Spatial Variability in Water Quality and Surface Sediment Diatom Assemblages in a Complex Lake Basin: Lake of the Woods, Ontario, Canada

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ABSTRACT. *Lake of the Woods (LOW) is an international waterbody spanning the Canadian provinces of Ontario and Manitoba, and the U.S. state of Minnesota. In recent years, there has been a perception that water quality has deteriorated in northern regions of the lake, with an increase in the frequency and intensity of toxin-producing cyanobacterial blooms. However, given the lack of long-term data these trends are difficult to verify. As a first step, we examine spatial and seasonal patterns in water quality in this highly complex lake on the Canadian Shield. Further, we examine surface sediment diatom assemblages across multiple sites to determine if they track within-lake differences in environmental conditions. Our results show that there are significant spatial patterns in water quality in LOW. Principal Component Analysis divides the lake into three geographic zones based primarily on algal nutrients (i.e., total phosphorus, TP), with the highest concentrations at sites proximal to Rainy River. This variation is closely tracked by sedimentary diatom assemblages, with [TP] explaining 43% of the variation in diatom assemblages across sites. The close correlation between water quality and the surface sediment diatom record indicate that paleoecological models could be used to provide data on the relative importance of natural and anthropogenic sources of nutrients to the lake.*

INDEX WORDS: *Water quality, diatoms, total phosphorus, spatial patterns, Lake of the Woods.*

INTRODUCTION

Lake of the Woods (LOW) is a waterbody of international importance, spanning the Canadian provinces of Ontario and Manitoba, and the state of Minnesota, USA. In addition, Shoal Lake, which is hydrologically linked to LOW, is a drinking water reservoir for the city of Winnipeg, Manitoba. Although algal blooms have been reported in the southern portion of the lake since the early 1800s (McElroy and Riggs 1943), anecdotal evidence suggests that water quality has deteriorated in the northern bays in recent years. Furthermore, algal identifications in the late-1990s found large popula-

tions of toxin-producing cyanobacteria at several locations in the lake (H. Kling and C. Herbert, unpublished data). In the absence of historical data, however, increases in bloom frequency and intensity are difficult to verify. Furthermore, data describing the relative importance of natural (e.g., geological) and anthropogenic sources of algal nutrients are scarce, and thus the relative sources of nutrients to the lake are not fully understood.

Due to the size and hydrological complexity of LOW (Fig. 1), the water quality is highly variable and difficult to monitor. Consequently, few studies have quantified seasonal or spatial patterns in water chemistry or biological assemblages across the lake. Recent measurements of nutrient concentrations and water transparency indicate that there is a

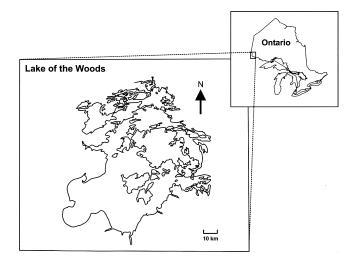*Corresponding author. E-mail: andrew.paterson@ene.gov.on.ca

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FIG. 1. *Map showing geographic location of Lake of the Woods, Ontario, Canada. Water quality and coring site locations are presented in Table 1.*

significant south to north gradient in water quality (Hissa and Mosindy 1991, Anderson *et al.* 2000). Late-summer readings of total phosphorus typically range from 20 to 50 $\mu g \cdot L^{-1}$ across the lake, with significantly higher values in southern regions. This gradient reflects differences in the morphometry of individual bays, and their proximity to the primary tributary, the Rainy River.

In cases where direct monitoring data are unavailable, lake sediments may provide a detailed archive of environmental conditions and variability through time (Smol 2002). Sediments preserve physical and chemical markers, and biological microfossils that can be examined at multiple spatial and temporal scales. For example, the remains of microscopic algae have been used extensively to understand present-day and historical water quality. Diatoms, in particular, are excellent indicators of many water quality variables (Stoermer and Smol 1999), including lake trophic status (Hall and Smol 1999), acidification (Battarbee *et al.* 1999), and climatic conditions (Smol and Cumming 2000).

The examination of single cores from the deepest basin of small to mid-sized inland lakes has been shown to be representative of average environmental conditions (Battarbee *et al.* 2001). However, comparatively few studies have examined variability in water quality and diatom communities across multiple sites in large, morphometrically-complex lakes (Kienel and Kumke 2002). In this study, we examine spatial and seasonal variability in water quality in a highly complex lake on the Canadian

Shield, with an emphasis on variation of algal nutrient concentrations. Furthermore, we examine diatom assemblages from surface sediment samples to determine whether they track within-lake differences in environmental conditions. Results from this study may be used to develop ecologically-meaningful management strategies for large lakes such as the Lake of the Woods, and to develop quantitative models for reconstructing environmental variables through time using paleolimnological techniques (Smol 2002). Moreover, the long-term development of LOW is of interest to a broad range of researchers, in addition to lake managers (e.g., Yang and Teller 2005).

