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Increased variability and sudden ecosystem state change in Lake Winnipeg, Canada, caused by 20th century agriculture

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Abstract

Eutrophication can initiate sudden ecosystem state change either by slowly pushing lakes toward a catastrophic tipping point beyond which self-reinforcing mechanisms establish an alternate stable state, or through rapid but persistent changes in external forcing mechanisms. In principle, these processes can be distinguished by determining whether historical changes in focal parameters (phytoplankton) exhibit transient (rising then declining) or continuously-elevated variability characteristic of alternate stable states or a “paradox of enrichment,” respectively. We tested this hypothesis in the south basin of Lake Winnipeg, Canada, a site with intense blooms of N₂-fixing cyanobacteria since 1990, but for which little is known of earlier limnological conditions, causes of eutrophication, or whether modern conditions represent an alternate stable state. Paleolimnological analysis revealed that the basin was naturally mesotrophic (~15–20 μg P L⁻¹) with diazotrophic cyanobacteria, productive diatoms, and phosphorus-rich sediments. Eutrophication accelerated during ca.1900–ca.1990, when sedimentary nitrogen, phosphorus and carbon contents increased 10–50%, δ¹⁵N enriched 3–4‰, and concentrations of many fossil pigments increased 300–500%. Nearly 75% of 20th century variability was explained by concomitant increases in production of livestock and crops, but not by climate. After ca.1990, the basin exhibited a rapid threefold increase in akinetes from *Aphanizomenon* and *Anabaena* spp. and 50% declines in pigments from chlorophytes and cyanobacteria because of sudden socio-economic reorganization of agriculture. Phytoplankton variability quantified using Gaussian generalized additive models increased continuously since the onset of agriculture for bloom-forming taxa, did not decline after state change, and suggested that recovery should not be affected by stable-state hysteresis.

Eutrophication remains the most significant global threat to the integrity of aquatic ecosystems despite 50 yr of research to identify the factors that degrade water quality (Carpenter et al. 1998; Schindler 2006). In cases where eutrophication has been caused by nutrient influx from discrete sources (e.g., municipal waste water, factory farms), significant improvements in water

quality have been achieved following diversion of point-source nutrients (Jeppesen et al. 2005). In contrast, eutrophication by nonpoint nutrient sources (e.g., agriculture, atmospheric deposition) has been more difficult to quantify and regulate, because diffuse fluxes are often intermittent (Bennett et al. 2001), derived from large-scale land-use practices (Carpenter et al. 1998), or are regulated by opposing management strategies for food production and environmental quality (Bunting et al. 2007). Such diffuse nutrient inputs are now the primary cause of aquatic pollution in many regions of the world (Carpenter et al. 1998).

Water quality degradation from diffuse nutrient sources arises for several reasons. First, agricultural inputs of phosphorus (P) and nitrogen (N) in commercial fertilizer and animal feed supplements often exceed agricultural outputs (Bunting et al. 2007). Second, excessive livestock densities can lead to manure production that overwhelms both soil

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Additional Supporting Information may be found in the online version of this article.

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storage capacities and regional requirements of crops. Third, application of N in commercial fertilizer or manure can lead to ammonia (NH_3) volatilization and N deposition at remote locations (Holtgrieve et al. 2011). In many instances, excess fertilization favors soil surpluses of P that are mobile and can leach into downstream aquatic ecosystems (Bennett et al. 2001). Such surpluses of soil P can last for millennia (Carpenter 2005), facilitate accumulation of soluble P within downstream lakes, and alter mechanisms regulating lake structure and function (Bunting et al. 2007).

Ecological theory predicts that persistent fertilization of lakes may lead to potentially-irreversible changes in the structure and function of lake ecosystems (Scheffer et al. 2001; Scheffer and Carpenter 2003; Carpenter 2003). In particular, analysis of small shallow lakes suggests that increased variation in focal water-column parameters (e.g., phytoplankton abundance, Chlorophyll *a*) and regulatory mechanisms are reliable indicators of state change from irradiance-sufficient mixed assemblages of benthic and planktonic primary producers to communities in turbid waters composed predominantly of buoyant cyanobacteria (Carpenter 2003; Carpenter and Brock 2006). This shift between states may arise from either rapid persistent changes in external forcing (Leavitt et al. 2009; Dakos et al. 2015) or comparatively small variation in environmental conditions (climate, food web) which are reinforced by internal feedback mechanisms within alternate states (e.g., vertical stratification, internal nutrients, macrophytes, shading) (Scheffer et al. 2001; Scheffer and Carpenter 2003). However, little is known of whether these regime shift hypotheses are relevant to large lakes (Janssen et al. 2014).

In principle, characterization of historical changes in the variability of key ecosystem components, such as phytoplankton abundance, can be used to distinguish between sudden ecosystem state change arising from establishment of alternate stable states from those which experience continuous forcing (Carpenter et al. 2011; Dakos et al. 2015). Lake ecosystems subject to prolonged slow forcing by a predominant mechanism, such as by eutrophication from land-use change, may exhibit rising variance and temporal autocorrelation in focal parameters prior to regime shifts to alternate stable states (Carpenter and Brock 2006; Scheffer et al. 2009). After transition, new stable states are characterized by lower temporal (and spatial) variability in focal parameters following the establishment of internal mechanisms which reinforce the new state (e.g., internal nutrient loading, loss of macrophytes, etc.) (Carpenter and Brock 2006; Scheffer and van Nes 2007; Dakos et al. 2015). In contrast, lakes forced by sudden but persistently-elevated nutrient influx, as well as those which initiate cyclic behavior or which fail to establish an alternate stable state, may exhibit a “Paradox of Enrichment” wherein bloom-forming taxa exhibit increased variability and diminished predictability following state change (Cottingham et al. 2000; Dakos et al. 2015). To date, analysis of variability has rarely been used to distinguish between these scenarios,

although ecological theory suggests the approach would be a powerful management tool (reviewed in Dakos et al. 2015).

In this paper, we analyzed profundal sediments for diverse chemical and biological parameters to test the hypothesis that the southern basin of Lake Winnipeg, Canada, has undergone sudden ecosystem state change due to cumulative effects of a century of agriculture (e.g., Carpenter 2005), rather than long-term climatic change (e.g., Paerl and Huisman 2008). We also sought to determine whether historical changes in phytoplankton variability were consistent with establishment of an alternative stable state. Lake Winnipeg is presently eutrophic (south basin $> 100 \mu\text{g TP L}^{-1}$); however, little is known of the baseline limnological conditions, the extent and causes of eutrophication, or whether outbreaks of diazotrophic cyanobacteria (*Aphanizomenon*, *Anabaena* spp.) since 1990 (Schindler et al. 2012) represent establishment of a self-reinforcing alternative stable state (Scheffer et al. 2001; Scheffer and Carpenter 2003). To address these issues, we created highly-resolved time series of historical N inputs (as $\delta^{15}\text{N}$, N content), P influxes (as TP and P fractions), aquatic carbon cycling ($\delta^{13}\text{C}$, C content), and algal abundance and community composition (pigments, microfossils from cyanobacteria and diatoms) for statistical comparison with coeval records of climatic variability, crop production, and livestock densities using variance partitioning analyses (Borcard et al. 1992; Hall et al. 1999). Historical changes in phytoplankton variability were then quantified using Gaussian generalized additive models of location and scale (Rigby and Stasinopoulos 2005).

Methods

Site description

Lake Winnipeg is a large (23,750 km²), shallow (mean depth = 12 m), polymictic, multi-basin, eutrophic lake ($> 100 \mu\text{g P L}^{-1}$) situated at 217.6 m above sea level (a.s.l.) in the Province of Manitoba (MB), Canada (Fig. 1, Supporting Information S1). Climate is sub-humid continental (Leavitt et al. 2006), but has experienced pronounced warming during fall, winter and spring since the 1800s (Hall et al. 1999). The 953,250 km² lake catchment is located mainly within the Canadian provinces of Manitoba (MB), Alberta (AB), Saskatchewan (SK), and Ontario (ON), with additional contributions from the northern United States of North Dakota (ND) and Minnesota (MN). More than 660,000 km² (69%) of the catchment is used for agriculture, which in Canada is divided evenly between areas for cultivation of crops (wheat, barley, oats, canola; also potatoes and corn in MB) and that used for pasture, forage, or zero-tillage management in support of the production of ~12 million beef cattle and ~15 million hogs per annum (Lake Winnipeg Initiative Consortium [LWIC] 2006; Manitoba Conservation and Water Stewardship [MCWS] 2006). More than 80% of the 6.6 million inhabitants of the watershed are located in urban areas,

