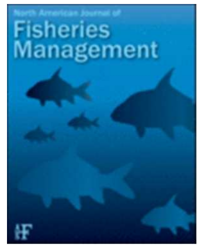


Estimating Age at a Specified Length from the von Bertalanffy Growth Function

Journal:	*North American Journal of Fisheries Management*
Manuscript ID	Draft
Manuscript Type:	Management Brief
Keywords:	Nonlinear modeling, Lake Whitefish, Walleye, Age and Growth, Population Dynamics
Note: The following files were submitted by the author for peer review, but cannot be converted to PDF. You must view these files (e.g. movies) online.	
OgleIsermann.R	

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

Derek H. Ogle*

Natural Resources Department, Northland College, 1411 Ellis Ave, Ashland, WI 54806, USA

Daniel A. Isermann

U. S. Geological Survey, Wisconsin Cooperative Fishery Research Unit, College of Natural Resources, University of Wisconsin-Stevens Point, 800 Reserve St., Stevens Point, WI 54481, USA

*Corresponding author: dogle@northland.edu)

Running title: Estimating Age at a Specified Length

<A>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.

<A>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 $t_{\rho'}$ 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 larger 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.

<A>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_∞ 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,

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

where L_0 is L_t when $t = 0$ (i.e., y-intercept; Figure 1). The fundamental similarity between equations (1) and (2) is seen when these equations are expressed, respectively, as:

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

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

This similarity suggests that the VBGF may be expressed as:

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

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).

Of more interest is that equation (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 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_∞ (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). 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.

<A>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 equation (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 (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_∞ 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). Thus, for conceptual consistency with previous parameterizations of the VBGF and because of the flexibility afforded by equation (3), we suggest using equation (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.

<A>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 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.

<A>Supplementary Information

R code for all figures and analyses.

<A>References

Allen, M. S., and L. E. Miranda. 1995. An evaluation of the value of harvest restrictions in managing crappie fisheries. North American Journal of Fisheries Management 15:766-772.

Baty, F., C. Ritz, S. Charles, M. Brutsche, J-P. Flandrois, and M-L Delignette-Muller. 2015. A toolbox for nonlinear regression in R: the package nlstools. Journal of Statistical Software 66:1-21.

Belnap, M. J. 2014. Stock characteristics of Lake Whitefish in Lake Michigan. Master's Thesis, University of Wisconsin-Stevens Point.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fisheries Investigations Series II, Volume 19, Ministry of Agriculture, Fisheries, and Food, Her Majesty's Stationery Office, London.

Brenden, T. O., E. M. Hallerman, B. R. Murphy, J. R. Copeland, and J. A. Williams. 2007. The New River, Virginia, Muskellunge fishery: population dynamics, harvest regulation modeling, and angler attitudes. Environmental Biology of Fish 79:11-25.

Brett, J. R. 1979. Environmental factors and growth. Pages 599-674 *in* W.S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish Physiology, volume VIII. Academic Press, London, UK.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inferences, second edition. Springer-Verlag, New York.

Clark, Jr., R. D. 1983. Potential effects of voluntary catch and release of fish in recreational fisheries. North American Journal of Fisheries Management 3:306-314.

Colvin, M. E., P. W. Bettoli, and G. D. Scholten. 2013. Predicting Paddlefish roe yields using an extension of the Beverton–Holt equilibrium yield-per-recruit model. North American Journal of Fisheries Management 33:940-949.

Ebener, M. P., R. E. Kinnunen, P. J. Schneeberger, L. C. Mohr, J. A. Hoyle, and P. J. Peeters. 2008. Management of commercial fisheries for Lake Whitefish in the Laurentian Great Lakes of North America. Pages 99-143 *in* M. J. Schechter, N. J. Leonard, and W. W. Taylor, editors. International Governance of Fisheries Ecosystems: learning from the past, finding solutions for the future. American Fisheries Society, Bethesda, Maryland.

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., and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, New Jersey.

Isermann, D. A., S. M. Sammons, P. W. Bettoli, and T. N. Churchill. 2002. Predictive evaluation of size restrictions as management strategies for Tennessee reservoir crappie fisheries. North American Journal of Fisheries Management 22:1349-1357.