METHODS

Site Description

By area, Lake of the Woods (LOW) is the second largest inland lake in the Province of Ontario, Canada. Excluding Shoal Lake to the northwest, the lake covers an area of approximately 385,000 ha, with two-thirds of its boundaries within Canada (Rusak and Mosindy 1997). At its widest dimensions, LOW spans 105 km from north to south, and 90 km from in an east-west direction (Fig. 1). The lake is hydrologically complex, comprised of a series of distinct basins and more than 14,500 islands (Heiman and Smith 1991). The main direction of flow through the lake is north through three channels into the Winnipeg River. Water levels have been managed since the mid 1890s by two dams near Kenora, Ontario, and presently, annual levels fluctuate between 0.9 and 1.2 meters (Minnesota Department of Natural Resources and Ontario Ministry of Natural Resources 1998). Rainy River enters LOW at its extreme southeast end, and provides approximately 70% of the tributary inflow to the lake. While most of the lake lies on Precambrian Shield bedrock, the southern portions of LOW and the Rainy River are underlain by old lake sediments deposited by glacial Lake Agassiz (Johnston 1915). Consequently, the large southern bay (i.e., Big Traverse Bay) is shallower, more turbid, and more productive than other regions of the lake (Rusak and Mosindy 1997).

Field and Laboratory Analyses

Twenty sampling locations were selected to span a broad gradient of total phosphorus concentrations (Fig. 1, Table 1), based on existing monitoring data (e.g., Ontario Ministry of the Environment, Lake

TABLE 1.   *Location of water quality and sediment core sampling locations, including site names and codes, geographical coordinates, and coring depths.*

Site Name	Site Code	Latitude (N)	Longitude (W)	Depth (m)
Thomspson Island North	PP1	49° 41.668	94° 29.481	20.5
Portage Bay	PP2	49° 43.542	94° 33.024	36.8
White Partridge Bay	PP3	49° 42.254	94° 35.970	14.7
Clearwater Bay West	PP4	49° 41.471	94° 47.795	53.7
Echo Bay	PP5	49° 38.129	94° 54.602	38.1
Cul-de-Sac	PP6	49° 37.564	94° 49.864	33.0
Ptarmigan Bay	PP7	49° 38.845	94° 41.478	20.9
Chisholm Island	PP8	49° 31.727	94° 23.268	16.5
Kennedy Island	PP9	49° 29.091	94° 36.352	20.0
Bishop Bay	PP10	49° 28.394	94° 48.420	9.2
Falcon Island at Monkey Rocks	PP11	49° 23.067	94° 46.099	8.7
Long Bay	PP12	49° 26.178	94° 02.569	18
Regina Bay	PP13	49° 24.094	94° 00.676	22
Whitefish Bay—Turtle Point	PP14	49° 21.372	94° 03.882	34
Whitefish Bay South	PP15	49° 12.263	94° 07.722	16
Turtle Lake	PP16	49° 11.541	94° 07.285	4.1
Sabaskong Bay	PP17	49° 09.423	94° 10.456	7.2
Little Traverse Bay	PP18	49° 15.010	94° 40.050	9.5
Bigsby Island	PP19	49° 09.002	94° 24.922	6.8
Big Traverse Bay	PP20	48° 59.868	94° 41.205	10.2

Partner Program (LPP), unpublished data). Within selected basins, sites were chosen based on lake-bed characteristics and their suitability for coring (e.g., areas of sediment deposition), and their proximity to existing Ontario Ministry of Natural Resources long-term monitoring stations. Water chemistry samples were collected in early-June and September, 2003, over a period of 3 to 5 days. In addition, monthly data collected by LPP volunteers are presented from five sites to show seasonal variation in total phosphorus concentrations. Secchi depth and temperature/oxygen profiles were taken on-site using an YSI Model 90 multimeter. Water samples were collected to the Secchi depth using a composite sampling bottle, and filtered through an 80 μm mesh filter. Phytoplankton and chlorophyll *a* were collected as unfiltered samples through a depth of two times the Secchi reading (i.e., the euphotic zone). Water samples were subsequently stored at 4°C and shipped to the Ontario Ministry of the Environment (MOE) Dorset Environmental Science Centre laboratory for analysis. All field and analytical techniques followed standard MOE protocols (Girard *et al*. 2005).

Duplicate surface sediment samples were collected at each site using a modified Glew gravity corer (Glew 1989) fitted with 90-cm Lucite core tubes (internal core diameter = 7.62 cm). In the laboratory, sediment digestion procedures followed Battarbee *et al*. (2001). The subsequent slurries were pipetted onto glass coverslips, allowed to evaporate overnight, and then mounted onto glass slides using Naphrax©, a mounting medium with a high refractive index. A minimum of 400 diatom valves were enumerated along transects using a Leica DMRB light microscope at a magnification of 1,000×. Diatom taxonomy followed Krammer and Lange-Bertalot (1986), Krammer and Lange-Bertalot (1988), Krammer and Lange-Bertalot (1991a), Krammer and Lange-Bertalot (1991b), Camburn and Charles (2000), and Ramstack *et al*. (2003).

Data Analysis

Species and environmental data were screened to identify and remove redundant or outlier variables and samples (Birks 1998). Diatom taxa that occurred at a relative abundance of at least one percent in one surface sample were included in subsequent analyses. This selection criterion reduced the total number of taxa from 121 to 36 (Table 2). Of the twenty initial sites, site PP-8 was removed from the analysis as water samples were available for June only, and no sediment cores were obtained from this location. Similarly, sediment cores could not be obtained from sites PP-14 or PP-20 on the day of sampling, and therefore diatom

TABLE 2. Diatom species names, codes, number of occurrences, effective number of occurrences (Hill's N2), and maximum and mean abundances in surface sediment from 17 sites in Lake of the Woods.