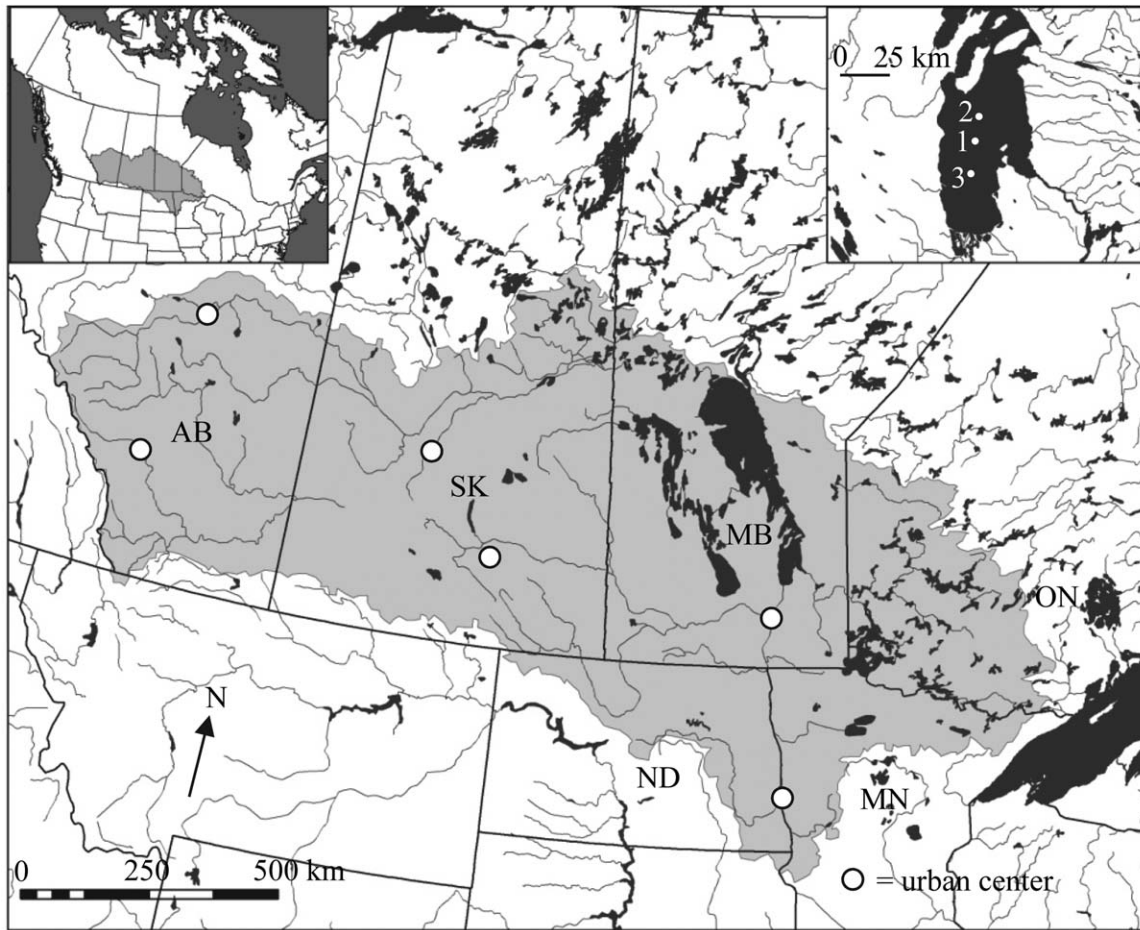


Fig. 1. Catchment area (grey shading) of Lake Winnipeg, Manitoba, Canada. This lake is the largest water body in Manitoba (MB), and receives drainage mainly from Canadian provinces of Alberta (AB), Saskatchewan (SK), and Ontario (ON), and US states of Minnesota (MN) and North Dakota (ND). Urban centers with > 200,000 inhabitants indicated with white open circles, and include the City of Winnipeg (pop. 750,000) in MB. Lake location within North America in upper left inset. Location of three sediment within south basin of Lake Winnipeg in upper right inset. Sediment cores were collected at 50.7825°N, 96.7756°W (Core 1), 50.9135°N, 96.7417°W (Core 2) and 50.6260°N, 96.7960°W (Core 3). See Supporting Information S1 for detailed site and catchment description.

although cities with populations > 200,000 are relatively uncommon (Fig. 1). Presently, more than 50% of nutrient influx is derived from MB (Supporting Information S1), particularly the Red River catchment (Yates et al. 2012; Donald et al. 2015). Further descriptions of the basin land-use characteristics and nutrient fluxes are provided in Supporting Information S1.

Historical development of eutrophication

At present, Lake Winnipeg receives ~96,000 tonnes N and ~7,900 tonnes P each year (Supporting Information S1); however, historical changes in limnological conditions within Lake Winnipeg are poorly known due to its large size, remote location, and potentially high spatial heterogeneity. Sporadic monitoring of the south basin during the 20th century suggests a shift from mesotrophic conditions recorded during both the 1920s (Lowe 1924; Bajkov 1930, 1934) and

late-1960s (Brunskill 1973; Crowe 1973; Brunskill and Graham 1979) to a more advanced state of eutrophy thereafter, as indicated by elevated concentrations of TP (~80 $\mu\text{g P L}^{-1}$) and TN (~700 $\mu\text{g TN L}^{-1}$) in the south basin during 1992–1996 (MCWS unpubl. data; Schindler et al. 2012). Similarly, surveys conducted during 2000–2005 revealed enriched concentrations of TP (> 100 $\mu\text{g P L}^{-1}$) and TN (~750 $\mu\text{g N L}^{-1}$) throughout the south basin, with soluble reactive P (SRP) accounting for ~50% of TP (> 50 $\mu\text{g P L}^{-1}$) during fall sampling (Schindler et al. 2012; MCWS unpubl. data). Occasional phytoplankton analyses conducted during the 20th century suggest that a diatom community composed mainly of *Stephanodiscus niagarae* Ehrenberg in 1920s (Lowe 1924), 1930s (Bajkov 1930, 1934), and 1969 (Crowe 1973; Brunskill and Graham 1979) was supplemented with, or replaced by, diazotrophic cyanobacteria (*Aphanizomenon*, *Anabaena*) and the diatom genus *Aulacoseira* by the 1990s (Kling 1998; Kling

et al. 2011). Interestingly, paleolimnological analysis of two sediment cores with low temporal resolution suggests that heterocystous cyanobacteria and *Aulacoseria* spp. have been present in Lake Winnipeg for several millennia (Kling 1998). Improved understanding of historical levels of lake production is essential both for optimizing ecosystem management strategies and to evaluate the proximity of lake state to potential catastrophic tipping points.

Field and laboratory methods

Three sediment cores (62.6–77.6 cm in length) were collected along a 35-km transect within the south basin of Lake Winnipeg in July 2006 using a Glew gravity corer deployed from the research vessel *MV Namao* (Fig. 1). The cores were sectioned in 7.5-mm intervals and sediment samples were either refrigerated (4°C) or frozen (−10°C) in darkness until analysis of individual strata for measures of sediment age (^{210}Pb , ^{137}Cs activities), past lake nutrient status (C, N, and P contents; $\delta^{15}\text{N}$, $\delta^{13}\text{C}$), algal abundance and gross community composition (pigments) and, for Core 1 alone, microfossils from diatoms and cyanobacteria.

Sediment chronology was established for each core by gamma spectrometric analysis of ^{210}Pb and ^{137}Cs activities in 15–16 lyophilized (48 h, 0.01 Pa) whole sediment samples distributed evenly over the length of the core (Appleby et al. 1986; Schelske et al. 1994). Sediment age and mass accumulation rates ($\text{g cm}^{-2} \text{yr}^{-1}$) were calculated using the constant rate of supply (CRS) calculation following Binford (1990).

Stable isotope ratios and elemental composition were determined on whole freeze-dried sediment samples using a ThermoQuest (F-MAT) Delta^{PLUS} XL isotope ratio mass spectrometer equipped with continuous flow (Con Flo II) unit and an automated Carlo Erba elemental analyzer following Savage et al. (2004). Stable N ($\delta^{15}\text{N}$) and C ($\delta^{13}\text{C}$) isotope ratios were expressed in the conventional δ -notation in units of per mil (‰) deviation from an atmospheric N_2 standard and an organic C standard calibrated previously against authentic Vienna Pee Dee Belemnite. Sample reproducibility was $<0.25\%$ and $<0.10\%$ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ determinations, respectively.

Sediment TP concentrations and four operationally-defined fractions of P were measured using the standard protocols of Engstrom and Wright (1984). All extracts were analyzed with a Lachat QuikChem model 8000 flow-injection auto-analyzer using the ascorbic acid method. TP was quantified as ortho-P extracted by sequential exposure to 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; $\text{NH}_4\text{Cl-P}$). The residue from the second aliquot was sequentially extracted with 0.1 M NaOH to measure non-apatite inorganic P (NAI-P; NaOH-P) composed of Fe- and Al-bound P, and 0.5 M HCl to determine apatite (carbonate)-bound P (AP; HCl-P). Finally, residual organically-bound P (OP; residual-P) was estimated as the difference between TP and

the sum of the inorganic P fractions. In general, EP is considered available to biota following release from sediments, AP includes P bound in crystal lattices of apatite grains and is largely biologically inert (Mayer et al. 2006), while NAI-P includes orthophosphate adsorbed on Fe- and Al-oxides, Fe and Al minerals such as vivianite or variscite, and Ca-P minerals other than crystalline apatite (Williams et al. 1980) and is considered to be the maximum potential particulate P that can be rendered soluble by diagenesis (Logan et al. 1979).

Algal abundance and community composition was quantified from analysis of fossil pigments and their derivatives. Pigments were extracted from lyophilized whole sediment samples, filtered (0.2- μm pore), and dried under pure N_2 gas using the standard methods of Leavitt and Hodgson (2001). Carotenoids, chlorophylls (Chls), and their derivatives were isolated and quantified using an Agilent model 1100 high-performance liquid chromatography (HPLC) system equipped with photo-diode array and fluorescence detectors, and calibrated with authentic standards. Analysis was restricted to pigments characteristic of siliceous algae and some dinoflagellates (fucoxanthin), mainly diatoms (diatoxanthin), cryptophytes (alloxanthin), chlorophytes (Chlorophyll *b*, pheophytin *b*), Nostocales cyanobacteria (canthaxanthin), total cyanobacteria (echinenone), total algae (β -carotene), as well as ubiquitous Chl *a* and its derivative pheophytin *a*. Isomeric carotenoids from chlorophytes (lutein) and cyanobacteria (zeaxanthin) were inseparable on our HPLC system and were presented together as lutein-zeaxanthin (potentially bloom-forming algae). Pigment concentrations were expressed as $\text{nmol pigment g}^{-1}$ sediment C, a metric which is linearly correlated to annual algal standing stock in whole-lake calibration studies (Leavitt and Hodgson 2001).

