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**Exploring optimal walleye exploitation rates for northern Wisconsin Ceded
Territory lakes using a hierarchical Bayesian age-structured model**

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Abstract

We assessed population dynamics of walleye (*Sander vitreus*) in multiple Ceded Territory lakes, supporting recreational and tribal fisheries, using a hierarchical Bayesian age-structured model. We used distributions of parameter estimates to develop a dynamic simulation model to forecast performances of walleye fisheries across these lakes under alternative recreational and tribal fishing scenarios. Application of a hierarchical approach allowed us to obtain more accurate estimates of stock–recruitment relationships, natural mortality, maturity and selectivity schedules, and growth parameters for individual lakes, especially for those with relatively uninformative data, and to characterize their variability among lakes. Using standing spawning stock biomass, recreational and tribal harvest, and probability of population collapse as performance metrics, our simulations suggest that northern Wisconsin walleye populations can sustain a regional optimal exploitation rate of about 20% on average given the existing recreational and tribal gear selectivities. However, lake-specific optimal exploitation rates may be higher or lower depending on estimated lake productivities, suggesting that effective management of the Ceded Territory walleye fisheries should account for variability in population dynamics among lakes.

Introduction

Sustainability of walleye (*Sander vitreus*) populations in northern Wisconsin Ceded Territory lakes has been an issue of concern to fisheries managers since off-reservation tribal hunting, fishing, and gathering rights were affirmed to Lake Superior Chippewa tribes. Consequently, these populations have been subjected to recreational (angling) and tribal (spearing) exploitation (Hansen et al. 1991; Schueller et al. 2008; Cichosz 2012). This multi-user fishery has been managed by setting total allowable catches (TAC) to not exceed, in not more than 1 in 40 occasions, an annual adult exploitation rate of 35%, which is presumed to ensure optimal sustainable yields for the walleye populations (Staggs et al. 1990). These TACs are implemented through lake-specific spearing quotas and angler bag and minimum length limits agreed upon between the Wisconsin Department of Natural Resources (WDNR) and the Great Lakes Indian Fish and Wildlife Commission (GLIFWC). Annual TAC quotas for individual lakes are established based on lake-specific adult density estimates from mark-recapture surveys or by using empirical relationships relating adult walleye abundance to lake area when population estimates are not available or deemed outdated (Staggs et al. 1990; Hansen et al. 1991; Nate et al. 2001). Mark-recapture surveys conducted on 29 northern Wisconsin lakes in 2010 showed that adult walleye densities ranged from 0.8 to 21.8 fish·ha⁻¹ (Cichosz 2012), and a log-linear lake area-adult walleye abundance regression suggested that average regional density for northern Wisconsin lakes is about 8.9 fish·ha⁻¹ (95% confidence interval = 2.92–26.71 fish·ha⁻¹) (Schueller et al. 2008).

Maximum TAC for all northern Wisconsin lakes has been set at 35% of adult abundance, apparently based on an implicit assumption that all lakes are equally productive. However, optimal fishery yields may vary from lake to lake depending on the balance between mortality

and recruitment dynamics of individual populations, with the maximum reproductive rate at low stock size determining the biological limits of fishing (Myers et al. 1999; Gibson and Myers 2003). Therefore, accounting for variability in walleye productivity among lakes is important because managing fisheries in all lakes as though they are equally productive may be suboptimal if this leads to overexploitation of some populations. Indeed, several studies have been conducted to assess the potential for walleye fisheries across northern Wisconsin lakes. For example, walleye recruitment variability was related to density-dependent and -independent factors, including temperature and competition with or predation by adult yellow perch (*Perca flavescens*), in Escanaba Lake (Hansen et al. 1998) and across multiple northern Wisconsin lakes (Beard et al. 2003a; Hansen et al. 2015). Schueller et al. (2008) evaluated the sustainability of walleye populations in northern Wisconsin across a range of initial densities using an age-structured simulation model based on estimates of walleye stock recruitment relationship in Escanaba Lake. Accordingly, walleye populations in northern Wisconsin were determined to support sustainable exploitation rates of 60–85% depending on allocations of angling and spearing harvest and minimum length limits for recreational fisheries. However, these exploitation rates were identified based on probabilities of extinction or population decline, and thus are not necessarily optimal. More recently, Hansen et al. (2011) assessed changes in walleye natural mortality in relation to fishing mortality and fish abundance using an age-structured population model. In addition to these studies focusing on walleye population dynamics, several whole-lake experiments have been conducted in northern Wisconsin to directly evaluate population responses to sustained exploitation rates. Specifically, Big Crooked and Sherman lakes were experimentally subjected to ten-year walleye exploitation rates of 35 and 50%, respectively, which led to declines in adult walleye densities and changes in growth and

maturation schedules in both lakes (U.S. Department of the Interior 1991; Schueller et al. 2005; Schmalz et al. 2011). Although previous studies have led to a better understanding of the status and dynamics of walleye populations in northern Wisconsin lakes, they have not covered the entire range of walleye productivity in the Ceded Territory because they focused on a few selected lakes with the best data available. As a result, patterns in walleye productivity in northern Wisconsin lakes remained to be investigated, which is essentially a prerequisite for the development of an effective fishing policy.

Relatively large amount of walleye demographic data are available for many northern Wisconsin lakes. However, many of the time-series data are still not informative enough to reliably assess population dynamics or long enough to provide sufficient contrast to accurately estimate stock–recruitment relationships for individual lakes. Under such circumstances, hierarchical Bayesian meta-analysis can be a useful method for improving assessment of walleye population dynamics across northern Wisconsin lakes, considering that these lakes likely possess biological and environmental similarities and are subjected to a joint fishery. Rather than simply pooling data, hierarchical Bayesian models assume an underlying probability distribution for parameters of interest that is common to all populations (i.e., the prior distribution) (Myers et al. 1999; Maunder 2003; Gelman et al. 2004). By analyzing data from multiple, related populations simultaneously, and thus allowing data sets with little information about parameters to borrow information from other data sets, hierarchical meta-analysis has the advantage of providing more accurate parameter estimates for populations with uninformative data (Gelman et al. 2004; Forrest et al. 2010). As such, hierarchical Bayesian analysis of walleye demographic data sets from the northern Wisconsin lakes could be used to obtain more accurate estimates of population parameters for individual lakes and to characterize their variability among these lakes.

Several previous studies have applied hierarchical Bayesian methods to assess population and fishery processes, including stock–recruitment relationships (Chen and Holtby 2002, Forrest et al. 2010, Su and Peterman 2012), growth of fish (Pilling et al. 2002; He and Bence 2007; He et al. 2008), and other specific aspects of fishery or population dynamics (e.g., catchability, intrinsic rate of population growth) (Meyer and Millar 1999, Millar and Methot 2002, Tsehaye et al. 2013). However, these studies either did not fully describe population dynamics or were based on simplified population models (such as the surplus production model), in large part due to the specific type of data available for these studies. In contrast, we were able to conduct a more comprehensive analysis of walleye population dynamics to estimate a whole set of population and fishery parameters because multiple types of fishery-dependent and -independent data were available for many of the northern Wisconsin lakes. Lake-specific data sets available included time-series of adult walleye abundances and age composition, age-0 walleye abundances, length-at-age, angling and spearing exploitation rates, and length composition of spearing harvest. The availability of such information allowed us to estimate stock–recruitment relationships, natural mortalities, maturity and selectivity schedules, and growth parameters for multiple lakes. Based on estimates of demographic parameters and associated uncertainties, we then developed a forecasting model to evaluate performances of the walleye fisheries regionally and in individual lakes under different exploitation rates and allocations of angling and spearing harvest. Our ultimate goal was to determine optimal walleye harvest policies (providing the largest sustainable harvest $\cdot \text{ha}^{-1}$) for the northern Wisconsin Ceded Territory lakes.

Methods

Study area and the management system

The Ceded Territory, covering the northern third of Wisconsin, has thousands of lakes (mostly < 400 ha), over 900 of which support walleye populations (Beard et al. 2003a; Cichosz 2012) (Fig. 1). The Ceded Territory contains 77% of Wisconsin's lakes, accounting for 53% of the total inland lake surface area in Wisconsin (Staggs et al. 1990). Walleye fisheries in some of these lakes are supported by stocking, while the fisheries in the majority of these lakes are sustained by natural reproduction (Nate et al. 2000). Recreational and tribal walleye fisheries in the Ceded Territory are managed using a "safe harvest" quota system, wherein the maximum acceptable risk of exploitation rates exceeding 35% is 1 in 40 occasions (Staggs et al. 1990; Hansen et al. 1991), i.e., given average adult densities and associated measures of error (*see below*). Under this management system, the tribes annually declare their target (percent) harvest for off-reservation lakes, and the WDNR then sets annual recreational angler bag limits (≤ 5 walleye·day⁻¹) such that total exploitation rate does not exceed 35% by increasing or lowering angling bag limits in response to tribal harvest each year, commonly known as a sliding bag limit system (Beard et al. 2003b).

As part of the walleye fishery management system, the WDNR and GLIFWC have monitored the status and trends of walleye populations in northern Wisconsin lakes since 1987 (Cichosz 2012). The status of walleye populations in these lakes have been evaluated using (a) mark-recapture experiments, to obtain spring adult population estimates (PEs) (expressed as means and associated coefficients of variation (CVs) based on repeated random samples), (b) electrofishing, to estimate fall age-0 (young-of-year) catch per effort (CPE) and abundance, and (c) creel surveys/census, to estimate/enumerate recreational/tribal harvest and effort (Cichosz 2012). In the WDNR mark-recapture experiments, fyke nets are used to capture adult walleyes for marking, and AC electrofishing is used to recapture walleyes (Hansen et al. 2000; Beard et al.

2003b). Mark-recapture surveys by the GLIFWC use pulsed-DC electrofishing to catch and recapture walleye. Adult age composition in these surveys has been determined based on fish aging using scales (for smaller fish) and dorsal fin spines (for larger fish). In addition, length-at-age data have been recorded for individual lakes. In this study, we selected 25 lakes from the Ceded Territory with age-specific adult PEs and five or more years of data on adult PEs and age-0 abundance, which we assumed to provide sufficient contrast to analyze stock–recruitment relationships and other population dynamics.

Population dynamics and parameter estimation

We assessed stock–recruitment relationships and other walleye population dynamics in two separate steps, described in separate sections below. Traditionally, stock recruitment analysis has been performed after time-series of spawning stock and recruitment have been estimated using another assessment model, typically based on fishery-dependent catch, age composition and effort data. Intuitively, it would be more appropriate to analyze the stock–recruitment relationship inside the stock assessment model because the analysis will automatically incorporate the uncertainty in stock and recruitment estimates into the stock–recruitment parameter estimates (Maunder and Punt, 2013). Yet, several recent simulation studies have shown that the estimates of the stock–recruitment relationship are actually often highly uncertain or biased (Magnusson and Hilborn 2007, Conn et al. 2010, Lee et al. 2012, Maunder and Piner 2015). Either way, the availability of direct fishery-independent estimates of walleye recruit and spawning stock abundances for the Ceded Territory lakes from annual electrofishing and mark-recapture surveys avoided the need for us to rely on model estimated stock and recruit abundances.

In a subsequent step, parameter estimates from the two assessments were used as inputs to build a forecasting model to simulate walleye population responses to fishing. Definitions of parameters and variables used in walleye estimation and simulation models are given in Table 1. The numbers of years of data of adult and age-0 abundance available for each of the selected lakes is shown in Table 2, with Escanaba Lake having the longest time-series data.

Stock–recruitment relationships

We assessed stock–recruitment relationships regionally and in individual lakes by fitting Ricker models to time series of spawner–recruit data from the 25 lakes assumed to have a sufficient number of years of data on adult and age-0 abundance. For spawners, we used the spring adult PEs. Age-0 walleye abundances (N_0) were calculated from electrofishing CPEs using a relationship developed by Hansen et al. (2004):

(1)
$$N_0 = 0.0345 * CPE^{1.564}$$

We fit stock–recruitment relationships to individual lakes simultaneously using a hierarchical model:

(2)
$$R_{i,t} = \alpha_i S_{i,t} e^{-\beta_i S_{i,t}}$$
$$\hat{R}_{i,t} = R_{i,t} e^{\omega_{i,t}}, \quad \omega_{i,t} \sim N(0, \sigma_{R,i}^2),$$
$$\hat{S}_{i,t} = S_{i,t} e^{v_{i,t}}, \quad v_{i,t} \sim N(0, \sigma_{S,i}^2),$$

where annual recruitment ($R_{i,t}$) is predicted for each lake (i) by year (t), with observed recruitments being $\hat{R}$. The deviations $\omega_{i,t}$ combine both measurement error, representing the difference between measured and actual recruitment, and process error, representing deviations from the direct proportionality assumption between stock and recruitment (i.e., according to the

stock–recruitment relationship) or inter-annual variability in recruitment. Similarly, considering that we do not observe spawning stock size directly, observed spawning stock size $\hat{S}_{i,t}$ was expressed as a function of actual spawning stock size $S_{i,t}$ estimated as parameters by accounting for measurement error $\nu_{i,t}$; $\sigma_{S,i}$ values were calculated externally based on the CVs (Evans et al. 2000) of adult PEs from the mark-recapture experiments described above (resulting in $\sigma_{S,i} = 0.06\text{--}0.18$). By accounting for both measurement and process errors, our model provided – in effect – a state-space representation of walleye recruitment dynamics.

