












ORIGINAL ARTICLE

Impacts of a century of land-use change on the eutrophication of large, shallow, prairie Lake Manitoba in relation to adjacent Lake Winnipeg (Manitoba, Canada)

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Abstract

1. Evaluation of large lake response to centennial changes in land use and climate can be complicated by high spatial and hydrological complexity within their catchments, particularly in regions of low relief. Furthermore, large lakes can exhibit abrupt changes in structure and function that obscure causes of eutrophication.
2. We provide the first quantification of historical trends in lake production, cyanobacterial abundance, sediment geochemistry and diatom composition since c. 1800 in Lake Manitoba, the 29th largest lake in the world, and compared them to Lake Winnipeg, a morphologically similar, adjacent basin with a 10-fold larger catchment and an abrupt increase in production around 1990.
3. Before 1900, Lake Manitoba was mesotrophic, with low sedimentary concentrations of carbon, phosphorus, nitrogen, cyanobacteria and algal pigments, as well as assemblages of low-light-adapted benthic diatoms. Analysis of pigment time-series with hierarchical generalised additive models revealed that Lake Manitoba eutrophied during 1900–1930 as a consequence of the development of intensive agriculture within its local catchment, but thereafter exhibited stable cyanobacterial densities with limited expansion of N₂-fixing cyanobacteria despite persistent eutrophication.
4. Lake Manitoba did not undergo an abrupt change as seen in Lake Winnipeg.
5. These findings suggest that catchment size had little influence on water quality degradation and that nutrient influx from proximal agricultural sources was sufficient to initially degrade these large prairie lakes. The abrupt change in Lake Winnipeg around 1990 required additional intensification of local land use that did not occur in the Lake Manitoba catchment.

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KEYWORDS

akinetes, cyanobacteria blooms, land-use change, nitrogen, pigments

1 | INTRODUCTION

The global degradation of fresh waters through eutrophication and the proliferation of toxic cyanobacterial blooms is often attributable to excessive nutrient loading (Glibert, 2020; Paerl et al., 2016; Taranu et al., 2015). As a result, eutrophication- and bloom-mitigation strategies have attempted to reduce nutrient inputs to lakes, succeeding primarily when improved water-treatment infrastructure has regulated discrete nutrient inputs (Bergbusch et al., 2021; Hamilton et al., 2016; Schindler et al., 2016). By contrast, diffuse nutrient sources are more difficult to regulate, in part owing to the large spatial scales of some biogeochemical disturbances (e.g., agriculture), and potential effects of intervening waterbodies on transmission of nutrients to downstream lakes (Bunting et al., 2016; Donald et al., 2015; Maheaux et al., 2016).

In principle, control of diffuse nutrient sources proximate to lakes may be critical in protecting surface water quality, especially when catchment features complicate nutrient export from land to fresh waters (Fraterrigo & Downing, 2008; Soranno et al., 1999). For example, landscape analysis of nutrient fluxes in large dendritic catchments reveals that upstream water bodies can capture high proportions of diffuse nutrients before they can impact downstream lakes (Donald et al., 2015; Goyette et al., 2019; Patoine et al., 2006; Soranno et al., 1999), although the effectiveness of this process may depend on meteorological conditions (Donald et al., 2015). Nutrient transport can also be complicated when upstream ecosystems differentially sequester nitrogen (N) or phosphorus (P), depending on their intrinsic production and stoichiometry (Dixit et al., 2000; Donald et al., 2015; Leavitt et al., 2006). Further, variation in edaphic, geological and climate features across very large catchments can lead to regional variability in nutrient export and transportation (Fraterrigo & Downing, 2008; Goyette et al., 2019). Together, these complex hydrological connections result in differential weighting of diffuse nutrient sources, making it difficult to predict how adjacent lakes may respond to apparently similar anthropogenic and climate forcing if they have different catchment sizes.

Mechanistic evaluation of lake response to long-term eutrophication may be further complicated by the occurrence of sudden, nonlinear changes in ecosystem structure and function, variously referred to as regime shifts, state changes, critical threshold exceedance, or flickering (Dakos et al., 2015; Scheffer et al., 2001; Su et al., 2021). In small lakes, these abrupt changes are often marked by a shift from transparent, macrophyte-rich conditions to turbid, phytoplankton-dominated states with buoyant cyanobacteria (Bogard et al., 2020) resulting from decadal-scale changes in nutrient influx (McGowan et al., 2005; Scheffer & Jeppesen, 2007). Here, rising temporal variance in planktonic primary production or cyanobacterial abundance has been suggested as a predictive marker of abrupt

transitions (Carpenter & Brock, 2006; Dakos et al., 2015; Scheffer et al., 2001), although recent studies suggest that rising variance is not a prerequisite of an abrupt change (Burthe et al., 2016; Ratajczak et al., 2018). By contrast, identification of the causes and mechanisms inducing sudden shifts can be more difficult for large lakes owing to greater spatial diversity of intrinsic lake characteristics and human activities inside large drainage basins (Guiry et al., 2020; Tomczak et al., 2022). In this situation, adjacent basins may not exhibit equivalent signs of abrupt ecosystem change and comparative evaluation of the patterns and processes underlying eutrophication may be useful to develop robust regional management and mitigation strategies.

Here we quantified historical changes in primary production (biomarker pigments, cyanobacterial akinetes, fossil diatom assemblages, sediment geochemistry) from four sediment cores collected from large, shallow, prairie Lake Manitoba (Manitoba, Canada) to establish the first eutrophication history of the basin. Despite being the 29th largest lake in the world (Lake Manitoba Stewardship Board [LMSB], 2008), little is known of the eutrophication history of Lake Manitoba, particularly in comparison to adjacent Lake Winnipeg, a well-studied site which underwent an abrupt ecological shift to abundant planktonic cyanobacteria after 1990 (Binding et al., 2018; Bunting et al., 2016; Schindler et al., 2012). We hypothesised that patterns of eutrophication would be similar in the southern basins of Lake Manitoba (this study) and Lake Winnipeg (Bunting et al., 2016) because both sites: are presently eutrophic; exhibit similar morphology and limnological conditions; have intensive agriculture in their immediate catchments; have experienced similar climate histories and forcing; and are separated by only 70 km (Agriculture and Agri-Food Canada [AAFC], 2005; Bunting et al., 2016; Deveson, 2007; Dibike et al., 2012). We also hypothesised that any differences in eutrophication histories may reflect the relative importance of proximate and distal nutrient sources, as their catchment areas differ by an order of magnitude (Manitoba 80,299 km²; Winnipeg 982,900 km²) (AAFC, 2005; Last, 1984).

2 | METHODS

2.1 | Site description

Lake Manitoba is a large (4706 km²), shallow (mean depth = 4.5 m), polymictic, multi-basin lake located in west-central Manitoba, Canada (Figure 1; Table S1). The lake lies in a glacial trough comprised of Palaeozoic carbonates overlain by glacial, fluvial and lacustrine Quaternary sediments (Last, 1984). The lake has a smaller north basin (1456 km²) with complex morphometry and rapid water residence time (c. 2 years), whereas the larger south basin (3250 km²)

