Admitting ageing error when fitting growth curves: an example using the von Bertalanffy growth function with random effects

Jason M. Cope and André E. Punt

Abstract: A way to explicitly incorporate ageing error into the estimation of von Bertalanffy growth function (VBGF) parameters using a random effects (RE) modeling framework is presented. This RE framework also accounts for the effects of selectivity on growth curve estimation by characterizing the distribution of true ages derived from multiple age reads using either an exponential or gamma distribution. Simulation testing across four life histories is used to compare the RE approach with standard nonlinear (SNL) approaches that use the primary, average, or median ages in growth estimation. Sensitivity tests compare the effects of assumed length and ageing error, selectivity, and recruitment variability on the estimation of growth curve parameters. Results support the use of the RE method using a gamma distribution over the SNL methods because RE method estimates of VBGF growth parameters were more precise across life histories and sensitivity trials. This general approach can be applied and expanded to other growth models. Applications demonstrate that the results from RE methods may differ in biologically important ways to those obtained from SNL approaches.

Résumé : Nous présentons une méthode pour incorporer de façon explicite l'erreur de détermination de l'âge dans l'estimation des paramètres de la fonction de croissance de von Bertalanffy (VBGF) dans le cadre de la modélisation à effets aléatoires (RE). Ce cadre RE tient aussi compte des effets de la sélectivité sur l'estimation de la courbe de Hcroissance en caractérisant la distribution des âges réels dérivée de lectures multiples des âges à l'aide des distributions exponentielle ou gamma. Nous effectuons une vérification par simulation sur quatre cycles biologiques afin de comparer la méthodologie RE avec les méthodes standard non linéaires (SNL) qui utilisent les âges primaires, moyens ou médians dans l'estimation de la croissance. Des tests de sensibilité servent à comparer les effets des erreurs présumées de longueur et d'âge, de la sélectivité et de la variabilité du recrutement sur l'estimation des paramètres de la courbe de croissance. Nos résultats appuient le choix de la méthode RE avec une distribution gamma plutôt que les méthodologies SNL parce que la méthode RE génère des estimations plus précises des paramètres de croissance de VBGF au cours des cycles biologiques et dans les tests de sensibilité. Cette méthodologie générale peut être étendue et s'appliquer à d'autres modèles de croissance. Les applications des méthodes RE révèlent que les résultats peuvent différer de ceux des méthodologies SNL de différentes manières qui ont des conséquences biologiques importantes.

[Traduit par la Rédaction]

Introduction

The biological relationship between age and length is fundamental to many fisheries population dynamics models. Estimates of growth drive size- and age-structured stock assessment models (Quinn and Deriso 1999), scale yield calculations (Beverton and Holt 1957; Gulland 1983; Haddon 2001), and are related to life history traits such as natural mortality (*M*) and age or length at maturity (Charnov 1993; Jensen 1998). Besides pure application, age and growth studies are also important in describing the basic biology and ecology of fishes (Weatherley and Gill 1987; Cailliet and Goldman 2004).

Although many growth curves are available, the von Bertalanffy growth function (VBGF; von Bertalanffy 1938) is the most widely used in fisheries, and its parameters are particularly useful in describing general fish growth (Chen et al. 1992; Quinn and Deriso 1999), deriving fisheries reference points (Clark 1991; Williams and Shertzer 2003) and estimating life history parameters (Beverton and Holt 1959; Beverton 1992). Most commonly, data will consist of one age and length measure per individual collected from many individuals, although data from length frequencies (Wang and Ellis 1998, 2005) or multiple measures of the same individual through tag–recapture (Fabens 1965; Wang 1998) and repeated-measures studies (Palmer et al. 1991) are also used.

Current VBGF estimation techniques use nonlinear regression or likelihood methods to fit deterministic relationships, assuming that all variance between the model and the data is due to heterogeneity in length at age (Quinn and Deriso 1999). This variance describes natural variation in the length at age attributable to individual growth processes and is commonly termed process error. This estimation ap-

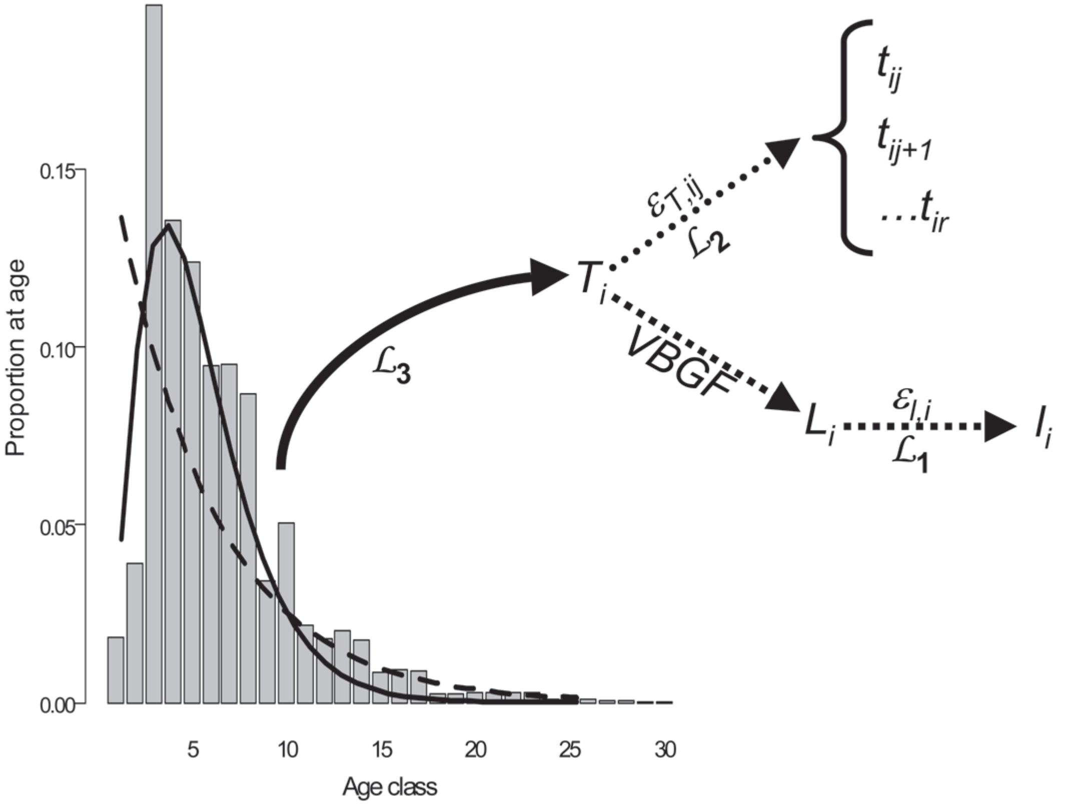
Received 25 April 2006. Accepted 17 October 2006. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 10 February 2007.
J19291

J.M. Cope[1] and A.E. Punt. School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020, USA.

[1] Corresponding author (e-mail: jcope@u.washington.edu).

doi:10.1139/F06-179

Fig. 1. Illustration of the data generation and subsequent fit to the random effects (RE) method. This example shows how the true age of individual i (T_i) is drawn from a population (shaded bars) and results in an observed length l_i (resulting from an expected length L_i and derived via the von Bertalanffy growth function (VBGF) from T_i with process error ε_L) and r age reads t_{ir} (T_i with ageing error $\varepsilon_{T,ij}$). Sources of stochasticity (with likelihood components $\mathcal{L}_x$) are noted at the arrows between the observed and expected values. Exponential (broken line) and gamma (solid line) fits to the true sample age population are also shown.



proach is referred to in this paper as the standard nonlinear (SNL) method.

Also frequent (especially in temperate fishes), but often overlooked, is measurement error in reading ageing structures. The formation of ageing structures (e.g., otoliths) and the subsequent interpretation of the growth record is not always consistent, leading to observation error in the assignment of age (Evans and Hoenig 1998; Campana 2001). Such error can greatly affect estimates of growth, mortality, recruitment, and yield (Tyler et al. 1989; Bradford 1991; Reeves 2003). Ageing error should therefore be considered when fitting growth curves.

To address this issue, multiple age reads of fish are often taken, and the precision of the reads is quantified (Beamish and Fournier 1981; Chang 1982; Campana 2001). Kimura and Anderl (2005) present a way to compare different measures of ageing precision, and Campana et al. (1995) and Cailliet et al. (1990) present graphical ways to summarize inter-read variation, bias, and precision. However, none of these studies accounted for ageing error when fitting growth curves.

Advances have been made to incorporate different types of error when fitting the VBGF. For example, individual variation in VBGF growth parameters (Sainsbury 1980; Wang and Thomas 1995; Pilling et al. 2002), seasonal variation in growth (Pitcher and MacDonald 1973; Cloern and Nichols 1978; Appledoorn 1982), autocorrelated error (Venugopalan and Prajneshu 1997), and stochastic environmental fluctuations (Prajneshu and Venugopalan 1999) have all been investigated, though none of these studies considered ageing error. Nummi (2000) presents a general method to incorporate error in the dependent variable for repeated-measures studies, though this does not apply to typical fisheries age and growth data (i.e., one length measurement per

Table 1. Estimated parameters of the standard nonlinear (SNL) and two random effects (RE_Exp, RE_Gamma) methods compared in this study.

