

Are Age-Structured Models Appropriate for Catch-Effort Data?

Donald Ludwig and Carl J. Walters

Institute of Animal Resource Ecology, The University of British Columbia, Vancouver, B.C. V6T 1W5

Ludwig, D., and C. J. Walters. 1985. Are age-structured models appropriate for catch-effort data? *Can. J. Fish. Aquat. Sci.* 42: 1066–1072.

Simulated data have been used to evaluate the performance of schemes for estimating optimum fishing effort using a simple stock-production model and R. B. Deriso's age-structured model. Even when the data are generated using Deriso's model, the simpler production model generally gives as good or better estimates for the optimal effort. The only exception to this result is when data are provided with unrealistically large contrasts in effort and catch per unit effort over time. The implication of these findings is that simple production models should often be used in stock assessments based on catch/effort data, even when more realistic and structurally correct models are available to the analyst; the best choice depends on how much contrast has occurred in the historical effort and catch per unit effort data, rather than on prior knowledge about which model structure is biologically more realistic.

Les auteurs ont utilisé des données simulées pour évaluer le rendement de plans d'estimation de l'effort de pêche optimum, à l'aide d'un simple modèle de production de stock et du modèle de R. B. Deriso structuré selon l'âge. En général, le simple modèle de production fournit des estimations aussi bonnes, voire meilleures de l'effort optimal même quand les données sont obtenues du modèle de Deriso, avec une seule exception : quand il y a beaucoup trop d'écart entre les données sur l'effort et les prises par unité d'effort en fonction du temps. Ces résultats indiquent que de simples modèles de production devraient souvent être utilisés pour les évaluations de stock basées sur les données de prises et d'effort, même quand des modèles plus réalistes et structurellement corrects sont disponibles; le meilleur choix dépend de l'écart qui s'est produit dans les données historiques sur l'effort et les prises par unité d'effort et non d'une connaissance antérieure du modèle le plus biologiquement réaliste.

Received August 14, 1984
Accepted February 19, 1985
(J7092)

Reçu le 14 août 1984
Accepté le 19 février 1985

Simple surplus production models have been widely used in fisheries management, but they suffer from lack of biological realism. In recent years, as computers have become more powerful, more elaborate models and estimation schemes have become feasible (Deriso 1980). It seems obvious that greater biological realism will lead to better estimates for variables such as optimal exploitation rate or optimal effort. However, the more elaborate the model is, the greater are its requirements for information. It is possible for difficulties associated with parameter estimation to degrade the performance of age-structured models below that of simplistic stock-production models.

In this paper we show that a simple surplus production model derived from Ricker's model for stock and recruitment can perform as well as Deriso's (1980) age-structured model for stock biomass dynamics, even when the catch/effort data series is generated by Deriso's model in the first place. Here, performance is tested by means of simulations with artificially generated data series. Such tests are an indispensable supplement to tests on actual fisheries data, since a model and estimation scheme may produce plausible parameter values, which are nevertheless extremely inaccurate or misleading. We argue that all estimation schemes should be tested with simulated data where the parameter values are known in advance, since accuracy and consistency cannot in principle be determined from "real data" where the parameters are unknown.

A Ricker Model for Surplus Production

By pretending that fishing is concentrated in a short period each year with fishing mortality rate proportional to effort, and that biomass of the following year will be related by a dome shaped curve to the stock remaining after harvest, it is simple to devise the following surplus production model:

$$(1) \quad B_{t+1} = S_t \exp(\alpha - \beta S_t + U_t)$$

$$(2) \quad S_t = B_t - C_t$$

$$(3) \quad C_t = B_t(1 - \exp(-qE_t))$$

where B_t denotes the population biomass in year t , S_t denotes the biomass remaining after harvest in year t , C_t denotes the harvest in year t , E_t denotes the observed effort in year t , U_t are independent normally distributed random variables, with mean 0 and variance σ^2 , and α , β , and q are parameters to be estimated from catch and effort data.

A parameter estimation scheme for this model is detailed in Ludwig and Hilborn (1983). The basic procedure is to seek estimates of α , β , and q that minimize the sum of the squared residuals in $\ln(B_{t+1}/S_t)$ when equations (1)–(3) are fitted to catch and effort data. Here, we use a simpler formulation than theirs, since we neglect the effect of errors in estimating effective effort. This is done to simplify the presentation, and to save computer time when considering test data. However, such

observation errors should not be neglected when employing actual data. In the absence of observation errors, the estimation procedure involves the following iterative scheme: (i) assume a value for q and compute B_t and S_t using equations (2) and (3); (ii) estimate α and β from linear regression of $\ln(B_{t+1}/S_t)$ on S_t using B_t 's and S_t 's from step (i); (iii) repeat steps (i) and (ii) while varying q so as to find that value where the sum of the squared residuals is minimized. Various search procedures for function minimization may be used at this stage.

