

Abstract.—Surplus-production models, because of their simplicity and relatively undemanding data needs, are attractive tools for many stock assessments. This paper reviews the logistic production model, starting with the basic differential equation and continuing with a description of the model development without the equilibrium assumption. It then describes several extensions, including “tuning” the model to a biomass index; partitioning fishing mortality by gear, time, or area; and making projections. Computation of confidence intervals on quantities of interest (e.g. maximum sustainable yield (MSY), effort at MSY, level of stock biomass relative to the optimum level) can be done through bootstrapping, and the bootstrap can also be used to construct nonparametric tests of hypotheses about changes in catchability. To fit the model, an algorithm that uses a forward solution of the population equations can be implemented on a small computer. An example of the utility of surplus-production models (illustrating several of these extensions) is given. The example is loosely based on swordfish (*Xiphias gladius*) in the North Atlantic Ocean, but is not intended to describe the actual status of that stock.

A suite of extensions to a nonequilibrium surplus-production model*

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Despite the prevalence of age-structured population models, surplus-production models—which generally do not incorporate age structure—remain useful for analysis of fish population dynamics. These models are of particular value when the catch cannot be aged, or cannot be aged precisely, and therefore age-structured models cannot be applied. Surplus-production models are also useful as a complement to age-structured models, providing another view of the data and the fisheries. An especially appealing aspect of production models is their simplicity; from a scientific point of view, this makes exploration of their properties easier; from a management point of view, it makes their results easier to present and understand (Barber, 1988).

In this paper, I show that another benefit of these models’ simplicity is that model extensions are easily made. Examples of such extensions include modeling several simultaneous or sequential fisheries on the same stock, “tuning” the model to a biomass index (as is often done in age-structured models; e.g. the CAGEAN model of Deriso et al.,

1985; the CAL model of Parrack, 1986; the ADAPT model of Gavaris, 1988), modeling changes in catchability or population characteristics (e.g. carrying capacity), and estimating missing values of fishing effort. Many of these extensions have not been presented before.

The comprehensiveness of a production model can be further increased by introducing another extension: computation of nonparametric estimates of variability in the results. These can be obtained by bootstrapping, and can be used both to describe the results more completely and to learn more about the model’s behavior under a variety of circumstances.

After reviewing the formulation of the simplest surplus-production model (the logistic model), a number of extensions to the model are described. An example, loosely based on swordfish, *Xiphias gladius*, in the North Atlantic Ocean, is presented to illustrate typical results from the model and the use of many of the extensions. The example, which is not intended to be an assessment of that stock, should not be used to make inferences about stock status.

Model formulation and fitting

Basic differential equations

Surplus-production models characterize a population as an undifferentiated biomass. The number of individuals present or harvested plays no part in these models, nor is age or size structure considered. A quantity termed "surplus production" is used to characterize population dynamics at different levels of population size (measured in biomass). Surplus production is the algebraic sum of three major forces: recruitment, growth, and natural mortality. The adjective "surplus" refers to the surplus of recruitment and growth over natural mortality; i.e. the net production. In this article, surplus production will often be termed simply "production," and the models termed "production models."

In the simplest production model, the logistic or Graham-Schaefer (Graham, 1935; Schaefer, 1954, 1957) model, a first-order differential equation describes the rate of change of stock biomass B_t due to production. In the absence of fishing, the population's rate of increase or decrease is assumed to be a function of the current population size only:

$$\frac{dB_t}{dt} = rB_t - \frac{r}{K}B_t^2, \quad (1)$$

where B_t is the population biomass at time t and r and K are parameters. The right side of Equation 1 is simply the start of the Taylor expansion of an arbitrary function $\Phi(B)$ passing through the origin (Lotka, 1924).

Equation 1 is written in the parameterization of population ecology, in which K represents the maximum population size, or carrying capacity, and r represents the stock's intrinsic rate of increase (in proportion per unit time). In this paper, both are assumed constant. Other parameterizations could be used, and indeed a slightly different parameterization is used for simplicity in the next section.

Adding fishing mortality F_t to the model, it becomes

$$\frac{dB_t}{dt} = (r - F_t)B_t - \frac{r}{K}B_t^2. \quad (2)$$

This model, like many fisheries models, is much simpler than the real world. In particular, it excludes such factors as environmental variation, interspecific effects, or the possible presence of more than one stable regime.

Time trajectories of biomass and yield

Integration of Equation 2 with respect to time allows modeling the biomass and yield through time.

Before integration, simplify notation by defining $\alpha_t = r - F_t$ and $\beta = r/K$ to express Equation 2 more simply as

$$\frac{dB_t}{dt} = \alpha_t B_t - \beta B_t^2. \quad (3)$$

Equation 3 can be conveniently solved for biomass under the assumption that F_t is constant and that therefore α_t is constant. This is a weak assumption, for if F_t varies, time can be divided into short periods of constant or nearly constant F and a solution found for each period. Fitting would then require knowing the catch and effort for each short period.

For the period beginning at $t = h$ and ending at time $t = h + \delta$, during which the instantaneous fishing mortality rate is F_h , the solution to Equation 3 is

$$B_{h+\delta} = \frac{\alpha_h B_h e^{\alpha_h \delta}}{\alpha_h + \beta B_h (e^{\alpha_h \delta} - 1)} \quad \text{when } \alpha_h \neq 0, \text{ or} \quad (4a)$$

$$B_{h+\delta} = \frac{B_h}{1 + \beta \delta B_h} \quad \text{when } \alpha_h = 0. \quad (4b)$$

Equation 4a is the familiar logistic equation. However, if $\alpha_h = 0$ (i.e. if $F_h = r$), Equation 4a is undefined and Equation 4b is used in its place.

Modeling the yield during the same period involves another integration with respect to time:

$$Y_h = \int_{t=h}^{h+\delta} F_h B_t dt, \quad (5)$$

where B_t , the biomass at instant t , is defined by Equations 4a and 4b; F_h is the (constant) instantaneous rate of fishing mortality during the time period; and Y_h is the yield taken during the period. Performing the integration in Equation 5,

$$Y_h = \frac{F_h}{\beta} \ln \left[1 - \frac{\beta B_h (1 - e^{\alpha_h \delta})}{\alpha_h} \right] \quad \text{when } \alpha_h \neq 0, \text{ or} \quad (6a)$$

$$Y_h = \frac{F_h}{\beta} \ln(1 + \delta \beta B_h) \quad \text{when } \alpha_h = 0. \quad (6b)$$

Equation 6a was apparently first given by Pella (1967) (and a similar form developed by Schnute [1977]); Equations 4b and 6b seem not to have been presented in fishery biology before now.

It follows from the definition of F that the estimated average biomass during the period is simply Y_h / F_h . The surplus production P_h during the time period can be determined by mass balance:

$$P_h = B_{h+\delta} - B_h + Y_h. \quad (7)$$

When yield is equal to surplus production, the population is in equilibrium.

