

Modeling Variation in Mass–Length Relations and Condition Indices of Lake Trout and Chinook Salmon in Lake Huron: a Hierarchical Bayesian Approach

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Abstract.—Commonly used approaches to studying mass–length relations and condition indices often do not adequately address covariance between mass–length parameters, usually ignore heterogeneity in individual variance for body mass at a given length, and assume that length distributions of fish samples are similar across regions and years. We used body mass at selected lengths as condition indices based on statistical modeling and a hierarchical Bayesian approach to inferences, and our approach allowed us to avoid using restrictive assumptions. We estimated spatial and annual variation in mass–length relations, where the process errors in parameters are drawn from a multivariate distribution. We also estimated region-, year-, and size-group-specific variance for individual variation in mass at given lengths. We applied our approach to study mass–length relations of lake trout *Salvelinus namaycush* (1977–2005) and Chinook salmon *Oncorhynchus tshawytscha* (1983–2004) in U.S. waters of Lake Huron. We found that small lake trout were able to maintain their condition in response to declines in prey availability, whereas Chinook salmon of the same size could not. Similarly, large Chinook salmon exhibited a greater and more rapid decline in body condition than did lake trout of the same size. We also found that spatial differences in recent temporal trends in condition of large fish altered the ranks of the three lake trout management regions. Ignoring spatial heterogeneity led to a biased overall average mass–length relation for lake trout. The large temporal variation in mass–length parameters suggested that it was better not to assume isometric growth for a specific year, even though the overall average exponent for Chinook salmon was nearly 3.0. In our study, conventional application of Fulton’s condition factor to a relatively narrow size range was able to capture qualitative long-term trends but missed some important short-term changes because of the additional variation of length-related bias and the limitation of sample sizes.

Mass–length relations and condition indices constitute a basis for studying physiological condition of fish populations (LeCren 1951; Murphy et al. 1990; Anderson and Neumann 1996; Blackwell et al. 2000) and are also major components in fishery stock assessment (Dutil et al. 1999; Quinn and Deriso

1999; Kimmerer et al. 2005). Many studies have continued to develop condition indices or improve their use in animal ecology, particularly in fishes (Green 2001; Brenden et al. 2003; Lai and Helser 2004; Gerow et al. 2005; Froese 2006). The visibility of condition indices in fisheries literature is very high, and declines in fish condition are commonly of concern (Lambert and Dutil 1997; Cardinale and Arrhenius 2000; Madenjian et al. 2003; Marshall et al. 2004). Such concerns often have direct connections with the

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decreases in fish survival or recruitment, as associated with poor energetic status (Henderson and Morgan 2002; Hartman and Margraf 2003; Van Horn 2003; Nalepa et al. 2005; Winter et al. 2005; Peters et al. 2007). It is surprising, however, that only a few published studies have addressed both spatial and annual variations in fish condition (Filbert and Hawkins 1995; Meretsky et al. 2000) or have compared changes in body condition among fish species and among size-groups within a fish population (Murphy et al. 1990; Porath and Peters 1997; Porath et al. 2003). Such comparisons are basic information required for ecosystem-based fishery management.

The scarcity of such studies stems partially from the limitation of condition indices or the ways these condition indices are applied. Commonly used condition indices are meaningful when comparing individuals of the same length or populations with similar length distributions, because fish often grow allometrically (Bolger and Connolly 1989; Cone 1989; Springer et al. 1990; Froese 2006). A difference in condition indices among populations differing in length distributions may only reflect static allometric growth rather than any difference in fish condition. One possible way to adequately apply common condition indices is to evaluate the condition of fish with different lengths and examine the length-specific condition responses to changes in the environment. Such approaches, however, typically encounter issues related to small sample size as data are partitioned into areas, time periods, and restricted size-categories.

Another approach for dealing with fish size effects on condition indices is to adopt a statistical modeling approach in which body mass is a power function of body length and plausible statistical assumptions are made to evaluate how parameters vary spatially and temporally. This approach has also been criticized because the two parameters of a power function are inversely related and cannot be used directly as condition indices (Bolger and Connolly 1989; Springer et al. 1990). Many recent studies have used body mass at two or more selected lengths as condition indices (e.g., Winters and Wheeler 1994; Filbert and Hawkins 1995; Meretsky et al. 2000), but these analyses usually require sampling efforts beyond regular and routine sampling programs (Kimmerer et al. 2005).

We build on general tactics of the statistical modeling approach to develop a new method for (1) quantifying spatial and annual variation in condition indices, (2) comparing annual changes in condition indices between two predatory fish species, and (3) showing size-specific changes in fish condition. Our method is based on a hierarchical Bayesian approach to statistical inference that has been applied to fish growth

models (Pilling et al. 2002; Helser and Lai 2004; He and Bence, in press). We applied our method to lake trout *Salvelinus namaycush* and Chinook salmon *Oncorhynchus tshawytscha* in Lake Huron, where there have been major changes in both growth and body condition of the two species. For comparative purposes, we also employed a conventional analysis of Fulton's condition factor (K ; Ricker 1975; Anderson and Neumann 1996; Nash et al. 2006) using the same data from which our improved condition indices were developed.

Methods

Study area and background.—We analyzed mass and length data for lake trout and Chinook salmon captured in U.S. waters of Lake Huron. Both species have been stocked in the Laurentian Great Lakes of North America since the late 1960s. Lake trout are stocked to rebuild self-sustaining populations of this native predator (Hansen 1999). Chinook salmon are stocked to support a recreational fishery and to control the invasive alewives *Alosa pseudoharengus*, particularly in Lakes Huron, Ontario, and Michigan (Tody and Tanner 1966; Kocik and Jones 1999). Since predator populations were reestablished in these lakes and since lake productivity declined in Lake Ontario, there have been declines in alewife size at age and population biomass (Henderson and Brown 1985; Jude and Tesar 1985; O'Gorman et al. 1997, 2004; Madenjian et al. 2003, 2005). From the low growth and low abundance levels, prey fish biomass further declined substantially during 2003–2005 in Lake Huron, and the population biomass of alewives decreased by 99% (S. Riley, J. Schaeffer, and E. Roseman, U.S. Geological Survey [USGS], Great Lakes Science Center, personal communication). The alewife is a key prey species in the Great Lakes, and the health of lake trout and Chinook salmon fisheries depend on food web balance (Stewart et al. 1981; Stewart and Ibarra 1991; Jones et al. 1993; Rand and Stewart 1998a, 1998b). Studies in Lake Michigan have suggested that declines in prey availability can have substantial effects on energetic status and survival of Chinook salmon (Holey et al. 1998; Peters et al. 2007). In this study, we analyzed how mass–length relations and body condition of the two predatory fish species in Lake Huron have responded to changes in lake productivity and prey fish biomass during the past three decades.

Lake trout and Chinook salmon data.—Lake trout mass–length relations and condition were analyzed from data collected during an annual spring (May and early June) gill-net survey in Michigan waters of Lake Huron from 1977 to 2005. The survey was conducted by the Alpena Fisheries Research Station of the

Michigan Department of Natural Resources (MDNR); the MDNR and Chippewa Ottawa Resource Authority have conducted the survey cooperatively since 1991. The survey used 1.83-m-high multifilament nylon gill nets that consisted of nine 30.5-m panels ranging in mesh size from 50.8 to 152.4 mm (mesh increment = 12.7 mm). The nets were set overnight on the bottom across depth contours of 10–50 m. Every lake trout captured in the survey was measured for total length (TL, nearest mm) and mass (nearest 0.01 kg). We used all data for 40,021 lake trout collected over the 29-year period. For the purpose of lake trout stock assessment and fisheries management, Lake Huron’s main basin has been divided into northern, north-central, and southern regions (Smith et al. 1961; Ebener 1998; Sitar et al. 1999; Wilberg et al. 2002; Johnson et al. 2004). Length and body mass information were available from at least 200 lake trout/region for each year.

Chinook salmon TL and body mass data for 1983–2004 were obtained from an annual creel survey of the sport fishery in Michigan waters of Lake Huron. The creel survey was conducted by the MDNR Charlevoix Fisheries Research Station (Rakoczy and Svoboda 1997; Bence and Smith 1999). Fish samples were collected at major ports on Lake Huron. Both TL (nearest mm) and body mass (nearest 0.01 kg) were measured at a site where charter boats and anglers returned to shore. We restricted our analysis to fish caught during August of each year because it was the month with the largest number of biological samples in most years. We used all data for 6,076 Chinook salmon collected during the 22-year period. At least 108 Chinook salmon were sampled in each year except 1990, when only 54 were sampled. Given that Chinook salmon forage over a much wider range than lake trout in Lake Huron (Adlerstein et al. 2007a, 2007b) and because of the much smaller annual sample size for Chinook salmon than for lake trout, we analyzed Chinook salmon samples without stratifying by lake regions.

In comparing body condition between lake trout and Chinook salmon and among size-groups within a species, we emphasized how condition indices changed among years. In doing so, we acknowledge that Chinook salmon condition should be higher than lake trout condition, because lake trout data were from May and early June collections and Chinook salmon data were from August collections. Anglers may also release fish with low body mass for a given length, although this is probably a rare occurrence. For these reasons, condition of sampled Chinook salmon may have been better than the population average during a given year.

