Measurement Errors and Uncertainty in Parameter Estimates for Stock and Recruitment

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A procedure is developed for estimating stock and recruitment parameters in the presence of measurement errors. It requires an independent assessment of the ratio of environmental and measurement error variances, and provides maximum likelihood estimates of the time series of errors as well as the average stock–recruit parameters. Measures of parameter uncertainty are also provided and are incorporated into an analysis of optimum spawning stocks. This analysis indicates that much higher, or at least more variable, spawning runs should be allowed in many Pacific salmon stocks. An immediate need in salmon management is to obtain estimates of the measurement error variance, so that recent historical data can be made more useful.

Key words: statistics, stock recruitment, optimum spawning, uncertainty

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Nous avons mis au point un méthode d'estimation des paramètres de stock et de recrutement quand les mensurations comportent des erreurs. La méthode est fondée sur une évaluation indépendante du rapport entre les variances de l'environnement et celles des mensurations, et donne des estimations de probabilité maximale de la série temporelle d'erreurs, de même que les paramètres moyens de stock et de recrues. Nous fournissons également des mesures de l'incertitude des paramètres, mesures incorpores dans une analyse de stocks reproducteurs optima. A la suite de cette analyse, on constate que, dans plusieurs stocks de saumons du Pacifique, il faudrait prévoir des remontées reproductrices beaucoup plus fortes, ou du moins plus variables. Dans la gestion du saumon, il faudrait tout d'abord estimer la variance des erreurs de mensurations, de façon à tirer meilleur profit des données historiques récentes.

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MEASUREMENT errors may have two effects upon the assessment of stock and recruitment: (1) the parameter estimates may be inconsistent, as a result of hidden correlations in the regression equations, and (2) the amount of information available may be overestimated. These effects are pointed out by Walters and Ludwig (1981). Here we extend that analysis to take account of the limited number of observations which are usually available. We develop a more elaborate estimation procedure and further explore the policy consequences of measurement errors.

A major conclusion of Walters and Ludwig is that estimates of numbers of spawners and recruits are of little value unless the accuracy of the estimates is also assessed. There is a parallel principle in the statistical estimation of model parameters: the statistical estimates are of little value unless they are accompanied by estimates of their accuracy. A similar principle applies to management decisions which are based (in part) upon parameter estimates: uncertainty about parameter values cannot be ignored in formulating management policy. These principles are valid even if observations are made with perfect accuracy. However, large observation errors (which are present in most fisheries data) result in substantial uncertainty in parameter estimates. The parameter uncertainty frequently overwhelms effects of density dependence in the stock–recruitment relationship. In such situations, more information is required before a rational strategy can be determined. Then the first task of the manager is to obtain such information. This will usually require purposeful manipulation of the number of spawners.

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Estimation of Observation Errors

We shall illustrate our procedure with the Ricker model. Other models are treated in the Appendix. If r_j and s_j denote the actual number of recruits and spawners in generation j, we assume that

$$(1) \quad r_j = s_{j-1}\, e^{a+b\, s_{j-1} + u_j},$$

where u_j are independent, normally distributed random variables, with mean 0 and variance σ_u^2. The observed numbers of recruits and spawners are given by R_j and S_j, respectively, where

$$(2) \quad R_j = r_j e^{v_j},\ S_j = s_j e^{v_j}.$$

Here v_j are independent, normally distributed, random variables with mean 0 and variance σ_v^2. Notice that the same relative error appears in numbers of recruits and spawners of a given generation. (Recruits are usually estimated as catch plus spawners, and we assume catch is measured with small error.) Our method can also be applied if the relative errors are different, but details will not be given here.

Given observations (R_j, S_j) for generations $j = 0, 1, 2, \ldots, n$, we seek to estimate the parameters a, b, σ_u^2, and σ_v^2 from these observations. It is shown in Kendall and Stewart (1973) that this problem is insoluble unless additional information about the errors is provided. We have chosen to prescribe the ratio

$$(3) \quad \lambda = \frac{\sigma_v^2}{\sigma_u^2}.$$

That is, all of our calculations depend upon the value of λ, which must be chosen beforehand. Other assumptions might be made, but this one leads to a relatively straightforward estimation procedure.

Once λ is prescribed, the parameters a, b, σ_u^2, and $v_0, v_1, \ldots, v_n$ may all be estimated by the method of maximum likelihood. Details are given in the Appendix. The logarithm of the likelihood of the observations is given by

$$(4) \quad L(a, b, \sigma_u^2, v_0, \ldots, v_n) = -\frac{1}{2\sigma_u^2}\left[\sum_{i=1}^{n} u_i^2 + \frac{1}{\lambda} v_i^2\right] - n \ln \sigma_u - (n+1)\ln(\lambda\sigma_u),$$

where $u_1, \ldots, u_n$ are determined from (1) and (2). All of the parameters except for σ_u^2 are determined by maximizing L. If σ_u^2 were determined in the same way, the estimate would be biased; σ_u^2 can be estimated from the residual sum of squares:

$$(5) \quad \hat{\sigma}_u^2 = \frac{1}{2n+1-(n+3)}\left[\sum_{i=1}^{n} \hat{u}_i^2 + \frac{1}{\lambda}\sum_{i=0}^{n} \hat{v}_i^2\right],$$

where $\hat{u}_i$ and $\hat{v}_i$ are the estimated values which maximize L.

The results of this procedure are illustrated in Fig. 1. The original data points are displayed, together with the best least squares fit with the Ricker model. The corrected data points are obtained from (2), where v_j are estimated by the maximum likelihood procedure with $\lambda = 1$. In Fig. 1, the original points are shown as numbers representing spawning years. They are joined to stars representing corrected points. Best fits to original and corrected data are shown for the Ricker model.

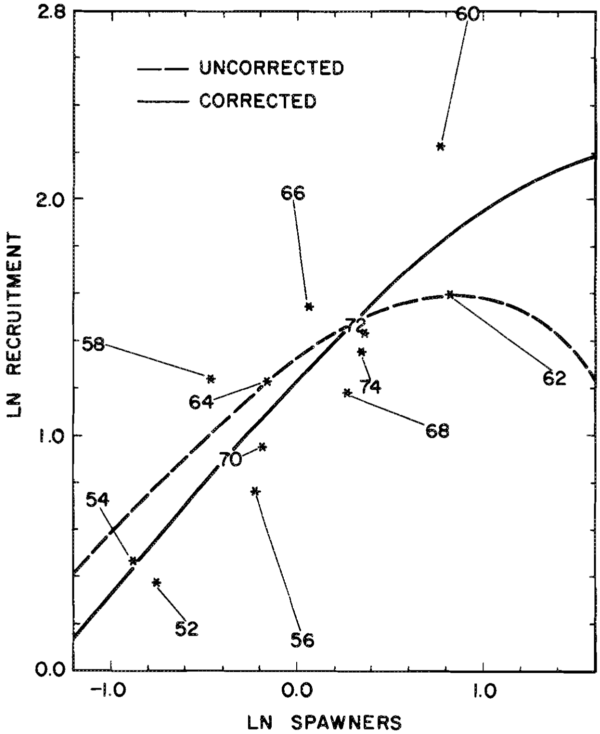

FIG. 1. The logarithm of the number of recruits in generation n is plotted against the number of spawners in generation $n-1$, for pink salmon in British Columbia statistical area 8. The original data points are plotted as numbers, which represent spawning years. The broken line curve is the best fit to the data, using the Ricker model. If observation errors are considered, whose variance is equal to the variance of the annual fluctuations in recruitment, then the original data points are corrected to the values shown with stars. The solid curve is the best fit to the corrected data, using the Ricker curve. The corrected slope is generally higher than the uncorrected slope, because of hidden correlation in the original data.

To assess the validity of the procedure, we have applied it to artificial data, starting with parameters $\hat{a}$, $\hat{b}$, and $\hat{\sigma}_u^2$ as estimated in Fig. 1. For the artificial data, s_i, $i = 0, \ldots, n-1$ were chosen such that ln s_i were uniformly distributed on an interval of width w, with the same center as for the original data. An important parameter is w, since it measures the amount of information provided about variation of the number of recruits with the number of spawners. Then sequences $\{u_i\}$ and $\{v_i\}$ were generated to be normally distributed with mean 0 and variance σ_u^2 and σ_v^2, respectively. The values of σ_u^2, σ_v^2, a, and b were those determined as in Fig. 1. Then (1) and (2) were used to generate the artificial data, subject to the constraint that $s_i \leq r_i$. The result of all this is a set of artificial data which resembles the original data, but for which the parameters are known. The amount of information in the artificial data is controlled by the number of points n, and the width w.

