FITTING THE GENERALIZED STOCK PRODUCTION MODEL BY LEAST-SQUARES AND EQUILIBRIUM APPROXIMATION¹

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ABSTRACT

A least-squares method for fitting the generalized stock production to fishery catch and fishing effort data which utilizes the equilibrium approximation approach is described. A weighting procedure for providing improved estimates of equilibrium fishing effort and an estimator of the catchability coefficient are developed. A computer program PRODFIT for performing the calculations is presented. The utility and performance of PRODFIT is illustrated with data from a simulated pandalid shrimp population.

The production model approach to fish stock assessment is simply an adaptation of the Lotka-Volterra population equations into the situation of a population exploited by man. The earliest such adaptation was by Graham (1935) in assessing the potential production from North Sea fish stocks. The major development of this approach in fisheries management, though, is due to Schaefer (1954, 1957) who initiated it as a management tool for the yellowfin tuna fishery of the eastern tropical Pacific Ocean. While there has been an attempt at a detailed extention of the production model approach to multispecies fisheries (Lord 1971), the usual application has been on a single species stock.

Mathematical formulation of the production model begins with the general differential equation

$$dP/dt = P_t g(P_t) - P_t h(f_t)$$
(1)

where P_t is the population size at time t, $P_tg(P_t)$ is the population production function encompassing the effects of reproduction and natural mortality (and growth in weight if biomass is the population unit), and $h(f_t)$ is the fishing mortality coefficient exerted by f_t units of fishing effort. Fishing effort is assumed to be standardized from nominal fishing effort such that $qf_t = F_t$, where F_t is the instantaneous coefficient of fishing mortality and q is a constant (the catchability coefficient), giving $qf_tP_t = dC/dt$, the rate of catch. At equilibrium, that is dP/dt = 0, the catch rate equals the production rate such that an equilibrium yield, Y, is obtained

$$Y = qfP = Pg(P). \tag{2}$$

The most general assumptions about the form of $P_{tg}(P_t)$ are that it should 1) approach zero as P_t approaches some environmental capacity, P_{max} , and 2) increase to some maximum at a population size smaller than the environmentally limited size. Practically, the function should be simple, since in any case the approach is a gross simplification of population dynamics. The most flexible, simple function advanced for $P_{tg}(P_t)$ is a simple case of Bernoulli's equation (Chapman 1967; Pella and Tomlinson 1969)

$$P_t g(P_t) = H P_t^m - K P_t \tag{3}$$

where H, K, and m are constant parameters.³ Equation (3) includes the logistic function when m = 2 (Schaefer 1954, 1957) and the Gompertz function $[K'P_t - H'P_t \ln P_t]$ as $m \rightarrow 1$ (Fox 1970). Equation (3), hereafter referred to as the generalized stock production model after Pella and Tomlinson (1969), approaches, zero at P_{\max} $= (K/H)^{1/(m - 1)}$ and has a maximum $P_{\text{opt}} =$ $[m^{1/(1 - m)}] \cdot P_{\max}$.

Three equilibrium relationships can be derived by the substitution of Equation (3) in Equation (2) to obtain

1) Yield and population size

$$Y = HP^{m} - KP,$$
(4)

2) Population size and fishing effort

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Manuscript accepted May 1974. FISHERY BULLETIN: VOL. 73, NO. 1, 1975.

³When formulated as in Equation (3), H and K are positive for m < 1, but are negative for m > 1.

$$P = \left(\frac{K}{H} + \frac{q}{H}f\right)^{\frac{1}{m-1}}$$
(5)

3) Yield and fishing effort

$$Y = f\left(\frac{Kq^{m-1}}{H} + \frac{q^m}{H}f\right)^{\frac{1}{m-1}}$$
(6)

The critical points, useful as management implications and previously derived by Pella and Tomlinson (1969), are:

$$f_{\rm opt} = K \left(\frac{1}{m} - 1\right) / q \tag{7}$$

$$P_{\rm opt} = \left[K / (mH) \right]^{\overline{m-1}} \tag{8}$$

and

$$Y_{\max} = H[K/(mH)]^{\frac{m}{m-1}} - [K^{m}/(mH)]^{\frac{1}{m-1}}, (9)$$

where $f_{\rm opt}$ is the amount of fishing effort required to produce $Y_{\rm max}$, the maximum sustainable average yield (MSAY),⁴ and $P_{\rm opt}$ is the equilibrium population size obtained at $f_{\rm opt}$. Figure 1 demonstrates the flexibility of the generalized stock production model with three values for m (0.5, 2.0, 4.0); each curve has the same value for $P_{\rm max}$ and $Y_{\rm max}$.

In utilizing the production model for analysis of the status of a particular population, the usual basic assumptions are that 1) the model is being applied to a closed single unit population, 2) the concept of equilibrium conditions⁵ applies to the population under analysis, and 3) the age-groups being fished have remained, and will continue to remain, the same. If one is able to obtain data which represent equilibrium conditions at three or more population levels, then no additional assumptions are needed to fit the production model. In most fishery data sets, however, no real period of equilibrium conditions will exist. Using data from the transitional states of a population requires the additional assumptions that both 1) time lags in processes associated with population change and 2) deviations from the stable age structure at any population level have negligible effects on the production rate, $P_{tg}(P)_{t}$ (Schaefer and Beverton 1963).

Schaefer (1954, 1957) pioneered the use of transitional state data for fitting a production model (the logistic form) to catch and fishing effort data. Schaefer's (1957) method for estimating the parameters consisted of approximating differential equation (1) with two finite difference equations and then iteratively solving them. Pella and Tomlinson (1969) greatly improved upon Schaefer's method by demonstrating that a catch history of a fishery could be predicted from the fishing effort history, initial estimates of the production model parameters, and the integrated form of Equation (1). Then final parameter estimates could be obtained by a pattern search routine which finds those parameters which minimize the residual sum of squared differences between



FIGURE 1.—Equilibrium relationships of the generalized stock production model for three values of m. (A) Equilibrium yield and population size; (B) population size and fishing effort; (C) equilibrium yield and fishing effort.

 $⁴Y_{max}$ is usually referred to as the maximum sustainable yield (MSY). The term MSY, however, does not convey that in reality the yield will fluctuate due to changes in the population even if the fishing effort and catchability coefficient remain constant. Hence, the "equilibrium yield" curve represents a curve of yield that is sustainable at some average level.

⁵The definition of equilibrium adopted here, essentially that of Beverton and Holt (1957), is: given a constant rate of fishing, including zero, a population will achieve a state where, on the average, it will not change in size or characteristics.

the observed and predicted catches. While these two estimation methods are very different in their degree of sophistication, they are fundamentally the same in that both methods utilize the prediction of population transitional state changes by the production model. For convenience, this approach will be subsequently referred to as the transition prediction approach.

