

Modeling Annual Growth Variation using a Hierarchical Bayesian Approach and the von Bertalanffy Growth Function, with Application to Lake Trout in Southern Lake Huron

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Abstract.—We compared two models for time-varying growth using a hierarchical Bayesian approach to inference. Both models were derived from the same time-invariant von Bertalanffy growth function (VBGF), and our model comparisons were based on the deviance information criterion. We fit models to length and age data for 15,675 individual lake trout *Salvelinus namaycush* collected during annual spring gill-net surveys in southern Lake Huron from 1976 to 2004. We found that a model structured with both year and cohort effects outperformed a model that only used the same year-specific VBGF parameters for all age-groups. For the better model, the full version that allowed all VBGF parameters to vary over time also outperformed alternatives for which some parameters were constant. Length at age changed greatly over the 1976–2004 period, and in some years different ages changed in different directions. These complex patterns, which were due to the combination of cohort-specific growth and year-specific changes in growth environment, were well captured by our model. When we modeled growth as varying over time, inferences about VBGF parameters differed between the two models, and correlations among VBGF parameters also differed from the usually reported relations based on time-invariant models.

Common applications of the von Bertalanffy growth function (VBGF) are descriptions of average size at age, although many studies have quantified variation in size at age due to either environmental or individual characteristics (von Bertalanffy 1938; Wang and Thomas 1995; Prajneshu and Venugopalan 1999). When interannual growth variations are the major concern, growth modeling and growth comparison are often based on two insufficient approaches: (1) to separate years or (2) to separate year-classes (e.g., Welch and McFarlane 1990; Chen and Mello 1999; Polacheck et al. 2004). When fitting a VBGF separately by year, one presumes that all age-groups in a year have experienced the same growth environment over their past lifespan. When fitting a VBGF separately by cohort, one presumes that growth conditions remain constant among years for a cohort. Both approaches thus restrict changes in parameters in the ways that do not reflect how growth changes among years.

An alternative approach is to model interannual growth of multiple cohorts via year-specific VBGF

parameters, either determined as functions of environmental variables (Millar and Myers 1990; Mallet et al. 1999; Millar et al. 1999) or estimated separately for each year (Szalai et al. 2003). This approach acknowledges that annual growth depends upon how year-specific conditions influence the growth of a given age and size and that size at each age reflects a sequence of growth conditions experienced by a cohort.

We recognize three major concerns for applying this alternative approach. First, using many parameters to obtain near perfect modeling fits, often does not lead to better understanding (McCullagh and Nelder 1989). We need to identify whether annual changes in growth are large enough to warrant inclusion in growth models. Second, parameter estimates can be biased when their covariance is not taken into account (Pilling et al. 2002; Helser and Lai 2004). We need to explicitly address potential correlations among VBGF parameters. Third, VBGF parameters can have different biological meanings when a VBGF is fit to growth increments versus length at age (Kirkwood 1983; Francis 1988; Quinn and Deriso 1999). We need to know whether parameter meaning will be the same when a parameter is allowed to vary among years.

To address the above three major concerns, we expanded the approach of Szalai et al. (2003) and

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developed and compared two expressions of the VBGF in the context of time-varying growth. Both expressions are derived from the same time-invariant VBGF but involve different assumptions such that VBGF parameters could have different meanings. We modified and generalized Szalai et al.'s (2003) approach to the relationships among parameters. They modeled L_{∞} as the primary time-varying parameter, assumed a linear relationship between L_{∞} and K , and estimated the parameters of that relationship. In contrast we allowed each of the VBGF parameters to vary over time and used a hierarchical structure that allows for statistical inferences about the direction and magnitude of any potential correlations among the VBGF parameters. Furthermore, to compare the two models and a number of variants of the best model differing in which parameters varied over time, we used the deviance information criterion (DIC), which is a generalized Akaike information criterion used to compare models for Bayesian analyses (Spiegelhalter et al. 2002; Gelman et al. 2004). The Bayesian approach and the use of DIC is a practical way to make inferences about model parameters and comparisons among models, particularly when models differed both in structure and in what process errors are incorporated.

For our study, we used lake trout *Salvelinus namaycush* in southern Lake Huron as an example. The lake trout was the top native predator in four of the five North American Great Lakes, but all populations were near extirpation by the 1950s (Hansen 1999). The current lake trout population in the main basin of Lake Huron is derived almost entirely from annual release of hatchery yearlings or fingerlings (Wilberg et al. 2002; Johnson et al. 2004; Madenjian et al. 2004). The management goal is to rebuild a self-sustaining population in the lake (Ebener 1998), and the status of the stock has been evaluated by using statistical catch-at-age modeling (Sitar et al. 1999). During the past 40 years of rehabilitation efforts, there has been substantial variation in lake trout growth in most of the Great Lakes (e.g., Elrod et al. 1996; Ferreri and Taylor 1996; Fabrizio et al. 2001). Accurate growth description and interpretation is important in the management process, for it will potentially influence the estimates of a number of critical quantities such as recruitment, mortality, and age-specific fishing selectivity.

Methods

Lake trout length-at-age data.—We analyzed data collected as part of an annual spring survey in the western main basin of Lake Huron (U.S. waters). The survey has been conducted in May and early June every year since 1975 by Michigan Department of Natural Resources (Sitar et al. 1999; Johnson et al.

2004). The survey used multifilament nylon gill nets that were 1.83 m deep and consisted of nine 30.5-m panels. Mesh sizes were 51–152 mm, with graded increments of 13 mm. The nets were set overnight on the bottom across depth contours of 10–50 m. We restricted our analysis to 1976–2004 data for age-4 to age-15 lake trout (1972 and later year-classes) collected from the southern portion of the surveyed region (offshore of the region from Harrisville to Harbor Beach). Observed ages ranged from 2 to 20, but individuals aged over 15 typically made up less than 0.2% of the observations for each year-class. We excluded fish younger than age 4 because we suspected that, on average, lake trout total length at ages 2 and 3 was greater in gill-net samples than in the population, based on examination of body lengths from ages 2–4. Data on length and age included at least 200 lake trout each year, and totaled 15,675 fish for the entire analysis.

Every lake trout captured in the survey was measured (total length; mm) and aged. Nearly all lake trout caught by the survey were of hatchery origin, and they were marked by fin clips before release from hatcheries. Ages of captured fish were determined based on fin clips or coded wire tags (Jefferts et al. 1963; Elrod and Schneider 1986). The few unmarked lake trout had their ages assigned based on scale readings. Overall, errors in age assignment and length-at-age measures were negligible.

