Sudden ecosystem state change in Lake Winnipeg, Canada, caused by eutrophication arising from crop and livestock production during the 20th century

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Abstract

Lake Winnipeg, Canada, has experienced severe blooms of N_2-fixing cyanobacteria since 1990; however, little is known of background limnological conditions, causes of eutrophication, or whether modern conditions represent a stable ecosystem state change. To address these issues, sedimentary records of nitrogen (N) inputs (as δ^{15}N, %N), phosphorus (P) influxes (total P, chemical fractions), lake production (δ^{13}C, %C), and algal abundance and community composition (pigments, algal microfossils) were analyzed in three cores from the lake's south basin. Under baseline conditions (ca. 1800-1900), the basin was mesotrophic (~15-20 μg P L^{-1}) with diazotrophic cyanobacteria (*Aphanizomenon*, *Anabaena*), mesotrophic and eutrophic diatoms (*Aulacoseira islandica*, *Stephanodiscus niagarae*), and sedimentary P fractions characteristic of hardwater prairie lakes. Eutrophication accelerated during a second phase (1900-1990), when N, P and C contents increased 10-50%, δ^{15}N enriched 3-4‰, and concentrations of most algal pigments increased 300-500%. Nearly 75% of this 20th century variability was explained by concomitant increases in production of livestock (mainly cattle and hogs) and crops (wheat, potatoes, canola), but not by variation in climate. A third phase (1990-present) was marked by 50% declines in pigments from chlorophtyes and cyanobacteria, a 10-fold increase in concentrations of akinetes from *Aphanizomenon* and *Anabaena* spp., and occurred because of a century of fertilization, rapid changes in economic policies, and agricultural diversification. We conclude that P influx must decline by ~50% to suppress N_2-fixing cyanobacteria (500% to re-establish baseline conditions) and that failure to regulate P influx may initiate a fourth phase in which pollution with N promotes potentially toxic cyanobacteria.

Introduction

Eutrophication remains the most significant environmental problem which threatens the integrity of aquatic resources throughout the world despite 50 years 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) (Schindler 1977), 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). Unfortunately, such diffuse nutrient inputs are now the primary cause of aquatic pollution in many regions of the world (Smith 2003; Schindler 2006).

Water quality degradation arises from diffuse nutrient sources for several main reasons. First, agricultural inputs of phosphorus (P) and nitrogen (N) in commercial fertilizer and animal feed supplements often exceed agricultural outputs (Foy et al. 2002; Bunting et al. 2007). Second, excessive livestock densities can lead to manure production that overwhelms both 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 (Vitousek et al. 1997). In many instance, excess fertilization favours soil surpluses of P that are mobile and can leach into

downstream aquatic ecosystems (Smith et al. 1995; Bennett et al. 2001). Such surpluses of soil P can last for millennia (Carpenter 2005), facilitate accumulation of soluble P within downsteam lakes, and alter mechanisms regulating lake structure and function (Leavitt et al. 2006; Bunting et al. 2007).

Ecological theory suggests 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 water-column parameters (e.g., P concentration) 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 (Cottingham et al. 2000; Carpenter 2003; Carpenter and Brock 2006). Interestingly, the shift between states may arise from either rapid persistent changes in external forcing (Leavitt et al. 2009) 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. Similarly, further research is required to quantify the patterns and controls of ecosystem state change at decadal scales, as recent studies suggest that surface blooms of N_2-fixing cyanobacteria may not represent the terminal state in the eutrophication sequence (Leavitt et al. 2006; Bunting et al. 2007; Xu et al. 2010).

In this paper, we analyzed profundal sediments for diverse chemical and biological parameters to test the hypothesis that Lake Winnipeg, Canada, has undergone sudden ecosystem state change due to cumulative effects of a century of agriculture, rather than climatic variability. Lake Winnipeg is presently eutrophic (south basin >100 μg TP L^{-1}); however, little is known of the baseline limnological conditions, the magnitude, timing or causes of eutrophication, or whether outbreaks of diazotrophic cyanobacteria (*Aphanizomenon*, *Anabaena* spp.) since 1990 represent an externally-forced increase in production (Carpenter 2003; Leavitt et al. 2009) or a self-reinforcing change between alternative stable states (Scheffer et al. 2001; Scheffer and Carpenter 2003). To address these issues, we created highly resolved time series of historical N inputs (as δ^{15}N, N content), P influxes (as TP and P fractions), aquatic production (δ^{13}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). We conclude that while the south basin of Lake Winnipeg is naturally mesotrophic, a century of crop and livestock development has increased lake production ~500%, allowed intensification of agricultural practices after 1980 to initiate a state change, and poised the lake on the threshold of a further shift to increased biomass and toxicity of cyanobacteria.

Methods

Site description – Lake Winnipeg is a large (23,750 km^2), shallow (mean depth = 12 m), polymictic, multi-basin, eutrophic lake (>100 μg P L^{-1}) situated at 217.6 m above sea level (a.s.l.) in the Province of Manitoba (MB), Canada (Fig. 1, Table 1). The 953,250 km^2 lake catchment is located mainly within four Canadian provinces (MB, Alberta [AB], Saskatchewan [SK], Ontario [ON]), with additional contributions from the northern United States, primarily North Dakota (ND) and Minnesota (MN). More than 660,000 km^2 (70%) 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 (LWIC 2006; MWS 2006). More than 80% of the 6.6 million inhabitants of the watershed are located in urban areas (Statistics Canada and U.S. Bureau of Census data), although cities with populations >200,000 are relatively uncommon (Fig. 1).

Climatic conditions vary with location in the catchment, with aridity generally increasing from east to west and north to south (Pham et al. 2009). Within the central watershed, the climate is characterized as sub-humid continental, with short warm summers (mean 19°C in July), cold winters (mean -16°C in January), low mean annual temperatures (~1^{o}C), and an average of 105 frost-free days (Leavitt et al. 2006). In addition, this region has experienced an ~3^{o}C increase in mean temperature since the 19th century, mainly as pronounced increases in fall, winter, and spring minimum temperatures. As a result, ice cover in southern MB has declined more than 35 days since 1860 (Hall et al. 1999).

Three major river systems flow into Lake Winnipeg, while the sole outflow, the Nelson River, drains northeast into Hudson Bay (Fig. 1). The Red and Assiniboine rivers join within City of Winnipeg and enter the lake from the south (~8% of total water inflow), the Saskatchewan River enters the lake from the northwest (~22%), and the Winnipeg River enters from the southeast (~40%) (Fig. 1). Well developed Chernozemic soils predominate throughout the catchments of the Red-Assiniboine and Saskatchewan river systems (Brunskill et al. 1980), while forest and peatland soil types (regosols, brunisols, luvisols, gleysols, organic peat) predominate in the Winnipeg River watershed (Smith et al. 1998).

Land use varies substantially among sub-basins. For example, the Red (~127,000 km^2) and Assiniboine river catchments (~41,500 km^2) are composed largely of arable land that supports cereal, feed and specialty crop production, range and pasture lands, and intensive cattle and hog operations (UARBSC 2000). These sub-basins also include the major urban centers of Winnipeg MB (pop. 742,000), Fargo-Moorehead ND, and Regina SK (each pop. 200,000), livestock processing centers, and several smaller cities (MWS 2006). Agricultural land use is broadly similar within the Saskatchewan River drainage basin (~416,000 km^2) (specialty, cereal, and forage crops; range and pasture lands; livestock feedlots), while major cities are located in SK (Saskatoon, pop. 200,000) and AB (Calgary, Edmonton, pop. >750,000 each), and substantial forestry is practiced along the northern boreal margin of the catchment (Jones and Armstrong 2001). In contrast, land-use within the Winnipeg River catchment (~137,000 km^2) is restricted mainly to mining, forestry, and recreational activities, with few large population centres (Patalas and Salki 1992; Smith et al. 1998).

Nutrient influx to Lake Winnipeg – At present, Lake Winnipeg receives ~96,000 tonnes N and ~7,900 tonnes P each year, both derived mainly from non-urban sources (Table 2). Decade-long mass flux estimates suggest that Manitoba represents the largest source of nutrients to Lake Winnipeg (47% TP, 49% TN), due to a combination of agricultural runoff, background and undefined sources, atmospheric loading, internal lake processes, and urban and industrial effluent (Bourne et al. 2002; MWS 2006). The remaining portion of annual TP and TN influx to the lake is derived from headwater jurisdictions within the US (35% TP, 21% TN), ON (13% TP, 21% TN), and the Canadian Prairies (SK and AB, 5% TP, 9% TN) (Bourne et al. 2002; MWS 2006). On average, ~84% of TP and ~70% of TN is delivered to the south basin of Lake Winnipeg via the Red (54% TP, 30% TN) and Winnipeg river systems (13% TP, 29% TN) (M. Stainton, G. McCullough, Fisheries and Oceans Canada [FOC], unpublished data). Despite these generalities, magnitude and importance of individual sources likely vary among years, such that TP loading to Lake Winnipeg is highly correlated ($r^2 = 0.97$) to catchment water yield, particularly from the Red River (Jones and Armstrong 2001; Bourne et al. 2002; MWS 2006).

Relatively little is known of how nutrient influx to Lake Winnipeg has varied in the past. Total annual influxes of N and P have risen at least 13% and 10%, respectively, since the early 1970s, primarily due to increased nutrient inputs from the Red and Winnipeg river systems (Jones and Armstrong 2001; Bourne et al. 2002; MWS 2006; LWIC 2006). These latter increases reflect elevated river discharge since the early 1990s, a 29% increase in flow-adjusted concentrations of TP in both the Red and Winnipeg

rivers during the past 40 yr, and a concomitant 58% increase in TN concentrations in the Red River and possibly the Winnipeg River (Jones and Armstrong 2001). Furthermore, unpublished hydrologic models have combined these data with continuous measurements of Red River discharge to predict that mean whole-lake TP concentrations varied from ~12 μg P L^{-1} during the arid 1930s to ~55 μg P L^{-1} ca. 2000, assuming constant nutrient export from land (G. McCullough, R. Hesslein, FOC, unpublished data). In addition, analysis of P fractions in a sediment core with low temporal resolution suggests that there have been few large-scale changes in P influx during the past ~500 years, other than a modest increase (<10%) in TP deposition during the 20th century (Mayer et al. 2006).

Historical development of eutrophication – Relatively little is known of the historical changes in limnological conditions within Lake Winnipeg 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 in the mid- to late-1920s (Lowe 1924; Bajkov 1930, 1934) and late-1960s (Crowe 1973; Brunskill 1973; Brunskill and Graham 1979) to a more advanced state of eutrophy thereafter (Brunskill et al. 1979a, 1979b, 1980), as indicated by elevated concentrations of TP (~80 μg P L^{-1}) and TN (~700 μg TN L^{-1}) in the south basin during 1992-1996 (Manitoba Water Stewardship [MWS] unpublished data). Similarly, surveys conducted during 2000-2005 revealed enriched concentrations of TP (>100 μg P L^{-1}) and TN (~750 μg N L^{-1}) throughout the south basin, with soluble reactive P (SRP) accounting for ~50% of TP (>50 μg P L^{-1}) during fall sampling (M. Stainton, FOC, unpublished data). Occasional phytoplankton analyses conducted during the 20th century suggest that a

diatom community composed mainly of *Stephanodiscus niagarae* Ehrenberg in 1920s (Lowe 1924), 1930a (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 (Brunskill et al. 1979a; Hecky et al. 1986; Kling 1998). 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).

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 *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; δ^{15}N, δ^{13}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 (g cm^{-2} yr^{-1}) were calculated using the constant rate of supply (CRS) calculation (Binford 1990).

Stable isotope ratios and elemental composition were determined on whole sediment samples using a ThermoQuest (F-MAT) Delta^{PLUS} XL isotope ratio mass spectrometer equipped with continuous flow (Con Flo II) unit, an automated Carlo Erba elemental analyzer as an inlet device, and following standard procedures of Savage et al. (2004). Stable N (δ^{15}N) and C (δ^{13}C) isotopic compositions were expressed in the conventional δ-notation in units of per mil (‰) deviation from atmospheric N_2 and an organic C standard which had been calibrated previously against authentic Vienna Pee Dee Belemnite. Sample reproducibility was <0.25‰ and <0.10‰ for δ^{15}N and δ^{13}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 0.5M 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 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 (48 h, 0.01 Pa) 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. Pigment analysis was restricted to taxonomically diagnostic carotenoids, including those characteristic of siliceous algae and some dinoflagellates (fucoxanthin), mainly diatoms (diatoxanthin), cryptophytes (alloxanthin), chlorophytes (Chl *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). All pigment concentrations were expressed as nmol pigment g^{-1} sediment C, a metric which is linearly correlated to annual algal standing stock in whole-lake calibration studies (reviewed in 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 ~10 aliquots (~0.10 mL) per interval were individually 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 ($\lambda_{excitation}$ = 450-480 nm). Microfossil concentrations were estimated as akinetes g^{-1} dry mass of whole sediment. 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 protocol reviewed in Laird and Cumming (2009). Whole 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 100× fluotar objective and differential interference contrast optics (1000× magnification; N.A. = 1.3) to determine species composition, microfossil concentration (valves g^{-1} dry mass sediment), and relative (%) species abundance. Taxonomy and nomenclature are

presented in detail in Laird and Cumming (2009) (boreal lake taxa) and Michels et al. (2007) (prairie lake taxa).

Historical changes in water-column TP concentrations were reconstructed from analysis of diatom species assemblages in Core 1 following standard paleolimnological procedures (Hall and Smol 1992). Nutrient preferences of individual species were obtained from a survey of diatom composition in surfacial sediments of 140 regional sites (124 MN lakes, 16 sites from Lake of the Woods, ON). Diatom-inferred TP (DI-TP) was reconstructed using a robust weighted-average model ($r^2_{\text{bootstrap}} = 0.75$, RMSEP = 0.20) using the computer program C2 (Juggins 2003) and covered a gradient of 5–364 μg P L^{-1}, as detailed in Hyatt et al. (2011). Principal components analysis (PCA) was performed on diatom relative abundance with a square-root transformation using the computer program C2 (Juggins 2003). Local assemblage zones were identified using stratigraphically constrained cluster analysis of diatom microfossil time series using CONISS® v. 2.0 (Grimm 1987). Local assemblage zones were estimated using the Euclidian distance dissimilarity coefficient.

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, δ^{15}N, δ^{13}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 (Appendix 1). Manitoba represents the largest source of nutrients to the lake, but development of provincial management strategies has been hampered by lack of historical context for

recent eutrophication and an understanding of the relative influence of climate, crop production, and animal husbandry practices (D. Williamson, MWS, pers. comm.). Consequently, we sought to quantify the statistical relationship between provincial land-use practices, climate, and water quality during the 20th century to better prioritize goals for lake remediation, even though we recognize that this approach will not account for nutrients influxes from headwater regions in southern and western portions of the catchment, or the unique effects of the City of Winnipeg. Fortunately, mass balance studies conducted within the Lake Winnipeg basin demonstrate that most nutrients from SK and AB are sequestered in intervening lakes and reservoirs prior to transmission to Lake Winnipeg (Leavitt et al. 2006; Finlay et al. 2010; B. Parker, Environment Canada, unpublished data), and that City of Winnipeg contributes 5-10% of TN and TP to the lake in most years. 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.

Climate records were obtained from Environment Canada weather stations located at Winnipeg St. Johns College (1900–1937) and Winnipeg Richardson International Airport (1938–2006). These records were blended without modification, as comparison of each with overlapping records from additional stations suggested that there was no measurable offset between sites for major meteorological time series. Potential climate predictors included monthly, seasonal, and annual total precipitation (mm; 1875–2006), annual rainfall (mm; 1875–2006), mean monthly and seasonal temperature (^{o}C; 1875–2006), and mean minimum and maximum temperatures on monthly, seasonal and annual scales (°C, 1875–2006). In addition, historical records of ice thaw and freeze for the Red

River at Winnipeg were used to estimate the regional ice-free season of the western Canadian plains 1900–1995, as described by Hall et al. (1999). Records of mean annual lake level (m a.s.l.) and discharge (m^3) from the 12 main tributary rivers and the sole outflow (Nelson River) were obtained from MWS.

Historical records of livestock populations, production, and associated agricultural products were obtained for MB from Census of Canada reports (Statistics Canada 1871–2006). Canadian census data have been variously available in MB at annual, 5-yr, and decadal intervals during the 20^{th} century. Consequently, annual estimates of all commercial livestock species density and production (e.g., beef cattle, dairy cattle, hogs, sheep, chickens, etc.) and their products (e.g., milk, fleece, eggs, etc.) were estimated for each year 1906–2006 by linear interpolation between census years (Appendix 1). Similarly, annual estimates of total, urban, and rural human populations were obtained for MB from Census of Canada reports (Statistics Canada 1871–2006) by linear interpolation among census data available at annual, 5-yr, or decadal intervals since 1871.

Crop production variables included a combination of areal estimates of diverse farming activities, fertilizer sales, and direct measurements of agricultural production. Historical records were obtained from Census of Canada reports (Statistics Canada 1871–2006) including number of farms (farms yr^{-1}), area (km^2) used for specific activities (e.g., cropland, pasture, summer-fallow), area seeded or planted with individual crop species (km^2), calendar day of year [DOY] of agricultural activities (seeding, heading, swathing, harvest) for major cultivars, and annual mass of products harvested for each crop (kg). In all cases, estimates of annual production were approximated by linear interpolation among census data collected at annual, 5- or 10-yr intervals since 1908. Annual fertilizer

sales (kg), farm expenditure on fertilizer and lime (CND$), and nutrient content (N, PO_4, K, potash) of purchased fertilizer (kg) were obtained from diverse sources, including Statistics Canada (1968–1977), fertilizer trade catalogues, the Canadian Fertilizer Institute, the Potash and Phosphate Institute (1978–2001), and Korol (2002). In general, chemical fertilizer use was limited prior to 1960.

Although too brief to be used in our statistical analysis, we also compiled annual records of limnological variables available for 1969 and 1992-2005 from MWS and FOC for concentrations (μg L^{-1}) of TP (1969, 1992–2005), TN (1992–2005), and Chl *a* (1992-2005). Similarly, annual records of commercial fish harvest from Lake Winnipeg (1883–2006) were obtained from MWS. However, although the lake supports a $20M commercial fishery, fish production and harvest were viewed, in part, as a response to eutrophication, rather than predictors of causal relationships, and were not included subsequent statistical analyses.

Numeric analyses – Constrained and partial canonical ordinations (ter Braak 1988) were used to evaluate the statistical relationships between fossil records of trophic status (pigments and stable isotopes; diatoms) and time series of explanatory variables related to climate (*C*), livestock (*L*), and crops (*A*). 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. In this procedure, 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). Separate VPA was conducted for indices of past lake trophic status (9 biomarker pigments, $\delta^{13}C$, $\delta^{15}N$, %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, USA).

VPA is most effective when there are similar numbers of predictors within explanatory categories and when predictors do not greatly outnumber response variables (Borcard et al. 1992; Hall et al. 1999). Consequently, several criteria were used to optimize predictor selection from the 191 candidate time series (Appendix 1). First, we eliminated time series less than 70 years in duration before interpolation because our objective was to identify the environmental factors best correlated with inter-decadal changes in lake production during the 20th century. Second, we used least-squares regression analysis of environmental time series within individual categories (e.g., *C*) to quantify the correlation among potential predictors. If two candidate time series were highly correlated, we eliminated a variable if we could assume its effect on mass flux (e.g., mass harvested, area cultivated) was 10-fold less than that of a well-correlated predictor (honeybees vs. hogs, minor specialty crops vs. wheat, etc.). Third, forward selection and Monte Carlo permutation testing was used separately for each category (*C*, *L*, *A*) within RDA to select the variables that explained significant (P <0.05) independent variation in fossil time series. Final predictors included six variables from livestock (total populations of cattle, hogs, horses, sheep, chickens + hens), crop (production of wheat,

oats, barley, canola, potatoes, corn), and climate categories (mean summer and winter temperature, summer and winter precipitation, ice-free period, Red River discharge). Although rural human population was also retained, we eliminated it from subsequent analyses because we were interested in the relative importance of individual human activities caused by elevated populations.

