Abstract. – Von Bertalanffy growth models appropriate for fitting to length-increment data by maximum likelihood are described. Models incorporating variation in growth among individuals, release-length-measurement error, and model error are developed and fit to southern bluefin tuna *Thunnus maccoyii* tag-return data. On the basis of likelihood ratio tests, a model in which individual variation in growth is represented by variation in L_∞ and which explicitly incorporates model error is selected as the most appropriate model for these data. The parameter estimates obtained were μ_{L_∞} = 186.9 cm, $\sigma_{L_\infty}^2$ = 218.8 cm^2, K = 0.1401/year, and σ_e^2 = 15.25 cm^2. Analyses of simulated data suggest that biased estimates of growth parameters can result if model error is not explicitly included in von Bertalanffy models incorporating individual variation in growth.

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Estimation of Southern Bluefin Tuna *Thunnus maccoyii* Growth Parameters from Tagging Data, using von Bertalanffy Models Incorporating Individual Variation

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Knowledge of the growth of a fish and, in particular, a mathematical description of the increase in length or weight with time, is important for understanding its population and fishery dynamics. Also, fish growth has been used directly or indirectly to calculate catch age composition (Hayashi 1974, Baglin 1977, Kume 1978, Skillman and Shingu 1980, Majkowski and Hampton 1983), mortalities (Beverton and Holt 1957, Pauly 1987) and yield-per-recruit (Beverton and Holt 1957, Ricker 1975) and to make inter- and intrapopulation comparisons (Brousseau 1979, Goldspink 1979, Kohlhorst et al.1980, Francis 1981).

Techniques for studying fish growth in length fall into three categories: (i) Direct measurements of age (such as those obtained by counting periodic protein and calcium depositions in scales, otoliths, vertebrae, fin rays, or some other hard tissue) and length; (ii) analysis of time series of length-frequency data (sometimes called modal progression analysis); and (iii) analysis of length-increment and time-at-liberty data from a mark-recapture experiment. In each case, a growth model is usually fit to the data. Various models have been proposed for fitting to these types of data (e.g., Brody 1927 and 1945, Ford 1933, Walford 1946, Richards 1959, Knight 1969), but by far the most used model in fisheries research is that of von Bertalanffy (1938). This model, originally formulated on physiological considerations, has three parameters that have the biological interpretations of average maximum length (L_∞), the average rate at which L_∞ is approached (K), and the theoretical average time at which length would be zero if growth had always occurred according to the model (t_0).

The study of growth by direct measurements of age (reviewed by Bagenal 1974, Brothers 1979, Beamish 1981, Prince and Pulos 1983) and length is not possible for many species. In particular, good estimates of the ages of older fish are frequently hard to come by. This was the case for Yukinawa's (1970) study of southern bluefin tuna *Thunnus maccoyii* age and growth from presumed annual rings on scales. He examined the scales of 2240 fish within the length range of 38–184 cm, but was able to age only about 15% of fish larger than 120 cm, and none of those larger than 153 cm. Similarly, Thorogood (1986) was unable to age significant numbers of large southern bluefin from examinations of their otoliths.

A major aspect of length-frequency analysis is the identification of age classes in the data. To do this, Harding (1949) and Cassie (1954) used probability paper, and Tanaka (1956) fit parabolas to the logarithms of observed length-frequencies. More recently, digital computers have been used, and the distribution of length-at-age has been assumed to be normal or lognormal (Hasselblad 1966, Kumar and Adams 1977, Macdonald 1969 and 1975, Macdonald and Pitcher 1979, Schnute and Fournier 1980, Fournier and Breen 1983). Pauly's method (Pauly 1987) of fitting growth curves to observed peaks in a time series of length-frequency data, commonly known as ELEFAN I, has received some recent attention, but it suffers from the assumption that length-at-age does not vary (Hampton and Majkowski 1987).

Some attempts have been made to study the growth of southern bluefin, using length-frequency data. Serventy (1956) plotted the progressions of length-frequency means and modes of juvenile age classes caught in Australian coastal waters, but did not attempt to quantify the results as a growth equation. Robins (1963) made the first attempt to quantify growth, obtaining a Walford growth transformation from an analysis of length-frequency modes of juvenile fish. Hearn (1986) identified a seasonal component to growth from analyses of similar data. Recently, promising results have been obtained with the application of MULTIFAN, a likelihood-based method for estimating von Bertalanffy growth parameters from length-frequency data, to southern bluefin tuna data (Fournier et al. 1990).

Length-increment and time-at-liberty data from a tagging experiment provide direct measurements of the growth of individual fish as long as the tag or the tagging procedure does not have a significant effect on growth. Using a von Bertalanffy model and a fitting procedure such as that proposed by Fabens (1965), estimates of L_∞ and K can be obtained, but without additional assumptions no estimate of t_0 is available.

Murphy (1977) analyzed the release and recapture data from 2578 tagged southern bluefin and derived estimates of L_∞ and K that he considered to be more reliable than those previously derived by other workers. Kirkwood (1983) obtained similar estimates from a smaller data set (*n* 794), excluding fish that had been at liberty for less than 250 days. In addition, he incorporated age-at-length observations from length-frequency modes to the estimation procedure to obtain an estimate of t_0.

None of the studies of southern bluefin growth, and indeed few studies of fish growth in general, take explicit account of variation in growth among individuals by the incorporation of parameters describing such variation into the model. Krause et al. (1967) gave the first thorough treatment of individual variability in growth when deriving conditional probability densities for body weight-at-age of chickens. Sainsbury (1980) recognised the importance of individual variability in fishes showing von Bertalanffy growth, and derived equations appropriate for length-at-age and length-increment data if both L_∞ and K showed individual variation. He also showed that biased estimates of mean growth parameters could result if individual variability in K existed and was ignored. Kirkwood and Somers (1984) developed a simpler model for length-increment data in which only L_∞ was variable and applied it to two species of tiger prawn.

A problem with these models (as pointed out by Kirkwood and Somers 1984) is that all the observed "error" is attributed to individual variation in L_∞ and/or K. It is, of course, reasonable to expect that there will also be error due to some animals not growing exactly according to the von Bertalanffy model, a so-called model error. For standard growth models not incorporating individual variability, all residual error is assumed to be model error. It is also reasonable to expect that, in the case of length-increment data, the initial or release length cannot always be measured exactly and therefore will be an additional source of error.