Growth models and growth parameters.—We modeled annual length increments based on the von Bertalanffy growth function (VBGF). There were multiple cohorts of fish, and the VBGF parameters were allowed to vary among years. We considered two different models derived from the same Fabens' time-invariant expression of the VBGF (Fabens 1965). The first we call the Fabens year-effect (FYE) model:

$$L_{y,a} - L_{y-1,a-1} = (L_{\infty,y-1} - L_{y-1,a-1}) [1 - \exp(-K_{y-1})] \quad (1)$$

Here, $L_{y,a}$ is the length of age- a fish in the population at the time of spring survey in year y . In our case, it is the median total length rather than the mean because of the lognormal error structure we used (see below). The model describes interannual growth in length for fish in a cohort as a function of the length one year earlier and one age younger. Growth of all cohorts in a given year is influenced by the same year-specific asymptotic length (L_{∞}) and the same year-specific Brody growth coefficient (K). The length for the youngest age recognized by the model is not expressed explicitly in equation (1) but is a third year-specific quantity needed to determine lengths for subsequent ages of

each cohort. We chose this to be length at age 3, L_3 , to be consistent with the parameterization of the next-described model below. We could have started the FYE model at any age before the start of the observed growth, and different choices are simply reparameterized versions of the same model.

We refer to our second model as the Fabens year-and-cohort-effect (FYCE) model, which incorporates an idea that the amount of growth experienced by a cohort when young influences their ability at later ages to realize potential growth:

$$L_{y,a} - L_{y-1,a-1} = (L_{\infty,y-1} - L_{y-1,a-1})[1 - \exp(-K_{y-1,a-1})] \quad (2a)$$

$$K_{y-1,a-1} = -\log_e \left(\frac{L_{\infty,y-1} - L_{3,y-a+3}}{L_{\infty,y-1} - L_{2,y-a+2}} \right) \quad (2b)$$

Here, equation (2a) differs from equation (1) in that K_{y-a} is replaced by $K_{y-1,a-1}$ and incorporates a combination of year and cohort effects, as indicated by equation (2b). Among the three time-varying parameters, L_{∞} , L_3 , and L_2 (length at age 2), only L_{∞} influences growth of all ages in a given year, whereas L_3 and L_2 only influence growth through cohort-specific effects on K . Such a cohort effect and the year-specific K in the FYE model (equation 1) are both assumptions subjected to empirical examination. We formulated the cohort effect so that the same relationship among K , L_{∞} , L_2 , and L_3 was retained, as is the case for the time-invariant VBGF (e.g., He and Stewart 2002; He et al. 2005).

In equation (2b), we could replace L_3 and L_2 by any other pairs of adjacent ages with time-invariant growth (Schnute and Fournier 1980). With time-varying growth, however, only a pair of early ages before subsequent time-varying growth can have the cohort effect we envision. We considered using the alternative pair L_2 and L_1 . By using L_3 and L_2 instead of the alternative, we assumed that the von Bertalanffy growth started at age 2 rather than age 1. We believed a priori that this was a better approximation because hatchery-origin lake trout experienced a substantial environmental transition as yearlings when they were released into Lake Huron, typically in May and June each year. In preliminary fitting of the model, we found that the FYCE model parameterized with L_2 and L_1 produced a much larger (worse) DIC value than when the L_3 and L_2 parameterization was used (see “Model comparisons and consideration of reduced models”).

We modeled among-year variation in the von Bertalanffy parameters through multiplicative errors and allowed potential correlations among time-varying

parameters by basing the errors on a multivariate distribution.

$$\gamma_{i,y} = \tilde{\gamma}_i \exp(\varepsilon_{\gamma_{i,y}}) \quad (3)$$

Here, $\gamma_{i,y}$ represents a time-varying von Bertalanffy parameter, which is determined by the central tendency parameter $\tilde{\gamma}_i$ and the process errors $\varepsilon_{\gamma_{i,y}}$. The $\tilde{\gamma}_i$ is an element of $\tilde{\gamma}$ consisting of $\{L_{\infty}, K, L_3\}^T$ or $\{L_{\infty}, L_2, L_3\}^T$ for the FYE and FYCE models, respectively, where the bar below a symbol denotes a vector. The $\varepsilon_{\gamma_{i,y}}$ is an element of the vector ε_y , which we assumed to be distributed as a multivariate normal with zero mean, such that ε_y approximates $N(\mathbf{0}, \Sigma_y)$. For the FYE model, ε_y is equal to $\{\varepsilon_{L_{\infty,y}}, \varepsilon_{K,y}, \varepsilon_{L_3,y}\}^T$. For the FYCE model, ε_y is equal to $\{\varepsilon_{L_{\infty,y}}, \varepsilon_{L_2,y-1}, \varepsilon_{L_3,y}\}^T$. The FYCE model allowed the process error for $L_{\infty,y}$ to be correlated with process errors for L_2 and L_3 that jointly determined the Brody growth coefficient (K) influencing growth of the youngest observed age (age 4) in year ($y + 1$).

Hierarchical Bayesian approach to inference.—We used a hierarchical Bayesian approach to inference that has been applied previously to growth models in fish by Pilling et al. (2002) and Helser and Lai (2004). In such an approach, inferences are made about a vector of parameters and a vector of hyperparameters, based on their posterior distributions, and these posterior distributions depend upon the likelihood, the prior distributions (priors), and the hyperprior distributions (hyperpriors). We specified the priors, hyperpriors, and likelihood as shown below, and we used Markov chain Monte Carlo (MCMC) methods to approximate the posterior distributions.

The parameters for the Bayesian analysis were not time-varying von Bertalanffy parameters ($\gamma_{i,y}$). Rather, they included those unknown quantities that determined $\gamma_{i,y}$ (equation 3; Table 1). The priors describe belief about possible values for these parameters before the data analysis, and we assumed lognormal distribution for positive random variables and normal distribution for ones that could be either positive or negative. The parameters also included standard deviations for log-transformed individual lengths at every age σ_a , because among-individual variation about the median length for each age and year contributed to the likelihood (below).

Hyperparameters (Table 1) determined the variance-covariance matrix Σ_{ε} , which in turn parameterized the prior for parameters that determined how the VBGF parameters varied over time. We followed Daniels and Kass (1999, 2001) and Barnard et al. (2000) in separating Σ_{ε} into a matrix containing correlations (r_{γ_i, γ_j}) and a diagonal matrix containing standard

TABLE 1.—Bayesian parameters (θ) and hyperparameters (ϕ) used in the growth models, including distributional parameters for priors (D) that are calculated from hyperparameters. Corresponding priors and hyperpriors were either normal (N) or lognormal (LN), sometimes after Fisher’s z -transformation (z) of the original parameter. A variance–covariance matrix, Σ , with a vector of expected values indicates a multivariate distribution. A scalar variance, σ^2 , with an expected value indicates a univariate distribution. Distributional parameters for priors and hyperpriors that were specified a priori are given in Table 2.