Explanatory and response variables were transformed and harmonized prior to multivariate analyses. First, all fossil time series were centered (mean = 0), standardized (variance = 1.0), and inspected for normal distribution, although no transformations were required. Because many explanatory variables were resolved more highly (annual) than the fossil time series (2.5-yr sample^{-1}, separated by 3-5 yr), all predictor time series were smoothed using a 3-year moving average, before being harmonized to fossil time series by sampling predictors at time intervals which matched those of the sedimentary records (17 intervals for pigments and isotopes, 19 for diatoms). In addition, all agricultural variables, most livestock predictors (except chickens + hens), and few climate variables (only Red River discharge) required $\log_{10}$ transformation to normalize variance.

Results

Sediment chronology – ^{210}Pb activity declined monotonically with depth in each of the Lake Winnipeg sediment cores (Fig. 2a), and 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 (± SE) rates of 50.0 ± 0.8, 64.6 ± 1.1, and 83.2 ± 0.9 mg cm^{-2} yr^{-1} for Cores 1, 2 and 3, respectively, although in each case mean 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. Mean SAR estimates were very similar to those obtained from previous studies (63.5–86.1 mg cm^{-2} yr^{-1}) of the south basin (Wilkinson and Simpson 2003).

Sedimentary geochemistry – Although the cores were taken from locations separated by ~35 km, they exhibited a high degree of similarity in elemental composition and stable isotope content throughout the past 200 years (Fig. 3). Consistent with the constant SAR, both N (~0.17% of dry mass) (Fig. 3b) and C contents (~1.5%) (Fig. 3c) were very 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 (~10:1) varied little either among cores or with burial depth and were characteristic of algal-derived material (data not shown). In contrast, δ^{15}N values increased linearly from background depleted levels (~4.5‰) ca. 1900 to an enriched maximum (~8.0‰) in surface sediments (Fig. 3a). Similarly, although δ^{13}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 from ca. 1800–1900, declined irregularly by ~1‰ until ca. 1990, then exhibited high temporal variability during the past 20 years, 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 essentially constant throughout the 19th century and increased by only 10-15% between ca. 1900 and the present day (Fig. 4a). In general, these increases reflected variation in NAI-P which accounted for ~45% TP content throughout the sediment record. NAI-P 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 concentrations (Fig. 4d) demonstrated little systematic variation through time, and accounted for ~30% and ~10% of TP content, with the exception of elevated EP content in surface sediments, and brief declines of AP in Core 1 (1 sample only) during the 1970s (Fig. 4b). Overall, residual 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 were relatively constant from ca. 1800–1900, 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), and chemically-stable indicators of total algal abundance (*β*-carotene, pheophytin *a*) (Fig. 5e), were constant throughout 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 exponentially in Core 1 sediments from baseline values between ca. 1800–1990 to 10-fold 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 cyanobacterial microfossil deposition ca. 1990 reflect either shading of other algae by positively buoyant N_2-fixing cyanobacteria, or a change in depositional processes as neutrally-buoyant phytoplankton are replaced by positively-buoyant diazotrophs (Bunting et al. 2007). Regardless, taken together, these patterns demonstrate that algal abundance increased ~three- to five-fold during the 20th century, with an ecosystem state change occurring ca. 1990. In contrast, ratios of labile to chemically-stable pigments (Chl *a* : pheophytin *a*) did not change with depth (not shown), indicating that preservation environments have 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 years (Fig. 6). Constrained cluster analysis of fossil valve concentrations identified three diatom zones in Core 1, including communities with low concentrations representing baseline conditions (Zone I, ca. 1800–1915), a period of slowly rising densities (Zone II, ca. 1915–1975), and an era of greatly increased diatom deposition (Zone III, ca. 1980-present). Although the same zones were also identified by cluster analysis of diatom relative (%) abundance (data not shown), there were only modest changes in species composition during the past 200

years. At all core intervals, mesotrophic *Aulacoseira islandica* (regional $TP_{optimum}$ = 15.4 μg P L^{-1}) accounted for 60-85% of sedimentary diatoms in Core 1 (Fig. 6), consistent with reports of its abundance in spring throughout the 20th century (Lowe 1923; Bajkov 1930, 1934; Kling 1998). Instead, transition from Zone I to II was marked by declines in abundance of eutrophic *Stephanodiscus niagarae* (TP_{opt} = 58.5) and mesotrophic *Aulacoseira subarctica* (O. Müller) Haworth (TP_{opt} = 21.5), coupled with modest increases in *A. islandica* and eutrophic *Stephanodiscus hantzschii* Grunow (TP_{opt} = 40.1). In contrast, the shift from Zone II to III revealed large increases in concentrations of several diatom taxa, including *A. islandica*, *Stephanodiscus minutulus* Håkansson (TP_{opt} = 41.7) and eutrophic *Stephanodiscus* spp. (*S. parvus* Stoermer and Håkansson, *S. hantzschia*), and the first occurrence of *Cyclostephanos* spp. (TP_{opt} = 33.3, 95.1). Interestingly, diatom-inferred TP concentrations did not vary substantially (range ~12 to ~20 μg P L^{-1}) during the past 200 years (Fig. 6), suggesting that while total diatom production increased through the 20th century (Figs. 5a, 6), factors other than nutrients regulated precise species composition (e.g., silica, light, turbulence, etc.). Consistent with this interpretation, total concentrations of diatom valves were correlated strongly (r^2 = 0.66, P<0.0001) with sedimentary concentrations of diatoxanthin, the pigment characteristic of diatoms.

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, $\delta^{13}C$, $\delta^{15}N$, 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 crops (66.5%) or livestock alone (62.0%) explained three-fold more variation in pigments and geochemistry (Fig. 7). Only cattle (correlated positively with hogs, negatively with horses) and chickens + hens (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 were retained in a RDA of fossils with crop predictors, although production of both these 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. Interestingly, multivariate analyses were unable to explain any significant (P <0.05) variation in past diatom community composition (% relative abundance) during 1904-1993, either in VPA or in RDA constrained uniquely to climate, crop, or livestock predictors.

Discussion

Analysis of highly resolved time series of sediment geochemistry and algal fossils demonstrated that southern Lake Winnipeg has undergone three phases of eutrophication since 1800. The first phase (ca. 1800-1900) includes baseline conditions prior to

eutrophication in which the south basin was mesotrophic (~15-20 μg 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. 5d), including diazotrophic *Aphanizomenon* and *Anabaena* spp. (Fig. 5f). Lake Winnipeg eutrophied during the second phase (ca. 1900–1990), 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 N_2-fixing cyanobacteria (Fig. 5). As in other prairie lakes (Hall et al. 1999; Leavitt et al. 2009), climatic variability during the 20th century had limited affect on water quality. Finally, during the third stage of eutrophication (ca. 1990-2006), southern Lake Winnipeg experienced a sudden persistent ecosystem state change (Scheffer et al. 2001; Scheffer and Carpenter 2003) defined by rising variance in biogeochemical cycles (Figs. 3, 4) and vernal algal populations (Fig. 5a, b; Fig. 6), a 50% reduction in pigments from summer-blooming algae (Fig. 5c-e), and a 10-fold increase in sedimentation of N_2-fixing cyanobacterial fossils (Fig. 5f). As described below, suppression of recent diazotrophic blooms will require a ~50% decline in nutrient influx (~500% to re-establish baseline conditions), while failure to reduce nutrients may result in a fourth phase of eutrophication in which toxic low-light adapted *Planktothrix* and *Microcystis* predominate such as seen in agricultural regions worldwide (Leavitt et al. 2006; Bunting et al. 2007; Xu et al. 2010).

Quantification of baseline conditions – Development of effective lake management strategies requires well defined scientific objectives for remediation of water quality. Unfortunately, due to its large size and relatively remote location (Fig. 1),

few limnological data exist prior to 1970 (Lowe 1924; Bajkov 1930, 1934; Brunskill 1973), and baseline conditions are unknown beyond preliminary analysis of fossil algae (Kling 1998) and phosphorus (Mayer et al. 2006) in poorly resolved cores. Here we demonstrate that the southern basin of Lake Winnipeg was naturally mesotrophic (TP = 15-20 μg TP L^{-1}) prior to intensification of European-style agriculture, with diatoms characteristic of regional eutrophic lakes (Cumming et al. 1995; Hall et al. 1999) (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 (Allan 1980; 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 (~0.6 mg P g^{-1} dry mass) (Fig. 4a) were similar to pre-agricultural values (0.8 $\pm$ 0.1 mg P g^{-1} dry mass) (Hall et al. 1999 and unpublished data) recorded in diverse lakes of the northern Great Plains (Allen et al. 1980; Triplett et al. 2009; Engstrom et al. 2009), other large shallow hardwater lakes (e.g., Lake Okeechobee) (Engstrom et al. 2006), and previous analysis of Lake Winnipeg sediments (Mayer et al. 2006). Second, fossil diatom communities were composed predominantly of taxa with inferred P requirements >15 μg TP L^{-1} (Fig. 6), such that abundance-weighted estimates of water-column P ranged 15-20 μg TP L^{-1} during the 19th century. Finally, 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 (Allen et al. 1980; Engstrom et al. 2009; Triplett et al. 2009). Unfortunately, the high proportion of biologically-unavailable P, combined with minimal temporal variability in P concentration (Fig. 4),

despite pronounced eutrophication (Fig. 5), suggest that historical changes in sedimentary P cannot be used to estimate baseline water-quality conditions within the lake.

Calculations based on combined analysis of total algal abundance (as fossil β-carotene) (Fig. 5e) and modern nutrient content suggest that baseline water-column concentrations of TP in the south basin ranged 15-20 μg TP L^{-1}, characteristic of other mesotrophic prairie lakes (Pham et al. 2008, 2009). Here we assumed that algal production during the 20th century was limited by the influx of P (Schindler 1977), that the relationship between algal density and P concentrations was consistent throughout 1800-1992, and that variations in fossil β-carotene concentrations were correlated linearly to changes in total algal abundance (Cuddington et al. 1999; Leavitt and Hodgson 2001). Therefore, given that mean ($\pm$ SD) water-column TP in the south basin was 80 $\pm$ 15 μg P L^{-1} during 1992-1996 (MWS unpublished data), and that sedimentary β-carotene concentrations in the three cores were between 4.33 $\pm$ 1.10 and 5.53 $\pm$ 1.74 -fold greater during the early 1990s than before 1900 (depending on whether mean [1960-1992] or maximum pigment concentrations were used), we estimate that the south basin contained 14.5 – 18.5 μg TP L^{-1} prior to eutrophication. These values agree well with the range inferred from analysis of fossil diatoms (Fig. 6; but *see* caveats below) and unpublished hydrological simulations of nutrient export (G. McCullough, R. Hesslein, FOC, unpublished data), and demonstrate that Lake Winnipeg should be managed for mesotrophic rather than oligotrophic conditions.

Mechanisms causing water-quality change during the 20th century – Water quality in the south basin of Lake Winnipeg was degraded substantially during the 20th century

(Fig. 5), largely due to the combined effects of crop and livestock production, but not climate change (Fig. 7). Specifically, abundance of all algal groups except diazotrophic cyanobacteria increased 300-500% (Fig. 5), δ^{15}N values increased 3-4 ‰ due to influx of enriched N (Fig. 3a) (Anderson and Cabana 2005; vander Zanden et al. 2005; Bunting et al. 2007), and δ^{13}C declined 1-2‰ consistent with increased primary production and reliance on respired CO_2 (Leavitt et al. 2006; Bunting et al. 2007). VPA explained almost 75% of historical variation in indices of lake trophic status (pigments, isotopes, %C, %N) between ca. 1900-1992 due to increased production of cattle, hogs, chicken, and major crop cultivars (canola, potatoes, wheat, etc.), while the unique effects of climate and its first-order interactions with crop and livestock production (*C*, *C*× *L*, *C*× A) explained a non-significant (P >0.15) fraction (4.1%) of historical change (Fig. 7). Such weak effects of pronounced warming (~3^{o}C increase, ~35 day decline in ice cover) have been documented for other lakes within the Lake Winnipeg catchment (Leavitt et al. 2009), 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).

Intensification of nutrient fluxes due to widespread crop production and animal husbandry is now the most significant mechanism causing eutrophication of fresh and coastal waters (Carpenter et al. 1998; Smith 2003). For example, grains such as wheat (~1×10^9 kg yr^{-1} in 1910s) and barley (0.3-0.5$\times10^9$ kg yr^{-1} in 1910s) have dominated production since regional farming began (Honey and Oleson 2006), but their harvest increased dramatically following World War II (WWII; 1939-1945), reaching 5×10^9 kg

yr^{-1} and 2×10^9 kg yr^{-1}, respectively, during the 1980s (Statistics Canada 1871-2006). Similarly, irrigation-intensive potato production increased linearly from stable values of ~0.1×10^9 kg yr^{-1} 1900-1950 to modern harvests >1×10^9 kg yr^{-1} (Statistics Canada 1871-2006) due to increased demand for processed food (Honey and Oleson 2006). Although canola was introduced after 1945, this crop 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 (~25% of Canadian canola crop). Interestingly, 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 (Fig. 3-6), because lake production was inversely correlated with horse density in VPA (horses were replaced by tractors), and because 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).

Degradation of water quality by livestock production arises most commonly when animal densities greatly exceed that of humans, and mass imbalances occur between nutrient importation to sustain forage and other crops and their 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, cattle populations were ~0.75×10^6 until ca. 1950, increased to ~1.5×10^6 by 1975, declined for 20 yr, and then peaked at ~1.75×10^6 in the 2000s (Statistics Canada 1906-2006). Similarly, MB hog populations were <0.75×10^6 until ~1980, after which

time densities increased exponentially to ~3×10^6 head by 2005. Interestingly, chicken and hen populations varied between 6- and 8×10^6 since the mid 1940s, after having increased rapidly during the early 20th century (Statistics Canada 1906-2006). Taken together, we find that MB biomass for these three species alone is ~12-fold greater than that of humans (~60 kg ind^{-1}), assuming market weights for chickens (2 kg ind^{-1}), hogs (112 kg ind^{-1}), and cattle (317 kg ind^{-1}). Given that Winnipeg (pop. 742,000) accounts for 5-10% of nutrient influx to Lake Winnipeg (Table 2), 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).

Strongly enriched (3-4‰) sedimentary $\delta^{15}N$ values recorded after 1900 are consistent with increased influx of N from agricultural (Anderson and Cabana 2005; vander Zanden et al. 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, 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. unpublished data), four cores from adjoining Lake Manitoba (Leavitt et al. unpublished data), and six other lakes within the catchment (Leavitt et al. 2007), all sites which receive substantial agricultural N, but not direct urban N. As reviewed elsewhere (Savage et al. 2004; Leavitt et al. 2007), 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 this interpretation, changes in fossil $\delta^{15}N$ were correlated more highly with growth of

Winnipeg's population during the 20th century (r^2 = 0.82, P <0.0001) than with changes in either MB cattle (r^2 = 0.74, P <0.0001) or hog populations (r^2 = 0.52, 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* (E*m*) flux framework (Leavitt et al. 2009) and empirical observations from more than 20 agriculturally-impacted lakes within the Canadian Prairies (Hall et al. 1999; Pham et al. 2008; Dröscher et al. 2009; Leavitt et al. 2009). Regional fall, winter, and spring mean and minimum temperatures have increased ~3°C since the late 1800s (Statistics Canada 1897-2006), leading to ~35 day 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 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 (MWS unpublished data) and was retained in the VPA (Fig. 7), there was no sustained interdecadal increase in hydrologic influx until 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 *m* influx to lakes by >10-fold whenever land-use practices prevent re-establishment of natural vegetation (reviewed in Dearing and Jones 2003).

Our statistical approach was unable to clearly isolate the unique effects of crop and livestock production on water quality degradation during the 20th century (Fig. 7),

mainly because of residual co-linearity among predictors following selection of environmental time series (*see* Methods). Additionally, cumulative explained variance (~75%) was lower than that recorded in VPA of other lakes in the catchment (87-97%) using identical protocols (Hall et al. 1999; Leavitt et al. 2009), likely because we did not include urban (~5-10% TP and TN) or US nutrient sources (~34% TP, 21% TN) (Table 2). Similarly, we were unable to partition the unique effects of N and P pollution as has been done in coastal marine systems (Savage et al. 2010), because TN has been rarely monitored and because TN in regional lakes includes a high proportion ($\geq$70%) of dissolved organic N of uncertain biological availability (Patoine et al. 2006; Leavitt et al. 2006; Bunting et al. 2010). High colinearity among sedimentary variables also prevented us from quantifying the unique effects of N and P on southern Lake Winnipeg using fossil time series, even though historical changes in total algal abundance (as β-carotene) were correlated strongly with sedimentary concentrations of P ($r^2 = 0.47 \pm 0.25$, $P < 0.02$), %N ($r^2 = 0.81 \pm 0.08$, $P < 0.0001$), and δ^{15}N values ($r^2 = 0.72 \pm 0.16$, $P < 0.0001$) in all three cores (1901-1992). Finally, the lack of historical variation in diatoms species composition prevented VPA of relative abundance data, and complicated interpretations of diatom-inferred TP concentrations (Fig. 6). Despite these caveats, the observation that changes in MB crop (wheat, canola, potatoes) and livestock production (cattle, hogs, chicken + hens) explained ~75% of variation in south basin production 1901-1992 allows regulatory agencies to develop more effective management strategies, as outlined below.

Ecosystem State Change – Nearly a century of eutrophication combined with rapid agricultural development during the past ~30 years appears to have initiated an

ecosystem state change ca. 1990 (Scheffer et al. 2001; Scheffer and Carpenter 2003), from diverse productive algal communities to modern assemblages composed mainly of buoyant diazotrophic *Aphanizomenon* and *Anabaena* spp. (Fig. 5) (Kling 1998). As predicted from theory (Cottingham et al. 2000; Carpenter 2003; Carpenter and Brock 2006), state change was also marked by elevated temporal variation in many lake characteristics, including production and deposition of diatoms (Fig. 5a, Fig. 6), cryptophytes (Fig. 5b), and summer bloom-forming algae (Figs 5c-d), carbon cycling (Fig. 3c), and relative composition of sedimentary P fractions (Fig. 4). At present, it is unclear whether the 50% decline in concentrations of ubiquitous fossil pigments (*β*-carotene, pheophytin *a*) after 1990 (Fig. 5e) reflects a true reduction in algal abundance due to shading by floating cyanobacteria (McGowan et al. 2005; Bunting et al. 2007), lateral transfer of these algae to lakeshores (LWIC 2006), or increased pigment degradation due to slower sinking of buoyant taxa (Cuddington et al. 1999; Leavitt and Hodgson 2001). Regardless, we inter that southern Lake Winnipeg has undergone a state change due to a persistent change in external forcing (Leavitt et al. 2009), rather than a transition between alternative stable states (Scheffer et al. 2001; Scheffer and Carpenter 2003; Carpenter 2005), because the south basin's polymictic status and poor light penetration (Z_{secchi} <1 m, Z_{mean} 9.7 m) prevent many internal mechanisms (internal nutrient loading, macrophytes, stratification, benthic algal production) (Fig. 6) needed to stabilize alternative states (Scheffer and Carpenter 2003). This distinction is important for managers because stabilizing feedback mechanisms associated with alternative stable states can substantially delay lake response to declines in external nutrient influx (Scheffer et al. 2001; Scheffer and Carpenter 2003).

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. Specifically, Canadian agricultural policies were modified in the 1980s and 1990s to comply with World Trade Organization, Canada-US, and North American Free Trade agreements and to increase exports (hogs, oilseeds, grains), deregulate transportation (railways), induce foreign investment, reduce governmental subsidies, and eliminate price controls, among other activities (Venema 2006). In particular, the National Farmers Union notes that modification (1984) and elimination (1996) of long-standing (since 1897) rail transportation subsidies (Crows Nest Pass Agreement, Western Grain Transportation Act) increased grain transportation costs more than three-fold, particularly for MB farmers 1500 km distant from coastal grain shipping ports (Novek 2003). Concomitantly, international prices for grains declined, the federal Gross Revenue Insurance Plan for farmers was eliminated (Bradshaw et al. 2004), and world pork demand tripled (Agriculture and Agri-Food Canada 1997; Novek 2003; Venema 2006).