For Core 1 alone, cyanobacterial akinetes (resting stages) were isolated from refrigerated sediments and prepared for microscopy following the modified protocol of Crumpton (1987). Whole sediment samples (~ 1 g) were diluted with 20 mL distilled water, sonicated three times, and preserved with glutaraldehyde (0.2 mL). Samples were homogenized and aliquots (~ 0.10 mL) were removed, diluted with distilled water, and fossils filtered onto a 0.45- μm pore membrane filter. Filters were mounted on cover slips using hydroxypropyl-methacrylate (HPMA) resin, air dried for 24 h, and permanently mounted onto glass microscope slides with HPMA resin. For each sample, ~ 200 cyanobacterial akinetes were identified and enumerated by counting random fields using an Olympus BX51 compound microscope equipped with Nomarski and phase-contrast optics, and epifluorescent detection ($\lambda_{\text{excitation}} = 450\text{--}480$ nm). Microfossil concentrations were estimated as akinetes g^{-1} wet mass of whole sediment, a metric linearly correlated to phytoplankton densities in large lakes (Bunting et al. 2007). Taxonomic identities were based on references from Bunting et al. (2007) and a standard reference collection.

Diatom microfossils (frustules, valves) were isolated from Core 1 sediments and prepared for microscopy following the standard protocols of Laird and Cumming (2009). Whole fresh sediments (0.2–0.3 g) were placed in a 20-mL glass vial with a mixture of concentrated HNO_3 : H_2SO_4 (50 : 50, by mole), heated for ~6 h at 70°C, and settled for 24 h. Samples were washed repeatedly to constant pH with distilled water. Suspensions of siliceous microfossils were spiked with known densities of artificial microspheres, evaporated onto cover slips, and mounted permanently onto glass microscope slides with Naphrax[®] medium. For each sample, ~400 diatom valves were identified and enumerated along transects using a Leica DMRB microscope equipped with a 100X fluotar objective and differential interference contrast optics (1000X magnification; N.A. = 1.3) to determine species composition, microfossil concentration (valves g^{-1} dry mass sediment), and relative (%) species abundance. Taxonomy, nomenclature and TP optima (TP_{opt}) of diatom species are presented in Michels et al. (2007), Laird and Cumming (2009), Hyatt et al. (2011), and Cumming et al. (2015). Broad changes in both the concentration and relative composition of fossil diatoms were identified from a stratigraphically-constrained cluster analysis using a Euclidian distance as measure of sample similarity (Grimm 1987).

Historical data

Time series of 191 environmental variables from MB were collected for the 20th century to both quantify the statistical relationships between fossil records of lake trophic status (pigments, %N, %C, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$) in the south basin prior to recent expansion of cyanobacterial blooms and identify potential causal agents related to regional variation in climate, livestock populations, and crop production (Supporting Information S2). We focused on the statistical relationships between Manitoba land-use practices, climate, and water quality during the 20th century because mass-balance studies of the entire Lake Winnipeg basin demonstrate that nutrients from other Canadian and USA regions are largely sequestered in prior to transmission to Lake Winnipeg (Bourne et al. 2002; Donald et al. 2015) and that the City of Winnipeg contributes 5–10% of TN and TP to the lake in most years (Supporting Information S1) (Bourne et al. 2002; MCWS unpubl. data). Finally, we used estimates of total agricultural production within MB for comparison with the fossil time series because agricultural activities within MB are largely restricted to land within the Lake Winnipeg catchment.

Details concerning sources and processing of environmental time series are presented in Supporting Information S2. Briefly, climate records were obtained from two Environment Canada weather stations located in the City of Winnipeg and included precipitation (mm), annual rainfall (mm), mean monthly, minimum, maximum and seasonal temperatures (°C). Historical records of ice thaw and freeze near Win-

nipeg were obtained from Hall et al. (1999), while mean annual lake level (m a.s.l.) and discharge (m^3) from tributary and outflow rivers were obtained from MCWS. Historical records of livestock and associated agricultural products were obtained for MB from Census of Canada reports (Statistics Canada 1871–2006), whereas human populations were obtained for MB from Census of Canada reports (Statistics Canada 1871–2006). Estimates of agricultural intensity included specific farm activities, fertilizer sales, and direct measurements of agricultural production, largely obtained from Census of Canada reports (Statistics Canada 1871–2006), the Canadian Fertilizer Institute, the Potash and Phosphate Institute, and previous publications (Korol and Rattray 1999; Korol 2002). In general, chemical fertilizer use was limited prior to 1960. Although too brief to be used in our statistical analysis, limnological variables from 1969 and 1992 to 2005 were collected from MCWS and Fisheries and Oceans Canada (FOC). Similarly, MCWS records of fish harvest were viewed mainly as a response to eutrophication, rather than predictors of causal relationships, and were not included in statistical analyses. As shown elsewhere, food-web state change in the absence of variation in allochthonous nutrient influx alters phytoplankton composition and vertical distribution but not total production (Leavitt et al. 1989; McGowan et al. 2005).

Numeric analyses

Constrained and partial canonical ordinations (ter Braak 1988) were used to evaluate the statistical relationships between fossil records of trophic status (pigments, stable isotopes, C and N content; diatoms) from Core 1 and time series of explanatory variables related to climate (C), livestock (L), and crops (A) as detailed in Supporting Information S2. Specifically, we used the variance partitioning analysis (VPA) protocol of Borcard et al. (1992), as modified by Hall et al. (1999) for paleolimnological applications, to estimate the fraction of historical variance in time series of fossil assemblages explained by categories of predictor variables (C , L , A) and their first- ($C \times L$, $C \times A$, $A \times L$) and second-order ($C \times L \times A$) interactions. Redundancy analysis (RDA) was used to partition variation in fossil assemblages because exploratory detrended correspondence analysis (DCA) suggested that fossil composition varied along environmental gradients in a linear rather than unimodal fashion (ter Braak 1986). Predictor and fossil time series were transformed if needed (\log_{10}), then centered (mean = 0), standardized (variance = 1.0), and harmonized to equivalent sampling intervals prior to analyses (see Supporting Information S2). Separate VPA was conducted for indices of past lake trophic status (nine biomarker pigments, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %C, %N) and diatom community composition (% relative abundance) for the periods 1901–1992 and 1904–1993, respectively. All computations were performed using CANOCO v. 4 (ter Braak 1990) (Microcomputer Power, New York, U.S.A.).

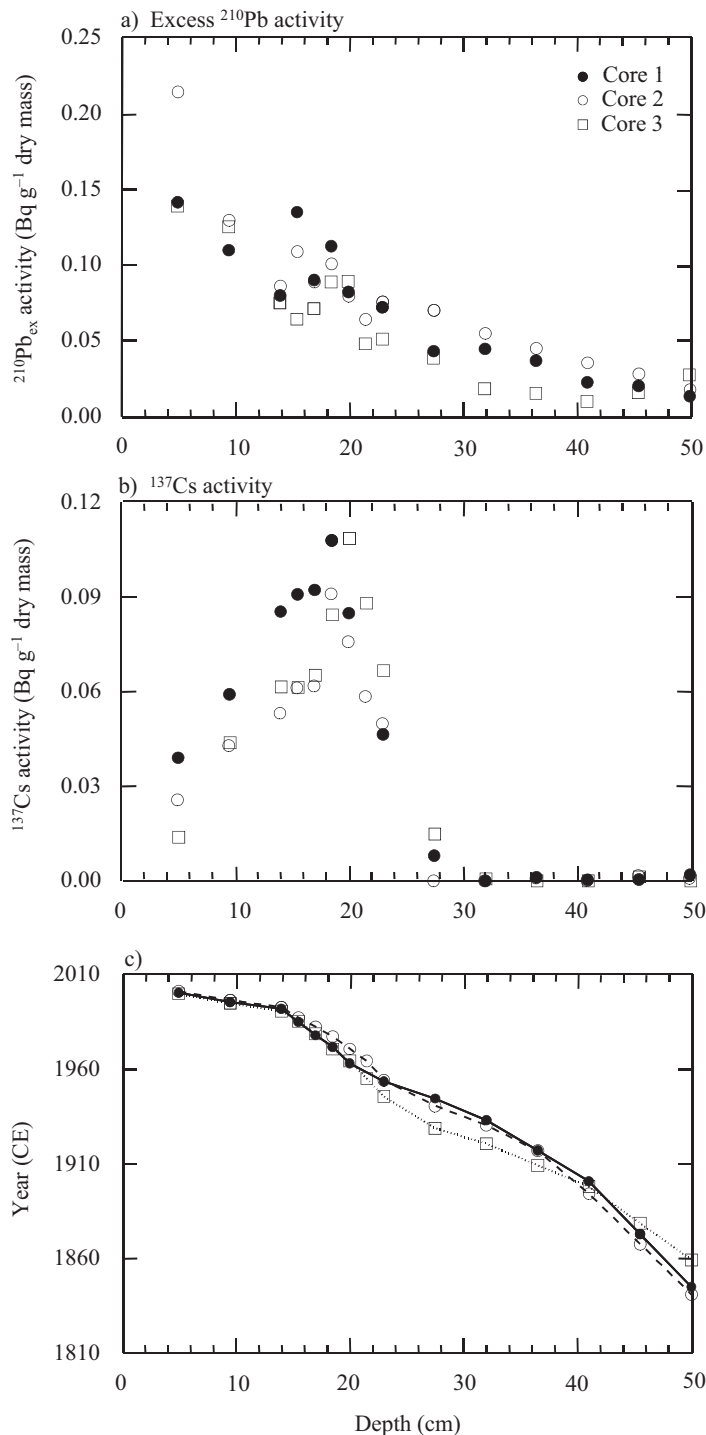


Fig. 2. Specific activities (Bq g^{-1} dry mass) of **(a)** ^{210}Pb and **(b)** ^{137}Cs in three cores from southern Lake Winnipeg as a function of burial depth. **(c)** Relationship between sediment age estimates from constant rate of supply calculation and ^{210}Pb activities for Cores 1 (closed circle, solid line), 2 (open circle, dashed line), and 3 (open square, fine line). Core locations are separated by 35 km (Fig. 1 inset).

