Mercury and water level management in lakes of northern Minnesota

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Abstract. Water level (WL) fluctuations substantially alter the fauna, flora, and microbial community of nearshore aquatic ecosystems. Water level management therefore has the potential to strongly influence a wide variety of ecosystem processes. Many northern temperate lake food webs experience substantial methylmercury contamination, which is partially mediated by the action of sulfate-reducing bacteria occurring in sediments that are periodically inundated. For lakes with elevated methylmercury, WL management could be designed to reduce methylmercury contamination. At the lake scale, this concept is supported by studies that identified statistical associations between fish mercury content and water level (WL) fluctuations. Here, we compiled a long-term dataset (1997–2015) of mercury content in young-of-year Yellow Perch (Perca flavescens) from six lakes on the border of the United States and Canada and examined whether mercury content was associated with WL fluctuation. Many WL metrics covary and appear to have strong associations with Yellow Perch mercury. However, these associations appear to vary by lake, and lake-specific models are needed to identify relationships between WL fluctuation and Yellow Perch mercury content. We used partial least-squares regression (PLSR) to identify the associations between Yellow Perch mercury content and WL metrics, temperature, and annual deposition data for lakes in northern Minnesota. These PLSR models not only showed some variation among lakes, but also supported strong associations between WL fluctuations and annual variation in Yellow Perch mercury content. The study lakes underwent a change in WL management in 2000, when winter WL minimums were increased by about 1 m in five of the six study lakes, which reduced annual WL fluctuation on those lakes. Using the PLSR models, we estimated how this change in WL management would have affected Yellow Perch mercury content. In four of the five study lakes in which annual WL fluctuation was reduced in 2000, the change in WL management likely reduced Yellow Perch mercury content, relative to the previous WL management regime.

Key words: lakes; mercury; methylmercury; water level fluctuations; Yellow Perch.

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INTRODUCTION

The magnitude and frequency of water level (WL) fluctuations are believed to strongly influence the flora and fauna of lakes and reservoirs, as many ecosystem processes are influenced by the regular drying and rewetting of nearshore sediments (Haxton and Findlay 2008, Leira and Cantonati 2008, Wantzen et al. 2008). For example, drying and rewetting alter macroinvertebrate and vegetation patterns (Haxton and Findlay 2008, Leira and Cantonati 2008). In addition to influencing the distribution of flora and fauna, WL fluctuations can strongly influence other ecosystem processes (Leira and Cantonati 2008). Water levels are regulated for multiple purposes in many lakes and reservoirs, which can present challenges and opportunities for resource managers (Jager and Smith 2008).

Many lakes and reservoirs with active WL management provide ecosystem services related to fish communities, especially commercial and recreational fishing (Holmlund and Hammer 1999), but many of these fish communities are experiencing mercury contamination (Scheuhammer et al. 2007). Mercury in the biosphere has increased as a result of human activities, and even relatively undeveloped locations may receive substantial atmospheric depositions of mercury (Driscoll et al. 2007, Munthe et al. 2007). This atmospheric deposition of mercury usually occurs in oxidized elemental form, which can then be converted to methylmercury (CH$_3$Hg$^+$) by sulfate-reducing bacteria in anoxic sediments (Selin 2009). Methylmercury can then enter the food web and bioaccumulate to relatively high concentrations as it moves up the food web (Selin 2009).

The drying and rewetting of sediments associated with WL fluctuations have the potential to substantially influence the production of methylmercury by sulfate-reducing bacteria. Nearshore sediments that have been recently inundated or have been dry for a long period before re-inundation are often favorable to sulfate-reducing bacteria because they are carbon-rich and can easily become anoxic (Benoit et al. 2003, Gilmour et al. 2004). A few studies have demonstrated that sediments that are periodically inundated produce more methylmercury than sediments that are permanently exposed or permanently inundated (Eckley et al. 2017, Xiang et al. 2018). In principle, larger WL fluctuations result in more periodically inundated sediments, which then translates into increased methylmercury entering the food web.

Variation in methylmercury inputs into the food web often is inferred by measuring a sentinel species. The sentinel species approach involves sampling a single species over space or time, usually at the same age or life stage. Ideally, the young of year of a species that feeds at lower trophic levels is used, so that the mercury inputs to the food web can be tied to a particular season or exposure period (Sorensen et al. 2005, Wiener et al. 2006, Larson et al. 2014). Using this approach, controls over spatial and temporal variation in methylmercury production can be inferred. Annual and longer-term patterns in WL fluctuations have been associated with methylmercury contamination in food webs in several studies (Sorensen et al. 2005, Mailman et al. 2006, Selch et al. 2007, Larson et al. 2014, Watras et al. 2019).

In an analysis of fourteen lakes in Minnesota, Sorensen et al. (2005) found strong associations between WL fluctuations and mercury concentrations in young-of-year Yellow Perch (Perca flavescens). As many of these lakes have WL fluctuations that are actively managed for multiple purposes, this raised the possibility that local management of WL fluctuations could minimize mercury contamination in these lakes. A follow-up study by Larson et al. (2014) using several years of additional data found that these WL associations with Yellow Perch mercury content varied by lake, with some lakes having little or no WL–mercury associations and others having very strong associations. Larson et al. (2014) hypothesized that lake-specific characteristics (specifically, morphology and productivity) might be the cause of differences in the WL effect on Yellow Perch mercury content. Here, we use previously published data (Sorensen et al. 2005, Larson et al. 2014, Christensen et al. 2017) to re-examine the role of WL management on Yellow Perch mercury content (as a surrogate for methylmercury inputs to the food web). The lakes that are the focus of this study occur on the boundary between Canada and the United States and are regulated by international treaty (IJC 2000). Water level fluctuations in these lakes are...
managed (via water release at dams) according to regulations that are regularly updated to achieve both environmental and economic goals (IJC 2000).