Parameter estimation

Parameter estimation for this model can be accomplished by a number of methods. The method presented here is a slight modification of one originated by Pella (1967), later used by Pella and Tomlinson (1969), and recently termed the "time-series method" by Hilborn and Walters (1992). Although it is not necessary to use equal time periods, the treatment in the balance of this paper assumes, for simplicity, that there are T equal time periods, indexed by $\tau = \{1, 2, \dots, T\}$, and that a period is one year in duration. The following symbols are used:

- B_τ population biomass at the start of year τ
- Y_τ yield in biomass during year τ
- P_τ surplus production during year τ ,
- f_τ fishing effort rate during year τ ,
- F_τ fishing mortality rate during year τ ,
- α_τ function of F_τ ; $\alpha_\tau = r - F_\tau$.

Estimates of the first five of these quantities are represented by $\hat{B}_\tau, \hat{Y}_\tau, \hat{P}_\tau, \hat{f}_\tau$, and \hat{F}_τ .

An important additional assumption is that, for all τ , $F_\tau = qf_\tau$; in other words, that fishing mortality rate is proportional to fishing effort rate and that the catchability coefficient q is constant. (The assumption of constant q is slightly relaxed later.)

The data required for fitting are, for each time period τ , data on effort f_τ and the yield Y_τ , where $\tau = \{1, 2, \dots, T\}$ and $T > 4$. The parameters to be estimated are r and K in Equation 1, q , and B_1 , the biomass at the beginning of the first year. The simplest procedure accumulates residuals in yield. To perform the estimation, the following algorithm is used:

- A1 Obtain starting guesses for the four parameters.
- A2 Beginning with the current estimate of B_1 , project the population through time according to Equations 4a and 4b. For each year of the projection, compute estimated yield from Equations 6a and 6b.
- A3 Compute the objective function to be minimized. Assuming a multiplicative error structure in yield, this is

$$\sum_{\tau=1}^T [\log(Y_\tau) - \log(\hat{Y}_\tau)]^2.$$

- A4 Monitor the objective function for convergence. If achieved, end. Otherwise, revise the parameter estimates (using a standard minimization scheme) and continue at step A2.

The simplex or "polytope" algorithm (Nelder and Mead, 1965; Press et al., 1986) works well as the minimization scheme in this application. Although

not as rapid computationally as some other methods, the simplex algorithm is quite robust to starting values and is easily manipulated (by restarts) to avoid local minima (see Press et al., 1986, p. 292). Rivard and Bledsoe (1978) used the Marquardt (1963) algorithm successfully for estimation in a similar model.

The estimation method just described uses the recorded effort in each year to estimate yield. Alternatively, one could use the recorded yield in each year to estimate the fishing mortality rate (or equivalently, the fishing effort rate). The solutions of Equations 6a and 6b for fishing mortality rate are

$$F_\tau = \frac{\beta Y_\tau}{\ln \left[\frac{\beta B_\tau (e^{\alpha_\tau - 1})}{\alpha_\tau} + 1 \right]} \quad \text{when } \alpha_\tau \neq 0, \text{ or} \quad (8a)$$

$$F_\tau = \frac{\beta Y_\tau}{\ln[1 + \beta B_\tau]} \quad \text{when } \alpha_\tau = 0. \quad (8b)$$

To use this approach, one must revise the second and third steps of the algorithm to become—

- A2' Beginning with the current estimate of B_1 , compute the estimated fishing effort for each year by solving Equation 8a or 8b and dividing by \hat{q} . Project the population to year-end with Equation 4.
- A3' Compute the objective function to be minimized. Assuming a multiplicative error structure in effort, this is

$$\sum_{\tau=1}^T [\log(f_\tau) - \log(\hat{f}_\tau)]^2.$$

This is equivalent to minimizing the sums of squared residuals in the logarithm of catch per unit of effort, i.e. to minimizing

$$\sum_{\tau=1}^T [\log(C_\tau / f_\tau) - \log(C_\tau / \hat{f}_\tau)]^2.$$

A significant practical advantage of the second approach is that it simplifies the analysis of data with some missing data on effort. During parameter estimation, effort is estimated for all years; for years of missing effort, the contribution to the objective function is simply defined to be zero. In contrast, the computations for the first approach are not possible without data on effort for each year.

Estimating effort from yield introduces two small practical difficulties. The first difficulty is that Equation 8a is not an explicit solution for effort (because α_τ includes f_τ), so it must be solved iteratively. This is accomplished by putting a starting guess \hat{F}_τ into the right-hand side of the equation, solving, and substituting the result repeatedly until convergence is achieved. A logical starting guess is $\hat{F}_\tau = Y_\tau / \hat{B}_\tau$.

The second difficulty involves a fundamental difference between predicting yield and predicting effort. For a given starting biomass and effort, one can always compute the corresponding yield. For a given starting biomass, however, there are some yields that can never be obtained, no matter how high the effort. Under these circumstances, the catch equation (6a or 6b) has no solution. Unless a tactic is devised for such cases, it becomes impossible to compute the objective function when they occur, and thus impossible to conduct its minimization. A tactic suggested by R. Methot¹ as useful in his stock-synthesis model (Methot, 1989, 1990) is to place a constraint on the maximum allowable value of F_t (and consequently of f_t). When an estimate of F_t reaches this constraint, it is not allowed to increase further, and the quantity $[\log(Y_t) - \log(\hat{Y}_t)]^2$ is added to the objective function along with the usual squared residual in effort. This allows computation of a reasonable value of the objective function for such regions of the solution space that may be encountered during optimization. In my experience, however, final estimates have always come from a solution in which yield is always matched exactly.

In fitting a linear regression, observation error in the predictor variables causes problems with the parameter estimates, including inconsistency and, in the bivariate linear case, bias towards zero (Thiel, 1971; Kennedy, 1979). The problems induced into nonlinear models are less well understood, but are believed to be similar. Schnute (1989) has illustrated how the choice of dependent variable in a fisheries model can affect the results substantially. In fisheries contexts, yield is usually observed more precisely than fishing effort; for that reason, it seems preferable on statistical grounds to use the second approach, estimating effort from yield, rather than estimating yield from effort.

Whichever approach is chosen, the estimation process results in direct estimates of B_1 , r , K , and q , which define unique estimates of the stock biomass levels B_2 , B_3 , ..., B_T and the stock's production during each period of time. The corresponding estimate of maximum sustainable yield (MSY) under the logistic model is $\hat{MSY} = \hat{K}\hat{r}/4$. According to the theory of production modeling, MSY can be attained as a sustainable yield only at one specific stock size; for the logistic model this is $B_{MSY} = K/2$, estimated by $\hat{B}_{MSY} = \hat{K}/2$. The instantaneous fishing mortality that generates MSY at B_{MSY} is $F_{MSY} = r/2$; the corresponding rate of fishing effort is $f_{MSY} = r/2q$, with estimates given by substituting \hat{r} and \hat{q} for the unknown true values in these two expressions.

The logarithmic objective function assumes multiplicative errors with constant variance. The solution obtained is the maximum-likelihood solution if the transformed residuals are independent, of constant variance, and normally distributed (see Seber and Wild, 1989). However, maximum-likelihood methods, while generally desirable, are not necessarily robust to outliers, nor do they necessarily have desirable small-sample properties. Use of a robust-regression method (such as least absolute values regression) would be an interesting research topic.