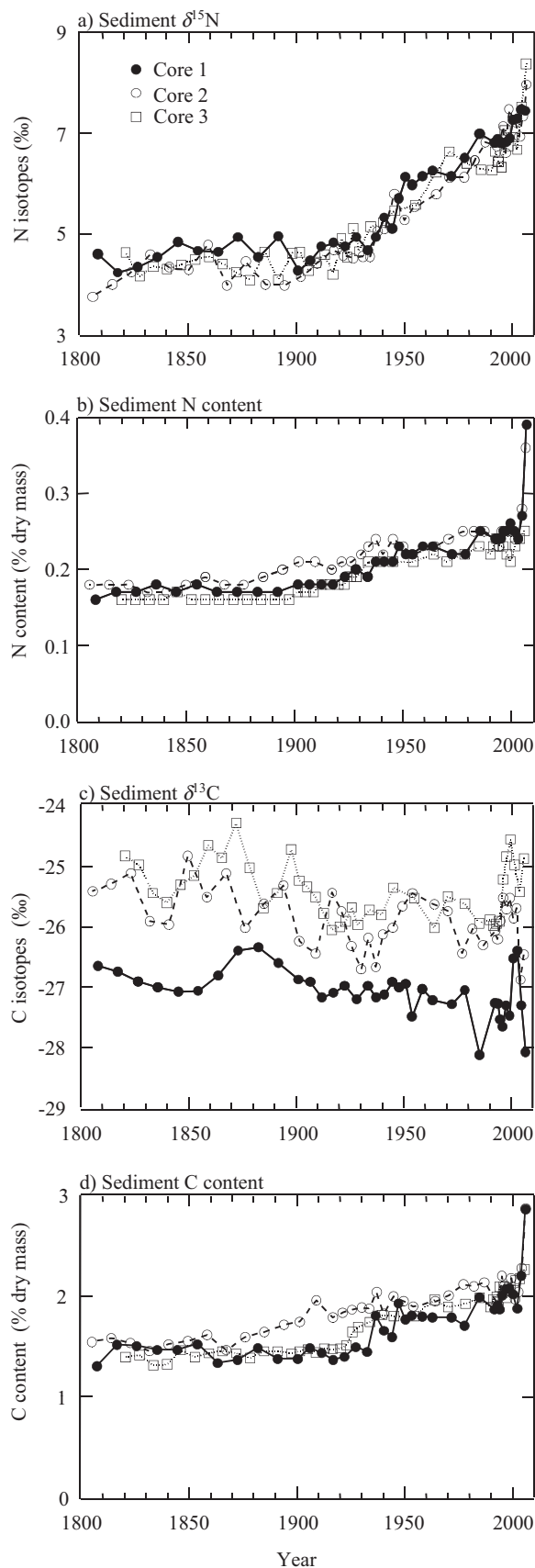
Historical changes in the temporal variability of phytoplankton abundance were estimated by application of Gaussian generalized additive models of location (mean) and scale (variance) (GAMLS) (Rigby and Stasinopoulos 2005) to fossil pigment time series representing the main functional groups of phytoplankton (Supporting Information S3; R Core Team 2015). Algal pigments have been identified as reliable metrics of changes in ecosystem variability during state changes (Carpenter et al. 2011). Similarly, sedimentary pigments accurately record known regime shifts among alternate stable states (McGowan et al. 2005), as well as historical increases the temporal variability of phytoplankton abundance arising from persistent fertilization (Hall et al. 1999; Cottingham et al. 2000). However, while fossil analyses have recorded increased variability associated with transient shifts among alternate stable states (“flickering”; Wang et al. 2012), this approach has been criticized for generating statistical artifacts because time series are based on observations that are unevenly separated in time and that each integrate different time intervals (Carstensen et al. 2013). To address these biases, we used the GAMLS approach with weighted time series to quantify historical trends in phytoplankton variability, as this procedure does not require uniform time series steps and corrects for variation in temporal resolution among samples. GAMLS were fit to fossil pigment time series for diatoms (diatoxanthin), cryptophytes (alloxanthin), chlorophytes (pheophytin *b*), colonial cyanobacteria (canthaxanthin) and total phytoplankton (β -carotene).

Based on empirical and theoretical considerations, we expected that phytoplankton variability would increase with lake fertilization until state change, then either decline if an alternate stable state were established (Carpenter et al. 2011; Dakos et al. 2015), or continue to increase if the lake exhibited a paradox of enrichment (Hall et al. 1999; Cottingham et al. 2000), failed to establish a stable state (Capon et al. 2015), or was subject to continuously elevated variance in forcing mechanism (Dakos et al. 2015). We sought to distinguish among these scenarios, because management strategies to reduce nutrients may be ineffective when hysteresis associated with establishment of a turbid water state slows lake recovery (Scheffer et al. 2001; Scheffer and van Nes 2007; Dakos et al. 2015).

Results

Sediment chronology

^{210}Pb activity declined with depth in each of the Lake Winnipeg sediment cores (Fig. 2a) in a pattern that suggested only limited mixing of surface sediments. Similarly, activity profiles for ^{137}Cs were well defined, with a clear maximum in ^{210}Pb -dated intervals corresponding to peak atmospheric nuclear testing in 1964 (Fig. 2b). Application of the CRS calculation also showed that bulk dry sediment accumulation rates (SAR) were high and similar over the



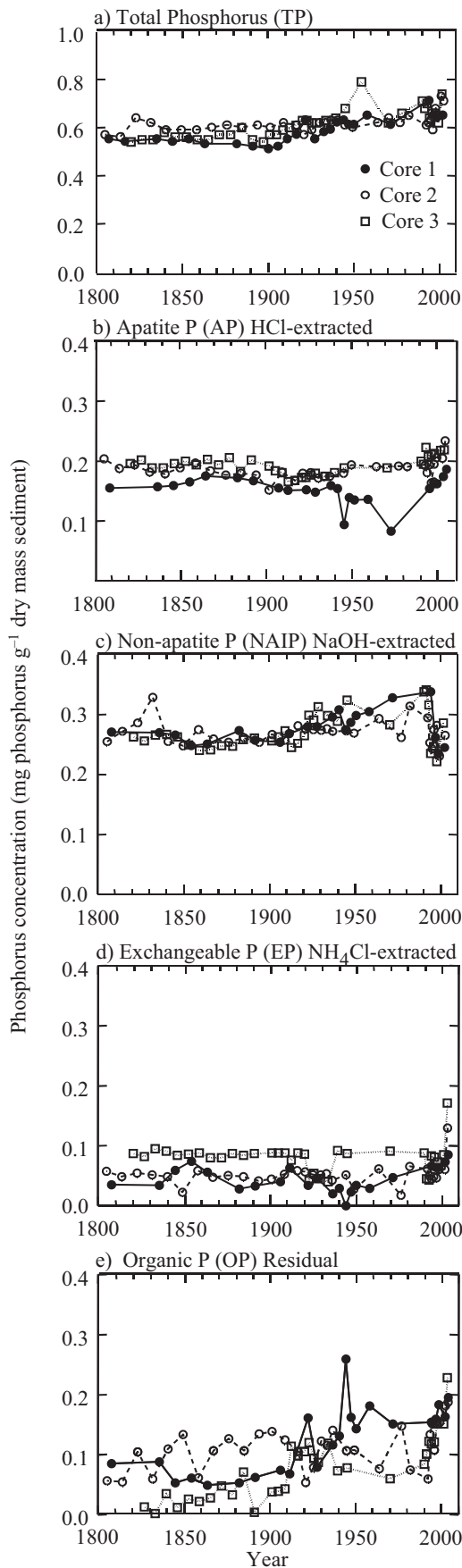
length of each core, with mean (\pm SE) rates of 50.0 ± 0.8 $\text{mg cm}^{-2} \text{yr}^{-1}$, 64.6 ± 1.1 $\text{mg cm}^{-2} \text{yr}^{-1}$, and 83.2 ± 0.9 $\text{mg cm}^{-2} \text{yr}^{-1}$ for Cores 1, 2 and 3, respectively, although in each case SAR increased slightly after ~ 1990 . Consequently, depth-age (Fig. 2c) and cumulative mass-depth relationships (not shown) were nearly linear prior to 1990 ($r^2 > 0.98$, $p < 0.0001$) (Fig. 2c) and sedimentary profiles encompassed 310, 218 and 185 yr for Cores 1 (77.6 cm), 2 (62.6 cm), and 3 (62.6 cm), respectively. Errors in determination of sediment age ranged from < 1 yr for surface samples, to ~ 5 yr in the mid-20th century, and ~ 20 yr for basal sediments. Mean SAR estimates were consistent with prior studies (63.5 – 86.1 $\text{mg cm}^{-2} \text{yr}^{-1}$) of the south basin (Wilkinson and Simpson 2003).