The following results are derived in Appendix A: after α , β , and q have been estimated, an optimum spawning stock S can be determined by choosing S to maximize discounted yield at equilibrium:

$$(4) \quad \delta S \exp(\alpha - \beta S + 1/2\sigma^2) - S = \text{maximum at } S = \hat{S}$$

where the discount factor $\delta = 0.9$. This corresponds to a 10% discount rate per year or per generation, depending upon the situation. Then the optimal effort is estimated by

$$(5) \quad \hat{E} = \frac{\alpha - \beta \hat{S} + \frac{1}{2}\sigma^2}{q}.$$

The Deriso Model

The model of Deriso (1980) considers two categories of biomass. If P_t denotes the biomass of prerecruitment juveniles and B_t denotes the biomass of catchable adults, prior to harvest in year t , then equation (8) of Deriso states that

$$(6) \quad P_{t+1} = (1 + \rho) l m P_t - \rho (l m)^2 P_{t-1} + R_{t+1}$$

$$(7) \quad R_{t+1} = (1 + \rho) S_t - \rho l^2 \frac{S_t}{B_t} S_{t-1} + (1 - m) P_{t+1}.$$

Here, ρ denotes the Brody growth coefficient (weight growth is assumed to be described by $W_{a+1} = W_k + \rho W_a$, where W_k is weight at recruitment and W_a is weight at age a). The fraction lost due to natural mortality is $1 - l$, and $1 - m$ denotes the fraction of individuals in P_t that become catchable in year t . Recruitment is assumed to depend only upon spawning biomass k years earlier:

$$(8) \quad R_{t+1} = S_{t+1-k} \exp(\alpha - \beta S_{t+1-k} + U_t).$$

This model assumes that random effects and density dependence are important only in the very early life stages. The concentration of these effects in the recruitment equation (8) greatly simplifies the analysis. We shall assume that catch and effort are related by (3), as before.

Although (1) and (8) are similar in appearance, their significance is quite different. This becomes apparent when α and β are estimated by linear regression. In the computations for the Deriso model, one must estimate P_{t+1} from (7), while using catch and effort data and equation (3) to estimate B and S for years $t - 1$, t , and $t + 1$. Then, R_{t+1} is estimated in terms of P_{t+1} , P_t , and P_{t-1} .

Thus, the calculation of R_{t+1} involves data from years $t + 1$, t , $t - 1$, $t - 2$, and $t - 3$. If S_{t+1-k} appears in that list, then 5 yr (generations) of catch and effort data are involved in the estimation of R_{t+1} ; otherwise, 6 yr (generations) of data are involved. In contrast with the Deriso model, the regression for the Ricker model involves only 2 successive yr (generations) for each data point.

These complications make it awkward to compensate for observation errors when using the Deriso model. Nevertheless,

a scheme analogous to the procedure in Ludwig and Walters (1981) and Ludwig and Hilborn (1983) has been devised and coded. It indicates that estimation performance deteriorates rapidly when observation errors are present. However, such a scheme is costly to run, so that extensive simulation trials are extremely expensive. Therefore, we have conducted our comparison on data without observation errors.

The estimation of parameters for the Deriso model is described in detail in Appendix B. The following is a summary of that description. In the absence of observation errors, parameter estimation for q , α , and β in the Deriso model proceeds as with the Ricker model, with one added step: (i) assume q and estimate R_t and S_t from equations (3) and (1); (ii) using the B_t and S_t estimates from step (i), solve equation (7) for time series of P_t estimates and then use these in equation (6) to solve for a time series of R_t estimates; (iii) regress the resulting estimates of $\ln(R/S_{t-k+1})$ versus S_{t-k+1} to get α and β ; (iv) repeat steps (i)–(iii) while varying q so as to search for that value that maximizes the likelihood function. The negative of the log likelihood function is given by

$$(9) \quad -\ln L = \frac{n}{2} \frac{1}{n-2} \sum_{t=1}^n U_t^2 + \sum_{t=1}^n \ln W_t$$

where n is the number of regression points and W_t is the contribution of the current year's recruitment to the current year's catch. The second sum in (9) comes from the Jacobian of the transformation of the random variables U_1, \dots, U_n to the catches C_1, \dots, C_n , which are the observations. Since this Jacobian involves q , it must be included in the likelihood function. If it is omitted, the performance of the Deriso scheme degrades very rapidly when the data have low contrast. Its importance was pointed out to us by J. Schnute (Pacific Biological Station, Nanaimo, B.C. V9R 5K6).

