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To cite this article: Derek H. Ogle & Daniel A. Isermann (2017) Estimating Age at a Specified Length from the von Bertalanffy Growth Function, North American Journal of Fisheries Management, 37:5, 1176-1180, DOI: [10.1080/02755947.2017.1342725](https://doi.org/10.1080/02755947.2017.1342725)

To link to this article: <http://dx.doi.org/10.1080/02755947.2017.1342725>

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 Published online: 08 Sep 2017.

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MANAGEMENT BRIEF

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 the use of standard frequentist methods to compute confidence intervals and compare estimates of age at the specified length among populations. We provide a parameterization of the von Bertalanffy growth function that has age at a specified length as a parameter. With this parameterization, age at a specified length is directly estimated, and standard methods can be used to construct confidence intervals and make among-group comparisons for this parameter. We demonstrate use of the new parameterization with two data sets.

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 in Beverton–Holt equilibrium yield models (denoted t_p by 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 resulted in increased use

of 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 to (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 higher t_r grows more slowly than a population with a lower t_r . Thus, t_r may be a useful parameter 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 SEs and confidence intervals (CIs) for t_r derived in this manner. However, likelihood profiles (Hilborn and Mangel 1997; Ritz and Streibig 2008) cannot be used to construct CIs for the derived t_r , and the usual methods (likelihood ratio tests: Kimura 1980; information criterion approaches: Burnham and Anderson 2002; or extra sum-of-squares tests: Ritz and Streibig 2008) for comparing models cannot be used to determine whether t_r differs among populations. These statistical shortcomings could be overcome if t_r was directly estimated as a parameter in the VBGF rather than being derived from other parameters in the VBGF.

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Received March 30, 2017; accepted June 9, 2017

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 the values derived from those 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 included as a parameter in the VBGF. Therefore, the objectives of this brief 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 to identify differences in t_r between populations.

THEORETICAL DEVELOPMENT

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

$$L_t = L_\infty \left[1 - e^{-K(t-t_0)} \right], \tag{1}$$

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

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

or, equivalently,

$$L_t = L_0 + (L_\infty - L_0)(1 - e^{-Kt}), \tag{2}$$

where L_0 is L_t when $t = 0$ (i.e., y -intercept; Figure 1). With simple additions (or subtractions) of zeroes, equations (1) and (2) can be expressed, respectively, as

$$L_t = 0 + (L_\infty - 0) \left[1 - e^{-K(t-t_0)} \right]$$

and

$$L_t = L_0 + (L_\infty - L_0) \left[1 - e^{-K(t-0)} \right].$$

Comparison of these expressions reveals the algebraic similarity between the two parameterizations. This similarity suggests that the VBGF may be expressed as

$$L_t = L_r + (L_\infty - L_r) \left[1 - e^{-K(t-t_r)} \right], \tag{3}$$

where $L_t = L_r$ when t is equal to 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 equation (3) reduces to equation (1) 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 equation (3) reduces to equation (2) with L_r replaced by L_0 . Thus, equations (1) and (2) are special cases of equation (3) and only differ in whether they are parameterized to estimate the x - or y -intercept (Figure 1). These intercepts may be of little biological interest (especially t_0) or poorly estimated because they are outside the domain or range of the data.

A specific value of L_r or t_r may be chosen so that equation (3) passes through any specific point on the VBGF curve (Figure 1), and a biologically interesting parameter is then estimated. 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 equation (3) to data. Conversely, and the focus of this brief, 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 equation (3) to data. Thus, because t_r is a parameter directly estimated from fitting equation (3) to data, all methods for computing CIs for function parameters may be used, and common statistical methods may be employed to identify differences in t_r among populations.

