Revisiting the von Bertalanffy Seasonal Cessational Growth Function of Pauly et al. (1992)

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Abstract

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# Introduction

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

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

(1)

where is a measure of the exponential rate of approach to the asymptote (Schnute and Fournier 1980) and is the theoretical time or age at which the mean length 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 Equation 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), uses

(2)

with . In Equation 2, 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 is the proportional decrease in growth at the depth of the growth oscillation (i.e., "winter"). Equation 2 may represent no seasonal oscillation in mean length (=0) or a reduced but not stopped increase in mean length (for 0<<1), a complete stop in the increase in mean length (=1), and a decrease in mean length (>1) during the “winter” (Figure 1). The point where the increase in mean length is smallest is called the "winter-point" () and is at because the sine function in Equation 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 >1 from Equation 2 were unrealistic for length (but not weight) data. Pauly et al. (1992) then proposed a modification to Equation 2 that included a no-growth period where mean length was not allowed to decrease. Specifically, their modification is

(3)

with . In Equation 3, is the “no-growth time” or the length of the no growth period (as a fraction of a year) and is found by “subtracting from the real age () the total no-growth time occurring up to age ” (Pauly et al. 1992). Furthermore, because the units of changed from in Equation 2 to in Equation 3, Pauly et al. (1992) suggested using in Equation 3, as here, to minimize confusion.

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

Pauly et al. (1992) provided a then ubiquitous but now obsolete 3.5-in “diskette” with a computer program to estimate the parameters of Equation 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 detailed description of how should be operationalized. This is an important step in using Equation 3 because is a function of , but it is also a function of and , which are parameters to be estimated during the model-fitting process. Thus, the values for change with each iteration of the non-linear model-fitting algorithm.

Therefore, the objectives of this note are to (i) operationalize the calculation of , (ii) provide an (open-source) algorithm for the calculation of and Equation 3 for use in model fitting, and (iii) demonstrate the use of this algorithm.

# Methods

The algorithm developed to fit Equation 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 215 Australian bonito (*Sarda australis*) sampled from commercial landings as detailed in Stewart et al. (2013). Stewart et al. (2013) fit Equation 2 to these data but constrained to not exceed 1. These data were chosen to illustrate how Equation 3 may provide a better and more appropriate fit then Equation 2 with the boundary condition of . 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 Equation 2, without constraining , to fish from ten locations. Data from three locations were chosen to be examined here to demonstrate how Equation 3 fits relative to Equation 2 with varying estimates of (i.e., site 2 had much greater than 1, site 4 had only slightly greater than 1, and Site 9 had much less than 1).

We used the “port” algorithm in the nls() function in R (R Development Core Team 2016) to estimate the parameters for both Equations 2 and 3 for all four data sets. For Equation 2, and were constrained to be positive, was constrained to be between 0 and 1, and was constrained to be positive for the mosquitofish data and between 0 and 1 for the Australian bonito data. For Equation 3, and were constrained to be positive and and were constrained to be between 0 and 1. The function with the lowest Akaike Information Criterion (AIC) value was chosen as the best fit model for each data set. Confidence intervals for each parameter were the 2.5% and 97.5% percentile values of non-parametric bootstrap parameter estimates computed with the nlsBoot() function from the nlstools package (Baty et al. 2015) in R.

# Results

## 3.1 Calculating

As noted by Pauly et al. (1992) the calculation of depends on the observed age () and the cumulative no-growth time prior to . In practice, the calculation of 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 and , such that the following algorithm may be used to convert from observed ages () to ages adjusted for cumulative prior to age (). With this may be calculated with the following six steps.

1. Shift the age () by subtracting the start of the no-growth () period (i.e., ; Chatzinikolaou and Richardson 2008) from, such that a whole number will represent the start of a no-growth period. For example, if =0.4, then =2.4 will become 2.0 and =2.9 will become 2.5.
2. Subtract the whole number age (i.e., fully completed growth years) from the shifted age from Step 1 such that the remaining decimal represents the fraction of a shifted year. For example, a 0 will result if the shifted age is 2.0 and a 0.5 will result if the shifted age is 2.5.
3. Substract the from the value from the previous step.
4. If the value from the previous step is negative, then the 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 time into a growth period.
5. Add the value from the previous step to the total growth time completed (i.e., the product of the number of growth periods completed and the length of the growth period ()).
6. Compute by adding back the that was subtracted in Step 1.