After the parameters in the Deriso model have been estimated, optimal \hat{S} and \hat{E} may be calculated, in analogy with (4) and (5). Details of the following calculations are given in Appendix C. It follows from (6), (7), and (8) that if E is held constant, then

$$(10) \quad S = \frac{1}{\beta} \left[\alpha + \frac{1}{2}\sigma^2 - \ln(1 - (1 + \delta)lm + \delta l^2 m^2) + \ln(1 - m) - \ln(e^{qE} + \delta l^2 e^{-qE} - (1 + \delta)l) \right].$$

The discounted harvest at equilibrium is maximized if

$$(11) \quad \delta e^{qE} S - S = \text{maximum}.$$

In our calculations, a discount factor of 0.9 was chosen. The optimal effort \hat{E} was determined from (11). Similar results were presented by Deriso (1980).

Simulation Trials

Some simulated catch and effort data are illustrated in Fig. 1. Initially, the stock was in a nearly unexploited state. Five years of low effort were followed by 10 yr of high effort, followed by a recovery period with low effort of 10 yr. Such sequences of efforts provide high contrast in both effort and catch per unit effort. The data were generated from the Deriso model by employing such a predetermined effort sequence, using parameter values that correspond to a long lived, slow growing species. The parameter values used were $k = 5$, $l = 0.9$, $m = 0.3$, $\rho = 0.2$, $\alpha = -0.5$, $\beta = 1$, and $q = 1$. Parameter σ^2 was set at 0.09, to give realistically large random variations in recruitment.

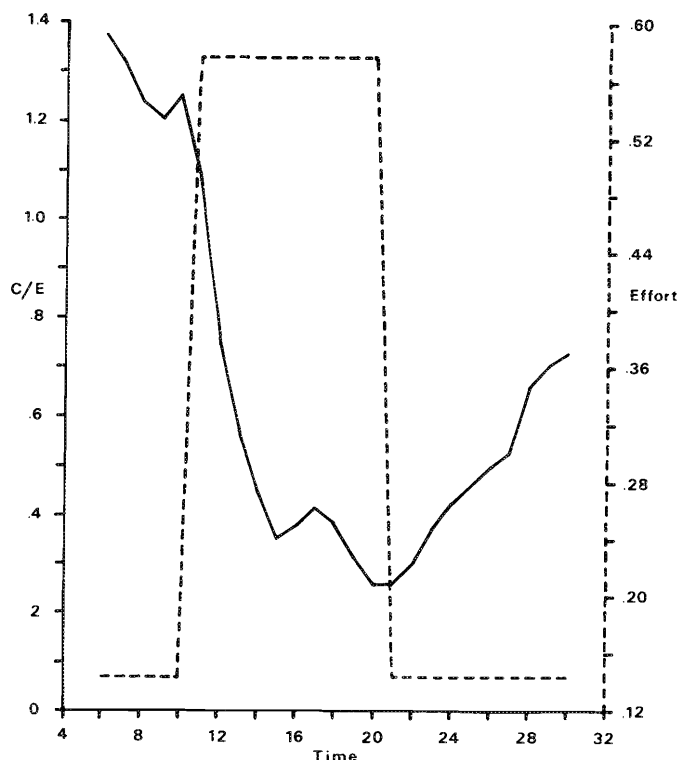


FIG. 1. Catch per unit effort (solid line) and effort (broken line) are plotted versus time for 25 yr of data. The data were generated by using the Deriso model with a set of pseudo-random normal deviates U_i , with $\sigma = 0.3$.

In parameter estimation trials, correct values for all but the last three parameters were assumed to be known a priori. That is, only q , α , and β were estimated from the data. With sufficiently informative data (i.e. with ratios of largest to smallest stock biomass and effort of at least 4), it is possible to estimate l in addition to α , β , and q . But attempts to estimate l and p together with the other three variables resulted in the likelihood function being maximized at impossible parameter values. This result is apparently at variance with Deriso (1980), who included seven parameters in his estimation procedure. However, he reported that the matrix of second partial derivatives was not positive definite at his estimated parameter values (p. 277), which implies that his optimization package did not find unique best estimates. We encountered similar difficulties when working with actual data from various stocks. We attribute this to a lack of contrast in the data, and to the effect of observation errors.

The Deriso and Ricker regressions to determine α and β given q (Fig. 2 and 3) are not directly comparable, due to differences in the underlying assumptions. For instance, note that the increases in catch per unit effort in years 15 and 16 are correctly attributed to high recruitment due to spawning in years 11 and 12, in the Deriso regression. But the Ricker regression attributes them to extraordinary recruitment in years 15 and 16. In spite of such differences, the two regressions are similar in one key respect: in both cases, information about the slope of the regression line comes mainly from the first few years (6–10) of data before the stock was heavily exploited, in combination with data from later years when the spawner biomass was low.

A series of simulation trials were performed to see how the performance of the estimation scheme would degrade as contrast in effort and catch per unit effort was reduced.