Manitoba government sought to offset resultant 40% declines in agricultural revenues and promoted 'the Manitoba advantage' (low feed-grain costs, intensive forage cultivation, 5.4×10^6 ha for waste assimilation, pro-business attitude) to both regional farmers and international hog producers facing severe environmental and regulatory constraints (e.g., North Carolina, Denmark, Netherlands, Taiwan) (Martin et al. 1999; Novek 2003; MB Agriculture and Food 2010). As a result, hog number increased five-

fold and operations intensified (~350% fewer farms, 8-fold increase in areal animal densities) during 1981-2000 (Schnaiberg and Gould 1994; Novek 2003; Venema 2006) while fodder corn production increased from 0.1 $\times 10^9$ kg yr^{-1} to ~1.2 $\times 10^9$ kg yr^{-1} (Statistics Canada 1871-2006). Between 1990 and 2010, agricultural diversification also increased annual harvest of canola and potatoes by ~2.5 $\times 10^9$ kg (500%) and ~0.7 $\times 10^9$ kg (275%), respectively, whereas production of other major grains declined slightly (wheat, barley, mixed grains, corn) or changed little (oats) relative to previous production (Statistics Canada 1871-2006). Such sudden increases in crop and livestock production increased nutrient runoff in southern MB, as recorded by elevated nutrient concentrations in all tributary rivers (Jones and Armstrong 2001), ~20% increases in water column concentrations of N and P (MWS unpublished data), and a decline in water column TN : TP ratios from ~8.5 to 6.3 since 1990 (MWS unpublished data).

Scientific and management implications – Sedimentary analyses provide a unique opportunity to improve scientifically-based strategies for lake remediation. By assuming Lake Winnipeg has been regulated mainly by the influx of P prior to regime shift ca. 1990, we propose that modern TP content in the south basin (~100 μg P L^{-1}) must be reduced ~five-fold to return the basin to mesotrophic conditions characteristic of the pre-agricultural era (~15-20 μg P L^{-1}). These targets are consistent with the P optimum of the predominant (60-80% of valves) diatom taxon, *Aulacoseira islandica* (~15.4 μg P L^{-1}), determined using a survey of >100 regional lakes, although we caution that factors other than nutrient influx (e.g., physical mixing, Si, light, etc.) appear to be regulating diatom species composition in the south basin (Fig. 6). Similarly, we recommend that modern

TP concentrations be reduced to ~50 μg P L^{-1} (50% decrease) to suppress current outbreaks of diazotrophic cyanobacteria and reduce the present surplus of water column SRP (~50% of TP), yet allow for the high interannual variability in river discharge which regulates nutrient influx to the lake. We infer that the lake will not show hysteresis in response to nutrient reduction because the recent state change appears to lack most internal mechanisms that would stabilize a turbid, cyanobacteria-rich state (e.g., anoxia, internal nutrient loading, bioavailable sedimentary P) (Fig. 4). Further, we believe that these thresholds (50%, 500% reductions) will also apply to the north basin of Lake Winnipeg, despite ~50% lower ambient TN and TP concentrations (MWS unpublished data), as most of the nutrients enter that site from the south basin.

Finally, we caution that failure to immediately reduce P influx may initiate a final transition in lake state from buoyant N_2-fixing *Aphanizomenon* and *Anabaena* to potentially toxic, but low-light adapted cyanobacteria (*Planktothrix*, *Microcystis*, *Cylindrospermopsis*) due to continued pollution with N, as has occurred in the Canadian Prairies (Patoine et al. 2006; Leavitt et al. 2007), Europe (Scheffer et al. 1990; Bunting et al. 2007), China (Paerl and Scott 2010; Xu et al. 2010), and elsewhere. These turbid polymictic lakes usually lie in catchments with P-rich soils due to natural geology or prolonged agriculture (Carpenter 2005), accumulate >50 μg P L^{-1} as bioavailable SRP during summer despite greatly elevated cyanobacterial biomass, and exhibit highly significant correlations (r^2 >0.7) between total algal biomass and N influx, but not P supply, in long-term (>20 yr) monitoring studies (e.g., Bunting et al. 2007). In addition, several of these sites have paleolimnological time series which demonstrate that diazotrophic cyanobacteria are replaced within decades by potentially toxic cyanobacteria

due to continued pollution of P-rich systems with N (Leavitt et al. 2006; Bunting et al. 2007). As demonstrated by three years of month-long, large-scale (>3000 L) mesocosm experiments, pollution of P-rich polymictic lakes with reduced N (urea, NH_3) can suppress N_2-fixing *Aphanizomonen* and *Anabaena* but increase total biomass and toxicity of *Microcystis* and *Planktothrix* by up to 400% when lakes have >50 μg SRP L^{-1} and dissolved N : P <20 : 1 (Finlay et al. 2010). Unfortunately, monitoring since 1992 demonstrates that southern Lake Winnipeg now exhibits these same characteristics, suggesting that the lake is already subject to damage by N pollution and that there may be substantial benefits to reducing both N and P influx (Paerl and Scott 2010).

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Table 1. Physical characteristics of Lake Winnipeg, modified from Brunskill et al. (1980).

	North Basin	Narrows	South Basin	Entire Lake
Latitude (^{o}N)				50^{o}00'-53^{o}50'
Longitude (^{o}W)				96^{o}15'-99^{o}15'
Surface area, A_0 (km^2)	17520	3450	2780	23750
Volume (km^3)	232.4	24.6	27.0	284
Mean depth (m)	13.3	7.2	9.7	12.0
Maximum depth (m)	19.0	61.0	14.0	36.0
Maximum length (m)	232	143	93	436
Maximum breadth (m)	111	30	46	111
Shoreline (km)	761	640	349	1750
Shoreline/ A_0	0.043	0.19	0.13	0.074
Development of Shoreline	1.6	3.1	1.9	3.2
Development of Volume	2.1	0.6	2.1	1.0
Mean depth/Maximum depth	0.70	0.20	0.69	0.33
Relative depth (%)	0.013	0.054	0.024	0.021
Mean hydraulic residence (yr)			0.57	3.28

Table 2. Estimated mean annual total phosphorus (TP) and nitrogen (TN) influx to Lake Winnipeg 1994–2001 (tonnes yr^{-1} rounded to nearest 100 tonnes) (Bourne et al. 2002, MWS unpublished data). Natural background and undefined sources include influx from forests, wildlife, and septic fields. Internal processes include gross N_2 fixation only, not denitrification (L. Hendzel, Fisheries and Oceans Canada, unpublished data). SK = Saskatchewan, MB = Manitoba, ON = Ontario.

Category	TP	%TP (%MB sources)	TN	%TN (% MB sources)
Upstream jurisdictions	*4,200*	*53*	*48,900*	*51*
US (Red R)	2,500	32	19,000	20
US (Souris R)	200	3	1,100	1
SK and AB (Assiniboine and Saskatchewan R)	400	5	8,300	9
ON (Winnipeg R)	800	10	16,800	17
ON (Other R)	300	3	3,700	4
MB Sources	*3,700*	*47*	*47,100*	*49*
MB Point Sources	700	9 (19)	5,100	5 (11)
City of Winnipeg	400	5 (11)	3,700	4 (8)
Other wastewater sources)	300	4 (8)	1,400	1 (3)
MB Watershed Processes	2500	32 (67)	23,200	24 (49)
Natural background and undefined sources	1,300	17 (35)	18,100	19 (38)
Present agriculture	1,200	15 (32)	5,100	5 (11)
Atmospheric deposition	500	6 (14)	9,500	10 (20)
Internal lake processes	n/a	n/a	9,300	10 (20)
Total annual load	*7,900*	*100*	*96,000*	*100*

Figure Legends

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 cores within south basin of Lake Winnipeg in upper right inset. *See* Site Description for land use, soil, and hydrological details.

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).

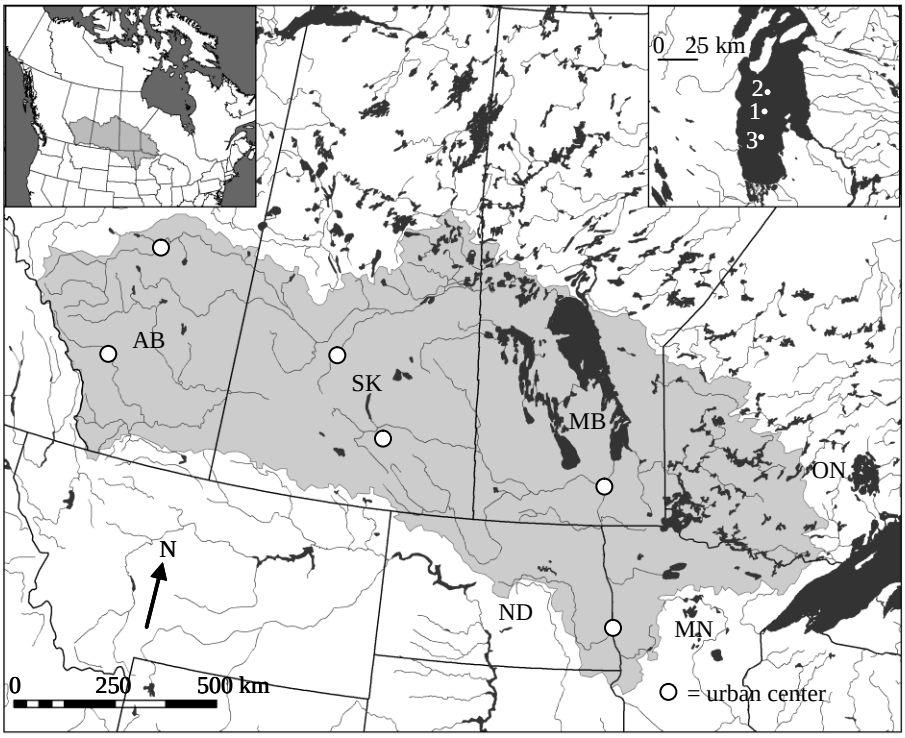
Fig. 3. Time series of whole-sediment (a) nitrogen (N) isotopes (δ^{15}N, ‰), (b) N content (% dry mass), (c) carbon (C) isotopes (δ^{13}C, ‰), and (d) C content (% dry mass) during 1800-2010 for three sediment cores from southern Lake Winnipeg. Symbols and lines as in Fig. 2.

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) non-apatite inorganic P extracted by NaOH, (d) exchangeable inorganic P extracted by NH_4Cl, and (e) residual or organic P during 1800-2010 for sediment cores (as Fig. 2) from southern Lake Winnipeg.

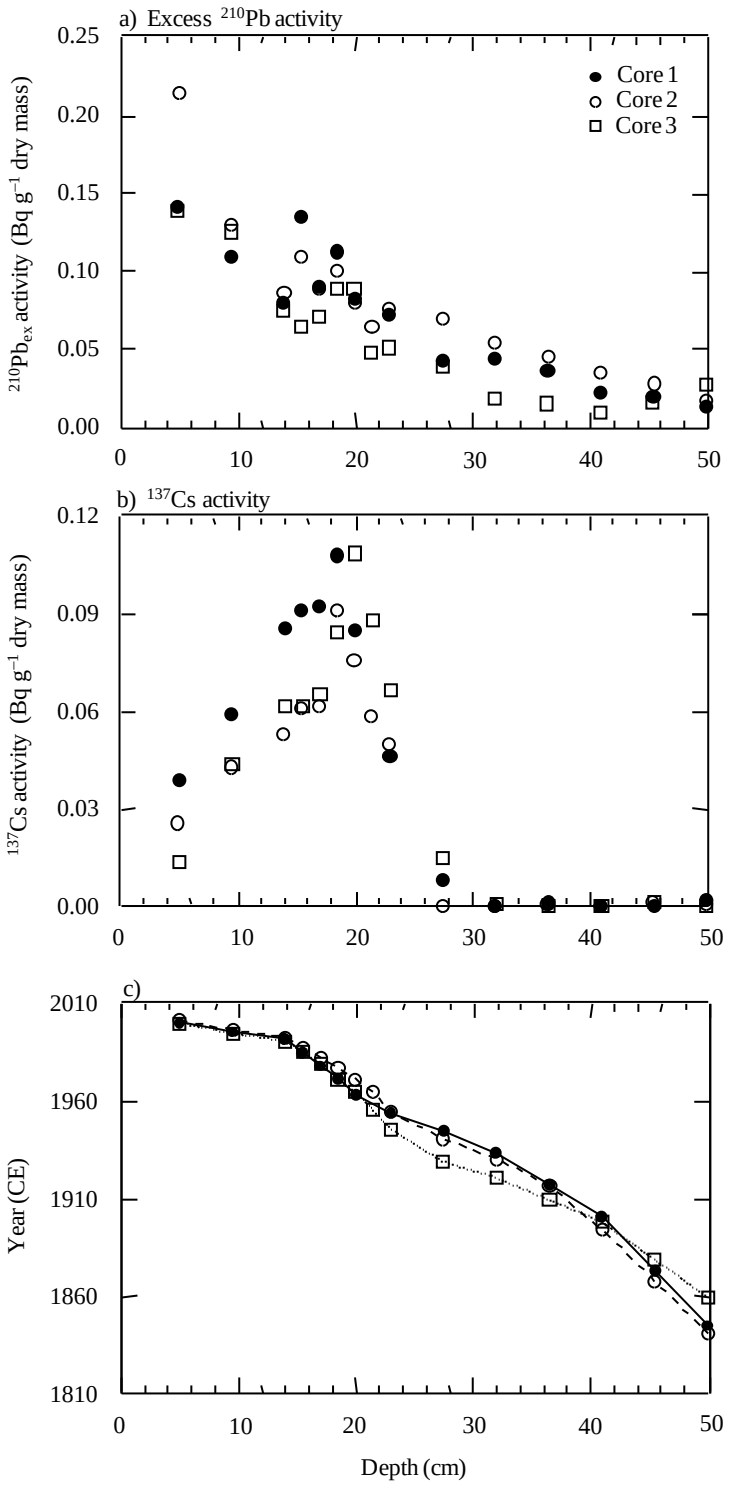
Fig. 5. Time series of fossil pigment concentrations (a-e) (nmol pigment g^{-1} sediment C) and (f) cyanobacterial akinetes (microfossils g^{-1} dry mass) during 1800-2010 for three cores from southern Lake Winnipeg. Core identities as Fig. 2. Pigment include (a) diatoxanthin mainly from diatoms, (b) 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* (black histograms, 10^5 scale) and *Aphanizomenon* (grey histograms, 10^4 scale).

Fig. 6. Time series of concentrations of valves from fossil diatom species in Core 1 during 1800-2010. All fossil concentrations are valves x 10^5 g^{-1} dry mass, except *Aulacoseira islandica* and total diatom abundance (valves 10^6 g^{-1} dry mass). Uppermost two panels include results of cluster analysis of diatom species and estimates of total water column phosphorus concentration (μg TP L^{-1}) estimated for the south basin from weighted average regression analysis of relative (%) diatom species composition.

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 both $C \times L$ and $A \times C$ interactions explained <0.3% of historical variation in lake production parameters.



Bunting et al. Fig. 1



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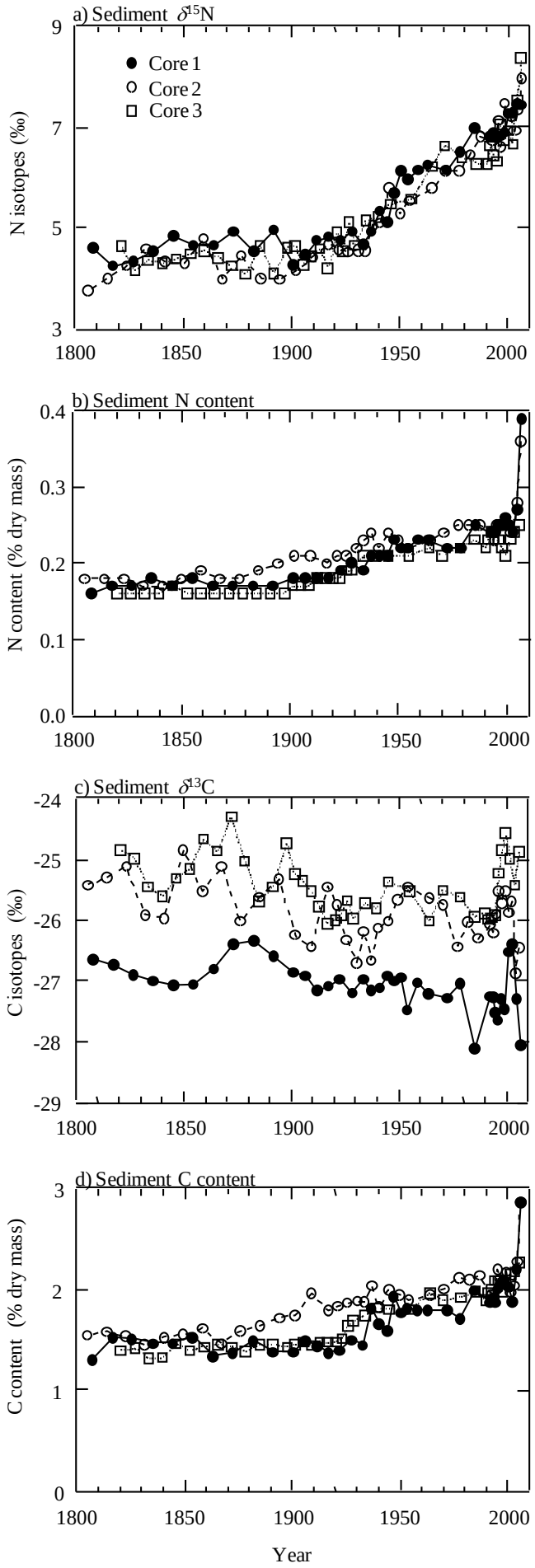

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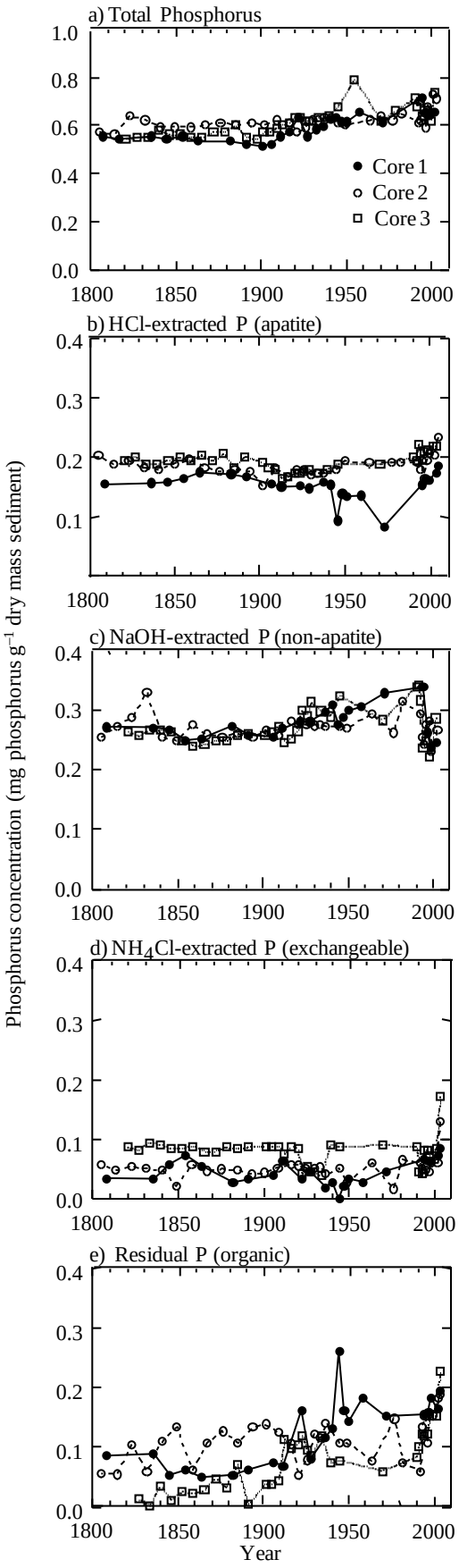

