

Flexible von Bertalanffy growth models incorporating Bayesian splines



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ABSTRACT

Understanding the growth rates of fish is vital for effective fisheries management. Historically a three-parameter von Bertalanffy growth model (VBGM) has most often been used to describe the somatic growth of fish. However, increasingly, populations are identified with patterns of growth that are not adequately described by the standard VBGM. We describe a more flexible growth model obtained by replacing the normally constant von Bertalanffy growth coefficient, k , with a piecewise constant function, K , of age. In principle this allows arbitrary monotonic growth to be approximated within a generalized von Bertalanffy structure. Posterior distributions of model parameters are approximated by the method of Hamiltonian Monte Carlo using the Stan software package. Spline smoothing of the K function is achieved by specifying a hierarchical random walk prior. We compare fits achieved using this new approach to observations of length-at-age of southern bluefin tuna (*Thunnus maccoyii*) with a range of existing growth models.

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1. Introduction

Knowledge of growth rates of harvested fish species is important for sound fisheries management. For example, harvest rates that optimize sustainable yields depend upon somatic growth rates. For some species growth curves are used to estimate the number or proportion of fish harvested annually from each age class based on length frequency samples from the catch. The age-structured model used to estimate the global population of southern bluefin tuna (SBT, *Thunnus maccoyii*) takes as a key data input estimates of catch-at-age of an Australian purse seine fishery that harvests juveniles. The purse seine catch-at-age is estimated by assigning ages to length samples using cohort slicing based on a growth curve (Kolody et al., 2016).

In fisheries applications, the three-parameter von Bertalanffy growth model (VBGM) is used to model size-at-age more frequently than any other growth model. The VBGM is an asymptotic growth curve with no inflexion points assuming absolute growth rate decreases continuously as animals approach their asymptotic length. As growth information for various species accumulates, the

identification of populations whose growth departs from the VBGM is becoming increasingly common.

Many or even most fish species undergo profound changes in their habitat or biology during their lifetime and often growth will be affected. Ricker (1979) suggested that the growth of a fish across its lifetime could be considered to consist of a series of stages or stanzas with transition from one stanza to the next occurring as the result of some crisis or discontinuity in development or a change in habitat (p. 689). The effect upon growth of the onset of sexual maturity has probably been investigated more often than that of any other life history stage (see e.g. Lester et al., 2004; Quince et al., 2008a,b; Roff, 1983). However, effects of other events have been described. For example, individuals of some fish species are known to change sex at certain times of life and, not surprisingly, this has been found to affect growth in some cases (Davis, 1982; Matthias et al., 2016; Higgins et al., 2015; Walker and McCormick, 2004). The growth of diadromous fish such as salmon has been observed to alter markedly when they move between freshwater and saltwater environments (Ricker, 1979). An apparent acceleration in the growth rate of Nile perch, modelled by Soriano et al. (1992), has been attributed to a shift in its diet from zooplankton to fish.

Working within a general framework described previously by Wang (1998), we replace the constant von Bertalanffy growth coefficient, k , with a function of age and we refer to this function as 'growth trajectory', or more simply as the K function. We propose a

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piecewise constant K function that facilitates flexible modelling of asymptotic growth whilst making minimal assumptions about the parametric form of the growth process.

Ultimately we seek to specify a model that satisfies the desiderata of Sandland and McGilchrist (1979) to a greater extent than existing models. That is, the model should be highly flexible and able to be fitted to a wide variety of shapes whilst, at the same time, retaining some of the biological interpretability associated with the standard VBGM (Sandland and McGilchrist, 1979, p. 257). We fit generalised von Bertalanffy growth models with piecewise constant growth trajectory functions to 2161 direct observations of length-age taken from southern bluefin tuna harvested by international fishing fleets using Bayesian methods. Spline smoothing of the log growth trajectory function is achieved by the specification of a hierarchical random walk prior. The results are compared to a range of existing parametric growth models that we fit to the same data.

2. Background

2.1. The VBGM

We consider the problem of estimating the average length of a population of animals as a function of age. As a starting point we first describe the three-parameter VBGM which, as mentioned, is the model most commonly used to describe fish growth. Letting l denote the mean length of individuals in the population as a function of age, a , the VBGM is characterised by the relationship:

$$\frac{dl}{da} = k(L_\infty - l(a)), \quad k > 0, \quad (1)$$

where L_∞ is an asymptotic mean length and k is a positive constant. The popularity of the VBGM in fisheries applications stems, at least in part, from the view amongst many fisheries scientists that the model has a biological foundation. However, the validity of the biological argument for the VBGM has been questioned (e.g. Ricker, 1979; Sandland, 1983) and the need for empirically based model comparison emphasised.

2.2. A generalisation of the VBGM

Wang (1998) describes a generalisation of Eq. (1) such that K can vary with age as well as with potentially age-dependent covariates. This generalised VBGM is characterised by the relationship:

$$\frac{dl}{da} = K(a, \mathbf{x}_a | \boldsymbol{\theta})(L_\infty - l(a)), \quad K(a, \mathbf{x}_a | \boldsymbol{\theta}) > 0 \quad \forall a, \quad (2)$$

where \mathbf{x}_a is a matrix of covariate values and $\boldsymbol{\theta}$ is a vector of parameters. This approach has been applied to wild populations to examine the effect on growth of latitude (Lloyd-Jones et al., 2012) and of inserting tags for mark-recapture purposes (Wang, 1998; Wang and Jackson, 2000). The effects of covariates are not considered in the present study, but we allow growth trajectory, K , to vary with age.

Wang (1998) gives the solution of Eq. (2) in its general form. Initially we restrict our attention to the special case where $l(0) = 0$, which is reasonable for most bony fish species. The solution of this special case can be expressed as:

$$l(a | L_\infty, \boldsymbol{\theta}) = L_\infty \left(1 - \exp \left(- \int_0^a K(u | \boldsymbol{\theta}) du \right) \right). \quad (3)$$

Strictly speaking, l must be continuously differentiable for Eq. (3) to be a solution of (2) and this places certain restrictions on the function K . However, Laslett et al. (2002) note that any cumulative

distribution function scaled by asymptotic length can be used as a growth model. Therefore, Eq. (3) forms a growth model provided:

$$\int_0^\infty K(u | \boldsymbol{\theta}) du = \infty. \quad (4)$$

We mention Eq. (2) to highlight the relationship between the K function we refer to as growth trajectory and the von Bertalanffy parameter, k , in Eq. (1).

The new models we describe below are compared with existing growth models some of which are not subject to the $l(0) = 0$ constraint. We briefly explain later how the approach we describe can also be easily extended to accommodate the growth of species where the assumption of zero length at birth is not appropriate.

3. Methods and materials

3.1. Piecewise constant growth trajectory function

The piecewise constant function is a popular choice to model the baseline hazard function in survival analysis problems (see e.g. Fahrmeir and Kneib, 2011; Ibrahim et al., 2001). As implied by Schnute and Richards (1990), survival and growth models are actually quite similar. In this sense the hazard function, central to survival analysis, is analogous to what we refer to as the K function within the generalised von Bertalanffy growth framework, Eq. (3).

