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# Hierarchical modelling of spatiotemporal dynamics of biological characteristics of Lake Whitefish, *Coregonus clupeaformis* (Mitchill), in Great Slave Lake, Northwest Territories, Canada, 1972–2004

Xinhua Zhu[1], A. Chris Day[1], W. E. Fred Taptuna[2], Theresa J. Carmichael[1], and Ross F. Tallman[1]

[1]Arctic Aquatic Research Division
Fisheries and Oceans Canada, Freshwater Institute
501 University Crescent, Winnipeg, MB  R3T 2N6

[2] Fisheries and Oceans Canada,
42043 Mackenzie Hwy, Hay River, NT  X0E 0R9

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**Foreword**

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

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# ABSTRACT

To monitor fisheries population dynamics, a fishery-dependent sampling program was initiated in 1972 for Lake Whitefish in Great Slave Lake (GSL). A set of fish biological data on scale age, fork length and dressed weight has been collected annually. The objectives of this study are to summarize the spatiotemporal variations in the biological characteristics and to evaluate the potential association of these biological characteristics with cumulative impacts from localized hydrology, meteorology, global climate changes and exploitation during 1972-2004.

Applying multimodel inference (MMI), relationships between log-transformed pairs of fork length and round weight were best described by a piece-wise regression model for fish in southern shallow areas and a cubic regression model for deep-water fish. In terms of the selected length-weight models, the relative condition index, $K_{LC}$, was derived to reflect the effects of changing mesh sizes and fishing efforts. Statistically, a conventional linear regression model, which is used to relate body mass proportionally to the cube of body length, did not support the change in the morphological relationship of the fish in GSL.

Three length-at-age growth models, von Bertalanffy, generalized, and logistic growth, were employed to select for better representation of the growth patterns of the fish populations. Among those, the generalized growth model performed the best for describing length-based growth patterns of the fish. Spatial comparison of growth patterns indicated that the fish growth traits changed along a southwest to northeast gradient in GSL.

Throughout the history of the fishery, the profound variation in Lake Whitefish harvest corresponded to changes in social and economic factors. Thus, despite the spatiotemporal variations in the biological metrics and harvest, there was no indication of a decline in stock status among management areas. However, information gaps and uncertainties in the fish biological assessment were identified and further analyses were recommended combining fishery-dependent and fishery-independent survey results.

# Modélisation hiérarchique de la dynamique spatiotemporelle des caractéristiques biologiques du grand corégone *Coregonus clupeaformis* (Mitchell) dans le Grand lac des Esclaves (Territoires du Nord-Ouest) Canada, 1972-2004

## RÉSUMÉ

Afin de surveiller la dynamique des populations de poissons, un programme d'échantillonnage dépendant de la pêche a été lancé en 1972 pour le grand corégone dans le Grand lac des Esclaves. Chaque année, des données biologiques sur les poissons ont été recueillies pour déterminer l'âge des écailles, la longueur à la fourche et le poids apprêté. Cette étude vise à résumer les variations sociotemporelles des caractéristiques biologiques et à évaluer le lien potentiel de ces caractéristiques biologiques avec les effets cumulés de l'hydrologie localisée, de la météorologie, des changements climatiques mondiaux et de l'exploitation entre 1972 et 2004.

En utilisant une interférence multimodèle (MMI), la relation morphologique entre les paires log-transformées de la longueur à la fourche et du poids brut a été mieux décrite par un modèle de régression séquentielle pour les poissons des zones peu profondes au sud et par un modèle de régression cubique pour les poissons des eaux profondes. En ce qui concerne les modèles longueur-poids choisis, l'indice de condition relative, $K_{LC}$, a été utilisé afin de mieux refléter les effets de la modification du maillage et de l'effort de pêche. Sur le plan statistique, un modèle de régression linéaire conventionnel, qui est utilisé pour relier la masse corporelle proportionnellement au cube de la longueur corporelle, n'a pas soutenu de modifications dans la relation morphologique du poisson dans le Grand lac des Esclaves.

Trois modèles de croissance de la longueur selon l'âge, de von Bertalanffy, généralisés, et le modèle logistique de la croissance, ont été utilisés afin de sélectionner le modèle qui offre une meilleure représentation des schémas de croissance des populations de poissons. Parmi ces modèles, le modèle de croissance généralisé a donné le meilleur rendement pour ce qui est de la description des schémas de croissance du poisson fondés sur la longueur. La comparaison spatiale des schémas de croissance indique que les paramètres de croissance du poisson ont changé le long d'un gradient sud-ouest/nord-est dans le Grand lac des Esclaves.

Tout au long de l'histoire de pêche, la profonde variation des captures du grand corégone dans le lac a correspondu à des changements dans les facteurs sociaux et économiques. Donc, en dépit des variations sociotemporelles dans les paramètres biologiques et les captures, rien n'indiquait une diminution du stock de grands corégones dans les zones de gestion. Toutefois, des lacunes dans les données et des incertitudes dans l'évaluation biologique du poisson ont été relevées et il a été recommandé de procéder à d'autres analyses combinant les résultats de relevés dépendants de la pêche et indépendants de la pêche.

# INTRODUCTION

Lake Whitefish, *Coregonus clupeaformis* (Mitchell), was first described as *Salmo clupeaformis* from the St. Marys River, below the falls, at the northern extremity of Lake Huron in 1818 by Mitchell (Carlander 1969, Scott and Crossman 1998). Currently, it is widely distributed from Atlantic coastal watersheds westward across Canada, and in the northern United States. Lake Whitefish populations have supported vigorous commercial fisheries in North American freshwater systems. For example, Lake Whitefish in the Great Lakes sustained overall production of 9,534 tonnes, for a total value of $18.64 million U.S. dollars in 2000 (Kinnunen 2003). Lake Huron alone contributed more than 50% of the overall Lake Whitefish production in terms of commercial fishery harvest (Figure 1) (Baldwin et al. 2009).

In Great Slave Lake (GSL), Lake Whitefish provided an important resource for commercial and subsistence users throughout exploration and settlement of the area by the Aboriginal residents (Keleher 1962). After a four-year feasibility study and the construction of roads for transportation and fish processing companies, a commercial Lake Whitefish fishery formally commenced in the Northwest Territories of Canada in the mid-1940s (Rawson 1947, 1949, 1951). Five years later, at its historical peak in harvest, over 4,000 tonnes of Lake Whitefish and Lake Trout (*Salvelinus namaycush*), combined, made it one of the largest commercial fisheries in the Northwest Territories (Figure 2). Along with local socioeconomic development, the Lake Whitefish fishery also experienced striking downturns to around 1,000 tonnes in 1997 and less than 500 tonnes in the mid-2000s. The increase in the Lake Whitefish fishery in the 1970s largely coincided with a decline in Lake Trout and a reduction in minimum gillnet mesh size (Duthie and Flett 1972, Day 2002, Read and Taptuna 2003, Tallman and Friesen 2007).

There are several similarities in Lake Whitefish harvests between the Great Lakes and GSL (Figures 1 and 2): harvests declined since the mid-1990s but increased slightly in recent years. The significant declines in coldwater Lake Whitefish harvests in the sub-polar region, to historically low levels, stimulated growing concerns about the sustainability of freshwater fish populations under cumulative impacts from hydrological modification, exploitation and a warming global climate (Reist et al. 2006, Ficke and Myrick 2007, Pörtner and Peck 2010). In 1972, a fishery-dependent sampling program was initiated for monitoring the Lake Whitefish fisheries in GSL. Through this program, a set of fish biological data on scale age, fork length and dressed weight has been routinely collected. In addition, six experimental netting programs were carried out to investigate gear selectivity by using multiple mesh sizes in 1972 (Bond and Turnbull 1973), 1974 (Bond 1975), 1977 (Moshenko and Low 1978a), 1980–81 (Roberge et al. 1985a), 1996 (Stewart et al. 1999) and 1997–1998 (Day 2002).

Despite realizing the tremendous importance of the fish and observing significant declines in fishery production in GSL, few studies have exclusively examined the relevance of dynamic changes in biological characteristics and hydroclimatic variability. Tallman and Friesen (2007) reviewed temporal changes in Lake Whitefish length and age between 1972 and 1995 when the harvest varied around an average of 1,136 ± 37 tonnes; their results documented an increase in size and age with commercial exploitation. To better understand fish population dynamics, we summarized the spatiotemporal variations in the biological characteristics and evaluated the potential associations of these biological characteristics with cumulative impacts from localized hydrology, meteorology, global climate changes and exploitation over the period from 1972-2004. In particular, alterations in life-history patterns can be monitored by examining growth at age, population size-structure and condition parameters, which may provide indications of resource utilization and the effectiveness of management strategies (Isely and Grabowski 2007). Also, size structure analysis on a fish population as a snapshot can reflect interactions among the dynamic rates of recruitment, growth and mortality (Neumann and Allen 2007).

Furthermore, several measures of fish condition are of keen interest to both fisheries scientists and managers because fish populations in better condition show faster growth rates, greater reproductive potential and higher survival under ideal supporting environmental conditions (Pope and Kruse 2007). The objectives of this study were to:

1) integrate information on fisheries biology from routine fish plant sampling programs during 1972–2004,

2) model time-varying growth at age, size structure and condition index, which emphasize the capacity for population self-regulation under changing biotic and abiotic environments, and

3) evaluate the possible drivers of biological variation under changing environmental conditions that may impact the Lake Whitefish population dynamics in the sub-polar freshwater system.

## MATERIALS AND METHODS

### STUDY AREA

GSL is situated between 61–63° N and 109–117° W, lying in the southwest corner of the District of Mackenzie, Northwest Territories, Canada (Figure 3). The surface area of the lake is $27.20 \times 10^3$ km$^2$ and it has a drainage area of $958 \times 10^3$ km$^2$ (Bond 1975), ranking it the fifth-largest lake (by surface area) in North America. Stretching 440 km from its extreme east end to the outlet of the Mackenzie River, the lake straddles two distinct physiographic regions: the erosion-resistant Precambrian Shield to the east and the Interior Plains to the west (French and Slaymaker 1993, MRBB 2004, Howell et al. 2009). The east arm of GSL is comprised of undulating topography with bedrock outcroppings forming hills and valleys that contain wetlands and lakes. It is much deeper than the rest of the lake, with an average depth of 249 m and a maximum depth of 614 m; GSL is known as the deepest lake in North America (MRBB 2004). The western half of GSL, sitting in the flat Interior Plains, is underlain by thick glacial, fluvial and lacustrine deposits. The surrounding area contains many wetlands and lakes (Woo et al. 2007). The mean depth in the main basin is 41 m with a maximum of 163 m. GSL receives north-flowing waters that connect the interior of the continent and drains into the Mackenzie River through Fort Providence in the southwest. Among those, 77% of the inflow is from the Slave River.

Over an annual cycle, daily air temperature within the Mackenzie River Basin varies between -50 to 30°C; the monthly average temperature typically ranges from -35 to -25°C during winter and between 15 and 20°C during summer (Woo et al. 2007). Water temperatures in the upper 10 m in the central and western parts of the lake are about 7.8°C in July and August (Rawson 1949). Within the entire Mackenzie Basin, annual precipitation shows a strong geographic gradient, exceeding 1,000 mm in the southwest mountainous areas and 300 mm in the northeast (Woo et al. 2007). Located in the southern area of the Arctic Circle, GSL is completely frozen for five and a half months each year. As a result of ice coverage from late-December to early-June, the growing season for aquatic life is rather short. However, lake ice conditions vary significantly from year to year (Blanken et al. 2007).

### DATA COLLECTION

#### Commercial harvest

Lake Whitefish have sustained an important fishery resource in the sub-polar region since 1944 when Rawson (1947) conducted a pioneering study on the potential commercial fisheries.

Because of its unique status, the Lake Whitefish fishery quickly became one of the largest freshwater fisheries in the Canadian Northwest Territories and an important economic asset to many Aboriginal communities. Commercial exploitation primarily targeted Lake Whitefish along with five other valuable species: Lake Trout, Inconnu (*Stenodus leucichthys nelma* (Pallas)), Northern Pike (*Esox lucius* (Linnaeus)), Walleye (*Sander vitreus* (Mitchill) and Burbot (*Lota lota* (Linnaeus)). As seasonal changes of ice freeze-up and break-up in the lake, commercial fisheries can be distinctly separated into summer (from June to September) and winter (from October to May) periods. Throughout the course of fisheries development, commercial harvest data have been compiled into a series of annual reports by Environment Canada and DFO. These long-term datasets record pertinent to Lake Whitefish harvests, including fish by administrative area delivered to fish plants, either on the basis of dressed or round weights. To standardize the weight records, a conversion factor (1.173) was applied to estimate total harvest in round weight (Keleher 1964).

The commercial fisheries have been managed by means of controls on total allowable catch (TAC), fishing effort and spatial restrictions. Seven administrative areas were designated by DFO to manage commercial fisheries in GSL, although the boundaries have been changed slightly over the time series. Before 1979, area III did not exist. Area IW is mainly used for winter fisheries. Almost all of the lake was used for commercial fishing during early fishery development stage; the east arm of GSL (area VI) has been completely closed to commercial fishing since 1974. At present, six administrative areas are designated for commercial fishing (Figure 3). A TAC quota system was applied to the entire lake until 1972 when area-specific TAC quotas were in place. TACs were implemented by setting area-based annual fishable quotas, which were adjusted by monitoring changes in annual harvests. The control of fishing effort involved setting a minimum legal mesh size for commercial gillnets. There was no limit on the number of gillnets that could be used in a single spatial area. The legal minimum mesh size was 140 mm (5½") knot to knot stretched mesh until regulation changes in 1977 when the minimum mesh size became 133 mm (5¼") (Day 2002, Tallman and Friesen 2007). In November 1997, the legal minimum mesh size in areas IE, II, III and IV changed to 127 mm. In areas IW and V the legal minimum mesh size was reduced from 133 mm to 127 mm in May 2000 and November 2000, respectively (Read and Taptuna 2003).

## Biological observations

Through long-term fish plant observation programs, a minimum of 200 Lake Whitefish were sampled from each of the six administrative areas fished during each sampling period. The sampling periods were based on a schedule of winter and summer periods (Read and Taptuna 1997, 2001, 2003). Boxes of fish were randomly selected from the catches of several harvesters as they arrived at fish plants. All Lake Whitefish in the box were sampled, up to a maximum of 70 fish per harvester. A total of 200 Lake Whitefish were sampled from at least three fishers in each administrative area and 10 additional fish were added to compensate for scale samples that were unsuitable for age determination.

During 1972–2004, fork length (measured to the nearest 1 mm) and round or dressed weight (to the nearest 5 g) were observed for a total of 83,838 individuals. Of the measured fish, scales were sampled for age determination from 52,226 individuals. Scale samples were removed from the left side of the fish, from an area just above the lateral line and below the dorsal fin. Many other alternative anatomical structures have been used for age estimates of Lake Whitefish in GSL or elsewhere, such as pelvic fins (Mills and Beamish 1980, Stewart et al. 1999) and otoliths (Roberge et al. 1985a, Hoyle 2005). Despite concerns over the accuracy of age determination from different ageing structures (Muir et al. 2008), scales (refer to unique protocols of Carlander (1969), Weatherley and Gill (1987), Campana (2001)) have become a staple material for age determination in northern Canada (Rawson 1947, 1951, Kennedy 1950, 1953, 1954, Bond

1975, Healey 1975, 1978, 1980, Moshenko and Low 1978a, b, Read and Taptuna 1997, 2001, 2003). For fish up to 20–25 years of age, however, Johnson (1976) found good agreement of age readings between scales and otoliths for Lake Whitefish from the Northwest Territories. Therefore, we considered scale reading a reliable method for ageing fish and reserve the disagreement among different ageing structures for further study.

Growth data on age-specific fork length and round weight were retrieved from the DFO Arctic stock assessment database. To narrow the seasonal differences within age groups, growth data in this study were limited to samples for a sampling period between June and September, 1972–2004. This arbitrary selection was supported by Kennedy (1953) who noted that Lake Whitefish growth is limited to a period from June to September, inclusive. Apart from the archived datasets, we also integrated age-based growth information for the fish from experimental fishery investigations (Bond and Turnbull 1973, Moshenko and Low 1978a, Stewart et al. 1999). To overcome the under-representation by small sample size ($n<5$), the length or weight-at-age growth analysis was limited to the age groups 2-21.

**Statistical analysis**

Three groups of statistical analyses are used to account for the biological characteristics of Lake Whitefish in GSL: the length-weight relationship, condition index and length or weight-at-age growth models. To estimate the coefficients of the allometric functions, paired length and weight data are usually log-transformed (natural logarithms). Logarithmic transformation is generally appropriate because morphological data tend to follow a lognormal distribution, as they are non-negative, with a positively-skewed distribution and variance that increases with the mean (Ebert and Russel 1994). We used four candidate numerical models, linear (LM), quadratic (QM), cubic (CM) and piecewise (PW, or broken-stick), to examine log-transformed length-weight relationship for Lake Whitefish. The QM and CM models assume that model parameter $b$ changes continuously with increasing body size, represented by polynomial functions. The PW model uses two straight line segments with different slopes that intersect at $L=C$, which assumes a marked morphological change (eq. 1).

$$LM: \log(W) = a_1 + b_1\log(L)$$

$$QM: \log(W) = a_1 + b_1\log(L) + b_2(\log(L))^2$$

(1)    $$CM: \log(W) = a_1 + b_1\log(L) + b_2(\log(L))^2 + b_3(\log(L))^3$$

$$PW: \log(W) = \begin{cases} a_1 + b_1\log(L), \log(L) \leq \log(C) \\ a_1 + (b_1 - b_2)\log(C) + b_2\log(L), \log(L) > \log(C) \end{cases}$$

Here, $L$ and $W$ are measured morphologic characters for fork length (mm) and round weight (g); $a$ and $b$ are the intercept and slope of the individual regression models, respectively.

To judge the best model performance among the candidate models, multi-model inference (MMI) was employed in terms of the small-sample, bias-corrected form of the Akaike information criterion (AIC), $AIC_c$, for model selection (Burnham and Anderson 2002, Anderson 2008). The model with the smallest $AIC_c$, $AIC_{c,min}$, was selected as the 'best' among the candidate models tested. The $AIC_c$ differences to $AIC_{c,min}$, $\Delta_i$, were computed for all of the candidate models. To quantify the plausibility of each model, given the data and the set of four models, the 'Akaike weight', $w_i$, is considered the weight of evidence in favor of model $i$ being the actual best model of the available set of models (eq. 2).

$$AIC = n\left(log\left(2\pi\frac{RSS}{n}\right) + 1\right)$$

$$AIC_c = AIC + \frac{2k(k+1)}{n-K-1}$$

(2)     $\Delta_i = \left| AIC_{c,i} - AIC_{c,min} \right|$

$$W_i = \frac{exp(-0.5\Delta_i)}{\sum_{i=1}^{4} exp(-0.5\Delta_i)}$$

where RSS is the residual sum of squares, *n* is the number of observations and *k* is the number of regression parameters plus 1. According to Burnham and Anderson (2002), models with $\Delta_i < 4$ have substantial support, while there is considerably less support for models with $4 < \Delta_i < 10$. Models with $\Delta_i > 10$ have essentially no support and might be omitted from further consideration;

After determining the best model, the average model or model-based average is applied to generate adjusted model parameters and residuals in terms of $w_i$ values. In LM, the allometric exponent *b* does not change as fork length changes. In models QM and CM, the exponent *b* is assumed to change continuously as fork length varies, following the first derivative of log-transformed weight with respect to log-transformed fork length. In PW, it is assumed that the allometric exponent takes two constant values, $b_1$ and $b_2$, before and after the breakpoint $L=C$ (eq. 3).

$$LM: b = b_1$$

$$QM: b = b_1 + 2b_2 \log(L)$$

(3)     $CM: b = b_1 + 2b_2 \log(L) + 2b_3 (\log(L))^2$

$$PW: b = b_1 \ \big| \ L < C$$

$$PW: b = b_2 \ \big| \ L \geq C$$

Condition index or the Fulton factor (Ricker 1975, Pope and Kruse 2007) is commonly used as a standard measure of energy reserve, growing condition and even habitat quality. Fish in good condition are expected to manifest a faster growth rate, greater reproductive potential and a higher survival rate than poorer-conditioned counterparts under comparable environmental conditions (Blukacz et al. 2010). The consequences of ideal ecological processes will ultimately be reflected by a series of biological indicators, such as a higher condition index. With respect to altered aquatic environments, therefore, the condition index, if interpreted appropriately, can characterize components of ecological and physiological processes affecting fisheries production and improve our understanding of population dynamics (Pope and Kruse 2007). Two condition indices are used in this study: Fulton's condition index ($K_F$), which is frequently used to describe the relative plumpness of fish, was estimated for Lake Whitefish using the formula (eq. 4),

(4)     $K_F = \frac{W}{L^3} x 10^5$

And the relative condition index, $K_{LC}$ (Le Cren 1951) (eq. 5),

(5)     $K_{LC} = \frac{W}{W'} x 100$

Here, *w'* is the length-specific round weight predicted by the average model in eq. (1) and AIC weight ($w_i$), which is incorporated with MMI (eq. 2).

Changes in length-at-age were described as size growth, commonly represented by the von Bertalanffy growth equation (VGM; von Bertalanffy 1938). There is no inflection point in length growth with increasing age. However, for many aquatic animals there are models that combine sigmoid curves to portray the growth trajectories by an explanatory variable *t*, such as the generalized von Bertalanffy growth model (GGM; Pauly 1979) and the logistic growth model (LGM; Ricker 1975).

$$VGM: L_t = L_\infty \left[ 1 - e^{-K(t-t_0)} \right]$$

(6) $$GGM: L_t = L_\infty \left[ 1 - e^{-K(t-t_0)} \right]^p$$

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

where, $L_\infty$, *K* and $t_0$ are model parameters of the asymptotic size attainable by the average fish if it could grow throughout its life, the Brody growth rate and time when length approaches zero, respectively (Ricker 1975). The exponent, *p*, is a dimensionless shape parameter.

The growth rate was differentiated from the original growth model to indicate changes in length by age,

$$VBM: dL_{a,t} \,/\, dt = \left( L_{a,\infty} - L_{a,t} \right) K_a$$

(7) $$GGM: dL_{a,t} \,/\, dt = L_{a,t} K_a P_a \times \frac{e^{-K_a(t-t_0)}}{1 - e^{-K_a(t-t_0)}}$$

$$LGM: dL_{a,t} \,/\, dt = L_{a,t} K_a e^{-K_a(t-t_0)} \times \left[ 1 + e^{-K_a(t-t_0)} \right]^{-1}$$

Where, subscript *a* specifies a temporal-specific parameter. $dL_{a,t}$ is the growth rate in year *a* and age *t*; it is assumed to follow a normal probability distribution. The hierarchical growth process is implemented in the model through a multi-level prior of temporal-specific parameters in the population growth model.

To run hierarchical Bayesian growth models (eq. 6), we constructed four model scenarios describing time-varying or invariant model parameters $L_\infty$ and *K*,

LCKC: constants in both $L_\infty$ and *K*, which is the conventional VBGE model

LCKV: constant $L_\infty$ and varying *K*

LVKC: varying $L_\infty$ and constant *K*

LVKV: varying both $L_\infty$ and *K*

Two kernel hyper-parameters, $L_{a,\infty}$ and $K_a$, are assumed to follow lognormal distribution functions with log-transformed mean $L_{a,\infty}$ and $K_a$ as well as their variances $\sigma^2_{L_\infty}$ and $\sigma^2_K$, as indicated in equation (6).