Species Name	Code	# occurrences	Hill's N2	Max	Mean
Achnanthes minutissima Kützing	AM012A	13	8.09	3.02	0.77
Amphora pediculus (Kützing) Grunow	AS001A	10	8.06	1.16	0.32
Asterionella formosa Hassall	AU031A	11	7.05	5.92	1.52
Aulacoseira alpigena (Grunow) Krammer	AU002A	13	7.74	3.61	0.98
Aulacoseira ambigua (Grunow) Simonsen	AU005A	17	9.53	27.11	7.72
Aulacoseira distans (Ehrenberg) Simonsen	AU003A	11	4.59	5.46	0.93
Aulacoseira granulata (Ehrenberg) Simonsen	AU032A	17	10.57	66.58	25.41
Aulacoseira pfaffiana (Reinsch) Krammer	AULPER	6	3.56	3.40	0.56
Aulacoseira cf. *perglabra*	AU020A	1	1.00	1.17	0.07
Aulacoseira subarctica (O. Müller) Haworth	AU020A	16	9.77	17.71	5.00
Aulacoseira cf. *subarctica*	1	3	2.64	1.16	0.14
Aulacoseira spp.	AU9999	9	4.49	15.65	2.62
Aulacoseira spp. 3	AULSP3	8	5.30	4.42	0.85
Aulacoseira valida (Grunow) Krammer	AU033A	5	3.89	2.38	0.35
Cocconeis placentula Ehrenberg	CO001A	12	8.06	1.60	0.38
Cyclostephanos dubius (Fricke) Round	CC001A	15	6.83	12.45	2.64
Cyclotella bodanica v. *lemanica* (O. Müller) Bachmann	CY058A	16	9.73	10.82	3.59
Cyclotella comensis Grunow	CY010A	9	6.02	17.36	4.23
Cyclotella michiganiana Kützing	CY005A	8	4.85	2.68	0.51
Cyclotella ocellata Pantocsek	CY009A	13	8.43	3.31	0.96
Cyclotella pseudostelligera Hustedt	CY002A	8	3.83	6.42	1.17
Fragilaria brevistriata Grunow	FR006A	13	7.58	3.20	0.73
Fragilaria capucina var. *mesolepta* (Rabenhorst) Rabenhorst	FR009B	3	2.21	1.32	0.14
Fragilaria capucina var. *vaucheriae* (Kützing) Lange-Bertalot	FR062A	12	4.91	16.12	2.72
Fragilaria construens (Ehrenberg) Grunow	FR002A	8	1.89	25.34	2.08
Fragilaria crotonensis Kitton	FR008A	14	8.57	22.39	6.67
Fragilaria pinnata Ehrenberg	FR001A	14	2.80	29.91	3.03
Fragilaria tenera (W. Smith) Lange-Bertalot	FR060A	13	6.89	5.21	1.21
Fragilaria ulna var. *acus* (Nitzch) Lange-Bertalot	FR072A	8	6.28	1.14	0.24
Gomphonema spp.	GO9999	3	1.95	1.20	0.11
Nitzschia amphibia Grunow	NI014A	3	2.15	1.05	0.10
Stephanodiscus medius Håkansson	ST014A	16	12.39	4.87	2.10
Stephanodiscus minutulus (Kützing) Cleve and Möller	ST021A	15	4.62	12.00	2.24
Stephanodiscus niagarae Ehrenberg	ST006A	17	11.25	6.93	2.71
Stephanodiscus parvus Stoermer and Håkansson	ST010A	17	9.16	24.71	6.78
Tabellaria flocculosa (Roth) KützingAC013A	TA001A	12	7.18	17.04	4.54

analysis was not completed. Although duplicate cores were taken at site PP-16, the diatom assemblage was dominated by small *Fragilaria* taxa, indicative of shallow waters and dense macrophyte growth not present at other sampling locations. This site was removed from subsequent analysis.

Prior to ordination analysis, environmental data were screened for normality and log-transformed where necessary (Table 3). Using June water chemistry, which corresponds to the period of diatom dominance in LOW (Chen *et al*. 2004), variation in water quality across sites was examined using Principal Components Analysis (PCA) (scaled species scores were divided by the standard deviation to

produce a correlation matrix; ter Braak and Šmilauer 1998). Detrended correspondence analysis (DCA), with detrending by segments, was used to determine the maximum amount of variation in the species data. Due to the long gradient length of the first DCA axis (2.58 standard deviation units), unimodal ordination techniques were deemed appropriate to explore the relationship between species and environmental data (e.g., Canonical Correspondence Analysis, CCA). However, as the number of measured environmental variables (23) exceeded the number of samples (16), correlated variables were removed to obtain a subset of 14 environmental variables. Variables were selected for removal if

TABLE 3.   Summary of physical and chemical variables measured for 20 sampling locations in Lake of the Woods in June, 2003.