Another management benchmark

An analogue of the management benchmark $F_{0.1}$ can be computed for this model (or for any production model). The derivative of equilibrium yield with respect to fishing mortality rate for this model is

$$\frac{dY_e}{dF} = K \left(1 - \frac{2F}{r} \right). \quad (9)$$

At $F = 0$, this derivative is equal to K . We define as $F_{0.1}$ for this model as the value of F at which Equation 9 equals $0.1 K$. Substitution into Equation 9 gives the following results: $F_{0.1} = 0.45 r$, and $Y_{0.1} = 0.2475 rK$ (where $Y_{0.1}$ is the equilibrium yield corresponding to $F_{0.1}$). An equivalent statement is that $F_{0.1}$ is 90% of F_{MSY} , and $Y_{0.1}$ is 99% of MSY. Punt (1990) used the concept of $F_{0.1}$ for a production model but did not explicitly state these relationships.

Penalty for large estimates of B_1

Logistic production theory implies that B_1 should always be less than K , but the objective functions used here are relatively insensitive to the estimate of B_1 . In practice, I have found that the estimate of B_1 obtained from some data sets tends to be much larger than the estimate of K . Such results could be eliminated by introducing a fixed constraint into the solution, but I have used another method successfully: adding a penalty term to the objective function when $\hat{B}_1 > \hat{K}$. Including this term, the complete logarithmic objective function (assuming residuals in effort) becomes

$$L = \sum_{t=1}^T [\log(f_t) - \log(\hat{f}_t)]^2 + \phi [\log(\hat{B}_1) - \log(\hat{K})]^2, \quad (10)$$

where $\phi \equiv 1$ if $\hat{B}_1 > \hat{K}$, and $\phi \equiv 0$, otherwise. While constraining the value of B_1 seems logical in accordance with the underlying population theory, such constraints can change the estimates of other parameters, compared to an unconstrained solution. The amount of change can be examined by estimating with and without the penalty term or fixed constraint.

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Extensions to the model

A great strength of the model presented here is the ease with which it can be extended and modified. Such extensions can include, for example, modeling fisheries divided by space, time, or gear type; analyzing data series including some years of no effort, as would occur during a closure; analyzing data series with years of missing or highly uncertain effort data; incorporating changes in catchability within the data series, perhaps after periods of closure or following regulatory changes; and tuning the model to fishery-independent estimates or indices of population biomass.

Missing data

Gaps in the effort and yield time series do not present a problem to these dynamic production model analyses. Years with no effort (and therefore no catch) can easily be treated by defining the residual to be zero. Although such years do not influence parameter estimation directly, the time lag during the years of closure carries information that is incorporated in fitting the model, and an estimate of population biomass for each missing year is made according to the logistic growth model. In contrast, years of closure contribute no information to production models that assume equilibrium conditions.

A slightly more difficult problem is the correct treatment of years in which effort is known to have existed, but for which the data are missing or highly uncertain. In such a case, the framework presented here can be used to estimate, simultaneously with the other parameters, effort levels for a limited number of such years within the series. As in any estimation scheme, the total number of estimated parameters should be kept reasonably small in comparison to the number of years of nonzero data. If residuals are constructed in effort (rather than yield) the estimation of missing effort becomes trivial, as a predicted effort is computed for each year during parameter estimation.

More than one data series

Another simple extension of the basic estimation framework is analysis of stocks fished by two or more different gear types, either in the same years or serially. For convenience, I refer to these as different fisheries on the same stock. To define the situation more precisely, there are J different fisheries, indexed by $j = \{1, 2, \dots, J\}$. The effort applied by fishery j in period τ is $f_{j\tau}$, the catchability coefficient of that fishery is q_j , and the yield in period τ is Y_{τ} . All q_j are

assumed time-invariant. The total instantaneous fishing mortality in period τ is

$$F_{\tau} = \sum_{j=1}^J q_j f_{j\tau}. \quad (11)$$

Biomass and yield projections can be computed by Equations 4a, 4b, 6a, and 6b as before. The estimated yield from fishery j in period τ is

$$\hat{Y}_{j\tau} = \frac{\hat{q}_j \hat{f}_{j\tau}}{\hat{F}_{\tau}} \hat{Y}_{\tau}, \quad (12)$$

where \hat{Y}_{τ} is the total yield in period τ . During parameter estimation, a residual is obtained for each fishery having nonzero effort in period τ . The contribution to the objective function for each period is thus composed of a sum of terms, one for each fishery with nonzero effort. In addition, the individual fisheries may carry different statistical weights to reflect varying levels of confidence in the data from each fishery. Inverse-variance weighting can be approximated by iteratively examining the mean-squared error (MSE) from each series, weighting, and re-estimating the parameters.

Model tuning

If an external series of population biomass estimates is available, it can be incorporated into the analysis in a procedure analogous to tuning an age-structured analysis. The external estimates are compared to the population estimates derived within the production model and the residuals incorporated in computation of the objective function. Rivard and Bledsoe (1978) suggested this possibility, but did not pursue the idea, and it has also been described by Hilborn and Walters (1992). The external biomass series need not be continuous, but may contain missing values; the series' contribution to the objective function is set to zero for years with missing values. An external *index* of biomass can be used similarly, with the cost of estimating one more parameter (the catchability associated with the index).

The model formulation involved in tuning the model is similar to that used when fitting more than one fishery. As in that situation, each year's contribution to the objective function consists of a sum of terms. Here, the sum includes a term from each fishery and a term for each biomass-estimate or index series. For a maximum-likelihood solution, the components should carry statistical weights inversely proportional to their variances.

Varying catchability

In many situations, catchability is thought to change relatively suddenly, perhaps because more efficient

gear for finding or catching the fish is introduced. In such cases, the formulation represented by Equations 11 and 12 can be used to estimate different catchability coefficients for segments of a single time series. In formulating such a model, the time segments would be treated as separate fisheries, each having nonzero catch and effort data only during its respective time period. Each additional time segment would add one additional parameter to the model.

A common concern is determining whether the improvement in fit obtained from a more complex model is statistically significant. A production model with added catchability parameters can be tested against the simpler model (with one estimated q) with a standard F -ratio test. (Here F refers to the F distribution of statistics, not to fishing mortality rate.) The test statistic F^* is

$$F^* = \frac{(SSE_s - SSE_c)/v_1}{SSE_c/v_2}, \quad (13)$$

where SSE_s and SSE_c are the error sums of squares of the simple and complex models, respectively; v_1 is the difference in number of estimated parameters between the two models; and v_2 is the number of data points less the total number of estimated parameters. The significance probability of F^* can be obtained from tables of the F -distribution with v_1 and v_2 degrees of freedom. As pointed out by a referee, this is equivalent to a likelihood-ratio test assuming log-normal error structure, which is implicit in using the SSE from log-transformed data. Because of the possibility of specification error, any such significance test must be considered approximate.

A nonparametric test of the null hypothesis $q_1 = q_2$ can also be conducted by examining a bias-corrected confidence interval on the ratio of the two catchability coefficients. (Construction of bias-corrected confidence intervals is described later.) As an example, assume that the alternative hypothesis is $q_1 \neq q_2$. The null hypothesis would be rejected at $P < 0.05$ if a 95% confidence interval on the ratio q_1/q_2 did not include the value 1.0. Like the F -test, this test is approximate because of the possibility of specification error.