In our base hierarchical model, stock–recruitment parameters were assumed to vary among lakes following a normal or lognormal distribution, with central tendency parameters $\bar{\alpha}$, $\bar{\beta}$, and $\bar{\sigma}_R$ and multiplicative and additive process errors $\varepsilon_{\alpha,i}$, and $\varepsilon_{\beta,i}$, respectively (eq. 3). $\varepsilon_{\alpha,i}$ and $\varepsilon_{\beta,i}$ were assumed to be correlated and follow a bivariate normal distribution with a vector of means $\underline{0}$ and variance–covariance matrix Σ ; thus, α_i and β_i would follow a bivariate lognormal-normal (LNN) distribution. $\sigma_{R,i}^2$ was assumed to follow an inverse-gamma distribution. We selected a model with LNN prior for α_i and β_i and inverse-gamma prior for $\sigma_{R,i}^2$ as the best (base) model among alternative models based on deviance information criterion (DIC) (*see section* Model sensitivity to prior assumptions). In fact, the inverse-gamma distribution is commonly used as a prior for variance (Gelman et al., 2004). Thus,

$$(3) \quad \alpha_i = \bar{\alpha} e^{\varepsilon_{\alpha,i}},$$

$$\beta_i = \bar{\beta} + \varepsilon_{\beta,i},$$

$$\begin{bmatrix} \varepsilon_{\alpha,i} \\ \varepsilon_{\beta,i} \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \Sigma_{\varepsilon}\right),$$

$$\sigma_{R,i}^2 \sim \text{Inv-gamma}(\alpha', \beta')$$

where, the parameters (including process errors or random effects) $\bar{\alpha}$, $\bar{\beta}$, $\varepsilon_{\alpha,i}$, $\varepsilon_{\beta,i}$, and $\sigma_{R,i}^2$ were estimated as first-level parameters; Σ_{ε} , α' , and β' were estimated as second-level parameters (also known as hyperparameters). Σ_{ε} was estimated through Cholesky decomposition as a function of the standard deviations of $\varepsilon_{\alpha,i}$, and $\varepsilon_{\beta,i}$ and an “off diagonal” parameter defining the correlation between the two (ADMB Project 2013). The expected (regional) $\bar{\sigma}_R^2$ was calculated as a derived variable as a function of the shape (α') and scale (β') parameters as

$$\frac{\beta'}{\alpha' - 1}.$$

We used a Bayesian approach for model fitting and to characterize uncertainty of parameter estimates. For our hierarchical Bayesian model, the joint posterior probability distribution for the unknown parameters and hyperparameters can be specified as

$$(4) \quad P(\theta, \varepsilon, \phi | X) \propto L(X | \theta, \varepsilon) P(\varepsilon | \phi) P(\theta) P(\phi)$$

where $L(X | \theta, \varepsilon)$ represents data likelihoods, $P(\varepsilon | \phi)$ and $P(\theta)$ prior probability distributions for the first-level parameters (ε and θ), $P(\phi)$ prior probability distributions (also known as hyperpriors) for the hyperparameters ϕ . For model fitting, we calculated the log of the joint posterior probability as the sum of (1) log-likelihood ($\log L$) of observed data, (2) log-priors ($\log P$) for first-level parameters and (3) log-hyperpriors for the second-level parameters, defined as follows. Log-likelihoods of observed recruit $\hat{R}$ and stock size $\hat{S}$ data were calculated as

$$(5) \quad \log L = - \sum_{i=1}^{25} \sum_t \left[\ln(\sigma_i) + \frac{(\text{dev}_{i,t})^2}{2 \text{sig}_i^2} \right]$$

where $dev_{i,t}$ is $\omega_{i,t}$ or $\nu_{i,t}$ (i.e., differences between log of predicted and observed $\hat{R}$ or $\hat{S}$ values), and sig_i is $\sigma_{R,i}$ or $\sigma_{S,i}$, respectively. Log-prior for the bivariate process errors $\varepsilon_{\alpha,i}$ and $\varepsilon_{\beta,i}$, inverse-gamma log-prior for the first-level parameter $\sigma_{R,i}^2$, and log-prior for the first-level parameters $\bar{\alpha}$ and $\bar{\beta}$ were, respectively, specified as:

$$(6) \quad \log P = -\left(\frac{25}{2}\right) \ln |\Sigma_{\varepsilon}| - 0.5 \sum_{i=1}^{25} [\underline{x}_i^T \Sigma_{\varepsilon}^{-1} \underline{x}_i],$$

$$\log P = \sum_{i=1}^{25} \left[\alpha' \ln(\beta') - \ln(\Gamma(\alpha')) - (\alpha' + 1) \ln(\sigma_{R,i}^2) - \frac{\beta'}{\sigma_{R,i}^2} \right],$$

$$\log P = -\frac{1}{2} [(\underline{x} - \underline{\mu})^T \Sigma^{-1} (\underline{x} - \underline{\mu})],$$

where the vector $\underline{x}_i = (\varepsilon_{\alpha,i}, \varepsilon_{\beta,i})$, $\underline{x} = (\bar{\alpha}, \bar{\beta})$, $\underline{\mu} = (2.5, 0.1)$, $\Sigma = \begin{bmatrix} 25^2 & 0 \\ 0 & 1^2 \end{bmatrix}$. The values of $\underline{\mu}$ were derived from preliminary analysis based on data likelihoods, and the corresponding standard deviations were assumed to be $10 \times \underline{\mu}$ with the intent for the priors to be only weakly informative so that the data would predominantly determine parameter estimates. Log-hyperpriors for the elements of Σ_{ε} and for α' and β' were specified as

$$(7) \quad \log P = -0.5 \left(\frac{x - \mu}{\sigma} \right)^2,$$

where x is either the standard deviation of $\varepsilon_{\alpha,i}$ or $\varepsilon_{\beta,i}$; the “off diagonal” parameter for Σ_{ε} ; or α' or β' . Just as above, the values of μ were selected based on preliminary analysis of data without hyperpriors, and the values of σ were set at $10 \times \mu$.

Posterior distributions of parameter estimates were obtained using Markov Chain Monte Carlo (MCMC) sampling. The Metropolis-Hastings algorithm within AD Model Builder

(Fournier et al. 2012) was used to obtain MCMC samples from the joint posterior distribution of parameter estimates. AD Model Builder implementation of MCMC involves first creating an approximate multivariate normal distribution, using the highest posterior density (HPD) estimates as the mode and the inverse of the Hessian at the mode as the variance-covariance matrix (i.e., an asymptotic variance co-variance). HPD parameter estimates were the values obtained when the maximum gradient of the objective function was less than 1.0×10^{-4} . Using the HPD estimates as starting values, the approximate multivariate normal distribution is then used as a “jumping distribution” for drawing random samples sequentially from the parameter space. At each step, AD Model Builder accepts or rejects the drawn random sample based on the posterior density calculated for the sample, thereby constructing the target posterior distribution (Gelman et al. 2004). The MCMC simulation was run for 1.1 million samples saving every 100th sample to produce a total saved sample size of 10,000 after 1,000 samples were discarded as burn-in. MCMC chains were evaluated for adequacy (convergence and sufficient information) using trace plots for each estimated parameter and derived variable, as a visual check to ensure the chain was well-mixed and did not show long-term patterns, the effective sample size, and similarity between the first 10% and last 50% of the chain using Geweke's (1992) Z-score test, where $Z < 2$ for well mixed chains with no long-term patterns. All MCMC diagnostics were conducted in R (R Development Core Team 2010) using the CODA package (Plummer et al. 2010). We summarized posterior distributions of parameters using HPD estimates as point estimates and 95% Bayesian credible intervals as measure of uncertainty.

To determine the extent to which our hierarchical meta-analysis improved (or not) stock–recruitment estimates, we also estimated stock–recruitment relationships independently for individual lakes, in which the stock–recruitment relationship estimated for a given lake would

not account for potential underlying similarities between lakes. For many of these lakes, the time-series spawner–recruit data provided unrealistically high α (e.g., $\alpha = 10493.93$ for North Twin lake) or negative β (e.g., $\beta = -0.17$ for Squirrel lake) suggesting an exponential increase in recruitment with stock size. Therefore, we excluded these lakes when calculating a regional average stock–recruitment relationship to compare with the regional stock–recruitment relationship from the hierarchical model.

Model sensitivity to prior assumptions

We conducted sensitivity analysis to determine the extent to which our parameter estimates may be influenced by our assumptions of prior distributions. Specifically, this is to test whether our choice of priors in the base model, assuming a bivariate lognormal-normal distribution for α_i and β_i and an inverse-gamma distribution for $\sigma_{R,i}^2$ (referred to as LNN–InvG hereafter), accommodated possible skewness and excess variability among parameters and has not caused over-shrinkage of parameter estimates toward average values. For this purpose, we fitted the hierarchical stock–recruitment model under alternative assumptions of prior distributions for α_i and β_i , including a bivariate lognormal-lognormal (LNLN) and a bivariate normal-normal (NN) distributions (referred to as LNLN and NN, respectively, hereafter). For these models, $\sigma_{R,i}$ was assumed to follow a lognormal distribution, with central tendency parameter $\overline{\sigma_R}$ and multiplicative process error $\varepsilon_{\sigma_R,i}$:

$$(8) \quad \sigma_{R,i} = \overline{\sigma_R} e^{\varepsilon_{\sigma_R,i}}$$

$$\varepsilon_{\sigma_R,i} \sim N(0, \sigma_{\sigma_R}^2)$$

Thus, in lieu of the inverse-gamma log-prior for $\sigma_{R,i}^2$ in equation 6, we specified a log-prior for the process errors $\varepsilon_{\sigma_{R,i}}$ and the first-level parameter $\bar{\sigma}_R$ as

$$(9) \quad \log P = -\sum_{i=1}^{25} \left[\ln(\sigma_{\sigma_R}) + \frac{\varepsilon_{\sigma_{R,i}}^2}{2\sigma_{\sigma_R}^2} \right],$$

$$\log P = -0.5 \left(\frac{\bar{\sigma}_R - 2.0}{20} \right)^2,$$

and log-hyperprior for the hyperparameter σ_{σ_R} was specified as in equation (7). Additionally, we evaluated an LNLN model with $\sigma_{R,i}$ assumed to follow an inverse-gamma distribution (referred to as LNLN–InvG hereafter).

To assess the effects alternative prior assumptions on the stock–recruitment parameter estimates, we calculated recruitment at unfished equilibrium as an “omnibus” metric summarizing the combined effects on α_i and β_i , which was calculated using the 10,000 MCMC samples of parameter estimates as:

$$(10) \quad R_0 = \frac{\ln(\alpha \text{SPR})}{b \text{SPR}}$$

where SPR was calculated by incorporating natural mortalities and maturity schedules estimated in the next section (Walters and Martell 2004). We assessed similarity between the samples of R_0 estimates obtained under the different prior assumptions using pairwise Geweke's (1992) Z-score tests, as described above (i.e., between the first 10% of the chain from the first model and the last 50% of the chain from second model). Even if model estimates may not be sensitive to our prior assumptions, we also calculated DIC (Spiegelhalter et al. 2002) to determine which model structure best described our stock–recruit data. The DIC calculations were based on saved 10,000 MCMC samples of parameter estimates and associated data likelihoods from MCMC runs

conducted under the various assumptions for prior distributions (Spiegelhalter et al. 2002). DIC was calculated as

$$(11) \quad \text{DIC} = \bar{D} + p_D$$

$$\bar{D} = \frac{1}{C} \sum_{c=1}^C -2 \ln(L(\text{data} | \theta_c))$$

$$p_D = \bar{D} - D(\bar{\theta})$$

Growth, natural mortality, maturity, and selectivity

We conducted an integrated analysis (Maunder 2003) (Fig. 2) to assess natural mortality and maturity and selectivity patterns using a statistical-catch-at-age framework (Deriso et al. 1985; Walters and Martell 2004; Fournier et al. 2012), wherein von Bertalanffy (VB) growth functions, logistic maturity and selectivity schedules, and survival curves were fit simultaneously to obtain values to match observed length-at-age of fish and age composition of adult PEs. Because there were many gaps in the time-series of adult PEs for many of the lakes and our goal was to obtain average mortality for use as input to our forecasting model (*see section* Forecasting model), we pooled annual adult PEs to obtain an average adult age composition for each lake to which a survival curve was fit. Given that there is no evidence that mortality has changed considerably over time, we believe our use of a pooled age distribution is reasonable. We estimated regional and lake-specific growth, maturity parameters, and natural mortality by fitting hierarchical Bayesian models to length-at-age and age composition data from the selected 25 lakes, with lake-specific parameters treated as random effects. Growth parameters were estimated by fitting the VB growth function to length-at-age data as

$$(12) \quad L_{i,a} = L_{\infty,i} (1 - e^{-K_i(a-t_{0,i})})$$

$$L_{i,a,j} = L_{i,a} e^{\xi_{i,a,j}}, \quad \xi_{i,a,j} \sim N(0, \sigma_{L,i}^2)$$

where ξ is random error representing individual variation in length-at-age with mean 0 and lake-specific standard deviation $\sigma_{L,i}$. We assumed that the VB growth parameters varied among lakes following a lognormal distribution, with central tendencies $\overline{L_\infty}$, $\overline{K}$, $\overline{t_0}$, and $\overline{\sigma_L}$ and multiplicative process errors $\varepsilon_{L_\infty,i}$, $\varepsilon_{K,i}$, $\varepsilon_{t_0,i}$, and $\varepsilon_{\sigma_L,i}$ with standard deviations σ_{L_∞} , σ_K , σ_{t_0} , and σ_{σ_L} , respectively, i.e.,

$$(13) \quad L_{\infty,i} = \overline{L_\infty} e^{\varepsilon_{L_\infty,i}}, \quad \varepsilon_{L_\infty,i} \sim N(0, \sigma_{L_\infty}^2)$$

$$K_i = \overline{K} e^{\varepsilon_{K,i}}, \quad \varepsilon_{K,i} \sim N(0, \sigma_K^2)$$

$$t_{0,i} = \overline{t_0} + \varepsilon_{t_0,i}, \quad \varepsilon_{t_0,i} \sim N(0, \sigma_{t_0}^2)$$

$$\sigma_{L,i} = \overline{\sigma_L} e^{\varepsilon_{\sigma_L,i}}, \quad \varepsilon_{\sigma_L,i} \sim N(0, \sigma_{\sigma_L}^2)$$

Thus, $\overline{L_\infty}$, $\overline{K}$, $\overline{t_0}$, $\overline{\sigma_L}$, $\varepsilon_{L_\infty,i}$, $\varepsilon_{K,i}$, $\varepsilon_{t_0,i}$, and $\varepsilon_{\sigma_L,i}$ were estimated as first-level parameters, and σ_{L_∞} , σ_K , σ_{t_0} , and σ_{σ_L} were estimated as second-level parameters or hyperparameters.