Variable Name	Code	Units	Min	Max	Mean	Median	Transformation
Alkalinity	ALK	mg·L $CaCO_3$	24.90	53.20	44.46	47.45	log (x)
Aluminum	Al	µg·L^{-1}	8.60	90.00	37.04	33.50	log (x)
Calcium	Ca	mg·L^{-1}	8.04	14.90	12.55	13.00	log (x)
Chloride	Cl	mg·L^{-1}	0.01	2.46	1.48	1.55	—
Colour (true)	Colour	TCU	6.00	35.00	19.31	18.50	log (x)
Conductivity	COND	µS·cm^{-1}	63.00	121.00	105.13	113.00	—
Dissolved inorganic carbon	DIC	mg·L^{-1}	6.42	13.00	10.75	11.70	log (x)
Dissolved organic carbon	DOC	µg·L^{-1}	5.20	10.30	7.97	8.30	—
Iron	Fe	µg·L^{-1}	11.20	102.00	42.96	32.65	log (x)
Potassium	K	mg·L^{-1}	0.81	1.16	1.02	1.02	log (x)
Magnesium	Mg	mg·L^{-1}	1.60	4.62	3.77	4.18	—
Manganese	Mn	mg·L^{-1}	1.81	17.20	5.78	4.72	log (x)
Sodium	Na	mg·L^{-1}	1.37	4.43	2.53	2.63	log (x)
Ammonium + ammonia	NH_4	µg·L^{-1}	16.00	92.00	49.10	41.00	log (x)
Nitrate + nitrite	NO_3	µg·L^{-1}	4.00	216.00	20.50	7.00	log (x)
Total Kjeldahl Nitrogen	TKN	µg·L^{-1}	321.00	640.00	491.00	501.50	log (x)
pH	pH	—	7.53	7.92	7.75	7.76	—
Total phosphorus	TP	µg·L^{-1}	6.80	25.40	15.47	16.35	log (x)
Silicate	SiO_3	mg·L^{-1}	0.18	2.72	1.37	1.10	log (x)
Sulphate	SO_4	mg·L^{-1}	2.70	6.20	3.86	3.95	log (x)
Chlorophyll *a*	Chl *a*	mg·L^{-1}	0.60	7.20	2.57	2.00	—
Maximum (coring) depth	Z	m	4.10	53.70	20.31	18.00	log (x)
Secchi depth	Secchi	m	1.70	5.50	3.17	2.90	—

they were highly correlated (r > 0.90) to "master" variables (e.g., Ca, Mg, Conductivity, and DIC were highly correlated with alkalinity). Forward selection was used in the CCA to reduce the remaining co-linearity in the explanatory variables. Monte Carlo permutation tests (999 simulations) were used to i) test the significance of each forward selected variable, and ii) test the significance of the first two CCA ordination axes. The significance of the PCA axes and the remaining CCA axes was tested using the broken-stick model (Jackson 1993). A partially-constrained CCA was run to determine the amount of variation explained by total phosphorus independent of lake depth, which followed a similar gradient from south to north. All ordinations were performed using Canoco version 4.0 for Windows (ter Braak and Šmilauer 1998).

RESULTS

Water Quality

The first ($\lambda = 0.55$) and second ($\lambda = 0.21$) PCA axes were significant, and captured 75.9% of the variation in the environmental data. The first axis showed a strong negative correlation with algal nutrient concentrations ([TP], [TKN], [DOC] and [SiO3]; see Table 3 for variable codes), and was positively correlated to Secchi depth (Fig. 2). The strongest correlates with the second PCA axis were pH and maximum depth (i.e., coring depth). PCA effectively separated the LOW sites into three distinct geographic zones (Fig. 2): 1) eastern sites or basins, characterized by low nutrients and alkalinity; 2) northwestern sites, with low nutrients but higher measures of pH and alkalinity; and, 3) sites situated along a south-north axis, from the Rainy River inflow to the south, to Kenora (Ontario) in the north. The central sites followed strong gradients of nutrients and maximum depth, with shallow, higher nutrient sites to the south (e.g., PP16, PP17), and deeper sites with lower nutrients to the north (e.g., PP1, PP2).

Seasonal patterns in [TP] were examined at five sites across the lake in 2002 and 2003 (Fig. 3). In general, spring concentrations were higher at LOW sites than in other Shield lakes in central Ontario (Ontario Ministry of the Environment 2004). Seasonally, two distinct patterns were observed across a broad spatial scale. The first, which was characterized by a rise in [TP] through the summer months, was observed at sites in the central core of the lake (Fig. 3). Specifically, sites in more south-
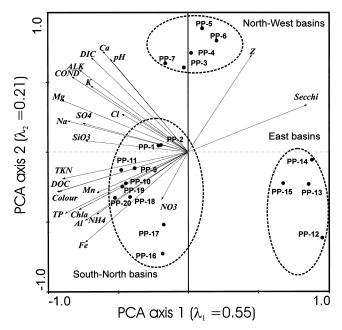
**FIG. 2.   *Principal components analysis (PCA)
biplot of 23 physical and chemical environmental
variables from 19 sites in Lake of the Woods. Sites
were separated into three distinct geographic
zones based on water quality data from June,
2003: sites in the south-north core, sites in the
northwest region, and sites in the eastern region
of the lake.***

ern regions of LOW (e.g., Fig. 3, sites D and E) showed a large rise in phosphorus in late August and September. Site B (Fig. 3), located north of Big Narrows and Tranquil Channel (channels located between sites PP9 and PP10, Fig. 1), also showed a rise in [TP], although less marked and delayed relative to sites in the south. The second pattern, which characterized sites in the eastern and northwestern regions of the lake (Fig. 3), showed a minimal change or a slight decrease in [TP] through the ice-free season. Sites with this pattern are isolated from the main channel flow from the Rainy River to the outflows near Kenora, Ontario.