In other cases, catchability is thought to vary in more subtle ways than the step function just suggested (Paloheimo and Dickie, 1964; Gulland, 1975; MacCall, 1976; Peterman and Steer, 1981; Winters and Wheeler, 1985), and one could incorporate any number of catchability models into the estimation framework. It would be straightforward to model a linear trend (increase or decrease) in catchability with time. This could be parameterized by estimating the first and last years' values of q and generating intermediate years' values by linear interpola-

tion, so that only one additional parameter would be estimated. One could also add some form of density-dependent catchability model with a minimal cost in terms of number of parameters estimated; the foundation of such an approach was presented by Fox (1975). However, it might prove difficult to distinguish varying catchability from trends in biomass itself. If so, the use of external estimates or indices of biomass, as explained above, might be especially valuable.

Bootstrap estimates of bias and variability

The bootstrap (Efron, 1982; Stine, 1990) is a sample reuse technique often used to estimate sampling variances, confidence intervals, bias, and similar properties of statistics, including parameter estimates. Major advantages of the bootstrap, compared to alternative methods (such as those based on the information matrix), are its flexibility and relative freedom from distributional assumptions. A minor drawback is that it demands a great deal of computer time.

Bootstrapping is often performed by resampling the original observations. However, in fitting nonequilibrium production models, the order of the catch-effort pairs is as significant as the data themselves. For time-series models (in the broad sense), Efron and Tibshirani (1986) describe a method, used here, that preserves the original time structure of the data. For each bootstrap trial (of which there may be 250 to several thousand), a set of synthetic observations is constructed by combining the ordered predictions from the original fit with residuals chosen at random (with replacement) from the set of residuals from the original fit. The model is then refit to this set of synthetic observations.

The bootstrap can be used to estimate bias in parameter estimates. The median estimation bias B'_θ in a parameter θ is estimated by

$$\hat{B}'_\theta = \hat{\theta}_m - \hat{\theta}, \quad (13a)$$

where $\hat{\theta}$ is the conventional estimator of θ , and $\hat{\theta}_m$ is the median value of θ obtained from the bootstrap trials (Efron, 1982; Efron and Gong, 1983). A bias-corrected estimator $\hat{\theta}_{BC}$ of a parameter θ can therefore be given by

$$\hat{\theta}_{BC} = \hat{\theta} - \hat{B}'_\theta. \quad (13b)$$

It appears that the median bias correction, rather than a mean correction, has been adopted in the bootstrapping literature because a mean correction (which would be expected to produce an "unbiased" estimate in the usual sense) can have extremely high variance (Hinkley, 1978). The resulting problems are

avoided by use of a median correction, which is quite resistant to outliers. However, the use of a median correction implies that the estimated bias correction will be nonzero for an estimator that is unbiased (in the usual sense) but arises from a distribution in which the median does not equal the mean. That is, the use of a median bias correction transforms the estimator into a median estimator.

Several methods have been developed for computing bias-corrected confidence intervals from the bootstrap (Efron, 1982; Efron, 1987; Noreen, 1989). The most widely used at present appears to be the BC method of Efron (1982). To compute a BC interval, let $N(z)$ be the cumulative distribution function (CDF) of the standard normal distribution and let N^{-1} be the inverse-normal CDF. Let \hat{C} be the empirical bootstrap CDF of the parameter θ ; i.e. $\hat{C}(g)$ is the proportion of realizations of $\hat{\theta}$ in the bootstrap distribution that falls below any arbitrary value g . Define the constant

$$z_0 \equiv N^{-1}[\hat{C}(\hat{\theta})], \quad (14)$$

where $\hat{\theta}$ is the conventional estimator. Then, the $(1 - 2\alpha)$ BC central confidence interval on $\hat{\theta}$ is defined as

$$\theta \in \left\{ \hat{C}^{-1}\left[N\left(2z_0 + N^{-1}(\alpha)\right)\right], \hat{C}^{-1}\left[N\left(2z_0 - N^{-1}(\alpha)\right)\right] \right\}. \quad (15)$$

This method assumes that a transformation exists under which the distribution of θ becomes normal and homoscedastic. However, the form of the transformation need not be known (Efron and Gong, 1983). Kizner (1991) constructed bootstrap confidence intervals on production-model results, but he did not state whether bias corrections were used.

This discussion of bootstrapping has referred to estimated "parameters" for simplicity, but the method can be used to estimate bias corrections and bias-corrected confidence intervals for any estimated quantity. Such quantities might include estimates of MSY , f_{MSY} , the population biomass in the final (or any other) year, $f_{0.1}$, projections of biomass levels (discussed next), and so forth.

Projections

Because a production model implicitly includes a recruitment function, it can be used to make projections based on hypothetical catch or effort quotas. As noted above, the historical population biomass trajectory is estimated during parameter estimation. The modeled population can then be projected forward in time by using the same population equations (4, 6, 8), and a proposed set of yields or effort rates. If the bootstrap is used following parameter estimation,

the results of each bootstrap trial can be projected forward. From the results, it is possible to compute bias-corrected point estimates and confidence intervals on the projection results.

Example: North Atlantic swordfish

Many aspects of the production model discussed above are illustrated in this example, which is loosely based on swordfish, *Xiphias gladius*, in the North Atlantic Ocean. The example comprises two analyses, the difference between them being the use of an abundance index for tuning the second analysis. Both the base analysis and the tuned analysis used the same yield and fishing-effort data (Table 1; Fig. 1); the tuned analysis also used a hypothetical index of abundance constructed for this purpose (Table 1; Fig. 1). In both analyses, errors were assumed to occur in fishing effort and to follow a lognormal distribution; in other words, the "second estimation approach" described previously was used. Each analysis included a projection of five years beyond the actual data; during those five years, it was assumed that a yield of 12,000 metric tons would be taken annually. Each analysis included a bootstrap with 1,000 trials.

This example is not intended as, and should not be considered to be, a formal assessment of the swordfish fishery. Such an assessment would normally include additional information and analysis, including age-structured population models and numerous sensitivity analyses. Also, the abundance index used here was developed solely to serve an example, and is not believed to be an accurate reflection of abundance over time.

The North Atlantic swordfish fishery enjoyed a high catch rate in 1962 and 1963, but it declined in the late 1960s (Fig. 1). The U.S. and Canadian portions of the fishery were sharply reduced in the early 1970s because of FDA regulations prohibiting interstate transportation or importation of fish with mercury concentrations exceeding the allowable level of 0.5 ppm (Hoey et al., 1989). In 1978, the FDA increased the allowable mercury content to 1 ppm, and since then, the catch has increased, but the CPUE has slowly declined (Fig. 1B). For the years 1971–73, early years of the FDA regulations, data are available on catch but not on fishing effort.

Results from the two analyses were similar, but they illustrate how tuning can influence the results of a production model. In each analysis, the model fits the effort data reasonably well (Fig. 2); however, because the hypothetical abundance index does not match the observed CPUE well (Fig. 1B), the fit in the last years of the tuned model was a compromise

between matching the observed effort (Fig. 2B) and matching the index (Fig. 2C). The tuned analysis gave lower estimates of MSY , f_{MSY} , and a less optimistic impression of the current level of the stock, as represented by the ratio B_{1992}/B_{MSY} (Table 2). It also estimated that the recent fishing mortality rate, as represented by the ratio F_{1991}/F_{MSY} , was somewhat higher.

