

LIKELIHOOD METHODS FOR THE VON BERTALANFFY GROWTH CURVE

DANIEL K. KIMURA¹

ABSTRACT

Likelihood methods for the von Bertalanffy growth curve are examined under the assumption of independent, normally distributed errors. The following are examined: determining the best method of estimation, relationships between methods of estimation, failure of assumptions, constructing confidence regions, and applying likelihood ratio tests. An example is presented illustrating many of the methods discussed in theory.

The paper may be viewed as an application of classic nonlinear least squares methods to the von Bertalanffy curve. As such, the concepts discussed are generally applicable and the paper may serve as an introduction to nonlinear least squares.

Since the application of the von Bertalanffy (1938) growth curve by Beverton and Holt (1957) to the yield per recruit problem, this curve has been widely used in fisheries biology. The original curve has been generalized (Richards 1959; Chapman 1961). However, this paper will not deal with the more general Chapman-Richards growth curve. Nor will it deal with the biological motivation for these curves which have been discussed by the cited authors. Instead, I confine my study to the classic von Bertalanffy curve and examine what appears to be reasonable methods for the statistical treatment of data.

THE MODEL AND ITS MAXIMUM LIKELIHOOD ESTIMATES

I assume that age-length data are available on some species, and that the relationship between age and length can be adequately described by the von Bertalanffy growth curve. Using the usual notation, the length of the u th individual of age t_u is assumed to be

$$\begin{aligned}l_u &= l_\infty(1 - \exp(-K(t_u - t_0))) + \epsilon_u \\ &= \mu(l_\infty, K, t_0, t_u) + \epsilon_u \\ &= \mu(t_u) + \epsilon_u\end{aligned}$$

where l_∞ is asymptotic length, K a constant describing how rapidly this length is achieved, t_0 the hypothetical age at length zero, and the ϵ_u 's independent $N(0, \sigma^2)$ random variables.

For this model, parameters can best be estimated using the method of maximum likelihood. The principal reasons why maximum likelihood estimates are desirable are that under very general conditions (much more general than described here) they are consistent (converge in probability to the correct value), asymptotically normal, and asymptotically attain (except under unusual circumstances) the smallest possible variance. It will not be necessary to expand on these properties because they are among the most important results in statistics, and are discussed to some extent in virtually every book on mathematical statistics.

Letting $S(l_\infty, K, t_0) = \sum_u (l_u - \mu(l_\infty, K, t_0, t_u))^2$, the likelihood function can be written as

$$\begin{aligned}\ell(l_\infty, K, t_0, \sigma^2) \\ = (2\pi\sigma^2)^{-N/2} \exp(-S(l_\infty, K, t_0)/2\sigma^2)\end{aligned}\quad (1)$$

where N is the number of observations. Since for any given value of σ^2 , say σ_0^2 , $\ell(l_\infty, K, t_0, \sigma_0^2)$ is maximized when $S(l_\infty, K, t_0)$ is minimized, it follows that the maximum likelihood (ML) estimates of (l_∞, K, t_0) , say $(\hat{l}_\infty, \hat{K}, \hat{t}_0)$, are the least squares (LS) estimates. These estimates shall be referred to as ML or LS depending on the property which is being emphasized.

The ML estimate of σ^2 is obtained in the usual way by first taking the log likelihood, calculating the partial derivative with respect to σ^2 , and setting this result equal to zero

$$\begin{aligned}\log(\ell(l_\infty, K, t_0, \sigma^2)) \\ = -(N/2)\log(2\pi\sigma^2) - S(l_\infty, K, t_0)/2\sigma^2\end{aligned}$$

¹Washington Department of Fisheries, Olympia, WA 98504.

$$\frac{\partial \log(\ell(l_\infty, K, t_0, \sigma^2))}{\partial \sigma^2}$$

$$= -N/2\sigma^2 + S(l_\infty, K, t_0)/2(\sigma^2)^2 = 0$$

$$\hat{\sigma}^2 = S(\hat{l}_\infty, \hat{K}, \hat{t}_0)/N.$$

Thus the problem of ML estimation for the von Bertalanffy curve reduces to finding LS estimates of (l_∞, K, t_0) . Note that this is a general property of the normal error model, since no special properties of the von Bertalanffy curve have been used.

The normal equations for finding ML estimates are obtained by taking the partial derivative of $S(l_\infty, K, t_0)$ with respect to the unknown parameters and setting the results equal to zero (i.e., $\partial S/\partial l_\infty = 0$; $\partial S/\partial K = 0$; $\partial S/\partial t_0 = 0$). Because these equations do not allow a simple solution, the graphical Ford-Walford method (Ricker 1975; actually the regression of l_{t+1} on l_t) has been widely used. The Ford-Walford plot, in addition to a plot of average length at age, should be adequate for determining the age range following the von Bertalanffy curve.

For the von Bertalanffy curve, proper ML estimates can only be found using iterative algorithms. A number of authors (Stevens 1951; Tomlinson and Abramson 1961; Allen 1966) have suggested specialized algorithms. Although these algorithms may have advantages when computers are not available, the easiest way to obtain ML estimates is to use any of the general purpose nonlinear LS computer programs available in BMD (Dixon 1976), BMDP (Dixon 1977), or SPSS (Nie et al. 1975). These programs have the flexibility of allowing complicated curves to be fit to data sets, which is especially useful if differences in growth curves among different populations are to be tested statistically. For example, it might be necessary to fit different growth curves to several populations, but with the constraint that the t_0 's be equal.

