Estimating Age at a Critical Length from the von Bertalanffy growth function

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Abstract

The average length of time (or age) for the mean length of a population of fish to reach a critical value is useful for understanding the dynamics of fish populations. The mean age at which a population reaches a mean length is most often estimated by fitting a von Bertalanffy growth function to length-at-age data and then rearranging the best-fit equation to solve for age at the critical length. This process precludes using some statistical methods to compute confidence intervals or to statistically compare estimates of mean age at the critical length among populations. We provide a new parameterization of the von Bertalanffy growth function that allows the mean age at a critical length to be directly estimated so that all methods to construct confidence intervals and make among-group comparisons for these values can be used. We demonstrate use of the new parameterization with two datasets.

Keywords: Growth, Critical Age, Critical Length, Nonlinear modeling

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# Introduction

The average length of time () for the mean length of a population of fish to reach a critical value () is useful for understanding the dynamics of fish populations. The metric is commonly used when simulating fish populations with the Jones (1957) modification of the Beverton and Holt (1957) equilibrium yield model, primarily as implemented in FAST (Slipke and Maceina, 2001) and FAMS (Slipke and Maceina, 2010). In this age-structured model, identifies the age (usually when converted from ) when fish recruit to the fishery, which is important for modeling fishing mortality under different management scenarios (e.g., Slipke et al., 1998; Brenden et al. 2007; Colvin et al, 2014). The value may also be valuable outside of this simulation modeling framework because it is a synthetic measure of growth prior to age . In other words, when considering the same , a population with a larger will have grown more slowly than a population with a lower . Thus, likely responds (or is related) to the many abiotic and biotic factors that affect growth of fish (Brett, 1979; Lorenzen, 2016).

Typically, has been estimated by fitting a von Bertalanffy growth function (VBGF) to length and age data and then algebraically rearranging the best-fit equation to solve for age given the critical length of (Slipke and Maceina, 2001). The delta method (Seber and Wild, 2003; Ritz and Streibig, 2008) or bootstrapping (Hilborn and Mangel, 1997; Ritz and Streibig, 2008) may be used to approximate standard errors and confidence intervals for derived in this manner. However, likelihood profiles (Hilborn and Mangel, 1997; Ritz and Streibig, 2008) cannot be used to construct confidence intervals for the derived and usual methods (extra sum-of-squares tests, likelihood ratio tests, or information criterion approaches; Ogle et al 201X) for comparing models cannot be used to determine if differs among populations. These statistical shortcomings could be overcome if was directly estimated as a function parameter rather than being derived from other function parameters.

Additionally, some parameters in the usual VBGFs may be illogical and poorly estimated (i.e., imprecise) because they represent values outside the domain of observed ages. In some instances, these parameters have been fixed at constant values (Isermann et al. 2007; Weber et al. 2011), which may negatively affect estimates of other parameters and values derived from these parameters, such as . In contrast, is unlikely to be outside the domain of observed ages and, thus, is likely to be logically and precisely estimated if it is a parameter in a VBGF.

Therefore, the objectives of this note are to (1) describe a VBGF that has as a directly estimated parameter and (2) to demonstrate how this VBGF can be used to directly estimate and identify differences in between populations.

# Theory

A variety of parameterizations of the VBGF have been used to model growth in length of fishes (Ogle et al., 201X). The most common parameterization (Beverton and Holt, 1957) is

(1)

where is the expected or mean length at time (or age) , is the asymptotic mean length, is a measure of the exponential rate at which approaches (Schnute and Fournier, 1980; Ogle et al., 201X), and is the theoretical time (hereafter, age) at which would be zero (i.e., the x-intercept; Figure 1). For use further below, Eq. (1) can be expressed as

(1a)

The original parameterization of the VBGF from von Bertalanffy (1938) is

(2)

where is when *t*=0 (i.e., y-intercept; Figure 1). Eq (2) can be algebraically shown to equal

which, for use further below, can also be expressed as

(2a)

The similarities of Eqs. (1a) and (2a) suggest that the VBGF may be expressed as

(3)

where is when *t* = . Thus, if , then represents the theoretical age at which would be zero (i.e., the x-intercept) and, if is replaced with , then Eq. (3) reduces to Eq. (1a). Similarly, if , then represents when *t* = 0 (i.e., the y-intercept), and, if is replaced with , then Eq. (3) reduces to Eq. (2a). Thus, Eqs. (1) and (2) are special cases of Eq. (3) and only differ in whether they are parameterized to estimate the x- or y-intercept (Figure 1). Note that Eq. (3) appears to have four parameters, but either is set to a constant value and is estimated, or is set to a constant value and is estimated. Thus, Eq. (3) will have three estimable parameters.