Figures 2 and 3 illustrate the results when the estimation procedure was applied to such artificial data sets, while assuming the correct value of $\lambda = 1$. In some cases, as in Fig. 2, the error corrections led to very accurate estimates. Fre-

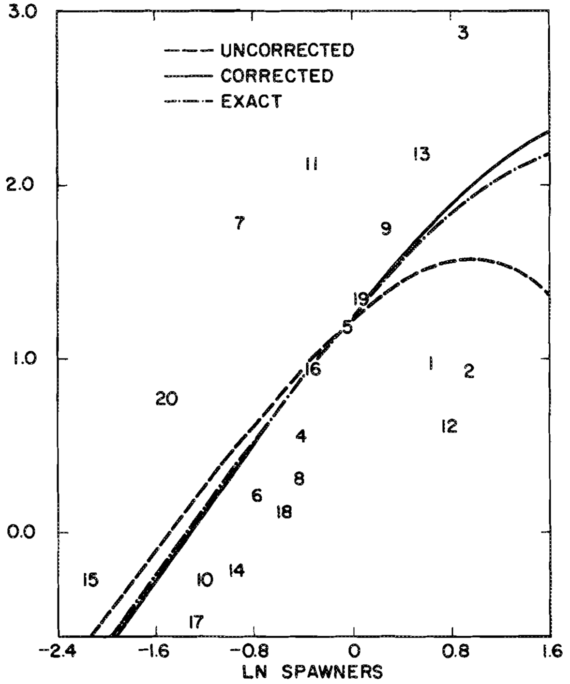

FIG. 2. Simulated stock and recruitment data, for the parameters estimated in Fig. 1. The curve labeled "exact" is the corrected fit from Fig. 1. The curve labeled "uncorrected" was the best fitting Ricker curve to the simulated data. The curve labeled "corrected" was obtained by assuming the observation errors had the same variance as the variance of annual fluctuations in recruitment.

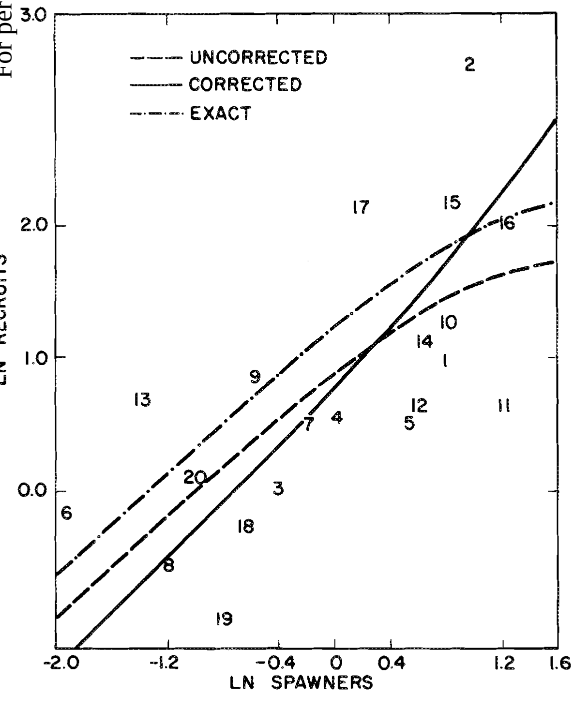

FIG. 3. A second set of simulated data, obtained under the same conditions as in Fig. 2.

quently, as in Fig. 3, the results were far from accurate, and the error correction did not improve the accuracy. For very large data sets ($50 \leq n \leq 100$) the error correction was more accurate and reliable. Although such an outcome is reassuring, it is irrelevant to most management problems, since such large sets are not yet available (and would be unreliable anyway, because of changes in stock parameters).

It is more important to assess the validity of the procedure if $10 \leq n \leq 20$. In this range, the width w has a decisive impact upon the estimates. Accuracy and reliability were both poor for widths w comparable to those available for historical British Columbian salmon data. Accuracy increased sharply if the width w was increased by a factor of 2 to 4, even if no observation error correction was used. This result emphasizes the need for management strategies which produce larger variations in the actual number of spawners.

Uncertainty in Parameter Estimates

The unreliability of the estimation procedure when applied to artificial data shows the need for estimates of parameter uncertainty. One approach would be to describe the distribution of the least squares estimates for large samples. However, fisheries managers are not confronted with many independent sets of data drawn from the same population, so the basic assumptions which underlie the conventional approach to estimation are not satisfied. On the contrary, the manager usually has one set of observations for each stock, and data from differing stocks will seldom have the same statistical properties.

A more appropriate procedure is to base all statistical inference upon the likelihood of the given observations, as a function of the parameters to be estimated. Such an approach has been adopted implicitly in equation (4), where the logarithm of the likelihood of the observations is displayed as a function of these parameters. The actual likelihood function will be extremely complicated. However, we may approximate it by a quadratic function, in the vicinity of the maximum likelihood estimates. As shown in the Appendix, the result is an approximation

$$(6)\quad L(a,b) \sim L(\hat{a}, \hat{b}, \hat{\sigma}_u^2, \hat{v}_0, \ldots, \hat{v}_n) - \frac{1}{2\sigma_u^2}[M'_{aa}(a-\hat{a})^2 + 2M'_{ab}(a-\hat{a})(b-\hat{b}) + M'_{bb}(b-\hat{b})^2].$$

The coefficients (M'_{aa}, M'_{ab}, M'_{bb}) are derived from a reduced information matrix, which takes account of variation of the estimated errors $v_0, \ldots, v_n$ with the parameters $\hat{a}$ and $\hat{b}$.

Up to this point, the calculations are hardly different from a conventional large-sample approach. The same information matrix appears in describing the distribution of the maximum likelihood estimates. However, we believe that it is more appropriate to regard (6) as the probability density function of the parameter values, based upon the information provided by the data. That is, the likelihood function describes the state of our knowledge of the parameter values, as determined by the observations. A difficulty with this Bayesian approach is that other information about the parameter values should be incorporated into a "prior distribution," which would multiply the likelihood. Such a prior distribution in essence incorporates additional (less-accurate) observations which are assigned lesser weight than the others. This possibility is considered in the Appendix. If equal weights are assigned to all observations and the likelihood function is used to describe the parameter distribution, this is equivalent to adopting a uniform, uninformative, prior parameter distribution.

Now the stock–recruitment relation (1) must be reexamined. If a and b are random variables distributed as in (6), then (1) takes the form

$$(7) \quad \hat{r} = s\, e^{\hat{a} + \hat{b}s + u + z},$$

where z is a random variable which accounts for the possible deviation of (a, b) from $(\hat{a}, \hat{b})$. If the approximation (6) is used, then $a + bs$ is a normally distributed random variable with mean $\hat{a} + \hat{b}s$, and with variance

$$(8) \quad \sigma_z^2(s) = C_{aa} + 2s\, C_{ab} + s^2 C_{bb}.$$

The parameter covariance matrix C is obtained from the inverse of the information matrix:

$$(9) \quad \begin{bmatrix} C_{aa} & C_{ab} \\ C_{ab} & C_{bb} \end{bmatrix} = \sigma_u^2 \begin{bmatrix} M'_{aa} & M'_{ab} \\ M'_{ab} & M'_{bb} \end{bmatrix}^{-1}$$

Uncertainty about the stock–recruitment relationship may be visualized by drawing two confidence intervals for $\ln \hat{r}$. In the first of these, we ignore year-to-year fluctuations in recruitment, which are expressed by u. Then an approximately 50% confidence interval will have width $\sigma_z(s)$ around the maximum likelihood estimate $\hat{r}$:

$$(10) \quad \hat{r} = s\, e^{\hat{a} + \hat{b}s}$$

The second interval takes the year-to-year fluctuations into account, and has width $\sqrt{\sigma_u^2 + \sigma_z^2(s)}$. These intervals are shown in Fig. 4, for the data of Fig. 1. Uncertainty is least in locating the "center of mass" of the data points. However, the slope of the fitted curve is much less certain. The same, or similar intervals would be drawn, even if a Bayesian approach were not adopted.

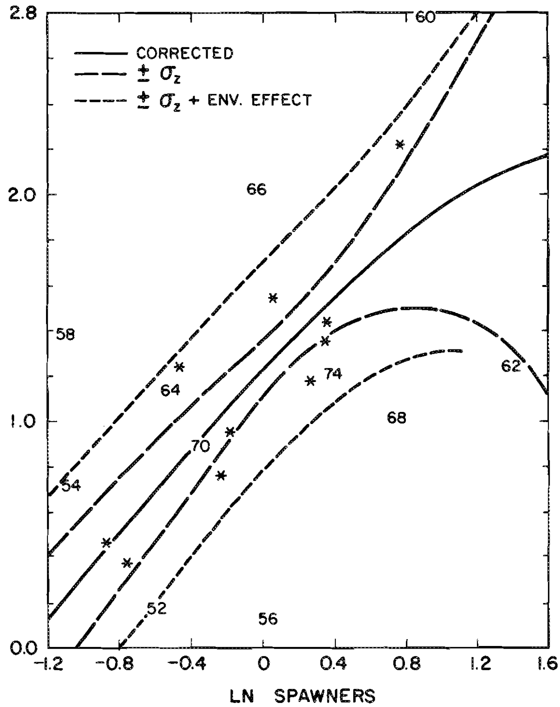

FIG. 4. Confidence intervals for the stock–recruitment relation, as fitted from the data of Fig. 1. The original data, the corrected data, and the solid curve are as shown in Fig. 1. The inner pair of broken line curves are separated by one standard deviation $\sigma_z(s)$, as defined in eq. (8). Thus the probability is ~50% that the correct (averaged) stock–recruitment relation will be between these curves, above any given point on the ln s axis. The outer pair of broken line curves show one standard deviation if the effects of year-to-year fluctuation are included.