Hierarchical model structure for modeling variation in body mass of a given length.—Our models used two

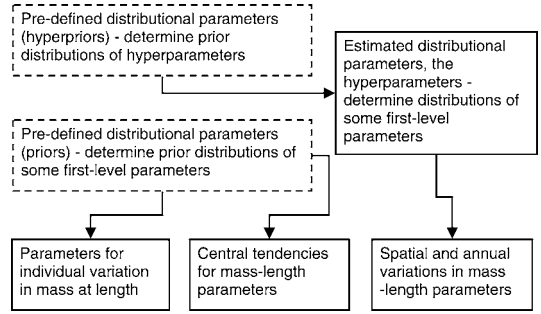


FIGURE 1.—Diagram depicting the relations between two parameter levels (parameters and hyperparameters; solid boxes) estimated for predicting Chinook salmon and lake trout body mass at length and their predefined distributional parameters (dashed boxes).

levels of parameters (Figure 1). In this subsection, we describe the functions of the first- and second-level parameters (the latter are also termed hyperparameters), and the links between the two levels. In the next subsection, we further describe the structure of our hierarchical Bayesian approach to inferences.

The first-level parameters included the central tendency parameters for an overall mass–length relation, the spatial and annual variation in parameters of mass–length relations, and the parameters for individual variation in body mass at a given length. These first-level parameters directly determined the distributions of individual mass at a given length:

$$W_{r,y,s,j} \sim \text{LN}(W_{r,y,L}, \sigma_{r,y,s}^2), \tag{1}$$

$$W_{r,y,L} = a_{r,y} b_{r,y}^L, \tag{2}$$

$$\log_e(a_{r,y}) = \log_e(a_r) \exp(\varepsilon_{a,r,y}), \tag{3}$$

and

$$b_{r,y} = b_r \exp(\varepsilon_{b,r,y}). \tag{4}$$

Here, $W_{r,y,s,j}$ is the j th observation of individual body mass (kg) from region r , year y , and size-group s ; LN indicates that $W_{r,y,s,j}$ follows a lognormal distribution; $W_{r,y,L}$ is the median body mass in region r and year y for a fish with a TL (mm) of L (Baskerville 1972; Sprugel 1983; Hayes et al. 1995); $\sigma_{r,y,s}^2$ is the variance of log-transformed body mass at length for a specific region, year, and size-group. The coefficient $a_{r,y}$ and exponent $b_{r,y}$ could vary among regions and years, with region-specific central tendencies ($\log_e[a_r]$ and b_r). We assumed that the process errors in mass–length parameters were multiplicative, and they were specific to the combination of a parameter, region, and year ($\varepsilon_{a,r,y}$ and $\varepsilon_{b,r,y}$). The two central tendency parameters

and their process errors were in different scales because of the linear relation after log transformation of both sides of equation (2).

All first-level parameters (i.e., $\log_e[a_r]$, b_r , $\varepsilon_{a,r,y}$, $\varepsilon_{b,r,y}$, and $\sigma_{r,y,s}^2$) were estimated in our models. From the first four parameters, the models calculated the power function coefficients $a_{r,y}$ and exponents $b_{r,y}$ (equations 3 and 4) and predicted body mass from body length (equation 2). These four parameters together with $\sigma_{r,y,s}^2$ described the distribution of individual mass at a given length (equation 1).

In our analysis, the among-individual variance $\sigma_{r,y,s}^2$ was specific to region, year, and size-group, and this distinguished our approach from many others that assume homogeneous variances. Ignoring variance heterogeneity when it does exist can lead to biased estimation of mass-length relations and biased prediction of body mass at length. We avoided these potential biases by explicitly estimating $\sigma_{r,y,s}^2$, which in turn appropriately weighted data from each region, year, and size-group. Our allowance for heterogeneous variances represented the same concept as inverse variance weighting in weighted least-squares regression (Neter et al. 1996). There were three spatial regions for lake trout and only one spatial region for Chinook salmon in our analysis, as described in the previous subsection. Based on residual plots of preliminary modeling fits, we defined four length-groups for each species (<350, 350–550, 550–750, and >750 mm for lake trout; <450, 450–650, 650–850, and >850 mm for Chinook salmon).

The second-level parameters (i.e., hyperparameters; Figure 1) represented another essential feature of our approach that distinguished our analyses from most other analyses of mass-length relations. Such a hierarchical model structure is useful when some parameters can be viewed as being related and, thus, as being a set of samples from a common probability distribution (Gelman et al. 2004:117). In our case, for each combination of region and year, we treated the pair of process errors that influenced $a_{r,y}$ and $b_{r,y}$ as repeated samples from a multivariate normal distribution:

$$\underline{\varepsilon}_{r,y} \sim N(\underline{0}, \Sigma_\varepsilon), \tag{5}$$

and

$$\Sigma_\varepsilon = \begin{bmatrix} \sigma_{\varepsilon a} & \\ & \sigma_{\varepsilon b} \end{bmatrix} \begin{bmatrix} 1 & r \\ r & 1 \end{bmatrix} \begin{bmatrix} \sigma_{\varepsilon a} & \\ & \sigma_{\varepsilon b} \end{bmatrix}. \tag{6}$$

Here, $\underline{\varepsilon}_{r,y}$ is a region- and year-specific vector that is normally distributed (N) and consists of $(\varepsilon_{a,r,y}, \varepsilon_{b,r,y})^T$; the zero vector ($\underline{0}$) is its mean for each region; and the variance-covariance matrix Σ_ε depends on three

hyperparameters: standard deviation $\sigma_{\varepsilon a}$ for the process errors $\varepsilon_{a,r,y}$, $\sigma_{\varepsilon b}$ for the process errors $\varepsilon_{b,r,y}$, and the correlation coefficient r between $\varepsilon_{a,r,y}$ and $\varepsilon_{b,r,y}$ (Daniels and Kass 1999, 2001; Barnard et al. 2000; Gelman et al. 2004; He and Bence, 2007). We used our models to estimate the three hyperparameters that determined the variances of process errors in a and b and the covariance between these process errors. Our intent in using this multivariate distribution for process errors was to avoid overfitting, which can occur when a large number of parameters are estimated without taking advantage of such a common distribution (Gelman et al. 2004:117). Our hierarchical model structure is similar in concept to a mixed-model analysis of variance applied in a non-Bayesian estimation of mass-length relations (Lai and Helser 2004).

Based on our preliminary analyses (using methods described below in *Model comparisons and consideration of reduced models*), we decided to use the same variance-covariance matrix Σ_ε for lake trout in the three lake regions; thus, we used a reduced form of equations (3)–(6) with lakewide central tendencies of $\log_e a$ and b . Our preliminary analyses agreed with Froese (2006) in that the correlation between a and b was invariant within a fish species.

Hierarchical Bayesian approach to inference.—Our statistical inferences on first-level parameters, hyperparameters, and predicted quantities were based on posterior distributions. On the logarithm scale, we specified the joint posterior density as the sum of the log-transformed likelihood function, log-transformed prior probability distributions, and log-transformed hyperprior probability distributions (Tables 1, 2). The likelihood function was based on the distribution specified by equation (1), and its distributional parameters were model-predicted body mass at length and model-estimated variance for individual variation in body mass at length. The prior probability distribution for a first-level parameter (prior) or a hyperparameter (hyperprior) encompassed our assumptions about all possible values for the parameter or hyperparameter. We assumed lognormal distributions for positive quantities and normal distributions for quantities that could be either positive or negative. For r , the normal distribution followed Fisher’s zeta transformation (inverse hyperbolic tangent; Neter et al. 1996; Zar 1999).

The hyperparameters in our models were the estimated distributional parameters that specified the prior for process errors ($\varepsilon_{a,r,y}$ and $\varepsilon_{b,r,y}$), while the hyperpriors for hyperparameters and the priors for other first-level parameters were assumed known and their distributional parameters were specified a priori

TABLE 1.—Log-posteriors, specified as the sum of log likelihood ($\log L$), log-priors ($\log P$), and log-hyperpriors ($\log \tilde{P}$), used to model variation in body mass at a given length in Lake Huron lake trout and Chinook salmon. The likelihood $L(\theta|X)$ quantifies how likely the set of parameters and hyperparameters (θ) is given the available data (X). The functions f with distributional parameters are specified as normal (N), lognormal (LN), multivariate normal (MN), or multivariate lognormal (MLN). Underlined symbol denotes a vector. Parameters, hyperparameters, and predicted quantities are defined in equations (1)–(6). In addition, γ is equal to $(a, b)^T$ and $z(r)$ is Fisher’s zeta transformation of the correlation coefficient r (Neter et al. 1996; Zar 1999). See Table 2 for more about these functions.