(8) $$L_{a,\infty} \sim \log normal\left( \overline{L}_\infty, \sigma^2_{L_\infty} \right)$$

$$K_a \sim \log normal\left( \overline{K}, \sigma^2_K \right)$$

Bayes' theorem, combined with a prior from a likelihood function and normalization, produces a posterior probability distribution, which is the conditional distribution of the uncertain quantity given the data. In the case of growth processes for Lake Whitefish in GSL, a non-hierarchical Bayesian growth model represents a posterior density for parameters ($p(\theta|\mathrm{d}L_{a,t})$) using Bayes' theorem,

$$(9) \qquad p\left(\theta = L_{a,t}K_a \mid dL_{a,t}\right) = \frac{\prod_a f(dL_{a,t}|\theta)\pi(\theta)}{\int_{-\infty}^{+\infty}\prod_a f(dL_{a,t}|\theta)\pi(\theta)d\theta}$$

For a hierarchical Bayesian growth model, it assigns hyper-parameters to yield joint posterior distributions,

$$(10) \qquad p\left(\theta' = L_a, K_a, \overline{L}_\infty, \overline{\sigma}_{L_\infty}, \overline{\sigma}_K \mid dL_a\right) =$$

$$\frac{\prod_a f\left(dL_a \mid L_{a,\infty}, K_a\right)\pi_1\left(L_{\infty,a}|\overline{L}_\infty, \overline{\sigma}_{L_\infty}\right)\mu_1\left(\overline{L}_\infty\right)v_1\left(\overline{\sigma}_{L_\infty}\right)\pi_2\left(K_a|\overline{K}, \overline{\sigma}_K\right)\mu_2\left(\overline{K}\right)v_2(\overline{\sigma}_K)}{\int_{-\infty}^{+\infty}\prod_a f\left(dL_a \mid L_{a,\infty}, K_a\right)\pi_1\left(L_{\infty,a}|\overline{L}_\infty, \overline{\sigma}_{L_\infty}\right)\mu_1\left(\overline{L}_\infty\right)v_1\left(\overline{\sigma}_{L_\infty}\right)\pi_2\left(K_a|\overline{K}, \overline{\sigma}_K\right)\mu_2\left(\overline{K}\right)v_2(\overline{\sigma}_K)d\theta'}$$

In the above mathematical expressions, $f(dL_a|\theta)$ is the probability density function of $dL_a$ on parameter vector $\theta$; $u_1(L_\infty)$ and $v_1\left(\sigma_{L_\infty}\right)$ are the median and variance vectors of the probability distribution density functions of $L_\infty$ and $\sigma_{L_\infty}$, respectively.

The implementation of these Bayesian models requires specification of the prior distributions of all unobserved quantities. Two types of priors are adopted to compose probability distribution functions of model parameters: informative and non-informative priors. Informative priors, based on literature values, are used to specify the probability distribution functions of modeled parameters, such as $L_\infty$ and $K$, to take into account the initial values. The reported average values for $L_\infty$ were 596 and 572 mm for female and male Lake Whitefish in the Great Lakes, and 558 and 544 mm in southern inland waters, respectively (Beauchamp et al. 2004). Cook et al. (2005) documented $L_\infty$ (total length) values of 634 (females) and 569 mm (males) for Lake Erie Lake Whitefish during 1989–1994, and 593 (females) and 576 mm (males) during 1995–2001. By integrating multiple datasets, Zhu and Johnson (unpubl. data) estimated growth parameters for Lake Erie Lake Whitefish and derived $L_\infty$ (total length) of 627.53 mm and $K$ of 0.2522. Bronte et al. (2003) reported Lake Whitefish growth patterns in Lake Superior, where $L_\infty$ ranged within 453–719 mm, with a median of 631.48 ± 18.55 mm in fork length, and $K$ was 0.156–0.496, with a median of 0.214 ± 0.017. In addition, in fishbase, $L_\infty$ values ranged between 440 and 798 mm total length, and 462 and 634 mm fork length. Our long-term biological measurements in GSL documented a maximum size of 648 mm fork length. After combining literature reviews and accumulated data sets, the boundaries for undifferentiated $L_\infty$ were set to 450 and 720 mm. For prior $K$, the Brody growth rate, Beauchamp et al. (2004) reported that $K$ values for female and male Lake Whitefish were 0.251 and 0.275 in the Great Lakes, and ranged between 0.22 and 0.231 in inland waters, respectively. The accumulated information on growth parameter $K$ provided a range of 0.156 to 0.496, with a median of 0.232 ± 0.014. Thus, the initial values for $K$ sampling boundaries were set to 0.1 and 0.5.

A critical issue when using the Markov chain Monte Carlo (MCMC) method is to determine when random samples have converged to the posterior distribution and incorporated the full range of uncertainties. Using OpenBUGS, we executed two chains (300000 iterations each) of Metropolis-Hasting with Gibbs sampling. Following a burn-in period of 50000 iterations, a total of 5000 samples for each chain were obtained by sampling in a thin of the 50th iteration to avoid highly auto-correlated neighboring values (Spiegelhalter et al. 2002). Model convergence and stationarity were diagnosed using the R-based evaluation package CODA (Convergence

Diagnosis and Output Analysis, version 0.13-5) for Gibbs sampling output (Plummer et al. 2006, Ntzoufras 2009). We used four available diagnostic tests to examine the model convergence and stationary under the combinations of initial model parameters. Of four diagnostic tests, the Geweke test was used to check for convergence of the mean of each posterior parameter, separately, from a single chain if the critical value |Z|<2. The Gelman-Rubin test examines a shrinking factor R≤1 through an ANOVA-type convergence test for multiple chains. The Raftery-Lewis diagnostic test focuses on the pre-specified degree of accuracy for specific quantiles instead of convergence of the mean. It is also very useful for testing the appropriateness of the values for burn-in, thin and total iterations. The fourth convergence diagnostic test, the Heldelberger-Welch test, is used to determine if stationarity of the Markov chain samples is achieved by examining single chains from univariate observations. Each test has the specific purpose of testing for convergence diagnosis (Carlin and Louis 2009).

The deviance information criterion (DIC) with *a priori* parsimonious predictive Bayesian statistics was employed to measure relative goodness of fit for the structural models that profiled the complexity and instability resulting from a particular parameterization (Burnham and Anderson 1998, McAllister and Kirkwood 1998, Millar and Meyer 2000, Spiegelhalter et al. 2002, Carlin and Louis 2009). As a generalization of the AIC that is based on the posterior distribution of the deviance statistic, DIC can be expressed as,

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

$$DIC = 2\overline{D} - \widehat{D}$$

(11)     *or*

$$DIC = \overline{D} + pD$$

$$pD = \overline{D} - \widehat{D}$$

where $f(y|\theta)$ is the likelihood function for the observed data vector *y* given the parameter vector $\theta$, and $h(y)$ is a standardization function of the data alone (Carlin and Louis 2009). $\overline{D}, \widehat{D}$ and *pD* are the posterior mean of the deviance as a measure of fit, the deviance of the posterior mean and the effective number of parameters as a measure of complexity in a Bayesian model, respectively (Lunn et al. 2009). DIC values are scale-free and have no intrinsic meaning. Similar to AIC, the minimum DIC value estimate will make the best short-term predictions (Lunn et al. 2009, Ntzoufras 2009). Therefore, it offers a straightforward means of comparing different models when using the same observed data.

Spiegelhalter et al. (2002) suggested that if models differ by only one or two DIC units then one cannot distinguish between the two models. If models differ by three to seven DIC units there is some support for the first model but the second model is clearly better. If the difference in DIC is greater than 10, essentially no support is found for the model with the higher DIC. Following the MMI (Burnham and Anderson 2002; Gelman 2006) strategies, the best growth models were determined with regard to a criterion of the smallest DIC and model-based average methodology was applied to project growth patterns of area-specific fish populations in GSL.

Pairwise correlation analysis was used to examine how variations in these biological parameters of Lake Whitefish relate to the changing local weather, hydrology, large scale climate-related environmental factors and exploitation in GSL system. Three significant levels, α=0.05, 0.01, and 0.001, were set if statistics tests like simple correlation and analysis of variance (ANOVA). All conventional statistical analyses were conducted with Stata version 11.

## RESULTS AND DISCUSSION

### RELATIONSHIPS BETWEEN FORK LENGTH AND ROUND WEIGHT

Over all of the administrative areas, minimum and maximum measurements for Lake Whitefish were 286–648 mm, 250–4692 g and for fork length and round weight, respectively (Table 1). Fish with smaller average sizes were recorded in the deeper area IV, with an average fork length 408.78 ± 0.22 mm, round weight 1040.54 ± 1.88 g and dressed weight 887.09 ± 1.60 g, respectively. Larger fish appeared in the shallow area IW, with an average fork length of 425.86 ± 0.35 mm. In terms of individual-based weight, larger fish were found along the shallow southern shore, in area III, with average round and dressed weights of 1166.17 ± 3.99 g and 994.17 ± 3.40g, respectively.

Conventionally, fish fork length and round weight relationships are described by a power function (Figure 4). The intercepts of simple linear models (LM) varied between -11.08 and -9.68, while the slopes ranged between 2.77 and 3.09. By including all of the observed samples in the statistical models, we found that Lake Whitefish growth patterns along the southern shore of GSL tended to be isometric ($b \approx 3$), compared with fish from deeper waters in areas IV and V ($b \approx 2.8$). The exponent value in deeper waters, $b<3$, indicated that fish growth followed a negative allometric relationship in a much slenderer form. It is well known that the value of coefficient $b$ represents the body form and directly demonstrates the effects of ecological factors, such as temperature, food supply, spawning condition, sex, age and season, as well as fishing effort and mesh size on recorded weight (Ricker 1973). When $b=3$, the body increases in all dimensions in the same proportion as it grows; this is termed isometric growth. If $b>3$, fish growth follows a positive allometric relationship with a much broader and deeper form. The numeric value of $b$ is almost always between 2.5 and 3.5 (Weatherley and Gill 1987). Differences in the allometric exponent $b$ may reflect the adaptive outcomes of fish living under different conditions.

Combined with four candidate models, the regression parameters and the corresponding $AIC_c$, $\Delta_i$ and $w_i$ values are summarized in Table 2. In terms of $AIC_c$ and $\Delta_i$, model PW was considered the best for Lake Whitefish in areas IW, IE and III (Figure 5), and model CM was the best in areas II, IV and V (Figure 6). Model QM only received less support in area IW (Table 2). However, the LM model was not supported in any of the areas, despite being the most commonly selected model. Using the PW model, breakpoint ranges in the regression slope were found at 392, 380 and 441 mm in shallow areas IW, IE and III, respectively, while in deep waters, they varied from 372 mm in area IV to 446 mm in area V and 460 mm in area II.

In terms of $w_i$ (Table 2), the relationship between measured morphometric pairs was best expressed by a single model, either model PW in area IE or model CM in areas II and IV. In the remaining administrative areas, $w_i$ indicated multi-model support of the length-weight relationship. In area IW, the length-weight relationship was substantially supported by the PW model whilst QM and CM models seemed to partially support this relationship as well. In areas III and V, the relationship was substantially supported by a combination of CM and PW. With regard to the multi-model supports, MMI were applied to the average model from a reconciliation of the relative contribution of $w_i$. Overall, it is evident that a simple linear model (LM) did not support the log-transformed length-weight relationship. From the quadratic fit of the residuals, it is clear that the assumption of linearity is more or less violated as the residuals of LM displayed either wider variation or evident curvature (Figure 5). The situation was clearly improved with the average model, especially in shallow areas (IW, IE, and III) and deep waters (area V). The residuals in areas II and IV were similar to the earlier results because of the prevalence of a single model (CM).

When studying allometric growth, linear regression models with log-transformed length-weight data are always the default option because it is conceptually and mathematically simple to estimate model parameters. Checking for breakpoints is very rare. The basic LM assumes that allometry does not change as body size increases. However, this assumption is usually violated by biological variation in somatic and gonadal development, seasonal changes in prey supply and population density (Weatherley and Gill 1987). During ontogeny, growth is a three-dimensional process, with an individual's length, width and depth changing over time. Therefore, the growth process is described by the simplest assumption that individual length, width and depth change continuously in proportion to one another with a constant allometric exponent - isometric growth (Quinn and Deriso 1999). However, fish species commonly exhibit changes in their allometric exponents. The present study indicates that information may be lost when linear models are selected arbitrarily, regardless of the existence of optional models. In all cases, the candidate models, CM, PW or QM, provided partially or substantially-supporting information on transitions in size increments while some characteristic pitfalls occurred because of a lack support by LM. By using the curvature exponent, the discontinuity is expressed as a breakpoint. More specifically, the existence of breakpoints (i.e., points of discontinuity in slope $b$) has been recognized since the allometric function was first proposed (Huxley 1932). However, estimating breakpoints visually is not appropriate and the use of regression models provides a better alternative (Hall et al. 2006). The location of the growth transition varies with fish in particular habitats or life stages. In areas IW and IE, there was a change from positive ($b>3$) to negative allometry ($b<3$), which was maintained invariantly. Fish in the remaining areas showed a discontinuity in allometry, from positive to negative and back, suggesting an evident shift during somatic development. Combined with information on migration, ontogeny and mortality, discontinuities can be useful since they can be caused by marked events in the life history of the species or fast ecological changes. Quite often, maturity can cause distinct changes in morphology and should be considered an important clue for addressing variability in population growth and reproductive schedules. In the present study, a marked breakpoint, ranging from 372 to 460 mm, was identified over spatial areas. There might be a transition in the ontogenic development of life history, such as maturity, of the species or fast ecological shifts responsible for this breakpoint. Roberge et al. (1985b) investigated the fall spawning run of Lake Whitefish in the Little Buffalo River, Northwest Territories, and documented average fork lengths of 376 and 389 mm in 1975 and 1979, respectively. These values are in the range of the breakpoints found in this study, despite variation among years. Wang et al. (2008) reported that the total length at which 50% of individuals were mature was 412–493 mm for male and 456–538 mm for female Lake Whitefish in the Great Lakes. Applying a fork length to total length conversion factor (1.118), the range of the breakpoint in GSL was derived as 416–514 mm in total length for Great Lakes Whitefish. Combined with studies on reproductive biology, we suggest the existence of a growth breakpoint in the fork length of Lake Whitefish in GSL, which coincides with 50% of mean size-at-maturity. Beauchamp et al. (2004) suggested there was inverse co-variation between age-at-maturity and the pre-reproductive growth rate in Great Lakes Whitefish. However, a significant shift in ages 3–4 can be seen between age- and length-at-maturity for Lake Whitefish in both the Great Lakes and inland waters (refer to Figure 3 in Beauchamp et al. 2004), supporting our hypothesis regarding changes in morphological attributes at first maturity. Therefore, spatial variation in allometric growth in fork length and round weight in GSL Lake Whitefish can indirectly reflect both plastic and adaptive responses to changes in exploitation, the environment and population abundance.

## CONDITION INDEX

Two condition indices were used in this analysis: $K_F$ and $K_{LC}$. During 1972–2004, $K_F$ values varied between 0.53 and 3.76 (mean = 1.50 ± 0.01). The other index, $K_{LC}$, ranged between

38.81 and 255.63, with an overall average of 100.58 ± 0.04. Despite different scales, the two condition indices were correlated ($r^2$=0.94, $p$<0.001). Being calculated from morphometric measurements of length and weight, $K_F$ seemed to be significantly size dependent, while $K_{LC}$ displayed no significant length-related bias which was ascribed as random variation of intra-population straits (Svanback and Ekov 2004, Rennie and Verdon 2008). Therefore, we selected $K_{LC}$ to further analyze spatiotemporal patterns over month, administrative area and mesh-size.

Using log-transformed fork length as a covariate, a significant difference in the relative condition index $K_{LC}$ was found, with significant interactions among month, administrative area, mesh size and fork length (ANCOVA, $F$=11.34, $p$<0.001). Among these explanatory variables, a marginal effect of fork length on $K_{LC}$ was found ($F$=4.78, $p$=0.03) and highly significant effects of month, administrative area, and mesh size were detected (Table 3). One-way ANOVA illustrated significant temporal differences in $K_{LC}$ under changing mesh size, from 127 mm ($F$=26.61, $p$<0.001), to 133 mm ($F$=195.82, $p$<0.001) and 140 mm ($F$=73.24, $p$<0.001). Using a Bonferroni multiple comparison test, monthly-averaged $K_{LC}$ decreased considerably with a mesh size of 127 mm, from 103.86 ± 0.68 in February, to 99.85 ± 0.33 in July and 96.78 ± 0.46 in September. However, there was no significant difference in $K_{LC}$ between March and August ($p$=0.285) or September ($p$=0.689), suggesting that similar condition states existed in winter and late summer seasons (Figure 7). When a mesh size of 133 mm was employed, monthly differences in $K_{LC}$ were found, especially between periods from August through October and from November to July. The mean values of the lowest and highest $K_{LC}$ periods were 96.01 ± 0.27 in October and 101.69 ± 0.09 in January. When the mesh size was increased to 140 mm, the lowest $K_{LC}$ value occurred in August. $K_{LC}$ in September was not significantly different from June ($p$=1.00) or August ($p$=1.00). Comparing $K_{LC}$ values under all three mesh sizes, average $K_{LC}$ was 101.65 ± 0.07, 98.50 ± 0.10 and 98.91 ± 0.10 in July, August and September, respectively. It is evident that $K_{LC}$ tended to increase with mesh-size, from 98.15 ± 0.20 with 127 mm mesh, to 99.15 ± 0.06 with 133 mm mesh and 102.61 ± 0.10 with 140 mm mesh, respectively.

However, two-way ANOVA found significant differences in Lake Whitefish condition index values from year ($F$=918.74, $p$<0.0001), area ($F$=96.11, $p$<0.0001) and the interaction between month and area ($F$=48.58, $p$<0.001). Over years, reductions in mesh size occurred in 1977 and during 1997 through 2000. During 1976–1979, historically low condition index values were detected across all areas (Figure 8). Since 1980, condition index values seem to have declined steadily, except in area III. When the legal minimum mesh size changed from 133 to 127 mm, $K_{LC}$ seemed to be unaffected. Because of increases in operating costs, some fishers still favour using a mesh-size of 133 mm.

## SIZE COMPOSITION

Size composition analysis included examining temporal variation in fork length, round weight and age. Two-way ANOVA showed that highly significant variation in Lake Whitefish fork length occurred over month ($F$=58.51, $p$<0.001), area ($F$=123.76, $p$<0.001), mesh size ($F$=35.45, $p$<0.001) and their interactions ($F$=26.73, $p$<0.001) (Table 4). Similarly, highly significant variation in round weight occurred by month ($F$=22.7, $p$<0.001), area ($F$=80.57, $p$<0.001), mesh size ($F$=45.17, $p$<0.001) and their interaction terms ($F$=35.76, $p$<0.001). Statistical analyses showed no significant correlations between either fork length or round weight and year at the critical level $\alpha$=0.05 (Figure 9). This suggested that despite dynamic inter-annual variations in fork length, there were no pronounced temporal patterns in size variation. Instead, inter-annual changes in fork length and round weight varied in diverse ways. The values were dynamic and decreased in areas IW (CI: 3.92% in length and 14.03% in weight), IE (CI: 1.71% in length and 6.84% in weight) and III (CI: 2.28% in length and 10.56% in weight). Size measurements showed slight increases in deeper waters, such as area IV (CI: 1.72% in length and 6.80% in

weight). In particular, average round weight decreased significantly over years in the eastern south shore areas (area IE: $r$=-0.3788, $p$=0.0427, area III: $r$=-0.6038, $p$=0.0023).

Using either log-transformed fork length or round weight as a covariate, ANCOVA found no significant impacts on Lake Whitefish age structure (Table 5), but significant differences appeared by year, area, the covariate and interaction between mesh size and the covariate. Area-specific average ages for Lake Whitefish increased through years in areas IE, IV and V ($p$<0.05), whereas no significant temporal patterns were found in areas IW, II and III (Table 6, Figure 10). Marginal impacts on the age composition were observed when the interaction between year and mesh size was considered.

Comparing changes in fork length, round weight and age over years and areas (Figure 9 and 10), it seemed that Lake Whitefish growth rates tended to decline gradually. Despite the gradual reductions in mesh sizes in 1977 and 1997–2000, reductions in body size and age were only discernable after 2–3 years (Figures 8 and 9). Our results using the Lake Whitefish dataset spanning 1972–2004 showed slight differences from a similar analysis by Tallman and Friesen (2007) that used data covering 1972–1995. Evident decline in fisheries yield (Figure 2) coincided with weak temporal trends in fork length and round weight. If the biological samples were sufficient and representative, the reduction in fisheries yield would clearly signify more surplus production and hyperstability for the Lake Whitefish population. However, the data were gathered exclusively using gillnets with limited mesh-sizes during biased commercial fisheries. The selectivity of gillnets creates a critical concern when commercial gillnets are used to assess growth and age structure. To reflect the status of the entire population, multi-mesh sampling protocols are recommended to obtain representative samples of the entire fish population (Jensen 1995). Moreover, the legal minimum mesh size changed at least three times. The effects of these changes in mesh size need to be separated from the samples when fishery-independent surveys using multiple mesh-sizes are not available.

## MODEL CONVERGENCE DIAGNOSES

For the Geweke diagnostic test, LVKV yielded a higher proportional convergence (>90%) of the model parameters than those of other models, which suggested there were no significant differences among the chains given the different initial values (Table 7). Lower proportional convergence (<50%) occurred in area IW with the GGM-LCKC model and in area V with LGM-LVKC.  For the Gelman-Rubin test, as much as 50% of the model parameters did not pass the tests in LCKC scenarios; better model behaviour was found with LVKV. Using bridge theory, the Heldelberger-Welch test showed that all of the growth model scenarios, except GGM-LCKC in area IE, were better model scenarios, with effective tests of stationarity and halfwidth occurring more than 94% of the time. In terms of the Raftery-Lewis diagnosis, the average dependence factor over all of the model parameters ranged between 50 and 64, with a grand mean of 51.46 ± 0.28. Combined with these stationarity tests, we found that a burnin period of 50000 and a thin interval of 50 were large enough to avoid local autocorrelations in the MCMC runs.

## MODEL SELECTION AND UNCERTAINTY

Of the hierarchical Bayesian growth models created for GSL Lake Whitefish, the best model ascribed by the smallest DIC value, the generalized growth model (GGM) with variation in both $L_\infty$ and $K$ (LVKV), was selected in shallow areas (IW, IE and III), and the model scenario that incorporated constant $L_\infty$ and varying $K$ (LCKV) was the best in deep areas (II, IV and V). The other models, in order of ascending DIC values and decreasing complexity ($pD$), were the logistic growth model (LGM) and the von Bertalanffy growth model (VBM) incorporated with LVKC, LCKV and LCKC scenarios (Table 8). The extent of the difference in DIC between LVKV and LCKV of the GGM provided substantial support or showed no meaningful difference in

areas IW, IE, III and V. Parameter *pD* is used to assess the effective number of parameters under two general conditions: approximately normal likelihoods and negligible prior information (Spiegelhalter et al. 2002). The negative values in the LCKC model scenario indicated that the posterior mean was a poor summary statistic when this anomaly occurred in models with very asymmetric posterior distributions (Carlin and Louis 2009). Similar to MMI by AIC, the differences ($\Delta_i$) and weights ($w_i$) between minimum and individual DIC values showed that scenarios LVKV and LCKV in GGM were better interpreted for the growth patterns of the fish, both in southern shallow waters (areas IW, IE and III) and in the deep area V. In the remaining deep areas (II and IV), fish growth was significantly characterized by GGM-LCKV. Therefore, of the three growth models, VBM and LGM were not considered ideal models and might be omitted from further consideration of Lake Whitefish growth patterns.

Using hierarchical Bayesian-structured models, the underlying uncertainties were separated into process ($\sigma^2$), observation ($\tau^2$) and hierarchical variance in $L_\infty$ ($\tau_{L\infty}^2$) and $K$ ($\tau_K^2$) (Table 8). Individual uncertainties in the best fit model, GGM-LVKV, showed a larger observation error $\tau^2$ and a smaller processor error $\sigma^2$ than in GGM-LCKV. With respect to hyper-parameters in the hierarchical model settings, the largest hierarchical uncertainties appeared in the scenario of constant parameters for $L_\infty$ and $K$ (LCKC). Spatial changes in individual uncertainties led to the smallest process errors and the largest time-varying errors ($\tau_K^2$) in deeper waters (areas II, IV and V), while larger process errors and smaller time-dependent $\tau_{L\infty}^2$ and $\tau_K^2$ appeared in shallow waters (areas IW, IE and III) (Figure 11). Two neighboring areas, IW and IE, showed significant differences in all uncertainty components ($|t|>33.29$, $p<0.001$).

In terms of goodness of fit of parameter estimates and DIC comparisons, the best fit of the GGM with LVKV and LCKV scenarios passed nearly all of the convergence and stationary diagnostics used for the two chains. Szalai et al. (2003) employed maximum likelihood estimates in [ADMB](ADMB) (automatic differentiation model builder) to model time-varying growth of Bloater, *Coregonus hoyi*, in Lake Michigan. He and Bence (2007) applied a hierarchical Bayesian approach to Lake Trout growth in Lake Huron and concluded that a model with varying growth parameters outperformed a model with time-invariant parameters, based on DIC values. Our growth model analyses further supported of time-varying growth characteristics of fish populations under changing population density, prey-predator rationale and exploitation pressure. Of the four hierarchical Bayesian growth models, LCKC is one of the most frequently used models for estimating von Bertalanffy growth model parameters. In our analysis, the LCKC-based VGM was the worst model.