Sedimentary geochemistry

Although the cores were taken from locations separated by ~ 35 km (Fig. 1), they exhibited a high degree of similarity in elemental composition and stable isotope values throughout the past 200 yr (Fig. 3). Consistent with the nearly constant SAR, both N ($\sim 0.17\%$ of dry mass) (Fig. 3b) and C contents ($\sim 1.5\%$) (Fig. 3c) were stable from ca. 1800–1900, increased gradually by 50%, then rose rapidly in sediments deposited ca. 2006 (Fig. 3b,d). Similarly, C: N mass ratios ($\sim 10 : 1$) varied little either among cores or with burial depth and were characteristic of algal-derived material (data not shown). In contrast, $\delta^{15}\text{N}$ values increased linearly from background depleted levels ($\sim 4.5\%$) early in the 20th century to an enriched maximum ($\sim 8.0\%$) in surface sediments (Fig. 3a). Similarly, although $\delta^{13}\text{C}$ values of whole sediment were consistently ~ 1 – 2% lower in Core 1 than at other sites (Fig. 3c), C isotope ratios in each core were relatively enriched and constant during the 19th century, declined irregularly by $\sim 1\%$ until ca. 1990, then exhibited high temporal variability during the past 20 yr, with a maximum ca. 2000 and a further minimum ca. 2006.

In all three cores, concentrations of TP and chemical fractions showed few pronounced changes in sediments deposited during the past two centuries (Fig. 4). For example, TP content was almost constant throughout the 19th century and increased only 10–15% by present day (Fig. 4a). In general, these increases reflected variation in NAI-P which accounted for $\sim 45\%$ TP content in most samples. NAI-P content was stable during ca. 1800–1900, increased gradually until ca. 1990, then declined sharply to minima in the early 2000s (Fig. 4c). In contrast, AP (Fig. 4b) and EP (Fig. 4d) concentrations demonstrated little systematic variation through time, and accounted for $\sim 30\%$ and $\sim 10\%$ of TP, respectively, with the exception of elevated EP content in surface

Fig. 3. Time series of whole-sediment (a) nitrogen (N) isotopes ($\delta^{15}\text{N}$, ‰), (b) N content (% dry mass), (c) carbon (C) isotopes ($\delta^{13}\text{C}$, ‰), and (d) C content (% dry mass) during 1800–2010 for three sediment cores from southern Lake Winnipeg. Symbols and lines as in Fig. 2.



sediments, and brief declines in AP concentration in Core 1 during the 1970s (Fig. 4b). Overall, the OP content was more variable among cores and through time (5–15% of TP), exhibiting an increase after 1900 in two cores (Fig. 4e).

Fossil pigments and cyanobacterial microfossils

In contrast to the relatively complacent geochemical records, analysis of algal fossils revealed three main patterns of community change consistent with pronounced eutrophication of Lake Winnipeg (Fig. 5). First, concentrations of pigments from diatoms (diatoxanthin) (Fig. 5a) and cryptophytes (alloxanthin) (Fig. 5b) which are common in spring algal communities (Kling et al. 2011), were relatively constant from ca. 1800 to ca. 1900, then increased steadily to irregular maxima in recent sediments. Second, biochemical fossils from summer bloom-forming chlorophytes (pheophytin *b*, Chl *b*) (Fig. 5c) and Nostocales cyanobacteria (canthaxanthin) (Fig. 5d), together with chemically-stable indicators of total algal abundance (β -carotene, pheophytin *a*) (Fig. 5e), were relatively constant during the 19th century, increased 300–500% to maxima in the late-1980s, then declined ~50% in sediments deposited since 1990. Third, concentrations of akinetes from diazotrophic cyanobacteria increased sharply in Core 1 sediments from baseline values between ca. 1800 and ca. 1900 to threefold higher abundances since that time (Fig. 5f). In general, microfossils from *Anabaena* spp. were always 10-fold more abundant than those from *Aphanizomenon* spp. throughout the 200-year record. Such concomitant changes in pigment and akinetes deposition ca. 1990 reflect either shading of other algae by positively buoyant N₂-fixing cyanobacteria (McGowan et al. 2005), or a change in depositional processes as neutrally-buoyant phytoplankton are replaced by positively-buoyant diazotrophs (Cuddington and Leavitt 1999; Bunting et al. 2007). Regardless, taken together, these patterns demonstrate that algal abundance increased ~three- to five-fold during the 20th century, and that an ecosystem state change initiated ca. 1990. Importantly, ratios of labile to chemically-stable pigments (Chl *a* : pheophytin *a*) did not change with depth (not shown), indicating that the preservation environment has been relatively constant since 1800 (Leavitt and Hodgson 2001).

Fossil diatoms

Diatoms were well preserved, abundant, and composed of taxa characteristic of productive waters throughout the past 200 yr (Fig. 6). Overall, total diatom concentrations were correlated strongly ($r^2 = 0.66$, $p < 0.0001$) with sedimentary concentrations of diatoxanthin, the pigment characteristic

Fig. 4. Time series of whole-sediment phosphorus (P) concentrations (mg P g⁻¹ dry mass), including (a) total P (TP), (b) apatite P extracted by HCl, (c) nonapatite inorganic P extracted by NaOH, (d) exchangeable inorganic P extracted by NH₄Cl, and (e) residual or organic P during 1800–2010 for sediment cores (as Fig. 2) from southern Lake Winnipeg.

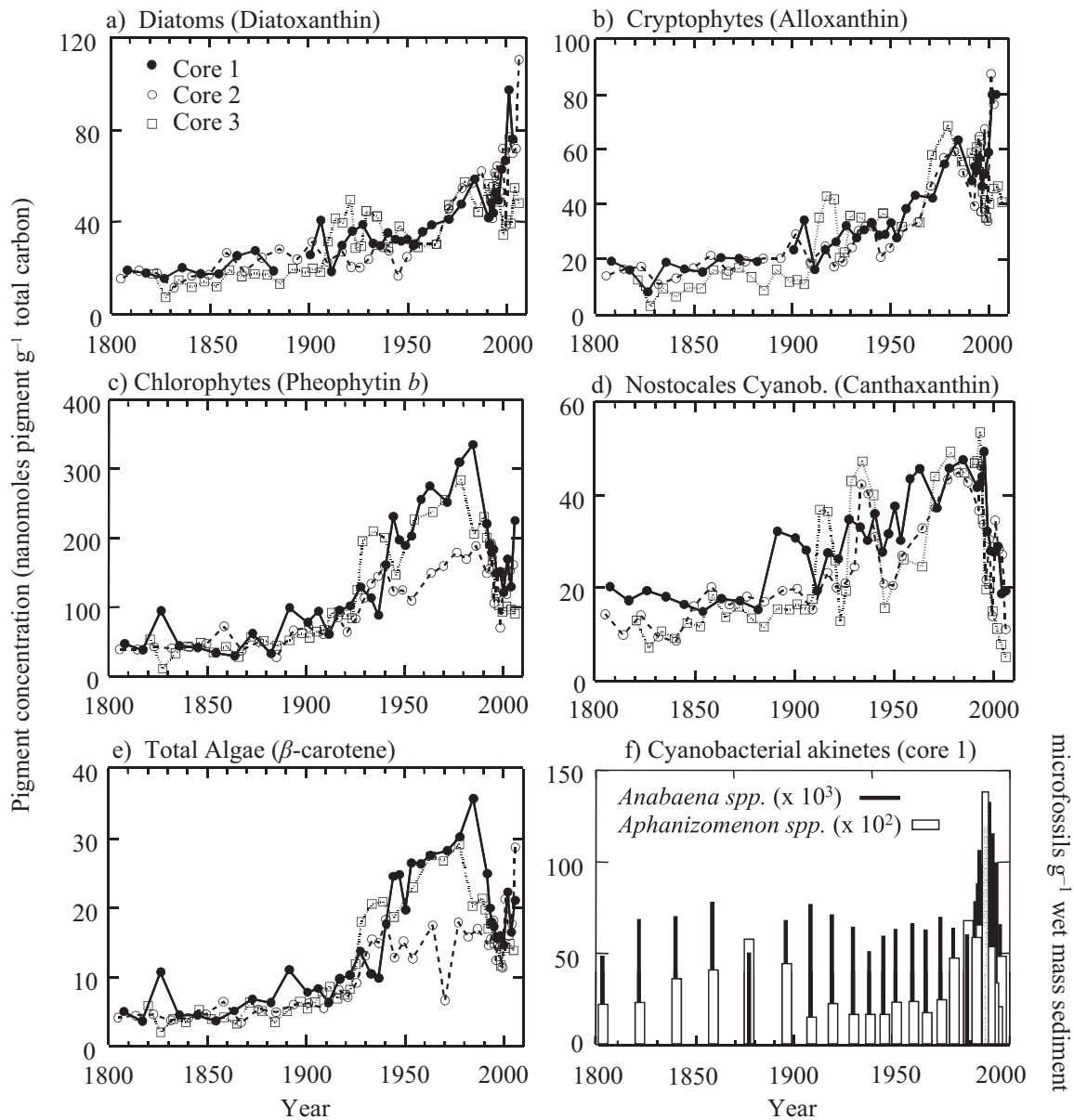


Fig. 5. Time series of fossil pigment concentrations (**a–e**) (nmol pigment g⁻¹ sediment C) and (**f**) cyanobacterial akinetes (microfossils g⁻¹ dry mass) during 1800–2010 for three cores from southern Lake Winnipeg. Core identities as Fig. 2. Pigments include (a) diatocanthin mainly from diatoms, (b) alloxanthin from cryptophytes, (c) pheophytin *b* from chlorophytes, (d) canthaxanthin from Nostocales cyanobacteria, and (e) ubiquitous β-carotene from all algae. (f) Fossil akinetes were quantified only in Core 1 and were derived from species of *Anabaena* (thin black histograms, 10³ scale) and *Aphanizomenon* (open histograms, 10² scale).