Probability of maturity at age was estimated by fitting a logistic function to age composition of adult PEs. Age composition of spearing harvest closely matched age composition of adults PEs, so we assumed that spearing selectivity was the same as the walleye maturity schedule:

$$(14) \quad V_{i,a}^{\text{spear}} = \frac{1}{1 + \exp(-h_i(a - m_i))}$$

where h and m were estimated for each lake as random effects parameters. We assumed that h and m varied among lakes following a lognormal distribution, with central tendencies $\overline{h}$ and

353 $\bar{m}$ and multiplicative process errors $\varepsilon_{h,i}$ and $\varepsilon_{m,i}$ for which the standard deviations were σ_h
 354 and σ_m , respectively.

$$\begin{aligned} 355 \quad (15) \quad h_i &= \bar{h} e^{\varepsilon_{h,i}}, & \varepsilon_{h,i} &\sim N(0, \sigma_h^2) \\ 356 \quad m_i &= \bar{m} e^{\varepsilon_{m,i}}, & \varepsilon_{m,i} &\sim N(0, \sigma_m^2) \end{aligned}$$

357 As with the stock–recruitment model above, the prior distributions for VB and maturity
 358 parameters were selected based on DIC comparisons. Here, we considered different
 359 combinations of normal and lognormal prior error distributions for the different parameters.

360 No length/age composition data were available to estimate vulnerability for the
 361 recreational fisheries, but Myers et al. (2014) showed that smaller walleyes were not targeted by
 362 the recreational walleye fishery in Escanaba Lake. Because minimum length limits are
 363 commonly used for the recreational fishery, we used a knife-age selectivity function for this
 364 fishery, i.e.,

$$365 \quad (16) \quad V_{i,a}^{\text{rec}} = \begin{cases} 0, & \text{if } L_{i,a} < 38 \text{ cm} \\ 1, & \text{otherwise} \end{cases}$$

366 where the length corresponding to each age is predicted by the VB growth function for each lake.
 367 Subsequently, fishing mortality was calculated as:

$$368 \quad (17) \quad F_{i,a} = -\ln(1 - u_{s,i} V_{i,a}^{\text{spear}} - u_{r,i} V_{i,a}^{\text{rec}})$$

369 where $u_{s,i}$ and $u_{r,i}$ are averages of annual spearing and recreational exploitation rates,
 370 respectively, recorded for each lake. Total mortality (Z) was then calculated as the sum of natural
 371 and fishing mortality:

$$372 \quad (18) \quad Z_{i,a} = M_{i,a} + F_{i,a}$$

Given that walleye natural mortality in northern Wisconsin lakes is higher for younger age classes and that our natural mortality estimates were based on adult age composition, we obtained natural mortality estimates for younger age classes (< 5 years old) from Hansen et al. (2011). Age-specific natural mortality for younger age classes was approximated as:

$$(19) \quad M_{a<5} = 0.7e^{-0.114a}$$

For older age classes, we estimated lake-specific natural mortalities as parameters. Again, we assumed that estimated natural mortality varied among lakes following a lognormal distribution, with a central tendency $\bar{M}$ and a multiplicative process error ($\varepsilon_{M,i}$) with a standard deviation σ_M .

$$(20) \quad M_{i,a \geq 5} = \bar{M}e^{\varepsilon_{M,i}}, \quad \varepsilon_{M,i} \sim N(0, \sigma_M^2)$$

Assuming a scaling age-0 abundance $N_{i,0} = 1$ (it does not really matter what the value of $N_{i,0}$ is in the calculation of $P_{i,a}$), numbers at older ages were predicted as:

$$(21) \quad N_{i,a+1} = N_{i,a}e^{-Z_{i,a}}$$

Because the probability of maturity at age was assumed to be equal to vulnerability to spear fishing, the age composition of mature fish was then calculated as:

$$(22) \quad N_{i,a}^{\text{mat}} = N_{i,a}V_{i,a}^{\text{spear}}$$

$$\text{tot}N_i^{\text{mat}} = \sum_a N_{i,a}^{\text{mat}}$$

$$P_{i,a} = \frac{N_{i,a}^{\text{mat}}}{\text{tot}N_i^{\text{mat}}}$$

Parameters were estimated by fitting predicted lengths at age ($L_{i,a}$) and predicted proportions by age ($P_{a,i}$) to observed lengths-at-age ($L_{i,a,j}$) and age composition of adult PEs ($\hat{P}_{a,i}$). As with the estimation stock–recruitment relationships above, we calculated the log of the posterior

probability as the sum of (1) log-likelihood ($\log L$) of observed data, (2) log-priors ($\log P$) for first-level parameters and (3) log-hyperpriors for the second-level parameters. Log-likelihood ($\log L$) of observed length-at-age data was calculated as,

$$(23) \quad \log L = - \sum_{i=1}^{25} \sum_j \left[\ln(\sigma_{L,i}) + \frac{(\ln(L_{i,a,j}) - \ln(L_{i,a}))^2}{2\sigma_{L,i}^2} \right],$$

and log-likelihood of the data on age composition of adult PEs, which was calculated assuming a multinomial distribution as a function of the effective sample size (n_i), observed ($\hat{P}$), and predicted proportions (P) at age was specified as

$$(24) \quad \log L = n_i \sum_i \sum_a \hat{P}_{i,a} \ln P_{i,a}.$$

Log-priors ($\log P$) of the process errors (ε_i^*) was calculated as:

$$(25) \quad \log P = - \sum_{i=1}^{25} \left[\ln(\sigma^*) + \frac{\varepsilon_i^{*2}}{2\sigma^{*2}} \right]$$

where σ^* is σ_{L_∞} , σ_K , σ_{t_0} , σ_{σ_L} , σ_h , σ_m , or σ_M , and ε_i^* is $\varepsilon_{L_\infty,i}$, $\varepsilon_{K,i}$, $\varepsilon_{t_0,i}$, $\varepsilon_{\sigma_L,i}$, $\varepsilon_{h,i}$, $\varepsilon_{m,i}$, or $\varepsilon_{M,i}$. Log-priors for each of the first-level parameters ($\overline{L_\infty}$, $\overline{K}$, $\overline{t_0}$, $\overline{\sigma_L}$, $\overline{h}$, $\overline{m}$, $\overline{M}$) and log-hyperpriors for all second-level parameters (σ_{L_∞} , σ_K , σ_{t_0} , σ_h , σ_m , and σ_M) were specified the same way as in eq. 7, with parameter values for prior distributions selected based on preliminary analysis of data and standard deviations set at 10 fold the mean values.

For the multinomial log-likelihood function, we used the same effective sample size (n_i) for all lakes. Effective sample sizes weight the relative importance of likelihood components corresponding to age compositions. The use of effective sample size, rather than actual sample size, is based on the recognition that the number of independent sample units is smaller than the actual number of fish aged due to nonrandomness of samples. However, this issue is not relevant

in our model because the multinomial log-likelihood (for age composition) was the only likelihood function in our integrated analysis (i.e., except for the log-likelihood function for length at age data to fit VB growth functions, which do not have any interactions with the model fits to age compositions). Therefore, parameter estimates are not affected by our choice of effective sample size. Indeed, the relative weightings of likelihood functions (hence the effective sample size) would have been an issue if we had used our integrated analysis to obtain estimates of population abundance (e.g., by fitting to harvest and effort data) along with age compositions, in which case there would be interaction between the two.

Posterior probability distributions were obtained for regional and lake-specific parameters using MCMC simulation the same way as with the stock–recruitment relationships above. Overall, we obtained posterior distributions for 260 parameters, including 3×26 stock–recruitment parameters (α , β and σ_R) and 7×26 growth and maturation/selectivity parameters (L_∞ , K , t_0 , σ_L , h , m , and M), a sub-sample of which was used as input to the forecasting model.

Forecasting model

To evaluate performances of walleye fisheries in northern Wisconsin regionally and in individual lakes under alternative harvest policies (exploitation rates and allocations of tribal and recreational harvest), we constructed an age-structured dynamic simulation model forecasting total (ages 1–18 years) and adult abundances of walleye and tribal and recreational harvest over a 100-year time horizon. We parameterized the walleye simulation model using regional and lake-specific posterior distributions of parameter estimates from the hierarchical Bayesian models described above. Thus, the simulation model forecasted walleye abundance-at-age for regionally and on a lake-by-lake basis. Regional and lake-specific recruitment to the first age class was

generated using stock–recruitment relationships, which included stochasticity to allow for interannual recruitment variation.

$$(26) \quad N_{i,0,t} = \alpha_i S_{i,t} e^{-\beta_i S_{i,t} + e_{i,t}}$$

Since the deviations $e_{i,t}$ in our estimation model combined measurement and process errors in recruitment, the actual standard of inter-annual variability in recruitment would be less than our estimates of $\sigma_{R,i}$. Hansen et al. (2004) acknowledged that a large part of variability in Wisconsin walleye recruitment was attributable to measurement error in the electrofishing estimates of walleye recruitment. Additionally, previous studies indicated that the average standard deviation of the logarithm of annual recruitment residuals over many fish species was around 0.6 (Beddington and Cooke 1983; Maunder and Deriso 2003). Therefore, we used one third of the estimated $\sigma_{R,i}$ as the standard deviation of inter-annual variability in forecasting future recruitment, which is quite conservative given that measurement errors in electrofishing CPE were estimated to be more than three times actual age-0 walleye variability (Hansen et al. 2004).

Numbers at age after recruitment were assumed to decrease exponentially over time and were calculated using an accounting equation of the form:

$$(27) \quad N_{i,a+1,t+1} = N_{i,a,t} e^{-M_{i,a}} \left(1 - u_{s,i} V_{i,a}^{\text{spear}} - u_{r,i} V_{i,a}^{\text{rec}} \right)$$

where M estimates were based on Hansen et al. (2011) for younger age classes and our own method for the five year and older age classes. Initial population density was set at abundance at unfished equilibrium, calculated for each lake based on $R0$ and natural mortality, with adult density being $R0 \times \text{SPR}$. Our estimates of adult density were within the range of equilibrium adult density calculated by Schueller et al. (2012), in which the median adult density at unfished equilibrium was $23.3 \text{ fish} \cdot \text{ha}^{-1}$ (with a range of $14\text{--}55 \text{ fish} \cdot \text{ha}^{-1}$).

We evaluated changes in walleye abundance under various combinations of tribal and recreational exploitation rates, assuming a logistic selectivity curve for spearing and a knife-age selectivity function for angling (with a minimum length limit of 38 cm), just as with the estimation model. Given that the selectivity schedule for the spear fishery was assumed to be the same as the walleye maturity schedule, the simulated age/size composition of spearing harvest would be the same as that for the adult population. In addition, we evaluated changes in walleye abundance under an alternative vulnerability schedule for the recreational fishery assuming that all adults were fully vulnerable to angling, just as with the tribal fisheries.

Given a knife-age selectivity function for angling, some adult fish would not be vulnerable to fishing in the recreational fishery depending on the minimum length limit, meaning that the amount of fish harvested under a given exploitation rate would be less in the recreational fishery than in the spearing fishery. To ensure the same number of fish would be harvested in both fisheries despite a minimum length limit for angling, we adjusted the exploitation rate (u_{adj}) for vulnerable age classes in the recreational fishery such that:

$$(28) \quad u_{adj} = \tilde{u}_r * \frac{adult}{vul}$$

where *adult* is the abundance of the adult population and *vul* is the total abundance of vulnerable age classes given the minimum length limit.