Correlations between nutrient concentrations and Secchi depth or algal biomass (e.g., chlorophyll *a*) have been presented for numerous lake ecosystems in many regions (e.g., Mazumder and Havens 1998, Kalff 2002), and are shown for LOW in Table 4. Seasonally, Secchi depth decreased in all sites from June to September. In contrast, [TP] increased over the same time period. Thus, Secchi depth showed a significant negative correlation with [TP] and [TN] across all sites in both time periods (Table 4). Sur-

prisingly, Secchi depth was only correlated with algal biomass (measured as chlorophyll *a*) in June, and this relationship was de-coupled in late summer. Furthermore, while [TP$_{June}$] and [TP$_{September}$] were significantly correlated ($r^2 = 0.88$, $p < 0.001$), there was no seasonal pattern for chlorophyll *a* when all sites were considered. Consequently, chlorophyll *a* was not significantly correlated with [TP$_{September}$], although it was with [TN$_{September}$]. Of the various nitrogen components, ammonium showed the highest correlation with chlorophyll *a* (Table 4).

Diatoms

Across sites, the diatom assemblages were dominated by planktonic taxa (60–98%), with the exception of the shallowest site (PP16, Z_{max} = 4.1 m), which was dominated by a distinctive benthic flora (70%) consisting primarily of small *Fragilaria* species (56%; *F. construens* (Ehrenberg) Grunow and *F. pinnata* (Ehrenberg)). These taxa are commonly found in shallow, meso- to eutrophic lakes (Ramstack *et al.* 2003). When all sites were included, the first DCA axis accounted for 33.1% of the species variation. However, site PP16 was identified as an outlier for the reasons mentioned above, and excluded from further analysis. In a revised DCA, the first axis accounted for 41.8% of the variation in the diatom data ($\lambda = 0.46$), and was strongly correlated with June [TP] ($r = 0.96$). The second DCA axis ($\lambda = 0.11$) was correlated with pH ($r = 0.74$) and maximum depth ($r = 0.64$), showing the importance of pH in structuring diatom communities, even across a relatively narrow environmental gradient.

Patterns in floristic variation that can be explained by measured environmental data were detected using CCA. Two variables ([TP] and pH) explained significant, independent source of variation in the diatom data as identified with forward selection. The first ($\lambda_1 = 0.43$) and second ($\lambda_2 = 0.10$) CCA axes captured 48.2% of the variation in the species-environment relationship (axis 1 = 39.4%). Axis one and two captured a nutrient and pH gradient, respectively (Fig. 4). The position of each taxon on the CCA biplot approximates its weighted-average optimum relative to other taxa. Taxa indicative of environments with higher [TP], including *Aulacoseira granulata* (Ehrenberg) Simonsen, *Cyclostephanos dubius* (Fricke) Round, and *Stephanodiscus* species, were found at higher relative abundances in the southern bays and central
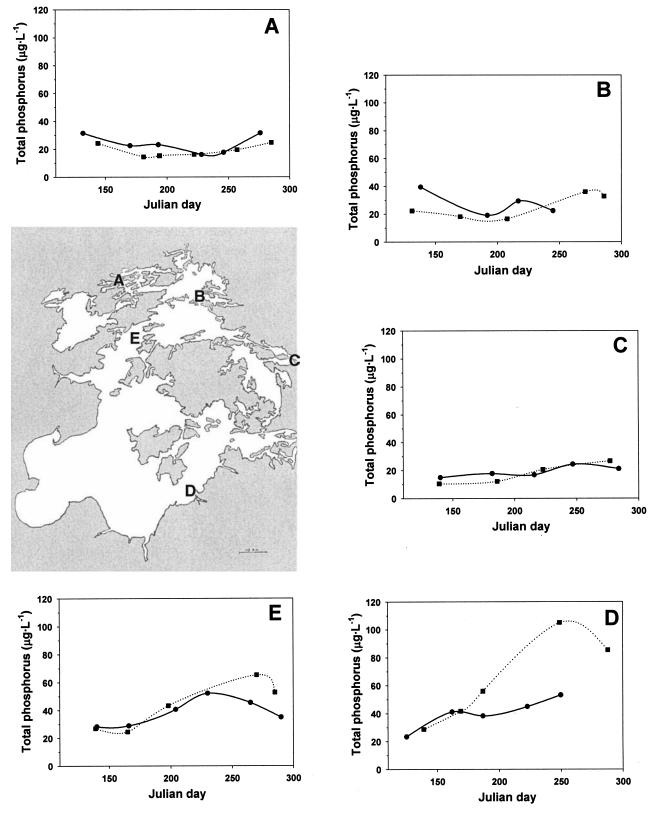
FIG. 3. *Seasonal and inter-annual variation in total phosphorus concentrations at five sites in Lake of the Woods in 2002 (solid line) and 2003 (dashed line). Data are from the Ontario Ministry of the Environment Lake Partner Program.*