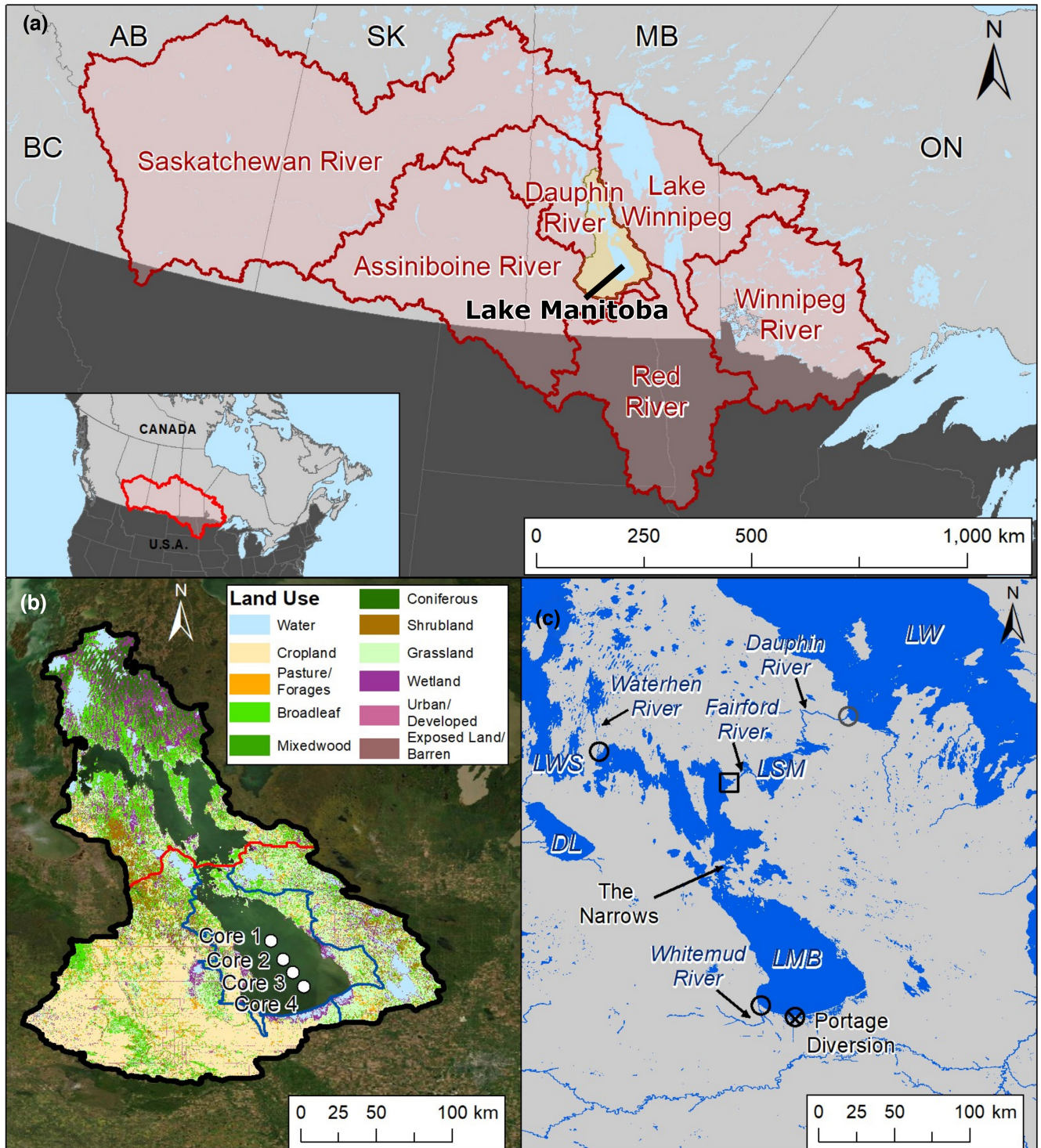


FIGURE 1 (a) Map of the Lake Winnipeg sub-watersheds across the provinces of British Columbia (BC), Alberta (AB), Saskatchewan (SK), Manitoba (MB) and Ontario (ON) in Canada and the United States. Lake Manitoba and its immediate watershed are highlighted. Watershed information from Commission for Environmental Cooperation (2010), DMTI Spatial Inc. (2014a, 2014b) and Natural Resources Canada (2021). (b) Immediate watershed of Lake Manitoba with land use and cover (AAFC, 2020). The watershed is divided into the areas that drain into the north and south basins (red). The blue line denotes the realised drainage of the south basin with the remaining area draining into the Whitemud River, small streams, or into groundwater. The coring locations are highlighted within the southern basin. Satellite imagery from Esri (2021). (c) Hydrology of Lake Manitoba with inflows (circles) and outflows (square) highlighted. The "X"-ed circle marks the Portage Diversion from the Assiniboine River. Sources of water that flow through Lake Manitoba (LMB) and into Lake Winnipeg (LW) are labelled: DL, Dauphin Lake; LSM, Lake St. Martin; LWS, Lake Winnipegosis. Also highlighted are the Narrows which separate the north and south basins of Lake Manitoba. (a) is presented in Lambert Conformal Conic projection, while (b) and (c) use a geographical coordinate system (WGS 1984).

exhibits a simple morphology and a long residence time (c. 28 years; Last, 1984). The two basins are effectively separated by “the Narrows” (51°05.06' N, 98°46.98' W; Figure 1), an 800-m wide, c. 1.5-m deep, channel that limits hydrological exchange between the basins.

The catchment of Lake Manitoba drains 80,299 km² of west-central Manitoba and east-central Saskatchewan (Figure 1). The northern area of catchment is relatively undeveloped spruce-aspen parkland, coniferous forest, and wetlands, whereas the southern catchment has been modified for intensive agriculture since the late 19th Century (AAFC, 2005; Deveson, 2007; Lake Manitoba Regulation Review Advisory Committee (LMRRAC), 2003). The south basin drains an area of 17,343 km² (Last, 1984) and is largely developed for cattle and forage production, with relatively minor cereal and marginal oilseed cropping (AAFC, 2020; Figure 1b). Regional climate is cold and continental, with mean annual temperatures of 2.6°C, and 526 mm/year of annual precipitation split between 404 mm/year of rain and 126 mm/year of snow over the 1981–2010 period (Environment and Climate Change Canada [ECCC], 2022a). Precipitation is the primary water source to the south basin with limited input from the north basin and the small Whitemud River that drains the southwestern portion of the catchment (Figure 1). Ground water constitutes a minor component of hydrological influx (Table S2; LMRRAC, 2003; Westdal et al., 2013). Water loss from the south basin is principally via surface evaporation, while the north basin outflows through the Fairford River (Figure 1; Table S2; LMRRAC, 2003). Since 1970, the south basin also has received intermittent inflow from the Assiniboine River through the Portage Diversion during the spring run-off season (Blais et al., 2016). During high spring-flow events, the Assiniboine River can account for c. 60% of P influx to Lake Manitoba, whereas N is imported mainly from the north basin (Blais et al., 2016; Westdal et al., 2013).

2.2 | Modern lake conditions

Analysis of unpublished data from Manitoba Ministry of Sustainable Development (MMSD) between 1991 and 2001 and those of Hughes and Williamson (2002) suggests that the south basin of Lake Manitoba is presently alkaline, sub-saline and eutrophic, with low water-column transparency and elevated concentrations of algal chlorophyll *a* (Chl-*a*), total phosphorus (TP) and total Kjeldahl nitrogen (TKN) during late summer (Table S3). Sporadic monitoring since 1928 suggests few marked trends in lake water chemistry in the south basin of Lake Manitoba during the 20th Century, other than a decline in lake-water conductivity and total dissolved solid (TDS) content since 1991 reflecting increased regional precipitation (Hughes & Williamson, 2002; MMSD, unpublished data).

The planktonic community of Lake Manitoba is poorly characterised. Occasional evaluation since 1999 suggests that phytoplankton assemblages are diverse, with abundant taxa characteristic of shallow, well-mixed waters (H. Kling, Winnipeg, MB, personal communication). Low-light-adapted colonial cyanobacteria appear to be

present in most seasons (e.g., *Planktolyngbya*, *Planktothrix*), while *Aphanizomenon* spp. can form surface blooms during summer. Based on limited sampling, chroococcoid cyanobacteria are thought to be common (*Aphanocapsa*, *Aphanothece*, *Cyanodictyon* and *Romeria* spp.), whereas chlorophytes such as *Pediastrum* spp. are well-represented (H. Kling, unpublished data). The current and historical status of the zooplankton community also is largely unknown. Commercial fish harvest increased from the late-1880s to maxima in the mid-20th Century, but has declined steadily since that time (Westdal et al., 2013) as cisco (*Coregonus artedii*) and walleye landings (*Sander vitreus*) have been replaced by yellow perch (*Perca flavescens*) and introduced carp (*Cyprinus carpio*) since the 1970s (LMRRAC, 2003).

2.3 | Land-use change around the south basin of Lake Manitoba

Historical census data (Statistics Canada, 1871–2006) of agricultural production in Manitoba was used to characterise the land-use history of the direct catchment of the south basin of Lake Manitoba (Figure 1b). Initial agricultural development began in the south of the catchment in the late 19th Century and focused on cereal crops including wheat, barley and oats (Deveson, 2007). Livestock production was initially limited, but cattle and forage production increased between c. 1900 and 1930, particularly along the eastern and western margins of the south basin where soil quality is too poor for expansive cereal production (AAFC, 2005; Deveson, 2007). Mechanised tillage was introduced in the 1930s, resulting in increased production of cereals and forage for cattle during the middle of the 20th Century. Forage and cattle production further increased in the 1990s, whereas the production of canola and other oilseeds has been marginal compared to other catchments in southern Manitoba (AAFC, 2005). Likewise, the exponential expansion of potato production and intensive hog operations recorded within the Red River catchment leading to Lake Winnipeg (Figure 1) since approximately 1980 has not occurred in the catchment of Lake Manitoba (Manitoba Clean Environment Commission [MCEC], 2007).