Isermann, D. A., D. W. Willis, B. G. Blackwell, and D. O. Lucchesi. 2007. Yellow Perch in South Dakota: population variability and predicted effect of creel limit reductions and minimum length limits. North American Journal of Fisheries Management 27:918-931.

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

Lorenzen, K. 2016. Toward a new paradigm for growth modeling in fisheries stock assessments: embracing plasticity and its consequences. Fisheries Research 180:4-22.

McCullough, B. D. 2008. Some details of nonlinear estimation. Pages 245-267 *in* M. Altman, J. Gill, and M. P. McDonald, editors. Numerical issues in statistical computing for the social scientist. John Wiley & Sons, Inc., Hoboken, New Jersey.

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

Quinn II, T. J., and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.

R Development Core Team. 2017. R: a language and environment for statistical computing, v3.3.3. 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 Bulletin 191.

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

Schnute, J., and D. Fournier. 1980. A new approach to length-frequency analysis: growth structure. Canadian Journal of Fisheries and Aquatic Sciences 37:1337–1351.

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

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

Slipke, J. W., and M. J. Maceina. 2014. Fisheries analysis and modeling simulator (FAMS), v1.64. American Fisheries Society, Bethesda, Maryland.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S, fourth edition. Springer, New York.

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

Weber, M. J., M. J. Hennen, M. L. Brown. 2011. Simulated population responses of Common Carp to commercial exploitation. North American Journal of Fisheries Management 31:269-279.

TABLE 1. Estimated parameters [L_∞, 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_∞	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

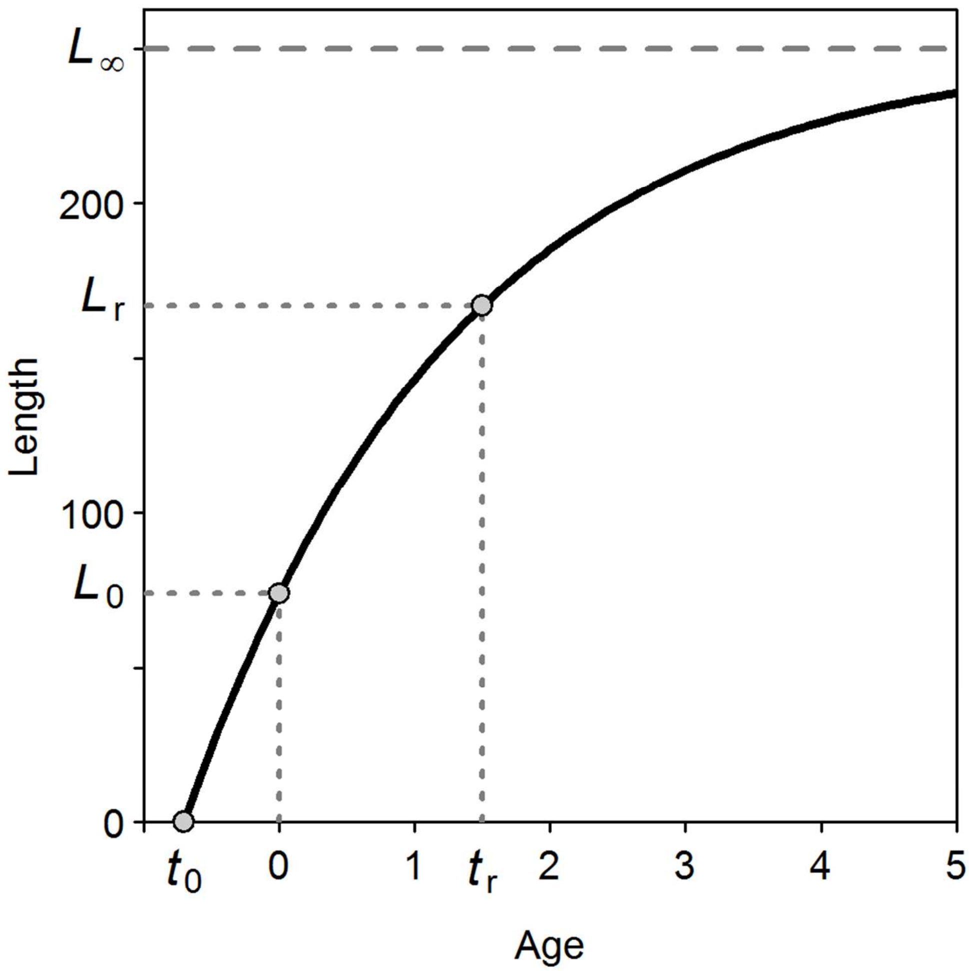
[a]Value derived by rearranging the equation to solve for *t* with a length of 480 mm.