We accounted for uncertainties in walleye population dynamics when evaluating performances of alternative harvest policies by repeating the 100-year simulations under 1,000 combinations of: (1) stock–recruitment relationships; (2) VB growth functions; (3) natural mortalities; and (4) maturity/vulnerability schedules. For each of the 1,000 simulations, the forecasting model read in a different set of input values from the posterior distributions of parameter estimates obtained using the MCMC simulations described above. We then compared

performances of harvest policies using: (1) the median and interquartile range (IQR) of the proportion of adult abundance remaining after 100 years of fishing; (2) the median and interquartile range of long-term sustainable angling and spearing harvests (calculated as the average harvest in years 50–100 to make sure the population is at stable equilibrium); and (3) probability of collapse based on the 1,000 simulations. It should be noted that the Ricker stock–recruitment model would not give a reliable prediction of collapse if juvenile mortality increased at low spawner abundances through depensation or Allee effects (Myers et al. 1999; Walters and Kitchell 2001). To account for potential depensatory population dynamics, we used 10% of the adult or population abundance at unfished equilibrium (as predicted by our simulation models) as a threshold below which the population was considered to have functionally collapsed (Worm et al. 2009). At 10% of unfished stock size, recruitment is presumed to be severely reduced, and the population would no longer play a substantial ecological role (Worm et al. 2009).

Results

Model fits and sensitivity analysis

Based on DIC, which was about 1403.86 for the lake-by-lake analysis (Table 2), we selected the LNN–InvG model (Table 3) as the best model among the alternative models evaluated (Table 4) to characterize the variation in stock–recruitment relationships of walleye populations among the Ceded Territory lakes. Except for the NN model, all the alternative model structures considered for model selection and sensitivity analysis met the criteria used to evaluate model convergence. i.e., the MCMC chains for the parameters estimated were judged to have converged to the underlying joint posterior probability distribution and to contain enough information to characterize uncertainty in parameter estimates; trace plots showed no

“stickiness”, effective sample sizes showed that saved MCMC samples contained sufficient information to characterize posterior probability distributions of parameter estimates and, the means of the first 10% and last 50% of the saved MCMC samples were similar, with the absolute values of Geweke’s (1992) Z-score of the differences between means of the first 10% and last 50% being < 2 for all parameters (Table 4). Using the base model estimate, we found that predicted values also matched observed stock–recruitment data (Fig. 3).

Stock–recruitment parameter estimates were not sensitive to our assumptions of prior distributions as evidenced by the test of similarity of R_0 estimates obtained under alternative prior assumptions, with the absolute value of the pairwise Geweke’s (1992) Z-scores being < 2 for almost all lakes (Table 4). Regional median R_0 estimates were in the range 20–23 fish·ha⁻¹ under the different prior assumptions; lake-specific median R_0 estimates under the different prior assumptions were also within a 1–6 units of each other (Table 4). For three lakes (Lac Vieux Desert, Squaw and Siskiwit), SPR values provided negative R_0 estimates, most likely because the Hansen et al. (2011) method (eq. 19) over-estimated natural mortality. Therefore, we used regional SPR when calculating R_0 for these lakes; negative equilibrium recruitment means that the population is headed to extinction (Walters and Martell 2004).

For the other population dynamics parameters, DIC values showed that the model with lognormal priors for all parameters except t_0 best described the VB and maturity functions for walleye in the Ceded Territory lakes. Apparently because the data are less noisy (Fig 4), the VB and maturity parameters were even less sensitive to prior distributional assumptions. By contrast, the stock–recruitment model fits show large residual errors (as is typical of other fisheries), with the lake-specific values of σ ranging from 1.6 to 2.4 (Fig. 3; Table 3), although these values represented both inter-annual variability in recruitment and measurement errors. For brevity, we

only report results from our analysis of sensitivity of the stock–recruitment relationships to alternative model structures.

Population dynamics

In addition to the DIC being higher (1403.86), estimates of stock–recruitment relationships obtained by fitting the Ricker model independently for each lake varied substantially among lakes, with the limited number of years of (apparently less informative) data for several lakes providing parameter estimates with very high degrees of uncertainty (CV) (Table 2) and unrealistically high α (e.g., $\alpha = 10493.93$ for North Twin lake) or negative β (e.g., $\beta = -0.17$ for Squirrel Lake and -0.11 for Bearskin Lake) (Table 2). With α ranging from 0.09 to 10493.93 and negative β for several lakes, it was not possible to provide reasonable regional estimates unless we excluded the lakes with biologically unrealistic parameter estimates. In contrast, the hierarchical Bayesian analysis resulted in reasonable estimates of α and β for all lakes, without over-shrinkage of parameter estimates, as ascertained by the insensitivity of our estimates to prior distributional assumptions (Table 3 and 4).

Stock–recruitment parameters from the hierarchical model also suggested that walleye productivity varied considerably among northern Wisconsin lakes, with regional (LNN–InvG) median R_0 estimated to be about 20 fish·ha⁻¹ (Table 4) and the associated stock–recruitment parameters being $\alpha = 2.768$ (95% Bayesian credible limits, CL = 1.366, 4.761), $\beta = 0.049$ (CL = 0.002, 0.103), and $\sigma = 1.964$ (CL = 1.931, 2.643) (Table 3; parameter estimates from alternative models are in Table A1). Lake-specific R_0 values ranged from 3.441 fish·ha⁻¹ for Annabelle Lake to 70.714 fish·ha⁻¹ for Escanaba Lake, with the corresponding stock–recruitment parameters estimated to be $\alpha = 2.077$ (CL = 0.508, 4.541), $\beta = 0.057$ (CL = -0.007 , 0.136), and $\sigma = 1.781$

(CL = 1.261, 2.364) for Annabelle Lake and $\alpha = 6.046$ (CL = 1.800, 11.860), $\beta = 0.029$ (CL = 0.003, 0.052), and $\sigma = 1.612$ (CL = 1.212, 1.887) for Escanaba Lake. Stock–recruitment parameters estimated for Escanaba Lake were similar under the hierarchical and lake-by-lake analyses, which is likely given the large amounts of (and apparently more informative) data for this lake.

VB growth parameters were estimated with lower degrees of uncertainty than stock – recruitment parameters (compare CLs in Table 3 and 5). Variability in VB growth parameters among lakes was also less pronounced (Table 5), with regional VB growth parameters estimated at $L_{\infty} = 68.61$ cm (95% CL = 64.31 cm, 73.41 cm), $K = 0.13$ yr⁻¹ (95% CL = 0.11 yr⁻¹, 0.15 yr⁻¹), and $t_0 = -1.23$ (95% CL = -1.43, -1.02). Lake Siskiwit was an extreme case, with the lowest L_{∞} (HPD = 47.63 cm; 95% CL = 46.25 cm, 49.07 cm) and the highest K (HPD = 0.24 yr⁻¹; 95% CL = 0.22 yr⁻¹, 0.27 yr⁻¹). Similarly, parameters of the logistic maturity and selectivity curves were estimated with relatively low error (Table 6), with a regional $m = 3.36$ (95% CL = 3.13, 3.63) and $h = 4.80$ (95% CL = 3.45, 6.22); however, the slope of the logistic function (h) varied more than the age at 50% maturity (m). Regional natural mortality was also estimated with relatively low error (Table 6), with HPD = 0.24 yr⁻¹ (95% CL = 0.17 yr⁻¹, 0.35 yr⁻¹), although very high or very low natural mortalities were estimated for some lakes.

Comparing performances of alternative harvest scenarios

Although walleye population responses to fishing were predicted to be highly variable due to high uncertainty in stock–recruitment parameter estimates, underlying trends were evident. While the magnitude of population responses to fishing would be higher or lower for individual lakes depending on their productivity, simulations based on the regional population

and fishery parameters showed that the performance of walleye fisheries would vary depending on exploitation rates and selectivity schedules assumed for recreational and tribal fisheries. Based on the regional parameter estimates, adult density, which is equivalent to standing stock biomass (SSB), decreased continuously as the exploitation rate increased. The effect of exploitation was slightly lower under the scenarios with a 38-cm minimum length limit for the recreational fishery (Fig. 5a) compared to fishing scenarios with logistic selectivity for both the recreational and tribal fisheries (Fig. 5b). Recreational and tribal harvest increased with increased fishing within exploitation rates in the range of 0–20%, and declined with exploitation rates above 20% (Fig. 5c and d). Assuming equal exploitation rates for the two fisheries, peak combined recreational and tribal harvest was about $1.7 \text{ fish} \cdot \text{ha}^{-1}$ on average under either of the two combinations of selectivity schedules assumed for the two fisheries (Fig. 5c and d). Similarly, the probability of collapse increased as the exploitation rate increased (Fig 5a and b), and the risk of collapse was lower under the scenarios with a 38 cm minimum length limit than logistic selectivity for the recreational fishery. Using SSB, total recreational and tribal harvest, and probability of population collapse as performance metrics, simulations suggested that northern Wisconsin walleye populations could sustain an optimal exploitation rate of about 20% on average given the existing combination of recreational and tribal selectivity schedules (Fig. 5).

Contour plots based on adult abundance under different combinations of recreational angling and tribal spearing exploitation rates in the range of 0–25% indicated that adult density would decrease continuously with exploitation rate (Fig. 6a). In contrast, combined recreational and tribal harvest increased with increased exploitation rates in the range of 1–15% (i.e., up to a total exploitation rate of 20%), but decreased when combined recreational and tribal exploitation

rate increased above 20% (Fig. 6b). These results indicate that a total exploitation rate of about 20% would yield the greatest long-term optimal harvests, assuming a 38-cm minimum length limit for the recreational fishery.

Regional adult abundance and harvest projections under a total exploitation rate of 35% (with a 38-cm minimum length limit for the recreational fishery) indicated that the largest changes in response to fishing would occur during the first ten years or so of the fisheries. Abundance and harvest stabilized in subsequent years, at a median adult density of about 4.30 fish·ha⁻¹ and total recreational and tribal harvest of about 1.20 fish·ha⁻¹ (Fig. 7). Given the population and fishery parameters estimated for each lake (Tables 3, 5 and 6), lake-specific optimal fishing scenarios can be higher or lower than was predicted to be optimal regionally. The most productive lakes, such as Escanaba ($R_0 = 70.714$ fish·ha⁻¹), Middle Eau Claire ($R_0 = 50.831$ fish·ha⁻¹), Sherman ($R_0 = 51.004$ fish·ha⁻¹), and Grindstone ($R_0 = 39.135$ fish·ha⁻¹) lakes would yield the highest optimal harvests, whereas low productivity lakes, such as Annabelle ($R_0 = 3.441$ fish·ha⁻¹), Squaw ($R_0 = 5.208$ fish·ha⁻¹), and Siskiwit ($R_0 = 6.318$ fish·ha⁻¹) lakes would provide the lowest optimal harvests, which is evident from our results showing probabilities of population collapse for individual lakes under various exploitation rates (Table 7).

Discussion

Hierarchical Bayesian meta-analysis has been used in a number of fisheries management applications as a means of making efficient use of uninformative data in the estimation of population dynamics parameters (Chen and Holtby 2002; Michielsens and McAllister 2004; Forrest et al. 2010). We expanded upon previous approaches by applying a hierarchical Bayesian meta-analysis with alternative prior distributional assumptions to identify an appropriate model

to describe population and fishery dynamics of walleye in multiple lakes in the Ceded Territory of northern Wisconsin. Although time-series demographic data were available for walleye in numerous lakes in northern Wisconsin, data sets for many of the lakes were not informative enough or did not provide sufficient contrast to accurately describe walleye population dynamics, especially their recruitment dynamics, resulting in unrealistic estimates of stock–recruitment relationships for several lakes. In contrast, by accounting for an assumed underlying similarity (Myers et al. 2001; Gelman et al. 2004) between lakes (which is plausible given the broad-scale biological, environmental, and anthropogenic factors affecting recruitment dynamics in individual lakes (Beard et al. 2003a)), a hierarchical Bayesian model allowed us to obtain biologically reasonable combinations of α and β for stock–recruitment curves that still fit observed data very well. As such, our results highlight that in contrast to models fit to individual lakes separately, assuming they share no similarities, and models that pool all the data, assuming all lakes are identical, hierarchical models combine “the best of both worlds” by modeling lakes’ similarities but also allowing estimation of individual parameters. Additionally, by considering alternative prior distributions, we were at the same time able to ensure that parameter values were primarily influenced by data; thus, our modeling framework accommodated possible skewness and excess variability among parameters and has not caused over-shrinkage of parameter estimates toward average values. This was also evident from our lake-specific estimates of unfished equilibrium recruitment (R_0) and adult abundance that reflected the observed recruitment data for individual lakes. Further, by comparing parameter estimates for individual lakes from the hierarchical analysis including and excluding Escanaba Lake, we showed that that lake-specific parameter estimates were not strongly influenced by the relatively

larger amount of data from Escanaba Lake (results not shown), suggesting lake-specific parameters were not pulled toward the regional average values.

In view of the above, we believe that the hierarchical approach allowed us to obtain more accurate posterior distributions of stock–recruitment parameters, natural mortalities, maturity and selectivity schedules, and growth parameters for individual lakes and to characterize the variability in population productivity among lakes. Given the estimated posterior distributions for the entire set of population and fishery parameters, it was possible for us to build a whole-population forecasting model that accounted for uncertainty in all input parameters, one that allowed us to evaluate the sustainability of alternative recreational and tribal harvest policies regionally and in individual lakes in the Ceded Territory of northern Wisconsin. Besides providing improved parameter estimates for individual lakes, our hierarchical Bayesian analysis provided regional posterior distributions of parameter estimates representing multiple walleye populations that can be used as priors in future assessments of walleye or similar populations in other lakes (i.e., posterior predictive distribution), especially when available data are uninformative.