It should be remembered that LS solutions obtained iteratively may be local rather than global minimizations of $S(l_\infty, K, t_0)$. With this in mind, initial values provided to any iterative procedure must represent the best available information. I recommend that the Ford-Walford method be used to calculate initial values. This guarantees that any LS solution which is obtained has smaller residual sum of squares than the Ford-Walford estimates.

LEAST SQUARES METHODS OF ESTIMATION

Under differing assumptions on the error variance, four different LS methods of estimation are appropriate. When these assumptions are met, each method provides ML estimates under the likelihood model (Equation (1)).

Let l_{ij} be the length of the j th individual of age t_i , and let \bar{l}_i and s_i^2 be the sample mean and sample variance of the lengths of individuals of age t_i , based on a sample size n_i . For each method, the assumption on the error variance and the appropriate sum of squares to be minimized when this assumption is correct, is given below.

- (a) All l_{ij} have constant variance:

$$\sum (l_{ij} - \mu(t_i))^2.$$

- (b) All \bar{l}_i have constant variance:

$$\sum (\bar{l}_i - \mu(t_i))^2.$$

- (c) The variance of l_{ij} varies with t_i , and at age t_i is equal to σ_i^2 :

$$\sum (n_i/s_i^2) (\bar{l}_i - \mu(t_i))^2.$$

- (d) All l_{ij} have constant variance (i.e., the same assumption as (a) above):

$$\sum n_i (\bar{l}_i - \mu(t_i))^2.$$

The dependent variables in methods (a) and (b) are formally of the form described by the likelihood model (Equation (1)). By this it is meant that they have constant variance, and assuming normality and independence, their likelihood is described by Equation (1). The dependent variables in methods (c) and (d) can be transformed into the form of Equation (1). This can be done by placing the weights $w_i = (n_i/s_i^2)$ (method (c)) and $w_i = n_i$ (method (d)) within the squared expressions. Doing so for method (c) gives the pseudoobservation $y_i = (\sqrt{n_i/s_i})\bar{l}_i$ with expectation $E(y_i) \approx (\sqrt{n_i/s_i})\mu(t_i)$ and variance asymptotically equal to unity (as $s_i \rightarrow \sigma_i$). Assuming normality and independence, the asymptotic likelihood of these y_i is described by Equation (1). Similarly for method (d), the pseudoobservation becomes $y_i = (\sqrt{n_i})\bar{l}_i$ with expectation $E(y_i) = (\sqrt{n_i})\mu(t_i)$ and variance σ^2 . Again assuming normality and inde-

pendence, the likelihood of these y_i is described by Equation (1). It follows that likelihood procedures applicable to unweighted methods (a) and (b) are also applicable to weighted methods (c) and (d) with few modifications. These arguments apply when fitting any function using LS estimation.

Selection of an appropriate LS method for a given problem can largely be made on the validity of the error assumption, but not solely on this basis. It is also useful to keep in mind the purpose of fitting the curve. For example, a curve fit with method (a) would do well in predicting the length of a randomly selected individual (if data were from random samples), and this property would be important in, say, modeling applications. Method (b), on the other hand, may best describe the growth of a species over its entire lifespan, a property which would be desirable when comparing growth among species. It should be noted that the practice of graphing the estimated curve and plotting average lengths observed at each age is visually biased toward method (b). Method (b) will generally look best on this type of plot.

Method (c) is appropriate when it is apparent that the variance at each age varies significantly. This assumption can be examined using Bartlett's or Cochran's tests (Dixon and Massey 1957) for the homogeneity of variance.

Method (d) is largely a computational device. In the following section it is shown that method (d) is nearly equivalent to method (a), but often requires much less computational effort.

NEAR EQUIVALENCE OF METHODS (A) AND (D)

Calculations for method (a) can be performed using method (d), with often a large savings in computational effort. It will be shown that methods (a) and (d) yield identical parameter estimates, and similar covariance matrix estimates of parameter estimates. These results are general properties of LS estimates under the assumptions of method (a), and are not dependent on the form of the function being fitted.

Identity of Parameter Estimates

For the von Bertalanffy curve using method (a), the sum of squares to be minimized is

$$S(l_\infty, K, t_0) = \sum_i \sum_j (l_{ij} - \mu(l_\infty, K, t_0, t_i))^2 .$$

The sum of squares to be minimized using method (d) is

$$S_w(l_\infty, K, t_0) = \sum_i n_i (\bar{l}_i - \mu(l_\infty, K, t_0, t_i))^2 .$$

The normal equation is derived for the parameter K say, using method (a), by taking the partial derivative of S with respect to K and setting the result equal to zero:

$$\begin{aligned} \frac{\partial S}{\partial K} &= \sum_i \sum_j -2(l_{ij} - \mu(t_i)) \mu'_K(t_i) \\ &= -\sum_i 2\mu'_K(t_i) n_i (\bar{l}_i - \mu(t_i)) = 0 . \end{aligned}$$

The normal equation is obtained for method (d) by taking the partial derivative of S_w with respect to K , yielding a result identical to that from method (a):

$$\frac{\partial S_w}{\partial K} = -\sum_i 2\mu'_K(t_i) n_i (\bar{l}_i - \mu(t_i)) = 0 .$$

Because this identity of the two normal equations is not due to any special property of K , normal equations obtained from methods (a) and (d) are identical, implying corresponding LS estimates are also identical.