2.4 | Sediment core collection

Four sediment cores, each between 35 and 45 cm in length, were collected along a north–south transect in the south basin of Lake Manitoba during September 2010 using a Glew gravity corer (Glew, 1989; Figure 1b). Cores 1–4 were recovered from water depths ranging from 5.4 to 6.7 m (Table S4). Cores were stored vertically and sectioned in the field using a Glew extruder into 9- or 7-mm-thick increments (Table S4). Samples were stored in darkness during transportation to laboratories and either refrigerated (4°C) or frozen (−10°C) before analyses. Subsequent sediment analyses were conducted on alternate strata (carbon [C] and N content, stable isotopes, pigments), or more widely spaced intervals (sediment P fractions, diatoms, cyanobacterial akinetes, radioisotopes).

2.5 | Palaeolimnological analyses

Age dating by radio-isotopic analysis of ^{210}Pb and ^{137}Cs was performed on c. 15 samples per core using an Ortec High-Purity Germanium (HPGe) Coaxial Well Photon Detector System (Appleby et al., 1986; Schelske et al., 1994). Sediment age–depth relationships and mass accumulation rates were calculated using the constant rate of supply (CRS) model of ^{210}Pb activity profiles (Binford, 1990) with dating uncertainty estimated by first-order propagation of counting error, assuming a normal distribution of gamma disintegrations (Schelske et al., 1994). Approximate ages of sediments older than around 1890 were estimated by extrapolating depth–age relationships recorded during the late 19th and early 20th centuries. Although ^{137}Cs activity was measured, it was not used as a supplemental dating marker because of indistinct peaks or apparent migration within the core.

Stable isotope ratios of freeze-dried sediments were estimated using a Thermo Finnigan Delta V stable isotope ratio mass spectrometer equipped with a continuous flow (ConFlo IV) interface and a Costech (ECS 4010) elemental analyser following the methods of Savage et al. (2004). Elemental ratios were estimated as mass of N or C relative to the dry mass of combusted sediment and were used to calculate C:N mass ratios. Stable isotope values were expressed using standard δ -notation with per mil (‰) units relative to the international standards of Pee Dee Belemnite for C isotopes ($\delta^{13}\text{C}$) and atmospheric nitrogen gas for N isotopes ($\delta^{15}\text{N}$).

Total and fractional P content of Cores 1 and 2 were determined from sediment subsamples using procedures adapted from Hieltjes and Lijklema (1980) and Engstrom and Wright Jr. (1984). Briefly, TP was quantified as ortho-P extracted from an aliquot of freeze-dried sediment in 30% H_2O_2 and 0.5 M HCl, while a second aliquot was extracted in 1 M NH_4Cl to estimate chemically exchangeable P (EP; NH_4Cl -P). The residue from the second aliquot was then sequentially extracted with 0.1 M NaOH to measure non-apatite inorganic P (NAI-P; NaOH-P), followed by 0.5 M HCl to determine apatite (carbonate)-bound P (AP; HCl-P). Residual organically bound P (OP; residual-P) was estimated as the difference between TP and the sum of the inorganic P fractions. All extracts were analysed on a Lachat QuikChem model 8000 flow-injection auto-analyser with P concentrations expressed as mg P/g dry mass of whole sediment.

Diatom analyses were conducted on Core 1 following the methods of Battarbee et al. (2001). Subsamples of wet sediments (c. 0.2–0.3 g) were digested in a 1:1 M solution of concentrated nitric and sulfuric acids in a c. 80°C water bath for c. 8 h. The solutions were brought to the pH of deionised water through repeated aspiration of the acidic supernatant and dilution with deionised water. Siliceous slurries were spiked with 0.6 mL of c. 6 μL of microsphere suspension (concentration = 2.0×10^7 spheres/mL) and then plated on coverslips in four dilutions. Coverslips were dried overnight and then mounted to slides using Naphrax® heated with a hotplate. Diatom valves were identified and enumerated using a Leica DMRB microscope under a $\times 100$ Fluotar objective (NA of objective = 1.3) and differential interference contrast optics at $\times 1000$ magnification. A minimum of 400

valves per sample were counted and identified to the lowest taxonomic unit possible using published (Cumming et al., 1995; Krammer & Lange-Bertalot, 1986, 1988, 1991a, 1991b) and online (Spaulding et al., 2021) references. Total diatom concentrations were calculated as valves $\times 10^7$ /g dry mass (Battarbee & Keen, 1982). Diatom accumulation rates were estimated by multiplying fossil concentration by dry mass accumulation rates.

Sedimentary pigments were extracted, filtered, and dried under N_2 gas following the procedures of Leavitt and Hodgson (2001). Concentrations of carotenoid, chlorophyll and derivative pigments were quantified using an Agilent 1100 high-performance liquid chromatographer (HPLC) equipped with a photodiode array spectrophotometer and calibrated using authentic standards (Leavitt & Hodgson, 2001). Sudan II (Sigma Chemical Corp.) was used as an internal reference standard. Pigment analysis was restricted to chemically stable, taxonomically diagnostic compounds characteristic of mainly diatoms (diatoxanthin), cryptophytes (alloxanthin), chlorophytes (pheophytin b) and Nostocales cyanobacteria (canthaxanthin), whereas ubiquitous β -carotene was used as a measure of total phototrophic production. Although other cyanobacterial markers were recorded (echinenone, some myxoxanthophyll, zeaxanthin), we focused on canthaxanthin because it was used in analysis of Lake Winnipeg (Bunting et al., 2016) and provided the most reliable fossil time series of cyanobacteria in Lake Manitoba sediments (i.e., consistently present, low variability, no co-elution). In addition, the ratio of labile Chl-*a* to stable pheophytin *a* was used as a metric of changes in the pigment preservation environment (Leavitt, 1993; Leavitt & Hodgson, 2001). Pigment concentrations were expressed as nmoles pigment/g total C as estimated from geochemical analysis.

Cyanobacterial akinetes (i.e., resting stages) were analysed in Core 1 using the modified protocol of Crumpton (1987). Sediment samples (c. 1 g) were diluted in 20 mL of distilled water and dispersed by sonication (3 \times) before being preserved in c. 0.2 mL of glutaraldehyde. Akinetes were filtered from homogenised aliquots using a 0.45- μm pore membrane filter. Filters were mounted to microscope coverslips using hydroxypropyl-methacrylate (HPMA) resin, allowed to dry for 24 h, and then mounted to glass microscope slides with additional HPMA resin. Each sample was enumerated until at least 200 cyanobacterial akinetes were counted using an Olympus BX51 compound microscope equipped with Nomarski and phase-contrast optics and epifluorescent detection (450–480 nm). Only the potentially N_2 -fixing cyanobacterial taxa *Dolichospermum*/*Anabaena* spp. and *Aphanizomenon* spp. were included in analysis and identification was based on Bunting et al. (2007) and a reference collection at PhycoTech Inc. Akinete concentrations were measured as remains/g wet sediments, which is linearly correlated to phytoplankton density in large lakes (Bunting et al., 2007).

2.6 | Data analysis

All numerical analyses were performed in R (version 4.0.4; R Core Team, 2021). The *tidyr* and *dplyr* packages (Wickham, 2021;

Wickham, François, et al., 2021) were used for data management, while most plots were created using the *ggplot2* and *cowplot* packages (Wickham, Chang, et al., 2021; Wilke, 2020). Diatom assemblages were delineated through time using broken-stick-validated constrained cluster analysis (CONISS) using the *rioja* package (Juggins, 2020). Cluster analysis was limited to Hellinger-transformed (Legendre & Gallagher, 2001) diatom abundance data from taxa that occurred at >1% in more than two samples.