Gulland (1961) established a second approach to fitting production models with transitional state data. Gulland's approach estimates the level of fishing effort which, if equilibrium obtained, would produce, on the average, the observed level of catch per unit effort in each year of the fishery. Then the set of paired catches per unit effort and estimated equilibrium fishing effort units are fitted to one of the equilibrium relationships given by, or derived from, Equation (4), (5), or (6). This approach will be referred to subsequently as the equilibrium approximation approach.

Clearly, the transition prediction and equilibrium approximation approaches are basically different. The transition prediction approach is obviously intimately based upon the transition state population assumptions. On the other hand, the degree to which the equilibrium approximation approach is dependent on these assumptions is unclear. This paper presents a least-squares method and a computer program PRODFIT, which uses the equilibrium approximation approach to estimate the parameters (and indices of their variability) of the generalized stock production model. A weighting procedure for providing improved estimates of equilibrium fishing effort and an estimator of the catchability coefficient are developed. The utility and performance of computer program PRODFIT is illustrated by fitting deterministic and stochastic data from a simulated pandalid shrimp population. Some cursory comparisons between the equilibrium approximation and transition prediction approaches are made by repeating the pandalid shrimp simulated data fits with GENPROD, the computer program written by Pella and Tomlinson (1969).

FITTING METHOD

The equilibrium approximation approach was first outlined in Gulland (1961), but is more fully explained in Gulland (1969:120). Gulland's method involves relating the annual catch per unit effort in year i, U_i , to the fishing effort averaged over some number of years, T. Gulland (1961) first defined T as the mean life expectancy of an individual in the fishable population, or Z^{-1} , where Z is the instantaneous total mortality coefficient and the value of Z^{-1} is rounded off to the nearest integer. Subsequently, Gulland (1969) defined T as the average fishable duration of a year class (again to the nearest whole year)—he provided the following example: if recruitment is at 4 yr and if most of the catch in year *i* consists of 4 to 9 yr-old fish, then the average fishable duration is about 3 yr so U_i would be related to an average of f_i , f_{i-1} and f_{i-2} . The general formulation for the average fishing effort in year *i* is

$$\bar{f}_{i} = \frac{1}{T} \sum_{j=i-T+1}^{i} f_{j}$$
(7)

A discussion of the rationale for, and performance of, Gulland's averaging method is given by Gulland (1969:120).

Weighted Average Fishing Effort Method

In this paper a different tack is taken which results in approximating equilibrium fishing effort with a weighted average. The catch per unit effort of the incoming year class j in year i, U_{ij} , is related to the amount of effort in year i; that of the previous year class, $U_{i,j-1}$, is related to the fishing effort in years i and i - 1; that of the year class which entered 2 yr previously, $U_{i,j-2}$, is related to the fishing effort in years i, i - 1, and i - 2; and so forth. The catch per unit effort of the total fishable population, assuming equal catchability, is

$$U_i = U_{i,j} + U_{i,j-1} + U_{i,j-2} + \cdots + U_{i,j-k+1}$$

for k year classes. For the simplest case where the incoming year class is recruited at the beginning of each year's fishing season, therefore,

$$U_{i} \sim \{ \boldsymbol{k} \cdot f_{i} + (\boldsymbol{k} - 1) \cdot f_{i-1} + \cdots + f_{i-k+1} \}.$$
(8)

Equation (8) suggests a weighted average of fishing effort over the total number of years that a year class contributes significantly to the fishery, or

$$\overline{f_i} = \left\{ k \cdot f_i + (k-1) \cdot f_{i-1} + \cdots + f_{i-k+1} \right\} / \left\{ k + (k-1) + \cdots + 1 \right\} .$$
(9)

An arithmetic average rather than a geometric average is suggested because most applications are on catch in weight, i.e. while year classes decline exponentially in terms of numbers they concomitantly increase in terms of mean weight per individual.

The weighting procedure can be more precise if it is known when during the year of record that recruitment occurs. For example, if recruitment occurs at midseason during the year of record for a fishable population of three year classes, $\overline{f_i}$ changes from $\{3f_i + 2f_{i-1} + f_{i-2}\}$ /6 to $\{2.5f_i + 1.5f_{i-1} + 0.5f_{i-2}\}$ /4.5. Further precision is gained if k is varied from year to year with the level of fishing effort, since at high fishing rates fewer year classes will contribute significantly to the catch than at low fishing rates. Further adjustments can be made for unequal catchability among the year classes.

The unweighted method of averaging the fishing effort, Equation (7), and the new weighted method, Equation (9), will be compared in a subsequent section of this paper.

Estimation Procedure

Gulland (pers. commun.)⁶ prefers an eye-fitted curve for estimating the equilibrium relationship between U_i and f_i because of the oversimplification of the method and the errors associated with usual catch and effort data. However, these reasons should not defer the seeking of a more precise method of fitting a curve nor the taking advantage of error estimation schemes, if the simplifications and assumptions are kept in mind. On the contrary, it will be demonstrated that, at least for some controlled conditions, the equilibrium approximation approach provides reasonably good results.

Equation (5) may be written in terms of catch per unit effort and averaged fishing effort as

$$U_{i} = \left[(Kq^{m-1} / H) + (q^{m} / H) \overline{f}_{i} \right]^{1/(m-1)}$$
(10)

or simply

$$U_i = (\alpha + \beta \overline{f_i})^{1/(m-1)}.$$
(11)

Equation (11) is a nonlinear function with three parameters which does not require simultaneous estimation of the catchability coefficient, q. The

critical points in terms of the parameters of Equation (11) are

$$f_{\rm opt} = (\alpha - \alpha m) / (m\beta)$$
(12)

$$U_{\rm opt} = (\alpha/m)^{1/(m-1)}$$
(13)

and

$$Y_{\max} = \frac{(\alpha - \alpha m) (\alpha / m)}{m \beta}^{1/(m-1)}$$
(14)

Given the data set $\{U_i, \overline{f_i}\}$, where i = 1...nobservations, the least-squares criterion for estimating the parameters α , β , and m is to minimize the function

$$S = \sum_{i=1}^{n} W_{i} (\mathbf{U}_{i} - \hat{\mathbf{U}}_{i})^{2}$$
(15)

where the W_i are statistical weights, and \hat{U}_i are the predicted equilibrium catches per unit effort from Equation (11). The statistical weights,

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$$W_i = (\hat{U}_i)^{-2},$$
 (16)

are derived from the assumption of the multiplicative error structure as suggested by Fox (1971). Weighting as in Equation (16) will usually give the greatest weight to observations at the highest level of averaged fishing effort; in many cases these also will be the most recent observations. Giving greater weight to observations at high effort levels will tend to give the greatest weight to observations with the greatest temporal and spatial coverage of the population. In addition, giving the greatest weight to the most recent data is especially advantageous when approaching the $Y_{\rm max}$ level during a period increasing fishing effort because the observations nearest the $Y_{\rm max}$ level receive the greatest weight.