In this paper, southern bluefin tuna tag-return data are analysed using three existing models, all of which are based on the von Bertalanffy model: the standard model, using the fitting procedure described by Fabens (1965), model (2) of Kirkwood and Somers (1984), and the Sainsbury (1980) model. In addition, models based on the latter two that incorporate model error and release-length-measurement error are derived and applied. The properties and assumptions of each of the models are investigated using computer simulation techniques.

Methods

Tagging methods and data

The primary method used to catch fish for tagging was commercial pole-and-line, using either live or dead bait, although on some occasions trolling was also used. Prior to release, the fork lengths of most fish selected for tagging were measured to the nearest centimeter on a measuring board. While the fish were restrained on the measuring board, one or two numbered tuna tags, each consisting of a molded plastic barbed head with a tubular plastic streamer glued to it (Williams 1982), were inserted forward into the musculature at an angle of about 45°, 1–2 cm below the posterior insertion of the second dorsal fin. For double-tagged fish, one tag was inserted on each side of the second dorsal fin. Ideally, the tag barb was anchored behind the second dorsal fin ray supports (pterygiophores).

The primary data used in this study consist of returns of southern bluefin tagged between 1962 and 1978 that were measured to the nearest centimeter at release, were thought to have reliable dates of release and recapture, and were at liberty for at least 250 days. These criteria were satisfied by 1800 returns. The last criterion was applied to eliminate the possible effect that the tagging operation might have on length growth and to minimize the biasing effect that seasonal fluctuations in growth, if present, might have on parameter estimation.

Most fish were 50–80 cm long when tagged, with the smallest 38 cm and the largest 104 cm. The range of recapture lengths was 51–185 cm, with most being in the range 60–100 cm. The times at liberty for the primary data set range from 250 days (the minimum allowed) to approximately 11 years.

Parameter estimation

Model 1: Standard von Bertalanffy model The form of the von Bertalanffy growth model appropriate for fitting to tag-return data (indexed by i) is, as described by Fabens (1965),

$$\delta l_i = (L_\infty - l_i)(1 - e^{-Kt_i}) + e_i \tag{1}$$

where δl_i is the length increment, l_i is the release length, t_i is the time at liberty, and e_i is a model error term (or residual), all for the ith observation. The error term e_i is assumed to be a normally-distributed random variable with an expected value of zero and variance σ_e^2. Thus, for given l_i and t_i, δl_i is a normally-distributed random variable with an expected value of $(L_\infty - l_i)(1 - e^{-Kt_i})$ and a variance of σ_e^2. Estimates of L_∞, K, and σ_e^2 can be obtained by nonlinear ordinary least squares (as in Kirkwood and Somers 1984) or by maximum likelihood (Kimura 1980). In the case of model 1, either technique can be applied, since the variance of δl_i is assumed to be constant with increasing t_i. However, in the models that incorporate individual variability (see below), the variance of δl_i increases with increasing t_i. This would require the use of weighted least-squares if this approach was followed. Since the weights would depend on the estimated K, an iterative procedure would be necessary to obtain the appropriate estimates. Therefore, the maximum-likelihood method, which is far more straightforward, is used to obtain parameter estimates for this and the models that follow.

For n observations of δl_i and t_i ($i = 1$ to n), the likelihood function is

$$L = \prod_{i=1}^{n} (2\pi\sigma_e^2)^{-\frac{1}{2}} \exp\left[-\frac{[\delta l_i - E(\delta l_i)]^2}{2\sigma_e^2}\right],$$

and estimates of L_∞, K, and σ_e^2 are found by minimizing

$$LL = -\ln L = \frac{n}{2}\ln(2\pi\sigma_e^2) + \frac{\sum_{i=1}^{n}[\delta l_i - E(\delta l_i)]^2}{2\sigma_e^2}.$$

This was accomplished for all the models described in this paper, using the minimization subroutine MINIM (programmed by D.E. Shaw, CSIRO Div. Math. Stat., P.O. Box 218, Lindfield 2070, Aust.), which uses the method of Nelder and Mead (1965). Equivalent subroutines are available in several commercially-available software packages.

Model 2: Kirkwood and Somers model Kirkwood and Somers (1984) described a model which allowed for individual variation in growth through an individually variable L_∞. Specifically, L_∞ was assumed to be normally distributed with mean μ_{L_∞} and variance $\sigma_{L_\infty}^2$. For given l_i and t_i, δl_i is a normally-distributed random variable whose expected value is given by

$$E(\delta l_i) = (\mu_{L_\infty} - l_i)(1 - e^{-Kt_i}) \tag{2}$$

and variance by

$$\mathrm{var}(\delta l_i) = \sigma_{L_\infty}^2 (1 - e^{-Kt_i})^2.$$

The negative log-likelihood function now becomes

$$LL = \sum_{i=1}^{n} \frac{\ln[2\pi\,\mathrm{var}(\delta l_i)]}{2} + \frac{[\delta l_i - E(\delta l_i)]^2}{2\,\mathrm{var}(\delta l_i)} \tag{3}$$

from which maximum likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, and K may be obtained.

Model 3: Kirkwood and Somers model with model error Let us now assume that the variance of δl_i is comprised of components due to both the individual variation in L_∞ and to a normally-distributed model error, e_i, having a mean of zero and variance σ_e^2. In this case, $E(\delta l_i)$ is unchanged from Equation (2) and the variance of δl_i is given by

$$\mathrm{var}(\delta l_i) = \sigma_{L_\infty}^2 (1 - e^{-Kt_i})^2 + \sigma_e^2. \tag{4}$$

Maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, K, and σ_e^2 can again be obtained by substituting the right sides of Equations (2) and (4) into Equation (3).

Model 4: Kirkwood and Somers model with model error and release-length-measurement error Because the tagging operation involves the handling of powerful, often violently struggling fish, it is quite reasonable to expect that release length will be measured with error. If possible, this error should be independently estimated and included in the growth model. On the other hand, measurement of a dead fish at recapture should not involve a significant error if competently carried out. In this study, recapture lengths are assumed to be measured without error.