## GROWTH PATTERNS

The relationships between fork length and round weight with age are illustrated in Figures 12 and 13. Across administrative areas, growth in fork length by individual fish was characterized by a non-linear relationship with age. As a result of mixed seasonal fisheries, variations in the measurable quantities of fork length and round weight per age group were quite apparent in terms of the fishery-dependent collections.

In the light of multiple model inference (MMI), two kernel growth parameters, $L_\infty$ and $K$, were further analyzed by means of the best model, GGM with LVKV and LCKV scenarios. The resulting average posterior values of $L_\infty$ and $K$ changed with area and through the time series, ranging from 492.80 to 553.13 mm and 0.1000 to 0.1630, respectively (Figure 14). Spatially, posterior $L_\infty$ varied between 493 and 504 mm in deeper areas (IV and V), 506 and 553 mm along the southern shore (areas IW, IE and III) and was 536 mm, with very dynamic variation, in transitional nearshore-offshore waters (area II). For the posterior parameter $K$, the average value over years was smallest and less dynamic ($K$=0.1168, CI=5.01%) in the shallow area IW, and largest and most dynamic in area IV ($K$=0.1343, CI=11.11%). Throughout the time series,

there was a tendency for steady decreases in both growth parameters, but no statistically pronounced variations were found. This was consistent with an earlier study by Kennedy (1953), which suggested there was a spatial increase in growth rate along a southwest to northeast gradient in the lake.

Joint posterior hyper-parameter distributions of $K$ and $L_\infty$ differed substantially among areas and years 1972, 1982, 1992 and 2002 (Figure 15 and 16). As $K$ increased, the posterior parameter $L_\infty$ diminished quickly, following a negative exponential function. The relationship between the hyper-parameters was not linear, as was described by the traditional growth model—VBM (Beauchamp et al. 2004). Negative linear correlations between $L_\infty$ and $K$ were much more significant in LVKV (Figure 15) ($r$: -0.4436~-0.7305, mean: -0.5855, $p<0.001$) than in LCKV ($r$: -0.3083~-0.6047, mean: -0.4462, $p<0.001$). ANOVA for spatiotemporal changes in the hierarchical growth parameters, $L_\infty$ and $K$, showed significant differences in both parameters among areas ($L_\infty$: $F=1048.75$, $p<0.001$; $K$: $F=7.79$, $p<0.001$). In fact, smaller and slower-growing fish appeared in the deep waters (areas IV and V), while larger and quicker-growing fish were distributed in the shallow waters, especially in area IW. In shallow waters in the southern shore areas, these two prime parameters jointly influenced the growth increments, but only parameter $K$ was responsible for changes in fish growth traits in deep waters. Combined with temporal variations in both hyper-parameters, the weighted average of the posterior growth parameters of GGM-LCKV and LVKV demonstrated faster Lake Whitefish growth in the 1980s, an intermediate rate in the 1970s and gradually slower rates from the 1990s onward (Figure 17). Over the whole time series, there was no explicit temporal patterns in both parameters ($L_\infty$: $F=2.05$, $p=0.11$; $K$: $F=0.07$, $p=0.97$). Therefore, our study did not provide clear evidence of a decline in growth rate and condition in Lake Whitefish, as has been observed in Lakes Michigan and Huron (Ebener et al. 2008, DeBruyn et al. 2008, Brenden et al. 2010). Beauchamp et al. (2004) compared Lake Whitefish growth patterns in the Great Lakes and inland lakes; they documented smaller $L_\infty$ (females 558 mm and males 544 mm) and a lower growth rate $K$ (females 0.22 and males 0.231) in inland lakes compared with fish in the Great Lakes ($L_\infty$: 596 mm for females and 572 mm for males, and $K$: 0.25 for females and 0.275 for males). The grand averages of $L_\infty$ and $K$ for Lake Whitefish in GSL were 522.22 ± 1.66 mm and 0.1253 ± 0.0010, which are equivalent to 89% (522.22/584) and 48% (0.1253/0.2655) of the parameter values in the Great Lakes, respectively.

## POSSIBLE DRIVERS OF BIOLOGICAL VARIATION

In this study, we examined time-varying biological characteristics, especially in the context of fork length and round weight relationships, condition index and growth patterns of Lake Whitefish populations in GSL over the period 1972–2004. Using conventional and Bayesian statistics, the present interpretation uncovered significant spatiotemporal variations in Lake Whitefish biological characteristics that are related to both intrinsic attributes and the capacity for environmental adaptation. In addition to the population capacity for self-regulation, we also addressed the linkage between biological productivity and a series of cumulative impacts from the local hydrographic and ecological changes in the lake ecosystem. In connection with predator-prey paradigms, several studies found that Lake Whitefish population dynamics were largely subject to a series of hydroclimatic processes in the Peace-Athabasca-Slave systems (Prowse et al. 2006), atmospheric teleconnections of climate change (Reist et al. 2006) and exploitation (Rouyer et al. 2008, Pörtner and Peck 2010). Of the dynamic processes that occur in the river-lake system, the remarkable dynamics in the water resources in the Slave-Mackenzie River Basins have imposed pronounced impacts on the hydroclimatic controls of GSL (Gibson et al. 2006a, b, Prowse et al. 2006). Considering the mixture of environmental changes and the cumulative impacts from both localized and global vectors, we were specifically interested in the potential drivers accounting for the biological traits of GSL Lake

Whitefish. This issue was addressed by examining available data on the hydroclimate (water level and flow runoff in the Slave River at Fitzgerald), local meteorology (air temperature and precipitation in Yellowknife) and biological attributes, including growth parameters $L_\infty$ and $K$, condition index and commercial harvest.

At three critical statistical levels ($\alpha$=0.1, 0.05, 0.005), hydroclimatic variables (water level and riverine inflow) significantly influenced the condition index ($K_{LC}$), the Brody growth rate ($K$) and asymptotic fork length ($L_\infty$) (Table 9). Statistical analysis indicated significant impacts between hydroclimatic variables and biological parameters, but these influences varied with temporal and spatial scales. In February, the correlation between riverine discharge and $K_{LC}$ was significantly negative ($r$=-0.39, $F$=4.62, $p$<0.05) in area II; in June, the Brody growth rate $K$ was positively related to water level ($r$=0.61, $F$=8.39, $p$<0.05) in the shallow area III. Both statistical results revealed inter-dependence between hydroclimatic conditions and biological production: increasing riverine inflow in winter may be detrimental to fish condition index $K_{LC}$ resulting from reduction of prey resource and the overwintering habitats the fish require in deep water, and higher summer water levels can facilitate increasing Brody growth rate in productive shallow waters (Figure 18). Accordingly, during 1960–2010, riverine inflow tended to increase in winter (February) ($r$=0.43, $F$=38.77, $p$<0.05) and gradually decreased in early summer (June) ($r$=-0.36, $F$=4.23, $p$<0.05). In addition to natural fluctuations, man-made water regulation in the Peace-Athabasca-Slave system by the W.A.C. Bennett Dam has occurred since 1967. Despite the absence of a significant difference in annual mean riverine inflow ($t$=0.05, $p_{2\text{-tailed}}$=0.96), monthly differences were significant, except in May ($p$=0.80), October ($p$=0.12) and November ($p$=0.29), between the periods of 1960–1971 and 1972–2010. As monthly average riverine discharge decreased after June, significant positive correlations between riverine inflow and $L_\infty$ were identified in area IE, but no significant effects on the Brody growth rate $K$ were found. Water level displayed dynamic inter-annual changes without pronounced tendencies in either February ($r$=0.19, $p$>0.01) or June ($r$=-0.19, $p$>0.10). Significant differences in water level were detected from March to May, leading to marked seasonal water level increases in GSL. The peak riverine inflow at Fitzgerald occurred in June and July, and water levels in GSL peaked in July and August before 1971, demonstrating a one-month lag between these locations.

In addition to hydroclimatic variables, local meteorological conditions, including air temperature, precipitation and wind, that prevail in a particular region may influence the regimes of water temperature and the flow of watercourses (Jonsson and Jonsson 2009). In GSL, positive correlations were detected between air temperature and $K_{LC}$, $K$ and $L_\infty$ in shallow areas IW and IE before May, and negative relationships were found during June through November, especially in the shallow area III (Table 9). This suggests that warmer winters may benefit growing conditions for overwintering schools while warmer summers may retard the growth efficiency of this cold-water fish (Figure 19). Fish are typically poikilothermic and their metabolic energy costs increase with water temperature (Weatherley and Gill 1987). For example, the scope of activity and swimming speed increases with temperature, demanding the energy costs related to activity in summer time. For fish in the deeper area IV, air temperature acts as a positive driver, increasing the growth rate $K$ over years. Within a year, monthly variation in air temperature showed a single warmer season that peaked in July. There was a noticeable increase in temperature over 1972–2010 compared to 1960–1971, but this increase is without statistical power. Over 1970–2010, winter (November through March) temperature increased gradually while summer (June) thermal condition displayed dynamic variation without a definite inter-annual pattern. In contrast, precipitation in February varied by year, with higher amounts in the mid-1980s. In summer (e.g., August), historically higher precipitation occurred in the 1970s and from mid-1990 through 2010. Monthly total rainfall differed significantly in May ($t$=2.40, $p$<0.05), June ($t$=2.19, $p$<0.05) and September ($t$=1.91, $p$<0.05), showing pronounced increases from May through September. As precipitation increased during the summer, significant

negative correlations between meteorological parameters and the biological attributes of the fish populations indicated that growth patterns were adversely impacted by warmer and rainier summer weather.

Commercial harvest is the interactive outcome between comprehensive anthropogenic activities and natural resources. For example, the harvest quota, which was set for conservative purpose, changed significantly from 1305 tonnes in areas II and IV during 1972–1976 to 727 tonnes from 1977 onward (Figure 20). The commercial harvest quota in the east arm (area VI) was set to zero since 1974 to reserve the local populations for recreational and subsistence uses. Over 1972–2010, commercial Lake Whitefish harvests only matched the quota in area IW and declined gradually in the remaining areas, possibly because of declining market values. Under such man-made influences, commercial Lake Whitefish harvests did not closely correlate with water levels, but positively related to riverine inflow in area III during August through December (Table 9). Significant correlations were found between harvest and precipitation and temperature, but these patterns varied by month and area in having either positive or negative rationales, which possibly reflected the complicated effects of climate changes on the commercial harvest. The resulting positive correlation between harvest and air temperature may link to preferred fishing behaviours nearshore (areas IW, IE and III) during August-September, and the positive correlation between total precipitation and harvest in area III may be beneficial for ice fishing in December (Table 9).

Gibson et al. (2006b) modeled water sources in GSL and found that seventy-four percent of the inflow originated from the Peace-Athabasca catchments, 21% was captured from other catchments bordering GSL and five percent was received from precipitation over the lake surface. Therefore, riverine inflow from Fitzgerald at the Slave River may predominantly influence the limnological and biological properties of the lake. In addition, alterations in biological traits are mainly attributed to variability in year class strength, population reproduction and the supporting capacity of the lacustrine food web. After conducting a series of hypothetical experiments in four freshwater lakes in the Northwest Territories, Healey (1975, 1980) corroborated the interrelationships between Lake Whitefish growth, recruitment and exploitation. His research suggested that heavy exploitation can stimulate a significant increase in length-at-age as well as recruitment in Lake Whitefish. Our results show a positive relationship between $K$ and harvest in the lightly-fished area III, which upholds Healey's inference, but the hypothesis is not support in areas IW, IE, II and IV that have experienced long-term fishing. Reckahn (1986) documented a close association between long-term growth patterns of Lake Whitefish in Lake Huron and fluctuations in hydroclimatic factors, suggesting that the water levels and temperature can account for 88% of the variation in growth. The analyses in present study showed that hydroclimate, local meteorology and exploitation all significantly influenced $K$, $L_\infty$ and $K_{LC}$ (Figure 21). These influences differed notably with the spatiotemporal scale. A positive relationship between summer (July) temperature and the condition index was found in the western shallow area (IW), while a negative effect of temperature was found in the shallower inflow area (area III) (Table 9). Given that water inflowing from the Slave River is of lower temperature, it may stimulate energy conservation in summer. During warmer seasons (from March through October), positive correlations between temperature and $K$ and $L_\infty$ further support our hypothesis that a warmer lake environment can facilitate rapid growth by Lake Whitefish if forage production is sufficient. In plume area III, warmer summers seemed to depress the growth potential of fish, suggesting there might be a thermal threshold beyond which cold-water salmonids cannot naturally adapt. Precipitation from April through August seems to constrain the condition index, resulting in negative relationships with the kernel growth parameters. In addition to hydrological factors, the waves of ecological modifications that have occurred in the Great Lakes have been primarily attributed to anthropogenic dimensions, such as habitat destruction in tributaries and inshore areas, excessive phosphorus loading in the

1960s–1970s, invasions of non-indigenous dreissenids (zebra and qugga mussels) and changes in climatic conditions (Beauchamp et al. 2004, Cook et al. 2005, Hoyle 2005, Mohr and Ebener 2005, Nalepa et al. 2005, Pothoven 2005, Nalepa et al. 2009, Rennie et al. 2009). Until now, there have been insufficient data to profile variation in supporting biological production components despite pioneering studies on production in fish (Rawson 1949), nekton (Rawson 1951) and benthic fauna (Rawson 1953). Compared with other northern freshwater lakes, GSL is somewhat productive, but productivity is significantly lower than in the Laurentian Great Lakes.

Projections from the Intergovernmental Panel on Climate Change (IPCC) climate models indicate a global increase in temperature of 1.4 °C by the mid-21st century (IPCC 2001). The boreal region in Canada will be highly responsive to predicted global warming brought about by increased anthropogenic gases, which will result in extensive melting of glaciers, thawing of permafrost and reduction in the extent of sea ice. In GSL, the melting of permafrost ice could potentially change drainage patterns, with localized increases in surface water (ACIA 2005). Such changes to the hydrologic system could significantly alter biotic and climatic processes because of ecosystem sensitivity. Our studies have summarized spatiotemporal dynamics in the biological traits of Lake Whitefish and found possible associations with hydroclimate, meteorology and exploitation. Finally, additional fieldwork and experimental research is necessary for precautionary management of this important natural resource considering the effects of multiple cumulative impacts.

## CONCLUSIONS

1) In terms of fish plant samples during 1972–2004, body size of the GSL Lake Whitefish varied with management area and year. A power function was conventionally used to describe the relationship between fork length and round weight, but this method was not supported by applying AIC to MMI. Model PW was considered the best for Lake Whitefish in areas IW, IE and III, and model CM was the best in areas II, IV and V. In terms of AIC weight, the average model was derived to better describe the fork length and round weight of GSL Lake Whitefish. A breakpoint range in the regression slope was found at 392, 380 and 441 mm in the shallow areas IW, IE and III, respectively, while in deep waters it varied from 372 mm in area IV to 446 mm in area V and 460 mm in area II. These breakpoints were marked by transitions in ontogenic development because of maturation.

2) Two condition indices were used in this analysis: $K_F$ and $K_{LC}$. $K_F$ values, calculated from morphometric measurements of length and weight, varied between 0.53 and 3.76 (mean = 1.50 ± 0.01). The other index, $K_{LC}$, ranged between 38.81 and 255.63 with a grand average of 100.58 ± 0.04, displayed no significant length-related bias but limited to a single population. $K_{LC}$ varied significantly by year, area and mesh-size used. Since 1980, the condition index declined steadily but varied by area.

3) Significant spatiotemporal variation in the size composition of the Lake Whitefish catch was found by ANOVA, indicating slight differences in the size distribution among areas. Larger temporal variation, measured by the coefficient of variation (CV), occurred in the southwest shallow waters (IW); values decreased along the southwest-east shore. Statistically significant decrease in yearly averages for fork length and round weight were found in areas IE and III over years. Area-based average age of Lake Whitefish showed a significant positive relationship with year in areas IE, IV and V, but no significant correlations were found in the rest of the lake. Combined with measurements of fork length and round weight, we suggest that a noticeable reduction in growth rate occurred over time.

4) Growth patterns of GSL Lake Whitefish were delineated by three candidate growth models: VBM, GGM and LGM. For each model, four hierarchical Bayesian scenarios were applied: LCKC, LCKV, LVKC and LVKV. MMI strategies were applied to model selection, leading to the best model, GGM with LVKV for fish growth in shallow waters and GGM-LCKV for deep-water fish. The posterior hyper-parameters $L_\infty$ and $K$ displayed clear spatiotemporal variations, ranging from 492.80 to 553.13 mm and 0.1000 to 0.1630, respectively. Spatially, smaller $L_\infty$ and larger $K$ values appeared in deep-water areas (areas IV and V), while larger $L_\infty$ and smaller $K$ values were found in the shallow southern waters (areas IW, IE and III). A traditional growth model, the von Bertalanffy growth model, was found to be inappropriate for studying growth patterns of GSL Lake Whitefish.

5) Pair-wise correlation analysis revealed that larger amounts of riverine inflow in winter may have negative effects on prey production and overwintering habitats. In summer, increasing temperature may compress the habitat range, stimulating an increase in energy costs for activity and swimming. However, the impact of temperature on fish growth differed by season: the effect was positive in winter and negative in summer and fall. $K$ was favoured by higher water levels in June and benefited from food consumption and growth. In addition, there was an evident impact of exploitation on growth traits ($K$ and $L_\infty$), especially in the rather heavily fished area IW. Factor analysis was used to identify the dominant factors affecting fish growth and other biological traits. The first two canonical components explained 39.66% of the cumulative variation in $K_{LC}$ that is associated with abiotic factors and exploitation. Although riverine inflow and precipitation in summer jointly influenced the condition index of fish in deeper waters, temperature and water levels in spring and winter profoundly impacted the condition index throughout the lake. The first two canonical components accounted for 54.34% of the total variation in the linkages between $K$ and hydroclimate, meteorology and exploitation. Among the factors selected, climate change exerts predominant impacts on variation in hydroclimate, meteorology and biological productivity in the lake.

6) This data summary serves as a first step towards integrating accumulated abiotic and fisheries data, and facilitates general communication within the working group. Thus, many gaps remain unresolved but urgent needs are ascribed to fishery-independent surveys and experimental research, which exclusively focus on quantitative stock assessment and precautionary management.

## ACKNOWLEDGEMENTS

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# APPENDIX: TABLES AND FIGURES

*Table 1. Summary statistics for fork length and round weight of Lake Whitefish sampled from commercial fisheries on GSL during 1972–2004.*

| Area | IW | IE | III | II | IV | V |
|------|------|------|------|------|------|------|
| | | | Fork length (mm) | | | |
| Min | 302 | 286 | 301 | 294 | 298 | 318 |
| Max | 599 | 580 | 581 | 607 | 648 | 589 |
| Mean | 425.86 | 417.09 | 418.92 | 411.62 | 408.78 | 421.90 |
| SD | 36.87 | 31.03 | 30.96 | 32.85 | 30.29 | 26.77 |
| SE | 0.35 | 0.24 | 0.38 | 0.26 | 0.22 | 0.23 |
| CV (%) | 8.66 | 7.44 | 7.39 | 7.98 | 7.41 | 6.34 |
| n | 11302 | 17026 | 6547 | 15702 | 19122 | 14139 |
| | | | Round weight (g) | | | |
| Min | 350 | 250 | 411 | 300 | 300 | 350 |
| Max | 3367 | 3226 | 4457 | 4692 | 4516 | 3343 |
| Mean | 1164.05 | 1130.69 | 1166.17 | 1059.30 | 1040.54 | 1101.23 |
| SD | 335.49 | 270.80 | 322.96 | 300.22 | 259.88 | 244.96 |
| SE | 3.16 | 2.08 | 3.99 | 2.40 | 1.88 | 2.06 |
| CV (%) | 28.82 | 23.95 | 27.69 | 28.34 | 24.98 | 22.24 |
| | | | Dressed weight (g) | | | |
| Min | 298 | 213 | 350 | 256 | 256 | 298 |
| Max | 2870 | 2750 | 3800 | 4000 | 3850 | 2850 |
| Mean | 992.38 | 963.94 | 994.17 | 903.08 | 887.09 | 938.83 |
| SD | 286.00 | 230.84 | 275.32 | 255.93 | 221.54 | 208.81 |
| SE | 2.69 | 1.77 | 3.40 | 2.04 | 1.60 | 1.76 |
| CV (%) | 28.82 | 23.95 | 27.69 | 28.34 | 24.97 | 22.24 |

*Table 2. Parameters and rooted sum of squares, MSE, corrected AIC$_c$, AIC$_c$ difference ($\Delta_i$) and Akaike weights ($w_i$) of the linear (LM), quadratic, (QM), cubic (CM) and piece-wise models (PW) between log-transformed fork length and round weight of GSL Lake Whitefish for management areas and all areas combined. Values corresponding to the best models are in bold characters.*

| Model | Parameter | IW | IE | III | II | IV | V | Lake |
|---|---|---|---|---|---|---|---|---|
| LM | a1 | -10.888 | -9.681 | -11.609 | -11.088 | -10.129 | -10.152 | -10.415 |
| | b1 | 2.960 | 2.767 | 3.088 | 2.995 | 2.836 | 2.835 | 2.884 |
| | MSE | 0.101 | 0.109 | 0.108 | 0.112 | 0.107 | 0.112 | 0.111 |
| QM | a1 | -19.368 | -26.747 | 47.300 | -0.558 | -7.319 | 29.579 | -2.128 |
| | b1 | 5.756 | 8.420 | -16.396 | -0.499 | 1.903 | -10.304 | 0.139 |
| | b2 | -0.230 | -0.468 | 1.611 | 0.290 | 0.078 | 1.086 | 0.227 |
| | MSE | 0.101 | 0.109 | 0.107 | 0.112 | 0.107 | 0.112 | 0.111 |
| CM | a1 | -198.101 | -293.250 | -1461.765 | -911.117 | -1074.396 | -1510.701 | -875.140 |
| | b1 | 94.170 | 140.948 | 732.261 | 451.819 | 532.784 | 752.849 | 433.683 |
| | b2 | -14.806 | -22.432 | -122.171 | -74.588 | -87.942 | -124.933 | -71.524 |
| | b3 | 0.801 | 1.213 | 6.821 | 4.131 | 4.863 | 6.936 | 3.957 |
| | MSE | 0.101 | 0.109 | 0.107 | 0.111 | 0.106 | 0.111 | 0.11 |
| PW | a1 | -12.044 | -12.073 | -10.179 | -10.701 | -12.461 | -9.305 | -12.463 |
| | b1 | 3.154 | 3.170 | 2.850 | 2.930 | 3.231 | 2.695 | 3.231 |
| | b2 | 2.932 | 2.716 | 3.676 | 3.426 | 2.785 | 3.351 | 2.857 |
| | log(B) | 5.972 | 5.940 | 6.089 | 6.131 | 5.919 | 6.100 | 5.916 |
| | MSE | 0.101 | 0.108 | 0.107 | 0.111 | 0.107 | 0.111 | 0.111 |
| | Model | IW | IE | III | II | IV | V | Lake |
| AIC$_c$ | LM | -19713 | -27277 | -10533 | -24297 | -31268 | -21837 | -131212 |
| | QM | -19717 | -27303 | -10642 | -24308 | -31267 | -21899 | -131245 |
| | CM | -19719 | -27308 | -10688 | **-24385** | **-31412** | **-21961** | -131550 |
| | PW | **-19724** | **-27333** | **-10690** | -24374 | -31332 | -21961 | -131334 |
| $\Delta_i$ | LM | 11.077 | 56.488 | 157.244 | 87.588 | 144.198 | 124.347 | 338.700 |
| | QM | 6.628 | 30.579 | 47.607 | 76.739 | 145.179 | 62.139 | 305.400 |
| | CM | 4.880 | 25.500 | 2.450 | **0.000** | **0.000** | **0.000** | **0.000** |
| | PW | **0.000** | **0.000** | **0.000** | 10.576 | 79.520 | 0.650 | 216.499 |
| $w_i$(%) | LM | 0.348 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | QM | 3.223 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | CM | 7.731 | 0.000 | 22.706 | **100.000** | **100.000** | **58.054** | **100.000** |
| | PW | **88.698** | **100.000** | **77.294** | 0.000 | 0.000 | 41.946 | 0.000 |