Up to now no mention has been made on the estimation of the catchability coefficient, q. This is because experience with GENPROD and stochastic simulation studies have indicated that poor results are frequently obtained from the simultaneous estimation of q (Pella and Tomlinson 1969; Fox 1971). Once that α , β , and m have been estimated, q may be treated as a conditional probabilistic variable and estimated as a mean value. Two tacks were selected, the difference method and the integral method.

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The difference method involves writing Equation (1) as a finite difference equation for the production model in terms of catch per unit effort and the estimates for α . β , and m as

$$\frac{1}{q}\frac{\Delta U_i}{\Delta t} = \frac{1}{\hat{\beta}} U_i^{\dot{m}} - \frac{\hat{\alpha}}{\hat{\beta}} U_i - f_i U_i$$
(17)

for each year $i; \Delta t$ is taken as one unit, Equation (17) is divided through by U_i , summed over the n - 2 yr that ΔU_i can be estimated, and then solved for \hat{q}_S ,

$$\hat{q}_{S} = \left[\sum_{i=2}^{n-1} \frac{\Delta \hat{U}_{i}}{U_{i}}\right] / \left[\frac{1}{\hat{\beta}}\sum_{i=2}^{n-1} U_{i}^{\hat{m}-1} - (n-2)\frac{\hat{\alpha}}{\hat{\beta}} - \sum_{i=2}^{n-1} f_{i}\right]$$
(18)

where

$$\Delta \hat{U}_i = (U_{i+1} - U_{i-1})/2.$$
(19)

This method has provided reasonable estimates with the logistic (m = 2) and Gompertz $(m \rightarrow 1)$ forms of the production model for several fisheries (Fox 1970).

Pella and Tomlinson (1969) observed that Equation (19) can be a poor estimator of the change in stock size during year i under certain circumstances. The integral method avoids this problem by writing Equation (17) as a differential equation

$$\frac{dU}{U(-\frac{\hat{\alpha}}{\hat{\beta}} - f^* + \frac{1}{\hat{\beta}} U^{\dot{m}-1})} = q \ dt, \qquad (20)$$

where f^* , the effective effort having been exerted between years *i* and *i* +1, is estimated by

$$\hat{f}^* = (f_i + f_{i+1})/2.$$
 (21)

The integral of Equation (20) after rearranging some terms is

$$\hat{\mathbf{q}}_{i} = \ln[|(zU_{i}^{1-\hat{m}} + \frac{1}{\hat{\beta}})/(zU_{i}^{1-\hat{m}} + \frac{1}{\hat{\beta}})|]/(z\hat{m} - z) (22)$$

where

$$z = -\hat{\alpha}/\hat{\beta} - \hat{f}^*.$$

The fact that Equation (22), as an estimator of q, gives negative values when the stock changes in one direction, depending on whether m is greater or less than 1, is remedied by taking the absolute value of q. Also, since q is constrained against being less than zero, the geometric mean will probably be a better estimator than the arithmetic

mean (this will be demonstrated to be so in at least one case), such that

$$\hat{q}_{I} = e^{\sum_{i=1}^{n-1} \ln |\hat{q}_{i}|/(n-1)}$$
(23)

becomes the integral estimator.

Variability Measures

Some measure of the variability of the parameter estimates can be made using the "delta" method (Deming 1943). If S is the weighted residual sum of squares for the final parameter estimates, a variability index matrix, V, is computed by

$$V = (X'WX)^{-1}S/(n-3)$$
(24)

where W is an n by n diagonal matrix of the statistical weights, X is an n by 3-parameter matrix of first partial derivatives of Equation (11) with respect to each parameter (given in the Appendix). The diagonal elements of V are variability indices of the parameter estimates and the off-diagonal elements of V are covariability indices. Since Equation (11) is nonlinear, the independent variable is not without error, the errors in the dependent variable are correlated, and the statistical weights are random variables, it is virtually impossible to make probability statements about the accuracy of the parameter estimates (Draper and Smith 1966). However, V gives some index of the variability inherent in the data which is useful largely for comparative purposes between different fisheries and data sets. For convenience, an error index may be formulated as

$$E_{\chi} = [100 \sqrt{V(\hat{X})}]/\hat{\chi}$$
 (25)

where \hat{X} is the estimated parameter and $V(\hat{X})$ is its corresponding variability index. Variability and error indices of Y_{\max}, f_{opt} , and U_{opt} also may be computed by the "delta" method (see Appendix) and the elements of V (Equation 24).

Program PRODFIT

A computer program PRODFIT, in FORTRAN IV language, was written to perform the calculations described above. A brief description of the program's options and mode of operation is given below.

DATA INPUT OPTION. Option 1.- A catch

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and fishing effort history, $\{C_i, f_i\}$, of $i = 1 \dots n$ years length and a vector of significant year class numbers $\{k_i\}$ are read in. There may be embedded zeros, if they are true zeros and do not simply reflect a lack of information. The only real problem with unreal zeros, however, occurs in the estimation of q. The catch per unit effort vector is computed internally and the averaged fishing effort vector is computed by Equation (9) with SUBROUTINE AVEFF.

Option 2.—If one wishes to compute the averaged fishing effort vector by another method or if data are obtained which represent equilibrium conditions, then this option is selected and the vectors of catch per unit effort and averaged (or equilibrium) fishing effort $\{U_i, f_i\}$ are read in directly. No estimate of q can be made, however.

STARTING VALUES OPTION. Option 1.— Initial estimates of the parameters are computed in SUBROUTINE INEST and the user provides the starting estimate for m, either 0, 1, or 2. Option 2.—Occasionally the data are so variable that INEST does not provide compatible starting values for the parameters. In this case, or in any case, the user may opt to enter directly all the initial parameter estimates.

MODEL OPTION. The user may allow PROD-FIT to estimate m to any desired precision. Frequently, however, the data are so variable that no significant reduction in the residual sum of squares is obtained by varying m. The user then has the option to fix m at 2, the logistic model (Schaefer 1957); at 1, the Gompertz model (Fox 1970); or at 0, the asymptotic yield model.