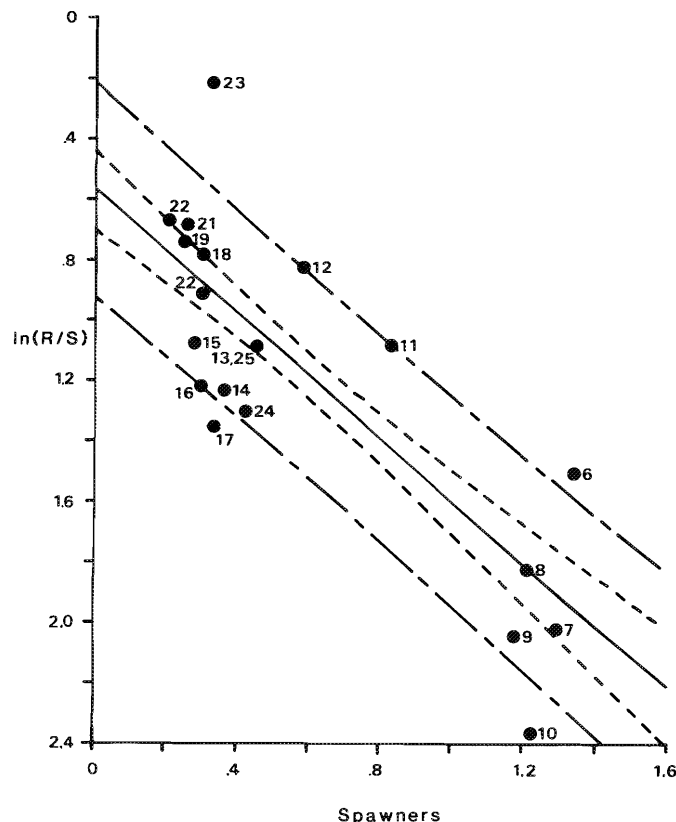


FIG. 2. Regression to determine stock-recruitment parameters using the Deriso model (negative logarithm of R/S versus the biomass of spawners). The solid curve is the least squares regression line. A 68% confidence band for the position of that line is given by the broken curves. The two outermost curves give 68% confidence limits for the position of the data points. The numbers next to the plotted points specify the year of spawning.

Sequences of 25 yr of data and 50 yr of data were generated. Because when $k = 5$, the Deriso regression for 25 yr of data has only 20 points, we emphasize results from the 50-yr sequences. However, the results for 25-yr sequences were similar. Also, to make our theoretical point, ratios of high and low efforts as great as 8 were considered, although actual data from most fisheries would not be nearly so informative.

The results of the simulation trials are summarized in Table 1. The primary statistic is the average squared deviation of the estimated optimum effort from the actual optimum effort. Loss in long term harvest due to estimation errors is approximately proportional to that squared deviation, since the graph of the value function versus (constant) effort can be approximated by a parabola near the optimal effort. Thus, the average of the squared deviation can be interpreted as a percentage of the optimal harvest that may be expected. The performance of the Deriso model drops as contrast in effort is reduced. The drop in performance is also reflected in an increased number of failures in the estimation procedure. A "failure" was defined as any case where at least one parameter estimate was physically impossible, or where the estimated optimal effort differed by more than 50% from the actual optimum.

Note in Table 1 that the Ricker model scheme actually performed slightly better than the correct (Deriso) model when effort contrast (E ratio) was low. Though this advantage is perhaps not significant (statistically or for management), the accuracy of the estimates of optimal effort was slightly better

TABLE 1. Results of 150 simulation trials, using the Deriso and Ricker procedures to estimate parameters for 50 yr of data. The parameters in the simulation are intended to represent a slow growing fish. The first column gives the ratio of efforts prescribed, according to the scheme illustrated in Fig. 1. The maximum and minimum catch per unit efforts have a similar ratio. The performance of each method is best measured by the average of the squared deviation of the estimated optimal effort from the true optimal effort. This average is also converted into a percentage of the optimum yield that would be obtained by using the estimated optimal effort. The resulting percentage is displayed in the column headed "value." The bottom two lines are the result of 150 simulation trials for 50 yr of data, where efforts are given by a sequence of pseudo-random numbers. Each effort has the form $E = E^* \exp(U)$, where U is normally distributed with mean 0 and variance σ_u^2 and E^* is the optimal constant effort. The values of σ_u^2 are displayed in the first column under the heading "random." The parameters are chosen to imitate a slow growing fish.