Management in the Presence of Uncertainty

It is clear from Fig. 4 that the effect of parameter uncertainty increases sharply at the ends of the spawner range where data are available. In most cases that we have examined, the effect is most pronounced at the upper end of that interval. Thus extrapolation of the stock–recruitment relation to such higher values is not warranted: on the basis of the data, we usually cannot predict the effect of a substantial increase in the number of spawners. Therefore, some unlikely possibilities may have large positive or negative effects on the expected performance of a given management strategy.

To focus the discussion, we shall consider policies which set escapement targets: if q is the target escapement, then $r - q$ of the recruits are harvested if $r > q$, and no harvesting is done if $r < q$. Such a policy cannot usually be achieved in practice, nor would it necessarily be most desirable. However, such policies have been shown to produce maximum expected yields (Mendelssohn 1979; Reed 1974; Walters 1981). They are useful as a standard of comparison with other policies, and only one parameter (q) specifies the policy.

How should q be determined? A simple approach is to compare the expected yield at equilibrium for each value of q. If parameter uncertainty is ignored, then we have

$$(11) \quad \hat{H}(q) = \underset{u}{E}\,[q\, e^{\hat{a} + \hat{b}q + u}] - q = q\, e^{\hat{a} + \hat{b}q + \frac{1}{2}\sigma_u^2} - q.$$

Then we determine $\hat{q}$ in such a way that $\hat{H}(q)$ has a maximum at $q = \hat{q}$.

If we account for current parameter uncertainty but not the effect of q on future uncertainty, then the expectation in (11) is taken over the distribution of z as well as u. Thus

$$(12) \quad \bar{H}(q) = \underset{u,z}{E}\,[q\, e^{\hat{a} + \hat{b}q + u + z}] - q = q\, e^{a + bq + \frac{1}{2}\sigma_u^2 + \frac{1}{2}\sigma_z^2(q)} - q.$$

The best choice $\bar{q}$ then becomes that value of q which maximizes $\bar{H}(q)$. This will generally be the "Bayes equivalent"

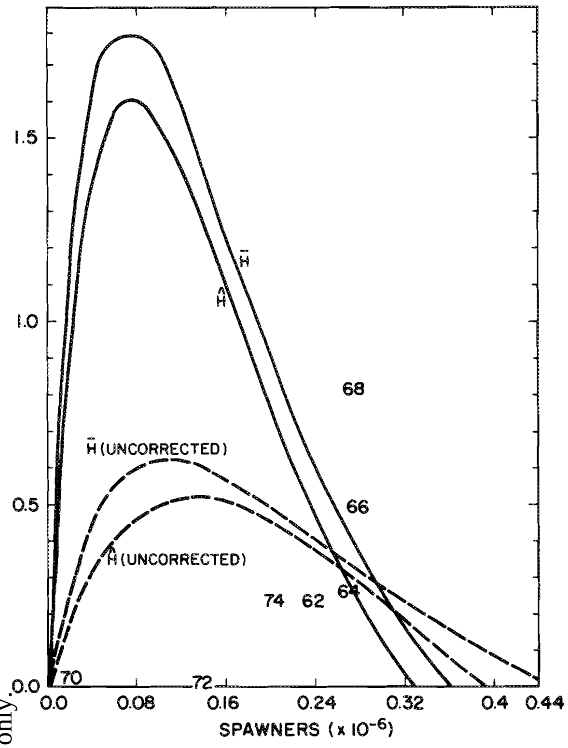

FIG. 5. Projected harvest at equilibrium versus the number of spawners, under four sets of assumptions for pink salmon from the Chignik River, Alaska.

optimal policy as defined by Mendelssohn (1980). The form of (12) is more complicated than (11), in view of (8).

Figure 5 shows $\hat{H}$ and $\bar{H}$ as functionsof q, where the parameters are estimated for data from Chignik River pink salmon. In this case, the parameter uncertainty makes little difference in either the best choice of q, or the yield at equilibrium. $\hat{H}$ (no error correction) uses the Ricker stock–recruitment relation, where the parameters are estimated by a linear regression using uncorrected observation. $\bar{H}$ (no error correction) takes the uncertainty in the estimated parameters into account. The stock–recruitment relation was averaged over the posterior distribution of parameter values. The curves labeled $\hat{H}$ and $\bar{H}$ were obtained by a similar process, where the variance of the observation error was set equal to the variance of the year-to-year fluctuation in recruitment ($\lambda = 1$). The parameters as estimated indicate extreme density dependence. Although there is a great variation in the harvest curves, the suggested optimal number of spawners differ only slightly.

Figure 6 shows a case where $\hat{H}$ has a local maximum, but $\bar{H}$ does not. If observation errors are neglected, then a rather low number of spawners appears to be optimal. However, if observation errors are accounted for, then the optimal number of spawners increases by a factor of three. If the effect of parameter uncertainty is also included, then there is no optimum level of spawners; then the indication is that the number of spawners should be increased as much as possible, until density dependence is apparent. Most pink salmon data lead

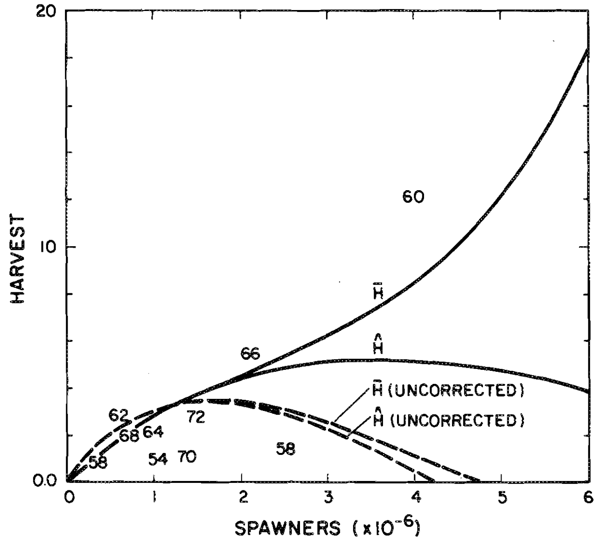

FIG. 6. Projected harvest curves as in Fig. 5, for pink salmon of the Atnarko River, B.C.

to curves resembling those of Fig. 6, rather than Fig. 5. The parameter uncertainty is so large that density-dependent effects are overwhelmed. The implication for management in this case is that escapements should be raised, to explore the possibility of large returns. One should not assign great precision to the values computed for $\hat{H}$ and $\bar{H}$. However, the qualitative difference between Fig. 5 and 6 is significant.

The determination of the spawning quota by examination of $\bar{H}$ is easy to make, but it is not easily justified on the basis of our assumptions. More elaborate schemes to determine q are examined in Ludwig and Walters (1981). These more complicated methods indicate that uncertainty in parameters is even more important than suggested by consideration of $\hat{H}$ and $\bar{H}$.

Uncertainty About the Basic Model

The preceding discussion has been based upon the assumption that the Ricker model is adequate to describe stock and recruitment. This assumption may be tested by carrying out an analogous procedure for other models of stock and recruitment. Two additional models are considered in the Appendix. Relative credibility can be assigned to the various models from the ratio of their likelihoods.

If (5) is substituted into (4) and the maximum-likelihood estimates of the parameters are chosen, then the log-likelihood of the Ricker model is given by

$$(14)\quad L^{*}_{\text{Ricker}} = -\frac{n-2}{2} - (n + 1 \ln \lambda - (2n + 1) \ln \sigma_u \text{ (Ricker).}$$

Similar formulas hold for the power model,

$$(15)\quad L^{*}_{\text{power}} = -\frac{n-2}{2} - (n + 1) \ln \lambda - (2n + 1) \ln \sigma_u \text{ (power),}$$

and for the three-parameter model that combines the Ricker and power models:

$$(16)\quad L^*_{\text{general}} = -\frac{n-3}{2} - (n+1)\ln\lambda - (2n+1)\ln\sigma_u \text{ (general).}$$

Suppose we calculate the likelihood ratio

$$(17)\quad \frac{\text{log likelihood of Ricker model}}{\text{log likelihood of power model}} = \left[\frac{\sigma_u(\text{power})}{\sigma_u(\text{Ricker})}\right]^{2n+1}$$

The model which produces the better fit will have the smaller value of σ_u. Then (17) is a quantitative expression of the degree of belief in the models which is inspired by the data. The eventual choice of the escapement quota can be based upon a suitable compromise between the values suggested by the various models.

A more elaborate approach would be to estimate Bayes posterior probabilities for the models, using the formulation developed by Wood (1974), then compute a Bayes equivalent policy by the procedure suggested in Mendelssohn (1980). It is not possible as yet to estimate numerically the optimal, long-term, adaptive policy (Walters 1981) for the problem, since the Bayes probabilities are not a complete description of the "information state" regarding each model.