WEIGHTING OPTION. The user may select the statistical weights as Equation (16) or may choose to not weight the observations, i.e., $W_i = 1$ for all *i*.

CATCHABILITY COEFFICIENT. The catchability coefficient, q, is estimated by Equation (22), but both the geometric and arithmetic averages are computed.

Program PRODFIT uses an adaptation of the same pattern search optimization routine, MIN, as contained in GENPROD (Pella and Tomlinson 1969) to locate the least-squares parameter estimates. A more sophisticated Taylor series approach (Draper and Smith 1966) was attempted initially, but severe distortion of the sum-ofsquares space prevented reasonable convergence. In order to facilitate termination of the searching procedure, the sum-of-squares space is searched with m and a transformation of the parameters α and β to

$$U_{\max} = \alpha^{1/(m-1)}$$
(26)

$$Y_{\max} = \frac{(\alpha - \alpha m)(\alpha/m)^{1/(m-1)}}{m\beta}$$
(27)

where U_{\max} is the unexploited population size in terms of catch per unit effort. Neither U_{\max} nor Y_{\max} change greatly with moderate changes in m.

The output of PRODFIT provides a listing of the input data, the transformed data, initial parameter estimates, the iterative solution steps, the final estimates of α , β , and m and their variability indices, the management implications of the final model U_{max} , U_{opt} , f_{opt} , and Y_{max} and their variability indices, the observed and predicted values and error terms, and estimates of the catchability coefficient, q.

A listing of program PRODFIT and a user's guide are available on request from the author.

COMPARATIVE EXAMPLES OF THE EQUILIBRIUM APPROXIMATION METHODS

Two methods of averaging fishing effort which attempt to approximate equilibrium conditions have been presented, the unweighted method (Equation 7) and the new weighted method (Equation 9). In order to compare these two methods, catch histories for a simulated pandalid shrimp fishery (Fox 1972) were generated using a generalized exploited population simulation model GXPOPS (Fox 1973). It should be noted, however, that the comparisons are, for the most part, simply illustrative. It is virtually impossible to demonstrate conclusively which is the better method because there is an infinite choice of life histories, parameter values, fishing effort histories, and stochastic variation representations.

Equilibrium values for the unexploited population biomass in terms of catch per unit effort (U_{\max}) , the maximum equilibrium yield (Y_{\max}) , and optimum fishing effort (f_{opt}) , were determined empirically by running the simulation model FOX: FITTING THE GENERALIZED STOCK PRODUCTION MODEL

(Table 1). The catchability coefficient, q, was assumed to be 1.0. Figure 2 presents the equilibrium values of catch per unit effort and yield at fishing effort values ranging from 0.0 to 1.3 for the simulated shrimp population. Above f = 1.3 the population level did not stabilize in 25 yr of simulation and at f = 2.0 the population was definitely extinguished. The equilibrium data for f = 0.0 to 1.3 were fit to the generalized stock production model with PRODFIT to illustrate the obtainable degree of correspondence. The generalized stock production model very closely approximates the equilibrium values for the simulated pandalid

TABLE 1.—Empirical management implications for the simulated pandalid shrimp population and those estimated for the generalized stock production model with PRODFIT.



FIGURE 2.—Fit of the generalized stock production model (line) to simulated equilibrium values (circles) of (A) catch per unit effort and (B) yield by computer program PRODFIT. Shaded areas represent nonequilibrium.

shrimp population being slightly low in the range of f = 0.7 to 1.1 and slightly high beyond f = 1.1 (Figure 2). The estimated parameters are also very close (Table 1).

The problem which confronts a fishery scientist is to estimate the parameters of Table 1, hence the equilibrium relationship of Figure 2, from catch and fishing effort data representing transitional rather than equilibrium states. To illustrate the efficacy of the equilibrium approximation approach and to provide a comparison between the two fishing effort averaging methods, a 12-yr fishing effort history was selected which approximates the rapid expansion of fishing for Pandalus borealis in Ugak Bay, Alaska. Exploiting the simulated shrimp population with the fishing effort history produced the catch and catch per unit effort history in Figure 3. Two comparisons were made, the first using the deterministic data shown in Figure 3 and the second introducing some random error.

Deterministic Comparison

The appropriate averaging time, k, for the weighted average method is four since the fishable part of the simulated shrimp population consists of four significant year classes. The appropriate averaging time, T, for the unweighted average method is 2 since the average duration of the fishable phase is 2 yr. The results of fitting the



FIGURE 3.—Catch (dots) and catch per unit effort (circles) calculated with a fishing effort history (triangles) from the simulated pandalid shrimp population.

12-vr catch and fishing effort history by both methods for a range of averaging times are given in Table 2. Examination of the appropriate row for each method in Table 2 clearly reveals that for this example the superior estimates were produced by the weighted average method. In fact, the maximum error among the weighted average estimates of m, Y_{max} , and U_{max} (the parameters used in searching for the least-squares solution) at k = 4 is only 1%.

The effect of different averaging times on the estimates of the parameters m, Y_{max} , and U_{max} is the same for both effort averaging methods. By increasing the averaging time, the estimates of mand Y_{max} decrease and the estimate of U_{max} increases. The residual sum of squares is minimum at the appropriate averaging time for the weighted method (i.e. at k = 4). For the unweighted method, however, the minimum residual sum of squares is at 1 yr greater than the appropriate criterion.

Another way of comparing the weighted and unweighted averaging methods is to examine how well they estimated the equilibrium fishing effort. The equilibrium fishing effort was computed for each year's observed catch per unit effort (Figure 3), using the production model fitted to the equilibrium data (Table 1) for interpolation. The estimated equilibrium fishing effort by the weighted average method was closest in 10 of the 12 yr and had a mean absolute error of less than one-third of the unweighted method (Table 3).

Estimates of the catchability coefficient, q, by the integral method, Equation (22), -geometric and arithmetic means-and the difference

TABLE 2.- Empirical and estimated parameters for the simulated pandalid shrimp catch history using the equilibrium approximation approach and two methods of averaging fishing effort.

Method	Averaging time (k or T)	ŵ	Ŷmax	Û _{max}	'ĝ	Mean squared error
Empirical	_	²0.60	5.60	17.96	1.00	-
Weighted	1	1.16	7.26	17,63	0.42	1.3830
average	2	1.35	6.48	17.61	0.62	0.3293
fishing	3	0.86	6.02	17.82	0.88	0.0686
effort ³	44	0.60	5.67	17.97	0.87	0.0500
	5	0.53	5.21	18.01	0.75	0.0913
	6	0.51	4.76	18.02	0.62	0.1236
Unweighted	1	1.16	7.26	17,63	0.42	1.3830
average	42	1.09	6.17	17.69	0.70	0.1323
fishing	3	0.35	6.10	18.07	1,12	0.0529
efforts	4	0.28	5.36	18.14	0.69	0.2797

¹Integral method, geometric mean ²Estimated, Table 1.

