Predicting mercury levels in yellow perch: use of water chemistry, trophic ecology, and spatial traits

Ben K. Greenfield, Thomas R. Hrabik, Chris J. Harvey, and Stephen R. Carpenter

Abstract: Recent research suggests that wetland abundance surrounding lakes, fish trophic position, and fish community composition may influence the bioavailability of mercury (Hg) to fish. To compare the importance of these spatial and biological factors to chemical factors known to influence bioavailability, we determined the relationship between 24 lake traits and Hg concentrations in yellow perch (*Perca flavescens*; whole fish samples) for 43 northern Wisconsin lakes. Independent variables included biological traits such as fish trophic position and body condition, spatial traits such as lake hydrologic position and surrounding wetland abundance, and chemical traits such as pH and water color. The strongest predictor of fish Hg levels was pH (R^2 = 0.42; p < 0.002). Of the biological traits measured, yellow perch body condition explained significant additional variation (final R^2 = 0.54; p = 0.024). Trophic position explained limited variability and population abundance of planktivores and piscivores were not correlated to perch Hg levels. Regression tree models indicated that small lakes with greater than 6% wetland in their watershed have moderately elevated fish Hg levels. Our results indicate that within-lake chemistry and fish growth patterns are stronger correlates of Hg levels in yellow perch than spatial traits, trophic position, or fish community attributes.

Résumé : Des travaux récents laissent croire que l'abondance des terres humides autour d'un lac, la position trophique des poissons et la composition de la communauté ichtyenne peuvent affecter la biodisponibilité du mercure aux poissons. Afin de comparer l'importance de ces facteurs spatiaux et biologiques avec celle des facteurs chimiques connus pour leur influence sur la biodisponibilité, nous avons déterminé la relation entre 24 caractéristiques de 43 lacs du nord du Wisconsin et les concentrations de mercure chez la Perchaude (*Perca flavescens*; échantillons de poissons entiers). Les variables indépendantes incluent des caractéristiques biologiques, telles que la position trophique des poissons et leur condition physique; les variables spatiales comprennent, par exemple, la position hydrologique du lac et l'abondance des terres humides adjacentes; les variables chimiques regroupent, entre autres, le pH et la couleur de l'eau. La variable explicative la plus significative de la concentration de mercure chez les poissons est le pH (R^2 = 0,42; p < 0,002). Parmi les caractéristiques biologiques mesurées, la condition physique des Perchaudes explique une partie significative additionnelle de la variation (R^2 final = 0,54; p = 0,024). La position trophique n'explique que peu de la variabilité et il n'y a pas de corrélation entre l'abondance des populations de planctonophages et de piscivores et les concentrations de mercure chez les Perchaudes. Des modèles d'arbres de régression indiquent que les petits lacs qui ont plus de 6% de terres humides dans leur bassin versant ont des concentrations moyennes de mercure chez les poissons. Nos résultats montrent que les caractéristiques chimiques du lac même et les taux de croissance des poissons sont de meilleures variables explicatives des concentrations de mercure chez les Perchaudes que les caractéristiques spatiales, la position trophique ou la structure de la communauté de poissons.

[Traduit par la Rédaction]

Introduction

Atmospherically deposited mercury (Hg) bioaccumulates in freshwater food webs. Therefore, many relatively undisturbed lakes have elevated levels of Hg in fish and wildlife. Elevated Hg concentrations in planktivorous fishes can be toxic for piscivorous fishes and wildlife and hazardous for human consumption (Wiener and Spry 1996). Methyl mercury (MeHg) is the predominant form in fish tissue (Grieb et al. 1990) because it is efficiently retained in tissue and biomagnifies in aquatic food webs (Kidd et al. 1995). Previous studies on the causes of elevated fish Hg levels have established the importance of among-lake differences in limnological characteristics and morphometry. Reductions in pH (Grieb et al. 1990; Suns and Hitchin 1990; Watras et al. 1998), increases in dissolved organic matter (Driscoll et al.

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B.K. Greenfield,[1,2] T.R. Hrabik,[3] C.J. Harvey, and S.R. Carpenter. Center for Limnology, University of Wisconsin–Madison, Madison, WI 53706, U.S.A.

[1]Corresponding author (e-mail: ben02@earthlink.net).
[2]Present address: San Francisco Estuary Institute, 180 Richmond Field Station, 1325 South 46th Street, Richmond, CA 94804, U.S.A.
[3]Present address: Department of Biology, University of Minnesota–Duluth, 211 Life Science, 10 University Drive, Duluth, MN 55812, U.S.A.

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1995; Watras et al. 1998), and reductions in lake size (Bodaly et al. 1993) all correlate with higher fish Hg levels. However, a lake's surrounding landscape or its ecological community composition may also influence Hg bioaccumulation in fish. We examine whether ecological or landscape factors influence Hg accumulation to the same degree as limnological and morphometric characteristics.

Models of Hg bioaccumulation often incorporate trophic position under the assumption that trophic position significantly influences bioaccumulation (Cabana and Rasmussen 1994). In piscivorous fishes, increased trophic position increases Hg bioaccumulation (Cabana and Rasmussen 1994; Cabana et al. 1994; Kidd et al. 1995). However, little is known about the influence of trophic position on contaminant levels for relatively short-lived, omnivorous fishes, which may be important intermediate links for biomagnification. Relative trophic position can be measured using stable isotope analysis, in which an organism's nitrogen isotope ratio is compared to that of other organisms in a food web (Peterson and Fry 1987).

Ecological interactions may cause increased fish contaminant levels by influencing contaminant levels of food or growth rate of the fish. Few studies have examined population abundances within the fish community to determine potential impacts of predation and competition on Hg accumulation rates. In two studies, reduced population abundance caused decreases in Hg accumulation due to increased growth rate (Verta 1990) or reduced consumption of contaminated benthos (Wong et al. 1997). These results suggest that in lakes with dense fish populations, fish would exhibit reduced growth rates, causing less growth dilution and leading to higher tissue Hg concentrations. Fish body condition (a measure of weight to length ratio) has been observed to correlate negatively with Hg levels (Suns and Hitchin 1990). Body condition indicates growth efficiency (Willis et al. 1991; Fechhelm et al. 1995) and potential for growth dilution.