Estimated median biases from each analysis were small. In the base analysis, no management benchmark was estimated to have a bias exceeding 1.5%

Table 1

Data used in two production model analyses loosely based on swordfish, *Xiphias gladius*, in the North Atlantic Ocean. Yield and standardized fishing-effort-rate data are from Hoey et al. (1993) with minor revisions. Hypothetical abundance index data are the mean of ages 3 through 5+ in numbers from Scott et al. (1992). The index was constructed solely for illustrative purposes, and is designated "hypothetical" because it probably is not a good indicator of total-stock biomass.

Year	Yield (t)	Fishing effort rate (10 ⁶ hooks/yr)	Hypothetical abundance index
1962	5,342	6.45	—
1963	10,189	8.54	—
1964	11,258	24.45	—
1965	8,652	25.30	—
1966	9,338	31.39	—
1967	9,084	28.90	—
1968	9,137	40.11	—
1969	9,138	43.23	—
1970	9,425	38.47	—
1971	5,198	—	—
1972	4,727	—	—
1973	6,001	—	—
1974	6,301	19.22	—
1975	8,776	22.97	—
1976	6,587	21.17	—
1977	6,352	18.14	—
1978	11,797	20.40	—
1979	11,859	40.13	—
1980	13,527	35.44	—
1981	11,126	34.85	1.000
1982	12,832	40.73	0.816
1983	14,423	55.10	0.488
1984	12,516	49.44	0.483
1985	14,255	59.55	0.526
1986	18,278	80.75	0.411
1987	19,959	98.91	0.377
1988	19,137	97.08	0.368
1989	17,008	90.46	0.359
1990	15,594	85.86	0.352
1991	13,212	69.86	—

of the corresponding uncorrected estimate (Table 2). Estimated median biases for the tuned analysis were only slightly higher; with only the estimated bias in f_{MSY} slightly exceeding 2%. Estimates of median bias in individual model parameters (such as r and K) were slightly higher yet, but only for B_1 was bias estimated as higher than about 2.5%.

Approximate 80% nonparametric confidence intervals computed by Equations 14 and 15 were derived from the bootstrap. These were computed for the individual model parameters, management benchmarks, indicators of stock position, and for each year's relative stock size estimate (Table 2; Fig. 3). A unitless nonparametric measure of the precision of estimates was constructed by dividing the bias-corrected 50% confidence interval (interquartile range; not shown here) by the corresponding median bias-corrected estimate. The resulting statistic, the relative interquartile range (RIR) is a nonparametric analog of the coefficient of variation. The RIR was of similar magnitude for both models, and was smallest in MSY and f_{MSY} , the benchmarks that do not depend on q . Estimates of the quantities that depend on q , and that thus involve absolute scaling, exhibited relative IQ ranges of about 50% (Table 2).

Estimates of relative biomass (B_t scaled to B_{MSY}) and fishing mortality rate (F_t scaled to F_{MSY}) were also similar from the two models (Fig. 3). They show a declining biomass through 1991, with an increase expected thereafter (at the projected harvest rate of 12,000 t/yr, which is less than the MSY estimates). As expected, the precision of estimates during the projection period was less than during the period for which data were available.

In summary, this example demonstrates that much more than MSY can be estimated from a production model. Biomass trajectories can be computed easily, as can estimated confidence intervals derived through the bootstrap. If an independent index of abundance is available, the model can be tuned to that index. Another useful feature is that projections can be used to estimate the probable effects of quotas or other management measures.

Discussion

The modeling framework described here is based on the logistic population model. The history of this model was summarized by Kingsland (1982), who pointed out that the model originated in the work of Verhulst (1845) and Robertson (1923), was popularized by Pearl and Reed (1920), and was also studied by Lotka (1924). The model was introduced to fishery science by Graham (1935) and Schaefer (1954,

1957). In modeling fish populations, one could just as easily use the exponential yield model of Fox (1970) or a model of more flexible shape, such as that of Pella and Tomlinson (1969) or its alternative formulation by Fletcher (1982). (Fletcher's formulation lacks the estimated exponent that has been found to complicate estimation [Ricker 1975, p. 326].) Unfortunately, those formulations can not supply an analytical formulation similar to Equations 6 and 8, which means that numerical integration would have to be used, as in the GENPROD computer program of Pella and Tomlinson (1969). Another alternative would be to use a discrete-time model, rather than the continuous-time model presented here. Such models are simpler mathematically, but usually entail assumptions that the growth, recruitment, and catching seasons are brief. The logistic model was used here because it is a simple case, not because using other models would be impractical or inferior.

For what types of stocks are the models presented here appropriate? Research is lacking to answer this question definitively, but general comments are possible. One group of fishes for which production models seem to work well is the tropical tunas. These species are characterized by relatively fast growth, relatively constant recruitment, and reduced annual seasonality in the life processes. Density dependence in growth has been demonstrated in a related species, *Scomber japonicus* (Prager and MacCall, 1988); such plasticity in growth would allow the compensation inherent in a production model to be expressed in a way beyond recruitment variability. For modeling fish stocks with more seasonality in growth, reproduction, and harvest, a discrete-time production model might prove superior to the continuous-time model presented here.

In many fish stocks, recruitment is extremely variable. Ordinary production models may not work well when applied to stocks with large recruitment fluctuations that are unrelated to population size, especially when the catch-effort series is short. If recruitment fluctuations can be linked to external factors (such as variation in rainfall or sea-surface temperature), a production model incorporating these factors might work well (Freon, 1986). It would be simple to modify the logistic model to incorporate an environmental factor, perhaps as an influence on r on an annual basis.

