Journal of Great Lakes Research Supplement xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Modeling spatiotemporal variabilities of length-at-age growth characteristics for slow-growing subarctic populations of Lake Whitefish, using hierarchical Bayesian statistics

Xinhua Zhu *, Ross F. Tallman, Kimberly L. Howland, Theresa J. Carmichael

Fisheries and Oceans Canada, Central and Arctic Region, Freshwater Institute, 501 University Crescent, Winnipeg, MB, R3T 2N6, Canada

ARTICLE INFO

Article history:
Received 10 May 2015
Accepted 21 August 2015
Available online xxxx

Communicated by Bruce Hanna

Index words:
Variability
Growth
Resilience
Subarctic great lake
Cumulative impact
Lake Whitefish

ABSTRACT

Though Lake Whitefish are ecologically, culturally and economically important to aboriginal communities in the Northwest Territories, Canada, growth characteristics of the fish populations have not received extensive interpretations, resulting in a lack of quantitative information to support fisheries management efforts in subarctic great lake systems. The overall objective of this study is to investigate spatiotemporal variations of growth characteristics of Lake Whitefish populations in Great Slave Lake (GSL) from 1972–2009. Using hierarchical Bayesian statistics, we structured four candidate growth models: generalized (GGM), logistic (LGM), Gompertz (PGM), and von Bertalanffy (VBM), with four parameterization scenarios combining all possible options of varying or constant L_∞ and K. In terms of deviance information criterion (DIC) and multimodel inference (MMI), the plausibility of the candidate models was evaluated to select the best combinations of growth models and the parameter scenarios. The GGM with varying L_∞ and K best delineated the fish growth characteristics in almost all areas of GSL, while the fish growth model parameterized with constant L_∞ and varying K performed best in the shallow western basin. The VGM where L_∞ and K were varied partially described fish growth in the shallow waters. Applying the MMI-based growth analysis, we found that smaller and slower-growing fish were mainly distributed in deep waters, while larger and faster-growing fish inhabited shallow waters. These spatiotemporal variations of fish growth characteristics have been attributed to the presence of coupled impacts derived from both climate-driven and anthropogenic events.

Introduction

Growth is a continuous additive process that incorporates two opposing ecophysiological processes, anabolism and catabolism, over a descriptive time interval (von Bertalanffy, 1938; Brett, 1979). Accurate estimates of growth parameters, associated with the descriptive changes in the time-specific length or weight of a fish, are essential for monitoring many aspects of fish population status (Hilborn and Walters, 1992), assessing fisheries regulations and management options (Weatherley and Gill, 1987; Quinn and Deriso, 1999), and implementing bio-manipulation of ecotrophic transfer efficiencies in aquaculture (Jobling, 2002). Together with the underlying changes in size-at-age information, these aspects of relative or allometric growth characteristics of fish populations may vary temporally between spatially discrete populations. This may ultimately influence the assessment of various demographic attributes, such as mortality, maturity, and recruitment, as well as management decisions against environmental regime shifts and cumulative impacts from increasing anthropogenic activities (Huxley, 1932; Ricker, 1975; Weatherley and Gill, 1987; Neill et al., 2004). Given the spatiotemporal variations of size-at-age for a studied population, for instance, it is possible to compare the fish population growth performance with other populations at different temporal and spatial scales. Furthermore, by incorporating these fish growth characteristics into fisheries management practices, harvest strategies can be optimized by balancing individual growth, population biomass, recruitment and mortality aspects of the studied fish populations (Jobling, 2002; Isely and Grabowski, 2007).

To explore fish growth characteristics, several sets of numerical expressions of time-specific length and weight measurements have been conventionally chosen, including the von Bertalanffy growth models (VBM; von Bertalanffy, 1938), Gompertz growth model (PGM; Gompertz, 1825), logistic growth model (LGM; Ricker, 1975) and generalized von Bertalanffy growth model (GGM; Pauly, 1979). Among these, VBM is the most commonly selected, given two model-related assumptions. The first assumption is that the selected model is the best choice. However, Gamito (1998) suggested that young fish growth

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* Corresponding author. Tel: +1 204 983 7795.
E-mail address: Xinhua.Zhu@dfo-mpo.gc.ca (X. Zhu).

http://dx.doi.org/10.1016/j.jglr.2015.08.013

Please cite this article as: Zhu, X., et al., Modeling spatiotemporal variabilities of length-at-age growth characteristics for slow-growing subarctic populations of Lake Whitefish, using hierarchical Bayesian statistics, J. Great Lakes Res. (2015), http://dx.doi.org/10.1016/j.jglr.2015.08.013

can be better described by the parabolic PGM, and that VBM performs better for older fish. The second assumption is that population-specific growth model parameters, Brody growth rate K and asymptotic length L_∞, are time invariant, provided that life history traits of fish growth vary in a consistent fashion (Jobling, 2002). However, many studies have documented that the traditional sets of VBM under these assumptions can often under-represent biological responses to spatiotemporal variations in population abundance, mortality, exploitation, and environmental conditions (Chen and Mello, 1999; Neill et al., 2004). It is unknown whether the selected growth models are robust enough to fit these types of data, and model uncertainties may be amplified if there is incomplete information on the population and surrounding environmental conditions (Francis and Shotton, 1997). It is therefore necessary to extend VBM-based simulations to either incorporate environmental variability (Mallet et al., 1999; Millar et al., 1999) or switch to the time-varying growth characteristics of the fishes under investigations (Chen and Mello, 1999; Szalai et al., 2003; He and Bence, 2007).

Lake Whitefish, *Coregonus clupeaformis*, is a commonly exploited coldwater salmonid that distributes extensively throughout North American freshwater ecosystems, from Atlantic coastal watersheds westward and northward across Canada and Alaska (Scott and Crossman, 1998). Since the inception of commercial fisheries in Great Slave Lake (GSL) in the mid-1940s, the annual commercial harvest for northern populations of Lake Whitefish in GSL alone peaked at about 1.7 million kg during the 1960s, before diminishing to around 416 thousand kg in 2009–2010 (Zhu et al., 2015). The pronounced variations of the fisheries production were synchronized with the decline of Lake Trout, *Salvelinus namaycush,* in the early 1970s and thereafter adjustments in minimum gillnet mesh sizes (Day, 2002; Read and Taptuna, 2003; Tallman and Friesen, 2007). To manage GSL commercial fisheries, a portion of the total annual quota is allotted to one of six administrative areas (Fig. 1). Lake Whitefish is assumed to be consisted of discrete stocks across the areas, but without genetic analyses until now. Recognizing the tremendous fluctuations of the fish production and importance of fisheries management in GSL, collection of biological data on fish by individual areas has constituted a long-term routine activity for monitoring commercial fish stock status (Rawson, 1949, 1951; Healey, 1975), spatial movement (Keleher, 1963), and exploitation (Healey, 1975; Read and Taptuna, 2003).

In this study, we aimed to assess 1) what type of growth model is the most appropriate to describe the growth characteristics of Lake Whitefish in GSL, and 2) what kind of hierarchical model scenarios, constant or time-varying, should be used to parameterize the selected model(s) for the slow-growing Lake Whitefish in GSL. To approach the overall objectives, we integrated the fish biological dataset collected over administrative areas from 1972–2009, and standardized the otolith-based age estimates from the scale ages to evaluate the spatiotemporal variations of the length-at-age attributes. We then applied hierarchical Bayesian statistics (Carlin and Louis, 2009) to construct multiple sets of length-at-age growth models for GSL Lake Whitefish. Applying deviance information criterion (DIC) and multimodel inference (MMI) approaches (Burnham and Anderson, 2002; Anderson, 2008), we aimed to select the best working models and evaluated robust estimates of the growth parameters of interest (Katsanevakis and Maravelias, 2008) where the available data supported more than one model.