Of more interest is that Eq. (3) may be used to estimate or for any point on the VBGF curve (Figure 1). For example, may be set to an age of biological interest such that the mean length at that age () is a parameter estimated from fitting Eq. (3) to data. Conversely, and the focus of this note, may be set to a length of biological interest such that the mean age for fish of that length () is a parameter estimated from fitting Eq. (3) to data. Thus, because is a parameter directly estimated from fitting Eq. (3) to data, all methods for computing confidence intervals for function parameters may be used and common statistical methods may be used to identify differences in among populations.

# Methods

We demonstrate use of Eq. (3) with two examples. First, length-at-age data for Lake Michigan lake whitefish (*Coregonus clupeaformis*) are used to demonstrate that the fit of Eq. (3) is equivalent to the fits of Eqs. (1) and (2), and that direct estimates of from Eq. (3) equal derived estimates of from Eqs. (1) and (2). Second, length-at-age data for Lake Winnibigoshish (Minnesota) walleye (*Sander vitreus*) are used to show how model comparison methods can be used to assess differences in (and other function parameters) between groups (i.e., sexes).

Lake whitefish were captured by commercial trap-netters from the spawning grounds of the Big Bay de Noc, Lake Michigan genetic stock in October 2012 and 2013. Total length (TL) was measured to the nearest mm and integer ages were estimated from thin-sectioned otoliths. Full collection details for these data are in Belnap (2014). As in Belnap (2014), we estimate the mean age required to reach 480 mm TL (i.e., *t*480), which is the TL at which lake whitefish are fully vulnerable to commercial and tribal harvest in Lake Michigan (Ebener et al., 2008). Eqs. (1)-(3) were fit to these data using the default Gauss-Newton algorithm of the nls() function in the R environment (R Development Core Team, 2017). Starting values were obtained by visually fitting each equation to the observed data (Ritz and Streibig, 2008; Ogle, 2016). Alternative starting values were used to confirm that a global rather than a local minimum was obtained (McCullough, 2008; Ogle et al. 201X). Results from fitting Eqs. (1) and (2) were algebraically rearranged to derive an estimate of . For each equation, 999 non-parametric bootstrap samples of mean-centered residuals were computed with the nlsBoot() function from the nlstools package v1.0-2 (Baty et al., 2015). A was derived for each bootstrap sample for Eqs. (1) and (2). To further compare the equivalency of Eqs. (1)-(3), predicted mean lengths at ages 8 and 20 were computed from each bootstrap sample for all three equations. Approximate 90% confidence intervals (CI) for each parameter and derived value were the 5% and 95% percentile values of parameter or derived value estimates. The 90% confidence intervals were used to eliminate the tail portion of the bootstrapped distributions to better compare the equivalency of estimated parameters and derived values across equations.

Gillnets were used to capture walleye from two locations in Lake Winnibigoshish in MONTH 2012. Total length was measured to the nearest mm, integer ages were estimated from thin-sectioned otoliths, and sex was determined by visually examining gonads. We estimated , because 432 mm is the lower end of a protective slot limit for Lake Winnibigoshish walleye. We used extra sum-of-squares tests in a sequential step-down process (as described in Ogle, 2016) to identify which of eight possible models best fit these data. The eight models were modifications of Eq. (3) where all, two, one, or no parameters differed between the two sexes. All models were fit with the default Gauss-Newton algorithm in nls() of R. The confint() function from the MASS package (Venables and Ripley, 2002) was used to construct 95% profile likelihood CI for all function parameters in the final model. The profile likelihood method, rather than bootstrapping, was used for these CI to illustrate that the likelihood profile method can be used to estimate CI for from Eq. (3).