	Method		
Parameters	SNL	RE_Exp	RE_Gamma
L_∞	×	×	×
k	×	×	×
t_0	×	×	×
CV_L	×	×	×
CV_T	NA	●	●
λ	NA	×	NA
γ	NA	NA	×
β	NA	NA	×

Note: RE_Exp, uses the exponential distribution to describe the sample population; RE_Gamma, uses the gamma distribution to describe the sampled population; ×, estimated within the model; ●, estimated external to the model; NA, not applicable or estimated. See Materials and methods for definitions of parameters.

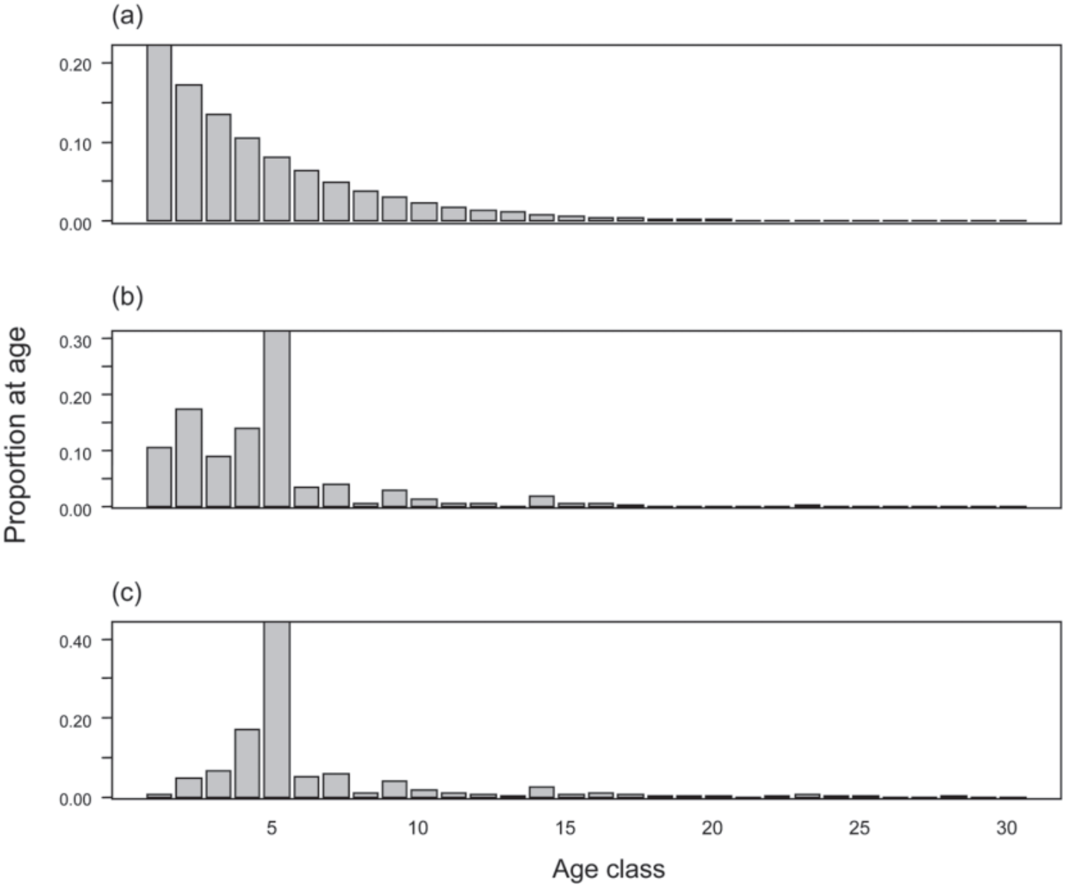
Table 2. Values used to parameterize the operating model for (*i*) each life history and (*ii*) each sensitivity.

	Parameter									
	M (year^{-1})	L_∞ (mm)	k (year^{-1})	t_0 (year)	ω (year)	CV_L	CV_T	ϕ_1 (year)	ϕ_2 (year)	σ_R
Life history base-case values										
1	0.075	500	0.05	0	100	0.1	0.1	5	5	0.6
2	0.15	500	0.09	0	50	0.1	0.1	4	4	0.6
3	0.25	500	0.152	0	30	0.1	0.1	3	2	0.6
4	0.5	500	0.303	0	10	0.1	0.1	2	1	0.6
Life history 3: base case and sensitivities										
Base case	0.25	500	0.152	0	30	0.1	0.1	3	2	0.6
Sensitivities										
Low CV_L	0.25	500	0.152	0	30	0.05[a]	0.1	3	2	0.6
High CV_L	0.25	500	0.152	0	30	0.2[a]	0.1	3	2	0.6
Low CV_T	0.25	500	0.152	0	30	0.1	0.05[a]	3	2	0.6
High CV_T	0.25	500	0.152	0	30	0.1	0.2[a]	3	2	0.6
$\Delta\mathrm{CV}_T$ low	0.25	500	0.152	0	30	0.1	0.05–0.20[a]	3	2	0.6
$\Delta\mathrm{CV}_T$ high	0.25	500	0.152	0	30	0.1	0.1–0.20[a,b]	3	2	0.6
Low σ_R	0.25	500	0.152	0	30	0.1	0.1	3	2	0.3[a]
High σ_R	0.25	500	0.152	0	30	0.10	0.1	3	2	1.0[a]
Low selectivity	0.25	500	0.152	0	30	0.1	0.1	0	0	0.6
High selectivity	0.25	500	0.152	0	30	0.1	0.1	0.4	0.3	0.6
$\Delta\mathrm{CV}_T$, selectivity high	0.25	500	0.152	0	30	0.1	0.10–0.20[a,b]	0.1	0.2	0.6

[a] Values that differ from the base case.

[b] The linear increase in CV_T is applied to ages 10–30 only.

Fig. 2. Simplified illustration of creating the sampled population of true ages given (*a*) natural mortality (M), (*b*) M and recruitment variability (σ_R), and (*c*) M, σ_R, and logistic selectivity (ϕ_1, ϕ_2; see eq. 8): (*a*) stable age distribution given a specified M; (*b*) the same age structure with added σ_R; (*c*) how the age structure in (*b*) is impacted by ϕ and is the age-structures sampled for simulation purposes.



sampled individual). Richards et al. (1992) present a way to account for ageing error from multiple age reads when developing age compositions, but not when fitting age and growth models.

Kimura (2000) addresses the problem of measurement error in age estimates when fitting growth models using an errors-in-variables approach based on functional regression. However, Kimura's approach requires the specification of a variance ratio term that is unknown. Although Kimura (2000) gives guidance in choosing this ratio, uncertainty associated with its value may greatly influence the resulting growth curve estimation.

This study presents an approach to explicitly incorporate ageing error into the estimation of the VBGF parameters using a random effects (RE) modeling framework. (A Microsoft Excel®-based application to implement the estimation approaches used in this paper is available from the corresponding author.) An RE approach is powerful in three main ways: (*i*) it allows for explicit incorporation of ageing error for multiple reads when estimating VBGF parameters, (*ii*) the only internally inestimable parameter can be derived from the age-at-length data, and (*iii*) an estimate of the sampled population from which the true ages is produced "corrects" the VBGF parameters for selectivity and may lead to an independent estimate of total mortality (Z; estimating mortality rates from this approach will be covered in a subsequent study). Simulation testing across four different life histories is used to compare the RE approach with three variants of the SNL approach based on using (*i*) the primary read only, (*ii*) the average age of multiple reads, and (*iii*) the median age of multiple reads. Each method is then applied to age and length data of four species (sand sole (*Psettichthys melanostictus*), cabezon (*Scorpaenichthys marmoratus*), greenspotted rockfish (*Sebastes chlorostictus*), and blackgill rockfish (*Sebastes melanostomus*)) to demonstrate the use of the RE approach.

Materials and methods

Model formulation

The models presented presume that the data set consists of one length and one or multiple age reads (r is the total number of age reads) per individual for n individuals. The methods presented can be extended straightforwardly to cases when the number of reads for each individual varies.

Standard von Bertalanffy growth function

The observed length at age (l_i) for the ith individual in the sample can be formulated as follows:

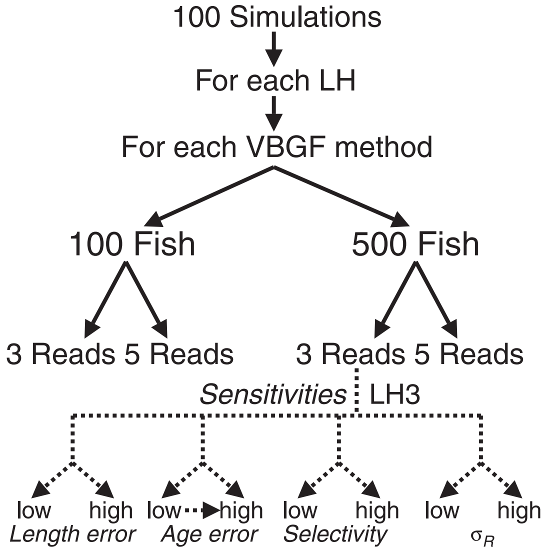
$$(1) \qquad l_i + L_i + \varepsilon_{L,i} \qquad \varepsilon_{L,i} \sim N(0, \sigma_{L,i}^2)$$

where L_i is calculated from the traditional three-parameter VBGF (Beverton and Holt 1957):

$$(2) \qquad L_i = L_\infty\{1 - \exp[-k(T_i - t_0)]\}$$

where L_i is the expected length at age for the ith individual, L_∞ is theoretical maximum length, k is the Brody growth coefficient, t_0 is theoretical age at length 0, and T_i is the true age of the ith individual.