of diatoms. During the 19th century, communities were composed mainly (~60%) of mesotrophic *Aulacoseira islandica* (O. Müller) Simonsen, along with subdominant mesotrophic (*A. distans* (Ehrenberg) Simonsen, *A. subarctica* (O. Müller) Haworth, *Stephanodiscus medius* Håkansson), meso-eutrophic (*A. ambigua* (Grunow) Simonsen, *S. minutulus* (Kützing) Cleve & Möller), and eutrophic taxa (*S. niagarae* Ehrenberg). In the early 20th century, concentrations of *S. niagarae* and *A. subarctica* decreased, while those of *S. minutulus* and eutrophic *S. hantzschii* Grunow increased. At the same time, *A. islandica*

remained abundant, consistent with reports of its predominance in spring throughout the 20th century (Lowe 1924; Bajkov 1930, 1934; Kling 1998). Constrained cluster analysis showed that communities were distinctive after ca. 1980 (Fig. 6), when concentrations of many fossil diatoms (except *S. niagarae*) increased two- to 20-fold. Notably, epiphytic diatoms were rare in all sediment intervals. Despite these patterns, there were few marked changes in species relative (%) composition during the past 200 yr (see Supporting Information S4), suggesting that while total diatom production

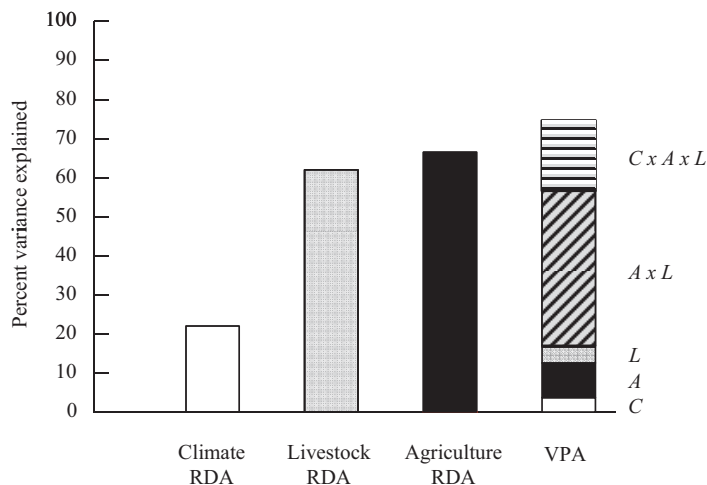
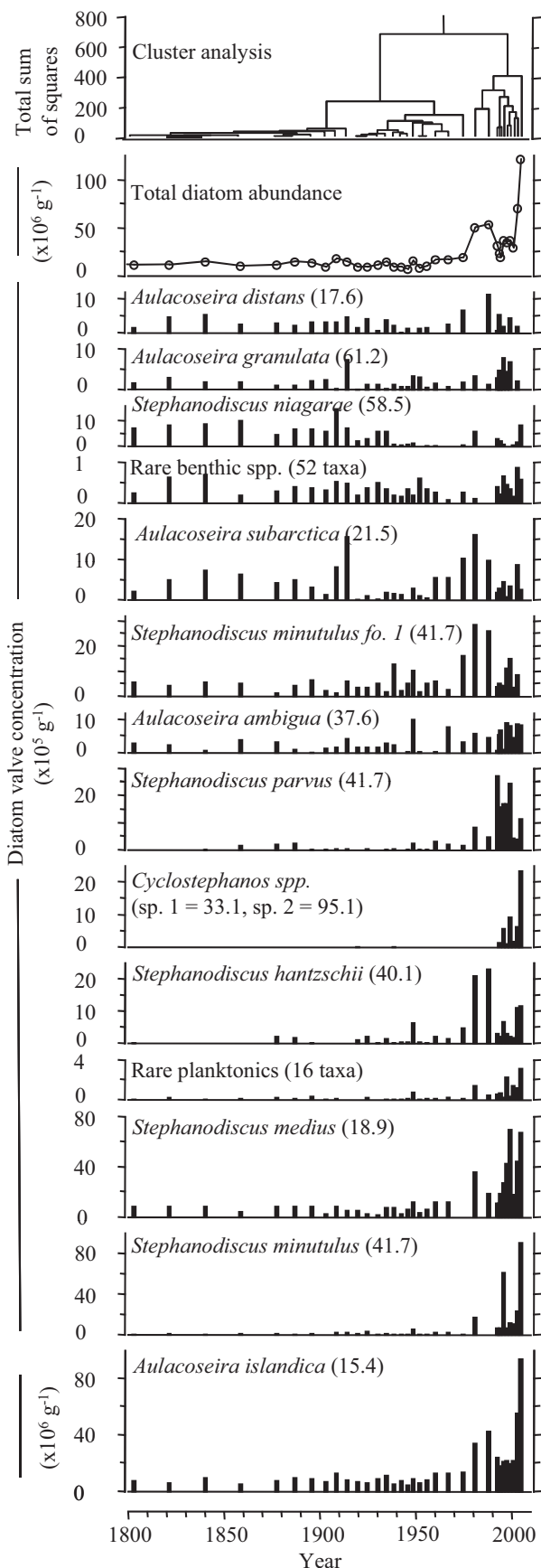


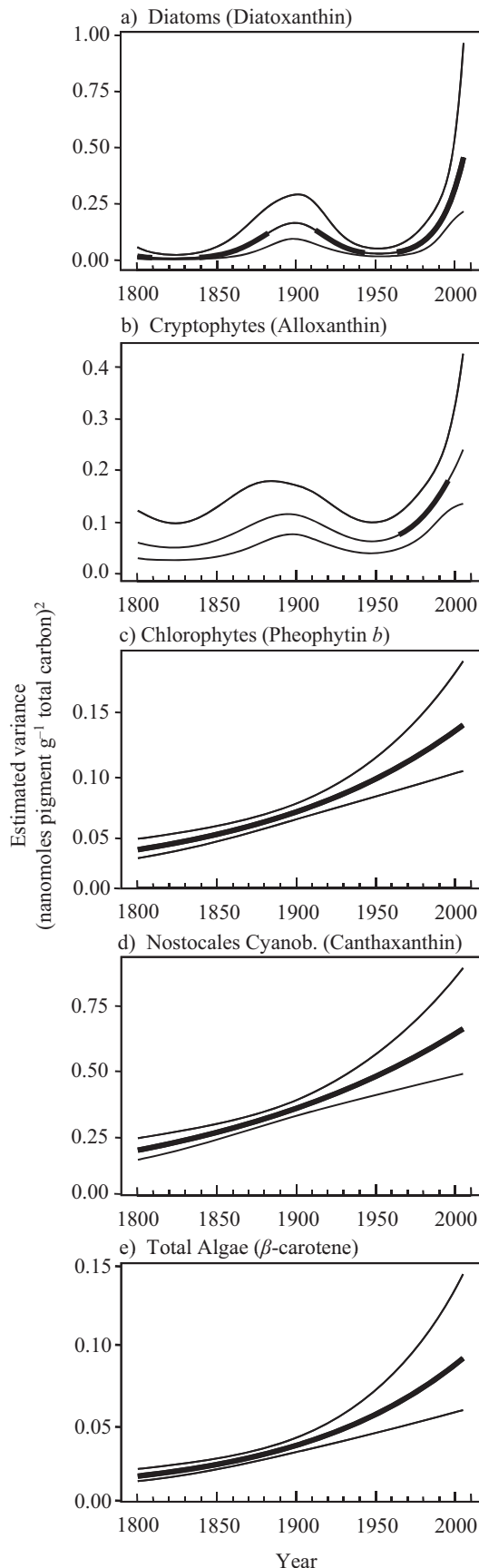
Fig. 7. Percent variation in fossil pigment concentrations (as in Fig. 5), C and N isotopes (‰), and C and N content (%) in sediments of Core 1 during 1901–1992 explained by redundancy (RDA) analysis of (a) climate variables alone (white histogram), (b) livestock variables alone (grey histogram), or (c) agriculture (crop) production variables alone (black histogram), or by (d) variance partitioning analysis of climate (C, white), crop production (A, black), and livestock production (L, grey), their first-order ($A \times L$, $C \times L$, $A \times C$), and second order ($A \times L \times C$) interactions. Note that both $C \times L$ and $A \times C$ interactions explained $< 0.3\%$ of historical variation in lake production parameters and are not presented.

increased throughout the 20th century (Figs. 5a, 6), factors other than nutrients regulated precise species composition (e.g., light, turbulence, etc.).

Variance partitioning analysis

VPA revealed that environmental variation associated with climate (C), crop-based agriculture (A), or livestock husbandry (L) explained 74.5% of historical changes in lake trophic status (fossil pigments, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C and N content) during 1901–1992 (Fig. 7). Comparison of unique and interactive categories revealed that most of the explained variation arose from interactions between crops and livestock ($A \times L = 39.6\%$; $A \times L \times C = 17.9\%$ explained variance) rather than from climate change ($C = 3.7\%$; $C \times A = 0.3\%$; $C \times L = 0.1\%$). Consistent with this interpretation, RDA with climate predictors alone explained only 22.0% of fossil change during the 20th century, whereas similar analysis using either crop (66.5%) or livestock variables alone (62.0%) explained threefold more variation in pigments and geochemistry

Fig. 6. Time series of concentrations of valves from fossil diatom species in Core 1 from southern Lake Winnipeg during 1800–2010. All fossil concentrations are valves $\times 10^5 \text{ g}^{-1}$ dry mass, except *Aulacoseira islandica* and total diatom abundance (valves $\times 10^6 \text{ g}^{-1}$ dry mass). The uppermost panel includes results of stratigraphically-constrained cluster analysis of diatom species densities. Approximate diatom species optimum for total phosphorus indicated in parentheses (from Hyatt et al. 2011; Cumming et al. 2015, and references therein).