Similarity of Covariance Matrix estimates

The asymptotic covariance matrix for parameters $\theta' = (\theta_1, \dots, \theta_p)$ estimated using ML theory is the inverse information matrix $I(\theta)^{-1}$ (Kendall and Stuart 1973), where $I(\theta) = (I_{ij})$,

$$I_{ij} = -E \frac{\partial^2 L(\theta, X)}{\partial \theta_i \partial \theta_j} ,$$

$L(\theta, X) = \log(\ell(\theta, X))$, and $\ell(\theta, X)$ is the likelihood function.

For nonlinear LS estimates, $I(\theta)^{-1}$ can be estimated using

$$\hat{\Sigma} = (Z'Z)^{-1} s^2$$

which is the formula used by nonlinear LS computer programs. Generally, $Z = (Z_{ij})$, where Z_{ij} is the partial derivative of the expectation of the i th observation with respect to the j th parameter

evaluated at the ML estimates, and s^2 is the mean square error.

For estimates calculated using method (a),

$$Z' = \begin{bmatrix} \frac{\partial\mu(t_1)}{\partial l_\infty} & \cdots & \frac{\partial\mu(t_1)}{\partial l_\infty} & \cdots & \frac{\partial\mu(t_I)}{\partial l_\infty} & \cdots & \frac{\partial\mu(t_I)}{\partial l_\infty} \\ \frac{\partial\mu(t_1)}{\partial K} & \cdots & \frac{\partial\mu(t_1)}{\partial K} & \cdots & \frac{\partial\mu(t_I)}{\partial K} & \cdots & \frac{\partial\mu(t_I)}{\partial K} \\ \frac{\partial\mu(t_1)}{\partial t_0} & \cdots & \frac{\partial\mu(t_1)}{\partial t_0} & \cdots & \frac{\partial\mu(t_I)}{\partial t_0} & \cdots & \frac{\partial\mu(t_I)}{\partial t_0} \end{bmatrix} \quad 3 \times N$$

evaluated at $(\hat{l}_\infty, \hat{K}, \hat{t}_0)$, with $s^2 = S(\hat{l}_\infty, \hat{K}, \hat{t}_0)/(N-3)$, $N = \sum_i n_i$ and I the number of age categories.

As was previously noted for method (d), it is often advantageous to view this model as being unweighted with transformed variables. From this point of view, $y_i = (\sqrt{n_i})\hat{l}_i$ is the dependent variable, with expectation $E(y_i) = (\sqrt{n_i})\mu(t_i)$. Under this parameterization, $\text{var}(y_i) = \sigma^2$ with

$$Z'_w = \begin{bmatrix} \sqrt{n_1} \frac{\partial\mu(t_1)}{\partial l_\infty} & \cdots & \sqrt{n_I} \frac{\partial\mu(t_I)}{\partial l_\infty} \\ \sqrt{n_1} \frac{\partial\mu(t_1)}{\partial K} & \cdots & \sqrt{n_I} \frac{\partial\mu(t_I)}{\partial K} \\ \sqrt{n_1} \frac{\partial\mu(t_1)}{\partial t_0} & \cdots & \sqrt{n_I} \frac{\partial\mu(t_I)}{\partial t_0} \end{bmatrix} \quad 3 \times I$$

again evaluated at $(\hat{l}_\infty, \hat{K}, \hat{t}_0)$, with $s_w^2 = S_w(\hat{l}_\infty, \hat{K}, \hat{t}_0)/(I-3)$.

It is easily verified that $Z'Z = Z'_w Z_w$ and, therefore, any differences in the covariance matrix estimates of parameter estimates must be due to differences in the estimates s^2 and s_w^2 of σ^2 . Although s^2 provides a better estimate than s_w^2 in terms of degrees of freedom ($N-3$ versus $I-3$), they should be similar in value, and hence it can be expected that methods (a) and (d) provide similar covariance matrix estimates of parameter estimates.

This analysis points out that good estimates of the covariance matrix of parameter estimates require having sufficient numbers of observations so that σ^2 is adequately estimated. From this point of view method (a) is superior to method (d). However, method (d) can be modified so that data are

not completely collapsed (averaged) at each value of the independent variable. Instead, data can be partitioned so that there are several dependent variable averages, and weights, at each value of the independent variable. A similar technique can be applied to method (c).

Another possibility would be to estimate σ^2 independent of the LS calculations by pooling the s_i^2 values. However, this estimate based on pure error would tend to underestimate the true σ^2 which will often contain a lack of fit component (see the following section for a discussion concerning pure error and lack of fit).

FAILURE OF ASSUMPTIONS

There are two ways in which the assumed model can fail: 1) growth may not follow the von Bertalanffy curve; or 2) error assumptions may not hold.

Failure of the von Bertalanffy Curve

Even when growth follows the von Bertalanffy curve, expected lengths at age from sample data may not. Discrepancies can be caused by bias in sampling, bias in age determination, or size selective survival in the natural population. Because samples tend to be biased toward larger individuals, age readers tend to under-age older individuals, and larger individuals of an age group tend to have better survival, these factors may bias the observed size upward for a given age.

When a number of length specimens are available at each age, a statistical measure of lack of fit (departure from the von Bertalanffy curve) can be calculated using the procedure described by Draper and Smith (1966). For this analysis, it is

necessary to assume that the error variance of individuals is constant (i.e., the variance assumption of method (a) holds). It is also important to remember that for nonlinear models (such as the von Bertalanffy curve) the procedure is not strictly valid, but is analogous to calculations valid under linear models.