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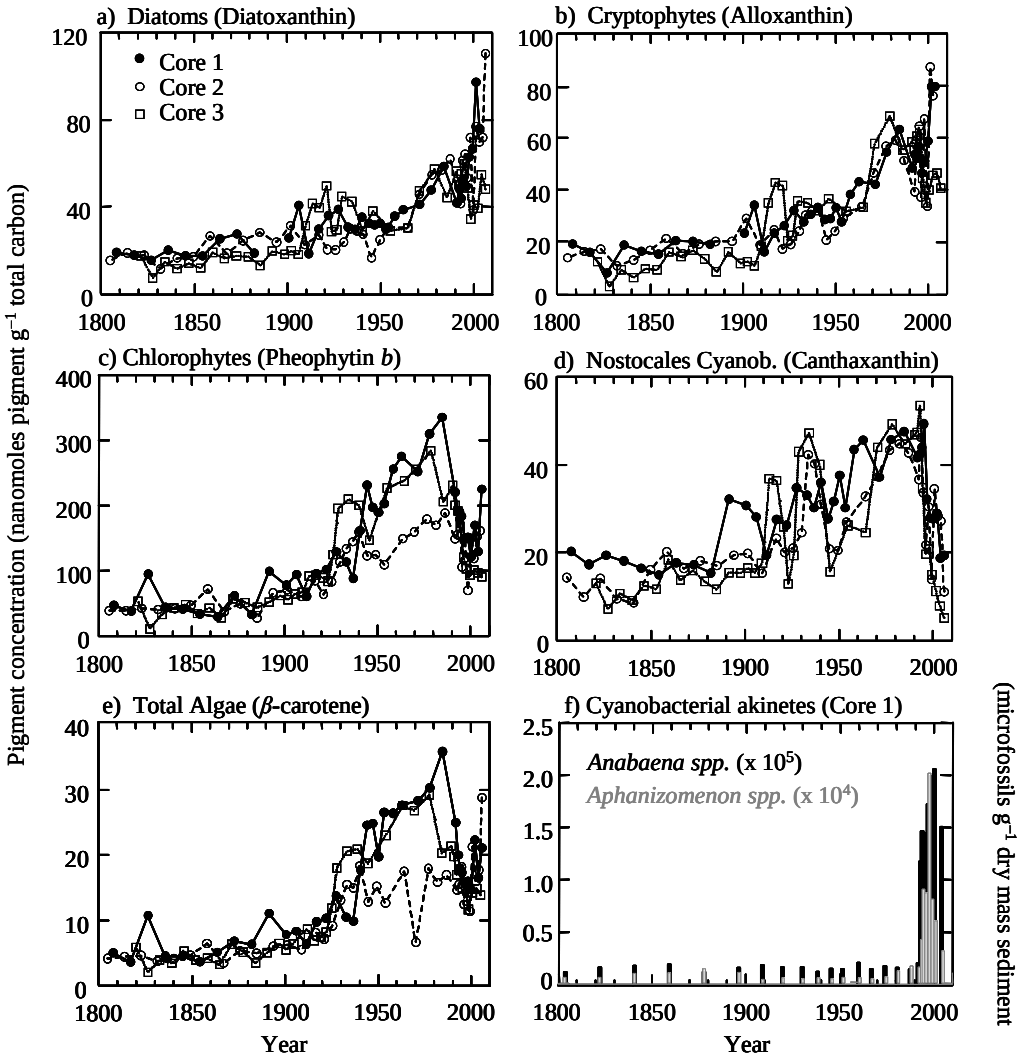

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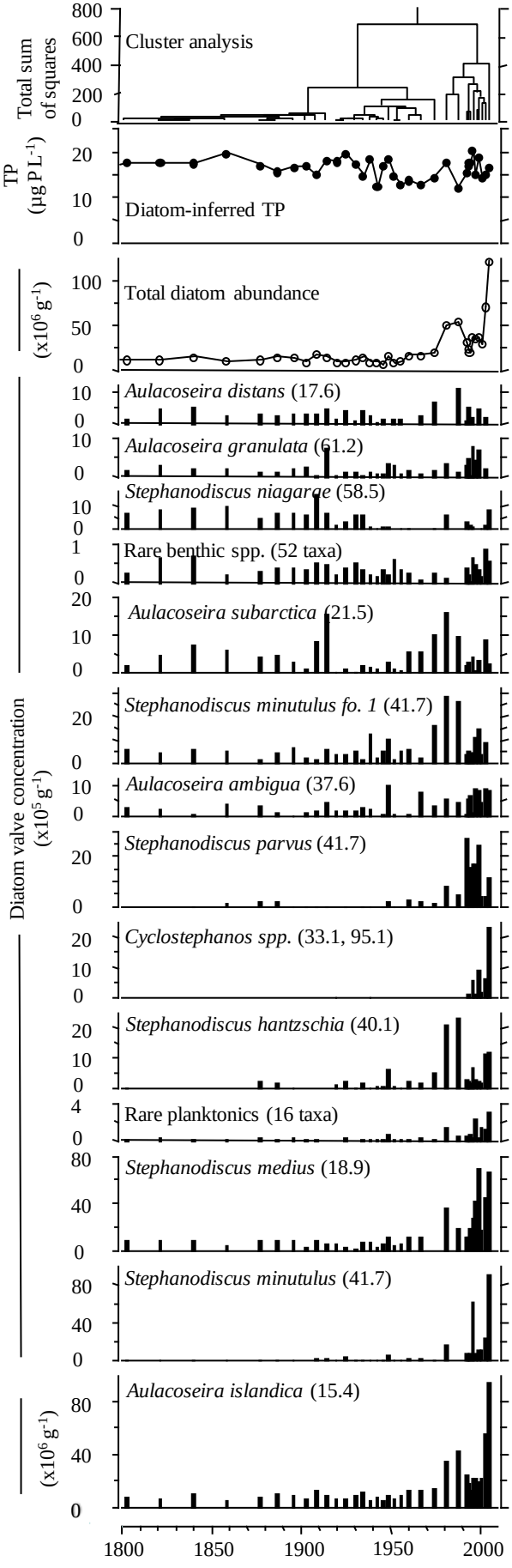
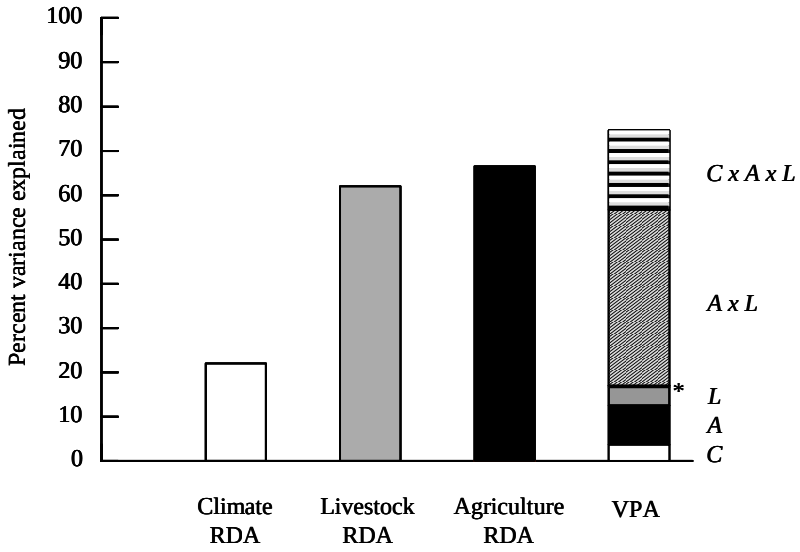


Bunting et al. Fig. 6



Bunting et al. Fig. 7

Appendix 1. Explanatory variables included initially in variance partitioning analysis (VPA). Variables are grouped into climate, livestock, and crops for VPA. Limnological variables provided by Manitoba Water Stewardship are listed separately. N = Number of variables within category; DOY–calendar day of year. Year of time series start and end are indicated for each variable.

Variable name	*N*	Start	End
Climate			
Monthly precip., mm	12	1875	2006
Seasonal precip., mm	4	1875	2006
Annual precip., mm	1	1875	2006
Annual rainfall, mm	1	1875	2006
Mean monthly max temperature, °C	12	1875	2006
Mean seasonal max temperature, °C	4	1875	2006
Mean monthly min temperature, °C	12	1875	2006
Mean seasonal min temperature, °C	4	1875	2006
Mean monthly temperature, °C	12	1875	2006
Mean seasonal temperature, °C	4	1875	2006
Mean annual temperature, °C	1	1875	2006
Ice breakup date, Red River at Winnipeg, DOY	1	1870	1995
Ice freeze-up data, Red River at Winnipeg, DOY	1	1870	1981
Ice-free season, Red River at Winnipeg, No. days	1	1870	1981
Annual flow, Black River, cm	1	1960	1992
Annual flow, Fisher River, cm	1	1961	2006
Annual flow, Pigeon River, cm	1	1957	1996
Annual flow, Berens River, cm	1	1980	1998
Annual flow, Icelandic River, cm	1	1958	2006
Annual flow, Bloodvein River, cm	1	1976	2006
Annual flow, Poplar River, cm	1	1968	1996
Annual flow, Manigotogan River, cm	1	1913	1996
Annual flow, Red River, cm	1	1882	2006
Annual flow, Winnipeg River, cm	1	1907	2006
Annual flow, Saskatchewan River, cm	1	1912	2006
Annual flow, Dauphin River, cm	1	1977	2006
Annual flow, Nelson River East, cm	1	1972	2006
Annual flow, Nelson River West, cm	1	1972	2006
Annual flow, Nelson River East and West, cm	1	1972	2006
Annual total inflow, cm	1	1980	1992
Annual lake level, m	1	1914	2006
Mean monthly lake level, m	1	1914	2006
Mean seasonal lake level, m	1	1914	2006

Livestock and Humans

Annual commercial fish harvest, kg	1	1883	2006
Annual cattle pop., No.	1	1921	2006
Annual bull pop., No.	1	1931	2006
Annual dairy cattle pop., No.	1	1931	2006
Annual beef cattle pop., No.	1	1931	2006
Annual heifer pop., No.	1	1931	2006
Annual steers pop., No.	1	1931	2006
Annual calves pop., No.	1	1931	2006
Annual hog pop., No.	1	1921	2006
Annual horse pop., No.	1	1906	2006
Annual sheep pop., No.	1	1906	2006
Annual chicken pop., No.	1	1916	2006
Annual turkey pop., No.	1	1916	1982
Annual duck pop., No.	1	1916	1972
Annual geese pop., No.	1	1916	1972
Annual bee colonies., No.	1	1924	2006
Annual milk prod., kg	1	1920	1977
Annual shorn fleece wool, kg	1	1920	1993
Annual honey prod., kg	1	1924	2006
Annual MB pop., No.	1	1871	2006
Annual City of Winnipeg, MB pop., No.	1	1871	2006
Annual City of Brandon, MB pop., No.	1	1871	2006

Crops

Annual fertilizer sales, kg	1	1945	2002
Annual fertilizer and lime sales, $	1	1968	2001
Annual fertilizer sales, $	1	1926	1970
Annual fertilizer sales, 1992 constant $	1	1971	2006
Annual chemical product sales, 1992 constant $	1	1971	2006
Annual N content in fertilizer sold, kg	1	1950	2002
Annual PO_4 content in fertilizer sold, kg	1	1950	2002
Annual potash content in fertilizer sold, kg	1	1968	2002
Annual nutrient (N+P+K) content in fertilizer sold, kg	1	1968	2002
Annual farm, No.	1	1921	2006
Annual agricultural land area, km^2	1	1921	2006
Annual pasture area, km^2	1	1951	1992
Annual cropland area, km^2	1	1921	2006
Annual summerfallow area, km^2	1	1913	2006
Annual seeded all wheat area, km^2	1	1908	2006
Annual seeded spring wheat area, km^2	1	1908	2006
Annual seeded durum wheat area, km^2	1	1941	2006
Annual seeded oat area, km^2	1	1908	2006
Annual seeded barley area, km^2	1	1908	2006
Annual seeded all rye area, km^2	1	1908	2006
Annual seeded spring rye area, km^2	1	1923	2006
Annual seeded fall rye area, km^2	1	1923	2006

Annual seeded mixed grain area, km^2	1	1910	2006
Annual seeded corn for grain area, km^2	1	1941	2006
Annual seeded buckwheat area, km^2	1	1925	2006
Annual seeded dry field pea area, km^2	1	1908	2006
Annual seeded flaxseed area, km^2	1	1908	2006
Annual seeded mustard seed area, km^2	1	1952	2004
Annual seeded sunflower area, km^2	1	1943	2006
Annual seeded canola area, km^2	1	1943	2006
Annual seeded tame hay area, km^2	1	1908	2006
Annual seeded sugarbeet area, km^2	1	1940	1998
Annual seeded fodder corn area, km^2	1	1910	2006
Annual seeded potato area, km^2	1	1908	2006
Annual seeded field root area, km^2	1	1908	1940
Annual planted tomato area, km^2	1	1940	2006
Annual planted cucumber area, km^2	1	1940	2006
Annual planted lettuce area, km^2	1	1940	2001
Annual planted dry onion area, km^2	1	1940	2006
Annual planted asparagus area, km^2	1	1940	2006
Annual planted celery area, km^2	1	1940	1996
Annual planted beans area, km^2	1	1940	2006
Annual planted fresh corn area, km^2	1	1940	2006
Annual planted cabbage area, km^2	1	1940	2006
Annual planted cauliflower area, km^2	1	1940	2006
Annual planted carrot area, km^2	1	1940	2006
Annual planted parsnip area, km^2	1	1940	1996
Annual planted beet area, km^2	1	1940	2006
Annual planted rutabaga and turnip area, km^2	1	1940	2006
Spring wheat seeding is general (DOY)	1	1952	1991
Spring wheat heading is general (DOY)	1	1952	1990
Spring wheat swathing is started (DOY)	1	1952	1990
Spring wheat swathing is general (DOY)	1	1952	1989
Spring wheat swathing is completed (DOY)	1	1952	1990
Spring wheat combining is started (DOY)	1	1952	1990
Spring wheat combining is general (DOY)	1	1952	1989
Spring wheat combining is completed (DOY)	1	1952	1990
Annual tame hay prod., kg	1	1908	2006
Annual all wheat prod., kg	1	1908	2006
Annual spring wheat prod., kg	1	1908	2006
Annual durum wheat prod., kg	1	1941	2006
Annual buckwheat prod., kg	1	1925	2006
Annual oat prod., kg	1	1908	2006
Annual all rye prod., kg	1	1908	2006
Annual spring rye prod., kg	1	1923	2006
Annual fall rye prod., kg	1	1923	2006
Annual barley prod., kg	1	1908	2006
Annual mixed grain prod., kg	1	1910	2006
Annual canola prod., kg	1	1943	2006
Annual flaxseed prod., kg	1	1908	2006
Annual mustard seed prod., kg	1	1952	2004
Annual sunflower seed prod., kg	1	1943	2006
Annual potato prod., kg	1	1908	2006

Annual carrot prod., kg	1	1940	2006
Annual parsnip prod., kg	1	1940	1996
Annual cauliflower prod., kg	1	1940	1996
Annual cabbage prod., kg	1	1940	2006
Annual beet prod., kg	1	1940	2000
Annual sugarbeet prod., kg	1	1940	1996
Annual rutabaga and turnip prod., kg	1	1940	1995
Annual field root prod., kg	1	1908	1940
Annual asparagus prod., kg	1	1940	2002
Annual cucumber prod., kg	1	1940	2006
Annual lettuce prod., kg	1	1940	2001
Annual tomato prod., kg	1	1940	2006
Annual celery prod., kg	1	1940	1996
Annual dry onion prod., kg	1	1940	2006
Annual corn for grain prod., kg	1	1941	2006
Annual fodder corn prod., kg	1	1910	2006
Annual dry field pea prod., kg	1	1908	2006
Annual fresh corn prod., kg	1	1940	2006
Annual soy bean prod., kg	1	1956	2006

Limnology

Annual Red River mean TN, mg L^{-1}	1	1974	2006
Annual Red River mean TP, mg L^{-1}	1	1970	2006
Annual Winnipeg River mean TN, mg L^{-1}	1	1978	2006
Annual Winnipeg River mean TP, mg L^{-1}	1	1978	2006
Annual Saskatchewan River mean TN, mg L^{-1}	1	1970	2006
Annual Saskatchewan River mean TP, mg L^{-1}	1	1970	2006
Annual Dauphin River mean TN, mg L^{-1}	1	1978	2006
Annual Dauphin River mean TP, mg L^{-1}	1	1978	2006
Annual Nelson River East mean TN, mg L^{-1}	1	1972	2006
Annual Nelson River East mean TP, mg L^{-1}	1	1972	2006
Annual South Basin L. Winnipeg mean TN, mg L^{-1}	1	1992	2005
Annual South Basin L. Winnipeg mean TP, mg L^{-1}	1	1992	2005
Annual Narrows Lake Winnipeg mean TN, mg L^{-1}	1	1992	2005
Annual Narrows Lake Winnipeg mean TP, mg L^{-1}	1	1992	2005
Annual North Basin Lake Winnipeg mean TN, mg L^{-1}	1	1992	2005
Annual North Basin Lake Winnipeg mean TP, mg L^{-1}	1	1992	2005
Annual South Basin mean Chl *a*, mg L^{-1}	1	1992	2005
Annual Narrows mean Chl *a*, mg L^{-1}	1	1992	2005
Annual North Basin mean Chl *a*, mg L^{-1}	1	1992	2005
Annual Red River P loading, kg yr^{-1}	1	1970	2006
Annual Winnipeg River P loading, kg yr^{-1}	1	1970	2006
Annual Saskatchewan River P loading, kg yr^{-1}	1	1970	2006
Annual Dauphin River P loading, kg yr^{-1}	1	1977	2006
Annual East Side Lake Winnipeg P loading, kg yr^{-1}	1	1970	2006
Annual West Side Lake Winnipeg P loading, kg yr^{-1}	1	1970	2006
Annual Atmospheric Deposition P loading, kg yr^{-1}	1	1970	2006

Annual City of Winnipeg P loading, kg yr^{-1}	1	1970	2006
Annual Total P loading, kg yr^{-1}	1	1970	2006
Annual Outflow P (from Nelson River), kg yr^{-1}	1	1972	2006
Annual P load retained, kg yr^{-1}	1	1972	2006
Annual % P retention	1	1972	2006
Annual Red River N loading, kg yr^{-1}	1	1970	2006
Annual Winnipeg River N loading, kg yr^{-1}	1	1970	2006
Annual Saskatchewan River N loading, kg yr^{-1}	1	1970	2006
Annual Dauphin River N loading, kg yr^{-1}	1	1977	2006
Annual East Side Lake Winnipeg N loading, kg yr^{-1}	1	1970	2006
Annual West Side Lake Winnipeg N loading, kg yr^{-1}	1	1970	2006
Annual Atmospheric Deposition N loading, kg yr^{-1}	1	1970	2006
Annual N Fixation loading, kg yr^{-1}	1	1970	2006
Annual City of Winnipeg, N loading, kg yr^{-1}	1	1970	2006
Annual total N loading, kg yr^{-1}	1	1970	2006
Annual Outflow N (from Nelson River), kg yr^{-1}	1	1972	2006
Annual N load retained, kg yr^{-1}	1	1972	2006
Annual % N retention	1	1972	2006

Sudden ecosystem state change in Lake Winnipeg, Canada, caused by eutrophication arising from crop and livestock production during the 20th century

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Abstract

Lake Winnipeg, Canada, has experienced severe blooms of N_2-fixing cyanobacteria since 1990; however, little is known of background limnological conditions, causes of eutrophication, or whether modern conditions represent a stable ecosystem state change. To address these issues, sedimentary records of nitrogen (N) inputs (as δ^{15}N, %N), phosphorus (P) influxes (total P, chemical fractions), lake production (δ^{13}C, %C), and algal abundance and community composition (pigments, algal microfossils) were analyzed in three cores from the lake's south basin. Under baseline conditions (ca. 1800-1900), the basin was mesotrophic (~15-20 μg P L^{-1}) with diazotrophic cyanobacteria (*Aphanizomenon*, *Anabaena*), mesotrophic and eutrophic diatoms (*Aulacoseira islandica*, *Stephanodiscus niagarae*), and sedimentary P fractions characteristic of hardwater prairie lakes. Eutrophication accelerated during a second phase (1900-1990), when N, P and C contents increased 10-50%, δ^{15}N enriched 3-4‰, and concentrations of most algal pigments increased 300-500%. Nearly 75% of this 20th century variability was explained by concomitant increases in production of livestock (mainly cattle and hogs) and crops (wheat, potatoes, canola), but not by variation in climate. A third phase (1990-present) was marked by 50% declines in pigments from chlorophtyes and cyanobacteria, a 10-fold increase in concentrations of akinetes from *Aphanizomenon* and *Anabaena* spp., and occurred because of a century of fertilization, rapid changes in economic policies, and agricultural diversification. We conclude that P influx must decline by ~50% to suppress N_2-fixing cyanobacteria (500% to re-establish baseline conditions) and that failure to regulate P influx may initiate a fourth phase in which pollution with N promotes potentially toxic cyanobacteria.