Spatial traits of lakes can be measured remotely using geographic information systems, and may allow natural resource managers to efficiently screen large numbers of lakes for those likely to have high fish Hg levels (Gergel et al. 1999). A lake's spatial traits include both its relative position in a watershed and the abundance of land-cover types surrounding the lake. Lake order, analogous to stream order, identifies lakes according to their hydrologic position with respect to other lakes and associated streams. Groundwater connection increases as lake order increases, causing increased alkalinity (Riera et al. 2000). Additionally, as lake order increases, catchment area increases, causing increased water color (Riera et al. 2000). Because both color and alkalinity affect fish Hg levels (Grieb et al. 1990; Watras et al. 1998), and because lake order is easy to measure, we evaluate lake order as a potential predictor of fish Hg concentrations.

Correlations between watershed attributes and aqueous Hg levels within a lake have been demonstrated through research at the landscape scale. Wetlands have been identified as significant sources of MeHg to adjacent lakes and rivers (Rudd 1995). Methyl mercury is produced and stored in wetlands (Rudd 1995), and wetland abundance correlates positively with river water MeHg concentration (Hurley et al. 1995). Additionally, wetlands are sources of dissolved organic matter, which reduces oxygen levels, thereby facilitating Hg methylation by sulfate-reducing bacteria (Gilmour et al. 1992; Crisman et al. 1998). However, little is known about the relationship between wetland abundance surrounding a lake and Hg concentrations in the lake biota (but see Driscoll et al. 1995).

In this study, we compare Hg concentrations in yellow perch (*Perca flavescens*) to the chemical, biological, and spatial attributes of 43 northern Wisconsin lakes. Our specific hypotheses are as follows: (*i*) yellow perch trophic position and planktivore population size will be positively correlated with Hg concentrations due to increased bioaccumulation and reduced growth dilution, respectively; (*ii*) yellow perch body condition will be negatively correlated to fish Hg because it will indicate fish growth efficiency; (*iii*) wetland abundance will be positively correlated to fish Hg, because wetlands are sources of MeHg; and (*iv*) lake hydrologic position will indicate Hg concentrations. Regarding hydrologic position, we expect to find the highest fish Hg levels in low alkalinity seepage lakes, intermediate Hg levels in lowland drainage lakes, which are alkaline but have elevated water color, and the lowest Hg levels in headwater drainage lakes. Hydrologic position and wetland abundance would be particularly useful predictors, because they would allow resource managers to identify lakes for potential consumption advisories using geographic information systems data.

Methods

Study site

Forty-three lakes from the Northern Highland Lake District, Wisconsin, U.S.A. were chosen for this study (46°N, 89°W). This region is characterized by 30–50 m of non-calcareous, sandy tills overlying granitic bedrock (Riera et al. 2000). Chosen lakes included all regional hydrologic types (drainage lakes, headwater lakes, and seepage lakes; Table 1). The study lakes also ranged widely in alkalinity and surrounding wetland abundance (Table 2). Five of the lakes have been routinely sampled as part of the North Temperate Lakes Long Term Ecological Research site (NTL-LTER), and one lake has been sampled as part of the Cascading Trophic Interactions Project (Bade et al. 1998).

Chemical data

Lakes were monitored for pH, alkalinity, total phosphorus, chlorophyll *a*, and color during June, July, and August of 1997–1999 (Table 2). Except as specified, all chemical data were collected and analyzed according to NTL-LTER protocols, which are available to the public for inspection at the NTL-LTER Web site (http://www.limnology.wisc.edu/catalog.html). Crampton Lake was sampled according to protocols outlined in Bade et al. (1998). Samples were collected monthly in each lake during the same season fish were collected with the exception that color data were collected in the year prior to fish collection for the NTL-LTER lakes and Crampton Lake. Total phosphorus, chlorophyll *a*, and pH were averaged over June, July, and August. Alkalinity and color were determined once, during midsummer. All parameters other than chlorophyll were collected 1 m below the lake surface, except in the five NTL-LTER lakes, where they were collected at the water surface. Color samples were filtered through 0.4-μm nucleopore filters and analyzed at 440 nm. Epilimnetic chlorophyll concentration was measured monthly to estimate primary productivity. Chlorophyll samples were collected on Fisher Type A/E glass fiber filters by raising and lowering sampling tubing at a constant rate while drawing water with a peristaltic pump. Samples were homogenized and stored in

Table 1. Characteristics of the sampled lakes, including area, hydrologic position, fish length, Hg concentration, number of fish sampled, and whether the lake was sampled for all fish biology parameters. Lake order is placed in parentheses next to hydrologic position.

Lake name	Area (ha)	Hydrologic position[a]	Fish length (mm)		Fish Hg ($\mu g \cdot g^{-1}$)		N	Biological sampling
			Mean	SD	Mean	SD		
Allequash[b]	174	D (1)	183	9.2	0.057	0.0106	5	Y
Arrowhead	38	H (0)	153	6.6	0.025	0.0023	3	Y
Beaver	25	D (2)	164	25.8	0.084	0.0258	5	
Big	325	D (3)	145	13.2	0.036	0.0098	3	Y
Big Gibson	48	S (–2)	156	23.5	0.141	0.0384	5	
Big Muskellunge[b]	357	S (–1)	144	11.5	0.044	0.0128	4	Y
Boulder	217	D (3)	97	20.2	0.054	0.0077	5	Y
Brandy	44	D (2)	131	36.4	0.048	0.0079	9	Y
Crampton[c]	26	S (–2)	136	5.5	0.170	0.0346	3	Y
Crystal[b]	36	S (–2)	208	3.5	0.101	0.0597	3	Y
Diamond	48	S (–2)	128	36.2	0.217	0.0841	6	Y
Flora	38	H (0)	138	15.7	0.139	0.0415	3	Y
Ike Walton	569	S (–1)	159	15.6	0.140	0.0141	2	
Island	361	D (4)	134	26.5	0.055	0.0181	6	Y
Johnson	33	D (2)	156	6.1	0.053	0.0232	3	Y
Katherine	214	H (0)	211	33.2	0.080	0.0212	2	
Katinka	70	S (–2)	149	2.1	0.066	0.0164	3	Y
Lehto	32	H (0)	127	26.2	0.106	0.0629	2	
Little Crooked	61	D (2)	151	9.3	0.075	0.0141	3	Y
Little Spider	87	H (0)	155	21.3	0.040	0.0045	7	
Little Sugarbush	17	S (–2)	105	25.1	0.048	0.0104	5	Y
Little Trout	408	S (–1)	140	35.4	0.042	0.0150	4	Y
Lower Kaubeshine	79	D (1)	143	35.9	0.043	0.0144	7	Y
Lynx	121	H (0)	137	8.6	0.110	0.0100	3	Y
McCullough	90	D (2)	155	1.4	0.068	0.0057	2	
Mid	104	D (2)	163	21.2	0.066	0.0163	2	
Minocqua	809	D (2)	171	17.7	0.064	0.0142	3	
Muskesin	46	S (–2)	146	32.1	0.120	0.0410	4	Y
Nixon	49	D (2)	154	22.9	0.091	0.0201	5	
Partridge	96	H (0)	152	19	0.021	0.0097	4	
Randall	48	D (2)	152	33.2	0.068	0.0092	2	
Round	72	D (3)	111	30.5	0.067	0.0307	8	Y
Sanford	36	H (0)	133	39.8	0.130	0.0721	6	Y
Sparkling[b]	64	S (–2)	142	14.7	0.058	0.0148	3	Y
Statenaker	84	S (–2)	144	24.7	0.103	0.0172	5	Y
Stearns	96	S (–2)	126	34.3	0.037	0.0143	7	Y
Tomahawk	1495	D (2)	142	12.6	0.042	0.0025	3	
Trout[b]	1568	D (2)	161	27	0.077	0.0215	4	Y
Upper Kaubeshine	71	H (0)	135	43.8	0.045	0.0106	7	Y
White Birch	46	D (1)	151	10.6	0.053	0.0122	3	Y
White Sand	299	D (2)	135	16	0.041	0.0183	4	Y
Wild Rice	152	D (3)	120	38.3	0.068	0.0277	7	Y
Wildcat	142	H (0)	146	5.3	0.015	0.0010	3	Y

