

A flexible maximum likelihood approach for fitting growth curves to tag-recapture data

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Abstract: We describe a novel maximum likelihood method for fitting general growth curves to tag-recapture data. The growth model allows for the asymptotic length and the time to tagging to vary from individual to individual, with other parameters being fixed. Unlike the Fabens approach, we do not take differences to fit the parameters, but instead model the joint density of the release and recapture lengths. We simulate data to examine the bias and precision of the estimated parameters obtained using our fitting method. We include simulations for which the time to tagging model is incorrect, but find that the growth curve is usually still fitted with small bias. Furthermore, we introduce a new growth curve that allows for different growth rates for juveniles and adults. The new growth curve needs sufficient data coverage before and after the transition from juvenile to adult for all parameters to be estimated precisely. We illustrate the method on real data by fitting this new growth curve to southern bluefin tuna tag-recapture data.

Résumé : On trouvera ici une méthode nouvelle de vraisemblance maximale pour ajuster les courbes générales de croissance à des données de marquage et de recapture. Le modèle de croissance permet d'inclure des variations individuelles dans la longueur asymptotique et l'âge au marquage, tous les autres paramètres étant fixes. Au contraire de la méthode de Fabens, nous n'utilisons pas les différences pour ajuster les paramètres, mais nous modélisons la densité conjointe des longueurs au marquage et à la recapture. Une simulation des données permet de déterminer l'erreur et la précision des paramètres estimés par notre méthode d'ajustement. Dans des simulations où le modèle de l'âge au marquage est incorrect, la courbe de croissance s'ajuste néanmoins avec de faibles erreurs. De plus, nous présentons une nouvelle courbe de croissance qui permet de tenir compte de l'existence de taux différents de croissance pour les jeunes et les adultes. La nouvelle courbe de croissance nécessite une gamme suffisante de données d'avant et d'après la transition de jeune à adulte pour pouvoir estimer les paramètres avec précision. L'ajustement de la nouvelle courbe de croissance à des données de marquage et de recapture du thon rouge du Sud donne une illustration concrète du fonctionnement de la méthode.

[Traduit par la Rédaction]

Introduction

Understanding how fish grow is a fundamental component of fish biology, and quantitative information on growth is critical to the stock assessment process. However, it is not only mean growth that is important to characterize, but also the variability among individuals. One of the primary sources of information used for estimating the growth rates of fish comes from tagging studies. In these studies, the length of a fish is measured and recorded when the fish is released and recaptured. The times of release and recapture are also recorded so that the time at liberty is known. The estimation of growth rates from these data presents a difficult challenge for several reasons: there are only two measurements per fish, the age at first release is not precisely

known, and fish vary in their growth from individual to individual.

Despite these obvious difficulties, several efficient methods of estimating growth curves from tag-recapture data have been developed (e.g., Fabens 1965; Francis 1988; Palmer et al. 1991). The estimation process involves determining both an appropriate parametric form for the growth curve and a reliable statistical procedure for fitting the data to the growth curve. The determination of the appropriate curve is often an iterative process using standard statistical model selection criteria. Nonparametric estimation of growth from tag-recapture data is generally not feasible because of the paucity and structure of the data. In any case, parametric models can provide insights into the underlying functional processes and allow for direct comparison of growth curves across time and space or between different populations or species. Moreover, differences among individuals can be captured by modeling some of the growth parameters as random variables.

A wide variety of parametric models has been used to model fish growth, with the von Bertalanffy (VB) growth model being the most ubiquitous. However, the generalized von Bertalanffy, the Richards, the Gompertz, and the logistic models have all been advocated (see Schnute 1981). In fact, any cumulative statistical distribution scaled by an asymptotic length could be used, although the growth curve preferably should have a biological motivation. Almost all modeling of

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fish growth has been based on modeling the growth rate as a continuous, smooth, monotonically decreasing function of age. However, recent analyses of growth in southern bluefin tuna (SBT) suggest that there is a marked change in the growth process somewhere during the transition from the juvenile to subadult part of the life cycle (Anonymous 1994; Hearn and Polacheck 2002). Hearn and Polacheck (2002) suggest this might also be a feature in other tuna species. In the SBT case, growth has been modeled as a two-stage process in which growth in each stage follows a different VB curve, with a discontinuity in the growth rates at the transition point between the two. However, Hearn and Polacheck (2002) identify problems both with the biological interpretation of this model and in statistically fitting it. Thus there is a need, at least in the case of SBT, for alternative growth models that can adequately represent the complex pattern of growth.

A large body of scientific literature exists on the statistical estimation of growth curves from tag-recapture data. The most widely used approach in fisheries' research has been the one developed by Fabens (1965). However, this approach does not take into account variability among individuals in their growth curves, cannot be applied to the full range of potential growth models, and is not asymptotically consistent (Maller and de Boer 1988). Extensions to the Fabens approach that can accommodate individual variability in growth within a VB model framework have been developed by Sainsbury (1980) and Hampton (1991), but these methods still bear some of the limitations of a Fabens-type approach. James (1991) and Wang (1998) have developed fitting procedures based on estimating equations as a statistically rigorous alternative to Fabens' method, but again there are problems in applying the estimating equations approach to more complicated growth models. As such, there remains a need for a flexible estimation method that can be adopted to a wide range of alternative growth models, that can accommodate individual variability in the growth parameters, and that can provide a statistical basis for selecting the most appropriate and parsimonious model.

In the current paper, we develop an alternative maximum likelihood approach for estimating growth curves from tag-recapture data that is based on estimating the joint density of tag and recapture lengths rather than modeling growth increments. This method allows for individual variability in growth by having selected parameters considered as random effects. Standard statistical tests based on likelihood theory and Akaike's information criteria (Akaike 1974) may be used to compare and select among alternative models. Although Wang et al. (1995) have proposed a similar approach, our method requires less restrictive assumptions and can easily be applied to a wide range of growth curves. Furthermore, we have developed a new growth curve that can accommodate a marked change in the growth pattern at some point in the life cycle. We apply our estimation method along with the proposed new growth curve to tag-recapture data for SBT.

Methods

The joint density of tag and recapture lengths for a general growth model

In this section, we derive the joint density of tag and recapture lengths for a single fish. This is formulated in terms

of a general model for fish growth in which the asymptotic length varies from fish to fish. Other parameters are fixed. The joint density is needed for maximum likelihood fitting of the growth model and inference about its relative fit.

In tag-recapture studies, a fish is tagged at time t_1 with length l_1 and is recaptured at time t_2 with length l_2 . We know that fish growth during the very early stages of life (e.g., during the egg and larval stages) follows a different process from subsequent growth. However, we do not have data with which to model this initial growth. We define t_0 to be the time at which a fish would have had length 0 if we were to project its postlarval growth trajectory backwards. We acknowledge that t_0 is a theoretical value with no real biological interpretation.

Let $A = t_1 - t_0$, then A varies from fish to fish, partly because the fish are spawned at different times (which results in t_0 varying between fish) and partly because there may be several tagging expeditions (so that t_1 varies). For convenience, we will refer to A simply as the age at tagging, keeping in mind that it is age relative to t_0 , not relative to birth.

We assume that a generic growth function $f(t)$ is available, where $f(t)$ is a monotone increasing function of time, t . It approaches 1 as $t \rightarrow \infty$ and is 0 when t is t_0 . The growth of each fish follows the form of $f(t)$, although with individual variations.

