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). The parameterization of the VBGF attributable to Beverton and Holt (1957) is most common and may be expressed as

with

where is the expected or average length at time (or age) , is the asymptotic mean length, is a measure of the exponential rate of approach to the asymptote (Schnute and Fournier 1980), and is the theoretical time or age (generally negative) 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). Equation 2 of the traditional VBGF has been modified, usually with a sine function, to model these seasonal oscillations in growth. The most popular of these modifications, from Hoenig and Choudaray Hanumara (1982) and Somers (1988), is

with and where modulates the amplitude of the growth oscillations and corresponds to the proportional decrease in growth at the depth of the oscillation (i.e., "winter"), and is the time between time 0 and the start of the convex portion of the first sinusoidal growth oscillation (i.e., the inflection point). If =0, then there is no seasonal oscillation and Equation 3 reduces to Equation 2 and the typical VBGF (Figure 1). If =1, then growth completely stops once a year at the "winter-point" (), whereas values of 0<<1 result in reduced, but not stopped, growth during the winter (Figure 1). Note that because the sine function in Equation 3 has a period (i.e., the growth period) of one year. Some confusion has surrounded the use of Equation 3, although Garcia-Berthou et al. (2012) carefully clarified its form.

Values of >1 (or <0) in Equation 3 allow seasonal decreases in mean length-at-age (Figure 1). A decrease in mean length with increasing age is unlikely for organisms whose skeletons largely preclude shrinkage (Pauly et al. 1992), although a seasonal decrease in mean length-at-age is possible if size-dependent overwinter mortality occurs (Garcia-Berthou *et al.*, 2012). Pauly *et al.* (1992) modified Equation 3 to include a true seasonal no-growth period where mean length was not allowed to decrease and smoothly transitioned into and out of the no-growth period. Specifically, their modification is

 with and where 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, Pauly *et al.* (1992) noted that the units of changed from in Equation 3 to in Equation 4. To eliminate confusion, they suggested using in Equation 4, as we do here.

Pauly *et al.* (1992) devised Equation 4 by assuming =1 and replacing in Equation 3 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 3 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 "diskette" that contained a computer program to estimate the parameters of Equation 4. The diskette is difficult (at best) to obtain 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 description of how was operationalized. This is an important step in using Equation 4 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 4 for use in model fitting, and (iii) demonstrate the use of this algorithm.

# Methods

The algorithm developed to fit Equation 4 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 Bonito (*Sarda australis*) sampled from commercial landings as detailed in Stewart *et al.* (2013). Stewart *et al.* (2013) fit Equation 3 to these data but constrained to not exceed 1. These data were chosen to illustrate how Equation 4 may provide a better and more appropriate fit then when the boundary condition of is returned for Equation 3. The remaining three data sets are from the examination of the invasive Eastern Mosquitofish (*Gambusia holbrooki*) in 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 3, but without constraining the value of , to fish from ten locations. Data from three locations were chosen to be examined here to demonstrate how Equation 4 fits relative to Equation 3 with varying estimates of (i.e., Site 9 had much less than 1, site 4 had only slightly greater than 1, and site 2 had much greater 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 3 and 4 for all four data sets. For Equation 3, 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 Bonito data. For Equation 4, 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. I attempted to further summarize each parameter with profile likelihood confidence intervals.

# 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 ().

1. Shift the age () by subtracting the start of the no-growth () period (i.e., ) 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 4 is easily implemented as an R function as shown in Appendix 2.

## 3.1 Examples of Fitting the Function

Equation 4 fit the Bonito data slightly better than Equation 3 with slightly lower residual sums-of-squares (RSS) and Akaike Information Criterion (AIC) values. 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). The from Equation 3 was equal to from Equation 4 multiplied by (Table 1). Graphically, there was little perceptual difference in the model fits (Figure 3).

## Mosquitofish Data --

# Discussion

* General
  + Parameters from real data seem reasonable
  + Other parameters by maths -- WP=ts+0.5, SNG=WP-NGT/2
  + Little practical difference between Equations 3 and 4 unless C>>1 and NGT>>0
* Model-Fitting
  + Fit Equation 3 first to see if C>=1
  + Problems due to 5 parameters
  + Bound parameters
* Assumptions
  + ts same time each year and age
  + NGT same length each year and age

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John Stewart (New South Wales Department of Primary Industries Fisheries) graciously provided the Bonito length-at-age data.

### Appendix A. R Function to Compute t’

################################################################  
## 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 4 (Somers (1988) 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) {  
 if (length(Linf)==5) { Kpr <- Linf[[2]]; t0 <- Linf[[3]]  
 ts <- Linf[[4]]; NGT <- Linf[[5]]  
 Linf <- Linf[[1]] }  
 tpr <- iCalc\_tpr(t,ts,NGT)  
 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))  
}

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Table 1: Parameter estimates and Akaike Information Criterion (AIC) from the fits of Equation 3 and Equation 4 to the Bonito and three sites of Mosquitofish data. The lower AIC between the two equations for the same dataset is boldfaced.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Equation 3 (Somers (1988) Function) | | | | | | |  | | | Equation 4 (Pauly et al. (1992) Function) | | | | | | | | |
|  |  | Mosquitofish | | |  | | |  | | | |  | | 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 the model fitting.

Figure Labels

Figure 1. Example VBGF using Equation 3 with =30, =0.3, =-0.1, =0.05 (with =0.55) and four different values of .

Figure 2. Example VBGF using Equation 4 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 length at age for Australian Bonito with the best-fit of Equation 4 (black line) and Equation 3, with fixed , superimposed (gray line). The parameter estimates (and 95% confidence intervals) from the model fits are shown in Table 1.





