

Effects of agriculture, urbanization, and climate on water quality in the northern Great Plains

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Abstract

The Qu'Appelle Valley drainage system provides water to a third of the population of the Canadian Great Plains, yet is plagued by poor water quality, excess plant growth, and periodic fish kills. Fossil algae (diatoms, pigments) and invertebrates (chironomids) in Pasqua Lake were analyzed by variance partitioning analysis (VPA) to determine the relative importance of climate, resource use, and urbanization as controls of aquatic community composition 1920–1994. From fossil analyses, we identified three distinct biological assemblages in Pasqua Lake. Prior to agriculture (ca. 1776–1890), the lake was naturally eutrophic with abundant cyanobacterial carotenoids (myxoxanthophyll, aphanizophyll), eutrophic diatoms (*Stephanodiscus niagarae*, *Aulacoseira granulata*, *Fragilaria capucina/bidens*), and anoxia-tolerant chironomids (*Chironomus*). Principal components (PCA) and dissimilarity analyses demonstrated that diatom and chironomid communities did not vary significantly ($P > 0.05$) before European settlement. Communities changed rapidly during early land settlement (ca. 1890–1930) before forming a distinct assemblage ca. 1930–1960 characterized by elevated algal biomass (inferred as β -carotene), nuisance cyanobacteria, eutrophic *Stephanodiscus hantzschii*, and low abundance of deep-water zoobenthos. Recent fossil assemblages (1977–1994) were variable and indicated water quality had not improved despite 3-fold reduction in phosphorus from sewage. Comparison of fossil community change and continuous annual records of 83 environmental variables (1890–1994) using VPA captured 71–97% of variance in fossil composition using only 10–14 significant factors. Resource use (cropland area, livestock biomass) and urbanization (nitrogen in sewage) were stronger determinants of algal and chironomid community change than were climatic factors (temperature, evaporation, river discharge). Landscape analysis of inferred changes in past algal abundance (as β -carotene; ca. 1780–1994) indicated that urban impacts declined with distance from point sources and suggested that management strategies will vary with lake position within the catchment.

Lake eutrophication remains a widespread problem despite intense research efforts to determine factors that regulate water quality (Schindler 1990; Williamson et al. 1999). Factors regulating eutrophication have been studied extensively in dimictic, soft-water, temperate lakes (e.g., Schindler 1990), but remain poorly understood in polymictic, hard-water, prairie lakes of the northern Great Plains where humans are important agents of environmental change (Allan 1980; Kenney 1990). Prairie lakes lie in large, fertile agricultural catchments that supply high concentrations of nutrients (Peters 1973) and are characterized by low nitrogen:phosphorus (N:P) ratios and surface blooms of nitrogen (N_2)-fixing cyanobacteria (Haertel 1976). The inability to

identify and regulate the agents that cause eutrophication continues to hamper management initiatives in prairie lakes (Allan and Kenney 1978; Kenney 1990).

Water quality in prairie lakes may be impacted by interactions among climate, resource use, and urban factors (Hammer 1971). Lakes of the northern Great Plains lie in semi-arid climates where precipitation deficits exceed 300 mm yr⁻¹ (Atmos. Environ. Serv. 1993) and alterations in the balance between precipitation, evaporation, and groundwater can concentrate dissolved nutrients, carbon, and salts (Hammer 1971; Williamson et al. 1999). Similarly, variability in ice cover leads to oxygen depletion, internal P generation, toxic build-up of ammonia and hydrogen sulfide, and fish kills during long winters (Barica 1987). Intensive resource use also alters aquatic communities and deteriorates water quality (Soranno et al. 1996). More than 95% of the arable grassland in western Canada (Stat. Can. 1991) has been converted to production of cereal crops and livestock using intensive European-style agricultural practices that increase soil erosion and bioavailable nutrient export (Clausen and Meals 1989). Additionally, fisheries management and hydrological regulation may alter nutrient supplies, nutrient cycling, and food-web composition (Kitchell 1992). Finally, urban populations have expanded more than 10-fold since 1900 as farmers shifted to urban centers (Stat. Can. 1901–1991), creating point sources of urban wastes. Unfortunately,