If growth is assumed to be negligible, a comparison of lengths-at-release and lengths-at-recapture (l_2) for animals at liberty for a very short time should provide a good estimate of release-length-measurement error. Such a comparison was made for 251 tag returns in which the release length was 50 cm or more (see Residuals Analysis section) and the period at liberty was 10 days or less. For this data set, the mean measurement error $\mu_m = (\Sigma\{l_2 - l_1\}/251)$ was 0.4861 cm with a variance, σ_m^2, of 5.2428 cm^2. At least some of this μ_m might be attributed to growth, since the average growth increment over a 10-day period is approximately 0.5 cm. In this paper, μ_m is assumed to be zero.

Because δl_i now depends on another random variable (l_i), it is convenient to assume that the length-at-recapture is a normally-distributed random variable. Equation (1) can be modified to describe the ith recapture length as

$$l_{2i} = [\mu_{L_\infty} - (l_i + \varepsilon_i)]\,[1 - e^{-Kt_i}] + l_i + \varepsilon_i + e_i, \qquad (5)$$

where ε_i is the normally-distributed release-length-measurement error. The expected value of l_{2i} is given by

$$E(l_{2i}) = [\mu_{L_\infty} - E(l_i)]\,[1 - e^{-Kt_i}] + E(l_i),$$

where $E(l_i)$ is equal to $l_i + \mu_m$. Collecting terms in ε_i, Equation (5) is rewritten as

$$l_{2i} = [\mu_{L_\infty} - l_i]\,[1 - e^{-Kt_i}] + l_i + e^{-Kt_i}\,\varepsilon_i + e_i.$$

The variance of l_{2i} is then given by

$$\mathrm{var}\,(l_{2i}) = \sigma_{L_\infty}^2\,(1 - e^{-Kt_i})^2 + \sigma_e^2 + \sigma_m^2\,e^{-2Kt_i}.$$

Given estimates of μ_m and σ_m^2, maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, K, and σ_e^2 can be obtained as before.

Model 5: Sainsbury model Sainsbury (1977, 1980) described a model that recognised individual variation in K, as well as in L_∞. He assumed that both were independent random variables, with K following a gamma distribution and L_∞ being normally distributed. He also assumed that, as an approximation, δl_i is normally distributed for given l_i and t_i, pointing out that this should involve little error if L_∞ is normally distributed (Sainsbury 1977). With μ_K and σ_K^2 denoting the mean and variance, respectively, of K, the relevant equations are

$$E(\delta l_i) = [\mu_{L_\infty} - l_i]\left[1 - \left[1 + \frac{\sigma_K^2\,t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}}\right]$$

and

$$\mathrm{var}\,(\delta l_i) = C_1\,\sigma_{L_\infty}^2 + C_2\,(\mu_{L_\infty} - l_i)^2, \qquad (6)$$

where

$$C_1 = 1 - 2\left[1 + \frac{\sigma_K^2\,t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}} + \left[1 + \frac{2\sigma_K^2\,t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}}$$

and

$$C_2 = \left[1 + \frac{2\sigma_K^2\,t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}} - \left[1 + \frac{\sigma_K^2\,t_i}{\mu_K}\right]^{-\frac{2\mu_K^2}{\sigma_K^2}}$$

Maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, μ_K, and σ_K^2 can be obtained as shown earlier.

Model 6: Sainsbury model with model error As shown in model 3, a model error can be included simply by adding the model error variance term to Equation (6) giving

$$\mathrm{var}\,(\delta l_i) = C_1\,\sigma_{L_\infty}^2 + C_2\,(\mu_{L_\infty} - l_i)^2 + \sigma_e^2.$$

Solution by maximum likelihood now requires that a fifth parameter, σ_e^2, be estimated from the data.

Model 7: Sainsbury model with model error and release-length-measurement error Using logic similar to that developed in model 4, length-at-recapture is now considered as the random variable and assumed to be normally distributed, with

$$E(l_{2i}) = \left[\mu_{L_\infty} - E(l_i)\right]\left[1 - \left[1 + \frac{\sigma_K^2\, t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}}\right] + E(l_i) \qquad (7)$$

and

$$\mathrm{var}\,(l_{2i}) = C_1\, \sigma_{L_\infty}^2 + C_2\,[\mu_{L_\infty} - E(l_i)]^2 + \sigma_e^2 + \sigma_m^2 E(e^{-2Kt_i}), \quad (8)$$

where

$$E(e^{-2Kt_i}) = \left[1 + \frac{2\sigma_K^2\, t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}}$$

Given the estimate of σ_m^2 derived for model 4, maximum-ikelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, μ_K, σ_K^2, and σ_e^2 can be obtained as before.

Estimation of t_0 An estimate of t_0 is required for many applications of the von Bertalanffy model, but this parameter cannot be estimated from tag-return data alone. To estimate t_0, one or more observations of age-at-length are required. Kirkwood (1983) described a maximum-likelihood method for determining t_0, along with L_∞ and K, if supplementary age-length data are available in addition to tag-return data. Such data can easily be accommodated in the models described above. Consider the case where n1 tag returns (δl_i and δt_i) and n2 age-length observations (l_j and t_j) are available. We now have two random variables, δl_i and l_j, which have normal probability density functions conditioned on l_i (release length) and δt_i, and t_j, respectively. Their expected values, for example in the case of model 3, are given by

$$E(\delta l_i) = (\mu_{L_\infty} - l_i)\,(1 - e^{-K\delta t_i})$$

$$E(l_j) = \mu_{L_\infty}\,(1 - e^{-K(t_j - t_0)})$$

and their variances by

$$\mathrm{var}\,(\delta l_i) = \sigma_{L_\infty}^2\,(1 - e^{-K\delta t_i})^2 + \sigma_{e1}^2$$

$$\mathrm{var}\,(l_j) = \sigma_{L_\infty}^2\,(1 - e^{-K(t_j - t_0)})^2 + \sigma_{e2}^2$$

where σ_{e1}^2 and σ_{e2}^2 are independent model error variances. Maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, K, t_0, σ_{e1}^2, and σ_{e2}^2 could, in theory, be found by minimizing

$$LL = \sum_{i=1}^{n1} \frac{\ln\,[2\pi\, \mathrm{var}\,(\delta l_i)]}{2} + \frac{[\delta l_i - E(\delta l_i)]^2}{2\, \mathrm{var}\,(\delta l_i)}$$

$$+ \sum_{j=1}^{n2} \frac{\ln\,[2\pi\, \mathrm{var}\,(l_j)]}{2} + \frac{[l_j - E(l_j)]^2}{2\, \mathrm{var}\,(l_j)}. \qquad (9)$$

However, the estimation of six parameters (or seven in the case of models 6 and 7) may prove unrealistic in many cases. In order to obtain an approximate estimate of t_0, I have employed a simpler procedure. It involves fixing the growth parameters estimated from tag-return data and estimating t_0 by minimizing only the second summation in Equation (9), using the same approximate age-length data as Kirkwood (1983). I did not attempt to estimate simultaneously all parameters using the combined length-increment and age-length data because of the approximate nature of the latter data.

