significant south to north gradient in water quality (Hissa and Mosindy 1991, Anderson *et al.* 2000).

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Partner Program (LPP), unpublished data).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 lakebed 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).

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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				0.77
Amphora pediculus (Kützing) Grunow	AS001A				0.32
Asterionella formosa Hassall	AU031A				1.52
Aulacoseira alpigena (Grunow) Krammer	AU002A				0.98
Aulacoseira ambigua (Grunow) Simonsen	AU005A				7.72
Aulacoseira distans (Ehrenberg) Simonsen	AU003A				0.93
Aulacoseira granulata (Ehrenberg) Simonsen	AU032A				25.41
Aulacoseira pfaffiana (Reinsch) Krammer	AULPER				ahra499 ocl6a0.7
Aulacoseira cf. *perglabra*	AU020A				
Aulacoseira subarctica (O. Müller) Haworth	AU020A				
Aulacoseira cf. *subarctica*	1				
Aulacoseira spp.	AU9999				
Aulacoseira spp. 3	AULSP3				
Aulacoseira valida (Grunow) Krammer	AU033A				
Cocconeis placentula Ehrenberg	CO001A				
Cyclostephanos dubius (Fricke) Round	CC001A				
Cyclotella bodanica v. *lemanica* (O. Müller) Bachmann	CY058A				
Cyclotella comensis Grunow	CY010A				
Cyclotella michiganiana Kützing	CY005A				
Cyclotella ocellata Pantocsek	CY009A				
Cyclotella pseudostelligera Hustedt	CY002A				
Fragilaria brevistriata Grunow	FR006A				
Fragilaria capucina var. *mesolepta* (Rabenhorst) Rabenhorst	FR009B				
Fragilaria capucina var. *vaucheriae* (Kützing) Lange-Bertalot	FR062A				
Fragilaria construens (Ehrenberg) Grunow	FR002A				
Fragilaria crotonensis Kitton	FR008A				
Fragilaria pinnata Ehrenberg	FR001A				
Fragilaria tenera (W. Smith) Lange-Bertalot	FR060A				
Fragilaria ulna var. *acus* (Nitzch) Lange-Bertalot	FR072A				
Gomphonema spp.	GO9999				
Nitzschia amphibia Grunow	NI014A				
Stephanodiscus medius Håkansson	ST014A				
Stephanodiscus minutulus (Kützing) Cleve and Möller	ST021A				
Stephanodiscus niagarae Ehrenberg	ST006A				
Stephanodiscus parvus Stoermer and Håkansson	ST010A				
Tabellaria flocculosa (Roth) KützingAC013A	TA001A				

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 Smilauer 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 Smilauer 1998).

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The first (λ = 0.55) and second (λ = 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-

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

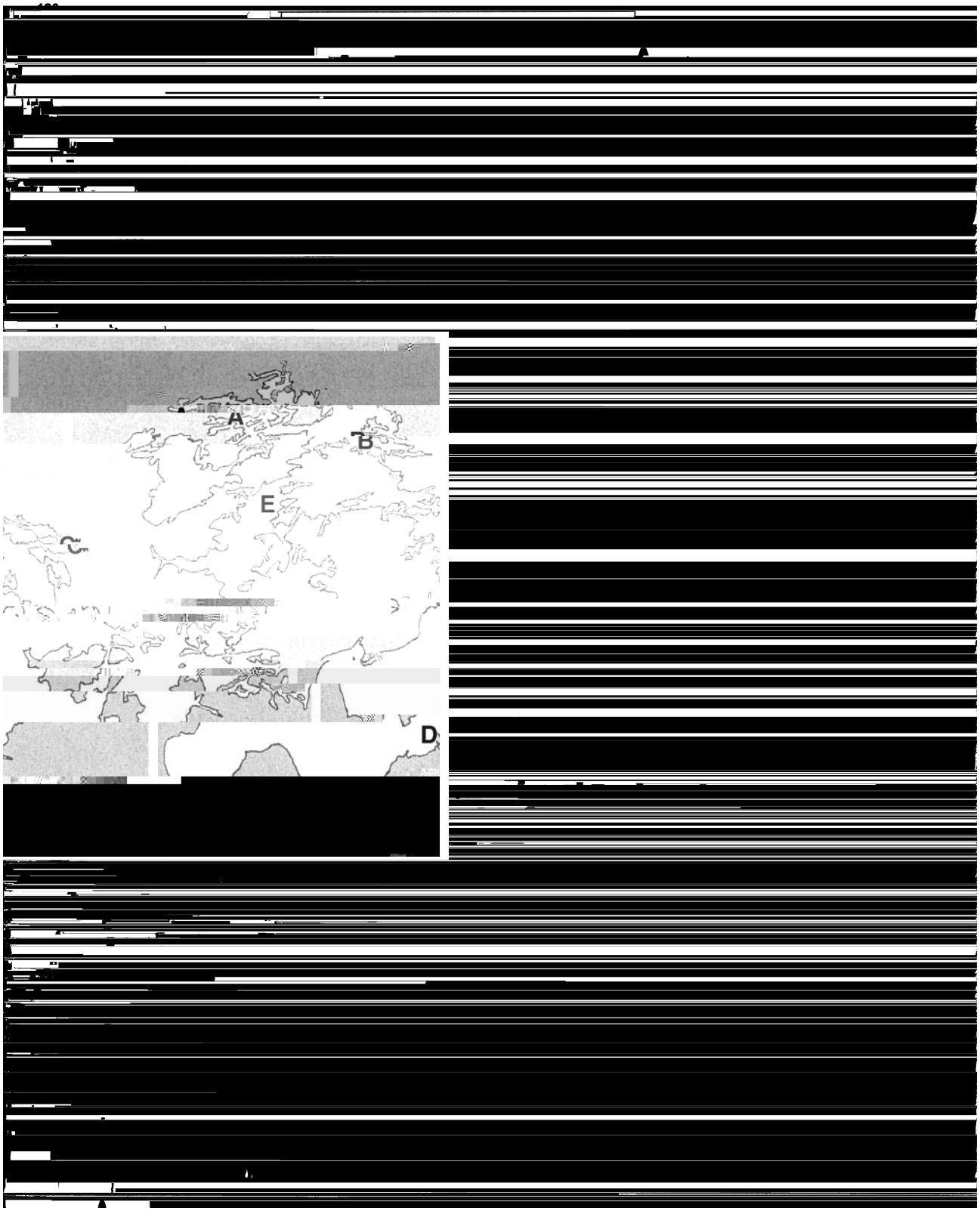

FIG. 3. Seasonal and inter-annual variation in total phosphorus concentrations at five sites in Lake of the Woods in 2002 (solid line) and 2003 (dashed line). Data are from the Ontario Ministry of the Environment Lake Partner Program.

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 gxrw5Tj0 TheA

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.

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.

$$t \quad D \quad t \qquad A^{ty} \qquad D \qquad ty$$

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

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.

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