Discussion

We have applied the procedures outlined above to various data sets on British Columbian and Alaskan Pacific salmon, for a range of assumptions about measurement errors. A common result is the pathological situation illustrated in Fig. 6: the optimum spawning stock cannot be established with any confidence, and it would be best (in the sense of maximizing expected harvests) to allow much higher or at least more variable escapements. This result is especially discouraging since salmon are supposed to be more manageable than many other fishes because spawning stocks can be enumerated directly. Perhaps we are naive to draw such conclusions from simple recruitment models, or have simply been too pessimistic about the magnitude of measurement errors.

It is worth questioning the wisdom of trying to fit simple models to the data, rather than multivariate models that account for various environmental influences on recruitment. Since recruitment appears so variable with respect to spawners in most fishes, it has even been suggested that the spawner–recruit relationship should be ignored entirely. We have argued (Walters and Ludwig 1981) that appearances can be deceptive, but there is a more fundamental reason to pursue the relationship no matter how variable it may be: spawning stock decisions represent a basic connection between present and future yields. To presume that the spawner–recruit relationship is meaningless is to pretend that today's harvest decision has no influence on the recruitment future of the fishery. In this long-term view of management, it is simply irrelevant to comment that recruitment can often be predicted more accurately from environmental factors than from spawning stock; it is the spawning stock that can be controlled through management decisions. Suppose we could construct and validate a model that "explained" the stochastic deviations u_j in terms of various environmental factors; to make an optimum spawning stock decision, we would then have to hypothesize future values or probability distributions for these factors. In most cases the resulting distributions for u_{j+1}, u_{j+2}, etc. would be hardly more credible than the distribution that we estimate directly from the past data without even asking what factors were involved.

It may also be that the mean spawner–recruit relationship has a more complex shape than can be captured by simple equations like the Ricker curve (Ward and Larkin 1964, Peterman 1977). Data are generally too poor to say anything about this problem, though there are sound biological reasons to expect complex responses (i.e. depensatory mortality effects, Peterman and Gatto 1978) at low spawning stocks.

We mentioned the importance of testing the estimation procedure for small sample sizes ($10 \le n \le 20$). Our concern is not that larger data sets are rarely available; rather, we suspect that stock–recruit "parameters" may not be stable for longer periods. Even in the absence of persistent environmental trends, we should expect to see changes in the internal characteristics (genetic composition, local spatial structure) of stocks. Some of these effects can be tracked by adaptive parameter estimation even if they cannot be predicted, provided the estimation has a relatively short data "memory."

We have not been able to establish satisfactory estimates of measurement error variance for any of the Pacific salmon data sets. We have heard scattered reports of instances where the usual counting procedure (fishery officer count, aerial surveys, etc.) was compared to some more accurate enumeration, with results differing by as much as 200%. In some cases the recording procedure alone (by abundance intervals rather than actual counts) has probably generated errors sufficient to make $\lambda \approx 1.0$ (eq. 3).

It may be worthwhile to invest in more accurate counting procedures, at least for some key index stocks. An alternative "investment" would be to increase the variability of spawning stocks. But it is more critical now to obtain estimates of the measurement error variance (or λ of eq. 3). Otherwise a great deal of recent historical data is going to remain less than useless until it becomes irrelevant for management purposes due to possible changes in underlying stock characteristics.

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KENDALL, M. G., AND A. STEWART. 1973. The advanced theory of statistics, Vol. II, 3rd ed. Hafner Pub. Co., New York, NY.

LUDWIG, D., AND C. J. WALTERS. 1981. Optimal harvesting with imprecise parameter estimates. Ecol. Model. (In press)

MENDELSSOHN, R. 1979. Determining the best tradeoff between expected economic return and the risk of undesirable events when managing a randomly varying population. J. Fish. Res. Board

Can. 36: 939–947.

1980. Using Markov decision models and related techniques for purposes other than simple optimization: analyzing the consequences of policy alternatives on the management of salmon runs. Fish. Bull. 78: 35–50.

PETERMAN, R. M. 1977. A simple mechanism that causes collapsing stability regions in exploited salmonid populations. J. Fish. Res. Board Can. 34: 1130–1142.

PETERMAN, R. M., AND M. GATTO. 1978. Estimation of functional responses of predators on juvenile salmon. J. Fish. Res. Board Can. 35: 797–808.

REED, W. J. 1974. A stochastic model for the economic management of a renewable animal resource. Math. Biosci. 22: 313–337.

WALTERS, C. J. 1981. Optimum escapements in the face of alternative recruitment hypotheses. Can. J. Fish. Aquat. Sci. 38: 678–689.

WALTERS, C. J., AND D. LUDWIG. 1981. Effects of measurement errors on the assessment of stock–recruit relationships. Can. J. Fish. Aquat. Sci. 38: 704–710.

WARD, F. J., AND P. A. LARKIN. 1964. Cyclic dominance in Adams River sockeye salmon. Int. Pac. Salmon Fish. Comm. Prog. Rep. 11: 116 p.

WOOD, E. F. 1974. A Bayesian approach to analysing uncertainty among stochastic models. Int. Inst. Appl. Syst. Anal. (Laxenburg, Austria) Res. Rep. 74–16: 19 p.

Appendix

Correction for Observation Errors

This Appendix describes a method for correcting observation errors, using maximum likelihood estimation. Details will be given for three models of stock and recruitment. Motivation and interpretation of these results are given in the body of the paper. Otherwise, this Appendix is self-contained.

LINEAR REGRESSION: THREE MODELS OF STOCK AND RECRUITMENT

We shall be concerned with linear models of the form

$$(1.1)\quad y_i = \sum_{p=1}^{m} x_{ip}a_p - u_i,\ 1,\ \ldots,\ n.$$

Here y_i and x_{ip} are determined from the observations. Specific examples are given below. The parameters of the model are $a_1, \ldots, a_m$, and the u_i are assumed to be independent, normally distributed, random variables, with mean 0 and variance σ_u^2. Our procedure can be extended to models where the parameters appear nonlinearly, but the estimation is more straightforward in the linear case.

Model a: the Ricker model — As in equation (1), let r_i denote the number of recruits in generation i, and let s_{i-1} denote the number of spawners in the previous generation. The Ricker model assumes that

$$(1.2a)\quad r_i = s_{i-1} \exp(a_1 + a_2 s_{i-1} - u_i),\ i = 1,\ \ldots,\ n.$$

After taking logarithms of both sides of (1.2a), we obtain the form (1.1, where $m = 2$ and

$$(1.3a)\quad y_i = \ln(r_i/s_{i-1}),$$

$$(1.4a)\quad (x_{i1}, x_{i2}) = (1, s_{i-1}).$$

Model b: the power model — With r_i and s_{i-1} defined as above, the power model assumes that

$$(1.2b)\quad r_i = s_{i-1}^{a_2} \exp(a_1 - u_i),\ i = 1,\ \ldots,\ n.$$

This results in the form (1.1), where $m = 2$ and

$$(1.3b)\quad y_i = \ln r_i,$$

$$(1.4b)\quad (x_{i1}, x_{i2}) = (1, \ln s_{i-1}).$$

Model c: the generalized Ricker model — The two preceding models may be combined in the form

$$(1.2c)\quad r_i = s_{i-1}^{a_3} \exp(a_1 + a_2 s_{i-1} - u_i).$$

In this case $m = 3$, and

$$(1.3c)\quad y_i = \ln r_i,$$

$$(1.4c)\quad (x_{i1}, x_{i2}, x_{i3}) = (1, s_{i-1}, \ln s_{i-1}).$$

MAXIMUM LIKELIHOOD AND THE METHOD OF WEIGHTED LEAST SQUARES

We shall ignore observation errors for the moment, to present the method of weighted least squares in its simplest form. Since u_i are normally distributed, the likelihood of the observations is given by

$$(1.5)\quad L = \exp\left[-\frac{1}{2\sigma_u^2}\sum_{i=1}^{n} w_i u_i^2 - \ln \sigma_u \sum_{i=1}^{n} w_i\right],$$

where u_i ($i = 1, \ldots, n$) are obtained from equation (1.1). The quantities $w_1, \ldots, w_n$ are weights which are attached to the observations. It may happen that early observations are less reliable than later ones, or the parameters of the model may have changed since the early years. Instead of disregarding early observations or anecdotal evidence, they may be assigned weights which are less than one. This modification of the procedure as described in the text is easy to make, and it promotes better use of the available information.

