RANDOM VARIABILITY AND PARAMETER ESTIMATION
FOR THE GENERALIZED PRODUCTION MODEL[1]

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ABSTRACT

Three alternative statistical models are proposed for estimating the parameters of the generalized production model by the method of least squares. A stochastic representation of the generalized production model is constructed and simulation (or the Monte Carlo Method) is employed to infer the effects of random variability on the variation in catch. The use of residuals examination for selecting the appropriate statistical model for least-squares estimation of the generalized production model parameters is demonstrated for the yellowfin tuna fishery in the eastern tropical Pacific Ocean. In both the simulation and actual fishery, statistical Model 3—assuming catch residual variance is proportional to the catch squared—best fulfills the assumptions of least-squares theory and should, therefore, provide the best least-square parameter estimates.

Mathematical models are powerful tools which are being used increasingly in resource management. A knowledge of mathematics allows a resource manager to construct from gathered data a representation of the real system and, coupled with statistical theory, allows estimation of the parameters of his model. Then, as is impossible in the real system, a manager may experiment on his model and derive outcomes which aid decisions about management of the real system. Results of model experimentation usually depend greatly on the formulation of the model and to some degree on the accuracy of the parameter estimates. Often precise statistical parameter estimation lags behind mathematical formulation, primarily because many mathematical models are robust, i.e., decisions are independent of parameter accuracy. This is one reason for the development of deterministic rather than stochastic models. However, it seems that it is always desirable to obtain the best possible parameter estimates from the data at hand.

A simple case of Bernoulli's equation has been suggested as a model for the growth of an organism by Richards (1959), Chapman (1961), and Taylor (1962)

$$dx/dt = Hx_t^m - Kx_t \qquad (1)$$

where x_t represents either weight or length at time t, and H, K, and m are parameters which may be given some physiological significance. Recently equation (1) has been advanced independently by Chapman (1967) and Pella and Tomlinson (1969) as a simple model for assessing the relation between exploitation and yield (or catch) from a living resource

$$dP/dt = HP_t^m - KP_t - qfP_t \qquad \text{for } m < 1$$
$$(2)$$
$$dP/dt = -HP_t^m + KP_t - qfP_t \quad \text{for } m > 1$$

where P_t is the population size (biomass or numbers), f is the amount of fishing effort, q is the coefficient of catchability, and H, K, and m are parameters. It is assumed that f is constant over the time period that equation (2) is used. Therefore, $qf = F$, the instantaneous fishing mortality coefficient, and $qfP_t = C_t$ the catch. Equation (2), referred to herein as the generalized production model after Pella and Tomlinson (1969), includes the logistic model used by

Graham (1935), Schaefer (1954, 1957), and others when $m = 2$, and the exponential model discussed by Fox (1970) if the limit is taken as $m \to 1$.

This type of production modeling is a stock assessment approach which has extreme mathematical and data requirement simplicity. Therein lies its primary virtue; for example, equation (2) contains only four parameters whereas the simplest Beverton and Holt (1957) type of model providing the same relation contains at least nine parameters. Estimation of the parameters of equation (2) requires only catch and fishing effort data while at the very least, the Beverton and Holt approach additionally requires age structure information. Discussion of the different assumptions for implementing each approach can be found in Schaefer and Beverton (1963). The generalized production model provides for a wide variety of shapes for the production curve and thus coupled with its mathematical simplicity represents an important tool for successfully managing exploitation.

Procedures for estimating the parameters of production models can be found in Schaefer (1954, 1957), Ricker (1958), Chapman, Myhre and Southward (1962), Gulland (1969), and Pella and Tomlinson (1969). However, it appears that in all cases, except Schaefer (1957), random variation about the deterministic predictions of the production model has been largely ignored in choosing a *statistical* model for estimating the parameters. Perhaps this is because of the apparent formidable nature of such variation. On the other hand, such variation may often be approximated in a simple manner to allow better estimates of the parameters than if ignored altogether. It is conceded that the generalized production model is at the very best only a good approximation of the actual biological dynamics, but this should not imply that better parameter estimates are unwarranted, unless its prime virtue of mathematical simplicity is compromised in the course of such action.

Several statistical models for estimating the parameters of mathematical models of biological relationships have been discussed variously by Zar (1968), Glass (1969), Hafley (1969), and Pienaar and Thomson (1969). While to the nonstatistician these papers may bear a strong resemblance to quibbling over apparent minor differences of results in the face of large data variability, the improper statistical model can lead to misleading conclusions or to significant errors, as several of the above authors demonstrated. Statistical models differ on the assumption about the manner in which variation or error enters the deterministic biological model. The technique employed by Pienaar and Thomson (1969) to assess fulfillment of the assumptions about variation is the graphing and examination of residuals, the differences between the observed data and those predicted by the model. Extensive discussion on the examination and analysis of residuals can be found in Anscombe (1961), Anscombe and Tukey (1963), and Draper and Smith (1966).

This paper presents a discussion of the nature of simple random variability and its relation to estimating the parameters of the generalized production model. An illustration of residuals examination in selecting the appropriate statistical model for the parameter estimating technique of Pella and Tomlinson (1969) is included. Data from the fishery for yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific Ocean were utilized in the illustration.