(Fig. 7). Only cattle (correlated positively with hogs, negatively with horses) and chickens (correlated positively with sheep) were retained by forward selection and Monte Carlo analysis as unique significant livestock predictors of change in fossil time series. Similarly, canola and potato production was retained in a RDA of fossils records with crop predictors; however, production of both cultivars was correlated positively with that of many other crops, particularly wheat. Finally, only winter precipitation (correlated positively with mean summer temperature, negatively with Red River discharge) was retained as a predictor in RDA constrained to use only climate variables. In contrast, multivariate analyses were unable to explain any significant ($p < 0.05$) variation in past diatom community composition (% relative abundance) during 1904–1993 (Supporting Information S4), either in VPA or in RDA constrained uniquely to climate, crop, or livestock predictors (analysis not shown).

Historical changes in phytoplankton variability

Gaussian GAMLS were significant for time series of all major functional groups, allowing estimation of historical patterns of variance in phytoplankton abundance (Fig. 8). Variance of the diatom (diatoxanthin) time series increased significantly during the late 19th and 20th centuries, but declined significantly in the early 20th century (Fig. 8a), while that of cryptophytes increased significantly only after ca. 1965 (Fig. 8b). In contrast, variation in time series of chlorophytes (pheophytin *b*) (Fig. 8c), Nostocales cyanobacteria (canthaxanthin) (Fig. 8d) and total phytoplankton (β -carotene) (Fig. 8e) increased significantly throughout each time series, particularly during the 20th century. Notably, variability of these three groups continued to increase following the apparent state change in ca. 1990, despite ~50% reduction in mean fossil concentrations (Fig. 5c–e).

Discussion

Analysis of highly resolved time series of sediment geochemistry and algal fossils demonstrated that southern Lake Winnipeg exhibited three phases of production since 1800 culminating in a sudden ecosystem state change. The first phase (ca. 1800 to ca. 1900) includes baseline conditions prior to eutrophication in which the south basin was mesotrophic ($\sim 15\text{--}20 \mu\text{g TP L}^{-1}$), with stable influx of N, P, and C (Figs. 3, 4), meso-eutrophic diatom species (*A. islandica*, *S. niagarae*, *S. medius*) (Fig. 6), and colonial cyanobacteria

Fig. 8. Time series of estimated variance of fossil pigment concentrations ($[\text{nmol pigment g}^{-1} \text{ sediment C}]^2$) calculated using Gaussian generalized additive models for location and scale applied to Core 1 from southern Lake Winnipeg. Pigments include **(a)** diatoxanthin (diatoms), **(b)** alloxanthin (cryptophytes), **(c)** pheophytin *b* (chlorophytes), **(d)** canthaxanthin (Nostocales cyanobacteria), and **(e)** ubiquitous β -carotene (all algae). Pointwise 95% confidence intervals enclose central trend. Intervals of significant rates of change in variance indicated with heavy lines.

(Fig. 5d), including diazotrophic *Aphanizomenon* and *Anabaena* spp. (Fig. 5f). Lake Winnipeg eutrophied slowly during the second phase (ca. 1900 to ca. 1990), when the coeval intensification of crop and livestock production (Fig. 7) increased influx of N (Fig. 3a,b) and P (Fig. 4) and allowed a three- to five-fold increase in abundance of most algae, except N₂-fixing cyanobacteria (Fig. 5). As in other prairie lakes (Hall et al. 1999; Leavitt et al. 2009; Maheaux et al. 2016), climatic variability during the 20th century had limited effects on water quality. Finally, southern Lake Winnipeg experienced a sudden ecosystem state change (Scheffer et al. 2001; Scheffer and Carpenter 2003) during the third stage (ca. 1990 to present), defined by a threefold increase in sedimentation of N₂-fixing cyanobacterial fossils (Fig. 5f), elevated sediment (Fig. 2) and diatom deposition (Fig. 6), and a 50% reduction in pigments from summer-blooming algae (Fig. 5c–e). However, Gaussian GAMLS of time series of summer taxa (Fig. 8) suggested that southern Lake Winnipeg experienced a persistent increase in phytoplankton variability characteristic of the Paradox of Enrichment (Cottingham et al. 2000) or increased variation in environmental forcing (Dakos et al. 2015), rather than establishment of an alternate stable state (Carpenter et al. 2011).

Quantification of baseline conditions

Estimation of background conditions is important for determining the proximity of lake state to critical thresholds related to eutrophication. Here we demonstrate that the southern basin of Lake Winnipeg was naturally mesotrophic (TP = 15–20 $\mu\text{g TP L}^{-1}$) prior to intensification of European-style agriculture, with diatoms characteristic of regional meso-eutrophic lakes (Hall et al. 1999; Cumming et al. 2015) (Fig. 6), abundant cyanobacteria (Fig. 5d), low but constant densities of diazotrophic *Aphanizomenon* and *Anabaena* spp. (Fig. 5f), and sedimentary P typical of productive hardwater lakes (Engstrom et al. 2006) (Fig. 4).

Several lines of evidence suggest that southern Lake Winnipeg was P-rich prior to development of the drainage basin. First, baseline concentrations of TP in sediments ($\sim 0.6 \text{ mg P g}^{-1}$ dry mass) (Fig. 4a) were similar to pre-agricultural values ($0.8 \pm 0.1 \text{ mg P g}^{-1}$ dry mass) recorded in diverse lakes of the northern Great Plains (Engstrom et al. 2009; Triplett et al. 2009), other large shallow hardwater lakes (e.g., Lake Okechobee) (Engstrom et al. 2006), and previous analysis of Lake Winnipeg sediments (Mayer et al. 2006). Second, fossil diatom communities during the 19th century were composed predominantly of taxa with elevated P requirements ($> 15 \mu\text{g TP L}^{-1}$; Hyatt et al. 2011; Cumming et al. 2015) (Fig. 6). Third, sediments were composed largely of inorganic forms of labile (NAI-P; 45%) and inert inorganic P (AP; 30%), similar to other eutrophic lakes of the northern Great Plains (Engstrom et al. 2009; Triplett et al. 2009). Fourth, calculations based on analysis of total algal abundance (as fossil β -carotene) (Fig. 5e) and modern nutrient content (see

Supporting Information S5) suggest that baseline water-column concentrations of TP in the south basin ranged 15–20 $\mu\text{g TP L}^{-1}$, similar to other mesotrophic prairie lakes (Pham et al. 2008) and the TP optimum of the predominant diatoms (Fig. 6). Given this naturally elevated nutrient status, we infer that Lake Winnipeg may have been particularly sensitive to fertilization-induced state change.

Mechanisms causing water-quality change during the 20th century

In many instances, establishment of a stable alternate state is characterized by a slow environmental change which pushes an ecosystem to a critical threshold after which a sudden regime shift takes place (Scheffer et al. 2001, 2009; Dakos et al. 2015). In the case of the southern basin of Lake Winnipeg, water quality has degraded progressively during the 20th century (Fig. 5) largely due to the combined effects of crop and livestock production, rather than climate change (Fig. 7). VPA explained almost 75% of historical variation in indices of lake trophic status (pigments, isotopes, %C, %N) between ca. 1900 and 1992 due to increased production of cattle, hogs, chicken, and major crop cultivars, while the unique effects of climate and its first-order interactions with crop and livestock production (C , $C \times L$, $C \times A$) explained a non-significant ($p > 0.15$) fraction (4.1%) of historical change (Fig. 7). Such weak effects of pronounced warming ($\sim 3^\circ\text{C}$ increase, ~ 35 d decline in ice cover since 1870) have been documented for 25 other lakes within the Lake Winnipeg catchment (Leavitt et al. 2009, 2014; Maheaux et al. 2016), and are consistent with theoretical and empirical expectations that changes in mass (m) influx (water, solutes, particles) can overwhelm effects on lakes of increased energy (E) influx (as temperature, irradiance, ice cover, wind energy) (Dröscher et al. 2009; Leavitt et al. 2009; Vogt et al. 2011).

Non-point nutrient influx due to crop production is now the primary cause of freshwater and coastal eutrophication (Carpenter et al. 1998). In Manitoba, grains such as wheat ($\sim 1 \times 10^9 \text{ kg yr}^{-1}$ in 1910s) and barley ($0.3\text{--}0.5 \times 10^9 \text{ kg yr}^{-1}$ in 1910s) have dominated production since regional farming began in the early 1800s (Honey and Oleson 2006), but their harvest increased dramatically following World War II (WWII; 1939–1945), reaching $5 \times 10^9 \text{ kg yr}^{-1}$ and $2 \times 10^9 \text{ kg yr}^{-1}$, respectively, during the 1980s (Statistics Canada 1871–2006). Similarly, irrigation-intensive potato production increased linearly from stable values of $\sim 0.1 \times 10^9 \text{ kg yr}^{-1}$ 1900–1950 to modern harvests $> 1 \times 10^9 \text{ kg yr}^{-1}$ (Statistics Canada 1871–2006) due to increased demand for processed food (Honey and Oleson 2006). Introduced in 1945, canola found favour only after 1960s (Honey and Oleson 2006), when its area seeded increased from $< 12,000$ ha in 1961, to 0.24×10^6 ha in 1971, and 1.15×10^6 ha in 2004 ($\sim 25\%$ of Canadian canola crop). Despite these patterns, we infer that the effects of crop production on water quality arose mainly due to mechanized tillage of soils and

manure application, rather than due to chemical fertilizer use because: there was little eutrophication during the 1800s despite substantial crop development (Figs. 3-6); lake production was inversely correlated with horse density in VPA (horses were replaced by tractors), and; use of chemical fertilizers was negligible prior to 1960 (Korol and Rattray 1999), yet coeval fossil pigment concentrations were ~70% of late 1980s maxima (Fig. 5).