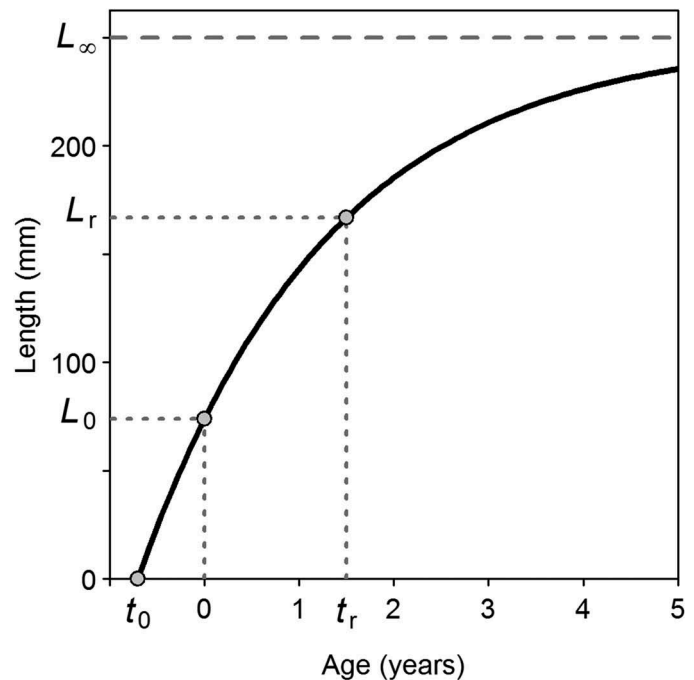


FIGURE 1. Examples of equations (1)–(3) with $L_\infty = 250$ mm, $K = 0.5$ /year, $t_0 = -0.7$ year, and $L_0 = 74$ mm (symbols are defined in the text). Three points on the curve are shown with gray circles: $(t_0, 0)$ specifically defines equation (1); $(0, L_0)$ specifically defines equation (2); and (t_r, L_r) generically defines equation (3).

Note that equation (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, equation (3) has three estimable parameters, as is the case for equations (1) and (2).

METHODS

We demonstrate the use of equation (3) to estimate t_r with two examples. First, we use length-at-age data for Lake Whitefish *Coregonus clupeaformis* in Lake Michigan to demonstrate that the fit of equation (3) is equivalent to the fits of equations (1) and (2) and that direct estimates of t_r from equation (3) equal the derived estimates of t_r from equations (1) and (2). Second, we use length-at-age data for Walleyes *Sander vitreus* in Lake Winnibigoshish (Minnesota) 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 trapnetters 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. The TLs of Lake Whitefish were measured to the nearest millimeter, and integer ages were estimated from thin-sectioned otoliths. Full collection details for these data are provided by Belnap (2014). As in the Belnap (2014) study, we estimate the age at which a mean TL of 480 mm was reached (i.e., t_{480}); this is the TL at which Lake Whitefish are fully vulnerable to commercial and tribal harvest in Lake Michigan (Ebener et al. 2008). Equations (1)–(3) were fit to these data by using the default Gauss–Newton algorithm of the nls() function in the R environment (see the Supplement available in the online version of this article for R code; 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 equations (1) and (2) were algebraically rearranged to estimate t_{480} . For each equation, 999 nonparametric bootstrap samples of mean-centered residuals were computed with the nlsBoot() function from the “nlstools” package version 1.0-2 (Baty et al. 2015). A value of t_{480} was derived from each bootstrap sample for equations (1) and (2). To further compare the equivalency of equations (1)–(3), the predicted mean lengths at ages 8 and 20 were computed from each bootstrap sample for all three equations. Approximate 90% CIs 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% CI was used instead of the 95% CI to eliminate the tail portion of the bootstrapped distributions to better compare the equivalency of estimated parameters and derived values across equations.