Introduction

Eutrophication remains the most significant environmental problem which threatens the integrity of aquatic resources throughout the world despite 50 years 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) (Schindler 1977), 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). Unfortunately, such diffuse nutrient inputs are now the primary cause of aquatic pollution in many regions of the world (Smith 2003; Schindler 2006).

Water quality degradation arises from diffuse nutrient sources for several main reasons. First, agricultural inputs of phosphorus (P) and nitrogen (N) in commercial fertilizer and animal feed supplements often exceed agricultural outputs (Foy et al. 2002; Bunting et al. 2007). Second, excessive livestock densities can lead to manure production that overwhelms both 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 (Vitousek et al. 1997). In many instance, excess fertilization favours soil surpluses of P that are mobile and can leach into

downstream aquatic ecosystems (Smith et al. 1995; Bennett et al. 2001). Such surpluses of soil P can last for millennia (Carpenter 2005), facilitate accumulation of soluble P within downsteam lakes, and alter mechanisms regulating lake structure and function (Leavitt et al. 2006; Bunting et al. 2007).

Ecological theory suggests 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 water-column parameters (e.g., P concentration) 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 (Cottingham et al. 2000; Carpenter 2003; Carpenter and Brock 2006). Interestingly, the shift between states may arise from either rapid persistent changes in external forcing (Leavitt et al. 2009) 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. Similarly, further research is required to quantify the patterns and controls of ecosystem state change at decadal scales, as recent studies suggest that surface blooms of N_2-fixing cyanobacteria may not represent the terminal state in the eutrophication sequence (Leavitt et al. 2006; Bunting et al. 2007; Xu et al. 2010).

In this paper, we analyzed profundal sediments for diverse chemical and biological parameters to test the hypothesis that Lake Winnipeg, Canada, has undergone sudden ecosystem state change due to cumulative effects of a century of agriculture, rather than climatic variability. Lake Winnipeg is presently eutrophic (south basin >100 μg TP L^{-1}); however, little is known of the baseline limnological conditions, the magnitude, timing or causes of eutrophication, or whether outbreaks of diazotrophic cyanobacteria (*Aphanizomenon*, *Anabaena* spp.) since 1990 represent an externally-forced increase in production (Carpenter 2003; Leavitt et al. 2009) or a self-reinforcing change between alternative stable states (Scheffer et al. 2001; Scheffer and Carpenter 2003). To address these issues, we created highly resolved time series of historical N inputs (as δ^{15}N, N content), P influxes (as TP and P fractions), aquatic production (δ^{13}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). We conclude that while the south basin of Lake Winnipeg is naturally mesotrophic, a century of crop and livestock development has increased lake production ~500%, allowed intensification of agricultural practices after 1980 to initiate a state change, and poised the lake on the threshold of a further shift to increased biomass and toxicity of cyanobacteria.

Methods

Site description – Lake Winnipeg is a large (23,750 km^2), shallow (mean depth = 12 m), polymictic, multi-basin, eutrophic lake (>100 μg P L^{-1}) situated at 217.6 m above sea level (a.s.l.) in the Province of Manitoba (MB), Canada (Fig. 1, Table 1). The 953,250 km^2 lake catchment is located mainly within four Canadian provinces (MB, Alberta [AB], Saskatchewan [SK], Ontario [ON]), with additional contributions from the northern United States, primarily North Dakota (ND) and Minnesota (MN). More than 660,000 km^2 (70%) 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 (LWIC 2006; MWS 2006). More than 80% of the 6.6 million inhabitants of the watershed are located in urban areas (Statistics Canada and U.S. Bureau of Census data), although cities with populations >200,000 are relatively uncommon (Fig. 1).

Climatic conditions vary with location in the catchment, with aridity generally increasing from east to west and north to south (Pham et al. 2009). Within the central watershed, the climate is characterized as sub-humid continental, with short warm summers (mean 19°C in July), cold winters (mean -16°C in January), low mean annual temperatures (~1^{o}C), and an average of 105 frost-free days (Leavitt et al. 2006). In addition, this region has experienced an ~3^{o}C increase in mean temperature since the 19th century, mainly as pronounced increases in fall, winter, and spring minimum temperatures. As a result, ice cover in southern MB has declined more than 35 days since 1860 (Hall et al. 1999).

Three major river systems flow into Lake Winnipeg, while the sole outflow, the Nelson River, drains northeast into Hudson Bay (Fig. 1). The Red and Assiniboine rivers join within City of Winnipeg and enter the lake from the south (~8% of total water inflow), the Saskatchewan River enters the lake from the northwest (~22%), and the Winnipeg River enters from the southeast (~40%) (Fig. 1). Well developed Chernozemic soils predominate throughout the catchments of the Red-Assiniboine and Saskatchewan river systems (Brunskill et al. 1980), while forest and peatland soil types (regosols, brunisols, luvisols, gleysols, organic peat) predominate in the Winnipeg River watershed (Smith et al. 1998).

Land use varies substantially among sub-basins. For example, the Red (~127,000 km^2) and Assiniboine river catchments (~41,500 km^2) are composed largely of arable land that supports cereal, feed and specialty crop production, range and pasture lands, and intensive cattle and hog operations (UARBSC 2000). These sub-basins also include the major urban centers of Winnipeg MB (pop. 742,000), Fargo-Moorehead ND, and Regina SK (each pop. 200,000), livestock processing centers, and several smaller cities (MWS 2006). Agricultural land use is broadly similar within the Saskatchewan River drainage basin (~416,000 km^2) (specialty, cereal, and forage crops; range and pasture lands; livestock feedlots), while major cities are located in SK (Saskatoon, pop. 200,000) and AB (Calgary, Edmonton, pop. >750,000 each), and substantial forestry is practiced along the northern boreal margin of the catchment (Jones and Armstrong 2001). In contrast, land-use within the Winnipeg River catchment (~137,000 km^2) is restricted mainly to mining, forestry, and recreational activities, with few large population centres (Patalas and Salki 1992; Smith et al. 1998).

Nutrient influx to Lake Winnipeg – At present, Lake Winnipeg receives ~96,000 tonnes N and ~7,900 tonnes P each year, both derived mainly from non-urban sources (Table 2). Decade-long mass flux estimates suggest that Manitoba represents the largest source of nutrients to Lake Winnipeg (47% TP, 49% TN), due to a combination of agricultural runoff, background and undefined sources, atmospheric loading, internal lake processes, and urban and industrial effluent (Bourne et al. 2002; MWS 2006). The remaining portion of annual TP and TN influx to the lake is derived from headwater jurisdictions within the US (35% TP, 21% TN), ON (13% TP, 21% TN), and the Canadian Prairies (SK and AB, 5% TP, 9% TN) (Bourne et al. 2002; MWS 2006). On average, ~84% of TP and ~70% of TN is delivered to the south basin of Lake Winnipeg via the Red (54% TP, 30% TN) and Winnipeg river systems (13% TP, 29% TN) (M. Stainton, G. McCullough, Fisheries and Oceans Canada [FOC], unpublished data). Despite these generalities, magnitude and importance of individual sources likely vary among years, such that TP loading to Lake Winnipeg is highly correlated ($r^2 = 0.97$) to catchment water yield, particularly from the Red River (Jones and Armstrong 2001; Bourne et al. 2002; MWS 2006).

Relatively little is known of how nutrient influx to Lake Winnipeg has varied in the past. Total annual influxes of N and P have risen at least 13% and 10%, respectively, since the early 1970s, primarily due to increased nutrient inputs from the Red and Winnipeg river systems (Jones and Armstrong 2001; Bourne et al. 2002; MWS 2006; LWIC 2006). These latter increases reflect elevated river discharge since the early 1990s, a 29% increase in flow-adjusted concentrations of TP in both the Red and Winnipeg

rivers during the past 40 yr, and a concomitant 58% increase in TN concentrations in the Red River and possibly the Winnipeg River (Jones and Armstrong 2001). Furthermore, unpublished hydrologic models have combined these data with continuous measurements of Red River discharge to predict that mean whole-lake TP concentrations varied from ~12 μg P L^{-1} during the arid 1930s to ~55 μg P L^{-1} ca. 2000, assuming constant nutrient export from land (G. McCullough, R. Hesslein, FOC, unpublished data). In addition, analysis of P fractions in a sediment core with low temporal resolution suggests that there have been few large-scale changes in P influx during the past ~500 years, other than a modest increase (<10%) in TP deposition during the 20th century (Mayer et al. 2006).

Historical development of eutrophication – Relatively little is known of the historical changes in limnological conditions within Lake Winnipeg 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 in the mid- to late-1920s (Lowe 1924; Bajkov 1930, 1934) and late-1960s (Crowe 1973; Brunskill 1973; Brunskill and Graham 1979) to a more advanced state of eutrophy thereafter (Brunskill et al. 1979a, 1979b, 1980), as indicated by elevated concentrations of TP (~80 μg P L^{-1}) and TN (~700 μg TN L^{-1}) in the south basin during 1992-1996 (Manitoba Water Stewardship [MWS] unpublished data). Similarly, surveys conducted during 2000-2005 revealed enriched concentrations of TP (>100 μg P L^{-1}) and TN (~750 μg N L^{-1}) throughout the south basin, with soluble reactive P (SRP) accounting for ~50% of TP (>50 μg P L^{-1}) during fall sampling (M. Stainton, FOC, unpublished data). Occasional phytoplankton analyses conducted during the 20th century suggest that a

diatom community composed mainly of *Stephanodiscus niagarae* Ehrenberg in 1920s (Lowe 1924), 1930a (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 (Brunskill et al. 1979a; Hecky et al. 1986; Kling 1998). 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).

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 *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; δ^{15}N, δ^{13}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 (g cm^{-2} yr^{-1}) were calculated using the constant rate of supply (CRS) calculation (Binford 1990).

Stable isotope ratios and elemental composition were determined on whole sediment samples using a ThermoQuest (F-MAT) Delta^{PLUS} XL isotope ratio mass spectrometer equipped with continuous flow (Con Flo II) unit, an automated Carlo Erba elemental analyzer as an inlet device, and following standard procedures of Savage et al. (2004). Stable N (δ^{15}N) and C (δ^{13}C) isotopic compositions were expressed in the conventional δ-notation in units of per mil (‰) deviation from atmospheric N_2 and an organic C standard which had been calibrated previously against authentic Vienna Pee Dee Belemnite. Sample reproducibility was <0.25‰ and <0.10‰ for δ^{15}N and δ^{13}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 0.5M 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 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 (48 h, 0.01 Pa) 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. Pigment analysis was restricted to taxonomically diagnostic carotenoids, including those characteristic of siliceous algae and some dinoflagellates (fucoxanthin), mainly diatoms (diatoxanthin), cryptophytes (alloxanthin), chlorophytes (Chl *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). All pigment concentrations were expressed as nmol pigment g^{-1} sediment C, a metric which is linearly correlated to annual algal standing stock in whole-lake calibration studies (reviewed in 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 ~10 aliquots (~0.10 mL) per interval were individually 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 ($\lambda_{excitation}$ = 450-480 nm). Microfossil concentrations were estimated as akinetes g^{-1} dry mass of whole sediment. 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 protocol reviewed in Laird and Cumming (2009). Whole 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 100× fluotar objective and differential interference contrast optics (1000× magnification; N.A. = 1.3) to determine species composition, microfossil concentration (valves g^{-1} dry mass sediment), and relative (%) species abundance. Taxonomy and nomenclature are

presented in detail in Laird and Cumming (2009) (boreal lake taxa) and Michels et al. (2007) (prairie lake taxa).

Historical changes in water-column TP concentrations were reconstructed from analysis of diatom species assemblages in Core 1 following standard paleolimnological procedures (Hall and Smol 1992). Nutrient preferences of individual species were obtained from a survey of diatom composition in surfacial sediments of 140 regional sites (124 MN lakes, 16 sites from Lake of the Woods, ON). Diatom-inferred TP (DI-TP) was reconstructed using a robust weighted-average model ($r^2_{\text{bootstrap}} = 0.75$, RMSEP = 0.20) using the computer program C2 (Juggins 2003) and covered a gradient of 5–364 μg P L^{-1}, as detailed in Hyatt et al. (2011). Principal components analysis (PCA) was performed on diatom relative abundance with a square-root transformation using the computer program C2 (Juggins 2003). Local assemblage zones were identified using stratigraphically constrained cluster analysis of diatom microfossil time series using CONISS® v. 2.0 (Grimm 1987). Local assemblage zones were estimated using the Euclidian distance dissimilarity coefficient.

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, δ^{15}N, δ^{13}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 (Appendix 1). Manitoba represents the largest source of nutrients to the lake, but development of provincial management strategies has been hampered by lack of historical context for

recent eutrophication and an understanding of the relative influence of climate, crop production, and animal husbandry practices (D. Williamson, MWS, pers. comm.). Consequently, we sought to quantify the statistical relationship between provincial land-use practices, climate, and water quality during the 20th century to better prioritize goals for lake remediation, even though we recognize that this approach will not account for nutrients influxes from headwater regions in southern and western portions of the catchment, or the unique effects of the City of Winnipeg. Fortunately, mass balance studies conducted within the Lake Winnipeg basin demonstrate that most nutrients from SK and AB are sequestered in intervening lakes and reservoirs prior to transmission to Lake Winnipeg (Leavitt et al. 2006; Finlay et al. 2010; B. Parker, Environment Canada, unpublished data), and that City of Winnipeg contributes 5-10% of TN and TP to the lake in most years. 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.

Climate records were obtained from Environment Canada weather stations located at Winnipeg St. Johns College (1900–1937) and Winnipeg Richardson International Airport (1938–2006). These records were blended without modification, as comparison of each with overlapping records from additional stations suggested that there was no measurable offset between sites for major meteorological time series. Potential climate predictors included monthly, seasonal, and annual total precipitation (mm; 1875–2006), annual rainfall (mm; 1875–2006), mean monthly and seasonal temperature (^{o}C; 1875–2006), and mean minimum and maximum temperatures on monthly, seasonal and annual scales (°C, 1875–2006). In addition, historical records of ice thaw and freeze for the Red

River at Winnipeg were used to estimate the regional ice-free season of the western Canadian plains 1900–1995, as described by Hall et al. (1999). Records of mean annual lake level (m a.s.l.) and discharge (m^3) from the 12 main tributary rivers and the sole outflow (Nelson River) were obtained from MWS.

Historical records of livestock populations, production, and associated agricultural products were obtained for MB from Census of Canada reports (Statistics Canada 1871–2006). Canadian census data have been variously available in MB at annual, 5-yr, and decadal intervals during the 20^{th} century. Consequently, annual estimates of all commercial livestock species density and production (e.g., beef cattle, dairy cattle, hogs, sheep, chickens, etc.) and their products (e.g., milk, fleece, eggs, etc.) were estimated for each year 1906–2006 by linear interpolation between census years (Appendix 1). Similarly, annual estimates of total, urban, and rural human populations were obtained for MB from Census of Canada reports (Statistics Canada 1871–2006) by linear interpolation among census data available at annual, 5-yr, or decadal intervals since 1871.

Crop production variables included a combination of areal estimates of diverse farming activities, fertilizer sales, and direct measurements of agricultural production. Historical records were obtained from Census of Canada reports (Statistics Canada 1871–2006) including number of farms (farms yr^{-1}), area (km^2) used for specific activities (e.g., cropland, pasture, summer-fallow), area seeded or planted with individual crop species (km^2), calendar day of year [DOY] of agricultural activities (seeding, heading, swathing, harvest) for major cultivars, and annual mass of products harvested for each crop (kg). In all cases, estimates of annual production were approximated by linear interpolation among census data collected at annual, 5- or 10-yr intervals since 1908. Annual fertilizer

sales (kg), farm expenditure on fertilizer and lime (CND$), and nutrient content (N, PO_4, K, potash) of purchased fertilizer (kg) were obtained from diverse sources, including Statistics Canada (1968–1977), fertilizer trade catalogues, the Canadian Fertilizer Institute, the Potash and Phosphate Institute (1978–2001), and Korol (2002). In general, chemical fertilizer use was limited prior to 1960.

Although too brief to be used in our statistical analysis, we also compiled annual records of limnological variables available for 1969 and 1992-2005 from MWS and FOC for concentrations (μg L^{-1}) of TP (1969, 1992–2005), TN (1992–2005), and Chl *a* (1992-2005). Similarly, annual records of commercial fish harvest from Lake Winnipeg (1883–2006) were obtained from MWS. However, although the lake supports a $20M commercial fishery, fish production and harvest were viewed, in part, as a response to eutrophication, rather than predictors of causal relationships, and were not included subsequent statistical analyses.

Numeric analyses – Constrained and partial canonical ordinations (ter Braak 1988) were used to evaluate the statistical relationships between fossil records of trophic status (pigments and stable isotopes; diatoms) and time series of explanatory variables related to climate (*C*), livestock (*L*), and crops (*A*). 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. In this procedure, 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). Separate VPA was conducted for indices of past lake trophic status (9 biomarker pigments, $\delta^{13}C$, $\delta^{15}N$, %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, USA).

VPA is most effective when there are similar numbers of predictors within explanatory categories and when predictors do not greatly outnumber response variables (Borcard et al. 1992; Hall et al. 1999). Consequently, several criteria were used to optimize predictor selection from the 191 candidate time series (Appendix 1). First, we eliminated time series less than 70 years in duration before interpolation because our objective was to identify the environmental factors best correlated with inter-decadal changes in lake production during the 20th century. Second, we used least-squares regression analysis of environmental time series within individual categories (e.g., *C*) to quantify the correlation among potential predictors. If two candidate time series were highly correlated, we eliminated a variable if we could assume its effect on mass flux (e.g., mass harvested, area cultivated) was 10-fold less than that of a well-correlated predictor (honeybees vs. hogs, minor specialty crops vs. wheat, etc.). Third, forward selection and Monte Carlo permutation testing was used separately for each category (*C*, *L*, *A*) within RDA to select the variables that explained significant (P <0.05) independent variation in fossil time series. Final predictors included six variables from livestock (total populations of cattle, hogs, horses, sheep, chickens + hens), crop (production of wheat,

oats, barley, canola, potatoes, corn), and climate categories (mean summer and winter temperature, summer and winter precipitation, ice-free period, Red River discharge). Although rural human population was also retained, we eliminated it from subsequent analyses because we were interested in the relative importance of individual human activities caused by elevated populations.