The assumed growth curve for the fish is

$$(1) \quad l(t) = L_{\infty} f(t; A, \theta)$$

where L_{∞} (the asymptotic length) is random from fish to fish with mean μ_{∞} and variance σ_{∞}^2 , A is random from fish to fish with density $p(\cdot)$, θ is a vector of fixed unknown parameters, and t is real time. For example, for the von Bertalanffy model,

$$f(t; A, \theta) = \begin{cases} 1 - \exp(-k(A + t - t_1)) & \text{if } t > t_1 - A \\ 0 & \text{otherwise} \end{cases}$$

so $\theta = \{k\}$ has only one component. Let $\delta t = t_2 - t_1$ be the time increment between tagging and recapture. To analyze tag-recapture data, we need the familiar equations

$$f(t_1; A, \{k\}) = 1 - \exp(-kA)$$

$$f(t_2; A, \{k\}) = 1 - \exp(-k(A + \delta t))$$

James (1991), Palmer et al. (1991), and Wang et al. (1995) have all discussed the estimation of von Bertalanffy parameters from tag-recapture data using this style of model. Our aim is to show that parameter estimation is still feasible for more complex and realistic growth models $f(\cdot)$ in eq. 1.

In this article, we assume that L_{∞} and A are both random variables. Models in which either L_{∞} or A are the same unknown constants for all fish are implausible, and models for which L_{∞} and A are different constants are overparameterized, so ours is the simplest realistic assumption. We denote random variables by capital letters. We follow James (1991), Palmer et al. (1991), and Wang et al. (1995) in assuming that L_{∞} and A are independent. We have no evidence to the contrary.

We assume for convenience that L_{∞} has a normal distribution. Intuitively, this seems reasonable, and we have no data

to refute it. We also assume that measurements are taken at times t_1 and t_2 (with $t_1 < t_2$), so that

$$(2) \quad l_1 = l(t_1) + \epsilon_1$$

$$(3) \quad l_2 = l(t_2) + \epsilon_2$$

where ϵ_1 and ϵ_2 represent measurement error. They are also normally distributed with mean 0 and variance σ^2 and are independent from fish to fish. We assume also that ϵ_1 and ϵ_2 are independent of L_∞ and A .

We are now in a position to derive the joint distribution of l_1 and l_2 . For the moment, we argue conditional upon a known value of A , say $A = a$. Then l_1 and l_2 are both the sum of normal random variables and hence are themselves normal. Their first and second moments are

$$\mu_1(a) = E(l_1|a) = \mu_\infty f_1$$

$$\mu_2(a) = E(l_2|a) = \mu_\infty f_2$$

$$\sigma_1^2(a) = \text{Var}(l_1|a) = \sigma_\infty^2 f_1^2 + \sigma^2$$

$$\sigma_2^2(a) = \text{Var}(l_2|a) = \sigma_\infty^2 f_2^2 + \sigma^2$$

$$\text{Cov}(l_1, l_2|a) = \sigma_\infty^2 f_1 f_2$$

$$\rho(a) = \text{Corr}(l_1, l_2|a) = \frac{\sigma_\infty^2 f_1 f_2}{\sigma_1(a) \sigma_2(a)}$$

where $f_1 = f(t_1; a, \theta)$ and $f_2 = f(t_2; a, \theta)$. Clearly, l_1 and l_2 are joint normal with conditional density

$$(4) \quad h(l_1, l_2|a) = \frac{1}{2\pi\sigma_1(a)\sigma_2(a)\sqrt{1-\rho(a)^2}} \exp\left\{-\frac{q_{12}(a)}{2(1-\rho(a)^2)}\right\}$$

where

$$q_{12}(a) = \frac{(l_1 - \mu_1(a))^2}{\sigma_1(a)^2} - 2\rho(a) \frac{(l_1 - \mu_1(a))(l_2 - \mu_2(a))}{\sigma_1(a)\sigma_2(a)} + \frac{(l_2 - \mu_2(a))^2}{\sigma_2(a)^2}$$

If A is random, the unconditional joint density of l_1, l_2 is

$$(5) \quad h(l_1, l_2) = \int_0^\infty h(l_1, l_2|a)p(a)da$$

There are several points to note. First, the joint density (eq. 5) involves a single integral, whereas Wang et al. (1995) have a double integral. Second, $l_2 < l_1$ is allowed, whereas Wang et al. (1995) do not allow it. Third, a more complex model for the measurement error may be desirable and can easily be incorporated. For example, in the case of SBT, recapture lengths are measured by fishermen and scientists, but tag lengths are measured by scientists only. The fishermen are believed to be less precise. Hence it may be desirable to structure the measurement errors so that $\text{Var}(\epsilon_2) > \text{Var}(\epsilon_1)$ when l_2 is measured by fishermen. Fourth, correlation between ϵ_1 and ϵ_2 may also be allowed for very easily, although it is likely to be poorly identified. Finally, condi-

tioning on nonlinear components to simplify the analysis of partially nonlinear models has a long history in statistics. A seminal paper is Halperin (1963).

The joint density for zero measurement error

It is useful to have a special formula for $h(l_1, l_2)$ when $\sigma^2 = 0$, because it is not immediately clear what eq. 5 reduces to. We first look at the von Bertalanffy model. It is possible then to calculate exactly what A must be if l_1, l_2 , and k are known: it is

$$(6) \quad a^* = -\frac{1}{k} \log\left(\frac{l_2 - l_1}{l_2 - dl_1}\right)$$

where $d = \exp(-k(t_2 - t_1))$. Arguing from first principles, we obtain

$$(7) \quad h_0(l_1, l_2) = \frac{1}{\sigma_\infty f_2^*} \phi\left(\frac{l_2/f_2^* - \mu_\infty}{\sigma_\infty}\right) p(a^*) \frac{1}{k} \left\{ \frac{1}{l_2 - l_1} - \frac{d}{l_2 - dl_1} \right\}$$

where $f_2^* = f(t_2; a^*, \theta)$ and $\phi(\cdot)$ is the standard normal density. If $l_2 \leq l_1$, then $h_0(l_1, l_2)$ is set to 0.

For general log-concave growth curves, the formula is

$$(8) \quad h_0(l_1, l_2) = \frac{1}{\sigma_\infty f_2^*} \phi\left(\frac{l_2/f_2^* - \mu_\infty}{\sigma_\infty}\right) p(a^*) \frac{\partial a^*}{\partial l_1}$$

suggesting that an explicit formula for a^* in terms of l_1 and l_2 is needed for each model. However, it is easy to prove that

$$\frac{1}{f_2^*} \frac{\partial a^*}{\partial l_1} = \left(l_2 \frac{\partial f_1^*}{\partial a^*} - l_1 \frac{\partial f_2^*}{\partial a^*} \right)^{-1}$$

so we really only need to differentiate $f(t; a, \theta)$ with respect to a and evaluate it at (t_1, a^*) and (t_2, a^*) . Note that a^* is the solution to $f_1/l_1 = f_2/l_2$, which may need to be solved numerically. A growth curve $f(t)$ is log-concave if $\log f(t)$ is concave: that is, any straight line joining two points on the curve $\log f(t)$ lies on or beneath the curve. Many of the commonly used simple growth curves are log-concave. For several examples, we confirmed numerically that $h(l_1, l_2)$ converges to $h_0(l_1, l_2)$ as $\sigma^2 \rightarrow 0$.