Fig. 3. Schematic of the simulation testing process. Solid lines are simulation pathways for each life history base case. Broken lines are simulations exploring sensitivity to different parameter values. The sensitivities are only examined for life history 3 (LH3) with 500 individuals and 3 reads.



The coefficient of variation of the normally distributed process error, CV_L, is assumed to be the same for all individuals in the population. The standard deviation of the process error in length for individual i, $\sigma_{L,i}$, is therefore given by $\sigma_{L,i} = CV_L L_i$. All variance in the data is therefore associated with estimated length process error, and L_∞, k, and t_0 are estimable parameters (Table 1). The likelihood function (L_1, Fig. 1) maximized to estimate the values of these parameters (coded in AD Model Builder; Otter Research Ltd. 2005*a*) is

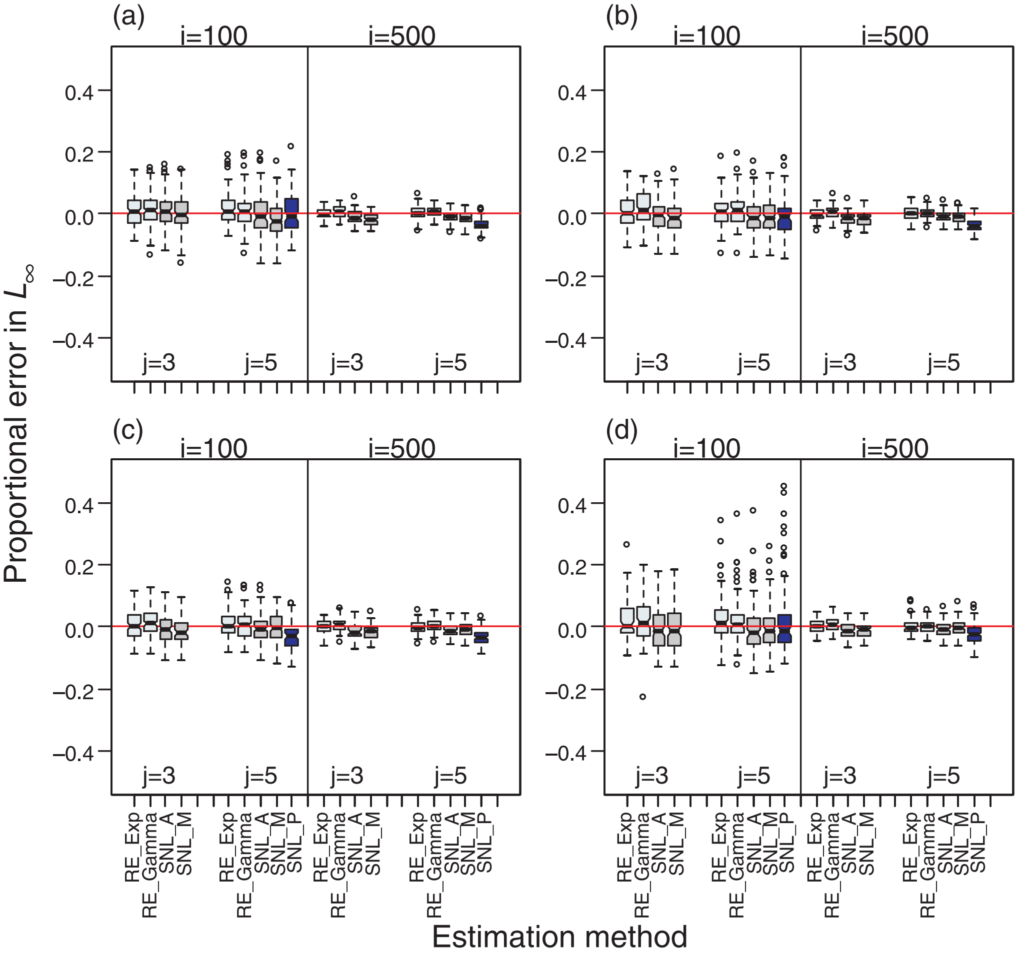
$$(3) \qquad L = \prod_i \frac{1}{\sqrt{2\pi}\,\sigma_{L,i}} \exp\left[-\frac{(l_i - L_i)^2}{2\sigma_{L,i}^2}\right]$$

Traditionally, only one age per individual is used to fit the VBGF. When multiple reads (t_{ij}: $j = 1, 2, \ldots, r$) are available for each individual i, three approaches are typically used to obtain the one age read per individual: (*i*) a primary age reader is established and only their read is used to fit the model, (*ii*) multiple reads are averaged, and (*iii*) the median value of the multiple reads is taken to decrease the influence of outliers.

Growth curve models with random effects

RE models allow one to fit nonGaussian, nonlinear models with additional variance components (e.g., error in the independent variable) by specifying an additional likelihood component based on (in the case of growth curves) the fit of the observed age reads to the expected true age ($\mathcal{L}_2$, Fig. 1) and a distribution for the ages of the sampled individuals ($\mathcal{L}_3$, Fig. 1). In this approach, one can envision sampling a true age T_i from the population (Fig. 1, bars), of which a length is measured — with process error — from the growth curve (e.g., VBGF). Likewise, multiple reads of the true age are obtained with observation error (Fig. 1). All three components (length ($\mathcal{L}_1$), age ($\mathcal{L}_2$), and sampled population ($\mathcal{L}_3$)) comprise the statistical model for the data.

Fig. 4. Proportional error ((estimated – true)/true) among four life histories in the estimates of the von Bertalanffy growth function (VBGF) parameter L_∞ for the two random effects (RE_Exp, random effects with exponential distribution; RE_Gamma, random effects with gamma distribution) and three standard nonlinear (SNL_A, averages of multiple reads; SNL_M, medians of multiple reads; SNL_P, primary reads only) methods when the number of individuals (*i*) sampled is either 100 or 500 and 3 or 5 age reads (*j*) are made. Box plot description: median, bold solid line; 1st and 3rd interquartile range, box; 1.5 times the interquartile range, whiskers; outliners, circles. The horizontal line denotes zero error. (*a*) Life history 1; (*b*) life history 2; (*c*) life history 3; (*d*) life history 4.



VBGF with random effects

A relationship between the observed and true ages can be formulated. For example

$$(4)\qquad t_{ij} = T_i + \varepsilon_{T,ij} \qquad \varepsilon_{T,ij} \sim N(0, \sigma^2_{T,i})$$

where the standard deviation of the age-reading error for individual i, $\sigma_{T,i}$, is based on that assumption that the CV of the ageing error is constant (i.e., $\sigma_{T,i} = \mathrm{CV}_T T_i$ (Kimura and Lyons 1991; Piner et al. 2005, 2006), where CV_T is the coefficient of variation of ageing error).

The value of CV_T cannot be estimated within the model because of lack of degrees of freedom (Otter Research Ltd. 2005*b*), although it can be estimated from the multiple age reads assuming that ageing is unbiased:

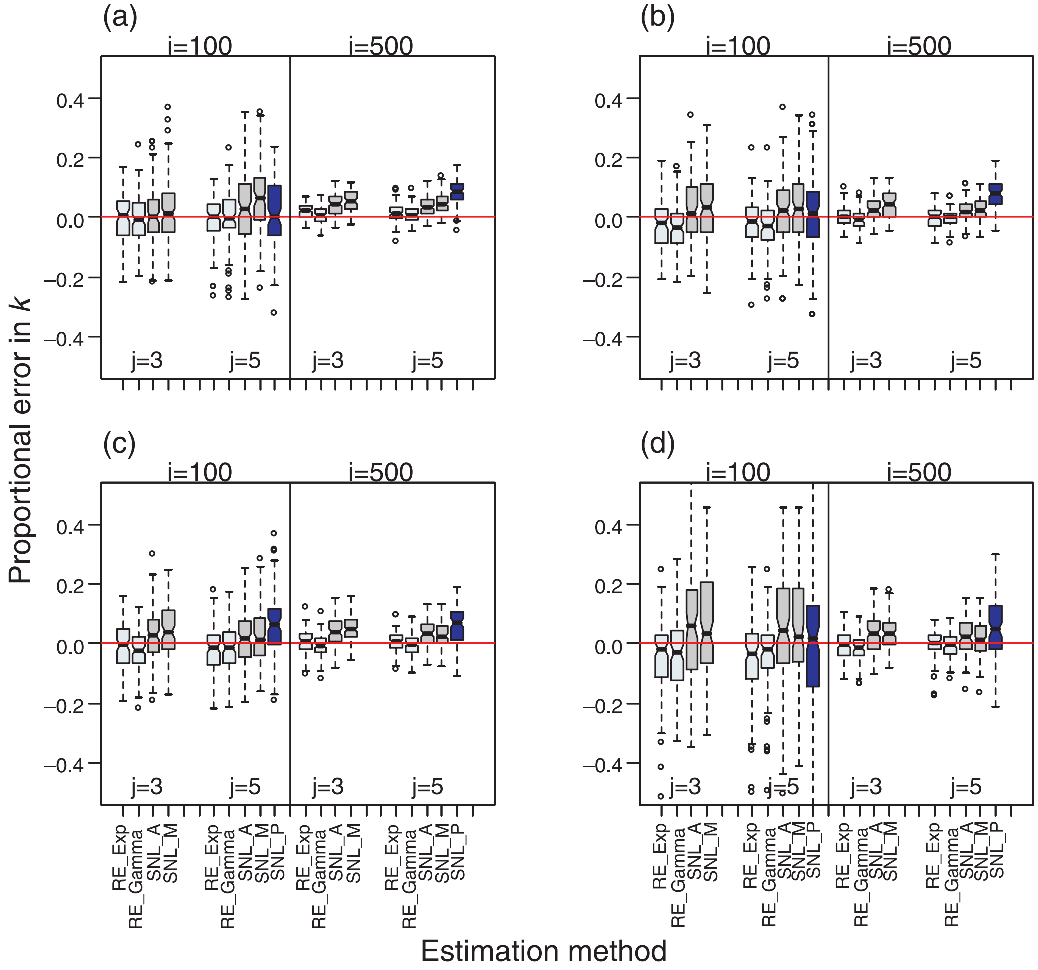
$$(5)\qquad \widehat{\mathrm{CV}}_T = \sqrt{\frac{\sum_{i=1}^{n} \mathrm{CV}^2_{t,i}}{n}}$$

where $\mathrm{CV}_{t,i}$ is the age coefficient of variation for each individual i.