We define knot locations, $0 = \tau_0 < \tau_1 < \dots < \tau_{J-1} < \tau_J$, where τ_j is greater than or equal to the maximum age observed so that the $j+1$ knots, τ_j , partition observed age. Letting $\mathbf{I}(\cdot)$ denote an indicator function which takes the value one when condition \cdot is true and zero otherwise, the piecewise constant growth trajectory function is defined as:

$$K(a | \boldsymbol{\theta} = \{\kappa_1, \dots, \kappa_J\}) = \sum_{j=1}^J \kappa_j \mathbf{I}(\tau_{j-1} \leq a < \tau_j), \quad \kappa_j > 0. \quad (5)$$

With sufficiently short interval lengths, the piecewise constant function can approximate an arbitrary function of age. The very simple degree-zero spline basis terms allow the integral in Eq. (3) to be evaluated for any set of κ_j as the sum of the areas of J rectangles and so readily updated within a Monte Carlo algorithm. We constrain the κ_j to be strictly positive to ensure the fitted length-at-age curve is monotonic. We refer to growth models incorporating this approach as 'VB-spline' models and call this first example VB_{spl1} to distinguish it from a slightly modified version that we describe below.

3.2. A slightly altered growth trajectory function

Exploratory modelling of the SBT data suggested that estimated growth trajectory in the first year might be substantially higher than in subsequent years. In an attempt to avoid a large change in the K function at age 1 we consider a second VB-spline model having a very slightly modified growth trajectory function from that defined in Eq. (5). This second spline model, which we refer to as VB_{spl2}, has K function:

$$K(a | \boldsymbol{\theta}) = \mathbf{I}(0 \leq a < \tau_1) \left\{ \kappa_1 + \frac{a(\kappa_2 - \kappa_1)}{\tau_1} \right\} + \sum_{j=2}^J \kappa_j \mathbf{I}(\tau_{j-1} \leq a < \tau_j). \quad (6)$$

The VB_{spl2} growth model is obtained by substituting Eq. (6) into the general growth model (3). This adjustment amounts to replacing the first constant interval of Eq. (5) with a linear interpolation from κ_1 to κ_2 between ages $\tau_0 = 0$ and τ_1 . The integral of the K function is then just the sum of the areas of one trapezium and $J - 1$ rectangles.

3.3. Alternative growth functions

We fit a range of alternative functions for mean length-at-age to the SBT data to allow the performance of the VB-spline models to be meaningfully assessed. Specifically, we consider the commonly applied three parameter VBGM discussed earlier, the VBlogk currently used to describe the growth of SBT and the four-parameter Richards growth model.

We parameterise the VBGM as:

$$l(a) = L_{\infty} [1 - \exp\{-k(a - a_0)\}] \quad (7)$$

The parameter L_{∞} is common to all of the models that we consider and is interpreted as mean asymptotic length (in cm) in each model. As described earlier, the von Bertalanffy coefficient, k , controls the shape of the VBGM with higher values of k corresponding to steeper early growth and increased curvature. The VBGM parameter a_0 is the implied age corresponding to zero mean length. However, the a_0 parameter is generally not interpreted literally. The a_0 parameter allows length-at-birth to be non-zero which can result in an improved fit to observed growth data even when length-at-birth is known to be approximately zero. In fisheries applications individuals very near zero length are often not observed and are typically of limited interest.

Laslett et al. (2002) describe an approach for fitting growth models to mark-recapture data where the ages of the animals at tagging are unknown. For reasons of parameter identifiability, Laslett et al. (2002) parameterised growth in terms of $(a - a_0)$ where a_0 is an age-at-zero-length nuisance parameter as appears in the three parameter VBGM (7). Within this more general framework, Laslett et al. (2002) propose a von Bertalanffy type model with a logistic K function. The K function, logistic in $(a - a_0)$, is expressed as:

$$K(a) = k_1 + \frac{k_2 - k_1}{1 + \exp\{-\beta(a - a_0 - \alpha)\}} \quad (8)$$

According to Eq. (8), the transition from k_1 to k_2 is centred at age $\alpha + a_0$, with the steepness of the transition controlled by the parameter β . It can be seen that if β is constrained to be positive, the right hand side of Eq. (8) approaches k_2 as a gets large. It follows that the case where $k_2 > k_1$ describes an increasing logistic function and $k_2 < k_1$ describes a decreasing logistic function. The VBlogk, is the solution to Eq. (2) assuming the logistic K function (8) and setting length at $a = a_0$ to zero. The resulting length-at-age model is given by:

$$l(a) = L_{\infty} \left[1 - \exp\{-k_2(a - a_0)\} \left\{ \frac{1 + \exp\{-\beta(a - a_0 - \alpha)\}}{1 + \exp(\beta\alpha)} \right\}^{(k_1 - k_2)/\beta} \right] \quad (9)$$

Various parameterisations of the Richards growth model (Richards, 1959) have been used, but according to Ratkowsky (1990), the parameterisation with the best statistical properties has the form:

$$l(a) = L_{\infty} \{1 + \exp(\phi - \rho a)\}^{-1/\delta} \quad (10)$$

Parameters δ and ρ are constrained to be positive. The Richards model has as special cases the logistic (when $\delta = 1$) and the Gompertz (as $\delta \rightarrow 0$) growth models.

3.4. Application to southern bluefin tuna

SBT is a large, moderately long-lived, pelagic fish species that is widely distributed throughout the temperate oceans of the southern hemisphere. The species is harvested by international fishing fleets and the characteristics of its growth are of considerable scientific interest. Previous studies (e.g. Hearn and Polacheck, 2003; Laslett et al., 2002) have concluded that growth of SBT is not adequately described by the standard VBGM. Hearn and Polacheck

(2003) fitted 'two-phase' von Bertalanffy models to tag-recapture data such that growth was assumed to switch from one von Bertalanffy curve to another upon reaching a particular length. The transition length was estimated from the data. Laslett et al. (2002) suggested the abrupt change in growth implied by the two-phase von Bertalanffy model seemed 'harsh from a biological viewpoint' (p. 979) and proposed the VBlogk as an alternative. The VBlogk permits a smooth transition between two growth stanzas by modelling growth trajectory as a logistic function of age. However, when the VBlogk has been fitted to SBT data previously (Laslett et al., 2002; Eveson et al., 2004; Polacheck et al., 2004) the estimated parameters of the logistic growth trajectory function have suggested a virtually instantaneous step-change between growth stanzas limiting its effective advantage over the model of Hearn and Polacheck (2003). The growth of SBT is currently assumed to be described by a seasonal VBlogk (see e.g. Polacheck et al., 2003; Eveson et al., 2004).

3.4.1. Direct length-age data

As with many other bony fish species, the age of harvested SBT can be inferred by examining small calcified structures called sagittal otoliths which are extracted from inside the head. Opaque zones are deposited in SBT otoliths each austral winter so that the age (in years) of the harvested individuals can be 'read' by counting the number of opaque zones in much the same way that the age of trees is inferred from growth rings in their trunks. An age reading coupled with a corresponding length measurement from the same fish at the time of harvest constitutes a 'direct observation of length-age'.