While our hierarchical meta-analysis of the population dynamics of walleye in northern Wisconsin lakes showed that productivities (particularly, stock–recruitment relationships) and associated optimal harvest rates varied among lakes, the estimated optimal exploitation rates (with a median of 20%) are within the range of those estimated for other walleye populations in North America, i.e., a median of 21% and a maximum of about 56% (Baccante and Colby 2003). Our estimates were also similar to those of Lester et al. (2014), which suggested that sustainable exploitation rates for walleye should be about $0.75 \cdot M$. Given our regional estimate of $M = 0.24$ across all age classes, Lester et al. (2014) would predict an optimal exploitation rate of 18% for

northern Wisconsin walleye populations. A recent analysis of walleye production and exploitation on Escanaba Lake also suggested that annual exploitation rates $> 20\%$ reduced surplus production (Rypel et al. 2015). Further, our estimates of mean optimal exploitation rates were similar to those suggested in previous studies of walleyes in Wisconsin, including Staggs et al. (1990) and Hansen et al. (1991). On the other hand, Schueller et al. (2008) concluded that an exploitation rate of 35% may be the most optimal for the walleye populations; however, their prediction was based on probability of population collapse.

Our estimates of optimal exploitation rates are also in concordance with existing walleye harvest policy in northern Wisconsin, which aims to ensure that total exploitation rate does not exceed 35% of the adult population in more than 1 out of 40 occasions (Beard et al. 2003b). However, walleye populations in these lakes are generally exploited at lower rates; adult walleye exploitation calculated as the sum of angling and spearing exploitation rates averaged about 13%, with only four out of 210 lakes (1.9%) sampled during 1990–1998 having experienced total exploitation rates that exceeded 35% (Beard et al. 2003b). However, these exploitation rates are lower than those found for walleye in other North American lakes (Baccante and Colby 2003), although some of the differences among the exploitation rates in our study and others could be the result of differences in how exploitation rates were calculated. For example, Serns and Kempinger (1981) calculated exploitation rates assuming age-3 and older walleye were fully vulnerable to fishing, while our study used exploitation rates as a proportion of adult walleye only. Yet, even if most northern Wisconsin lakes are typically exploited below the predicted optimal exploitation rate, managing the walleye populations in these lakes under the same harvest policy may not necessarily result in optimal yields given the variability in walleye productivity among these lakes. Thus, walleye management policies for northern Wisconsin

lakes should account for the variability in productivity among lakes when formulating mismanagement policies. Ignoring the variability among these populations may lead to high-risk management strategies being adopted for the least productive lakes, such as Squaw and Siskiwit lakes. Conversely, assuming the same optimal exploitation rate for all lakes may lead to under-exploitation of the most productive lakes, such as Escanaba, Sherman, Middle Eau Claire, and Grindstone lakes.

Our results suggest that the walleye fisheries would perform better under size-selective harvest policies in which only the largest age classes are vulnerable to fishing (lower probability of collapse; higher SSB) (Fig 4). This is not surprising because delaying the age at entry of fish to the harvestable population reduces the risk of overexploitation by allowing fish to mature and spawn prior to harvest (Frisk et al. 2002). Even though it would result in suboptimal harvests, the walleye population was predicted to sustain exploitation rates over 35% under a 38 cm minimum length limit for the recreational fishery. This implies that under highly size-selective harvest policies, it may not be necessary to control exploitation rates, and the fishery can be left to self-regulate. Indeed, inland fisheries managers generally rely on passive regulations, such as bag and length limits, to regulate fisheries (Beard et al. 2003b; Post et al. 2002). However, recent evidence suggests that self-regulation may not always maintain exploitation rates at sustainable levels and a precautionary approach should be used to manage recreational fisheries (Radomski et al. 2001; Cox et al. 2002; Allen et al. 2013).

Our results indicated that current Ceded Territory management policies (1 in 40 maximum acceptable risk of exploitation rates exceeding 35%) and size-selectivity in the recreational fishery are likely sufficient to sustain walleye populations in many northern Wisconsin lakes, but not in all of them, suggesting the need for lake-specific management

policies. However, with hundreds of lakes in northern Wisconsin that differ in ecosystem characteristics, responsive lake-specific walleye management in the Ceded Territory may be infeasible. Instead, regionally conservative management policies could be implemented to avoid overexploitation in certain populations (low walleye productivity systems) at the expense of some populations being potentially underexploited (high walleye productivity systems). Under the “adult exploitation $\leq 35\%$ ” management system, mean adult density and age-0 walleye relative abundance declined significantly in the Ceded Territory during 1990–2011 (Hansen et al. 2015), and mean adult walleye densities are now below the desired goal of ≥ 7.4 fish·ha⁻¹ for naturally reproducing walleye populations in the Ceded Territory (U.S. Department of the Interior 1991). These negative trends in adult densities and walleye recruitment further suggest that a conservative regional approach is needed for Ceded Territory walleye management. Considering our estimates of regional optimal exploitation rates and the variability in productivity among lakes, a reduction in the Ceded Territory of Wisconsin total allowable catch walleye exploitation rate from $\leq 35\%$ to about 20% may ensure optimal sustainable yields for most of the lakes in this tribally and recreationally important fishery. This is also reasonable considering the estimates of Lester et al. (2014) and Rypel et al. (2015), and the experimental fishing studies on Big Crooked and Sherman lakes (Schueller et al. 2005; Schmalz et al. 2011; G.G. Sass unpublished data).

Although our results could be used to guide walleye management policies, future research could expand on our analysis of variability in life-history characteristics among northern Wisconsin lakes. Variability in life history characteristics among populations is of critical interest to population ecologists aiming not only to understand the inherent within-species variability, but also to explore potential environmental covariates explaining variability in life

history characteristics (Myers et al. 2001; Helser and Lin 2004). Although they did not use a hierarchical modeling approach, Beard et al. (2003a) analyzed data from 162 northern Wisconsin lakes during 1990–1999 to develop a regional stock–recruitment model for walleye and identified density-independent factors explaining variability in recruitment, including temperature (as represented by calendar year) and yellow perch density. Their findings were similar to those of other studies on walleye stock–recruitment relationships (e.g., Madenjian et al. 1996; Hansen et al. 1998). Similarly, Sass and Kitchell (2005) found strong correlations between walleye growth and surrogate measures of lake productivity. Therefore, a logical next step to our study would be to explore potential relationships between our estimates of lake-specific population parameters and environmental covariates identified by Beard et al. (2003a), Sass and Kitchell (2005), and others. Identifying variance components associated with density-independent effects on lake productivity may help explain variability in stock–recruitment and other population parameters among lakes and can lead to improved parameter estimation with relatively low error. Similarly, (Hanson et al., 2004), accounting for density-independent covariates may help explain inter-annual variability in recruitment for individual lakes, especially persistent change or “nonstationarity” in recruitment dynamics (Walters and Martell, 2004). In this regard, accounting for temporal autocorrelation may be expected to explain some of the inter-annual variability in recruitment, but our *post hoc* analysis of serial-autocorrelation of recruitment residuals showed that temporal autocorrelation (estimated to be about 0.05 on average for individual lakes) did not account for a large amount of variability in annual recruitment.

Though the parameter estimates for walleye populations in northern Wisconsin from our hierarchical meta-analysis may be generally more realistic than estimates from independent

analyses, alternative model assumptions (i.e., observation and/or process submodel hypotheses) can be considered to minimize potential bias regarding some aspects of our assessment. Particularly, while some population parameters are potentially correlated, we assumed that all parameters were independent except for the Ricker α and β , and this may have led to some bias in our estimates. For example, growth parameters L_{∞} and K are generally known to be negatively correlated among fishes (Helser and Lin 2004). Therefore, accounting for these correlations may lead to somewhat better estimates. Further, our age-structured model did not track population numbers over time, but pooled together age composition data over time. Although it would be computationally more expensive, developing a full hierarchical Bayesian statistical catch-at-age model that accounts for these and other potential correlations could lead to more accurate representations of the dynamics of walleye populations in northern Wisconsin lakes. Finally, aging bias may occur due to the use of scales and dorsal fin spines instead of otoliths, pointing to the need to apply an aging error correction matrix. However, Koenigs et al. (2013) suggested that there is minimal difference between otoliths and dorsal spines in aging older age classes. In addition, any potential age estimation bias associated with the Wisconsin Ceded Territory's walleye sampling protocols, which have been in place since 1990, would only be significant for the older age classes (e.g., ages 10+), and thus would have negligible effects on our estimates of natural mortality; based on our age composition data, these age classes comprise a very low proportion of total walleye densities. Finally, while we selected the best model to represent walleye dynamics in the Ceded Territory using DIC results and MCMC diagnostics, alternatively we may use multi-model averaging using DIC weights to make inferences based on all candidate models that fit the data well enough to appear plausible. However, because the difference in DIC between the best model and alternative models is greater than 10, DIC weights would be close to

1 for the best selected model (Burnham and Anderson 2002). In addition, Wilberg and Bence (2008) showed using simulations that DIC usually selected the structurally most appropriate model and that estimates based on the selected model and on model averaging were almost equally unbiased. Either way, given that our model estimates were not very sensitive to assumptions on priors, we anticipate that inferences made based on model averaging would not be very different from those based on the best selected model.

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References

- ADMB Project. 2013. Random Effects in AD Model Builder: ADMB-RE User Guide. ADMB Foundation, Honolulu, Hawaii.
- Allen, M.S., Ahrens, R.N.M., Hansen, M.J., and Arlinghaus, R. 2013. Dynamic angling effort influences the value of minimum-length limits to prevent recruitment overfishing. *Fish. Manag. Ecol.* **20**(2-3): 247–257.
- Baccante, D.A., and Colby. 2003. Harvest, density and reproductive characteristics of North American walleye populations. *Ann. Zool. Fennici* **33**: 601–615.
- Beard, T.D., Hansen, M.J., and Carpenter, S.R. 2003a. Development of a regional stock–recruitment model for understanding factors affecting walleye recruitment in northern Wisconsin lakes. *Trans. Am. Fish. Soc.* **132**(2): 382–391.
- Beard, T.D., Rasmussen, P.W., Cox, S., and Carpenter, S.R. 2003b. Evaluation of a management system for a mixed walleye spearing and angling fishery in northern Wisconsin. *N. Am. J. Fish. Manage.* **23**(2): 481–491.
- Beddington, J.R., and Cooke, J.G. 1983. The Potential yield of fish stocks. FAO Fish. Tech. Pap., Rome, Italy.
- Burnham, K.P., and Anderson, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. 2nd ed. Springer, New York.
- Chen, D.G., and Holtby, L.B. 2002. A regional meta-model for stock–recruitment analysis using an empirical Bayesian approach. *Can. J. Fish. Aquat. Sci.* **59**(9): 1503–1514.
- Cichosz, T.A. 2012. Wisconsin Department of Natural Resources 2010-2011 Ceded Territory Fishery Assessment Report. Annual report, Department of Natural Resources, Bureau of Fisheries Management, Madison, Wisconsin.

- 823 Conn, P.B., Williams, E.H., and Shertzer, K.W. 2010. When can we reliably estimate the
824 productivity of fish stocks? Can. J. Fish. Aquat. Sci. **67**(3): 511–523.
- 825 Cox, S.P., Beard, T.D., and Walters, C. 2002. Harvest control in open-access sport fisheries: hot
826 rod or asleep at the reel? Bull. Mar. Sci. **70**(2): 749–761.
- 827 Deriso, R.B., Quinn II, T.J., and Neal, P.R. 1985. Catch-Age Analysis with Auxiliary
828 Information. Can. J. Fish. Aquat. Sci. **42**(4): 815–824.
- 829 Evans, M., Hastings, N., and Peacock, B. 2000. Statistical Distributions, 3rd edition. Wiley and
830 Sons, New York.
- 831 Forrest, R.E., McAllister, M.K., Dorn, M.W., Martell, S.J.D., and Stanley, R.D. 2010.
832 Hierarchical Bayesian estimation of recruitment parameters and reference points for
833 Pacific rockfishes (*Sebastes* spp.) under alternative assumptions about the stock–recruit
834 function. Can. J. Fish. Aquat. Sci. **67**(10): 1611–1634.
- 835 Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen, A.,
836 and Sibert, J. 2012. AD Model Builder: using automatic differentiation for statistical
837 inference of highly parameterized complex nonlinear models. Optim. Meth. Softw. **27**:
838 233–249.
- 839 Frisk, M.G., Miller, T.J., and Fogarty, M.J. 2002. The population dynamics of little skate
840 *Leucoraja erinacea*, winter skate *Leucoraja ocellata*, and barndoor skate *Dipturus laevis*:
841 predicting exploitation limits using matrix analyses. ICES J. Mar. Sci. **59**(3): 576–586.
- 842 Gelman, A., Carlin, J.B., Stern, H.S., and Rubin, D.B. 2004. Bayesian Data Analysis. In 2nd
843 edition. Chapman and Hall/CRC.