Given the models for the errors in observed lengths (eqs. 1–2) and estimated ages (eq. 4), the RE model lastly requires characterizing the distribution of the true ages. This distribution has biological meaning, as it is the true age composition of the sampled population. For the purposes of this paper, either the exponential (Fig. 1, broken line) or gamma distribution (Fig. 1, solid line) is used to describe the sampled population. These two distributions were chosen because the exponential distribution is a simplistic, continuous representation of an age structure decaying over time and is a special case of the gamma distribution (Casella and Berger 2002), which contains one more parameter, but is flexible enough to characterize vagaries in the sampled age composition attributable to trends in recruitment and (or) sampling selectivity.

The complete likelihood function for the RE model is given by

Fig. 5. Proportional error ((estimated – true)/true) among four life histories in the estimates of the von Bertalanffy growth function (VBGF) parameter *k* for the two random effects (RE_Exp, random effects with exponential distribution; RE_Gamma, random effects with gamma distribution) and three standard nonlinear (SNL_A, averages of multiple reads; SNL_M, medians of multiple reads; SNL_P, primary reads only) methods when the number of individuals (*i*) sampled is either 100 or 500 and 3 or 5 age reads (*j*) are made. Box plot description: median, bold solid line; 1st and 3rd interquartile range, box; 1.5 times the interquartile range, whiskers; outliers, circles. The horizontal line denotes zero error. (*a*) Life history 1; (*b*) life history 2; (*c*) life history 3; (*d*) life history 4.



(*i*) Exponential model:

$$L = \prod_i \int \frac{1}{\sqrt{2\pi}\,\sigma_{L,i}} \exp\left[-\frac{(l_i - L_T)^2}{2\sigma_{L,i}^2}\right] \prod_j \frac{1}{\sqrt{2\pi}\,\sigma_{T,i}} \times \exp\left[-\frac{(t_{ij} - T_i)^2}{2\sigma_{T,i}^2}\right] \lambda \exp(-\lambda T)\,\mathrm{d}T \tag{6}$$

(*ii*) Gamma model:

$$L = \prod_i \int \frac{1}{\sqrt{2\pi}\,\sigma_{L,i}} \exp\left[-\frac{(l_i - L_i)^2}{2\sigma_{L,i}^2}\right] \prod_j \frac{1}{\sqrt{2\pi}\,\sigma_{T,i}} \times \exp\left[-\frac{(t_{ij} - T_i)^2}{2\sigma_{T,i}^2}\right] \frac{(T/\beta)^{(\gamma-1)} \exp[-(T/\beta)]}{\beta\Gamma(\gamma)}\,\mathrm{d}T \tag{7}$$

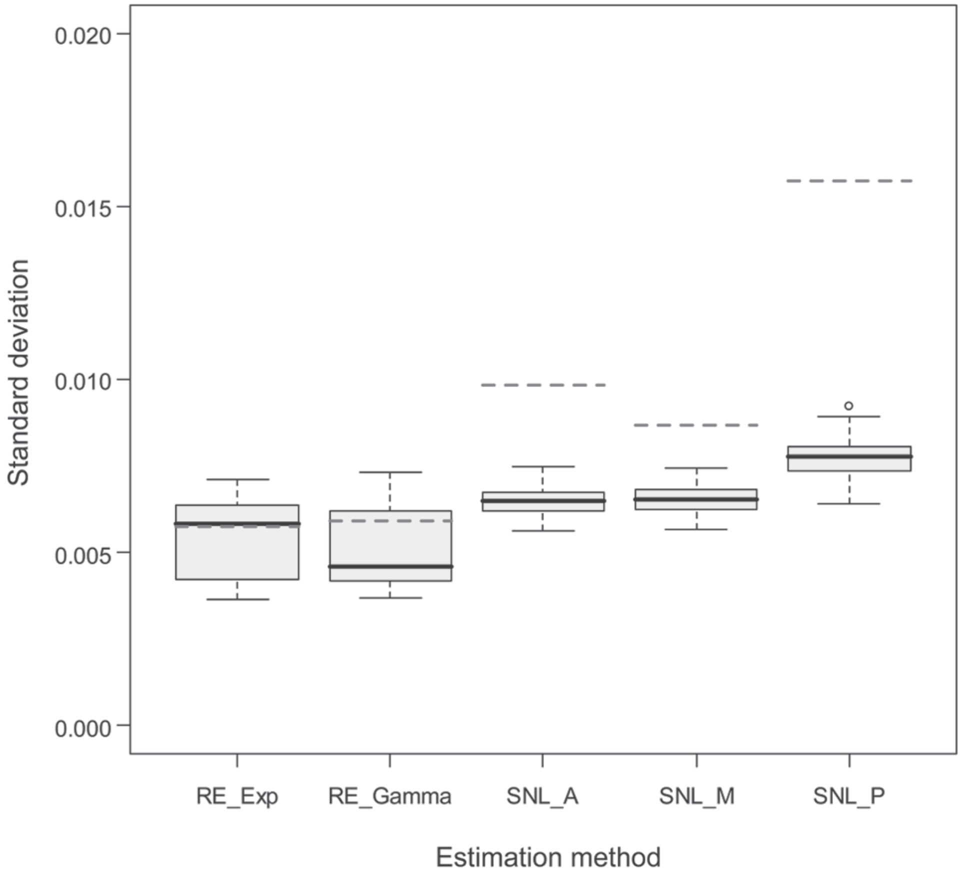
The RE model was implemented using the AD Model Builder RE module (ADMB-RE; Otter Research Ltd. 2005*b*), which is based on using the Laplace approximation to integrate over the random effects (Skaug and Fournier 2006) and partial separability of the objective function to increase computational efficiency and speed when handling hundreds to thousands of random effects (Gay 1996). Table 1 lists all the parameters for each method and indicates which are estimated either internal or external to the model.

Simulation testing

Base case

Lengths with multiple age reads were generated to evaluate the ability of the three SNL and two RE methods to estimate the values for the VBGF parameters. An (operating) model that captures relevant processes and dynamics with known relationships and produces data with acceptable error structures was created and used to generate artificial data sets. These data sets were then used by each of the estimation methods, and the resulting estimated parameter values were compared with true values.

Fig. 6. Box plots of the asymptotic standard deviations (solid lines within box) for the von Bertalanffy growth function (VBGF) growth parameter k for 100 simulations compared with the root mean square error (RMSE, broken lines).



Data generation began by first simulating an age-structured population from which to sample the true ages. Four life histories were considered, corresponding roughly to the blackgill (*Sebastes melanostomus*), blue (*Sebastes mystinus*), olive (*Sebastes serranoides*), and calico (*Sebastes dalli*) rockfishes and differing in longevity (ω), natural mortality (M), and age-specific selectivity (Table 2). Sampled populations of true ages (Fig. 2) were created through the interaction of M, lognormal recruitment variability (σ_R), and a two-parameter (ϕ_1, ϕ_2) model of logistic selectivity interact to create a sampled population of true ages

$$(8) \qquad \phi_l = \{1 + \exp[-\log(19)(L_i - \phi_1)/\phi_2]\}^{-1}$$

where ϕ_l is selectivity at length l, ϕ_1 is the length at 50% selectivity (determined by age), and ϕ_2 is the difference between the length at 95% selectivity and that at 50% selectivity. A specified number (either 100 or 500) of true-aged individuals was then sampled from this population. Length at age was then calculated using eqs. 1 and 2 with process error based on a CV_L set to 0.1 (Bowker 1995). The ratio M/k was set to 1.65 (Charnov 1993), so specifying M also specified the VBGF k value. Multiple age reads (either 3 or 5) were generated from each true age assuming a constant ageing observation error CV_T of 0.1 (Campana 2001; Dunn et al. 2002). The base case parameter values for each life history are listed (Table 2). After generating the length-at-age data, each of the five methods was then applied and the resulting parameter estimates were stored. This data-generation – model fit procedure was repeated for a total of 100 simulations for each life history, estimation method, and individual–read combination (Fig. 3).

