Estimation of Growth and Mortality Parameters for Use in Length-Structured Stock Production Models

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Abstract

The suggestion of some authors that linear methods of fitting von Bertalanffy growth curves generate biases may be premature, at least in one case discussed here, where the direction of the observed bias is explainable by the use of a predictive instead of a functional regression. When growth parameters are needed for length-converted catch curves or length-based cohort analysis, an inverse regression (age on length) may be appropriate. This can be computed through ordinary linear regression. An estimator for the total mortality, based on mean length, is derived for use when recruitment occurs periodically rather than continuously. Surplus-production models employing total mortality as the independent variable may become tilted to the left if natural mortality is compensatory. When growth parameters are unknown, surplus production can be modelled as a function of Z/K. When available data are limited to a small portion of the surplus production curve, fitting curves by regression may give unreasonable results. In this case, one can constrain a parameter to the value of an independent estimate so that the other estimates become more reasonable.

Introduction

Surplus production modelling as a function of total instantaneous mortality Z, or as a function of Z/K, was proposed by Csirke and Caddy (1983) as an alternative to collecting and calibrating data on fishing effort. Total mortality data can be obtained in a variety of ways, the simplest of which utilize data on mean length in a sample.

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Linear Methods of Fitting Growth Curves

Vaughan and Kanciruk (1982) suggested that traditional linear methods of fitting the von Bertalanffy growth equation (e.g., the Ford-Walford plot) be abandoned in favor of nonlinear regression because of bias in the parameter estimates. If this is so, it places an added burden on fishery biologists without ready access to appropriate computer facilities. However, Vaughan and Kanciruk (1982) used an ordinary predictive linear regression instead of a functional regression line (D. Vaughan, pers. comm.). This resulted in a lower value of L_∞ and a higher value of K than if a functional line had been used. Thus, the direction of the bias observed by Vaughan and Kanciruk (1982) is explainable by the choice of regression line. Monte Carlo simulation studies are needed to see if the magnitude of the bias is accounted for by the type of regression line. Until then, it seems premature to abandon the linear methods for fitting the growth curve.

Predicting Age from Length

Estimates of the time Δt required to grow through a given length interval are needed for applications such as length-converted catch curves and length-based cohort analysis. Given unbiased estimates of the mean ages at the limits of the length interval, it follows that an unbiased estimate of the average time to grow through the interval Δt is given by the difference of the two mean ages since Δt is a linear function of two random variables. The mean age at any length L can be determined by an inverse regression of the von Bertalanffy growth equation, i.e.,

$$t = \frac{-1}{K} \log_e (1 - L/L_\infty) + eL^c \qquad \ldots 1)$$

where eL^c is a random error term which can be a function of L (if $c \neq 0$). This can be fitted by ordinary least squares linear regression if L_∞ is fixed. One can then iteratively search for the value of L_∞ which gives the best fit. Since the linearization does not involve transformation of the dependent variable, the assumed error structure is unchanged. (The same is not true when linearizing the von Bertalanffy equation by $\log_e (1 - L/L_\infty) = -Kt + Kt_o$ where t is the independent variable. In this case, assuming the error structure independent of t implies that the variability in length about age decreases with age).

To examine the importance of using equation (1) instead of the usual regression of length on age, growth parameters were estimated by both methods using nonlinear regression for two data sets from the literature (Table 1). For the butterfly fish *Chaetodon miliaris*, K and L_∞ were both about 20% lower in the regression of age on length. For the shark *Carcharhinus obscurus*, the residuals increased with the dependent variable so that weights, proportional to the square of the independent variable, were used. In this case, K was about 60% lower, and L_∞ about 5% higher in the regression of age on length than in the regression of length on age.

To see the effect of the difference in growth parameter estimates on a length-converted catch curve, an example from Pauly (1984) was recomputed using new growth parameter estimates which differed from the original estimates by the percentages mentioned above. When K and L_∞ were both decreased by about 20%, the values of Δt increased by 70% for the smallest length class to over 600% for the highest (Table 2), while the estimated value of Z changed from 1.8 to 1.0.