Symbol	Type	Description	Priors, hyperpriors, and definition of distributional parameters
$\tilde{\gamma}$	θ	Vector of medians with $(\tilde{L}_\infty, \tilde{K}, \tilde{L}_3)^T$ or $(\tilde{L}_\infty, \tilde{L}_2, \tilde{L}_3)^T$ for the Fabens year-effect (FYE) or Fabens year-and-cohort effect (FYCE) model, respectively.	$LN(\underline{\mu}_{\tilde{\gamma}}, \Sigma_{\tilde{\gamma}})$
$\underline{\epsilon}_y$	θ	Yearly vectors of stochastic process errors corresponding to (L_∞, K, L_3) or (L_∞, L_2, L_3) for the FYE or FYCE model, respectively.	$N(\underline{0}, \Sigma_\epsilon)$
σ_a	θ	Standard deviation of log-transformed individual lengths at age a (one parameter each for ages 4–15).	$LN(\mu_{\sigma_a}, \sigma_{\sigma_a}^2)$
$\sigma_{\epsilon_{\gamma_i}}$	ϕ	Standard deviations for $\underline{\epsilon}_y$, corresponding to (L_∞, K, L_3) or L_∞, L_2, L_3 in the FYE or FYCE model, respectively.	$LN(\mu_{\sigma_{\epsilon}}, \sigma_{\sigma_{\epsilon}}^2)$
r_{γ_i, γ_j}	ϕ	Correlation coefficient between $\epsilon_{\gamma_i, y}$ and $\epsilon_{\gamma_j, y}$. Both γ_i and γ_j can represent any of L_∞, K , and L_3 or L_∞, L_2 , and L_3 for the FYE or FYCE model, respectively.	$z(r_{\gamma_i, \gamma_j}) \sim N(\mu_r, \sigma_r^2)$ $z(r_{\gamma_i, \gamma_j}) = \frac{1}{2} \log_e \left(\frac{1 + r_{\gamma_i, \gamma_j}}{1 - r_{\gamma_i, \gamma_j}} \right)$
Σ_ϵ	D	Variance–covariance matrix used in prior for $\underline{\epsilon}_y$.	$S \cdot R \cdot S$
S	D	Diagonal matrix of SDs used in representing Σ_ϵ in separable form.	$\begin{bmatrix} \sigma_{\epsilon_{\gamma_1}} & 0 & 0 \\ 0 & \sigma_{\epsilon_{\gamma_2}} & 0 \\ 0 & 0 & \sigma_{\epsilon_{\gamma_3}} \end{bmatrix}$
R	D	Correlation matrix used in representing Σ_ϵ in separable form.	$\begin{bmatrix} 1 & r_{\gamma_1, \gamma_2} & r_{\gamma_1, \gamma_3} \\ r_{\gamma_1, \gamma_2} & 1 & r_{\gamma_2, \gamma_3} \\ r_{\gamma_1, \gamma_3} & r_{\gamma_2, \gamma_3} & 1 \end{bmatrix}$

deviations ($\sigma_{\epsilon_{\gamma_i}}$). We used hyperpriors to describe belief about possible values for the components of these two matrices. If the resulting correlation matrix is positive definite, this separation provides independent control of each standard deviation and correlation. When sample size for multivariate observations is relatively small, as was true for the number of years in our study, the separation approach defines weakly informative priors better than the widely used inverted Wishart prior (Daniels and Kass 1999; Barnard et al. 2000; Gelman et al. 2004).

We chose distributional parameters for all priors and hyperpriors to be weakly informative. Thus, the priors were with plausible central tendency values and with moderate probability density at the edge of the range of values we considered possible (Table 2). The specified medians for the prior on $\tilde{\gamma}$ are within the range of point estimates for the corresponding VBGF parameters for lake trout in Great Lakes studies. We used a multivariate normal prior for $\log_e(\tilde{\gamma}_i)$ and followed Pilling et al. (2002) and Helser et al. (2004) in using very large variance and zero covariance. The lognor-

TABLE 2.—Distributional parameters specified for the priors and hyperpriors given in Table 1.

Symbol	Description	Values
$\underline{\mu}_{\tilde{\gamma}}$	Mean vector for the prior on $\log_e(\tilde{\gamma})$ with $\tilde{\gamma} = (L_\infty, K, L_3)^T$ or $(L_\infty, L_2, L_3)^T$ for the FYE or FYCE model, respectively. μ_{L_∞} , expected value for among-year average $\log_e(L_\infty)$. μ_K , expected value for among-year average $\log_e(K)$. μ_{L_2} , expected value for among-year average $\log_e(L_2)$. μ_{L_3} , expected value for among-year average $\log_e(L_3)$.	$\log_e(650)$ $\log_e(0.25)$ $\log_e(150)$ $\log_e(280)$
$\Sigma_{\tilde{\gamma}}$	Variance–covariance matrix used in prior on $\log_e(\tilde{\gamma})$.	$\begin{bmatrix} 0.5 & 0 & 0 \\ 0 & 0.5 & 0 \\ 0 & 0 & 0.5 \end{bmatrix}$
$\mu_{\sigma_a}, \sigma_{\sigma_a}^2$	Mean and variance for the prior on $\log_e(\sigma_a)$.	$\log_e(0.2), 0.5$
$\mu_{\sigma_{\epsilon}}, \sigma_{\sigma_{\epsilon}}^2$	Mean and variance for the hyperprior on $\log_e(\sigma_{\epsilon_{\gamma_i}})$.	$\log_e(0.2), 0.08$
μ_r, σ_r^2	Mean and variance for the hyperprior on z -transformed r_{γ_i, γ_j} .	$0, 2$

TABLE 3.—The log of posterior density, with ignored constants dropped. A log-transformed univariate normal density ($-g_N$) and a log-transformed multivariate normal density ($-g_{MN}$) were used to define each component, including the log likelihood, the log of prior density (priors), and the log of hyperprior density (hyperpriors). See Tables 1 and 2 for definitions of parameters and hyperparameters, and prior values for distributional parameters. Curly braces indicate a list of all parameters of that type.