Sensitivities

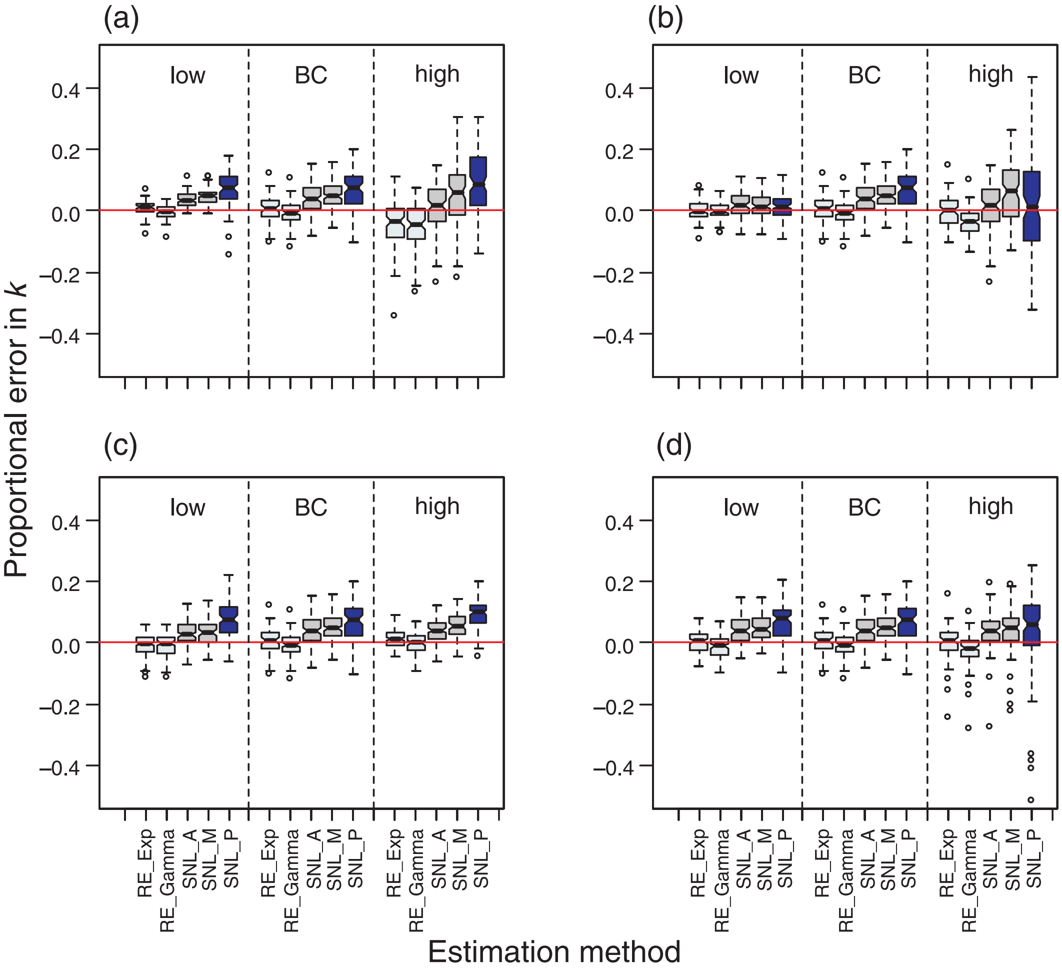
The sensitivity of the simulation results to the specifications of the base case operating model was explored by changing the values assumed for the extent of length error, ageing error, selectivity, and recruitment variation. High and low values for each of these processes were specified for life history 3 (Table 2) to capture a realistic range of values. In addition, the impact of violating the assumption that the ageing error CV is independent of age was explored in three ways: (*i*) CV_T increasing from 0.05 to 0.20 across all ages (trial: ΔCV_T low), (*ii*) CV_T increasing from 0.10 to 0.20 from ages 10 to 30 (trial: ΔCV_T high), and (*iii*) CV_T increasing from 0.10 to 0.20 from ages 10 to 30 with selectivity modified to include the sampling of more older ages (trial: ΔCV_T, selectivity high; Table 2).

Results

Base case

Performance of the various estimation methods is consistent across the four life histories (Figs. 4 and 5). Little gain in accuracy (no error in median estimation) or precision (spread of the box plot) is evident when the number of reads

Fig. 7. Proportional error in the estimate of the von Bertalanffy growth function (VBGF) growth parameter k for sensitivities based on varying the extent of (*a*) length and (*b*) ageing error; (*c*) sampling selectivity; and (*d*) recruitment variability.



was increased from 3 to 5 (a subset of trials using only 2 reads also showed little difference from those using 3), but both accuracy and precision increased when the number of individuals sampled increased from 100 to 500 (i.e., improved estimates of the VBGF parameters k and L_∞ occur with increased sampling, rather than with the number of times an individual is aged).

The estimates of L_∞ and k showed less proportional error when derived from the RE methods (Figs. 4 and 5). Both RE and SNL methods demonstrated bias when sample size was low, but precision was always greatest with the RE approaches. When the number of individuals sampled increased, the RE approaches were both more accurate and precise. This is particularly apparent when estimating k; SNL methods tended to overestimate the value of this parameter (Fig. 5). The estimates of k were the most biased and least precise when only the primary read was used. Imprecision tended to also increase as M increased (e.g., compare the results for life history 1 with those for life history 4 in Fig. 5). Precision is an important consideration when evaluating the overall usefulness of each method, because one will not usually have the luxury of 100 samples of 500 individuals, so a method with poor precision may result in estimates that differ substantially from the true values. The high precision of the RE methods compared with the SNL methods may translate into important differences when applied to typical age and growth data (see forthcoming applied examples).

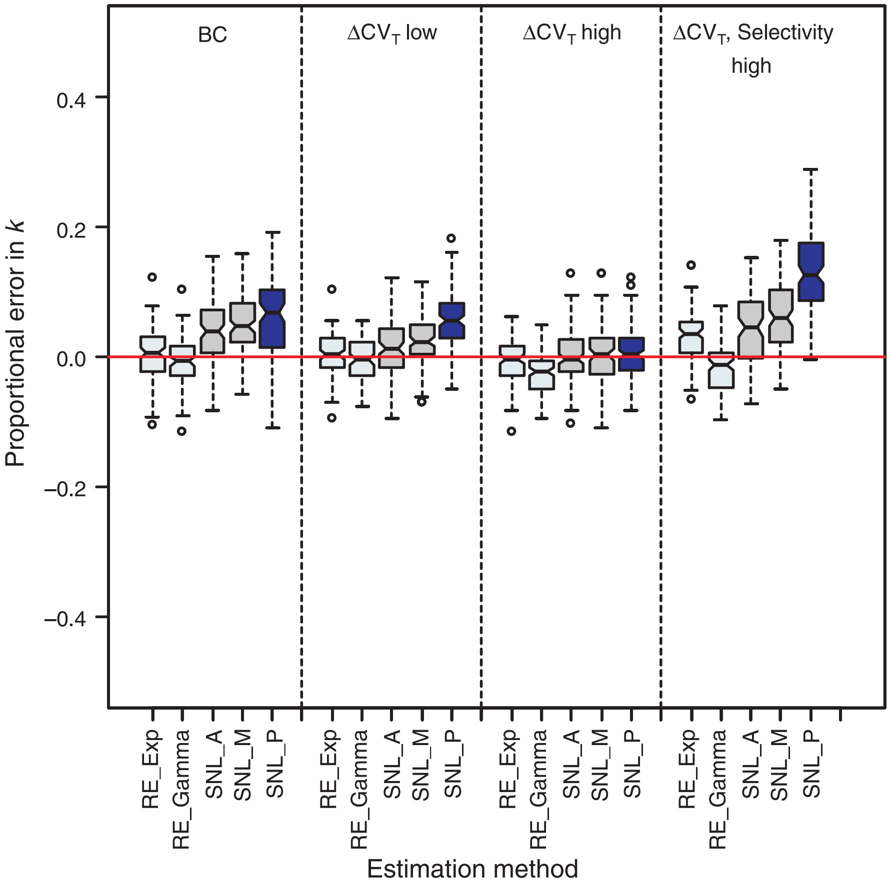
Proportional error was lower for L_∞ (Fig. 4) than for k (Fig. 5) and was negatively correlated between these two parameters (e.g., positive proportional error in L_∞ meant negative proportional error in the k). This correlation is as expected given the known correlation between these parameters (Quinn and Deriso 1999).

The asymptotic standard deviations (based on inverting the Hessian matrix) for the estimates of k are lowest for the RE methods (Fig. 6), although all of the methods had relatively low standard deviations. The asymptotic standard deviations for the RE methods provide a better reflection of the true error associated with estimating k than is the case for the SNL methods (Fig. 6).

Sensitivities: life history 3 (500 individuals, 3 reads)

Sensitivity results are shown only for k and life history 3 when 500 individuals are sampled and when 3 age reads are made. We chose this subset because there was very little qualitative difference in the results among the four life histo-

Fig. 8. Proportional error in the estimate of the von Bertalanffy growth function (VBGF) growth parameter *k* for sensitivity trials based on changing CV_T with age. BC refers to the base case for life history 3. The specifications of the other trials can be found in Table 2.



ries, between L_∞ and *k*, and between 3 and 5 age reads when 500 individuals were sampled.