Numerical computation of the integral

Computation of the integral in eq. 5 is not straightforward. When maximizing a likelihood, the integral needs to be computed separately for each fish at each step of the likelihood maximization. If there are 1000 fish in the study, and the likelihood optimization routine takes 500 steps to find the optimal parameters, the integral will need to be computed 500 000 times. For large-scale applications, a fast and accurate quadrature method is required. We used Gauss-Hermite integration after using a robust search method to locate the approximate maximum of the integrand. For details, refer to Appendix A.

A new growth curve: the von Bertalanffy with logistic growth rate parameter

Extensive tagging studies of southern bluefin tuna were undertaken during the 1960s and 1980s. This large database has enabled researchers to examine the adequacy of the von Bertalanffy growth curve, which has traditionally been the standard for this species. As noted in the Introduction, recent analyses suggest that a more complex model incorporating a two-stage growth process is required (Hearn and Polacheck 2002).

Wang (1998) has proposed the following generalization of the von Bertalanffy growth curve. Suppose a fish has length 0 at time t_0 . Then the growth rate at time t is given by

$$l'(t) = (L_\infty - l(t))k(t)$$

where $k(t)$, the function that controls the growth rate, may depend on time. The solution is

$$l(t) = L_\infty(1 - \exp(-K(t_0, t)))$$

where $K(t_0, t) = \int_{t_0}^t k(u)du$. Hearn and Polacheck (2002) argue that for SBT $k(t)$ should be a constant value, k_1 say, for juvenile tuna and a lower value, k_2 , for adult tuna. Thus $k(t)$ is a step function

$$(9) \quad k(t) = \begin{cases} k_1 & \text{for } t < t_0 + \alpha \\ k_2 & \text{otherwise} \end{cases}$$

In this model, α is the age at which juveniles become adults, denoted by t^* in Hearn and Polacheck (2002). The Hearn and Polacheck model is slightly more general than this, but the extra generality is only mildly supported by the data.

The step function (eq. 9) seems harsh from a biological viewpoint. We would at least like to allow for the possibility of a slower transition between juvenile and adult growth. In addition, the step function may cause problems for statistical analysis. For example, the likelihood in Hearn and Polacheck's (2002) analysis has two modes, which might be caused by the step function.

We propose instead modeling $k(t)$ by a logistic curve:

$$(10) \quad k(t) = k_1 + (k_2 - k_1) \frac{1}{1 + \exp(-\beta(t - t_0 - \alpha))}$$

For $t \ll t_0 + \alpha$, $k(t) \approx k_1$, and for $t \gg t_0 + \alpha$, $k(t) \approx k_2$. As t increases, $k(t)$ makes a smooth transition from k_1 to k_2 . The rate of transition is governed by β , being sharper for larger β . As $\beta \rightarrow \infty$, eq. 10 reduces to the step function given in eq. 9. An advantage of the logistic form is that it can be explicitly integrated, yielding the growth curve

$$l(t) = L_\infty \left[1 - e^{-k_2(t-t_0)} \left\{ \frac{1 + e^{-\beta(t-t_0-\alpha)}}{1 + e^{\beta\alpha}} \right\}^{-(k_2-k_1)/\beta} \right]$$

if $t \geq t_0$. Of course, $l(t) = 0$ if $t < t_0$. In the notation of eq. 1, $\theta = \{k_1, k_2, \alpha, \beta\}$ has four components, in contrast to the ordinary von Bertalanffy curve, which has one. We propose calling this the von Bertalanffy growth curve with logistic growth rate and abbreviating it as the "VB log k " model. The traditional von Bertalanffy curve is recouped if

$k_1 = k_2 = k$. Note that the VB log k model is not a member of the Schnute (1981) class.

The VB log k model could be further generalized to three or more phases in growth, reflecting different growth conditions for multiple life stages. It is also possible to generalize the von Bertalanffy by using a logistic rate $k(t)$ on the length scale: $l(t) = L_\infty(1 - e^{-k(t)(t-t_0)})$. However, this model does not have a simple growth rate interpretation, so we leave it for future investigation.

Estimation

Wang et al. (1995) suggest that a gamma distribution be used for $p(\cdot)$, the distribution of A , although we prefer the lognormal. In fact, an advantage of our approach is that any well-behaved parametric model for A can be adopted. Once the models for A and growth $f(t)$ have been decided upon, the unknown parameters can be estimated by maximizing the log-likelihood

$$\sum_{i=1}^n \log h(l_{1i}, l_{2i})$$

where n is the number of fish, and (l_{1i}, l_{2i}) are the two measurements for fish i . A numerical optimization algorithm with bound constraints is needed to fit the model.

After successfully maximizing the log-likelihood, the user may wish to estimate the realized values of A and L_∞ for each fish. One way to do this is to calculate the estimated posterior distribution using Bayes' theorem.

Thus, for a given fish, we can calculate

$$p(A = a | l_1, l_2) = \frac{h(l_1, l_2 | a)p(a)}{h(l_1, l_2)}$$

by plugging in the maximum likelihood estimates of the unknown parameters. This distribution gives the plausible range of values of A compatible with the data l_1 and l_2 . Of course, calculating this conditional distribution might be practical if there are only a few fish, but often there are hundreds. The user really requires a single summary statistic for each fish. The mean would probably be chosen, although other summary statistics, such as the median, mode, trimmed mean, and so on, could be used if desired. The mean requires a one-dimensional integration. It is worth noting that the mode of A given l_1 and l_2 is already determined for each fish if the method outlined in Appendix A for calculating the likelihood is followed. Typically, we find little difference between the mean and the mode.

Similarly, we can calculate $q(L_\infty | l_1, l_2)$, the density of the asymptotic length given the data. In practice, we would probably use the mean of $q(L_\infty | l_1, l_2)$ as a point estimate of the asymptotic length for a particular fish. The direct approach yields a double integral, but this can be avoided by exploiting the joint normality of L_∞ , l_1 , and l_2 when a is known. The formula is

$$(11) \quad E(L_\infty | l_1, l_2) = \frac{\int_0^\infty E(L_\infty | l_1, l_2, a) h(l_1, l_2 | a)p(a)da}{h(l_1, l_2)}$$

where

Table 1. Mean parameter estimates (and standard deviations) from applying our new estimation method to simulated von Bertalanffy data.

Distribution of A	Assumed	Mean growth parameter estimates (standard deviation)				Mean parameter estimates for A (standard deviation)			
		σ	μ_∞	σ_∞	k	σ	u	v	p
True									
LogN(0.5,0.5)	LogN(u,v)	0	100.3 (1.8)	5.0 (0.4)	0.50 (0.02)	0.01(0.02) ^a	0.50 (0.06)	0.50 (0.04)	—
		0	99.9 (0.8)	5.0 (0.2)	0.50 (0.01)	— ^b	0.50 (0.03)	0.50 (0.03)	—
LogN(0.5,0.5)	LogN(u,v)	2	100.1 (2.2)	4.7 (1.0)	0.50 (0.04)	2.0 (0.2)	0.50 (0.06)	0.50 (0.04)	—
LogN(0.5,0.5)	LogN(u,v)	4	99.7 (3.0)	4.3 (2.2)	0.51 (0.05)	3.9 (0.4)	0.49 (0.08)	0.50 (0.04)	—
Multimodal	Gaus.Mixt.(u,v,σ_c,p)	2	100.0 (3.3)	5.1 (1.1)	0.50 (0.05)	2.1 (0.5)	1.1 (0.06)	2.1 (0.14)	0.80 (0.05)
Multimodal	LogN(u,v)	2	100.6 (2.9)	4.8 (1.1)	0.49 (0.04)	2.0 (0.2)	0.21 (0.05)	0.31 (0.03)	—

Note: For each model, we ran 100 simulations with 100 recaptures per simulation. Data were generated with $L_\infty \sim N(100, 25)$ and $k = 0.5$. Times at liberty were taken to be $\Gamma(1,1)$ distributed. The standard deviation of the measurement error, σ , was varied, as was the distribution on the true and assumed age at tagging A . LogN(u,v) denotes a lognormal with mean u and standard deviation v on the log scale; Gaus.Mixt.(u,v,σ_c,p) denotes a Gaussian 2-component mixture with means u and v , common standard deviation σ_c , and proportion p belonging to the first component.