We initially sourced direct observations of length-age from 16,595 harvested SBT recorded on the database of the Commission for the Conservation of Southern Bluefin Tuna (CCSBT). Juvenile observations of length-age mostly come from an Australian commercial purse seine fleet that operates in the Great Australian Bight over the austral summer. Juveniles captured by purse seine are typically transferred live via towing pontoons to tuna farms for fattening prior to harvest and export (Ellis and Kiessling, 2015). Otoliths are extracted from individuals that die during the towing process. From about the age of three or four years, SBT are harvested by longline fleets operating in the eastern Atlantic, Indian and western Pacific Oceans. Recent longline catch of SBT has occurred chiefly during the austral winter by vessels fishing under the flags of Japan, Taiwan, South Korea and New Zealand. Otoliths are extracted from a random sample of longline-caught SBT by onboard observers. Information on the length-at-age of adult SBT comes predominantly from length measurements and otolith samples of individuals caught by Indonesian longline fleets operating on the SBT spawning grounds south of Java. The Indonesian fleet which targets yellowfin and bigeye tuna catch adult SBT as bycatch during the SBT spawning season, mostly between September and March. A full description of the SBT length-age data is given in Farley et al. (2007).

Following recent analyses of these data (Eveson et al., 2004; Polacheck et al., 2003), we exclude observations corresponding to individuals harvested between the months of May and September as well as individuals harvested by the Indonesian fleet on the spawning grounds estimated to be less than 15 years old. We assume the growth characteristics of individuals 15 years and older caught on the spawning grounds are more representative of the SBT population at the same ages than the younger individuals caught on the spawning grounds. Observations from SBT harvested between May and September are excluded because of uncertainty in the timing of opaque zone deposition in otoliths. Young adults harvested on the spawning grounds are excluded because fast growing individuals are thought to begin migrating to the spawning grounds at a younger age than slower growing individuals (Farley et al., 2014). These restrictions result in the exclusion of 9742 observations. The

distinctness of zones in otoliths is variable and the age-reading process is subject to error. Scientists that perform age-readings of SBT are required to record a readability rating on a six point scale for each otolith. We exclude all readings where the readability was rated less than three. This leads to the exclusion of a further 4697 observations leaving 2161 for analysis.

An assumed age, conditional on the age reading and the month of harvest, was calculated also as described by Eveson et al. (2004). Spawning in SBT occurs mostly between the months of September and March and a common birthday of 1 January for all SBT is considered a reasonable approximation (Eveson et al., 2004; Leigh and Hearn, 2000). Opaque zones are deposited in otoliths over winter some time between the months of May and September (Clear et al., 2000). So, using similar notation to Eveson et al. (2004), if q_i is the number of opaque zones counted on an otolith extracted from fish i and r_i is the Julian day this fish was harvested, then the assumed age of fish i in years is given by:

$$a_i = \begin{cases} q_i + \frac{r_i}{365} & \text{if harvested Jan–Apr,} \\ q_i - 1 + \frac{r_i}{365} & \text{if harvested Oct–Dec.} \end{cases} \quad (11)$$

The harvest date of the direct length-age data on the CCSBT database are given only to month accuracy, so the fifteenth day of the specified month was assumed in all cases. The lengths of aged individuals are measured at the time of harvest, so the fitted data consist of $n=2161$ pairs of length and age values (l_i, a_i) from fish $i=1, \dots, n$ summarised in Fig. 1. The marginal histograms shown in Fig. 1 reveal that the observations used for modelling span the observed ages of SBT quite well. Relatively fewer observations of individuals between the ages of about 7 and 14 years are fitted because the Japanese, Taiwanese and New Zealand flagged vessels that harvest SBT in these age classes operate chiefly during the austral winter and, as mentioned above, observations from individuals harvested between April and September are excluded from

analyses of length-at-age. As a result the majority of length-age observations of SBT between 7 and 14 years available on the CCSBT database were excluded from the analysis, but sufficient observations of these age classes were able to be sourced from longline fishing at other times of year. The ages assigned to each fish will, in general, include some error. However, our approach is consistent with that used by Eveson et al. (2004) who assumed the process was unbiased (p. 295).

Using Eq. (11), the maximum age assumed among the 2161 observations considered was between 39 and 40 years. This being the case, we chose to partition the interval 0–40 years into 40 sub-intervals of unit length. Alternative partitioning schemes could have been chosen, but we prefer to use interval lengths equal to an integer number of years to avoid differences in seasonal growth between intervals.

3.5. The observation model

We assume a standard observation model for individual length-at-age with normally distributed errors. If function l defines the mean length-at-age of the population, conditional on parameters, Ω , the measured length, l_i of fish i harvested at age a_i is assumed to be normally distributed about $l(a_i)$ with variance σ^2 . This is expressed as:

$$l_i = l(a_i|\Omega) + \epsilon_i, \quad \epsilon_i \sim \text{Normal}(\text{mean} = 0, \text{std. dev.} = \sigma). \quad (12)$$

The same observation model (12) is used for the five alternative growth functions considered in the present study. This model has likelihood function:

$$\text{like}_l(\Omega, \sigma) = (\sqrt{2\pi}\sigma)^{-n} \exp\left(-\frac{1}{2} \sum_{i=1}^n \frac{(l_i - l(a_i|\Omega))^2}{\sigma^2}\right). \quad (13)$$

The assumption of normally distributed errors with constant variance in Eq. (12) is consistent with previous analyses of SBT growth based on direct length-age data (e.g. Eveson et al., 2004; Polacheck et al., 2003). Kolody et al. (2016) survey approaches used to model the growth of commercially important tuna and billfish species internationally. They note that constant coefficient of variation is often assumed, but state a personal view (Kolody et al., 2016, p. 186) that constant variance is likely to be more appropriate in many cases, singling out SBT. Models that accommodate alternative mean-variance relationships can be readily defined with a Bayesian approach where appropriate. Residual analysis, described later, suggests the assumption of constant standard deviation (and equivalently constant variance) is reasonable for the SBT data.

3.6. Model fitting and prior distributions

We specify a weakly informative Normal(mean = 185, std. dev. = 30) prior for mean asymptotic length parameter, L_∞ . This parameter is common to all models that we fit in this study. The lengths of very many harvested SBT have been measured and even amongst the oldest fish observed lengths greater than 200 cm are uncommon and lengths greater than 220 cm are very rare. Laslett et al. (2004) suggested the assumption of a mean asymptotic length of 185 cm for SBT was reasonable.