Explanatory and response variables were transformed and harmonized prior to multivariate analyses. First, all fossil time series were centered (mean = 0), standardized (variance = 1.0), and inspected for normal distribution, although no transformations were required. Because many explanatory variables were resolved more highly (annual) than the fossil time series (2.5-yr sample^{-1}, separated by 3-5 yr), all predictor time series were smoothed using a 3-year moving average, before being harmonized to fossil time series by sampling predictors at time intervals which matched those of the sedimentary records (17 intervals for pigments and isotopes, 19 for diatoms). In addition, all agricultural variables, most livestock predictors (except chickens + hens), and few climate variables (only Red River discharge) required $\log_{10}$ transformation to normalize variance.

Results

Sediment chronology – ^{210}Pb activity declined monotonically with depth in each of the Lake Winnipeg sediment cores (Fig. 2a), and 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 (± SE) rates of 50.0 ± 0.8, 64.6 ± 1.1, and 83.2 ± 0.9 mg cm^{-2} yr^{-1} for Cores 1, 2 and 3, respectively, although in each case mean 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. Mean SAR estimates were very similar to those obtained from previous studies (63.5–86.1 mg cm^{-2} yr^{-1}) of the south basin (Wilkinson and Simpson 2003).

Sedimentary geochemistry – Although the cores were taken from locations separated by ~35 km, they exhibited a high degree of similarity in elemental composition and stable isotope content throughout the past 200 years (Fig. 3). Consistent with the constant SAR, both N (~0.17% of dry mass) (Fig. 3b) and C contents (~1.5%) (Fig. 3c) were very 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 (~10:1) varied little either among cores or with burial depth and were characteristic of algal-derived material (data not shown). In contrast, δ^{15}N values increased linearly from background depleted levels (~4.5‰) ca. 1900 to an enriched maximum (~8.0‰) in surface sediments (Fig. 3a). Similarly, although δ^{13}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 from ca. 1800–1900, declined irregularly by ~1‰ until ca. 1990, then exhibited high temporal variability during the past 20 years, 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 essentially constant throughout the 19th century and increased by only 10-15% between ca. 1900 and the present day (Fig. 4a). In general, these increases reflected variation in NAI-P which accounted for ~45% TP content throughout the sediment record. NAI-P 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 concentrations (Fig. 4d) demonstrated little systematic variation through time, and accounted for ~30% and ~10% of TP content, with the exception of elevated EP content in surface sediments, and brief declines of AP in Core 1 (1 sample only) during the 1970s (Fig. 4b). Overall, residual 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 were relatively constant from ca. 1800–1900, 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), and chemically-stable indicators of total algal abundance (*β*-carotene, pheophytin *a*) (Fig. 5e), were constant throughout 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 exponentially in Core 1 sediments from baseline values between ca. 1800–1990 to 10-fold 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 cyanobacterial microfossil deposition ca. 1990 reflect either shading of other algae by positively buoyant N_2-fixing cyanobacteria, or a change in depositional processes as neutrally-buoyant phytoplankton are replaced by positively-buoyant diazotrophs (Bunting et al. 2007). Regardless, taken together, these patterns demonstrate that algal abundance increased ~three- to five-fold during the 20th century, with an ecosystem state change occurring ca. 1990. In contrast, ratios of labile to chemically-stable pigments (Chl *a* : pheophytin *a*) did not change with depth (not shown), indicating that preservation environments have 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 years (Fig. 6). Constrained cluster analysis of fossil valve concentrations identified three diatom zones in Core 1, including communities with low concentrations representing baseline conditions (Zone I, ca. 1800–1915), a period of slowly rising densities (Zone II, ca. 1915–1975), and an era of greatly increased diatom deposition (Zone III, ca. 1980-present). Although the same zones were also identified by cluster analysis of diatom relative (%) abundance (data not shown), there were only modest changes in species composition during the past 200

years. At all core intervals, mesotrophic *Aulacoseira islandica* (regional $TP_{optimum}$ = 15.4 μg P L^{-1}) accounted for 60-85% of sedimentary diatoms in Core 1 (Fig. 6), consistent with reports of its abundance in spring throughout the 20th century (Lowe 1923; Bajkov 1930, 1934; Kling 1998). Instead, transition from Zone I to II was marked by declines in abundance of eutrophic *Stephanodiscus niagarae* (TP_{opt} = 58.5) and mesotrophic *Aulacoseira subarctica* (O. Müller) Haworth (TP_{opt} = 21.5), coupled with modest increases in *A. islandica* and eutrophic *Stephanodiscus hantzschii* Grunow (TP_{opt} = 40.1). In contrast, the shift from Zone II to III revealed large increases in concentrations of several diatom taxa, including *A. islandica*, *Stephanodiscus minutulus* Håkansson (TP_{opt} = 41.7) and eutrophic *Stephanodiscus* spp. (*S. parvus* Stoermer and Håkansson, *S. hantzschia*), and the first occurrence of *Cyclostephanos* spp. (TP_{opt} = 33.3, 95.1). Interestingly, diatom-inferred TP concentrations did not vary substantially (range ~12 to ~20 μg P L^{-1}) during the past 200 years (Fig. 6), suggesting that while total diatom production increased through the 20th century (Figs. 5a, 6), factors other than nutrients regulated precise species composition (e.g., silica, light, turbulence, etc.). Consistent with this interpretation, total concentrations of diatom valves were correlated strongly (r^2 = 0.66, P<0.0001) with sedimentary concentrations of diatoxanthin, the pigment characteristic of diatoms.

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, $\delta^{13}C$, $\delta^{15}N$, 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 crops (66.5%) or livestock alone (62.0%) explained three-fold more variation in pigments and geochemistry (Fig. 7). Only cattle (correlated positively with hogs, negatively with horses) and chickens + hens (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 were retained in a RDA of fossils with crop predictors, although production of both these 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. Interestingly, multivariate analyses were unable to explain any significant (P <0.05) variation in past diatom community composition (% relative abundance) during 1904-1993, either in VPA or in RDA constrained uniquely to climate, crop, or livestock predictors.

Discussion

Analysis of highly resolved time series of sediment geochemistry and algal fossils demonstrated that southern Lake Winnipeg has undergone three phases of eutrophication since 1800. The first phase (ca. 1800-1900) includes baseline conditions prior to

eutrophication in which the south basin was mesotrophic (~15-20 μg 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. 5d), including diazotrophic *Aphanizomenon* and *Anabaena* spp. (Fig. 5f). Lake Winnipeg eutrophied during the second phase (ca. 1900–1990), 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 N_2-fixing cyanobacteria (Fig. 5). As in other prairie lakes (Hall et al. 1999; Leavitt et al. 2009), climatic variability during the 20th century had limited affect on water quality. Finally, during the third stage of eutrophication (ca. 1990-2006), southern Lake Winnipeg experienced a sudden persistent ecosystem state change (Scheffer et al. 2001; Scheffer and Carpenter 2003) defined by rising variance in biogeochemical cycles (Figs. 3, 4) and vernal algal populations (Fig. 5a, b; Fig. 6), a 50% reduction in pigments from summer-blooming algae (Fig. 5c-e), and a 10-fold increase in sedimentation of N_2-fixing cyanobacterial fossils (Fig. 5f). As described below, suppression of recent diazotrophic blooms will require a ~50% decline in nutrient influx (~500% to re-establish baseline conditions), while failure to reduce nutrients may result in a fourth phase of eutrophication in which toxic low-light adapted *Planktothrix* and *Microcystis* predominate such as seen in agricultural regions worldwide (Leavitt et al. 2006; Bunting et al. 2007; Xu et al. 2010).

Quantification of baseline conditions – Development of effective lake management strategies requires well defined scientific objectives for remediation of water quality. Unfortunately, due to its large size and relatively remote location (Fig. 1),

few limnological data exist prior to 1970 (Lowe 1924; Bajkov 1930, 1934; Brunskill 1973), and baseline conditions are unknown beyond preliminary analysis of fossil algae (Kling 1998) and phosphorus (Mayer et al. 2006) in poorly resolved cores. Here we demonstrate that the southern basin of Lake Winnipeg was naturally mesotrophic (TP = 15-20 μg TP L^{-1}) prior to intensification of European-style agriculture, with diatoms characteristic of regional eutrophic lakes (Cumming et al. 1995; Hall et al. 1999) (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 (Allan 1980; 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 (~0.6 mg P g^{-1} dry mass) (Fig. 4a) were similar to pre-agricultural values (0.8 $\pm$ 0.1 mg P g^{-1} dry mass) (Hall et al. 1999 and unpublished data) recorded in diverse lakes of the northern Great Plains (Allen et al. 1980; Triplett et al. 2009; Engstrom et al. 2009), other large shallow hardwater lakes (e.g., Lake Okeechobee) (Engstrom et al. 2006), and previous analysis of Lake Winnipeg sediments (Mayer et al. 2006). Second, fossil diatom communities were composed predominantly of taxa with inferred P requirements >15 μg TP L^{-1} (Fig. 6), such that abundance-weighted estimates of water-column P ranged 15-20 μg TP L^{-1} during the 19th century. Finally, 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 (Allen et al. 1980; Engstrom et al. 2009; Triplett et al. 2009). Unfortunately, the high proportion of biologically-unavailable P, combined with minimal temporal variability in P concentration (Fig. 4),

despite pronounced eutrophication (Fig. 5), suggest that historical changes in sedimentary P cannot be used to estimate baseline water-quality conditions within the lake.

Calculations based on combined analysis of total algal abundance (as fossil β-carotene) (Fig. 5e) and modern nutrient content suggest that baseline water-column concentrations of TP in the south basin ranged 15-20 μg TP L^{-1}, characteristic of other mesotrophic prairie lakes (Pham et al. 2008, 2009). Here we assumed that algal production during the 20th century was limited by the influx of P (Schindler 1977), that the relationship between algal density and P concentrations was consistent throughout 1800-1992, and that variations in fossil β-carotene concentrations were correlated linearly to changes in total algal abundance (Cuddington et al. 1999; Leavitt and Hodgson 2001). Therefore, given that mean ($\pm$ SD) water-column TP in the south basin was 80 $\pm$ 15 μg P L^{-1} during 1992-1996 (MWS unpublished data), and that sedimentary β-carotene concentrations in the three cores were between 4.33 $\pm$ 1.10 and 5.53 $\pm$ 1.74 -fold greater during the early 1990s than before 1900 (depending on whether mean [1960-1992] or maximum pigment concentrations were used), we estimate that the south basin contained 14.5 – 18.5 μg TP L^{-1} prior to eutrophication. These values agree well with the range inferred from analysis of fossil diatoms (Fig. 6; but *see* caveats below) and unpublished hydrological simulations of nutrient export (G. McCullough, R. Hesslein, FOC, unpublished data), and demonstrate that Lake Winnipeg should be managed for mesotrophic rather than oligotrophic conditions.

Mechanisms causing water-quality change during the 20th century – Water quality in the south basin of Lake Winnipeg was degraded substantially during the 20th century

(Fig. 5), largely due to the combined effects of crop and livestock production, but not climate change (Fig. 7). Specifically, abundance of all algal groups except diazotrophic cyanobacteria increased 300-500% (Fig. 5), δ^{15}N values increased 3-4 ‰ due to influx of enriched N (Fig. 3a) (Anderson and Cabana 2005; vander Zanden et al. 2005; Bunting et al. 2007), and δ^{13}C declined 1-2‰ consistent with increased primary production and reliance on respired CO_2 (Leavitt et al. 2006; Bunting et al. 2007). VPA explained almost 75% of historical variation in indices of lake trophic status (pigments, isotopes, %C, %N) between ca. 1900-1992 due to increased production of cattle, hogs, chicken, and major crop cultivars (canola, potatoes, wheat, etc.), while the unique effects of climate and its first-order interactions with crop and livestock production (*C*, *C*× *L*, *C*× A) explained a non-significant (P >0.15) fraction (4.1%) of historical change (Fig. 7). Such weak effects of pronounced warming (~3^{o}C increase, ~35 day decline in ice cover) have been documented for other lakes within the Lake Winnipeg catchment (Leavitt et al. 2009), 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).

Intensification of nutrient fluxes due to widespread crop production and animal husbandry is now the most significant mechanism causing eutrophication of fresh and coastal waters (Carpenter et al. 1998; Smith 2003). For example, grains such as wheat (~1×10^9 kg yr^{-1} in 1910s) and barley (0.3-0.5$\times10^9$ kg yr^{-1} in 1910s) have dominated production since regional farming began (Honey and Oleson 2006), but their harvest increased dramatically following World War II (WWII; 1939-1945), reaching 5×10^9 kg

yr^{-1} and 2×10^9 kg yr^{-1}, respectively, during the 1980s (Statistics Canada 1871-2006). Similarly, irrigation-intensive potato production increased linearly from stable values of ~0.1×10^9 kg yr^{-1} 1900-1950 to modern harvests >1×10^9 kg yr^{-1} (Statistics Canada 1871-2006) due to increased demand for processed food (Honey and Oleson 2006). Although canola was introduced after 1945, this crop 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 (~25% of Canadian canola crop). Interestingly, 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 (Fig. 3-6), because lake production was inversely correlated with horse density in VPA (horses were replaced by tractors), and because 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).

Degradation of water quality by livestock production arises most commonly when animal densities greatly exceed that of humans, and mass imbalances occur between nutrient importation to sustain forage and other crops and their 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, cattle populations were ~0.75×10^6 until ca. 1950, increased to ~1.5×10^6 by 1975, declined for 20 yr, and then peaked at ~1.75×10^6 in the 2000s (Statistics Canada 1906-2006). Similarly, MB hog populations were <0.75×10^6 until ~1980, after which

time densities increased exponentially to ~3×10^6 head by 2005. Interestingly, chicken and hen populations varied between 6- and 8×10^6 since the mid 1940s, after having increased rapidly during the early 20th century (Statistics Canada 1906-2006). Taken together, we find that MB biomass for these three species alone is ~12-fold greater than that of humans (~60 kg ind^{-1}), assuming market weights for chickens (2 kg ind^{-1}), hogs (112 kg ind^{-1}), and cattle (317 kg ind^{-1}). Given that Winnipeg (pop. 742,000) accounts for 5-10% of nutrient influx to Lake Winnipeg (Table 2), 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).

Strongly enriched (3-4‰) sedimentary $\delta^{15}N$ values recorded after 1900 are consistent with increased influx of N from agricultural (Anderson and Cabana 2005; vander Zanden et al. 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, 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. unpublished data), four cores from adjoining Lake Manitoba (Leavitt et al. unpublished data), and six other lakes within the catchment (Leavitt et al. 2007), all sites which receive substantial agricultural N, but not direct urban N. As reviewed elsewhere (Savage et al. 2004; Leavitt et al. 2007), 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 this interpretation, changes in fossil $\delta^{15}N$ were correlated more highly with growth of

Winnipeg's population during the 20th century (r^2 = 0.82, P <0.0001) than with changes in either MB cattle (r^2 = 0.74, P <0.0001) or hog populations (r^2 = 0.52, 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* (E*m*) flux framework (Leavitt et al. 2009) and empirical observations from more than 20 agriculturally-impacted lakes within the Canadian Prairies (Hall et al. 1999; Pham et al. 2008; Dröscher et al. 2009; Leavitt et al. 2009). Regional fall, winter, and spring mean and minimum temperatures have increased ~3°C since the late 1800s (Statistics Canada 1897-2006), leading to ~35 day 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 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 (MWS unpublished data) and was retained in the VPA (Fig. 7), there was no sustained interdecadal increase in hydrologic influx until 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 *m* influx to lakes by >10-fold whenever land-use practices prevent re-establishment of natural vegetation (reviewed in Dearing and Jones 2003).

Our statistical approach was unable to clearly isolate the unique effects of crop and livestock production on water quality degradation during the 20th century (Fig. 7),

mainly because of residual co-linearity among predictors following selection of environmental time series (*see* Methods). Additionally, cumulative explained variance (~75%) was lower than that recorded in VPA of other lakes in the catchment (87-97%) using identical protocols (Hall et al. 1999; Leavitt et al. 2009), likely because we did not include urban (~5-10% TP and TN) or US nutrient sources (~34% TP, 21% TN) (Table 2). Similarly, we were unable to partition the unique effects of N and P pollution as has been done in coastal marine systems (Savage et al. 2010), because TN has been rarely monitored and because TN in regional lakes includes a high proportion ($\geq$70%) of dissolved organic N of uncertain biological availability (Patoine et al. 2006; Leavitt et al. 2006; Bunting et al. 2010). High colinearity among sedimentary variables also prevented us from quantifying the unique effects of N and P on southern Lake Winnipeg using fossil time series, even though historical changes in total algal abundance (as β-carotene) were correlated strongly with sedimentary concentrations of P ($r^2 = 0.47 \pm 0.25$, $P < 0.02$), %N ($r^2 = 0.81 \pm 0.08$, $P < 0.0001$), and δ^{15}N values ($r^2 = 0.72 \pm 0.16$, $P < 0.0001$) in all three cores (1901-1992). Finally, the lack of historical variation in diatoms species composition prevented VPA of relative abundance data, and complicated interpretations of diatom-inferred TP concentrations (Fig. 6). Despite these caveats, the observation that changes in MB crop (wheat, canola, potatoes) and livestock production (cattle, hogs, chicken + hens) explained ~75% of variation in south basin production 1901-1992 allows regulatory agencies to develop more effective management strategies, as outlined below.

Ecosystem State Change – Nearly a century of eutrophication combined with rapid agricultural development during the past ~30 years appears to have initiated an

ecosystem state change ca. 1990 (Scheffer et al. 2001; Scheffer and Carpenter 2003), from diverse productive algal communities to modern assemblages composed mainly of buoyant diazotrophic *Aphanizomenon* and *Anabaena* spp. (Fig. 5) (Kling 1998). As predicted from theory (Cottingham et al. 2000; Carpenter 2003; Carpenter and Brock 2006), state change was also marked by elevated temporal variation in many lake characteristics, including production and deposition of diatoms (Fig. 5a, Fig. 6), cryptophytes (Fig. 5b), and summer bloom-forming algae (Figs 5c-d), carbon cycling (Fig. 3c), and relative composition of sedimentary P fractions (Fig. 4). At present, it is unclear whether the 50% decline in concentrations of ubiquitous fossil pigments (*β*-carotene, pheophytin *a*) after 1990 (Fig. 5e) reflects a true reduction in algal abundance due to shading by floating cyanobacteria (McGowan et al. 2005; Bunting et al. 2007), lateral transfer of these algae to lakeshores (LWIC 2006), or increased pigment degradation due to slower sinking of buoyant taxa (Cuddington et al. 1999; Leavitt and Hodgson 2001). Regardless, we inter that southern Lake Winnipeg has undergone a state change due to a persistent change in external forcing (Leavitt et al. 2009), rather than a transition between alternative stable states (Scheffer et al. 2001; Scheffer and Carpenter 2003; Carpenter 2005), because the south basin's polymictic status and poor light penetration (Z_{secchi} <1 m, Z_{mean} 9.7 m) prevent many internal mechanisms (internal nutrient loading, macrophytes, stratification, benthic algal production) (Fig. 6) needed to stabilize alternative states (Scheffer and Carpenter 2003). This distinction is important for managers because stabilizing feedback mechanisms associated with alternative stable states can substantially delay lake response to declines in external nutrient influx (Scheffer et al. 2001; Scheffer and Carpenter 2003).

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. Specifically, Canadian agricultural policies were modified in the 1980s and 1990s to comply with World Trade Organization, Canada-US, and North American Free Trade agreements and to increase exports (hogs, oilseeds, grains), deregulate transportation (railways), induce foreign investment, reduce governmental subsidies, and eliminate price controls, among other activities (Venema 2006). In particular, the National Farmers Union notes that modification (1984) and elimination (1996) of long-standing (since 1897) rail transportation subsidies (Crows Nest Pass Agreement, Western Grain Transportation Act) increased grain transportation costs more than three-fold, particularly for MB farmers 1500 km distant from coastal grain shipping ports (Novek 2003). Concomitantly, international prices for grains declined, the federal Gross Revenue Insurance Plan for farmers was eliminated (Bradshaw et al. 2004), and world pork demand tripled (Agriculture and Agri-Food Canada 1997; Novek 2003; Venema 2006).