Our objectives were to (1) identify lake and site-specific conditions that might drive spatial variation in WL–mercury associations, (2) use multivariate methods to identify WL–mercury relationships on a lake-specific basis, and (3) use these lake-specific models to evaluate whether different WL management scenarios have influenced mercury content in young-of-year Yellow Perch. We specifically explored the possibility that other environmental characteristics of these lakes might be associated with among-lake variation in the effect of WL on fish mercury content. For example, among-lake variation in Secchi depth (associated with organic carbon in these lakes), chlorophyll a (associated with productivity), and land cover features has been shown to drive spatial variation in mercury content in lakes from this region (Sorensen et al. 2005, Wiener et al. 2006, Kolka et al. 2019). To accomplish these objectives, we analyzed annual measurements of mercury in tissues of young-of-year Yellow Perch from six large lakes during 1997–2015, which have been reported in previous publications (Sorensen et al. 2005, Larson et al. 2014, Christensen et al. 2017).

METHODS

Study sites

The Rainy Lake–Namakan Reservoir complex is located on the border between the United States and Canada. The complex consists of naturally occurring lakes that have been impounded. Water levels are regulated for multiple purposes (e.g., hydropower, flood control, fisheries). Thirteen sites in six lakes from the Rainy Lake–Namakan Reservoir complex in or near Voyageurs National Park (Minnesota, USA) were sampled between 2013 and 2015 (Crane Lake, Lake Kabetogama, Little Vermilion Lake, Namakan Lake, Rainy Lake, and Sand Point Lake; Table 1, Fig. 1). Fish were collected between mid-September and early November each year. Fish were collected with 15.2- or 30.5-m bag seines with 6.4-mm mesh (bar), following procedures approved by the National Park Service’s Institutional Animal Care and Use Committee.

Regulations for WL fluctuations in the Rainy Lake–Namakan Reservoir complex are determined by the International Joint Commission (IJC) in the form of Rule Curves (IJC 2000). The IJC Rule Curves indicate bands of permitted maximum and minimum water levels that are allowed throughout the year (Christensen et al. 2004). Modest changes in the IJC Rule Curves occurred in 2000, specifically designed to reduce overall annual water level changes in five of the six lakes sampled here (all except Rainy Lake).

Water level estimates

Water level metrics calculated here were similar to those used in Sorensen et al. (2005) and Larson et al. (2014). All water level data were obtained from the Lake of the Woods Water Control Board, which provided daily averages for the entire study period. Within-year minimum WL and maximum WL were used to calculate water level rise (WLR). Mean and standard deviation (SD) in daily WL also were calculated. In addition, change in maximum water level ($\Delta_{\text{maxWL}}$) from the previous year was calculated. Water levels in the Rainy Lake–Namakan Reservoir complex follow a seasonal pattern, with early-spring minimums and early- to mid-summer maximums. The WLR, minimum, maximum, mean, and SD in WL were calculated for the entire year, for the spring (April–June), and for the summer (July–September).

Surface area estimates

The inundated surface area at 0.1 m water level elevation increments (between the minimum WL and maximum WL for each lake) was estimated for five of the six lakes using a sequence of geoprocessing tools in a GIS environment (Environmental Systems Research Institute [ESRI] 2019). Inundation area estimates were calculated using the 10-m digital elevation model (DEM) developed by Morin et al (2016); surface area estimates were not calculated for Little Vermilion Lake as it was not covered by the spatial extent of the DEM. The number of inundated DEM raster cells at each 0.1-m WL elevation was determined using ESRI Spatial Analyst tools. The approximate inundated surface area (in square meters) for each lake was then calculated using standard geometry tools, and the series of inundated surface area
Table 1. Sites from which young-of-year Yellow Perch were captured and mercury content measured.

| Lake                  | Site | Latitude  | Longitude  | USGS site number     | Years of Yellow Perch Hg data | Data sources |
|-----------------------|------|-----------|------------|----------------------|-------------------------------|--------------|
| Crane Lake            | 1    | 48.309780 | -92.495530 | 481835092294401      | 2001–03, 2013–15             | 1,2          |
| Crane Lake            | 2†   | 48.307610 | -92.481670 | 481827092285401      | 2001–10, 2013–15             | 1,2,3        |
| Lake Kabetogama†      | 1‡   | 48.432080 | -92.870970 | 482556092521601      | 2001–10, 2013–15             | 1,2,3        |
| Lake Kabetogama       | 2    | 48.434280 | -92.818080 | 482603092490501      | 2001–03, 2013–15             | 1,2          |
| Little Vermilion Lake†| 1‡   | 48.304390 | -92.429610 | 4818180922524201     | 2001–10, 2013, 2015          | 1,2,3        |
| Little Vermilion Lake†| 2    | 48.297470 | -92.421890 | 481751092251901      | 2001–03, 2013, 2015          | 1,2          |
| Namakan Lake          | 1‡   | 48.431440 | -92.679780 | 482553092404801      | 2001–10, 2013–15             | 1,2,3        |
| Namakan Lake          | 2    | 48.428030 | -92.687690 | 482541092411601      | 2001–03, 2013–15             | 1,2          |
| Rainy Lake            | 1‡   | 48.596920 | -93.058630 | 483549093030001      | 2001–10, 2013–15             | 1,2,3        |
| Rainy Lake            | 2    | 48.604220 | -93.094500 | 483615093054001      | 2001–03, 2015                | 1,2          |
| Sand Point Lake‡      | 0‡   | 48.334940 | -92.475920 | 482006092283301      | 1997, 1999, 2000–10, 2013–15 | 1,2,3        |
| Sand Point Lake       | 1    | 48.381360 | -92.520830 | 482241092311501      | 2001–03, 2013–15             | 1,2          |
| Sand Point Lake       | 2    | 48.404530 | -92.484330 | 482416092290401      | 2001–03, 2013–15             | 1,2          |

Notes: USGS site numbers refer to site data available through the website https://waterdata.usgs.gov/nwis. Data sources are (1) Sorensen et al. (2005), (2) Christensen et al. (2017), and (3) Larson et al. (2014).
† Buffers around site are only partially covered by elevation maps.
‡ Sites used in the partial least-squares regression analysis and among-lake comparisons.

Fig. 1. Locations where annual young-of-year Yellow Perch were collected in the Rainy Lake–Namakan Reservoir complex.
estimates for each 0.1-m WL elevation were compiled in tabular format.