We expect the ‘true’ growth trajectory function to be continuous and smooth. The piecewise constant functions of the VB-spline models satisfy neither of these conditions, but modelling the $\gamma_j = \ln(\kappa_j)$ as a random walk has a smoothing effect on jump discontinuities in the growth trajectory function at the locations of the knots. The random walk is defined by $\gamma_j \sim N(\text{mean} = \gamma_{j-1}, \text{std. dev.} = \sigma\gamma)$ for $j \geq 3$. We uncouple γ_1 from the random walk on γ_j because of an *a priori* expectation that growth of SBT in the first year might be fundamentally different from later years (Laslett et al.,

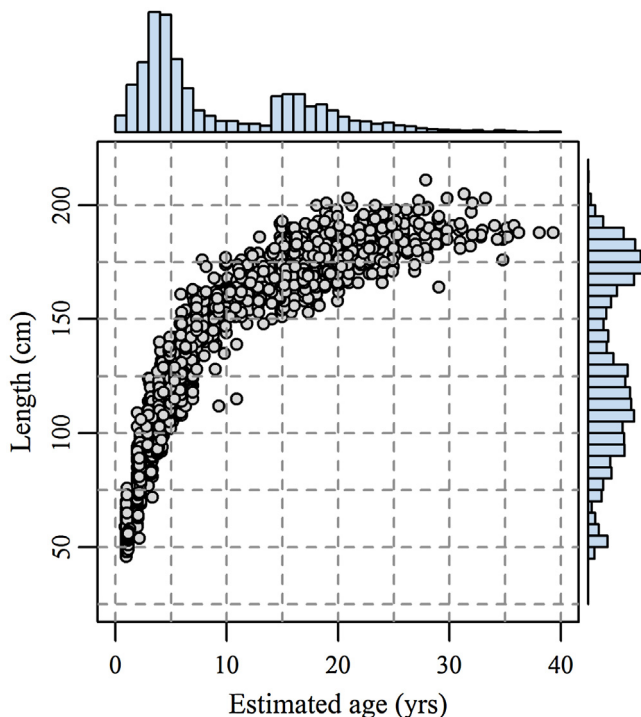


Fig. 1. Measured caudal fork length versus estimated age of 2161 southern bluefin tuna used to model growth. The histograms show the marginal distributions of estimated age (top margin) and measured length (right margin).

2002, p. 977). The use of the random walk prior achieves P-spline smoothing of the degree zero B-spline basis functions (Fahrmeir and Kneib, 2011). The assumption of lognormally distributed κ_j ensures a monotonic growth curve. For log-scale parameters γ_1 and γ_2 we specify Normal (mean = -1, std. dev. = 1) priors.

We specified half-Cauchy priors (see Gelman, 2006) with a scale parameter of 5 for both the standard deviation of the errors, σ , and the standard deviation of the random walk of the log scale γ_j parameters, σ_γ . The density we refer to as the half-Cauchy is a Cauchy distribution (see Johnson et al., 1994, Chapter 16) with location parameter zero, folded about the zero line so that negative values have zero probability density. The scale parameter of the half-Cauchy defines the positive number at which the density is reduced to half its value at the mode, where the mode occurs at zero. Increasing the scale parameter of a half-Cauchy distribution produces a flatter density function.

In summary, the priors for the VB-spline models were specified as:

$$\begin{aligned} L_\infty &\sim \text{Normal}(\text{mean} = 185, \text{std. dev.} = 30), \\ \sigma &\sim \text{half-Cauchy}(\text{scale} = 5), \\ \gamma_j &\sim \text{Normal}(\text{mean} = -1, \text{std. dev.} = 1) \quad \text{for } j = 1, 2, \\ \gamma_j &\sim \text{Normal}(\text{mean} = \gamma_{j-1}, \text{std. dev.} = \sigma_\gamma) \quad \text{for } j = 3, \dots, 40, \\ \sigma_\gamma &\sim \text{half-Cauchy}(\text{scale} = 5). \end{aligned} \quad (14)$$

An attempt was made as far as possible to define priors consistently across models. However, given the models have different parameters, it is not clear in some cases how this would be achieved. Stan assumes flat priors for all parameters unless otherwise specified, but improper priors are not appropriate for parameters of nonlinear regression models (Wakefield, 2013, p. 91). The VBGM is familiar to fisheries scientists meaning that for the VBGM and the models based on the von Bertalanffy, the VBlogk and the two VB-spline models, we have some prior knowledge about plausible parameter values. The strictly positive lognormal priors implicit for $\kappa_1 = \exp(\gamma_1)$ and $\kappa_2 = \exp(\gamma_2)$ have means of $e^{-1/2} \approx 0.61$, standard deviations of $e^{-1/2}\sqrt{e-1} \approx 0.80$, medians of $e^{-1} \approx 0.37$ and modes of $e^{-2} \approx 0.14$.

The parameters of the Richards model on the other hand are not at all well known. Therefore some experimentation was required to determine reasonable priors for the parameters of the Richards model.

The priors for parameters not defined in Eq. (14) were specified as:

$$\begin{aligned} k_1, k_2, k &\sim \text{Lognormal}(\text{location} = -1, \text{scale} = 1), \\ a_0 &\sim \text{Normal}(\text{mean} = 0, \text{std. dev.} = 2), \\ \alpha &\sim \text{Uniform}(\text{min} = 0, \text{max} = 40), \\ \beta &\sim \text{Uniform}(\text{min} = 0, \text{max} = 30), \\ \rho, \delta &\sim \text{Lognormal}(\text{location} = -1, \text{scale} = 1), \\ \phi &\sim \text{Normal}(\text{mean} = 0, \text{std. dev.} = 10). \end{aligned} \quad (15)$$

The VBlogk parameter α can technically be negative, but is assumed to be non-negative (pers. comm. Paige Eveson, CSIRO, Hobart 2016). Dortel et al. (2015) considered only positive values, assuming a gamma prior for this parameter. Lognormal(-1, 1) priors for parameters k , k_1 and k_2 ensure these have the same priors as the VB-spline parameters κ_1 and κ_2 .

Given 2161 direct observations of length-age, we expect the data to be informative. Nevertheless, the need to specify priors for comparison of Bayesian models introduces at least technical subjectivity. To check for sensitivity to the specified priors, we repeat the comparison of the same models, but with more diffuse priors. The models with diffuse priors (Eq. S1 and Eq. S2) are described in greater detail in the Supplemental Materials. Posterior summaries of the models with diffuse priors are also provided in the Supplemental Materials (Table S6).

The Stan software package (Stan Development Team, 2014) was used to fit Bayesian models. The posterior distributions of each of the five models were approximated using the No U-Turn Sampler, a version of Hamiltonian Monte Carlo (HMC, Neal, 2011), originally termed Hybrid Monte Carlo (Duane et al., 1987). Four sequences of 26,000 iterations with different sets of initial values were generated for each model. The first 1000 iterations from each chain were discarded as 'warm-up' and then every fifth iteration from the remaining 25,000 was retained to reduce autocorrelation in the retained sample. Trace plots were examined for evidence of non-convergence and to gauge the extent of mixing.

3.7. Model comparison

The leave-one-out information criterion (LOO-IC) is based on the model expected log posterior density (ELPD) of out-of-sample data (see Vehtari et al., 2015). The LOO-IC is just the ELPD multiplied by negative two which puts LOO-IC on the deviance scale familiar for comparison of other information criteria. Better model fit is suggested by higher ELPD and, equivalently, lower LOO-IC. By estimating the fit of out-of-sample data the ELPD, like other information criteria, seeks to avoid selecting models that are over-fitted to the observed data. We used the loo package (Vehtari et al., 2015) to compute values of the LOO-IC for each model as a basis for comparing the goodness of fits achieved by each model.