Description	Equation	Number of observations	Values for distributional parameters
Log-likelihood	$\log L(\underline{\theta} \underline{X} \sum_r \sum_y \sum_s f_{LN}(W_{r,y,s,j} W_{r,y,L}, \sigma_{r,y,s}^2)$	Number of fish by region, year and size-group	$W_{r,y,L}$ and $\sigma_{r,y,s}$ are estimated by the model
Log-prior for $\sigma_{r,y,s}$	$\log P(\sigma_{r,y,s}) = f_{LN}(\sigma_{r,y,s} \mu_{\sigma_{r,y,s}}, \sigma_{\sigma_{r,y,s}}^2)$	Sum of numbers of regions, years and size-groups	$\log_e(0.1), 2.0$
Log-prior for $\tilde{\gamma}$	$\log P(\tilde{\gamma}) = f_{MLN}(\tilde{\gamma} \underline{\mu}_a, \underline{\mu}_b, \Sigma_\gamma)$	1	$-20, \log_e(2.72), \begin{bmatrix} 2 & 0 \\ 0 & 2 \end{bmatrix}$
Log-prior for $\underline{\varepsilon}_{r,y}$	$\log P(\underline{\varepsilon}_{r,y}) = f_{MN}(\underline{\varepsilon}_{r,y} \underline{0}, \Sigma_\varepsilon)$	Sum of numbers of regions and years	Σ_ε is determined by estimated hyperparameters.
Log-hyperprior for σ_{ε_i}	$\log P(\sigma_{\varepsilon_i}) = f_{LN}(\sigma_{\varepsilon_i} \mu_{\sigma_{\varepsilon_i}}, \sigma_{\sigma_{\varepsilon_i}}^2)$	2	$\log_e(0.1), 2.0$
Log-hyperprior for $z(r)$	$\log P[z(r)] = f_N[z(r) \underline{\mu}_r, \sigma_r^2]$	1	0, 2

(Figure 1; Table 1). These prespecified distributional parameters were plausible but only weakly informative, and posterior distributions were not sensitive to the priors and hyperpriors (Appendix 1). Thus, the complete posterior distributions were primarily determined by the data or the likelihood function (Schnute 1994; Punt and Hilborn 1997).

We used Markov chain Monte Carlo (MCMC) methods to approximate the posterior distributions of parameters, hyperparameters, and predicted quantities such as likelihood value and our condition indices. Most of these quantities were transformed so that the prior distributions would be normally distributed, and this improved the performance of the MCMC methods. We generated MCMC chains using the Metropolis–Hastings algorithm as implemented in AD Model Builder software (Otter Research 2001). Diagnostic procedures were largely the same as those used by He and Bence (2007) and are summarized in Appendix 2. Predicted quantities were calculated at each cycle of all parameters and hyperparameters in the MCMC chains. From the saved MCMC chains, we calculated the average and equal-tailed probability intervals for each transformed parameter and hyperparameter. In the

report of our results, we summarized all marginal posterior distributions on back-transformed scales. The back-transformation to nominal parameters was an antilog calculation in most cases. For r , the back-transformation was a hyperbolic tangent.

Model comparisons and consideration of reduced models.—We used the deviance information criterion (DIC) to compare alternative models, and the purpose of such comparisons was to evaluate whether it was necessary to quantify spatial and annual variation in mass–length relations and predicted body mass at a given length. The DIC is used to compare models in Bayesian analyses and is similar in concept to Akaike’s information criterion, which is more widely used in non-Bayesian applications. A model with the lowest DIC should produce the lowest parameter uncertainty and the best predictions of out-of-sample observations (Spiegelhalter et al. 2002; Gelman et al. 2004).

$$DIC = -2 \log_e L(\check{\underline{\theta}}|M) + n_e, \tag{7}$$

where $n_e = -2 \log_e L(\check{\underline{\theta}}|M) - [-2 \log_e L(\check{\underline{\theta}}|M)]$, $\log_e L(\check{\underline{\theta}}|M)$ is average log-likelihood over the MCMC

TABLE 2.—A log-transformed univariate normal density function (f_N) for a sample of k independent observations (i.e., the number of observations in Table 1) and a log-transformed multivariate normal density function (f_{MN}) with ignored constants dropped. The two functions were used to specify the likelihood function, priors, and hyperpriors in Table 1. Here, μ is an expected value of variable x , σ^2 is a scalar variance, an underlined symbol denotes a vector, and Σ is a variance–covariance matrix. Note that $f_{LN}(x) = f_N(\log_e x)$ and $f_{LMN}(x) = f_{MN}(\log_e x)$, after ignored constants are dropped.

Description	Equation
Log-univariate normal	$f_N(x \underline{\mu}, \sigma^2) = -k \log_e \sigma - \sum_{i=1}^k \frac{(x_i - \underline{\mu})^2}{2\sigma^2}$
Log-multivariate normal	$f_{MN}(\underline{x} \underline{\mu}, \Sigma) = -(\frac{k}{2}) \log_e \Sigma - 0.5 \sum_{i=1}^k [(\underline{x}_i - \underline{\mu})^T \Sigma^{-1} (\underline{x}_i - \underline{\mu})]$

chain given a model M , $\log_e L(\bar{\theta} | M)$ is the log-likelihood calculated at mean values for the transformed parameters and hyperparameters over the MCMC chain with M , and n_e is a measure of model complexity, referred to as the effective number of parameters. Spiegelhalter et al. (2002) suggested that a model with a DIC score that is seven points lower than alternative models has substantially better predictive ability.

In addition to the full lake trout model in which parameters varied among regions and years, we evaluated four reduced models: (1) southern and north-central regions of Lake Huron were combined for comparison with the northern region; (2) northern and north-central regions were combined for comparison with the southern region; (3) time-invariant mass-length relations were used for each region, and among-individual variation was only assessed among regions and size-groups (i.e., not among years); (4) spatial- and time-invariant mass-length relations were used for all data, and among-individual variation was only assessed among size-groups. For Chinook salmon, there was only one region and thus the only reduced model was the time-invariant model.

Condition indices.—For each combination of region and year, we used posterior median body masses at 500 and 700 mm TL as condition indices and evaluated each index based on its marginal posterior distribution. We chose these two particular lengths because they were both well within the distribution of sampled lengths in each region and year and also allowed for a meaningful contrast between fish of different lengths that can feed on prey of different sizes (Madenjian et al. 1998, 2006; Mason et al. 1998).

Our condition indices relied on our model producing valid predictions of body mass at a given length. We looked at region- and year-specific a and b , and we plotted $\log_e a$ versus b to verify that there were no outliers in the changing mass-length relations. For each combination of region and year, we also looked at differences between observed and predicted body mass on a log scale and plotted the residuals versus body length. Our models produced approximately symmetric distributions of prediction residuals about the zero line because the models estimated and used the variance $\sigma_{r,y,s}^2$ for individual variation in mass at length. We did not present the large numbers of such plots in an effort to limit the length of this paper.

Our condition indices differed from most other condition indices in their assumptions about data. Using conventional condition indices, the underlying assumption is a similar length distribution across regions and years. Using our condition indices, the assumption is that individual variation in mass at

length is similar within a size-group from a given region and year (equation 1). Thus, applying conventional condition indices requires special sampling effort to collect a large number of fish for each region, year, and size-group of a narrow range. In contrast, applying our condition indices with our statistical modeling approach only requires routine data for each region and year as long as the data cover a similar overall size range. To show the consequence of using condition indices in a conventional fashion when the assumption of similar length distributions may be invalid, we applied K to our lake trout and Chinook salmon data:

$$K = 10^5 \times W/(L^3), \quad (8)$$

where W is body mass (g) and L is body length (TL, mm). We calculated K for each individual fish and averaged the K -values for a specified size-group or age of interest.

Results

Model Selection and Spatial and Annual Variation in Mass–Length Relation

For lake trout, the full model that specified spatial and annual variation in mass-length relation had the lowest DIC (i.e., was the best model); for Chinook salmon, the full model that specified annual variation in mass-length relation had the lowest DIC (Table 3). Each full model was far superior to reduced models that ignored some or all spatial and annual variation in the mass-length relation. Thus, use of additional parameters to quantify the region- and year-specific mass-length relation for lake trout and the year-specific mass-length relation for Chinook salmon substantially improved prediction of observed body mass at length, and was therefore warranted.

For both lake trout and Chinook salmon, the process errors for $\log_e a$ and b were correlated with each other, and r was near 1.0 (95% probability interval = 0.996–0.999). The positive r for the process errors indicated an inverse correlation between a and b , because the value for $\log_e a$ was negative and a larger multiplicative error caused a to be smaller (equations 1–4).

Chinook salmon exhibited much larger variation in mass-length relations among years than lake trout did among years and regions. The σ_{ea} and σ_{eb} were larger for Chinook salmon (95% probability interval = 0.05–0.10) than for lake trout (0.04–0.05). Thus, the multiplicative errors used in equations (3) and (4) for Chinook salmon had 95% probability intervals as wide as 0.82–1.22, while the range was much smaller for lake trout. The large temporal variation in parameters suggested that it was better not to assume isometric

TABLE 3.—Comparison of models used to predict body mass at a given length for lake trout in three management regions of Lake Huron and Chinook salmon throughout the main basin of the lake. The deviance information criterion (DIC) was used to compare models (Δ DIC = difference in DIC between a given model and the best model—i.e., that with the lowest DIC; EP = effective number of parameters; ES = effective sample size for the negative log-likelihood, which was a summary variable saved from Markov chain Monte Carlo chains and was used for the calculations in equation 7).

Model	DIC	Δ DIC	EP	ES
Lake trout				
Full model with region- and time-varying parameters, with unequal variances for observation errors among regions, years, and size-groups	-67,301.4	0.0	443	477
Reduced model with northern region and combined north-central and southern regions	-66,400.5	900.9	327	715
Reduced model with southern region and combined northern and north-central regions	-65,892.9	1,408.5	332	698
Separate time-invariant models for three regions with unequal variances for observation errors among regions and size-groups	-59,300.5	8,000.9	16	4,000
Region- and time-invariant model, with unequal variances for observation errors among size-groups	-58,729.6	8,571.8	6	3,977
Chinook salmon				
Full model with time-varying parameters and unequal variances for observation errors among size-groups and years	-7,771.4	0.0	120	3,500
Reduced, time-invariant model, with unequal variances for observation errors among size-groups	-6,210.7	1,560.6	6	4,000

growth for a specific year, even though the overall average b for Chinook salmon was nearly 3.0 (Table 4).

