Ecological Modelling 355 (2017) 1–11

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Flexible von Bertalanffy growth models incorporating Bayesian splines

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ARTICLE INFO

Article history:
Received 4 November 2016
Received in revised form 28 March 2017
Accepted 28 March 2017
Available online 14 April 2017

Keywords:
Southern bluefin tuna
Growth
Bayesian modelling
Piecewise constant model
Spline smoothing

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.

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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http://dx.doi.org/10.1016/j.ecolmodel.2017.03.026
0304-3800/

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:

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

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:

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

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:

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

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:

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

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, $0 = \tau_0 < \tau_1 < \cdots < \tau_{J-1} < \tau_J$, 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:

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

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 $\mathrm{VB}_{\mathrm{spl1}}$ 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 $\mathrm{VB}_{\mathrm{spl2}}$, has K function:

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

The $\mathrm{VB}_{\mathrm{spl2}}$ 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.