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REVIEWS

A technical note on seasonal growth models

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Abstract The growth of many organisms is seasonal, with a dependence on variation in temperature, light, and food availability. A growth model proposed by Somers (Fishbyte 6:8–11, 1988) is one of the most widely used models to describe seasonal growth. We point out that three different formulae (beyond numerous typographical errors) have been used in the literature referring to Somers (Fishbyte 6:8–11, 1988). These formulae correspond to different curves and yield different parameter estimates with different biological interpretations. These inconsistencies have led to the wrong identification of the period of lowest growth rate (winter point) in some papers of the literature. We urge authors to carefully edit their formulae to assure use of the original definition in Somers (Fishbyte 6:8–11, 1988).

Keywords von Bertalanffy growth function · Seasonality · Temperature · Fishery models · Somers' (1988) growth model

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Introduction

The growth of most plant species and ectothermic animals, such as fish, reptiles, crustaceans, and many invertebrate taxa, is strongly seasonal, with a dependence on temperature, light, and food supply (e.g., Pauly 1990; Alcoverro et al. 1995; Adolph and Porter 1996; Coma et al. 2000; Böhlenius et al. 2006). Even at tropical latitudes, the growth of fish and other organisms is often seasonal, depending on minor variations in temperature (Pauly 1990; Pauly et al. 1992) or increased food availability during the rainy season (Bayley 1988). Therefore, understanding and accounting for seasonality in growth is essential for understanding the ecology, evolution, and management of fish and many organisms.

Numerous models to describe the seasonal growth of organisms have been proposed (Table 1). Nearly all of these models are modifications of the traditional von Bertalanffy growth model that allow for seasonal oscillations in length within each growth year. The model originally proposed by Hoenig and Hanumara in an unpublished report (Hoenig and Hanumara 1990; Pauly et al. 1992), but most often cited from its description in Somers (1988), is highly popular, probably due to its availability in a number of software programs, including FAO-ICLARM Stock Assessment Tools (FiSAT; Gayanilo et al. 2005) and its predecessors, such as ELEFAN. Following other authors (e.g., Pauly 1998), we will continue to refer to this model as Somers' model. Declarations of the

Table 1 Number of citations, by February 2012, for the most widely used seasonal growth models, according to Google Scholar and ISI Web of Knowledge (ISI WOK)

Model	Citations according to Google Scholar	Citations according to ISI WOK
Pitcher and MacDonald (1973)	83	59
Cloern and Nichols (1978)	67	42
Pauly and Gaschütz (1979)	159	118
Somers (1988)	92	54
Pauly et al. (1992)	40	26
Porch et al. (2002)	20	14

The ISI counts for Pauly and Gaschütz (1979) and Somers (1988) are approximate because these references are cited in many different ways. Note that the number of papers actually using these models is much higher because many of the papers only cite the software used. For instance, the citation counts for Gayanilo and Pauly (1997), whose software only uses Somers (1988) among these models, are 828 and 146, respectively

formula for Somers' model have been inconsistent, perhaps due to the relative difficulty in obtaining the literature where this model was first developed. Thus, we aim to clarify the formula for Somers' model and show that other formulae that appear in the literature are incorrect and have led to mistaken biological interpretations.

Somers' (1988) growth model

The traditional parameterization of the von Bertalanffy growth model was proposed by Beverton and Holt (1957) and is

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

where *L(t)* is the expected or average length at time (or age) t; L_∞ is the model asymptote for average length; K is a measure of the exponential rate of approach to the asymptotic length (Schnute and Fournier 1980); and t_0 is the theoretical time or age (generally negative) at which the average length would be zero. These definitions apply to length-at-age data, whereas the parameters have different meanings when applied to tagging data (Francis 1988). The t_0 parameter is not of biological interest and is, rather, an important modeling artifact to adjust the model for the initial size of the animal (Beverton and Holt 1957), as most of the fitted models do not pass through the origin (Schnute and Fournier 1980).

Pitcher and Macdonald (1973) and Pauly and Gaschütz (1979) modified this traditional von Bertalanffy growth model to incorporate seasonal growth oscillations by including a sine function with a period of 1 year. However, Somers (1988) showed that those modifications produced a model that only fulfilled the definition of t_0 (i.e., $L(t_0) = 0$) under a very strict circumstance (i.e., the seasonal oscillations began at $t = t_0$). Thus, Somers (1988) proposed the following formula for modeling seasonal growth that rectified this situation:

$$\begin{aligned} L(t) &= L_\infty(1 - \exp(-K(t - t_0) - S(t) + S(t_0))), \\ &\text{with} \quad S(t) = (CK/2\pi)\sin(2\pi(t - t_S)), \\ &\text{so} \quad S(t_0) = (CK/2\pi)\sin(2\pi(t_0 - t_S)), \end{aligned}$$

and where C modulates the amplitude of the growth oscillations and corresponds to the proportion of decrease in growth at the depth of the oscillation (i.e., "winter"); t_s is the time between time 0 and the start of the convex portion of the first sinusoidal growth oscillation (i.e., the inflection point); and the rest of the variables and parameters are as defined above. If $C = 0$, then there is no seasonal oscillation and the model reduces to the typical von Bertalanffy growth model. If $C = 1$, then growth completely stops once a year at the "winter-point" (WP $= t_s + 0.5$), whereas values of $0 < C < 1$ result in reduced, but not stopped, growth during the winter. Values of $C > 1$ (or < 0) allow seasonal decreases in average length-at-age, and might not seem realistic in organisms whose skeletons largely preclude shrinkage (Pauly et al. 1992), but could result from size-dependent over-winter mortality.