*Table 3. ANCOVA for variation in relative condition index, $K_{LC}$, with month, administrative area, mesh size and fork length. Log-transformed fork length is treated as a covariate.*

| Source | Partial SS | *df* | MS | *F* | *p>F* |
|---|---|---|---|---|---|
| Model | 882714.56 | 149 | 5924.26 | 55.06 | 0.000 |
| Month | 9203.13 | 9 | 1022.57 | 9.50 | 0.000 |
| Area | 3983.39 | 5 | 796.68 | 7.40 | 0.000 |
| Month x Area | 30735.38 | 35 | 878.15 | 8.16 | 0.000 |
| Mesh | 4828.64 | 2 | 2414.32 | 22.44 | 0.000 |
| Month x Mesh | 2188.29 | 7 | 312.61 | 2.91 | 0.005 |
| Area x Mesh | 6815.53 | 7 | 973.65 | 9.05 | 0.000 |
| Month x Area x Mesh | 11145.69 | 9 | 1238.41 | 11.51 | 0.000 |
| Lnlen | 514.72 | 1 | 514.72 | 4.78 | 0.029 |
| Month x Lnlen | 9010.79 | 9 | 1001.20 | 9.31 | 0.000 |
| Area x Lnlen | 3939.51 | 5 | 787.90 | 7.32 | 0.000 |
| Month x Area x Lnlen | 30664.65 | 35 | 876.13 | 8.14 | 0.000 |
| Mesh x Lnlen | 4971.15 | 2 | 2485.57 | 23.10 | 0.000 |
| Month x Mesh x Lnlen | 2196.44 | 7 | 313.78 | 2.92 | 0.005 |
| Area x Mesh x Lnlen | 6942.13 | 7 | 991.73 | 9.22 | 0.000 |
| Month x Area x Mesh x Lnlen | 10977.25 | 9 | 1219.70 | 11.34 | 0.000 |
| Residual | 9004329.6 | 83688 | 107.59 | | |
| Total | 9887044.1 | 83837 | 117.93 | | |

*Table 4. ANOVA examining variation in fork length (a) and round weight (b) of Lake Whitefish by month, administrative area and mesh size.*

**(a) Fork length**

| Source | Partial SS | *df* | MS | *F* | *p>F* |
|---|---|---|---|---|---|
| Model | 46.33 | 74 | 0.63 | 120.76 | 0.000 |
| Month | 2.73 | 9 | 0.30 | 58.51 | 0.000 |
| Area | 3.21 | 5 | 0.64 | 123.76 | 0.000 |
| Month x Area | 14.68 | 35 | 0.42 | 80.92 | 0.000 |
| Mesh | 0.37 | 2 | 0.18 | 35.45 | 0.000 |
| Month x Mesh | 0.26 | 7 | 0.04 | 7.03 | 0.000 |
| Area x Mesh | 0.98 | 7 | 0.14 | 27.07 | 0.000 |
| Month x Area x Mesh | 1.25 | 9 | 0.14 | 26.73 | 0.000 |
| Residual | 434.25 | 83763 | 0.01 | | |
| Total | 480.58 | 83837 | 0.01 | | |

**(b) Round weight**

| Source | Partial SS | *df* | MS | *F* | *p>F* |
|---|---|---|---|---|---|
| Model | 467.22 | 74 | 6.31 | 116.07 | 0.000 |
| Month | 11.11 | 9 | 1.23 | 22.70 | 0.000 |
| Area | 21.91 | 5 | 4.38 | 80.57 | 0.000 |
| Month x Area | 174.22 | 35 | 4.98 | 91.51 | 0.000 |
| Mesh | 4.91 | 2 | 2.46 | 45.17 | 0.000 |
| Month x Mesh | 4 | 7 | 0.57 | 10.51 | 0.000 |
| Area x Mesh | 15.74 | 7 | 2.25 | 41.34 | 0.000 |
| Month x Area x Mesh | 17.51 | 9 | 1.95 | 35.76 | 0.000 |
| Residual | 4556.36 | 83763 | 0.05 | | |
| Total | 5023.58 | 83837 | 0.06 | | |

**(c) Age**

| Source | Partial SS | *df* | MS | *F* | *p>F* |
|---|---|---|---|---|---|
| Model | 33623.98 | 67 | 501.85 | 182.05 | 0.000 |
| Month | 1175.62 | 8 | 146.95 | 53.31 | 0.000 |
| Area | 8004.12 | 5 | 1600.82 | 580.71 | 0.000 |
| Month x Area | 3745.09 | 35 | 107.000 | 38.82 | 0.000 |
| Mesh | 406.16 | 2 | 203.08 | 73.67 | 0.000 |
| Month x Mesh | 36.95 | 5 | 7.39 | 2.68 | 0.020 |
| Area x Mesh | 433.15 | 5 | 86.63 | 31.43 | 0.000 |
| Month x Area x Mesh | 167.63 | 7 | 23.95 | 8.69 | 0.000 |
| Residual | 173781.6 | 521158 | 2.76 | | |
| Total | 177405.6 | 52225 | 3.40 | | |

*Table 5. ANCOVA examining variation in Lake Whitefish age structure with year, administrative area and mesh size when log-transformed fork length (a) or round weight (b) were used as a covariate.*

(a)

| Source | Partial SS | *df* | MS | *F* | *p>F* |
|---|---|---|---|---|---|
| Model | 71440.63 | 40 | 1786.02 | 879.57 | 0.000 |
| Year | 5729.37 | 30 | 190.98 | 94.05 | 0.000 |
| Area | 16041.93 | 5 | 3208.39 | 1580.05 | 0.000 |
| Mesh | 0.73 | 1 | 0.73 | 0.36 | 0.549 |
| log(L) | 2500.34 | 1 | 2500.34 | 1231.35 | 0.000 |
| Year x Mesh | 7.84 | 1 | 7.84 | 3.86 | 0.050 |
| Mesh x log(L) | 57.77 | 2 | 28.88 | 14.22 | 0.000 |
| Residual | 105964.93 | 52185 | 2.03 | | |
| Total | 177405.56 | 52225 | 3.40 | | |

(b)

| Source | Partial SS | *df* | MS | *F* | *p>F* |
|---|---|---|---|---|---|
| Model | 67561.98 | 40 | 1689.05 | 802.44 | 0.000 |
| Year | 4928.45 | 30 | 164.28 | 78.05 | 0.000 |
| Area | 17675.71 | 5 | 3535.14 | 1679.49 | 0.000 |
| Mesh | 2.00 | 0 | 2.00 | 0.95 | 0.330 |
| log(W) | 2151.43 | 1 | 2151.43 | 1022.11 | 0.000 |
| Year x Mesh | 12.22 | 1 | 12.22 | 5.81 | 0.016 |
| Mesh x log(W) | 113.20 | 2 | 56.60 | 26.89 | 0.000 |
| Residual | 109843.58 | 52185 | 2.10 | | |
| Total | 177405.56 | 52225 | 3.40 | | |

*Table 6. Decadal comparison of age composition for Lake Whitefish collected from GSL commercial fisheries during 1972-2004.*

| Year | Area | IW | IE | II | III | IV | V |
|------|------|------|------|------|------|------|------|
| 1970-1979 | Range | 5-16 | 6-18 | 5-16 | | 5-17 | 5-19 |
| | Mean | 9.61 | 9.87 | 8.79 | | 9.86 | 10.78 |
| | SD | 1.52 | 1.54 | 1.42 | | 1.55 | 1.64 |
| | SE | 0.04 | 0.02 | 0.02 | | 0.02 | 0.02 |
| | N | 1848 | 4659 | 5157 | | 5604 | 5441 |
| 1980-1989 | Range | 5-20 | 5-20 | 5-20 | 6-17 | 5-19 | 5-21 |
| | Mean | 10.55 | 10.28 | 9.50 | 10.60 | 10.71 | 11.60 |
| | SD | 2.05 | 1.72 | 1.74 | 1.89 | 1.64 | 2.04 |
| | SE | 0.04 | 0.03 | 0.03 | 0.05 | 0.02 | 0.03 |
| | N | 2723 | 4679 | 3643 | 1548 | 4539 | 3418 |
| 1990-1999 | Range | 4-19 | 7-16 | 5-19 | 5-16 | 6-17 | 5-17 |
| | Mean | 10.26 | 10.51 | 9.41 | 10.31 | 10.87 | 11.33 |
| | SD | 2.10 | 1.37 | 1.90 | 1.55 | 1.72 | 1.97 |
| | SE | 0.06 | 0.04 | 0.06 | 0.05 | 0.04 | 0.06 |
| | N | 1127 | 1088 | 1137 | 957 | 1721 | 963 |
| 2000-2004 | Range | 6-16 | 7-16 | 6-15 | 6-17 | 6-18 | 7-18 |
| | Mean | 10.75 | 10.61 | 10.06 | 10.29 | 11.24 | 12.90 |
| | SD | 1.58 | 1.37 | 1.57 | 1.50 | 1.65 | 1.90 |
| | SE | 0.07 | 0.06 | 0.09 | 0.10 | 0.09 | 0.19 |
| | N | 504 | 515 | 325 | 210 | 317 | 103 |

*Table 7. Diagnosis of hierarchical Bayesian growth model convergence for Lake Whitefish over the GSL administrative areas. Three candidate growth models, von Bertalanffy growth model (VBM), generalized von Bertalanffy growth model (GGM) and logistic growth model (LGM), were included. For each growth model, four model scenarios were examined. LCKC assumed constant asymptotic fork length ($L_\infty$) and Brody growth rate (K). LCKV had constant $L_\infty$ and varying K. LVKC had varying $L_\infty$ and constant K. Both $L_\infty$ and K varied simultaneously in LVKV. Using the R-based CODA package, four measures of convergence, Geweke, Gelman-Rubin, Raftery-Lewis and Heidelberger-Welch tests, were applied to two chains of Gibbs sampling.*

| Area | Model | Scenario | N | Geweke | | Gelman-Rubin | | Dependence factor | | Stationarity test | | Halfwidth test | |
|------|-------|----------|---|--------|--------|--------------|--------|-------------------|--------|-------------------|--------|----------------|--------|
| | | | | Chain 1 | Chain 2 | Chain 1 | Chain 2 | Chain 1 | Chain 2 | Chain 1 | Chain 2 | Chain 1 | Chain 2 |
| IW | GGM | LCKC | 364 | 93.13 | 92.31 | 56.59 | 56.59 | 51.54 | 51.32 | 99.45 | 98.63 | 99.45 | 98.63 |
| | GGM | LCKV | 381 | 76.64 | 74.54 | 58.53 | 58.53 | 50.67 | 50.71 | 96.85 | 98.16 | 96.85 | 98.16 |
| | GGM | LVKC | 381 | 92.91 | 92.13 | 58.53 | 58.53 | 52.65 | 52.16 | 99.74 | 100.00 | 99.74 | 100.00 |
| | GGM | LVKV | 397 | 95.72 | 95.47 | 60.20 | 60.20 | 51.63 | 51.92 | 99.75 | 100.00 | 99.75 | 100.00 |
| | LGM | LCKC | 364 | 92.31 | 92.86 | 56.59 | 56.59 | 50.72 | 50.86 | 99.18 | 99.45 | 99.18 | 99.45 |
| | LGM | LCKV | 380 | 93.16 | 91.58 | 58.42 | 58.42 | 50.17 | 50.10 | 100.00 | 99.21 | 100.00 | 99.21 |
| | LGM | LVKC | 380 | 95.79 | 94.74 | 58.42 | 58.42 | 51.84 | 51.68 | 97.89 | 99.74 | 97.89 | 99.74 |
| | LGM | LVKV | 396 | 96.46 | 96.21 | 60.10 | 60.10 | 50.45 | 50.44 | 99.49 | 98.99 | 99.49 | 98.99 |
| | VBM | LCKC | 364 | 94.51 | 95.05 | 56.59 | 56.59 | 50.14 | 50.26 | 99.73 | 99.18 | 99.73 | 99.18 |
| | VBM | LCKV | 380 | 93.16 | 93.95 | 58.42 | 58.42 | 49.99 | 50.10 | 99.21 | 99.74 | 99.21 | 99.74 |
| | VBM | LVKC | 380 | 96.05 | 93.16 | 58.42 | 58.42 | 50.28 | 50.30 | 98.95 | 99.47 | 98.95 | 99.47 |
| | VBM | LVKV | 396 | 93.43 | 93.94 | 60.10 | 60.10 | 50.18 | 50.18 | 99.49 | 99.49 | 99.49 | 99.49 |
| IE | GGM | LCKC | 532 | 46.39 | 47.11 | 49.28 | 49.28 | 54.36 | 54.35 | 68.59 | 67.33 | 68.59 | 67.33 |
| | GGM | LCKV | 579 | 95.34 | 95.68 | 51.47 | 51.47 | 50.87 | 50.84 | 99.48 | 99.48 | 99.48 | 99.48 |
| | GGM | LVKC | 579 | 72.02 | 73.58 | 51.47 | 51.47 | 60.86 | 60.06 | 100.00 | 100.00 | 100.00 | 100.00 |
| | GGM | LVKV | 604 | 94.54 | 93.87 | 53.48 | 53.48 | 50.84 | 51.19 | 99.67 | 99.34 | 99.67 | 99.34 |
| | LGM | LCKC | 553 | 96.56 | 95.66 | 49.19 | 49.19 | 51.03 | 51.01 | 99.82 | 99.46 | 99.82 | 99.46 |
| | LGM | LCKV | 578 | 93.77 | 93.60 | 51.38 | 51.38 | 50.21 | 50.12 | 99.65 | 99.13 | 99.65 | 99.13 |
| | LGM | LVKC | 578 | 93.08 | 93.94 | 51.38 | 51.38 | 51.77 | 51.66 | 99.48 | 99.31 | 99.48 | 99.31 |
| | LGM | LVKV | 603 | 95.19 | 94.86 | 53.40 | 53.40 | 50.10 | 50.07 | 99.50 | 99.50 | 99.50 | 99.50 |
| | VBM | LCKC | 553 | 94.03 | 93.85 | 48.42 | 49.19 | 50.67 | 50.80 | 99.64 | 99.64 | 99.64 | 99.64 |
| | VBM | LCKV | 578 | 95.85 | 93.08 | 51.38 | 51.38 | 50.21 | 50.11 | 98.96 | 99.13 | 98.96 | 99.13 |
| | VBM | LVKC | 578 | 94.64 | 95.85 | 51.38 | 51.38 | 50.31 | 50.32 | 99.65 | 99.83 | 99.65 | 99.83 |
| | VBM | LVKV | 603 | 96.68 | 95.19 | 53.40 | 53.40 | 50.49 | 50.47 | 99.67 | 99.50 | 99.67 | 99.50 |
| III | GGM | LCKC | 343 | 95.63 | 95.04 | 46.36 | 46.36 | 51.92 | 52.02 | 94.75 | 94.17 | 94.75 | 94.17 |
| | GGM | LCKV | 359 | 96.66 | 97.77 | 48.75 | 48.75 | 50.86 | 50.77 | 99.44 | 99.72 | 99.44 | 99.72 |
| | GGM | LVKC | 359 | 98.61 | 97.77 | 48.75 | 48.75 | 54.04 | 54.00 | 98.89 | 99.72 | 98.89 | 99.72 |
| | GGM | LVKV | 374 | 91.71 | 94.92 | 50.80 | 50.80 | 51.05 | 50.87 | 99.73 | 100.00 | 99.73 | 100.00 |
| | LGM | LCKC | 343 | 95.04 | 96.50 | 46.36 | 46.36 | 51.26 | 51.07 | 99.71 | 98.83 | 99.71 | 98.83 |
| | LGM | LCKV | 358 | 93.85 | 93.85 | 48.60 | 48.60 | 50.41 | 50.34 | 98.88 | 99.16 | 98.88 | 99.16 |
| | LGM | LVKC | 358 | 94.97 | 96.37 | 48.60 | 48.60 | 52.27 | 51.69 | 99.44 | 99.44 | 99.44 | 99.44 |
| | LGM | LVKV | 373 | 92.76 | 91.96 | 50.67 | 50.67 | 50.20 | 50.24 | 99.73 | 98.93 | 99.73 | 98.93 |
| | VBM | LCKC | 343 | 93.29 | 93.00 | 46.36 | 46.36 | 50.88 | 50.93 | 99.71 | 99.42 | 99.71 | 99.42 |
| | VBM | LCKV | 358 | 91.62 | 93.30 | 48.60 | 48.60 | 50.15 | 50.15 | 98.04 | 98.04 | 98.04 | 98.04 |
| | VBM | LVKC | 358 | 95.53 | 93.30 | 48.60 | 48.60 | 50.48 | 50.40 | 100.00 | 100.00 | 100.00 | 100.00 |
| | VBM | LVKV | 373 | 96.78 | 96.78 | 50.67 | 50.67 | 50.39 | 50.40 | 99.46 | 99.20 | 99.46 | 99.20 |

| Area | Model | Scenario | N | Geweke | | Gelman-Rubin | | Dependence factor | | Stationarity test | | Halfwidth test | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Chain 1 | Chain 2 | Chain 1 | Chain 2 | Chain 1 | Chain 2 | Chain 1 | Chain 2 | Chain 1 | Chain 2 |
| II | GGM | LCKC | 574 | 94.77 | 94.08 | 48.78 | 48.78 | 51.89 | 51.89 | 98.61 | 98.78 | 98.61 | 98.78 |
| | GGM | LCKV | 601 | 95.34 | 94.68 | 51.08 | 51.08 | 50.50 | 50.59 | 99.67 | 99.83 | 99.67 | 99.83 |
| | GGM | LVKC | 601 | 95.34 | 94.51 | 51.08 | 51.08 | 51.57 | 51.58 | 99.33 | 99.50 | 99.33 | 99.50 |
| | GGM | LVKV | 627 | 96.33 | 96.49 | 53.11 | 53.11 | 50.70 | 50.56 | 99.36 | 99.68 | 99.36 | 99.68 |
| | LGM | LCKC | 574 | 95.64 | 95.30 | 48.78 | 48.78 | 51.28 | 51.28 | 99.65 | 99.48 | 99.65 | 99.48 |
| | LGM | LCKV | 600 | 95.17 | 95.00 | 51.00 | 51.00 | 50.12 | 50.18 | 99.00 | 98.83 | 99.00 | 98.83 |
| | LGM | LVKC | 600 | 96.83 | 98.17 | 51.00 | 51.00 | 51.84 | 51.68 | 99.67 | 99.50 | 99.67 | 99.50 |
| | LGM | LVKV | 626 | 95.37 | 95.37 | 53.04 | 53.04 | 50.21 | 50.14 | 99.52 | 99.36 | 99.52 | 99.36 |
| | VBM | LCKC | 574 | 95.82 | 95.99 | 48.78 | 48.78 | 50.50 | 50.45 | 99.30 | 99.13 | 99.30 | 99.13 |
| | VBM | LCKV | 600 | 94.83 | 95.00 | 51.00 | 51.00 | 50.12 | 50.04 | 99.83 | 99.83 | 99.83 | 99.83 |
| | VBM | LVKC | 600 | 95.33 | 95.33 | 51.00 | 51.00 | 50.21 | 50.34 | 99.00 | 99.00 | 99.00 | 99.00 |
| | VBM | LVKV | 626 | 91.21 | 93.29 | 53.04 | 53.04 | 50.42 | 50.32 | 99.36 | 99.20 | 99.36 | 99.20 |
| IV | GGM | LCKC | 532 | 98.50 | 97.93 | 48.87 | 48.87 | 54.12 | 54.78 | 99.44 | 99.44 | 99.44 | 99.44 |
| | GGM | LCKV | 447 | 94.41 | 96.20 | 58.17 | 58.17 | 51.29 | 51.23 | 99.33 | 99.55 | 99.33 | 99.55 |
| | GGM | LVKC | 557 | 95.69 | 94.43 | 51.17 | 51.17 | 52.27 | 52.26 | 98.38 | 98.38 | 98.38 | 98.38 |
| | GGM | LVKV | 581 | 94.84 | 94.66 | 53.18 | 53.18 | 50.82 | 51.02 | 99.31 | 99.66 | 99.31 | 99.66 |
| | LGM | LCKC | 532 | 96.24 | 97.18 | 48.87 | 48.87 | 51.36 | 51.44 | 98.50 | 98.50 | 98.50 | 98.50 |
| | LGM | LCKV | 556 | 95.14 | 95.68 | 51.08 | 51.08 | 50.23 | 50.23 | 98.92 | 98.74 | 98.92 | 98.74 |
| | LGM | LVKC | 556 | 97.12 | 95.68 | 51.08 | 51.08 | 51.11 | 51.08 | 99.82 | 99.46 | 99.82 | 99.46 |
| | LGM | LVKV | 580 | 95.86 | 96.55 | 53.10 | 53.10 | 50.31 | 50.18 | 99.66 | 99.66 | 99.66 | 99.66 |
| | VBM | LCKC | 532 | 92.29 | 90.79 | 48.87 | 48.87 | 50.77 | 50.65 | 99.44 | 99.44 | 99.44 | 99.44 |
| | VBM | LCKV | 556 | 95.86 | 96.40 | 51.08 | 51.08 | 50.14 | 50.26 | 99.28 | 99.64 | 99.28 | 99.64 |
| | VBM | LVKC | 556 | 94.60 | 95.50 | 51.08 | 51.08 | 50.42 | 50.38 | 99.82 | 99.64 | 99.82 | 99.64 |
| | VBM | LVKV | 580 | 95.17 | 95.34 | 53.10 | 53.10 | 50.21 | 50.27 | 99.48 | 99.48 | 99.48 | 99.48 |
| V | GGM | LCKC | 427 | 94.61 | 94.15 | 56.21 | 56.21 | 60.91 | 61.57 | 99.30 | 99.30 | 99.30 | 99.30 |
| | GGM | LCKV | 447 | 94.41 | 96.20 | 58.17 | 58.17 | 51.29 | 51.23 | 99.33 | 99.55 | 99.33 | 99.55 |
| | GGM | LVKC | 447 | 95.08 | 96.20 | 58.17 | 58.17 | 63.30 | 63.76 | 100.00 | 100.00 | 100.00 | 100.00 |
| | GGM | LVKV | 466 | 94.21 | 92.92 | 59.87 | 59.87 | 51.55 | 51.63 | 99.79 | 99.79 | 99.79 | 99.79 |
| | LGM | LCKC | 427 | 94.15 | 95.32 | 56.21 | 56.21 | 52.76 | 53.24 | 100.00 | 100.00 | 100.00 | 100.00 |
| | LGM | LCKV | 446 | 93.95 | 95.52 | 58.07 | 58.07 | 50.55 | 50.52 | 99.55 | 99.55 | 99.55 | 99.55 |
| | LGM | LVKC | 446 | 48.88 | 48.21 | 58.07 | 58.07 | 55.08 | 55.00 | 99.78 | 99.78 | 99.78 | 99.78 |
| | LGM | LVKV | 465 | 95.91 | 95.27 | 59.78 | 59.78 | 50.88 | 50.72 | 98.92 | 99.78 | 98.92 | 99.78 |
| | VBM | LCKC | 427 | 95.08 | 95.78 | 56.21 | 56.21 | 50.32 | 50.29 | 100.00 | 99.53 | 100.00 | 99.53 |
| | VBM | LCKV | 446 | 93.95 | 95.96 | 58.07 | 58.07 | 50.22 | 50.29 | 99.55 | 99.10 | 99.55 | 99.10 |
| | VBM | LVKC | 446 | 95.96 | 95.52 | 58.07 | 58.07 | 50.27 | 50.29 | 99.33 | 98.88 | 99.33 | 98.88 |
| | VBM | LVKV | 465 | 95.70 | 94.41 | 59.78 | 59.78 | 50.19 | 50.16 | 99.14 | 99.57 | 99.14 | 99.57 |

