



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

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

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Running title: Estimating Age at a Specified Length

## 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 using 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 datasets.

## 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 in Beverton–Holt equilibrium yield models (was  $t_p$  in 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 (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 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 approaches (Burnham and Anderson 2002)] 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 parameter in the VBGF rather than being derived from other parameters in the VBGF.

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 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 identify differences in  $t_r$  between populations.

## Theoretical Development

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

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

where  $L_t$  is the expected or mean length at time (hereafter, age)  $t$ ,  $L_\infty$  is the asymptotic mean length,  $K$  is a measure of the exponential rate at which  $L_t$  approaches  $L_\infty$  (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,

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

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:

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

$$L_t = L_0 + (L_\infty - L_0)(1 - e^{-K(t-t_0)})$$

Comparing these expressions reveals the algebraic similarity between the two parameterizations.

This similarity suggests that the VBGF may be expressed as:

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

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 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 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 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 do equations (1) and (2).

#### <A>Methods

We demonstrate using equation (3) to estimate  $t_r$  with two examples. First, length-at-age data for Lake Michigan Lake Whitefish *Coregonus clupeaformis* are used to demonstrate that the fit of equation (3) is equivalent to the fits of equations (1) and (2), and that direct estimates of  $t_r$  from equation (3) equal derived estimates of  $t_r$  from equations (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 age 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). Equations (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 equations (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 from each bootstrap sample for equations (1) and (2). To further compare the equivalency of equations (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%, rather than 95%, 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 equation (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 equation (3).

## <A>Results

Point estimates for all parameters and derived values, including  $t_{480}$ , shared between equations (1)-(3) were equivalent (Table 1). Confidence intervals for all parameters and derived values shared between equations (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  $L_{\infty}$  ( $F = 147.43$ ,  $df = 1, 482$ ,  $P < 0.001$ ) and  $t_{432}$  ( $F = 128.30$ ,  $df = 1, 482$ ,  $P < 0.001$ ) parameters, but not  $K$  ( $F = 3.21$ ,  $df = 1, 481$ ,  $P = 0.074$ ), differed significantly between male and female Lake Winnibigoshish Walleye (Figure 2). Best-fit model equations for both sexes are:

$$\text{Female: } L_t = 432 + (671 - 432)(1 - e^{-0.17(t-3.87)})$$

$$\text{Male: } L_t = 432 + (585 - 432)(1 - e^{-0.17(t-4.76)})$$

The  $L_{\infty}$  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 asymptotic mean length than males.

## 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 age for any specific mean length, rather than only intercept values as with the typical and original VBGFs. We expect 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) match 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 confidence intervals for  $t_r$  (e.g., profile likelihood) and determine if  $t_r$  differs among populations (e.g., extra sums-of-squares tests).

A direct estimate of  $t_r$  (though estimated as  $t_0$ ) may also be made by replacing  $L_t$  in equation (1) with  $L_t - L_r$  (i.e., subtracting  $L_r$  from each observed length). However,  $L_\infty$  from fitting this modified equation is underestimated by a constant  $L_r$ . If  $L_r$  is also subtracted from  $L_\infty$  in equation (1), then  $L_\infty$  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,  $L_\infty$  is dropped from the Schnute and Fournier (1980) parameterization and both  $L_\infty$  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 derived and *ad hoc*, estimate of  $t_r$  (or  $L_r$ ). In addition, direct

estimates of  $L_{\infty}$  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 the data are representative of the population of interest.

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#### Supplementary Information

R code for all figures and analyses.

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TABLE 1. Estimated parameters [ $L_{\infty}$ ,  $K$ ,  $t_0$ ,  $L_0$ , and, for equation (3),  $t_{480}$ ], derived variables ( $t_{480}$  for equations 1 and 2), and predicted mean lengths-at-ages 8 ( $L_8$ ) and 20 ( $L_{20}$ ), with 90% confidence intervals in parentheses, and residual sum-of-squares (RSS) from fitting equations (1)-(3) to the Big Bay de Noc genetic stock of Lake Whitefish.