Model selection

An important part of this study was to select the most appropriate growth model for use in southern bluefin tuna stock assessments. Although L provides a means of comparing the goodness of fit of the various growth models with the tagging data, it is not immediately clear whether the more complex models result in a statistically-significant improvement in fit to the data. Likelihood ratio tests (Mendenhall and Scheaffer 1973, Kendall and Stuart 1979, Kimura 1980) can be used to address this question.

Likelihood ratio tests Let λ be defined by

$$\lambda = \frac{L(\phi_0)}{L(\phi_a)},$$

where $L(\phi_0)$ and $L(\phi_a)$ are the maximum-likelihood function values under the null hypothesis (the simple model is correct) and the alternative hypothesis (the more complex model is correct), ϕ_0 is the set of maximum-likelihood estimates of r parameters under the null hypothesis, and ϕ_a is the set of maximum-likelihood estimates of r+s parameters under the alternative hypothesis. Under certain regularity assumptions that hold under most circumstances for large sample sizes (Mendenhall and Scheaffer 1973), $-2\log_e\lambda$ behaves as a χ^2 random variable with s degrees of freedom. Therefore $-2\log_e\lambda$ may be compared with a critical χ^2 value (pertaining to a suitable rejection region) and the null hypothesis either accepted or rejected. For example, a value of $-2\log_e\lambda$ of more than 3.84 would lead to rejection of the simple model in favor of a model with one extra parameter (df 1) with a rejection region (significance level) of 0.05 on the χ^2 distribution.

Simulations

Assessment of model performance One hundred simulated data sets were produced and analysed by the models described above. The simulated data sets were produced by simulating values of δl_i (for each of the 1736 observations comprising the edited data set), using the following equation,

$$\delta l_i = [L_{\infty i} - (l_i + \varepsilon_i)]\,[1 - e^{-K_i t_i}] + e_i.$$

$L_{\infty i}$ and e_i were sampled from normal distributions, and K_i from a gamma distribution defined by the model 7 maximum-likelihood estimates of their respective μ's and σ^2's. The release-length-measurement error, ε_i, was sampled from a normal distribution with a mean of 0 and a variance of 5.2428 cm^2. Subroutine GGNML of the International Mathematical and Statistical Library (IMSL) was used to generate random normal deviates. IMSL subroutine GGAMR was used to generate gamma deviates. Actual values of l_i and t_i from the edited data set were used.

A second set of simulations was undertaken, assuming $L_{\infty i}$ and K_i to be correlated with a correlation coefficient of 0.80. Correlated normal deviates were generated, using IMSL subroutine GGNSM. This was done to test the sensitivity of the models to the assumption of independence of $L_{\infty i}$ and K_i observations. In this set of simulations, K was assumed, for simplicity, to be normally distributed, rather than gamma distributed. With the values of μ_K and σ_K^2 encountered in this study, the gamma and normal distributions are virtually indistinguishable, and therefore the normal approximation should result in little or no error. This was confirmed in a small number of simulations where analyses of simulated data, produced using normally-distributed K_i values (uncorrelated with $L_{\infty i}$), gave results virtually identical to simulations where K_i was gamma distributed.

Analysis of the 100 simulated data sets by each of the models described above provided 100 sets of parameter estimates for each. The means and standard errors of these estimates were calculated to (i) derive approximate confidence intervals for the maximum-likelihood estimates produced by the models and (ii) compare model performance, i.e., their ability to estimate known parameter values.

Testing the assumption of normally-distributed l_{2i} The assumption that, given l_i and t_i, the random variable δl_i (or l_{2i} in the case of models 4 and 7) is normally distributed, is central to all the models described. This assumption is most questionable for model 7, where K variability and release-length-measurement error could have unpredictable effects on the distribution of l_{2i}. This assumption was tested for 30 combinations of l and t by generating 5000 values of l_{2i} for each combination, using the following equation.

$$l_{2i} = [L_{\infty i} - (l + \varepsilon_i)]\,[1 - e^{-K_i t}] + l + \varepsilon_i + e_i.$$

A χ^2 goodness-of-fit test (IMSL subroutine GPNOR) with 50 equiprobable categories was then applied to identify possible departures from a normal distribution with mean and variance given by Equations (7) and (8), respectively. Values of l of 50, 60, 70, 80, 90, and 100 cm were combined with values of t of 2, 4, 6, 8, and 10 years to produce the 30 combinations.

Results

Residuals analysis

Using model 1, an analysis of residuals was carried out on the primary data set. An initial fit of model 1 to the 1800 observations yielded estimates of L_∞, K, and σ_e^2 of 195.614 cm, 0.131914/year, and 24.8193 cm^2, respectively. Standardized residuals ($R_i = e_i/\sigma_e$) were calculated and plotted against t_i (Fig. 1) and against l_i (Fig. 2). Examination of Figure 1 reveals an even distribution of standardized residuals about zero and no obvious relationship with time at liberty. However, Figure 2 suggests that the fit model may not be appropriate over the entire range of release lengths observed. For release lengths less than 50 cm, there are 54 positive residuals but only 8 negative residuals, indicating that observed growth was faster than the model would predict for these smaller fish. For release lengths of 50 cm and larger, the pattern of residuals is unremarkable. On this basis, observations with release lengths smaller than 50 cm were excluded from further analyses.