Table 1. Comparison of two procedures for fitting growth curves. Butterfly fish data from Pauly (1984), shark data from Hoenig (1979).

Millet-seed butterfly fish *(Chaetodon miliaris)*

Length on age	Age on length	% change[a]
K .0031 day^{-1}	K .0024 day^{-1}	−22.6
L_∞ 127 mm	L_∞ 101 mm	−20.5
t_o −30 days	t_o 6.0 days	—

Dusky shark *(Carcharhinus obscurus)*

Length on age[b]	Age on length[b]	% change[a]
K .029 $year^{-1}$	K .012 $year^{-1}$	−58.6
L_∞ 481 cm	L_∞ 502 cm	+4.4
t_o −6.9 year	t_o −6.9 year	—
Length on age[c]	**Age on length[c]**	**% change[a]**
K .035 $year^{-1}$	K .013 $year^{-1}$	−62.9
L_∞ 439 cm	L_∞ 482 cm	+9.8
t_o −6.3 year	t_o −6.4 year	—

[a]100 (2nd col.—1st col)/1st col.
[b]Regression weighted by length squared.
[c]Unweighted regression.

Table 2. Effects of different procedures for obtaining growth parameter estimates on length-converted catch curve computations. Data are for banded grouper *(Epinephelus sexfasciatus)* from Pauly (1984).

Lower class limit (cm)	N	Δt^a	Δt^b	% increase in Δt^c
4	5	.15	.26	71.5
6	29	.16	.29	76.2
8	114	.18	.33	82.1
10	161	.20	.37	89.8
12	143	.22	.44	100.5
14	118	.25	.53	115.4
16	61	.28	.67	138.2
18	50	.33	.92	178.8
20	32	.40	1.46	267.8
22	17	.50	3.83	667.7
24	4	.67	—	—
26	4	1.03	—	—

[a]Based on L_∞ = 30.9 cm; K = .51 $year^{-1}$.
[b]Based on decreasing K by 22.6% and L_∞ by 20.5%; i.e., K = .39474, L_∞ = 24.5655.
[c]% increase in Δt = 100 (2nd estimate—1st)/1st.

Estimation of Total Mortality from Mean Length When Reproduction Occurs Periodically

Methods for estimating the total instantaneous mortality rate, Z, from length-frequency data have been available since Beverton and Holt (1956) derived the formula

$$Z = \frac{K(L_\infty - \bar{L})}{\bar{L} - L'} \qquad \ldots 2)$$

where K and L_∞ are parameters of the von Bertalanffy growth equation, $\bar{L}$ is the mean length of fish above L', while L' is the lower limit of length class in which the animals are fully vulnerable to the sampling gear. This and other approaches, which assume continuous recruitment (i.e., throughout the year), were reviewed by Pauly (1983) and Hoenig et al. (1983) (see also Wetherall et al., Part I, this vol.).

When recruitment occurs once a year as a discrete event, an analogous model can be derived by equating the mean length with a function of the growth parameters and mortality rate. The method can also be used when recruitment occurs with other periodicity if the quantities are expressed in appropriate time units (see also Damm, Part I, this vol.). Thus,

$$\overline{L} = \sum_{i=t'}^{t_{max}} N_i \overline{L}_i \Big/ \sum_{i=t'}^{t_{max}} N_i$$

$$\overline{L} = \sum_{i=t'}^{t_{max}} e^{-Zi}\, \overline{L}_i \Big/ \sum_{i=t'}^{t_{max}} e^{-Zi}$$

$$= \frac{(\Sigma e^{-Zi}\, \overline{L}_i)(1 - e^{-Z})}{e^{-Zt'} - e^{-Z(t_{max}+1)}} \qquad \ldots 3)$$

where $\overline{L}_i$ is the mean length at age i, N_i is the number of animals at age i, and t' and t_{max} are the youngest and oldest ages fully represented in the sample. Note that $\overline{L}$, the sample mean, is the mean of those fish whose ages are fully represented in the sample. This implies that one should choose a left truncation point (L') that lies in a "trough" between two peaks in a length-frequency distribution.