To estimate the parameters $a_1, \ldots, a_m$, we maximize L as a function of them. This is equivalent to minimizing the sum of squares

$$(1.6)\quad M(a) = \frac{1}{2}\sum_{i=1}^{n} w_i u_i^2.$$

At the minimizing value $\hat{a}_p$, $p = 1, \ldots, m$, we must have

$$(1.7)\quad \frac{\partial M}{\partial a_p} = \sum_{i=1}^{n} w_i u_i x_{ip} = 0,\ p = 1,\ \ldots,\ m.$$

In view of (1.1), (1.7) takes the form

$$(1.8)\quad \sum_{q=1}^{m} M_{pq}\hat{a}_q = \sum_{i=1}^{n} w_i y_i x_{ip},\ p = 1,\ \ldots,\ m$$

where the information matrix (M_{pq}) is given by

$$(1.9)\quad M_{pq} = \frac{\partial^2 M}{\partial a_p\, \partial a_q} = \sum_{i=1}^{n} w_i x_{ip} x_{iq}.$$

The Form of Observation Errors

One cannot correct for observation errors without some assumptions about the way in which they appear. In the present case, we assume that the actual numbers of recruits and spawners cannot be observed. The observations will be denoted by R_i and S_i, respectively. Moreover, we shall assume that the same relative error appears in both spawners and recruits:

$$(1.10)\quad R_i = r_i\, e^{v_i},\ S_i = s_i\, e^{v_i},\ i = 0, \ldots, n,$$

where v_i, $i = 0, \ldots, n$ are assumed to be independent, normally distributed, random variables, with mean zero and variance σ_v^2.

The form (1.1) still holds, but x_{ip} *and* y_i are not observable. In terms of observable variables, (1.2a) implies that

$$(1.11a)\quad u_i = a_1 + a_2 S_{i-1}\, e^{-v_{i-1}} - \ln (R_i/S_{i-1}) - v_{i-1} + v_i.$$

Similarly, (1.2b) and (1.2c) imply that

$$(1.11b)\quad u_i = a_1 + a_2 \ln S_{i-1} - a_2\, v_{i-1} - \ln R_i + v_i,$$

$$(1.11c)\quad u_i = a_1 + a_2\, S_{i-1}\, e^{-v_{i-1}} + a_3 \ln S_{i-1} - a_3\, v_{i-1} - \ln R_i + v_i.$$

Many other assumptions could be accomodated within the scheme presented below. A common feature of the models treated here is that u_i depends only upon v_i, v_{i-1}, and the model parameters. This restriction could be dropped, but it would complicate the calculation of $v_0, \ldots, v_n$ below.

Maximum Likelihood Estimation of the Observation Errors

In view of the presence of v_i in (1.11), the likelihood (1.5) must be modified to

$$(1.12)\quad L(a,v) = \exp\left[-\frac{M(a,v)}{\sigma_u^2} - \sum_{i=1}^{n} w_i \ln \sigma_u - \sum_{i=0}^{n} w_{i+1} \ln \sigma_v \right]$$

where

$$(1.13)\quad M(a,v) = \frac{1}{2} \sum_{i=1}^{n} w_i u_i^2 + \frac{1}{2\lambda} \sum_{i=0}^{n} w_{i+1}\, v_i^2.$$

The parameter λ is given by (3). As is explained there, λ must be prescribed to estimate the parameters and observation errors.

The parameters $a_1, \ldots, a_m$ and the errors $v_0, \ldots, v_n$ will be estimated by maximizing the likelihood, i.e. by minimizing $M(a,v)$. The minimizing values $\hat{a}$ and $\hat{v}$ must satisfy

$$(1.14)\quad \frac{\partial M}{\partial v_j}(\hat{a},\hat{v}) = \sum_{i=1}^{n} w_i\, \hat{u}_i\, \frac{\partial \hat{u}_i}{\partial v_j} + \frac{1}{\lambda} w_{j+1}\, \hat{v}_j = 0,\quad j = 0, \ldots, n,$$

$$(1.15)\quad \frac{\partial M}{\partial a_p}(\hat{a},\hat{v}) = \sum_{i=1}^{n} w_i\, \hat{u}_i\, \hat{x}_{ip} = 0,\ p = 1, \ldots, m.$$

$$(1.16)\quad \frac{\partial M}{\partial v_j}(\hat{a},\hat{v}) = w_{j+1}\left[\hat{u}_{j+1} \frac{\partial \hat{u}_{j+1}}{\partial v_j} + \frac{1}{\lambda} v_j \right] + w_j\, u_j \frac{\partial \hat{u}_j}{\partial v_j} = 0.$$

In particular, from (1.11) we obtain

$$(1.17a)\quad \frac{\partial u_{j+1}}{\partial v_j} = -1 - a_2\, s_j,\ \frac{\partial u_j}{\partial v_j} = +1.$$

$$(1.17b)\quad \frac{\partial u_{j+1}}{\partial v_j} = -a_2,\ \frac{\partial u_j}{\partial v_j} = 1.$$

$$(1.17c)\quad \frac{\partial u_{j+1}}{\partial v_j} = -a_2\, s_j - a_3,\ \frac{\partial u_j}{\partial v_j} = 1.$$

In each case, $\frac{\partial u_j}{\partial v_k} = 0$ unless $k = j$ or $k = j - 1$.

Newton's Method

Since the system (1.15)−(1.16) is nonlinear, we shall solve it by an iterative method. Suppose that we have an initial guess a^0, v^0. Then we write

$$(1.18)\quad \begin{cases} a_p = a_p^0 + \delta a_p,\ p = 1, \ldots, m, \\ v_j = v_j^0 + \delta v_j,\ j = 0, 1, \ldots, n, \end{cases}$$

and we attempt to satisfy the equations

$$(1.19)\quad \frac{\partial M}{\partial v_j}(a^0 + \delta a,\ v^0 + \delta v) = 0,\ j = 0, \ldots, n,$$

$$(1.20)\quad \frac{\partial M}{\partial a_p}(a^0 + \delta a,\ v^0 + \delta v) = 0,\ p = 1, \ldots, m.$$

If equations (1.19) and (1.20) are expanded by Taylor's theorem, and quadratic and higher powers of δa and δv are neglected, the result is the approximate system

$$(1.21)\quad \frac{\partial M}{\partial v_j}(a^0,v^0) + \sum_{k=0}^{n} \frac{\partial^2 M}{\partial v_j \partial v_k}(a^0,v^0)\, \delta v_k + \sum_{q=1}^{m} \frac{\partial^2 M(a^0,v^0)}{\partial v_j \partial a_q}\, \delta a_q = 0,\ j = 0, \ldots, n,$$

$$(1.22)\quad \frac{\partial M}{\partial a_p}(a^0,v^0) + \sum_{k=0}^{n} \frac{\partial^2 M}{\partial v_j \partial v_k}(a^0,v^0)\, \delta v_k + \sum_{q=1}^{m} \frac{\partial^2 M\,(a^0,v^0)}{\partial a_p \partial a_q}\, \delta a_q = 0,\ p = 1, \ldots, m.$$

The system (1.21)−(1.22) is linear in δv and δa; the method of solution is given below. Then the next approximation v^1, a^1 is obtained from (1.18). Since the system (1.21)−(1.22) is only an approximation, v^1 and a^1 may still not satisfy (11.19) and (1.20) to sufficient accuracy. If not, further approximations v^2, a^2, etc. may be obtained by repeating the procedure described above. If the initial guess is sufficiently accurate, the number of significant figures doubles with each iteration. Thus, success in applying Newton's method depends upon obtaining an accurate first guess a^0, v^0.

A good initial guess may be obtained by varying the parameter λ. If $\lambda = 0$, then no corrections are made to the observations, and $v_i = 0$, $i = 0, \ldots, n$. Then δa_p, $p = 1, \ldots, m$ may be obtained by solving (1.22) with $a_p^0 = 0$, $p = 1, \ldots, m$, which is equivalent to (1.8). Now we may choose a small value of λ, and use $v_i^0 = 0$, $i = 0, \ldots, n$, and $a_p^0 = \delta a_p$, $p = 1, \ldots, m$. If λ is small enough, the subsequent iterations must converge. Then we may increase λ slightly, and iterate again to obtain v and a.

Some computing time is saved if the initial guess is made by extrapolation in λ. Suppose that we have a solution of (1.15)−(1.16) for some value of λ:

$$(1.23)\quad \frac{\partial M}{\partial v_j}(a(\lambda), v(\lambda), \lambda) = 0,\ j = 0, \ldots, n,$$

$$(1.24)\quad \frac{\partial M}{\partial a_p}(a(\lambda), v(\lambda), \lambda) = 0,\ p = 1, \ldots, m.$$

If (1.23) and (1.24) are differentiated with respect to λ, the result is

$$(1.25)\quad \frac{\partial^2 M}{\partial v_j \partial \lambda} + \sum_{k=0}^{n} \frac{\partial^2 M}{\partial v_j \partial v_k}\frac{\partial v_k}{\partial \lambda} + \sum_{q=1}^{m} \frac{\partial^2 M}{\partial v_j \partial a_q}\frac{\partial a_q}{\partial \lambda} = 0,\qquad j = 0, \ldots, n,$$

$$(1.26)\quad \frac{\partial^2 M}{\partial a_p \partial \lambda} + \sum_{k=0}^{n} \frac{\partial^2 M}{\partial a_p \partial v_k}\frac{\partial v_k}{\partial \lambda} + \sum_{q=1}^{m} \frac{\partial^2 M}{\partial a_p \partial a_q}\frac{\partial a_q}{\partial \lambda} = 0,\qquad p = 1, \ldots, m.$$

This system has the same form as (1.21)–(1.22), and it may be solved in the same way. The only difference is in first term in each equation. These terms are obtained from (1.15)−(1.16):

$$(1.27)\quad \frac{\partial^2 M}{\partial v_j \partial \lambda} = -\frac{1}{\lambda^2} w_{j+1} v_j,\ j = 0, \ldots, n.$$

$$(1.28)\quad \frac{\partial^2 M}{\partial a_p \partial \lambda} = 0,\ p = 1, \ldots, m.$$

If the solutions of (1.23)−(1.26) are known for $\lambda = \lambda_0$, then an initial guess for $\lambda = \lambda_1$ is given by

$$(1.29)\quad v_j^0(\lambda_1) = v_j(\lambda_0) + (\lambda_1 - \lambda_0)\frac{\partial v_j}{\partial \lambda}(\lambda_0),\ j = 0, \ldots, n,$$

$$(1.30)\quad a_p^0(\lambda_1) = a_p(\lambda_0) + (\lambda_1 - \lambda_0)\frac{\partial a_p}{\partial \lambda}(\lambda_0),\ p = 1, \ldots, m.$$

This procedure will lead to convergent Newton iterations if $\lambda_1 - \lambda_0$ is small enough. The combined Newton's method and extrapolation can fail only if successive increments in λ must be taken smaller and smaller. This situation is explained below.