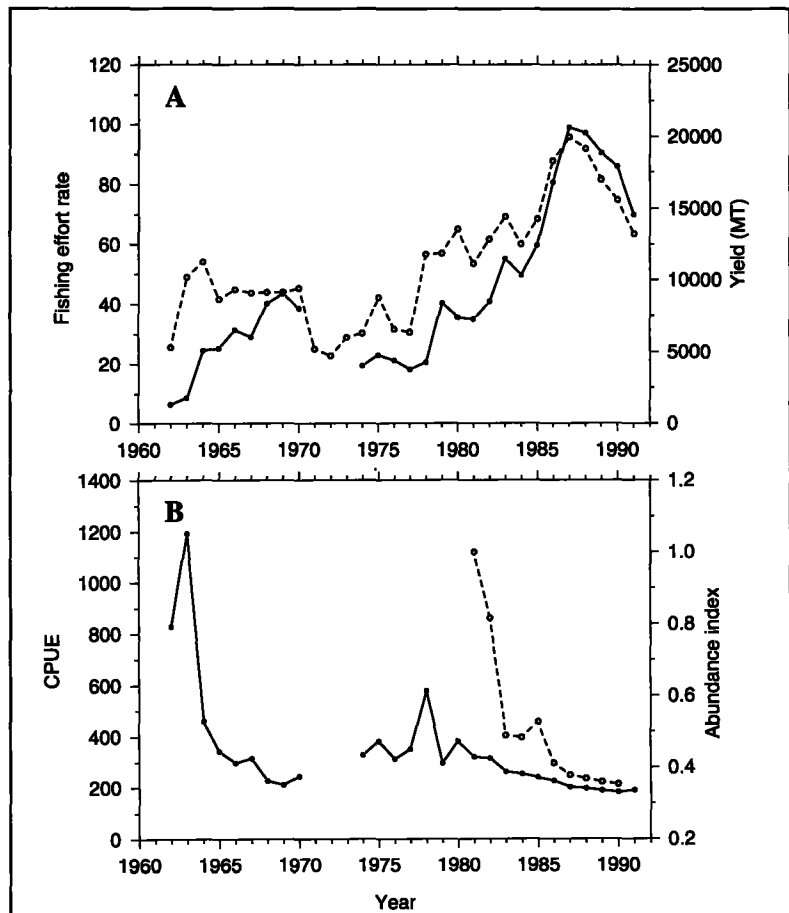


Figure 1

Data used to fit production model examples loosely based on swordfish, *Xiphias gladius*, in the North Atlantic Ocean. (A) Standardized effort rate (•) and total yield (◦). (B) CPUE trajectory (•) computed from data in (A), and index of abundance (◦) used to tune the second example. The index, which was used for illustrative purposes only, is not a good measure of total-stock abundance.

Other extensions

Many other extensions to the production model have been published. An incomplete list includes these: Fox (1975, 1977) presented a logistic production model with mixing of two stocks; Deriso (1980) and Hilborn (1990) demonstrated different methods of fitting production models to age-structured populations (but see also Ludwig and Walters, 1985); Freon (1986) introduced environmental variables into a production model that used the equilibrium assumption; Laloë (1989) and Die et al. (1990) incorporated fished area into production models; Polovina (1989) demonstrated a system of production models in which some parameters are common among models; and Hoenig and Warren (1990) demonstrated Bayesian

and empirical Bayes methods for fitting production models. Most of the extensions described by these investigators could be combined with techniques presented here (e.g. tuning, bootstrapping), as required for a particular analysis.

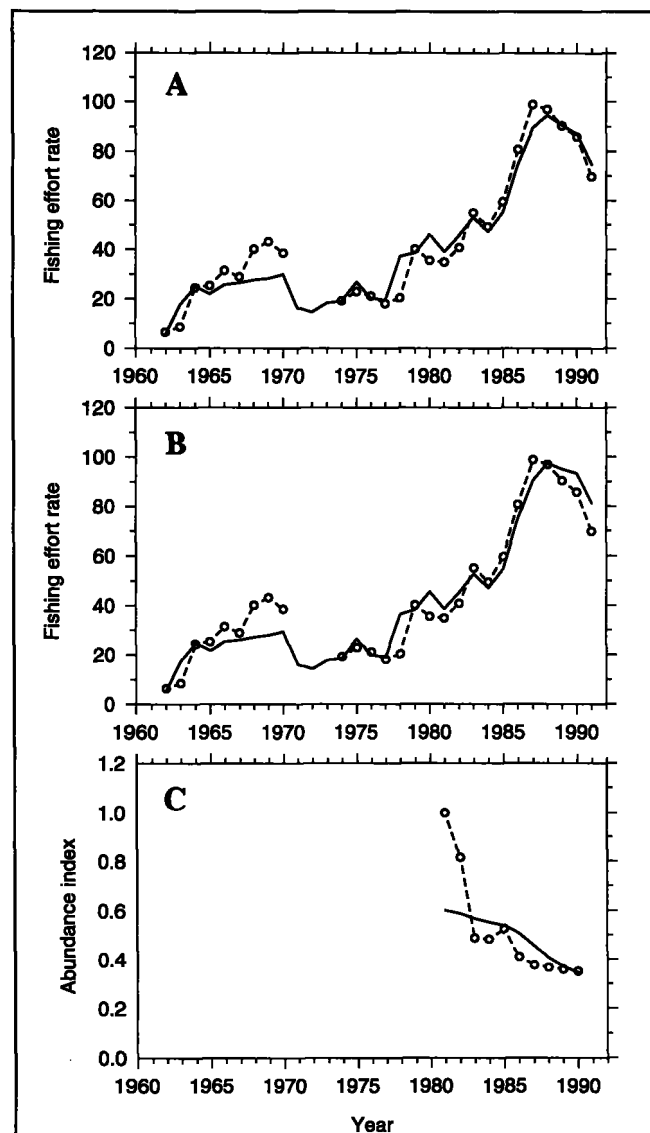


Figure 2

Goodness-of-fit of two production model analyses loosely based on swordfish, *Xiphias gladius*, in the North Atlantic Ocean. These analyses are illustrative and are not intended as an assessment of swordfish. Model 2 differs from Model 1 in being tuned to a hypothetical index of abundance. (A) Observed (○) and estimated (—) fishing effort rate from Model 1. (B) Observed (○) and estimated (—) effort rate from Model 2. (C) Observed (○) and estimated abundance-index from Model 2.

Autocorrelation

Because catch and effort data are usually autocorrelated, the residuals from fitting—whether computed in yield or effort—may also be autocorrelated. A matter of statistical concern is whether a method of fitting that takes the autocorrelation into account (such as one based on time-series analysis *sensu* Box and Jenkins [1976]) might be more appropriate. Some results relevant to this question were obtained by Ludwig et al. (1988) in a study that used two different objective functions to fit production models to simulated data. The first was a total-least-squares objective function, which did not take autocorrelation into account; the second, an approximate-likelihood objective function, which did. Ludwig et al. (1988) found that the two methods produced very similar estimates; the authors concluded that the added complexity of the approximate-likelihood method was probably not warranted. In addition, the approximate-likelihood method frequently failed to converge from poor starting values. This does not mean that autocorrelation should be ignored in all fisheries modeling; however, it was not a major concern in the study cited.

Process error

The model presented here assumes that the production of biomass is a deterministic function of the current biomass; stochasticity occurs only in the observation of catch or effort or in the relation of fishing effort to fishing mortality rate (if effort is being estimated from catch). In reality, production is undoubtedly stochastic to some degree. In recognition of this, fisheries models that explicitly incorporate process error have been developed (e.g. Ludwig et al., 1988; Sullivan, 1992). Because process errors are propagated forward in time, it would seem that time-series fisheries models (e.g. production models), should include corrections for process errors, so that the system can be modeled as correctly as possible.

Despite the undeniable logic of including process error in fisheries models, there are also negative aspects, and the practical merit of including process error in fisheries applications remains a topic for research. The theory of models including process error was largely developed in process control (Kalman, 1960), a field in which large data sets are common. Including both observation error and process error in a model generally entails either estimating a large number of nuisance parameters (the process errors), making strong assumptions about the form or value of the process error component, or both. In some cases, the need to estimate additional parameters can make it difficult or impossible to estimate parameters of interest, such as MSY, without additional

Table 2

Results of two bootstrapped production model analyses loosely based on swordfish, *Xiphias gladius*, in the North Atlantic Ocean. The base model used only yield and standardized effort data. The tuned model also used a hypothetical index of abundance (Table 1). Each conventional parameter estimate is designated $\hat{\theta}$, the corresponding bias-corrected estimate is designated $\hat{\theta}_{BC}$. Nonparametric bias-corrected 80% confidence intervals are derived from the bootstrap; as with most fishery analyses, these are conditional on correct model structure and probably underestimate true uncertainty (see text). The relative interquartile (IQ) range, a unitless measure of precision, is the 50% confidence interval divided by the median bias-corrected estimate. All results are rounded to three significant digits.