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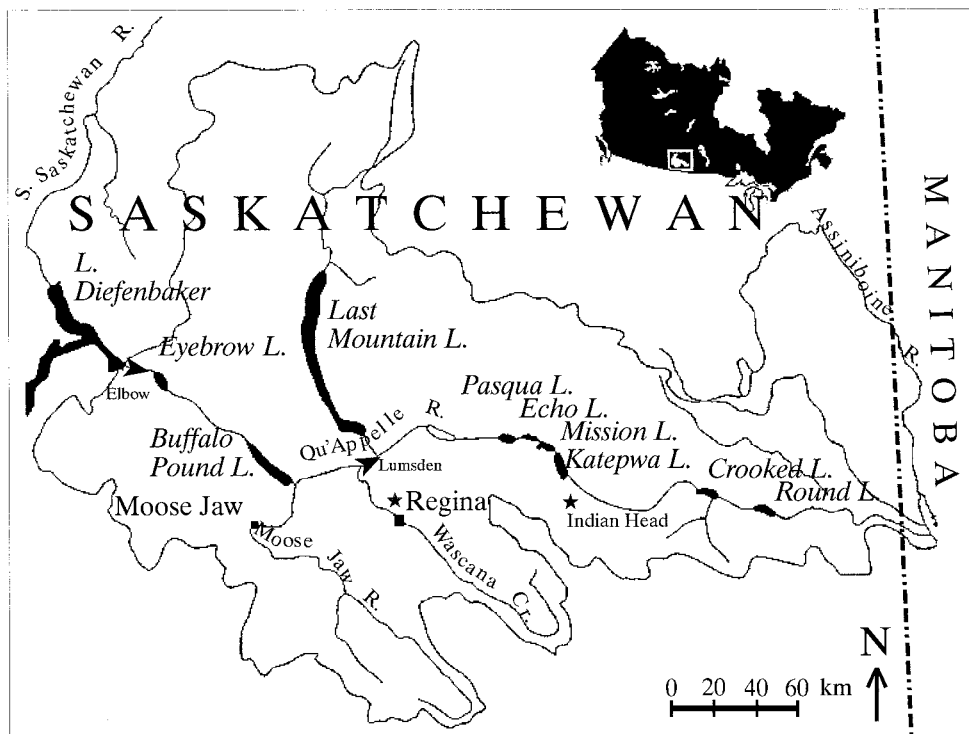


Fig. 1. Qu'Appelle River drainage basin and lakes, urban centers (■), meteorological stations (★), and hydrologic stations (▶).

it is uncertain how urban factors, climate, and resource use presently interact to regulate water quality on the northern Great Plains.

This study used canonical ordination-based variance partitioning (*sensu* Borcard et al. 1992) to quantify relationships between highly resolved fossil analyses of algae and invertebrates and century-long annual records of 83 environmental factors that influence water quality. We focused on the Qu'Appelle Valley drainage system because it supplies water to nearly a third of the population in the western Canadian prairies and because lakes within the drainage are characterized by poor water quality (Barica 1987), surface blooms of toxic cyanobacteria (*Aphanizomenon*, *Anabaena*, *Microcystis*; Hammer 1971; Graham 1997), excessive macrophyte growth (Chambers 1989), and kills of commercially important fishes (Qu'Appelle Basin Study Bd. 1972). In particular, we quantified pre-agricultural communities of Pasqua Lake to benchmark subsequent biotic change in response to climate, resource use, and urbanization. Past changes in total algal abundance were also quantified in six other regional lakes to determine the role of landscape position in mediating lake response to environmental change (Webster et al. 1996).

Site description—The Qu'Appelle Valley drains 52,000 km² (50°00'N–51°30'N, 101°30'W–107°10'W) and extends over 400 km from headwaters near Lake Diefenbaker to its confluence with the Assiniboine River (Fig. 1). More than 95% of the drainage area is composed of agricultural fields (wheat, barley, canola) and pastures (cattle, swine), while the cities of Regina and Moose Jaw are main point-sources of

nutrients (Qu'Appelle Basin Study Bd. 1972). Regional climate is subhumid with annual precipitation of 420 mm and moisture deficits exceeding 400 mm yr⁻¹ (Atmos. Environ. Serv. 1993). Summers are short (105 frost-free days) and warm (mean temp. 19°C), whereas winters are long and cold (–16°C). Lakes are ice-covered from late November to late April (Hammer 1971).