**Site buffer characteristics**
For each study site, a 200 m radius buffer was generated around the center of the sampling location (whole lake land cover data are not available). Land cover and slope were characterized within each site buffer, using a 2010 land cover dataset developed by Olmanson and Bauer (2017) and a slope raster generated from the same 10-m DEM (Morin et al. 2016) that was used to estimate the inundated surface areas. Land cover and slope data for each site were used to identify whether land cover conditions around the sampling location were driving differences in the relationship between water level elevation and Hg content. Land cover types from the Level 1 classification scheme (consisting of urban/developed, extraction, agriculture, forest, open water, and wetlands land cover types) were summarized to determine the percent coverage of each land cover type within a buffered area. The overall net change in slope (total) and standard deviation (SD) of slope change within each site buffer were calculated for the partial area covered by the DEM. Partial coverage is indicated in the appended data tables (Tables 1, 4, Data S1). Site buffer characteristics were not generated for Little Vermilion Lake, as it falls completely outside the spatial extent of the DEM. Geospatial data summary data are available online (https://doi.org/10.5066/P96TWNJL).

**Atmospheric deposition of mercury and sulfate**
The deposition of mercury and sulfate was measured by the National Atmospheric Deposition Program (NADP). For mercury, annual data from the Fernberg monitoring location (MN18) were obtained from the NADP website (NADP 2012a). For sulfate, annual data from the Sullivan Bay monitoring location (MN32) also were collected from the NADP website (NADP 2012b).

**Temperature data**
Water temperature data were not available for most of the lakes over the time scales needed for analysis. Instead, air temperatures and Eq. 1 from Chezik et al. (2014) were used to calculate annual degree-days for each lake. All data were obtained from the National Oceanic and Atmospheric Administration’s National Climatic Data Center (http://www.ncdc.noaa.gov/data-access). Station USW0014918 in nearby International Falls, Minnesota, was used for all of the lakes in this study. In this formulation, the degree-days for a single day (DD; °C-days) are calculated as follows:

\[
DD = \frac{T_{\text{max}} - T_{\text{min}}}{2} - T_s
\]

where \( T_s \) is the threshold temperature under consideration (e.g., 0°C or 5°C) and \( T_{\text{max}} \) and \( T_{\text{min}} \) are the daily maximum and minimum temperatures, respectively. Negative daily DD estimates are discarded, and the positive daily DD estimates are summed for the year. We calculated DDs for a \( T_s \) of 0°C, 5°C, 10°C, and 15°C.

**Fish mercury analysis**
Fish mercury data (Table 1) were compiled from previous reports: Sorensen et al. (2005), Larson et al. (2014), and Christensen et al. (2017). Methods for estimating the mercury content for young-of-year Yellow Perch were consistent with those used in Sorensen et al. (2005) and previously described in Larson et al. (2014). Fish wet weight (WW) and total length were measured, and then, fish were dried for 24 h at 70°C and weighed again to estimate moisture content. Length measurements were made using a ruler with 1 mm demarcations, estimated to the nearest 0.5 mm. Weights were measured using a balance accurate to 0.1 mg. Dried fish were then shredded and ground with mortar and pestle and kept frozen until analysis. Total Hg was measured using USEPA method 245.6 (EPA 1991) on a whole fish basis, as methylmercury generally is >90% of total mercury in fish (Sandheinrich and Wiener 2011). Detection limits varied based on the data source from 0.5 to about 3 ng mercury per gram of wet fish (Sorensen et al. 2005, Larson et al. 2014, Christensen et al. 2017). Quality control details are available in the individual publications listed above, and the laboratory reports on concentrations are available upon request. For this analysis, we used only mercury content
for young-of-year Yellow Perch on a dry mass basis.

**Chlorophyll a and Secchi depth**

Chlorophyll a concentration and Secchi depth were collected according to methods described in Christensen et al. (2017). Briefly, water samples for chlorophyll a were collected from nearshore sites by NPS personnel using a Van Dorn-type sampler. Seston was filtered onto glass fiber filters in the dark and was frozen as quickly as possible (Christensen et al. 2017). Samples were shipped to the Natural Resources Research Institute Laboratory in Duluth, Minnesota, for the analysis of chlorophyll a using spectrophotometric methods (Ameel et al. 1998). Water temperature was measured about 1 m below the lake surface with a multiparameter sonde calibrated according to USGS methods (Wagner et al. 2006). Because sites were shallow, Secchi depth was measured by moving out into the lake until the Secchi disk was no longer visible at the bottom of the lake.

**Statistical methods**

Data were compiled using R statistic software Version 3.6.1 (R Development Core Team 2019). All statistics were completed in R. Individual package version numbers are included in the code in Data S1. Although Yellow Perch mercury content is reported per unit dry mass, we explored the possibility that there were size-driven differences in mercury content. Pearson’s correlation coefficients between mercury content and length or total dry mass were low (0.18 and 0.23, respectively), and visual inspection of bivariate plots between these variables suggested little or no additional association between size and mercury content. Therefore, we did not perform any additional mass-based or length normalization on the mercury content.

*Estimating effect sizes of simple WL metrics.*—Correlation coefficients between young-of-year Yellow Perch mercury content and WL fluctuations were estimated using a Bayesian approach that is analogous to Pearson’s correlation coefficient (see documentation for the Bayesian First Aid package; Bååth 2014). These are referred to as Pearson’s correlation coefficients hereafter, but they actually use a t-distribution that is relatively robust to outliers, and this approach is capable of easily estimating uncertainty in the estimate of the correlation coefficient. Correlations were performed at each site (13 sites total), using the maximum water level elevation (Max WL), the annual water level rise (WLR), the spring WLR (Spring WLR), and the change in maximum water level since the previous year (ΔmaxWL). These were the primary predictors identified as most strongly associated with Yellow Perch mercury content in previous publications (Sorensen et al. 2005, Larson et al. 2014). The resulting correlation coefficients (the effect sizes of these WL variables on Yellow Perch mercury content) were then themselves correlated with three lake characteristics (area periodically inundated, proportion of the maximum lake size that is periodically inundated, and the mean percent increase in surface area per 0.1 m increase in water level elevation) and five site characteristics (Secchi depth, chlorophyll a, percent of buffer that is classified as open water, that is, lake, percent of buffer that is classified as wetlands, and the total slope within the buffer). Correlation coefficients were calculated with 95% credible intervals. If those credible intervals do not overlap zero, then we consider it strong evidence that the correlation is nonzero (McCarthy 2007). Correlations between WLR and fish mercury content at site Rainy Lake 2 would not converge and therefore are not estimated using this method.