Note: SD, standard deviation.
[a]S = seepage; H = headwater; D = drainage; lake order in parentheses.
[b]NTL-LTER lake.
[c]Cascading Trophic Interactions lake.

methanol for 24 h prior to spectrophotometric determination of chlorophyll concentration. For the NTL-LTER lakes, chlorophyll data were taken from Sanderson (1998).

Biological data

Biological traits measured included yellow perch body condition, age, total length, length at ages 1–3, total Hg concentration, stable nitrogen isotope ($\delta^{15}N$) signature, and population density, total density of other planktivorous fishes, and predator density (Table 2). Fish sampling was conducted between June and August in 1998 and 1999. Crampton Lake was sampled in 1997 and 1999. Yellow perch were collected by a combination of angling, beach seines, vertical gill nets, fyke nets, and electrofishing.

To evaluate the impact of planktivore and piscivore density, 30 of the lakes were sampled to estimate relative abundances of major feeding guilds. In these lakes, three fyke nets were set in the litto-

Table 2. Descriptive statistics of selected variables measured in the study lakes during the summers of 1997–1999. Transformation column indicates the transformation that was used to achieve normality prior to linear regression analysis.

Attribute	No. lakes	Minimum	Maximum	Mean	SD	Transformation
Limnology						
Alkalinity (meq·L^{-1})	43	7	1 859	569	395	Square root
Phosphorus (μg·L^{-1})	43	2.3	30.0	13.2	7.1	Square root
Chlorophyll (μg·L^{-1})	43	1.4	35.5	7.0	6.2	Log
Water color (440 nm)	43	0.22	6.02	1.45	1.19	Log
pH	43	5.6	9.1	7.7	0.8	None
Fish biology						
Yellow perch abundance	30	6	1 385	244	327	Log
Other planktivore abundance	30	5	1 288	288	346	Log
Piscivore abundance	30	3	518	92	104	Log
Perch body condition	30	–0.19	0.17	0.00	0.08	None
Perch Hg concentration (μg·g^{-1})	43	0.02	0.22	0.07	0.04	Log
Perch corrected $\delta^{15}N$	43	1.3	8.1	4.7	1.9	None
Perch length (mm)	43	97	211	146	22	None
Length at age 1 (mm)	30	48	86	63	10	Log
Perch age (years)	30	1[a]	7[a]	3	1.0	Square root
Spatial						
Lake order	43	–2	4	0.5	1.8	None
Total watershed area (ha)	42	66	2 541	539	571	Log
Percent wetlands	43	0	76	17	17	Arcsin(square root)
Maximum depth (m)	43	2	36	12	7.6	Square root
Lake area (ha)	43	17	1 568	204	337	$(Log)^{-1}$
SDF[b]	43	1.04	4.21	1.88	0.66	Log
Perimeter (m)	43	1327	49 927	8665	9826	$(Log)^{-1}$

Note: SD, standard deviation.
[a]Youngest and oldest fish; averages across lakes were 1.3 and 5.7 years, respectively.
[b]SDF = shoreline development factor = length / $[2(\pi \cdot \text{area})^{0.5}]$.

ral zone and a vertical gill net with five mesh sizes (19-, 32-, 51-, 64-, and 89-mm stretch mesh) was set in the pelagic zone for one diel cycle. Additionally, two 30-min electrofishing transects were performed. We grouped fishes as planktivores or piscivores based on general feeding habits described in Becker (1983). Piscivorous fish species included burbot (*Lota lota*), lake trout (*Salvelinus namaycush*), northern pike (*Esox lucius*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieui*), walleye (*Stizostedion vitreum*), and muskellunge (*Esox masquinongy*). Planktivores included pumpkinseed (*Lepomis gibbosus*), rock bass (*Ambloplites rupestris*), warmouth (*Lepomis gulosus*), black crappie (*Pomoxis nigromaculatus*), and bluegill (*Lepomis macrochirus*).

Yellow perch relative body condition was based on residuals from a linear regression of log-transformed total length and body mass (n = 1487) (Fechhelm et al. 1995). Fish under 75 mm were eliminated from the analysis owing to the difficulty of measuring their mass in the field. Twenty-seven extreme outliers were removed using a studentized residual test. The remaining 1460 residuals were averaged by lake to calculate each lake's relative body condition. Yellow perch age and length at ages 1–3 were determined by reading at least five scales collected posterior to the pectoral fin, assuming a constant size ratio of body length to scale diameter.

We determined the tissue Hg wet weight concentration of 183 fish from the 43 study lakes. The number of fish sampled per lake ranged between 2 and 9, with at least three fish sampled for 38 of the lakes. When possible, fish chosen for analysis were approximately 150 mm in length, to reduce variability in Hg concentrations caused by variability in fish length (Table 1). Whole fish were ground and acid digested and total Hg concentration was determined using flow-injection, cold vapor atomic absorption spectroscopy at the Wisconsin State Lab of Hygiene (Sullivan and Delfino 1982). The limit of detection is 4 ng·g^{-1} and the limit of quantification is 10 ng·g^{-1}. Quality control included analytical and procedural blanks, calibration standards, a standard reference material (lobster hepatopancreas, National Research Council of Canada), and recovery of spiked samples. Differences between replicates averaged 7% (n = 21, standard deviation, SD = 7%) and recovery of spikes averaged 95% (n = 22, SD = 8%). For 14 of the fish, ranging in whole body concentration from 0.03–0.25 μg·g^{-1}, a muscle sample was also analyzed to enable determination of the muscle to body concentration ratio.