Eight major water bodies (7.7–552 km²) form a gradient of trophic status within the central Qu'Appelle Valley and include two headwater reservoirs and six natural lakes (Tables 1, 2). Reservoirs were created by damming the South Saskatchewan River (1968; Lake Diefenbaker) and flooding a shallow lake (1952, Buffalo Pound; Wiens 1987). The natural lakes are spring fed, lie in broad glacial outwash valleys, and were formed by deposition of alluvial fans from inflowing rivers (Christiansen 1960). Pasqua Lake occupies the upstream position of a central chain of four lakes, known as the Fishing Lakes, and is the first lake to receive point-source discharges from Regina and Moose Jaw. Hydrology of the Qu'Appelle River is highly variable, with spring runoff dominating annual discharge (Allan and Kenney 1978). All lakes except Katopwa exhibit low relative depth (*sensu* Wetzel 1983) and are polymictic (Table 1; Hammer 1971). Lake Diefenbaker and Buffalo Pound Lake contain freshwater [<0.5 g total dissolved solids (TDS) liter⁻¹], whereas eastern lakes are subsaline (~ 0.5 mg TDS liter⁻¹). Salinity is highest in Last Mountain Lake and can exceed 1.5 g TDS liter⁻¹. Composition of aquatic communities varies with productivity among lakes, as discussed by Graham (1997). In general, zooplankton in Pasqua Lake include *Diacyclops thomasi*, *Leptodiaptomus*, several *Daphnia* (*D. galeata-men-*

Table 1. Physical characteristics of the Qu'Appelle lakes and reservoirs (modified from Qu'Appelle Basin Study Bd. 1972). A_0 = surface area.

Lake	Distance down-stream (km)	N lat	W long	Elevation (m asl)	A_0 (km ²)	Depth (m)		Relative depth (%)	Total capacity (m ³ × 10 ⁶)
						Mean	Max		
Diefenbaker	0	51°07'	106°38'	552.0	500.0	33.0	62.0	0.24	9,400.0
Buffalo Pound	95	50°39'	105°30'	509.3	29.1	3.0	5.5	0.09	87.5
Last Mountain	145	50°05'	105°14'	490.1	226.6	7.9	30.8	0.18	1,807.2
Pasqua	200	50°47'	104°00'	479.0	20.2	5.8	15.5	0.30	120.8
Echo	215	50°41'	103°49'	479.0	12.5	9.8	21.9	0.55	122.1
Mission	230	50°45'	103°44'	478.2	7.7	8.2	17.1	0.55	62.9
Katepwa	240	50°42'	103°39'	478.2	16.2	14.3	23.2	0.51	233.2
Crooked	315	50°36'	102°44'	451.7	15.0	7.9	16.5	0.38	120.9
Round	330	50°32'	102°22'	442.3	10.9	7.6	13.1	0.35	83.9

dotae, *D. pulicaria*, *D. retrocurva*), and abundant rotifers. Northern pike (*Esox lucius*) and walleye (*Stizostedion vitreum*) are common piscivores; planktivores include cisco (*Coregonus artedii*) and yellow perch (*Perca flavescens*).

Qu'Appelle lakes have been subject to intensive resource use in both terrestrial and aquatic habitats. Aborigines harvested fish before European settlement, whereas commercial fisheries began in the 1880s (Hammer 1971). Fish stocking has been common, especially from 1930 to 1955, when walleye, whitefish (*Coregonus clupeaformis*), pike, and lake trout (*Salvelinus namaycush*) were added to all lakes [Fish. Branch, Sask. Environ. Resour. Manage. (SERM) unpubl. data]. In addition to the arable lands of the drainage basin, uplands are used for cattle, swine, and poultry production. Many lakes have received sewage from local municipalities, in particular Regina and Moose Jaw, since 1882. Similarly, the hydrology of the system has been altered for energy production, water supply, and flood control (Weins 1987).

Methods

Historical data—Continuous annual data for 83 variables were collected to determine the impacts of environmental change on water quality (1890–1995) and were assigned to climate, resource use, or urban categories (Table 3). Complete records of monthly and annual precipitation (mm; 1911–1995), and mean monthly minimum and maximum temperatures (°C; 1891–1995) were obtained from the En-

vironment Canada weather station at Indian Head, a central location in the Qu'Appelle drainage (Fig. 1). Monthly and annual gross evaporation (mm yr⁻¹) from small to medium water bodies (3–469,000 MI) was estimated using a modified Meyer formula (Martin 1988) and climate data (1911–1993) obtained from Agriculture Canada (Prairie Farm Rehab. Admin., Regina).