Different growth models may be substituted for $\overline{L}_i$ in equation (3), notably the seasonally oscillating growth model of Pauly and Gaschütz (1979).

If the simple, nonoscillating von Bertalanffy growth equation is selected, one obtains

$$\overline{L} = L_\infty - \frac{L_\infty (1-e^{-Z})(e^{-t'(Z+K)} - e^{-(t_{max}+1)(Z+K)})\, e^{Kt_o}}{(1-e^{-(Z+K)})(e^{-Zt'} - e^{-Z(t_{max}+1)})} \quad .$$

Finally, if there is no reason to believe the older age groups are underrepresented, then t_{max} can be taken to be infinite and

$$\overline{L} = L_\infty - \frac{L_\infty (1-e^{-Z})\, e^{-k(t'-t_o)}}{1-e^{-(Z+K)}} \quad .$$

Rearranging this to eliminate t_o gives

$$\frac{L_\infty - L'}{L_\infty - \bar{L}} = \frac{1 - e^{-(Z + K)}}{1 - e^{-Z}}$$

which leads to the estimator

$$Z = \log_e \left(\frac{e^{-K} (\bar{L} - L_\infty) + L_\infty - L'}{\bar{L} - L'} \right) \qquad \ldots 4)$$

Using equation (2) as an approximation to (4) results in a positive bias whose severity increases in absolute and relative magnitude as L' approaches $\bar{L}$ (Table 3).

Table 3. Effect of using an estimator assuming continuous recruitment when recruitment occurs at discrete (annual) intervals. $K = 0.3\ \text{year}^{-1}$; $L_\infty = 40$ cm; $t_o = 0$ year. Table gives estimates of Z derived from equations (2) and (4).

	$L' = 10$ cm			$L' = 15$ cm			$L' = 20$ cm		
$\bar{L}$	eq. (2)	eq. (4)	% bias[a]	eq. (2)	eq. (4)	% bias[a]	eq. (2)	eq. (4)	% bias[a]
15.0	1.5	.83	80.7	—	—	—	—	—	—
20.0	.60	.42	42.9	1.20	.71	69.0	—	—	—
25.0	.30	.23	30.4	.45	.33	36.4	.90	.57	57.8
30.0	.15	.12	25	.20	.16	25	.30	.23	30.4

[a] $\% \text{ bias} = \dfrac{(\text{eq. (2)} - \text{eq. (4)}) \times 100}{\text{eq. (4)}}$

Production Modelling Using Mortality Estimates Derived from Mean Length

If natural mortality rate is compensatory, then a plot of equilibrium yield versus total mortality rate may be expected to be asymmetrical and shifted to the left. In this case, transforming the data may produce a more appropriate model (J. Caddy, pers. comm.). However, problems with parameter estimation can artificially distort the shape of a production curve.

If the Beverton-Holt mortality estimator is used when the periodic spawning model is more appropriate, the effect will be to widen the curve (Fig. 1). The estimates of MSY and natural mortality rate (the left x-axis intercept) will remain relatively unaffected but the value of Z_{opt} can be greatly overinflated. The curve will be flatter-domed making it harder to locate Z_{opt}. The value of $\bar{L}_{opt}$ will remain unchanged, however.