STATISTICAL MODELS

Schaefer (1957) recognized that the production model is not deterministic and represented environmentally induced variation as an additive term consisting of a random variable η multiplied by population size. In terms of the generalized production model

$$dP/dt = KP_t - HP_t^m - qfP_t + \eta P_t . \quad (3)$$

His parameter-estimating procedure used a finite difference approximation of equation (3) divided through by P_t for the case when $m = 2$. By summing over many time periods the effects of variation are eliminated since the expected value (or mean) of η is zero. Schaefer's formulation of the error term, while reasonable and convenient for his estimating technique, pro-

duces a complex statistical model on integrating equation (3). Therefore, his statistical model was given no further consideration.

Pella and Tomlinson (1969) also mentioned that the generalized production model is not deterministic. They pointed out several sources of error in Schaefer's finite difference approximation of population change and estimation procedure, and advanced a "least-squares" searching procedure as an alternative. In doing so, however, apparently no consideration was given to statistical implications of their technique. The Pella-Tomlinson procedure integrates equation (2) over the time period during which the fishing effort is assumed constant, Δt, to give

$$\widehat{P}_t = \left[\frac{H}{K (\pm) q f} - \left(\frac{H}{K (\pm) q f} - P_0^{1-m} \right) \right.$$

$$\left. \times e^{\mp (K (\pm) qf) (1-m) t} \right]^{\frac{1}{1-m}} \quad (4)$$

where P_0 is the population size at the beginning of the time period, and the upper signs applying when $m < 1$ and the lower when $m > 1$. Starting with initial guesses of the parameter values, an estimated catch history, $\{\widehat{C}_i\}$ where $i = 1 \ldots n$ time periods, is calculated from the known fishing effort history, $\{f_i\}$, by the formula

$$\widehat{C}_i = qf_i \cdot \sum_{j=1}^{N} \frac{1}{2} (\widehat{P}_{i,j} + \widehat{P}_{i,j+1}) \cdot \Delta t_i / N \quad (5)$$

where $\widehat{P}_{i,j}$ are found from equation (4) over $j = 1 \ldots N$ subintervals of each time interval i. The fitting criterion, S, is computed from the known catch history, $\{C_i\}$, of n time periods as

$$S = \sum_{i=1}^{n} (C_i - \widehat{C}_i)^2 = \sum_{i=1}^{n} \epsilon_i^2 \quad (6)$$

where the ϵ_i are residuals. The initial parameter guesses are then modified in a searching routine with their computer program GENPROD until those parameter values which minimize S are located.

The statistic S is a "least-squares" criterion. For the parameters of a nonlinear model which minimize S to be the *best* least-squares estimates, the residuals, ϵ_i, must: 1) be independent, 2) have an expected value (or mean) of zero, and 3) have constant variance (i.e., not correlated with t, $\widehat{C}_i$, or f_i).[3] Consequently, the proper statistical model for the Pella-Tomlinson fitting technique must both fulfill the three assumptions and be biologically rational. It is also important that the statistical model be simple, i.e., one which requires no additional parameters to be estimated.

Ignoring for the moment that equation (5) is an approximation, the choice of equation (6) as the least-squares estimate criterion tacitly assumes

$$C_i = \widehat{C}_i + \epsilon_i \quad (7)$$

giving

$$\overline{P}_i = \widehat{P}_i + (1/qf_i) \cdot \epsilon_i \quad (8)$$

where $\overline{P} = \int_0^1 P \, dt$ for ease of notation. Equation (7), referred to hereafter as statistical Model 0, is biologically tantamount to assuming random variation in population size approaches being infinitely great in an unexploited population. This denies the concept of an environmentally limited maximum population size or "carrying capacity" which is usually a foundation of the production model. Therefore, Model 0 assumed by Pella and Tomlinson is intrinsically unattractive even though it may be a reasonable approximation at intermediate exploited population levels.

There are three simple statistical models (among many) which are commonly assumed, biologically reasonable, and involve calculating S as a weighted sum of squares or from transformed data.

Model 1. Additive Error

$$\overline{P}_i = \widehat{P}_i + \epsilon_{1i} \quad (9)$$

so

$$C_i = \widehat{C}_i + (qf_i) \cdot \epsilon_{1i} \quad (10)$$

[3] Additionally, if the ϵ_i are normally distributed then it can be shown that the least-squares estimates are also the maximum likelihood estimates which have minimum variance as the number of data grows large—hence are global best estimates (e.g., see Draper and Smith, 1966).

giving

$$S_1 = \sum_{i=1}^{n} [(C_i - \widehat{C}_i)/f_i]^2 \quad (11)$$

as the appropriate criterion to be minimized.

Model 2. Multiplicative Error

$$\bar{P}_i = \widehat{P}_i \cdot \epsilon_{2i} \quad (12)$$

so

$$C_i = \widehat{C}_i \cdot \epsilon_{2i} \quad (13)$$

or

$$\ln C_i = \ln \widehat{C}_i + \ln \epsilon_{2i} \quad (14)$$

giving

$$S_2 = \sum_{i=1}^{n} (\ln C_i - \ln \widehat{C}_i)^2 \quad (15)$$

as the appropriate criterion to be minimized.