Quantity estimated	Base model					Tuned model				
	$\hat{\theta}$	$\hat{\theta}_{BC}$	80% lower CL	80% upper CL	Relative IQ range	$\hat{\theta}$	$\hat{\theta}_{BC}$	80% lower CL	80% upper CL	Relative IQ range
Management benchmarks										
MSY	13,800	13,700	11,800	15,100	11.8%	13,400	13,400	11,700	14,900	11.7%
F_{MSY}	0.257	0.259	0.161	0.393	45.3%	0.264	0.269	0.169	0.432	50.9%
f_{MSY}	72.6	71.1	61.7	82.2	14.5%	68.7	68.3	0.590	0.781	14.1%
B_{MSY}	53,800	53,100	37,400	79,700	40.7%	50,900	50,000	33,600	71,900	39.6%
B_{1992}/B_{MSY}	0.932	0.929	0.755	1.17	21.8%	0.829	0.820	0.650	1.01	23.6%
F_{1991}/F_{MSY}	1.03	1.03	0.750	1.32	28.3%	1.18	1.18	0.892	1.53	29.3%
Directly estimated parameters										
r	0.514	0.517	0.323	0.785	45.3%	0.528	0.537	0.337	0.865	50.9%
K	108,000	106,000	74,800	159,000	40.7%	102,000	100,000	67,200	144,000	39.6%
q	0.00354	0.00363	0.00236	0.00541	43.3%	0.00384	0.00393	0.00260	0.00612	45.7%

information or assumptions. (For an example, see Conser et al., 1992, and Prager, 1993). This would not be a serious objection if estimates made by models without process error were known to be severely flawed, but to my knowledge the fisheries literature includes no comprehensive comparisons of equivalent models with and without process error.

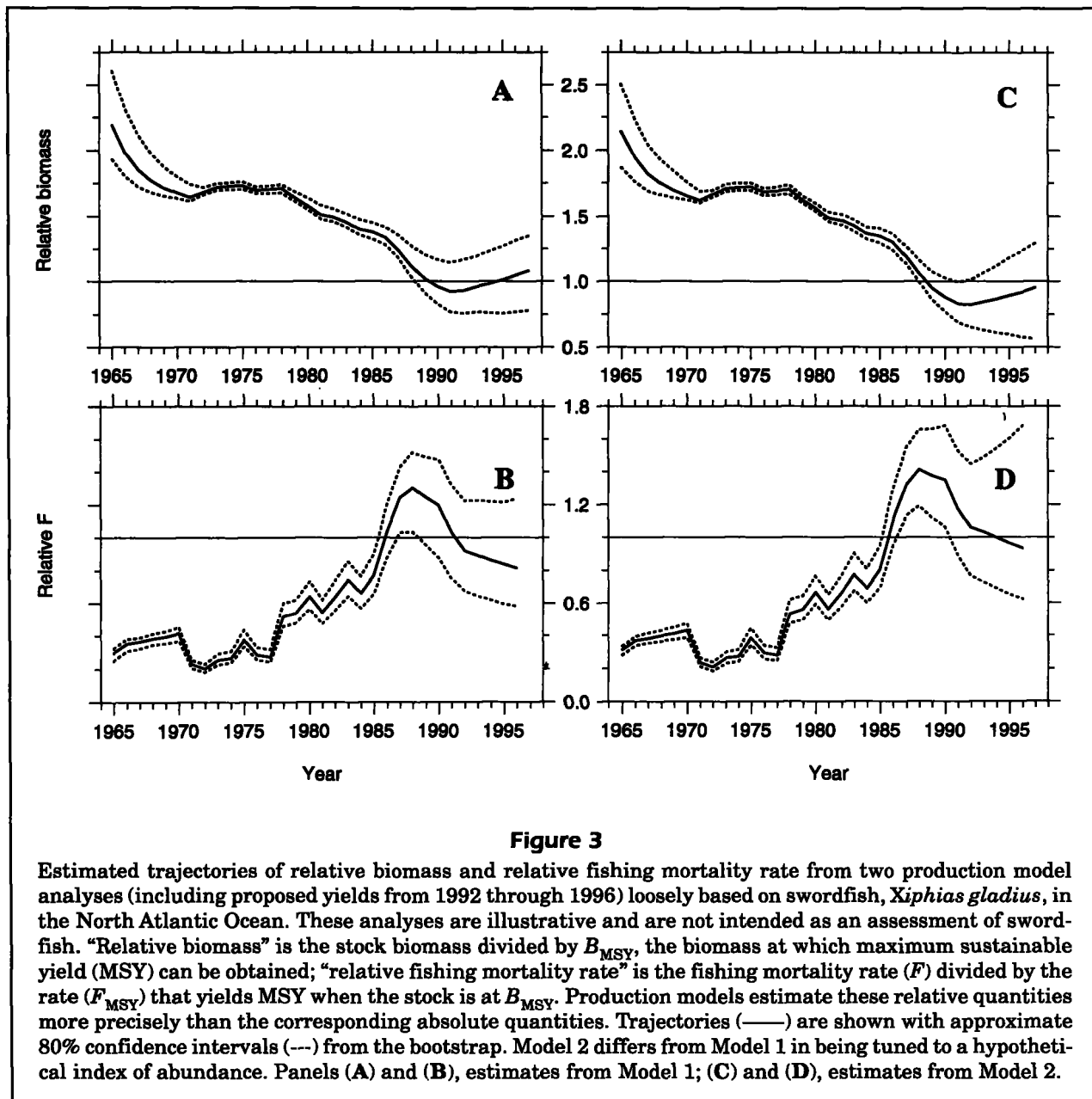
The work by Ludwig et al. (1988) does shed some light on this question, as their simulations and models included both types of error. The authors found that when observation error was ignored (its variance assumed to be zero) during parameter estimation, the resulting estimates were biased and resulted in an average loss in harvest value of at least 20%. In contrast, when the relative variance of the process error component was assumed to be half of its correct value, a substantially smaller loss in harvest value resulted. Unfortunately, Ludwig et al. (1988) did not present results for estimation under the assumption that process error was zero. Further research into estimation methods for systems with both process error and observation error would allow fishery scientists and managers to better balance complexity and accuracy in population models.