When growth parameter estimates are unknown, production can be modelled as a function of Z/K by simply plotting equilibrium yield versus $(L_\infty - L)/(L - L')$ (see Csirke and Caddy (1983) and Pauly (1984)). A sensitivity analysis reveals that errors in the value of L_∞ are somewhat magnified

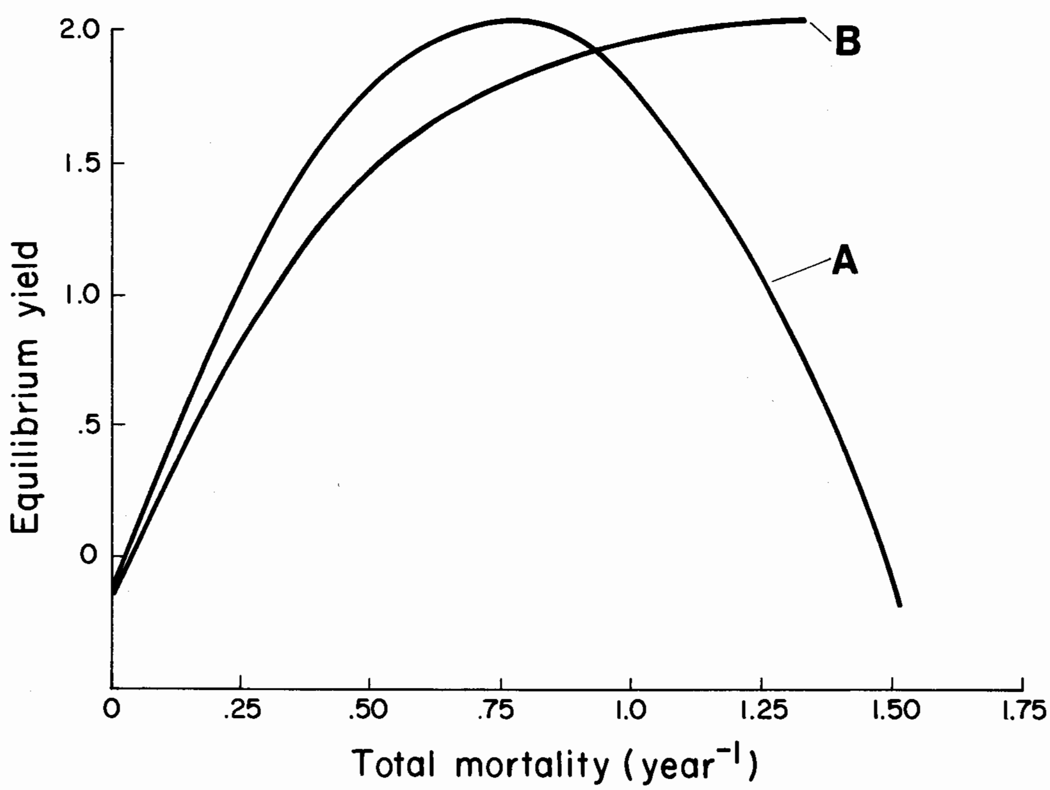

Fig. 1. Production curves generated using two models for estimating mortality. Curve A represents the model $Y_{EQ} = 4Z^2 + 6Z - .5$. Assuming that $L_\infty = 40$, $K = 0.3$ and $L' = 10$, Z values were converted to mean lengths using equation 4. Curve B was generated by converting the mean lengths back to Z values using equation (2) and represents effect of assuming recruitment to be continuous and using estimator (2) when the estimator for discrete recruitment (4) would be appropriate.

when estimating Z_{opt}/K: a 10% increase in the value of L_∞ caused an 18% increase in $(Z/K)_{opt}$ (Fig. 2).

Optimum length can be obtained from Z_{opt}/K using the relationship (Pauly 1984):

$$\frac{Z_{opt}}{K} = \frac{L_\infty - \bar{L}_{opt}}{\bar{L}_{opt} - L'}$$

Thus,

$$\bar{L}_{opt} = \frac{L_\infty + \left(\frac{Z_{opt}}{K} \cdot L'\right)}{\frac{Z_{opt}}{K} + 1}$$