*Table 8. Deviance Information Criterion (DIC) values and model uncertainties for selecting the best growth model among the four model scenarios. $\overline{D}$, $\widehat{D}$ and pD are the posterior mean of the deviance, the deviance of the posterior mean and the effective number of parameters in the model, respectively. Uncertainties are accounted for by the components of process ($\sigma^2$), observation ($\tau^2$) and the variances of hierarchical $L_\infty$ ($\tau^2_{L_\infty}$) and K ($\tau^2_k$), respectively. $\Delta_i$ and $w_i$ are the difference and weight between the minimum and individual DIC values, respectively. See Table 7 for descriptions of models and model scenarios.*

| Area | Model | Scenario | $\overline{D}$ | $\widehat{D}$ | pD | DIC | $\Delta_i$ | $w_i$ | $\sigma^2$ | $\tau^2$ | $\tau^2_{L_\infty}$ | $\tau^2_K$ |
|------|-------|----------|------|------|------|------|------|------|------|------|------|------|
| IW | GGM | LVKV | 1801 | 1783 | 17.77 | 1819 | 0 | 66.13 | 2.08 | 22.70 | 0.07 | 0.02 |
|    |     | LCKV | 1808 | 1796 | 12.25 | 1820 | 1 | 33.17 | 1.98 | 22.52 | 0.08 | 2.98 |
|    |     | LVKC | 1814 | 1800 | 13.84 | 1828 | 9 | 0.70 | 1.71 | 23.19 | 8.53 | 0.02 |
|    |     | LCKC | 1843 | 1844 | -0.95 | 1842 | 23 | 0.00 | 1.74 | 24.17 | 8.20 | 3.16 |
|    | LGM | LVKC | 1836 | 1821 | 14.95 | 1851 | 32 | 0.00 | 2.19 | 24.85 | 7.83 | 0.02 |
|    |     | LVKV | 1835 | 1818 | 17.37 | 1853 | 34 | 0.00 | 2.89 | 24.79 | 0.06 | 0.02 |
|    |     | LCKV | 1845 | 1833 | 12.05 | 1858 | 39 | 0.00 | 2.75 | 24.68 | 0.08 | 2.83 |
|    |     | LCKC | 1867 | 1868 | -1.28 | 1865 | 46 | 0.00 | 2.17 | 25.69 | 8.14 | 3.03 |
|    | VBM | LVKV | 1906 | 1871 | 34.65 | 1941 | 122 | 0.00 | 5.76 | 24.74 | 0.08 | 0.02 |
|    |     | LVKC | 1917 | 1889 | 28.20 | 1945 | 126 | 0.00 | 4.38 | 25.54 | 6.41 | 0.02 |
|    |     | LCKV | 1922 | 1894 | 28.38 | 1951 | 132 | 0.00 | 5.50 | 25.17 | 0.08 | 2.84 |
|    |     | LCKC | 1938 | 1922 | 16.62 | 1955 | 136 | 0.00 | 3.30 | 26.60 | 6.34 | 2.98 |
| IE | GGM | LVKV | 2389 | 2361 | 28.31 | 2417 | 0 | 57.69 | 2.34 | 22.58 | 0.08 | 0.02 |
|    |     | LCKV | 2397 | 2377 | 20.64 | 2418 | 1 | 42.31 | 2.11 | 22.34 | 0.09 | 3.05 |
|    |     | LVKC | 2417 | 2392 | 24.79 | 2441 | 24 | 0.00 | 1.67 | 23.90 | 7.81 | 0.03 |
|    |     | LCKC | 2481 | 2482 | -0.87 | 2480 | 63 | 0.00 | 1.67 | 25.60 | 7.33 | 3.07 |
|    | VBM | LVKV | 2483 | 2432 | 51.29 | 2534 | 117 | 0.00 | 5.02 | 23.25 | 0.08 | 0.02 |
|    |     | LVKC | 2497 | 2455 | 42.40 | 2540 | 122 | 0.00 | 3.70 | 24.09 | 6.58 | 0.03 |
|    |     | LCKV | 2499 | 2454 | 45.14 | 2544 | 127 | 0.00 | 4.52 | 23.37 | 0.08 | 3.03 |
|    |     | LCKC | 2538 | 2522 | 16.02 | 2554 | 137 | 0.00 | 1.93 | 25.84 | 6.97 | 2.83 |
|    | LGM | LVKC | 2553 | 2529 | 24.12 | 2577 | 160 | 0.00 | 1.65 | 30.97 | 7.38 | 0.04 |
|    |     | LVKV | 2563 | 2536 | 27.41 | 2591 | 173 | 0.00 | 2.88 | 31.28 | 0.08 | 0.04 |
|    |     | LCKV | 2583 | 2565 | 18.42 | 2602 | 184 | 0.00 | 2.66 | 31.05 | 0.11 | 3.19 |
|    |     | LCKC | 2611 | 2612 | -0.87 | 2610 | 193 | 0.00 | 1.60 | 32.76 | 7.18 | 3.20 |
| III | GGM | LVKV | 1320 | 1301 | 18.87 | 1338 | 0 | 49.66 | 2.12 | 19.31 | 0.07 | 0.02 |
|    |     | LCKV | 1325 | 1311 | 13.66 | 1339 | 0 | 42.53 | 1.93 | 18.90 | 0.10 | 3.12 |
|    |     | LVKC | 1325 | 1308 | 17.23 | 1342 | 4 | 7.81 | 1.67 | 19.50 | 8.23 | 0.03 |
|    | LGM | LVKC | 1342 | 1324 | 17.69 | 1360 | 21 | 0.00 | 2.07 | 20.94 | 7.93 | 0.04 |
|    |     | LVKV | 1343 | 1324 | 19.51 | 1363 | 24 | 0.00 | 2.89 | 20.88 | 0.07 | 0.03 |
|    |     | LCKV | 1361 | 1347 | 14.25 | 1375 | 37 | 0.00 | 2.53 | 21.03 | 0.12 | 2.96 |
|    | GGM | LCKC | 1378 | 1379 | -0.78 | 1377 | 39 | 0.00 | 1.72 | 21.79 | 8.14 | 2.95 |
|    | LGM | LCKC | 1403 | 1404 | -1.03 | 1402 | 64 | 0.00 | 2.02 | 23.72 | 7.57 | 3.02 |
|    | VBM | LVKC | 1410 | 1380 | 29.30 | 1439 | 101 | 0.00 | 3.73 | 21.34 | 6.73 | 0.03 |
|    |     | LVKV | 1415 | 1382 | 32.48 | 1447 | 109 | 0.00 | 5.13 | 21.70 | 0.07 | 0.02 |
|    |     | LCKC | 1437 | 1425 | 11.83 | 1449 | 111 | 0.00 | 2.05 | 23.45 | 6.85 | 3.10 |
|    |     | LCKV | 1424 | 1395 | 28.72 | 1452 | 114 | 0.00 | 4.81 | 21.49 | 0.08 | 3.23 |

| Area | Model | Scenario | $\overline{D}$ | $\widehat{D}$ | $pD$ | DIC | $\Delta_i$ | $w_i$ | $\sigma^2$ | $r^2$ | $\tau^2_{L_\infty}$ | $\tau^2_K$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| II | GGM | LCKV | 2447 | 2426 | 21.32 | 2469 | 0 | 92.38 | 1.98 | 21.43 | 0.09 | 3.02 |
| | | LVKV | 2446 | 2418 | 27.85 | 2474 | 5 | 7.62 | 2.16 | 21.92 | 0.08 | 0.02 |
| | | LVKC | 2463 | 2436 | 26.32 | 2489 | 20 | 0.00 | 1.67 | 22.90 | 8.22 | 0.03 |
| | | LCKC | 2530 | 2531 | -0.81 | 2529 | 61 | 0.00 | 1.71 | 24.44 | 8.42 | 3.11 |
| | LGM | LVKC | 2607 | 2581 | 26.49 | 2634 | 165 | 0.00 | 1.50 | 29.79 | 7.08 | 0.04 |
| | | LVKV | 2621 | 2591 | 30.21 | 2651 | 183 | 0.00 | 2.87 | 30.27 | 0.08 | 0.04 |
| | | LCKV | 2652 | 2631 | 20.56 | 2672 | 204 | 0.00 | 2.64 | 30.57 | 0.12 | 2.96 |
| | | LCKC | 2682 | 2683 | -0.82 | 2681 | 213 | 0.00 | 1.40 | 32.32 | 7.12 | 3.20 |
| | VBM | LCKV | 2654 | 2601 | 52.31 | 2706 | 237 | 0.00 | 5.12 | 25.16 | 0.07 | 3.13 |
| | | LCKC | 2678 | 2649 | 29.08 | 2707 | 238 | 0.00 | 2.75 | 27.33 | 6.83 | 3.07 |
| | | LVKV | 2650 | 2592 | 57.54 | 2707 | 239 | 0.00 | 5.61 | 25.49 | 0.07 | 0.02 |
| | | LVKC | 2659 | 2609 | 49.39 | 2708 | 239 | 0.00 | 4.33 | 26.37 | 6.58 | 0.02 |
| IV | GGM | LCKV | 2126 | 2111 | 14.23 | 2140 | 0 | 100.00 | 1.57 | 22.83 | 0.11 | 3.44 |
| | | LVKV | 2325 | 2297 | 28.29 | 2353 | 213 | 0.00 | 2.06 | 24.61 | 0.08 | 0.03 |
| | | LVKC | 2333 | 2307 | 26.46 | 2360 | 220 | 0.00 | 1.50 | 25.14 | 8.26 | 0.04 |
| | LGM | LVKC | 2365 | 2338 | 26.74 | 2391 | 252 | 0.00 | 1.90 | 26.98 | 8.14 | 0.05 |
| | | LVKV | 2370 | 2341 | 28.76 | 2398 | 259 | 0.00 | 2.84 | 27.04 | 0.07 | 0.05 |
| | | LCKV | 2418 | 2397 | 20.47 | 2438 | 298 | 0.00 | 2.59 | 28.22 | 0.13 | 2.97 |
| | GGM | LCKC | 2441 | 2441 | -0.61 | 2440 | 300 | 0.00 | 1.53 | 29.47 | 8.14 | 3.26 |
| | LGM | LCKC | 2478 | 2479 | -0.97 | 2477 | 337 | 0.00 | 1.76 | 31.81 | 7.71 | 3.00 |
| | VBM | LVKC | 2486 | 2438 | 47.74 | 2533 | 393 | 0.00 | 4.39 | 28.14 | 6.81 | 0.04 |
| | | LVKV | 2482 | 2429 | 53.03 | 2535 | 395 | 0.00 | 6.01 | 27.55 | 0.11 | 0.03 |
| | | LCKV | 2499 | 2451 | 47.39 | 2546 | 406 | 0.00 | 5.84 | 27.50 | 0.11 | 3.18 |
| | | LCKC | 2563 | 2542 | 21.19 | 2584 | 444 | 0.00 | 2.76 | 32.81 | 7.69 | 3.07 |
| V | GGM | LCKV | 2126 | 2111 | 14.12 | 2140 | 0 | 64.68 | 1.57 | 22.83 | 0.11 | 3.44 |
| | | LVKV | 2121 | 2101 | 19.78 | 2141 | 1 | 35.32 | 1.68 | 23.08 | 0.10 | 0.01 |
| | | LVKC | 2145 | 2128 | 17.00 | 2162 | 22 | 0.00 | 1.14 | 24.41 | 7.42 | 0.02 |
| | | LCKC | 2182 | 2182 | -0.85 | 2181 | 41 | 0.00 | 1.08 | 25.52 | 7.05 | 3.49 |
| | LGM | LVKC | 2189 | 2171 | 17.64 | 2206 | 67 | 0.00 | 1.37 | 26.99 | 6.96 | 0.03 |
| | | LVKV | 2198 | 2177 | 20.78 | 2218 | 79 | 0.00 | 2.64 | 27.47 | 0.07 | 0.03 |
| | | LCKV | 2212 | 2197 | 14.48 | 2226 | 87 | 0.00 | 2.38 | 27.12 | 0.10 | 3.28 |
| | | LCKC | 2234 | 2236 | -1.17 | 2233 | 94 | 0.00 | 1.28 | 28.65 | 6.57 | 3.12 |
| | VBM | LVKV | 2282 | 2234 | 47.64 | 2329 | 190 | 0.00 | 7.01 | 25.13 | 0.13 | 0.03 |
| | | LVKC | 2319 | 2286 | 33.18 | 2352 | 212 | 0.00 | 5.70 | 27.62 | 6.14 | 0.02 |
| | | LCKV | 2321 | 2287 | 34.18 | 2355 | 215 | 0.00 | 7.11 | 26.33 | 0.09 | 3.43 |
| | | LCKC | 2337 | 2316 | 21.44 | 2359 | 219 | 0.00 | 5.13 | 28.24 | 6.05 | 3.09 |

Table 9. Pair-wise correlation coefficients for hydroclimatic conditions (data collected from the *Environment Canada Data Explorer*, local meteorological conditions at the Yellowknife weather station and biological attributes of GSL Lake Whitefish. Superscript symbols denote significance levels: *, $p<0.10$; **, $p<0.05$; ***, $p<0.005$. Relationships that are not significant are denoted as ns.

| | | Condition factor ($K_{LC}$) | | | | | Body growth rate ($K$) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | IW | IE | III | II | IV | IW | IE | III | IV | V |
| Water level (m) | Jun | ns | ns | ns | ns | ns | ns | ns | 0.69*** | ns | Ns |
| | Jul | ns | ns | ns | ns | ns | ns | ns | 0.54** | ns | ns |
| | Aug | ns | ns | ns | ns | ns | ns | ns | 0.55** | ns | ns |
| | Sep | ns | ns | ns | -0.39** | ns | ns | ns | 0.52** | ns | ns |
| Flow runoff (m³/s) | Feb | ns | ns | ns | -0.34* | ns | ns | ns | ns | ns | ns |
| | Mar | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | May | ns | ns | ns | ns | ns | ns | ns | 0.44* | ns | ns |
| | Jun | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Aug | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Sep | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Oct | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Dec | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| Air temperature (°C) | Jan | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Feb | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Apr | ns | 0.41** | ns | ns | ns | ns | ns | ns | ns | 0.48** |
| | May | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Jun | ns | ns | ns | ns | ns | ns | ns | -0.48* | ns | ns |
| | Jul | 0.48** | ns | -0.45** | ns | ns | ns | ns | ns | ns | ns |
| | Aug | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Sep | ns | ns | ns | ns | ns | ns | ns | ns | ns | 0.41* |
| | Nov | ns | -0.35* | ns | -0.36* | ns | ns | ns | -0.50* | 0.41** | ns |
| | Dec | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| Precipitation (mm) | Jan | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Feb | ns | 0.33* | 0.48* | ns | ns | 0.55** | ns | 0.48* | ns | ns |
| | Mar | ns | ns | ns | ns | ns | ns | ns | ns | 0.36* | ns |
| | Apr | -0.34* | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | May | ns | ns | ns | ns | ns | ns | -0.62*** | ns | ns | ns |
| | Jun | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Jul | -0.35* | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Aug | ns | ns | -0.63*** | ns | ns | ns | ns | ns | ns | ns |
| | Sep | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Oct | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Dec | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| Condition index ($K_{LC}$) | IW | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | IE | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | III | ns | ns | ns | ns | ns | ns | ns | 0.50* | ns | ns |
| | IV | ns | ns | ns | ns | ns | ns | ns | ns | ns | Ns |
| | V | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| $K$ | IE | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | III | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | III | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | IV | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| $L_\infty$ (mm) | IE | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | III | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |

Table 9. Continued.

| | | Asymptotic fork length ($L_\infty$) | | | | | Harvest (tonne) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | IW | IE | III | II | V | IW | IE | III | II | IV | V |
| Water level (m) | Jun | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Jul | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Aug | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Sep | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| Flow runoff ($m^3/s$) | Feb | ns | ns | ns | ns | ns | ns | ns | ns | ns | 0.40** | -0.38** |
| | Mar | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | May | ns | 0.43** | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Jun | ns | 0.34* | ns | ns | ns | ns | ns | ns | ns | ns | 0.41** |
| | Aug | ns | 0.43** | ns | ns | 0.44* | ns | ns | 0.42** | ns | ns | ns |
| | Sep | ns | 0.43** | ns | ns | ns | ns | ns | 0.36* | ns | ns | ns |
| | Oct | ns | 0.36* | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Dec | ns | ns | ns | ns | ns | ns | ns | 0.41** | ns | ns | ns |
| Air temperature (°C) | Jan | ns | ns | ns | 0.36* | ns | ns | ns | -0.46** | ns | ns | ns |
| | Feb | ns | ns | ns | ns | ns | ns | ns | ns | ns | 0.32* | ns |
| | Apr | 0.43* | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | May | 0.42* | ns | ns | ns | ns | -0.35* | ns | ns | ns | ns | ns |
| | Jun | ns | ns | -0.57** | ns | ns | ns | ns | ns | ns | ns | ns |
| | Jul | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Aug | ns | ns | ns | ns | ns | 0.35* | 0.31* | ns | ns | ns | ns |
| | Sep | ns | ns | ns | ns | ns | ns | ns | 0.53** | ns | ns | ns |
| | Nov | ns | ns | -0.57** | ns | ns | ns | -0.34* | -0.35* | -0.37** | ns | -0.38** |
| | Dec | ns | ns | ns | ns | ns | 0.32* | ns | ns | ns | ns | ns |
| Precipitation (mm) | Jan | 0.53** | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Feb | ns | ns | 0.56** | ns | ns | ns | ns | ns | ns | ns | ns |
| | Mar | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Apr | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | May | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Jun | ns | 0.35* | ns | ns | ns | ns | ns | ns | 0.37** | ns | ns |
| | Jul | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | Aug | ns | ns | ns | ns | ns | ns | ns | ns | ns | -0.50*** | ns |
| | Sep | ns | ns | ns | ns | ns | ns | ns | 0.43** | ns | ns | ns |
| | Oct | ns | ns | ns | ns | -0.48** | ns | ns | -0.40* | ns | -0.32* | ns |
| | Dec | ns | ns | ns | ns | ns | ns | ns | 0.50** | ns | ns | ns |
| Condition index ($K_{LC}$) | IW | 0.54** | ns | ns | ns | ns | 0.58*** | ns | ns | ns | ns | ns |
| | IE | ns | ns | ns | ns | ns | -0.38** | ns | ns | ns | ns | ns |
| | III | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| | IV | ns | ns | ns | ns | ns | 0.46** | ns | ns | ns | ns | ns |
| | V | ns | ns | ns | ns | ns | ns | ns | 0.41* | ns | ns | ns |
| $K$ | IE | ns | ns | ns | ns | ns | ns | -0.45** | ns | ns | ns | ns |
| | III | ns | ns | ns | ns | ns | ns | ns | 0.46* | ns | ns | ns |
| | III | ns | ns | ns | ns | ns | ns | ns | ns | -0.36* | ns | ns |
| | IV | ns | ns | ns | ns | ns | ns | ns | ns | ns | -0.43** | ns |
| $L_\infty$ (mm) | IE | ns | ns | ns | ns | ns | ns | -0.51** | ns | ns | ns | ns |
| | III | ns | ns | ns | ns | ns | ns | ns | 0.50** | ns | ns | ns |
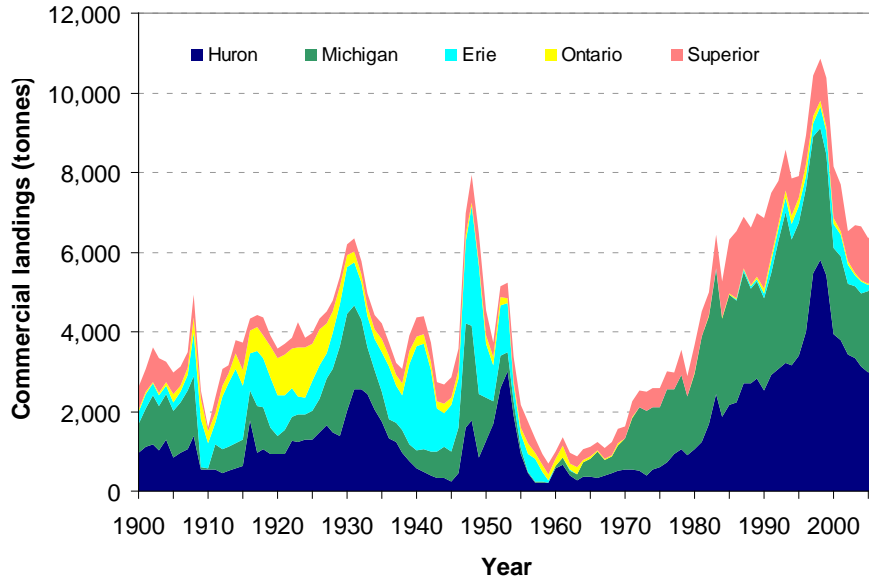
*Figure 1. Commercial harvest of Lake Whitefish in the Laurentian Great Lakes from 1900 to 2006. Peak harvests in the 1930s and 1950s were caused by strong year classes and increased fishing effort with trap nets. Lower harvests were primarily caused by sea lamprey predation, introductions of invasive species, habitat loss and eutrophication. Colours correspond to individual Great Lakes: Huron (dark blue), Michigan (green), Erie (light blue), Ontario (yellow) and Superior (pink).*
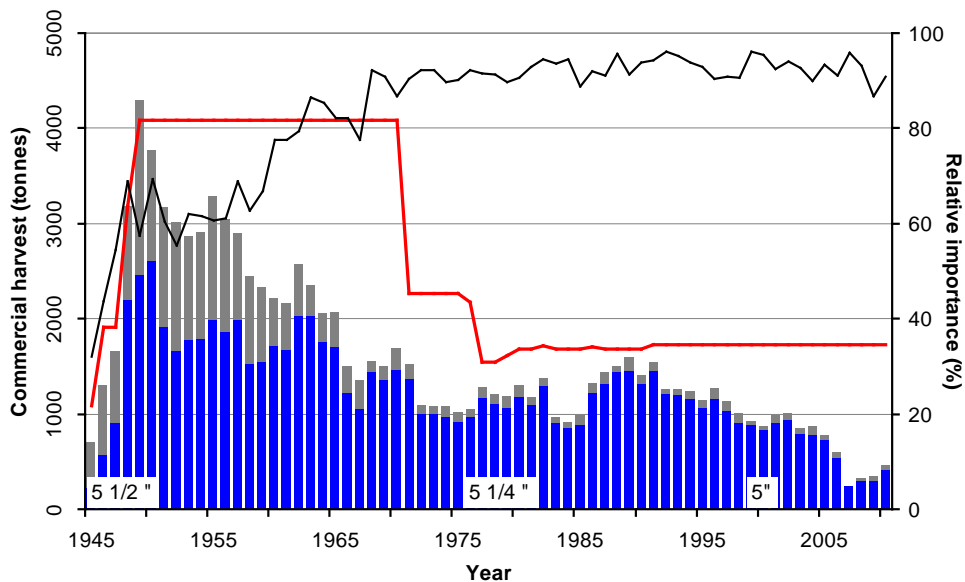