Parameter/ Variable	Equation (1)	Equation (2)	Equation (3)
$L_{\infty}$	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) <sup>a</sup>	8.04 (7.02, 8.67) <sup>a</sup>	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

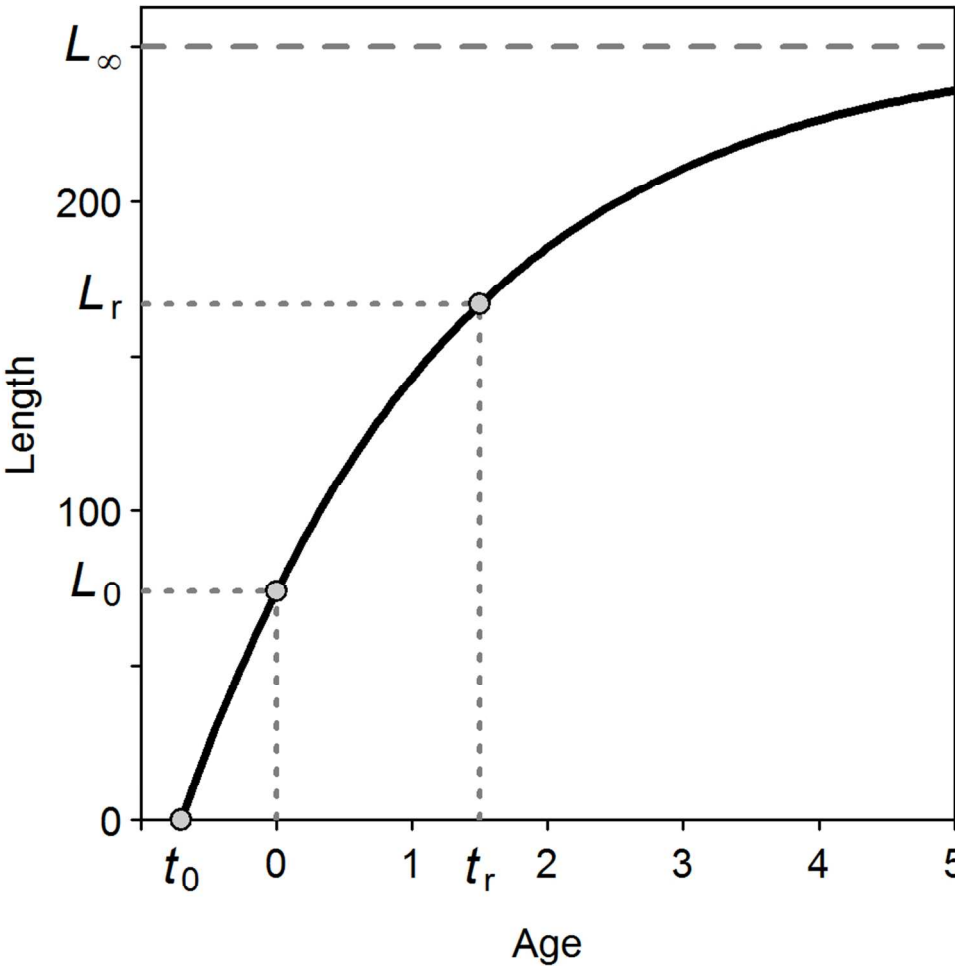
<sup>a</sup>Value derived by rearranging the equation to solve for  $t$  with a length of 480 mm.



## Figure Labels

FIGURE. 1. Examples of equations (1)-(3) with  $L_{\infty} = 250$ ,  $K = 0.7$ ,  $t_0 = -0.7$ , and  $L_0 = 74$ . 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).