^aParameters were estimated using likelihood for measurement error and setting lower bound on σ at 0.001.

^bParameters were estimated using likelihood for no measurement error.

$$(12) \quad E(L_\infty | l_1, l_2, a) = \mu_\infty + \frac{\sigma_\infty^2}{\sigma^2 + \sigma_\infty^2 (f_1^2 + f_2^2)} (f_1(l_1 - \mu_\infty f_1) + f_2(l_2 - \mu_\infty f_2))$$

Thus, the conditional means $E(L_\infty | l_1, l_2)$ can be calculated by substituting eq. 12 into eq. 11 and using one-dimensional integration. It is reassuring to note that this yields the correct result when $\sigma^2 = 0$, in which case $l_1 = L_\infty f_1$ and $l_2 = L_\infty f_2$, and it is readily checked that $E(L_\infty | l_1, l_2, a) = L_\infty$. Of course, the bivariate conditional distribution $p(A, L_\infty | l_1, l_2)$ could also be calculated, although there seems little point.

Results

Simulated data

To test our proposed model fitting procedure and its generality, we carried out a number of simulations. We generated growth data according to various models, looking at the effect of different growth curves, different distributions on the age at tagging, and different amounts of measurement error.

Initially, we considered the traditional von Bertalanffy (VB) curve. In all model runs, L_∞ was taken to be normally distributed with mean 100 and standard deviation 5, and k was taken to be 0.5, such that 95% of the average maximum length was achieved by age 6. The times at liberty were generated according to a $\Gamma(1,1)$ distribution, which was chosen to be representative of tagging studies in which most recaptures occur quickly and subsequently decrease (in this case, 63% within the first year and 95% within 3 years).

At first, ages at tagging, A , were generated according to a lognormal distribution with mean and standard deviation on the log scale of 0.5 and 0.5, respectively (which we will denote by $A \sim \text{LogN}(0.5, 0.5)$). This gives a positively skewed distribution with a mode around 1.5 years of age. The effect of varying the amount of measurement error was investigated by setting σ equal to 0, 2, and 4 in different simulations. For each situation, 100 simulations using a sample size of 100 recaptures per simulation were carried out.

We now summarize the results from the above simulations. The parameter estimates obtained using the new estimation method were all unbiased, except for a slight underestimation of the variability in L_∞ as the measurement error increased (Table 1, rows 1 to 4). Otherwise, the effect of increasing the measurement error was only to increase the standard deviation of the parameter estimates. Note that in the case of zero measurement error, we ran simulations using both the likelihood based on the joint density developed for measurement error (eq. 5) and the likelihood based on the joint density for no measurement error (eq. 8). The two methods gave comparable estimates (Table 1, rows 1 and 2).

With such a small sample size and relatively short times at liberty, there is not much information on older fish with which to discern the distribution of L_∞ . Hence, it is not too surprising that the variability in L_∞ is slightly biased; perhaps more surprising is that the mean value is estimated correctly. Increasing the sample size from 100 to 500 or, alternatively, changing the distribution on the times at liberty to be uniform on [1,7] eliminated the slight bias in the standard deviation of L_∞ when σ was equal to 4.

For many studies, the ages at tagging may not follow a simple distributional form. For example, in the case of SBT, fish spawn from October to April, and tagging is performed most commonly during January. This results in a multimodal distribution for the release ages. Thus, it is important that our estimation method works for a variety of distributions for A . We generated values for A that we believe are representative of the real ages at tagging for SBT using the following steps. Firstly, from the true tagging data for SBT, we took a random sample of 100 fish and retained their release date and integer age (an integer age had been assigned to each fish based on its release length, and this age is likely to be accurate for young fish). Next, we generated a “birth date” for each fish from a normal distribution with a mean of zero (representative of January 1) and a standard deviation of 1.5 months (so that roughly 95% of the birth dates fell between October 1 and April 1). Lastly, we calculated a release age for each fish by taking its integer age (in years) and adding the difference between its release date and birth date (expressed in decimal years).

The distribution of release ages generated in the above manner has distinct modes at ages 1 and 2 and is clearly not lognormal (Fig. 1). A Gaussian mixture model appears to be an appropriate choice. Thus, we applied our estimation method to simulated data that included such ages at tagging assuming that they follow a two-component Gaussian mixture distribution with means u and v , a common standard deviation σ_c , and a proportion p belonging to the first component. We again generated times at liberty according to a $\Gamma(1,1)$ distribution, and tag and recapture lengths according to a VB curve with $k = 0.5$ and L_∞ random normal with mean 100 and standard deviation 5. The standard deviation of the measurement error was taken to be 2. The mean parameter estimates for L_∞ , k , and σ were unbiased (Table 1, second last row), which shows that the method works even for fairly complex distributions for A .

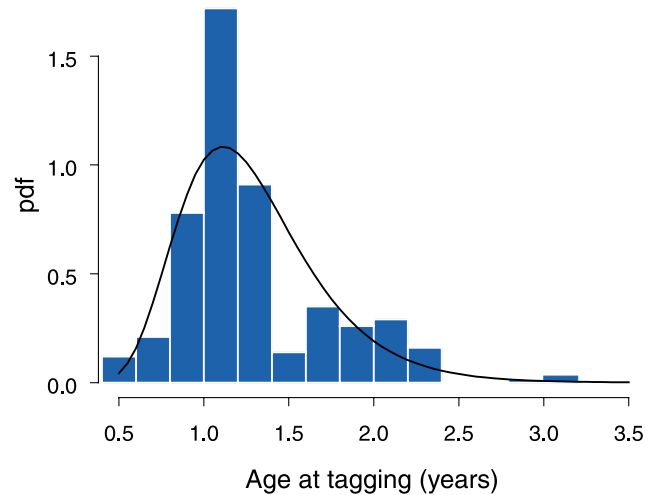
To investigate the robustness of our method to the distribution assumed for A , we reran the above simulations assuming a lognormal distribution for A . Again, the growth parameter estimates were unbiased (Table 1, last row). In this case, the lognormal distribution gave a fair approximation to the true distribution of A , as shown in Fig. 1 where the fitted lognormal curve is overlaid on the histogram of release ages. In most situations, the researcher will have some information about the release ages, and the method appears to be quite robust provided a reasonable distribution for A is chosen. For example, in the above simulations, we could have chosen the gamma distribution instead of the lognormal and achieved equally good results.