Calculation of the Observation Errors

Now we turn to the solution of (1.21). Assume for the moment that δa_p, $p = 1, \ldots, m$ are known. We define g_k, $k = 0, \ldots, n$ and h_{pk}, $p = 1, \ldots, m$; $k = 0, \ldots, n$ as the solutions of the systems

$$(1.31)\quad \sum_{k=0}^{n} \frac{\partial^2 M}{\partial v_j \partial v_k}(a^0, v^0) g_k = \frac{\partial M}{\partial v_j}(a^0, v^0),\ j = 0, \ldots, n,$$

$$(1.32)\quad \sum \frac{\partial^2 M}{\partial v_j \partial v_k}(a^0, v^0)\, h_{pk} = \frac{\partial^2 M(a^0, v^0)}{\partial a_p \partial v_j}\qquad j = 0, \ldots, n;\ p = 1, \ldots, m.$$

Since the system (1.21) is linear in δv, we obtain

$$(1.33)\quad \delta v_j = -g_j - \sum_{p=1}^{m} h_{pj}\, \delta a_p.$$

Now we evaluate the coefficient matrix in (1.31) and (1.32). It follows from differentiating (1.16) that

$$(1.34)\quad \frac{\partial^2 M}{\partial v_j \partial v_k} = w_{j+1}\left[\frac{\partial u_{j+1}}{\partial v_j}\frac{\partial u_{j+1}}{\partial v_k} + u_{j+1}\frac{\partial^2 u_{j+1}}{\partial v_j \partial v_k} + \frac{\delta^{jk}}{\lambda}\right] + w_j \frac{\partial u_j}{\partial v_j}\frac{\partial u_j}{\partial v_k},$$

where $\delta^{jk} = 0$ if $j \neq k$, and $\delta^{jj} = 1$. The first derivatives which appear in (1.34) are given by (1.17), and the second derivatives are obtained by differentiating those equations. Thus for each of the three models we have, respectively,

$$(1.35a)\quad \frac{\partial^2 u_{j+1}}{\partial v_j \partial v_j} = a_2 s_j,\ \frac{\partial^2 u_j}{\partial v_j \partial v_j} = 0,\ \text{if } j = 0, \ldots, n.$$

$$(1.35b)\quad \frac{\partial^2 u_i}{\partial v_j \partial v_j} = 0 \text{ for all } i, j, k.$$

$$(1.35c)\quad \frac{\partial^2 u_{j+1}}{\partial v_j \partial v_j} = a_2 s_j,\ \frac{\partial^2 u_j}{\partial v_j \partial v_j} = 0,\ \text{if } j = 0, \ldots, n.$$

In every case,

$$(1.36)\quad \frac{\partial^2 u_i}{\partial v_j \partial v_k} = 0 \text{ where } j = k, \text{ and unless } i = j + 1 \text{ or } i = j.$$

The relations (1.17) and (1.36) imply that only the diagonal terms and those adjacent to the diagonal are different from zero in $\left(\frac{\partial^2 M}{\partial v_j \partial v_k}\right)$. In particular, (1.34) takes the form

$$(1.37)\quad \frac{\partial^2 M}{\partial v_j \partial v_j} = w_{j+1}\left[\left(\frac{\partial u_{j+1}}{\partial v_j}\right)^2 + u_{j+1}\frac{\partial^2 u_{j+1}}{\partial v_j^2} + \frac{1}{\lambda}\right] + w_j\left(\frac{\partial u_j}{\partial v_j}\right)^2, j = 0, \ldots, n,$$

$$(1.38)\quad \frac{\partial^2 M}{\partial v_j \partial v_{j+1}} = \frac{\partial^2 M}{\partial v_{j+1}\partial v_j} = w_{j+1}\frac{\partial u_{j+1}}{\partial v_{j+1}}\frac{\partial u_{j+1}}{\partial v_j},\quad j = 0, \ldots, n.$$

All of the remaining elements of $\left(\frac{\partial^2 M}{\partial v_j \partial v_k}\right)$ are zero. Systems which have such a "tri-diagonal" form are important in numerical analysis. Efficient solution subroutines are available at most large computer installations. The number of operations necessary to solve such a system is proportional to the first power of $n + 1$, rather than a higher power.

Calculation of the Parameter Estimates

After g_k and h_{pk} have been calculated, the form (1.33) may be substituted into (1.22). The result is

$$(1.39)\quad \left(\frac{\partial M}{\partial a_p} - \sum_{k=0}^{n}\frac{\partial^2 M}{\partial a_p \partial v_k} g_k\right) + \sum_{q=1}^{m}\left(\frac{\partial^2 M}{\partial a_p \partial a_q} - \sum_{k=1}^{n}\frac{\partial^2 M}{\partial a_q \partial v_k} h_{qk}\right)\delta a_q = 0,$$

The system (1.39) is a corrected form of the ordinary regression equations (1.8). The corrected information matrix (M'_{pq}) is given by

$$(1.40)\quad M'_{pq} = \frac{\partial^2 M}{\partial a_p \partial a_q} - \sum_{k=0}^{n}\frac{\partial^2 M}{\partial v_k \partial a_p} h_{qk}.$$

Since the additional parameters $v_0, \ldots, v_n$ must be estimated, the corrected matrix (M'_{pq}) corresponds to less information that was expressed in (M_{pq}). If the variance ratio λ becomes too large, the matrix (M'_{pq}) may become singular, or no longer positive-definite. In such a case, there is no longer enough information to produce any estimate of the parameter. As this situation is approached, the increments in λ which produce convergent Newton iterations become smaller and smaller. The lack of information is also reflected in the increasing size of confidence regions for the parameters, as will be shown below.

The maximum likelihood estimate for σ_u is obtained by differentiating (1.12) as a function of σ_u, holding λ fixed. The result is

$$(1.41)\quad \hat{\sigma}_u^2 = \frac{2M(\hat{a},\hat{v})}{\sum_{i=1}^{n} w_i + \sum_{i=0}^{n} w_i}.$$

The numerator in (1.41) is just the residual sum of squares. To correct the bias in this estimate, we may set

$$(1.42)\quad \tilde{\sigma}_u^2 = \frac{2M(\hat{a},\hat{v})}{n - p}.$$

A more refined Bayesian approach would be to treat σ_u^2 like the other parameters, and work with their joint posterior distribution. The present, cruder procedure seems to be adequate to deal with fisheries data.

Uncertainty in the Parameter Estimates

To assess the precision in our estimates $\hat{a}$, we return to (1.13), and we determine v_j as functions of a_p from (1.14):

$$(1.43)\quad \frac{\partial M}{\partial v_j}(a,v(a)) = 0, j = 0, \ldots, n.$$

If (1.43) is differentiated with repect to a_p, the result is

$$(1.44)\quad \frac{\partial^2 M}{\partial a_p \partial v_j} + \sum_{k=0}^{n}\frac{\partial^2 M}{\partial v_j \partial v_k}\frac{\partial v_k}{\partial a_p} = 0, p = 1, \ldots, m.$$

By comparing (1.44) and (1.32), we see that, at $\hat{a}$, $\hat{v}$,

$$(1.45)\quad \frac{\partial v_k}{\partial a_p} = -h_{pk}, p = 1, \ldots, m; k = 0, \ldots, n.$$

Furthermore, the total second derivatives of M are given by (compare (1.40))

$$(1.46)\quad \frac{\partial^2 M(a,v(a))}{\partial a_p \partial a_q} = \frac{\partial^2 M}{\partial a_p \partial a_q} + \sum_{k=0}^{n}\frac{\partial^2 M}{\partial a_p \partial v_k}\frac{\partial v_k}{\partial a_q} = M'_{pq}.$$

Since the first derivatives of M are zero at $\hat{a}$, $\hat{v}$, we obtain the approximate form

$$(1.47)\quad M(a,v(a)) \sim M(\hat{a},\hat{v}) + \frac{1}{2}\sum_{p,q=1}^{m} M'_{pq}(a_p - \hat{a}_p)(a_q - \hat{a}_q).$$

Then if we fix $\sigma_u = \tilde{\sigma}_u$ and set $v = v(a)$, the likelihood takes the form (6). When considered as a function of a, the likelihood is proportional to a multivariate normal density, with mean $\hat{a}$, and with a covariance matrix given by (9).