- 844 Geweke, J. 1992. Evaluating the accuracy of sampling-based approaches to the calculation of
845 posterior moments. *In* Bayesian Statistics. *Edited by* J.M. Bernardo, J.O. Berger, A.P.
846 Dawid, and A.F.M. Smith. Oxford University Press, Oxford, UK. pp. 169–193.
- 847 Gibson, F., and Myers, R.A. 2003. A meta-analysis of the habitat carrying capacity and
848 maximum reproductive rate of anadromous alewife in eastern North America. *In* Status
849 and conservation of shads worldwide; Biodiversity, status, and conservation of the
850 world's shads. American Fisheries Society. pp. 211–222.
- 851 Hansen, G.J.A., Carpenter, S.R., Gaeta, J.W., Hennessy, J.M., Vander Zanden, M.J., and
852 Tierney, K. 2015. Predicting walleye recruitment as a tool for prioritizing management
853 actions. *Can. J. Fish. Aquat. Sci.* **72**(5): 661–672.
- 854 Hansen, J.F., Sass, G.G., Gaeta, J.W., Hansen, G.A., Isermann, D.A., Lyons, J., and Vander
855 Zanden, M.J. 2015. Largemouth bass management in Wisconsin: intra- and inter-specific
856 implications of abundance increases. *In* Proceedings of the Black Bass Diversity:
857 Multidisciplinary Science for Conservation Symposium. American Fisheries Society,
858 Bethesda, MD. pp. 31–50.
- 859 Hansen, M.J., Beard, T.D., and Hewett, S.W. 2000. Catch rates and catchability of walleyes in
860 angling and spearing fisheries in northern Wisconsin lakes. *N. Am. J. Fish. Manage.*
861 **20**(1): 109–118.
- 862 Hansen, M.J., Bozek, M.A., Newby, J.R., Newman, S.P., and Staggs, M.D. 1998. Factors
863 affecting recruitment of walleyes in Escanaba Lake, Wisconsin, 1958–1996. *N. Am. J.*
864 *Fish. Manage.* **18**(4): 764–774.

- 865 Hansen, M.J., Fayram, A.H., and Newman, S.P. 2011. Natural mortality in relation to age and
866 fishing mortality on walleyes in Escanaba Lake, Wisconsin, during 1956–2009. N. Am. J.
867 Fish. Manage. **31**(3): 506–514.
- 868 Hansen, M.J., Newman, S.P., and Edwards, C.J. 2004. A reexamination of the relationship
869 between electrofishing catch rate and age-0 walleye density in northern Wisconsin lakes.
870 N. Am. J. Fish. Manage. **24**(2): 429–439.
- 871 Hansen, M.J., Staggs, M.D., and Hoff, M.H. 1991. Derivation of safety factors for setting harvest
872 quotas on adult walleyes from past estimates of abundance. Trans. Am. Fish. Soc. **120**(5):
873 620–628.
- 874 He, J.X., and Bence, J.R. 2007. Modeling Annual Growth Variation using a Hierarchical
875 Bayesian Approach and the von Bertalanffy Growth Function, with Application to Lake
876 Trout in Southern Lake Huron. Transactions of the American Fisheries Society **136**(2):
877 318–330.
- 878 He, J.X., Bence, J.R., Johnson, J.E., Clapp, D.F., and Ebener, M.P. 2008. Modeling variation in
879 mass-length relations and condition indices of lake trout and Chinook salmon in Lake
880 Huron: A hierarchical Bayesian approach. Trans. Am. Fish. Soc. **137**(3): 801–817.
- 881 Helser, T.E., and Lin, H. 2004. A Bayesian hierarchical meta-analysis of fish growth: with an
882 example for North American largemouth bass, *Micropterus salmoides*. Ecol. Model. **178**:
883 399–416.
- 884 Koenigs, R.P., Bruch, R.M., and Kamke, K.K. 2013. Impacts of Aging Error on Walleye
885 Management in the Winnebago System. North American Journal of Fisheries
886 Management **33**(5): 900–908.

- 887 Lee, H.-H., Maunder, M.N., Piner, K.R., and Methot, R.D. 2012. Can steepness of the stock–
888 recruitment relationship be estimated in fishery stock assessment models? *Fish. Res.*
889 **125–126**: 254–261.
- 890 Lester, N.P., Shuter, B.J., Venturelli, P., and Nadeau, D. 2014. Life-history plasticity and
891 sustainable exploitation: a theory of growth compensation applied to walleye
892 management. *Ecol. Appl.* **24**(1): 38–54.
- 893 Madenjian, C.P., Tyson, J.T., Knight, R.L., Kershner, M.W., and Hansen, M.J. 1996. First-year
894 growth, recruitment, and maturity of walleyes in western Lake Erie. *Trans. Am. Fish.*
895 *Soc.* **125**(6): 821–830.
- 896 Magnusson, A., and Hilborn, R. 2007. What makes fisheries data informative? *Fish. Fish.* **8**(4):
897 337–358.
- 898 Maunder, M.N. 2003. Paradigm Shifts in Fisheries Stock Assessment: From Integrated Analysis
899 to Bayesian Analysis and Back Again. *Nat. Resour. Model.* **16**(4): 465–475.
- 900 Maunder, M.N., and Deriso, R.B. 2003. Estimation of recruitment in catch-at-age models. *Can. J.*
901 *Fish. Aquat. Sci.* **60**(10): 1204–1216.
- 902 Maunder, M.N., and Piner, K.R. 2015. Contemporary fisheries stock assessment: many issues
903 still remain. *ICES J. Mar. Sci.* **72**(1): 7–18.
- 904 Meyer, R., and Millar, R.B. 1999. BUGS in Bayesian stock assessments. *Can. J. Fish. Aquat.*
905 *Sci.* **56**(6): 1078–1087.
- 906 Michielsens, C.G., and McAllister, M.K. 2004. A Bayesian hierarchical analysis of stock–recruit
907 data: quantifying structural and parameter uncertainties. *Can. J. Fish. Aquat. Sci.* **61**(6):
908 1032–1047.

- 909 Millar, R.B., and Methot, R.D. 2002. Age-structured meta-analysis of U.S. West Coast rockfish
910 (Scorpaenidae) populations and hierarchical modeling of trawl survey catchabilities. *Can.*
911 *J. Fish. Aquat. Sci.* **59**(2): 383–392.
- 912 Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rate of fish at
913 low population sizes. *Can. J. Fish. Aquat. Sci.* **56**(12): 2404–2419.
- 914 Myers, R.A., MacKenzie, B.R., Bowen, K.G., and Barrowman, N.J. 2001. What is the carrying
915 capacity for fish in the ocean? A meta-analysis of population dynamics of North Atlantic
916 cod. *Can. J. Fish. Aquat. Sci.* **58**: 1464–1476.
- 917 Myers, R.A., Smith, M.W., Hoenig, J.M., Kmiecik, N., Luehring, M.A., Drake, M.T., Schmalz,
918 P.J., and Sass, G.G. 2014. Size- and sex-specific capture and harvest selectivity of
919 walleyes from tagging studies. *Trans. Am. Fish. Soc.* **143**(2): 438–450.
- 920 Nate, N.A., Bozek, M.A., Hansen, M.J., and Hewett, S.W. 2000. Variation in walleye abundance
921 with lake size and recruitment source. *N. Am. J. Fish. Manage.* **20**(1): 119–126.
- 922 Nate, N.A., Bozek, M.A., Hansen, M.J., and Hewett, S.W. 2001. Variation of adult walleye
923 abundance in relation to recruitment and limnological variables in northern Wisconsin
924 lakes. *N. Am. J. Fish. Manage.* **21**(3): 441–447.
- 925 Pilling, G.M., Kirkwood, G.P., and Walker, S.G. 2002. An improved method for estimating
926 individual growth variability in fish, and the correlation between von Bertalanffy growth
927 parameters. *Can. J. Fish. Aquat. Sci.* **59**(3): 424–432.
- 928 Plummer, M., Best, N., Cowles, K., and Vines, K. 2010. Output analysis and diagnostics for
929 MCMC, R package version 0.14-2. Available: [CRAN.Rproject.org/package = coda](http://CRAN.Rproject.org/package=coda).

- 930 Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson,
931 L., and Shuter, B.J. 2002. Canada's recreational fisheries: the invisible collapse?
932 Fisheries **27**(1): 6–17.
- 933 Radomski, P.J., Grant, G.C., Jacobson, P.C., and Cook, M.F. 2001. Visions for recreational
934 fishing regulations. Fisheries **26**(5): 7–18.
- 935 Rypel, A.L., Goto, D., Sass, G.G., and Vander Zanden, M.J. 2015. Production rates of walleye
936 and their relationship to exploitation in Escanaba Lake, Wisconsin, 1965–2009. Can. J.
937 Fish. Aquat. Sci. **72**(6): 834–844.
- 938 Sass, G.G., and Kitchell, J.F. 2005. Can growth be used as a surrogate measure of walleye
939 (*Sander vitreus*) abundance change? Can. J. Fish. Aquat. Sci. **62**(9): 2159–2168.
- 940 Schmalz, P.I., Fayram, A.H., Isermann, D.A., Newman, S.P., and Edwards, C.J. 2011. Harvest
941 and exploitation. In Biology, Management, and Culture of Walleye and Saugeulture.
942 Edited by B.A. Barton. American Fisheries Society, Bethesda, MD. pp. 375–401.
- 943 Schueller, A.M., Fayram, A.H., and Hansen, M.J. 2012. Simulated equilibrium walleye
944 population density under static and dynamic recreational angling effort. N. Am. J. Fish.
945 Manage. **32**(5): 894–904.
- 946 Schueller, A.M., Hansen, M.J., and Newman, S.P. 2008. Modeling the sustainability of walleye
947 populations in northern Wisconsin lakes. N. Am. J. Fish. Manage. **28**(6): 1916–1927.
- 948 Schueller, A.M., Hansen, M.J., Newman, S.P., and Edwards, C.J. 2005. Density dependence of
949 walleye maturity and fecundity in Big Crooked Lake, Wisconsin, 1997–2003. N. Am. J.
950 Fish. Manage. **25**(3): 841–847.
- 951 Serns, S.L., and Kempinger, J.J. 1981. Relationship of angler exploitation to the size, age, and
952 sex of walleyes in Escanaba Lake, Wisconsin. Trans. Am. Fish. Soc. **110**(2): 216–220.

- 953 Spiegelhalter, D.J., Best, N.G., Carlin, B.P., and Van Der Linde, A. 2002. Bayesian measures of
954 model complexity and fit. *J. R. Stat. Soc. Ser. B* **64**(4): 583–639.
- 955 Staggs, M.D., Moody, M.H., Hansen, M.J., and Hoff, M.H. 1990. Spearing and sport angling for
956 walleye in Wisconsin's ceded territory. Administrative Report, Department of Natural
957 Resources, Bureau of Fisheries Management, Madison, Wisconsin.
- 958 Su, Z., and Peterman, R.M. 2012. Performance of a Bayesian state-space model of semelparous
959 species for stock–recruitment data subject to measurement error. *Ecological Modelling*
960 **224**(1): 76–89.
- 961 Tsehaye, I., Catalano, M., Sass, G., Glover, D., and Roth, B. 2013. Prospects for Fishery-Induced
962 Collapse of Invasive Asian Carp in the Illinois River. *Fisheries* **38**(10): 445–454.
- 963 U.S. Department of the Interior. 1991. Casting light upon the waters: a joint fishery assessment
964 of the Wisconsin Ceded Territory. Bureau of Indian Affairs, Minneapolis, Minnesota.
- 965 Walters, C.J., and Martell, S.J.D. 2004. *Fisheries Ecology and Management*. Princeton
966 University Press, Princeton, New Jersey.
- 967 Walters, C., and Kitchell, J.F. 2001. Cultivation/depensation effects on juvenile survival and
968 recruitment: implications for the theory of fishing. *Can. J. Fish. Aquat. Sci.* **58**(1): 39–50.
- 969 Wilberg, M.J., Bence, J.R., 2008. Performance of deviance information criterion model selection
970 in statistical catch-at-age analysis. *Fish. Res.* **93**, 212–221.
- 971 Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J.,
972 Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M.,
973 McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A.,
974 Watson, R., and Zeller, D. 2009. Rebuilding global fisheries. *Science* **325**(5940): 578–
975 585.
- 976

- 977 Table 1. List of parameters and variables used in the hierarchical Bayesian meta-analysis of
 978 northern Wisconsin walleye (*Sander vitreus*) population dynamics.