The residual sum of squares calculated using method (a) can be partitioned into a pure error component (S_{pe}) and a lack of fit components (S_{lof}). Estimates of these components are

$$S_{pe} = \sum (n_i - 1) s_i^2$$

and
$$S_{lof} = S(\hat{l}_\infty, \hat{K}, \hat{t}_0) - S_{pe} .$$

For a linear model with no lack of fit,

$$\hat{F} = (S_{lof} / (I - 3)) / (S_{pe} / (N - I))$$

would have an F -distribution with $\nu_1 = I - 3$ and $\nu_2 = N - I$ degrees of freedom. While recognizing that the von Bertalanffy curve is not a linear model, this statistic may still serve as a tentative examination for lack of fit.

Even if the data show significant lack of fit, the von Bertalanffy curve may still provide the most useful growth analysis. Rejection of the von Bertalanffy curve must ultimately be based on superior alternative curves or methods of analysis.

Failure of Error Assumptions

When a number of length specimens are available at each age, parameter estimates should be robust against violations of the normality assumption. As was previously shown, estimates can be viewed as solutions to a LS problem with observations $y_i = (\sqrt{n_i}) \bar{l}_i$ which are always approximately normally distributed due to the central limit theorem.

The most likely form of heteroscedasticity is the varying of variance with age. Method (c) provides an appropriate analysis for this case.

If observations are correlated, there will be no practical remedy. Efficient estimates will generally depend on the $N \times N$ correlation matrix of errors. This matrix will generally not be estimable.

CONSTRUCTING CONFIDENCE REGIONS

For method (a), confidence regions of approxi-

mate size $1 - q$ around ML estimates $(\hat{l}_\infty, \hat{K}, \hat{t}_0)$ can be constructed using the relationship

$$\begin{aligned} S(l_\infty, K, t_0) &= S(\hat{l}_\infty, \hat{K}, \hat{t}_0) \left[1 + \frac{3}{N-3} F(3, N-3, 1-q) \right] \\ &= c_q \text{ (Draper and Smith 1966)} \end{aligned}$$

where $F(3, N-3, 1-q)$ is the $(1-q)$ th percentile of the F -distribution with $\nu_1 = 3$ and $\nu_2 = N-3$ degrees of freedom. That is, values of (l_∞, K, t_0) which satisfy $S(l_\infty, K, t_0) = c_q$ form a three-dimensional surface enclosing the true value of (l_∞, K, t_0) with approximate probability $1 - q$. The probability level would be exactly $1 - q$ if the growth model was linear, but for nonlinear models (such as the von Bertalanffy curve) this value is only approximated. Although methods exist which provide confidence regions with exact values for q (Hartley 1964), such methods are inferior to that of Draper and Smith in that they: 1) have a degree of arbitrariness in the selection of a region, 2) do not follow contours of equal likelihood, and 3) are more complex to apply.

The relationship defining a contour is

$$S(l_\infty, K, t_0) - c_q = 0$$

where $S(l_\infty, K, t_0)$

$$\begin{aligned} &= \sum_u [l_u^2 - 2l_\infty l_u (1 - \exp(-K(t_u - t_0))) \\ &\quad + l_\infty^2 (1 - \exp(-K(t_u - t_0)))^2] \end{aligned}$$

and $c_q = S(\hat{l}_\infty, \hat{K}, \hat{t}_0) \left[1 + \frac{3}{N-3} F(3, N-3, 1-q) \right] .$

Therefore, $S(l_\infty, K, t_0) - c_q = A l_\infty^2 + B l_\infty + C$

where $A = \sum_u (1 - \exp(-K(t_u - t_0)))^2$

$$B = -2 \sum_u l_u (1 - \exp(-K(t_u - t_0)))$$

and $C = \sum_u l_u^2 - c_q .$

Solutions exist for the three-dimensional contour problem whenever $B^2 - 4AC \geq 0$.

Points on the three-dimensional contour are easily calculated by conditioning on a value for t_0 , and calculating the two-dimensional cross section (l_∞, K) by stepping through plausible values for K , and when $B^2 - 4AC \geq 0$, calculating $l_\infty = (-B \pm \sqrt{B^2 - 4AC}) / (2A)$. By varying t_0 also, this algorithm will generate the entire three-dimensional confidence region.

Although points on the contour surface are easily calculated, the fact that three parameters are involved in the von Bertalanffy curve greatly limits the usefulness of confidence regions. This is due to the simple fact that three-dimensional regions are difficult to display.

The simplest solution to this problem is to condition on \hat{t}_0 , and graph the resulting two-dimensional cross section (l_∞, K). It must be remembered that this region is not a true confidence region since more extreme values of (l_∞, K) may occur at a different value of t_0 . Thus this procedure will give only a rough idea of our confidence in the estimates (\hat{l}_∞, \hat{K}). A more time consuming solution is to graph a series of cross sections, or possibly a three-dimensional graph.

If method (b) is used to estimate parameters, the analysis follows as in method (a), by simply replacing l_u with \bar{l}_u and N with I .

If weighted methods (c) or (d) is used to estimate parameters, confidence regions are defined by the relationship

$$S_w(l_\infty, K, t_0) = S_w(\bar{l}_\infty, \bar{K}, \hat{t}_0) \left[1 + \frac{3}{I-3} F(3, I-3, 1-q) \right] = c'_q.$$

Computations proceed as in the unweighted case, but with

$$A_w = \sum_u w_u (1 - \exp(-K(t_u - t_0)))^2,$$

$$B_w = -2 \sum_u w_u \bar{l}_u (1 - \exp(-K(t_u - t_0)))$$

$$\text{and } C_w = \sum_u w_u \bar{l}_u^2 - c'_q.$$

For method (c) $w_u = n_u / s_u^2$, and for method (d) $w_u = n_u$.

