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Technical note

An algorithm for the von Bertalanffy seasonal cessation in growth function of Pauly et al. (1992)

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ABSTRACT

Pauly et al. (1992; Australian Journal of Marine and Freshwater Research 43:1151–1156) introduced a modified von Bertalanffy seasonal growth function that allowed for a period of no growth. Pauly et al. (1992) provided special purpose software to fit the model to length-at-age data, but this software is no longer available and specific details to implement a critical aspect of the new growth function were not clear. I provide details for this critical aspect of the function, implement it in the open-source R environment, and briefly demonstrate the use of this function with four data sets. With this, the growth function of Pauly et al. (1992) is now readily available to all scientists with access to software that can fit nonlinear models to data. Thus, this growth function may be implemented in more situations and its fit rigorously compared to the results from other models of fish growth.

1. Introduction

Mean length-at-age for many fish (Haddon, 2011) and other aquatic animals (e.g., Hota, 1994; Harwood et al., 2014) is often modeled using the von Bertalanffy growth function (VBGF; von Bertalanffy, 1938). A common foundation for several parameterizations of the VBGF is:

$$L_t = L_\infty\left(1 - e^{-q}\right)$$

where L_t is the expected or mean length at time (or age) t, L_∞ is the asymptotic mean length, and q is at least a function of t. For example, the most common parameterization of the VBGF attributable to Beverton and Holt (1957) uses:

$$q = K(t - t_0) \quad (1)$$

where K is a measure of the exponential rate at which L_t approaches L_∞ (Schnute and Fournier, 1980) and t_0 is the theoretical time or age at which L_t would be zero.

Many fish exhibit seasonal oscillations in growth as a response to seasonal changes in environmental factors such as temperature, light, and food supply (e.g., Bayley, 1988; Pauly et al., 1992; Bacon et al., 2005; Garcia-Berthou et al., 2012; Carmona-Catot et al., 2014). Various modifications of Eq. (1) have been used to model these seasonal oscillations in growth. The most popular of these modifications, from Hoenig and Choudaray Hanumara (1982) and Somers (1988), with a clarification by Garcia-Berthou et al. (2012), is:

$$q = K(t - t_0) + S(t) - S(t_0) \quad (2)$$

with $S(t) = \frac{CK}{2\pi}sin(2\pi(t - t_s))$. In Eq. (2), t_s is the amount of time between time 0 and the start of the convex portion of the first sinusoidal growth oscillation (i.e., the inflection point) and C is the proportional decrease in growth at the depth of the growth oscillation (i.e., "winter"). Eq. (2) may represent no seasonal oscillation in mean length (i.e., reduces to Eq. (1); $C = 0$), a reduced, but not stopped, increase in mean length ($0 < C < 1$), a complete stop in the increase in mean length ($C = 1$), or a decrease in mean length ($C > 1$) during the "winter" (Fig. 1). The point where the increase in mean length is smallest is called the "winter-point" (WP) and is at $t_s + \frac{1}{2}$ because the sine function in Eq. (2) has a period (i.e., the growth period) of one year.

Pauly et al. (1992) argued that a decrease in mean length with increasing age is unlikely for organisms whose skeletons largely preclude shrinkage and, thus, values of $C > 1$ in Eq. (2) were unrealistic for length (but not weight) data (however, see Nickelson and Larson, 1974; Huusko et al., 2011; and Garcia-Berthou et al., 2012). Pauly et al. (1992) then proposed a modification to Eq. (2) that included a no-growth period where mean length was not allowed to decrease. Specifically, their modification was:

$$q = K'\left(t' - t_0\right) + V\left(t'\right) - V(t_0) \quad (3)$$

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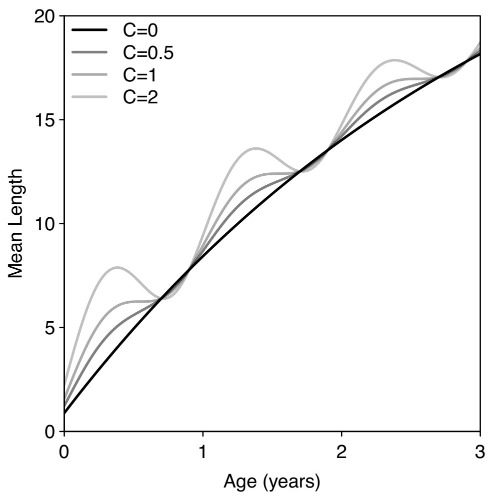

Fig 1. Example of Eq. (2) (Somers, 1988 VBGF) with $L_\infty = 30$, $K = 0.3$, $t_0 = -0.1$, $t_s = 0.05$ (with $WP = 0.55$) and four values of C.