A refit of model 1 to the amended data set (1738 observations) provided estimates of L_∞, K, and σ_e^2 of 200.120 cm, 0.125836/year, and 23.6157 cm^2, respectively. Using these parameter estimates, standardized

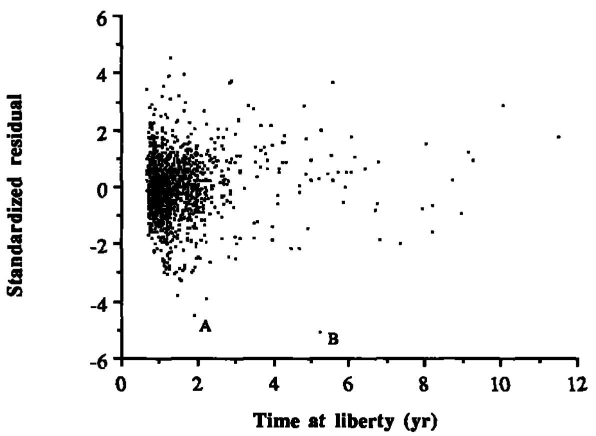

Figure 1

Plot of standardized residuals against time-at-liberty following an initial fit of model 1 to the primary data set (n 1800). The parameter estimates used were L_∞=195.614 cm, K=0.131914/year, and σ_e^2=24.8193 cm^2. The observations labeled A and B are those identified as outliers.

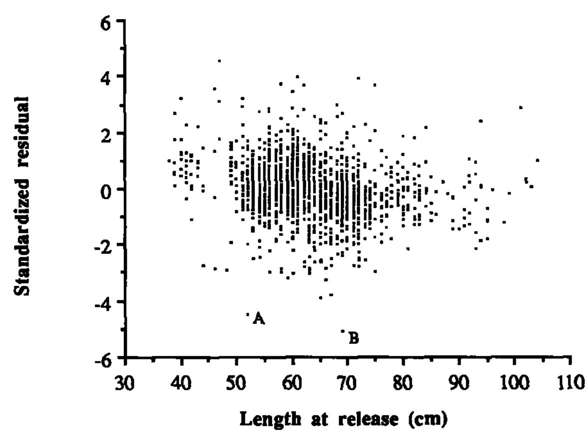

Figure 2

Plot of standardized residuals against release length following an initial fit of model 1 to the primary data set (n 1800). The parameter estimates used were L_∞=195.614 cm, K=0.131914/year, and σ_e^2=24.8193 cm^2. The observations labeled A and B are those identified as outliers.

residuals were recalculated and checked for outliers. Models 2–7 incorporate individual variability in growth parameters, necessitating the use of a quite severe criterion in the definition of an outlier. An observation was classified as an outlier only if the absolute value of its standardized residual was greater than 4.4172. Under the assumptions of model 1, only one in 2000 observations would exceed this value due to chance alone. Two observations were classified as outliers on this basis and rejected from further analyses. These observations are indicated in Figures 1 and 2. The final data set to which all models were fitted consisted of 1,736 observations.

Parameter estimates

Parameter estimates for the seven models fitted to the final data set are given in Table 1. The estimates differ substantially among some models, which is not surprising since they are based on rather different assump-

Table 1

Southern bluefin tuna growth parameter estimates derived for the seven models described.

Model no.	Model description	μ_{L_∞} (cm)	μ_K/yr	$\sigma_{L_\infty}^2$ (cm^2)	σ_K^2/yr^2	σ_e^2 (cm^2)	t_0 (yr)	LL
1	Fabens	201.1	0.1251			22.96	−0.6884	5183.66
2	Kirkwood and Somers	157.2	0.1892	555.8			−0.2506	5224.31
3	Kirkwood and Somers, with model error	186.9	0.1401	218.8		15.25	−0.5437	5150.86
4	Kirkwood and Somers, with model error and release-length error	186.2	0.1409	238.2		10.92	−0.5396	5151.06
5	Sainsbury	175.2	0.1563	100.7	0.1665E-02		−0.4660	5207.39
6	Sainsbury, with model error	188.3	0.1384	177.8	0.8824E-04	15.00	−0.5620	5150.80
7	Sainsbury, with model error and release-length error	188.0	0.1387	193.0	0.1014E-03	10.56	−0.5601	5150.97

Table 2

Estimates of mean and standard deviation of length-at-age (in cm), based on the parameter estimates for models 1 to 7.

	Model 1		Model 2		Model 3		Model 4		Model 5		Model 6		Model 7	
Age	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	38.3	4.8	33.1	5.0	36.3	4.8	36.6	4.5	35.6	8.5	36.6	5.2	36.6	4.9
2	57.4	4.8	54.5	8.2	56.0	5.9	56.0	5.7	55.4	12.2	56.2	6.4	56.1	6.3
3	74.3	4.8	72.2	10.8	73.1	7.0	73.1	6.9	72.3	14.7	73.2	7.5	73.2	7.5
4	89.2	4.8	86.9	13.0	88.0	8.0	88.0	8.0	86.6	16.3	88.1	8.5	88.0	8.6
5	102.4	4.8	99.0	14.8	100.9	8.9	100.9	9.0	98.8	17.3	101.0	9.3	100.9	9.5
6	114.0	4.8	109.0	16.3	112.2	9.7	112.1	9.9	109.3	17.7	112.2	10.0	112.1	10.2
7	124.2	4.8	117.3	17.6	121.9	10.4	121.8	10.6	118.2	17.8	122.0	10.6	121.9	10.8
8	133.3	4.8	124.2	18.6	130.4	11.1	130.3	11.3	125.8	17.6	130.5	11.0	130.4	11.3
9	141.2	4.8	129.9	19.5	137.8	11.6	137.6	11.9	132.4	17.3	138.0	11.4	137.8	11.7
10	148.3	4.8	134.6	20.2	144.2	12.1	144.0	12.4	138.0	16.8	144.4	11.8	144.3	12.0
11	154.5	4.8	138.5	20.8	149.8	12.5	149.6	12.8	142.9	16.3	150.1	12.0	149.9	12.4
12	160.0	4.8	141.7	21.2	154.7	12.9	154.4	13.2	147.1	15.8	155.0	12.3	154.8	12.6
13	164.8	4.8	144.4	21.6	158.9	13.2	158.6	13.5	150.7	15.2	159.2	12.5	159.1	12.8
14	169.1	4.8	146.6	22.0	162.5	13.5	162.2	13.8	153.8	14.7	163.0	12.6	162.8	13.0
15	172.9	4.8	148.4	22.3	165.7	13.7	165.3	14.1	156.5	14.2	166.2	12.8	166.0	13.1
16	176.2	4.8	149.9	22.5	168.5	13.9	168.1	14.3	158.8	13.7	169.0	12.9	168.8	13.3
17	179.1	4.8	151.2	22.7	170.9	14.1	170.5	14.5	160.9	13.3	171.5	13.0	171.3	13.4
18	181.7	4.8	152.2	22.8	173.0	14.3	172.5	14.7	162.6	12.8	173.6	13.1	173.4	13.5
19	184.0	4.8	153.1	23.0	174.8	14.4	174.3	14.8	164.2	12.5	175.5	13.2	175.3	13.6
20	186.0	4.8	153.8	23.1	176.4	14.5	175.9	14.9	165.5	12.1	177.2	13.3	176.9	13.7