Model 3. Additive Proportional Error

$$\bar{P}_i = \widehat{P}_i + \widehat{P}_i \cdot \epsilon_{3i} \quad (16)$$

so

$$C_i = \widehat{C}_i + \widehat{C}_i \cdot \epsilon_{3i} \quad (17)$$

giving

$$S_3 = \sum_{i=1}^{n} [(C_i - \widehat{C}_i)/\widehat{C}_i]^2 \quad (18)$$

as the appropriate criterion to be minimized.

Model 1 assumes constant variation at all population levels. This is perhaps the least biologically reasonable of the three suggested alternative statistical models since it is easier to conceive that under equilibrium conditions a population will fluctuate more radically near its environmentally limited maximum size than at smaller sizes under *constant* exploitation. Model 1 is usually employed as a statistical model when variation is expected to arise from experimental or measurement error. Assuming adequate statistics of catch and fishing effort exist, it is more likely that variation will arise from environmental influences on the parameters of the model. Models 2 and 3 assume that variation in population size decreases with population size and that variation in catch increases with the size of the catch. Models 2 and 3 approximate the stochastic representation of equation (2) suggested by Pella and Tomlinson [their equation (14)]

$$dP/dt = \eta_1 [(\pm)HP_t^m (\mp) KP_t] - \eta_2 qfP_t \quad (19)$$

where η_1 and η_2 are continuous random variables.

Other statistical models obviously could be constructed, such as

$$\bar{P}_i = \widehat{P}_i + \widehat{P}_i^c \cdot \epsilon_i \quad (20)$$

where c could assume any value—Models 1 and 3 are actually special cases with $c = 0$ or 1 respectively. However, this would introduce another parameter to be estimated. The four previously described statistical models will suffice.

Returning to the point that equation (5) is a numerical approximation of integration, equations (7), (10), (13), (14), and (17) are not strictly true for the Pella-Tomlinson procedure. Accurate representations would include an additional error term due to linear approximation. However, as provided for, the linear approximation error may be reduced by increasing the value of N in equation (5). As will be demonstrated later, this error is very small in relation to the magnitude of the ϵ_i even at small values of N. The choice of N, on the other hand, can be critical to obtaining good estimates of several parameters.

We now have three alternative statistical models which fulfill the goals of simplicity and biological rationality to various degrees. It remains to be determined which of them fulfills the assumptions of least-squares theory for obtaining the best parameter estimates.

STOCHASTIC SIMULATION

An analytical solution for the appropriate statistical model is not possible since the actual causes of variability and the relationships to their effects on the generalized production model

are unknown. However, a commonly used approach, simulation (or the Monte Carlo method), may be employed to infer probable effects of variability and lead to selection of the "best" statistical model. This simulation study consisted of constructing a stochastic (or probabilistic) analogue of the generalized production model and then simulating the catches at various levels of constant fishing effort. Inferences will be drawn about the propriety of all four statistical models from residual variation produced in the catches. Also, the sensitivity of catch residual variation to parameter variation will be demonstrated.

The generalized production model can be written in a form that is more easily discussed biologically

$$dP/dt = P_t K [(P_\infty{}^{m-1} - P_t{}^{m-1}) / P_\infty{}^{m-1}] - qfP_t \qquad (21)$$

The signs (+ or —) are set for convenience assuming $m > 1$. The usual biological interpretation of the constants is as follows: K is "the intrinsic rate of natural increase", $P_\infty = (K/H)^{1/(m-1)}$ is the asymptotic environmentally limited maximum population size or "carrying capacity", and m is the determinant of the proportion of P_∞ at which the maximum rate of production occurs. The stochastic analogue of equation (21) is

$$dP/dt = P_t \kappa [(\pi^{\mu-1} - P_t{}^{\mu-1}) / \pi^{\mu-1}] - \gamma f P_t \qquad (22)$$

where $\{ \kappa, \pi, \mu, \gamma \}$ are stochastic variables with expected values (or means) $\{ K, P_\infty, m, q \}$ respectively, and distributions and variances to be specified. The parameters of equation (21) were considered to be stochastic variables since they are actually average conditions determined by many environmental inter-relationships.

The distributions and variances of the stochastic variables are unknown as are their expected values to be estimated from the fishery data. Some broad inferences about the distributions can be made, however, from biological and mathematical implications of the production model. The "intrinsic rate of natural increase",

κ, was assumed to be approximately normally distributed $[\sim N (K, \sigma^2{}_1)]$, because K is the resultant rate of a linear combination of rates—birth rate — death rate (P in numbers), or birth rate + growth rate — death rate (P in biomass) —-so may be either positive or negative at any given time. Negative values for π and γ are biologically and physically meaningless so they were assumed to be approximately log-normally distributed $[\sim \log N (P_\infty, \sigma^2{}_2)$ and $\sim \log N (q, \sigma^2{}_3)$ respectively]. The integrated forms of equations (2), (21), or (22) do not exist for $m = 1$; therefore μ was assumed to be given by $[1 + (m - 1)\xi]$ where ξ was assumed to be approximately log-normally distributed with a mean of one $[\sim \log N (1, \sigma^2{}_4)]$. This resulted in μ having a mean of m with a range of minus infinity to one, or one to plus infinity, depending on whether m is less or greater than one.