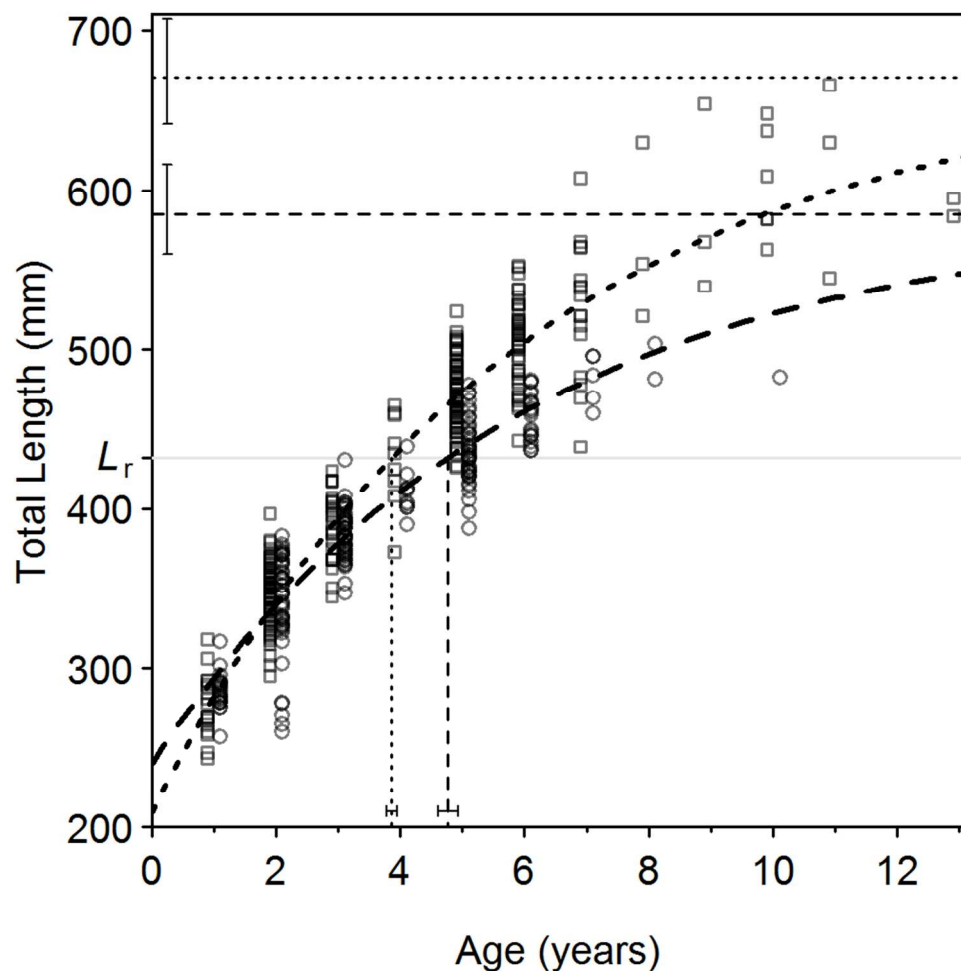
FIGURE. 2. Fits of equation (3) to female (open squares, dotted line) and male (open circles, dashed line) total length-at-age data for Walleye captured from Lake Winnibigoshish in September, 2012. Points are slightly offset from the integer ages to reduce overlap between sexes. Point estimates and 95% confidence intervals are shown for each sex along the y-axis for  $L_{\infty}$  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.



Examples of equations (1)-(3) with  $L_{\infty} = 250$ ,  $K = 0.7$ ,  $t_0 = -0.7$ , and  $L_0 = 74$ . 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).

88x88mm (300 x 300 DPI)





Fits of equation (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  $L_\infty$  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.

88x88mm (300 x 300 DPI)





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1 June 2017

Dr. Daugherty,

Enclosed is a modified version of our manuscript (ID UJFM-2017-0045) entitled "Estimating Age at a Specified Length from the von Bertalanffy Growth Function." We modified the manuscript based on the constructive suggestions by your Associate Editor and two anonymous reviewers for the journal. In addition, we have provided responses to the reviewer's concerns or suggestions in the attached pages, with the reviewer's specific comments followed, in bold, by our response. We believe that all concerns were adequately addressed in the new manuscript or in our responses.

Thank you for your continued consideration of our manuscript. We look forward to your response regarding the suitability of the revised manuscript for publication as a management brief in the *North American Journal of Fisheries Management*. Please contact me if you have any questions or concerns related to the manuscript or our responses to the reviewer's suggestions.

Respectfully,

A handwritten signature in black ink, appearing to read "Derek H. Ogle".