Pigment concentrations from the four cores were modelled with a hierarchical generalised additive model (HGAM; Pedersen et al., 2019) using the *mgcv* package (Wood, 2017, 2021). The HGAM used a Gamma location-scale family and estimated trends in pigment concentrations and variances (Wood et al., 2016). Pigment concentrations were modelled using factor smooths (i.e., the interactions of factors with a smooth effect) for each combination of the four cores and five pigments, for a total of 20 factors (Pedersen et al., 2019). The shape term of the distribution was modelled with a similar factor smooth, and a smooth of each sample's log-transformed temporal interval to account for the differences in temporal resolution across samples and cores. The smoothness parameter of the model was estimated using restricted maximum likelihood (REML; Wood, 2011; Wood et al., 2016). The same method was used in a separate HGAM to compare trends in pigment concentration in Core 1 to those of Lake Winnipeg published by Bunting et al. (2016). This HGAM used 10 factor smooths accounting for the five pigments in each lake (Pedersen et al., 2019). Pigment variance estimates were obtained by calculating the product of the mean and shape estimates, while 95% Bayesian credible intervals for the variance were obtained by running 10,000 simulations and taking the 2.5% and 97.5% quantiles of the posterior distribution. The first derivative of the estimated smooth trends was used to identify periods of statistically significant change (Simpson, 2018) in concentrations and variances using the *gratia* package (Simpson, 2021). Periods of significant change were identified as periods where the 95% credible interval of the derivative excluded 0.

3 | RESULTS

3.1 | Chronology

Activity of ^{210}Pb declined monotonically until background activity was reached below c. 20 cm depth in Cores 1 and 3, whereas more irregular declines in ^{210}Pb activity in Cores 2 and 4 suggested local variation in sedimentation patterns (Figure 2). Activities of ^{137}Cs broadly peaked between c. 11 and c. 17 cm depending on the core, and declined slowly towards the surface sediments in most cores (Figure 2). The precise fit of the CRS models varied among cores, with a three-phase history of sedimentation for most locations (except Core 2) encompassing a near-linear age–depth relationship in the uppermost 10–13 cm (c. 1950), increased sedimentation to c. 25 cm (c. 1900), and a third phase of lower sedimentation before that

point. By contrast, sedimentation rates appeared relatively constant throughout Core 2. In each case, estimates of sedimentation before c. 1900 (25 cm) are uncertain as a consequence of the large SEs associated with relatively low unsupported ^{210}Pb activity and the need to extrapolate the depth–age relationships from early 20th-Century sediments to deeper samples (Figure 2).

3.2 | Geochemistry

The four cores displayed similar patterns in stable isotopes and sedimentary geochemistry through time (Figure 3). In all cores, values of $\delta^{15}\text{N}$ remained stable at c. 6‰, while $\delta^{13}\text{C}$ declined over the 20th Century. This pattern was most apparent in Core 1, where $\delta^{13}\text{C}$ values of c. –11‰ near 1900 declined steeply to surface values of c. –17‰. Patterns in N% and C% were similar within and among cores (Figure 3) with low and stable values during the 19th Century giving way to elevated content after c. 1900. The magnitude of changes during the 20th Century were similar among cores, although in Core 1, C% and N% content also rose sharply at c. 1900. These trends resulted in C:N ratios that were relatively elevated during the 19th Century but declined during the 20th Century, particularly in Core 1 (Figure 3).

Sedimentary TP content of Core 1 rose c. 50% over the 20th Century, whereas that of Core 2 remained relatively stable until increased variability in sediments deposited after c. 2000 (Figures 3 and S1). Insoluble apatite P was a consistent fraction of the sedimentary P pool (10%–15% of TP) throughout both cores, as was exchangeable P (2%–3%), whereas non-apatite P (c. 5%) and organic P (20%–35%) fractions doubled over the course of the 20th Century, particularly after c. 1950 in Core 1 (Figure S1).

3.3 | Diatoms

Constrained cluster analysis revealed three diatom assemblages occurred in the south basin of Lake Manitoba since c. 1800 (Figure 4). The first assemblage that occurred between c. 1800 and 1890 and had low fossil concentrations, being characterised mainly by benthic fragilarioid species (*Staurosirella pinnata* Ehrenberg, *Staurosira construens* Ehrenberg, *Pseudostaurosira brevistriata* Grunow) and some meso-eutrophic and eutrophic planktonic taxa (*Stephanodiscus niagarae* Ehrenberg, *Aulacoseira ambigua* Grunow, *A. granulata* Ehrenberg), leading to a core-wide minimum ratio of benthic: planktonic (B:P) species (<5). The second assemblage occurred between c. 1890 and 1930 and was marked by a five-fold increase in total diatom concentrations, reflecting increases in *P. brevistriata*, *S. construens* and *S. pinnata*, declines in *Aulacoseira* spp., and greatly elevated B:P ratios (≤c. 50) (Figure 4). The third assemblage occurred after c. 1930 and was marked by high but variable diatom concentrations, reduced abundance of *S. construens*, increased proportions of *S. pinnata*, *Fragilaria capucina* Desmazières and *Fragilaria mesolepta* Rabenhorst, and moderate B:P ratios (10–15). Abundances of

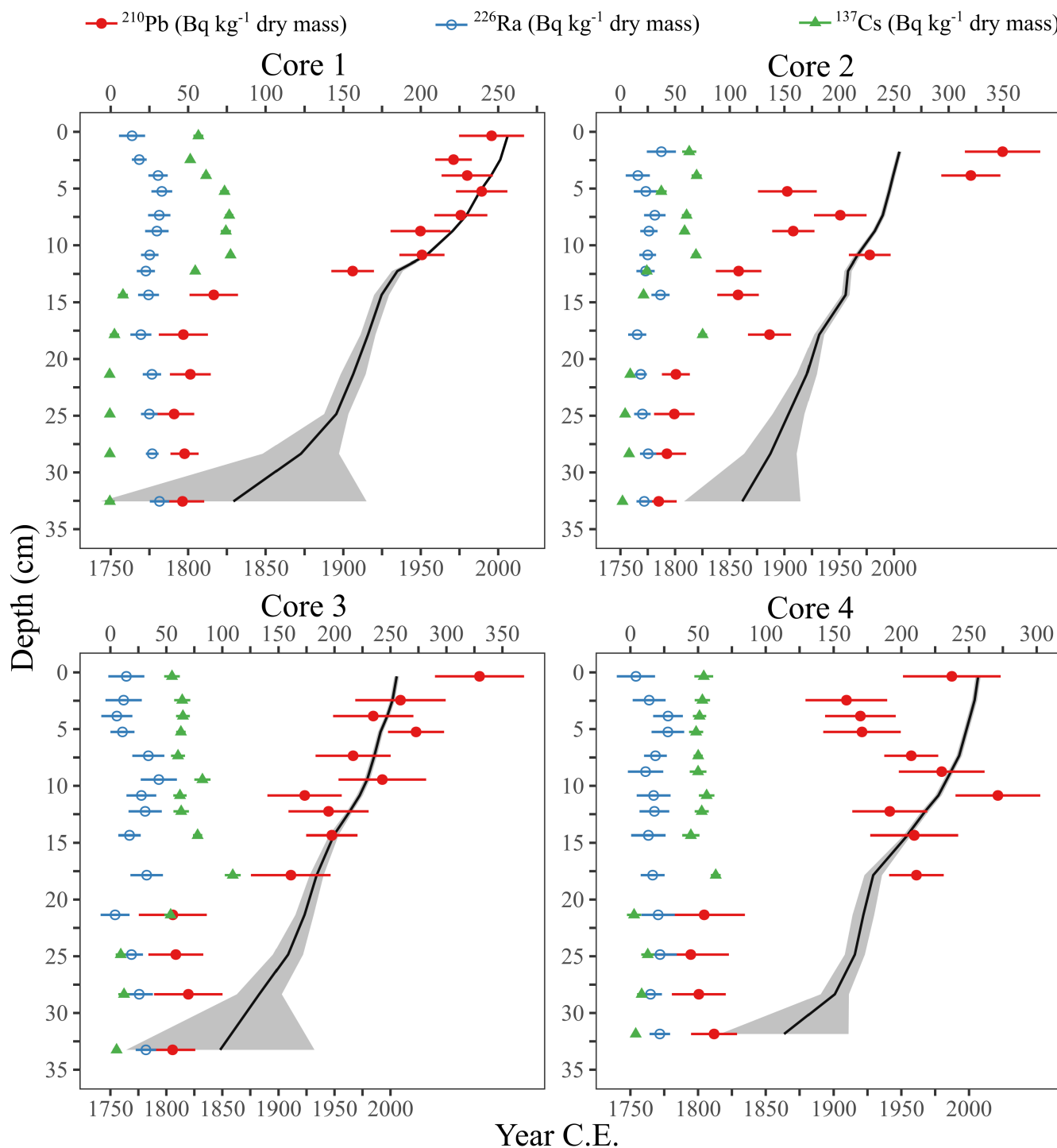


FIGURE 2 Activities of ^{210}Pb (closed points), ^{226}Ra (open points) and ^{137}Cs (closed triangles) in four cores from Lake Manitoba plotted by burial depth (cm). Radioisotope activities are presented in Bq/kg dry mass. The solid line represents the age-depth relationship determined by a constant rate of supply (CRS) model. Grey shading represents error estimates of the age-depth model. Core position identified in Figure 1.

planktonic *Aulacoseira* spp. and *Stephanodiscus* spp. remained low in this assemblage. Overall, patterns of diatom accumulation rates were similar to those recorded by the diatom-specific pigment diatoxanthin with low values in the 19th Century peaking c. 1900 and then declining to relatively stable values in the latter half of the 20th Century (Figure 4).