⁴Stuation (9); Program PRODFIT, unweighted estimates option.
 ⁴Appropriate averaging time.
 ⁵Equation (7); Program PRODFIT, unweighted estimates option.

TABLE 3.-Comparison of two estimates of equilibrium fishing effort for the simulated pandalid shrimp population catch history

Equilibrium		Weig	ghted estimate ¹	Unweighted average estimate ²		
Year	effort ³	Effort	Error	Effort	Error	
1	0.0000	0.0000	-0.0000	0.0000	-0.0000	
2	0.0072	0.0116	-0.0044	0.0145	-0.0073	
3	0.0109	0.0099	0.0010	0.0160	-0.0051	
4	0.0412	0.0515	-0.0103	0.0575	-0.0163	
5	0.0897	0.0891	0.0006	0.1210	-0.0313	
6	0.0896	0.0801	0.0095	0.0680	0.0016	
7	0.0692	0.0726	-0.0034	0.0500	0.0192	
8	0.1327	0.1516	0.0189	0.1685	-0.0358	
9	0.4031	0.4195	-0.0164	0.5405	-0.1374	
10	0.7461	0.7094	0.0367	0.9090	~0.1629	
11	0.7800	0.7887	-0.0087	0.8785	-0.0985	
12	0.9356	1.0025	-0.0669	0.9905	-0.0549	
Mean a	absolute error		0.0147		0.0475	
'Eau	ation (9): k = 4					

²Equation (7); T = 2. ³Calculated from Table 1 parameters.

method, Equation (18), for the weighted (k = 4)and unweighted (T = 2) fishing effort averaging techniques are given in Table 4. The best estimator within either effort averaging method was the integral method's geometric mean, with the weighted average fishing effort method being closest to the assumed value, 1.0.

Stochastic Comparison

In the deterministic comparison, the catch and fishing effort data were known precisely, the catch per unit effort was always exactly proportional to the average population size, and the population did not fluctuate. However, the stochastic nature of population processes, temporal and spatial changes in the availability and vulnerability of the population to fishing, and the use of sample data to represent an entire fishery all introduce considerable variability in real catch and effort data. Under the assumption that the component sources of variability are independent and random variables with constant expected values and variances, an approximation of the overall variability

TABLE 4.—Estimates of the catchability coefficient, q, by three methods for the weighted and unweighted fishing effort averaging techniques. Actual value of q is 1.0.

	Integral		
Effort averaging method	Geometric mean	Arithmetic mean	Difference method ²
Weighted 73	0.8684	1.1949	1.3283
Unweighted 74	0.6978	1.3558	2.6606

quation ²Equation (22) ²Equation (18)

³Equation (9); k = 4 ⁴Equation (7); T = 2

FOX: FITTING THE GENERALIZED STOCK PRODUCTION MODEL

TABLE 5.--- Empirical and estimated parameters for the five replicated stochastic catch histories using the equilibrium approximation approach and two methods of averaging fishing effort.

Method	Replicate	ŵ	Ýmax	Ûmax	'ĝ	Mean squared error
Empirical		²0.60	5.60	17.96	1.00	³ 0.0100
Weighted	1	1.03	5.80	17.49	0.53	0.0136
average	2	0.00	8.65	18.99	1.56	0.0107
fishing	3	0.60	5.73	17.97	0.87	0.0083
effort	4	1.04	5.07	18.68	0.95	0.0047
	5	0.24	6.68	18.40	1.13	0.0145
	Mean	0.58	6.39	18.30	1.01	0.0104
	⁵SEx	0.21	0.62	0.26	0.17	0.0018
Unweighted	1	2.19	6.70	17.10	0.65	0.0110
average	2	0.44	6.64	18.62	1.74	0.0130
fishing	3	1.41	6.27	17.54	0.90	0.0100
efforte	4	2.17	6.45	18.06	0.89	0.0095
	5	1.34	6.26	17.79	0.95	0.0117
	Mean	1.51	6.46	17.82	1.03	0.0110
	SEx	0.32	0.09	0.25	0.19	0.0006

¹Integral method, geometric mean ²Estimate, Table 1.

Assumed value. 4Equation (9); k = 4; Program PRODFIT, weighted estimates option. 9Standard error of the mean. 4Equation (7); T = 2; Program PRODFIT, weighted estimates option.



FIGURE 4.-Results (dots) of five stochastic simulated catch trials for the equilibrium approximation approach to fitting the generalized stock production model with the weighted averaging method. Circles are the true values.

structure is the multiplicative error model (Fox 1971)

$$C_i = C_i^* \cdot \epsilon_i \tag{28}$$

where C_i is the observed catch in year i, C_i^* is the expected catch, and ϵ_i is a random variable with an expected value of 1 and standard deviation σ . In practice, however, the ϵ_i are usually correlated because some (or all) of the component sources of variability do not meet the assumptions.

An ideal (i.e., in the sense that the ϵ_i are independent and random) error structure was chosen to illustrate the estimation ability of the two equilibrium approximation methods, because the "true" error structure of any given population and fishery is unique and largely unknown. Five independent sets of 12 pseudorandom, normally distributed variables, δ , as with an expectation of zero and a standard deviation of 0.1 were produced with the Library Subroutine RAND (University of Washington Computer Center, Seattle). The sets of δ 's were used to produce five stochastic catch data sets from the deterministic catch history (Figure 3) and Equation (28), with ϵ_i defined as $1 + \delta_i$.

The results of fitting the five replicate sets of catch and effort data by the weighted (Equation 9) and unweighted (Equation 7) averaging methods are given in Table 5. The effects of even moderate variability on the parameter estimates for both averaging methods are apparent. On the average, two $(m \text{ and } Y_{\max})$ of the three determining parameters $(m, Y_{max}, and U_{max})$ are closer to the empirical values for the weighted effort averaging method. The important observation, however, is that all the unweighted estimates of Y_{max} fall above the empirical value and that the average over the five replicates is significantly different from the empirical value with probability greater than 0.999.

Plots of the empirical equilibrium yields and those determined from the generalized stock production model parameters estimated by the weighted average method are compared in Figure 4. Equilibrium yield, for the most part, is estimated reasonably well in each replicate for the range of estimated "equilibrium" fishing effort, 0.0 to 1.0 (Table 3). The exception is replicate 4 where the empirical equilibrium yield is substantially underestimated above f = 0.8. Beyond the range of data, f = 1.0 to 1.3, the equilibrium yield is estimated reasonably well on the average, but not individually. None of the fitted models, of course, reveal that there is no equilibrium yield in the range of f = 1.6 to 2.0 for the simulated shrimp population (Figure 2).