Livestock management degrades water quality most commonly when animal densities greatly exceed that of humans, leading to imbalances between nutrient importation to sustain forage and crops and nutrient export in agricultural products (e.g., Bennett et al. 2001; Bunting et al. 2007). With the exception of the 1930s (drought) and 1940s (WWII), human populations in MB increased linearly from ca. 1850 to present, and now exceed 1.26×10^6 individuals, mainly in City of Winnipeg (~55%). In contrast, the total MB biomass of chickens (2 kg ind^{-1}), hogs (112 kg ind^{-1}), and cattle (317 kg ind^{-1}) exceeds that of humans (~60 kg ind^{-1}) by ~12-fold (Statistics Canada 1871–2006), with a near-exponential expansion of hog populations from less than 0.75×10^6 before ~1980 to $\sim 3 \times 10^6$ head by 2005. Given that Winnipeg (pop. 742,000) accounts for 5–10% of nutrient influx to Lake Winnipeg (Supporting Information S1), we infer that livestock wastes may contribute strongly to the eutrophication of Lake Winnipeg, either as direct runoff or via their use as fertilizers (Bunting et al. 2007; Yates et al. 2012).

Urban development contributed significantly to fertilization of southern Lake Winnipeg with nitrogen. Strongly enriched (3–4‰) sedimentary $\delta^{15}\text{N}$ values recorded after 1900 are consistent with increased influx of N from agricultural (Anderson and Cabana 2005; Bunting et al. 2007) or urban sources (Savage et al. 2004; Leavitt et al. 2006). Although it is difficult to distinguish among N sources (Mayer and Wassenaar 2012), we infer that the City of Winnipeg is the most likely source of enriched N, despite accounting for only 5–10% of TN influx, as similar enrichments have not been recorded in eight cores from the north basin of Lake Winnipeg (Bunting et al. 2012), four cores from adjoining Lake Manitoba (Leavitt et al. 2014), and 25 other lakes within the catchment (Pham et al. 2008; Leavitt et al. 2009; Maheaux et al. 2016), all sites which receive substantial agricultural N, but not urban N. As reviewed elsewhere (Savage et al. 2004; Leavitt et al. 2006), urban wastewater treatment can enrich dissolved N by 10–25‰ due to intense isotopic fractionation during NH_3 volatilization or denitrification of waste N. Consistent with the inferred importance of urban N, changes in fossil $\delta^{15}\text{N}$ were correlated more highly with growth of Winnipeg's population during the 20th century ($r^2 = 0.82$, $p < 0.0001$) than with those of the main livestock ($r^2 = 0.52$ –74, $p < 0.0001$).

Limited unique effects of climatic variability on eutrophication of southern Lake Winnipeg during the 20th century

(Fig. 7) are consistent with predictions of the Energy-mass (Em) flux framework (Leavitt et al. 2009) and empirical observations from more than 25 agriculturally-impacted lakes within the Canadian Prairies (Pham et al. 2008; Leavitt et al. 2009, Maheaux et al. 2016). Regional fall, winter, and spring mean and minimum temperatures have increased ~3°C since the late 1800s (Statistics Canada 1871–2006), leading to ~35 d increase in ice-free season in southern MB (Hall et al. 1999). Although similar magnitudes of climatic variation affect lakes worldwide (reviewed in Adrian et al. 2009), recent syntheses suggest that unique effects of global warming (air temperature, ice cover, wind) can be overridden by changes in mass influx associated with agricultural development and a modified hydrologic regime (Pham et al. 2008; Dröscher et al. 2009; Leavitt et al. 2009). Similarly, although Red River discharge also varied 10-fold among decades (MCWS unpubl. data; McCullough et al. 2012) and was retained in the VPA (Fig. 7), there was no sustained inter-decadal increase in hydrologic influx until ca. 1990, and climatic variables uniquely explain only ~4% of historical variation in lake production parameters (Fig. 7). Instead, we note that conversion of terrestrial ecosystems to agriculture within lake catchments increases mass influx to lakes by > 10-fold (reviewed in Dearing and Jones 2003), a proportion far greater than the increase in energy influx associated with global warming (Leavitt et al. 2009).

Ecosystem state change

Socio-economic analyses suggest that ecosystem state change occurred because of a sequence of international (Venema 2006), federal (Bradshaw et al. 2004), and provincial (Martin et al. 1999; Novek 2003) policy decisions which intensified MB agriculture, especially hog, potato and canola production, following a century of intensive exploitation for grains (Supporting Information S6). Regulatory changes allowed regional hog populations to increase by 500% (800% in areal densities) during 1981–2000, while harvest of individual MB fodder crops increased 275–1000% to a total of $3.4 \times 10^9 \text{ kg yr}^{-1}$. Together with increased runoff (McCullough et al. 2012), agricultural changes increased water-column concentrations of N and P by 20%, reduced TN: TP ratios from ~8.5 to 6.3, and elevated internal nutrient loading (Nürnberg and LaZerte 2016; MCWS unpubl. data), thereby favouring a sudden transition to a self-sustaining alternate stable state (Fig. 5). However, despite these patterns, analysis of phytoplankton variability suggests either that a stable state has not yet been established, or that variation in external forcing has continued to increase (Dakos et al. 2015).

Application of Gaussian GAMLS to weighted fossil pigment time series demonstrated that phytoplankton variability increased after ecosystem state stage (ca. 1990), particularly for phytoplankton which bloom in summer (Fig. 8). Further, this variability did not arise from oscillations in

mean conditions due to establishment of limit cycles, as the GAMLS spline captures the temporal evolution of mean values (Rigby and Stasinopoulos 2005). Significant increases in estimated variance also preceded the state change by over 100 yr, consistent with theoretical expectations that rising variance is an early warning indicator of sudden ecosystem state (Carpenter and Brock 2006; Dakos et al. 2015), the early onset of agriculture in MB (ca. 1815), and the strong statistical association of algal abundance and regional agricultural development during the 20th century (Fig. 7). We infer that rising variance does not reflect changes in the temporal resolution or observation intervals of the fossil time series (Carstensen et al. 2013) because accumulation rates are nearly constant prior to 1990 (Fig. 2), GAMLS is insensitive to irregular sample intervals (Rigby and Stasinopoulos 2005), and sample prior weights account for changes in sediment compaction and accumulation rate in the GAMLS. Similarly, we infer that sediment bioturbation did not alter estimates of past phytoplankton variability because composition of past cladoceran (Suchy et al. 2010; Bunting et al. 2012) and other invertebrate taxa (B.J. Hann, University of MB, unpubl. data) did not change appreciably since 1900, deepwater oxygen status appears unchanged (Nürnberg and LaZerte 2016), and ²¹⁰Pb profiles suggest only limited mixing of sediments (Fig. 2). Although variance is expected to scale with mean pigment concentration, and may in part explain elevated variation in recent cryptophyte and diatom populations (Figs. 5a,b, 6, 8a,b), the persistent rise in variability of total phytoplankton and summer taxa (Fig. 8c–e), despite 50% declines in fossil concentration (Fig. 5c–e), is more consistent with the Paradox of Enrichment (Cottingham et al. 2000).

At present, we cannot determine whether continued increases in the variability of primary producers reflects persistent increases in external forcing (Hall et al. 1999; McCullough et al. 2012; Dakos et al. 2015), the inability of large lakes to establish alternate stable states (Janssen et al. 2014; Capon et al. 2015), or the possibility that blooms of N₂-fixing cyanobacteria do not represent a terminal stable state in lake eutrophication (Leavitt et al. 2006; Bunting et al. 2007; Xu et al. 2010). For example, although the *Save Lake Winnipeg Act* (2011) and other provincial legislation now regulates future livestock and crop management, shifts in regional climate systems may continue to favour increased runoff of existing soil nutrient stores (McCullough et al. 2012; Reid et al. 2016; but see Leavitt et al. 2014). Similarly, while the turbid south basin of Lake Winnipeg ($Z_{\text{secchi}} < 1$ m, $Z_{\text{mean}} 9.7$ m) does not appear to have ever supported sufficient macrophytes to reinforce a clear-water state (few epiphytic diatoms; Fig. 6), mass budgets suggest that internal nutrient loading may be enhancing phytoplankton production, despite the polymictic and aerobic conditions (Nürnberg and LaZerte 2016). Finally, the persistently elevated P content of southern Lake Winnipeg ($> 50 \mu\text{g}$ soluble reactive P L⁻¹) (MCWS unpubl. data), combined with increased N influx

(Fig. 3a), may initiate an additional state change from buoyant N₂-fixing *Aphanizomenon* and *Anabaena* to potentially toxic, but low-light adapted cyanobacteria (*Planktothrix*, *Microcystis*, *Cylindrospermopsis*), such as has occurred elsewhere in the Canadian Prairies (Leavitt et al. 2006; Donald et al. 2011), Europe (Bunting et al. 2007), and China (Paerl and Scott 2010; Xu et al. 2010).

The absence of an alternate stable state characterized by lower phytoplankton variability suggests that Lake Winnipeg should not exhibit hysteresis following reduced nutrient influx (Carpenter et al. 2011; Dakos et al. 2015). Although bottom deposits currently represent a substantial source of P to the water column (Nürnberg and LaZerte 2016), the relatively constant fraction of exchangeable P in sediments (Fig. 3) suggests that internal nutrient loading has been important for over 200 yr and that it did not alter substantially following state change in ca. 1990. Similarly, the low abundance of macrophytes since 1800 inferred from fossil diatoms suggests an absence of internal biotic mechanisms stabilizing alternate states (Scheffer and Carpenter 2003), such as seen in other large shallow lakes (Capon et al. 2015). The important consequence of these observations is that effective nutrient management of the Lake Winnipeg basin should reduce phytoplankton abundance in direct proportion to external nutrient influx, possibly without the decades-long delay seen in other lake ecosystems (Jeppesen et al. 2005).

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