tions. The effect of these differences on the mean and standard deviation of length-at-age is shown in Table 2. Despite the differences in parameter estimates, mean length-at-age is virtually identical for all models up to age 7. This allows the calculation of an approximate age-at-release for each observation that should contain little error and that is essentially independent of which set of parameter estimates is used to convert the release length to age. With this information, a presumed age-at-recapture incorporating individual variation can be calculated by adding the presumed age-at-release to the observed period at liberty. A plot of presumed age-at-recapture (calculated using the model 3 parameter estimates) against recapture length is shown in Figure 3.

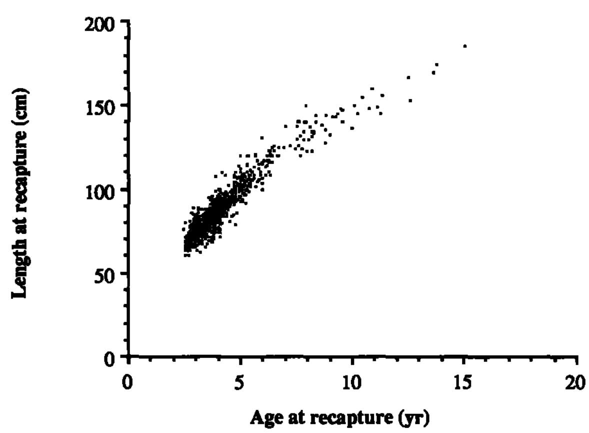

Figure 3

Plot of recapture length against presumed age-at-recapture for tag returns comprising the final data set (n 1736).

Model 1 produced the highest estimate of μ_{L_∞} and the lowest estimate of μ_K. The probable explanation for this is that the estimates are biased by the three observations with the greatest recapture lengths (Fig. 3). Because there is no individual variation in this model, the estimate of L_∞ is forced upward to compensate for these influential observations. In model 2, such observations can be accommodated by individual variation in L_∞; thus the estimate of μ_{L_∞} falls by more than 20% and the estimate of μ_K rises by more than 50%. When a model error term is added (model 3), the differences in relation to model 1 are less dramatic. The addition of release-length-measurement error (model 4) has little effect on the model-3 estimates, with the exception of σ_e^2, which is somewhat lower in model 4. Similar effects of adding model error and release-length-measurement error can be seen in comparisons of the parameter estimates for models 5, 6, and 7.

The estimates of $\sigma_{L_\infty}^2$ are substantially higher for models that assume constant K (models 2, 3, and 4) than for those that assume individual variability in K

Table 3

Values of the 97.5 percentile of the L_∞ distributions derived for models 2–7. These values may be compared with an observed maximum size in the catch of 225 cm.

Model no.	97.5 percentile of the L_∞ distribution (cm)
2	203.4
3	216.0
4	216.5
5	194.8
6	214.4
7	215.2

(models 5, 6, and 7). An approximate consistency test for derived L_∞ distributions is to compare an upper percentile (e.g., 97.5) of the distribution with the observed maximum size in a large sample of the catch (Kirkwood and Somers 1984). The largest southern bluefin ever measured by Japanese researchers during many years of length-frequency sampling is 225 cm (Yukinawa 1970, Shingu 1978). This may be compared with the derived 97.5 percentile of the L_∞ distributions for models 2–7 (Table 3). While by no means a definitive test, the comparisons suggest that the L_∞ distributions derived for models 3, 4, 6, and 7 (models that include model error) are more consistent with the observed maximum length than the distributions derived for models 2 and 5 (models that do not include model error).

The estimate of σ_K^2 for model 5 fell substantially with the addition of model error (models 6 and 7). The value of σ_K^2 for model 7 represents a coefficient of variation of approximately 7%. It should be pointed out here that the log-likelihood surface was very flat with respect to both $\sigma_{L_\infty}^2$ and σ_K^2, i.e., relatively large changes in either parameter resulted in only very small changes in LL. This matter is explored further using simulation techniques.

Model selection

The minimum negative log-likelihood function values given in Table 1 are indicators of the goodness of fit of the models to the data. Model 2 (3 parameters) provided a substantially poorer fit to the data than model 1 (3 parameters) and therefore need not be tested. Also, the inclusion of release-length-measurement error resulted in slightly worse fits to the data, eliminating models 4 and 7 from further consideration. The only likelihood ratio tests that are required are: (1) the null hypothesis (H_0) that model 1 is the correct model against the alternative that model 3 (4 parameters) is correct; (2) the H_0 that model 1 is the correct model against the alternative that model 6 (5 parameters) is correct; and (3) the H_0 that model 3 is the correct model against the alternative that model 6 is correct. H_0 was rejected for both tests (1) and (2) ($P<0.001$), indicating that the more complex models 3 and 6 provide significantly better fits to the data than model 1. For test (3), H_0 was accepted ($P>0.05$), suggesting that the additional complexity of the extra parameter (σ_K^2) in model 6 did not result in a significantly improved fit over model 3. On this basis, model 3 was adopted as the most appropriate model for these data.

Simulations

Assessment of model performance The results of analyses of 100 simulated data sets, produced assuming independence of $L_{\infty i}$ and K_i, are given in Table 4. These suggest that all of the models, with the possible exception of model 2, provide unbiased estimates of μ_{L_∞} and μ_K. This is somewhat surprising in view of the wide range of estimates of these parameters obtained from analyzing real data with the same models (Table 1). In particular, one might have expected, on the basis of analyses of the real data, that models 2 and 5 would have given biased estimates of μ_{L_∞} and μ_K for the simulated data also. The estimates of these parameters obtained from the real data, using the above models, even lie outside the approximate 95% confidence bounds calculated from the simulated data. A possible explanation for this is that the simulated data do not contain all the growth-related features of the real data. Such unaccounted-for structure, if it affected the performance of the models differently, could produce such inconsistencies. This, in fact, was observed in the case of the apparently biased estimates given by model 1 for the real data.