*Multivariate analysis of WL effects.*—Many metrics of WL fluctuations covary, and therefore, it is difficult to identify which WL characteristics will best represent potential effects on mercury accumulation (Sorensen et al. 2005, Larson et al. 2014). We used partial least-squares regression (PLSR) to identify associations between young-of-year Yellow Perch mercury content and many metrics of WL fluctuations that covary. Partial least-squares regression is similar to principal component analysis (PCA; Manly 2005), in that axes of covariation among variables are identified. However, PLSR has a predictor–response structure that is used to identify the components (Carrascal et al. 2009). Partial least-squares regression is useful in cases where sample sizes are low and many strongly correlated predictor variables are believed to be important (Carrascal et al. 2009). Essentially, PLSR identifies the components of variation (presumed to represent latent variables) in the predictor variables that
are related to variation in a response variable (Garthwaite 1994, Carrascal et al. 2009). Cross-validation can then be used to prevent overfitting of the data. We implemented this analysis using the PLS package in R (Mevik and Wehrens 2007). Cross-validation was used to select components that were related to response variables using the leave-one-out method employed in the plsr() function. Twenty-three potential predictors were included in the PLSR analysis, including all of the WL variables described above, annual degree-days for 0°, 5°, 10°, and 15°C, annual precipitation, annual mercury deposition, and annual sulfate deposition (all parameters that have been suggested to influence Yellow Perch Hg content in these lakes; Sorensen et al. 2005, Larson et al. 2014). We ran an individual PLSR with all 23 of these potential predictor variables for each of the sites with more than 12 yr of data (six sites, one in each lake). The root-mean-square error of prediction (RMSEP) was used to determine whether the inclusion of a component was strongly supported by the data: If the inclusion of a component lowered the RMSEP, then the component was considered supported and was included in the model (Mevik and Wehrens 2007). In cases where the RMSEP was at a minimum in the model with no components, we assumed no strong associations existed between the components and the response variable. Examples of the code are provided in the statistical appendix (Data S1).

A hydrologic model developed by Thompson (2015) uses inflow data as inputs and predicts WLs under different WL management scenarios. Two WL management scenarios were used in this analysis, one based on the management regime that began in 1970 (the 1970 Rule Curves) and one based on the management regime that began in 2000 (the 2000 Rule Curves; IJC 2000). For the period 2000–2014, this hydrologic model can be used to estimate the WLs as if the 1970 Rule Curves had been retained. The same model was used to estimate WLs as if the 2000 Rule Curves were used. During the 2000–2014 period, the 2000 Rule Curves were in effect, but for consistency and a more meaningful comparison of the two WL management strategies we used the model estimated WL values for this exercise instead of using actual WL values. Thus, this hydrologic model provides estimated WL fluctuation estimates for a given WL management strategy. These WL estimates were then used as the predictor data in PLSR models that had strongly supported components to estimate young-of-year Yellow Perch mercury content. Code for making the predictions is included in the statistical appendix (Data S1).

To incorporate potential error in the models, we used a jackknife approach to estimate mercury in young-of-year Yellow Perch from 2000 to 2014. Essentially, the jackknife approach involved dropping one of the observations (observations here are the annual means at a site), refitting the PLSR model using the remaining observations, making predictions using that model, and repeating the process until estimates had been made from all the possible combinations of data that lacked one observation.

**RESULTS**

Yellow Perch mercury content from separate sites within the same lake covariates

Correlation coefficients between sites within a single lake were large (all were ≥0.80) and only in Lake Kabetogama did the 95% credible interval of a correlation coefficient (r) overlap zero (Fig. 2). This indicates that within a particular lake, different sites tend to vary the same way over time, although these correlations are estimates from only 4–6 yr (Fig. 2). Correlations between Yellow Perch mercury (Hg) content and individual WL parameters were similar within a particular lake, with all 95% credible intervals overlapping from within a particular lake (Table 2). For example, the 95% credible interval of the r estimate for the association between Yellow Perch Hg content and Max WL in Crane Lake Site 1 (~0.30 to 0.95) and Site 2 (0.05–0.87) had broad overlap (Table 2). As would be expected, sites with more years of sampling tended to have narrower 95% credible intervals on the estimated correlation coefficient, because the correlation coefficient can be estimated more accurately. We used the median correlation coefficients as our estimate of the effect size of WL effects on Yellow Perch Hg content for subsequent analyses.

Variation in water level effects on Yellow Perch Hg content among lakes

There was substantial among-lake variation in the effect size (i.e., correlation coefficient) of
WL fluctuations on young-of-year Yellow Perch Hg content. For example, the correlation between Yellow Perch Hg content and WLR was 0.88 (0.66–0.97) at the Rainy Lake site with the most data but was indistinguishable from zero at the Little Vermilion Lake site with the most data (0.23 [−0.35 to 0.71]; Table 2). There are also differences among the lakes in their morphological characteristics (Table 3) and among sites in water quality and land cover characteristics (Table 4). Differences among lakes in morphology do not appear to be associated with differences in the effect size of WL fluctuations on Yellow Perch Hg content (Table 5). For example, lake-to-lake variation in the correlation coefficient between WLR and Yellow Perch Hg content ($r_{\text{WLR-Hg}}$) does not appear to be associated with differences among lakes in the proportion of the lake that is periodically inundated (Table 5, using data from the lake site with the most data). Using all of the sites (except those in Little Vermilion Lake), there was a strong association between Secchi depth and $r_{\text{MaxWL-Hg}}$ (the correlation between max WL and Yellow Perch Hg; Table 6), but there were no other strong associations between site properties and other correlation coefficients between WL variables and Yellow Perch Hg.