One of the advantages of our estimation method is its ability to generalize to a wide range of growth curves. To illustrate this, we ran simulations on growth data generated from a logistic curve, a generalized von Bertalanffy (GVB) curve, as well as a von Bertalanffy curve with a logistic growth rate (VB log k , as described in the Methods section). The logistic curve can be expressed as

$$(13) \quad l(t) = L_\infty(2(1 + \exp(-k(t - t_0)))^{-1} - 1)$$

parameterized such that $l(t) = 0$ when $t = t_0$ and $l(t)$ approaches L_∞ as $t \rightarrow \infty$. The equation for a GVB curve is

Fig. 1. Histogram of simulated realistic ages at tagging for southern bluefin tuna, scaled such that the total area of the bars is one. The line shows the fitted probability density function (pdf) assuming a lognormal distribution.



$$(14) \quad l(t) = L_\infty(1 - \exp(-k(t - t_0)))^r$$

for $r > 0$. Note that the logistic and GVB curves are both special cases of the Richards' growth curve. In our simulations for all models, we took L_∞ to be normally distributed with mean 100 and standard deviation 5, A to be $\text{LogN}(0.5, 0.5)$, the times at liberty to be $\Gamma(1,1)$, and σ to be 2.

For the logistic curve, we set $k = 0.5$, and for the GVB curve, we set $k = 0.5$ and $r = 2$. These two curves have a slower rate of growth than the VB curve, and the GVB curve has an inflection point at age $\log(2)/0.5 \approx 1.4$ (Fig. 2a). For the logistic and GVB models, we ran 100 simulations with 100 recaptures per simulation. For both models, all parameter estimates were accurate with the exception of σ_∞ , which shows a small negative bias and larger variability (Table 2). As with our simulations for the VB model, this is not surprising because we are generating data that has very little information on older fish. We illustrate a typical simulated data set for the logistic model along with the true curve (Fig. 2b). The asymptotic length is not reached until approximately age 10 but there is little data exceeding age 6. Still, μ_∞ is estimated very accurately and with more extensive data coverage, σ_∞ would be estimated with greater accuracy and precision as well.

For the VB log k model, we set $k_1 = 0.8$, $k_2 = 0.3$, $\alpha = 1.5$, and $\beta = 4$, giving a fairly rapid reduction in growth rate from about age 0.5 to age 2.5 (Fig. 3). To avoid identifiability problems, we did not optimize over β because β appears to be highly correlated with k_1 and k_2 . Furthermore, we increased the sample size to 500 recaptures in each of the 100 model runs because the data are otherwise insufficient to discriminate between likelihoods for many sets of parameter values. Even for this more complex growth model, the parameter estimates were accurate and unbiased (Table 3, row 1).

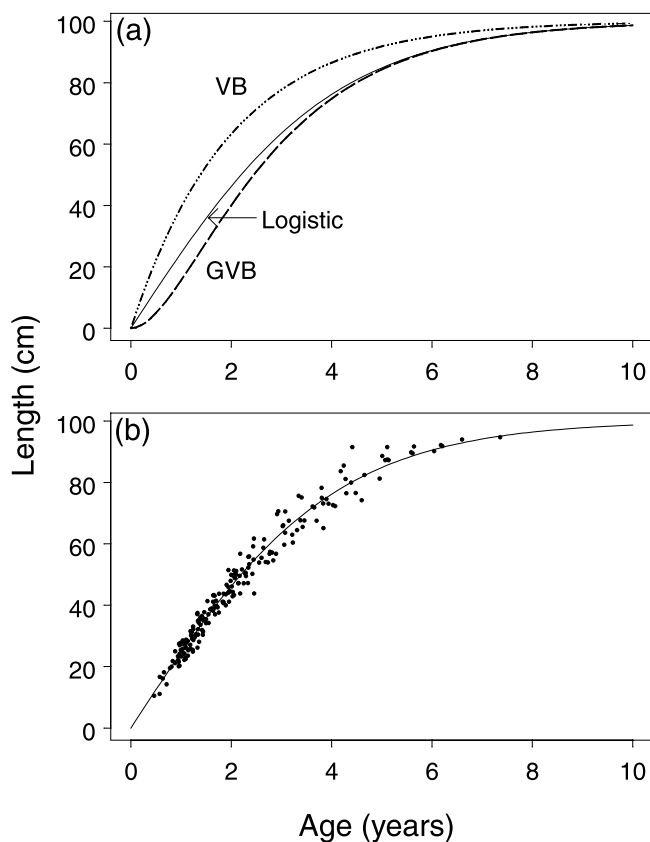
The necessity to fix β can be relaxed if the data are more comprehensive such that there is sufficient information before and after the transitional stage in the growth rate; however, care must still be used. We increased α to 2.5 so

Table 2. Mean parameter estimates (and standard deviations) from applying our new estimation method to simulated logistic and generalized von Bertalanffy (GVB) growth curves.

Growth curve	Mean growth parameter estimates (standard deviation)					Mean parameter estimates for A (standard deviation)	
	μ_∞	σ_∞	k	r	σ	$\mu_{\log A}$	$\sigma_{\log A}$
Logistic	100.0 (2.9)	4.2 (1.5)	0.50 (0.03)	—	2.0 (0.2)	0.51 (0.07)	0.49 (0.03)
GVB ($r = 2$)	100.2 (3.3)	4.4 (1.3)	0.50 (0.05)	2.1 (0.6)	2.0 (0.2)	0.49 (0.15)	0.50 (0.07)

Note: For each model, we ran 100 simulations with 100 recaptures per simulation. Data were generated assuming $L_\infty \sim N(100, 25)$, $k = 0.5$, age at tagging $A \sim \text{LogN}(0.5, 0.5)$ and $\sigma = 2$. Times at liberty were taken to be $\Gamma(1, 1)$ distributed.

Fig. 2. (a) Comparison between the von Bertalanffy (VB), logistic, and generalized von Bertalanffy (GVB) growth curves with $L_\infty = 100$ and $k = 0.5$ for all curves and $r = 2$ for the GVB curve. (b) A typical simulated data set to which we are fitting the logistic growth curve.

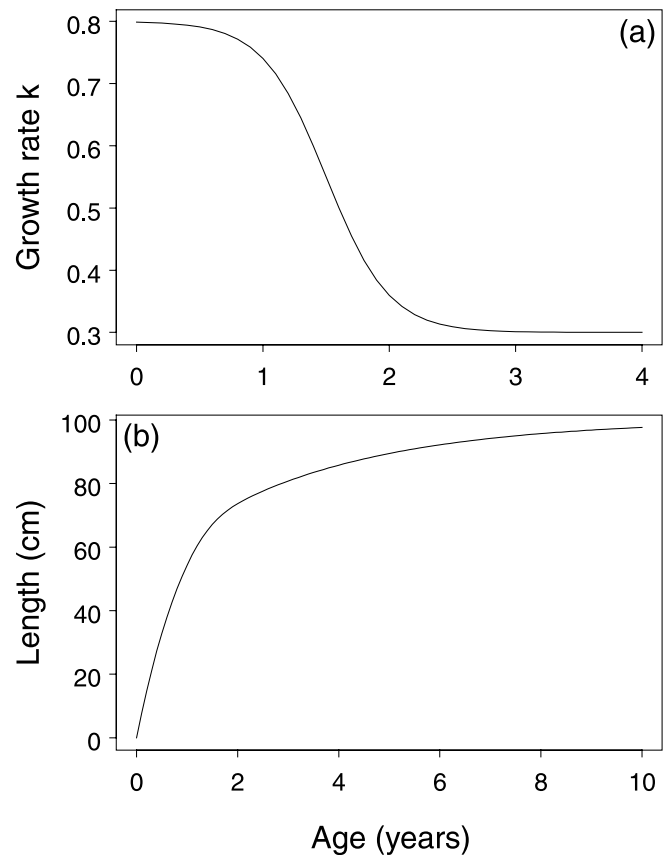


that there was more data before the transition and also changed the times at liberty to be uniform over the interval [1,7] and then ran simulations in which β was allowed to vary. In several data sets, either β , k_1 , or k_2 converged to one of its set bounds. Nevertheless, for the 82 of the 100 model runs in which this did not occur, the mean estimates for the parameters were good (Table 3, row 2). Note that the coefficient of variation in β is much larger than in any of the other parameters.