Materials and methods

Study area: GSL is situated between 61–63° N and 109–117° W, in the southwest part of the District of Mackenzie, Northwest Territories, Canada (Fig. 1). The surface area of the lake is 28.57×10^3 km^2 with a drainage area of 958×10^3 km^2, ranking it the ninth-largest lake (by surface area) in the world (Bond, 1975; Munawar, 1987). The lake stretches

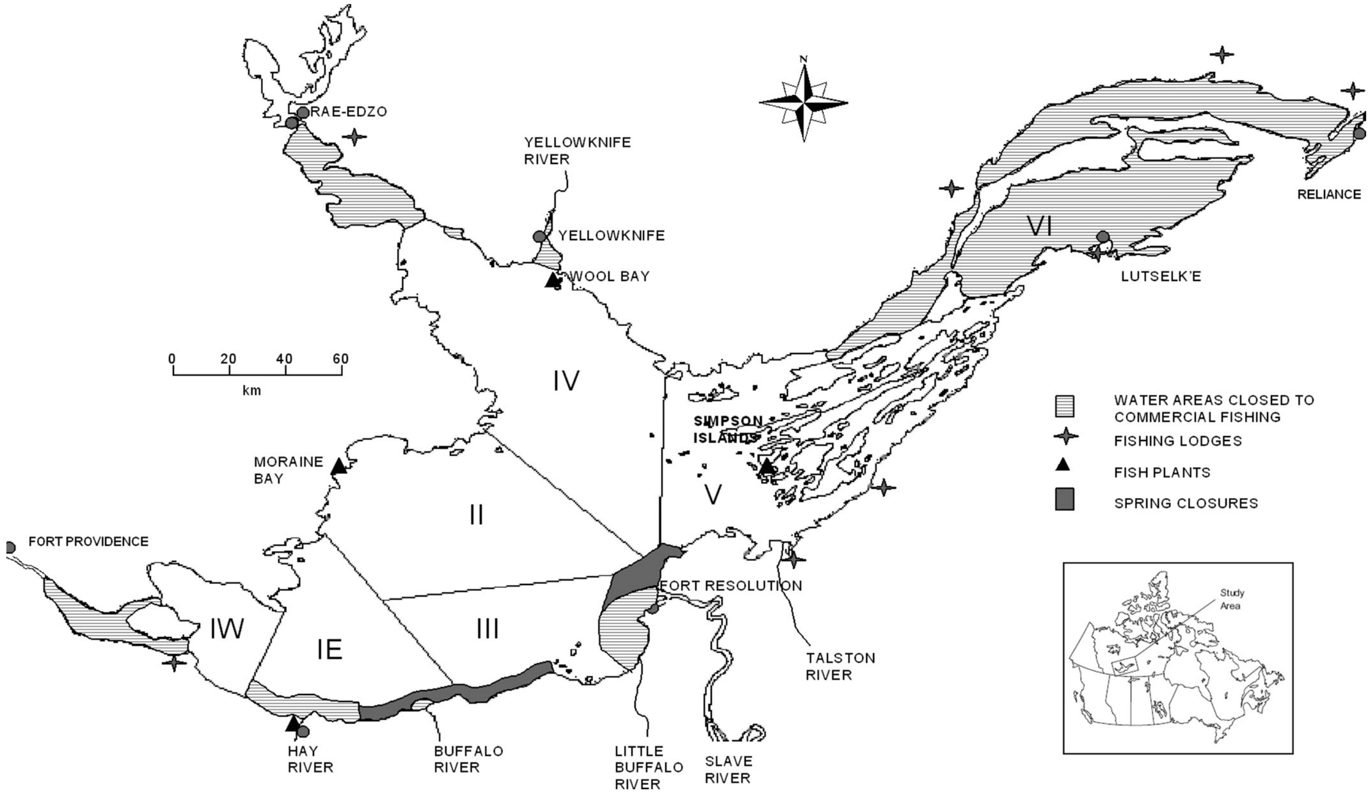

Fig. 1. Map of administrative areas (IE, IW, II, III, IV, V, and VI) with long-term biological samplings for Lake Whitefish since 1972. Areas closed to commercial fishing (lined fill indicates year-round closure; solid fill indicates spring closure) and the locations of fish plants (triangles) and fishing lodges (stars) are also indicated.

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440 km from its extreme east end to the outlet of the Mackenzie River, straddling two distinct physiographic regions: the erosion-resistant Precambrian Shield to the east and the Interior Plains to the west (MRBB, 2004). The eastern arm of GSL is comprised of undulating topography, with bedrock outcroppings that form hills and valleys. With an average depth of 249 m and a maximum depth of 614 m, GSL is the deepest lake in North America (MRBB, 2004). Sitting in the flat Interior Plains, the main basin of GSL is underlain by thick glacial, fluvial, and lacustrine deposits. The mean depth of the main basin is 41 m, with a maximum of 163 m. GSL receives north-flowing riverine inflows and drains to the Mackenzie River through Fort Providence in the southwest. Historically, almost the entire lake has been open to commercial fisheries, with the exception of the east arm of GSL, which was completely closed to commercial fisheries in 1974 and has been managed exclusively for subsistence and sport fisheries since (Read and Taptuna, 2003). Seasonal closures have also been in place along the south shore of the main basin since 2001 for the protection of inconnu, *Stenodus leucichthys*, stocks which congregate in these areas in spring (Read and Taptuna, 2003).

Data source: During 1972–2009, a series of fisheries biological observations, either from fishery-dependent fish plant sampling or fishery-independent research programs, were over six administrative areas of the lake (Fig. 1). During the sampling periods, measurements of fork length (to the nearest 1 mm) and round or dressed weight (to the nearest 5 g) were conducted for a total of 88,171 Lake Whitefish. Scales of 54,573 fish were collected from the region of the body ventral to the anterior edge of the dorsal fin and above the lateral line. Our recent comparative study on 307 Lake Whitefish captured by the use of multi-panel experimental gillnets in Area III between July 10 and August 15, 2012, documented that the otoliths of these are the best hard structure for age estimates, and that scale readings produce similar age estimates to the otoliths up to age 9 (Zhu et al., 2015). Beginning at age 10, the underestimated ages when using the scale readings tended to be linearly augmented. Thus, it was necessary to standardize otolith-based age estimates for the fish in terms of archived scale readings. We used a Bayesian regression model to fit log-transformed otolith-based (y_i) and scale-based age (x_i), structured with homoscedastic normal errors,

$$y_i \sim \text{normal}\ (\mu_i, \sigma^2),$$

$$\mu_i = \beta_1 + \beta_2\, x_i.$$

Here, $\beta = (\beta_1, \beta_2)$, are priors which conform normal probability distribution function (pdf), $\beta_i \sim$ normal (0, 0.01). Parameter σ is prior which follows uniform pdf, $\sigma \sim$ uniform (0.001, 10.0).

After the assessment of age errors from reading structures, we then examined how sampling seasons and sample size impacted the accuracy of length-at-age estimations. As suggested by Kennedy (1953), the length-at-age data were limited to the summer months of June through September, leading to a total sample of 43,641 individuals for this study. The effect of an age-specific sample size was mainly a result of insufficient observations ($n < 10$), which lead to the ages 4–20 being included in the present analysis. As a result, six sets of 38 (years) × 17 (ages) metrics were structured for the following Bayesian statistic analyses.

Model construction and Bayesian statistics

Four deterministic candidate growth models were used to describe length-at-age growth of Lake Whitefish (Table 1). VBM is characterized by a concave length-at-age growth curve with increasing age t while sigmoid curves, like GGM, LGM and PGM, can portray growth traits with an explicit inflection point of sigmoidal curves (Katsanevakis and Maravelias, 2008). Normally, three model parameters associated with the growth patterns of fish were expressed for L_∞, K and t_0 as of asymptotic length, Brody growth rate and the time when length approaches zero, respectively (Ricker, 1975). To simplify the estimation of growth model parameters, we assumed that $t_0 = 0$, which is consistent with similar studies (Beauchamp et al., 2004). The additional model parameter P is a dimensionless shape parameter in GGM that describes the curvilinearity of the approach to the asymptote L_∞ (McLaren, 1993).

Table 1
Characteristics of the four growth models used for quantifying length-at-age relationships of Lake Whitefish in Great Slave Lake.