Integrating equation (22) from P_0 to P_t yields

$$\widehat{P}_t = \left\{ \pi^{1-\mu} \left(\frac{\kappa}{\kappa - \gamma f} \right) - \left[\pi^{1-\mu} \left(\frac{\kappa}{\kappa - \gamma f} \right) - P_0{}^{1-\mu} \right] e^{(\kappa - \gamma f)(1-\mu)t} \right\}^{\frac{1}{1-\mu}} ; \qquad (23)$$

this is the stochastic analogue of equation (4). Expected values and arbitrary variances $(\sigma^2{}_1, \sigma^2{}_2, \sigma^2{}_3, \sigma^2{}_4)$ were chosen to allow:

Stochastic variable	Expected value	Approximate 99% range
κ	5.60	5.30-5.90
μ	2.00	1.95-2.06
π (10^8)	1.40	1.07-1.83
γ (10^{-5})	7.00	6.63-7.39

The expected values were rounded approximate values obtained in the example following this section. In the same manner as the previously described Pella-Tomlinson technique, equations (5) and (23) were used to simulate a 48-year catch history at each of 13 levels of fishing effort. The continuous stochastic variable case was approximated by setting $N = 10$ in equation (5). At each iteration, the stochastic variables $\{ \kappa, \pi, \mu, \gamma \}$ were drawn at random from their respective probability distributions, produced

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with a random number generator by the multiplicative congruential method (subroutine RAND, University of Washington Computer Center). The variances and means of residuals and log-residuals were calculated at each fishing effort level.

The results of the simulation trials are given in Table 1. It was obvious from the formulation of equation (23) that Model 0—assuming constant residual variance—was inappropriate, the simulation trials add confirmation. Model 1—assuming residual standard deviation proportional to fishing effort—is also rejected over any moderate range of fishing effort. A close approximation, however, is obtained for $f \leqslant 22{,}000$.

Model 2—assuming constant log-residual variance—appears to be valid up to $58{,}000 \leqslant f < 65{,}000$, where a trend of increasing variance begins. The hypothesis of common log-residual variance for $f \leqslant 65{,}000$ was tested by Bartlett's t-test (Snedecor and Cochran, 1967). The result is not significant (uncorrected $\chi^2 = 7.72$, 9 df, Pr >0.50). Including the log-residual variance for $f = 70{,}000$, however, significance is approached (corrected $\chi^2 = 16.35$, 10 df, Pr <0.10).

Model 3—assuming residual standard deviation proportional to catch—fulfills the assumption about as well as Model 2. The proportional relationship between the residuals standard deviations and deterministic catch (Figure 1) appears to be different between catches given by fishing effort below and above that which pro-
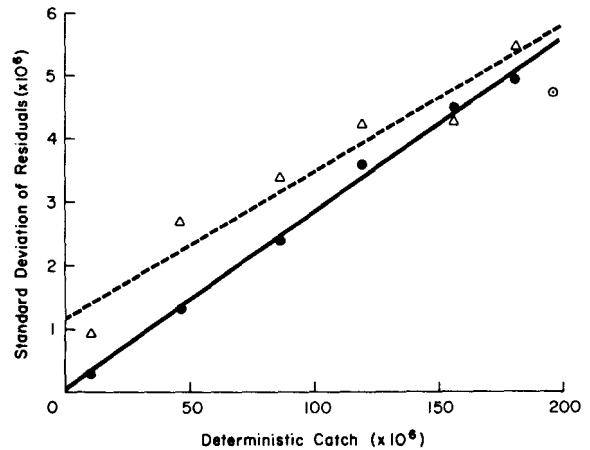

FIGURE 1.—Standard deviation of the residuals, ϵ_3, plotted against the deterministic catch, $\widehat{C}$, for statistical Model 3. $\bullet$ = fishing effort below maximum sustainable yield (MSY) level. $\triangle$ = fishing effort above MSY level. $\odot$ = fishing effort at MSY level.

duces the maximum sustainable yield (MSY) $(C = 196 \times 10^6)$. Regression analysis reveals that variance about regression, $S_{yx}{}^2$, is highly significantly different between below and above MSY levels ($F = 9.90$; 4, 4 df; Pr <0.01), but the regression coefficients, $\widehat{b}$, are not significantly different ($t = 1.47$; 5 df; Pr >0.20)—Table 2. The "above MSY" regression has a y-intercept, which must be zero, significantly different from zero ($t = 3.30$; 4 df; Pr <0.05). It appears that Model 3, like Model 2, is valid up to $58{,}000 \leqslant f < 65{,}000$ (Figure 1).

TABLE 1.—Results of the stochastic catch simulation trials of the generalized production model.