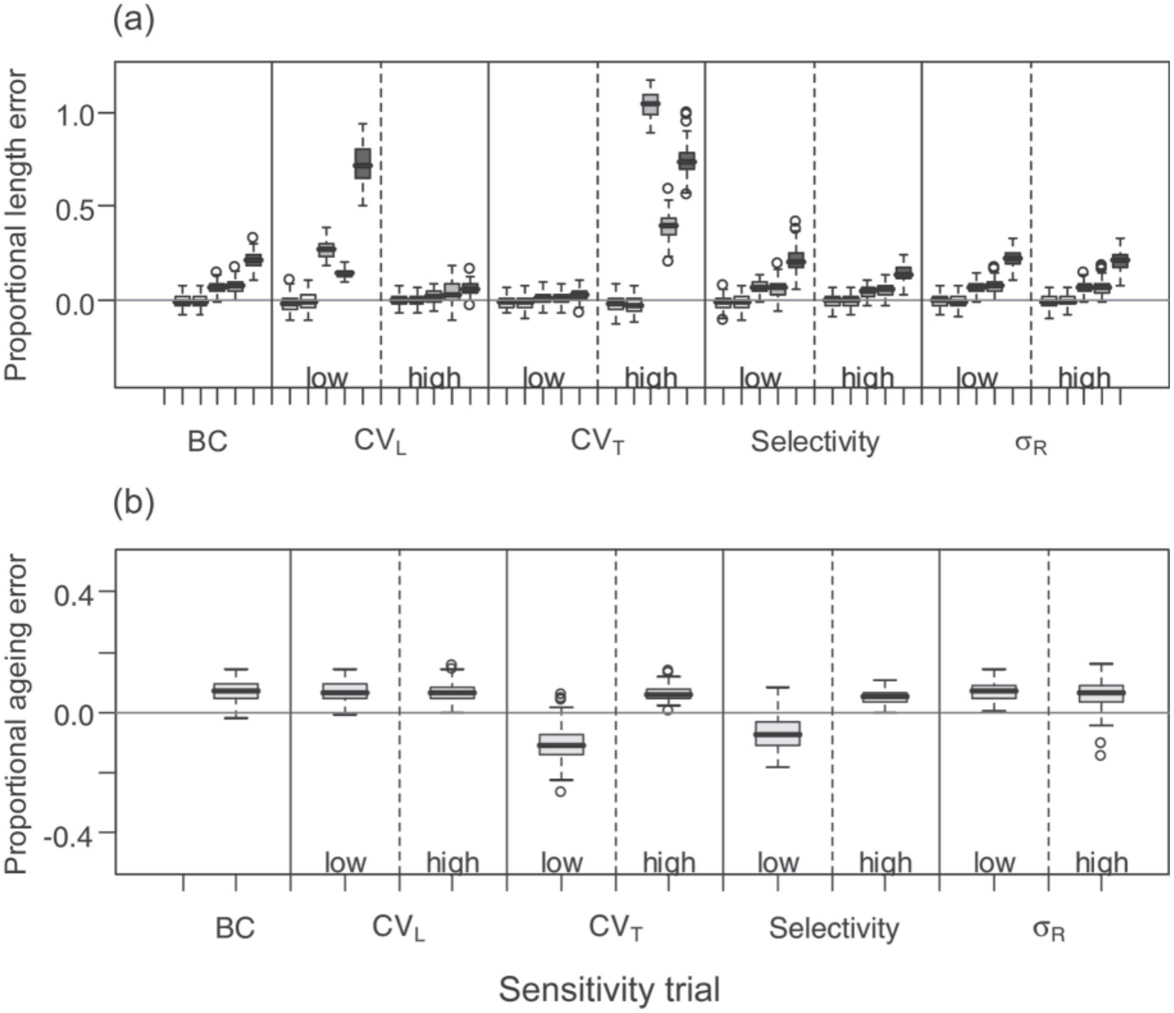
Both RE methods are robust to the factors considered in the sensitivity analysis. Specifically, the RE methods always exhibited the greatest precision and often the highest accuracy (Fig. 7). Increasing length error and recruitment variability led to the greatest overall decrease in precision. High length error also led to a negative bias in the estimate of *k* for the RE methods, whereas all levels of length and ageing error, selectivity, and recruitment variability led to positive biases for the SNL methods. The SNL method based on the primary read only (SNL_P in Fig. 7) was particularly sensitive to factors considered in the sensitivity analyses. Precision in the SNL methods was also sensitive to high ageing error. Increasing recruitment variation generally led to poorer precision, but had little effect on accuracy, whereas all methods were relatively insensitive to changes in selectivity.

The RE approaches remain the most accurate and precise even when CV_T changes linearly with age (Fig. 8). There is little difference between the base case and the ΔCV_T low trial because overall, the amount of ageing error is similar. The differences between the methods are less apparent in the ΔCV_T high trial, but this is attributable to fewer ages with ageing error being sampled. When the number of ages with ageing error being sampled is increased (trial ΔCV_T, high selectivity), the advantages of using the RE approaches are again apparent, particularly when the gamma distribution is assumed. Low selectivity across much of the younger ages causes the exponential distribution to be a poor approximation to the sampled population, whereas the gamma distribution captures this selectivity, providing more accurate and precise estimates of *k* than the other methods.

Varying the specifications of the operating model had little influence on the estimates of CV_L among the RE methods, and these estimates were generally precise and accurate (Fig. 9*a*). However, the estimates of CV_L among the SNL methods were biased for most of the trials. The greatest inaccuracy and imprecision in SNL methods resulted from low length error and high ageing error. This bias is attributable to ageing error increasing the estimate of process error. Only when ageing error was low did the SNL methods estimate the extent of process error with low bias. Estimates of CV_L were generally insensitive to selectivity and recruitment variability.

The estimates of CV_T do not depend on the choice of how the age structure of the sampled population is modeled (gamma or exponential), because they are based on eq. 5. These estimates are generally positively biased (a product of estimating the CV from few age reads), but the extent of bias is generally insensitive to the specifications of the oper-

Fig. 9. Proportional error in the estimates of (*a*) length error (CV_L) and (*b*) ageing error (CV_T) for the base case (BC) and the sensitivity trials. For the length error plot, each trial grouping reads, from left to right, RE_Exp, RE_Gamma, SNL_A, SNL_M, and SNL_P. For the ageing error plot, the proportional error shown is for the random effects methods.



ating model (Fig. 9*b*). However, the extent of overestimation was relatively low and had no impact on the estimation of the VBGF parameters, thus perhaps explaining the negligible difference in parameter estimation when 5 age reads were used (Fig 5).

Applying the RE methods: examples

Four examples of applying the VBGF estimation methods are given in Table 3. This table proceeds from relatively faster to slower life histories, and the examples differ in gender, number of individuals aged, and number of age reads available. The differences in the estimates of *k* between the exponential and gamma RE models for female sand sole, female greenspotted rockfish, and male cabezon are indicative of strong selection for older individuals in the sampled population. This strong selection also biases the estimates from the SNL methods (illustrated in Table 3). Additionally, differences in results between the RE and SNL methods for sand sole and cabezon can be attributed to the relatively large amount of ageing error. The results for male greenspotted rockfish and blackgill rockfish differ little among the RE and average and (or) median SNL approaches. It is noteworthy that except for blackgill rockfish, the estimates of *k* from the SNL_P approach differs the most from the other methods.

Discussion

Since the inception of the VBGF (von Bertalanffy 1934, 1938), there has been a steady evolution in its use and estimation. Beverton and Holt (1957) popularized the current form of the VBGF by changing the original three-parameter formulation to include t_0 rather than L_0. Several estimation techniques, ranging from linear fitting (Walford 1946; Stamatopoulos and Caddy 1989) to nonlinear least squares (Tomlinson and Abramson 1961; Marquardt 1963), iterative fitting (Rafail 1973), and likelihood (Kimura 1980) methods have subsequently been proposed. Kimura (2000) then suggested a functional regression approach to explicitly incorporate ageing error. The RE approach developed here is a natural step in the evolution of fitting growth curves, as it makes maximum use of information contained in multiple-aged individuals. The RE approach performs better than traditional methods across a wide range of life histories and under different rates of process and observation error, sam-

Table 3. Results of fitting the von Bertalanffy growth function to age and length data with multiple reads for four species based on the five estimation methods.

				Sample size		L_∞ (mm)		k (year^{-1})		t_0 (year)		Error	
Species	Gender	Method	No. of reads	*N*	*n*	Mean	SD	Mean	SD	Mean	SD	Length	Age
Sand sole (*Psettichthys melanostictus*)[a]	F	RE_Exp	2	426	269	388	7	0.688	0.065	–0.01	0.10	0.10	0.24
		RE_Gamma	2	426	269	410	8	0.566	0.031	0.00	0.00	0.09	0.24
		SNL_A/M	2	426	269	385	6	0.652	0.064	–0.29	0.12	0.10	—
		SNL_P	1	426	—	375	5	0.780	0.074	–0.26	0.11	0.10	—
	M	RE_Exp	2	178	121	348	38	0.414	0.156	–0.84	0.44	0.13	0.25
		RE_Gamma	2	178	121	359	45	0.432	0.168	–0.57	0.38	0.13	0.25
		SNL_A/M	2	178	121	331	20	0.468	0.113	–0.92	0.30	0.10	—
		SNL_P	1	178	—	311	12	0.604	0.123	–0.72	0.26	0.10	—
Cabezon (*Scorpaenichthys marmoratus*)[b]	F	RE_Exp	3	379	379	612	18	0.203	0.014	–1.27	0.08	0.11	0.17
		RE_Gamma	3	379	379	615	19	0.200	0.014	–1.27	0.08	0.11	0.17
		SNL_A	3	379	379	593	14	0.222	0.013	–1.22	0.07	0.10	—
		SNL_M	3	379	379	584	13	0.232	0.014	–1.19	0.07	0.10	—
		SNL_P	1	379	—	546	10	0.284	0.018	–1.16	0.09	0.10	—
	M	RE_Exp	3	238	238	424	7	0.478	0.038	–0.74	0.09	0.10	0.20
		RE_Gamma	3	238	238	426	7	0.465	0.038	–0.76	0.09	0.10	0.20
		SNL_A	3	238	238	420	6	0.508	0.037	–0.71	0.09	0.10	—
		SNL_M	3	238	238	422	6	0.485	0.038	–0.83	0.10	0.10	—
		SNL_P	1	238	—	409	5	0.582	0.051	–0.74	0.10	0.10	—
Greenspotted rockfish (*Sebastes chlorostictus*)[a]	F	RE_Exp	2	180	80	380	10	0.087	0.005	0.00	0.00	0.07	0.12
		RE_Gamma	2	180	80	402	14	0.077	0.005	0.00	0.00	0.07	0.12
		SNL_A/M	2	180	80	373	17	0.092	0.100	0.40	1.03	0.10	—
		SNL_P	1	180	—	383	25	0.072	0.100	–2.44	2.01	0.10	—
	M	RE_Exp	2	150	50	404	16	0.074	0.009	–0.50	0.72	0.07	0.09
		RE_Gamma	2	150	50	412	19	0.072	0.009	–0.29	0.75	0.07	0.09
		SNL_A/M	2	150	50	401	21	0.074	0.100	–0.62	0.87	0.10	—
		SNL_P	1	150	—	410	23	0.069	0.100	–0.86	0.91	0.10	—
Blackgill rockfish (*Sebastes melanostomus*)[c]	C	RE_Exp	2,3	112	108, 94	495	27	0.057	0.012	–0.50	2.01	0.16	0.13
		RE_Gamma	2,3	113	108, 95	499	28	0.056	0.012	–0.35	2.01	0.16	0.13
		SNL_A	2,3	114	108, 96	500	18	0.057	0.008	–0.87	1.39	0.10	—
		SNL_M	2,3	115	108, 97	503	19	0.054	0.008	–1.91	1.44	0.10	—
		SNL_P	1	116	—	492	19	0.057	0.009	–2.54	1.80	0.10	—