The application of an information criterion to select between a set of candidate models does not guarantee the best fitting model is adequate. Moreover, the practical significance of differences between model fit is not always clear from differences in information criteria scores. For this reason we recommend examination of residuals as routine practice for assessing the adequacy of growth models. We use 'realised' residuals (see e.g. Gelman et al., 2004, p. 174) calculated as the difference between the observed values and their fitted values conditional on a single random draw from the posterior distribution of the parameter space, Ω .

4. Results

4.1. Parameter estimates

Numerical summaries of the posterior distributions of key parameters of each fitted model are provided in Table 1.

The effective posterior sample size values, posteff , and potential scale reduction factor, R , in Table 1 describe characteristics of the HMC chains used to approximate the posterior distributions of the parameters. The effective posterior sample sizes are estimates of the information content of the retained HMC sample accounting for autocorrelation and are expressed in terms of the equivalent number of independent draws from the posterior distributions of each parameter. Estimated effective sample sizes of 2000 and above (Table 1) indicate that our retained HMC samples are more than adequate to permit full posterior inference. The potential scale reduction factor, \hat{R} , is a convergence diagnostic for MCMC algorithms based on the ratio of the variance of samples pooled from multiple chains to the within chain variance (see Gelman and Rubin,

Table 1
Statistical summaries of posterior distributions of key parameters of the five models fitted. Graphical summaries of the κ parameters of the VB_{spl1} and VB_{spl2} models are shown in Fig. 2

Model	Parameter	Percentiles			95% HPDI ^a	posteff	\hat{R}
		25%	Median	75%			
VB _{spl1}	L_∞	190	192	195	(186, 205)	2.8×10^3	1
	σ_γ	0.11	0.14	0.18	(0.06, 0.29)	4.3×10^3	1
	σ	8.70	8.79	8.88	(8.53, 9.05)	2.0×10^4	1
VB _{spl2}	L_∞	190	192	195	(186, 205)	3.3×10^3	1
	σ_γ	0.11	0.14	0.19	(0.06, 0.29)	4.3×10^3	1
	σ	8.69	8.78	8.87	(8.51, 9.03)	2.0×10^4	1
VBGM	L_∞	183	183	184	(182, 184)	1.8×10^4	1
	k	0.178	0.180	0.181	(0.174, 0.185)	1.8×10^4	1
	a_0	-1.17	-1.14	-1.10	(-1.24, -1.03)	1.8×10^4	1
	σ	8.85	8.94	9.03	(8.68, 9.21)	1.9×10^4	1
VBlogk	L_∞	192	194	197	(188, 204)	1.3×10^4	1
	k_1	0.23	0.26	0.30	(0.19, 0.34)	1.5×10^4	1
	k_2	0.07	0.09	0.10	(0.04, 0.12)	1.5×10^4	1
	α	1.51	3.06	4.69	(0.00, 6.60)	1.5×10^4	1
	β	0.21	0.25	0.31	(0.14, 0.46)	1.6×10^4	1
	a_0	-0.79	-0.73	-0.67	(-0.91, -0.55)	1.6×10^4	1
	σ	8.70	8.79	8.88	(8.53, 9.06)	2.0×10^4	1
	L_∞	180	180	180	(179, 181)	2.0×10^4	1
	ϕ	-3.70	-3.32	-2.97	(-4.41, -2.31)	1.7×10^4	1
Richards	ρ	0.25	0.25	0.25	(0.244, 0.259)	1.9×10^4	1
	δ	0.02	0.03	0.04	(0.005, 0.059)	1.7×10^4	1
	σ	9.22	9.32	9.41	(9.05, 9.61)	1.9×10^4	1

^a HPDI = highest posterior density interval.

1992). Values of \hat{R} approaching unity are consistent with algorithm convergence.

Posterior estimates of the mean asymptotic length parameter, L_∞ , of the VB-spline models and the VBlogk were larger than anticipated, each greater than 190 cm. Recent analyses of SBT growth using the VBlogk (e.g. Laslett et al., 2002; Polacheck et al., 2003, 2004; Eveson et al., 2004) have estimated asymptotic lengths between about 183 cm and 187 cm.

The posterior distributions of the κ_j parameters of the VB-spline models are summarised graphically in Fig. 2. Together these define the posterior growth trajectory functions, K , which are of key interest in the present study. The form of the estimated growth trajectory functions (Fig. 2) supports previous findings to the extent that the growth trajectory of older SBT tends to be lower than that of very young SBT.

Comparison of the piecewise constant growth trajectory functions (Fig. 2a and b) and the logistic K function of the VBlogk (Fig. 2c) is instructive. The VBlogk captures the basic trend of the growth trajectory functions of the VB-spline models. Beyond this, the posterior growth trajectory functions of the VB-spline models give some suggestion that the decline in growth trajectory pauses between the ages of about 3 and 8 years. This feature is admittedly subtle. However, a verified change in growth trajectory around 8 years of age would be intriguing because this would coincide approximately with the earliest onset of sexual maturity (Farley et al., 2014).

Relatively fewer length-age observations were fitted from individuals between the ages of 7 and 14 years. Nevertheless, the posterior K functions are estimated quite precisely over this interval (Fig. 2). Overall, the number of observations used to fit the model is more than adequate and the random walk spline smoothing improves the precision of the estimated κ_j generally. The precision of the posterior distribution of the K function declines as mean length approaches asymptotic length. This can be understood by considering Eq. (2) in the case where $l(a) - L_\infty \rightarrow 0$. As expected length approaches asymptotic length, the model estimated absolute growth rate, which is informed by the observed data, becomes progressively less sensitive to the value of the K function. The K

function of the VBlogk model is more precise at older ages (Fig. 2c) because of the assumption that its form is logistic. The posterior precision of the VB-spline growth trajectory functions could be improved by specifying a more informative prior for the κ_j such as a gamma process prior (Kalbfleisch, 1978). We prefer the random walk because we have stronger prior knowledge about the smoothness of the growth trajectory function than its level.

The parameters σ_γ of the VB-spline models control the degree of spline smoothing of their random walks on γ_j and are determined by the data. Values approaching zero reflect increased smoothness, whilst $\sigma_\gamma = 0$ would imply a perfectly flat growth trajectory curve – effectively a two parameter VBGM. The posterior distribution of this parameter in both VB-spline models is much more precise than their half-Cauchy priors indicating the observed data are informative on this parameter. Our posterior belief about credible values of σ_γ suggests this value is greater than zero even after decoupling γ_1 from the random walk.

A reviewer pointed out that the random walk prior for the log K function results in marginal priors for the individual γ_j that increase in standard deviation as j increases, adding this likely contributes to the increasing posterior uncertainty in K with age, evident in Fig. 2a and b. We found that alternatively modelling the log K function as an autoregressive AR(1) process, as suggested by the reviewer, resulted in a considerable reduction in the posterior uncertainty in the K function for older age classes compared with the random walk functions described here. The performance of the AR(1) models is not described further in the present study, but will be looked at more closely in future work.