E ratio	Deriso			Ricker		
	$(E - E^*)^2$	Value (%)	Failures	$(E - E^*)^2$	Value (%)	Failures
8	0.00038	99	0	0.00120	97	0
4	0.00094	98	0	0.00091	98	0
2	0.0027	92	9	0.00113	97	5
1.5	0.0038	91	27	0.00182	95	30
Random						
0.5	0.00263	94	0	0.00148	96	0
0.2	0.00293	93	15	0.00247	94	13

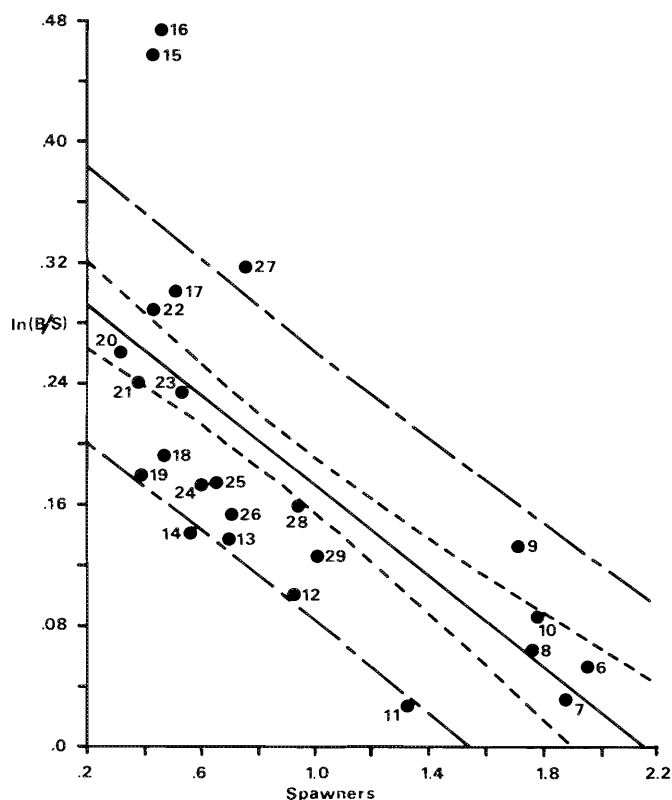


FIG. 3. Regression to determine stock-production parameters using the Ricker model (logarithm of B/S versus the biomass of spawners). The solid and broken curves have the same significance as in Fig. 2.

than when using Deriso's scheme. Since the Deriso model in fact had the correct structure, it outperformed the Ricker model when data with very large contrast were provided. But this advantage was lost when realistically low levels of effort contrast were tested.

One might suspect that this surprising result is due to the

special form of the effort sequence used. To test this idea, pseudo-random sequences of efforts were generated, with varying degrees of expected contrast. Figure 4 shows such a sequence of efforts. The results of 150 simulation runs are shown in Table 1. Again, the basic pattern is clear: the Ricker scheme performs about as well as the Deriso scheme at realistically low levels of contrast.

One might also suspect that our special choice of parameters was responsible for the good performance of the Ricker model. To test this idea, data were generated with Deriso's parameter estimates for haddock (*Melanogrammus aeglefinus*), a fast growing species for which a high exploitation rate is appropriate. The parameter values used were $k = 2$, $l = 0.51$, $m = 0.42$, $\rho = 0.85$, $\alpha = 1.1$, $\beta = 1$, and $q = 1$. The results (Table 2) are consistent with the preceding results; the Ricker scheme is almost as good as the correct Deriso model, except that more estimation failures occur at low effort contrast. We emphasize that the Deriso model also requires that parameters m , l , and ρ be specified or estimated. This requirement, and the greater computational complexity, raises grave questions about its practical utility.

Why Does the Ricker Model Perform So Well?

A clue to understanding the good performance of the Ricker model comes from comparison of Fig. 2 and 3. Although the two regressions are similar, the vertical scales on the two figures are very different. The difference in $\ln(B/S)$ is approximately 5 times as great in the Deriso regression as in the Ricker regression. For data that correspond to $k = 2$ (imitation haddock data) the corresponding factor is 2.

This disparity in variation carries through to parameter estimates: the maximum likelihood estimates will have standard errors that differ by corresponding factors. Our statistic $(\hat{E} - E^*)$ is roughly proportional to the variance of the estimated \hat{E} . Therefore, other things being equal, the Ricker estimates should produce an estimated \hat{E} whose variance is lower by a factor of 25

TABLE 2. Results of 150 simulation trials for 25 yr of data. The parameters in the simulation are intended to imitate the dynamics of a faster growing fish than in Table 1.