Note: When there are only two reads, the average and median age methods are the same (denoted here as SNL_A/M). Gender designations are as follows: F, female; M, male; C, combined gender data. The number of reads includes the primary read and may be a mixture of one to two additional reads (e.g., blackgill rockfish). *N*, total number of primary reads; *n*, total number of additional reads (not all ageing structures were read more than once).

[a] Don Pearson, NOAA Fisheries, Southwest Fisheries Science Center, Fisheries Ecology Division, 110 Shaffer Road, Santa Cruz, CA 95060, USA, unpublished data.

[b] Grebel 2003.

[c] Stevens et al. 2004.

pling conditions, and assumed population dynamics. Beyond benefits to model fitting, the RE approach may also provide information on the underlying population the samples are taken from and thus be informative of other population parameters, such as mortality rate. The general RE framework is also flexible enough to be extended to other growth models (e.g., the Gompertz or Schnute growth models; Schnute 1981).

The need for proper age estimates and subsequent growth models that incorporate uncertainty in ageing has been recognized for years (Lai and Gunderson 1987; Campana 2001). The general method presented here addresses this need and offers two main advantages over traditional growth curve estimation methods.

Including ageing error

First and most obviously, the RE method explicitly accounts for ageing error. The RE method is advantageous compared with functional regression approaches because it does not require the specification of an error ratio that is usually only roughly estimated. The only unknown parameter in the RE method not estimated by maximizing the likelihood function (σ_T) can be estimated directly from the multiple age reads and showed little influence on growth curve estimation even when estimated with some bias. Even when the extent of ageing error changes with age, the assumption of a constant ageing error CV is robust, although a simple modification to the likelihood functions (eqs. 6 and 7) could explicitly account for the ageing error CV changing with age.

There are still issues concerning ageing error that need further consideration. The simulations used here ignore bias in age reading. Although nonrandom errors between readers can be corrected with further training, systematic nonrandom errors in the growth structure itself can be harder to resolve (Campana 2001). In addition, ageing error may become skewed for older individuals (e.g., underageing of older individuals). Exploring the impact of alternative formulations of ageing error (i.e., log-normal) in the RE method using simulations may help address this issue.

Likewise, alternative assumptions regarding process error can also be explored with alternative model formulations. Bowker (1995) demonstrated that the CV of length in many fish decreases with age. A simple modification to the present model is to allow the CV in length to change with age, though the qualitative results presented here are not expected to change.

Accounting for selectivity

Second, the RE method treats the ages represented in the sample as random. This is a key reason for improved performance when different portions of the population are sampled and for the overall stability–precision of the RE method. Besides the exponential and gamma models, other distributions may more appropriately describe the sampling of ages. These can easily be accounted for by modifying the likelihood for the true age distribution in eqs. 6 or 7. Based on the current results, the gamma is recommended over the exponential distribution given that it is more flexible, has only one additional parameter, and contains the exponential distribution as a special case. This advantage is most apparent when selectivity for the younger ages is low.

One caveat of the current model formulation is that it does not correct for selectivity of individuals with varying growth rates (k) or maximum sizes (L_∞). Overall, selectivity can be visualized in two dimensions, of which the current method only corrects for the first: (*i*) selectivity across size and age classes and (*ii*) selectivity across variability of growth within a given size or age class. Therefore, younger, faster-growing and older, slower-growing individuals may be disproportionately represented in a given sample, leading to biased estimation of growth parameters (Parma and Deriso 1990; Vaughan and Burton 1994; Sinclair et al. 2002). One way to approach this problem may be to reformulate selectivity as a function of length rather than of age, a more realistic representation of selectivity. Troynikov (1999) and Taylor et al. (2005) introduce ways to account for size-selective mortality when estimating the standard process error formulation of the VBGF. Further investigation is needed to determine how these or other ideas may be incorporated into the RE method to account for size-selective mortality.

General recommendations

The inclusion of ageing error and the use of an RE framework in the estimation of the VBGF is an improvement over other standard, nonlinear estimation approaches. This highlights the importance of recording ageing error when undertaking age and growth studies. Typically only 20%, if any, of the ageing structures are reread (Kimura and Lyons 1991; Kimura and Anderl 2005). This number is sufficient for characterizing general ageing imprecision and bias, as well as assessing quality control among readers, but reduces the ability to account for the influence of ageing error in age and growth fits. Often the decision is made to allocate finite resources to ageing more individuals only once rather than ageing fewer individuals more times. This study demonstrates consistent bias in parameter estimates when using only one age read regardless of the sample size and method used to incorporate the information obtained from multiple reads. This study also demonstrates that two or three reads is generally sufficient to adequately characterize the ageing error, and we recommend more effort be allocated to collecting and ageing more fish once this minimum number of reads is acquired. Although the RE approach works with a mixed data set of singly and multiply aged individuals, increasing the number of multiple-aged fish within a study may lead to substantial and biologically relevant improvements to growth fits.

Acknowledgements

A self-standing, executable program that interacts with Microsoft® Excel to perform the RE methods described in this paper is available from JMC for general use. Thanks go to A. MacCall for the initial brainstorming session that lead to this investigation. Thanks go to D. Fournier and H. Skaug for their assistance regarding ADMB-RE. B. Horness, D. Pearson, and M. Schirripa were generous in providing ageing samples from NOAA Fisheries surveys for use in testing these methods. Thanks also go to J. Grebel, B. Matta, and M. Stevens for providing age and growth data sets to explore. Z.T. A'mar, G. Fay, M. Haltuch, and D. Kinzey provided considerable discussion during this work, and two anonymous reviewers offered valuable suggestions that greatly improved the presentation and readability of this paper. Support for JMC and AEP was provided by National Marine Fisheries Service (NMFS) grant NA07FE0473.

References

Appledoorn, R.S. 1982. Variation in the growth rate of *Mya arenaria* and its relationship to the environment as analyzed through principle component analysis and the omega parameter of the von Bertalanffy equation. Fish. Bull. **81**: 75–84.

Beamish, R.J., and Fournier, D.A. 1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. **38**: 982–983.

Beverton, R.J.H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. J. Fish Biol. **41**(Suppl. B): 137–160.

Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. Chapman and Hall, London, UK.

Beverton, R.J.H., and Holt, S.J. 1959. A review of the life-spans and mortality rates of fish in nature, and their relationship on growth and other physiological characteristics. *In* Ciba Foundation Colloquia on Ageing. Vol. 5. The lifespan of animals. J. & A. Churchill Ltd., London, UK.

Bowker, D.W. 1995. Modeling the patterns of dispersion of length at age in teleost fishes. J. Fish Biol. **46**(3): 469–484.

Bradford, M.J. 1991. Effects of ageing errors on recruitment time series estimated from sequential population analysis. Can. J. Fish. Aquat. Sci. **48**: 555–558.

Cailliet, G.M., and Goldman, K.J. 2004. Age determination and validation in chondrichthyan fishes. *In* Biology of sharks and their relatives. *Edited by* J. Carrier, J.A. Musick, and M.R. Heithaus. CRC Press LLC, Boca Raton, Fla. pp. 399–447.

Cailliet, G.M., Yudin, K.G., Tanaka, S., and Taniuchi, T. 1990. Growth characteristics of two populations of *Mustelus manazo* from Japan based upon cross-readings of vertebral bands. NOAA Tech. Rep. No. 90.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. **59**(2): 197–242.

Campana, S.E., Annand, M.C., and McMillan, J.I. 1995. Graphical and statistical methods for determining the consistency of age determination. Trans. Am. Fish. Soc. **124**: 131–138.

Casella, G., and Berger, R.L. 2002. Statistical inference. Duxbury, Pacific Grove, Calif.

Chang, W.Y.B. 1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. **39**: 1208–1210.

Charnov, E.L. 1993. Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford University Press, Oxford, UK.