Further examples of values relative to values are shown in Figure 2. This algorithm for computing is implemented in an R (R Development Core Team 2016) function as shown in Appendix 1. With this, Equation 3 is easily implemented as an R function as shown in Appendix 2.

## 3.1 Examples of Fitting the Function

Equation 3 fit the Australian bonito data slightly better than Equation 2 with a slightly lower AIC value (Table 1). The length of the no-growth period was estimated to be 0.133 or 13.3% of the year. The parameters were equal and the parameters were similar, but the parameters differed somewhat between the two models (Table 1). Graphically, there was little perceptual difference in the fits of the two functions (Figure 3A).

Equation 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>>1 in Equation 2; e.g., Site 2; Table 1; Figure 3B) or no evidence for a cessation in growth (i.e., C<1 in Equation 2; e.g. Site 9; Table 1; Figure 3D). However, Equation 2 appeared to respond too dramatically to one sample of ages (approx. 0.4) at Site 2, and Equation 3 likely provides more realistic estimates of mean length throughout the seasonal cessation in growth period in this example (Figure 3B). Equation 3 fit better than Equation 2 when a cessation in growth was evident without an apparent decline in mean length with age for mosquitofish (i.e., Site 4; Table 1; Figure 3C).

# Discussion

Pauly et al. (1992) introduced a novel function for modeling the seasonal cessation in growth in length of fishes. The growth function proposed by Pauly et al. (1992) incorporates only cyclic seasonal effects (Wang and Jackson 2000) and, thus, assumes that , or equivalently or , occur are at the same time each year, that the is greater than 0 and, if so, is the same length each year, and that the mean length does not decrease over time. These are stringent assumptions that are likely not appropriate for all species, locations, and time. Thus, Equation 3 is very likely not the globally best seasonal growth model, as illustrated here with the mosquitofish examples.

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 35 journal (excludes citations in books, dissertations, and reports) publications written in English actually fit Equation 3 to data. One of those (Chatzinikolaou and Richardson, 2008) used the special purpose LDFA software (XXX) to fit Equation 3 to length frequency data, whereas it is not clear how the other (Beguer et al., 2011) fit the model.

Perhaps the growth function of Pauly et al. (1992) has not been widely adopted because it was not clear how to actually fit the model the length-at-age data. Alternatively, it may be that this function does not adequately represent seasonal growth trajectories, though we are unaware of any rigorous comparison between Equation 3 and other seasonal growth models. The carefully described algorithm and R function provided here for computing , which allows for Equation 3 to be statistically fit to seasonal age data, appears to provide reasonable parameter estimates for the four examples provided. Thus, the Pauly et al. (1992) growth function is now available to all scientists with access to software that can fit nonlinear models to data. Thus, with the methods presented in this note, Equation 3 can now be implemented in more situations and its fit rigorously compared to the results from other models.

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### Appendix A. R Function to Compute

################################################################  
## internal function to compute t-prime  
################################################################  
iCalc\_tpr <- function(t,ts,NGT) {  
 ## Step 1  
 SNG <- ts+(1-NGT)/2  
 tmp.t <- t-SNG  
 ## Step 2 (in parentheses) and Step 3  
 tmp.t2 <- (tmp.t-floor(tmp.t))-NGT  
 ## Step 4  
 tmp.t2[tmp.t2<0] <- 0  
 ## Step 5 (in parentheses) and Step 6 (also returns value)  
 (floor(tmp.t)\*(1-NGT)+tmp.t2) + SNG  
}

## 

### Appendix B. R Function for Equation 3 (Pauly et al. (1992) Function)

################################################################  
## Main Function  
## Linf, t0 as usual  
## Kpr = K-prime as defined in Pauly et al. (1992)

## (units are different than usual K)  
## ts = start of sinusoidal growth (maximum growth rate)  
## NGT = "No Growth Time" = "fraction of a year where no

## growth occurs"  
## tpr = "t-prime" = age (t) minus cumulative NGT prior to t  
################################################################  
  
VBSCGF <- function(t,Linf,Kpr=NULL,t0=NULL,ts=NULL,NGT=NULL) {  
 ## Allow parameters to be sent as one vector in Linf

if (length(Linf)==5) { Kpr <- Linf[[2]]; t0 <- Linf[[3]]  
 ts <- Linf[[4]]; NGT <- Linf[[5]]  
 Linf <- Linf[[1]] }