TABLE 4. Correlation matrix of selected environmental variables from Lake of the Woods in June and September, 2003. Significant correlations are shown in normal (p < 0.05) and bold font (p < 0.01), respectively.
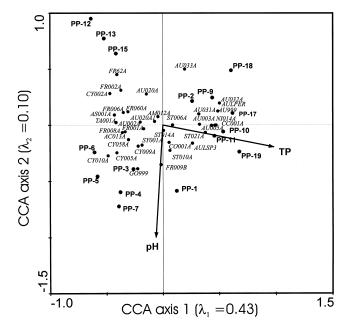
JUNE	Depth	Chl a	NO$_3$	TKN	NH$_4$	TN	TP	TN:TP	Secchi
Depth	—								
Chl a	**–0.59**	—							
NO$_3$									
TKN	–0.50	**0.72**	—	—					
NH$_4$		0.49		**0.84**	—				
TN	–0.53	**0.72**		**0.90**	**0.76**	—			
TP	**–0.65**	**0.81**	0.47	**0.81**	**0.64**	**0.87**	—		
TN:TP	0.55	**–0.75**		**–0.72**	**–0.60**	**–0.72**	**–0.95**	—	
Secchi		**–0.79**		**–0.78**	**–0.60**	**–0.81**	**–0.88**	**0.87**	—

SEPTEMBER	Depth	Chl a	NO$_3$	TKN	NH$_4$	TN	TP	TN:TP	Secchi
Depth	—								
Chl a		—							
NO$_3$	–0.49		—						
TKN		**0.71**		—					
NH$_4$		**0.85**		**0.74**	—				
TN		0.55	**0.60**	**0.95**	0.53	—			
TP	**–0.75**		**0.71**	0.52		**0.68**	—		
TN:TP	**0.65**		**–0.59**				**–0.88**	—	
Secchi	**0.67**		**–0.72**	–0.48		**–0.65**	**–0.81**	**0.75**	—

FIG. 4. Canonical Correspondence Analysis (CCA) biplot of diatom assemblages and forward-selected environmental variables (pH and TP) from 17 sites in Lake of the Woods. Biplot shows relationship of sites, environmental variables, and key diatom taxa (see Table 2 for species codes).

core of LOW (Fig. 4, see Table 2 for taxa codes). In contrast, species more commonly found at lower [TP] (e.g., *Cyclotella* species, *Asterionella formosa* Hassall, *Tabellaria flocculosa* (Roth) Kutzing) were found in deeper sites in the northwestern and eastern regions of the lake. The relative abundances of dominant diatom taxa (relative abundance > 5% in at least in one site) are plotted against a gradient of [TP] (Fig. 5). Finally, species richness (not shown) and diversity (Magurran 2003) decreased along the first DCA axis. In general, sites with high [TP] showed lower biological diversity, and were dominated by *Aulacoseira granulata* (Fig. 5).

DISCUSSION

Water Quality

The Lake of the Woods (LOW) basin is spatially-complex. Although a continuous hydrological connection is maintained throughout, the lake is composed of hundreds of distinct bays, and thousands of islands. Lake chemistry is further influenced by the heterogeneous surficial geology characteristic of the region, with large areas of exposed bedrock in the north and east, and thicker
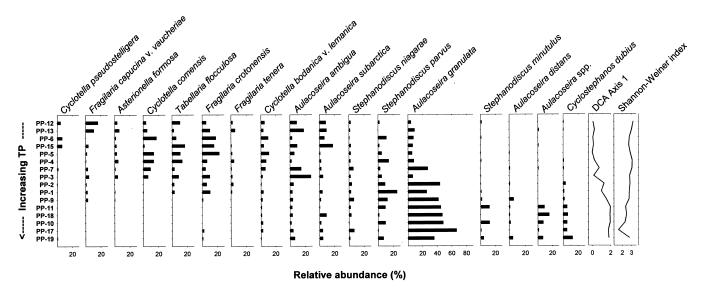
FIG. 5. *Diagram showing the relative abundance of dominant diatom taxa (occurring at a relative abundance of more than 5% in one sample) in sites arranged by increasing concentrations of total phosphorus. Also shown are DCA Axis 1 scores, and the Shannon-Weiner index of diversity.*

glacial deposits in southern regions (Johnston 1915). This variability was shown with PCA, which indicated a strong primary gradient of algal nutrient concentrations. This pattern closely follows geological boundaries, and is significantly correlated with Secchi depth measurements. The sites with the lowest measured [TP] and highest water transparency are located in the eastern region of the lake, which is isolated from the main direction of flow.

Rainy River, which contributes an estimated 70% of the total inflow, is an important source of nutrients to LOW. During the ice-free season of 1999, Anderson *et al.* (2000) reported a strong correlation of [TP] concentrations in Rainy River and LOW (i.e., Big Traverse Bay, southern LOW), with river [TP] ranging between 21–39 $\mu g \cdot L^{-1}$. While there is minimal information regarding Rainy River basin characteristics on the northern side of the U.S.-Canada border, detailed descriptions exist for Minnesota, which comprises 41% of the river's drainage area. The catchment area can be broadly divided into two geologic areas, the Canadian Shield and the glacial bed of Lake Agassiz. The latter region, which is located downstream of Rainy Lake (Rainy Lake, 2003, mean [TP]: 15 $\mu g \cdot L^{-1}$) and encompasses the southern shores of LOW, is dominated by wetlands (~ 75% peat, by area). Soils in the Agassiz lowlands are organic, clay-rich, and relatively deep, exceeding 5 metres in places (Minnesota Pollution Control Agency 2004).