3.4 | Fossil pigments and cyanobacteria akinetes

Analysis with HGAMs revealed substantial and significant increases in fossil pigment concentrations during the 20th Century, although there were also differences in the magnitude and timing of change across pigments and cores (Figure 5). In all four cores, the

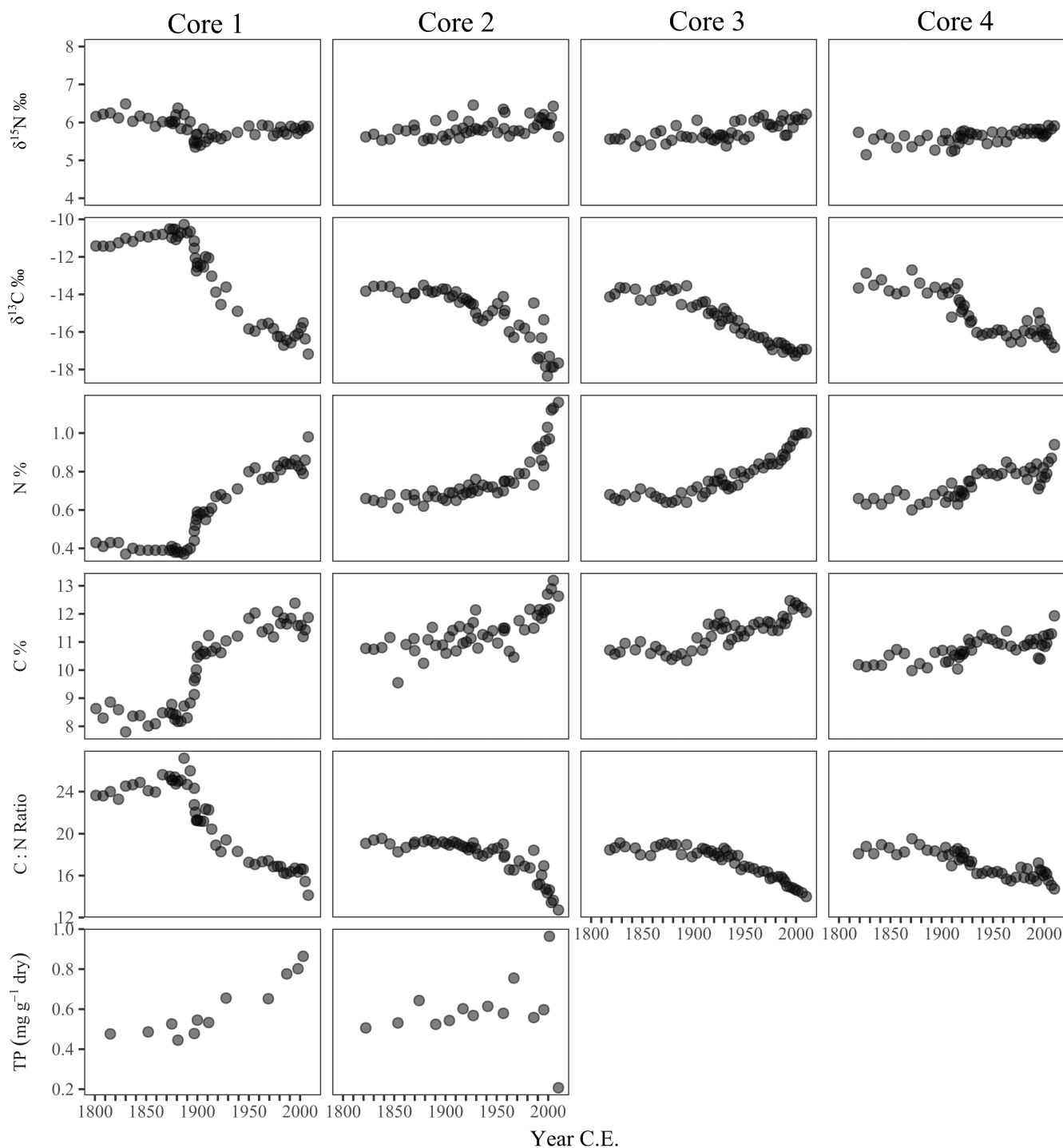


FIGURE 3 Historical changes in sediment stable isotope values ($\delta^{15}\text{N}$ ‰, $\delta^{13}\text{C}$ ‰), elemental content (N% and C% dry mass), C:N mass ratios and total phosphorus (TP mg/g dry mass sediment) in four cores from Lake Manitoba.

ratio of Chl-*a*:pheophytin *a* declined sharply from the top of core to relatively stable values in sediments deposited before c. 1950 (Figure S2). Concentrations of the mainly diatom biomarker diatoxanthin exhibited marked maxima at the end of the 19th Century in Cores 1 and 2 before declining slowly through the 20th Century, while elevated values were also recorded in Cores 3 and 4 during the early 1800s. Concentrations of pigments from cryptophytes (alloxanthin) and chlorophytes (pheophytin *b*) increased steadily after

c. 1880 in all cores, with statistically significant rates of increase in the first half of the 20th Century (Figure 5). Concentrations of canthaxanthin from potentially N_2 -fixing colonial Nostocales cyanobacteria also increased two- to three-fold in all cores c. 1900 then plateaued (Core 1) or declined slightly (Cores 2–4) in the last half of the 20th Century. Trends in total production (as β -carotene) incorporated many of these pigment-specific patterns, with evidence of increased primary production early in the 20th Century and stable

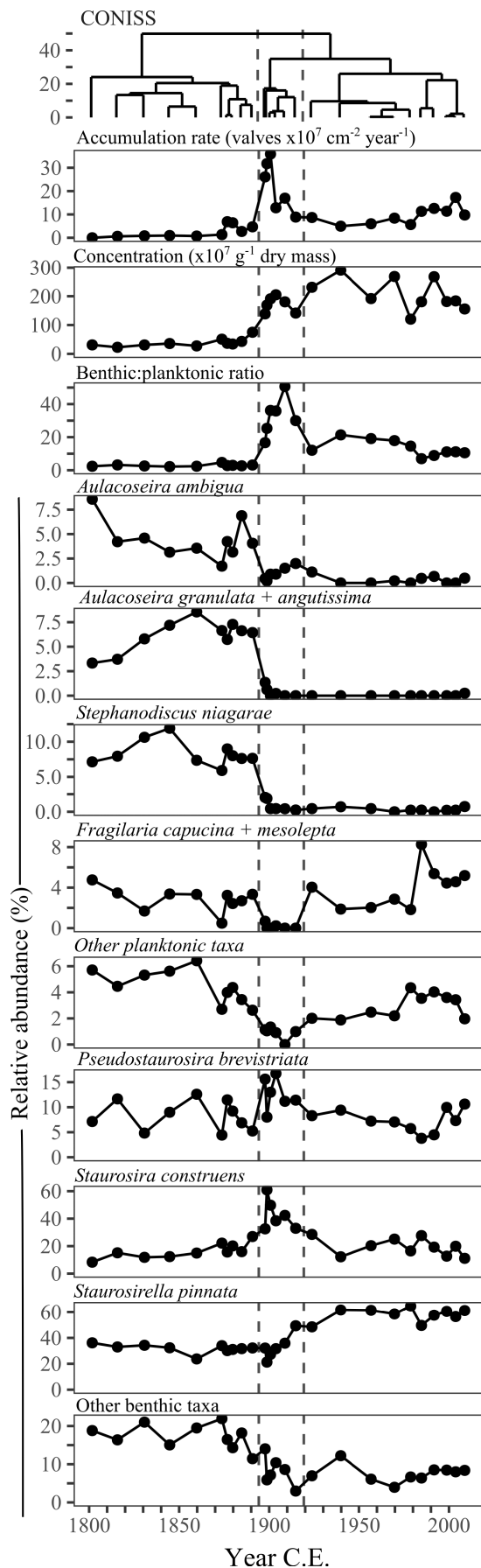


FIGURE 4 Relative abundances of common diatom taxa (>5% relative abundance) and total diatom concentrations of Lake Manitoba Core 1 plotted by age. Vertical lines represent periods of assemblage change as determined by broken-stick-validated constrained cluster analysis (CONISS). Diatom accumulation rate (valves $\times 10^7 \text{ cm}^{-2} \text{ year}^{-1}$), diatom concentrations (valves $\times 10^7/\text{g}$ dry mass), and abundance ratios of benthic: planktonic species also are presented.

concentrations after c. 1950 in three cores, whereas Core 2 exhibited more muted evidence of eutrophication (Figure 5).