Model	Number of parameter	Shape
Generalized von Bertalanffy growth model (GGM) $L_t = L_\infty[1-e^{-K(t-t_0)}]^P$	4	Sigmoidal
Logistic growth model (LGM) $L_t = \frac{L_\infty}{1+e^{-K(t-t_0)}}$	3	Sigmoidal
Gompertz growth model (PGM) $L_t = L_\infty e^{-(\frac{1}{K}e^{-K(t-t_0)})}$	3	Sigmoidal
Standard von Bertalanffy growth model (VBM) $L_t = L_\infty[1-e^{-K(t-t_0)}]$	3	Concave

To parameterize hierarchical Bayesian models, we composed four model scenarios in connection with two kernel model parameters L_∞ and K,

LCKC: constants for both L_∞ and K
LCKV: constant L_∞ and varying K
LVKC: varying L_∞ and constant K
LVKV: varying both L_∞ and K.

For each administrative area, the length-at-age data were modeled with the combinations of four models by four model scenarios. With regards to Bayes' theorem, the combination of a prior from a likelihood function and its normalization results in a posterior probability distribution, which is a conditional distribution of the probability given the data (Carlin and Louis, 2009). For Lake Whitefish length-at-age growth analyses, a non-hierarchical Bayesian growth model representing a posterior density for the parameters ($p(\theta|dL_{a,t})$) using Bayes' theorem was developed:

$$p(\theta = L_{a,t}K_a|dL_{a,t}) = \frac{\prod_a f(dL_{a,t}|\theta)\pi(\theta)}{\int_{-\infty}^{+\infty} \prod_a f(dL_{a,t}|\theta)\pi(\theta)d\theta}.$$

Here, a and t were year and age, respectively. For each hierarchical Bayesian growth model, hyper-parameters were assigned to yield joint posterior distributions:

$$\begin{aligned} &p(\theta' = L_{a,\infty}, K_a, \overline{L}_\infty, \overline{K}, \overline{\sigma}_{L_\infty}, \overline{\sigma}_K|dL_a) \\ &= \frac{\prod_a f(dL_a|L_{a,\infty}, K_a)\pi_1(L_{\infty,a}|\overline{L}_\infty, \overline{\sigma}_{L_\infty})\mu_1(\overline{L}_\infty)\upsilon_1(\overline{\sigma}_{L_\infty})\pi_2(K_a|\overline{K}, \overline{\sigma}_K)\mu_2(\overline{K})\upsilon_2(\overline{\sigma}_K)}{\int_{-\infty}^{+\infty} \prod_a f(dL_a|L_{a,\infty}, K_a)\pi_1(L_{\infty,a}|\overline{L}_\infty, \overline{\sigma}_{L_\infty})\mu_1(\overline{L}_\infty)\upsilon_1(\overline{\sigma}_{L_\infty})\pi_2(K_a|\overline{K}, \overline{\sigma}_K)\mu_2(\overline{K})\upsilon_2(\overline{\sigma}_K)d\theta'}. \end{aligned}$$

In the above mathematical expressions, $f(dL_a|\theta)$ is the pdf of dL_a of parameter vector θ; $\mu_1(\overline{L}_\infty)$ and $\upsilon_1(\overline{\sigma}_{L_\infty})$ are the median and variance vectors of the probability distribution functions (pdfs) of $\overline{L}_\infty$ and $\overline{\sigma}_{L_\infty}$, respectively. $\mu_2(\overline{K})$ and $\upsilon_2(\overline{\sigma}_K)$ are the pdfs of $\overline{K}$ and $\overline{\sigma}_K$, respectively.

When accounting for time-varying growth patterns, a certain part of pdfs was applied to specify hierarchical Bayesian models and the priors of model parameters. Two kernel model parameters, $L_{a,\infty}$ and K_a, are assumed to follow a lognormal pdf with log-transformed means $\overline{L}_\infty$ and $\overline{K}$. The Gelman or vague prior (Gelman, 2006) is used to construct a posterior pdf describing model process error (σ) and

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precisions for composing hierarchical priors, σ_{L_∞} and σ_K of the kernel model parameters, L_∞ and K as:

$$L_{a,\infty} \sim \mathrm{lognormal}\left(\overline{L_\infty}, \overline{\sigma_{L_\infty}{}^2}\right)$$

$$K_a \sim \mathrm{lognormal}\left(\overline{K}, \overline{\sigma_K{}^2}\right)$$

$$\overline{\sigma^2_{L_\infty}} \sim \mathrm{uniform}(0.001, 100)$$

$$\overline{\sigma^2_K} \sim \mathrm{uniform}(0.001, 100)$$

$$P \sim \mathrm{uniform}(0.1, 5.0).$$

The implementation of hierarchical Bayesian models requires specification of initial values for all priors. Informative priors, based on published information and observed values, are specified as the starting points of modeled parameters estimated, such as L_∞ and K. Reported values for L_∞ range from 479.5 mm in Lake Superior (Bronte et al., 2003) to 701.0 mm in Lake Huron (Chu and Koops, 2007), with arithmetic average fork length of 566.3 ± 11.6 mm (Table 2). Growth parameter K varies between 0.080 and 0.680, with an arithmetic mean of 0.282 ± 0.132. During 1972–2009, the maximum size for Lake Whitefish collected in GSL was 648 mm in fork length. Applying a factor of 1.15, thus, the boundaries for sex-undifferentiated L_∞ were set to 408 and 745 mm. In addition, the shape parameter, P, in GGM, is specified as greater than 0 and less than 5. If $P = 1$, it becomes the standard VBM, otherwise, it is a generalized form of the growth model.

$$\overline{L_\infty} \sim \mathrm{uniform}(408, 745)$$

$$\overline{K} \sim \mathrm{uniform}(0.1, 0.7)$$

To implement Markov Chain Monte Carlo (MCMC) methods, JAGS (just another Gibber sampler, http://mcmc-jags.sourceforge.net/) is a program for analysis of Bayesian hierarchical models using MCMC. An R environment (www.r-project.org) package R2jags (http://cran.r-project.org/web/packages/R2jags/index.html) was used to implement three Markov chains. A total of 300,000 Metropolis–Hasting iterations with Gibbs sampling were run, following a burn-in period of 50,000 iterations. For each Markov Chain, 1000 samples were obtained by using the 250th iteration to avoid highly auto-correlated neighboring values (Spiegelhalter et al., 2002). We used the R-based evaluation package CODA (Convergence Diagnosis and Output Analysis, version 0.13-5) to examine model convergence and stationarity of the Gibbs sampling outputs (Plummer et al., 2006; Carlin and Louis, 2009; Ntzoufras, 2009). Among convergence tests, the Gelman–Rubin test examines a shrinking factor $R \le 1$ through an ANOVA-type convergence test for multiple chains. The Heidelberg–Welch diagnostic was used to assess the stationarity of three Markov chains under specific numbers of samples in terms of half-bridge theory.

We used the deviance information criterion (DIC) with a priori parsimonious predictive Bayesian statistics to evaluate the relative goodness of fit of the structural models that profiled the complexity and instability that resulted from a particular parameterization (Burnham and Anderson, 2002; Spiegelhalter et al., 2002; Carlin and Louis, 2009). As a generalization of AIC that is based on the posterior distribution of the deviance statistic, DIC can be expressed as:

$$D(\theta) = -2\log f(y|\theta) + 2\log h(y)$$

$$\mathrm{DIC} = \hat{D} + 2pD\mathrm{or}\mathrm{DIC} = \overline{D} + pD$$

where $f(y|\theta)$ is the likelihood function for the observed data vector y given the parameter vector θ, and $h(y)$ is a standardization function of the data alone (Carlin and Louis, 2009). $\hat{D}$, $\overline{D}$, and pD are the deviance of the posterior mean, the posterior mean of the deviance as a measure of fit, and the effective number of parameters as a measure of complexity in the Bayesian model, respectively (Lunn et al., 2009).