Description	Equation
Log of posterior density for the vectors of transformed parameters ($\check{\theta}$) and hyperparameters ($\check{\phi}$), given the data \underline{X} . See specification for each of the six components below.	$\begin{aligned} \log_e P(\check{\theta}, \check{\phi} \underline{X}) &= \log_e L(\check{\theta} \underline{X}) \\ &+ \log_e P(\log_e \check{\gamma}) + \log_e P(\{\log_e \sigma_a\}) \\ &+ \log_e P(\{z(r_{i,\gamma_j})\}) + \log_e P(\{\log_e \sigma_{\varepsilon_{\gamma_i}}\}) \\ \check{\theta} &= \{\log_e \check{\gamma}, \{\log_e \sigma_a\}\} \\ \check{\phi} &= \{\{z(r_{i,\gamma_j})\}, \{\log_e \sigma_{\varepsilon_{\gamma_i}}\}\} \end{aligned}$
The negative log of the general univariate normal density, g_N , used for defining the likelihood, a prior component, and two hyperprior components below.	$g_N(x \mu, \sigma^2) = k \log_e \sigma + \sum_{i=1}^k \frac{(x_i - \mu)^2}{2\sigma^2}$
The negative log of the general multivariate normal distribution, g_{MN} , used for defining two prior components below.	$g_{MN}(\underline{x} \underline{\mu}, \Sigma) = \left(\frac{k}{2}\right) \log_e (\Sigma) + \left(\frac{k}{2}\right) \sum_{i=1}^k \left[(\underline{x}_i - \underline{\mu})^T \Sigma^{-1} (\underline{x}_i - \underline{\mu}) \right]$
The negative log likelihood. $L_{y,a,i}$ is the i th individual length for year y and age a ; and $L_{y,a}$ is determined given the model and its parameters.	$-\log_e L(\check{\theta} \underline{X}) = \sum_{a=4}^{a=15} \sum_{y=1976}^{y=2004} g_N [(\log_e L_{y,a,i}) \log_e L_{y,a}, \sigma_a^2]$ <p style="text-align: center;">k varies for a given age in a given year</p>
The negative log prior for transformed median von Bertalanffy growth function (VBGF) parameters, $\check{\gamma}$	$-\log_e P(\log_e \check{\gamma}) = g_{MN}(\log_e \check{\gamma} \underline{\mu}_{\check{\gamma}}, \Sigma_{\check{\gamma}})$ <p style="text-align: center;">$k = 1$</p>
The negative log prior for $\underline{\varepsilon}_y$, the stochastic process errors influencing time-varying VBGF parameters.	$-\log_e P(\{\underline{\varepsilon}_y\}) = g_{MN}(\{\underline{\varepsilon}_y\} \underline{0}, \Sigma_{\varepsilon})$ <p style="text-align: center;">$k = 28$ years for the FYE model $k = 29$ years for the FYCE model</p>
The negative log prior for transformed σ_a , the SD for log-transformed individual lengths at age a .	$-\log_e P(\{\log_e \sigma_a\}) = g_N(\{\log_e \sigma_a\} \mu_{\sigma_a}, \sigma_{\sigma_a}^2)$ <p style="text-align: center;">$k = 12$, for ages 4 through 15</p>
The negative log prior for transformed $\sigma_{\varepsilon_{\gamma_i}}$, the SD for $\varepsilon_{\gamma_i,y}$.	$-\log_e P(\{\log_e \sigma_{\varepsilon_{\gamma_i}}\}) = g_N(\{\log_e \sigma_{\varepsilon_{\gamma_i}}\} \mu_{\sigma_{\varepsilon}}, \sigma_{\sigma_{\varepsilon}}^2)$ <p style="text-align: center;">$k = 3$ in a full model</p>
The negative log prior for transformed r_{γ_i,γ_j} , the correlation coefficient between $\varepsilon_{\gamma_i,y}$ and $\varepsilon_{\gamma_j,y}$.	$-\log_e P(\{z(r_{ij})\}) = g_N(\{z(r_{ij})\} \mu_r, \sigma_r^2)$ <p style="text-align: center;">$k = 3$ in a full model</p>

mal prior for σ_a had a 95% probability interval from 0.05 to 0.80, which substantially exceeded the range of point estimates we knew of for lake trout in the Great Lakes. The hyperprior for r_{γ_i,γ_j} produced a 95% probability interval nearly between -1 and $+1$. We had little information on annual variations in the von Bertalanffy parameters, and with a truly flat prior for the standard deviations of process errors, neither FYE nor FYCE models were stable in convergence. We therefore specified the lognormal hyperprior for $\sigma_{\varepsilon_{\gamma_i}}$, where both values near zero and “large enough” were within a 95% hyperprior. The “large enough” means that for such a $\sigma_{\varepsilon_{\gamma_i}}$, there is a 95% prior probability interval for $\varepsilon_{\gamma_i,y}$ that allows for a doubling or halving of an annual value from the median of the prior for a von Bertalanffy parameter. For example, with an among-

year median of 280 mm for L_3 , such a prior for the $\varepsilon_{\gamma_i,y}$ leads to a discernible (nonnegligible) prior probability for the annual L_3 as large as 560 mm, which exceeds the mean length we observed at age 4 for all but 1 year.

We wrote the complete log posterior density as sum of the log likelihood, the log of the priors, and the log of the hyperpriors (Table 3). It is convenient to work on the log scale when conducting MCMC simulations to determine the joint posterior distribution of parameters and hyperparameters. The likelihood $L(\check{\theta} | \underline{X})$ is about the vector of parameters $\check{\theta}$ given a set of data \underline{X} . We based the likelihood on a lognormal distribution so that $L_{y,a,i}$ approximates $LN[\log_e(L_{y,a,i}), \sigma_a^2]$, where $L_{y,a,i}$ is the i th observation on individual lengths for age a and year y ; and $L_{y,a}$ is from equation (1) or (2) and depends on all the parameters except for σ_a^2 . In MCMC

simulations of the posterior densities, we used the vectors of transformed parameters ($\check{\theta}$) and hyperparameters ($\check{\phi}$) based on their assumed probability distributions.

Approximation of the posterior distribution.—We summarized marginal posterior distributions on back-transformed scales based on the mean and 95% equal-tailed probability intervals for the transformed parameters and hyperparameters. Note that transformed percentiles are invariant to the transformation, whereas the transformed mean will not necessarily be the mean on the transformed scale. In the special case of the lognormal distribution, the antilog back-transformation of the mean for the log-scale (normal) variable is the median, which is why $L_{y,a}$ in equations (1) and (2) represents the median. In general, however, our posterior distributions may not be exactly lognormal as assumed. We maintained consistency in our summaries of the posterior distributions. For Fisher's Zeta transformation of correlation coefficients, the back-transformation is hyperbolic tangent.