APPLYING LIKELIHOOD RATIO TESTS

Likelihood ratio (LR) tests provide a general

method for the statistical comparison of growth curves. It is a well-known and often exploited fact that once a general probability model has been specified (Ω), hypothesis tests of linear constraints on parameters in this model can be derived using the LR criterion. Alternatively viewed, linear constraints on parameters in Ω imply a simplified model ω . Tests of linear constraints on Ω are thus equivalent to testing ω against Ω .

The LR criterion can be used on the single sample problem, when it is desired to test whether a sample came from a population with some "known" values for any or all of the parameters (l_∞, K, t_0); or for the multisample problem comparing von Bertalanffy curves in different populations. The first problem will be solved by the simplest application of theory derived mainly in the context of the second problem. When a single parameter is being tested in the one or two sample problem, it makes good sense to simply use a Z -statistic (since ML estimates are asymptotically normal) and forego the more extensive calculations required for LR tests. One advantage that the Z test has over the LR test for the two sample problem is that σ^2 does not need to be equal in the two populations.

Consider I different populations each following the von Bertalanffy curve with parameters ($l_{\infty i}, K_i, t_{0i}$), $i = 1, \dots, I$. These populations would typically be the same species in different habitats, males and females, etc. Let l_{ij} be the length of the j th observation in the i th population, of age t_{ij} , $j = 1, \dots, n_i$, $N = \sum_i n_i$, with variance σ^2 independent of i . Note that the meaning of subscripts has been changed from what was used in previous sections.

Letting $S(l_\infty, K, t_0) = \sum_i \sum_j (l_{ij} - \mu(l_{\infty i}, K_i, t_{0i}, t_{ij}))^2$, the likelihood function under (Ω) can be written as

$$\ell(l_\infty, K, t_0, \sigma^2) = (2\pi\sigma^2)^{-N/2} \exp(-S(l_\infty, K, t_0) / 2\sigma^2)$$

where $l_\infty = (l_{\infty 1}, \dots, l_{\infty I})$,

$K = (K_1, \dots, K_I)$,

and $t_0 = (t_{01}, \dots, t_{0I})$.

Although the above parameterization is appropriate for unweighted methods (a) and (b), the reader can verify that no additional problems arise using weighted methods (c) and (d).

Previously, it was shown that likelihood functions of the form $\ell(l_\infty, K, t_0, \sigma^2)$ are maximized by LS estimates ($\hat{l}_\infty, \hat{K}, \hat{t}_0$), with the ML estimate of σ^2 being

$$\hat{\sigma}^2 = S(\hat{l}_\infty, \hat{K}, \hat{t}_0)/N.$$

This is true whether or not there are any linear constraints placed on the parameters being estimated. Substituting $\hat{\sigma}^2$ into $\ell(l_\infty, K, t_0, \sigma^2)$ yields the maximum value of the likelihood function

$$\max (\ell(l_\infty, K, t_0, \sigma^2)) = (2\pi\hat{\sigma}^2)^{-N/2} \exp(-N/2).$$

The LR for the hypothesis

H_ω : that the parameters (l_∞, K, t_0) satisfy some set of r linear constraints, say R

against the alternative

H_Ω : that the parameters (l_∞, K, t_0) possibly satisfy no linear constraints

$$\max (\ell(l_\infty, K, t_0, \sigma^2))$$

$$\text{is } \Lambda = \frac{\ell(l_\infty, K, t_0, R)}{\max (\ell(l_\infty, K, t_0, \sigma^2))}.$$

$$(l_\infty, K, t_0)$$

Letting $\hat{\sigma}_\omega^2$ and $\hat{\sigma}_\Omega^2$ be the ML estimates of σ^2 under ω and Ω , respectively, this LR becomes

$$\Lambda = \frac{(2\pi\hat{\sigma}_\omega^2)^{-N/2} \exp(-N/2)}{(2\pi\hat{\sigma}_\Omega^2)^{-N/2} \exp(-N/2)} = (\hat{\sigma}_\Omega^2 / \hat{\sigma}_\omega^2)^{N/2}.$$

Under H_ω , the test statistic $-2 \log(\Lambda) = -N \log(\hat{\sigma}_\Omega^2 / \hat{\sigma}_\omega^2)$ will have asymptotically a X_r^2 distribution. A derivation of this distribution given by Kendall and Stuart (1973) can be modified to accommodate the present model.

Because LR tests are based on statistics having asymptotically a X_r^2 distribution, the validity of this test is dependent on the sample sizes used in calculating the test statistic. Assuming H_ω is true and that the error variance of individual observations is constant, the LR test statistic calculated using method (a) will be based on more observations than the LR test statistic calculated using method (d), and hence could be expected to better follow the X_r^2 distribution. However, method (d) may be modified so that there are several dependent variable averages and weights at each value of the independent variable (see the section comparing methods (a) and (d)), and the number of

observations maintained above the required level. A similar technique can be applied to method (c).

The problem of constructing LR tests thus reduces to one of finding LS estimates for a number of different probability models. These models are generated by placing appropriate linear constraints on the general model Ω , depending on the hypothesis being tested. For the single sample problem, linear constraints take the form of fixing any or all of the parameters (l_∞, K, t_0) to their hypothesized values. In this case, the degrees of freedom of X_r^2 is equal to the number of parameters fixed. For the multisample problem, linear constraints take the form of fitting von Bertalanffy curves so that any or all of the parameters are equal in any or all of the I populations. In this case, the degrees of freedom of X_r^2 is equal to the number of linear equations needed to specify the particular constraints. For example, $I-1$ linear equations are needed to specify equality of any parameter over I populations.