Chen, Y., Jackson, D.A., and Harvey, H.H. 1992. A comparison of von Bertalanffy and polynomial functions in modeling fish growth data. Can. J. Fish. Aquat. Sci. **49**: 1228–1235.

Clark, W.G. 1991. Groundfish exploitation rates based on life history parameters. Can. J. Fish. Aquat. Sci. **48**: 734–750.

Cloern, J.E., and Nichols, F.H. 1978. A von Bertalanffy growth model with a seasonally varying coefficient. J. Fish. Res. Board Can. **35**: 1479–1482.

Dunn, A., Francis, R.I.C.C., and Doonan, I.J. 2002. Comparison of the Chapman–Robson and regression estimators of *Z* from catch-curve data when non-sampling stochastic error is present. Fish. Res. **59**(1–2): 149–159.

Evans, G.T., and Hoenig, J.M. 1998. Testing and viewing symmetry in contingency tables, with application to readers of fish ages. Biometrics, **54**: 620–629.

Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth, **29**: 265–289.

Gay, D. 1996. More AD of nonlinear AMPL models: computing Hessian information and exploiting partial separability. *In* Computational differentiation: techniques, applications, and tools. *Edited by* M. Berz, C. Bischof, G. Corliss, and A. Griewank. Society for Industrial and Applied Mathematics (SIAM), Philadelphia, Pa. pp. 173–184.

Grebel, J.M. 2003. Age, growth, and maturity of cabezon, *Scorpaenichthys marmoratus*, in California. M.S. thesis, Moss Landing Marine Laboratories, San Jose State University, Calif.

Gulland, J.A. 1983. Fish stock assessment: a manual of basic methods. John Wiley & Sons, Chichester, UK.

Haddon, M. 2001. Modelling and quantitative methods in fisheries. Chapman and Hall, London, UK.

Jensen, A.L. 1998. Simulation of relations among fish life history parameters with a bioenergetics-based population model. Can. J. Fish. Aquat. Sci. **55**(2): 353–357.

Kimura, D.K. 1980. Likelihood estimates for the von Bertalanffy growth curve. Fish. Bull. **77**: 765–776.

Kimura, D.K. 2000. Using nonlinear functional relationship regression to fit fisheries models. Can. J. Fish. Aquat. Sci. **57**(1): 160–170.

Kimura, D.K., and Anderl, D.M. 2005. Quality control of age data at the Alaska Fisheries Science Center. Mar. Freshw. Res. **56**(5): 783–789.

Kimura, D.K., and Lyons, J.J. 1991. Between-reader bias and variability in the age-determination process. Fish. Bull. **89**(1): 53–60.

Lai, H.L., and Gunderson, D. 1987. Effects of ageing error on estimates of growth, mortality and yield per recruit for walleye pollock (*Theragra chalcogramma*). Fish. Res. **5**: 287–302.

Marquardt, D.W. 1963. An algorithm for least-squares estimation of nonlinear parameters. J. Soc. Indust. Appl. Math. **11**(2): 431–441.

Nummi, T. 2000. Analysis of growth curves under measurement errors. J. Appl. Stat. **27**(2): 235–243.

Otter Research Ltd. 2005*a*. An introduction to AD Model Builder. Version 7.0.1. For use in non-linear modeling and statistics. Otter Research Ltd., Sydney, B.C.

Otter Research Ltd. 2005*b*. Random effects in AD Model Builder: ADMB-RE user guide. Otter Research Ltd., Sydney, B.C.

Palmer, M.J., Phillips, B.F., and Smith, G.T. 1991. Application of nonlinear models with random coefficients to growth data. Biometrics, **47**: 623–635.

Parma, A.M., and Deriso, R.B. 1990. Dynamics of age and size composition in a population subject to size-selectivity mortality: effects of phenotypic variability in growth. Can. J. Fish. Aquat. Sci. **47**: 274–289.

Pilling, G.M., Kirkwood, G.P., and Walker, S.G. 2002. An improved method for estimating individual growth variability in fish, and the correlation between von Bertalanffy growth parameters. Can. J. Fish. Aquat. Sci. **59**(3): 424–432.

Piner, K.R., Hamel, O.S., Menkel, J.L., Wallace, J.R., and Hutchinson, C.E. 2005. Age validation of canary rockfish (*Sebastes pinniger*) from off the Oregon coast (USA) using the bomb radiocarbon method. Can. J. Fish. Aquat. Sci. **62**(5): 1060–1066.

Piner, K.R., Wallace, J.R., Hamel, O.S., and Mikus, R. 2006. Evaluation of ageing accuracy of bocaccio (*Sebastes paucispinis*) rockfish using bomb radiocarbon. Fish. Res. **77**(2): 200–206.

Pitcher, T.J., and MacDonald, P.D.M. 1973. Two models for seasonal growth in fishes. J. Appl. Ecol. **10**(2): 599–606.

Prajneshu, and Venugopalan, R. 1999. von Bertalanffy growth model in a random environment. Can. J. Fish. Aquat. Sci. **56**: 1026–1030.

Quinn, T.J., and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Rafail, S.Z. 1973. A simple and precise method for fitting a von Bertalanffy growth curve. Mar. Biol. **19**: 354–358.

Reeves, S.A. 2003. A simulation study of the implications of age-reading errors for stock assessment and management advice. ICES J. Mar. Sci. **60**(2): 314–328.

Richards, L.J., Schnute, J.T., Kronlund, A.R., and Beamish, R.J. 1992. Statistical models for the analysis of ageing errors. Can. J. Fish. Aquat. Sci. **49**(9): 1801–1815.

Sainsbury, K.J. 1980. Effect of individual variability on the von Bertalanffy growth equation. Can. J. Fish. Aquat. Sci. **37**: 241–247.

Schnute, J.T. 1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. **38**: 1128–1140.

Sinclair, A.F., Swain, D.P., and Hanson, J.M. 2002. Disentangling the effects of size-selective mortality, density, and temperature on length-at-age. Can. J. Fish. Aquat. Sci. **59**(2): 372–382.

Skaug, H., and Fournier, D. 2006. Automatic approximation of the marginal likelihood in non-Gaussian hierarchical models. Computational Statistics & Data Analysis, **51**: 699–709.

Stamatopoulos, C., and Caddy, J.F. 1989. Estimation of von Bertalanffy growth parameters: a versatile linear regression approach. J. Cons. Int. Explor. Mer, **45**: 200–208.

Stevens, M.M., Andrews, A.H., Cailliet, G.M., Coale, K.H., and Lundstrom, C.C. 2004. Radiometric validation of age, growth, and longevity for the blackgill rockfish (*Sebastes melanostomus*). Fish. Bull. **102**(4): 711–722.

Taylor, N.G., Walters, C.J., and Martell, S.J.D. 2005. A new likelihood for simultaneously estimating von Bertalanffy growth parameters, gear selectivity, and natural and fishing mortality. Can. J. Fish. Aquat. Sci. **62**(1): 215–223.

Tomlinson, P.K., and Abramson, N.J. 1961. Fitting a von Bertalanffy growth curve by least squares. California Department of Fish and Game, Sacramento, Calif. Fish. Bull. No. 116.

Troynikov, V.S. 1999. Use of Bayes theorem to correct size-specific sampling bias in growth data. Bull. Math. Biol. **61**: 355–363.

Tyler, A.V., Beamish, R.J., and McFarlane, G.A. 1989. Implications of age determination errors to yield estimates. *In* Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. *Edited by* R.J. Beamish and G.A. McFarlane. Can. Spec. Publ. Fish. Aquat. Sci. No. 108. pp. 27–35.

Vaughan, D.S., and Burton, M.L. 1994. Estimation of von Bertalanffy growth parameters in the presence of size-selected mortality: a simulated example with red grouper. Trans. Am. Fish. Soc. **123**(1): 1–8.

Venugopalan, R., and Prajneshu. 1997. von Bertalanffy growth model with autocorrelated errors. Indian J. Fish. **44**: 63–67.

von Bertalanffy, L. 1934. Untersuchungen uber die Gestzlichkeit des Wachstums. 1. Teil. Allgemeine Grundlagen der Theorie; mathematische and physiologische Gesetzlichkeiten des Wachstums bei Wassertieren. Arch. Entwicklungsmech. Org. (Wilhelm Roux), **131**: 613–652.

von Bertalanffy, L. 1938. A quantitative theory of organic growth. Hum. Biol. **10**: 181–213.

Walford, L. 1946. A new graphical method of describing the growth of animals. Biol. Bull. **90**: 141–147.

Wang, Y.-G. 1998. An improved Fabens method for estimation of growth parameters in the von Bertalanffy model with individual asymptotes. Can. J. Fish. Aquat. Sci. **55**: 397–400.

Wang, Y.-G., and Ellis, N. 1998. Effect of individual variability on estimation of population parameters from length–frequency data. Can. J. Fish. Aquat. Sci. **55**: 2393–2401.

Wang, Y.-G., and Ellis, N. 2005. Maximum likelihood estimation of mortality and growth with individual variability from multiple length–frequency data. Fish. Bull. **103**: 380–391.

Wang, Y.-G., and Thomas, M.R. 1995. Accounting for individual variability in the von Bertalanffy growth model. Can. J. Fish. Aquat. Sci. **52**: 1368–1375.

Weatherley, A.H., and Gill, H.S. 1987. The biology of fish growth. Academic Press, London, UK.

Williams, E.H., and Shertzer, K.W. 2003. Implications of life-history invariants for biological reference points used in fishery management. Can. J. Fish. Aquat. Sci. **60**(6): 710–720.