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

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Abstract

Estimating the average time required (i.e., age) for the mean length of fish in a population to reach a specific value (e.g., legal harvest length) is useful for understanding population dynamics and simulating the potential effects of length-based harvest regulations. The mean 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 statistically comparing estimates of mean age at the specified length among populations. We provide a new parameterization of the von Bertalanffy growth function that allows the mean age at a specified length to be directly estimated so that standard 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: Nonlinear modeling, Lake Whitefish, Walleye, von Bertalanffy

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# Introduction

The average length of time () required for fish in a population to reach a specified mean length () is useful for understanding the dynamics of fish populations. The value usually represents the age when fish become vulnerable to fishing mortality as (originally denoted as ) 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 expanded the use of 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., 2014). The value may also be valuable outside of this modeling framework because it provides a measure of cumulative growth up to age 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 , a population with a larger grew slowly compared to a population with a lower . Thus, may be useful for comparing growth among populations.

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 specified length (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 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 (Ritz and Streibig, 2008), likelihood ratio tests (Kimura, 19890), or information criterion (Burnham and Anderson, 2002) approaches) 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 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 . 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

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

(1)

where is the expected or mean length at time (hereafter, age) , is the asymptotic mean length, is a measure of the exponential rate at which approaches (Schnute and Fournier, 1980), and is the theoretical 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) has 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 a specific 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 specific 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 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 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). Results from fitting Eqs. (1) and (2) were algebraically rearranged to estimate . 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 function parameter, derived estimate, and predicted 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 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 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 in Lake Winnibigoshish reached the minimum slot length limit (432 mm) before and achieved a longer maximum mean length than males.

# 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 more flexible in that it may be used to estimate mean length for any specific age or mean age for any specific length, rather than only intercept values as with the typical and original VBGFs. Point- and bootstrapped-interval estimates for mean age at a specific length (i.e., ) from Eq. (3) match those derived from estimated parameters from Eqs. (1) and (2). 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 specified length differs among populations. We suggest using Eq. (3) when interest lies in estimating mean age at a specific length or determining if the mean age at a specific length differs among populations.

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# Supplementary Information

R code for all figures and analyses.

# References

Allen, M. S., Miranda, L. E., 1995. An evaluation of the value of harvest restrictions in managing crappie fisheries. N. Am. J. Fish. Manag. 15, 766-772. DOI: 10.1577/1548-8675(1995)015<0766:AEOTVO>2.3.CO;2

Baty, F., Ritz, C., Charles, S., Brutsche, M., Flandrois, J-P., Delignette-Muller, M-L., 2015. A toolbox for nonlinear regression in R: The package nlstools. J. Stat. Soft. 66, 1-21. DOI: [10.18637/jss.v066.i05](http://dx.doi.org/10.18637/jss.v066.i05)

Belnap, M. J., 2014. Stock characteristics of lake whitefish in Lake Michigan. M. Sc. Thesis, University of Wisconsin-Stevens Point.

Bertalanffy, L. von, 1938. A quantitative theory of organic growth (inquiries on growth laws II). Hum. Biol. 10, 181–213.

Beverton, R. J. H., Holt, S. J., 1957. On the Dynamics of Exploited Fish Populations. United Kingdom Ministry of Agriculture; Fisheries. DOI: 10.1007/978-94-011-2106-4

Brenden, T. O., Hallerman, E. M., Murphy, B. R., Copeland, J. R., Williams, J. A., 2007. The New River, Virginia, muskellunge fishery: population dynamics, harvest regulation modeling, and angler attitudes. Environ. Biol. Fish. 79, 11-25. DOI: 10.1007/s10641-006-9089-1

Brett, J. R., 1979. Environmental factors and growth. in: Hoar, W. S., Randall, D. J., Brett, J. R. (Eds), Fish Physiology, vol. VIII. Academic Press, London, UK, pp. 599-675.

Burnham, K. P., Anderson, D. R., 2002. Model Selection and Multi-Model Inferences, Second Edition. Springer-Verlag, New York, New York.