Different formulae incorrectly referred to as Somers' model

Many different formulae referred to as Somers' model appear in the literature. Most of these formulae are obvious (but uncorrected) typographic errors (e.g., Hanumara and Ghedari 1993; Fiori and Morsán 2004; Botter-Carvalho et al. 2007; Simpfendorfer et al. 2008; Bilgin et al. 2009a; Martínez-Muñoz and Ortega-Salas 2010; Herrmann et al. 2011). However, three others (Table 2), while still incorrect, require

Table 2 The formulae referred to as Somers' (1988) model in the literature, plus a fourth possible one for comparison. See the text for interpretation and further details on the parameters

Formula no.	Equation	References using the formula
1	$L(t) = L_\infty(1 - \exp(-K(t - t_0) - S(t) + S(t_0)))$	Somers (1988), Hoenig and Hanumara (1990), Pauly (1990), Pauly et al. (1992), Gayanilo and Pauly (1997), and many other papers
2	$L(t) = L_\infty(1 - \exp(-K(t - t_0) + S(t) - S(t_0)))$	Defeo et al. (1992), Pauly (1998), Etim et al. (2002), Contreras et al. (2003), García and Duarte (2006), Chatzinikolaou and Richardson (2008), Bilgin et al. (2009a)
3	$L(t) = L_\infty(1 - \exp(-K(t - t_0) - S(t) - S(t_0)))$	None found
4	$L(t) = L_\infty(1 - \exp(-K(t - t_0) + S(t) + S(t_0)))$	Bellido et al. (2000), Gayanilo et al. (2005: 54), Deval and Göktürk (2008), Deval (2009)

more discussion and clarification because they differ only subtly, are more pervasive, and lead to equivalent predictions of length-at-age, but incorrect interpretations for t_0 and t_s.

The four formulae shown in Table 2 differ only in the signs that appear in front of $S(t)$ and $S(t_0)$, but are not mathematically equivalent (Fig. 1). Formulae 3 and 4 do not conform to the definition of t_0, i.e., $L(t_0) \neq 0$ (Fig. 1), which is evident by substituting $t = t_0$ into these two formulae. Thus, formulae 3 and 4 suffer from the same problem that Somers (1988) corrected. In addition, formulae 3 and 4 do not produce mean lengths at age $N + t_0$, where N is a non-negative integer, that are identical to the traditional von Bertalanffy growth model (Fig. 1). Thus, formulae 3 and 4 should be dismissed as useful models.

Formulae 1 and 2 share the positive attributes of having $L(t_0) = 0$ and mean lengths at age $N + t_0$ that are equivalent to the traditional von Bertalanffy growth model (Fig. 1). However, inspection of Fig. 1 shows that the growth trajectories between $N + t_0$

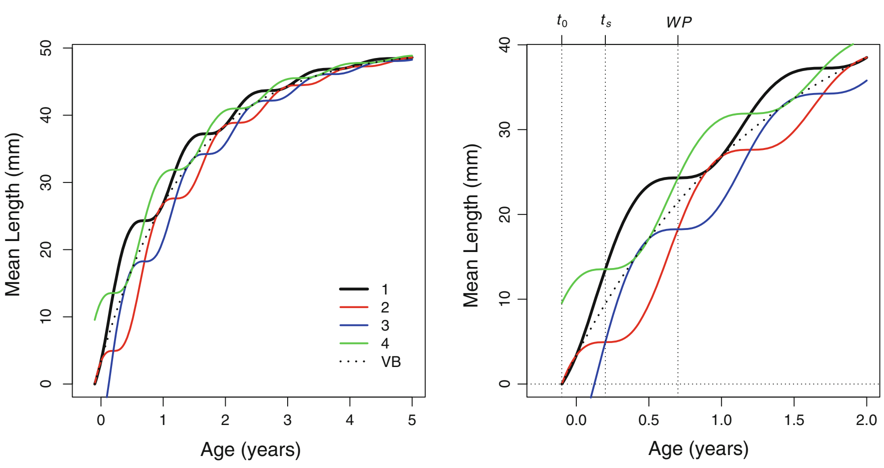

Fig. 1 The Somers' model formulae used in the literature (formula numbers as in Table 2) and the traditional non-seasonal von Bertalanffy model (VB) represented for the following hypothetical parameters: $L_\infty = 50.0$, $K = 0.70$, $t_0 = -0.2$, $C = 1$, $t_S = 0$. The *right pane* contains the same results as the *left pane* but is focused on the first 2 years of the growth trajectory and have the t_0, t_s, and WP parameters labeled for the correct Somers' (1988) model (i.e., formulae 1)

and $N + 1 + t_0$ are quite different for the two formulae. The WP, where seasonal growth is at a minimum (or growth is 0 if $C = 1$ as in Fig. 1), should be found half-way between the start of consecutive oscillation periods. The value of WP only equals $t_s + 0.5$ for formula 1; in fact, the WP for formula 2 is at t_s (Fig. 1).