SBT tag-recapture data

To illustrate the method on real data, we used tag-recapture data from SBT that were released in the 1980s. A total of 1412 recaptures were included in the analysis. The times at liberty ranged from 270 days (an imposed minimum to re-

Fig. 3. (a) Logistic growth rate with $k_1 = 0.8$, $k_2 = 0.3$, $\alpha = 1.5$, and $\beta = 4$. (b) von Bertalanffy curve with logistic growth rate (parameters as above) and $L_\infty = 100$.



move the effects of seasonal growth) to 4356 days (12 years), with 95% of the returns occurring in the first 3 years.

We began by using our method to fit the standard von Bertalanffy growth curve. We assumed that the ages at tagging followed a lognormal distribution, because our simulations in the previous section using release ages generated from the SBT tagging data indicated this was a reasonable assumption. Furthermore, we assumed that the measurement errors in release and recapture lengths, ϵ_1 and ϵ_2 , were normally distributed with mean = 0 and common variance σ^2 . We proceeded to make the model more complex by fitting the VB log k growth curve, leaving all other assumptions the same. Finally, we fit both the VB and the VB log k growth curves incorporating a more complicated error structure in which the error variance in recapture lengths differed according to the measurer, scientific staff or fishermen.

Table 3. Mean parameter estimates (and standard deviations) from applying our new estimation method to simulated von Bertalanffy logistic k growth data.

dt	n	α	Mean growth parameter estimates (standard deviation)							Mean parameter estimates for A (standard deviation)	
			μ_∞	σ_∞	k_1	k_2	α	β	σ	$\mu_{\log A}$	$\sigma_{\log A}$
$\Gamma(1,1)$	100	1.5	99.7 (2.2)	5.0 (0.4)	0.81 (0.06)	0.31 (0.04)	1.5 (1.1)	4 ^a	2.0 (0.1)	0.50 (0.05)	0.50 (0.02)
Unif(1,7)	82 ^b	2.5	100.4 (2.1)	5.0 (0.3)	0.83 (0.08)	0.30 (0.09)	2.4 (0.3)	4.3 (1.8)	1.9 (0.4)	0.48 (0.08)	0.51 (0.02)

Note: We ran n simulations with 500 recaptures per simulation. Data were generated with $L_\infty \sim N(100,25)$, $k_1 = 0.8$, $k_2 = 0.3$, $\alpha = 1.5$ or 2.5 (as specified in the table), and $\beta = 4$, age at tagging $A \sim \text{LogN}(0.5,0.5)$, and $\sigma = 2$. The distribution on the times at liberty, dt , was varied from a gamma distribution ($\Gamma(1,1)$) to a uniform distribution (Unif(1,7)).

^aFixed at 4 to avoid identifiability problems.

^bOf the 100 simulations, 82 did not have identifiability problems in which β , k_1 , or k_2 converged to a set bound.

Table 4. Parameter estimates from applying our estimation method to 1980s southern bluefin tuna tag–recapture data ($n = 1412$).

Growth curve	Error structure	Parameter estimates										–log likelihood	AIC
		μ_∞	σ_∞	k_1	k_2	α	β^a	$\mu_{\log A}$	$\sigma_{\log A}$	σ	σ_f		
VB	Simple	160.6	8.8	0.28	—	—	—	0.55	0.17	3.9	—	9633.1	19 278.2
VB	Sci./Fish.	162.0	7.1	0.27	—	—	—	0.56	0.18	2.9	4.2	9611.3	19 236.6
VB log k	Simple	188.2	10.9	0.22	0.16	3.0	30	0.58	0.16	3.7	—	9609.7	19 237.4
VB log k	Sci./Fish.	186.6	9.3	0.22	0.17	2.9	30	0.58	0.18	2.6	4.1	9585.7	19 191.4

Note: Negative log-likelihood values and Akaike’s information criteria (AIC) are also given. Results are for the von Bertalanffy (VB) and von Bertalanffy logistic k (VB log k) growth curves with both simple and measurer-dependent (Sci./Fish.) error structures.

^a β constrained to be ≤ 30 .

Scientists measured all release lengths so there was no need to make this distinction for ϵ_1 . In particular,

$$\text{var}(\epsilon_1) = \sigma^2$$

$$\text{var}(\epsilon_2) = \begin{cases} \sigma^2 & \text{if measured by a scientist} \\ \sigma^2 + \sigma_f^2 & \text{if measured by a fisherman} \end{cases}$$

For a given growth curve (either the VB or VB log k), the estimates of the growth parameters were very similar regardless of the error structure assumed (Table 4). However, the fits were significantly better when the measurer-dependent error structure was included, as indicated by the smaller Akaike information criteria (AIC) values (Table 4). This suggests that the more complex error structure is a worthwhile addition as it explains a significant amount of the residual variation.

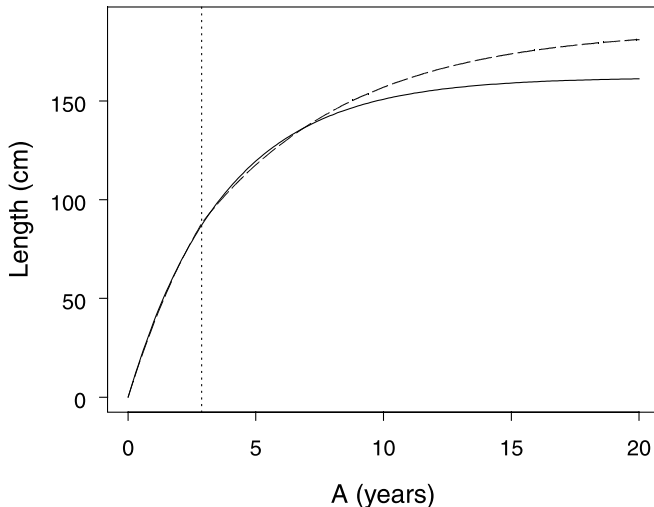
Both of the VB log k models gave a significantly improved fit compared with the VB model with an equivalent error structure. Again this is indicated by the smaller AIC values. The mean fitted curves for the VB and VB log k models with measurer-dependent error variance are very similar up until about age 7, at which point the VB log k curve becomes progressively higher than the VB curve (Fig. 4). To further compare and evaluate these models, we calculated residuals for the fitted recapture lengths (Fig. 5). To calculate these fitted values requires a realized value of A and L_∞ for each fish, which we estimated using the procedures described in the Methods section (under Estimation). Briefly, for each fish we calculated the mean of the posterior distribution for A and for L_∞ given the fish’s release length

and recapture length. Two features of the residual plots are worth noting. First, the improved fit of the VB log k model over the VB model is apparent in the residuals for large fish. We see that the mean asymptotic length is being underestimated in the VB model. Second, the reason for incorporating a measurer-dependent error structure seems clear because the residuals are markedly smaller for lengths measured by scientists than for those measured by fishermen.

