Technical note

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

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### A B S T R A C T

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.

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## 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) $t$, $L_\infty$ 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:

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

where $K$ is a measure of the exponential rate at which $L_t$ approaches $L_\infty$ (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:

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

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:

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

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

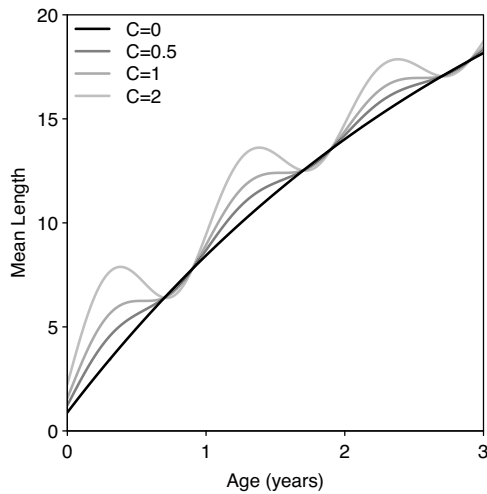*E-mail address:* dogle@northland.edu

**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 $C$.
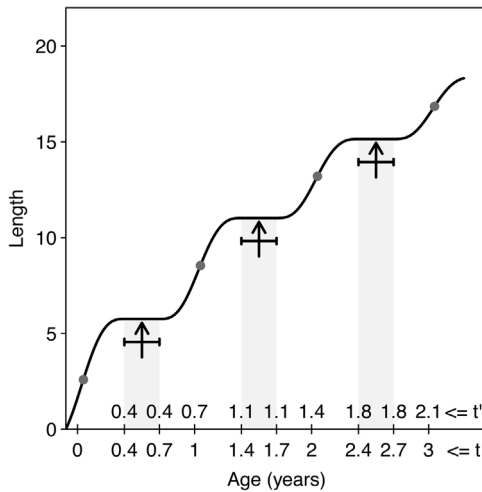


**Fig. 2.** Example of Eq. (3) (Pauly et al., 1992 VBGF) with $L_\infty = 30$, $K' = 0.35$, $t_0 = -0.1$, $NGT = 0.3$, and $t_s = 0.05$ (with $WP = 0.55$). Each $t_s$ is shown by a gray point, "winter point" ($WP$) by a vertical arrow, and no-growth period by the horizontal interval centered on the $WP$ 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.

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 $2\pi$ 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 $L_\infty$.

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 ($1 - NGT$).
   - For $t = 1.4$: $0 + 1(1 - 0.3) = 0.7$; and for $t = 3.0$: $0.3 + 2(1 - 0.3) = 1.7$.

**Table 1**

Parameter estimates (and 95% confidence intervals) from the fits of Eq. (1) (Typical VBGF), Eq. (2) (Somers, 1988 VBGF), and Eq. (3) (Pauly et al., 1992 VBGF) to the Australian bonito and three sites of Eastern mosquitofish data. The Akaike Information Criterion (AIC) value and the difference in AIC from the minimum AIC for models fit to the same data (△AIC) are also shown for each equation.