Trends in pigment variance were similar to those of pigment concentration, with significant increases generally occurring in the early- and mid-20th Century followed by declining variance after c. 1930 for diatoms (diatoxanthin) and c. 1950 for colonial cyanobacteria (canthaxanthin). Trends in the variance of cryptophytes (alloxanthin) and chlorophytes (pheophytin *b*) were more variable with declines or plateaus throughout the late 20th and early 21st centuries (Figure S3). Variance in total production, as β -carotene, was slightly more variable in the latter half of the 20th Century than before, but exhibited few intervals of significantly increasing variability (Figure S3).

Based on analysis of Core 1, concentrations of akinetes from N_2 -fixing cyanobacteria (*Dolichospermum/Anabaena* spp., *Aphanizomenon* spp.) were negligible in the south basin of Lake Manitoba until c. 1970, after which levels exhibited a brief peak (Figure 5). Following this rise, akinete concentrations were slightly elevated but variable, with densities since 1970 varying in direct proportion to the three-year running mean volume of water diverted into the south basin from the Assiniboine River ($R^2 = 0.88$, $p = 0.004$). Overall, algal micro-fossils were composed mainly of remains from *Pediastrum* spp. (>99% of all soft fossils), particularly before 1970.

4 | DISCUSSION

Analyses of pigments, geochemistry and diatom assemblages in four sediment cores from southern Lake Manitoba were consistent with initial eutrophication beginning c. 1900, concomitant with the introduction of intensive agricultural practices to the landscape (AAFC, 2005; Deveson, 2007). Despite substantial initial eutrophication c. 1900–1930, highlighting the lake's sensitivity to land-use alterations, and general continued increases in lake production after c. 1950, measures of cyanobacterial production showed stable or declining trends over the latter half of the 20th Century. These trends were also recorded in fitted HGAM trends of pigment variance and do not suggest that Lake Manitoba has undergone an abrupt ecological change to cyanobacterial dominance, as had occurred in adjacent Lake Winnipeg as a result of the intensive land-use alterations in its catchment since 1980 (Bunting et al., 2016). Instead, modest increases in diazotrophic cyanobacteria in Lake Manitoba after 1970 were correlated with hydrological inputs via the Portage Diversion,

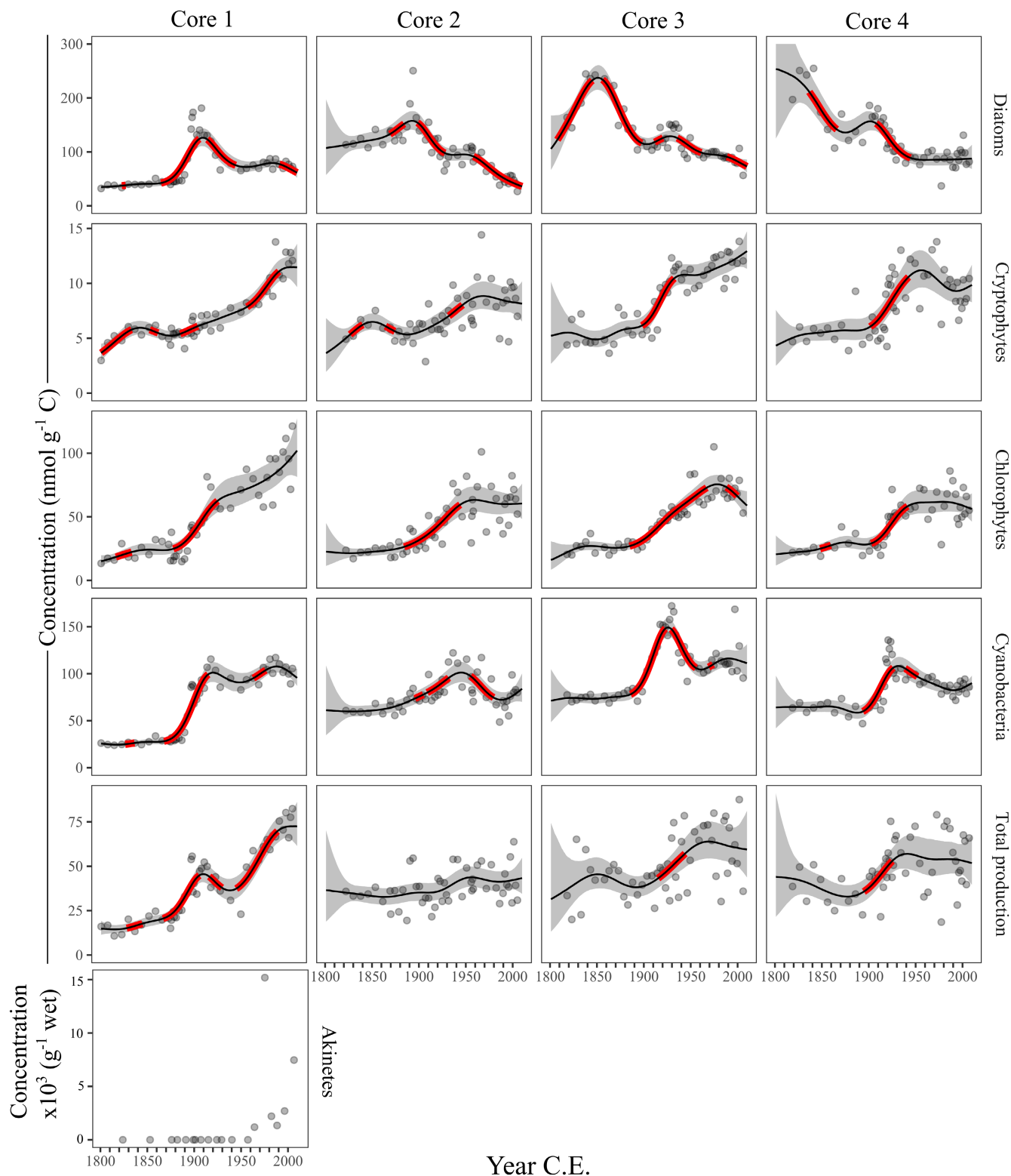


FIGURE 5 Concentrations (nmol pigment/g C) of select sedimentary pigments and N_2 -fixing cyanobacterial akinetes plotted by age in four cores from Lake Manitoba. In all plots, solid lines are fitted HGAM trends, shaded areas represent 95% confidence intervals of the model fit, and bold red sections are periods of statistically significant temporal change in pigment concentration. Pigments represent mainly diatoms (diatoxanthin), cryptophytes (alloxanthin), chlorophytes (pheophytin *b*), Nostocales cyanobacteria (canthaxanthin) and total phototrophic production (β -carotene). Total akinete concentrations are comprised of the sum of remains from N_2 -fixing *Anabaena*/*Dolichospermum* and *Aphanizomenon* spp. expressed as concentration of akinetes $\times 10^3$ /g wet sediment.

the main modern source of P to the southern basin of Lake Manitoba (Blais et al., 2016). Therefore, although both Lake Manitoba and Lake Winnipeg experienced a similar onset of eutrophication, which are likely to have been the consequence of regional agricultural development, subsequent eutrophication and the occurrences of abrupt ecological changes were dependent on how land-use intensified in the catchments proximate to each lake. These findings suggest that management of large lakes should prioritise mitigation of nutrient sources immediately adjacent to the lake basin before regulation of distal sources (Bunting et al., 2016; Rattan et al., 2017; Yates et al., 2012).