As a rule of thumb for multi-model inference (MMI), Spiegelhalter et al. (2002) suggested DIC difference between individual and minimum DIC, Δ_i:

$$\Delta_i = \mathrm{DIC}_i - \mathrm{DIC}_{min}$$

here, DIC_i and DIC_{min} are DIC in model i and minimum, respectively. If two models differ by only one or two DIC units (Δ_i) then one cannot distinguish between the two models and both are supported. If models differ by three to seven DIC units there is some support for the second model, but the first model is clearly better. When the DIC difference is greater than 10 there is no support for the second model. Therefore, DIC offers a straightforward means of comparing different models when using the same observed data.

Table 2

Literature values of the growth model parameters of asymptotic total length (TL_∞) or fork length (FL_∞) and Brody growth rate (K) for several different Lake Whitefish populations. The relation, total length (TL: mm) = 1.12 × fork length (FL: mm), was used.

Lake	Location	Year	TL_∞ (mm)	FL_∞ (mm)	K	Source
Lake Superior	Apostle Islands	1981	704.0	628.6	0.17	Bronte et al. (2003)
		1990	569.0	508.0	0.25	
		1999	537.0	479.5	0.31	
Lake Erie		1989–1994	569.0	508.0	0.40	Cook et al. (2005)
		1989–1994	634.0	566.1	0.28	
		1995–2001	576.0	514.3	0.32	
		1995–2001	593.0	529.5	0.31	
Lake Erie	West Central Basin	1995–2003	630.1	562.6	0.50	Chu and Koops (2007)
	East Central Basin	1997–2003	607.1	542.1	0.25	
	Pennsylvania Ridge	1989–2002	602.1	537.6	0.31	
	Eastern Basin	1993–1998	605.1	540.3	0.68	
Lake Ontario		1992–2004	703.1	627.8	0.08	
Lake Huron	Georgian Bay	1981–2003	785.1	701.0	0.35	
	East Lake Huron	1981–2003	687.1	613.5	0.12	
	West Lake Huron	1985–2002	703.1	627.8	0.22	
Lake Michigan		2000–2003	637.1	568.8	0.12	
Great Lakes		1950–1999	667.5	596.0	0.25	Beauchamp et al. (2004)
		1950–1999	640.6	572.0	0.28	
Inland		1971–2001	625.0	558.0	0.22	
		1971–2001	609.3	544.0	0.23	

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For each fitted estimation model the DIC weight (w_i) was calculated as (Burnham and Anderson, 2002):

$$w_i = \frac{e^{-\frac{1}{2}\Delta_i}}{\sum_{i=1}^{R} e^{-\frac{1}{2}\Delta_i}}.$$

The multi-model average over a model set was calculated using w_i for the comparative model parameters:

$$\beta_{\mathrm{DIC}} = \sum_{i=1}^{R} \beta_i w_i$$

where β_i is the appropriate parameter.

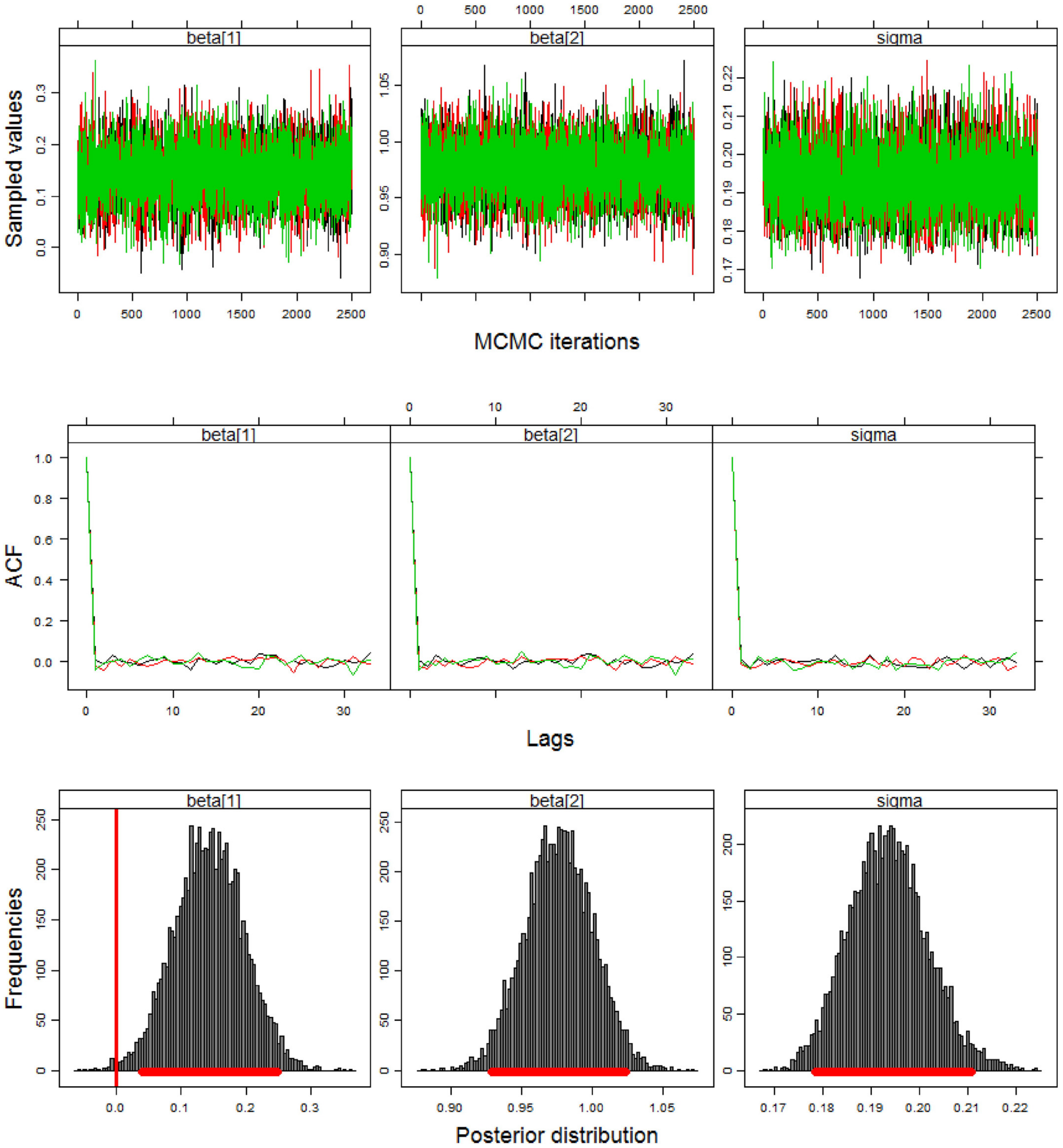

Fig. 2. Trace plots (upper panel), auto-correlated function (middle panel) and frequency distribution (lower panel) of Bayesian regression model parameters used to standardize otolith-based length-at-age estimates from scale-based measurements for Lake Whitefish.

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Results

Standardization of otoliths-based ages from scale-based readings

Associated with our previous age comparison study (Zhu et al., 2015), the discrepancies of the average age estimates between the otoliths- and scale-based ages were statistically significant beyond age 9 ($F_{1163} = 73.43$, $P < 0.0001$). We fitted a Bayesian regression model by running three chains of parallel Gibbs samplers for 250,000 iterations each, and thinned each chain by taking every 250th observation to avoid highly auto-correlated values. Consequently, a total of 1000 samples for each Markov chain were retained to estimate the values of β_1, β_2 and σ. The posterior distributions of model parameters suggested acceptable degree of convergence (Fig. 2). Based on the lag 1 auto-correlated function (ACF) of three overlapped chains, we discarded the first 50,000 iterations from each chain to complete sampler "burn-in". The posterior model parameters conformed to a normal distribution, with an interquartile range from 0.037 to 0.248 for β_1, 0.930 to 1.024 for β_2 and 0.178 to 0.211 for σ. The posterior means were accounted into 0.142 ± 0.054, 0.977 ± 0.024, and 0.194 ± 0.008 for β_1, β_2 and σ, respectively.

