

Estimating Age at a Specified Length from the von Bertalanffy Growth Function

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Abstract

Estimating the time required (i.e., age) for fish in a population to reach a specific length (e.g., legal harvest length) is useful for understanding population dynamics and simulating the potential effects of length-based harvest regulations. The age at which a population reaches a specific mean length is typically 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 specified length. This process precludes use of some statistical methods for computing confidence intervals and comparing estimates of age at the specified length among populations. We provide a parameterization of the von Bertalanffy growth function that allows age at a specified length to be directly estimated so that standard methods to construct confidence intervals and make among-group comparisons for this parameter can be used. We demonstrate use of the new parameterization with two datasets.

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1. Introduction

The length of time (t_r) required for fish in a population to reach a specified mean length (L_r) is useful for understanding the dynamics of fish populations. The t_r value usually represents the age when fish become vulnerable to fishing mortality as (originally denoted as $t_{\rho'}$) in Beverton-Holt equilibrium yield models (Beverton and Holt, 1957). These models have long been used to simulate fishery responses to changes in fishing mortality (Beverton and Holt, 1957; Ricker, 1975; Quinn and Deriso, 1999). Release of the Fisheries Analysis and Simulation Tools (FAST; Slipke and Maceina, 2001) and Fisheries Analysis and Modeling Simulator (FAMS, Slipke and Maceina, 2014) software packages facilitated using these Beverton-Holt models to simulate the effects of length-based harvest regulations on freshwater fisheries (e.g., Isermann et al., 2002; Brenden et al., 2007; Colvin et al., 2013). The t_r value may also be valuable outside of this modeling framework because it provides a measure of cumulative growth up to age t_r that likely responds (or is related) to abiotic and biotic factors that affect growth of fish (Brett, 1979; Lorenzen, 2016). For example, at a fixed L_r , a population with a larger t_r grows more slowly than a population with a lower t_r . Thus, t_r may be useful for comparing growth among populations.

Typically, t_r 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 specified length L_r (Beverton and Holt, 1957; Gulland, 1973; Clark, 1983; Allen and Miranda, 1995; 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 t_r 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 t_r and usual methods (extra sum-of-squares tests (Ritz and

Streibig, 2008), likelihood ratio tests (Kimura, 1980), or information criterion (Burnham and Anderson, 2002) approaches) for comparing models cannot be used to determine if t_r differs among populations. These statistical shortcomings could be overcome if t_r was directly estimated as a function parameter rather than being derived from other function parameters.

Additionally, some parameters in the usual VBGF 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 t_r . In contrast, t_r 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 t_r as a directly estimated parameter and (2) demonstrate how this VBGF can be used to directly estimate t_r and identify differences in t_r between populations.

2. Theory

The most commonly used parameterization of the VBGF from Beverton and Holt (1957) is

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \quad (1)$$

where L_t is the expected or mean length at time (hereafter, age) t , L_∞ is the asymptotic mean length, K is a measure of the exponential rate at which L_t approaches L_∞ (Schnute and Fournier, 1980), and t_0 is the theoretical age at which L_t would be zero (i.e., the x-intercept; Figure 1). For use further below, Eq. (1) can be expressed as

$$L_t = 0 + (L_\infty - 0)(1 - e^{-K(t-t_0)}) \quad (1a)$$

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

$$L_t = L_\infty + (L_\infty - L_0)e^{-Kt} \quad (2)$$

where L_0 is L_t when $t = 0$ (i.e., y-intercept; Figure 1). Eq (2) can be algebraically shown to equal

$$L_t = L_0 + (L_\infty - L_0)(1 - e^{-Kt})$$

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

$$L_t = L_0 + (L_\infty - L_0)(1 - e^{-K(t-0)}) \quad (2a)$$

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

$$L_t = L_r + (L_\infty - L_r)(1 - e^{-K(t-t_r)}) \quad (3)$$

where $L_t = L_r$ when $t = t_r$. Thus, when $L_r = 0$, t_r is the theoretical age at a mean length of zero (i.e., the x-intercept) and Eq. (3) reduces to Eq. (1a) with t_r replaced by t_0 . Similarly, when $t_r = 0$, L_r is the mean length at age zero (i.e., the y-intercept) and Eq. (3) reduces to Eq. (2a) with L_r replaced by L_0 . 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).

Of more interest is that Eq. (3) may be used to estimate L_r or t_r for any point on the VBGF curve (Figure 1). For example, t_r may be set to a specific age of biological interest such that the mean length at that age (L_r) is a parameter estimated from fitting Eq. (3) to data. Conversely, and the focus of this note, L_r may be set to a specific length of biological interest such that the age (t_r) for fish of that mean length is a parameter estimated from fitting Eq. (3) to data. Thus, because t_r 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 t_r among populations.