Approximate errors for the parameter estimates can be obtained by inverting the observed information matrix $\{\partial^2 l / \partial p_i \partial p_j\}$, where l is the maximum log-likelihood and p is the vector of parameters. Parameters on the boundary of the parameter space must be regarded as fixed. We used this method for the VB log k model with simple error structure (Table 4, row 3). The estimates 0.220 of k_1 and 0.163 of k_2 have standard errors of 0.011 and 0.013, respectively, with correlation 0.918. Thus the estimate of $k_1 - k_2$ is 0.057 with standard error 0.017, confirming that k_1 and k_2 are significantly different and that a simple VB model is inadequate. Similarly, for the VB log k model with measurer-dependent error variance (Table 4, row 4), the estimate of $k_1 - k_2$ is 0.053 with standard error 0.019, leading to the same conclusion.

For the VB log k models, β , the parameter that governs the rate at which the growth rate changes was optimized at a set upper bound of 30. This means an almost instantaneous switch in growth rate from k_1 to k_2 at age α . However, in the previous section we saw that the estimate of β can be high even if the true value of β is low when the data coverage is inadequate. To check this, we ran a number of simulations of 1400 fish with parameters close to those for the fitted VB

Fig. 4. Mean growth curves for the 1980s southern bluefin tuna tag-recapture data. The solid line is the von Bertalanffy fit and the broken line is the von Bertalanffy logistic k fit, both from models incorporating a measurer-dependent error structure. The dotted vertical line shows the estimated transition point, α , for the von Bertalanffy logistic k model.



log k model with simple error structure (Table 4, row 3), but with $\beta = 3$. The times at liberty were sampled from the observed times. We found that β was estimated correctly more than half the time, but converged to 30 (the upper bound) in the remaining runs. The other parameters were all estimated with minimal bias and good precision regardless of the estimate of β . Hence, we cannot be certain of the rate of transition between the phases, but we expect the other parameter estimates to be unaffected.

Discussion

The results from this paper show that the maximum likelihood method we propose for fitting growth models to tag-recapture data is a viable alternative to the methods already in existence. By modeling the joint density of l_1 and l_2 , we avoid the inconsistency problems that result from applying Fabens' method. However, in return, we must model the distribution of A .

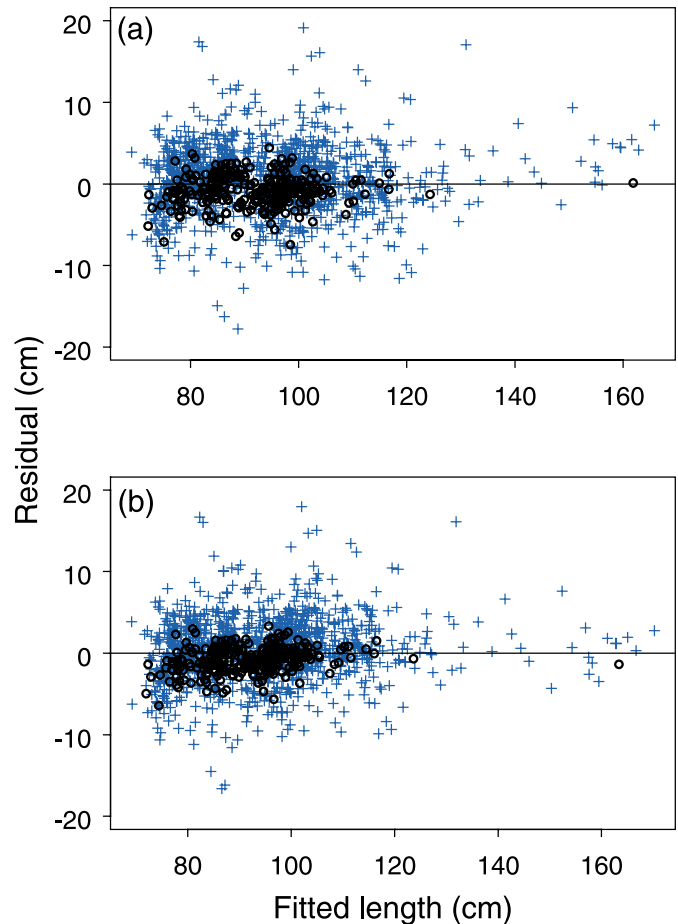
Wang (1998) has recommended fitting growth models using first-order estimating equations. This appears attractive because it also is statistically rigorous, yet it avoids the need to model A . We therefore consider this method more closely for our own situation. James (1991) has described the method for the von Bertalanffy model, but it may be extended to other more realistic models following the principles outlined by Wang (1998). For the VB log k model, let

$$S(t_1, t_2) = k_2(t_2 - t_1) + \frac{k_2 - k_1}{\beta} [\log(1 + e^{-\beta(t_2 - t_1 - \alpha)}) - \log(1 + e^{\alpha\beta})]$$

and

$$\eta(t_1, t_2, l_1, l_2) = l_2 - l_1 - (\mu_\infty - l_1)(1 - e^{-S(t_1, t_2)})$$

Fig. 5. Residuals between the actual and fitted recapture lengths for (a) the von Bertalanffy model and (b) the von Bertalanffy logistic k model fit to the 1980s southern bluefin tuna tag-recapture data. Both models incorporate a measurer-dependent error structure; the pluses indicate length measurements made by fishermen, whereas the open circles indicate length measurements made by scientists.



For fish i , let $S_i = S(t_{1i}, t_{2i})$ and $\eta_i = \eta(t_{1i}, t_{2i}, l_{1i}, l_{2i})$. The five unknown parameters $\{\mu_\infty, k_1, k_2, \alpha, \beta\}$ may be estimated by solving the five nonlinear equations

$$\begin{aligned} \sum_{i=1}^n \eta_i &= 0; & \sum_{i=1}^n \frac{\partial S_i}{\partial k_1} \eta_i &= 0; & \sum_{i=1}^n \frac{\partial S_i}{\partial k_2} \eta_i &= 0; \\ \sum_{i=1}^n \frac{\partial S_i}{\partial \alpha} \eta_i &= 0; & \sum_{i=1}^n \frac{\partial S_i}{\partial \beta} \eta_i &= 0 \end{aligned}$$

We attempted to solve these equations for the 1980s tagging data using commercial routines, with starting values near the maximum likelihood estimates for the VB log k model with simple error structure. We obtained $\hat{\mu}_\infty = 164.5$, $\hat{k}_1 = 0.265$, $\hat{k}_2 = 0.263$, $\hat{\alpha} = -0.606$, and $\hat{\beta} = 12.5$. These are suspiciously close to a simple VB solution. Suppose that \tilde{k} and $\tilde{\mu}_\infty$ are the solutions of the simple VB estimating equations. It is then easy to show that setting $k_1 = k_2 = \tilde{k}$, $\alpha = 0$, $\beta \rightarrow \infty$, and $\mu_\infty = \tilde{\mu}_\infty$ will solve the VB log k estimating equations—in fact, α and β merely need to satisfy $\sum_{i=1}^n \zeta_i \eta_i = 0$, where $\zeta_i = \log(1 + e^{-\beta(t_{2i} - t_{1i} - \alpha)})$, so other combinations of α and

β may suffice. Hence, a simple VB model always provides one solution. It is possible that the equations have other solution classes, but the existence of a simple VB solution is already an unsatisfactory feature.

There are other problems with these estimating equations: they do not yield estimates of σ_∞ and the residual variance parameters, and there is no way of estimating and testing for structure in the residual variation. These problems might be solved by moving to second-order estimating equations. However, we recommend staying with maximum likelihood, at least until the estimating equations approach is better understood.