Model convergence diagnoses and selections

The Gelman–Rubin diagnostic test for all of growth model parameters and variances varied in the range of 1.00 and 1.03, indicating the convergence of three Markov chains. Among these Markov chains, the Heidelberger–Welch test showed that all of the growth model scenarios, except GGM and LGM with LCKC in area IE, showed a fairly strong performance (>99% Markov chains passed the test) with effective stationarity and halfwidth tests.

Model selection was assessed in terms of the rule of thumb that the smaller DIC value the better the model. In terms of DIC values, the best growth models were consistently preferred by GGM with LVKV for the fish in GSL (Table 3), except area IE where GGM with LCKV was the best. Models PGM, LGM and LCKC had no support for lake whitefish

Table 3

Model comparison and selections in terms of Deviance Information Criterion (DIC) values, differences with the smallest values (Δ_i) and the weight (w_i) for Lake Whitefish length-at-age growth in the different areas of Great Slave Lake. Four hierarchical Bayesian growth models, generalized von Bertalanffy growth model (GGM), logistic growth model (LGM), Gompertz growth model (PGM), and standard von Bertalanffy growth model (VBM), were used. For each growth model, four model scenarios were examined, including LCKC as constant values for asymptotic fork length (L_∞) and the Brody growth rate (K), LCKV with constant L_∞ and varying K, LVKC for varying L_∞ and constant K as well as LVKV for varying both L_∞ and K simultaneously. The bold numbers are selected by use of MMI.

Model	Scenario	Area	DIC	Δ_i	w_i	Model	Scenario	Area	DIC	Δ_i	w_i
GGM	LVKV	IW	2105	0	**0.83**	GGM	LVKV	II	2395	0	**1.00**
VBM	LVKV	IW	2109	3	**0.17**	VBM	LVKV	II	2482	87	0.00
GGM	LCKV	IW	2128	22	0.00	GGM	LCKV	II	2495	100	0.00
VBM	LCKV	IW	2128	23	0.00	GGM	LVKC	II	2527	132	0.00
VBM	LVKC	IW	2147	42	0.00	VBM	LCKV	II	2548	153	0.00
GGM	LVKC	IW	2149	43	0.00	VBM	LVKC	II	2567	172	0.00
PGM	LVKV	IW	2193	88	0.00	GGM	LCKC	II	2596	200	0.00
VBM	LCKC	IW	2193	88	0.00	VBM	LCKC	II	2620	225	0.00
PGM	LCKV	IW	2194	89	0.00	PGM	LVKV	II	2647	252	0.00
GGM	LCKC	IW	2195	89	0.00	PGM	LVKC	II	2649	254	0.00
PGM	LVKC	IW	2197	92	0.00	PGM	LCKV	II	2660	265	0.00
PGM	LCKC	IW	2237	131	0.00	PGM	LCKC	II	2721	326	0.00
LGM	LVKV	IW	2255	150	0.00	LGM	LVKV	II	2787	392	0.00
LGM	LVKC	IW	2256	150	0.00	LGM	LVKC	II	2787	392	0.00
LGM	LCKV	IW	2269	164	0.00	LGM	LCKV	II	2825	430	0.00
LGM	LCKC	IW	2291	186	0.00	LGM	LCKC	II	2853	458	0.00
GGM	LCKV	IE	2491	0	**1.00**	GGM	LVKV	IV	2277	0	**1.00**
GGM	LVKV	IE	2638	147	0.00	GGM	LCKV	IV	2304	26	0.00
VBM	LVKV	IE	2642	151	0.00	VBM	LVKV	IV	2306	29	0.00
VBM	LCKV	IE	2754	262	0.00	GGM	LVKC	IV	2321	43	0.00
GGM	LVKC	IE	2780	289	0.00	VBM	LCKV	IV	2327	49	0.00
VBM	LVKC	IE	2781	290	0.00	VBM	LVKC	IV	2330	52	0.00
GGM	LCKC	IE	2831	340	0.00	PGM	LVKV	IV	2365	88	0.00
VBM	LCKC	IE	2832	340	0.00	PGM	LVKC	IV	2367	89	0.00
PGM	LVKV	IE	2935	444	0.00	PGM	LCKV	IV	2384	107	0.00
PGM	LCKV	IE	2936	445	0.00	VBM	LCKC	IV	2389	111	0.00
PGM	LVKC	IE	2939	448	0.00	GGM	LCKC	IV	2390	112	0.00
PGM	LCKC	IE	2980	489	0.00	LGM	LVKV	IV	2427	150	0.00
LGM	LVKC	IE	3058	567	0.00	LGM	LVKC	IV	2428	151	0.00
LGM	LVKV	IE	3058	567	0.00	PGM	LCKC	IV	2447	169	0.00
LGM	LCKV	IE	3072	581	0.00	LGM	LCKV	IV	2472	195	0.00
LGM	LCKC	IE	3096	605	0.00	LGM	LCKC	IV	2506	228	0.00
GGM	LVKV	III	1571	0	**0.97**	GGM	LVKV	V	2182	0	**1.00**
VBM	LVKV	III	1578	7	**0.03**	VBM	LVKV	V	2229	47	0.00
GGM	LCKV	III	1614	43	0.00	GGM	LCKV	V	2246	64	0.00
VBM	LCKV	III	1620	49	0.00	VBM	LCKV	V	2259	77	0.00
PGM	LVKV	III	1623	52	0.00	GGM	LVKC	V	2286	105	0.00
GGM	LVKC	III	1624	54	0.00	VBM	LVKC	V	2291	110	0.00
PGM	LVKC	III	1628	58	0.00	GGM	LCKC	V	2302	120	0.00
PGM	LCKV	III	1629	59	0.00	VBM	LCKC	V	2303	121	0.00
VBM	LVKC	III	1636	65	0.00	PGM	LVKV	V	2323	141	0.00
LGM	LVKV	III	1655	85	0.00	PGM	LCKV	V	2328	146	0.00
LGM	LVKC	III	1656	85	0.00	PGM	LVKC	V	2355	173	0.00
GGM	LCKC	III	1661	91	0.00	PGM	LCKC	V	2387	205	0.00
VBM	LCKC	III	1666	96	0.00	LGM	LVKV	V	2440	258	0.00
PGM	LCKC	III	1668	98	0.00	LGM	LVKC	V	2442	260	0.00
LGM	LCKV	III	1673	102	0.00	LGM	LCKV	V	2445	263	0.00
LGM	LCKC	III	1703	133	0.00	LGM	LCKC	V	2482	300	0.00