AN EXAMPLE

As an example illustrating some of the methods that have been presented, growth data (Table 1) for Pacific hake, *Merluccius productus*, from Dark (1975), was analyzed using method (b). The reader can test his understanding of methods, as well as the correctness of his computer programs, by duplicating this analysis.

A first step in nonlinear LS analysis is the selection of a general purpose iterative nonlinear LS computer program. Such programs take initial estimates and attempt to find LS estimates. For the present analysis, BMD07R of the BMD biomedical computer programs (Dixon 1976) was used. This choice was dictated by program availability.

TABLE 1.—Average length at various ages for male and female Pacific hake taken off California, Oregon, and Washington during 1965-69 (adopted from Dark 1975).

Age (years)	Female		Male	
	Sample size	Mean length (cm)	Sample size	Mean length (cm)
1.0	385	15.40	385	15.40
2.0	36	28.03	28	26.93
3.3	17	41.18	13	42.23
4.3	135	46.20	83	44.59
5.3	750	48.23	628	47.63
6.3	1,073	50.26	1,134	49.67
7.3	1,459	51.82	1,761	50.87
8.3	626	54.27	432	52.30
9.3	199	56.98	93	54.77
10.3	97	58.93	21	56.43
11.3	44	59.00	8	55.88
12.3	11	60.91	—	—
13.3	6	61.83	—	—

Suitable programs are also available in BMDP (Dixon 1977), SPSS (Nie et al. 1975), and from a number of other sources.

Initial values were obtained from Ford-Walford plots (Ricker 1975) which provided estimates \bar{l}_∞ and \bar{K} ; and from the weighted average

$$\bar{t}_0 = \frac{\sum_i [\log(1 - \bar{l}_i / \bar{l}_\infty) / \bar{K} + t_i] (\bar{l}_\infty - \bar{l}_i)}{\sum_i (\bar{l}_\infty - \bar{l}_i)}$$

where \bar{l}_i is the average length at age t_i . For these initial calculations, it was convenient to round ages to whole years. This disallows direct comparisons of Ford-Walford and LS estimates. Besides initial estimates, BMDO7R also requires a FORTRAN subroutine (provided in the Appendix) which evaluates $\mu(t_u)$ and its partial derivatives.

Table 2 contains the initial Ford-Walford estimates ($\bar{l}_\infty, \bar{K}, \bar{t}_0$) and the final LS estimates ($\hat{l}_\infty, \hat{K}, \hat{t}_0$) obtained from BMDO7R. LS fits of growth curves are graphed in Figure 1.

From Figure 1 there appears to be a difference in l_∞ between sexes. As a further examination of this difference, cross sections of the approximate 95% confidence regions around $(\bar{l}_\infty, \bar{K})$, generated by conditioning on \bar{t}_0 , were graphed (Figure 2) using

TABLE 2.—Least squares (LS) estimates of von Bertalanffy parameters for male and female Pacific hake, based on data in Table 1.

Item	l_∞	K	t_0
Male:			
Ford-Walford initial estimates	55.83	0.43	0.35
LS estimates	55.98	0.386	0.171
Standard deviation of LS estimates	1.083	0.039	0.142
Female:			
Ford-Walford initial estimates	60.60	0.35	0.32
LS estimates	61.23	0.296	-0.057
Standard deviation of LS estimates	1.214	0.029	0.175

methods previously described. These regions not only show a difference in l_∞ between sexes, but also indicate a difference in K .

As a final step in this analysis, LR tests for equality of von Bertalanffy parameters between males (population 1) and females (population 2) were performed. It was necessary to fit data to five models corresponding to hypotheses of interest (Table 3).

The difficulty of fitting these models depends somewhat on the nonlinear LS program used. If derivative-free programs are available, the user will be saved the complex task of specifying derivatives. If programs allow for constraints, only the model Ω need be specified. Nonlinear LS programs available in BMDP have these features.

For BMDO7R, the Appendix provides FORTRAN subroutines which evaluate $\mu(t_u)$ and its

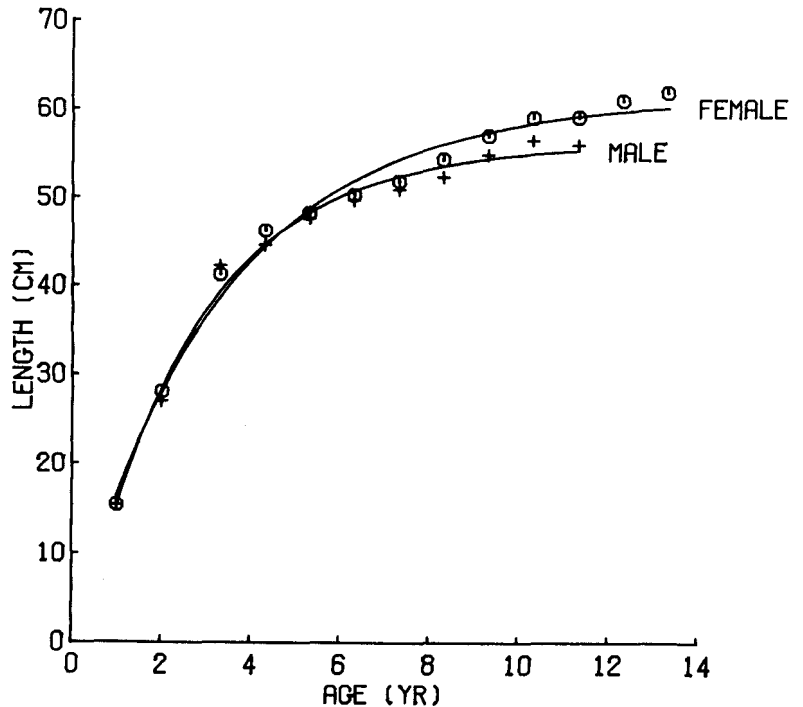


FIGURE 1.—Plots of average length at each age (from Table 1), for male and female Pacific hake, with graphs of estimated von Bertalanffy curves (from Table 2).