Fishing effort f	Deterministic catch (10^6) $\widehat{C}$	Deterministic population size (10^6) $\overline{P}$	Mean residual		Residual variance	
			$\overline{\epsilon}$ (10^6)	$\overline{\ln \epsilon}$ (10^{-2})	$S^2(\epsilon)$ (10^{12})	$S^2(\ln \epsilon)$ (10^{-4})
1,000	9.6775	138.25	−0.0706	−0.7765	0.0844	9.1231
5,000	45.9375	131.25	−0.0599	−0.1713	1.7538	8.3187
10,000	85.7500	122.50	0.0143	−0.0218	5.7506	7.8882
15,000	119.4375	113.75	0.2155	0.1357	13.0288	9.0945
22,000	156.3100	101.50	−0.7088	−0.4956	20.4779	8.3884
29,000	181.1775	89.25	−1.1161	−0.6551	24.6701	7.5760
40,000	196.0000	70.00	−0.6563	−0.3646	22.6228	5.9845
51,000	181.1775	50.75	0.5173	0.2404	30.1457	9.1269
58,000	156.3100	38.50	−0.1051	−0.1044	18.4686	7.6021
65,000	119.4375	26.25	0.5438	0.3927	18.1894	12.5489
70,000	85.7500	17.50	0.2865	0.2577	11.5283	15.4564
75,000	45.9375	8.75	−0.3734	−0.9846	7.2114	34.2285
79,000	9.6775	1.75	−0.2770	−3.4017	0.8834	102.6439

TABLE 2.—Regression analysis for statistical Model 3 of standard deviation of catch residuals, $S(\epsilon_3)$, on deterministic catch, $\widehat{C}$, with levels of fishing effort below and above that which produces the maximum sustainable yield (MSY).

Effort level regression	Degrees of freedom	Σx^2	Σxy	Σy^2	$\hat{b}$	Degrees of freedom	Sum of squares	$S^2 y/x$
Below MSY	5	21421.9	601.047	16.9475	0.028058	4	0.083566	0.020892
Above MSY	5	21421.9	498.146	12.4109	0.023254	4	0.826986	0.206746

In conclusion, the assumption of statistical Models 0 and 1 were rejected by the simulation study. Statistical Models 2 and 3 were found to be valid over a wide and similar range of fishing effort. Their range of validity includes up to and well beyond the level of fishing effort producing the MSY ($f = 40,000$), the most likely range in which a fishery would operate. Employing Model 3 has a theoretical advantage over Model 2 in a least-squares estimating procedure. With Model 3, the actual residual variance is minimized. Whereas with Model 2 the log-residual variance is minimized and the parameters are best least-squares estimates only in the transformed model. The theoretical advantage of Model 3 may serve as a criterion for choosing it when no other criteria exist.

Several additional simulation trials were made to demonstrate the relative degree of influence that random variability in each parameter exerts on the variance of the catch residuals. The upper two standard deviations of each stochastic variable was set equal to 25% of their mean, the level of fishing effort was set at 40,000 (MSY-producing level), and four trials of 500 time periods each were made. Each parameter in turn was allowed to vary with the remaining three constant (Table 3). The variation in catch was most sensitive to varying the exponent, m, and least sensitive to varying the catchability coefficient, q. This, of course, implies the relative precision of the parameters if they had been ac-

tual estimates. One should not, however, generalize on the order of precision since these results obtain specifically for the assumed probability distributions and expected values. This exercise does demonstrate a frequently employed method for implying which parameters, given their estimates, are most critical and perhaps deserving of additional independent estimation.

RESIDUALS EXAMINATION: AN EXAMPLE

The data of catch, catch per unit effort, and fishing effort from the eastern tropical Pacific yellowfin tuna fishery (Pella and Tomlinson, 1969; Table 6) are plotted in Figure 2. Apparently the population and fishery dynamics are
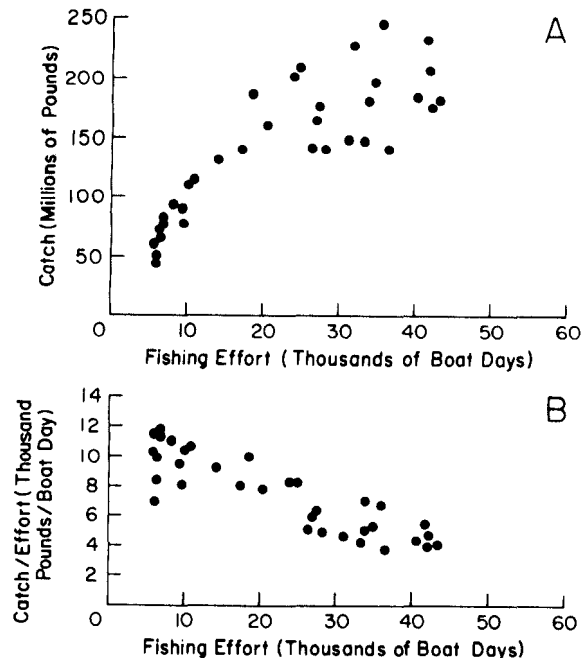
FIGURE 2.—Data from the eastern tropical Pacific yellowfin tuna fishery, 1934-67, plotted as (A) catch vs. fishing effort, and (B) catch per unit effort vs. fishing effort.