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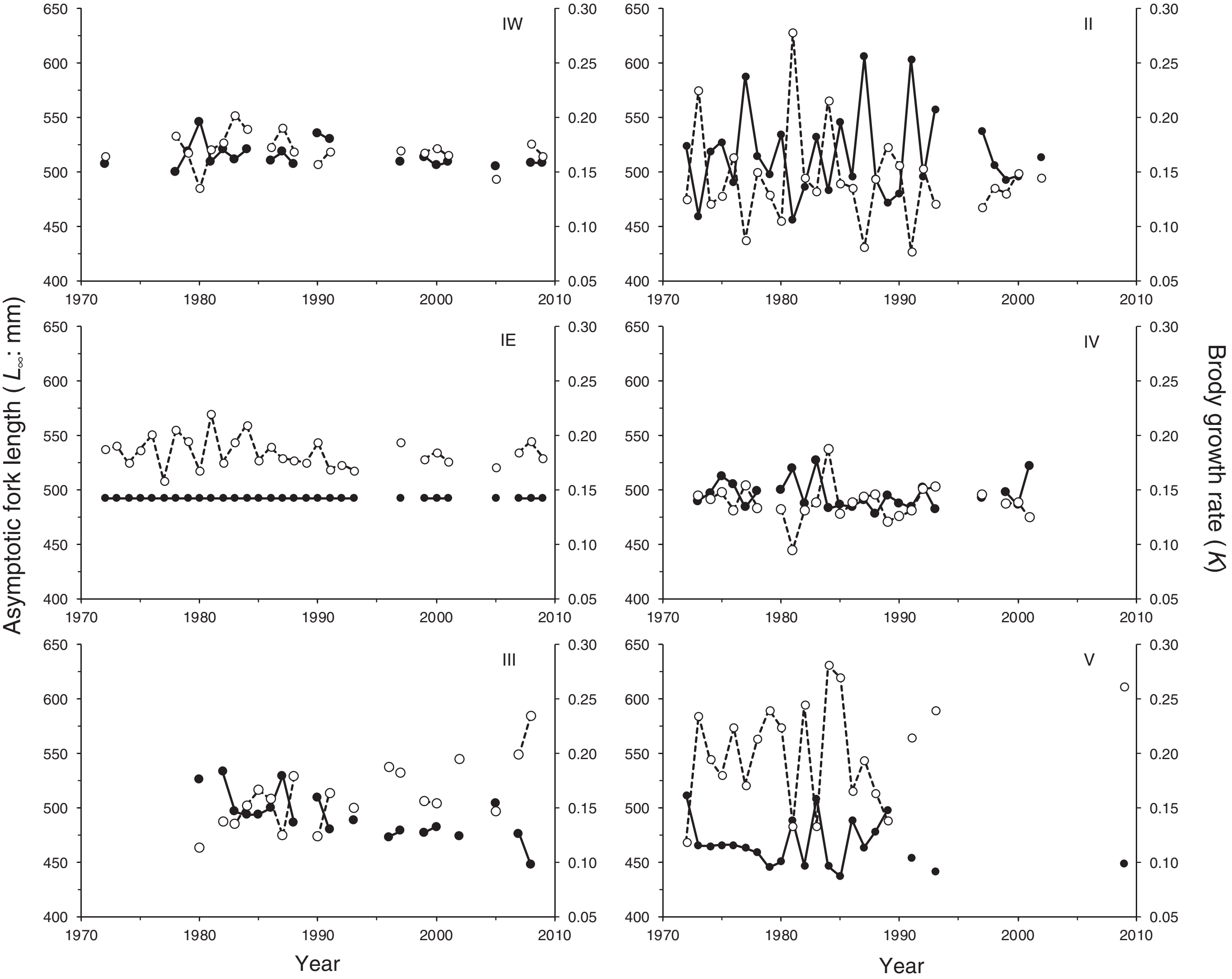

Fig. 3. Temporal changes in the posterior hyper-parameters of asymptotic fork length (L_∞: mm, solid circles with solid lines) and the Brody growth rate (K: open circles with broken lines) for Lake Whitefish across the administrative areas (indicated in the upper right corner of each panel) of GSL.

growth in GSL, despite their conventional use for some fish species in various other aquatic systems. Incorporated with different model structures and DIC weight (w_i), MMI elucidated that two supporting models, GGM with LVKV and VBM with LVKV, better represented growth characteristics of fish in the shallow areas IW and III. Fish growth in IE, though in shallow waters, was best supported by GGM with LCKV. In the deep waters (areas II, IV and V), one model, GGM with LVKV, is able to delineate fish growth. VBM with LVKV had some degree of support in areas IW and III, but, GGM with LVKV was clearly better.

Growth patterns

We estimated model-averaging hierarchical model parameters by use of composite DIC weights (w_i); the average posterior values of L_∞ and K varied from 437.5 to 606.5 mm and 0.078 to 0.281 per year, respectively (Fig. 3). Spatially, the median values of posterior model parameter L_∞ varied between 492.0 and 515.0 mm, except area V where the median posterior L_∞ was quite smaller (467.0 mm) (Table 4). Spatial variations in the model parameter K, with the global average of 0.166 ± 0.003 per year, were 30% greater for fish in areas IW, IE and III than those in areas II and IV, while model parameter L_∞ was 1% smaller than that in deep-water areas. Combined with two model posterior parameters L_∞ and K, growth in length-at-age for lake whitefish tended to be faster in southern shallow areas (areas IW, IE and III) than those in deep water areas (areas II and IV). Fish in area V

Table 4
Summary of hierarchical model parameters constructed for Bayesian statistics of otolith-based length-at-age growth of Lake Whitefish in Great Slave Lake.

Parameter	Shallow water area		
	IW	IE	III
L_∞ (mm)	515.0 ± 2.5	492.8 ± 0.1	492.4 ± 4.8
K	0.171 ± 0.003	0.184 ± 0.002	0.161 ± 0.007
P	1.17 ± 0.01	1.08 ± 0.01	0.80 ± 0.01
σ	0.04 ± 4.27 × 10^{-5}	0.05 ± 4.58 × 10^{-5}	0.04 ± 0.01
$\tau_{L\infty}$	0.03 ± 0.01	2.21 ± 0.04	0.06 ± 0.01
τ_K	0.123 ± 0.001	0.088 ± 2.94 × 10^{-5}	0.231 ± 0.003
Parameter	Deep water area		
	II	IV	V
L_∞ (mm)	515.3 ± 7.4	495.9 ± 2.6	466.5 ± 4.5
K	0.143 ± 0.008	0.139 ± 0.003	0.202 ± 0.010
P	0.69 ± 0.01	0.71 ± 0.01	0.75 ± 0.01
σ	0.04 ± 4.38 × 10^{-5}	0.05 ± 6.10 × 10^{-5}	0.04 ± 3.76 × 10^{-5}
$\tau_{L\infty}$	0.09 ± 4.93 × 10^{-4}	0.04 ± 4.65 × 10^{-4}	0.05 ± 3.32 × 10^{-4}
τ_K	0.33 ± 0.01	0.17 ± 0.01	0.30 ± 0.01

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were rather different from fish in the other areas, characterized by the smallest L_∞ (466.5 ± 4.6 mm), greatest K (0.202 ± 0.010 per year) and largest coefficient of variation (CV = 29%). Of three uncertainty indicators, model process error (σ), hierarchical variance $\tau_{L\infty}$ and τ_K, process errors were the least while hierarchical variance in K was the greatest over all spatial areas. Given that GGM-LCKV has been selected in area IE, there was the greatest hierarchical variance in estimating model parameter K.

Associated with the hierarchical models with the best fits, the joint posterior hyper-parameter distributions for kernel model parameters K and L_∞ differed substantially among areas and years. This was exemplified by comparing the bivariate correlations in 1972, 1982, 1991, 2000 and 2009 (Fig. 4). The correlations between the kernel model parameters K and L_∞ varied by these time periods and spatial areas, being significantly negative from −0.739 to −0.831 per year in western basin (areas IW and IE) to −0.747 to −0.941 per year in deeper waters (areas II, IV and V) and shallow area III. In particular, Lake Whitefish in the western basin showed relatively higher K, without a significant difference in K between 1972 and 2009 ($K_{1972} = 0.151$ vs. $K_{2009} = 0.152$). In areas II, III and IV, significant inter-decadal changes in the pair of parameters can be seen, reflecting the tendency of reductions in both growth parameters over the time series. The growth patterns of this species in area V reflected a relatively different growth pattern: increasing Brody growth rate K, from 0.119 ± 0.003 per year in 1972 to 0.262 ± 0.001 per year in 2000, and reducing asymptotic fork length L_∞ from 511.7 ± 0.4 mm to 448.7 ± 0.2 mm in 2000. The values of shape parameter, P, in GGM, ranged of 0.80 ± 0.01 and 1.17 ± 0.01 in southern shallow areas (IW, IE and III) as well as from 0.69 ± 0.01 to 0.75 ± 0.01 in the deeper areas (II, IV and V). Moreover, for the fish in the southern shallow areas, the P values averaged 1.02, which was much closer to 1 as expressed in the standard VBM. For the fish in the deep-water areas, the average P value was 0.72, indicating the presence of one inflection point during the young-of-year stage.