Overall Average Mass–Length Relation

When full models were used to estimate region- and year-specific mass–length relations for lake trout and year-specific mass–length relations for Chinook salmon, these models also estimated the overall average relations for Lake Huron. These overall averages are defined by the central tendency parameters for the power function coefficient and exponent (Table 4, full model). Reduced time-invariant models for both species produced overall average mass–length relations that were similar to those obtained using the full models. When the lake trout model was further reduced to also remove the regional effects, the resulting mass–length relation was substantially different from the overall average relation estimated using the full model.

The average a from the full model was larger than the 95% probability interval for a from the spatial- and time-invariant model, and the average b from the full model was smaller than the 95% probability interval for b from the spatial- and time-invariant model. Thus, if we desired to have an average mass–length relation over all regions and years, the lake trout model with invariant parameters produced a biased estimate even though all available data were used. The bias stemmed from the fact that the spatial- and time-invariant model weighted each fish the same, but sample sizes, individual variation, and mass–length parameters varied substantially among regions.

From the average parameters and their probability intervals, Chinook salmon had a larger a and a smaller b than lake trout had (Table 4). The difference in b might only reflect a difference in body forms between the two fish species. The difference in a , however,

TABLE 4.—Posterior distributions summarized for the coefficient a and exponent b of an overall average mass–length relation for lake trout and Chinook salmon in Lake Huron (see Table 3 for model descriptions). Markov chain Monte Carlo (MCMC) distributions for these parameters were generated from transformed scale based on assumed probability distributions; we report the back-transformed MCMC means and limits of equal-tailed 95% probability intervals (lower = 2.5%; upper = 97.5%). A standard weight equation proposed by Piccolo et al. (1993) for lake trout was also included (Piccolo–Hubert–Whaley [PHW] model).

Species	Model	a			b		
		Average	2.50%	97.50%	Average	2.50%	97.50%
Lake trout	Spatially and time invariant	4.33×10^{-9}	4.20×10^{-9}	4.47×10^{-9}	3.134	3.130	3.139
	Time invariant	4.61×10^{-9}	2.30×10^{-9}	6.18×10^{-9}	3.123	3.080	3.227
	Full	4.88×10^{-9}	4.10×10^{-9}	5.80×10^{-9}	3.116	3.088	3.144
	PHW	2.08×10^{-9}			3.246		
Chinook salmon	Time invariant	1.05×10^{-8}	8.54×10^{-9}	1.29×10^{-8}	2.999	2.961	3.035
	Full	1.06×10^{-8}	4.83×10^{-9}	1.81×10^{-8}	2.998	2.920	3.114

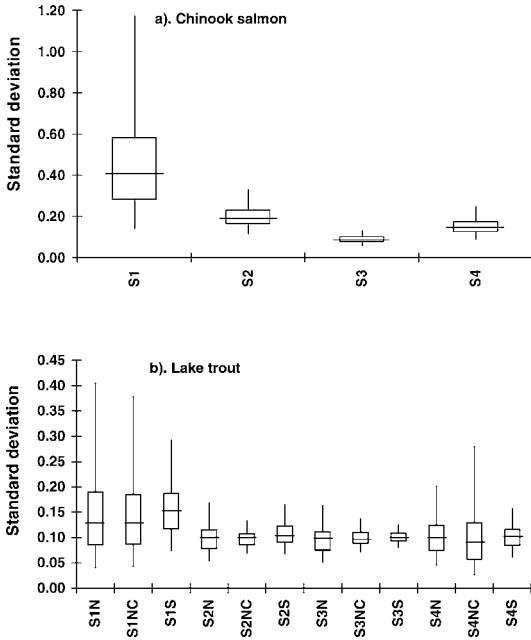


FIGURE 2.—Box plot (horizontal line = median, box = quartiles, vertical line = equal-tailed 95% probability interval) of standard deviations for individual variation in mass at length for (a) four Chinook salmon size-groups (S1–S4) throughout Lake Huron and (b) each size-group of lake trout within the lake’s three management regions (N = northern, NC = north-central, and S = southern). The posterior marginal distributions based on the average (over years) log-scale values from the Markov chain Monte Carlo samples are summarized (see text for further description).

indicated much larger body mass for Chinook salmon than for lake trout at relatively small length.

In comparison with a standard weight equation for lake trout in North America (Piccolo et al. 1993; Hubert et al. 1994), the overall average mass–length relation for lake trout from Lake Huron had a much larger *a* and a much smaller *b* (Table 4). To evaluate changes in lake trout body condition among lake regions, years, and size-groups, our references were from the overall average mass–length relation for lake trout in Lake Huron.

Individual Variation in Body Mass at Length

Chinook salmon mass at a given length had the lowest individual variation in the 650–850-mm length-group and the highest variation in fish less than 450 mm; the differences among four size-groups were substantial based on differences in the 95% probability intervals (Figure 2a). There was also evidence that individual variation in lake trout mass at length varied among length-groups and regions, based on the much

lower DIC in our preliminary analyses for models that allowed for these differences than for models that did not (this was also true for Chinook salmon). There is some suggestion for higher individual variation for the smallest lake trout length-groups, but it is difficult to pinpoint specific differences among size-group and region combinations, as each 95% probability interval overlapped the others (Figure 2b).

Predicted Body Mass at 500 and 700 mm as Condition Indices

The posterior medians, interquartile ranges, and 95% probability intervals of our new condition indices showed differences among regions, among years, between species, and between size-groups (Figure 3).

Lake trout body mass at 500 mm TL was the highest in southern Lake Huron and the lowest in northern Lake Huron. Most yearly medians in the northern region were below the lakewide overall median, and most yearly medians in the southern region were above the lakewide overall median ($\chi^2 = 6.138, P < 0.05$). Until the end of the entire time series, annual variation within each region did not show a clear trend. The 2005 median in the southern region was below 95% probability intervals for all previous years. The 2004 and 2005 medians in the north-central region were below 95% probability intervals for all previous years except 1982, 1987, and 1994. In the northern region, annual variation was larger than in the other two regions, and the 2004 and 2005 medians were the lowest among the last 20 years.

Lake trout body mass at 700 mm TL was also the highest in southern Lake Huron and the lowest in the northern region, but temporal trends altered the spatial pattern in recent years. After 1990, more yearly medians in the northern region were above the lakewide overall median than in previous years; in contrast, more yearly medians in the north-central and southern regions were below the lakewide overall median than in previous years. The temporal differences were not statistically significant in the northern (chi-square $\chi^2 = 0.013, P = 0.91$) and north-central ($\chi^2 = 1.168, P = 0.28$) regions, but in the southern region there were significantly more yearly medians below the lakewide overall median after 1990 than previously ($\chi^2 = 5.531, P < 0.02$). During 2002–2005, lake trout body mass at 700 mm in the southern region became the lowest lakewide.

In southern Lake Huron, the decline in lake trout body mass at 700 mm separated the time series into three periods (Figures 3f, 4a). The 95% probability intervals for yearly medians before 1982 had no overlap with the intervals for the other years, except for the slight overlap with the intervals for 1988 and