While the simulations indicate that estimates of the mean parameters are relatively unbiased and precise, this is not the case for estimates of their variances. In particular, it is clear that reliable estimates of σ_K^2 cannot be obtained from this data set, since estimates from the simulated data ranged from practically zero to 25% (expressed as the coefficient of variation). This could be due in part to the loss of information on K-variability incurred because of the necessary exclusion from the analyses of fish at liberty for less than 250 days.

The mean values of $\sigma_{L_\infty}^2$ are reasonably consistent with the estimates obtained from the real data. The estimates from models 2, 3, and 4 are positively biased, while those from model 5 are negatively biased. The estimates from model 7 are unbiased, but have a coefficient of variation of 45%. The estimates of σ_e^2 are somewhat less than those obtained from the real data, except in the case of model 1.

Table 4

Results of analyzing 100 simulated data sets generated using model 7, assuming independence of L_∞ and K_i. The true parameter values (i.e., those input to the simulation model) were those estimated from the real data using model 7 (Table 1).

Parameter		Model						
		1	2	2	4	5	6	7
μ_{L_∞} (cm)	mean	189.5	179.9	189.1	190.7	188.1	189.1	189.0
	SE	5.8	5.0	5.0	9.2	5.7	5.9	4.8
	lower c.b.*	178.3	170.0	179.4	172.6	177.0	177.6	179.5
	upper c.b.	200.8	189.8	198.8	208.8	199.2	200.7	198.4
μ_K/yr	mean	0.1372	0.1498	0.1376	0.1362	0.1400	0.1379	0.1378
	SE	0.0071	0.0074	0.0062	0.0093	0.0070	0.0074	0.0061
	lower c.b.	0.1233	0.1352	0.1256	0.1179	0.1263	0.1234	0.1259
	upper c.b.	0.1510	0.1644	0.1497	0.1544	0.1536	0.1525	0.1497
$\sigma_{L_\infty}^2$ (cm^2)	mean		699.2	249.7	288.4	27.1	178.1	186.3
	SE		64.2	44.1	100.5	42.3	93.4	84.8
	lower c.b.		573.4	163.3	91.4	−55.8	−5.0	20.1
	upper c.b.		825.0	336.1	485.4	110.0	361.2	352.4
σ_K^2/yr^2	mean					0.1176 E-2	0.1973 E-3	0.1839 E-3
	SE					0.1509 E-2	0.2503 E-3	0.1476 E-3
	lower c.b.					0.8806 E-3	−0.2932 E-3	−0.1054 E-3
	upper c.b.					0.1472 E-2	0.6879 E-3	0.4733 E-3
σ_e^2 (cm^2)	mean	20.11		11.13	6.67		10.08	6.04
	SE	0.75		0.97	1.11		1.49	1.17
	lower c.b.	18.63		9.22	4.50		7.16	3.75
	upper c.b.	21.59		13.03	8.85		13.00	8.32

*95% confidence bound assuming variables to be normally distributed.

The results of the simulations in which $L_{\infty i}$ and K_i were assumed to be correlated are given in Table 5. These results are essentially identical to those in Table 4; therefore, the assumption of independence does not affect parameter estimation in this instance.

Testing the assumption of normally-distributed l_{2i} Tests of normality of l_{2i} were performed for 30 combinations of l and t. For each of the combinations, the statistic G (χ^2 distributed with 49 degrees of freedom) and the probability, *P*, of wrongful rejection of the null hypothesis of normally-distributed l_{2i} were calculated (Table 6). In each case, *P* is greater than 0.10, and usually substantially so; therefore the null hypothesis is not rejected for any of the combinations of l and t.

Discussion

The estimation of von Bertalanffy growth parameters is one of the more frequently applied analyses in fisheries research. Despite this, the interpretation of the parameter estimates is often ill-founded. This is particularly so with L_∞, which is frequently given the interpretation of maximum possible length. This would be the case only if every fish grew exactly according to the derived model, i.e., there was no model error or individual variation in growth. In reality, the growth of all individual fish will not follow a single von Bertalanffy growth curve exactly; there will be variations among individuals resulting from exogenous (environmental) and endogenous (genetic) effects (Francis 1988). The correct interpretation of L_∞ estimated in the standard way is that it is the average maximum length that would be attained in the population represented by the data being analysed. Models have been proposed in this paper that take explicit account of model error and individual variation in growth, thereby eliminating the need for such interpretations.

Previous estimates of southern bluefin growth parameters have differed substantially (Table 7). The previous estimates of L_∞ obtained from tag-return data are somewhat smaller than the estimate derived using model 1 in this paper. This is possibly because

Table 5

Results of analyzing 100 simulated data sets generated using model 7, assuming correlated $L_{\infty i}$ and K_i pairs. The true parameter values (i.e., those input to the simulation model) were those estimated from the real data using model 7 (Table 1).

		Model						
Parameter		1	2	2	4	5	6	7
μ_{L_∞} (cm)	mean	188.2	178.5	187.6	187.3	186.3	187.1	184.6
	SE	6.6	4.9	5.0	5.1	5.6	6.4	7.8
	lower c.b.*	175.3	168.9	177.7	177.3	175.4	174.6	169.4
	upper c.b.	201.1	188.2	197.5	197.4	197.2	199.6	199.9
μ_K/yr	mean	0.1389	0.1517	0.1395	0.1398	0.1423	0.1404	0.1442
	SE	0.0083	0.0075	0.0065	0.0066	0.0072	0.0080	0.0111
	lower c.b.	0.1226	0.1370	0.1268	0.1269	0.1280	0.1248	0.1224
	upper c.b.	0.1553	0.1664	0.1521	0.1527	0.1563	0.1560	0.1661
$\sigma_{L_\infty}^2$ (cm^2)	mean		688.6	251.3	270.6	38.6	180.9	151.0
	SE		64.3	35.4	36.2	54.2	91.2	94.4
	lower c.b.		562.7	181.9	199.6	−67.6	2.2	−34.0
	upper c.b.		814.6	320.6	341.6	144.7	359.6	336.1
σ_K^2/yr^2	mean					0.1208 E-2	0.2105 E-3	0.4301 E-3
	SE					0.1608 E-3	0.2771 E-3	0.4383 E-3
	lower c.b.					0.8928 E-3	−0.3327 E-3	−0.4290 E-3
	upper c.b.					0.1523 E-2	0.7536 E-3	0.1289 E-2
σ_e^2 (cm^2)	mean	20.33		11.05	6.74		9.99	4.53
	SE	0.79		1.05	1.06		1.74	2.79
	lower c.b.	18.78		8.99	4.66		6.57	−0.95
	upper c.b.	21.88		13.12	8.82		13.41	10.00

*95% confidence bound assuming variables to be normally distributed.