Fig. 2. Annual variation in young-of-year whole fish Yellow Perch mean total mercury content in multiple sites from the same lake. Units for Yellow Perch mercury content are ng g$^{-1}$ dry mass. The solid line is a 1:1 line. Pearson's correlation coefficients ($r$) are reported with 95% confidence intervals. Each point is a separate year. For Sand Point Lake, closed circles are data from Site 0, and open circles are from Site 2.
Latent variables related to water level fluctuations strongly influence Yellow Perch Hg content

Partial least-squares regression analysis indicated strong associations between WL fluctuations and young-of-year Yellow Perch mercury content in five of the six study lakes (Data S1, Fig. 3). Only sites with 12+ yr of data were used for this analysis. For each of these five lakes (Crane Lake, Lake Kabetogama, Namakan Lake, Rainy Lake, and Sand Point Lake), the first component was very similar (Table 7). The first component explained between 42.9% and 79.2% of the variation in Yellow Perch Hg content and always included the Spring WL rise, with greater rise leading to greater mercury content (Table 7). Only WL variables had correlations of >0.30 with this first component. Therefore, this first component (or latent variable) can be understood as representing the WL fluctuation effect. Lake Kabetogama, Namakan Lake, and Rainy Lake had second components that were supported by the cross-validation as well, and these second components were all positively associated with degree-days (i.e., this component could be understood as the temperature effect; Table 8). No lake had a third component that was supported by cross-validation.

Statistical models indicate water level management changes cause changes in Yellow Perch Hg content

In the five lakes that had PLSR models supported by cross-validation, these models were

Table 2. Estimates of the effect size of associations between characteristics of water level variation and whole young-of-year Yellow Perch total mercury content (per unit dry mass).

| Lake          | Site | Years of data | Max WL (95% CI) | WLR (95% CI) | Spring WLR (95% CI) | Δmax WL (95% CI) |
|---------------|------|---------------|-----------------|--------------|---------------------|-----------------|
| Crane Lake    | 2†   | 13            | 0.57 (0.05, 0.87)| 0.54 (0.02, 0.86)| 0.57 (0.09, 0.86) | 0.57 (0.07, 0.87)|
| Lake Kabetogama | 2   | 6             | 0.67 (−0.11, 0.97)| 0.75 (0.07, 0.98) | 0.63 (−0.17, 0.96) | 0.66 (−0.15, 0.97) |
| Little Vermilion Lake | 2   | 5             | −0.21 (−0.90, 0.71) | −0.20 (−0.92, 0.70) | −0.17 (−0.88, 0.73) | 0.12 (−0.75, 0.86) |
| Namakan Lake  | 2†   | 13            | 0.72 (0.33, 0.92) | 0.61 (0.14, 0.88) | 0.59 (0.11, 0.87) | 0.53 (0.02, 0.85) |
| Rainy Lake    | 2†   | 13            | 0.82 (0.51, 0.96) | 0.88 (0.66, 0.97) | 0.82 (0.52, 0.95) | 0.51 (0.01, 0.84) |
| Sand Point Lake | 2   | 6             | 0.59 (−0.28, 0.96) | 0.60 (−0.24, 0.96) | 0.65 (−0.17, 0.97) | 0.75 (0.07, 0.98) |

Notes: Effect size estimates are correlation coefficients (with 95% credible intervals). Abbreviations are Max WL, maximum annual WL; WLR, annual water level rise; Δmax WL, change in maximum WL since last year; NA indicates the model would not converge. Bold indicates a nonzero correlation coefficient.

† Sites used in the partial least-squares regression analysis and among-lake comparisons.

Table 3. Morphological characteristics of study lakes with respect to changes in lake surface area.

| Lake            | Max lake surface area (km²) | Minimum lake surface area (km²) | Area periodically inundated (km²) | Percentage of max periodically inundated (%) | Mean % increase in surface area (% per 0.1 m) |
|-----------------|-----------------------------|---------------------------------|----------------------------------|---------------------------------------------|----------------------------------------------|
| Crane Lake      | 12.9                        | 9.5                             | 3.4                              | 26.1                                        | 0.86                                         |
| Lake Kabetogama | 103.5                       | 75.7                            | 27.8                             | 26.9                                        | 0.91                                         |
| Little Vermilion Lake | NA                      | NA                              | NA                               | NA                                          | NA                                           |
| Namakan Lake    | 100.8                       | 81.5                            | 19.4                             | 19.2                                        | 0.61                                         |
| Rainy Lake      | 1007                        | 787.1                           | 220.3                            | 21.9                                        | 0.94                                         |
| Sand Point Lake | 39.7                        | 29.1                            | 10.5                             | 26.5                                        | 0.79                                         |

Note: Max indicates maximum lake surface area.
used to estimate the effects of the two WL management scenarios. These were the models previously described in Tables 7, 8, and included a one-component model for Crane Lake and Sand Point Lake, and two-component models for Lake Kabetogama, Namakan Lake, and Rainy Lake (as mentioned above, no model was supported for Little Vermilion Lake). The two WL management scenarios included one scenario that used the 1970 Rule Curves and another scenario that used the 2000 Rule Curves prescribed by the International Joint Commission for these lakes (IJC 2000), for the period from 2000 to 2014. Model predictions of Yellow Perch Hg content for Crane Lake, Namakan Lake, Sand Point Lake, and Lake Kabetogama were higher under the 1970 Rule Curve scenario (Fig. 4). For Rainy Lake, both management scenarios yield similar annual variation in fish mercury content (Fig. 4), which is not surprising since the 1970 and 2000 Rule Curves for Rainy Lake are almost identical (IJC 2000).

DISCUSSION

The management of water level fluctuations to maximize economic and ecological benefits simultaneously continues to be a major concern.