4.1 | Eutrophication of Lake Manitoba

Water quality degradation in Lake Manitoba during the 20th Century largely reflected the historical development of crop and cattle production with the southern lake catchment. The local catchment of Lake Manitoba's south basin was initially developed for the agricultural production of cereals and cattle in the late 19th Century (AAFC, 2005; Deveson, 2007; Westdal et al., 2013), whereas the immediate catchment of the northern basin has remained largely undeveloped (AAFC, 2020). Furthermore, mechanised tillage was introduced in the 1930s, resulting in increased cattle forage and cereals production thereafter. However, unlike much of southern Manitoba, there was not a shift away from cereals towards potatoes and hogs, with only modest increases in oilseeds (canola) during the 1980–1990s (Bunting et al., 2016; Deveson, 2007; MCEC, 2007; Schindler et al., 2012). Likewise, there has not been meaningful urban growth within the lake's catchment. Instead, the southern catchment of Lake Manitoba only exhibited increased forage for cattle production after 1980 (AAFC, 2005; MCEC, 2007).

Before the agricultural development of its catchment, the south basin of Lake Manitoba likely exhibited mesotrophic conditions, as suggested by historically low sedimentary concentrations of P, N and C, low fossil pigment concentrations, low concentrations of diatom and cyanobacteria micro-fossils, and a planktonic diatom assemblage indicative of meso-eutrophic conditions. Such naturally mesotrophic conditions also have been reconstructed for a variety of presently eutrophic prairie lakes (Bjorndahl et al., 2022; Dixit et al., 2000; Hall et al., 1999; Maheaux et al., 2016; Pham et al., 2008; Vinebrooke et al., 1998), confirming that, despite high baseline fertility, water quality has declined over much of the prairies since the onset of European-style agriculture.

Substantial increases in biological production, particularly by diatoms, suggest that horse-drawn and later mechanised tillage mobilised the naturally high amounts of P, N and probably silicon (Si) (Allan & Williams, 1978; Edlund et al., 2009; Gibson et al., 2000), from soils into Lake Manitoba, as seen elsewhere in the Prairies during the late 19th and early 20th centuries (Dixit et al., 2000; Hall et al., 1999). Initially elevated diatom production in Lake Manitoba gave way to sustained levels of cryptophytes (alloxanthin), chlorophytes (pheophytin *b*), and colonial cyanobacteria (canthaxanthin), suggesting

that Si supply declined either as a result of droughts or erosion control measures of the late 1930s and 1940s (Schindler et al., 1996), or of possible changes in competitive regimes that may have favoured non-siliceous taxa with higher nutrient optima and tolerances (chlorophytes and cyanobacteria) following the widespread application of chemical fertilisers beginning in the 1960s (Deveson, 2007; Karamanos, 2007; Yates et al., 2012). Geochemically, eutrophication in Lake Manitoba during the 20th Century was marked by increased concentrations of sedimentary C and organic P from land, whereas declines in C:N ratios marked a trend towards increasing production by aquatic phototrophs (Bunting et al., 2016; Hall et al., 1999). In addition, whole-sediment $\delta^{13}\text{C}$ signatures declined from values characteristic of sedimentary carbonates that underlie the basin (c. 10‰; Last, 1984; Valero-Garcés et al., 1997) towards those common to algal-derived carbon (−20‰ to 25‰). This pattern infers a large change in carbon source and cycling resulting from the eutrophication (Hecky & Hesslein, 1995). Together these features are characteristic of initial lake eutrophication following land-use change in the Canadian Prairies (Bunting et al., 2016; Edlund et al., 2009, 2017; Leavitt et al., 2006).

Analysis of fossil diatoms suggests that benthic populations have been an important source of primary production in Lake Manitoba throughout the past 200 years. Interestingly, most phyto-benthic diatoms (by abundance) did not decline during initial fertilisation of Lake Manitoba, in contrast to patterns seen in other lakes undergoing cultural eutrophication (Vadeboncoeur et al., 2003). Before c. 1890, assemblages were composed mainly (c. 65%) of benthic or tychoplanktonic fragilarioid taxa (*S. pinnata*, *S. construens*, *P. brevistriata*) consistent with presumed mesotrophic conditions and the ability of these species to outcompete other taxa in turbid, low-light environments (Gushulak et al., 2021; Gushulak & Cumming, 2020). Unexpectedly, the burst of diatom production in the early 20th Century was driven by these benthic taxa, whereas populations of planktonic taxa (*A. ambigua*, *A. granulata*, *S. niagarae*) generally collapsed during initial eutrophication. Although speculative, we infer that the rapid expansion of bottom-dwelling diatom populations c. 1900 may have constrained the magnitude of planktonic diatom response to land-use change through competition for Si (Schelske et al., 1986), rather than N or P, as populations of other algae and cyanobacteria also increased at the same time. As shown elsewhere, sedimentary populations of tychoplanktonic species can act as biological hotspots in lakes, acting as a seedbank for annual blooms of both diatoms and cyanobacteria (Gushulak et al., 2021).

Initial agricultural development may have increased soil erosion, lake turbidity, and the influence of water transparency on algal assemblages in Lake Manitoba (Bere & Tundisi, 2011). Changes in light regime are inferred by substantial declines in benthic diatom taxa (excluding tychoplanktonic, low-light-adapted fragilarioids) concomitant with agricultural development in the catchment c. 1890. Lake transparency appears to have stabilised after c. 1930 as inferred from the generally stable abundances of benthic/tychoplanktonic taxa (e.g., *S. pinnata*, *S. construens*, *S. brevistriata*) during the remainder of the 20th Century (Gushulak et al., 2021; Gushulak

& Cumming, 2020), even though individual species varied through time. We argue that light may have penetrated to the bottom of Lake Manitoba, at least seasonally, in order to support such a substantial phytobenthos.

Total lake production continued to increase after c. 1930, but with only limited changes in sedimentary geochemistry, diatom assemblage composition and cyanobacterial production. This general biogeochemical stability is consistent with the modest changes in land-use practices and absence of urban development within the southern catchment during the last 80 years (AAFC, 2005; Deveson, 2007; Westdal et al., 2013). During this period, farming practises evolved to expand cattle and forage production, with only marginal increases in oilseed production and no other major changes in crop selection (AAFC, 2005, 2020). Instead, minor geochemical changes (increased N and P content, reduced C:N ratios, depleted $\delta^{13}\text{C}$ values) were recorded after opening of the Portage Diversion in 1970. Mass budgets confirm that intermittent hydrological inputs from the Assiniboine River are a major source of P, but not N, during flood years (Blais et al., 2016), producing low N:P conditions which can favour diazotrophic cyanobacteria (Hayes et al., 2019; Orihel et al., 2012). Consistent with this interpretation, akinete concentrations from *Dolichospermum/Anabaena* spp. and *Aphanizomenon* spp. were correlated positively with inflow via the diversion since 1970. However, as populations of Nostocales cyanobacteria (as canthaxanthin) remained stable during the past 80 years, and considering that heterocytous cyanobacteria account for only a small fraction of both modern and fossil algal assemblages, we infer that N_2 -fixation remains only a small fraction of N influx to Lake Manitoba. Furthermore, as Lake Manitoba lacks major urban wastewater inputs (Bourne et al., 2002), it does not display the rising $\delta^{15}\text{N}$ values seen in Lake Winnipeg (Bunting et al., 2016; Mayer & Wassenaar, 2012) and other prairie lakes receiving urban N inputs (Leavitt et al., 2006). Instead, eutrophication of Lake Manitoba arose primarily from increased nutrient influx result from historical changes in agriculture within the local catchment of the south basin.

4.2 | Eutrophication and abrupt changes in large prairie lakes

Analysis with HGAMs shows that although Lake Manitoba experienced rapid eutrophication in the early 20th Century, it did not undergo the abrupt change to cyanobacterial dominance that has been well-reported in adjacent Lake Winnipeg after 1990 (Bunting et al., 2016; Schindler et al., 2012). While both lakes exhibited clear signs of initial eutrophication c. 1900 (increased chlorophytes, cyanobacteria; change in diatom assemblages), production of colonial cyanobacteria (as canthaxanthin) was stable after c. 1950 in Lake Manitoba and exhibited static or declining variation until the 21st Century. By contrast, concentrations and variances of most fossil pigments increased until 1990 in Lake Winnipeg, after which time densities of akinetes from diazotrophic cyanobacteria increased three- to five-fold (Bunting et al., 2016). Such rising variance prior

to an abrupt shift to surface blooms of cyanobacteria is a key indicator of nonlinear and abrupt changes in shallow lake ecosystems (Randsalu-Wendrup et al., 2016) and is consistent with other palaeolimnological assessments of eutrophied lakes that have undergone documented shifts towards turbid, cyanobacteria-rich states (McGowan et al., 2005; Scheffer & Jeppesen, 2007). Although Lake Manitoba also exhibited minor increases in fossil akinetes after c. 1970, the declining variance prior to that time, 10-fold lower akinete densities than in Lake Winnipeg, and linear relation to water influx from the Portage Diversion are not consistent with the operation of mechanisms leading an abrupt ecosystem change.