Additional major sources of phosphorus to the Rainy River include atmospheric deposition, non-agricultural rural runoff, and stream bank erosion (Minnesota Pollution Control Agency 2004). In contrast to other river basins in central and southern Minnesota, agriculture plays a minimal role in the contribution of phosphorus (Minnesota Pollution Control Agency 2004), and thus, the primary sources of TP to the Rainy River are natural in origin. This is supported by historical evidence that algal blooms occurred in southern regions of the LOW prior to the establishment of large populated areas. Accounts from the early to mid-19th century report the existence of "a green scum of vegetable matter" (quote by Major J. Delafield, 1823; McElroy and Riggs 1943), and that "the water became tinged with green, deriving from a minute vegetable growth . . . [that] gave the appearance to the lake of a vast expanse of dirty green mud" (quote by S. J. Dawson, 1857; LOW Museum, Kenora, Ontario, pers. comm.). Furthermore, an Ontario Ministry of the Environment report (Salbach 1973) cited anecdotal evidence that algal blooms had been occurring near the Rainy River inflow for several decades, in reference to a severe bloom in 1972.

Despite evidence that algal blooms have occurred in the past, nutrient concentrations and the formation of severe blooms may vary annually, depending on variability in climate, water stability, and other stochastic processes (e.g., Gibson *et al.*

1996, Bradshaw *et al*. 2002). In 2002 and 2003, a large seasonal variation in [TP] was observed at several sites in LOW (Fig. 3), although there was a good correlation between nutrient concentrations in June and September across all sampling locations. Sites located in the northwestern region of the lake showed a pattern observed in many Shield lakes, with [TP] declining through the ice-free season. In stratified lakes and bays, the seasonal loss of nutrients is generally controlled by the settling of plankton and other material from the epilimnion to deeper waters, returning to the water column during fall turnover (Kalff 2002).

In contrast, sites located in the southern and central regions of the lake followed a pattern more typical of shallow lakes (Scheffer 1998), or lakes off the Canadian Shield, with increasing [TP] through the ice-free season. In general, the amplitude of this increase was greater at sites with higher initial (i.e., June) concentrations. Furthermore, late-summer TP concentrations in Big Traverse Bay commonly exceed those recorded in the Rainy River (e.g., Anderson *et al*. 2000), indicating the importance of other sources or inputs of nutrients. These facts suggest that internal loading may be an important source of nutrients to the water column, through sediment resuspension, changes in redox conditions, and/or microbial processes (Jeppesen *et al.* 1997, Søndergaard *et al*. 2003).

The resuspension of lake sediments may be facilitated by wind action across the relatively large fetch of the southern bays (Scheffer 1998). Using equations presented in Cyr (1998), the depth of the wave-mixed layer was estimated at 12 metres during storm events in the large southern bay (i.e., Big Traverse Bay, site PP20, maximum depth = 10.5 meters). Moreover, the release of inorganic phosphate through the mineralization of organic material may be stimulated by increased temperatures in late-summer (Jeppesen *et al*. 1997), or the increased sedimentation of organic matter with increased productivity of phytoplankton (Istvánovics and Pettersson 1998).

While the Rainy River and internal loading are likely important sources of TP to sites in the central core of the lake, the water quality of more isolated bays may be influenced by local factors. This is evident in a comparison of sites in the northwest and eastern regions of the lake. These sites share similar nutrient concentrations, but differ substantially in alkalinity and pH. In part, this may be explained by the proximity of the northwestern sites to the Trans-Canada highway, as well as local differences in surficial geology. In addition, recent surveys of sewage disposal systems in the Clearwater Bay region (northwestern LOW), suggest that shoreline development may have a significant impact on water quality. Approximately 25% of the septic systems examined failed to meet Provincial guidelines and required remediation (Heiman and Smith 1991). Furthermore, anecdotal evidence and video footage suggest that periphyton growth is enhanced at locations proximate to shoreline development (B. Corbett, Ontario Ministry of the Environment, pers. comm.). This information, in conjunction with fisheries data, has led to the closing of the winter lake-trout fishery and significant restrictions on future development in the region (Ontario Ministry of Natural Resources 1988).

[TP] and Chlorophyll *a*

Phosphorus is the nutrient that most commonly limits the algal biomass of lakes on the Precambrian Shield (Schindler 1975, Hecky and Kilham 1988, Kalff 2002). However, while a significant correlation between [TP] and chlorophyll *a* was observed in the LOW in June, this relationship was not significant in September. A similar pattern has been observed in other meso-eutrophic temperate lakes, and may represent an increased importance of factors other than nutrient concentrations (e.g., light, temperature) in regulating phytoplankton abundance in late-summer or autumn (Smith and Shapiro 1981). Furthermore, with a seasonal increase in nutrient enrichment, nitrogen may become a more important predictor of algal biomass than phosphorus, as suggested by the stronger relationship between total nitrogen and cyanobacteria dominance in nutrient-rich lakes (Downing *et al*. 2001). Indeed, nitrogen-species were significantly correlated with chlorophyll *a* across sites in LOW in September (Table 4).