Table 4. Water quality and land cover conditions at sites where juvenile Yellow Perch were collected to measure body mercury (Hg) content.

| Lake          | Site | Years of data | Average annual mean Hg (ng g/DW) | Water Temp | Secchi depth (m) | Chl a (µg/L) | Lake (ºC in 200 m buffer) | Wetlands (% in 200 m buffer) | Slope (total range) | Slope (sd) |
|---------------|------|---------------|----------------------------------|------------|----------------|--------------|---------------------------|------------------------------|-------------------|-----------|
| Crane Lake    | 1    | 6             | 644.7 (298.2)                   | 11.0       | 1.9            | 1.1          | 55.0                      | 0                            | 29.1              | 4.6       |
| Crane Lake    | 2    | 13            | 613.2 (276.7)                   | 10.7       | 1.6            | 2.1          | 45.7                      | 0                            | 29.5              | 5.6       |
| Lake Kabetogama | 2 | 13          | 169.7 (46.5)                    | 14.5       | 2.0            | 7.1          | 52.2                      | 0                            | 32.8              | 7.5       |
| Lake Kabetogama | 2 | 6            | 237.1 (108.6)                   | 15.2       | 2.3            | 9.0          | 33.6                      | 0                            | 32.5              | 7.0       |
| Little Vermilion Lake² | 1 | 5          | 375.6 (109.1)                   | 11.1       | 1.3            | 3.6          | 68.8                      | 0.2                          | 19.3              | 3.9       |
| Little Vermilion Lake † | 2 | 5          | 461.4 (75.5)                    | 11.3       | 1.8            | 2.3          | NA                        | NA                           | NA                | NA        |
| Namakan Lake  | 1‡   | 13            | 282.6 (109.8)                   | 15.0       | 2.4            | 2.0          | 82.9                      | 0                            | 19.6              | 3.9       |
| Namakan Lake  | 2‡   | 6             | 333.5 (117.0)                   | 14.9       | 2.5            | 1.3          | 54.9                      | 0                            | 34.9              | 6.6       |
| Rainy Lake    | 1‡   | 13            | 225.1 (97.3)                    | 14.7       | 2.0            | 1.3          | 83.0                      | 13.3                         | 8.0                | 1.3       |
| Rainy Lake    | 2‡   | 4             | 247.7 (93.7)                    | 14.4       | 1.5            | 1.3          | 72.6                      | 2.5                          | 20.6              | 4.6       |
| Sand Point Lake † | 0‡  | 16           | 523.4 (225.7)                   | 11.7       | 1.8            | 1.8          | 51.0                      | 5.0                          | 19.1              | 3.6       |
| Sand Point Lake | 1 | 6            | 564.0 (295.5)                   | 10.6       | 1.9            | 1.5          | 53.8                      | 0                            | 34.7              | 6.6       |
| Sand Point Lake | 2 | 6            | 500.2 (208.1)                   | 7.5        | 1.5            | 2.5          | 69.1                      | 10.8                         | 15.7              | 2.9       |

Notes: Median water temperature, Secchi depth, and chlorophyll a content are reported from Christensen et al. (2017). NA means very little buffer data available, and therefore, no estimates were made.

† Buffers around site are only partially covered by elevation maps, and therefore, slope estimates are not complete.

‡ Sites used in the partial least-squares regression analysis and among-lake comparisons.

Table 5. Correlation coefficients (with 95% credible intervals) between the effect of water level fluctuations and lake morphology.

| Effect size | Area periodically inundated | Proportion of max periodically inundated | Mean % increase in surface area |
|-------------|-----------------------------|----------------------------------------|--------------------------------|
| r<sub>MaxWL-Hg</sub> | 0.42 (−0.54, 0.94) | −0.49 (−0.95, 0.50) | 0.08 (−0.78, 0.85) |
| r<sub>WLR-Hg</sub> | 0.55 (−0.45, 0.97) | −0.33 (−0.93, 0.63) | 0.23 (−0.93, 0.90) |
| r<sub>SpringWLR-Hg</sub> | 0.38 (−0.60, 0.93) | −0.29 (−0.91, 0.66) | 0.15 (−0.75, 0.87) |
| r<sub>ΔmaxWL-Hg</sub> | −0.06 (−0.86, 0.74) | −0.03 (−0.81, 0.82) | −0.08 (−0.84, 0.79) |

Notes: Effect sizes (correlation coefficient between a water level metric and Yellow Perch Hg content; r) from five sites were included in this analysis (Crane Lake 2, Lake Kabetogama 1, Namakan Lake 1, Rainy Lake 1, and Sand Point Lake 0). Little Vermilion Lake is not included in this analysis because elevation data were not available. Abbreviations are Max WL, maximum annual WL; WLR, annual water level rise; Δmax WL, change in maximum WL since last year, NA.
for many natural resource managers. Several studies have found evidence that periodically inundated sediments can increase methylmercury production by sulfate-reducing bacteria (Eckley et al. 2017, Xiang et al. 2018). Moreover, ecosystem-scale studies have found statistical associations between fish methylmercury content and water level fluctuations (Sørensen et al. 2005, Selch et al. 2007, Watras et al. 2019). The large lakes studied here are subject to active water level fluctuations. Table 6. Correlation coefficients (with 95% credible intervals) between the effect of water level fluctuations and site-specific characteristics.

| Effect size | Secchi depth | Chl a | Surface water area in buffer | Wetlands in buffer | Slope (total range) |
|-------------|--------------|-------|------------------------------|--------------------|--------------------|
| $r_{\text{MaxWL-Hg}}$ | 0.54 (0.02, 0.90) | $-0.24 (-0.74, 0.37)$ | 0.26 (−0.34, 0.76) | 0.19 (−0.43, 0.72) | $-0.17 (-0.72, 0.44)$ |
| $r_{\text{WLR-Hg}}$ | 0.32 (−0.29, 0.82) | $-0.12 (-0.75, 0.51)$ | 0.22 (−0.40, 0.78) | 0.36 (−0.23, 0.87) | $-0.26 (-0.80, 0.38)$ |
| $r_{\text{SpringWLR-Hg}}$ | 0.19 (−0.40, 0.72) | $-0.29 (-0.80, 0.33)$ | $-0.18 (-0.42, 0.72)$ | 0.39 (−0.20, 0.85) | $-0.27 (-0.79, 0.34)$ |
| $r_{\text{ΔmaxWL-Hg}}$ | 0.03 (−0.56, 0.62) | $-0.35 (-0.84, 0.24)$ | $-0.19 (-0.72, 0.43)$ | $-0.07 (-0.65, 0.51)$ | 0.25 (−0.36, 0.78) |

Notes: Effect sizes (correlation coefficient between a water level metric and Yellow Perch Hg content; $r$) from eleven sites were included in this analysis (Table 4). Little Vermilion Lake is not included in this analysis because elevation data were not available. Bold indicates a nonzero correlation coefficient. Abbreviations are Max WL, maximum annual WL; WLR, annual water level rise; Δmax WL, change in maximum WL since last year, NA.