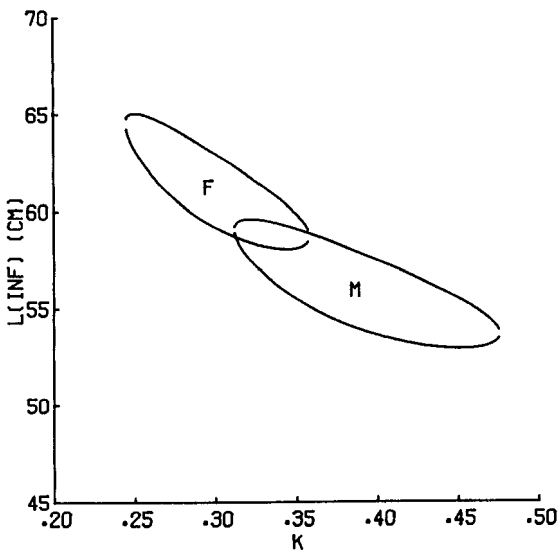


FIGURE 2.—Cross sections of approximate 95% confidence regions around least squares estimates (\hat{l}_∞, \hat{K}), generated by conditioning on \hat{t}_0 (see text), for male (M) and female (F) Pacific hake. Letters M and F are centered on least squares estimates.

partial derivatives for the five models. These subroutines are general in the sense that they allow comparisons of any number of populations. Probably these subroutines are compatible with the requirements of BMDP3R, but this program was not readily available for a test. Also, minor modifications may be necessary to comply with requirements of particular computer systems.

Results of LR tests (Table 3) indicate there is a significant difference ($\alpha = 0.002$) in l_∞ between sexes, a borderline significant difference ($\alpha = 0.05$) in K , but no significant difference in t_0 .

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TABLE 3.—Likelihood ratio tests comparing von Bertalanffy parameter estimates for male (1) and female (2) Pacific hake, based on data in Table 1 ($N = 24$ observations).

Hypthesis	Linear constraints	Equivalent model	$\hat{l}_{\infty 1}$	$\hat{l}_{\infty 2}$	\hat{K}_1	\hat{K}_2	\hat{t}_{01}	\hat{t}_{02}	Residual sum of squares ($N\hat{\sigma}^2$)	$\hat{\chi}_r^2 = -N \log (\hat{\sigma}_a^2 / \hat{\sigma}_w^2)$	df (r)	$P(\chi_r^2 > \hat{\chi}_r^2)$
H_Ω	none	$l_{ij} = l_{\infty i}(1 - \exp(-K_i(t_{ij} - t_{0i})))$	55.98	61.23	0.386	0.296	0.171	-0.057	48.22			
$H_{\omega 1}$	$l_{\infty 1} = l_{\infty 2}$	$l_{ij} = l_{\infty}(1 - \exp(-K_i(t_{ij} - t_{0i})))$	59.40	59.40	0.297	0.337	-0.111	0.087	71.60	9.49	1	0.002
$H_{\omega 2}$	$K_1 = K_2$	$l_{ij} = l_{\infty i}(1 - \exp(-K(t_{ij} - t_{0i})))$	57.44	60.14	0.330	0.330	-0.021	0.095	58.34	3.74	1	0.053
$H_{\omega 3}$	$t_{01} = t_{02}$	$l_{ij} = l_{\infty i}(1 - \exp(-K_i(t_{ij} - t_{0i})))$	58.45	60.77	0.361	0.313	0.057	0.057	50.76	1.23	1	0.267
$H_{\omega 4}$	$l_{\infty 1} = l_{\infty 2}$ $K_1 = K_2$ $t_{01} = t_{02}$	$l_{ij} = l_{\infty}(1 - \exp(-K(t_{ij} - t_{0i})))$	59.29	59.29	0.320	0.320	0.010	0.010	79.76	12.08	3	0.007
											3(-1)	

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APPENDIX

This appendix contains FORTRAN subroutines required by BMDO7R to fit models corresponding to the five hypotheses in Table 3. These subroutines evaluate $\mu(t_u)$ and its partial derivatives. To use these subroutines, the following three instructions need to be understood.

1. The variable NG must be set equal to the number of populations to be compared.

2. The first NG variables of the data input must be "design variables," followed by age. That is, the first NG variables for observation l_{ij} must consist

of $NG-1$ zeros and a single one, the one occurring in the i th position; followed by age (t_{ij}). Next comes length and statistical weights (if weighting is used).

3. The parameters to be estimated are referenced in the order all l_∞ 's first, all K 's second, and all t_0 's last. Relative positions of l_∞ 's, K 's, and t_0 's amongst themselves are simply the order of population number. It should be noted that the number of parameters fitted under the five hypotheses of Table 3 are $H_0: 3 \times NG$; $H_{\omega 1}, H_{\omega 2}, H_{\omega 3}: (2 \times NG) + 1$; $H_{\omega 4}: 3$.