Discussion

Model performance and selection criteria

There are several competing hypotheses as to which specific sets of candidate growth models with different model scenarios are used to describe the most appropriate growth of subarctic Lake Whitefish populations (Kennedy, 1953; Healey, 1980; Beauchamp et al., 2004). Among the candidate expressions, VBM is the most commonly used deterministic model, and selected as ‘best-fitting’, by assuming that time-invariant growth parameters are applied to the constant surrounding environment in which the fish inhabit over certain temporal scales. That may be the case for controlled experimental conditions; however, associated with the typical oligotrophic subarctic great lake system, our results for Lake Whitefish length-at-age growth indicate that this ‘best-fitting model’, VBM, was not supported by the observed data. Instead, time-varying model scenarios were preferred as the better model interpretation. Naturally, it reflects the reality of fish in the variable environment, which may modify fish growth patterns to diverge more or less from idealized growth trajectories (Weatherley and Gill, 1987). Day and Taylor (1997) suggested that one set of models could not perfectly interpret overall changes in somatic energy allocation from birth until maturity. VBM may provide a good description of somatic growth in adulthood, but fish growth in immature stages usually follows different growth curves in comparison to adults (Gamito, 1998; Quinn and Deriso, 1999; Lester et al., 2004). Moreover, growth variability between sexes and spatial scales for some species can be considerable; one version of a constantly-parameterized VBM is unlikely to capture these differences (Punt et al., 2006).

Recently, time-varying model scenarios have been increasingly favored as a result of its interpretation either by maximum likelihood estimates (Szalai et al., 2003; Katsanevakis and Maravelias, 2008) or hierarchical Bayesian statistics (He and Bence, 2007). Other than the use of appropriate statistic P-values, model performance is evaluated by using DIC in stochastic Bayesian statistics which incorporates likelihood to generate posterior estimates of model parameters (Carlin and Louis, 2009). When working with multiple candidate models, model selection is used to assess the evidence for a single ‘best’ model. Subsequent inferences and parameter estimates are conditional upon that model (Burnham and Anderson, 2002). In addition to the best model selection, other model information can be further incorporated by using MMI strategies, which weigh the relative contributions of individual model parameters, using DIC weight, to the individual model scenarios. Through this process, the deterministic growth model with LCKC scenarios was omitted to avoid biasing point estimates and generating false evaluations of accuracy (Katsanevakis, 2006). Similarly, there are several studies to underpin fish time-varying growth, such as Bloater (*Coregonus hoyi*) in Lake Michigan (Szalai et al., 2003), Lake Trout in Lake Huron (He and Bence, 2007) and Gilthead Seabream (*Sparus aurata*) in the Gulf of Lions (Mercier et al., 2011).

When multiple sets of growth models and scenarios are supported by observations, model selections and parameterizations may be species-specific and habitat dependent, taking into account population response to the spatial variations in environmental conditions, forage supplies and multispecies interactions. Katsanevakis (2006) reported that GGM was the best model for Rougheye Rockfish (*Sebastes aleutianus*) in southeastern Alaska (with a w_i of 59%), but it was the second best growth model for female Striped Seabream (*Lithognathus mormyrus*) in the Canadian archipelago (with a w_i of 21%). Kopf et al. (2011) reported that a standard growth model, VBM, showed the best fit with observed length-at-age growth for Striped Marlin (*Kajikia audax*) in the southwest Pacific Ocean. In addition to GGM and VBM, Ainsley et al. (2011) demonstrated that the PGM was the best fit for total length-at-age in the Whitebrow Skate (*Bathyraja minispinosa*) from the eastern Bering Sea. GGM and VBM both stem from the same family of logistic-originated functions. With the shape parameter $P =$ 1 in GGM, it becomes the most commonly used VBM with no inflection point for $t > 0$. Given the case of $P \neq 1$ in GGM, we would expect a sigmoidal length-at-age curve with an inflection point, representing faster growth at young and slower growth at adult stages. For GSL Lake Whitefish, P values varied close to 1 in the southern shallow areas (IW, IE and III), and less than 1 ($P = 0.72$) in the deep-water areas (II, IV and V), suggested spatial variations of length-at-age growth characteristics of this species. To calibrate these model results, more work is needed to investigate the impacts of diverse habitats on the growth of fish during their life histories.

Cumulative environmental associations with time-varying growth dynamics

We first used hierarchical Bayesian statistical analyses to reveal the evidence of time-varying growth characteristics for slow-growing Lake Whitefish populations in a subarctic great lake: characterized by relatively smaller values of K and L_∞ as well as substantial spatial difference in length-at-age growth. Compared to the growth parameters of southern populations of Lake Whitefish in the Laurentian Great Lakes (Bronte et al., 2003; Beauchamp et al., 2004; Cook et al., 2005; Chu and Koops, 2007), the average values of L_∞ and K for the GSL fish were smaller at 16% and 50%, respectively (Table 2). Over two decades (1981–1999), the growth parameters of Lake Whitefish in Lake Superior varied in the reduction of L_∞ (24%) and an increase of K (84%), reflecting the shift of modal age classes from ages 4–7 in 1983 to ages 5–17 in 1998 (Bronte et al., 2003). Since 1989, changes in the fish growth and conditions have been functionally associated with the decline of energy-rich and preferred amphipod, *Diporeia* spp. and establishment of non-indigenous dreissenids, like Zebra Mussel (*Dreissena polymopha*) and Quagga Mussel (*Dreissena bugensis*) in the Great Lakes (Cook et al., 2005; Pothoven, 2005; Lumb et al., 2007; DeBruyne et al., 2008). In GSL,

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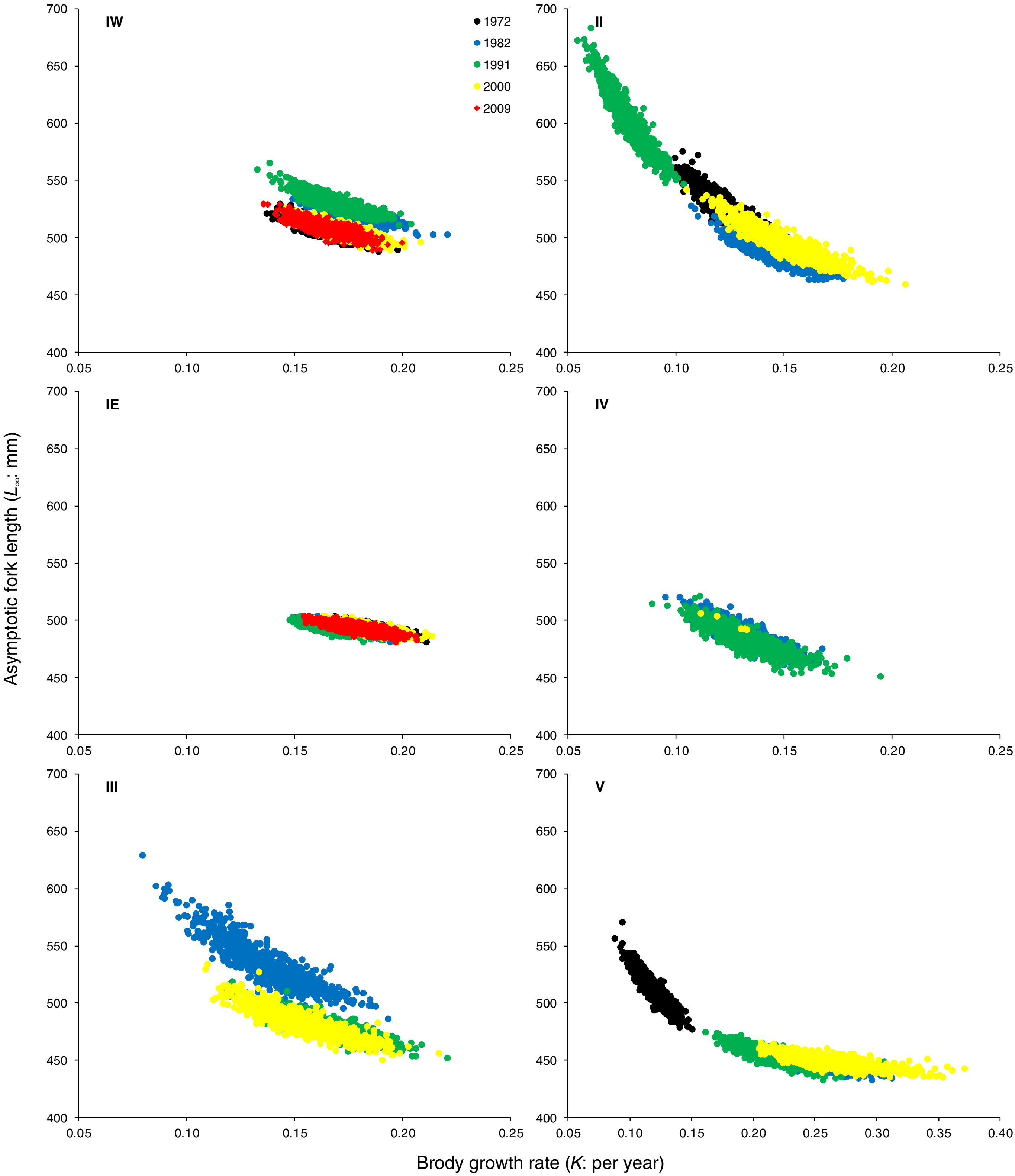