Manitoba government sought to offset resultant 40% declines in agricultural revenues and promoted 'the Manitoba advantage' (low feed-grain costs, intensive forage cultivation, 5.4×10^6 ha for waste assimilation, pro-business attitude) to both regional farmers and international hog producers facing severe environmental and regulatory constraints (e.g., North Carolina, Denmark, Netherlands, Taiwan) (Martin et al. 1999; Novek 2003; MB Agriculture and Food 2010). As a result, hog number increased five-

fold and operations intensified (~350% fewer farms, 8-fold increase in areal animal densities) during 1981-2000 (Schnaiberg and Gould 1994; Novek 2003; Venema 2006) while fodder corn production increased from 0.1 $\times 10^9$ kg yr^{-1} to ~1.2 $\times 10^9$ kg yr^{-1} (Statistics Canada 1871-2006). Between 1990 and 2010, agricultural diversification also increased annual harvest of canola and potatoes by ~2.5 $\times 10^9$ kg (500%) and ~0.7 $\times 10^9$ kg (275%), respectively, whereas production of other major grains declined slightly (wheat, barley, mixed grains, corn) or changed little (oats) relative to previous production (Statistics Canada 1871-2006). Such sudden increases in crop and livestock production increased nutrient runoff in southern MB, as recorded by elevated nutrient concentrations in all tributary rivers (Jones and Armstrong 2001), ~20% increases in water column concentrations of N and P (MWS unpublished data), and a decline in water column TN : TP ratios from ~8.5 to 6.3 since 1990 (MWS unpublished data).

Scientific and management implications – Sedimentary analyses provide a unique opportunity to improve scientifically-based strategies for lake remediation. By assuming Lake Winnipeg has been regulated mainly by the influx of P prior to regime shift ca. 1990, we propose that modern TP content in the south basin (~100 μg P L^{-1}) must be reduced ~five-fold to return the basin to mesotrophic conditions characteristic of the pre-agricultural era (~15-20 μg P L^{-1}). These targets are consistent with the P optimum of the predominant (60-80% of valves) diatom taxon, *Aulacoseira islandica* (~15.4 μg P L^{-1}), determined using a survey of >100 regional lakes, although we caution that factors other than nutrient influx (e.g., physical mixing, Si, light, etc.) appear to be regulating diatom species composition in the south basin (Fig. 6). Similarly, we recommend that modern

TP concentrations be reduced to ~50 μg P L^{-1} (50% decrease) to suppress current outbreaks of diazotrophic cyanobacteria and reduce the present surplus of water column SRP (~50% of TP), yet allow for the high interannual variability in river discharge which regulates nutrient influx to the lake. We infer that the lake will not show hysteresis in response to nutrient reduction because the recent state change appears to lack most internal mechanisms that would stabilize a turbid, cyanobacteria-rich state (e.g., anoxia, internal nutrient loading, bioavailable sedimentary P) (Fig. 4). Further, we believe that these thresholds (50%, 500% reductions) will also apply to the north basin of Lake Winnipeg, despite ~50% lower ambient TN and TP concentrations (MWS unpublished data), as most of the nutrients enter that site from the south basin.

Finally, we caution that failure to immediately reduce P influx may initiate a final transition in lake state from buoyant N_2-fixing *Aphanizomenon* and *Anabaena* to potentially toxic, but low-light adapted cyanobacteria (*Planktothrix*, *Microcystis*, *Cylindrospermopsis*) due to continued pollution with N, as has occurred in the Canadian Prairies (Patoine et al. 2006; Leavitt et al. 2007), Europe (Scheffer et al. 1990; Bunting et al. 2007), China (Paerl and Scott 2010; Xu et al. 2010), and elsewhere. These turbid polymictic lakes usually lie in catchments with P-rich soils due to natural geology or prolonged agriculture (Carpenter 2005), accumulate >50 μg P L^{-1} as bioavailable SRP during summer despite greatly elevated cyanobacterial biomass, and exhibit highly significant correlations (r^2 >0.7) between total algal biomass and N influx, but not P supply, in long-term (>20 yr) monitoring studies (e.g., Bunting et al. 2007). In addition, several of these sites have paleolimnological time series which demonstrate that diazotrophic cyanobacteria are replaced within decades by potentially toxic cyanobacteria

due to continued pollution of P-rich systems with N (Leavitt et al. 2006; Bunting et al. 2007). As demonstrated by three years of month-long, large-scale (>3000 L) mesocosm experiments, pollution of P-rich polymictic lakes with reduced N (urea, NH_3) can suppress N_2-fixing *Aphanizomonen* and *Anabaena* but increase total biomass and toxicity of *Microcystis* and *Planktothrix* by up to 400% when lakes have >50 μg SRP L^{-1} and dissolved N : P <20 : 1 (Finlay et al. 2010). Unfortunately, monitoring since 1992 demonstrates that southern Lake Winnipeg now exhibits these same characteristics, suggesting that the lake is already subject to damage by N pollution and that there may be substantial benefits to reducing both N and P influx (Paerl and Scott 2010).

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Table 1. Physical characteristics of Lake Winnipeg, modified from Brunskill et al. (1980).

	North Basin	Narrows	South Basin	Entire Lake
Latitude (^{o}N)				50^{o}00'-53^{o}50'
Longitude (^{o}W)				96^{o}15'-99^{o}15'
Surface area, A_0 (km^2)	17520	3450	2780	23750
Volume (km^3)	232.4	24.6	27.0	284
Mean depth (m)	13.3	7.2	9.7	12.0
Maximum depth (m)	19.0	61.0	14.0	36.0
Maximum length (m)	232	143	93	436
Maximum breadth (m)	111	30	46	111
Shoreline (km)	761	640	349	1750
Shoreline/ A_0	0.043	0.19	0.13	0.074
Development of Shoreline	1.6	3.1	1.9	3.2
Development of Volume	2.1	0.6	2.1	1.0
Mean depth/Maximum depth	0.70	0.20	0.69	0.33
Relative depth (%)	0.013	0.054	0.024	0.021
Mean hydraulic residence (yr)			0.57	3.28

Table 2. Estimated mean annual total phosphorus (TP) and nitrogen (TN) influx to Lake Winnipeg 1994–2001 (tonnes yr^{-1} rounded to nearest 100 tonnes) (Bourne et al. 2002, MWS unpublished data). Natural background and undefined sources include influx from forests, wildlife, and septic fields. Internal processes include gross N_2 fixation only, not denitrification (L. Hendzel, Fisheries and Oceans Canada, unpublished data). SK = Saskatchewan, MB = Manitoba, ON = Ontario.

Category	TP	%TP (%MB sources)	TN	%TN (% MB sources)
Upstream jurisdictions	*4,200*	*53*	*48,900*	*51*
US (Red R)	2,500	32	19,000	20
US (Souris R)	200	3	1,100	1
SK and AB (Assiniboine and Saskatchewan R)	400	5	8,300	9
ON (Winnipeg R)	800	10	16,800	17
ON (Other R)	300	3	3,700	4
MB Sources	*3,700*	*47*	*47,100*	*49*
MB Point Sources	700	9 (19)	5,100	5 (11)
City of Winnipeg	400	5 (11)	3,700	4 (8)
Other wastewater sources)	300	4 (8)	1,400	1 (3)
MB Watershed Processes	2500	32 (67)	23,200	24 (49)
Natural background and undefined sources	1,300	17 (35)	18,100	19 (38)
Present agriculture	1,200	15 (32)	5,100	5 (11)
Atmospheric deposition	500	6 (14)	9,500	10 (20)
Internal lake processes	n/a	n/a	9,300	10 (20)
Total annual load	*7,900*	*100*	*96,000*	*100*

Figure Legends

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 cores within south basin of Lake Winnipeg in upper right inset. *See* Site Description for land use, soil, and hydrological details.

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).

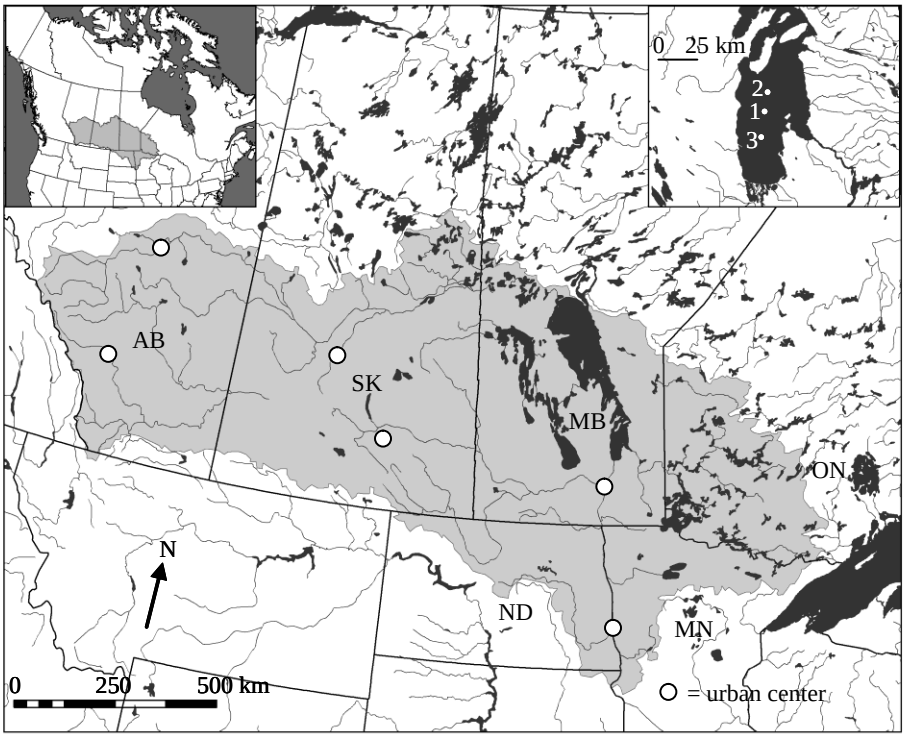
Fig. 3. Time series of whole-sediment (a) nitrogen (N) isotopes (δ^{15}N, ‰), (b) N content (% dry mass), (c) carbon (C) isotopes (δ^{13}C, ‰), and (d) C content (% dry mass) during 1800-2010 for three sediment cores from southern Lake Winnipeg. Symbols and lines as in Fig. 2.

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) non-apatite inorganic P extracted by NaOH, (d) exchangeable inorganic P extracted by NH_4Cl, and (e) residual or organic P during 1800-2010 for sediment cores (as Fig. 2) from southern Lake Winnipeg.

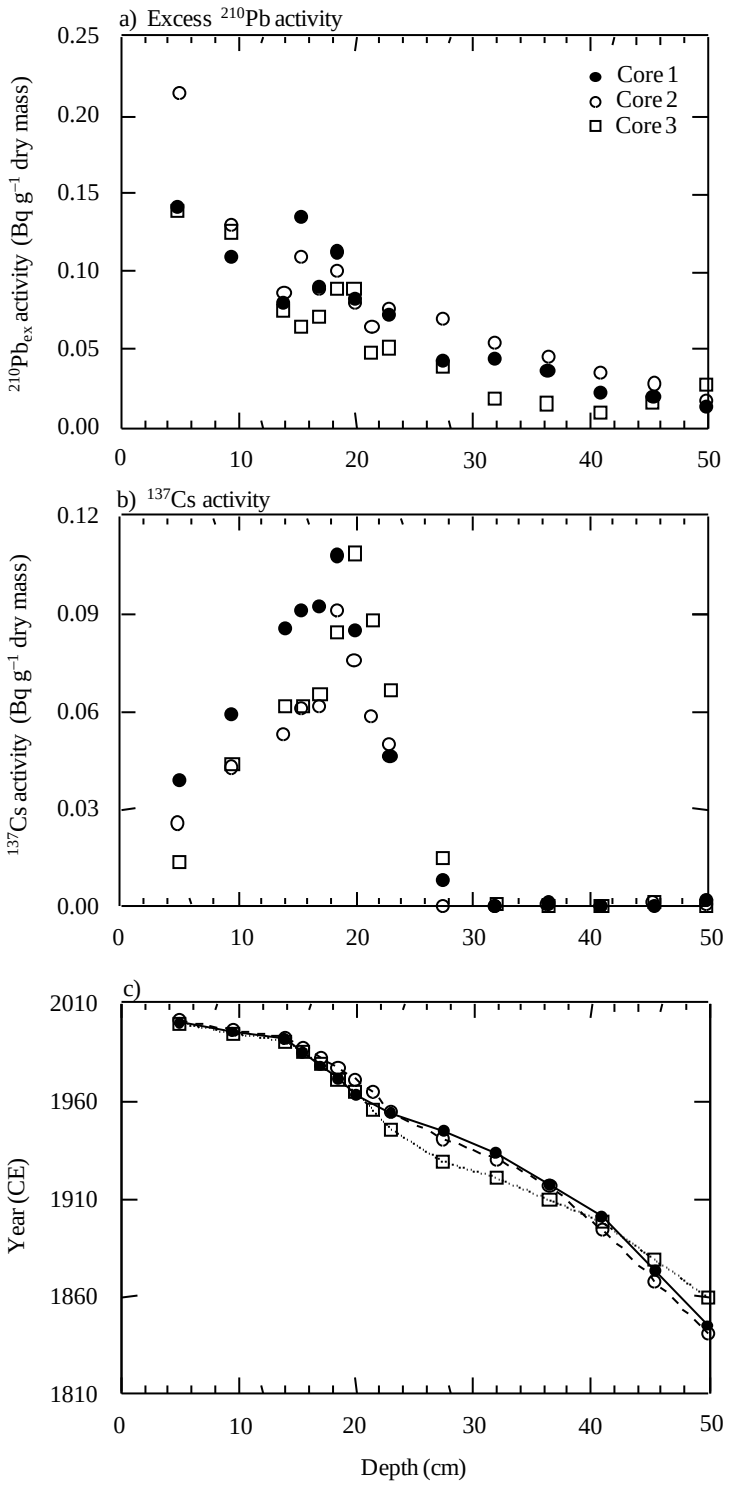
Fig. 5. Time series of fossil pigment concentrations (a-e) (nmol pigment g^{-1} sediment C) and (f) cyanobacterial akinetes (microfossils g^{-1} dry mass) during 1800-2010 for three cores from southern Lake Winnipeg. Core identities as Fig. 2. Pigment include (a) diatoxanthin mainly from diatoms, (b) 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* (black histograms, 10^5 scale) and *Aphanizomenon* (grey histograms, 10^4 scale).

Fig. 6. Time series of concentrations of valves from fossil diatom species in Core 1 during 1800-2010. All fossil concentrations are valves x 10^5 g^{-1} dry mass, except *Aulacoseira islandica* and total diatom abundance (valves 10^6 g^{-1} dry mass). Uppermost two panels include results of cluster analysis of diatom species and estimates of total water column phosphorus concentration (μg TP L^{-1}) estimated for the south basin from weighted average regression analysis of relative (%) diatom species composition.

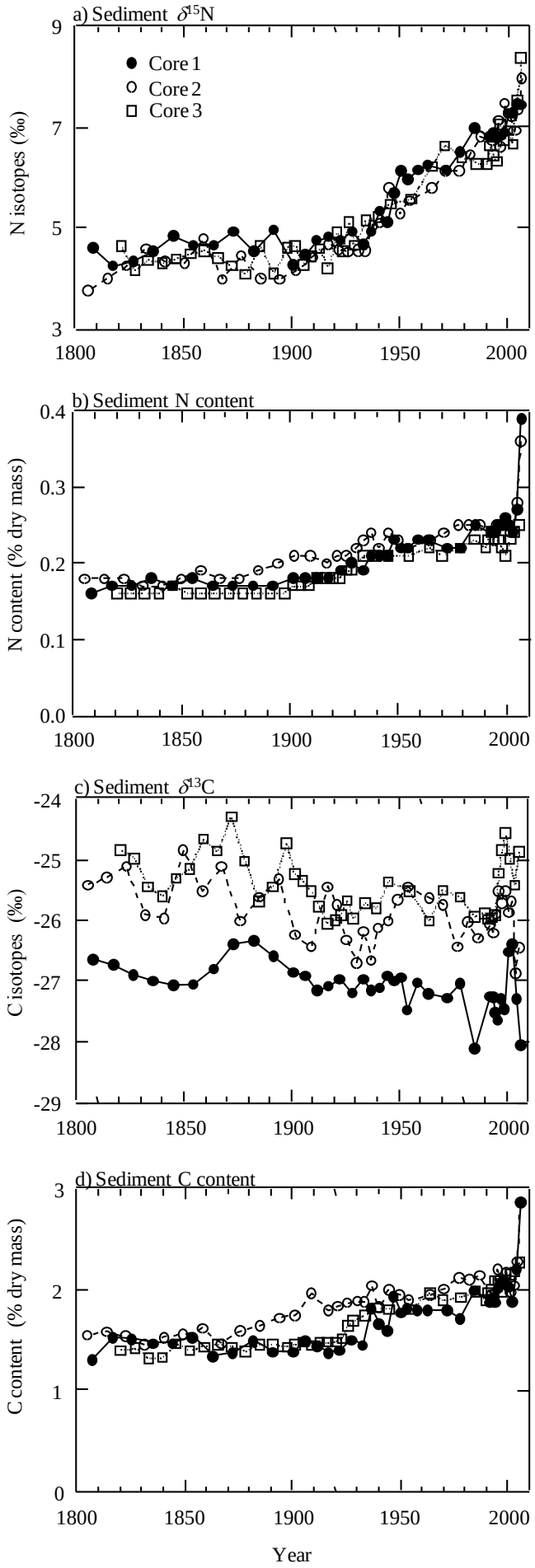
Fig. 7. Percent variation in fossil pigment concentrations (as in Fig. 5), C and N isotopes (‰), and C and N content (%) in sediments of Core 1 during 1901-1992 explained by redundancy (RDA) analysis of (a) climate variables alone (white histogram), (b) livestock variables alone (grey histogram), or (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 both $C \times L$ and $A \times C$ interactions explained <0.3% of historical variation in lake production parameters.