*Figure 2. Temporal changes in commercial harvests and quotas (red line) for Lake Whitefish (dark blue) and Lake Trout (grey) in GSL from 1944 through 2010. The relative importance (black line) of Lake Whitefish to Lake Trout was consistently elevated until 1970 and has been maintained above 90% since. The minimum legal mesh size was changed from 140 mm (5½") in 1944 to 133 mm (5¼") in 1977 and 127 mm (5") in 1998-2000.*
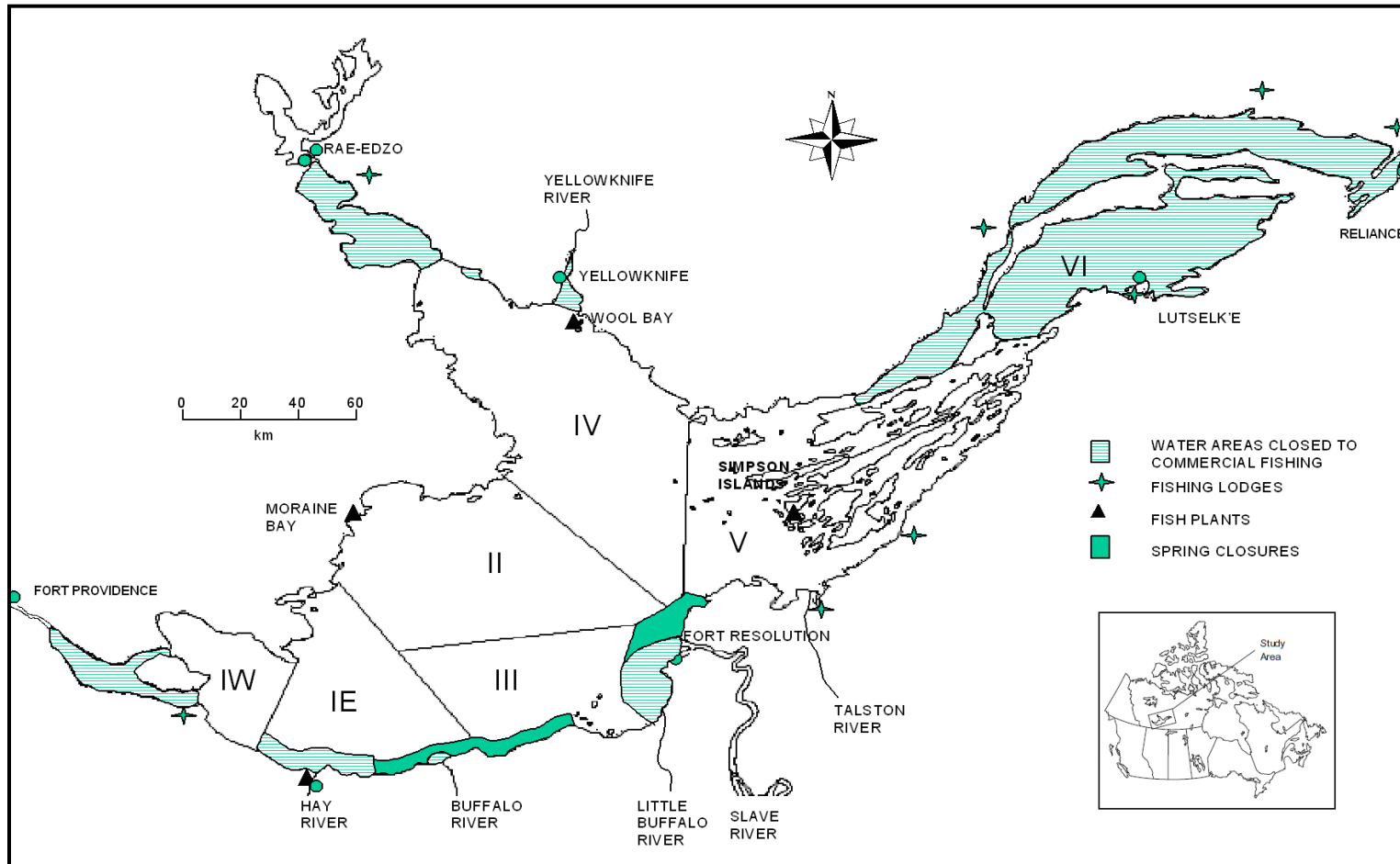
*Figure 3. Map showing designated administrative areas (IE, IW, II, III, IV, V and VI) for fisheries management of Lake Whitefish and Lake Trout in GSL. Areas closed to commercial fishing (lined fill indicates year-round closure; solid fill indicates spring closure) and the locations of fish plants (triangles) and fishing lodges (stars) are also indicated (modified from Read and Taptuna 2003, Day et al. 2013).*
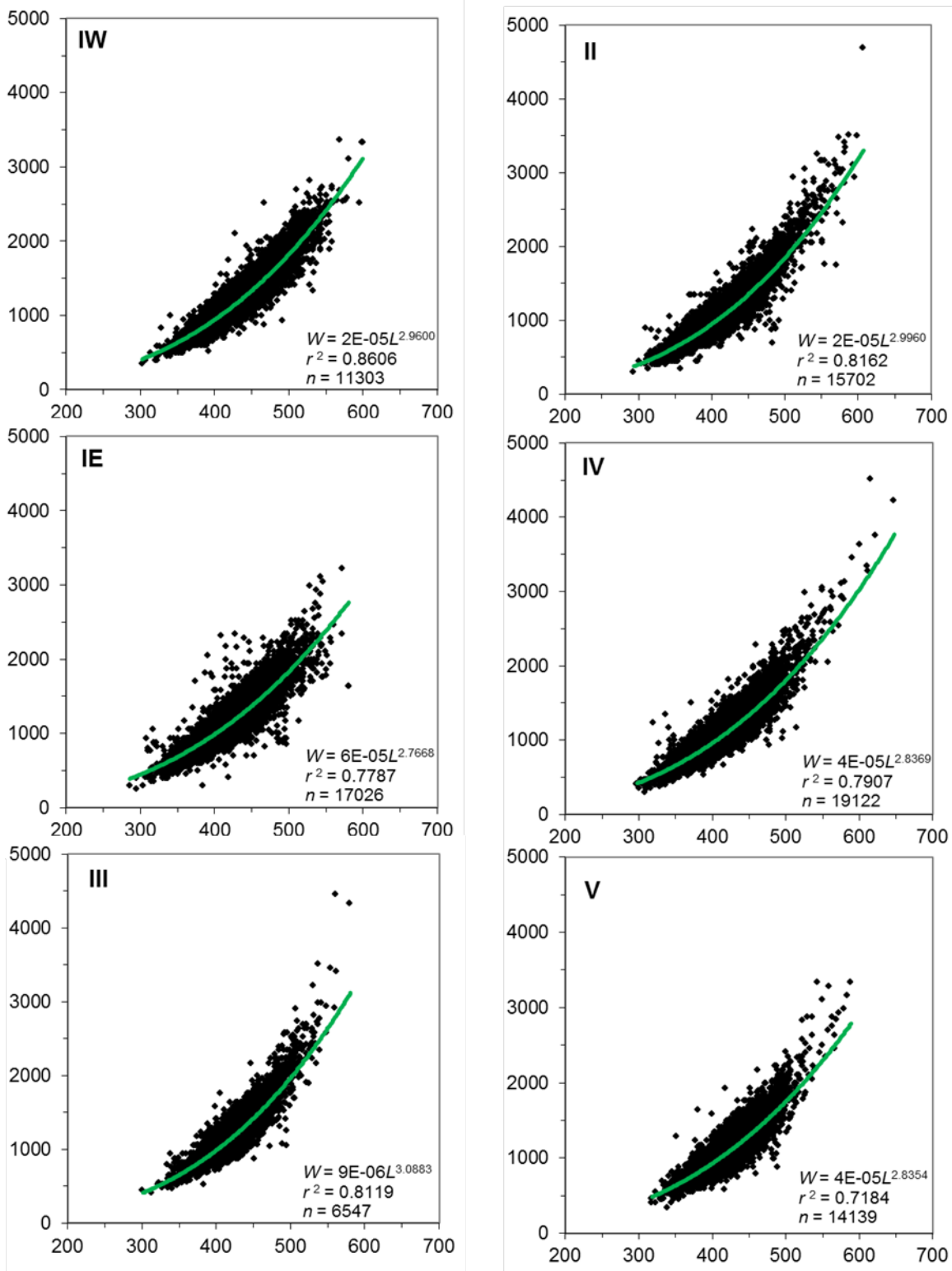
*Figure 4. Relationships between fork length and round weight of Lake Whitefish by GSL administrative areas during 1972-2004. Regression coefficients, correlation and sample sizes are provided within individual panels.*
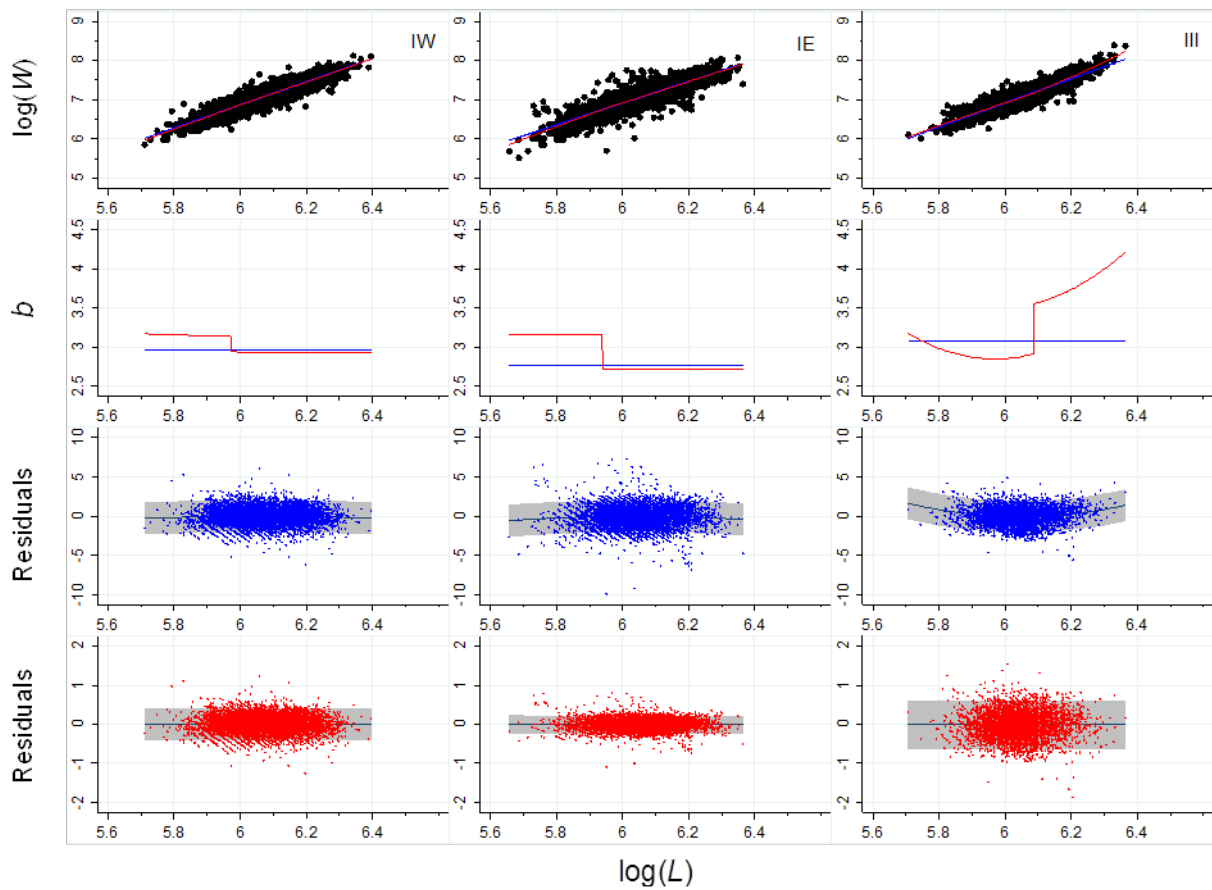
*Figure 5. Comparison of regression models of log-transformed pairs of fork length and round weight (upper panel black dots: observed) for GSL Lake Whitefish in shallow waters of areas IW (left), IE (middle) and III (right column). The allometric exponent b (second panel), residuals for linear (third panel blue) and average (bottom panel red) models, and quadratic regression with 95% CI (grey), are provided for shallow areas.*
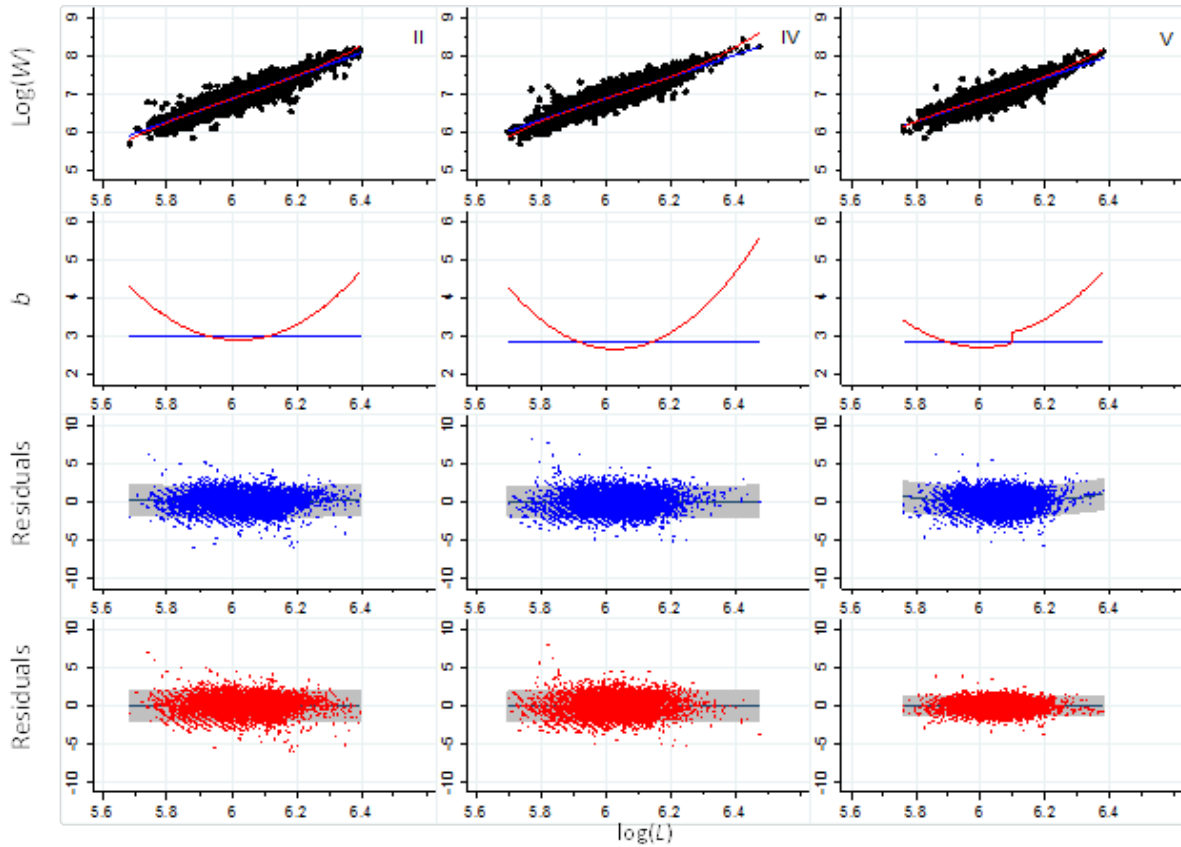
*Figure 6. Comparison of regression models of log-transformed pairs of fork length and round weight (upper panel black dots: observed) for GSL Lake Whitefish in the deep waters of areas II (left), IV (middle) and V (right column). The allometric exponent b (second panel), residuals from linear (third panel blue) and average (bottom panel red) models, and quadratic regression with 95% CI (grey), are provided for deep areas.*
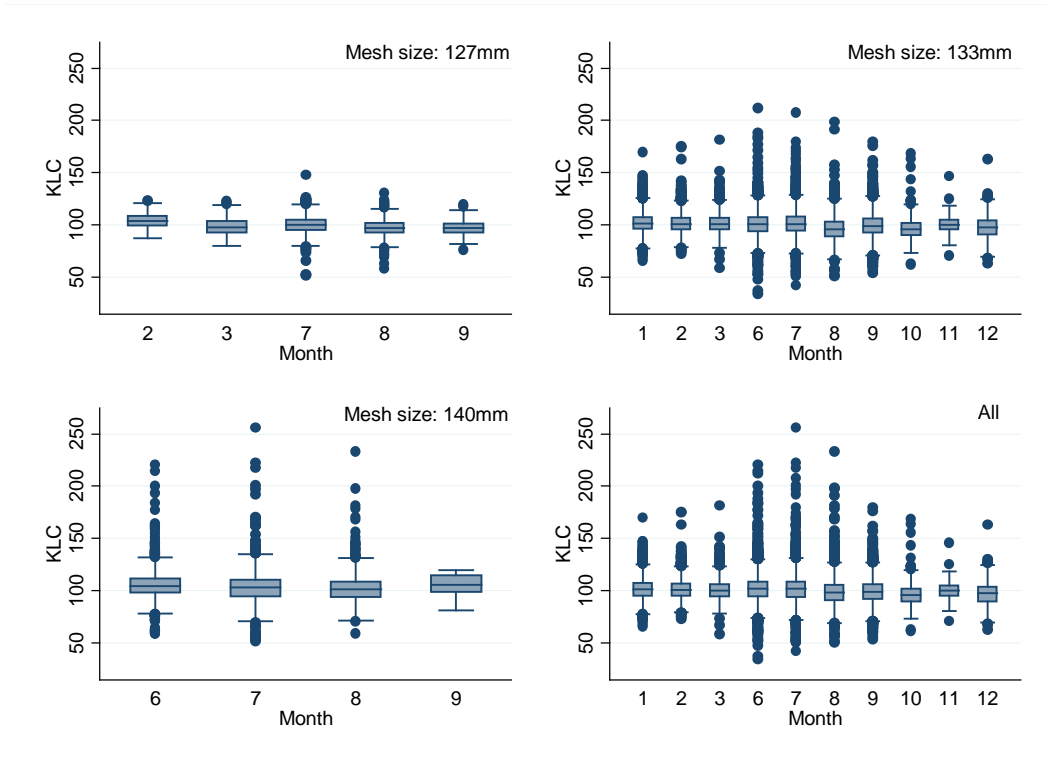
*Figure 7. Monthly changes in relative condition index, $K_{LC}$, by means of different mesh sizes.*
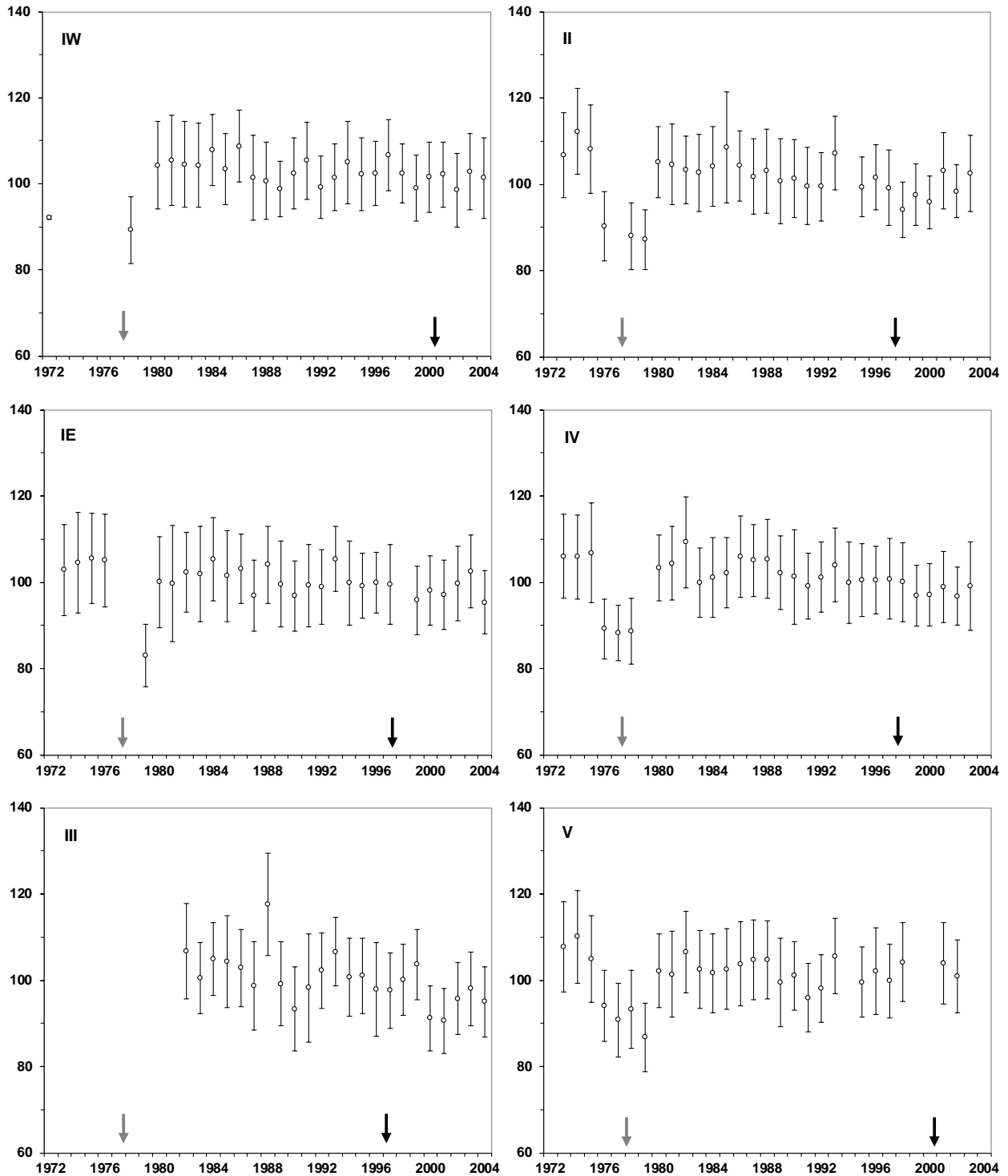
Figure 8. Inter-annual changes in relative condition index (K$_{LC}$) values, expressed by the mean plus one standard error, for Lake Whitefish in GSL. The minimum legal mesh size started at 140 mm (5½") in 1944, was 133 mm (5¼") from 1977 (grey arrow) to 1997 and changed to 127 mm in 1998-2000 (black arrow).
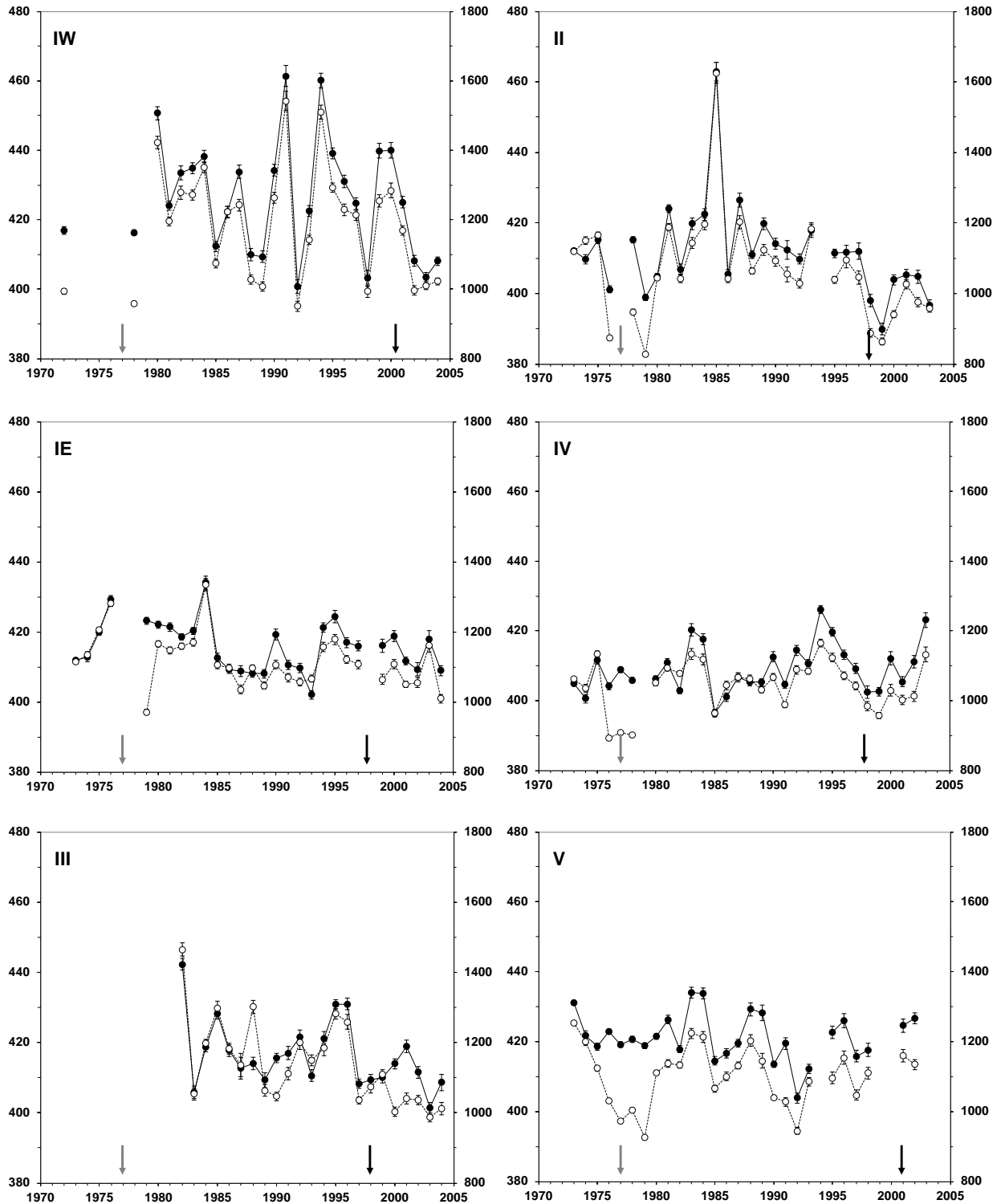