| Eq | Parameter Estimates (95% Confidence Intervals) | | | | | | | AIC | △AIC |
|---|---|---|---|---|---|---|---|---|---|
| | $L_\infty$ | $K$ | $K'$ | $t_0$ | $t_s$ | $C$ | $NGT$ | | |
| Australian Bonito (n = 251) | | | | | | | | | |
| 1 | 77.3 (59.8,164.8) | 0.22 (0.06,0.42) | – | −2.28 (−3.46,−1.48) | – | – | – | 1444.3 | 8.9 |
| 2 | 71.9 (59.6,141.5) | 0.27 (0.08,0.47) | – | −1.92 (−3.06,−1.13) | 0.09 (0.00,0.20) | 1.00[a] (0.44,1.00) | – | 1435.9 | 0.05 |
| 3 | 71.7 (58.7,127.8) | – | 0.31 (0.10,0.75) | −1.64 (−2.81,−0.70) | 0.09 (0.01,0.16) | – | 0.13 (0.00,0.46) | 1435.4 | – |
| Mosquitofish (Site 2) (n = 751) | | | | | | | | | |
| 1 | 66.8 (47.7,138.0) | 0.28 (0.11,0.49) | – | −0.74 (−0.94,−0.59) | – | – | – | 4355.8 | 196.4 |
| 2 | 35.9 (34.4,37.6) | 2.01 (1.69,2.36) | – | −0.02 (−0.04,−0.01) | 0.88 (0.87,0.89) | 1.95 (1.84,2.05) | – | 4159.4 | – |
| 3 | 35.1 (33.9,36.8) | – | 4.64 (3.28,6.62) | 0.43 (0.36,0.50) | 0.92 (0.91,0.93) | – | 0.43 (0.37,0.48) | 4175.4 | 16.0 |
| Mosquitofish (Site 4) (n = 686) | | | | | | | | | |
| 1 | 266.9 (70.7,623.6) | 0.07 (0.03,0.35) | – | −0.72 (−0.79,−0.53) | – | – | – | 4198.5 | 138.6 |
| 2 | 46.0 (40.3,56.7) | 1.05 (0.64,1.55) | – | −0.20 (−0.28,−0.14) | 0.75 (0.72,0.78) | 1.28 (1.14,1.44) | – | 4070.6 | 10.7 |
| 3 | 44.0 (39.0,58.0) | – | 1.60 (0.88,2.55) | 0.07 (−0.03,0.18) | 0.76 (0.70,0.80) | – | 0.26 (0.15,0.46) | 4059.9 | – |
| Mosquitofish (Site 9) (n = 887) | | | | | | | | | |
| 1 | 46.7 (43.4,51.6) | 0.86 (0.69,1.03) | – | −0.33 (−0.39,−0.28) | – | – | – | 5031.5 | 35.7 |
| 2 | 41.6 (39.2,45.4) | 1.31 (0.97,1.67) | – | −0.21 (−0.31,−0.15) | 0.72 (0.65,0.77) | 0.62 (0.45,0.78) | – | 4995.8 | – |
| 3 | 47.0 (42.4,57.2) | – | 0.77 (0.52,1.09) | −0.41 (−0.50,−0.18) | 0.61 (0.55,0.65) | – | 0.00 (0.00,0.27) | 5018.4 | 22.6 |

[a] $C$ was constrained to be less than or equal to 1 during model fitting.

6. Compute $t'$ by adding the *SNG* that was subtracted in Step 1 to the Step 5 result.
   - For $t = 1.4$: $0.7 + 0.4 = 1.1$; and for $t = 3.0$: $1.7 + 0.4 = 2.1$.

The $t'$ values that result from this algorithm are then input values, along with observed lengths, to a function for fitting Eq. (3) with any nonlinear model fitting software. For convenience, an R (R Development Core Team, 2016) function to represent Eq. (3), including use of the algorithm to compute $t'$, is included in the vbFuns() function of the FSA package v0.8.8 (Ogle, 2016a). Use of this function is demonstrated in the Supplementary information.

### 2.2. Demonstrating the algorithm

The algorithm developed to fit Eq. (3) is demonstrated with four data sets. The first data set is the fork lengths (mm) and decimal ages (the number of opaque zones observed on otolith thin sections plus the proportion of the year after the designated birthdate) from 251 Australian bonito (*Sarda australis*) sampled from commercial landings as detailed in Stewart et al. (2013). Stewart et al. (2013) fit Eq. (2) to these data but constrained $C$ to not exceed 1. These data were chosen to illustrate how Eq. (3) may provide a better and more appropriate fit than Eq. (2) with the boundary condition of $C = 1$. The remaining three data sets are for invasive Eastern mosquitofish (*Gambusia holbrooki*) from southern France to southern Spain detailed by Carmona-Catot et al. (2014). Standard lengths (mm) were measured for each fish and annual ages were estimated from length frequencies and analysis of scales, with decimal ages determined from capture date and estimated birth dates for a cohort. Carmona-Catot et al. (2014) fit Eq. (2), without constraining $C$, to fish from ten locations. Data from three of these locations were chosen to demonstrate how Eq. (3) fits relative to Eq. (2) with varying estimates of $C$ (i.e., $C$ much greater than 1 for Site 2, $C$ only slightly greater than 1 for Site 4, and $C$ much less than 1 for Site 9).