I. Subroutine FUN for hypothesis Ω .

```

SUBROUTINE FUN(F,D,P,X)
  DIMENSION D(1),P(1),X(1)
C  NG IS THE NUMBER OF POPULATIONS TO BE
C  COMPARED
  NG=2
C  SUBROUTINE FUN FOR HYPOTHESIS  $\Omega$ :
C  NG DIFFERENT GROWTH CURVES
  IND=NG+1
  XL=0.
  XK=0.
  XT=0.
  II=NG
  III=NG+NG
  DO 10 I=1,NG
  II=II+1
  III=III+1
  XL=XL+X(I)*P(I)
  XK=XK+X(I)*P(II)
  XT=XT+X(I)*P(III)
10  CONTINUE
  XX=EXP(-XK*(X(IND)-XT))
  F=XL*(1.-XX)
  II=NG
  III=NG+NG
  DO 20 I=1,NG
  II=II+1
  III=III+1
  D(I)=0.
  D(II)=0.
  D(III)=0.
  IF(X(I).EQ.0.) GO TO 20
  D(I)=1.-XX
  D(II)=XL*XX*(X(IND)-XT)
  D(III)=-XL*XX*XK
20  CONTINUE
  RETURN
  END

```

II. Subroutine FUN for hypothesis ω_1 .

```

SUBROUTINE FUN(F,D,P,X)
  DIMENSION D(1),P(1),X(1)
C  NG IS THE NUMBER OF POPULATIONS TO BE
C  COMPARED
  NG=2
C  SUBROUTINE FUN FOR HYPOTHESIS  $\omega_1$ :  $l_\infty$ 'S
C  EQUAL
  IND=NG+1
  XK=0.
  XT=0.
  II=1
  III=1+NG
  DO 10 I=1, NG
  II=II+1
  III=III+1
  XK=XK+X(I)*P(II)
  XT=XT+X(I)*P(III)
10  CONTINUE
  XL=P(1)
  XX=EXP(-XK*(X(IND)-XT))
  F=XL*(1.-XX)
  II=1
  III=1+NG
  DO 20 I=1,NG
  II=II+1
  III=III+1
  D(II)=0.
  D(III)=0.
  IF(X(I).EQ.0.) GO TO 20
  D(II)=XL*XX*(X(IND)-XT)
  D(III)=-XL*XX*XK
20  CONTINUE
  D(1)=1.-XX
  RETURN
  END

```

III. Subroutine FUN for hypothesis ω_2 .

```

SUBROUTINE FUN(F,D,P,X)
  DIMENSION D(1),P(1),X(1)
C  NG IS THE NUMBER OF POPULATIONS TO BE
C  COMPARED
  NG=2
C  SUBROUTINE FUN FOR HYPOTHESIS  $\omega_2$ : K'S
C  EQUAL
  IND=NG+1
  INDX=NG+1
  XL=0.
  XT=0.
  III=NG+1
  DO 10 I=1,NG
  III=III+1
  XL=XL+X(I)*P(I)
  XT=XT+X(I)*P(III)
10  CONTINUE
  XK=P(INDX)
  XX=EXP(-XK*(X(IND)-XT))
  F=XL*(1.-XX)
  III=NG+1
  DO 20 I=1,NG
  III=III+1
  D(I)=0.
  D(III)=0.
  IF(X(I).EQ.0.) GO TO 20
  D(I)=1.-XX
  D(III)=-XL*XX*XK
20  CONTINUE
  D(INDX)=XL*XX*(X(IND)-XT)
  RETURN
  END

```

IV. Subroutine FUN for hypothesis ω_3 .

```

SUBROUTINE FUN(F,D,P,X)
  DIMENSION D(1),P(1),X(1)
C  NG IS THE NUMBER OF POPULATIONS TO BE
C  COMPARED
  NG=2
C  SUBROUTINE FUN FOR HYPOTHESIS  $\omega_3$ :  $t_0$ 'S
C  EQUAL
  IND=NG+1
  INDX=NG+NG+1
  XL=0.
  XK=0.
  II=NG
  DO 10 I=1,NG
  II=II+1
  XL=XL+X(I)*P(I)
  XK=XK+X(I)*P(II)
10  CONTINUE
  XT=P(INDX)
  XX=EXP(-XK*(X(IND)-XT))
  F=XL*(1.-XX)
  II=NG
  DO 20 I=1,NG
  II=II+1
  D(I)=0.
  D(II)=0.
  IF(X(I).EQ.0.) GO TO 20
  D(I)=1.-XX
  D(II)=XL*XX*(X(IND)-XT)
20  CONTINUE
  D(INDX)=-XL*XX*XK
  RETURN
  END

```

V. Subroutine FUN for hypothesis ω_4 .

```

SUBROUTINE FUN(F,D,P,X)
  DIMENSION D(1),P(1),X(1)
C  NG IS THE NUMBER OF POPULATIONS TO BE
C  COMPARED
  NG=2
C  SUBROUTINE FUN FOR HYPOTHESIS  $\omega_4$ : ALL
C  CURVES IDENTICAL
  IND=NG+1
  XL=P(1)
  XK=P(2)
  XT=P(3)
  XX=EXP(-XK*(X(IND)-XT))
  F=XL*(1.-XX)
  D(1)=1.-XX
  D(2)=XL*XX*(X(IND)-XT)
  D(3)=-XL*XX*XK
  RETURN
  END

```