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 (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). Various modification of Equation 1 have been used to model these seasonal oscillations in growth. The most popular of these modifications is from Hoenig and Choudaray Hanumara (1982) and Somers (1988) and 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"). If =0, then there is no seasonal oscillation and Equation 2 reduces to the typical VBGF in Equation 1 (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 2 has a period (i.e., the growth period) of one year. Some confusion has surrounded the use of Equation 2, although Garcia-Berthou et al. (2012) carefully clarified its form.

Values of >1 (or <0) in Equation 2 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 2 to include a 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

(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, Pauly et al.(1992) noted that the units of changed from in Equation 2 to in Equation 3. To eliminate confusion, they suggested using in Equation 3, as we do here.

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 "diskette" that contained a computer program to estimate the parameters of Equation 3. 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 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 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 when the boundary condition of is returned for Equation 2. 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 2, 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 3 fits relative to Equation 2 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 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 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 value of non-parametric bootstrap parameter estimates computed with the nlsBoot() function from the nlstools package in R (Baty et al. 2015).

# 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 3 is easily implemented as an R function as shown in Appendix 2.

## 3.1 Examples of Fitting the Function

Equation 3 fit the Bonito data slightly better than Equation 2 with a slightly lower AIC value. 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 appears 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 during the seasonal cessation in growth period in this situation (Figure 3B). When a cessation in growth is evident without an apparent decline in mean length with age for Mosquitofish (i.e., Site 4; Figure 3C), Equation 3 fit better than Equation 2 (Table 1).

# Discussion

Pauly et al. (1992) introduced a novel function for modeling the seasonal cessation in growth of fishes. While Pauly et al. (1992) appears to have been cited often, it also appears that few of these functions actually used the described function and most of those that did simply used their special purpose software, which is now largely unavailable. Unfortunately, the description in Pauly et al. (1992) lacked sufficient detail to operationalize the fitting of their function without their special-purpose software. Here, we fill this gap by providing an algorithm, both in descriptive form and as a function for use in the open-source R environment, for computing the t’, a foundational component of the growth function from Pauly et al. (1992). In addition, the supplement provides the R code we used to demonstrate the fitting of this function to four data sets from the recent literature. We feel that our work has made this potentially useful model more readily available to fisheries scientists.

* 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

### Acknowledgments

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### 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 2 and Equation 3 to the Bonito and three sites of 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) | | | | | | | | |
|  |  | 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 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.