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1. Iadine Chadès, Sam Nicol, Tracy M. Rout, Martin Péron, Yann Dujardin, Jean-Baptiste Pichancourt, Alan Hastings, Cindy E. Hauser. 2017. Optimization methods to solve adaptive management problems. *Theoretical Ecology* **10**:1, 1-20. [Crossref]
2. Ricardo T. Lemos. 2016. An alternative stock-recruitment function for age-structured models. *Ecological Modelling* **341**, 14-26. [Crossref]
3. Timothy E. Walsworth, Daniel E. Schindler. 2016. Long time horizon for adaptive management to reveal predation effects in a salmon fishery. *Ecological Applications* **26**:8, 2695-2707. [Crossref]
4. James T. Thorson, Anna Rindorf, Jin Gao, Dana H. Hanselman, Henning Winker. 2016. Density-dependent changes in effective area occupied for sea-bottom-associated marine fishes. *Proceedings of the Royal Society B: Biological Sciences* **283**:1840, 20161853. [Crossref]
5. Clay E. Porch, Matthew V. Lauretta. 2016. On Making Statistical Inferences Regarding the Relationship between Spawners and Recruits and the Irresolute Case of Western Atlantic Bluefin Tuna (Thunnus thynnus). *PLOS ONE* **11**:6, e0156767. [Crossref]
6. Peter Sheldon Rankin, Ricardo T. Lemos. 2015. An alternative surplus production model. *Ecological Modelling* **313**, 109-126. [Crossref]
7. Elizabeth N. Brooks, Jonathan J. Deroba. 2015. When "data" are not data: the pitfalls of post hoc analyses that use stock assessment model output. *Canadian Journal of Fisheries and Aquatic Sciences* **72**:4, 634-641. [Abstract] [Full Text] [PDF] [PDF Plus]
8. Jonathan A. Hare, Elizabeth N. Brooks, Michael C. Palmer, James H. Churchill. 2015. Re-evaluating the effect of wind on recruitment in Gulf of Maine Atlantic Cod (Gadus morhua) using an environmentally-explicit stock recruitment model. *Fisheries Oceanography* **24**:1, 90. [Crossref]
9. S. Subbey, J. A. Devine, U. Schaarschmidt, R. D. M. Nash. 2014. Modelling and forecasting stock-recruitment: current and future perspectives. *ICES Journal of Marine Science* **71**:8, 2307-2322. [Crossref]
10. Arliss J. Winship, Michael R. O'Farrell, Michael S. Mohr. 2014. Fishery and Hatchery Effects on an Endangered Salmon Population with Low Productivity. *Transactions of the American Fisheries Society* **143**:4, 957-971. [Crossref]
11. James T. Thorson, Ian G. Taylor, Ian J. Stewart, André E. Punt. 2014. Rigorous meta-analysis of life history correlations by simultaneously analyzing multiple population dynamics models. *Ecological Applications* **24**:2, 315-326. [Crossref]
12. James T. Thorson, Mark D. Scheuerell, Eric R. Buhle, Timothy Copeland. 2013. Spatial variation buffers temporal fluctuations in early juvenile survival for an endangered Pacific salmon. *Journal of Animal Ecology* n/a-n/a. [Crossref]
13. Masatoshi Sugeno, Stephan B. Munch. 2013. A semiparametric Bayesian approach to estimating maximum reproductive rates at low population sizes. *Ecological Applications* **23**:4, 699-709. [Crossref]
14. Gavin Fay, Andre E. Punt. 2013. Methods for estimating spatial trends in Steller sea lion pup production using the Kalman filter. *Ecological Applications* 130228133738005. [Crossref]
15. T. Rougier, P. Lambert, H. Drouineau, M. Girardin, G. Castelnaud, L. Carry, M. Aprahamian, E. Rivot, E. Rochard. 2012. Collapse of allis shad, Alosa alosa, in the Gironde system (southwest

France): environmental change, fishing mortality, or Allee effect?. *ICES Journal of Marine Science* **69**:10, 1802-1811. [Crossref]

16. ThorsonJames T., CopeJason M., BranchTrevor A., JensenOlaf P.. 2012. Spawning biomass reference points for exploited marine fishes, incorporating taxonomic and body size information. *Canadian Journal of Fisheries and Aquatic Sciences* **69**:9, 1556-1568. [Abstract] [Full Text] [PDF] [PDF Plus] [Supplemental Material]
17. Zhenming Su, Randall M. Peterman. 2012. Performance of a Bayesian state-space model of semelparous species for stock-recruitment data subject to measurement error. *Ecological Modelling* **224**:1, 76-89. [Crossref]
18. Kazumi Sakuramoto, Naoki Suzuki. 2012. Effects of process and/or observation errors on the stock���recruitment curve and the validity of the proportional model as a stock���recruitment relationship. *Fisheries Science* **78**:1, 41. [Crossref]
19. Jonas Knape, Perry de Valpine. 2012. Are patterns of density dependence in the Global Population Dynamics Database driven by uncertainty about population abundance?. *Ecology Letters* **15**:1, 17-23. [Crossref]
20. Kassandra Fronczyk, Athanasios Kottas, Stephan Munch. 2011. Flexible modeling for stock-recruitment relationships using Bayesian nonparametric mixtures. *Environmental and Ecological Statistics* . [Crossref]
21. James T.ThorsonJ.T. Thorson, JimBerksonJ. Berkson. 2010. Multispecies estimation of Bayesian priors for catchability trends and density dependence in the US Gulf of Mexico. *Canadian Journal of Fisheries and Aquatic Sciences* **67**:6, 936-954. [Abstract] [Full Text] [PDF] [PDF Plus]
22. NickCaputiN. Caputi, RoyMelville-SmithR. Melville-Smith, Simonde LestangS. de Lestang, AlanPearceA. Pearce, MingFengM. Feng. 2010. The effect of climate change on the western rock lobster (Panulirus cygnus) fishery of Western Australia. *Canadian Journal of Fisheries and Aquatic Sciences* **67**:1, 85-96. [Abstract] [Full Text] [PDF] [PDF Plus]
23. James T. Thorson, Jim Berkson. 2010. Evaluating single- and multi-species procedures to estimate time-varying catchability functional parameters. *Fisheries Research* **101**:1-2, 38-49. [Crossref]
24. Shizhen Wang, Gary Morishima, Rishi Sharma, Larry Gilbertson. 2009. The Use of Generalized Additive Models for Forecasting the Abundance of Queets River Coho Salmon. *North American Journal of Fisheries Management* **29**:2, 423-433. [Crossref]
25. Jon T. Schnute, Laura J. Richards. Surplus Production Models 105-126. [Crossref]
26. . References 320-338. [Crossref]
27. Joanna D. Tober Griffin, Andrew H. Fayram. 2007. Relationships between a Fish Index of Biotic Integrity and Mean Length and Density of Brook Trout and Brown Trout in Wisconsin Streams. *Transactions of the American Fisheries Society* **136**:6, 1728-1735. [Crossref]
28. Steven L Haeseker, Michael L Jones, Randall M Peterman, James R Bence, Wenjing Dai, Gavin C Christie. 2007. Explicit consideration of uncertainty in Great Lakes fisheries management: decision analysis of sea lamprey (Petromyzon marinus) control in the St. Marys River. *Canadian Journal of Fisheries and Aquatic Sciences* **64**:10, 1456-1468. [Abstract] [PDF] [PDF Plus]

29. Shijie Zhou. 2007. Discriminating alternative stock–recruitment models and evaluating uncertainty in model structure. *Fisheries Research* **86**:2-3, 268-279. [Crossref]

30. BERNT-ERIK SÆTHER, MAGNAR LILLEGÅRD, VIDAR GRØTAN, FLURIN FILLI, STEINAR ENGEN. 2007. Predicting fluctuations of reintroduced ibex populations: the importance of density dependence, environmental stochasticity and uncertain population estimates. *Journal of Animal Ecology* **76**:2, 326-336. [Crossref]

31. Robert Kope. 2006. Cumulative effects of multiple sources of bias in estimating spawner���recruit parameters with application to harvested stocks of Chinook salmon (Oncorhynchus tshawytscha). *Fisheries Research* **82**:1-3, 101. [Crossref]

32. Perry de Valpine, Ray Hilborn. 2005. State-space likelihoods for nonlinear fisheries time-series. *Canadian Journal of Fisheries and Aquatic Sciences* **62**:9, 1937-1952. [Abstract] [PDF] [PDF Plus]

33. Greg G Sass, James F Kitchell. 2005. Can growth be used as a surrogate measure of walleye (Sander vitreus) abundance change?. *Canadian Journal of Fisheries and Aquatic Sciences* **62**:9, 2159-2168. [Abstract] [PDF] [PDF Plus]