Mixing regimes and the relative loss of phytoplankton to sinking may vary significantly among the sampling locations. These processes, which show the greatest inter-site variation during thermal stratification, may influence the phytoplankton assemblage and algal biomass independent of nutrient concentrations (Watson *et al*. 1997, Scheffer 1998). The importance of mixing regime is supported by a significant negative correlation between maximum depth [TP] and chlorophyll *a* in June (Table 4). Other factors, such as the presence and abundance of aquatic plants (Canfield *et al*. 1984), variability in light quantity and quality (Scheffer 1998), differ-

ential grazing rates (Pace 1984), variation in the proportion of [TP] that is bioavailable, and spatial heterogeneity in the formation of algal blooms (Anderson *et al.* 2000) all add to the complexity in the [TP]-chlorophyll relationship.

Spatial Variability and Diversity of Diatom Assemblages

A large number of published studies have shown the importance of lakewater pH and related variables (e.g., alkalinity, conductivity) as main drivers structuring diatom communities (Stoermer and Smol 1999, Battarbee *et al.* 1999). However, given the relatively short environmental gradient of pH among sites (Table 3), a greater portion of the floristic variation in LOW was explained by a gradient of nutrient concentrations. Partially-constrained ordination analyses determined that [TP] explained a significant portion of the diatom variation, independent of maximum depth, although these variables were significantly correlated in the dataset.

Excluding site PP-16, a shallow, macrophyte-dominated bay, the southern sampling sites were dominated by taxa common to meso-eutrophic lakes and reservoirs (e.g., *Cyclostephanos dubius* and *Stephanodiscus* species), and heavily-silicified *Aulacoseira* taxa (Dixit *et al.* 1999, Ramstack *et al.* 2003, Bennion *et al.* 1996). Large relative abundances of *Aulacoseira* species (> 40%), which are frequently found in turbulent or frequently-mixed waters that reduce cell sinking rates and facilitate the inoculation of resting cells from sediments (Carrick *et al.* 1993, Agbeti *et al.* 1997), suggest that the shallow, southern bays are well-mixed. In contrast, *Cyclotella* species, *Asterionella formosa*, *Tabellaria flocculosa*, and other planktonic, mesotrophic taxa (Hall and Smol 1992, Bennion *et al.* 1996) were more abundant in the northwestern and eastern sites. These sites are generally deeper, and well-stratified in late-summer.

Variations in lake morphometry and basin characteristics may have significant impacts of water chemistry, and consequently, diatom assemblages. For example, Big Narrows and Tranquil Channel (located between sites PP-9 and PP-10, Fig. 1) are narrow channels that form a significant barrier to flow, and effectively divide the central core of LOW into a northern and southern region. North of these channels, a decline in importance of *Aulacoseira* taxa may be indicative of increased water column stability. This decline is coupled with an increase in the relative abundance of *Stephanodiscus* species, taxa with similar nutrient requirements. Diatom assemblages at sites in the east and northwest were more typical of stratified, mesotrophic lakes on the Canadian Shield (Hall and Smol 1996). Floristic variability in assemblages within a single hydrological system has been demonstrated elsewhere, and can be related to a variety of factors, including lake depth (Kingston *et al.* 1983), proximity to riverine inputs or thermal bars (Likhoshway *et al.* 1995), or water chemistry.

Declining species diversity with increasing [TP] may be related to the decreased importance of diatoms relative to other phytoplankton under such conditions. The replacement of vernal diatoms with chlorophytes and filamentous cyanobacteria (e.g., *Anabaena, Aphanizomenon*) in productive lakes has been observed in Europe and North-America (e.g., Reynolds 1984). This variability may also be explained, in part, by inter-site differences in sedimentation rate (Smol 1981). At sites with lower sedimentation rates, the top 1 cm of lake sediment represents a greater period of deposition, and thus may accumulate a more diverse flora. Furthermore, sedimentation rate may vary directly with nutrient levels (i.e., higher primary production), although this is difficult to discern with the present data.

CONCLUSIONS

Marked variability in water quality was observed among sites in LOW. This variation was related to inter-site differences in morphometry (e.g., depth), and their proximity to Rainy River, the primary source of tributary inflow to the lake. Sites located in more isolated regions have a distinct water quality, and are likely more sensitive to local disturbances (e.g., shoreline development).

Severe cyanobacterial blooms in LOW have been reported for decades to centuries and are, in part, related to elevated nutrient concentrations. Sedimentary deposits from Glacial Lake Agassiz represent a significant natural-source of [TP] to the lake. Furthermore, the large, shallow southern basin is well-mixed suggesting that internal loading may also form an important part of the nutrient budget of this region of the lake. Other factors not specifically measured here, including variations in water temperature, wind intensity, water column stability, and competition for nutrients or elements other than phosphorus (e.g., nitrogen limitation), may also vary annually and contribute to the production and

distribution of algal blooms in lakes (Hyenstrand *et al*. 1998, Downing *et al*. 2001).

Thus, disentangling the specific causes and origins of algal blooms is a non-trivial task. In part, this uncertainty may be reduced through the development of paleoecological models to reconstruct natural (i.e., pre-development) phosphorus concentrations (Hall and Smoll 1999), and to measure long-term changes in nutrient concentrations across a broad spatial scale in LOW. The close correlation between water chemistry and diatom assemblages indicate that these models are possible, and may provide data on the relative importance of natural and anthropogenic sources of nutrients to the lake.

ACKNOWLEDGMENTS

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