Hearn and Polacheck (2003) were the first to suggest that the assumption of von Bertalanffy growth in SBT might be inappropriate. Analyses using the VBlogk (Eveson et al., 2004; Laslett et al., 2002) can be seen as a refinement of this first attempt. We have already mentioned that the mean asymptotic lengths of the VB-spline and VBlogk models estimated in the present study are significantly higher than estimated in previous analyses that fitted the VBlogk model. Therefore, given the dependence of absolute growth rate on the product of the K function and L_∞ implied in Eq. (2), it is not surprising that the growth trajectory function of the

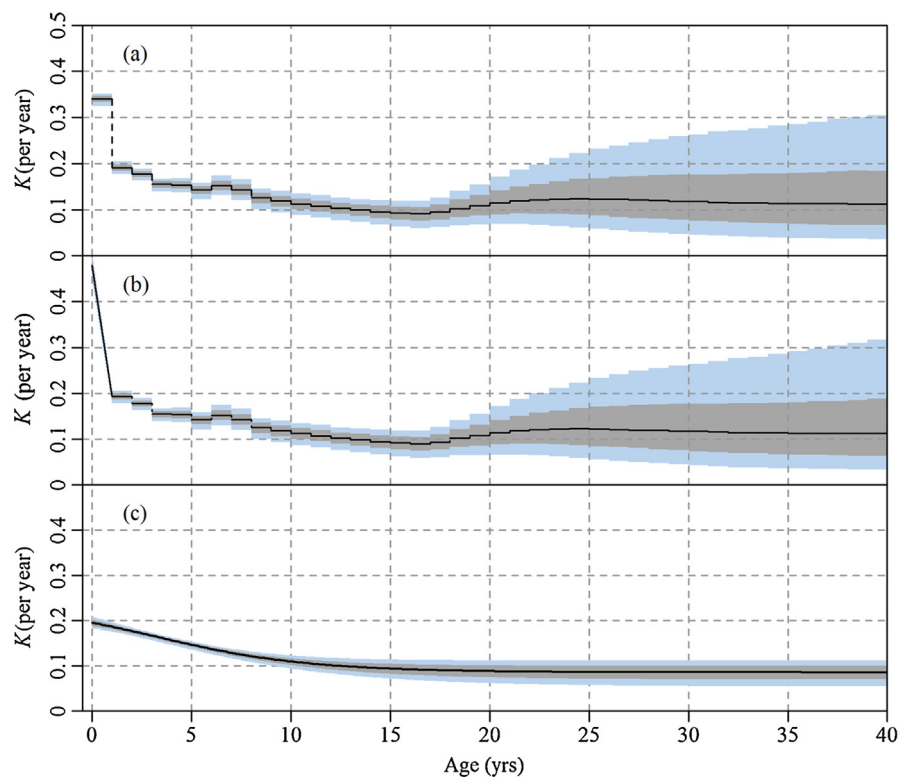


Fig. 2. Posterior growth trajectory functions for the (a) VB_{spl1} , (b) VB_{spl2} and (c) $VBlogk$ models. The black lines are the posterior medians. The shaded regions are 50% (innermost) and 80% (outermost) credible intervals.

$VBlogk$ estimated in the present study is generally lower than estimated in these previous studies. Also notable is the gradual decline of the growth trajectory function evident in the posterior distribution of the $VBlogk$ growth trajectory function (Fig. 2c). This is in contrast to previous applications of the $VBlogk$ model to SBT growth data where relatively very high values of the β parameter suggested essentially a step change from k_1 to a lower level k_2 typically occurring at around 3 years of age. We have used HMC to fit the $VBlogk$ in a Bayesian framework whereas the previous analyses fitted the $VBlogk$ using maximum likelihood (see Laslett et al., 2002; Polacheck et al., 2003). Additionally, the previous studies included tag-recapture data either alone (Laslett et al., 2002) or in combination with length-age data derived from otoliths (Eveson et al., 2004; Polacheck et al., 2003, 2004) where we have used only the length-age data.

4.2. Model selection

Model selection criteria for the fitted models are compared in Table 2. This table also includes estimates of the effective number of parameters, p_{eff} , for each model.

We emphasise that the estimated effective number of parameters for the VB-Spline models is approximately 10 (see Table 2) even though their piecewise constant K functions each include 40 discrete intervals. The difference between the number of parameters estimated and the effective parameters occurs as a result of the spline smoothing of the K function and is expected in hierarchical models (see e.g. Spiegelhalter et al., 2002). So while the VB-spline models have more effective parameters than conventional parametric growth models, the difference is not as great as might have been expected. Furthermore, according to LOO-IC, which accounts for the effective number of parameters, the VB-spline models fit the data better than the VBGM and the Richards models and are on a par with the $VBlogk$. This suggests the VB-spline models do

not overfit the SBT data. The model comparison statistics (Table 2) were generated using the compare function (Vehtari et al., 2015) in R version 3.2.2 (R Core Team, 2014). The Weight statistic provides an estimate of the probabilities that each model best describes the data generating process. The LOO-IC based Weight suggests that VB_{spl2} is likely to describe the growth of SBT better than the other models, although its advantage over the $VBlogk$ and VB_{spl1} is probably marginal. At the time of writing, the compare function included in the current version of the loo package no longer provides the estimated model weights.

The adequacy of each model can be better understood by examining distributions of residuals. We have plotted realised residuals versus age (Fig. 3) because fitted values are less evenly spread. The vertical scale of the residual plots makes them quite insensitive to model error because of the relatively large variability in the true length-at-age of SBT. Nevertheless some evidence of lack of fit is apparent in the VBGM (Fig. 3c) and Richards (Fig. 3e) residual plots. The other three models appear to fit the data well.

The distribution of realised residuals shown in Fig. 3 gives no reason to doubt the assumption of constant error variance assumed for the observation model Eq. (12). The adequacy of the constant variance assumption for the SBT data is shown more clearly by the nearly flat loess smooth fitted to the root absolute standardised residuals of the scale-location plot for the VB_{spl1} model (Fig. 4).

It is evident from the plots of realised residuals (Fig. 3) that the VBGM and the Richards model tend to underestimate the lengths of SBT older than about 25 years whereas the other models do a better job of predicting the lengths of these individuals. The fitted models also differ in their predicted lengths at ages less than one year. To illustrate this we compare the fitted models in Fig. 5 focusing on posterior mean length-at-age up to two years of age. The VB-Spline models assume zero length at birth whereas the other models do not. Also apparent in Fig. 5 is that the l_2 growth curve is smooth at age one, while l_1 is unsmooth.

Table 2
Model comparison statistics. Expected log predictive density (ELPD) of new data, leave-one-out information criterion (LOO-IC), effective number of parameters (p_{eff}) and model weight. The ΔELPD are differences in estimated expected log predictive density of new data compared with VBspl2 with standard errors in parentheses.

Model	ELPD	ΔELPD	LOO-IC	p_{eff}	Weight
VBspl1	-7768.3	-2.5 (0.5)	15,536.6	10.0	0.1
VBspl2	-7765.9	–	15,531.7	10.0	0.8
VBGM	-7802.8	-37.1 (7.9)	15,605.6	4.2	0.0
VBlogk	-7767.6	-1.9 (2.3)	15,535.1	5.8	0.1
Richards	-7889.5	-123.8 (14.1)	15,779.0	4.4	0.0

Note: LOO-IC = -2ELPD .