TABLE 3.—Catch residual variance produced by variation in each stochastic variable of the generalized production model.

Stochastic variable	Expected value	Approximate 95% range	Residual variance	
			$S^2(\epsilon)$ (10^{12})	$S^2(\ln \epsilon)$ (10^{-4})
μ	2.00	1.67-2.50	46.0834	11.9100
κ	5.60	4.20-7.00	36.8604	9.7958
π (10^8)	1.40	1.12-1.75	30.7556	8.1498
γ (10^{-5})	7.00	5.60-8.75	17.1333	4.4781

well described by a production model—good relationships are observed in Figure 2. These data were used by Pella and Tomlinson in exemplifying their technique; for comparative purposes the same data are utilized here. The results of this section, however, should be considered as just an example and not a recommendation on management.

The parameters of the generalized production model for the tuna fishery were estimated by the Pella-Tomlinson computer program, GENPROD, replacing the fitting criterion, S, with those of each alternative statistical model [equations (11), (15), and (18)]. Each parameter was searched to five digits or until the improvement in S was less than 0.01% at three levels of numerical approximation in equation (5)— $N = 1, 3, 5$—(Table 4). Increasing the precision of numerical approximation greatly changed the parameter estimates between $N = 1$ and 3, but only slightly between $N = 3$ and 5. The most sensitive parameter is H, followed in order by K, q, m, and r. Consequently, the estimates of the average environmentally limited maximum population size, $\bar{P}_\infty$, and average optimum population size $\bar{P}_{opt}$, vary with the level of pre-

cision. Pella and Tomlinson indicated that unreasonable estimates were obtained for the catchability coefficient, q, (presumably with $N = 1$) and made an arbitrary selection of a "reasonable" estimate. "Reasonable" catchability coefficients are obtained here with $N = 3$, making unnecessary the arbitrary selection of a reasonable estimate. The management implications of maximum equilibrium catch, C_{max}, and optimum fishing effort, f_{opt}, are surprisingly robust to the degree of precision of the numerical approximation. Schaefer (1957) mentioned previously, however, that these two management implications are robust to changes in the estimate of q in his estimating method; Pella and Tomlinson also mentioned the phenomenon for their technique. The S criteria values were reduced about 7% or less by choosing $N = 3$, as against $N = 1$ and reduced a negligible 0.2% or less by choosing $N = 5$ (S_1 and S_2 increased minutely due to the level of precision chosen for S). Obviously, the error due to approximation in equation (5), as previously stated, is negligible for these data with $N \geqslant 3$.

Turning to the effects of the alternative statistical models (with $N = 5$), it may be seen

TABLE 4.—Parameters and management implications of the generalized production model for the eastern tropical Pacific yellowfin tuna fishery, 1934-67, estimated with the Pella-Tomlinson technique (GENPROD) using four different statistical models and three levels of precision, N, in equation (5).

| Model | Parameters | | | | | Management implications | | | | $\overset{2}{S}$ Criterion |
	$\hat{m}$	$\hat{H}$ (10⁻⁵)	$\hat{K}$	¹$\hat{r}$	$\hat{q}$ (10⁻⁵)	$\bar{P}_\infty$ Pounds (10⁶)	C_{max} Pounds (10⁶)	f_{opt} Boat days	$\bar{P}_{opt}$ Pounds (10⁶)	
					$N = 1$					
20	1.4	--	--	--	45._ _	--	182.6	35,300	--	$1.78\_ .\times10^{16}$
0	1.4	2900.1	33.26	.820	27.00	44.6	182.6	35,200	19.2	1.7858×10^{16}
1	1.9	0.17064	15.21	.904	21.69	52.7	186.2	33,210	25.8	4.7140×10^{7}
2	1.6	34.502	16.65	.879	18.10	64.0	182.5	34,500	29.2	8.2214×10^{-1}
3	2.0	0.00748	7.57	.865	11.50	101.2	191.5	32,900	50.6	7.8762×10^{-1}
					$N = 3$					
0	1.5	59.999	7.65	.842	7.36	162.7	184.5	34,660	72.3	1.7197×10^{16}
1	2.2	0.00013	5.90	.921	10.00	113.0	188.6	32,200	58.6	4.5291×10^{7}
2	1.8	0.17092	5.86	.952	7.70	147.4	184.0	33,800	70.7	8.0355×10^{-1}
3	2.0	0.00408	5.59	.835	8.50	136.9	191.5	32,900	68.5	7.3769×10^{-1}
					$N = 5$					
0	1.5	55.802	7.28	.843	7.10	170.4	183.9	34,200	75.7	1.7185×10^{16}
1	2.2	0.00010	5.38	.921	9.11	124.0	188.7	32,210	64.3	4.5296×10^{7}
2	1.8	0.15820	5.61	.926	7.40	153.9	184.1	33,700	73.8	8.0371×10^{-1}
3	2.1	0.00054	5.06	.845	8.10	142.7	192.6	32,700	72.7	7.3608×10^{-1}