34. Kazumi SAKURAMOTO. 2005. Does the Ricker or Beverton and Holt type of stock-recruitment relationship truly exist?. *Fisheries Science* **71**:3, 577-592. [Crossref]

35. John A. Vucetich, Rolf O. Peterson. 2004. The influence of prey consumption and demographic stochasticity on population growth rate of Isle Royale wolves Canis lupus. *Oikos* **107**:2, 309-320. [Crossref]

36. Elizabeth A. Fulton, John S. Parslow, Anthony D.M. Smith, Craig R. Johnson. 2004. Biogeochemical marine ecosystem models II: the effect of physiological detail on model performance. *Ecological Modelling* **173**:4, 371-406. [Crossref]

37. Dennis Dunning, Quentin Ross, Stephan Munch, Lev Ginzburg. Measurement Error Affects Risk Estimates for Recruitment to the Hudson River Stock of Striped Bass 231-246. [Crossref]

38. Russell B Millar. 2002. Reference priors for Bayesian fisheries models. *Canadian Journal of Fisheries and Aquatic Sciences* **59**:9, 1492-1502. [Abstract] [PDF] [PDF Plus]

39. Leah R. Gerber, Peter M. Kareiva, Jordi Bascompte. 2002. The influence of life history attributes and fishing pressure on the efficacy of marine reserves. *Biological Conservation* **106**:1, 11-18. [Crossref]

40. Daniel G Kehler, Ransom A Myers, Christopher A Field. 2002. Measurement error and bias in the maximum reproductive rate for the Ricker model. *Canadian Journal of Fisheries and Aquatic Sciences* **59**:5, 854-864. [Abstract] [PDF] [PDF Plus]

41. J T Schnute, A R Kronlund. 2002. Estimating salmon stock#recruitment relationships from catch and escapement data. *Canadian Journal of Fisheries and Aquatic Sciences* **59**:3, 433-449. [Abstract] [PDF] [PDF Plus]

42. Perry de Valpine, Alan Hastings. 2002. FITTING POPULATION MODELS INCORPORATING PROCESS NOISE AND OBSERVATION ERROR. *Ecological Monographs* **72**:1, 57-76. [Crossref]

43. Ann E. Krause, Daniel B. Hayes, James R. Bence, Charles P. Madenjian, Ralph M. Stedman. 2002. Measurement Error Associated With Surveys of Fish Abundance in Lake Michigan. *Journal of Great Lakes Research* **28**:1, 44-51. [Crossref]

44. E Rivot, E Prévost, E Parent. 2001. How robust are Bayesian posterior inferences based on a Ricker model with regards to measurement errors and prior assumptions about parameters?. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:11, 2284-2297. [Abstract] [PDF] [PDF Plus]

45. Donald Ludwig, Marc Mangel, Brent Haddad. 2001. Ecology, Conservation, and Public Policy. *Annual Review of Ecology and Systematics* **32**:1, 481-517. [Crossref]

46. A. C. Wertheimer, W. W. Smoker, T. L. Joyce, W. R. Heard. 2001. Comment: A Review of the Hatchery Programs for Pink Salmon in Prince William Sound and Kodiak Island, Alaska. *Transactions of the American Fisheries Society* **130**:4, 712-720. [Crossref]

47. E. E. Holmes. 2001. Estimating risks in declining populations with poor data. *Proceedings of the National Academy of Sciences* **98**:9, 5072-5077. [Crossref]

48. D G Chen, N B Hargreaves, D M Ware, Y Liu. 2000. A fuzzy logic model with genetic algorithm for analyzing fish stock-recruitment relationships. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:9, 1878-1887. [Abstract] [PDF] [PDF Plus]

49. Hanna Kokko, Jan Lindström. 1998. Seasonal density dependence, timing of mortality, and sustainable harvesting. *Ecological Modelling* **110**:3, 293-304. [Crossref]

50. John M. Fryxell, J. Bruce Falls, E. Ann Falls, Ronald J. Brooks. 1998. LONG-TERM DYNAMICS OF SMALL-MAMMAL POPULATIONS IN ONTARIO. *Ecology* **79**:1, 213-225. [Crossref]

51. W R Gould, L A Stefanski, K H Pollock. 1997. Effects of measurement error on catch#-effort estimation. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:4, 898-906. [Abstract] [PDF] [PDF Plus]

52. W E Ricker. 1997. Cycles of abundance among Fraser River sockeye salmon (Oncorhynchus nerka). *Canadian Journal of Fisheries and Aquatic Sciences* **54**:4, 950-968. [Abstract] [PDF] [PDF Plus]

53. J T Schnute, A R Kronlund. 1996. A management oriented approach to stock recruitment analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **53**:6, 1281-1293. [Citation] [PDF] [PDF Plus]

54. Atsushi Yamauchi, Yoshiharu Matsumiya. 1996. Optimal Expected Escapement Policy with Imprecie Recruit Estimation. *Fisheries science* **62**:1, 35-39. [Crossref]

55. Josh Korman, Randall M. Peterman, Carl J. Walters. 1995. Empirical and theoretical analyses of correction of time-series bias in stock-recruitment relationships of sockeye salmon (Oncorhynchus nerka). *Canadian Journal of Fisheries and Aquatic Sciences* **52**:10, 2174-2189. [Abstract] [PDF] [PDF Plus]

56. Carl Walters. 1995. Estimation of historical stock sizes and recruitment anomalies from relative abundance time series. *Canadian Journal of Fisheries and Aquatic Sciences* **52**:7, 1523-1534. [Crossref]

57. Larry D. Jacobson, Alec D. MacCall. 1995. Stock-recruitment models for Pacific sardine (Sardinops sagax). *Canadian Journal of Fisheries and Aquatic Sciences* **52**:3, 566-577. [Abstract] [PDF] [PDF Plus]

58. Stephen R. Carpenter, Richard C. Lathrop, Alejandro Muñoz-del-Rio. 1993. Comparison of Dynamic Models for Edible Phytoplankton. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:8, 1757-1767. [Abstract] [PDF] [PDF Plus]

59. Daniel E. Lane. 1992. Management Science in the Control & Management of Fisheries: an Annotated Bibliography. *American Journal of Mathematical and Management Sciences* **12**:2-3, 101-152. [Crossref]

60. Charles A.S. Hall. 1988. An assessment of several of the historically most influential theoretical models used in ecology and of the data provided in their support. *Ecological Modelling* **43**:1-2, 5-31. [Crossref]

61. Bernard A. Megrey, Vidar G. Wespestad. A review of biological assumptions underlying fishery assessment models 31-69. [Crossref]

62. Wayne M. Getz, Michael O. Bergh. Quota setting in stochastic fisheries 259-274. [Crossref]

63. D. Ludwig, C. J. Walters, Justin Cooke. 1988. COMPARISON OF TWO MODELS AND TWO ESTIMATION METHODS FOR CATCH AND EFFORT DATA. *Natural Resource Modeling* **2**:3, 457. [Crossref]

64. Joseph F. Koonce, Brian J. Shuter. 1987. Influence of Various Sources of Error and Community Interactions on Quota Management of Fish Stocks. *Canadian Journal of Fisheries and Aquatic Sciences* **44**:S2, s61-s67. [Abstract] [PDF] [PDF Plus]

65. A.P. Dobson, R.M. May. 1987. The effects of parasites on fish populations—theoretical aspects. *International Journal for Parasitology* **17**:2, 363-370. [Crossref]

66. Joseph E. Swierzbinski. 1987. BOOK REVIEW. *Natural Resource Modeling* **2**:2, 331. [Crossref]

67. D. Noakes, D.W. Welch, M. Stocker. 1987. A TIME SERIES APPROACH TO STOCK-RECRUITMENT ANALYSIS: TRANSFER FUNCTION NOISE MODELLING. *Natural Resource Modeling* **2**:2, 213. [Crossref]

68. E. M. P. Chadwick. 1985. Fundamental research problems in the management of Atlantic salmon, Salmo salar L., in Atlantic Canada. *Journal of Fish Biology* **27**:sa, 9-25. [Crossref]

69. Donald Ludwig, Carl J. Walters. 1985. Are Age-Structured Models Appropriate for Catch-Effort Data?. *Canadian Journal of Fisheries and Aquatic Sciences* **42**:6, 1066-1072. [Abstract] [PDF] [PDF Plus]

70. Carl J. Walters. 1985. Bias in the Estimation of Functional Relationships from Time Series Data. *Canadian Journal of Fisheries and Aquatic Sciences* **42**:1, 147-149. [Abstract] [PDF] [PDF Plus]

71. Qisheng Tang. 1985. Modification of the ricker stock recruitment model to account for environmentally induced variation in recruitment with particular reference to the blue crab fishery in Chesapeake Bay. *Fisheries Research* **3**, 13-21. [Crossref]

72. . References 239-249. [Crossref]

73. D. Ludwig, C.J. Walters. 1982. Optimal harvesting with imprecise parameter estimates. *Ecological Modelling* **14**:3-4, 273-292. [Crossref]