Dr. Derek H. Ogle  
Professor of Mathematical Sciences and Natural Resources

**Reviewer: 1**

Comments to the Author: Well-written paper on novel parameterization of von Bertalanffy fish growth model that allows estimating Age|Length or Length|Age for any chosen age or length of interest to the user. These estimates are actual model parameters, so standard model outputs or other frequentist inference methods (e.g., profile likelihood) can be used for inference. I recommend this manuscript be accepted with minor edits. David F. Staples 5/3/17

- line 25: instead of 'some' statistical methods, perhaps note that use of standard frequentist methods

**AUTHOR'S RESPONSE: Done.**

- line 28: make clear that the re-parameterization of the model includes the  $L_r$  or  $t_r$  of interest as model parameters so inference on them is based on standard model output; abstract does say these are 'directly estimated', which is basically the same thing, but I think explicitly stating these are parameters in the model would be more clear.

**AUTHOR'S RESPONSE: Done, though we focused only on  $t_r$  as that is the focus of the manuscript.**

- line 78: as discussed with Dr. Ogle in email pasted below, this equation has a typo

Email correspondence with Dr. Ogle:

You are right about the equation on line 78. The plus after  $L_{inf}$  should be a minus. Thus, it should be  $L_t = L_{inf} - (L_{inf} - L_0)e^{(-Kt)}$ . This can be seen in von B's (see attached) equation 6 (where his  $l$  is my  $L_t$ , his  $L$  is my  $L_{inf}$ , and his  $l_0$  is my  $L_0$ ). In addition, the algebra then works out:

New line 78 (expanded):  $L_{inf} - L_{inf}e^{(-Kt)} + L_0e^{(-Kt)}$

Line 80 (expanded):  $L_0 + L_{inf} - L_{inf}e^{(-Kt)} - L_0 + L_0e^{(-Kt)} =$   
 $L_{inf} - L_{inf}e^{(-Kt)} + L_0e^{(-Kt)}$

**AUTHOR'S RESPONSE: Corrected.**

- line2 87-91: I recommend using some of model parameter discussion from email below to further clarify the derivation of the model.

Email correspondence with Dr. Ogle:

Regarding the other discussion. I was trying to take the two most prevalent parameterizations of the VBGF and show, with judicious zeroes, that they are the same functional form. However, to fit the model, a point on the line that the model goes through must be chosen. Von B chose for the model to go through the y-intercept (i.e., the point  $(0, L_0)$ ) and Beverton and Holt chose for the model to go through the x-intercept (i.e., the point  $(t_0, 0)$ ). So, von B estimated the mean length when the age is zero ( $L_0$ ) and B&H estimated the age when the mean length is zero ( $t_0$ ). I am arguing that you can choose any other point (i.e.,  $(t_r, L_r)$ ) such that if you specify  $t_r$  you estimate  $L_r$ , but if you specify  $L_r$  then you estimate  $t_r$ . In this way, you fit the same model (i.e., same predictions, etc.), but you can estimate a third parameter ( $L_r$  or  $t_r$ ) that may be of more interest than either  $L_0$  or  $t_0$ .

**AUTHOR'S RESPONSE: We made additions to this section of the manuscript. However, we feel that the salient points of the e-mail discussion are already in the manuscript. For example, the last sentence of the first paragraph in the Theoretical Developments section notes that the two original parameterizations were parameterized to estimate the x- or y-intercept and the first sentence of the next paragraph (now slightly modified) indicates that another point could have been chosen (and we are allowing the user to choose that point). Perhaps the only part of the e-mail communication that is missing in the manuscript is that a point must be chosen so that the model can be fit. We feel that this is at least implicit in the current manuscript and that an explicit statement of such does not add much clarity.**

- lines 100-102: perhaps this would be better before the paragraph starting at line 92

**AUTHOR'S RESPONSE:** We did not change the order of the second and third paragraphs of the Theoretical Developments section (as this comment suggests). The second paragraph discusses how the user can choose either  $L_r$  or  $t_r$  to estimate the other. We feel that it is important to make this point immediately after "deriving" the new parameterization and noting that the original parameterizations simply chose  $L_r=0$  and  $t_r=0$ . Specifically, the topic sentence of the second paragraph is likely going to be a question the reader has after reading the paragraph before it. We want to answer that question immediately. In addition the third paragraph (the one suggested to be moved here) makes more sense after noting that the user must choose a value for  $L_r$  or  $t_r$ .