We approximated the posterior distribution using MCMC simulation with the Metropolis-Hastings algorithm, as implemented in AD model Builder (Otter Research 2001). For each chain we saved values for all transformed parameters and hyperparameters, as well as the negative log likelihood associated with that set of parameters and hyperparameters. The chain length for the MCMC simulations was 1,000,000 cycles for each model. For computing time and data management reasons we thinned the chains by saving every 200th cycle. We dropped a burn-in period of the initial 1,000 values of the thinned chain, so that our inferences were based on a saved chain of 4,000. The burn-in period was not determined separately for each chain (Cowles et al. 1999) but was the same for all chains that were determined to be adequate (based on applying the diagnostics described below).

For each model and for each parameter, hyperparameter, and the summary variable of negative log likelihood (Cowles and Carlin 1996), we calculated Gelman and Rubin convergence statistics, based on three parallel chains starting at randomly selected locations for each parameter or hyperparameter (Gelman et al. 2004). To identify any unusual structure that might indicate a poorly defined posterior but was not accounted for by the Gelman and Rubin convergence statistics, we examined trace plots, chain autocorrelation functions, and effective sample sizes for all models (Thiebaut and Zwiers 1984). We verified that the univariate distribution plots were similar among four subchains of equal length, such that the saved chains were not unduly influenced by a long transient.

For our best model, we also compared observed

means of log-transformed length at age to posterior prediction intervals. To generate these intervals we first generated expected log-scale lengths at age for each age and year corresponding to the parameters from each cycle of the MCMC chain. We then added observation error to each of these expected values and saved the results. The observation error was a random draw distributed as $N[0, \sigma_a^2/n]$, where n is the number of observations for a given age and year, and σ_a^2 is the observation error variance parameter for that MCMC cycle. We calculated 50% and 90% posterior prediction intervals as the equal-tailed intervals that contained 50% or 90% of these saved results, respectively.

Model comparisons and consideration of reduced models.—We used DIC to compare alternative models; a model with the lowest DIC should do the best at predicting out-of-sample observations (Spiegelhalter et al. 2002; Gelman et al. 2004):

$$DIC = -2\overline{\log_e[L(\check{\theta}|M)]} + n_e \quad (4)$$

$$n_e = -2\log_e[L(\check{\theta}|M)] - \left\{ -2\log_e[L(\bar{\theta}|M)] \right\}$$

Here, $\overline{\log_e[L(\check{\theta}|M)]}$ is average log likelihood over the MCMC chain given model M ; $\log_e[L(\bar{\theta}|M)]$ is the log likelihood calculated at the mean values for the transformed parameters and hyperparameters, which were over the MCMC chain with model M ; and n_e is a measure of model complexity, which can be interpreted as the effective number of parameters.

We first considered the full FYE and FYCE models and selected the model with the lowest (best) DIC. We then compared the selected full model with its reduced versions, where one or more of the von Bertalanffy parameters were assumed to be constant over time. For the FYCE model, we only considered three reduced versions that allowed no parameters to vary; only L_∞ to vary; or only L_2 and L_3 to vary in combination. We did not consider other reduced versions where only L_2 or L_3 varied, with or without time-varying L_∞ , because L_2 and L_3 operated together in providing the cohort effects on the growth coefficient K . Process errors for all reduced models were still assumed to be lognormal. The correlations (r_{γ_i, γ_j}) and standard deviations ($\sigma_{\varepsilon \gamma_i}$) retained the same hyperpriors as for the corresponding r_{γ_i, γ_j} and $\sigma_{\varepsilon \gamma_i}$ in the full Σ_ε . The reduced Σ_ε is a scalar variance when only one von Bertalanffy parameter varies and is absent if none varies.

Results

Model Performance

For the negative log likelihoods of the models and those parameters and hyper-parameters that determined median length at age for each year, the Gelman and

TABLE 4.—Model comparisons based on deviance information criteria (DIC; equation 4). Change in DIC (Δ DIC) is the difference between the DICs for a given model and the “best” model (the lowest DIC); n_e is the effective number of parameters; and ES indicates the effective sample size for the negative log likelihood. The negative log likelihood is a summary variable saved from Markov Chain Monte Carlo chains and used for DIC and n_e calculations (equation 4).

Model	Time varying	DIC	n_e	Δ DIC	ES
FYE	All	-33,378.30	79.2	33.7	2,585
FYCE	All	-33,412.00	76.4		1,223
	L_2, L_3	-33,331.00	59.5	81	1,889
	L_∞	-32,373.80	40.1	1,038.2	3,573
	None	-29,585.00	15.2	3,827	4,000

Rubin statistics were all close to 1.0 (i.e., within 0.001). The minimum effective sample size was larger than 500 and was typically larger than 1,000 (Tables 4, 5). We conclude that the saved MCMC chains were sufficiently long. We saw no indications in our examinations of the trace plots, autocorrelation function, and subchains that there might be a problem with convergence or an initial transient. The autocorrelation function for a given quantity was typically close to zero by lag 8 of the saved chain.

The 95% posterior probability intervals for parameters and hyperparameters (Table 5; Figure 1) can be compared with the 95% prior-probability intervals, as

TABLE 5.—Posterior distributions and effective sample size (ES) for von Bertalanffy parameters, and SDs and correlations among their process errors for the full Fabens year-and-cohort effect (FYCE) and Fabens year-effect (FYE) models. The growth coefficient K^* for the FYCE model is based on an average among years and lake trout ages, and the value for a given age and year was calculated from equation 2b. We assumed that the K from the FYCE model was distributed as lognormal as in the FYE model. Markov Chain Monte Carlo (MCMC) distributions were generated on transformed scales based on corresponding probability distributions (see text), and we report the back-transformation of the MCMC mean and equal-tailed 95% probability intervals (PI).