Note that Eq. (3) appears to have four parameters, but either L_r is set to a constant value and t_r is estimated or t_r is set to a constant value and L_r is estimated. Thus, Eq. (3) has three estimable parameters, as do Eqs. (1) and (2).

3. Methods

We demonstrate use of Eq. (3) for estimating t_r 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 t_r from Eq. (3) equal derived estimates of t_r 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 t_r (and other function parameters) between groups (i.e., sexes).

Lake whitefish were captured by commercial trap-netters from locations in and around Green Bay, Lake Michigan in October 2012 and 2013 and were genetically assigned to the Big Bay de Noc stock. 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 at which a mean TL of 480 mm was reached (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). Results from fitting Eqs. (1) and (2) were algebraically rearranged to estimate t_{480} . 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 t_{480} 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 function parameter, derived t_{480} estimate, and predicted mean length-at-age were the 5th and 95th percentile values of the 999 bootstrap 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 September 2012. Total length was measured to the nearest mm, integer ages were estimated from cracked otoliths viewed with a fiber optic light, and sex was determined by visually examining gonads. We estimated t_{432} because 432 mm was the lower end of a protective slot limit for Lake Winnibigoshish walleye in 2012. 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 t_{432} from Eq. (3).

4. Results

Point estimates for all parameters and derived values, including t_{480} , 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 L_{∞} ($F_{1,482} = 147.43$, $P < 0.001$) and t_{432} ($F_{1,482} = 128.30$, $P < 0.001$) parameters, but not K ($F_{1,481} = 3.21$, $P = 0.074$), differed significantly between male and female Lake Winnibigoshish walleye (Figure 2). The L_{∞} was greater for female (95% CI: 641-707 mm) than male (95% CI: 560-616 mm) walleye, whereas t_{432} 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 in Lake Winnibigoshish reached the minimum slot length limit (432 mm) before and achieved a longer maximum mean length than males.

5. Conclusion

Eq. (3) is a simple parameterization of the VBGF that includes the typical and original VBGF parameterizations as special cases. However, Eq. (3) is flexible in that it may also be used to estimate mean length for any specific age or age for any specific mean length, rather than only intercept values as with the typical and original VBGFs. We expect the primary use of Eq. (3) among fisheries scientists will be to estimate age at a specific length (i.e., t_r). Thus, we demonstrated that point- and bootstrapped-interval estimates for t_r from Eq. (3) match those derived from parameters estimated with Eqs. (1) and (2). We also showed how Eq. (3) allows use of likelihood profile methods to estimate confidence intervals and model selection procedures to statistically determine if age at the specified mean length differs among populations.

A direct estimate of t_r (but as t_0) may also be made by replacing L_t in Eq. (1) with $L_t - L_r$ (i.e., subtracting L_r from each observed length). However, L_{∞} from fitting this modified equation is underestimated by a constant L_r . If L_r is also subtracted from L_{∞} in Eq. (1), then L_{∞} will be estimated on the original scale. These two *ad hoc* modifications simply convert Eq. (1) to Eq. (3).

Thus, for conceptual consistency with previous parameterizations of the VBGF and because of the flexibility afforded by Eq. (3), we suggest using Eq. (3), rather than *ad hoc* approaches, when interest lies in estimating or testing for differences among populations in L_{∞} , K , and a specific point on the growth curve, such as t_r .

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Supplementary Information

R code for all figures and analyses.

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249 Table 1. Estimated parameters (L_{∞} , K , t_0 , L_0 , and, for Eq. (3), t_{480}), derived variables (t_{480} for
 250 Eqs. (1) and (2)), and predicted mean lengths-at-ages 8 (L_8) and 20 (L_{20}), with 90% confidence
 251 intervals in parentheses, and residual sum-of-squares (RSS) from fitting Eqs. (1)-(3) to the Big
 252 Bay de Noc genetic stock of lake whitefish.

Parameter/ Variable	Eq. (1)	Eq. (2)	Eq. (3)
L_{∞}	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)
t_0	-2.386 (-9.834, 1.027)	--	--
L_0	--	206.31 (-214.67, 380.72)	--
t_{480}	8.04 (7.09, 8.65) ^a	8.04 (7.02, 8.67) ^a	8.04 (7.03, 8.64)
L_8	479.38 (469.10, 489.68)	479.38 (468.89, 489.62)	479.38 (469.42, 489.57)
L_{20}	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 $L_{\infty} = 250$, $K = 0.7$, $t_0 = -0.7$, and $L_0 = 73.8$. Three points on the curve are shown with gray circles -- $(t_0, 0)$ specifically defines Eq. (1), $(0, L_0)$ specifically defines Eq. (2), and (t_r, L_r) generically defines Eq. (3).

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