Dates of harvest and consequently assumed ages of the modelled SBT observations are resolved only to the nearest month. This results in groups of individuals having identical assumed ages. These groups can be distinguished in Fig. 5. Among individuals harvested at around one year of age, it would appear that those harvested in February and later tend to be smaller than those harvested in December and January despite our assumption that those harvested in February are slightly older. This probably occurs as

a result of one-year-olds available to the Australian SBT fleet in February being spawned later than those captured earlier in the fishing season. Spawning activity in SBT tends to peak twice a year leading to a bimodal length frequency distribution of one year olds (Itoh and Tsuji, 1996; Leigh and Hearn, 2000).

Tables and plots of the tests of sensitivity to prior distributions are included in Supplemental Materials. The higher variance priors used to check sensitivity to prior assumptions do result in small, but noticeable changes to the marginal posterior distributions of some individual model parameters (Table S6). Eveson et al. (2007) noted that high correlations between parameters of the VBGM mean that very similar length predictions can be given from models

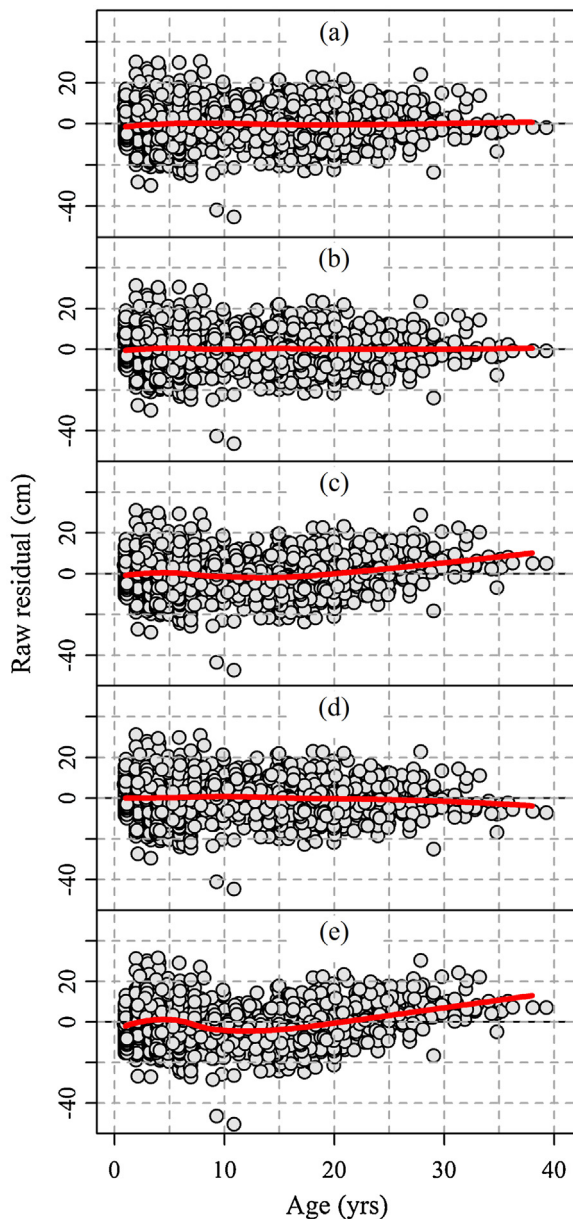


Fig. 3. A single realisation of residuals versus calculated age for (a) VBspl1 (b) VBspl2, (c) VBGM, (d) VBlogk and (e) Richards models. Loess smoothers are fitted to the residuals to help identify trends.

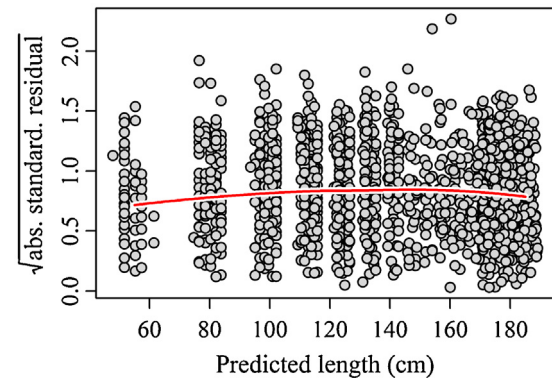


Fig. 4. A scale-location plot for the VBspl1 model showing a single realisation of the square root of absolute standardised residuals versus predicted length. A loess smoother is fitted to the residuals to help identify trends.

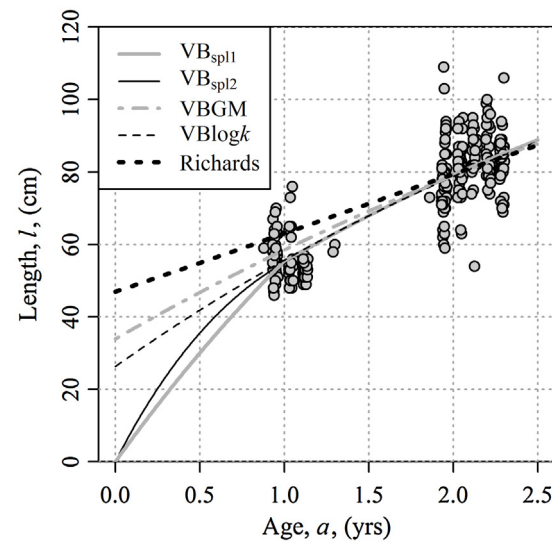


Fig. 5. Comparison of posterior mean length-at-age estimated by the five fitted models up to 2.5 years of age. The measured lengths of individual southern bluefin tuna aged less than 2.5 years are shown as grey circles. The ages plotted in the figure include a small random component (i.e. a jitter) to allow observations with the same assumed ages to be more easily distinguished.

with different sets of parameter values over a restricted range (p. 604). Similar correlations exist between the parameters of the other growth models and as these models have more parameters there is increased scope for different sets of parameter values to give nearly identical growth curves. Correlation matrices for all models are provided in Supplemental Materials (Tables S1–S5). We investigate differences in predicted length-at-age for each model with the two alternative sets of prior distributions by plotting posterior distributions of the difference for ages 0–40 (Fig. S1). These suggest that, generally, the posterior distributions of mean length-at-age are insensitive to the two alternative priors specified for the model parameters. Posterior mean length at age according to the VBlogk model is slightly larger for the oldest SBT when the diffuse priors are assumed. The difference is less than a centimetre, on average, for 40 year olds. The model comparison statistics are almost identical when the models are fitted with either set of priors (Tables 2 and S7).

Perhaps surprisingly, the HMC algorithms of both VB-spline models updated considerably faster than the VBlogk model. Specifically, it took around six hours on a 1.7 GHz laptop to generate the four chains of the VB_{spl1} posterior, just over eight hours for the VB_{spl2} posterior and 22 h for the VBlogk. This benefit is negated by the generally higher effective sample sizes realised for the VBlogk parameters from their HMC sequences (Table 1).