<i>E</i> ratio	Deriso			Ricker		
	$\overline{(E - E^*)^2}$	Value (%)	Failures	$\overline{(E - E^*)^2}$	Value (%)	Failures
8	0.00228	99.9	0	0.00384	99.9	0
4	0.00238	99	0	0.00261	99	0
2	0.0084	97.5	2	0.0090	97.5	4
1.5	0.0191	95	10	0.0124	96.5	20
Random						
0.5	0.0136	96.5	1	0.0192	95	20
0.2	0.0268	93	29	0.0168	95.5	20

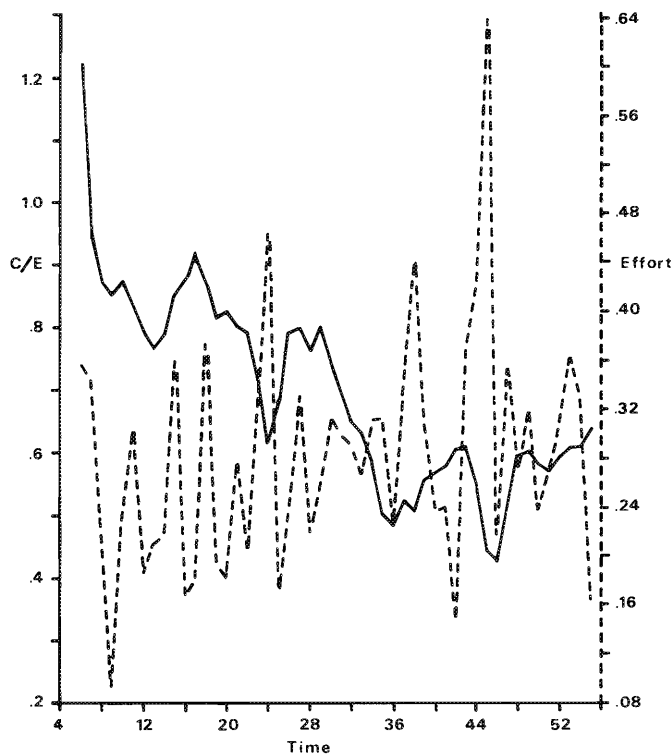


FIG. 4. Catch per unit effort (solid line) and effort (broken line) are plotted versus time for a pseudo-random sequence of efforts. The optimal effort E was multiplied by a log normally distributed pseudo-random number with mean 0 and standard deviation of 0.3.

when $k = 5$, and the Deriso $\ln(R/S)$ regression has 5 times the Ricker $\ln(B/S)$ standard error. Except when data are very informative, this advantage for the Ricker model cancels whatever advantage is provided by the superior structure of the Deriso regression.

To understand the difference in variation of $\ln B/S$ between the two models, we rewrite (7) in the approximate form

$$(12) \quad B = S[G + H \exp(\alpha - \beta(S - \bar{S}))].$$

Here, G and H depend upon data from preceding years, and \bar{S} denotes the mean spawning biomass. All of the density-independent growth and mortality is lumped into G , and H multiplies the density-dependent part, which is due to recruitment. For a long lived, slow growing species (for which age structure is presumably most important), H will be much smaller than G . Thus, we have approximately

$$(13) \quad \ln B/S \sim \ln G + \frac{H}{G} \exp(\alpha - \beta(S - \bar{S})).$$

The Ricker model consists in approximating (13) by

$$(14) \quad \ln B/S \sim \alpha^* - \beta^*(S - \bar{S}).$$

We have added asterisks to α and β in (14) to distinguish them from the corresponding quantities for the Deriso model. Comparing equations (13) and (14), we see that the amount of density dependence seen by the Ricker regression will be approximately H/G times the corresponding quantity for the Deriso regression.

A similar argument shows that this relationship also applies to variation in the estimated optimal effort, as computed by the two methods. Increasing the regression variance by a factor H/G results in correspondingly degraded estimates of optimal effort, unless the regression is provided with highly contrasting spawning stocks.

Conclusions

The phenomenon described above is not really surprising. It illustrates the general principle that the complexity of models and of decision procedures should be compatible with the amount of information available. Because of the large costs (direct and due to foregone harvest) of obtaining information about fish stocks, we suspect that management strategies in fisheries will always be developed in a twilight zone of inadequate information.

The implications are clear for models of population dynamics. The initial choice should be a minimal model that encompasses the basic variables that are measured (catch and effort), the decision variable (effort or exploitation rate), and a density-dependent effect, which determines desirable limits of stock abundance. Beyond that, each additional complication must be justified by the significance of its effect upon the basic variables, and by the adequacy of the information that is pertinent and available.

To obtain reasonable estimation performance with the Deriso model for data with moderate effort contrast, we had to assume correct values for ρ , l , m , and k . These parameters would ordinarily be estimated from age composition data. Therefore, even having more detailed data available to support some parameter estimates does not imply better performance of the more realistic surplus production model. Age-structured data do little to resolve uncertainties about q , since l (or its instantaneous rate equivalent M) and q are difficult to separate, as noted

graphically by Paloheimo (1980). However, such data may lead to improved estimation performance for α and β by providing more information about relative year class strengths.