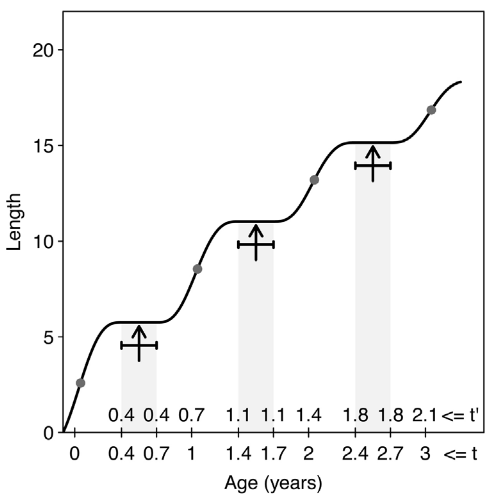

Fig. 2. Example of Eq. (3) (Pauly et al., 1992 VBGF) with $L_\infty = 30$, $K' = 0.35$, $t_0 = -0.1$, $NGT = 0.3$, and $t_s = 0.05$ (with $WP = 0.55$). Each t_s is shown by a gray point, "winter point" (WP) by a vertical arrow, and no-growth period by the horizontal interval centered on the WP arrow and the gray region that extends to the x-axis. Ages adjusted for the NGT (i.e., t') are shown above the x-axis.

with $V(t) = \frac{K'(1-NGT)}{2\pi} sin\left(\frac{2\pi}{1-NGT}(t - t_s)\right)$. In Eq. (3), NGT is the "no-growth time" or the length of the no growth period (as a fraction of a year) and t' is found by "subtracting from the real age (t) the total no-growth time occurring up to age t" (Pauly et al., 1992). Furthermore, because the units of K changed from $year^{-1}$ in Eq. (2) to $(1 - NGT)^{-1}$ in Eq. (3), Pauly et al. (1992) suggested using K' in Eq. (3) to minimize confusion with K in Eq. (2).

Pauly et al. (1992) devised Eq. (3) from Eq. (2) by assuming $C = 1$ and replacing 2π with $\frac{2\pi}{1-NGT}$ (i.e., restricting the seasonal oscillation to the growth period and noting that K' only operates during the growth period). Their modification may be described geometrically (though not algorithmically) in two steps. First, Eq. (2) with (fixed) $C = 1$ is fit to the observed lengths and ages that have had the cumulative NGT subtracted (i.e., using t'). This growth trajectory is then separated at each WP and horizontal segments that are NGT units long are inserted at these points. This forms a growth trajectory over the real ages (t) that smoothly transitions into and out of the no-growth periods (Fig. 2).

The growth function in Pauly et al. (1992) does not appear to have been widely used. Pauly et al. (1992) has been cited at least 70 times (from Google Scholar and ResearchGate searches on 31-May-16); though it appears that only two of 43 English journal citations (excludes book, dissertation, report, other non-journal citations, and journals not published in English) actually fit Eq. (3) to data. Of these, Chatzinikolaou and Richardson (2008) used the special purpose LFDA software (www.mrag.co.uk/resources/lfda-version-50) to fit Eq. (3) to length frequency data, whereas it is not clear how Beguer et al. (2011) fit the function, though they pre-specified rather than estimated L_∞.

Perhaps the growth function of Pauly et al. (1992) has not been widely adopted because it is not clear how to actually fit the function to length-at-age data. Pauly et al. (1992) provided a then ubiquitous, but now obsolete, 3.5-in "diskette" with a computer program to estimate the parameters of Eq. (3). However, the last diskette has been lost and the source code is no longer available (D. Pauly, pers. comm.). Pauly et al. (1992) did describe the operations performed by their program, but there is no equation for t' or detailed description of how t' should be operationalized. This lack of specificity may limit use of Eq. (3) because the relationship between t and t' is not a simple linear shift in scale, is not one-to-one, and depends on how t relates to t_s, NGT, and the number of completed no-growth periods prior to t.

Therefore, the objectives of this note are to (i) operationalize the calculation of t', (ii) provide an algorithm for the calculation of t' to be used when fitting Eq. (3) to observed data, and (iii) illustrate the use of this algorithm with real data. With this description, Eq. (3) can now be implemented in more situations and rigorously compared with other growth models (e.g., Eqs. (1) and (2).

2. Methods

2.1. Calculating t'

As noted by Pauly et al. (1992) the calculation of t' in Eq. (3) depends on the observed age (t) and the cumulative no-growth time prior to t. In practice, the calculation of t' also depends on the position of the no-growth period within a year. Here, the position of the no-growth period is defined relative to the start of the no-growth period (SNG), which Chatzinikolaou and Richardson (2008) showed to be $SNG = WP - \frac{NGT}{2} = t_s + \frac{1}{2} - \frac{NGT}{2}$. With this, the following six-step algorithm may be used to compute ages adjusted for cumulative NGT prior to age t (i.e., t') from observed ages (i.e., t). Below each step are example calculations of t' for $t = 1.4$ and $t = 3.0$ assuming $t_s = 0.05$ and $NGT = 0.3$ which result in $WP = 0.55$ and $SNG = 0.4$ (as in Fig. 2).

1. Subtract the SNG from t so that integer values are at the start of a growth period.
   - For $t = 1.4$: $1.4 - 0.4 = 1.0$; and for $t = 3.0$: $3.0 - 0.4 = 2.6$.
2. Subtract the number of completed full growth periods from the Step 1 result such that the remaining decimal represents the proportion completed of a year that started with the most recent growth period.
   - For $t = 1.4$: $1.0 - 1 = 0.0$; and for $t = 3.0$: $2.6 - 2 = 0.6$.
3. Substract the NGT from the Step 2 result.
   - For $t = 1.4$: $0.0 - 0.3 = -0.3$; and for $t = 3.0$: $0.6 - 0.3 = 0.3$.
4. If the Step 3 result is negative, then the observed age is within the no-growth period and the negative value should be replaced with a zero. Otherwise, the positive value represents the amount of the most recent growth period completed.
   - For $t = 1.4$: -0.3 is replaced with 0; and for $t = 3.0$: 0.3 is not changed.
5. Add the Step 4 result to the product of the number of completed full growth periods (as used in Step 2) and the length of the growth periods $(1 - NGT)$.