*Figure 9. Spatiotemporal variations in fork length (mm; filled circles) and round weight (g; open circles) for Lake Whitefish. Minimum legal mesh size for gillnets was initially set at 140 mm (5½"); this limit was reduced to 133 mm (5¼") in 1976/77 (grey arrow) and 127mm (5") during 1998-2000 (black arrow), respectively.*
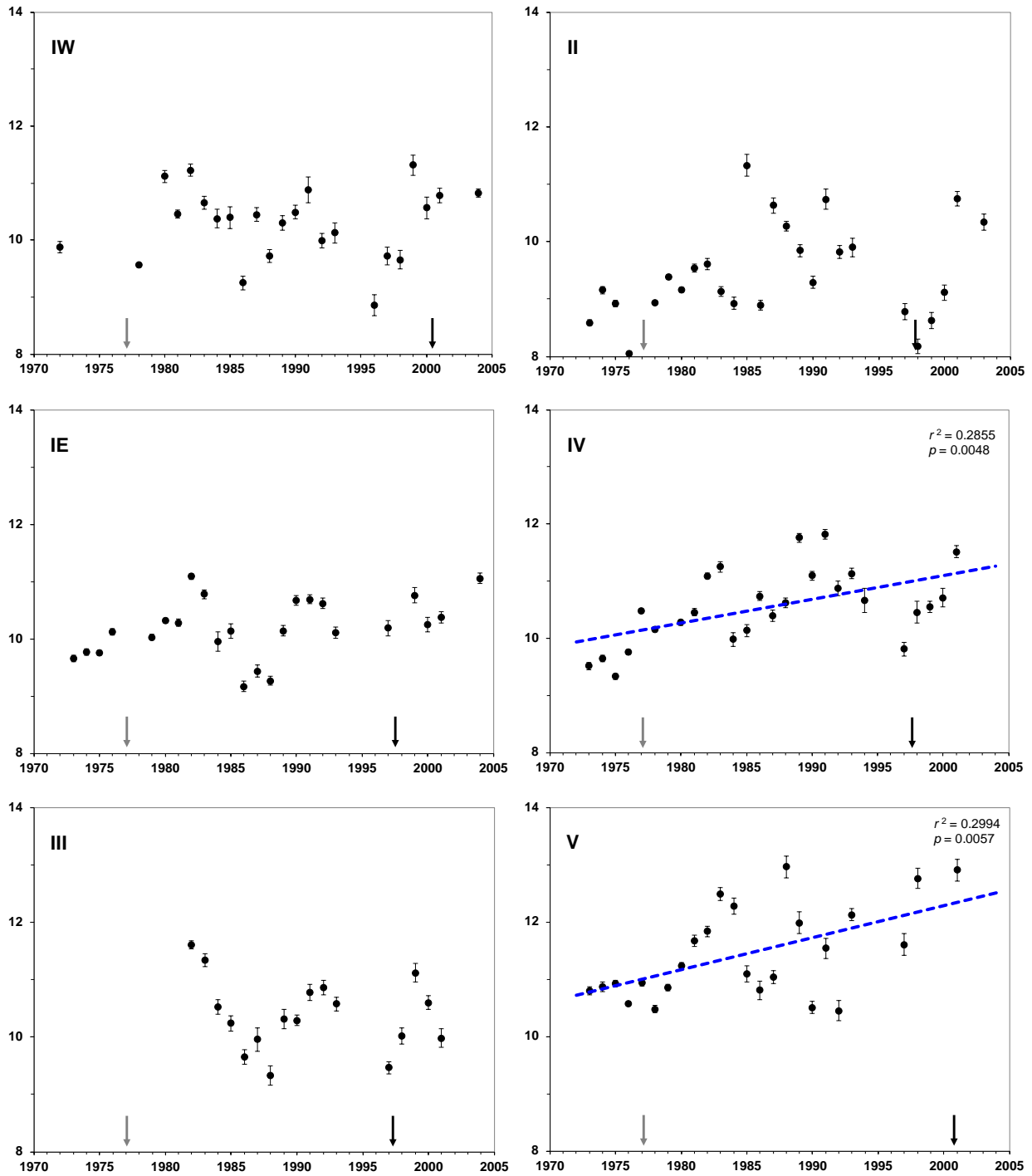
*Figure 10. Spatiotemporal changes in the average age of Lake Whitefish collected from commercial fisheries on GSL during 1972 through 2004. Minimum legal mesh size for gillnets was initially set at 140 mm (5½"); this limit was reduced to 133 mm (5¼") in 1976/77 (grey arrow) and 127mm (5") during 1998-2000 (black arrow), respectively.*
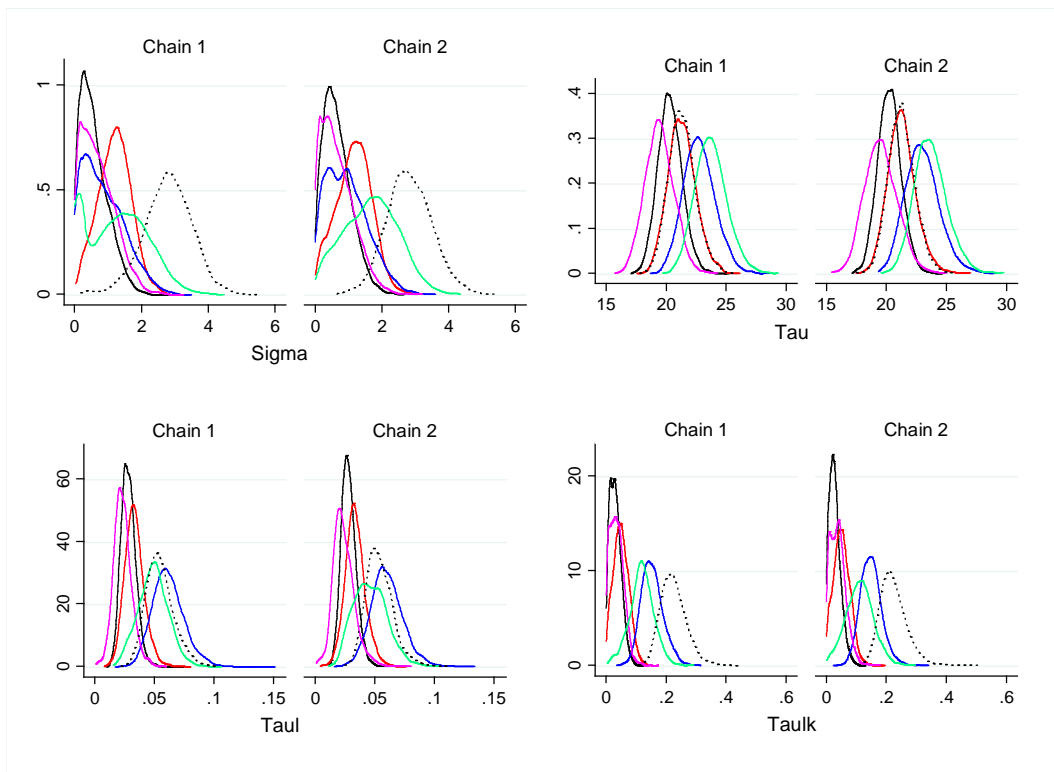
*Figure 11. Posterior probability density functions for hyper-parameter uncertainties when a two-chain LVKV model was used. Coloured lines represent spatial variation (black line, area IE; red line, area IW; blue line, area II; pink line, area III; green line, area IV; dotted line, area V). Uncertainty parameters Sigma, Tau, Taul and Tauk are components of process, observation, time-varying $L_\infty$ and K, respectively.*
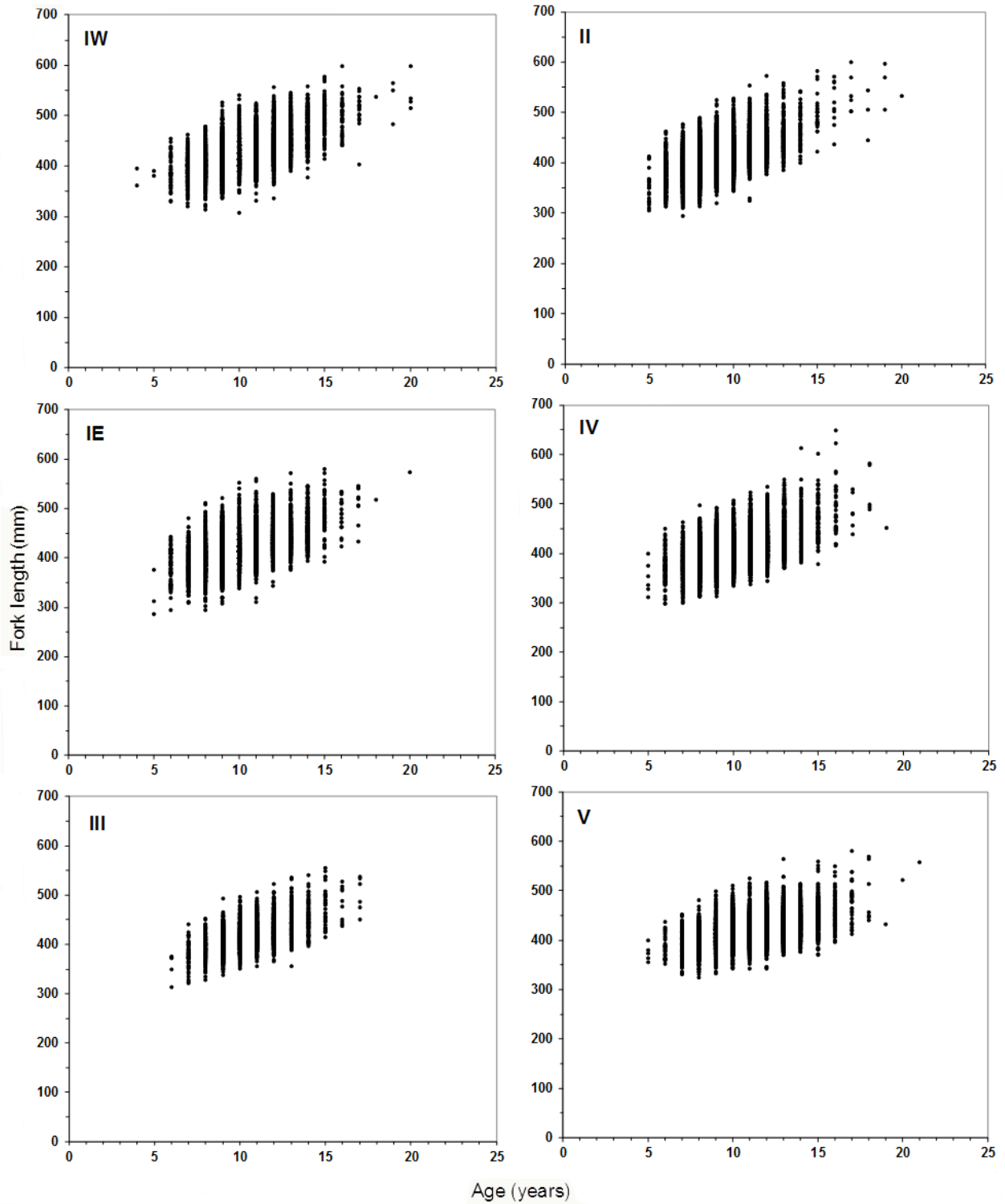
*Figure 12. Spatial variation in the relationship between fork length (mm) and age (years) for Lake Whitefish. Data are combined over a biological collection period from 1972-2004.*
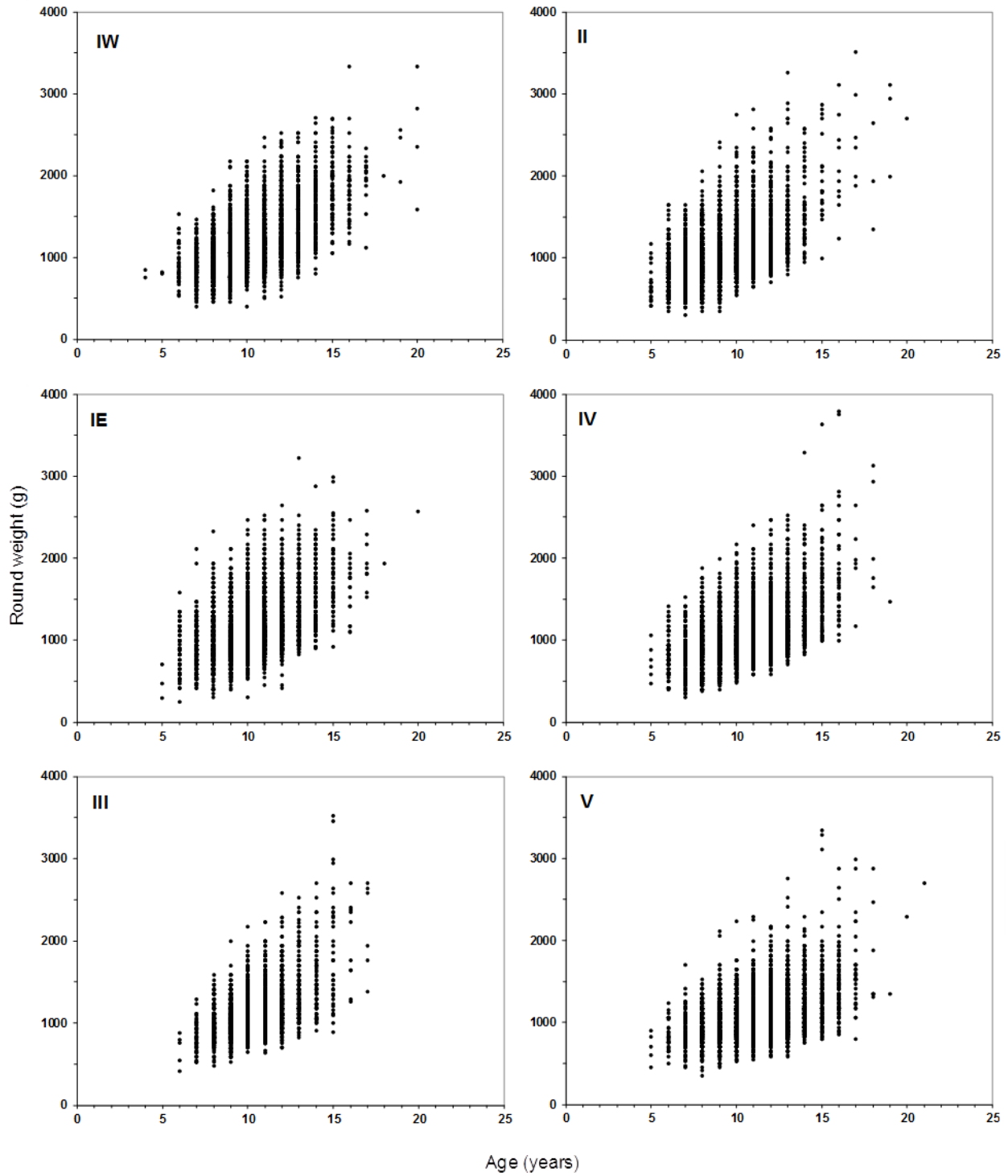
Figure 13. Spatial variation in the relationship between round weight (g) and age (years) for Lake Whitefish. Data are combined over a biological collection period from 1972-2004.
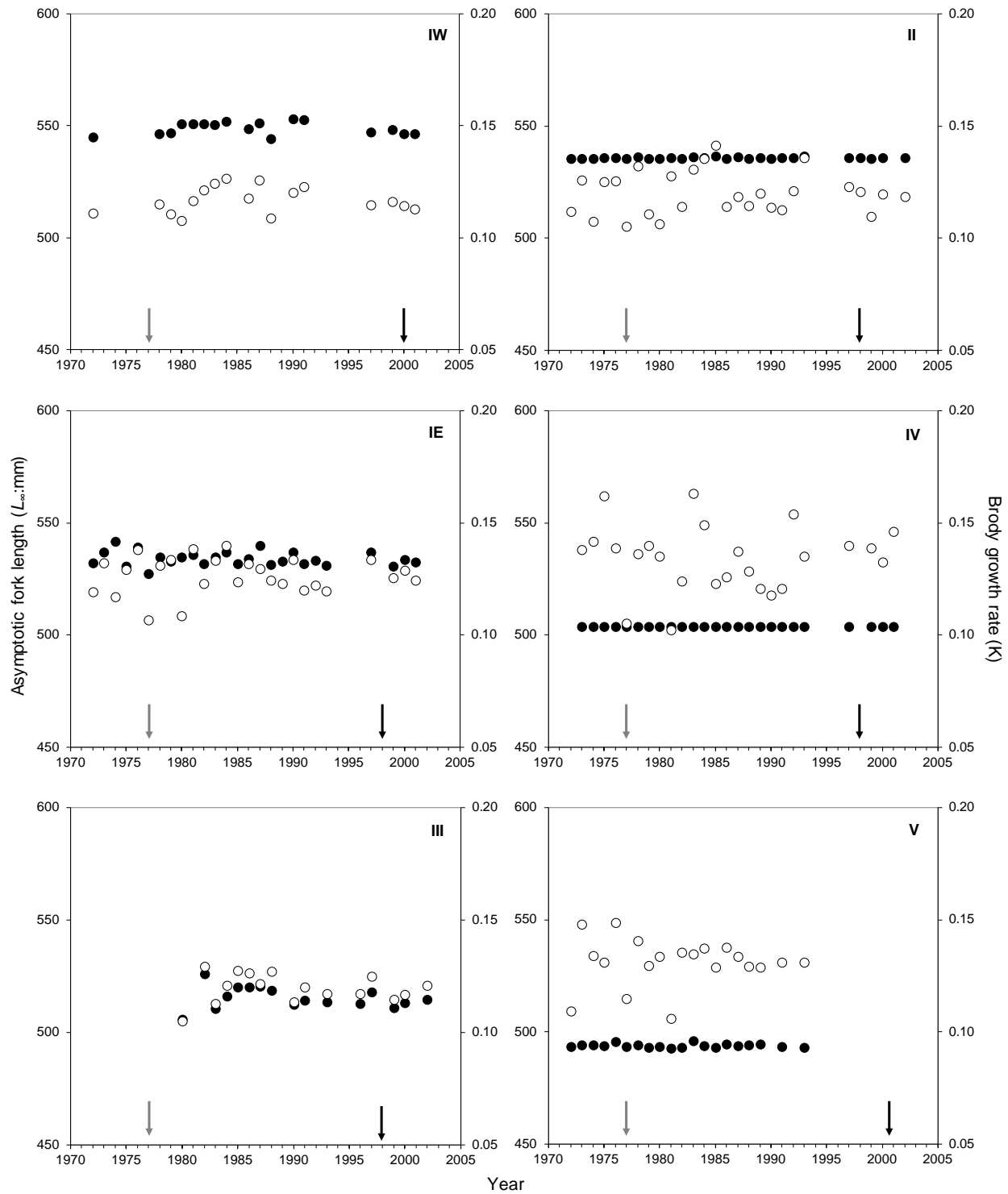
*Figure 14. Temporal changes in posterior hyper-parameters of asymptotic fork length ($L_\infty$: mm, solid circles) and the Brody growth rate (K: open circles) for Lake Whitefish across administrative areas of GSL. Minimum legal mesh size for gillnets was initially set at 140 mm (5½"); this limit was reduced to 133 mm (5¼") in 1976/77 (grey arrow) and 127mm (5") during 1998-2000 (black arrow), respectively.*
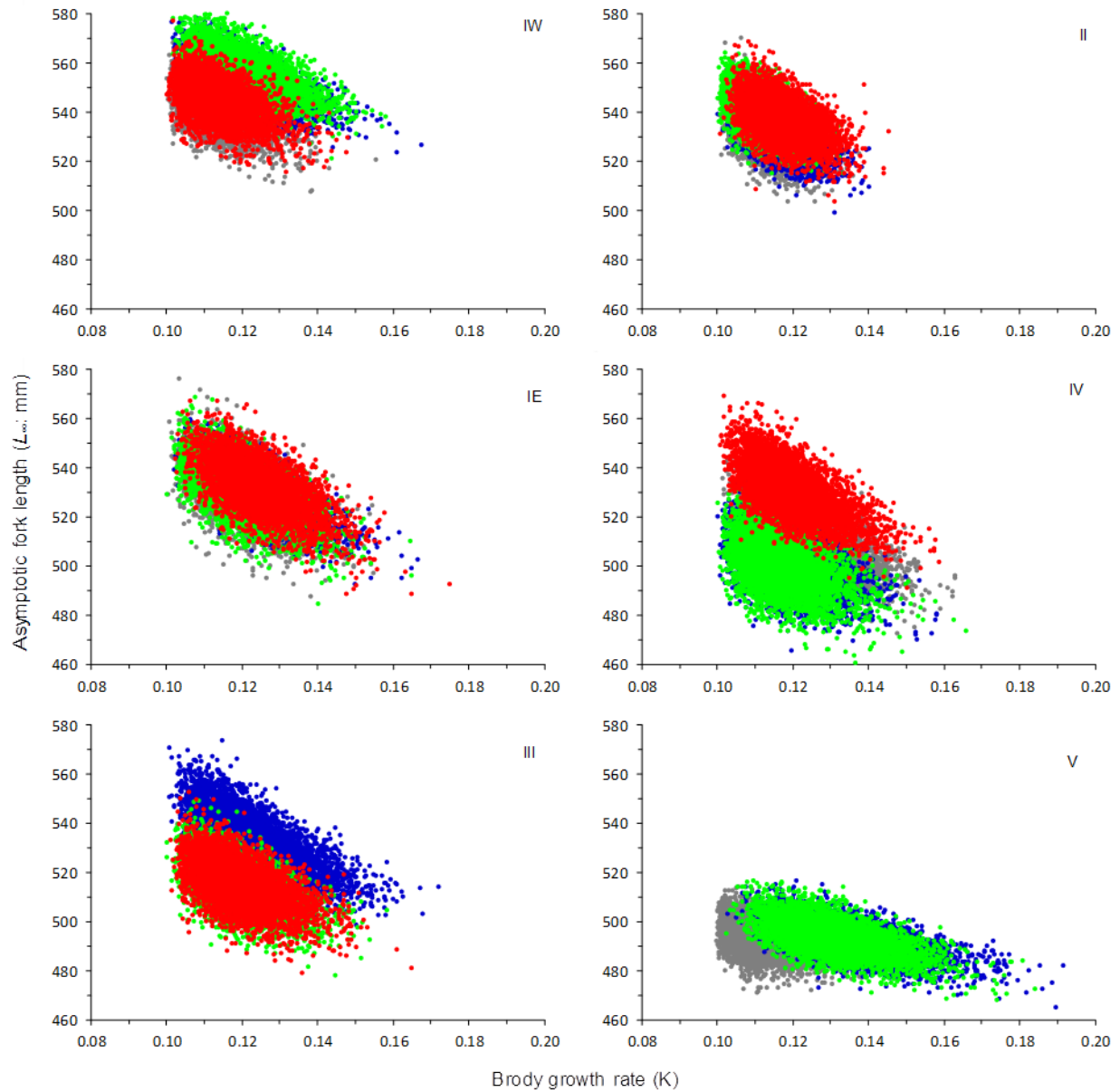
*Figure 15. Joint posterior hyper-parameter distributions for the Brody growth rate (K) and asymptotic fork length (L$_\infty$) obtained from a time-varying hierarchical growth model, GGM- LVKV, for Lake Whitefish. Coloured dots show temporal variation in the hyper-parameters in 1972 (grey), 1982 (dark blue), 1992 (green) and 2002 (red).*
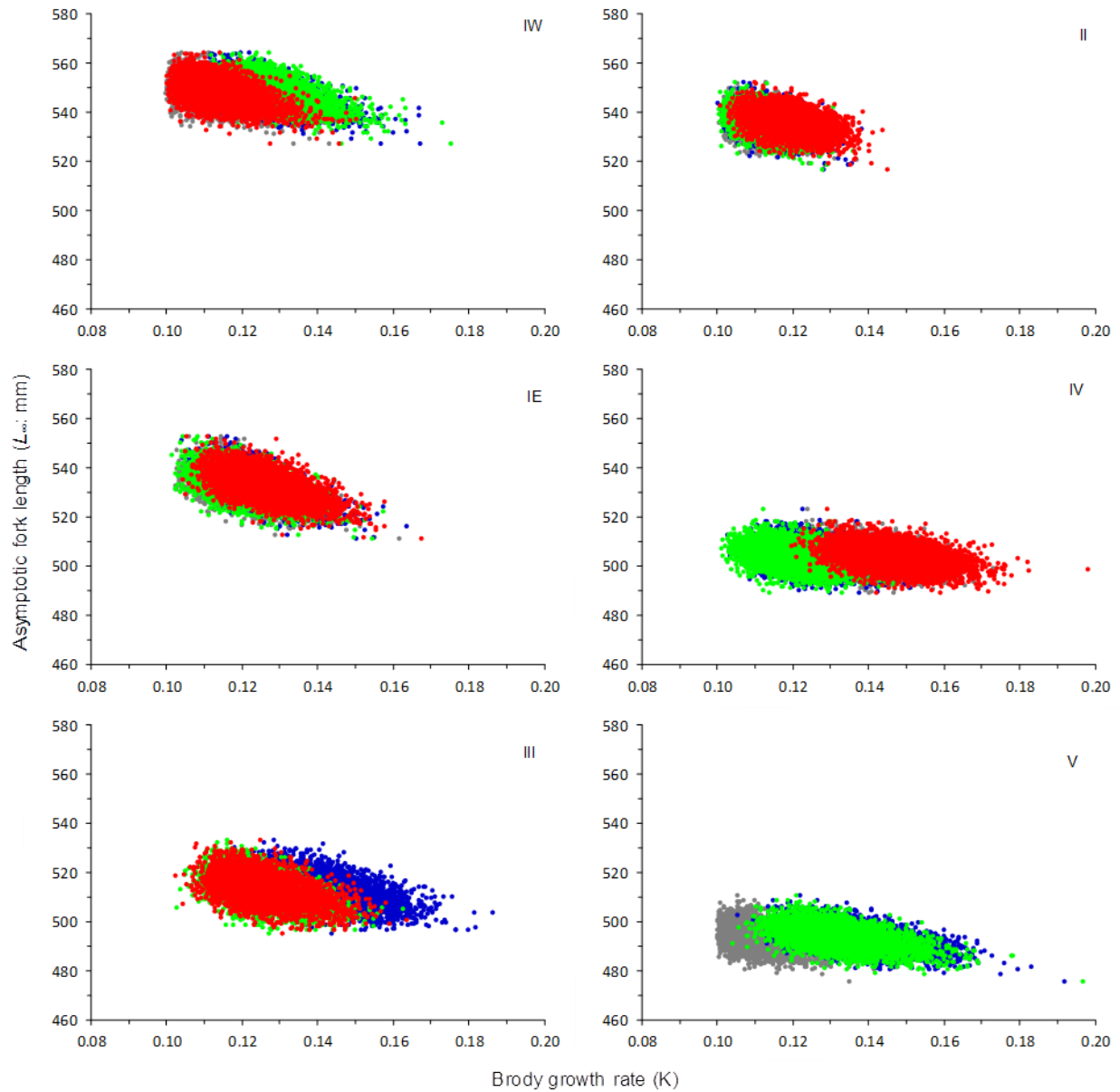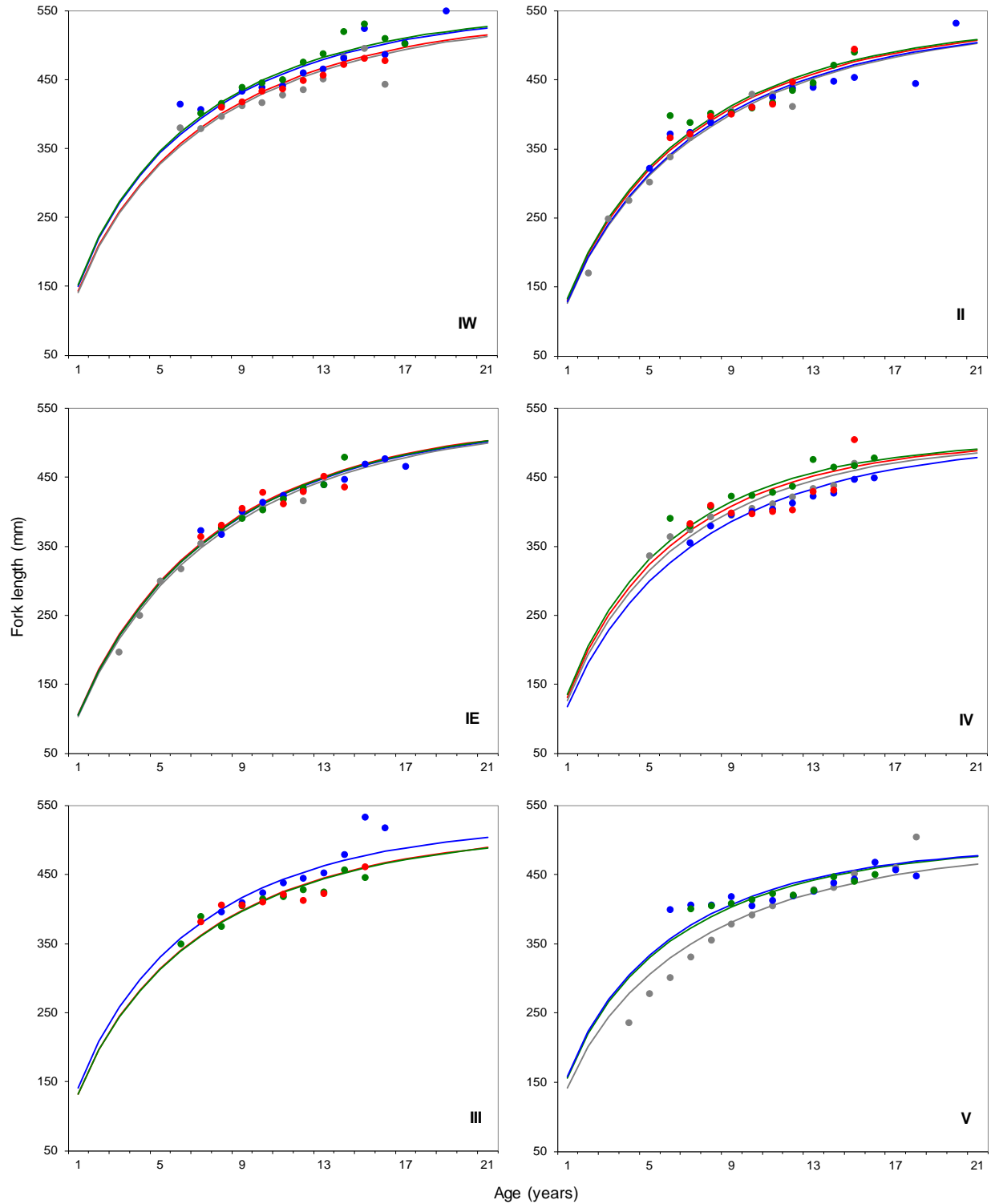
*Figure 16. Joint posterior hyper-parameter distributions for the Brody growth rate (K) and asymptotic fork length (L∞) obtained from a time-varying hierarchical growth model, GGM- LCKV, for Lake Whitefish. Coloured dots show temporal variation in the hyper-parameters in 1972 (grey), 1982 (dark blue), 1992 (green) and 2002 (red).*