Gill nets were used to capture Walleyes from two locations in Lake Winnibigoshish during September 2012. The TLs were measured to the nearest millimeter, integer ages were estimated from cracked otoliths viewed with a fiber optic light, and sex was determined by visual examination of the gonads. We estimated t_{432} because 432 mm was the lower end of a protective slot limit for Lake Winnibigoshish Walleyes in 2012. We used extra sum-of-squares tests in a sequential step-down process (as described by Ogle 2016) to identify which of eight possible models best fit these data. The eight models were modifications of equation (3), where all parameters, two parameters, one parameter, or no parameter differed between the two sexes. All models were fit with the default Gauss–Newton algorithm in the nls() function of R. The confint() function from the MASS package (Venables and Ripley 2002) was used to construct 95% profile likelihood CIs for all function parameters in the final model. The profile likelihood method, rather than bootstrapping, was used for these CIs to illustrate that this method can be used to estimate the CI for t_{432} from equation (3).

RESULTS

Point estimates for all parameters and derived values, including t_{480} , shared among equations (1)–(3) were equivalent for Lake Whitefish of the Big Bay de Noc genetic stock (Table 1). The CIs for all parameters and derived values shared among equations (1)–(3) were similar but not exactly equal due to the inherent stochasticity of the bootstrap method (Table 1). Lake Whitefish reached a TL of 480 mm at approximately 8 years of age.

The L_∞ ($F = 147.43$; $df = 1, 482$; $P < 0.001$) and t_{432} ($F = 128.30$; $df = 1, 482$; $P < 0.001$) parameters differed significantly between male and female Walleyes in Lake Winnibigoshish, whereas K did not ($F = 3.21$; $df = 1, 481$; $P = 0.074$; Figure 2). Best-fit model equations for both sexes were

$$L_t = 432 + (671 - 432) \left[1 - e^{-0.17(t-3.87)} \right] \text{ for females}$$

and

$$L_t = 432 + (585 - 432) \left[1 - e^{-0.17(t-4.76)} \right] \text{ for males.}$$

The L_∞ was greater for female (95% CI = 641–707 mm) than male (95% CI = 560–616 mm) Walleyes, whereas t_{432} was lower for females (95% CI = 3.78–3.95 years) than males (95% CI = 4.61–4.93 years). These results suggest that female Walleyes in Lake Winnibigoshish reached the minimum slot length limit (432 mm) before males and achieved a longer asymptotic mean length than males.

TABLE 1. Estimated parameters (L_∞ , K , t_0 , L_0 , and, for equation [3], t_{480} ; symbols are defined in the text), derived variables (t_{480} for equations [1] and [2]), and predicted mean TLs at age 8 (L_8) and age 20 (L_{20}), with 90% confidence intervals in parentheses, and residual sum of squares (RSS) from fitting equations (1)–(3) to data from Lake Whitefish of the Big Bay de Noc genetic stock.

Parameter/variable	Equation (1)	Equation (2)	Equation (3)
L_∞ (mm)	550.83 (540.45, 572.97)	550.83 (540.99, 574.34)	550.83 (541.33, 577.59)
K (/year)	0.197 (0.108, 0.300)	0.197 (0.097, 0.297)	0.197 (0.093, 0.306)
t_0 (years)	–2.386 (–9.834, 1.027)		
L_0 (mm)		206.31 (–214.67, 380.72)	
t_{480} (years)	8.04 (7.09, 8.65) ^a	8.04 (7.02, 8.67) ^a	8.04 (7.03, 8.64)
L_8 (mm)	479.38 (469.10, 489.68)	479.38 (468.89, 489.62)	479.38 (469.42, 489.57)
L_{20} (mm)	544.08 (537.65, 550.31)	544.08 (538.22, 549.73)	544.08 (538.65, 550.62)
RSS	320,685.4	320,685.4	320,685.4

^aValue derived by rearranging the equation to solve for t with a TL of 480 mm.