Table 6 provides a comparison of the catchability coefficient estimates by three techniques for each fishing effort averaging method. Clearly the best estimates were produced by the geometric mean for the integral method, with the mean estimate by the weighted average fishing effort procedure being slightly better than that of the unweighted average procedure.

COMPARATIVE EXAMPLES OF THE EQUILIBRIUM APPROXIMATION **AND TRANSITION PREDICTION** APPROACHES

Computer program GENPROD (Pella and Tomlinson 1969) was employed to fit the deterministic and stochastic catch and effort histories of the simulated shrimp to compare the results of the transition prediction and equilibrium approximation approaches. The reader is cautioned, as in the previous section, that these results are largely illustrative and should not be misconstrued as being valid for all cases in which a production model may be employed.

Deterministic Comparison

The comparison of equilibrium parameters in Table 7 reveals that the equilibrium approximation approach provided estimates that were closer to all the empirical values except m, where the two approaches estimated the same value as the empirical equilibrium fit. GENPROD estimated parameters which predicted the simulated catch history (Figure 3) extremely well-the largest error was only 0.05, the sum of squared errors was 0.00659, and the R statistic, a measure of improvement in the fit over simply using the mean catch as a predictor (Pella and Tomlinson 1969), was 0.99994. Utilizing the empirical equilibrium parameters in the generalized production model, however, resulted in a poorer, but still good, prediction of the transition state catches-the maximum error was 0.50, the sum of squared errors was 0.48515, and the R statistic was 0.99544. Apparently due to failure of the assumptions regarding population lag and age structure shifts or problems with precision in the numerical integration, the accuracy of some equilibrium parameter estimates by the transition prediction approach

TABLE 6.—Estimates of the catchability coefficient, q, from the five replicated stochastic catch histories by three methods for the weighted and unweighted fishing effort averaging procedures. Actual value of q is 1.0.

Effort averaging method	Estimation method	Mean ĝ	Range of <i>q</i>
Weighted F1	Integral method ²		
0	Geometric mean	1.008	0.53-1.56
	Arithmetic mean	1.660	1.27-2.41
	Difference method ³	1.503	1.35-1.77
Unweighted 74	Integral method		
5	Geometric mean	1.028	0.65-1.74
	Arithmetic mean	1.546	1.12-2.11
	Difference method	4.459	2.22-10.47

²Equation (22). ³Equation (18). ⁴Equation (7); T = 2.

were sacrificed in order to reduce the sum of squared errors by nearly 99%.

Stochastic Comparison

The results of fitting the five replicate stochastic catch histories by the equilibrium approximation and transition prediction approaches are given in Table 8. Of the four common parameters $(m, Y_{max},$ U_{\max} , and q), the equilibrium approximation approach estimates were closer to the empirical values of m, Y_{max} , and q, both on the average and for most of the replicates. The transition prediction approach estimates were closer, on the average, to the empirical value for U_{max} . The transition prediction approach provided one extremely poor estimate of q (replicate 3) and all replicate estimates are above the empirical value-the latter phenomenon could be related to the accuracy of the numerical integration scheme in GENPROD (Fox 1971). The additional parameter required by GENPROD, the ratio of the initial to unexploited population size (P_0/P_{max}) , was estimated very well.

There is considerable variability in the estimates of the most frequently desired parameter, Y_{max} , by either approach (Table 8) in spite of assuming an ideal error structure (independent,

TABLE 7.-Empirical and estimated parameters for the simulated pandalid shrimp catch history using the equilibrium approximation and transition prediction approaches

Approach	ŵ	Ŷ _{max}	Û max	ĝ	P ₀ /P _{max}
Empirical	10.60	5.60	17.96	1.00	1.00
Equilibrium approximation ²	0.60	5.67	17.97	0.87	
Transition prediction ³	0.60	5.92	17.69	1.32	1.16

Estimated, Table 1. ²Program PRODFIT, k = 4, unweighted estimates option. ³Program GENPROD, KK = 3, DEL = 3, unweighted estimates.

TABLE 8.—Empirical and estimated parameters for the five replicated stochastic catch histories using the equilibrium approximation and transition prediction approaches.

Method	Replicate	ŵ	Ŷ _{max}	Û _{max}	â	P ₀ /P _{max}	Mean squared error
Empirical	_	10.60	5.60	17.96	1.00	1.000	²0.0100
Equilibrium	1	1.03	5.80	17.49	0.53		0.0136
approximation approach ³	2	0.00	8.65	18.9 9	1.56	_	0.0107
	3	0.60	5.73	17.97	0.87	-	0.0083
	4	1.04	5.07	18.68	0.95	_	0.0047
	5	0.24	6.68	18.40	1.13	_	0.0145
	Mean	0.58	6.39	18.30	1.01	_	0.0104
	⁴SEx	0.21	0.62	0.26	0.17	-	0.0018
Transition	1	1.7	5.81	17.72	1.34	0.738	0.0105
prediction approach ⁵	2	0.0	9.09	18.15	1.18	1.095	0.0131
	3	2.1	6.69	17.29	3.97	1.211	0.0086
	4	1.7	5.26	17.83	1.40	1.313	0.0053
	5	0.0	9.34	19.21	1.52	0.797	0.0126
	Mean	1.10	7.24	18.04	1.88	1.031	0.0100
	SEx	0.45	0.84	0.32	0.52	0.113	0.0014

¹Estimated, Table 1. ²Assumed value. ³Program PRODFIT; k = 4, weighted estimates option. ⁴Standard error of the mean. ⁵Program GENPROD; KK = 3, DEL = 3, weighted estimates. The program was modified slightly from the version of Pella and Tomlinson (1969) by replacing f_{opt} with Y_{max} as one of the determining parameters to allow fitting the case where m = 0 (i.e. $f_{opt} = x$ at $m \ge 0$). Identical solutions were obtained for the remaining three cases with either version.

random and with constant expectation and variance), the observed catch being within 20% of the expected catch with probability 0.95, and the fishing effort being known without error. The maximum error for the equilibrium approximation approach was +54% (replicate 2) and for the transition prediction approach was +67% (replicate 5). The problem with these maximum errors (as well as an additional replicate of the transition prediction approach) was estimating m as 0.0, where Y_{\max} occurs at infinite fishing effort. It is not unreasonable, however, to obtain $\hat{m} = 0.0$ since the data series is so short and the best value for m is about 0.60. Considering these results and the true relationship between yield and effort (Figure 2) it would be prudent to adopt an alternative *m* estimation strategy for short data series.