Figure Labels

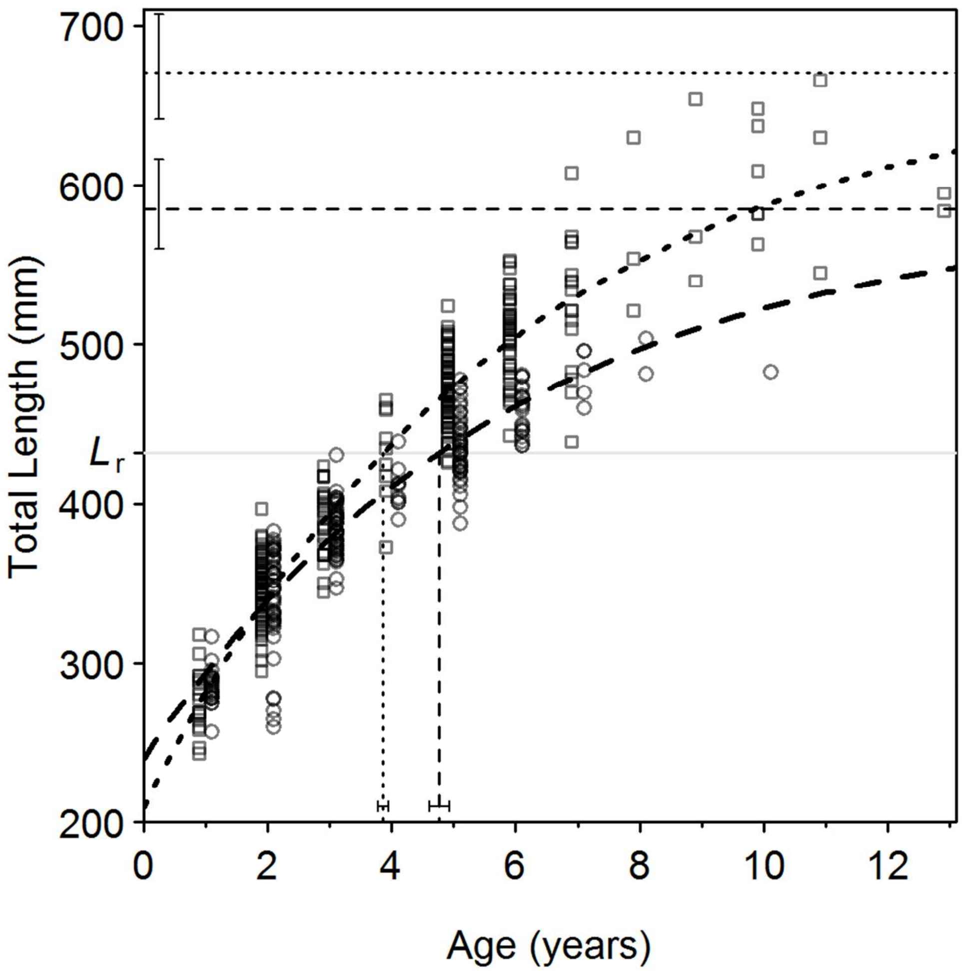
FIGURE. 1. Examples of equations (1)-(3) with L_∞ = 250, K = 0.7, t_0 = -0.7, and L_0 = 74. Three points on the curve are shown with gray circles: $(t_0, 0)$ specifically defines equation (1), $(0, L_0)$ specifically defines equation (2), and (t_r, L_r) generically defines equation (3).

.

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_∞ 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_∞ = 250, K = 0.7, t0 = -0.7, and L0 = 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 1
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_∞ and along the x-axis for t_{432}. The gray horizontal line is at Lr = 432 mm. One 581 mm age-16 male is not shown.
Figure 2
88x88mm (300 x 300 DPI)