¹ $r = P_0/P_\infty$
² Pella and Tomlinson (1969; Table 5).

that the most sensitive estimate is H, followed in succession by the estimates of m, K, q, and r. The estimates of the management implications C_{max} and f_{opt} are, for all practical purposes, the same among statistical models, but less similar than among levels of precision. This may be offered as an argument against considering alternative statistical models. But consider the plot of the data in Figure 2; one could draw an average line by eye through the data and arrive at estimates of C_{max} and f_{opt} just as accurate as those estimated by the sophisticated least-squares search technique. The point is that with *good* data most rational statistical procedures should provide similar estimates of C_{max} and f_{opt}. One cannot be certain that this will be so with data of lesser quality or different range. The values of m which determine the shape of the yield curve, on the other hand, are very different between Models 0 and 3. This could have a significant effect on an economic analysis of the yield curve.

In the absence of other criteria for choosing a particular statistical model, the "fit"—least sum of squared residuals—is often selected (Glass, 1969), and is perhaps a reasonable criterion if the goal is interpolation. The goal here is to obtain the best possible parameter estimates in order to make, in essence, extrapolations or predictions. In the latter case the best criterion is not the "fit", but the degree of assumption fulfillment. Statistical Model 3 provided estimates that were least influenced by the addition of error—comparing the parameters' precision between N equalling 1 and 5—inferring the greatest confidence in its estimates. It was also seen from the simulation study that Model 3 best fulfilled the assumptions of a least-squares procedure. Model 3, ironically, "fits" the data the worst, although only by about 6%.

Pienaar and Thomson (1969) have suggested the utilization of an important tool for selecting a statistical model which best fulfills the assumptions of the estimating procedure—residuals examination. Various plots of the residuals suggested by Draper and Smith (1966) were made for the four statistical models (Figure 3). Each statistical model gives a mean residual near zero fulfilling one of the least-squares assumptions (Figure 3A). Plots of residuals against time (Figure 3B) indicate: 1) variation increases with time in Model 0 from 1934 through 1961, violating the assumption of constant residual variance; 2) Model 1 tends to over-correct as there is a propensity for variation to decrease from 1940 through 1967; and 3) Models 2 and 3 are nearly identical in controlling time-oriented variation. Runs—consecutive residuals of the same sign—are evident in all four models, indicating violation of the assumption of residual independence. There are only ten runs in Model 3 giving a probability less than 0.01 that the arrangement of signs is random (Figure 3B). Draper and Smith (1966) suggest, however, that unless the ratio of degrees of freedom to number of observations is small (here 29/34), the effect can be ignored. The dependence of consecutive residuals is undoubtedly due to vitiation of the assumption of no time lags in the fish population. With changes in fishing effort the age structure of the population is altered as well. It might be possible to average out these effects by considering a time period longer than one year, say the average life-span of an individual. That would be about 3 years for a yellowfin tuna, the approximate mean length of the runs. However, that would also reduce the number of observations to eleven and the fishing effort, assumed constant in integration of the model, would vary considerably.

An increase in residual variation with deterministic catch is obvious for Model 0 (Figure 3C), again violating the assumption of constant residual variance. As in the time plot, Model 1 tends to over-correct for the phenomenon exhibited by Model 0. Models 2 and 3 stabilize the variance as might be expected. In the final plot, residuals against fishing effort, the same conclusions may be reached (Figure 3D).