Parameter group	Model	Corresponding parameter	Back-transformed mean for parameter	PI		ES
				2.50%	97.50%	
Central tendency \bar{y}	FYCE	L_∞ (mm)	787	770	807	2,265
		L_2 (mm)	219	191	251	925
		L_3 (mm)	385	370	400	1,136
		K^*	0.333	0.315	0.351	548
	FYE	L_∞ (mm)	798	766	835	946
		K	0.311	0.254	0.378	1,211
L_3		377	358	396	1,633	
Correlation r_{y_i, y_j}	FYCE	$L_\infty:L_2$	-0.265	-0.621	0.187	1,568
		$L_\infty:L_3$	-0.274	-0.634	0.175	1,947
		$L_2:L_3$	0.908	0.797	0.957	727
	FYE	$L_\infty:K$	-0.791	-0.917	-0.514	1,941
		$L_\infty:L_3$	0.398	-0.163	0.742	1,581
		$K:L_3$	-0.689	-0.857	-0.360	1,338
SD $\sigma_{\varepsilon_{y_i}}$ for stochastic process errors ε_{y_i}	FYCE	L_∞	0.056	0.040	0.080	2,445
		L_2	0.320	0.251	0.411	1,896
		L_3	0.094	0.074	0.120	2,208
	FYE	L_∞	0.100	0.075	0.132	987
		K	0.484	0.363	0.645	1,228
		L_3	0.124	0.094	0.166	1,133

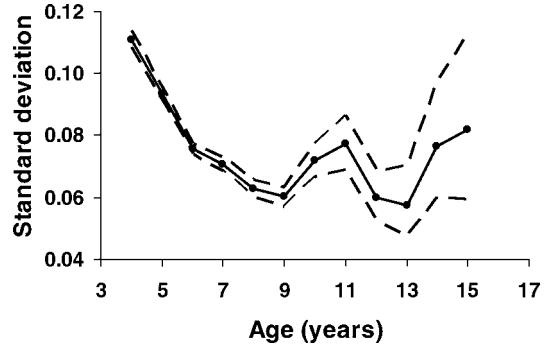


FIGURE 1.—Posterior means (dots) and 95% posterior probability intervals (dashed lines) for SDs of log-transformed individual lake trout lengths at ages 4–15, based on the Fabens year-and-cohort-effect (FYCE) model as applied to fish in southern Lake Huron.

defined by distributional parameters in Table 2. The comparison suggested that the data largely determined posterior distributions for parameters and hyperparameters. For the von Bertalanffy parameters, the posterior medians were larger than the prior medians, and were more concentrated within the 95% prior probability interval. For log-transformed individual lengths at age, the posterior standard deviations σ_a at some old ages were near to the lower end of the 95% prior interval, but these posteriors were not noticeably

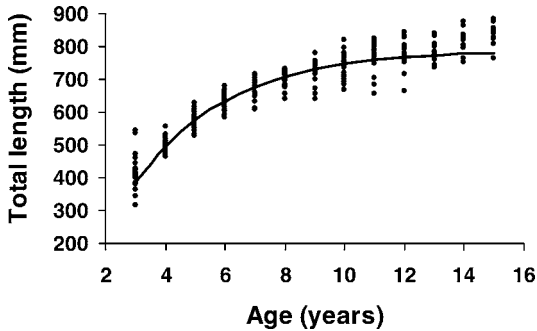


FIGURE 2.—Observed (dots) versus modeled among-year values for length at age (line) based on the full Fabens year- and-cohort-effect (FYCE) model as applied to lake trout in southern Lake Huron. Observed values are antilogs of annual mean $\log(\text{length at age})$. Modeled values are the antilogs of the posterior means for among-year averages of $\log(\text{length at age})$.

altered when we changed the 95% prior interval from (0.05, 0.80) to (0.02, 0.40) by altering the median parameter from $\log_e(0.2)$ to $\log_e(0.1)$. Similarly, for the process errors in L_3 and L_∞ , the posterior standard deviations were centered within the lower end of the 95% prior interval; for the process errors in L_2 , the posterior standard deviation was centered within the upper end of the 95% prior interval; and for the process errors in K , the posterior standard deviations were centered beyond the upper end of the 95% prior interval. We evaluated alternative priors that were more consistent with the initially obtained posteriors. If the priors were dominant in determining the initial posteriors, this change should have led to a substantial additional shift in the posteriors. When, for example, we altered the median and standard deviation for the priors from the values in Table 2 to $\log_e(0.1)$ and 0.08 for L_3 and L_∞ ; $\log_e(0.25)$ and 0.15 for L_2 ; and $\log_e(0.3)$ and 0.3 for K , the posteriors were only slightly altered (i.e., posterior means were within 11% and changes were typically less than 6%).

Model Comparison and Posterior Prediction

The DIC was much larger (worse) in the FYE model than the FYCE model, and the full FYCE model was far superior over its reduced versions based on the same criteria (Table 4). Thus, the model that involves both year-specific and cohort-specific effects on the VBGF parameters and allows all of these parameters to vary among years outperformed the alternatives. The overall model complexity was less than was indicated by the nominal 108 parameters for the full FYCE model because the effective number was 77. This lower number is largely a consequence of the assumption that year-specific process errors came from a common

probability distribution. The effective number of parameters per year of data was 2.7, including all parameters and hyperparameters that were required regardless of our time series length. Only 1.9 effective parameters were added for each additional year of data, although there were three process errors each year in the model.

From the full FYCE model, the antilog of posterior means for the among-year averages of \log length at each age was similar to those from a model with constant growth parameters. These average values described the general growth pattern well but ignored the observed year-to-year variation in size at age (Figure 2). There was some apparent lack of fit for ages 14–15, where the observed values tended to exceed the average modeled value. For each age and year, the modeled length at age (antilog of posterior mean \log length at age) was consistent with observed antilog of average \log length at age. Figure 3 show the excellent match between observed and modeled length at age for ages 4 through 10. For ages 4–9, which contributed most of the data, 57% and 90% of observed lengths at age were in the 50% and 90% posterior predictive intervals, respectively (Table 6). Although the percentages within the posterior predictive intervals were modestly below the expected percentages for ages 10–15, this was caused by the observed variation being larger than was modeled rather than by modeled values being consistently less than observed values. Observations were often missing for these oldest ages. Thus, the apparent lack of fit for older fish in Figure 2 actually appears to result from not accounting for time-varying growth.

The observed dynamics and trends differed among age-groups, indicating the combined effect of cohort-specific growth and year-to-year changes in growth environment. Age-8 and older fish generally had stable length at age until the late 1990s, when a decline and subsequent increase occurred. Younger fish showed declines in size at age over most of the time series, although there was a less marked decline for age-4 fish than the other ages. All ages showed some increase in size at age near the end of the time series, the increase occurring earlier for younger ages.