Fig. 3. Mean measured and predicted whole fish young-of-year Yellow Perch total mercury (ng g$^{-1}$ dry mass). Predictions are derived from partial least-squares regression models that were validated using cross-validation. Crane Lake and Sand Point Lake models included one component, and other lakes included two components (see Tables 3, 4). The solid line is a 1:1 line.
level management within an adaptive management framework, and the overall evidence examined here suggests that water level management can influence methylmercury contamination of food webs in most of these lakes.

In previous studies on the lakes in this analysis, year-to-year changes in maximum WL appeared to be strongly associated with annual variation in young-of-year Yellow Perch mercury content (Sorensen et al. 2005, Larson et al. 2014), which makes conceptual sense, as changes in the year-to-year maximum WL correspond to the area of sediments that are exposed for longer time periods (i.e., more than a year). In the current analysis, the statistical associations between Yellow Perch mercury content and year-to-year maximum WL were not stronger than other metrics of WL fluctuations that were indicative of within-year drying and inundation. The individual WL metrics that were most strongly associated with Yellow Perch mercury content varied by lake. For example, in Little Vermilion Lake, the associations between WL fluctuation and Yellow Perch Hg content were absent, while in Rainy Lake these associations were very strong.

Variation among lakes in the strength of associations between WL metrics and Yellow Perch Hg content did not appear to be related to lake morphology or land cover characteristics in our analysis. However, the data for these characteristics were not available for Little Vermilion Lake, which was the lake with the weakest association between WL fluctuation and Yellow Perch Hg content. Little Vermilion Lake has a more

Table 7. The first component of a partial least-squares regression analysis relating water level (WL) fluctuations, degree-days, precipitation, sulfate deposition, and mercury deposition to total mercury content (per unit dry mass) in whole young-of-year Yellow Perch (collected at the end of September).

| Variables                                   | Crane Lake (Site 2) | Kabetogama Lake (Site 1) | Namakan Lake (Site 1) | Rainy Lake (Site 1) | Sand Point Lake (Site 0) |
|---------------------------------------------|---------------------|--------------------------|-----------------------|---------------------|--------------------------|
| % variance explained (predictors)           | 46.5                | 42.8                     | 46.4                  | 48.1                | 47.6                     |
| % variance explained (mean Yellow Perch Hg ng per g DW) | 54.2                | 42.9                     | 61.7                  | 79.2                | 62.3                     |
| Loadings                                    |                     |                          |                       |                     |                          |
| Annual maximum WL                           | 0.30                | 0.35                     | 0.31                  | 0.30                | –                        |
| Annual WL rise                              | –                   | 0.34                     | 0.31                  | –                   | 0.30                     |
| Change in maximum WL from last year         | –                   | –                        | –                     | –                   | –                        |
| Annual minimum WL                           | –                   | –                        | –                     | –                   | –                        |
| Annual mean WL                              | –                   | –                        | –                     | –                   | –                        |
| Annual standard deviation WL                | –                   | –                        | –                     | –                   | –                        |
| Spring maximum WL                           | 0.30                | 0.32                     | 0.31                  | 0.30                | –                        |
| Spring WL rise                              | 0.30                | 0.31                     | 0.30                  | 0.30                | 0.30                     |
| Spring minimum WL                           | –                   | –                        | –                     | –                   | –                        |
| Spring mean WL                              | –                   | –                        | –                     | –                   | –                        |
| Spring standard deviation WL                | –                   | –                        | –                     | –                   | –                        |
| Summer maximum WL                           | 0.30                | 0.33                     | –                     | 0.30                | –                        |
| Summer WL rise                              | –                   | 0.32                     | –                     | –                   | –                        |
| Summer minimum WL                           | –                   | –                        | –                     | –                   | –                        |
| Summer mean WL                              | –                   | 0.33                     | –                     | –                   | –                        |
| Summer standard deviation WL                | –                   | 0.33                     | –                     | –                   | –                        |
| Degree-days (0°C)                           | –                   | –                        | –                     | –                   | –                        |
| Degree-days (5°C)                           | –                   | –                        | –                     | –                   | –                        |
| Degree-days (10°C)                          | –                   | –                        | –                     | –                   | –                        |
| Degree-days (15°C)                          | –                   | –                        | –                     | –                   | –                        |
| Precipitation (mm)                          | –                   | –                        | –                     | –                   | –                        |
| Sulfate deposition                          | –                   | –                        | –                     | –                   | –                        |
| Mercury deposition                          | –                   | –                        | –                     | –                   | –                        |

Notes: Loadings are equivalent to a correlation between the component and the individual variable. Only loadings of 0.3 or more are shown. Cross-validation supported the inclusion of each of these components. Each of these sites had >12 yr of data. Spring refers to April–June; summer refers to July–September. No components were supported for Little Vermilion Lake.
Vermilion Lake had no strongly supported components. have strongly supported second components, while Little July'sion of each of these components. Each of these sites had 0.3 or more are shown. Cross-validation supported the inclu-

The second component of a partial least-squares regression analysis relating water level (WL) fluctuations, degree-days, precipitation, sulfate deposition, and mercury deposition to total mercury content (per unit dry mass) in whole young-of-year Yellow Perch (collected at the end of September).