## Adjust ages for NGT (i.e., compute t-prime)  
 tpr <- iCalc\_tpr(t,ts,NGT)

## Equation 3 (i.e., Pauly et al. (1992) growth function)  
 q <- Kpr\*(tpr-t0) +  
 (Kpr\*(1-NGT)/(2\*pi))\*sin((2\*pi)/(1-NGT)\*(tpr-ts)) -  
 (Kpr\*(1-NGT)/(2\*pi))\*sin((2\*pi)/(1-NGT)\*(t0-ts))  
 Linf\*(1-exp(-q))  
}

### Online Supplement

R code for all figures and analyses.

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Table 1: Parameter estimates and Akaike Information Criterion (AIC) from the fits of Equation 2 and Equation 3 to the Australian bonito and three sites for mosquitofish data. The lower AIC between the two equations for the same dataset is boldfaced.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Equation 2 (Somers (1988) function) | | | | | | |  | | | Equation 3 (Pauly et al. (1992) function) | | | | | | | | |
|  | Australian | Mosquitofish | | |  | | |  | | | | Australian | | Mosquitofish | | |
|  | bonito | Site 2 | Site 4 | Site 9 | |  | | |  | | bonito | | Site 2 | | Site 4 | Site 9 | |
|  | 71.8  (59.6,125.8) | 35.9  (34.5,37.6) | 46.0  (40.1,56.2) | 41.6  (39.1,44.9) | |  | | |  | | 71.7  (58.5,123.8) | | 35.1  (33.8,36.8) | | 44.0  (38.9,57.6) | 38.1  (36.4,39.8) | |
|  | 0.27  (0.09,0.46) | 2.01  (1.68,2.35) | 1.05  (0.63,1.57) | 1.31  (1.00,1.71) | |  | | |  | | 0.31  (0.10,0.75) | | 4.64  (3.25,6.70) | | 1.60  (0.85,2.57) | 2.14  (1.78,2.94) | |
|  | -1.9  (-3.0,-1.2) | -0.02  (-0.04,-0.01) | -0.20  (-0.28,-0.14) | -0.21  (-0.30,-0.15) | |  | | |  | | -1.6  (-2.8,-0.7) | | 0.43  (0.35,0.50) | | 0.07  (-0.04,0.18) | -0.12  (-0.16,-0.02) | |
|  | 0.09  (0.00,0.19) | 0.88  (0.87,0.89) | 0.75  (0.72,0.78) | 0.72  (0.66,0.76) | |  | | |  | | 0.09  (0.00,0.17) | | 0.92  (0.91,0.93) | | 0.76  (0.69,0.79) | 0.75  (0.73,0.78) | |
|  | 1.00a  (0.44,1.00) | 1.95  (1.82,2.05) | 1.28  (1.13,1.44) | 0.62  (0.46,0.80) | |  | | |  | | 0.13  (0.00,0.49) | | 0.43  (0.37,0.48) | | 0.26  (0.16,0.45) | 0.00  (0.00,0.08) | |
|  |  |  |  |  | |  | | |  | |  | |  | |  |  | |
| AIC | 1435.9 | **4159.4** | 4070.6 | **4995.8** | |  | | | AIC | | **1435.4** | | 4175.4 | | **4059.9** | 5109.5 | |

a was constrained to be less than 1 during model fitting.

### Figure Labels

Figure 1. Example VBGF using Equation 2 with =30, =0.3, =-0.1, =0.05 (with =0.55) and four different values of .

Figure 2. Example VBGF using Equation 3 with =30, =0.35, =-0.1, =0.3, and =0.05 (with =0.55). Each is shown by a gray point, by a vertical arrow, and no-growth period by the horizontal interval centered on the arrow and the gray region that extends to the x-axis. The ages adjusted for the (i.e., ) are shown above the x-axis.

Figure 3. Fork lengths at age for Australian Bonito (A) and standard lengths at age for mosquitofish at Sites 2 (B), 4 (C), and 9 (D) with the best-fits of Equation 3 (black line) and Equation 2 (gray line) superimposed. Parameter estimates (and 95% confidence intervals) from the model fits are shown in Table 1.