As a potential predictor of fish Hg levels, we calculated yellow perch relative trophic position using stable isotope analysis. Trophic position was estimated for each lake as average perch $\delta^{15}N$ minus Cladocera $\delta^{15}N$ ($\delta^{15}N = [(R_{sample}/R_{standard}) - 1]1000$, where $R = {}^{15}N/{}^{14}N$; Peterson and Fry 1987). While $\delta^{15}N$ may vary among lakes for several reasons (Gu et al. 1996), the difference between perch and Cladocera within a lake should be proportional to the trophic position of perch relative to herbivores (Cabana and Rasmussen 1996). Cladocera were collected for stable isotope analysis using replicate water column tows of a 150-μm mesh Wisconsin net. From each lake several hundred individual herbivorous Cladocera were sorted, pooled, and dried for stable isotope analysis. Ground whole body fish samples were dried at 65°C and analyzed for $\delta^{15}N$. Samples were analyzed using a Micromass NC2500 continuous-flow mass spectrometer (U.S. Environmental Protection Agency, Mid-Continent Ecology Division, Duluth, Minn.) and a Finnigan Delta+ infrared mass spectrometer (Water Research Center, University of Alaska, Fairbanks, Alaska). Seven paired samples indicated no significant difference between machines.

Table 3. Pearson product–moment correlation between yellow perch Hg and selected lake attributes.

Attribute	No. lakes	Correlation coefficient
Alkalinity	43	–0.65
pH	43	–0.65
Body condition	30	–0.59
Corrected $\delta^{15}N$	43	0.38
Lake order	43	–0.26
Water color	43	0.25
Length at age 1	30	0.23
Length at age 2	30	–0.23
Length at age 3	28	–0.11
Length	43	0.07
Age	30	0.02

Spatial data

Spatial data included lake morphometry, watershed area, lake order, and surrounding wetland abundance (Table 2). Data on lake area, perimeter, maximum depth, and watershed area were obtained with ArcView using methods and sources described in Gergel et al. (1999). We define watershed area as the direct drainage watershed. In drainage lakes, the watershed boundary extended up to the outlet of the immediate upstream lake. Total watershed area, terrestrial watershed area, and total watershed to lake area ratio were all examined. Lake order was determined using a modification of the method of Riera et al. (2000). Lake order is a numerical surrogate for groundwater influx and hydrologic position along a drainage network, with the highest number indicating the lake lowest in a watershed. We define lake order as follows: –2 indicates isolated seepage lakes, –1 indicates seepage lakes connected by intermittent streams, 0 indicates headwater drainage lakes, and 1 through 4 indicate drainage lakes, with the number indicating the order of the stream that exits the lake (Riera et al. 2000). Wetland proportion was determined for a zone 500 m distant from the lakeshore that fell within the drainage area. Wetlands were defined using the methods of Gergel et al. (1999) and included terrestrial wetlands, emergent macrophytes, and floating macrophytes. Wetland proportion data were arcsin(square root) transformed.

Statistical analyses

Data were categorized as chemistry, fish biology, or spatial traits (Table 2) and models were built using each separate category and all categories in combination. Regression trees and linear regression were both used to determine the best fitting models. Regression trees are a binary partitioning approach whereby a data set is progressively split into subsets that most significantly reduce the variability of the response variable (Clark and Pregibon 1992). We did not transform predictor variables because regression tree results are invariant to predictor variable transformation (Clark and Pregibon 1992). For each group of potential predictor variables, we built trees in which the minimum number of lakes per node was five and the minimum proportionate reduction of error (PRE) per split was 0.01. Of the resulting tree, we determined optimal tree size by cross-validation and tree pruning (Clark and Pregibon 1992; Lamon and Stow 1999). Specifically, for each potential tree, at each potential tree size, the data set was split into 10 subsets, a separate tree was built in the absence of each subset, and the accuracy with which the tree predicted each subset was determined. Cross-validation was repeated by bootstrapping 1000 times and the tree size with the lowest average variance was selected. In instances where the difference was ambiguous between tree sizes, we used a combination of box plot inspections and biological interpretation to determine optimum tree size. Residual plots of final trees were examined for homoscedasticity and normality. For final tree results, we report PRE as an indicator of the total amount of variability that a specific tree explained.

Forward selection stepwise linear regression was performed following Draper and Smith (1998). We built models using all potential predictor variables and a subset of predictor variables chosen based on Pearson product–moment correlations and visual inspection. Addition and removal of variables were conducted manually based on p values, biological interpretation, and examination of plots. Unless otherwise noted, the cutoff point for predictor variable addition was $p < 0.05$; evaluations at higher cutoff levels ($p < 0.10$) did not change the final results observed. We used standard residual plots to examine final models for homoscedasticity and normality, and when necessary, transformed predictor variables (Table 2). For all models, Hg concentration was log transformed and then averaged by lake, unless otherwise specified. All correlation coefficient (r) values reported in the text are Pearson product–moment correlation coefficients.

Results

Within- versus among-lake variability

The tissue Hg concentration of the 183 sampled fish ranged from 0.01–0.31 $\mu g \cdot g^{-1}$ (Table 1). The mean concentration by lake was 0.075 $\mu g \cdot g^{-1}$, the standard deviation averaged 0.021, and the standard error averaged 0.011. Analysis of covariance using lake as a categorical predictor and fish length as a covariate indicated that the majority of variability in fish Hg levels was explained by interlake variations ($R^2 = 0.78$; $p < 0.0001$). Fish length explained a significant but very small proportion of variance ($R^2 = 0.04$; $p < 0.0001$). The effects of among-lake variation (MS = 1.23; 42 df) and fish length (MS = 2.91; 1 df) were greater than unexplained variance (MS = 0.08; 139 df). Regression analysis of the ratio of muscle (M) to whole body (B) Hg concentration produced a relationship of $B = 0.004 + 0.64M$ ($R^2 = 0.995$; $p < 0.0001$; $n = 14$).

Fish Hg was most strongly correlated with alkalinity and pH. Mercury concentration was negatively correlated with body condition and positively related to corrected $\delta^{15}N$. Correlation with age, total length, and length at ages 1–3 (indices of growth rate) were relatively weak (Table 3).

Regression tree analysis

Regression trees were built using exclusively chemical, biological, or spatial data. Of the three types of data, trees based on biological data explained the most variability in fish Hg levels, with a total proportionate reduction of error (PRE) of 0.64. Trees based on limnological data explained a similar amount of variability (PRE = 0.56) and spatial trees explained the least variability (PRE = 0.33).