<i>Symbol</i>	<i>Description</i>
<i>Index variables</i>	
i	Lake
t	Year
j	Individual fish
a	Age
<i>Parameters and derived quantities</i>	
N	Abundance at the beginning of the year
R	Predicted number of recruits
$\hat{R}$	Observed number of recruits
S	Predicted spawning stock
$\hat{S}$	Observed spawning stock
α	Recruits per spawner at low stock size
β	Degree of compensation
ω	Deviations in annual recruitment
σ_R	Standard deviation of inter-annual recruitment variability
ν	Spawning stock measurement error
σ_S	Standard deviation of measurement error for spawning stock
$\overline{\alpha}$	Median α
$\overline{\beta}$	Mean β
ε_α	Process error for α
ε_β	Process error for β
Σ	Variance-covariance matrix between ε_α and ε_β
ε_{σ_R}	Process error for σ_R
σ_{σ_R}	Standard deviation of ε_{σ_R}
L	Length of fish
K	Growth coefficient
t_0	Time at zero length
L_∞	Asymptotic length
ζ	Individual variation in length-at-age
σ_L	Standard deviation of ζ
$\overline{L_\infty}$	Median L_∞
$\overline{K}$	Median K
$\overline{t_0}$	Mean t_0
ε_{L_∞}	Process error for L_∞
ε_K	Process error for K

ε_{t_0}	Process error for t_0
σ_{L_∞}	Standard deviation of ε_{L_∞}
σ_K	Standard deviation of ε_K
σ_{t_0}	Standard deviation of ε_{t_0}
V^{spear}	Tribal spearing selectivity/maturation probability
V^{rec}	Recreational angling selectivity
h	Slope of the logistic selectivity/maturation function
m	Age at 50% maturity/vulnerability
$\bar{h}$	Median h
$\bar{m}$	Median m
ε_h	Process error for h
ε_m	Process error for m
σ_h	Standard deviation of ε_h
σ_m	Standard deviation of ε_m
V^{rec}	Angling selectivity
F	Instantaneous fishing mortality
u_s	Spearing exploitation rate
u_r	Angling exploitation rate
M	Instantaneous natural mortality (yr^{-1})
$\bar{M}$	Median natural mortality
Z	Total instantaneous mortality rate (yr^{-1})
ε_M	Process error for M
σ_M	Standard deviation of ε_M
N^{mat}	Number of mature fish at age
$\text{tot}N^{\text{mat}}$	Total number of mature fish
P	Predicted proportion of mature fish at age
$\hat{P}$	Observed proportion of mature fish at age
n	Effective sample size
α'	Shape parameter for inverse-gamma distribution
β'	Scale parameter for inverse-gamma distribution
R_0	Recruitment at unfished equilibrium
SPR	Spawners per recruit in the absence of fishing
DIC	Deviance information criterion
$\bar{D}$	Average deviance, measuring model fit
p_D	Effective number of parameters
C	Number of MCMC samples saved minus burn-in
θ	All estimated parameters
$D(\bar{\theta})$	Deviance evaluated at the HPD parameter estimates

980 Table 2. Ricker stock–recruitment parameters (and associated % asymptotic coefficients of
 981 variation) for northern Wisconsin walleye (*Sander vitreus*) estimated for individual lakes
 982 independently; the regional values were calculated by excluding lakes with unreasonably large α
 983 and negative β . Number of years of data used in estimating stock–recruitment parameters are
 984 shown for each lake.

Lake	Years of data	α	β	σ
Regional	–	9.88	0.29	2.15
Butternut (Forest)*	23	19.46 (133.72)	0.29 (52.38)	3.04 (14.74)
Franklin	6	5.91 (125.30)	0.35 (56.13)	1.98 (28.87)
Bearskin	10	0.09 (183.01)	–0.11 (67.78)	2.17 (22.36)
Squirrel	24	0.19 (149.54)	–0.17 (68.63)	1.66 (14.43)
Big Arbor Vitae	7	9.86 (243.68)	0.13 (113.08)	1.56 (26.73)
Pelican	8	6.09 (261.92)	0.38 (86.20)	3.52 (25.00)
Big St Germain	6	16.12 (545.42)	0.36 (182.03)	4.58 (28.87)
Plum	7	21.32 (0.57)	0.18 (18.33)	1.3 (26.73)
Star	7	312.46 (0.07)	0.44 (30.02)	1.64 (26.73)
North Twin	6	10493.93 (0.06)	1.29 (44.67)	1.9 (28.87)
Lac Vieux Desert	7	14.12 (685.67)	0.65 (185.94)	2.9 (26.73)
Sherman	18	18.09 (98.91)	0.12 (80.08)	1.99 (16.67)
Squaw	22	0.5 (127.07)	–0.04 (340.54)	1.68 (15.08)
Butternut (Price)*	6	5.31 (218.68)	0.14 (144.40)	1.97 (28.87)
Wolf	16	1.82 (263.00)	0.04 (374.31)	3.17 (17.68)
Big Crooked	21	0.86 (134.92)	0 (9349.02)	3.98 (15.43)
Escanaba	46	6.64 (41.55)	0.03 (41.29)	1.4 (10.43)
Grindstone	6	137.95 (0.03)	0.6 (38.98)	1.16 (28.87)
Round	6	3.84 (129.63)	0.05 (488.74)	1.44 (28.87)
Bass Patterson	18	15.94 (82.09)	0.14 (38.66)	1.67 (16.67)
Lower Eau Claire	6	0.28 (283.71)	–0.21 (179.54)	2.63 (28.87)
Middle Eau Claire	7	3.05 (117.04)	–0.08 (127.43)	0.83 (26.73)
Siskiwit	17	1.57 (65.71)	0.08 (77.42)	1.78 (17.15)
Pine	7	18.09 (279.25)	0.23 (77.05)	2.35 (26.73)
Annabelle	9	2.84 (108.83)	0.14 (95.05)	1.46 (23.57)

985 *These two lakes with the same name are differentiated by the county where they are located.

Table 3. Highest posterior density (HPD) estimates and lower and upper 95% Bayesian credible limits of regional and lake-specific Ricker stock–recruitment parameters for northern Wisconsin walleye (*Sander vitreus*) populations estimated using the base (LNN–InvG) model.

Lake	α	β	σ
Regional	2.768 (1.366, 4.761)	0.049 (0.002, 0.103)	1.964 (1.931, 2.643)
Butternut (Forest)	2.731 (0.775, 5.495)	0.049 (−0.005, 0.120)	2.401 (2.208, 3.534)
Franklin	2.059 (0.413, 5.064)	0.057 (−0.004, 0.139)	1.881 (1.452, 3.015)
Bearskin	3.312 (0.702, 6.406)	0.045 (0.000, 0.075)	1.973 (1.591, 2.962)
Squirrel	2.988 (1.082, 5.284)	0.047 (0.000, 0.090)	1.813 (1.398, 2.352)
Big Arbor Vitae	2.719 (0.687, 5.524)	0.050 (0.000, 0.102)	1.787 (1.278, 2.456)
Pelican	1.643 (0.312, 4.619)	0.062 (−0.005, 0.146)	2.203 (1.989, 3.671)
Big St Germain	2.292 (0.363, 5.708)	0.054 (−0.006, 0.123)	2.254 (2.164, 3.783)
Plum	3.733 (0.949, 8.084)	0.041 (−0.006, 0.088)	1.759 (1.154, 2.517)
Star	3.548 (0.896, 7.456)	0.043 (−0.005, 0.097)	1.861 (1.357, 2.976)
North Twin	3.261 (0.668, 7.447)	0.045 (−0.009, 0.113)	2.101 (1.862, 3.646)
Lac Vieux Desert	1.777 (0.362, 4.901)	0.060 (−0.004, 0.144)	2.362 (2.301, 3.828)
Sherman	5.231 (1.637, 10.080)	0.033 (−0.006, 0.072)	1.844 (1.423, 2.541)
Squaw	1.674 (0.542, 3.980)	0.062 (−0.001, 0.150)	1.757 (1.346, 2.235)
Butternut (Price)	2.514 (0.463, 5.260)	0.052 (−0.005, 0.115)	1.838 (1.348, 3.213)
Wolf	2.285 (0.679, 4.923)	0.054 (−0.001, 0.127)	2.263 (2.043, 3.602)
Big Crooked	2.003 (0.579, 4.725)	0.057 (0.000, 0.123)	2.304 (2.096, 3.413)
Escanaba	6.046 (1.800, 11.860)	0.029 (0.003, 0.052)	1.612 (1.212, 1.887)
Grindstone	4.192 (0.937, 10.360)	0.039 (−0.004, 0.098)	1.854 (1.365, 2.901)
Round	3.111 (0.786, 6.687)	0.046 (−0.004, 0.107)	1.791 (1.140, 2.477)
Bass Patterson	3.484 (1.143, 6.504)	0.043 (0.000, 0.084)	1.818 (1.458, 2.446)
Lower Eau Claire	2.461 (0.517, 5.359)	0.052 (−0.006, 0.124)	1.921 (1.487, 3.111)
Middle Eau Claire	5.014 (1.146, 11.500)	0.034 (−0.020, 0.071)	1.772 (1.159, 2.553)
Siskiwit	1.749 (0.528, 4.116)	0.061 (0.000, 0.141)	1.728 (1.223, 2.363)
Pine	2.018 (0.404, 4.756)	0.057 (0.000, 0.131)	1.924 (1.489, 2.960)
Annabelle	2.077 (0.508, 4.541)	0.057 (−0.007, 0.136)	1.781 (1.261, 2.364)

991 Table 4. Median recruitment at unfished equilibrium, R_0 , (fish·ha⁻¹) of northern Wisconsin
 992 walleye (*Sander vitreus*) under alternative assumptions of prior distributions for α , β and σ , and
 993 average pairwise Geweke's (1992) Z-scores for R_0 to test for similarity in R_0 estimates among
 994 models; at the bottom are average Geweke's (1992) Z-scores for α , β , and σ to test for similarity
 995 of the first 10% and the last 50% of MCMC samples within a given model, including DIC
 996 values.

Lake	R_0				R_0 Z-score
	LNN-InvG	LNLN-InvG	LNN	LNLN	
Regional	20.147	20.907	22.143	23.211	1.334
Butternut (Forest)	20.071	20.241	21.460	22.241	1.964
Franklin	13.374	13.269	15.523	15.869	1.386
Bearskin	25.672	25.689	25.204	25.151	0.356
Squirrel	21.115	21.412	21.655	21.853	0.118
Big Arbor Vitae	13.633	13.585	14.279	13.804	0.044
Pelican	7.851	7.122	10.120	9.715	0.043
Big St Germain	15.244	15.431	18.029	18.805	0.595
Plum	31.631	32.965	35.037	36.702	1.949
Star	25.808	26.514	26.507	27.243	1.032
North Twin	17.614	18.119	16.435	16.854	0.772
Lac Vieux Desert	6.728	6.356	12.586	12.606	2.264
Sherman	51.004	52.008	51.524	52.609	1.206
Squaw	5.208	5.076	4.748	4.466	1.695
Butternut (Price)	16.489	16.844	17.951	18.450	1.664
Wolf	14.702	14.899	16.421	16.868	1.907
Big Crooked	12.424	12.462	14.151	14.389	1.110
Escanaba	70.714	70.060	71.633	71.183	1.437
Grindstone	39.135	40.927	39.558	41.493	0.697
Round	24.701	25.944	26.776	28.258	1.916
Bass Patterson	17.033	16.360	17.501	16.994	0.919
Lower Eau Claire	16.753	17.336	18.925	19.705	0.829
Middle Eau Claire	50.831	51.001	54.661	54.298	0.000
Siskiwit	6.318	6.073	5.652	5.275	1.586
Pine	7.488	6.959	9.511	8.949	1.406
Annabelle	3.441	3.167	2.991	2.363	0.353
α Z-score	1.214	0.876	1.048	1.011	
β Z-score	0.623	0.506	0.679	0.242	
σ Z-score	0.642	0.978	1.040	1.317	
DIC	1356.103	1383.967	1378.196	1385.128	

997

998 Table 5. Highest posterior density (HPD) estimates and lower and upper 95% Bayesian credible
 999 limits of regional and lake-specific growth parameters for northern Wisconsin walleye (*Sander*
 1000 *vitreus*).

Lake	L_{∞} (cm)	K	t_0
Regional	68.61 (64.31, 73.41)	0.13 (0.11, 0.15)	-1.23 (-1.43, -1.02)
Butternut (Forest)	63.93 (59.03, 68.81)	0.15 (0.13, 0.18)	-0.91 (-1.13, -0.71)
Franklin	74.85 (69.60, 80.14)	0.14 (0.12, 0.16)	-0.54 (-0.66, -0.41)
Bearskin	70.00 (64.03, 76.76)	0.13 (0.10, 0.15)	-1.20 (-1.42, -0.98)
Squirrel	76.63 (68.20, 86.61)	0.10 (0.08, 0.11)	-1.31 (-1.53, -1.11)
Big Arbor Vitae	84.71 (74.19, 96.67)	0.09 (0.07, 0.11)	-1.67 (-1.97, -1.42)
Pelican	70.23 (64.57, 75.82)	0.13 (0.11, 0.15)	-1.05 (-1.22, -0.87)
Big St Germain	85.52 (76.10, 95.30)	0.10 (0.08, 0.11)	-0.85 (-1.01, -0.69)
Plum	68.58 (63.27, 73.84)	0.14 (0.12, 0.16)	-0.89 (-1.07, -0.71)
Star	79.07 (69.72, 89.10)	0.09 (0.07, 0.11)	-1.95 (-2.21, -1.66)
North Twin	81.69 (72.42, 91.54)	0.10 (0.08, 0.12)	-1.00 (-1.17, -0.80)
Lac Vieux Desert	81.38 (71.96, 91.62)	0.09 (0.07, 0.11)	-1.66 (-1.95, -1.43)
Sherman	62.33 (57.48, 67.44)	0.14 (0.12, 0.17)	-1.25 (-1.48, -0.97)
Squaw	58.29 (53.85, 62.51)	0.14 (0.12, 0.16)	-1.15 (-1.36, -0.94)
Butternut (Price)	75.84 (67.49, 85.65)	0.10 (0.08, 0.12)	-1.29 (-1.52, -1.06)
Wolf	60.91 (57.99, 63.30)	0.22 (0.19, 0.25)	-0.94 (-1.13, -0.74)
Big Crooked	60.99 (58.50, 63.47)	0.22 (0.19, 0.25)	-0.94 (-1.15, -0.77)
Escanaba	78.92 (71.55, 87.15)	0.10 (0.08, 0.11)	-2.02 (-2.28, -1.76)
Grindstone	65.10 (61.95, 68.88)	0.17 (0.15, 0.19)	-0.93 (-1.10, -0.75)
Round	54.74 (52.58, 57.40)	0.22 (0.20, 0.25)	-0.45 (-0.59, -0.31)
Bass Patterson	64.03 (58.39, 70.00)	0.13 (0.10, 0.15)	-1.78 (-2.09, -1.48)
Lower Eau Claire	58.55 (55.91, 61.01)	0.21 (0.18, 0.23)	-0.87 (-1.05, -0.70)
Middle Eau Claire	61.85 (57.33, 66.88)	0.15 (0.12, 0.18)	-1.61 (-1.91, -1.29)
Siskiwit	47.63 (46.25, 49.07)	0.24 (0.22, 0.27)	-0.99 (-1.16, -0.83)
Pine	77.47 (67.92, 87.96)	0.09 (0.07, 0.10)	-1.75 (-2.03, -1.49)
Annabelle	68.05 (61.14, 74.63)	0.10 (0.08, 0.12)	-1.81 (-2.08, -1.53)

1001

1002 Table 6. Highest posterior density (HPD) estimates and lower and upper 95% Bayesian credible
 1003 limits of regional and lake-specific natural mortality and the parameters of the logistic
 1004 maturity/spearing selectivity function for northern Wisconsin walleye (*Sander vitreus*).