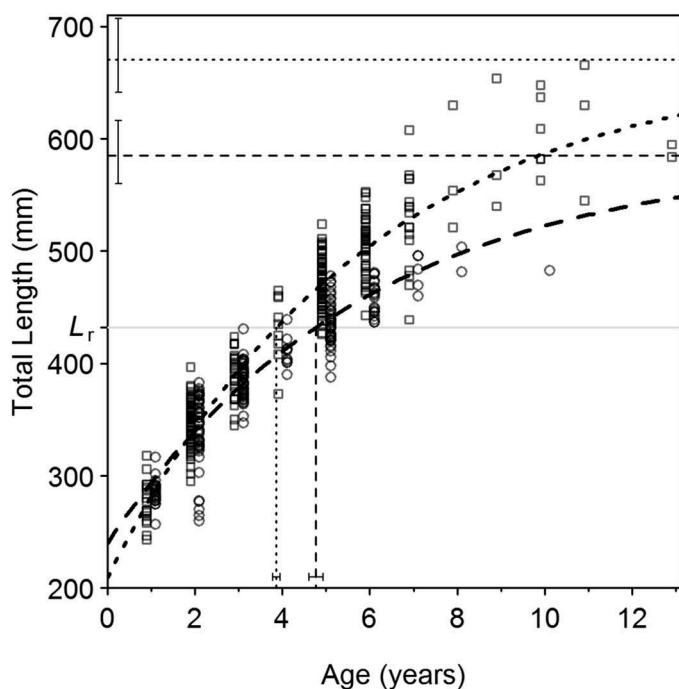


FIGURE 2. Fits of equation (3) to TL-at-age data for female (open squares, dotted line) and male (open circles, dashed line) Walleyes captured from Lake Winnibigoshish in September 2012. Points are slightly offset from the integer ages to reduce overlap between the sexes. Point estimates and 95% confidence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

DISCUSSION

Equation (3) is a simple parameterization of the VBGF that includes the typical and original VBGF parameterizations as special cases. However, equation (3) is flexible in that it may also be used to estimate mean length for any specific age or to estimate age for any specific mean length rather than only intercept values as with the typical and original VBGFs. We

expect that the primary use of equation (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 equation (3) matched those derived from parameters estimated with equations (1) and (2). We also showed how, in contrast to equations (1) and (2), standard frequentist methods can be used with equation (3) to estimate CIs for t_r (e.g., profile likelihood) and to determine whether t_r differs among populations (e.g., extra sum-of-squares test).

A direct estimate of t_r (though estimated as t_0) can also be obtained by replacing L_t in equation (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 equation (1), then L_∞ will be estimated on the original scale. These two ad hoc modifications simply convert equation (1) to equation (3). Additionally, the VBGF parameterizations of Schnute and Fournier (1980) and Francis (1988) have two or three parameters, respectively, that represent mean lengths at specific ages. Specific mean lengths could be chosen in these parameterizations such that ages at those mean lengths are estimated. However, L_∞ is dropped from the Schnute and Fournier (1980) parameterization, and both L_∞ and K are dropped from the Francis (1988) parameterization.

Equation (3) is an alternative parameterization of the VBGF that allows a direct and conceptually consistent—rather than a derived and ad hoc—estimate of t_r (or L_r). In addition, direct estimates of L_∞ and K are maintained with equation (3). It is important to note, however, that equation (3) is not a fundamentally new growth model. Thus, the usual cautions and caveats related to the applicability, fitting, and data requirements of a VBGF (Knight 1968; Roff 1980; Day and Taylor 1997; Lester et al. 2004; Katsanevakis and Maravelias 2008; Haddon 2011; Van Poorten and Walters 2015) still apply to equation (3). Equation (3) can be used to directly estimate three growth-related parameters of interest, but those estimates

are only useful if the VBGF is an adequate model of the data and if the data are representative of the population of interest.

ACKNOWLEDGMENTS

We thank M. Belnap for use of the Lake Whitefish data, which were obtained during a project funded by the Great Lakes Fishery Commission. We also thank the Minnesota Department of Natural Resources for use of the Walleye data from Lake Winnibigoshish. This paper was improved by discussions with and reviews by T. Brenden and two anonymous reviewers. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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