Inferences for Parameters and Hyperparameters

Inferences for the FYE and FYCE models were similar for some parameters and hyperparameters and different for others. From both models, the inferences about among-year medians for the von Bertalanffy growth parameters were similar (Table 5). The standard deviations for \log -transformed length at age decreased from age 4 to age 9, then fluctuated at older ages, and the patterns were also nearly identical between the

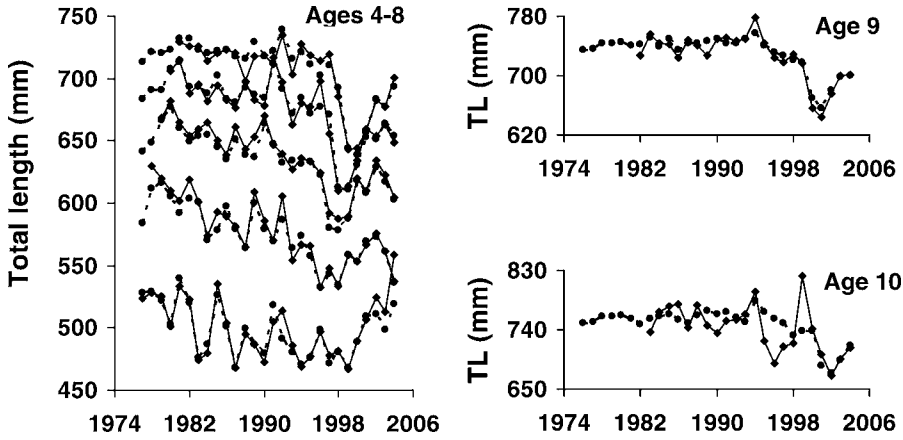


FIGURE 3.—Observed (diamonds) and modeled (dots) values for lengths at ages 4–8 (left panel) and 9–10 (two right panels) for lake trout in southern Lake Huron, 1976–2004, based on the full Fabens year-and-cohort-effect (FYCE) model. Observed values are antilogs of mean $\log(\text{length at age})$. Modeled values are the antilogs of the posterior means for $\log(\text{length at age})$.

FYCE and FYE models (Figure 1 only shows the results from the FYCE model). Interannual variations in the von Bertalanffy parameters were much larger for the FYE model than the FYCE model. This is indicated by the larger standard deviations associated with interannual variation for L_∞ and K (Table 5) and by greater interannual variation in K for the FYE model than the average (over ages) calculated K for the FYCE model (Figure 4). The variation for year-specific K from the FYE model was even larger than that for age-specific K from the FYCE model (Figure 4b). For the FYE model, the annual growth coefficients K were negatively correlated with the annual L_3 and L_∞ , whereas the posterior 95% probability interval for the correlation between L_3 and L_∞ overlapped zero (Table 5). For the FYCE model, L_2 and L_3 were positively correlated with each other, whereas the 95% posterior probability intervals for their correlation with L_∞ overlapped zero (Table 5). The among-age average K for the FYCE model seemed to be unrelated to L_2 and L_3 , and this

TABLE 6.—Percentage of observed log-scale mean lake trout length (mm) at age and year, which were within their respective posterior prediction intervals from the Fabens year-and-cohort-effect model.

Age	Number of observations	Posterior prediction interval	
		50%	90%
4	28	60.7	96.4
5	27	51.9	81.5
6	26	69.2	88.5
7	25	52.0	88.0
8	24	58.3	95.8
9	23	47.8	91.3
10–15	94	45.7	83.0

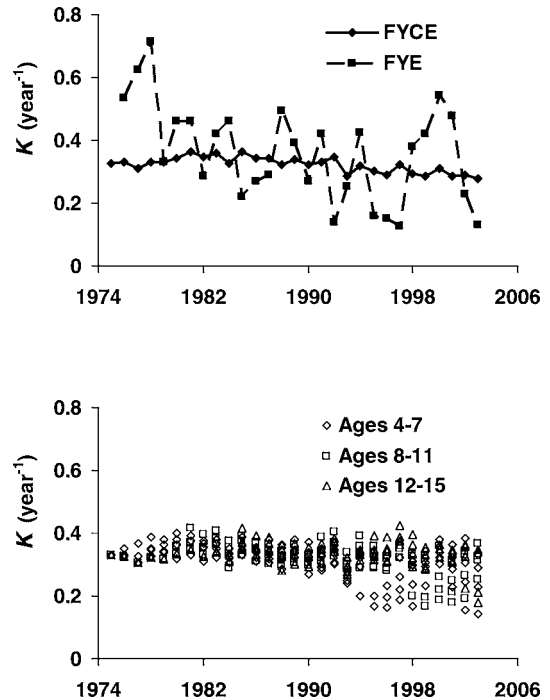


FIGURE 4.—Values for the time-varying growth coefficient, K (per year), based on the Fabens year-effect (FYE) and Fabens year-and-cohort-effect (FYCE) models as applied to lake trout in southern Lake Huron: (upper) antilogs of posterior means for $\log_e(K)$, which for the FYCE model was calculated as an annual average over age-specific values for the given year; (lower) age-specific values for the antilogs of posterior means for $\log_e(K)$, based on the FYCE model.

average K showed a negative correlation with the year-specific L_∞ from 1975 to 1993, after which the relationship seemed to break down (Figure 5). There were substantial decreases in both L_∞ and K for the period from 1994 to 2003 (Figure 5b, c).

Discussion

We demonstrated methods that explicitly acknowledge the interaction between cohort-specific growth and year-to-year changes in growth conditions, and showed that these methods can dramatically improve how well growth models fit length-at-age data. In southern Lake Huron, lake trout growth showed considerable annual variations. A conventional way to model such time-varying growth is to treat length at age within a year as a growth trajectory that can be generated from a model with year-specific parameters. In our preliminary investigations, however, this traditional method led to much worse modeling fits than either the FYCE or FYE models. The comparison suggests that when annual growth variations are substantial, it is critical to account for two effects of size at age of a cohort in the previous year. First, if fish were large for their age in the previous year, it is likely they will remain large for their age after another year of growth. Second, the growth increment itself will typically be a function of the starting size.

Our identification of “best” models was empirical, and it is premature to conclude that the full FYCE model generally best describes growth of the Great Lakes lake trout, or growth of fish in general. In our application, we modeled observed length at age from 1976 through 2004, whereas in many early years the 1972 year-class was the oldest cohort because lake trout stocking to the lake began in the early 1970s. Similar data structures also arise when evaluating growth from back-calculated growth increments. With other kinds of data, where all ages are present in the first year of annual surveys, the FYCE model would require two additional cohort specific parameters for each partial cohort included in the analysis. In these situations, the FYE model should be much easier to use than the FYCE model and may be advantageous by requiring fewer parameters. The relative performance of a range of models should continue to be evaluated when these models are applied to different data sets. Given the data available in our application, our results provided support for the idea that growth at very young ages influences a fish cohort to annually realize potential growth in future growth environments.