Table 8. The second component of a partial least-squares regression analysis relating water level (WL) fluctuations, degree-days, precipitation, sulfate deposition, and mercury deposition to total mercury content (per unit dry mass) in whole young-of-year Yellow Perch (collected at the end of September).

| Variables                  | Lake Kabetogama (Site 1) | Namakan Lake (Site 1) | Rainy Lake (Site 1) |
|----------------------------|--------------------------|----------------------|---------------------|
| % variance explained       | 19.4                     | 14.2                 | 21.2                |
| % variance explained       | 23.6                     | 21.4                 | 8.0                 |
| (predictors)               |                          |                      |                     |
| (mean Yellow Perch Hg ng per g DW) |                       |                      |                     |
| Loadings                   |                          |                      |                     |
| Annual maximum WL          | –                        | –                    | –                   |
| Annual WL rise             | –                        | –                    | –                   |
| Change in maximum WL from last year | –                    | –                    | –                   |
| Annual minimum WL          | –                        | 0.38                 | –0.34               |
| Annual mean WL             | –                        | –                    | –                   |
| Annual standard deviation WL | –                    | –                    | –                   |
| Spring maximum WL          | –                        | –                    | –                   |
| Spring WL rise             | –                        | –                    | –                   |
| Spring minimum WL          | –                        | 0.36                 | –0.34               |
| Spring mean WL             | –                        | –                    | –                   |
| Spring standard deviation WL | –0.31               | –                    | –                   |
| Summer maximum WL          | –                        | –                    | –                   |
| Summer WL rise             | –                        | –                    | –                   |
| Summer minimum WL          | –                        | –                    | –0.31               |
| Summer mean WL             | –                        | –                    | –                   |
| Summer standard deviation | –                        | –                    | –                   |
| Degree-days (0°C)          | 0.36                     | 0.34                 | –                   |
| Degree-days (5°C)          | 0.38                     | 0.33                 | 0.31                |
| Degree-days (10°C)         | 0.40                     | 0.35                 | 0.32                |
| Degree-days (15°C)         | 0.41                     | 0.38                 | 0.30                |
| Precipitation (mm)         | –                        | –                    | –                   |
| Sulfate deposition         | –                        | –                    | –                   |
| Mercury deposition         | –                        | –                    | –                   |

Notes: Loadings are equivalent to a correlation between the component and the individual variable. Only loadings of 0.3 or more are shown. Cross-validation supported the inclusion of each of these components. Each of these sites had >12 yr of data. Spring refers to April–June; summer refers to July–September. Crane Lake and Sand Point Lake did not have strongly supported second components, while Little Vermilion Lake had no strongly supported components.

Many of the WL metrics covary, so identifying a single WL metric to use as a surrogate for WL effects is perhaps an oversimplification. The use of partial least-squares regression (PLSR) allowed us to incorporate many different WL metrics (and other environmental variables) into a more inclusive model than had been used in previous analyses (Larson et al. 2014). The PLSR models also demonstrated lake-specific differences analogous to those seen when using individual WL metrics (Larson et al. 2014). For example, PLSR could not identify any WL-influenced latent variables that might be driving annual variation in Little Vermilion Lake, consistent with the single-metric correlations. But PLSR also was able to identify some commonalities among lakes that the previous studies and analyses did not detect. For example, Yellow Perch mercury content in Lake Kabetogama appeared unrelated to WL effects in Larson et al.’s (2014) analysis, but in the PLSR analysis, a latent component correlated with a few WL metrics appeared to be strongly associated with annual variation in fish mercury content. A very similar latent component appeared in every other lake (except Little Vermilion Lake). Although it is still unclear why quantitative differences exist in the magnitude of these WL–fish mercury associations among lakes, qualitatively these associations appear more similar among lakes than they did in the single variable modeling approach (Larson et al. 2014). Whatever spatial differences do occur also appears to be driven by lake-wide characteristics, since different sites within the same lake appeared to vary similarly over time (although the magnitude of the concentration may not be identical at different sites within the same lake). This also was the conclusion of
Sorensen et al. (2005) in an overlapping set of lakes but a shorter sampling interval. Overall, the PLSR models suggested that WL rise (in spring and in some lakes annually) was positively associated with young-of-year Yellow Perch mercury content. These are WL characteristics that were altered in five of these lakes (all but Rainy Lake) when a new WL management regime was adopted by the International Joint Commission in 2000 (IJC 2000). These rule curves reduced the winter drawdown, and thus the spring rise, in Namakan Reservoir by approximately 1 m, whereas changes in Rainy Lake were minimal.

Because a detailed hydrological model exists that can be used to compare what the WL fluctuations would have been given two different management scenarios (Thompson 2015), we were able to quantitatively compare Yellow Perch Hg content under the two most recent water level management regimes (the 1970 and 2000 Rule Curves). The effect of the WL management change is most apparent in Crane Lake and Sand Point Lake, where the PLSR model indicates that Yellow Perch Hg content would be lower under the 2000 Rule Curves than the 1970 Rule Curves. For Lake Kabetogama and Namakan Lake, the PLSR model

Fig. 4. Predicted whole fish young-of-year Yellow Perch total mercury content (ng g$^{-1}$ dry mass) in response to changes in water level (WL) management. Predictions are based on partial least-squares regression (PLSR) models and two WL management scenarios generated from a hydrological model spanning 2000–2014. Points are means of jackknifed PLSR models (error bars are standard deviations from the jackknifed estimates). The solid line is a 1:1 line.
indicates that the 2000 Rule Curve would have slightly less fish Hg content compared with the 1970 Rule Curve. Finally, for Rainy Lake there was no difference in fish Hg content between these Rule Curve scenarios, as expected because the WL management did not substantially change for Rainy Lake. Overall, these results suggest that the implementation of the 2000 Rule Curves likely decreased Yellow Perch mercury content in the lakes of the Namakan Reservoir complex, relative to what would have occurred under the 1970 Rule Curves.

Methylmercury contamination of fisheries remains a major management concern (Sandheinrich and Wiener 2011), and it appears that certain WL management strategies may influence the magnitude of this problem. Previous research has shown that differences in reservoir construction, initial inundation, and overall purpose may influence mercury content in fish (Dembkowski et al. 2014, Willacker et al. 2016), but here we show that different WL management scenarios in the Rainy Lake–Namakan Reservoir complex were associated with changes in fish mercury content and similar results might be expected from other impounded lakes. The management for methylmercury contamination is rarely the only consideration in WL management, but models such as those developed in this study could be used to evaluate different WL management scenarios so that consideration for multiple uses and ecosystem services of a waterway could be incorporated.

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**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3465/full