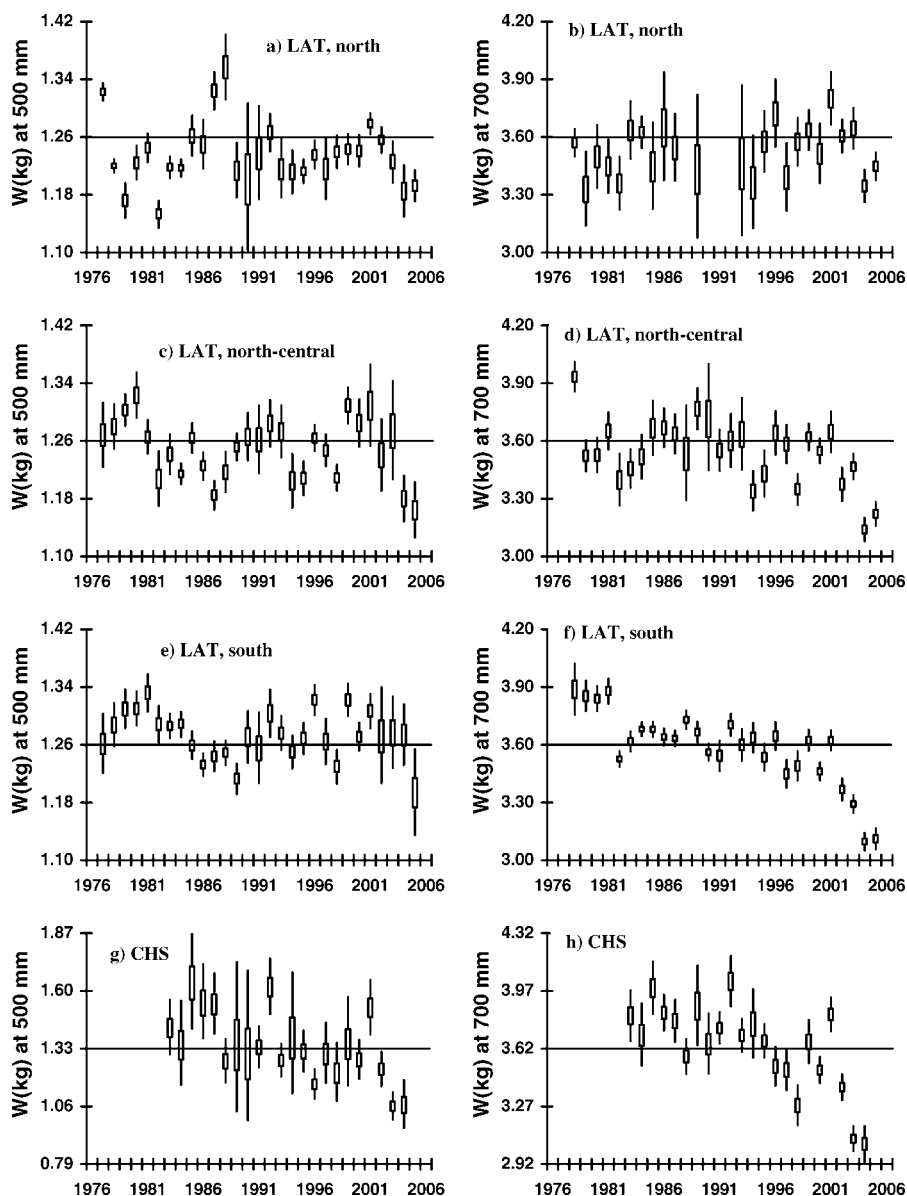


FIGURE 3.—Body mass (W) at 500 (a, c, and e) and 700 mm total length (b, d, and f) for lake trout (LAT) in three Lake Huron management regions (northern, north-central, and southern) from 1977 to 2005; (g) body mass at 500 mm for Chinook salmon (CHS) throughout Lake Huron during 1983–2004; and (h) body mass at 700 mm for CHS (lakewide). The posterior marginal distribution is summarized (box = quartiles; vertical line = equal-tailed 95% probability interval; horizontal line = lakewide overall median).

1992. The 95% probability intervals for yearly medians after 2001 had no overlap with the intervals for previous years, except for the slight overlap between the two intervals for 1997 and 2002. During 1982–2001, the temporal pattern suggested a declining trend in body mass at 700 mm across years, but the linear

trend was not statistically significant ($P = 0.07$; Figure 4a). Yearly medians before 1982 and after 2001 were outside of the 95% prediction intervals of the time trend for 1982–2001.

At both 500 and 700 mm TL, Chinook salmon body mass declined across years (Figure 3g, h). The time

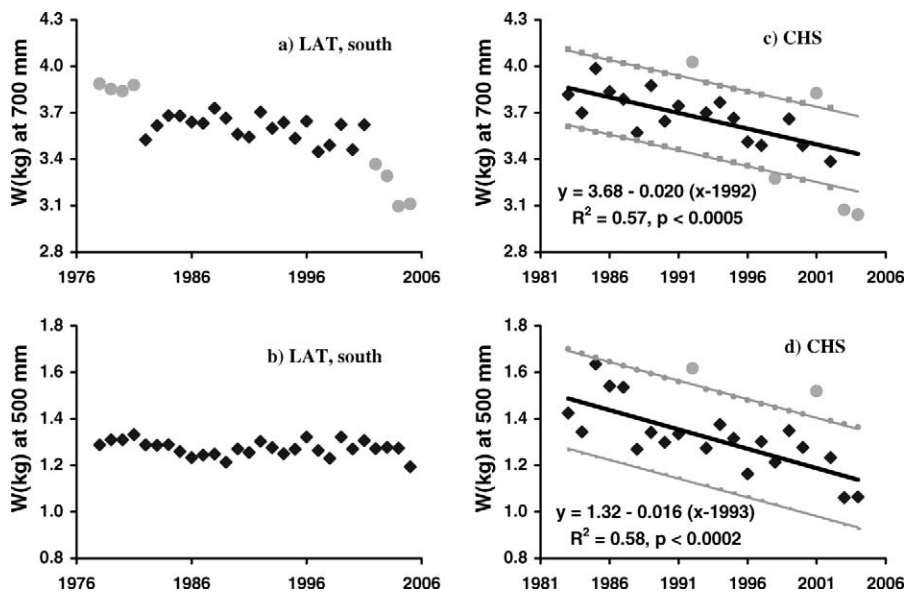


FIGURE 4.—Comparison of lake trout (LAT) and Chinook salmon (CHS) body mass (W) at total length in Lake Huron: (a) 700-mm LAT in the southern management region, 1978–2005; (b) 500-mm LAT in the southern region; (c) 700-mm CHS in the main basin, 1983–2004; and (d) 500-mm CHS in the main basin. The southern region was chosen because LAT there showed the largest regional decline in W at length (see text and Figure 3). Yearly values (diamonds) are the medians of posterior distributions estimated using the best models (Table 4); the linear regression of W on year is represented by the thick solid line. Thin solid lines show the 95% prediction interval for a regression. Circles indicate yearly values that are outside of 95% prediction intervals or that do not share intervals with other years (see text and Figure 3).

trends were significant ($P < 0.0003$; Figure 4c, d), and there was no difference between slopes for indices at the two selected lengths ($P = 0.24$). Despite similarity in the declining trends, there were still noticeable differences between small and large Chinook salmon. In 1998, the median body mass at 500 mm was still similar to most annual medians, while the median body mass at 700 mm was unusually low. The yearly median body masses at 500 mm were the lowest in 2003 and 2004, but they were still predictable by the time trend. Yearly medians for Chinook salmon body mass at 700 mm were the lowest in 1998, 2003, and 2004, and they were below the 95% prediction intervals of the time trend.

In comparison with Chinook salmon, annual variation in lake trout body mass at 500 mm (southern region) was negligible, and decline in lake trout body mass at 700 mm (southern region) was also nearly negligible until 2002 (Figures 3, 4). By the end of the time series, Chinook salmon body mass at 500 mm fell below that of lake trout; previously, this was only seen in 1996. Similarly, by 2003 and 2004, Chinook salmon body mass at 700 mm fell below that of lake trout, and such a reverse contrast was seen previously only in 1988 and 1998.

Fulton's Condition Factor

Mean K for large lake trout and Chinook salmon showed a general decline over time (Figure 5). For age-7 lake trout in southern Lake Huron and age-3 Chinook salmon lakewide, the time trends were nonsignificant ($P > 0.06$; Figure 5a, b). For a size range of 650–750 mm (chosen to be centered at 700 mm), the declines were significant for both species, and K declined faster for Chinook salmon than for lake trout ($P < 0.05$; Figure 5c, d), which agreed qualitatively with results for mass at 700 mm TL.

When we focused on the most recent drop in body condition, however, the 95% prediction intervals from these example applications suggested that the drop for lake trout in southern Lake Huron started in 2003 (Figure 5a) or even 2004 (Figure 5c), which is 1 or 2 years later than the decline identified by our new condition indices (Figures 3f, 4a). The decline for Chinook salmon started in 2004 (Figure 5b, d) and was also 1 year later than that identified by our condition indices (Figures 3h, 4c). Based on the 650–750-mm size range, only because the K -values for lake trout in 2002 and 2003 were not considered to be substantially below the trend of previous years, the slow declines during 1982–2003 appeared to be considerable in

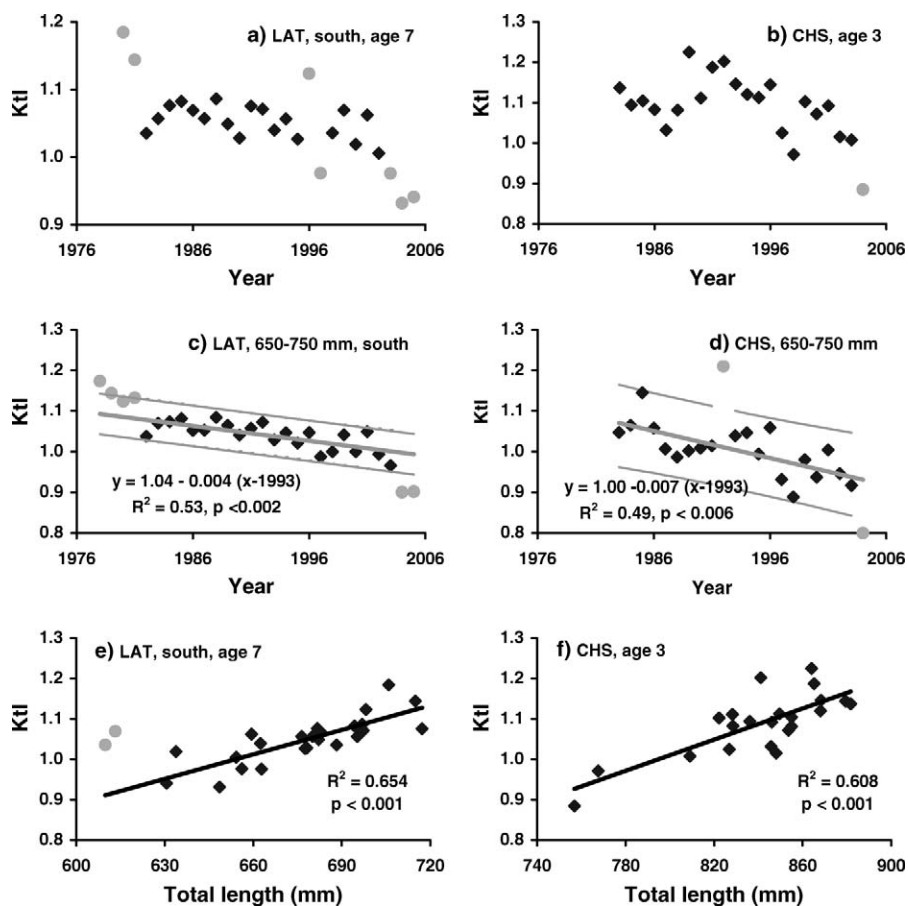


FIGURE 5.—Fulton's condition factor (K ; equation 8) averaged across Lake Huron salmonids of selected sizes and ages: (a) age-7 lake trout (LAT) in the southern management region during 1983–2004; (b) age-3 Chinook salmon (CHS) in the main basin during 1983–2004; (c) 650–750-mm (total length, TL) LAT; (d) 650–750-mm CHS; (e) K versus TL in age-7 LAT; and (f) K versus TL in age-3 CHS. Panels (e) and (f) illustrate the potential for length-based bias. Thick lines represent linear regressions; thin lines represent the 95% prediction interval of a regression. Circles indicate yearly values that are outside of 95% prediction intervals or that do not share intervals with other years.