Finally, we emphasize that the information that is important for management is primarily derived from variation in stock size. There is no way to estimate optimal biomass limits or exploitation rates without substantial contrast in effort and in catch per unit effort. This need for contrast is not unique to surplus production analysis; it is equally important for making valid inferences about detailed biological relationships such as density-dependent growth and juvenile survival. Therefore, we are not going to escape the statistical problems raised by surplus production analysis just by resorting to more careful biological investigations and detailed modelling.

References

- DERISO, R. B. 1980. Harvesting strategies and parameter estimation for an age-structured model. *Can. J. Fish. Aquat. Sci.* 37: 268–282.
- LUDWIG, D., AND R. HILBORN. 1983. Adaptive probing strategies for age-structured fish stocks. *Can. J. Fish. Aquat. Sci.* 40: 559–569.
- LUDWIG, D., AND C. J. WALTERS. 1981. Measurement errors and uncertainty in parameter estimates for stock and recruitment. *Can. J. Fish. Aquat. Sci.* 38: 711–720.
- PALOHEIMO, J. E. 1980. Estimation of mortality rates in fish populations. *Trans. Am. Fish. Soc.* 109: 378–386.

Appendix A: Optimal Catch and Effort Calculation for the Surplus Production Model

Here we assume that the stock can be maintained at a constant biomass after harvest, which will be denoted by S . The total expected discounted yield V is then given by

$$(A.1) \quad V = B - S + \sum_{t=1}^{\infty} \delta^t \left[\int U [S \exp(\alpha - \beta S + U) - S] \right]$$

where δ is a yearly (or generational) discount factor and B is the initial biomass before harvest. Since U is assumed to be normally distributed with mean 0 and variance σ^2 , the expectation is given by

$$(A.2) \quad \int U [S \exp(\alpha - \beta S + U)] = S \exp(\alpha - \beta S + \frac{1}{2}\sigma^2).$$

Moreover, the sum on the right-hand side of (A.1) is a geometrical series. When these facts are employed, (A.1) becomes

$$(A.3) \quad V = B - S + \frac{\delta}{1 - \delta} [S \exp(\alpha - \beta S + \frac{1}{2}\sigma^2) - S]$$

or

$$(A.4) \quad V = B + \frac{1}{1 - \delta} [\delta S \exp(\alpha - \beta S + \frac{1}{2}\sigma^2) - S].$$

Therefore, V is maximized by maximizing (4), as claimed there.

That maximization may be performed efficiently as follows: (4) is maximized if \hat{S} satisfies

$$(A.5) \quad (1 - \beta \hat{S}) \exp[\ln \delta + \alpha + \frac{1}{2}\sigma^2 - \beta \hat{S}] = 1.$$

If we define

$$(A.6) \quad A = \ln \delta + \alpha + \frac{1}{2}\sigma^2 - 1$$

$$(A.7) \quad T = 1 - \beta \hat{S}$$

then (A.5) may be rewritten as

$$(A.8) \quad T \exp(A + T) = 1.$$

The root T of this equation may be found by the following iteration scheme: let $T_0 = 0$, and

$$(A.9) \quad T_{n+1} = (1 + T_n)/(1 + \exp(A + T_n)).$$

The iterations converge rapidly to a root < 1 if $A > -1$.

Once the root is found, we may solve (A.7) to obtain

$$(A.10) \quad \hat{S} = \frac{1 - T}{\beta}.$$

In order to calculate the corresponding effort, we note from (3) that the stock remaining after harvest is

$$(A.11) \quad S = B \exp(-qE).$$

Thus, assuming the expected increase in biomass, the appropriate effort is chosen so that

$$(A.12) \quad \alpha - \beta \hat{S} + \frac{1}{2}\sigma^2 - qE = 0.$$

i.e. so that the expected stock after harvest is \hat{S} . Thus, equation (5) follows from (A.12).

Appendix B: Likelihood Function for the Deriso Model

There is subtlety in the derivation of the likelihood function for the Deriso model, which requires an extended explanation. The likelihood function is derived from a density function on the space of possible observations, which expresses the probability density of such observations, given a particular set of parameters \vec{p} . In the case of the Deriso model, \vec{p} will include q and any of the parameters ρ , l , m , and k that one attempts to estimate. The parameters α and β appear linearly at a crucial stage, and therefore they are treated separately. The efforts E_t are not regarded as random variables, but instead as “fixed inputs.”