Although the literature on fitting growth models to tag-recapture data is vast, most methods in existence bear some limitation: they do not allow for individual variability in growth, are restrictive in the way in which individual variability can be incorporated, give inconsistent parameter estimates, are inflexible in the error structures that can be assumed, or are not easily generalized to growth functions other than the von Bertalanffy. Our proposed maximum likelihood method appears to overcome these weaknesses.

In the case of a random L_∞ , our method can easily be generalized to any growth function. This was suggested in the derivation of the likelihood, which used a generic growth function, $f(t)$, and illustrated in our simulations using a range of growth functions.

Although we only allowed for individual variability in growth through a random asymptotic length, the likelihood equations can be derived for other random effects. For example, in the von Bertalanffy model, we might want to assume a random k parameter instead. We can adapt the argument presented in the Methods section and condition on both A and k , but a double integration is now required and would be time-consuming computationally. Alternatively, we can use modified Sheiner-Beal linearization to make the model linear in its random effects (Jones 1993, chapt. 7). If these are Gaussian, we avoid any integration problems, even where L_∞ and k are both random. However, we concur with the arguments summarized in the discussion of Wang et al. (1995) that reject the need for letting both k and L_∞ vary.

As a final point, the VB log k growth curve that we proposed shows potential as a growth curve for modeling SBT and other large pelagic species. The improved fit from applying this model compared with the simple von Bertalanffy lends support to the idea of a two-stage growth process for SBT.

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Appendix A

We discuss the efficient and accurate numerical computation of the integral in eq. 5. Denote the integrand by

$$g(a) = h(l_1, l_2 | a) p(a)$$

for given l_1 and l_2 . Note that $g(a)$ is proportional to the conditional distribution of A given l_1 and l_2 . Consideration of several examples with A lognormal suggests that $g(a)$ is often unimodal and nearly Gaussian in appearance. We can exploit this observation to integrate $g(a)$ efficiently. We first need to find the mode and spread of $g(a)$. After considerable experimentation, we decided on the following scheme.

1. Use an efficient and robust search method (e.g., Brent's method) to locate the maximum of $g(a)$ (Brent 1973, chapt. 5). This is best done on the log scale, because $g(a)$ is approximately Gaussian near its maximum and hence approximately quadratic on the log scale. Denote the location of the maximum by μ_g .
2. Estimate the standard deviation of $g(a)$ by

$$\sigma_g = \sqrt{-1 / z''(\mu_g)}$$

where $z(a) = \log g(a)$. A simple way of calculating $z''(\mu_g)$ is to fit a quadratic to $\log g(a)$ in the neighbourhood of μ_g .

Once we have good estimates of μ_g and σ_g , we can use any accurate quadrature method to calculate eq. 5. We preferred to use Gauss–Hermite integration because it does not require many function evaluations. Define $g(a) = 0$ for $a < 0$. Thus

$$\begin{aligned} h(l_1, l_2) &= \int_0^\infty g(a) da \\ &= \int_{-\infty}^\infty g(a) da \\ &= \sqrt{2} \sigma_g \int_{-\infty}^\infty g(\sqrt{2} x \sigma_g + \mu_g) dx \\ &\approx \sqrt{2} \sigma_g \sum_{k=1}^m w_k e^{x_k^2} g(\sqrt{2} x_k \sigma_g + \mu_g) \end{aligned}$$

where x_k ($k = 1, 2, \dots, m$) and w_k ($k = 1, 2, \dots, m$) are the abscissae and weights of m -point Gauss–Hermite quadrature. Note that $\sum_{k=1}^m w_k = \sqrt{\pi}$ for any m , so that the above version of Gauss–Hermite quadrature is exact if $g(a)$ is proportional to a Gaussian density with mean μ_g and standard deviation σ_g . For a 20-point quadrature, the composite factors $w_k e^{x_k^2}$ range from 0.491 to 0.899, whereas the weights w_k range from 0.462 down to 2.23×10^{-13} . Hence it is best to use the composite factors $w_k e^{x_k^2}$ directly. Experimentation with this integration scheme confirmed that it is very accurate provided good values of μ_g and σ_g have been found.

For maximum likelihood estimation, $\log h(l_1, l_2)$ is required rather than $h(l_1, l_2)$. A stable method of computing this is

$$\begin{aligned} (15) \quad \log h(l_1, l_2) &= \log g(\mu_g) + \log \int_0^\infty \exp(\log g(a) - \log g(\mu_g)) da \\ &= \log g(\mu_g) + \log \int_{-\infty}^\infty z_0(a) da \\ &\approx \log g(\mu_g) + \log \sigma_g \\ &\quad + \log \sum_{k=1}^m w_k e^{x_k^2} \{\sqrt{2} z_0(\sqrt{2} x_k \sigma_g + \mu_g)\} \end{aligned}$$

where $z_0(a) = \exp(\log g(a) - \log g(\mu_g))$ if $a \geq 0$ and is 0 otherwise. In $z_0(a)$, $\log g(a)$ is computed directly, not by taking logs of exponentials. Thus $\log g(a) = \log h(l_1, l_2|a) + \log p(a)$, where

$$\begin{aligned} \log h(l_1, l_2|a) &= -\log(2\pi) - \log \sigma_1(a) - \log \sigma_2(a) \\ &\quad - 0.5 \log(1 - p(a)^2) - \frac{q_{12}(a)}{2(1 - p(a)^2)} \end{aligned}$$

and if $p(a)$ is lognormal with parameters $\mu_{\log A}$ and $\sigma_{\log A}$,

$$\begin{aligned} \log p(a) &= -0.5 \log(2\pi) - \log \sigma_{\log A} - \log a \\ &\quad - 0.5(\log a - \mu_{\log A})^2 / \sigma_{\log A}^2 \end{aligned}$$

Computation of $\log g(a)$ rather than $g(a)$ avoids overflow problems: a value of $g(a)$ of e^{-1000} may be truncated to 0 on a computer, but $\log g(a) = -1000$ is computed very accurately. In $z_0(a)$, $\log g(a) - \log g(\mu_g)$ is computed before exponentiating. Also, $z_0(\mu_g) = 1$ at μ_g and $0 \leq z_0(a) \leq 1$ for all a , so that the sum in eq. 15 and its log may be computed accurately for any set of parameters. If $g(a)$ is proportional to a Gaussian curve with mean μ_g and standard deviation σ_g ($\sigma_g \ll \mu_g$), then

$$\sum_{k=1}^m w_k e^{x_k^2} \{\sqrt{2} z_0(\sqrt{2} x_k \sigma_g + \mu_g)\} = \sqrt{2} \pi \approx 2.5066$$

However, when fitting the model in row 1 of Table 4, for example, we found that this quantity varied between about 1.8 and 3.5, so that approximating $g(a)$ by a Gaussian curve (a common statistical procedure, sometimes called Laplace's approximation) is not accurate.

When the measurement error is small, $g(a)$ can exhibit a very small spread. In this case, Gauss–Hermite integration is particularly useful because it makes use of the mode and spread of the distribution. However, precise values of these parameters are required in order to achieve accurate integration. Occasionally, we have encountered situations in which A given l_1 and l_2 is not unimodal. This seems to occur when A has a complicated distribution or when the growth curve is complex and the measurement error is substantial. We have found that Simpson's rule or the extended trapezoidal rule is satisfactory under such circumstances, although it tends to be slower than Gauss–Hermite integration.