We also recommend that analysts consider additional variants of the models we used. For example, in preliminary analyses we modeled the process errors as multivariate autoregressive processes and allowed for

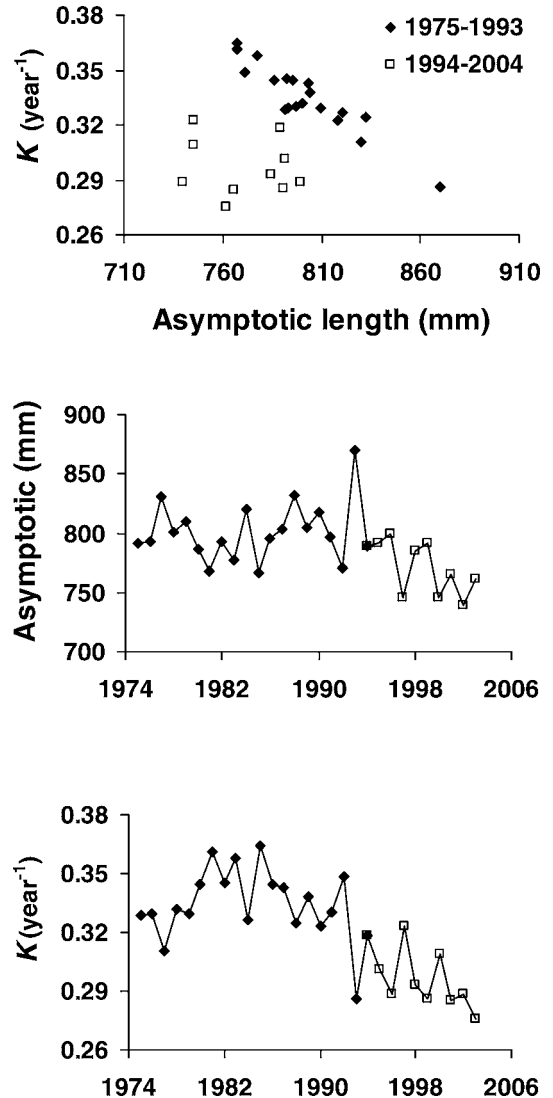


FIGURE 5.—Time-varying asymptotic length (mm) and growth coefficient K (per year) based on the Fabens year-and-cohort-effect (FYCE) model as applied to lake trout in southern Lake Huron. Shown are the antilogs for the posterior means of $\log_e(K)$ (lower panel) and $\log_e(L_\infty)$ (middle panel). $\log_e(K)$ was calculated as an annual average over age-specific values for a given year.

autocorrelations in the parameters. We abandoned this approach because the alternative models did not substantially alter DIC or other modeling results; also, the posteriors for autocorrelations were sensitive to the priors, although the posteriors for other quantities were not. With other data sets, however, incorporating such elaborations might improve model fits. Furthermore, we only modeled changes in growth and length at age

among years and assumed that age-specific variances for length at age were constants among years. This assumption should be tested in future studies when there are sufficient data for most ages and years in a time series.

Differences in annual variations of L_∞ and K were large between the FYCE and FYE models, suggesting that the two parameters, particularly K , might have different meanings in different models. A purely empirical application of growth models often presumes that the primary purpose is to obtain reliable estimates or predictions of size at age over time. A goal of using the von Bertalanffy growth function, however, is often to make use of parameter estimates in other models or other practical applications. The von Bertalanffy growth parameters, such as L_∞ and K , have been used to compare populations or species (Ricker 1979), quantify random variations in length at a given age (Prajeshu and Venugopalan 1999), provide a prior value for natural mortality (Pauly 1980), predict critical age or length for maximum biomass (Deriso 1987), estimate age or length at 50% of maturity (Roff 1984; Jensen 1996; He and Stewart 2001, 2002), and assess extinction risk (Musick 1998). In these contexts, one should be aware of potential differences in parameter meanings, depending upon the model and procedure used when parameters were estimated. For example, with the Pauly (1980) equation, using year-specific von Bertalanffy parameters from the FYE model would lead to nonsensical estimates of annual variation in natural mortality.

Estimated correlations among time-varying growth parameters also suggested different parameter meanings. The negative correlation between K and L_∞ from the FYE model was consistent with findings from the conventional use of the VBGF. In contrast, the results from the FYCE model showed that a negative relationship or no relationship were both possible. The FYE model maintains that all ages have the same growth coefficient (K), as is true for the time-invariant model. The FYCE model maintains the same mathematical relationship among the growth coefficient (K), early growth, and asymptotic length as does the time-invariant model. Such a mathematical relation leads to different ages having different K values in any given year under the condition of time-varying growth, and a summary annual value for K is actually an average among ages. It is not surprising that the FYE model appears to allow K to vary more freely than the FYCE model.

Furthermore, we found some differences in how the VBGF parameters were correlated with one another between models and some divergence with literature reports on correlation among these parameters. For the

FYE model, the negative correlation between K and L_3 may be a new observation. In contrast, we did not find strong evidence of L_2 and L_3 being correlated with the among-age average K for the FYCE model. In the conventional time-invariant VBGF or Ford–Walford plot, the correlation should be positive because rapid growth and large size at young age will lead to small Ford–Walford slope and large K that allows for rapid approach to the asymptotic length (e.g., He and Stewart 2002; He et al. 2005). To some extent, our results suggest that care is needed when equating among-population correlations among growth parameters with temporal correlations of the parameters within populations.

For both the FYE and FYCE models, the posterior distributions do not suggest that size at young ages is strongly correlated with asymptotic length. These results are consistent with the idea that the interactions between fish growth and environment may involve stage-specific differences (e.g., He and Stewart 2002; He et al. 2005).

Modeling time-varying growth provides both a new foundation and challenges for growth comparisons. When there is a combination of cohort-specific growth and year-to-year changes in growth conditions, it will often be subjective and inadequate to represent the long-term pattern using length at one or two selected ages. This is partially because length at age involves growth history from past conditions and can show different patterns for different ages. On the other hand, confusion can result from examining patterns in observed mean length at all ages, without use of a model for the growth process. Effects of initial size and temporal variations in growth conditions have proven hard to disentangle this way and can be obscured by variations in sample sizes (He et al. 2005). In southern Lake Huron, we observed sharp declines in length at age for ages 6–8, beginning in the mid-1990s, followed by a fairly sharp increase in length at these ages by the end of 1990s (Figure 3). We attribute the recent increase in length at age to increased length at the youngest ages. Our analysis strongly suggests that growth conditions for fish older than age 4 did not improve later in the time series because our estimates of average K and asymptotic length decreased rather than increased. Similar conclusion might have been reached by using other approaches, but a comprehensive synthesis will, at least implicitly, invoke a time-varying growth model. Using a formal approach to modeling time-varying growth offers the advantage of an objective basis for studying how growth changed over time and will allow for rigorous temporal and spatial comparisons of growth differences.

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