The biological tree displayed highest Hg levels for fish with low relative body condition and lowest Hg levels for fish with high body condition and low $\delta^{15}N$ signature (Fig. 1). The limnological tree indicated that Hg levels were highest in lakes of pH less than 6.7 (Fig. 2). The spatial tree indicated that small lakes (area < 63.9 ha) with abundant wetlands (abundance > 5.7%) had elevated Hg levels (Fig. 3). Among the three separate regression trees, the most significant single predictors observed were pH, which reduced er-

Fig. 1. Final tree results for biological predictors of fish Hg levels. Mean Hg levels are reported (μg·g^{-1} wet weight), with the higher levels in right-hand branches. PRE, proportionate reduction of error; condition, yellow perch body condition; δ^{15}N, perch corrected nitrogen isotope signature.

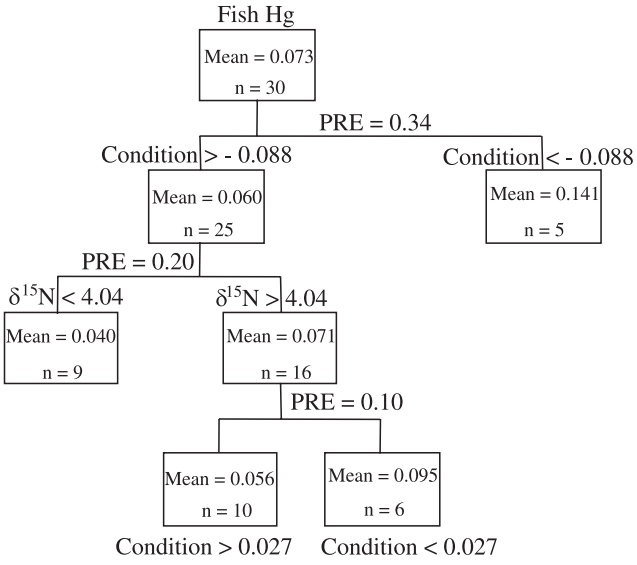


Fig. 2. Final tree results for chemical predictors of fish Hg levels. Mean Hg levels are reported (μg·g^{-1} wet weight), with the higher levels in right-hand branches. PRE, proportionate reduction of error; P, epilimnetic phosphorus (μg·L^{-1}).

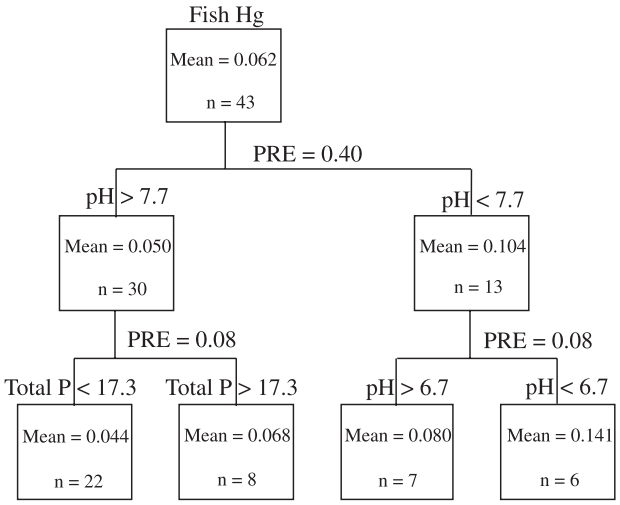


Fig. 3. Final tree results for spatial predictors of fish Hg levels. Mean Hg levels are reported (μg·g^{-1} wet weight), with the higher levels in right-hand branches. PRE, proportionate reduction of error; area, lake area (ha).

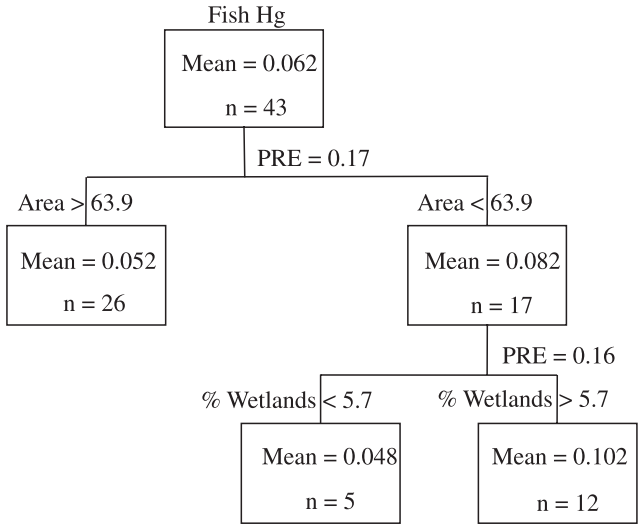
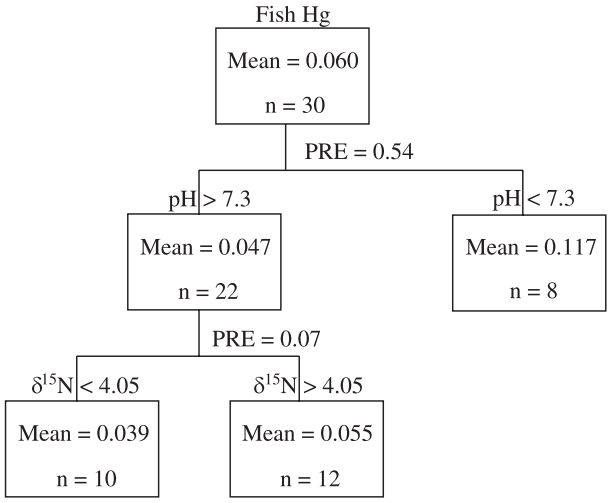


Fig. 4. Final tree results of tree combining the best predictors generated in separate models. Mean Hg levels are reported (μg·g^{-1} wet weight), with the higher levels in right-hand branches. PRE, proportionate reduction of error; δ^{15}N, perch corrected nitrogen isotope signature.



ror by 0.48 over two splits, and fish body condition, which reduced error by 0.44 over two splits.

To evaluate the relative importance of limnological, biological, and spatial predictors in the same model, we built a tree using the predictors retained in the separate tree models: pH, phosphorus, fish body condition, fish δ^{15}N, lake area, and percent wetland abundance (Fig. 4). In this tree, the majority of variability was explained by pH, with a PRE of 0.54. Among the lakes with pH greater than 7.3, the lowest perch Hg concentrations were found in lakes where corrected perch δ^{15}N was less than 4.05. This split improved the PRE by 0.07, producing a final model that explained 0.61 of the total variance.