*Figure 17. Projections of fork length-at-age growth patterns by the best hierarchical Bayesian growth model (GGM) for Lake Whitefish (lines), compared with observed fork length-at-age (dots) by areas in 1972 (grey), 1982 (dark blue), 1992 (green) and 2001 (red).*
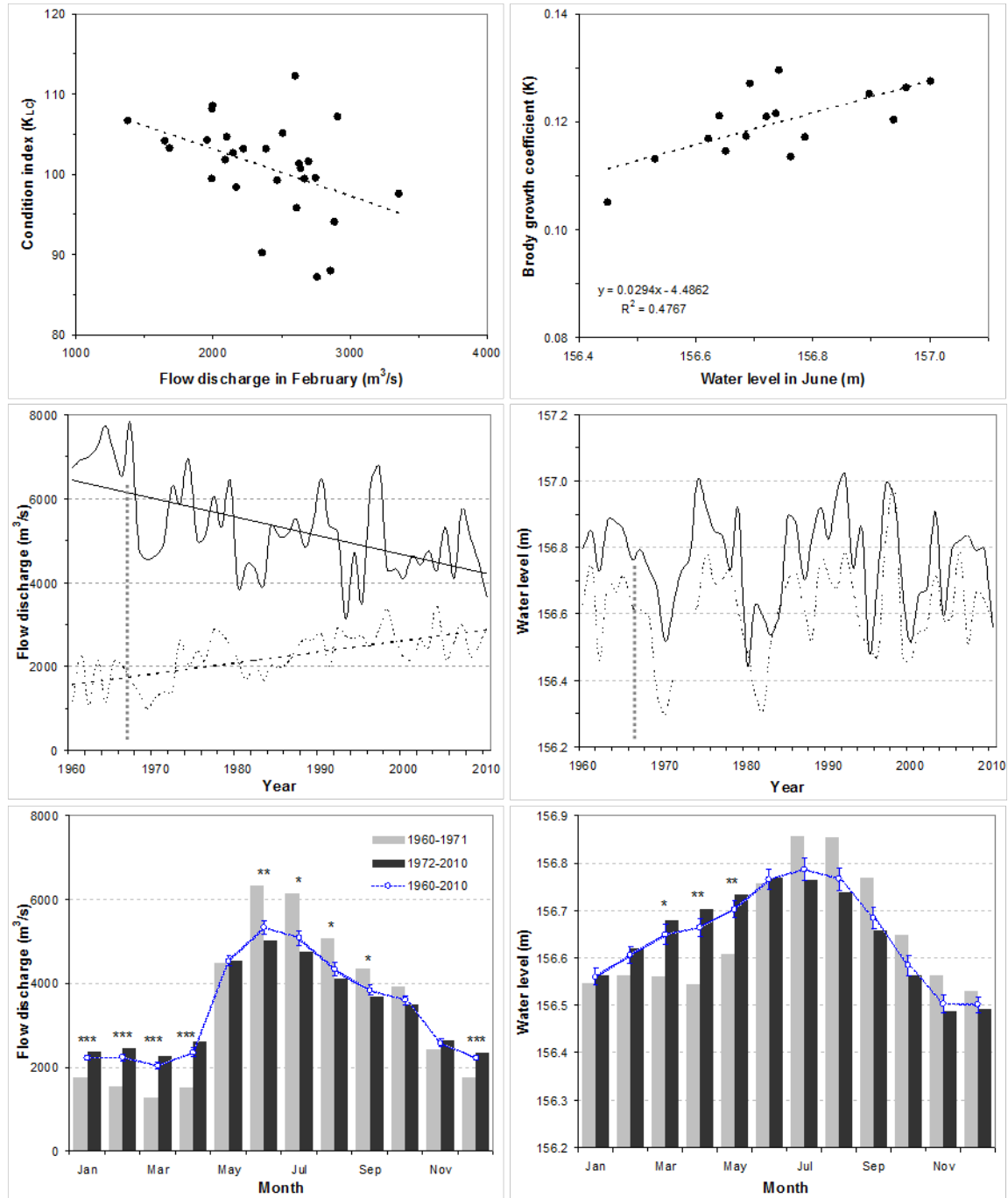
*Figure 18. Correlation between $K_{LC}$ and K versus flow discharge at Fitzgerald and water levels in GSL. Observed (black dots) and estimated (lines) values in the upper panel are expressed between riverine inflow in February and $K_{LC}$, as well as between water level in June and K. Changes in water level and riverine inflow in February (broken line) and June (solid line) from 1960-2010 are shown in the middle panel. Grey dotted lines show the time when the W.A.C. Bennett Dam was completed. The bottom panel shows seasonal variations in both hydrological parameters. Significance levels are labeled by α=0.5 (\*), 0.05 (\*\*) and 0.001 (\*\*\*).*
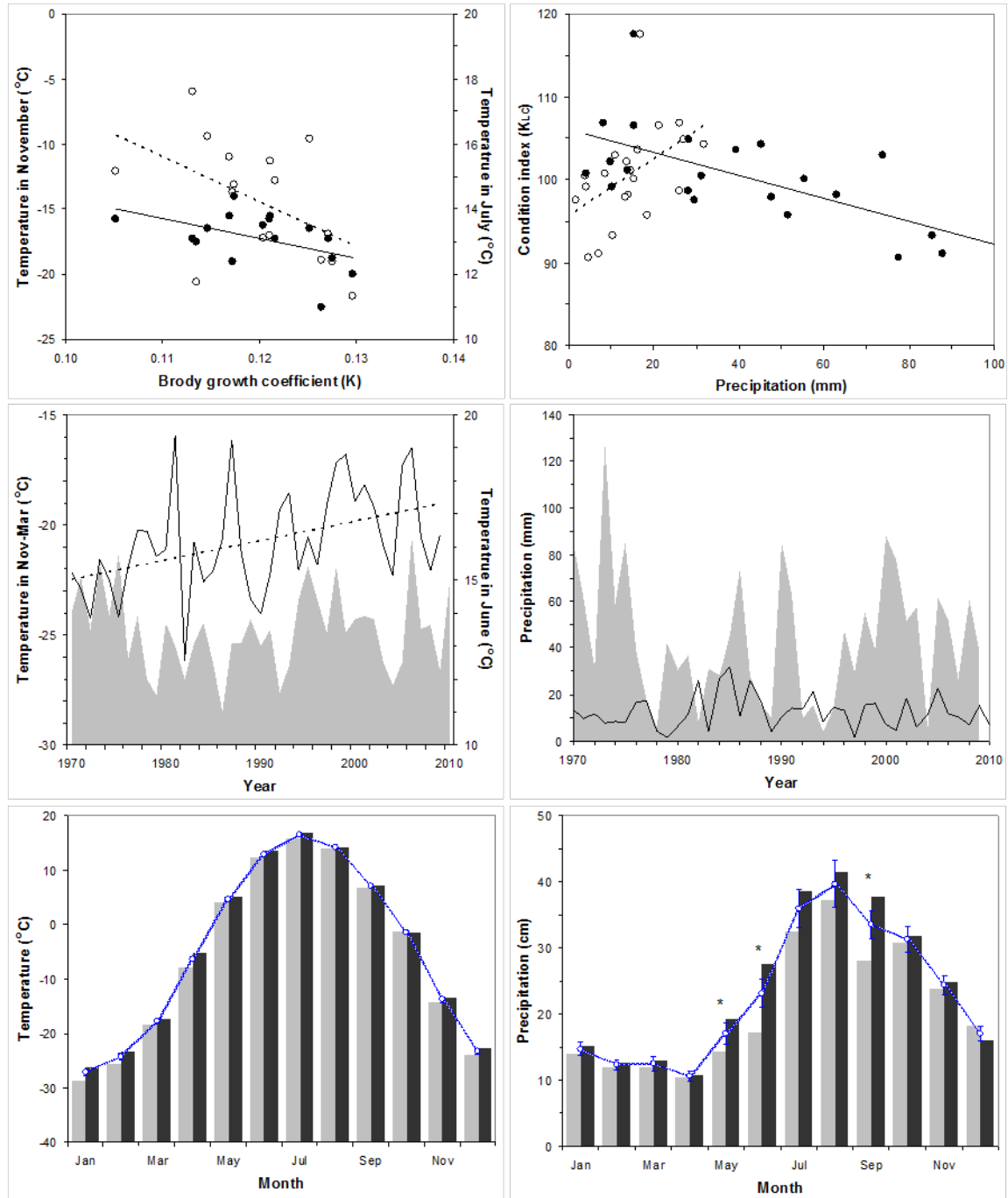
*Figure 19. Correlations between temperature in winter (November: open dots) or summer (June: solid circles) and K (lines) (left upper panel). Correlations between $K_{LC}$ and precipitation in February (open circles) or August (sold circles) (right upper panel). Temperature in winter (January-March: line) increased through 1970-2010, but no evident patterns in temperature and precipitation during April-August (grey area) are found in the middle panels. In the lower panels, a single-period seasonal pattern appears in both temperature and precipitation (black bar); there was a noticeable increase in precipitation during 1972-2010. Significance levels are labeled by α=0.5 (*), 0.05 (**) and 0.001 (***).*
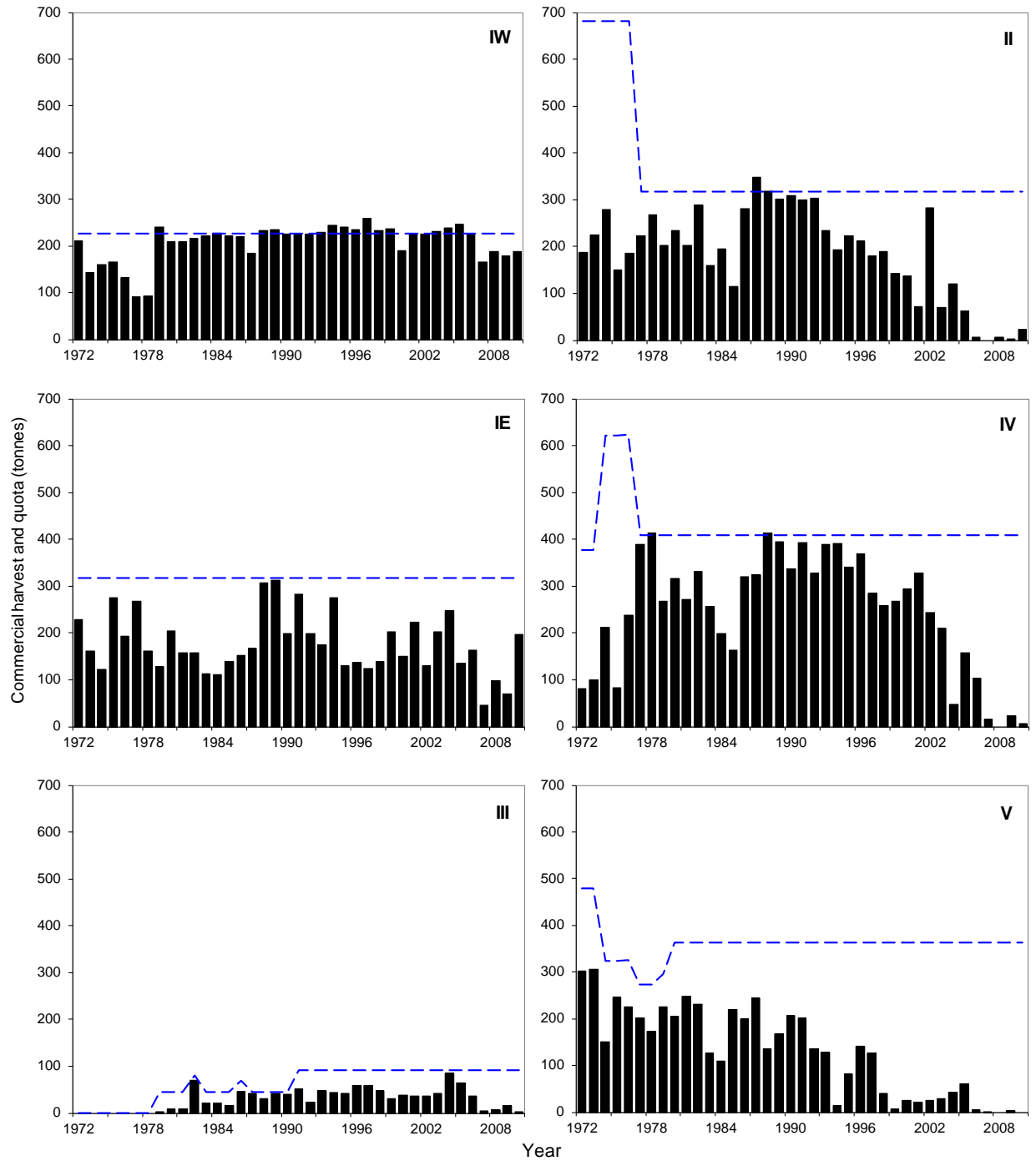
*Figure 20. Area-specific commercial harvest (solid bar) and quota (blue dotted lines) for GSL Lake Whitefish over 1972-2010. Total harvest in shallow waters (areas IW, IE and III) accounted for 43% of the harvest, while 57% of the harvest was from deeper waters (areas II, IV and V). The higher quotas in the deeper waters in the mid-1970s were suddenly reduced as a result of an impractical amount of fish production. Over years, harvest in IW, close to a fish plant, maintained the quota for winter fisheries only, and fisheries landings in the remaining areas diminished as a result of declining market values.*
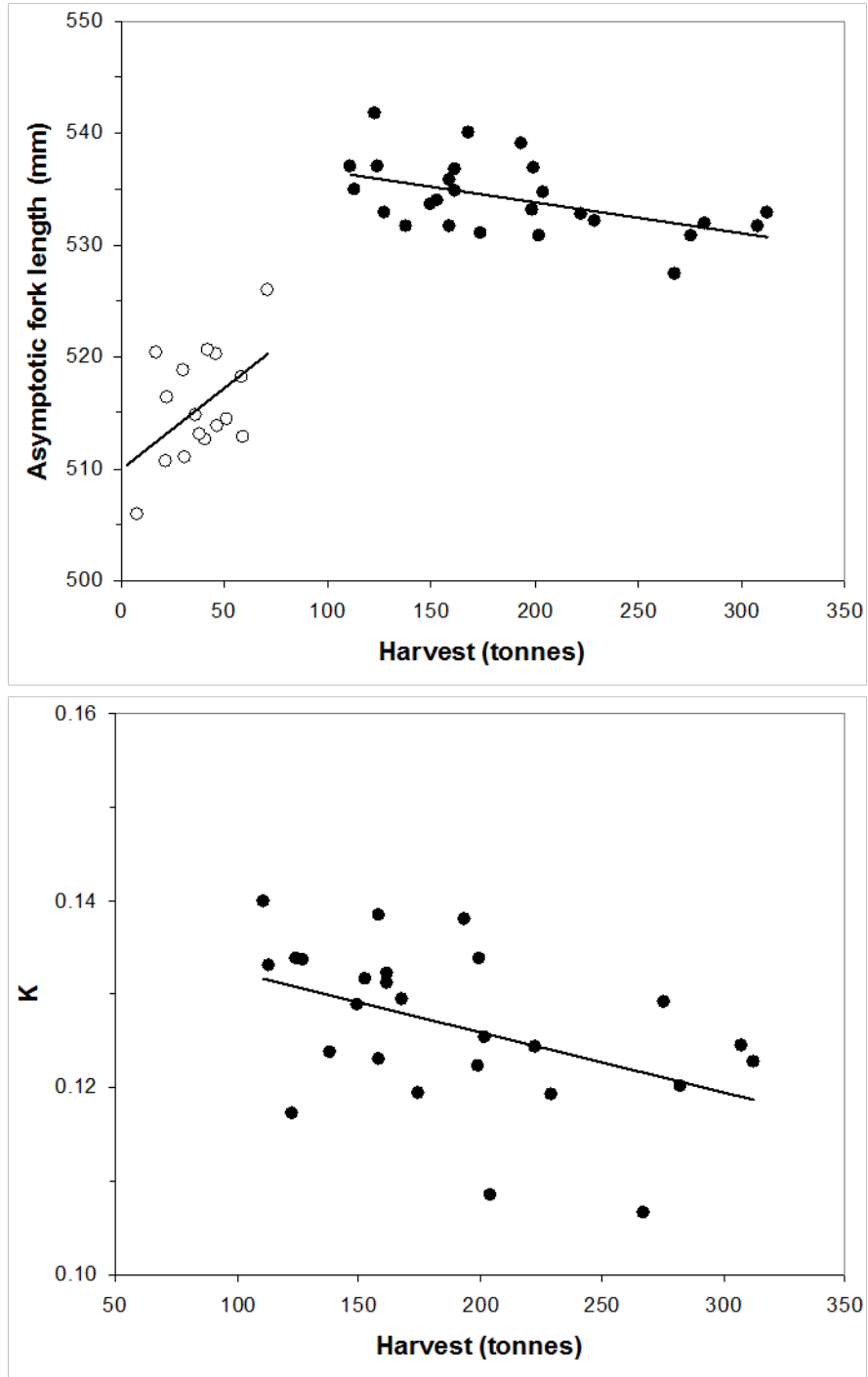
*Figure 21. Effects of exploitation on Lake Whitefish asymptotic fork length (L∞: upper) and Brody growth rate (K: bottom). A positive effect on L∞ is shown in the lightly fished area III (open circles) and a negative effect is shown in the heavily fished area IE (solid circles). A significant effect of exploitation in area IE manifested as a negative effect on the Brody growth rate.*