Alternative strategies which could be adopted for short data series are 1) to consistently assume one of the special cases of the generalized stock production model, either the logistic form (m = 2)or the Gompertz form $(m \rightarrow 1)$, or 2) fit both special cases and select the one with the least sum of squared errors. Table 9 presents the parameters estimated by the two approaches through fixing the value for m at 1 (actually 1.001) and 2. For comparative purposes, the results of these alternative strategies are summarized in Table 10. Fixing m at 1 or 2 resulted in average estimates of $Y_{\rm max}$ nearer the empirical value with less variability than obtained by allowing m to be freely estimated for both the equilibrium approximation

and transition prediction approaches. The empirical value of m is 0.6; hence assuming $m \rightarrow 1$ produced estimates nearer the empirical value of Y_{max} than assuming m = 2. For any given data set, however, one could not determine a priori which value of *m* to assume. The strategy of fitting both $m \rightarrow 1$ and m = 2 and then selecting that which provided the least-squares parameter estimates worked very well in comparison with freely estimating m under three criteria: 1) more accurate average estimate, 2) smaller average percentage error, and 3) smaller maximum overestimate. Comparing the equilibrium approximation and transition prediction approaches with the same three criteria reveals that the equilibrium approximation approach was superior [1) 0.5% vs. 5.2%, 2) 3.6% vs. 8.5%, and 3) 3.6% vs. 18.4%)].

DISCUSSION

The simple, illustrative calculations on the simulated pandalid shrimp population, of course, did not determine which of the approaches was better for general use in fitting the generalized stock production model. However, some additional guidance can be gained through examining some of their relative weaknesses with regard to the number of data points and the number of parameters they require.

The moving average of fishing effort in the equilibrium approximation approach results in the exclusion of points at the beginning of the data TABLE 9.—Estimated parameters for the five replicated stochastic catch histories using the equilibrium approximation and transition prediction approaches for fixed estimates of m.

Method	m	Replicate	Ŷ _{max}	Û _{max}	ĝ	P ₀ /P _{max}	Mean squared error
Equilibrium	1	1	5.80	17.51	0.54	_	0.0136
approximation		2	5.63	17.99	1.36		0.0155
approach ¹		3	5.56	17.66	0.99		0.0087
		4	5.05	18.72	0.92	_	0.0048
		5	5.78	17.73	0.95		0.0166
		Mean	5.57	17.92	0.96	_	0.0118
	2	1	6.27	16.73	0.29	_	0.0182
		2	6.27	17.17	1.14		0.0267
		3	6.06	16.92	0.88	_	0.0139
		4	5.86	17.65	0.77	_	0.0115
		5	6.35	16.94	1.19	-	0.0260
		Mean	6.16	17.08	0.85	—	0.0193
Transition	1	1	5.44	18.18	1.10	0.778	0.0107
prediction		2	6.00	18.16	1.79	1.014	0.0170
approach ²		3	6.39	17.81	2.97	1.058	0.0096
		4	4.66	18.08	1.07	1.162	0.0058
		5	6.10	18.40	1.87	0.715	0.0142
		Mean	5.72	18.13	1.76	0.945	0.0115
	2	1	5.95	17.61	1.38	0.720	0.0107
		2	6.47	17.83	2.40	0.962	0.0201
		3	6.63	17.37	3.62	1.210	0.0084
		4	5.30	17.73	1.35	1.361	0.0051
		5	6.51	17.89	2.29	0.604	0.0165
		Mean	6.17	17.69	2.21	0.971	0.0122

¹Program PRODFIT: k = 4, weighted estimates option. ²Program GENPROD; KK = 3, DEL = 5, weighted estimates

TABLE 10.—Summary of Y_{max} estimates by alternative strategies with the equilibrium approximation and transition prediction approaches for five replicated stochastic catch histories. Empirical value of Y_{max} is 5.60.

Method/strategy	Ŷ _{max} Mean	Standard error of mean	Average percentage error	Range
Equilibrium approximation approach1				
1. Estimate m	6.39	0.62	17.8	5.07-8.65
2. Assume $m \rightarrow 1$	5.57	0.14	3.6	5.05-5.80
3. Assume m = 2	6.16	0.09	10.0	5.86-6.35
 Least-squares, m = 1 or 2 	5.57	0.14	3.6	5.05-5.80
Transition prediction approach ²				
1. Estimate m	7.24	0.84	31.7	5.26-9.34
2. Assume $m \rightarrow 1$	5.72	0.31	10.0	4.66-6.39
3. Assume m = 2	6.17	0.25	12.4	5.30-6.63
4. Least-squares, $m = 1$ or 2	5.89	0.24	8.5	5.30-6.63

¹Program PRODFIT. ²Program GENPROD.

set unless either there was no fishing prior to the first record of the set or some information is available on the approximate level of catch and effort. One should check carefully to ensure that critical points (those being the only points at high, low, or intermediate levels of fishing) are not excluded or that the fitted model does not deviate greatly from where they might reasonably be expected to lie. If fishing effort was reasonably constant or negligible prior to the first record, dummy data of length k - 1 can be employed to allow use of the first few data points. Also, since the average fishable duration, T, is less than the number of significant fishable year classes, k, the unweighted averaging method will result in fewer data being excluded In any case, the sensitivity of the parameter estimates to alternative averaging times should be explored.

No data points are excluded with the transition prediction approach, a positive factor which should be considered even if one is satisfied with the parameter estimates obtained with the equilibrium approximation approach. On the other hand, the transition prediction approach utilizes five parameters while the equilibrium approximation approach utilizes only three, so that with few significant year classes in the fishable population there is little difference between the required number of data points. For example, the transition prediction approach statistically requires six points, while the equilibrium approximation approach with four significant year classes will require, in general, seven points. With a large number of significant year classes in the fishable population or a relatively high age at first capture, however, the major concern for either approach is the likelihood of failure of the transition state population assumptions.

The results summarized in Table 7 illustrate a general shortcoming in simultaneously estimating a large number of parameters, i.e. large deviations from model can be statistically reduced in a least-squares estimation procedure at the expense of the accuracy of certain "desired" parameters. The transition prediction approach, fitting a "free-form" type of curve with five parameters, is relatively more susceptible than the equilibrium approximation approach which fits a monotonically decreasing curve with only three parameters. On the other hand, estimates from the equilibrium approximation approach can be very sensitive to the placement of one data point in certain cases (e.g., a data point at an intermediate level of fishing with clusters of points at both low and high levels of fishing).