To further illustrate the differences between these four formulae, we used the non-linear least squares fitting function "nls" in the R environment (R Development Core Team 2011) to fit each formulae to length and age data for anchoveta (*Engraulis ringens*), from Fig. 9 in Cubillos et al. (2001) and available in the FSAdata package (Ogle 2011a). The data and script for fitting these models and reproducing the illustrations of this paper are available in the supplementary information to this article. Simpler instructions on how to fit Somers' growth model with R are available elsewhere (Ogle 2011b).

The fitted curves to these data are identical for the four formulae (Fig. 2). Thus, if one was only interested in predicting mean length-at-age, then each formula would provide the exact same results. However, the estimates of t_0 and t_s differ among the four formulae (Table 3). As expected from Fig. 1, formulae 1 and 2 will always have the same estimated t_0, as will formulae 3 and 4. Also, as expected from Fig. 1, formulae 1 and 3 will always have the same values of

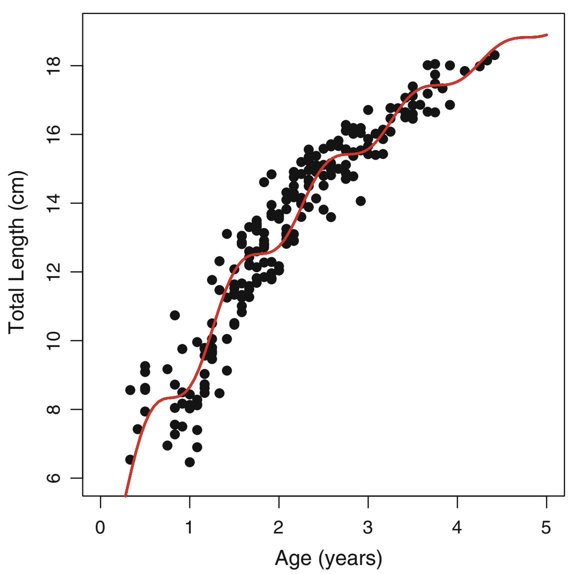

Fig. 2 The Somers' model fitted to the anchoveta data (see Table 3 for parameter estimates)

Table 3 Parameter estimates for the anchoveta data using the four published formula for Somers' model

Formula no.	t_0	t_S
1	−0.6044	0.2898
2	−0.6044	−0.2102
3	−0.3783	0.2898
4	−0.3783	−0.2102

Identical estimates were obtained for the rest of parameters ($L_\infty = 21.959$, $K = 0.3673$, $C = 0.9549$) and predicted mean length-at-age

t_s, as will formulae 2 and 4. The WP is at $N + 0.7898$ years (as observed in Fig. 2) and is only $t_s + 0.5$ for formulae 1 and 3; for formulae 2 and 4, WP actually equals t_s, i.e., $N -0.2102$ (Table 3).

Gayanilo et al. (2005) and other authors state that $\mathrm{WP} = t_s + 0.5$ while reporting formula 4, which are not consistent. Because the FiSAT software seems to provide correct results and Gayanilo and Pauly (1997) use formulae 1, we suspect that this is a typographical error. However, the literature contains some examples of wrong interpretations of the parameters derived from these inconsistencies. For instance, the top graph of Fig. 4 of Chatzinikolaou and Richardson (2008) reports $t_s = 0.08$ and $\mathrm{WP} = 0.58$, which would correspond to a WP in early July, whereas the fitted curve clearly shows that WP is around early January (0.08); the same inconsistency can be observed in their bottom graph of Fig. 4. Similarly, Bilgin et al. (2009b) state "for males, however, the slow growth period started in May ($\mathrm{WP} = 0.407$)" whereas their Fig. 5a clearly shows that May is the time with the highest growth rate and the minimum is rather in November ($\mathrm{WP} = 0.407 + 0.5$). Our results for the anchoveta data also suggest a similar inconsistency in Cubillos et al. (2001).

Conclusions

We have shown important errors in the formulae reported by many papers that use Somers' (1988) seasonal growth model. While all formulae provide equivalent fits to the length-at-age data, the differences in the formula have implications in the estimates obtained for the t_0 and t_s parameters and, more importantly, their biological interpretation. These inconsistencies have led to the wrong identification of the period of lowest growth rate (winter point) in some papers in the literature. The original formula proposed by Somers (1988) should be used in all cases for the sake of priority and correct interpretation of parameter estimates. The differences between the formulae are subtle (i.e., differences in signs); thus, we urge authors to carefully edit their formulae to assure that they use and report Somers' (1988) original formulation.

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