The "port" algorithm in the nls() function in R was used to estimate the parameters for Eqs. (1)–(3) for all four data sets. All starting values were obtained by visually fitting the VBGF to the observed data (Ritz and Streibig, 2008; Ogle, 2016b). Values of $L_\infty$, $K$, and $K'$ were constrained to be positive, $t_s$ and $NGT$ were constrained to be between 0 and 1, and $C$ was constrained to be between 0 and 1 for the Australian bonito data and positive for the mosquitofish

data. Alternative starting values were used to confirm that a global rather than a local minimum was obtained (McCullough, 2008). The growth function with the lowest Akaike Information Criterion (AIC) value, computed from least-squares results because normally distributed errors with a constant variance were assumed (Burnham and Anderson, 2002), was chosen as the better fit for each data set (Ritz and Streibig, 2008). However, if the difference in AIC between two models was less than 2, then the models were considered indistinguishable (Burnham and Anderson, 2002). Confidence intervals for each parameter were the 2.5% and 97.5% percentile values of parameter estimates from 999 non-parametric bootstrap samples of mean-centered residuals computed with the nlsBoot() function from the nlstools package v1.0-2 (Baty et al., 2015) in R. All code used in these analyses is in the Supplementary information.

### 3. Results

The fit of Eqs. (2) and (3) to the Australian bonito data were indistinguishable (Table 1; Fig. 3A). The $t_s$ estimates were equal and the estimates of $L_\infty$ and $t_0$ were similar between the two functions (Table 1). The length of the no-growth period was estimated with Eq. (3) to be 0.13 or 13% of the year.

Eq. (3) did not fit the mosquitofish data better in situations where there was some evidence for a decrease in mean length with increasing age (i.e., $C \gg 1$ in Eq. (2); e.g., Site 2; Table 1; Fig. 3B) or no evidence for a cessation in growth (i.e., $C < 1$ in Eq. (2); e.g., Site 9; Table 1; Fig. 3D). However, Eq. (2) appeared to respond too dramatically to one sample of ages (approx. 0.4) at Site 2, and Eq. (3) likely provides more realistic estimates of mean length throughout the seasonal cessation in growth period in this example (Fig. 3B). Eq. (3) fit better than Eq. (2) when a cessation in growth was evident without an apparent decline in mean length with age for mosquitofish (e.g., Site 4; Table 1; Fig. 3C).