Linear regression analysis

For stepwise regression, we chose six predictor variables that had relatively high correlation coefficients with Hg (Table 3): two limnological traits (pH and water color), two biological traits (body condition and corrected δ^{15}N), and two spatial traits (lake order and lake area). Additionally, we built a forward selection model including all potential predictors (Table 2). Both models selected pH and fish body

Fig. 5. The relationship between lake pH and yellow perch Hg concentration (n = 43; r = –0.65). Note log y-axis.

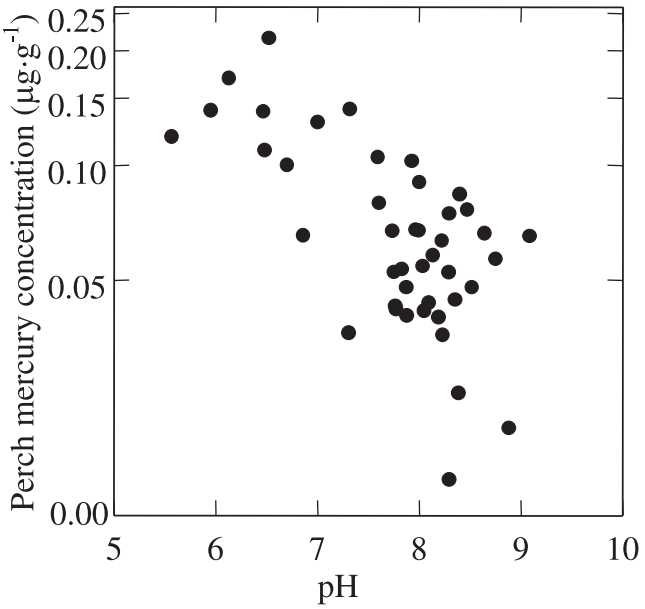
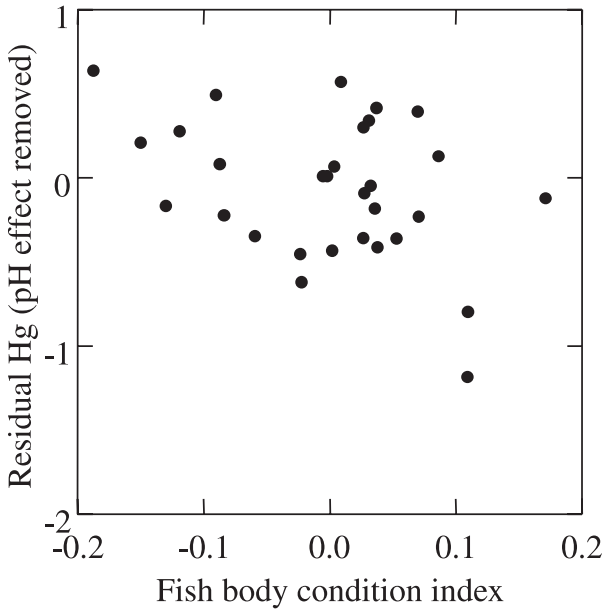


Fig. 6. The relationship between yellow perch relative body condition and the residual error from the pH vs. Hg regression (n = 30; r = –0.38).



condition in the final model. As in the limnological and mixed predictor regression tree models, pH explained the most variability in fish Hg levels (R^2 = 0.42; p = 0.0018). Fish body condition explained significant additional variability, as indicated by a partial F test (F = 5.74; p = 0.024) and also a linear regression of the residuals of the pH versus Hg regression (p = 0.037; R^2 = 0.15; Fig. 6). The combined model (log(Hg) = –0.188 – 0.343pH – 2.39condition; R^2 = 0.54) indicated that both predictors were negatively correlated with yellow perch Hg levels (Figs. 5 and 6). No predictors added significantly to the variability explained by the pH and body condition model.

Biological patterns

Regression analyses indicated that neither abundance of yellow perch (p = 0.77), planktivores (p = 0.55), nor piscivores (p = 0.1) was significantly correlated with perch Hg. However yellow perch abundance was significantly correlated with epilimnetic phosphorus (R^2 = 0.27; p = 0.003). Body condition of yellow perch, the strongest biological predictor of Hg levels in both the biological tree model and the combined multiple regression model, was also negatively correlated with pH. The correlation between condition and pH (r = –0.46) makes it difficult to confirm a significant body condition effect on Hg independent of pH. To determine whether body condition is correlated with fish Hg levels for individual fish within lakes, we performed an analysis of covariance (ANCOVA) using lakes as covariates and individual fish body condition as the predictor variable. For the 128 fish taken from the 30 lakes analyzed for biological data (Table 1), we determined that body condition was significantly related to Hg levels ($F_{1,128}$ = 4.113; p = 0.045), independently of the lake effect. Because fish in a given lake experience the same pH, we infer that body condition is related to Hg independently of pH.

Spatial patterns

Initial examination of scatterplots and correlation coefficients did not identify any spatial lake attributes as significantly related to fish Hg levels. However, based on previous research, and the results of the regression tree, we expected some influence of surrounding wetland abundance on Hg patterns. Therefore, we further examined subsets of the data to identify the circumstances in which wetland abundance was correlated to fish Hg levels. When only circumneutral lakes (7 < pH < 8.8) were examined, there was a significant but weak positive relationship (p = 0.029; R^2 = 0.15; n = 31). When lakes were further constrained by deletion of seepage lakes, this strengthened the positive association between wetland abundance and perch Hg levels (p = 0.001; R^2 = 0.39; n = 25) (Fig. 7). Thus the strongest correlation between wetland abundance and fish Hg levels was found for circumneutral drainage lakes. Lake order was not significantly related to mean Hg levels (one-way analysis of variance, ANOVA; p = 0.46; 6 df), nor was watershed area (linear regression analysis using total watershed area; p = 0.20; 40 df). However, hydrologic position did affect the variability among lakes. The coefficient of variation (CV) of fish Hg concentration was higher in seepage (CV = 0.57; n = 13) and headwater (CV = 0.66; n = 10) lakes than in drainage lakes (CV = 0.25; n = 20) (Fig. 8).

Discussion

Our findings indicate that: (*i*) lake pH explained the majority of variability in Hg concentrations; (*ii*) fish-specific biological traits (body condition or $\delta^{15}N$) explained additional variability beyond that explained by pH; and (*iii*) watershed attributes, such as percent wetland abundance, did not correlate strongly with Hg concentrations, and were generally

Fig. 7. The relationship between perch Hg concentration and proportion wetlands when drainage lakes of circumneutral pH are considered (n = 25; r = 0.63).