Fig. 4. Joint posterior hyper-parameter distributions for the Brody growth rate (K) and asymptotic fork length (L_∞: mm) obtained from multimodel averaging a set of hierarchical growth models for Lake Whitefish. Colored dots show temporal variation in the hyper-parameters in 1972 (black), 1982 (blue), 1991 (green), 2000 (yellow) and 2009 (red). Separate distributions are presented for each GSL administrative area (indicated in the upper right corner of each panel).

the consequence of a marked spatial difference in length-at-age growth of the fish may be a result of cumulative environmental effects, such as a short-growing season, stratified thermal structure, regulated water inflow and nutrient inputs in the typical oligotrophic lake (Kennedy, 1953; Healey, 1980). In fact, time-varying growth attributes can reflect simultaneous modifications in year-class strength and adaptions to varying environmental conditions, such as temperature, pH, and changes in the forage base (Neill et al., 2004).

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Among the environmental variables affecting the GSL ecosystems, water level, air temperature, and precipitation may impact the development of different time-varying patterns of Lake Whitefish. As more than 77% of runoff comes through Slave River into GSL, it largely modifies the seasonal and inter-decadal variations of water level and nutrient inputs along with other connecting river systems (MRBB, 2004). As a critical limnological indicator, water level is directly related to the water balance and lake functioning which is strongly associated with riverine discharge, precipitation, and climate-driven evaporation (Gibson et al., 2006; Pörtner and Peck, 2010). In addition, changes in GSL water level may also stem from anthropogenic water regulation since the completion of the W.A.C. Bennett Dam in the Peace Rivera major headwater basin of the Slave River in 1967. Combined with climate and water regulation, it appears to modify the amplitude of water level changes and the magnitude of peak levels, which cumulatively contributing to a seasonal shift towards an earlier annual peak in water levels in the lake (Gibson et al., 2006; Prowse et al., 2006).

Considering these impacts of cumulative environmental modifications from both localized and global vectors, our study of Lake Whitefish spatiotemporal growth patterns may constitute a vector of biological indicators to seasonal changes of wind action, vertical mixing and heat exchange, and riverine inflow (Rawson, 1950). For example, as a result of rapid heating in shallow areas, fish in areas IW, IE and III first displayed active feeding activities, faster growth (higher *K*) and constant asymptotic body size (Healey, 1980). The duration of warming seasons may also benefit through the extension of growing seasons, given sufficient nutrient inputs and higher productivity (Healey, 1975). In contrast to the shallow areas, the existence of the thermocline in summer months has stabilized colder thermal habitats in the deep waters of the lake (Rawson, 1950), preventing vertical migrations through the thermal structure. The strong wind actions in some years may break this stabilized thermal structure, resulting in vertical mixture of energy and nutrients. Consequently, despite low growth rate, the presence of significant variations in fish growth can support this possibility. Therefore, the current study is consistent with the suggestion of Reckahn (1986) that fluctuations in water levels and temperature can largely account for growth patterns in Lake Whitefish.

Density-dependent effects on growth rates

In addition to these abiotic effects on fish growth characteristics, several biological and ecological mechanisms are also available to explain the spatiotemporal variability of fish growth, including density effects and competitive interactions over food supplies and territories (Brett, 1979; Weatherley and Gill, 1987). Density-dependent growth attributes have been well documented in salmonids, such as Brown Trout, *Salmo trutta* (Parra et al., 2011). At the population level, cohort-specific mass growth can be affected by the density of conspecifics throughout life histories. Specifically, pre-recruit abundance and growth potential are primary drivers of subsequent trajectories in fish population dynamics. Therefore, density-dependent growth among recruits is a key process in the regulation of fish populations (Lorenzen and Enberg, 2001). For Lake Whitefish, several studies have supported the density-dependent or -independent population growth patterns during individual life histories. For instance, the density-dependent growth of young-of-the-year whitefish was related to the abundance of benthic prey, recruitment success, and reductions in mortality sources (Hoagman, 1974; Claramunt et al., 2010). In the mid-1990s, adult Lake Whitefish in southern Lake Michigan underwent a pronounced decline in growth rates that coincided with an increase in relative abundance, providing evidence of density-dependent mechanisms (DeBruyne et al., 2008). In northern Lake Michigan, the relationship between population growth and relative abundance displayed density-independent trends, possibly as a result of a trophic regime shift from *Diporeia* spp., a higher quality food, to lower quality non-indigenous dreissenid mussels (Pothoven, 2005). All of these studies provide evidence that ecosystem disturbances have significant impacts on Lake Whitefish growth and production dynamics. However, in GSL, there are no existing reports of food web changes from aquatic invasive species. Kennedy (1953) suggested there was a tendency for growth rates to increase from southwest to northeast within GSL, from moderately oligotrophic to extremely oligotrophic gradients. If we accept the prevalence of density-dependent growth mechanisms, it would be natural to conclude that there should be an uneven distribution of lake whitefish density, which would be highest in area IW and lowest in area IV.

Overall, we constructed four length-at-age growth models, parameterized with constant or time-varying probabilistic model parameters for GSL Lake Whitefish. By applying convergence tests, DIC and MMI, the best length-at-age growth models were characterized as having the highest proportional stationarity among the sampling chains and the lowest DIC values. Compared with conventional growth models, such as VBM-LCKC, our modeling results explicitly demonstrated that the implementation of a DIC-based MMI approach can substantially reduce the observation errors, combinations of candidate model parameter scenarios, as well as uncertainties that account for a series of abiotic and biological interactions. Using hierarchical Bayesian statistics, the modeling of time-varying growth offers the advantage of providing an objective basis for studying how fish growth changes over time and will allow for rigorous temporal and spatial comparisons of growth differences with changing environmental conditions and population structures. This new approach introduced in this study makes it possible to explain the inter-annual and inter-area variation in the growth characteristics of Lake Whitefish and strengthen the ability to more effectively manage these important commercial fish populations in arctic ecosystems, if time-varying growth characteristics of the fish populations are well integrated.

Acknowledgments

We are grateful to the DFO staff who involved in collecting, processing, and creating this long-term dataset by monitoring commercial fisheries and sports fishing lodges on GSL. George Low, Fred Taptuna, Chris Day, Deanna Leonard, Kevin Hedges, Marie-Julie Roux, and Melanie Toyne provided considerable helps and constructive discussions throughout a regional advisory process meeting to review these results. Drs. Marten Koops, DFO Great Lakes Laboratory for Fisheries and Aquatic Sciences, Darren Gillis, University of Manitoba, and Mark Ebener, Chippewa Ottawa Resource Authority, provided many knowledgeable comments on the early version of the manuscript. This study was funded by Northwest Territories Cumulative Impacts Monitoring Program (NWT-CIMP project No. 00132) and DFO Aboriginal Fisheries Strategy.

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Please cite this article as: Zhu, X., et al., Modeling spatiotemporal variabilities of length-at-age growth characteristics for slow-growing subarctic populations of Lake Whitefish, using hierarchical Bayesian statistics, J. Great Lakes Res. (2015), http://dx.doi.org/10.1016/j.jglr.2015.08.013