5. Discussion

The approximation of baseline hazard functions using piecewise constant models incorporating hierarchical Bayesian smoothing has proved to be a flexible approach for problems in survival analysis. To the authors' knowledge this paper provides the first example exploring the use of this strategy to model growth. The fisheries stock assessment software SS3 (Stock Synthesis 3) includes an age-specific K growth model, mentioned briefly in Methot and Wetzel (2013), but the K function is not smoothed.

The VB-spline growth models we describe are more flexible than growth models typically applied in fisheries science, but retain the useful constraint of monotonicity. The retention of the K function is helpful as it facilitates comparison with the VBGM familiar to fisheries biologists. The incorporation of a more flexible growth trajectory model allows length-at-birth to be constrained to be zero without biasing the rest of the growth curve (Fig. 5). We expect this feature results in more accurate prediction of the lengths of fish younger than the observed sample.

The difference between the two VB-spline models that we describe in this paper is almost trivial. We describe both models because, despite their similarity, each has slight advantages over the other. The VB_{spl1} provides a natural introduction to the VB-spline approach and tends to be computationally more efficient than the VB_{spl2}. On the other hand, VB_{spl2} gives a smoother growth curve at the location of the first internal knot and so, using the phraseology of Laslett et al. (2002), is less biologically harsh. It would be of some interest to fit observations of younger SBT with ages estimated from daily otolith circuli as described in Itoh and Tsuji (1996), but these observations were not available to the present study.

The VB-Spline models and the VBlogk all estimate a higher asymptotic length than has been estimated for SBT recently. It would be of interest to discover the cause of this. Since 2002, growth of SBT has been estimated by jointly modelling direct length-at-age data and tag-recapture data. Laslett et al. (2002) show using simulation that, unlike most earlier methods used to estimate von Bertalanffy growth parameters from tagging data, the approach they use to model tag recapture data does not introduce bias. Smaller, seemingly more reasonable, estimates of the VBlogk parameter β in the

present study might reflect the model fitting capabilities of the Stan software. Although, this last point is speculative.

The methods of capture used by commercial fishing fleets are not intended to catch a random sample of the harvested population. It is possible that the growth of the harvested SBT from which the sample is selected differs from the population as a whole over and above the allowances we make for young adults caught by the Indonesian fleet. In this case the fitted growth model is more reasonably regarded as the mean length-at-age of the harvested population rather than the entire population (Kolody et al., 2016). The length-at-age of the catch of harvested fish populations is of interest for fisheries stock assessment purposes. In any case, the purpose of the present study is to examine the utility of models we propose to describe growth as suggested by a realistic set of data rather than to provide an authoritative description of the growth of SBT.

Biphasic growth models (Lester et al., 2004; Shuter et al., 2005; Quince et al., 2008b) have been fitted to a number of fish species based on assumed changes in growth trajectory at the onset of sexual maturity. The application to SBT provides some indication of how the flexibility of the new model can potentially reveal aspects of growth that more structured parametric models cannot. Distinct changes in growth trajectory at particular ages could be symptomatic of biologically important changes in life stage. Comparisons of growth trajectory functions for different species might make these effects clearer and perhaps provide additional insights.

Most shark species give birth to live young. For these species the assumption of zero length at birth would not be appropriate. It would be straight forward to adapt the VB-spline models to such applications by estimating a mean length at birth parameter, say L_0 , and modelling growth relative to L_0 analogous to the treatment of the VBGM described in Cailliet et al. (2006).

The VB-spline models do have some important drawbacks. In our experience, the VB-spline models do not perform well when fitted to data that are not informative of an asymptotic length. Also, it is inconvenient to fully describe the fitted VB-spline models because they have relatively many parameters. More structured parametric models are likely to be a better choice for concisely describing length-at-age of fish populations where these are found to adequately fit the observed data. For the SBT data the VBlogk provides a good fit, although the K function shown in Fig. 2c does not really support the 'two-stanza' growth assumption that originally motivated the VBlogk. Despite some limitations, we believe the VB-spline model has considerable potential for exploratory modelling of growth as well as for model selection and validation. For example, the similarity in the present study between the growth trajectory of the VB-spline models and the parametric VBlogk increases our confidence that the fitted VBlogk model describes the growth of SBT well.

Where growth data are not well described by conventional parametric models, flexible VB-spline models might be preferable to multimodel inference which is sometimes advocated at present (e.g. Katsanevakis, 2006; Katsanevakis and Maravelias, 2008). For analyses of growth where the primary objective is to identify possible changes in growth behaviour with age, we suggest the VB-spline models provide an attractive alternative to models that have been used in the past. Ontogenetic changes in the characteristics of growth are more clearly illustrated from the growth trajectory function or K function than can be appreciated from a growth curve. The VB-spline models are well suited to analyses of possible temporal changes in growth or cohort effects. Comparative analyses of multiple species or populations are another obvious application.

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Appendix A. Stan code for the VB_{spl1} model

In this appendix we provide annotated Stan code used to fit the VB-Spline model, VB_{spl1}.

The model takes as input integers, n and J , which are the numbers of animals fitted and the number of piecewise constant intervals in the K function respectively, and a vector of measured lengths, $length$.

The $n \times J$ matrix, X , codifies the ages of the observed animals such that if the i th animal was measured at age a_i , element $x_{ij} = \min(\tau_{j+1}, a_i) - \min(\tau_j, a_i)$ where τ_0, \dots, τ_J are ages coinciding with the locations of the $J+1$ knots of the K function.

The definite integral of the K function evaluated between zero and a_i is then the scalar product of $X[i,]$, the i th row of X , and κ , the vector of κ parameters.

The prior for L_{inf} would generally need to be modified when fitting the model to data from a different species.

Text following double forward slashes treated as comments.

```
data
{
  int<lower = 0> n;           // number of animals fitted
  int<lower = 0> J;           // number of K function intervals
  real<lower = 0> length[n]; // vector of measured lengths
  row_vector[J] X[n];       // ages as an n by J matrix
}
parameters
{
  real<lower = 0> L_inf;      // Asymptotic length
  vector[J] gam;            // Vector of piecewise log K function
  real<lower = 0> sigma;      // Error standard deviation
  real<lower = 0> sigma_gam;  // Standard deviation of random walk
}
transformed parameters
{
  vector[J] kappa;          // Vector of piecewise K function levels
  real integral_K[n];       // definite integral of K function for each fish
  real mu_len[n];           // conditional mean length-at-age of each fish
  kappa <- exp(gam);
  for (i in 1:n)
  {
    integral_K[i] <- dot_product(kappa, X[i]);
    mu_len[i] <- L_inf*(1 - exp(-integral_K[i]));
  }
}
model
{
  L_inf ~ normal(185,30);
  sigma ~ cauchy(0,5);
  sigma_gam ~ cauchy(0,5);
  gam[1] ~ normal(-1,1);
  gam[2] ~ normal(-1,1);
  for (j in 3:J)
  {
    gam[j] ~ normal(gam[j-1], sigma_gam);
  }
  length ~ normal(mu_len, sigma);
}
```

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2017.03.026>.

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