- line 143: perhaps note why profile likelihood may be useful. I think it is better than standard Wald-type CI's for inference on a single parameter from a multi-parameter model because it accounts for effects of maximizing the likelihood across the nuisance parameters as the parameter of interest varies. This can be especially useful for sparse data sets, e.g., I've used this approach to find multi-modal profiles or even distinct regions of support for parameters in a bi-phasic growth model (Honsey et al 2017, Eco Apps 27(1)); however, I would note that I'm not sure how the `confint()` function would handle such a situation with distinct likelihood modes.

**AUTHOR'S RESPONSE:** We feel that addressing this suggestion is beyond the scope of our paper, which is to simply provide the alternative parameterization and show how standard statistical methods can be used with it. Suggesting why the profile likelihood method is useful would likely require describing the method in more detail, describing other alternative methods (e.g., Wald CIs as this reviewer did), etc. We feel that this (a) would distract from our core message and (b) is not needed for a brief. We do provide references when first mentioning the likelihood profile method. The interested reader could follow-up with these.

## Reviewer: 2

Comments to the Author: This paper presents a method for estimating age at a given length, along with its uncertainty, from a von Bertalanffy growth model. While the idea is quite simple, I've not seen it done before and it is "neater" than the alternative bootstrapping method. The paper is well written and presented, and I have just a couple of suggestions.

1) The authors should mention the similarity of their new VB parameterization with the so-called "Schnute parameterization" (Quinn and Deriso 1999). The Schnute model is in terms of two length and age pairs ( $L_1, t_1$ ) and ( $L_2, t_2$ ), but taking ( $L_r, t_r$ ) in eq 3 to be ( $L_1, t_1$ ) and  $t_2=\infty$  such that  $L_2=L_{\infty}$ , yields the same result. Presumably, one could use the Schnute parameterization with  $L_1$  and  $L_2$  assumed fixed instead of  $t_1$  and  $t_2$ , and estimate  $t_1$  and  $t_2$  as parameters.

**AUTHOR'S RESPONSE:** Done. Also added reference to Francis parameterization.

2) This is minor, but very few results are given for the second example in terms of the stepwise model selection and the chosen model (e.g., the parameter estimates for males and females for the final model are not specified). While these results aren't really necessary, I think readers might still like to see them.

**AUTHOR'S RESPONSE:** The step-wise results are contain in the ( $F=\#$ ,  $df=\#$ ,  $P=\#$ ) results. We had included (and kept) confidence intervals for the two parameters that did differ between the sexes. We have added the best-fit equations for each sex. We have kept the results concise because (a) this is a brief and (b) we want the focus on the new parameterization and its use in these examples, not so much the specific results in these examples.

## Associate Editor

Comments to the Author: This manuscript was well written and should be of interest to fisheries managers. The typo on line 78 has been recognized by the author and presumably will be fixed. The reviewers had some minor issues that

should be addressed. I think management staff are likely to use this method for calculating (and more importantly, comparing) age for a specified length. However, I can also see it being misused in terms of people wanting to ignore the goodness of fit for the VBGF model. As such, I would like to see some general guidelines for minimum data requirements, such as the distribution of age classes, minimum sample sizes of aged fish, a minimum goodness of fit for the VBGF. If the overall fit to the VBGF model is poor, I assume we would get wide CI for  $t_r$ , which should be a good reason for managers to collect better data. But, it still would be nice to have some general guidelines for data requirements.

**AUTHOR'S RESPONSE:** This statement is true – the results will only be as good as the data from which they are computed. We have included this caveat in the new final paragraph. However, we did not provide general guidelines for data requirements as (a) that is not the focus of this paper, (b) we do not provide any new insight into this matter, and (c) they are the same for our parameterization as for any other VBGF parameterization.