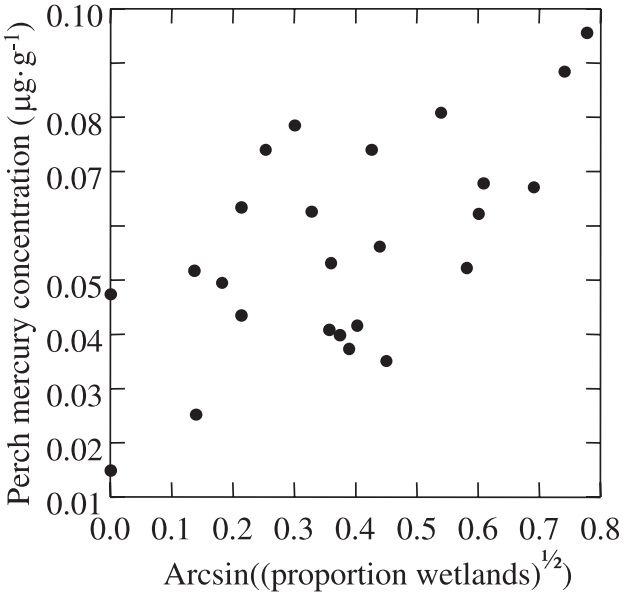
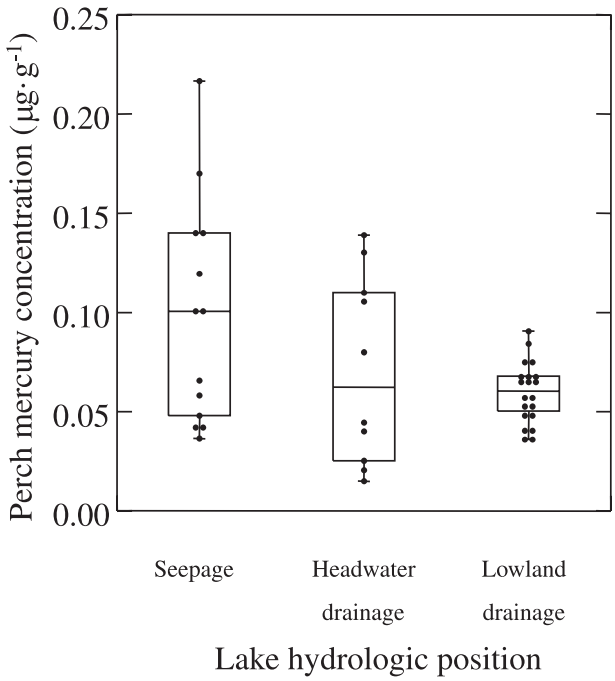


Fig. 8. The relationship between lake hydrologic position and yellow perch Hg concentration. Seepage lakes have lake orders of –2 and –1, headwater drainage lakes have lake order of 0, and lowland drainage lakes have lake orders between 1 and 4. Refer to Methods for additional description of lake order.



only relevant for subsets of the lakes. Although biological traits were significant in most models, surprisingly little variability was explained by trophic position (as estimated by $\delta^{15}N$) or community interactions (abundance of piscivores or planktivores).

When lakes were examined using a combination of all predictor types, pH explained the most variability. This finding corroborates earlier studies demonstrating the correlation between pH and Hg bioaccumulation (e.g., Grieb et al. 1990; Suns and Hitchin 1990; Watras et al. 1998). In fact, the correlation between pH and fish Hg in our study (r = –0.65) is virtually identical to that for yellow perch found by Grieb et al. (1990) (r = –0.63). Studies on the mechanism of this relationship indicate that more acidic lakes have higher aqueous MeHg concentrations, leading to higher availability at the base of the food web (Xun et al. 1987; Watras et al. 1998). Additionally, acidification may stimulate sediment MeHg production by sulfate-reducing bacteria (Gilmour et al. 1992).

Biological predictors

Other studies have demonstrated the potential importance of both diet shift (Snodgrass et al. 2000) and zooplankton food web complexity (Stemberger and Chen 1998) for MeHg bioaccumulation in omnivores. However, we found no evidence that trophic position impacted yellow perch Hg levels to the same extent as pH did. The tree models and correlation coefficients indicated that $\delta^{15}N$ was correlated with Hg concentration in yellow perch but did not explain much of the variation in Hg levels. Yellow perch are opportunistic omnivores that forage on zooplankton, benthic invertebrates, and small fishes as a function of perch size and prey availability (Becker 1983). However, yellow perch exhibit several life history attributes that may weaken the impact of trophic position on Hg levels. These include a relatively short life span, which reduces the potential for biomagnification from food-borne sources (de Freitas et al. 1974), and diet variability between pelagic and benthic sources, which may cause inconsistency in prey Hg concentrations (Cabana et al. 1994). Our results contrast with the high impact of trophic position for Hg levels in large, long-lived piscivores (Cabana et al. 1994; Kidd et al. 1995). For omnivorous yellow perch evaluated within a single region, among-lake chemical variation is much more influential on contaminant levels than dietary variation. Therefore, models of Hg accumulation based on trophic position (e.g., Cabana and Rasmussen 1994) may not be appropriate for species such as yellow perch.

Contrary to our expectations, we observed no effect of abundance of yellow perch, other planktivores, or piscivores on the concentration of Hg in yellow perch. Competition and predation have been demonstrated to impact fish Hg concentrations in a manipulated lake (Verta 1990) and increased benthivorous fish abundance has been shown to increase Hg transfer rates from benthic invertebrates to fishes (Wong et al. 1997). Nevertheless, the lack of significant relationships between our fish abundance estimates and yellow perch Hg concentrations may indicate that these mechanisms have little impact on many natural systems. In our data set, the lack of significant relationship between yellow perch abundance and Hg concentrations may result from the positive correlation between abundance and phosphorus concentration. If the increased abundances are facilitated by higher nutrient availability, then they may not indicate competition or individual growth rate.

Some comparative studies have standardized for fish size by developing a size-to-Hg regression for each lake (e.g., Bodaly et al. 1993). However, among-lake variation in fish

size explained little variability in Hg levels for the yellow perch in our study and the study by Watras et al. (1998). In our ANCOVA using a lake effect and a fish length effect, among-lake differences explained the majority of variation in Hg, indicating that for yellow perch in the size range caught during our study, fish size was relatively unimportant.