Lake	h	m	M
Regional	4.80 (3.45, 6.22)	3.36 (3.13, 3.63)	0.24 (0.17, 0.35)
Butternut (Forest)	6.80 (3.55, 11.98)	3.10 (3.07, 3.13)	0.25 (0.23, 0.27)
Franklin	7.68 (1.75, 18.01)	2.81 (2.56, 3.04)	0.12 (0.08, 0.16)
Bearskin	6.66 (4.00, 11.44)	3.09 (3.02, 3.15)	0.50 (0.46, 0.54)
Squirrel	6.76 (1.11, 13.11)	3.13 (3.08, 3.18)	0.42 (0.4, 0.45)
Big Arbor Vitae	5.23 (3.72, 7.69)	3.34 (3.16, 3.54)	0.51 (0.45, 0.56)
Pelican	2.67 (2.26, 3.10)	4.17 (3.96, 4.38)	0.17 (0.12, 0.22)
Big St Germain	2.64 (2.32, 3.08)	4.34 (4.14, 4.55)	0.02 (0.00, 0.05)
Plum	5.12 (2.49, 7.90)	3.16 (3.09, 3.24)	0.15 (0.11, 0.19)
Star	2.08 (1.88, 2.36)	4.03 (3.67, 4.38)	0.40 (0.30, 0.51)
North Twin	4.18 (3.38, 5.18)	3.50 (3.25, 3.74)	0.73 (0.62, 0.87)
Lac Vieux Desert	2.37 (2.13, 2.62)	4.68 (4.46, 4.90)	0.29 (0.23, 0.35)
Sherman	7.88 (2.19, 19.49)	2.88 (2.62, 3.07)	0.23 (0.2, 0.27)
Squaw	4.52 (4.30, 4.77)	3.29 (3.12, 3.45)	0.60 (0.54, 0.66)
Butternut (Price)	5.50 (3.26, 8.11)	3.13 (3.07, 3.22)	0.28 (0.24, 0.33)
Wolf	5.71 (3.01, 10.00)	3.12 (3.03, 3.20)	0.02 (0.00, 0.04)
Big Crooked	5.75 (2.69, 10.24)	3.10 (3.02, 3.18)	0.02 (0.00, 0.05)
Escanaba	11.81 (7.61, 19.64)	2.69 (2.67, 2.72)	0.79 (0.75, 0.83)
Grindstone	5.85 (3.26, 9.64)	3.12 (3.05, 3.20)	0.25 (0.20, 0.30)
Round	4.39 (2.53, 6.82)	3.31 (3.18, 3.47)	0.23 (0.18, 0.29)
Bass Patterson	2.33 (2.20, 2.48)	4.05 (3.92, 4.18)	0.57 (0.53, 0.63)
Lower Eau Claire	3.10 (0.83, 5.95)	3.44 (3.32, 3.59)	0.19 (0.14, 0.23)
Middle Eau Claire	4.36 (1.97, 7.10)	3.26 (3.16, 3.39)	0.23 (0.19, 0.27)
Siskiwit	2.30 (2.10, 2.48)	4.41 (4.19, 4.64)	0.39 (0.34, 0.46)
Pine	7.14 (4.76, 10.25)	2.85 (2.76, 2.93)	0.67 (0.59, 0.75)
Annabelle	5.20 (3.11, 7.69)	3.21 (3.08, 3.36)	0.58 (0.53, 0.65)

1005

1006

1007 Table 7. Median adult walleye (*Sander vitreus*) densities at unfished equilibrium (D) (fish·ha⁻¹)
1008 and probabilities of population collapse for the selected 25 lakes under various exploitation rates
1009 (divided equally between recreational and tribal fisheries), assuming a 38-cm minimum length
1010 limit for the recreational fishery.

Lake	D	$u = 0.20$	$u = 0.35$	$u = 0.50$	$u = 0.65$
Regional	23.28	0.03	0.24	0.55	0.60
Butternut (Forest)	26.44	0.01	0.06	0.11	0.20
Franklin	29.16	0.03	0.23	0.41	0.47
Bearskin	20.19	0.05	0.15	0.22	0.30
Squirrel	18.48	0.02	0.11	0.20	0.31
Big Arbor Vitae	11.49	0.11	0.33	0.44	0.54
Pelican	14.68	0.42	0.70	0.85	0.93
Big St Germain	40.67	0.05	0.43	0.76	0.90
Plum	43.59	0.01	0.05	0.11	0.16
Star	17.57	0.06	0.20	0.35	0.40
North Twin	14.08	0.03	0.06	0.13	0.16
Lac Vieux Desert	17.94	0.26	0.46	0.53	0.60
Sherman	52.93	0.00	0.00	0.00	0.01
Squaw	8.01	0.62	0.78	0.83	0.85
Butternut (Price)	19.35	0.10	0.24	0.35	0.41
Wolf	42.85	0.03	0.31	0.64	0.85
Big Crooked	38.45	0.03	0.50	0.83	0.90
Escanaba	45.10	0.00	0.01	0.01	0.01
Grindstone	38.25	0.01	0.06	0.08	0.12
Round	30.84	0.02	0.12	0.31	0.40
Bass Patterson	11.29	0.12	0.25	0.39	0.58
Lower Eau Claire	24.61	0.08	0.42	0.70	0.80
Middle Eau Claire	46.88	0.00	0.00	0.02	0.07
Siskiwit	8.99	0.66	0.81	0.84	0.86
Pine	11.12	0.07	0.16	0.20	0.30
Annabelle	4.99	0.38	0.46	0.61	0.70

1011

Figure captions

Fig. 1. Map showing Wisconsin counties with the Ceded Territory of Wisconsin shaded in gray.

Fig. 2. Schematic diagram for the age-structured integrated analysis (Maunder 2003) of growth, natural mortality, selectivity, and maturity of walleye (*Sander vitreus*) populations in northern Wisconsin lakes; i represents lake and a represents age; the six parameters estimated by the model as random effects are indicated in boldface, known model inputs are represented by ovals, and observed data (i.e., length-at-age data and age composition of adult PEs) to which predicted values are fit through optimization (*optim*) are represented by rounded squares. Remaining symbols are defined in the Methods section.

Fig. 3. Stock–recruitment relationships fit to age-0 and adult walleye (*Sander vitreus*) abundance data from the selected 25 northern Wisconsin lakes based on the hierarchical Bayesian meta-analysis with LNN–InvG priors (continuous lines) and lake-by-lake analyses (broken lines).

Fig. 4. Predicted age compositions of adult population estimates based on the hierarchical Bayesian model (lines) fit to observed data (symbols) of age compositions of adult population estimates (PEs) (from mark-recapture surveys) of walleye (*Sander vitreus*) populations from the selected 25 northern Wisconsin lakes.

Fig. 5. Proportions (median and interquartile range) of initial walleye (*Sander vitreus*) adult abundance remaining after 100 years (a and b) and corresponding long-term sustainable recreational and spearing harvest ($\text{fish}\cdot\text{ha}^{-1}$) (c and d) under various exploitation rates using

regional parameter estimates, assuming a logistic selectivity curve for the spearing fishery and a 38-cm minimum length limit for the recreational fishery (a and c); and a logistic selectivity curve for the spearing and recreational fisheries (i.e., no minimum length limit for the recreational fishery) (b and d). Proportions of adults remaining were calculated by dividing final abundance (i.e., year 100) by the initial (i.e., year 1), assumed to be at an unfished equilibrium. Values in parentheses are proportions of collapse associated with the respective exploitation rates.

Fig. 6. Contour plots of performances of northern Wisconsin walleye (*Sander vitreus*) fisheries under different combinations of recreational and tribal exploitation rates (0–25%) and a 38-cm minimum length limit for the recreational fishery using regional parameter estimates. Plots display median (a) predicted proportion of adult abundance remaining after 100 years and (b) combined long-term recreational and tribal harvest (fish·ha⁻¹).

Fig. 7. Regional model trajectories (median and interquartile range) of northern Wisconsin adult walleye (*Sander vitreus*) abundance and harvest under a 35% exploitation rate (17.5% recreational and 17.5% spearing), assuming a 38-cm minimum length limit for the recreational fishery.

Fig. 1.

Fig. 2.

Fig. 3.

Age

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Appendix

Table A1: Highest posterior density (HPD) estimates of regional and lake-specific Ricker stock–recruitment parameters (α , β , σ) for northern Wisconsin walleye (*Sander vitreus*) under alternative assumptions of prior distributions (see Table 3 for LNN–InvG model estimates).

Lake	LNLN–InvG	LNN	LNLN
Regional	2.751, 0.047, 1.965	2.831, 0.046, 2.113	2.799, 0.043, 2.114
Butternut (Forest)	2.681, 0.047, 2.401	2.753, 0.046, 2.852	2.710, 0.044, 2.852
Franklin	2.033, 0.056, 1.882	2.169, 0.051, 2.052	2.131, 0.049, 2.051
Bearskin	3.209, 0.042, 1.978	3.192, 0.043, 2.231	3.092, 0.041, 2.230
Squirrel	2.918, 0.045, 1.811	2.941, 0.045, 1.769	2.859, 0.042, 1.769
Big Arbor Vitae	2.669, 0.047, 1.802	2.700, 0.047, 1.689	2.629, 0.045, 1.686
Pelican	1.602, 0.066, 2.201	1.971, 0.053, 2.872	1.920, 0.052, 2.861
Big St Germain	2.264, 0.053, 2.253	2.492, 0.049, 3.004	2.461, 0.046, 3.000
Plum	3.651, 0.039, 1.757	3.909, 0.039, 1.512	3.838, 0.036, 1.521
Star	3.482, 0.040, 1.859	3.512, 0.041, 1.957	3.449, 0.038, 1.962
North Twin	3.219, 0.042, 2.102	3.152, 0.043, 2.677	3.111, 0.040, 2.675
Lac Vieux Desert	1.762, 0.062, 2.350	2.148, 0.052, 3.201	2.112, 0.050, 3.201
Sherman	5.091, 0.032, 1.840	5.189, 0.032, 1.860	5.104, 0.031, 1.863
Squaw	1.667, 0.064, 1.762	1.610, 0.058, 1.662	1.588, 0.058, 1.654
Butternut (Price)	2.481, 0.050, 1.837	2.530, 0.048, 1.869	2.492, 0.046, 1.882
Wolf	2.259, 0.053, 2.256	2.372, 0.049, 2.727	2.321, 0.047, 2.738
Big Crooked	1.991, 0.057, 2.300	2.090, 0.052, 2.734	2.049, 0.051, 2.727
Escanaba	5.913, 0.029, 1.612	6.092, 0.029, 1.431	6.011, 0.029, 1.431
Grindstone	4.109, 0.036, 1.851	4.111, 0.038, 1.952	4.054, 0.035, 1.954
Round	3.074, 0.043, 1.789	3.163, 0.043, 1.660	3.120, 0.040, 1.662
Bass Patterson	3.391, 0.041, 1.830	3.460, 0.041, 1.811	3.382, 0.039, 1.823
Lower Eau Claire	2.452, 0.050, 1.921	2.538, 0.048, 2.176	2.501, 0.045, 2.179
Middle Eau Claire	4.810, 0.033, 1.774	5.400, 0.032, 1.542	5.209, 0.031, 1.550
Siskiwit	1.741, 0.062, 1.733	1.671, 0.057, 1.550	1.642, 0.057, 1.552
Pine	1.971, 0.057, 1.918	2.100, 0.052, 2.152	2.041, 0.051, 2.159
Annabelle	2.062, 0.056, 1.780	2.040, 0.053, 1.640	2.000, 0.051, 1.641