Table 6

Values of the goodness-of-fit test statistic, G (χ^2 distributed with 49 degrees of freedom), and the probability, *P*, of wrongful rejection of the null hypothesis of normally-distributed recapture lengths. Each test consisted of 5000 recapture lengths generated for a specific combination of release length and time-at-liberty. For the purpose of calculating G statistics, the simulated recapture lengths were classified into 50 equiprobable categories.

Release length (cm)		Time-at-liberty (yr)				
		2	4	6	8	10
50	G	42.02	56.00	58.16	51.68	44.68
	P	0.75	0.22	0.17	0.37	0.65
60	G	57.54	50.86	52.38	38.74	46.84
	P	0.19	0.40	0.34	0.85	0.56
70	G	46.50	37.84	38.92	49.84	42.44
	P	0.58	0.88	0.85	0.44	0.73
80	G	56.68	45.62	60.92	40.42	48.58
	P	0.21	0.61	0.12	0.80	0.49
90	G	51.58	56.70	53.94	45.42	58.86
	P	0.37	0.21	0.29	0.62	0.16
100	G	54.96	45.70	46.70	31.94	43.78
	P	0.26	0.61	0.57	0.97	0.68

previous studies did not restrict the data to those observations where release length was at least 50 cm and time at liberty at least 250 days (except Kirkwood 1983 in the case of the latter restriction).

The estimates of L_∞ and K based on length-frequency data only (Shingu 1970, Hynd and Lucas 1974, Kirkwood 1983) and those based on scale (Yukinawa 1970) and otolith readings (Thorogood 1986) must be treated with caution because they were estimated from samples which consisted of no, or very few, larger fish (in the case of length-frequency data, modes are rarely visible beyond 100 cm). As discussed by Knight (1968), this almost inevitably leads to biased estimates of the growth parameters.

The analyses of both real and simulated data indicate that biased parameter estimates may result if model error is ignored. In addition, the incorporation of

Table 7
Southern bluefin tuna growth parameter estimates derived by other workers.

Source	Method	L_∞ (cm)	K/yr	t_0 (yr)	n
Shingu (1970) (data from Robins 1963)	Length-frequency	222.5	0.140	0.011	?
Shingu (1970)	Tag return	187.4	0.149	0.021	?
Yukinawa (1970)	Scales	219.7	0.135	0.040	1025
Hynd and Lucas (1974)	Length-frequency	220.0	0.150		?
Murphy (1977)	Tag return	180.8	0.146	−0.011	2578
Hearn (unpubl.)	Tag return	178.6	0.117	−0.010	629
Kirkwood (1983)	Tag return	185.3	0.155		794
	Tag return*	209.0	0.125		794
	Length-frequency	184.2	0.166	−0.036	77
	Length-frequency*	214.8	0.133	−0.095	77
	Tag return and length-frequency	184.4	0.157	−0.215	794+77
	Tag return and length-frequency*	207.6	0.128	−0.394	794+77
Thorogood (1986)	Otoliths	261.3	0.108	−0.157	~480

*Time-at-liberty and/or age assumed to be the dependent variable.

model error to both the Kirkwood and Somers model and the Sainsbury model resulted in significantly better fits to the data. This suggests that growth models that include individual variability should, if possible, include model error in the estimation procedure.

Release-length-measurement error did not prove to be a significant source of error in this case. However, its effect should, if possible, be tested in tag-recapture growth studies and, if significant, incorporated into the model as shown in this paper. This will be essential if negative length increments are included in the data set being analysed.

Sainsbury (1980) showed that an underestimate of mean K can result if substantial individual variability in K is present but ignored. There are a number of indications from southern bluefin data that the level of individual variability in K is not substantial. First, there is virtually no difference in estimates of μ_{L_∞} and μ_K between models 3 and 6 and between models 4 and 7. (The only difference in the models in each case is that both the latter models incorporate individual variability in K.) If the real level of individual variability in K was substantial, we might expect, on the basis of Sainsbury's (1980) observation, that models 3 and 4 would have given overestimates of μ_{L_∞} and underestimates of μ_K compared with models 6 and 7. Second, analyses of length-frequency modes suggest that the variance of length-at-age increases with increasing age (W.S. Hearn, CSIRO Div. Fish., GPO Box 1538, Hobart 7001, Aust., pers. commun.). This, as Sainsbury (1980) notes, is more the rule than the exception in fish populations, and is indicative of variation in L_∞ having the dominant effect on overall variation in length-at-age. Third, modes are clearly visible in the length-frequency data for at least the first four age-classes (Kirkwood 1983). Majkowski et al. (1987) give a general condition for the visual or statistical separability of length-frequency modes as $|\mu_i - \mu_{i-1}| < 2\min(\sigma_i,\ \sigma_{i+1})$, where μ_i and σ_i are the mean length and its standard deviation, respectively, of age-class i. Applying this condition to the mean-length and standard-deviation-at-age data given in Table 2, we find that only for models 3 and 4 (no variation in K) and models 6 and 7 ($\sigma_K/\mu_K = 0.07$) is the condition satisfied for separating age-classes 3 and 4. On this basis, we could conclude that the visibility of at least four modes in the length-frequency data would preclude levels of K variability much greater than those derived for models 6 and 7.

The problem of selecting the most appropriate model for use in stock assessment was addressed, using likelihood ratio tests. These indicated that model 1 was inadequate, and that a significantly better description of the data was provided by incorporating individual variation in L_∞ (model 3). However, the incorporation of individual variation in K or release-length-measurement error could not be justified.

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