### 4. Conclusion

The algorithm described here for computing $t'$, which allows for Eq. (3) to be statistically fit to seasonal age data, appears to provide reasonable parameter estimates for the four examples provided. Eq. (3) is likely not the globally best seasonal growth model as demonstrated here with three of four data sets. However, perhaps a better understanding of the utility of the Pauly et al. (1992) growth
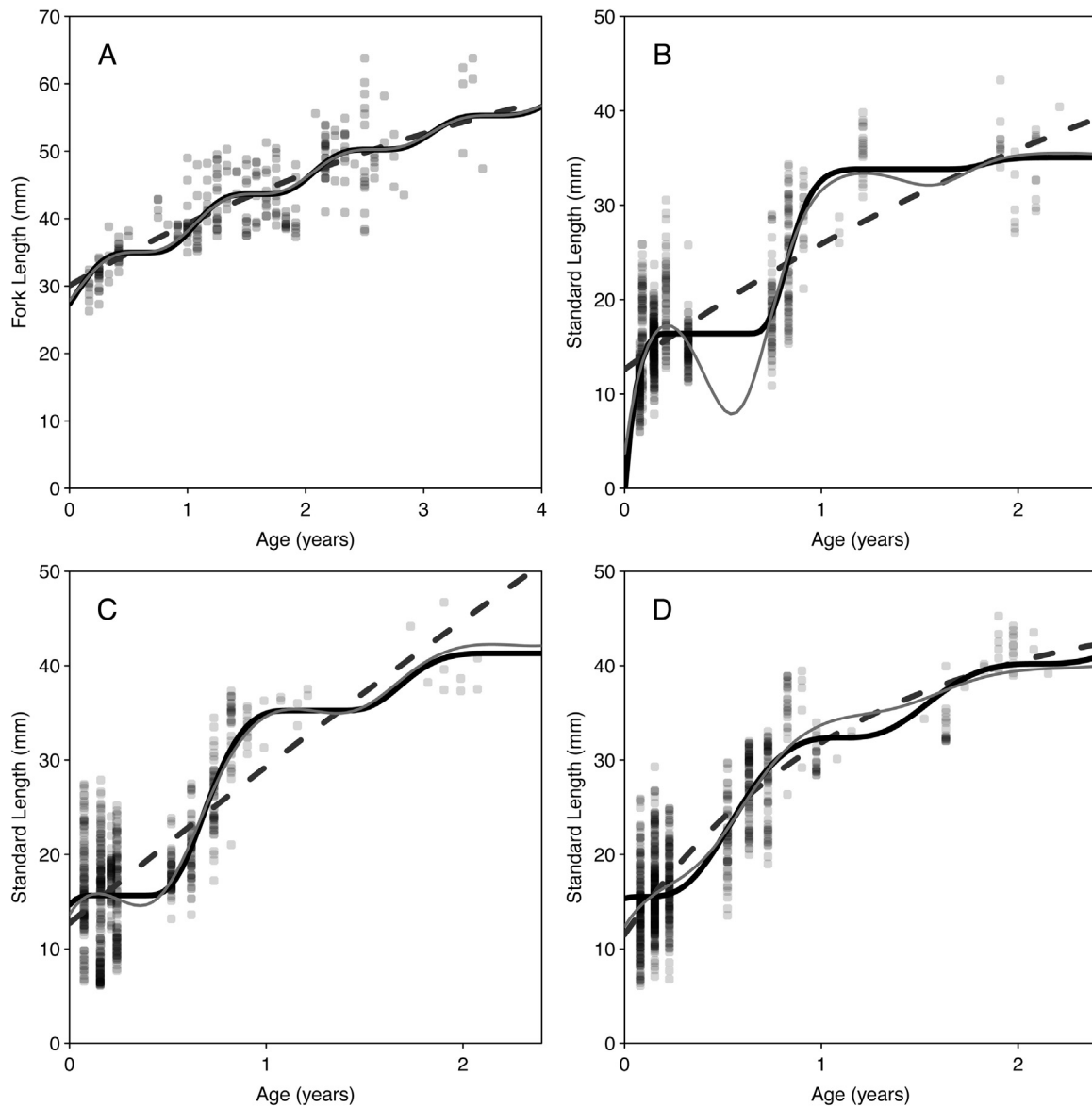
**Fig. 3.** Fork lengths at age for Australian bonito (A) and standard lengths at age for Eastern mosquitofish at Sites 2 (B), 4 (C), and 9 (D) with the best fits of Eq. (1) (Typical VBGF; dashed line), Eq. (2) (Somers, 1988 VBGF; gray solid line), and Eq. (3) (Pauly et al., 1992 VBGF; black solid line) superimposed. Parameter estimates (and 95% confidence intervals) from the model fits are shown in Table 1.

function for modeling seasonal growth of fishes will be forthcoming now that this function is readily available to all scientists with access to software (e.g., R) that can fit nonlinear models to data.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2016.09.020.

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