas of research which are likely to lead to an improvement in the model are described.

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Appendix I: Derivation of Equations Used in the Text

Let the number of smolts entering the sea, N_s, be given by

$$N_s = N_o \exp(-k_1 - k_2) \quad \text{(A1)}$$

where N_o = the smolt population before any mortalities

k_1 = mortality due to sawbills

k_2 = other mortalities

While they are at sea during their post-smolt and adult life, the fish will suffer an additional mortality, k_3. Hence, the number of adults returning, A_r, will be given by:

$$A_r = N_o \exp(-k_1 - k_2 - k_3) \quad \text{(A2)}$$

In fact, k_3 may be a density dependent mortality, ie

$$k_3 = u(N_s) \quad \text{(A3)}$$

where u is the density dependent function,

then $$A_r = N_o \exp[-k_1 - k_2 - u(N_s)] \quad \text{(A4)}$$

We wish to know what will happen to A_r when the sawbill-induced mortality k_1 is varied. Suppose then that k_1 is changed by an amount dk_1. This will change the population of smolts, N_s, entering the sea to N'_s.

$$N'_s = N_o \exp[-(k_1(1-d)+k_2)] \quad \text{(A5)}$$

whence

$$N'_s = N_s \exp[dk_1] \quad \text{(A6)}$$

Now, the number of returning adults is changed to A'_r which is given by:

$$A'_r = N_o \exp[-(k_1(1-d) + k_2 + u(N_s \exp(dk_1)))] \quad \text{(A7)}$$

The proportionate change, P, in returning adults is given by:

$$P = (A'_r - A_r)/Ar \quad \text{(A8)}$$

And substituting (A4) and (A7) into (A8) we obtain

$$P = \exp[dk_1 + u(N_s) - u(N_s \exp(dk_1))] - 1 \quad \text{(A9)}$$

Using equation (A9), it is therefore, possible to examine the effect on P of changes in sawbill-induced mortality by altering d.

If there is no density dependence, equation (A9) reduces to:

$$P = \exp(dk_1) - 1 \quad \text{(A10)}$$

and if dk_1 is small this further simplifies to:

$$P = dk_1 \quad \text{(A11)}$$

Thus, for a small decrease in sawbill-induced mortality and in the absence of density dependence, the proportionate change in the number of returning adults is equal to the absolute reduction in mortality due to sawbills.

Appendix II: Sensitivity Analysis

The estimates of model parameters are clearly subject to considerable uncertainty and this in turn leads to uncertainty in the estimation of the state variable, in this case P, the proportionate change in the number of returning adults. It is desirable, therefore, to quantify the effects of these uncertainties on the model output. To this end a sensitivity analysis has been performed on the model using the Fourier Amplitude Sensitivity Test (FAST) method of Cukier *et al.* (1978) which gives global sensitivity coefficients for non-linear multiparameter models. The model in this analysis consists of text equations (7) and (2) where the "parameters" are:

C – the number of smolts eaten by sawbills

N_s – the mean number of smolts entering the sea

k_2 – non-sawbill mortality

b – the coefficient of density dependence.

The first three parameters determine k_1 using equation (7), then equation (2) is solved using estimates of k_1 and b.

The FAST method involves simultaneously disturbing all the parameters in the model according to chosen uncertainty ranges. It is then possible to quantify how much of the variance in the state variable is due to each parameter. Table AII.I shows the results of the analysis. It has been assumed that the estimate of N_s is fairly precise (ie it changes by only 10%) while all the other parameters vary by a factor of 2. In Table AII.Ia low value of k_2 has been assumed and it can be seen that most of the sensitivity in P is due to C, the number of smolts eaten. Appendix Table 1b shows the output when k_2 is assumed to be large. Now the greatest sensitivity is due to both k_2 and C. It is encouraging, however, to see that if k_2 is low, which it probably is, then the most important parameter is C and that this quantity is perhaps the least difficult to measure.

It is important to realise that the calculated sensitivities (ie the partial variances) are dependent on the chosen nominal parameter values and the uncertainty range. Thus, if these values have been chosen incorrectly then the sensitive analysis will be misleading. If for example the uncertainty on N_s is increased its sensitivity increases. The analysis does show, however, that more work on a precise estimate of C should be worthwhile.

Appendix Table I

Output from FAST method for (a) a low value of k_2 and (b) a high value of k_2. In both cases d=0.9. For each parameter the maximum value taken is the nominal value x uncertainty range and the minimum value is nominal value ÷ uncertainty range. The partial variance indicates how much of the variance of the state variable P is due to that parameter.

(a)

Parameter	Nominal value	Uncertainty range	Partial variance
C	35,000	2.0	0.4609
N_s	172,000	1.1	0.0271
k_2	0.3	2.0	0.1021
b	0.000005	2.0	0.2757

Value of P at nominal parameter values = 0.0603
Mean value of P = 0.0620
Coefficient of variation of P = 0.5815

(b)

Parameter	Nominal value	Uncertainty range	Partial variance
C	35,000	2.0	0.2444
N_s	172,000	1.1	0.0630
k_2	0.9	2.0	0.3935
b	0.000005	2.0	0.1775

Value of P at nominal parameter values = 0.0305
Mean value of P = 0.3295
Coefficient of variation of P = 0.8042

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