contrast to the conclusion based on predicted body mass at 700 mm. Based on either age 3 or the 650–750-mm size range, the K -value for Chinook salmon in 1998 was not especially low because it was predictable by the 95% prediction interval of the time trend, which also contrasted with observations for body mass at 700 mm.

For age-based K , 60–65% of the temporal variation was explained by changes in length at age (Figure 5e, f). Variation in length-based K could not be explained by changes in length, in part because the variation in average length within the size-class did not have a clear trend over time as did the average length within a given age. However, this is not necessarily always the case. For example, we calculated K for the 650–850-mm Chinook salmon length-group, which we defined when

allowing heterogeneity among individual variability in mass at length (see Methods). For this length-group, average length decreased over time and nearly 50% of the variation in K was explained by changes in average length. Given that (1) b for mass-length relationships often diverged from 3.0 and (2) changes in length at age and body condition often occur simultaneously, there were no clear ways to separate real changes in body condition and length effect on K based on either age or a wide range of length.

In principle, all size-related bias or additional variation could be avoided by using small enough size-groups, but this leads to problems associated with small sample sizes. On average, there were 460 lake trout available for our analysis for each region in a given year and 276 Chinook salmon available for

analysis for a given year. In the size range used for the example application of K , the minimum yearly sample number was 28 for lake trout from southern Lake Huron and 8 for Chinook salmon. Special and additional sampling effort would be needed to supply sufficient samples for a predefined narrower size range. This is true also for applying relative weight because the calculation of relative weight often must be size specific (Murphy et al. 1990).

Discussion

We used posterior median body mass at 500 and 700 mm TL as condition indices. The two particular lengths were case-specific details that were driven by characteristics of the data and the biology of lake trout and Chinook salmon in U.S. waters of Lake Huron. Such details will differ in studies of fish in other ecosystems. Our approach to condition indices should be widely applicable because it maintains the following attributes: (1) allows comparison of small and large fish in their responses to ecosystem changes; (2) avoids problems associated with length-related bias, particularly when length distribution and the mass-length relation are changing among regions and years; (3) makes better use of data through statistical modeling but does not attempt to directly use the two inversely related mass-length parameters as condition indices; and (4) acknowledges that changes in mass-length relations and changes in fish condition result from the same processes. This is true because changes in mass-length relations are due to differences in how body condition varies among fish of different ages and lengths. While there is a conceptual difference between mass-length relations and condition indices (LeCren 1951), use of mass-length relations is not limited to evaluating fish body form.

Except for the substantial difference in assumptions about available data as detailed in our method justification, our condition indices are conceptually similar to conventional condition indices. We used the lakewide overall median body mass at 500 and 700 mm as reference indices and compared region- and year-specific indices to the references. Ratios of our region- and year-specific condition indices to the references can be calculated, although statistical inference of changes in body condition does not require the additional calculation of a ratio or relative weight. The posterior median body mass at the given length could be used to calculate K , and the result would be conceptually similar to Froese's (2006) mean Fulton's condition factor. The advantage of doing this, however, is not clear to us because the underlying reason for dividing mass by the cube of length (equation 8) is partially to adjust for variations in length among

samples, an issue our approach has addressed through statistical modeling and prediction of mass at a specific length.

We believe that use of conventional condition indices will continue, but appropriate application and interpretation will depend on specific objectives and circumstances. In our application, such indices identified general temporal trends when based on restricted size ranges but had difficulty with short-term changes due to (1) variation in sizes within the chosen size range and (2) small sample sizes. Such difficulty can be more problematic in detecting potential relations between fish condition and covariates. Often, fish size distributions will vary substantially among regions and years due to variations in mortality, recruitment, and growth, in a way that would produce length-related biases for conventional indices when applied to broad size ranges. In many cases, as was true for our application, sustainable and standard data collections will only provide moderate or small sample sizes within sufficiently restricted size ranges; we believe that a statistical modeling approach like ours could provide some benefits because overall samples are usually sufficient for using such approaches.

When using predicted mass at selected lengths as condition indices, our method is more parsimonious than separately conducting a large number of regressions for many regions and years. The nominal number of parameters was more than six per year and region, including a , b , and standard deviations of among-individual variations for four size-groups. In our full model for lake trout, the n_e was reduced to 5.1 per region and year, including all additional required parameters and hyperparameters regardless of time series length or number of spatial units (Table 3). The n_e was less than 6.0 because the model considered the process errors (spatial and temporal variations in mass-length parameters) as coming from a common probability distribution, and the variances of individual variations in mass at length (varied among regions, years, and size-groups) were also drawn from a common probability distribution. In the full model for Chinook salmon, n_e was only slightly less than the nominal number of parameters, because the time series was shorter than that for lake trout and there was only one spatial unit. In conducting a large number of separate regressions for each region and year, a total of six parameters would be always required in our case: two parameters for each mass-length relation and four additional weighting factors for four size-groups based on variances of prediction residuals from preliminary modeling fit (Neter et al. 1996). Furthermore, conducting separate regressions for each time period and region often leads to use of an oversimplified model

structure that does not consider variance heterogeneity and does not analyze correlation and covariance between mass-length parameters. Our statistical modeling approach has the potential for pattern descriptions that are even more parsimonious when warranted, as we would have simplified the model structure if a simpler model had performed better based on DIC or we could have included additional structure for representing more complex patterns and relations observed. We believe our methods will have more application in future studies because of the need for extracting more information on changes in condition from limited data and continuing progress in computing technology (e.g., Otter Research 2001).

Our results suggest that in Lake Huron, small lake trout were still able to maintain body condition in response to low prey availability, while Chinook salmon of the same size could not. Large Chinook salmon had greater and more rapid declines in body condition than did lake trout of the same size. Body condition of large lake trout after 2001 indicated further substantial changes in prey availability that were not predicted by the long-term trends. Body condition of large Chinook salmon indicated a similar change 1 year later because food availability changes started in southern Lake Huron. Our results also suggest that recent temporal trends in lake trout condition altered the spatial patterns. Both the temporal trends and changes in fish condition ranks among different regions of Lake Huron were associated with a severe decline in alewife abundance that first occurred in the southern part of the lake. Alewives were the dominant prey until the middle 1990s, but by 2002 it became difficult to find alewives in lake trout stomachs collected from southern Lake Huron. The condition of large lake trout was a better indication of reduced food availability than that of small lake trout because adults rely more on large-sized prey fish (Mason et al. 1998) and declines in alewife abundance were at first confined to older and larger fish (S. Riley, J. Schaeffer, and E. Roseman, personal communication).

Our findings have direct implications for fishery management. In 1998, 2003, and 2004, Chinook salmon physical appearance (i.e., low body mass at length) led many anglers and field biologists to express alarm about possible health consequences. In 2003 and 2004, total recreational harvest of Chinook salmon fell below the lake trout harvest for the first time during the past 40 years, suggesting a substantial decline in Chinook salmon abundance, since these species' relative stocking numbers have not changed. For lake trout, southern Lake Huron has historically produced the best sport fishery. There were no obvious changes in the fishery and in our assessment catch that would

indicate a decline in lake trout abundance, even though estimated body mass at 700 mm declined to the lowest level in the time series by 2002. Coincident with the changes in condition indices for the two fish species, the different fishery responses suggested that recent forage conditions in Lake Huron were unable to support the population abundance of Chinook salmon that was formerly possible, whereas lake trout fisheries were little affected. Our results suggest that adequate condition indices can provide a timely signal of ecosystem changes that often require the immediate attention of fishery managers.