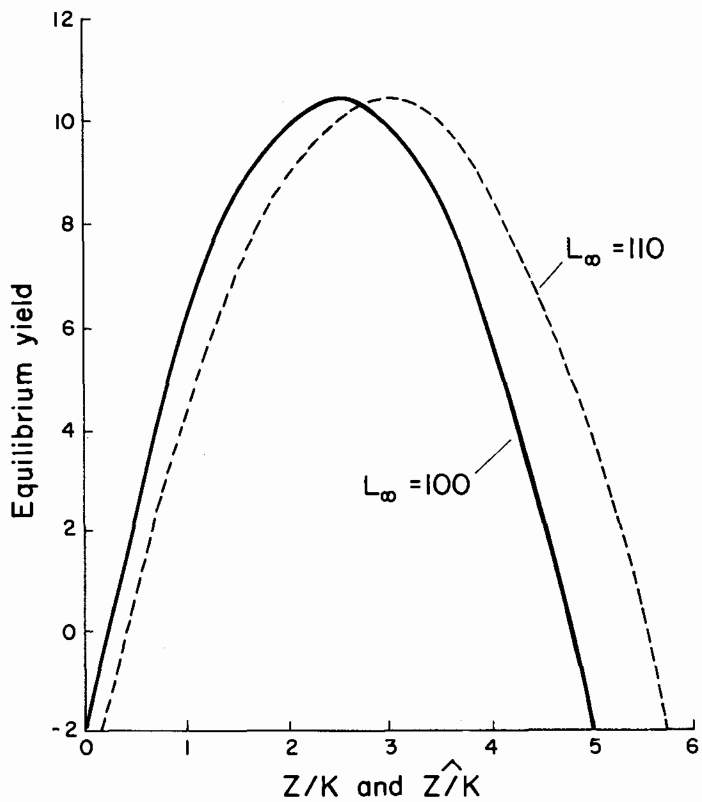

Fig. 2. Sensitivity analysis for the value of L_∞ in the relationship $Z/K = (L_\infty - \bar{L})/(\bar{L} - L')$. One curve uses a value of L_∞ which is 10% greater than the other. MSY is little affected while $(Z/K)_{opt}$ increases by about 18%.

Replacing Z_{opt} by any value of Z allows one to establish the relationship between Z (or Z/K) and the mean length of animals above L' in the catch.

When stock production data are limited or overly noisy, it may be necessary to incorporate an independently derived estimate of one parameter in the estimation procedure in order to obtain reasonable estimates of the other parameters. For example, the production curve can be constrained to have height equal to an estimate of MSY obtained independently from a comparative study. Or, the production curve can be forced to have a left X-axis intercept equal to a given value of M or M/K.

Let the production parabola be described by

$$Y = b_1 X^2 + b_2 X + b_3$$

where X denotes either Z or Z/K. The parabola has a maximum height of

$$-b_2^2 / 4b_1 + b_3$$

which will be constrained to a value of d using the method of Lagrange multipliers.

The task is to minimize

$$\Sigma (Y - b_1 X^2 - b_2 X - b_3)^2 + \lambda (-b_2{}^2 + 4b_1 b_3 - 4b_1 d)$$

where λ is a Lagrange multiplier, by setting the partial derivatives with respect to each parameter equal to zero. The resulting system of four equations can be solved simultaneously using Newton's method (Hoenig and Hoenig 1986).

Discussion

Length-based surplus production modelling is an important new tool for fisheries biologists. However, careful attention to technical details is required to avoid insidious systematic errors, which will remain undetected if a simple goodness-of-fit criterion is used to assess the validity of a model.

If an inappropriate mortality model or a poor estimate of L_∞ is used, the stock production model may be distorted in shape or shifted in location. Even so, the MSY can be estimated. If the methodology used does not change, then the fishery can be managed on the basis of the relationship between equilibrium yield and the X variable since it will remain a simple function of the true mortality rate. Difficulties arise, however, when estimates derived from such a production curve, such as Z_{opt} and M or Z_{opt}/K and M/K, are taken out of this context and used for other purposes.

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