Clark, Jr., R. D. 1983. Potential effects of voluntary catch and release of fish in recreational fisheries. N. Am. J. Fish. Manag. 3, 306-314. DOI: 10.1577/1548-8659(1983)3<306:PEOVCA>2.0CO;2

Colvin, M. E., Bettoli, P. W., Scholten, G. D., 2013. Predicting paddlefish roe yields using an extension of the Beverton–Holt equilibrium yield-per-recruit model. N. Am. J. Fish. Manag. 33, 940-949. DOI: 10.1080/02755947.2013.820242

Ebener, M. P., Copes, F. A., 1985. Population statistics, yield estimates, and management considerations for two lake whitefish stocks in Lake Michigan. N. Am. J. Fish. Manag. 5, 435-448. DOI: 10.1577/1548-8659(1985)5<435:PSYEAM>2.0.CO;2

Gulland, J. A., 1973. Manual of Methods for Fish Stock Assessment: Part 1 Fish Population Analysis. Food and Agriculture Organization of the United Nations.

Hilborn, R., Mangel, M., 1997. The Ecological Detective: Confronting Models with Data. Princeton University Press, Princeton, New Jersey.

Isermann, D. A., Sammons, S. M., Bettoli, P. W., Churchill, T. N., 2002. Predictive evaluation of size restrictions as management strategies for Tennessee reservoir crappie fisheries. N. Am. J. Fish. Man. 22:1349-1357. DOI: [10.1577/1548-8675(2002)022<1349:PEOSRA>2.0.CO;2](http://dx.doi.org/10.1577/1548-8675%282002%29022%3C1349:PEOSRA%3E2.0.CO;2)

Isermann, D. A., Willis, D. W., Blackwell, B. G., Lucchesi, D. O., 2007. Yellow perch in South Dakota: Population variability and predicted effect of creel limit reductions and minimum length limits. N. Am. J. Fish. Man. 27:918-931. DOI: 10.1577/M06-222.1

Kimura, D. K., 1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. 77:765-776.

Lorenzen, K., 2016. Toward a new paradigm for growth modeling in fisheries stock assessments: Embracing plasticity and its consequences. Fish. Res. 180:4-22. DOI: 10.1016/j.fishres.2016.01.006

McCullough, B. D., 2008. Some details of nonlinear estimation, in: Altman, M., Gill, J., McDonald M. P. (Eds), Numerical Issues in Statistical Computing for the Social Scientist. John Wiley & Sons, Inc., Hoboken, New Jersey, pp. 245-267.

Ogle, D. H., 2016. Introductory Fisheries Analysis with R. Chapman & Hall/CRC Press, Boca Raton, Florida.

Quinn II, T. J., Deriso, R. B., 1999. Quantitative Fish Dynamics. Oxford University Press, New York, New York.

R Development Core Team, 2017, R: A Language and Environment for Statistical Computing, v3.4.1. R Foundation for Statistical Computing, Vienna, Austria.

Ricker, W. E., 1975. Computation and Interpretation of Biological Statistics in Fish Populations. Fisheries Research Board of Canada 191.

Ritz, C., Streibig, J. C., 2008. Nonlinear Regression with R. Springer, New York, New York.

Schnute, J., Fournier, D., 1980. A new approach to length-frequency analysis: growth structure. Can. J. Fish. Aquat. Sci. 37, 1337–1351. DOI: 10.1139/f80-172

Seber, G. A. F., Wild, C. J., 2003. Nonlinear regression. John Wiley & Sons, New York, New York.

Slipke, J. W., Maceina, M. J., 2001. Fisheries analysis and simulation tools (FAST). Auburn University, Department of Fisheries and Allied Aquaculture, Auburn, Alabama.

Slipke, J. W., Maceina, M. J., 2014. Fisheries analysis and modeling simulator (FAMS). Version 1.64. American Fisheries Society, Bethesda, Maryland.

Venables, W. N., Ripley, B. D., 2002. Modern Applied Statistics with S, fourth edition. Springer, New York, New York.

Weber, M. J., Hennen, M. J., Brown, M. L., 2011. Simulated population responses of common carp to commercial exploitation. N. Am. J. Fish. Man. 31:269-279. DOI: 10.1080/02755947.2011.574923

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. 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 and along the x-axis for . The gray horizontal line is at *Lr* = 432 mm. One 581 mm age-16 male is not shown.