# Results

Point estimates for all parameters and derived values, including , shared between Eqs. (1)-(3) were equivalent (Table 1). Confidence intervals for all parameters and derived values shared between Eqs. (1)-(3) were similar, but not exactly equal due to the inherent stochasticity of the bootstrap method (Table 1). Lake whitefish from the Big Bay de Noc genetic stock reached a total length of 480 mm at approximately 8 years of age.

The (*F*1,482 = 147.43, *P* < 0.001) and (*F*1,482 = 128.30, *P* < 0.001) parameters, but not *K* (*F*1,481 = 3.21, *P* = 0.074), differed significantly between male and female Lake Winnibigoshish walleye (Figure 2). The was greater for female (95% CI: 641-707 mm) than male (95% CI: 560-616 mm) walleye, whereas was lower for female (95% CI: 3.78-3.95 years) than male (95% CI: 4.61-4.93 years) walleye. These results suggest that female walleye reach the minimum slot length limit (432 mm) before and can achieve a longer maximum mean length than male walleye in Lake Winnibigoshish.

# Conclusion

Eq. (3) is a simple parameterization of the VBGF that includes the traditional and original VBGF parameterizations as special cases. However, Eq. (3) is more flexible in that it may be used to estimate mean length for any chosen age or mean age for any chosen length, rather than only at the axes (i.e., intercepts) as with the common and original VBGFs. Point and bootstrapped interval estimates for mean age at a critical length (i.e., ) from Eq. (3) match those derived from estimated parameters from Eqs. (2) and (3). However, use of Eq. (3) allows for use of likelihood profile methods to estimate confidence intervals and model selection procedures to statistically determine if mean age at the critical length differs among populations. We suggest using Eq. (3) when interest lies in estimating mean age at a critical length or determining if the mean age at a critical length differs among populations.

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### Supplementary Information

R code for all figures and analyses.

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Table 1. Estimated parameters (, *K*, , , and, for Eq. (3), ), derived variables ( for Eqs. (1) and (2) and predicted mean lengths-at-ages 8 () and 20 ()), with 90% confidence intervals in parentheses, and AICc from fitting Eqs. (1)-(3) to the Big Bay de Noc genetic stock of lake whitefish.

|  |  |  |  |
| --- | --- | --- | --- |
| Parameter/ Variable | Eq. (1) | Eq. (2) | Eq. (3) |
|  | 550.83 (540.45, 572.97) | 550.83 (540.99, 574.34) | 550.83 (541.33, 577.59) |
| *K* | 0.197 (0.108, 0.300) | 0.197 (0.097, 0.297) | 0.197 (0.093, 0.306) |
|  | -2.386 (-9.834, 1.027) | -- | -- |
|  | -- | 206.31 (-214.67, 380.72) | -- |
|  | 8.04 (7.09, 8.65)a | 8.04 (7.02, 8.67)a | 8.04 (7.03, 8.64) |
|  | 479.38 (469.10, 489.68) | 479.38 (468.89, 489.62) | 479.38 (469.42, 489.57) |
|  | 544.08 (537.65, 550.31) | 544.08 (538.22, 549.73) | 544.08 (538.65, 550.62) |
| RSS | 320685.4 | 320685.4 | 320685.4 |

### aValue derived by rearranging the equation to solve for *t* with a length of 480 mm.

### Figure Labels

Fig. 1. Examples of Eqs. (1)-(3) with = 250, = 0.7, *t*0 = -0.7, and *L*0 = 73.8. Three points on the curve are shown with gray circles -- () specifically defines Eq. (1), (0) specifically defines Eq. (2), and () generically defines Eq. (3).

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Fig. 2. Fit of Eq. (3) to female (open squares, dotted line) and male (open circles, dashed line) to total length-at-age data for walleye captured from Lake Winnibigoshish in MONTH, 2012. Points are slightly offset from the integer ages to reduce overlap between the sexes. Point estimates and 95% confidence intervals are shown for each sex along the y-axis for and along the x-axis for . The gray horizontal line is at *Lr* = 432 mm. One 581 mm age-16 male is not shown.