Body condition indicates fish nutritional status at a given age (Fechhelm et al. 1995) and may influence Hg bioaccumulation rate. Among the biological predictors we evaluated, fish body condition displayed the strongest correlation with Hg concentrations. Although fish body condition has received little attention in bioaccumulation literature, Suns and Hitchin (1990) demonstrate a negative relationship between fish Hg and body condition among 16 lakes. However, lake acidity impacts body condition (Mills et al. 2000). Because of limited sample size, Suns and Hitchin (1990) were unable to distinguish a relationship between body condition and Hg beyond the impact of pH.

In our study, lower pH lakes had fish with lower body condition. However, two lines of evidence in our study indicated that fish with lower body condition had higher Hg concentrations, and that this relationship was independent of pH. First of all, analysis of residuals demonstrated that once the correlation between Hg and pH was removed, Hg was still negatively correlated with body condition. Additionally, ANCOVA with a lake effect and a body condition effect showed a significant relationship between body condition and fish Hg, even after the effects of all among-lake variations (including pH) were removed.

Based on our results, we hypothesize that body condition indicates fish growth patterns that cause elevated Hg concentrations. Fast growing fishes exhibit "growth dilution"; they reach a given size more efficiently, have spent proportionately less energy consuming and respiring to reach that size, and therefore have lower tissue contaminant concentrations per unit mass (de Freitas et al. 1974; Norstrom et al. 1976). Body condition is correlated with growth rate (Willis et al. 1991) but body condition is more indicative of current environmental constraints on growth than measures of past growth. For example, growth in individual years can be variable due to fluctuations in population densities (Fechhelm et al. 1995) but scale-derived age only estimates growth rate of prior years. Because body condition changes rapidly in response to environmental perturbation (e.g., Mills et al. 2000), it will be sensitive to conditions that change growth dilution. Finally, body condition is much easier to estimate than growth rate, requiring only length and mass data. Future research could evaluate the use of body condition guidelines for fish consumption advisories.

The fact that more acidic lakes may contain fish with lower body condition has been observed in previous studies (Suns and Hitchin 1990; Mills et al. 2000), but its implications for Hg bioaccumulation merit further consideration. More acidic lakes may have fish with lower body condition because of reduced availability of preferred food items (Mills et al. 2000) or the physiological stress associated with ion balance maintenance (Dennis and Bulger 1995). We know of no examinations of whether reduced growth efficiency (as indicated by body condition) is part of the mechanism by which acidic lakes have higher Hg bioaccumulation in fish. Watras et al. (1998) observed a steeper and more significant relationship between pH and fish Hg than between pH and Hg of lower trophic levels (crustacean zooplankton or planktonic seston), suggesting that Hg biomagnification in fish (as compared to lower trophic levels) is more significant in low pH lakes. Future studies could explicitly evaluate the relationship between pH, body condition, and biomagnification to determine whether increased biomagnification is an additional mechanism for higher fish Hg concentrations in low pH lakes.

Spatial predictors

Although we selected lakes that ranged widely in lake order and wetland abundance, neither trait was strongly related to fish Hg levels. Our data did not support the hypothesis that higher fish Hg levels would occur in seepage and lowland drainage lakes. We attribute the increased variation of fish Hg concentrations among seepage lakes to the fact that those lakes have the greatest among-lake variability in pH. The variability in pH among seepage lakes results from weak connections to underlying groundwater, which reduces alkalinity (Riera et al. 2000 and references therein). The lack of increase for lowland lakes indicates that for this region, correlates of lake order such as catchment size and water color are relatively unimportant.

The spatial tree model indicated that smaller lakes have higher fish Hg levels, which is consistent with the work of Bodaly et al. (1993). They attribute the negative correlation between lake size and fish Hg to higher water temperatures in smaller lakes causing increased methylation. Observations of increased methylation in warm littoral sediments (Ramlal et al. 1993) indicate that smaller lakes have higher biota Hg levels due to increased within-lake methylation. However, reduction of lake size may also increase the effect of allochthonous inputs of organic matter by increasing the proportionate influx of wetland-derived materials compared to the total lake volume.

Despite evidence that wetlands are sources of MeHg, in this study they only exerted quantitative impacts on fish Hg levels when (*i*) within-lake chemistry was controlled for by examining only circumneutral lakes or (*ii*) there was a relatively strong potential for watershed loading into the lake (i.e., drainage lakes or small lakes). In regression tree models, wetland abundance only correlated with elevated Hg levels in small lakes, suggesting that reduction in lake size increases the potential for input of wetland-derived MeHg or methylation substrate (i.e., dissolved organic carbon, DOC), rather than simply increasing within-lake methylation rates. In our linear regression models, the observation that perch Hg and wetland abundance were only correlated in drainage lakes supports the general conclusion that lake–wetland interactions are stronger and more easily predicted for drainage lakes. This is consistent with Gergel et al. (1999), who observe that lowland lakes have stronger lake–wetland interactions in wetland input of allochthonous DOC, which may increase Hg methylation (Gilmour et al. 1992; Crisman et al. 1998) and reduce photodegradation rates (Sellers et al. 1996). When we constrained pH in the linear regression model of wetland abundance versus fish Hg, the correlation strengthened. Previous research demonstrates that pH affects Hg methylation and consequent bioavailability to fish (Xun

et al. 1987; Watras et al. 1998), and our results indicate that this within-lake Hg speciation overshadows the effect of MeHg loading from adjacent wetlands.

Although our data range widely in wetland abundance, the range in concentrations of DOC is generally lower than the range found in other studies (Driscoll et al. 1995; Gergel et al. 1995; Watras et al. 1998). As DOC has been linked to wetland loading of MeHg into lakes (Driscoll et al. 1995), the relatively weak impact of wetland abundance we observed may be partially attributable to the relatively low range in DOC.

In our study, variability among lakes in hydrologic position, surrounding habitat features, and fish community traits did not strongly influence Hg levels in yellow perch. Given our initial objective of predicting biota Hg levels using remotely sensed data, it is unfortunate that in northern Wisconsin lakes, we can best predict Hg levels in those systems lacking conditions conducive to high Hg bioaccumulation (i.e., only in alkaline systems). However, spatial features could be used to identify lakes likely to have high fish contaminant levels. For example, based on our regression tree models, lakes smaller than 64 ha and having greater than 6% wetlands within a catchment buffer strip would be the lakes most likely to have high biota Hg levels. Also, if data on pH or a correlate (e.g., alkalinity or conductivity) were readily available, they could be used in combination with hydrologic position (seepage versus drainage) and wetland abundance to identify the lakes likely to have the highest contaminant levels. In regions containing thousands of lakes, such as the Great Lakes states and provinces of the U.S.A. and Canada, such approaches may be useful to identify high-risk lakes.

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