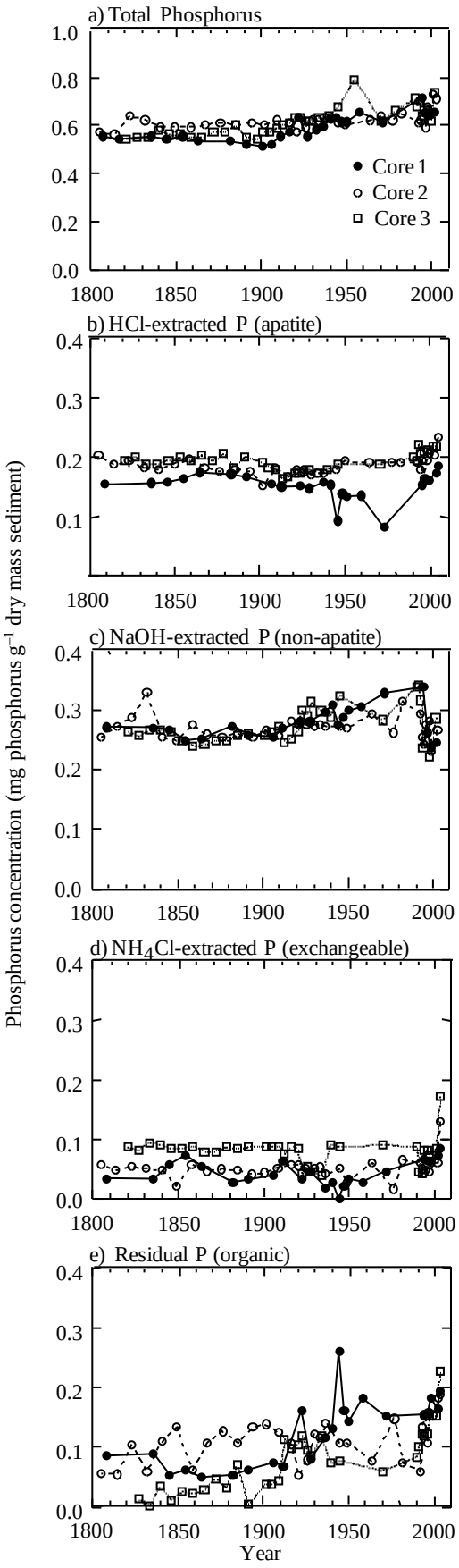
Bunting et al. Fig. 1



Bunting et al. Fig. 2



Bunting et al. Fig. 3



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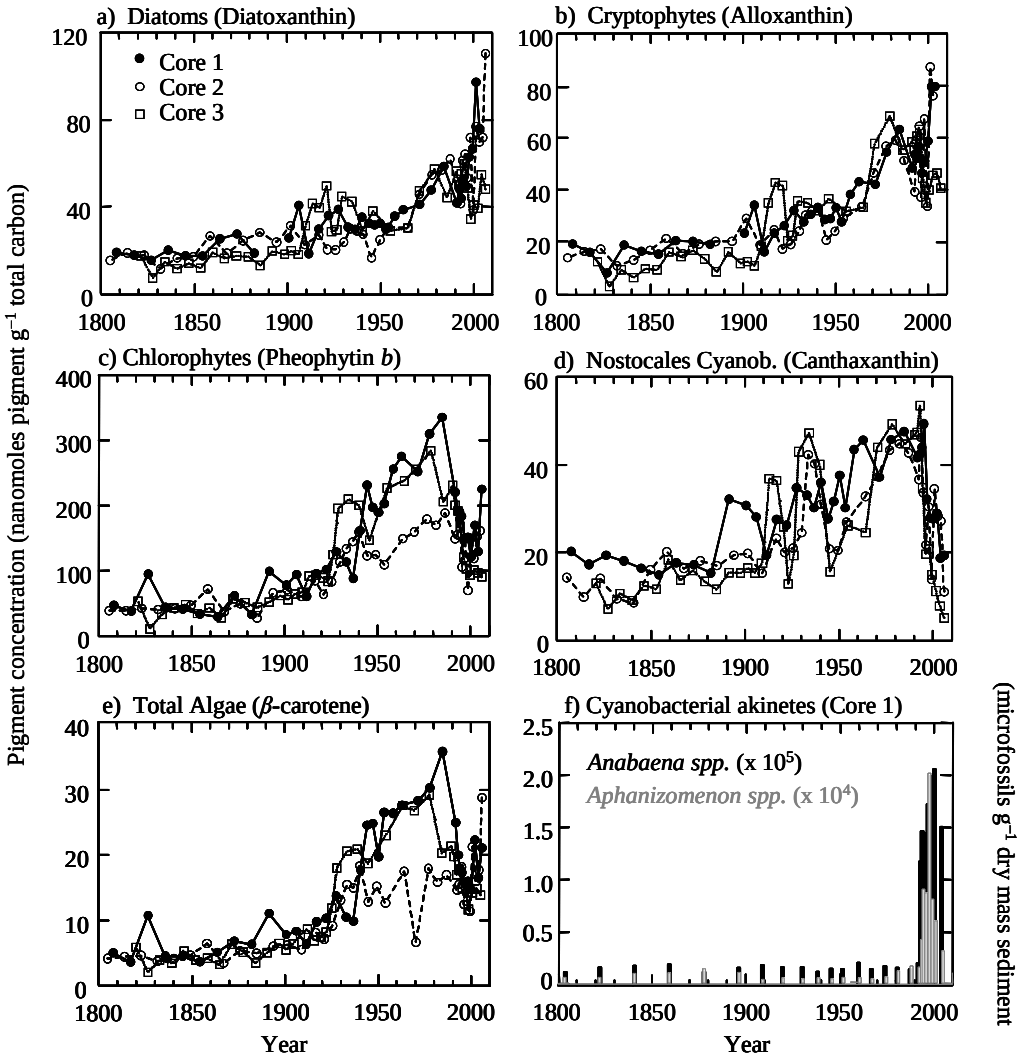

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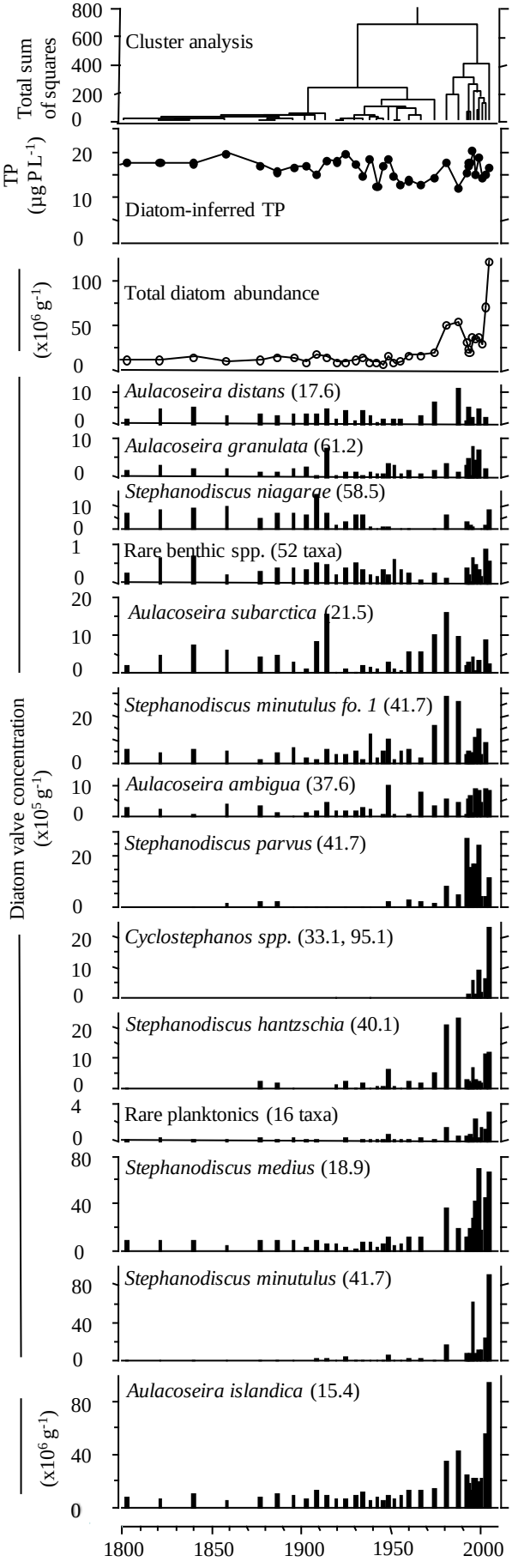

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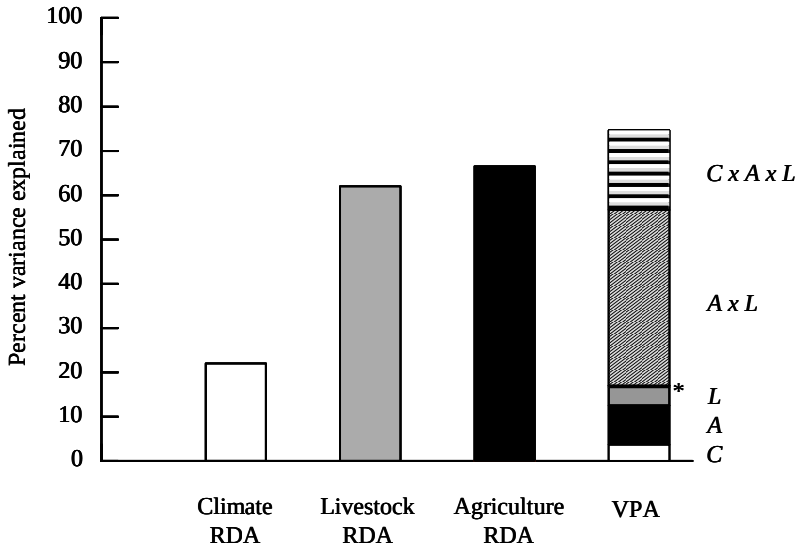

Bunting et al. Fig. 7

Appendix 1. Explanatory variables included initially in variance partitioning analysis (VPA). Variables are grouped into climate, livestock, and crops for VPA. Limnological variables provided by Manitoba Water Stewardship are listed separately. N = Number of variables within category; DOY–calendar day of year. Year of time series start and end are indicated for each variable.

Variable name	*N*	Start	End
Climate			
Monthly precip., mm	12	1875	2006
Seasonal precip., mm	4	1875	2006
Annual precip., mm	1	1875	2006
Annual rainfall, mm	1	1875	2006
Mean monthly max temperature, °C	12	1875	2006
Mean seasonal max temperature, °C	4	1875	2006
Mean monthly min temperature, °C	12	1875	2006
Mean seasonal min temperature, °C	4	1875	2006
Mean monthly temperature, °C	12	1875	2006
Mean seasonal temperature, °C	4	1875	2006
Mean annual temperature, °C	1	1875	2006
Ice breakup date, Red River at Winnipeg, DOY	1	1870	1995
Ice freeze-up data, Red River at Winnipeg, DOY	1	1870	1981
Ice-free season, Red River at Winnipeg, No. days	1	1870	1981
Annual flow, Black River, cm	1	1960	1992
Annual flow, Fisher River, cm	1	1961	2006
Annual flow, Pigeon River, cm	1	1957	1996
Annual flow, Berens River, cm	1	1980	1998
Annual flow, Icelandic River, cm	1	1958	2006
Annual flow, Bloodvein River, cm	1	1976	2006
Annual flow, Poplar River, cm	1	1968	1996
Annual flow, Manigotogan River, cm	1	1913	1996
Annual flow, Red River, cm	1	1882	2006
Annual flow, Winnipeg River, cm	1	1907	2006
Annual flow, Saskatchewan River, cm	1	1912	2006
Annual flow, Dauphin River, cm	1	1977	2006
Annual flow, Nelson River East, cm	1	1972	2006
Annual flow, Nelson River West, cm	1	1972	2006
Annual flow, Nelson River East and West, cm	1	1972	2006
Annual total inflow, cm	1	1980	1992
Annual lake level, m	1	1914	2006
Mean monthly lake level, m	1	1914	2006
Mean seasonal lake level, m	1	1914	2006

Livestock and Humans

Annual commercial fish harvest, kg	1	1883	2006
Annual cattle pop., No.	1	1921	2006
Annual bull pop., No.	1	1931	2006
Annual dairy cattle pop., No.	1	1931	2006
Annual beef cattle pop., No.	1	1931	2006
Annual heifer pop., No.	1	1931	2006
Annual steers pop., No.	1	1931	2006
Annual calves pop., No.	1	1931	2006
Annual hog pop., No.	1	1921	2006
Annual horse pop., No.	1	1906	2006
Annual sheep pop., No.	1	1906	2006
Annual chicken pop., No.	1	1916	2006
Annual turkey pop., No.	1	1916	1982
Annual duck pop., No.	1	1916	1972
Annual geese pop., No.	1	1916	1972
Annual bee colonies., No.	1	1924	2006
Annual milk prod., kg	1	1920	1977
Annual shorn fleece wool, kg	1	1920	1993
Annual honey prod., kg	1	1924	2006
Annual MB pop., No.	1	1871	2006
Annual City of Winnipeg, MB pop., No.	1	1871	2006
Annual City of Brandon, MB pop., No.	1	1871	2006

Crops

Annual fertilizer sales, kg	1	1945	2002
Annual fertilizer and lime sales, $	1	1968	2001
Annual fertilizer sales, $	1	1926	1970
Annual fertilizer sales, 1992 constant $	1	1971	2006
Annual chemical product sales, 1992 constant $	1	1971	2006
Annual N content in fertilizer sold, kg	1	1950	2002
Annual PO_4 content in fertilizer sold, kg	1	1950	2002
Annual potash content in fertilizer sold, kg	1	1968	2002
Annual nutrient (N+P+K) content in fertilizer sold, kg	1	1968	2002
Annual farm, No.	1	1921	2006
Annual agricultural land area, km^2	1	1921	2006
Annual pasture area, km^2	1	1951	1992
Annual cropland area, km^2	1	1921	2006
Annual summerfallow area, km^2	1	1913	2006
Annual seeded all wheat area, km^2	1	1908	2006
Annual seeded spring wheat area, km^2	1	1908	2006
Annual seeded durum wheat area, km^2	1	1941	2006
Annual seeded oat area, km^2	1	1908	2006
Annual seeded barley area, km^2	1	1908	2006
Annual seeded all rye area, km^2	1	1908	2006
Annual seeded spring rye area, km^2	1	1923	2006
Annual seeded fall rye area, km^2	1	1923	2006

Annual seeded mixed grain area, km^2	1	1910	2006
Annual seeded corn for grain area, km^2	1	1941	2006
Annual seeded buckwheat area, km^2	1	1925	2006
Annual seeded dry field pea area, km^2	1	1908	2006
Annual seeded flaxseed area, km^2	1	1908	2006
Annual seeded mustard seed area, km^2	1	1952	2004
Annual seeded sunflower area, km^2	1	1943	2006
Annual seeded canola area, km^2	1	1943	2006
Annual seeded tame hay area, km^2	1	1908	2006
Annual seeded sugarbeet area, km^2	1	1940	1998
Annual seeded fodder corn area, km^2	1	1910	2006
Annual seeded potato area, km^2	1	1908	2006
Annual seeded field root area, km^2	1	1908	1940
Annual planted tomato area, km^2	1	1940	2006
Annual planted cucumber area, km^2	1	1940	2006
Annual planted lettuce area, km^2	1	1940	2001
Annual planted dry onion area, km^2	1	1940	2006
Annual planted asparagus area, km^2	1	1940	2006
Annual planted celery area, km^2	1	1940	1996
Annual planted beans area, km^2	1	1940	2006
Annual planted fresh corn area, km^2	1	1940	2006
Annual planted cabbage area, km^2	1	1940	2006
Annual planted cauliflower area, km^2	1	1940	2006
Annual planted carrot area, km^2	1	1940	2006
Annual planted parsnip area, km^2	1	1940	1996
Annual planted beet area, km^2	1	1940	2006
Annual planted rutabaga and turnip area, km^2	1	1940	2006
Spring wheat seeding is general (DOY)	1	1952	1991
Spring wheat heading is general (DOY)	1	1952	1990
Spring wheat swathing is started (DOY)	1	1952	1990
Spring wheat swathing is general (DOY)	1	1952	1989
Spring wheat swathing is completed (DOY)	1	1952	1990
Spring wheat combining is started (DOY)	1	1952	1990
Spring wheat combining is general (DOY)	1	1952	1989
Spring wheat combining is completed (DOY)	1	1952	1990
Annual tame hay prod., kg	1	1908	2006
Annual all wheat prod., kg	1	1908	2006
Annual spring wheat prod., kg	1	1908	2006
Annual durum wheat prod., kg	1	1941	2006
Annual buckwheat prod., kg	1	1925	2006
Annual oat prod., kg	1	1908	2006
Annual all rye prod., kg	1	1908	2006
Annual spring rye prod., kg	1	1923	2006
Annual fall rye prod., kg	1	1923	2006
Annual barley prod., kg	1	1908	2006
Annual mixed grain prod., kg	1	1910	2006
Annual canola prod., kg	1	1943	2006
Annual flaxseed prod., kg	1	1908	2006
Annual mustard seed prod., kg	1	1952	2004
Annual sunflower seed prod., kg	1	1943	2006
Annual potato prod., kg	1	1908	2006

Annual carrot prod., kg	1	1940	2006
Annual parsnip prod., kg	1	1940	1996
Annual cauliflower prod., kg	1	1940	1996
Annual cabbage prod., kg	1	1940	2006
Annual beet prod., kg	1	1940	2000
Annual sugarbeet prod., kg	1	1940	1996
Annual rutabaga and turnip prod., kg	1	1940	1995
Annual field root prod., kg	1	1908	1940
Annual asparagus prod., kg	1	1940	2002
Annual cucumber prod., kg	1	1940	2006
Annual lettuce prod., kg	1	1940	2001
Annual tomato prod., kg	1	1940	2006
Annual celery prod., kg	1	1940	1996
Annual dry onion prod., kg	1	1940	2006
Annual corn for grain prod., kg	1	1941	2006
Annual fodder corn prod., kg	1	1910	2006
Annual dry field pea prod., kg	1	1908	2006
Annual fresh corn prod., kg	1	1940	2006
Annual soy bean prod., kg	1	1956	2006

Limnology

Annual Red River mean TN, mg L^{-1}	1	1974	2006
Annual Red River mean TP, mg L^{-1}	1	1970	2006
Annual Winnipeg River mean TN, mg L^{-1}	1	1978	2006
Annual Winnipeg River mean TP, mg L^{-1}	1	1978	2006
Annual Saskatchewan River mean TN, mg L^{-1}	1	1970	2006
Annual Saskatchewan River mean TP, mg L^{-1}	1	1970	2006
Annual Dauphin River mean TN, mg L^{-1}	1	1978	2006
Annual Dauphin River mean TP, mg L^{-1}	1	1978	2006
Annual Nelson River East mean TN, mg L^{-1}	1	1972	2006
Annual Nelson River East mean TP, mg L^{-1}	1	1972	2006
Annual South Basin L. Winnipeg mean TN, mg L^{-1}	1	1992	2005
Annual South Basin L. Winnipeg mean TP, mg L^{-1}	1	1992	2005
Annual Narrows Lake Winnipeg mean TN, mg L^{-1}	1	1992	2005
Annual Narrows Lake Winnipeg mean TP, mg L^{-1}	1	1992	2005
Annual North Basin Lake Winnipeg mean TN, mg L^{-1}	1	1992	2005
Annual North Basin Lake Winnipeg mean TP, mg L^{-1}	1	1992	2005
Annual South Basin mean Chl *a*, mg L^{-1}	1	1992	2005
Annual Narrows mean Chl *a*, mg L^{-1}	1	1992	2005
Annual North Basin mean Chl *a*, mg L^{-1}	1	1992	2005
Annual Red River P loading, kg yr^{-1}	1	1970	2006
Annual Winnipeg River P loading, kg yr^{-1}	1	1970	2006
Annual Saskatchewan River P loading, kg yr^{-1}	1	1970	2006
Annual Dauphin River P loading, kg yr^{-1}	1	1977	2006
Annual East Side Lake Winnipeg P loading, kg yr^{-1}	1	1970	2006
Annual West Side Lake Winnipeg P loading, kg yr^{-1}	1	1970	2006
Annual Atmospheric Deposition P loading, kg yr^{-1}	1	1970	2006

Annual City of Winnipeg P loading, kg yr^{-1}	1	1970	2006
Annual Total P loading, kg yr^{-1}	1	1970	2006
Annual Outflow P (from Nelson River), kg yr^{-1}	1	1972	2006
Annual P load retained, kg yr^{-1}	1	1972	2006
Annual % P retention	1	1972	2006
Annual Red River N loading, kg yr^{-1}	1	1970	2006
Annual Winnipeg River N loading, kg yr^{-1}	1	1970	2006
Annual Saskatchewan River N loading, kg yr^{-1}	1	1970	2006
Annual Dauphin River N loading, kg yr^{-1}	1	1977	2006
Annual East Side Lake Winnipeg N loading, kg yr^{-1}	1	1970	2006
Annual West Side Lake Winnipeg N loading, kg yr^{-1}	1	1970	2006
Annual Atmospheric Deposition N loading, kg yr^{-1}	1	1970	2006
Annual N Fixation loading, kg yr^{-1}	1	1970	2006
Annual City of Winnipeg, N loading, kg yr^{-1}	1	1970	2006
Annual total N loading, kg yr^{-1}	1	1970	2006
Annual Outflow N (from Nelson River), kg yr^{-1}	1	1972	2006
Annual N load retained, kg yr^{-1}	1	1972	2006
Annual % N retention	1	1972	2006