Precision of estimates

Production models tend to estimate some quantities much more precisely than others. Hilborn and Wal-

ters (1992) discuss this phenomenon at some length; the comments here reflect my own experiences. For most stocks, the main biological reference points (MSY, f_{MSY}) are estimated relatively precisely. However, absolute levels of stock biomass B_t and fishing mortality rate F_t are usually estimated much less precisely. This occurs because very few data sets contain sufficient information to estimate q well. (The example illustrates this point well—Table 2.) By dividing biomass and fishing-mortality estimates by estimates of the corresponding biological reference points, the effects of imprecision in estimating q can be removed. The relative levels thus obtained are useful measures in their own right: the relative level of biomass $\hat{B}_t / \hat{B}_{MSY}$ describes whether a population is above or below the level at which MSY can be obtained, and the relative level of fishing mortality rate $\hat{F}_t / \hat{F}_{MSY}$ suggests whether an increase or decrease in fishing effort might provide a higher sustainable yield.

When two or more catchability coefficients are estimated, ratios of catchability coefficients are typically estimated more precisely than the individual values of q . Thus it is possible to compare two different gears without being able to estimate very precisely the catchability of either one. If a parameterization involving K and r is used in fitting, the estimates of these quantities are usually quite imprecise.



cise, but because they are correlated, the corresponding estimates of MSY and optimum effort can nonetheless be quite precise.

The estimate of B_1 , the starting biomass in the first year, is usually quite imprecise even when normalized to B_{MSY} . It is also my impression that it can be biased for some data sets, although this does not significantly affect relative biomass estimates beyond the first few years. I would therefore not recommend using a production model to draw any inferences about the population biomass during the first few (perhaps 2 to 4) years, unless auxiliary information is available. Such information might comprise a biomass index (for tuning) or knowledge to support us-

ing an assumption of the type $B_1 = sK$, where s is a proportionality constant known a priori. Punt, 1990, provides an example. This indeterminacy in production modeling is similar to the inability of sequential population (age-structured) analyses to say much about population dynamics in the most recent years unless auxiliary information is used. In practice, it does not seem to degrade the estimates of MSY and optimum effort when a reasonably long time series is used.

Validity of bias corrections and confidence intervals

Bootstrap confidence intervals are approximations, and bias-correction methods can at times worsen the

approximation. DiCiccio and Tibshirani (1987) demonstrate an example in which "the BC and BC_a methods seem to pull the percentile interval in the wrong direction and hence the coverage gets worse." (The BC_a method, due to Efron [1987], incorporates a second-order correction to the BC method.) In that example, bias correction for the point estimate would also have made it worse. The example presented by DiCiccio and Tibshirani (1987) (estimating the variance of a correlation coefficient, true value 0.9, from a data set of 15 observations) seems rather extreme, but it does serve to emphasize that model results, including estimated bias corrections, must not be accepted blindly.

Confidence intervals estimated by bootstrap methods entail fewer assumptions than those made by parametric methods, but most likely are still optimistic. In a study of an econometrics equation (including a lagged term) that was fit by generalized least squares with an estimated covariance matrix, Freedman and Peters (1984) found the bootstrap estimates of standard error far superior to those made with asymptotic assumptions. The bootstrap estimates were 20% to 30% too low, but estimates from asymptotic formulas were too low by factors of almost three. One reason for underestimation by the bootstrap was that, due to the effect of fitting, the residuals used for resampling were smaller than the true values of the disturbance term (Freedman and Peters, 1984). A suggested correction is given by Stine, 1990, p. 338.

There are other reasons why estimated confidence intervals for fisheries models are likely to be optimistic. The time frame encompassed by the data used to fit fisheries models is usually short and does not encompass the full range of environmental variation that can add unexplained variation to observed data. As the time series becomes longer, the random effects of environmental variation tend to become more extreme, making earlier confidence intervals appear overly optimistic (Steele and Henderson, 1984). Another cause of optimistic confidence intervals is the use of preliminary models (e.g. ANOVA) to construct abundance indices; such models tend to filter the indices and thus reduce apparent variance. There may also be systematic errors in the data (from, e.g. gradual changes in q or gradual or sudden changes in the proportion of the catch reported); these can bias the results, but the confidence intervals include only the effects of variability, not bias from model misspecification. Schenker (1985) stated that "bootstrap confidence intervals should be used with caution in complex problems." It is probably appropriate to consider estimated confidence intervals from fisheries population models to be, in general, minimum estimates.

Is there life after death?

The concept of maximum sustainable yield was given its epitaph about 15 years ago in a critical review by Larkin (1977). Notwithstanding the title of his paper, Larkin's main target was not the concept of MSY itself, but what he called the "religion" of applying MSY dogmatically to every stock. Undoubtedly, one must recognize that MSY is not an immutable quantity, and that model results should not be used dogmatically. However, compensation in population dynamics does give rise to some form of maximum sustainable yield. Whether MSY is estimable from the data available for a given stock, and whether it is a useful concept given the stock's dynamics, are reasonable questions that, even if answered in the negative, do not invalidate the concept of MSY.

In a response to Larkin's (1977) paper, Barber (1988) pointed out that MSY, far from being dead, was still in widespread use. Barber cited the utility of MSY as a formal management objective; its simplicity and ability to be understood by the fishing industry, administrators, and managers; and the grounding of the MSY concept in basic ecological theory. He concluded by repeating Holt's (1981) suggestion that MSY be considered part of a multi-faceted management scheme.

Shortly following Larkin's (1977) paper, Sissenwine (1978) discussed several shortcomings of MSY as the basis for optimum yield (OY), the "legally mandated immediate objective of marine fisheries management in the coastal waters of the United States beyond the territorial sea of the individual states." In this section, I address those items not discussed earlier. Sissenwine pointed out that it is difficult to estimate q , and that q may vary with population size. This difficulty might be overcome, to some degree, by the methods described earlier for estimating changes in q . More importantly, this problem is not unique to production models. The common use of CPUE series to tune age-structured models also requires strong assumptions about q . Indeed, because an age-structured model generally provides little information about a cohort before it has been substantially fished, its estimate of population biomass in a year close to the present may be more influenced by random variations in q than would a similar estimate from a production model.

Sissenwine (1978) made a number of criticisms of production models fit by equilibrium assumption. The methods described here do not use the equilibrium assumption and are not subject to those problems. Once the assumption is dropped, one is much less likely to get a good, but spurious, fit, when modeling a population whose dynamics are not approximated

by the model. This is an excellent reason (but not the only one) to avoid the equilibrium assumption.

A final important point raised by Sissenwine (1978) is that, because the world is stochastic, one is truly more interested in maximum average yield (MAY) than MSY. Several studies (Doubleday, 1976; May et al., 1978; Sissenwine, 1978) have shown that in general $MAY < MSY$; thus harvesting MSY indefinitely would lead to stock collapse. This result does not make production models less useful, but does emphasize the necessity to use their results in the context of other knowledge about the stock and as part of an evolving view of stock dynamics. Fishery assessment and management are dynamic processes that must adapt to changing conditions and new knowledge. It is inconceivable that we will ever know enough about any wild stock to establish a management regime that could be effective into the indefinite future. The failure of MSY to be such a regime is no failure at all.

Notes added in proof

1 I have recently been made aware of several production-model applications that were circulated in the Collected Papers of the International Commission on Southeast Atlantic Fisheries (ICSEAF). Pertinent documents include those by Butterworth et al., 1986; Andrew et al., 1989; and Punt, 1989.

2 Anyone attempting to implement the methods described here should be aware that Equation 6, when solved for F , can be double-valued.

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