Models 2 and 3 apparently fulfill the assumptions of the least-squares procedure while Models 0 and 1 violate the assumption of constant residual variance. Invoking the previously mentioned criterion for choosing between Models 2 and 3, the best statistical model for this fishery is Model 3.
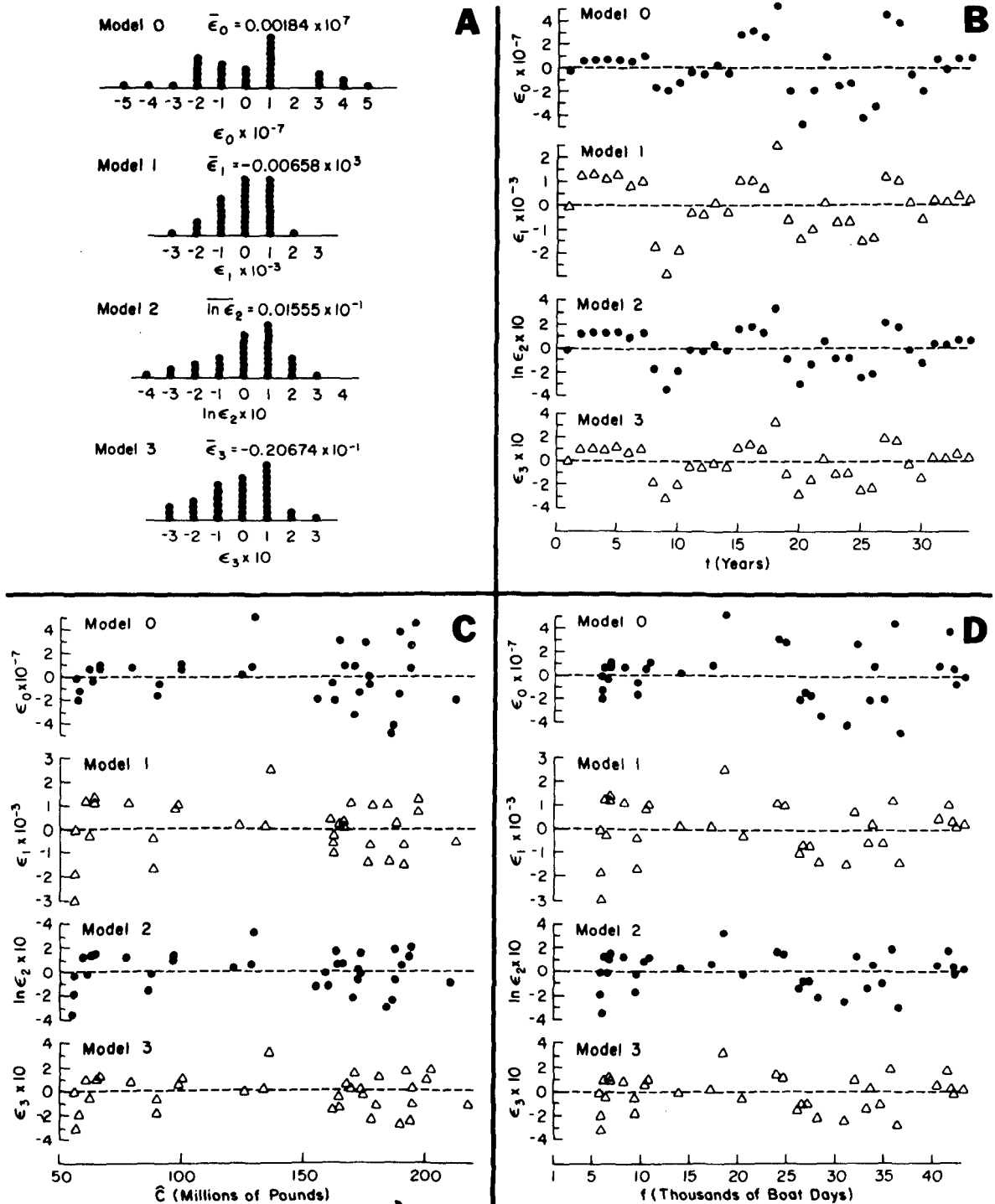
FIGURE 3.—Plots of residuals, ϵ_i, for statistical Models 0, 1, 2, 3, from the generalized production model for the eastern tropical Pacific yellowfin tuna fishery, 1934-67. A. Frequency distributions. B. Residuals against time. C. Residuals against deterministic catch, $\hat{C}_i$. D. Residuals against fishing effort, f_i.

The referee of this paper has raised an important point regarding application of the various statistical models to actual fishery data. In a non-overexploited fishery, generally, the quality and level of catch and effort values increase with time. Relatively speaking, Model 0 in this case places greater weight on more recent data than do Models 1, 2, or 3, and in the absence of any other criteria it might represent the intuitive choice. However, if the quality of the data were a more significant contributor to unequal residence variance than the statistical model, one would expect, in this case, a decrease in the residuals plotted for Model 0 against time, catch, and fishing effort in contrast to the apparent increase for the yellowfin tuna fishery (Figure 3). If one has reason to suspect a significant difference in quality of the data, as would be suggested by a decrease in the residual plots of Model 0, perhaps a solution is to partition the data at the point in time where a significant quality increase occurs. Then fit each set of data individually placing greater weight on the parameter estimates for the more recent set. The specter of the suitability of employing production models over long time periods is also raised by this point. But it is outside the scope of this paper and the reader is referred to the papers cited previously.

SUMMARY

In using a least-squares procedure for estimating parameters of a mathematical model, such as the Pella-Tomlinson technique, there are three assumptions about the residuals for obtaining the best least-squares estimates: 1) the residuals are independent, 2) the residuals have an expected value of zero, and 3) the variance of the residuals is constant (Anscombe and Tukey, 1963; Draper and Smith, 1966; Snedecor and Cochran, 1967). We have observed from the simulation study that two (of four alternative) simple statistical models which are biologically sound—Model 2 (using a logarithmic transformation) and Model 3 (weighting by the inverse of the squared deterministic catch) — fulfill the statistical assumptions for obtaining good least-squares estimates of the generalized production model parameters over a wide range of fishing effort.

On applying these four statistical models in estimating the parameters of the generalized production model for the eastern tropical Pacific yellowfin tuna fishery, residuals examination revealed that the same two statistical models, Models 2 and 3, fulfilled the least-squares estimation assumptions. Models 0 (assumed by Pella and Tomlinson, 1969) and 1 did not. Model 3 was selected as the best model since it involves the direct minimization of the actual residual variance, and is therefore considered to be theoretically superior to Model 2.

Finally, anyone using the generalized production model and the Pella-Tomlinson estimating technique should be aware of, in addition to the proper statistical model, the effect of the value of N in equation (5) on the parameter estimates.

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