Utilizing the production model approach for assessing the effects of exploitation presents significant problems in addition to choice of the parameter estimation procedure or the length of the data series. These additional problems are 1) maintaining a constant catchability coefficient throughout the data series, 2) assessing the effects of changes in the constitution of the fishery, and 3) assessing the effects of time lags in population production processes.

The basic components of the overall effective catchability coefficient are 1) the relative efficiency of various types and classes of fishing gear and 2) the manner in which the gear is employed relative to the availability and vulnerability of the population, and its subunits, to capture. Heterogeneity in the efficiency of various gear classes, or vessels, within a fishing season can be alleviated by adjusting for their estimated relative fishing powers-currently the best method for estimating fishing power is by analysis of variance with the computer program FPOW (Berude and Abramson 1972). The major problem remaining, however, is adjusting for among-year changes in efficiency of the standard gear. Rothschild (1970) discussed and provided examples of problems associated with changes in the catchability

coefficient related to areal deployment of the fishing gear. The expansion of fishing across a gradient of population density will increase or decrease the effective catchability coefficient depending on the direction of the density gradient and fishing expansion. Year-to-year shifts in the population location and density relative to the fishing effort deployment also could likewise create trends in the catchability coefficient. Age-specific differences in the catchability would cause shifting of the overall effective catchability coefficient with changes in fishing effort. For example, if the catchability of fish declined with age, then the overall effective catchability of the fishable population would increase with increasing fishing effort since the relative proportion of younger age groups would most likely increase.

Alterations in the constitution of the fishery probably are the most difficult problems to overcome satisfactorily. Expansion of the fishery across several stocks, either independent or with some mixing, can result in rather large shifts in the productivity estimates (Joseph 1970; Inter-American Tropical Tuna Commission 1972). Changes in the relative levels of fishing effort exerted by different gear types which exploit different age groups of the population, either voluntarily or through a change in minimum size limit regulations, can similarly have significant impact on the shape of the production model curve (Lenarz et al. 1974). The latter problem identifies a major shortcoming of the production model approach; i.e., the impact on total yield by altering the selectivity of fishing gear can not be assessed a priori without considerable additional information.

The effects of time lags in population production processes (e.g., reproduction, growth, and mortality, both density-independent and densitydependent) can result in either overestimation or underestimation of the population productivity, or in population cycling which may never result in reaching an equilibrium state (Wangersky and Cunningham 1957; Walter 1973).

In summary, both the equilibrium approximation and the transition prediction fitting methods are useful, one or the other more so under conditions outlined above. Application of the production model to catch and fishing effort data is relatively simple, the primary virtue of the approach. The interpretation of the results and the formulation of advice for managing the resource, however, can be extraordinarily complicated by a variety of factors. Therefore, the proper perspective of production model analysis is that it is little more than a regression model, yet very useful for making "first estimate" projections of the relationship between the level of exploitation and expected equilibrium yield.

ACKNOWLEDGMENTS

Douglas G. Chapman and Gerald J. Paulik of the University of Washington, Seattle, and Brian J. Rothschild of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif. reviewed an early manuscript and offered useful suggestions for improvement.

LITERATURE CITED

- BERUDE, C. L., AND N. J. ABRAMSON.
 - 1972. Relative fishing power, CDC 6600, FORTRAN IV. Trans. Am. Fish. Soc. 101:133.

BEVERTON, R. J. H., AND S. J. HOLT.

- 1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. 2, 19, 533 p. CHAPMAN, D. G.
- 1967. Statistical problems in the optimum utilization of fisheries resources. Int. Stat. Inst., Bull. 42(1):268-290.
- DEMING, W. E. 1943. Statistical adjustment of data. John Wiley & Sons, N.Y., 261 p.
- DRAPER, N. R., AND H. SMITH.
 - 1966. Applied regression analysis. John Wiley & Sons, N.Y., 407 p.
- Fox, W. W., Jr.
 - 1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish Soc. 99:80-88.
 - 1971. Random variability and parameter estimation for the generalized production model. Fish. Bull., U.S. 69:569-580.
 - 1972. Dynamics of exploited pandalid shrimps and an evaluation of management models. Ph.D. Thesis, Univ. Washington, Seattle, 223 p.
 - 1973. A general life history exploited population simulator with pandalid shrimp as an example. Fish. Bull., U.S. 71:1019-1028.

GRAHAM, M.

- 1935. Modern theory of exploiting a fishery, and application to North Sea trawling. J. Cons. 10:264-274. GULLAND. J. A.
 - 1961. Fishing and the stocks of fish at Iceland. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. 2, 23(4), 52 p.
 1969. Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO (Food Agric. Organ. U.N.) Man. Fish. Sci. 4, 154 p.

INTER-AMERICAN TROPICAL TUNA COMMISSION.

1972. Annual report of the Inter-American Tropical Tuna Commission, 1971, 129 p.

Joseph, J.

- 1970. Management of tropical tunas in the eastern Pacific Ocean. Trans. Am. Fish. Soc. 99:629-648.
- LENARZ, W. H., W. W. FOX, JR., G. T. SAKAGAWA, AND
- B. J. ROTHSCHILD.
- 1974. An examination of the yield per recruit basis for a minimum size regulation for Atlantic yellowfin tuna, *Thunnus albacares*. Fish. Bull., U.S. 72:37-61.

LORD, G.

1971. Optimum steady state exploitation of a multispecies population with predator-prey interactions. Univ. Wash., Fish. Res. Inst., Cent. Quant. Sci. For. Fish. Wildl., Quant. Sci. Pap. 29, 8 p.

Pella, J. J., and P. K. Tomlinson.

1969. A generalized stock production model. Inter-Am. Trop. Tuna Comm., Bull. 13:419-496.

ROTHSCHILD, B. J.

1970. A systems view of fishery management with some notes on the tuna fisheries. Univ. Wash., Cent. Quant. Sci. For. Fish. Wildl., Quant. Sci. Pap. 14, 78 p.

SCHAEFER, M. B.

- 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Inter-Am. Trop. Tuna Comm., Bull. 1:25-56.
- 1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 2:245-285.

SCHAEFER, M. B., AND R. J. H. BEVERTON.

1963. Fishery dynamics—their analysis and interpretation. In M. N. Hill (editor), The sea, Vol. 2, p. 464-483. John Wiley & Sons, N.Y.

WALTER, G. G.

- 1973. Delay-differential equation models for fisheries. J. Fish. Res. Board Can. 30:939-945.
- WANGERSKY, P. J., AND W. J. CUNNINGHAM.
 - 1957. Time lag in population models. Cold Spring Harbor Symp. Quant. Biol. 22:329-338.