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References

- Adlerstein, S. A., E. S. Rutherford, D. F. Clapp, J. A. Clevenger, and J. E. Johnson. 2007a. Chinook salmon seasonal movements in Lake Huron determined from coded wire tag recoveries. *North American Journal of Fisheries Management* 27:792-803.
- Adlerstein, S. A., E. S. Rutherford, J. A. Clevenger, J. E. Johnson, D. F. Clapp, and A. P. Woldt. 2007b. Lake trout movements in U.S. waters of Lake Huron interpreted from coded wire tag recoveries in recreational fisheries. *Journal of Great Lakes Research* 33:186-201.
- Anderson, R. O., and R. M. Neumann. 1996. Length, weight, and associated structural indices. Pages 447-482 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Barnard, J., R. McCulloch, and X. Meng. 2000. Modeling covariance matrices in terms of standard deviations and correlations, with application to shrinkage. *Statistica Sinica* 10:1281-1311.
- Baskerville, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. *Canadian Journal of Forestry* 2:49-53.
- Bence, J. R., and K. D. Smith. 1999. An overview of recreational fisheries of the Great Lakes. Pages 259-305 in W. W. Taylor and C. P. Ferreri, editors. *Great Lakes*

- fisheries policy and management. Michigan State University Press, East Lansing.
- Blackwell, B. G., M. L. Brown, and D. W. Willis. 2000. Relative weight (W_r) status and current use in fisheries assessment and management. *Reviews in Fisheries Science* 8:1–44.
- Bolger, T., and P. L. Connolly. 1989. The selection of suitable indices for the measurement and analysis of fish condition. *Journal of Fish Biology* 34:171–182.
- Brenden, T. O., B. R. Murphy, and J. B. Birch. 2003. Statistical properties of the relative weight (W_r) index and an alternative procedure for testing W_r differences between groups. *North American Journal of Fisheries Management* 23:1136–1151.
- Cardinale, M., and F. Arrhenius. 2000. Decreasing weight-at-age of Atlantic herring (*Clupea harengus*) from the Baltic Sea between 1986 and 1996: a statistical analysis. *ICES Journal of Marine Science* 57:882–893.
- Cone, R. S. 1989. The need to reconsider the use of condition indices in fishery science. *Transactions of the American Fisheries Society* 118:510–514.
- Cowles, M. K., and B. P. Carlin. 1996. Markov chain Monte Carlo convergence diagnostics: a comparative review. *Journal of the American Statistical Association* 91:883–904.
- Daniels, M. J., and R. E. Kass. 1999. Nonconjugate Bayesian estimation of covariance matrices and its use in hierarchical models. *Journal of the American Statistical Association* 94:1254–1263.
- Daniels, M. J., and R. E. Kass. 2001. Shrinkage estimators of covariance matrices. *Biometrics* 57:1173–1184.
- Dutil, J.-D., M. Castonguay, D. Gilbert, and D. Gascon. 1999. Growth, condition, and environmental relationships in Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence and implications for management strategies in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1818–1831.
- Ebener, M. P., editor. 1998. A lake trout rehabilitation guide for Lake Huron. Great Lakes Fishery Commission, Ann Arbor, Michigan.
- Filbert, R. B., and C. P. Hawkins. 1995. Variation in condition of rainbow trout in relation to food, temperature, and individual length in the Green River, Utah. *Transactions of the American Fisheries Society* 124:824–835.
- Froese, R. 2006. Cube law, condition factor, and weight-length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* 22:241–253.
- Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. *Bayesian data analysis*, 2nd edition. CRC Press, Boca Raton, Florida.
- Gerow, K. G., R. C. Anderson-Sprecher, and W. A. Hubert. 2005. A new method to compute standard-weight equations that reduces length-related bias. *North American Journal of Fisheries Management* 25:1288–1300.
- Green, A. J. 2001. Mass/length residuals: measures of body condition or generators of spurious results. *Ecology* 82:1473–1483.
- Hansen, M. J. 1999. Lake trout in the Great Lakes: basinwide stock collapse and binational restoration. Pages 417–453 in W. W. Taylor and C. P. Ferreri, editors. *Great Lakes fisheries policy and management*. Michigan State University Press, East Lansing.
- Hartman, K. J., and F. J. Margraf. 2003. U.S. Atlantic coast striped bass: issues with a recovered population. *Fisheries Management and Ecology* 10:309–312.
- Hayes, D. B., J. K. T. Brodziak, and J. B. O’Gorman. 1995. Efficiency and bias of estimators and sampling designs for determining length–weight relationships of fish. *Canadian Journal of Fisheries and Aquatic Sciences* 52:84–92.
- He, J. X., and J. R. Bence. 2007. Modeling annual growth variation using a hierarchical Bayesian approach and the von Bertalanffy growth function, with application to lake trout in southern Lake Huron. *Transactions of the American Fisheries Society* 136:318–330.
- Helsler, T. E., and H. Lai. 2004. A Bayesian hierarchical meta-analysis of fish growth: with an example for North American largemouth bass, *Micropterus salmoides*. *Ecological Modelling* 178:399–416.
- Henderson, B. A., and E. H. Brown, Jr. 1985. Effects of abundance and water temperature on recruitment and growth of alewife (*Alosa pseudoharengus*) near South Bay, Lake Huron, 1954–1982. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1608–1613.
- Henderson, B. A., and G. E. Morgan. 2002. Maturation of walleye by age, size and surplus energy. *Journal of Fish Biology* 61:999–1011.
- Holey, M. E., R. E. Elliot, S. V. Marcquenski, J. G. Hnath, and K. D. Smith. 1998. Chinook salmon epizootics in Lake Michigan: possible contributing factors and management implications. *Journal of Aquatic Animal Health* 10:202–210.
- Hubert, W. A., R. D. Gipson, and R. A. Whaley. 1994. Interpreting relative weights of lake trout stocks. *North American Journal of Fisheries Management* 14:212–215.
- Johnson, J. E., J. X. He, A. P. Woldt, M. P. Ebener, and L. C. Mohr. 2004. Lessons in rehabilitation stocking and management of lake trout in Lake Huron. Pages 161–175 in M. J. Nickum, P. M. Mazik, J. G. Nickum, and D. D. MacKinlay, editors. *Propagated fish in resource management*. American Fisheries Society, Symposium 44, Bethesda, Maryland.
- Jones, M. L., J. F. Koonce, and R. O’Gorman. 1993. Sustainability of hatchery-dependent salmonine fisheries in Lake Ontario: the conflict between predator demand and prey supply. *Transactions of the American Fisheries Society* 122:1002–1018.
- Jude, D. J., and F. J. Tesar. 1985. Recent changes in the inshore forage fish of Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1154–1157.
- Kimmerer, W., S. R. Avent, S. M. Bollens, F. Feyrer, L. F. Grimaldo, P. B. Moyle, M. Nobriga, and T. Visintainer. 2005. Variability in length–weight relationships used to estimate biomass of estuarine fish from survey data. *Transactions of the American Fisheries Society* 134:481–495.
- Kocik, J. F., and M. L. Jones. 1999. Pacific salmonines in the Great Lakes basin. Pages 455–488 in W. W. Taylor and C. P. Ferreri, editors. *Great Lakes fisheries policy and management*. Michigan State University Press, East Lansing.
- Lai, H., and T. Helsler. 2004. Linear mixed-effects models for weight–length relationships. *Fisheries Research* 70:377–387.