Differences in the histories of agricultural development within the local catchments of Lake Manitoba and Lake Winnipeg may be responsible for their contrasting trajectories of eutrophication during the past 40 years (Bunting et al., 2016; Rattan et al., 2017; Yates et al., 2012). Agriculture in the immediate catchment of Lake Winnipeg shifted from cereal-cropping to production of potatoes, canola, and hogs during the 1980s and early 1990s, and was the primary driver of the abrupt change in Lake Winnipeg (Bunting et al., 2016). These land-use changes resulted in increased export of terrestrial nutrients to Lake Winnipeg (Rattan et al., 2017; Yates et al., 2012) via the Red River which provides c. 70% and c. 35% of Lake Winnipeg's annual TP and TN influx, respectively (Zhang & Rao, 2012). Agricultural run-off, combined with influx of nutrient-rich, secondary-treated effluent from the City of Winnipeg (Soto et al., 2019), enhanced eutrophication and caused the abrupt change to cyanobacterial dominance in Lake Winnipeg in the early 1990s (Binding et al., 2018; Kling et al., 2011). In comparison, land-use change in the catchment of Lake Manitoba since 1980 has been mainly restricted to expansion of forage production for cattle populations that have been resident for nearly a century (AAFC, 2005; Deveson, 2007), while there has been no potato or hog production, limited cereal production, and only marginal introduction of canola during the past four decades (AAFC, 2005, 2020).

Climate variability also may have affected primary production, but does not yet appear to be a major factor regulating the eutrophication of Lake Manitoba or its differential history relative to Lake Winnipeg. For example, regional mean temperatures have increased by c. 1.5°C over the past century (ECCC, 2022b) and may have favoured expansion of cyanobacterial blooms, particularly in later decades (Paerl et al., 2016). However, in their variance partitioning analysis of nearby Lake Winnipeg, Bunting et al. (2016) found that temperature changes had only minor effects on algal and cyanobacterial production relative to those imparted by a century of altered crop and livestock production. Given that variation in prairie air temperatures is spatially coherent at the scale of hundreds of km (Pham et al., 2008; Vogt et al., 2011), we infer that atmospheric warming is unlikely to have differentially affected two large lakes separated by only 70 km. Likewise, while a documented 50% increase in summer precipitation across southern Manitoba during the 1990s increased N and P run-off to lakes (Dibike et al., 2012; McCullough et al., 2012; Manitoba Ministry of Agriculture [MMA], 2022), subsequent mass balance studies

show that precipitation alone cannot initiate sudden and differential eutrophication among the basins (Rattan et al., 2017). Instead, uniquely elevated nutrient concentrations due to fertiliser and manure applications in local catchments is a prerequisite to water-quality degradation following increased rainfall and run-off (Rattan et al., 2017; Yates et al., 2012). However, despite these patterns, we note that because the Portage Diversion increases P influx to Lake Manitoba during wet intervals, it is possible that predicted increases in precipitation and flooding (Dibike et al., 2012) may threaten future water quality in Lake Manitoba.

Finally, analysis of ratios of labile to chemically-stable pigments suggest that eutrophication may have altered the deep-water environment within Lake Manitoba. For example, Chl-*a*: pheophytin *a* ratios declined from maxima in surface sediments to more stable values in materials deposited before 1930–1950, in a pattern which suggests a selective loss of labile pigments (Hurley & Armstrong, 1991; Leavitt, 1993; Leavitt & Hodgson, 2001). In most lakes, over 95% of pigment losses occur during sinking following cell senescence, while further exponential losses of labile molecules continue for 10–20 years after deposition. Typically, changes in Chl-*a*: pheophytin *a* ratios in older sediments reflect changes in either primary production, development of deep-water anoxia, or the depth distribution of primary producers (reviewed in Leavitt & Hodgson, 2001). In the case of Lake Manitoba, we expect that the increases in pigment ratios in the early 20th Century reflect the initially elevated benthic production (see above) which would be expected to reduce pigment loss during sinking. Likewise, we interpret the presence of greatly elevated ratios of Chl-*a* (labile precursor) to pheophytin *a* (stable product) in surficial deposits (>5:1) as potentially recording the presence of live benthic algae. In either case, we infer that our reconstructions of past primary production are not greatly biased by changes in lake conditions, as Lake Manitoba is polymictic and should not develop sustained deep-water anoxia that affects pigment preservation. As well, we restricted our pigment analyses to compounds known to be chemically stable in sediment over the course of centuries (Leavitt & Hodgson, 2001). Furthermore, given the similar morphometry and modern limnological conditions in Lake Manitoba and Lake Winnipeg, we infer that differential preservation is unlikely to have caused observed differences in fossil time series.

5 | CONCLUSIONS

Palaeolimnological analyses of fossil pigments, geochemical markers and diatoms in four cores has produced the first record of eutrophication history for Lake Manitoba, despite it being the 29th largest lake in the world. These records indicate that the basin eutrophied from baseline mesotrophic conditions c. 1900 as a consequence of agricultural development of its immediate catchment. Despite marked increases in lake production during the early 20th Century, Lake Manitoba has not undergone the abrupt shift towards diazotrophic cyanobacteria seen in adjacent Lake Winnipeg (Bunting et al., 2016),

as indicated by declining variance in primary production after c. 1940–1950, stable concentrations of pigments from colonial cyanobacteria for c. 80 years, and persistently low densities of fossil akinetes from diazotrophic *Aphanizomenon* spp. and *Dolichospermum/Anabaena* spp. Given that the southern basins of lakes Manitoba and Winnipeg are separated by only 70 km, and are of comparable morphology, nutrient status and climate forcing (Dibike et al., 2012; McCullough et al., 2012), we infer that the lack of an abrupt change in Lake Manitoba reflects differential land-use practices that have occurred since the late 20th Century in the immediate catchments of each lake (Bunting et al., 2016; Rattan et al., 2017; Yates et al., 2012). In addition, we conclude that 10-fold variation in catchment size did not greatly affect the predisposition of the lakes to eutrophication, as both lakes initially eutrophied owing to the agricultural development of their immediate catchments (Bunting et al., 2016).

The south basin of Lake Manitoba has not yet undergone an abrupt change to profuse cyanobacterial blooms, yet markers of total production, cryptophytes and chlorophytes have continued to increase over the past several decades. This continued eutrophication may be in part a consequence of increased nutrient influx via the Portage Diversion that appears to be modifying aquatic stoichiometry to favour diazotrophic taxa, based on increases in akinete concentrations (Blais et al., 2016). Managers of Lake Manitoba should be wary of its continued eutrophication and should focus on the mitigation of proximal diffuse nutrient sources in the local catchment and limit unnecessary transfers of water via the Portage Diversion to prevent further water-quality degradation.

AUTHOR CONTRIBUTIONS

Conceptualisation: Cale A. C. Gushulak, Brian F. Cumming, Peter R. Leavitt; Developing methods: Cale A. C. Gushulak, Peter R. Leavitt; Conducting the research: Cale A. C. Gushulak, Stefano Mezzini, Katherine E. Moir, Lynda Bunting, Björn Wissel, Daniel R. Engstrom, Kathleen R. Laird, Ann St. Amand; Data analysis: Cale A. C. Gushulak, Stefano Mezzini, Gavin L. Simpson; Data interpretation: Cale A. C. Gushulak, Stefano Mezzini, Peter R. Leavitt; Preparation of figures & tables: Cale A. C. Gushulak, Stefano Mezzini, Katherine E. Moir; Writing: All authors.

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peoples, and the homeland of the Métis Nation. We dedicate this paper to our inspirational phycologist and friend, Ann St. Amand, who passed away on 07 October 2023. The world is a lesser place without her.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data from this study are available on GitHub at <https://github.com/simpson-lab/wpg-mb-lakes>.

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