In the Deriso model (3), (6)–(8), the catches are determined in terms of the normally distributed random variables U_t ; for the moment we write the corresponding density as $f(\vec{U}, \vec{p}) d\vec{U}$, where $f(\vec{U}, \vec{p})$ is a product of one-dimensional Gaussian densities. It is important to recognize that $f(\vec{U}, \vec{p})$ is not the likelihood function, since the likelihood L is derived from a density on the space of possible catches. The connection between f and L is made by equating the corresponding elements:

$$(B.1) \quad L(\vec{C}, \vec{p}) d\vec{C} = f(\vec{U}, \vec{p}) d\vec{U}.$$

This connection implies that

$$(B.2) \quad L(\vec{C}, \vec{p}) = f(\vec{U}, \vec{p}) \frac{\partial(\vec{C})}{\partial(\vec{U})}$$

where $\partial(\vec{C})/\partial(\vec{U})$ is the Jacobian of the transformation from the random variables U to the observed C . For simple models such as the surplus production model, this Jacobian is present, but it does not depend upon the parameter to be estimated. Therefore it may safely be ignored. However, in the case of the Deriso model, the Jacobian depends strongly upon the parameter q , as will be seen below.

In order to calculate $\partial(\vec{C})/\partial(\vec{U})$, we first express (6) and (7) in terms of the observed catches and efforts. It follows from (2) and (3) that

$$(B.3) \quad S_t = C_t \frac{e^{-qE_t}}{1 - e^{-qE_t}}$$

and

$$(B.4) \quad B_t = \frac{C_t}{1 - e^{-qE_t}}.$$

Now (7) may be written in the form

$$(B.5) \quad \frac{C_{t+1}}{1 - e^{-qE_{t+1}}} = (1 - m)P_{t+1} + \dots$$

where the dots denote terms that depend upon data from years (or generations) before $t + 1$. A similar treatment of (6) and a substitution produces

$$(B.6) \quad C_{t+1} = (1 - e^{-qE_{t+1}})(1 - m)(R_{t+1} + \dots).$$

If (8) is employed in B.6, we finally see how U_t influences C_{t+1} . Earlier variables U_{t-1} , etc., also influence C_{t+1} , but no future variables such as U_{t+1} can have an effect. We conclude that the Jacobian $\partial(\vec{C})/\partial(\vec{U})$ is the determinant of a triangular matrix, and hence it is a product of diagonal elements. In fact, from (8) we have

$$(B.7) \quad \frac{\partial R_{t+1}}{\partial(U_t)} = R_{t+1}.$$

Therefore

$$(B.8) \quad \frac{\partial(\vec{C})}{\partial(\vec{U})} = (1 - m)^n \prod_t (1 - e^{-qE_{t+1}})R_{t+1}.$$

The preceding result may be inserted into (B.2) in order to compute the likelihood function. Since U_t are assumed to be normally distributed with variance σ^2 , the log likelihood is given by

$$(B.9) \quad \ln L(C, p) = \frac{-1}{2\sigma^2} \sum_t U_t^2 - n \ln \sigma - n \ln (1 - m) - \sum_t \ln [(1 - e^{-qE_{t+1}})R_{t+1}].$$

In the formulation (B.9), the parameter vector p includes α , β , and σ , as well as q , etc. The computation of parameter estimates becomes much more manageable if we divide it into two stages. In the first stage, q , etc., are fixed and α and β are estimated by an ordinary regression, i.e. by minimizing

$$\sum_t U_t^2.$$

Then σ is estimated by

$$(B.10) \quad \hat{\sigma}^2 = \frac{1}{n - 2} \sum \hat{U}_t^2$$

where \hat{U}_t is the residual when α and β are replaced by their least squares estimates $\hat{\alpha}$ and $\hat{\beta}$.

In the second stage, q and any additional free parameters are estimated by minimizing

$$(B.11) \quad -\ln L = n \ln \hat{\sigma} + \sum_t \ln [(1 - e^{-qE_{t+1}})R_{t+1}].$$

This is the expression that appears in (9).

Appendix C: Optimal Catch and Effort Calculation for the Deriso Model

The calculation of optimal effort proceeds in analogy with Appendix A. The derivation (A.1)–(A.3) carries over, if the expression in square brackets is interpreted as a catch. Thus, (A.3) may be written as

$$(C.1) \quad \text{maximize} \left[-S + \frac{\delta}{1 - \delta} C \right]$$

as a function of the (constant) effort. From (2) and (3) it follows that

$$(C.2) \quad C = S(e^{qE} - 1).$$

If (C.2) is substituted into (C.1), the result is (11).

It still remains to calculate S as a function of E , assuming equilibrium conditions. This calculation involves (6)–(8). Assuming constant conditions and averaging as in (A.2), (6) becomes

$$(C.3) \quad P[1 - (1 + \rho)lm + \rho l^2 m^2] = S \exp [\alpha + \frac{1}{2}\sigma^2 - \beta S].$$

If (C.3) is substituted into (7), the result is

$$(C.4) \quad \frac{[1 - (1 + \rho)lm + \rho l^2 m^2]}{1 - m} [e^{qE} - (1 + \rho)l + \rho l^2 e^{-qE}] = \exp [\alpha + \frac{1}{2}\sigma^2 - \beta S].$$

If (C.4) is solved for S , the result is (10).