- Lambert, Y., and J. Dutil. 1997. Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2388–2400.
- LeCren, E. D. 1951. The length–weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *Journal of Animal Ecology* 20:201–219.
- Madenjian, C. P., T. J. Desorcie, and R. M. Stedman. 1998. Ontogenic and spatial patterns in diet and growth of lake trout in Lake Michigan. *Transactions of the American Fisheries Society* 127:236–252.
- Madenjian, C. P., T. O. Hoeoek, E. S. Rutherford, D. M. Mason, T. E. Croley, E. B. Szalai, and J. R. Bence. 2005. Recruitment variability of alewives in Lake Michigan. *Transactions of the American Fisheries Society* 134:218–230.
- Madenjian, C. P., J. D. Holuszko, and T. J. Desorcie. 2003. Growth and condition of alewives in Lake Michigan, 1984–2001. *Transactions of the American Fisheries Society* 132:1104–1116.
- Madenjian, C. P., J. D. Holuszko, and T. J. Desorcie. 2006. Spring–summer diet of lake trout on Six Fathom Bank and Yankee Reef in Lake Huron. *Journal of Great Lakes Research* 32:200–208.
- Marshall, C. T., C. L. Needle, N. A. Yaragina, A. M. Ajiad, and E. Gusev. 2004. Deriving condition indices from standard fisheries databases and evaluating their sensitivity to variation in stored energy reserves. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1900–1917.
- Mason, D. M., T. B. Johnson, and J. F. Kitchell. 1998. Consequences of prey fish community dynamics on lake trout (*Salvelinus namaycush*) foraging efficiency in Lake Superior. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1273–1284.
- Meretsky, V. J., R. A. Valdez, M. E. Douglas, M. J. Brouder, O. T. Gorman, and P. C. Marsh. 2000. Spatiotemporal variation in length–weight relationships of endangered humpback chub: implications for conservation and management. *Transactions of the American Fisheries Society* 129:419–428.
- Murphy, B. R., M. L. Brown, and T. A. Springer. 1990. Evaluation of the relative weight (W_r) index, with new applications to walleye. *North American Journal of Fisheries Management* 10:85–97.
- Nalepa, T. F., L. C. Mohr, B. A. Henderson, C. P. Madenjian, and P. J. Schneeberger. 2005. Lake Whitefish and *Diporeia* spp. in the Great Lakes: an overview. Pages 3–20 in L. C. Mohr and T. F. Nalepa, editors. *Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes*. Great Lakes Fishery Commission Technical Report 66.
- Nash, R. D., A. H. Valencia, and A. J. Geffen. 2006. The origin of Fulton’s condition factor—setting the record straight. *Fisheries* 31:236–238.
- Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. *Applied linear statistical models*. McGraw-Hill, New York.
- O’Gorman, R., O. E. Johannsson, and C. P. Schneider. 1997. Age and growth of alewives in the changing pelagia of Lake Ontario, 1978–1992. *Transactions of the American Fisheries Society* 126:112–126.
- O’Gorman, R., B. F. Lantry, and C. P. Schneider. 2004. Effect of stock size, climate, predation, and trophic status on recruitment of alewives in Lake Ontario, 1978–2000. *Transactions of the American Fisheries Society* 133:855–867.
- Otter Research. 2001. *An introduction to AD Model Builder version 6.02 for use in nonlinear modeling and statistics*. Otter Research, Sidney, British Columbia, Canada.
- Peters, A. K., M. L. Jones, D. C. Honeyfield, and J. R. Bence. 2007. Monitoring energetic status of Lake Michigan Chinook salmon using water content as a predictor of whole-fish lipid content. *Journal of Great Lakes Research* 33:253–263.
- Piccolo, J. J., W. A. Hubert, and R. A. Whaley. 1993. Standard weight equation for lake trout. *North American Journal of Fisheries Management* 13:401–404.
- Pilling, G. M., G. P. Kirkwood, and S. G. Walker. 2002. An improved method for estimating individual growth variability in fish, and the correlation between von Bertalanffy growth parameters. *Canadian Journal of Fisheries and Aquatic Sciences* 59:424–432.
- Porath, M. T., and E. J. Peters. 1997. Use of walleye relative weights (W_r) to assess prey availability. *North American Journal of Fisheries Management* 17:628–637.
- Porath, M. T., E. J. Peters, and D. L. Eichner. 2003. Impact of alewife introduction on walleye and white bass condition in Lake McConaughy, Nebraska, 1980–1995. *North American Journal of Fisheries Management* 23:1050–1055.
- Punt, A. E., and R. Hilborn. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. *Reviews in Fish Biology and Fisheries* 7:35–63.
- Quinn, T. J., II, and R. B. Deriso. 1999. *Quantitative fish dynamics*. Oxford University Press, New York.
- Rakoczy, G. P., and R. F. Svoboda. 1997. Sportfishing catch and effort from the Michigan waters of Lakes Michigan, Huron, Erie, and Superior, April 1, 1994–March 31, 1995. Michigan Department of Natural Resources, Fisheries Division, Technical Report 97-4, Ann Arbor.
- Rand, P. S., and D. J. Stewart. 1998a. Dynamics of salmonine diets and foraging in Lake Ontario, 1983–1993: a test of a bioenergetic model prediction. *Canadian Journal of Fisheries and Aquatic Sciences* 55:307–317.
- Rand, P. S., and D. J. Stewart. 1998b. Prey fish exploitation, salmonine production, and pelagic food web efficiency in Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 55:318–327.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191.
- Schnute, J. 1994. A general framework for developing sequential fisheries models. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1676–1688.
- Sitar, S. P., J. R. Bence, J. E. Johnson, M. P. Ebener, and W. W. Taylor. 1999. Lake trout mortality and abundance in southern Lake Huron. *North American Journal of Fisheries Management* 19:881–900.
- Smith, S. H., H. J. Buettner, and R. Hile. 1961. *Fishery statistical districts of the Great Lakes*. Great Lakes Fishery Commission Technical Report 2.

- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit (with discussion). *Journal of the Royal Statistical Society B* 64:583–640.
- Springer, T. A., B. R. Murphy, S. Gutreuter, R. O. Anderson, L. E. Miranda, D. C. Jackson, and R. S. Cone. 1990. Properties of relative weight and other condition indices. *Transactions of the American Fisheries Society* 119:1048–1058.
- Sprugel, D. G. 1983. Correcting for bias in log-transformed allometric equations. *Ecology* 64:209–210.
- Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–1988. *Canadian Journal of Fisheries and Aquatic Sciences* 48:909–922.
- Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Transactions of the American Fisheries Society* 110:751–763.
- Thiebaut, H. J., and F. W. Zwiers. 1984. The interpretation and estimation of effective sample size. *Journal of Climate and Applied Meteorology* 23:800–811.
- Tody, W. H., and H. A. Tanner. 1966. Coho salmon for the Great Lakes. Michigan Department of Conservation, Fish Division, Fish Management Report 1, Ann Arbor.
- Van Horn, S. L. 2003. Lake Norman striped bass management: a conflict between fishery managers and anglers. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 55(2001): 316–323.
- Wilberg, M. J., J. R. Bence, and J. E. Johnson. 2002. Survival of juvenile lake trout stocked in western Lake Huron during 1974–1992. *North American Journal of Fisheries Management* 22:213–218.
- Winter, A., G. Swartzman, and L. Ciannelli. 2005. Early- to late-summer population growth and prey consumption by age-0 pollock (*Theragra chalcogramma*), in two years of contrasting pollock abundance near the Pribilof Islands, Bering Sea. *Fisheries Oceanography* 14:307–320.
- Winters, G. H., and J. P. Wheeler. 1994. Length-specific weight as a measure of growth success of adult Atlantic herring (*Clupea harengus*). *Canadian Journal of Fisheries and Aquatic Sciences* 51:1169–1179.
- Zar, J. H. 1999. *Biostatistical analysis*, 4th edition. Prentice-Hall, Upper Saddle River, New Jersey.

Appendix 1: Sensitivity Analyses of Posterior Distributions to Prior Distributions

Through preliminary analyses, we ensured that posterior distributions were not sensitive to the weakly informative priors and hyperpriors. For individual variation in mass at length, the standard deviation (σ) was assumed to be lognormally distributed, for which the predefined variance of 2.0 was very large; the predefined log-scale mean was -2.30 , while the size- and region-specific posterior means had large deviations from the prior mean (deviation range = -0.154 to 0.391 for lake trout; -0.152 to 1.389 for Chinook salmon). When we changed this prior mean from -2.30 to -1.61 (30% increase) and changed the prior variance from 2 to 3 (50% increase), no noticeable change in resulting posterior parameter distributions were evident and none of the quantities represented in tables and figures was appreciably changed. The central tendencies for coefficient a and exponent b were also assumed to be lognormally distributed, for which we also used a large variance of 2.0; the prior mean b was 2.72, while the posterior average b was 3.00 for Chinook salmon and 3.12 for lake trout. When we changed the prior

mean from 2.72 to 2.42 (11% decrease) and changed the variance from 2 to 3 (50% increase), no noticeable changes in resulting posterior parameter distributions were evident and none of the quantities represented in tables and figures was appreciably changed. For process errors in a and b , the σ was assumed to be lognormally distributed; the prior log-scale mean was -2.30 , while the posterior means were -3.17 and -3.19 from the lake trout model and -2.81 and -2.92 from the Chinook salmon model. When we increased or decreased the prior mean by 30% and increased the variance by 50%, only negligible changes in posterior means or distributions occurred. For the zeta-transformed correlation coefficient r between the process errors, the prior of the normal distribution had a mean of 0 and the variance of 2 made the possible values for back-transformed r range from -1 to 1 (i.e., maximum range). When we increased variance on the transformed scale from 2 to 3, we observed no changes in posterior distributions for any of the parameters and quantities represented in tables and figures.

Appendix 2: Markov Chain Monte Carlo Calculation and Diagnostics

We used the Metropolis–Hastings algorithm as implemented in AD Model Builder (Otter Research 2001) to generate chains for the Markov chain Monte Carlo (MCMC) calculations. The chain length was 1,000,000 cycles for each model. For computing time and data management reasons, we thinned the chains by saving every 200th cycle. We dropped a burn-in period of the initial 1,000 values of the thinned chain, so that our inferences were based on a saved chain of 4,000. The chain length and burn-in period were adequate for all transformed parameters, hyperparameters, and negative log-likelihood values based on standard diagnostics as applied by He and Bence (2007). We checked the trace plots, autocorrelation functions, and subchains for all estimated and predicted quantities, and we found no potential problems with convergence or an initial transient. For every parameter and hyperparameter that determined body mass at length, the Gelman–Rubin statistics (Gelman et al. 2004) based on three parallel chains were close to 1.0 (i.e., within 0.001), and the minimum effective sample size (Thiebaut and Zwiers 1984) from the saved MCMC chain was larger than 300 for lake trout and larger than 143 for Chinook salmon. For the negative log-likelihood values of all models, the Gelman–Rubin statistics were also close to 1.0, and the minimum

effective sample sizes from the saved MCMC chains were larger than 477 (Table 3). These standard methods for MCMC diagnostics are reviewed by Cowles and Carlin (1996).

While the achieved effective sample sizes indicated that the chain lengths were long enough to approximate the posterior distribution, they were not excessive for this purpose. The AD Model Builder algorithm for MCMC chains adjusts the step size during the burn-in period to achieve generally recommended acceptance rates (e.g., Gelman et al. 2004) of 0.2–0.5. Nevertheless, even when thinned to save every 200th cycle, the resulting chain exhibited substantial serial correlation, suggesting that the thinning led to little loss of information. We believe the long period correlations in our chain were the result of (1) relatively high posterior correlations among some parameters and (2) the AD Model Builder MCMC procedure of sampling all parameters simultaneously in each cycle of the chain. For our application, the computation time associated with running a long chain was not a limitation; however, in cases where computation time could be a limitation, investigators may want to consider reparameterization to reduce correlations and sampling parameters in strategically chosen blocks (Gelman et al. 2004).