Historical records of ice thaw and freeze for the Red River at Winnipeg, Manitoba, were used to estimate the regional ice-free season of the western Canadian plains 1870–1981 (Rannie 1983). The Red River record was used because available historical records for the Qu'Appelle Valley (1967–1994) were too brief and because Red River ice records reflected trends on the Qu'Appelle River, as indicated by the significant correlation among ice-thaw dates ($r^2 = 0.50$, $P < 0.001$, $n = 26$; 1969–1994). To complete the Red River record between 1981 and 1995, we estimated thaw dates as the date when the river first rose 4 feet (1.22 m) above the mean winter level, based on a regression ($r^2 = 0.75$, $P < 0.001$, $n = 43$) developed for 1935 to 1981 (A. Warkentin pers. comm.): thaw date = $0.762 \times$ river-rise date + 30.61, where dates were reported as calendar day of year (DOY). Dates of river freezing were unavailable for 1981 to 1995 and were estimated as the mean date of freezing 1977–1981.

Annual discharge volume (Mliters yr⁻¹) was estimated for two sites on the Qu'Appelle River (1912–1995; A. Banga pers. comm.). The Lumsden site (Fig. 1) measured the volume of water conveyed by the Qu'Appelle River to Pasqua

Table 2. Mean chemical and biological characteristics of selected Qu'Appelle lakes, June–August 1994. Nitrogen-fixing cyanobacteria and total cyanobacteria (blue-greens) expressed as percent of total algal biovolume [modified from Graham (1997) and Leavitt *et al.* (unpubl. data)]. Data for Pasqua Lake from Allan and Roy (1980), except chlorophyll concentration from Hammer (1973). NA—Values not available.

Lake	Cond.	pH	Diss. N	Diss. P	N:P	Chl	% N ₂ fixers	% Cyano.
	(μ S cm ⁻¹)		(μ g liter ⁻¹)	(μ g liter ⁻¹)		(μ g liter ⁻¹)		
			±SD				Mean (range)	
Diefenbaker	380 ± 16	7.8 ± 0.7	205 ± 86	93 ± 71	3.1 ± 2.6	4.9 ± 3.9	17.2 (7–32)	17.2 (7–32)
Buffalo Pound	482 ± 24	8.4 ± 0.6	499 ± 24	185 ± 124	3.4 ± 2.2	6.3 ± 3.2	17.4 (4–26)	33.1 (13–46)
Last Mountain	2,062 ± 48	9.1 ± 1.0	578 ± 180	132 ± 50	5.0 ± 2.9	10.8 ± 2.9	61.2 (17–96)	66.9 (30–96)
Pasqua	2,100	8.5	NA	267	2.5	25.5	NA	NA
Katepwa	1,160 ± 43	8.5 ± 0.5	762 ± 259	286 ± 53	2.7 ± 0.9	13.0 ± 8.3	20.0 (10–33)	42 (17–55)
Crooked	1,338 ± 25	9.1 ± 0.5	1,062 ± 540	602 ± 120	1.7 ± 0.7	21.7 ± 15.3	37.6 (6–62)	56 (44–74)

Table 3. Explanatory variables included in historical datasets. Variables were grouped into one of three categories: climate, resource use, or urban factors. N—Number of variables included under a variable name; DOY—calendar day of year.

Variable name	N	Start and end of record	
Climate			
Monthly gross evap., mm	12	1911	1993
Seasonal gross evap., mm	4	1911	1993
Annual gross evap., mm	1	1911	1993
Annual net evap., mm	1	1911	1993
Monthly precip., mm	12	1911	1993
Seasonal precip., mm	4	1911	1993
Annual precip., mm	1	1911	1993
Mean monthly max temperature, °C	12	1891	1995
Mean seasonal max temperature, °C	4	1891	1995
Mean monthly min temperature, °C	12	1891	1995
Mean seasonal min temperature, °C	4	1891	1995
Ice breakup date, Red River at Winnipeg, DOY	1	1870	1995
Ice freezeup date, Red River at Winnipeg, DOY	1	1870	1981
Ice-free season, Red River at Winnipeg, No. days	1	1870	1981
Annual flow, Qu'Appelle R. at Lumsden, Mliters	1	1912	1995
Resource use			
Annual flow, Lake Diefenbaker reservoir, Mliters	1	1959	1995
Annual commercial fish harvest, kg	1	1920	1992
Annual number of fish stocked, No. fish	1	1924	1994
Livestock biomass, Qu'Appelle watershed, t	1	1881	1995
Area of field crops, Qu'Appelle watershed, ha	1	1881	1995
Area of farmland, Qu'Appelle watershed, ha	1	1920	1995
Urban			
Regina pop., No.	1	1881	1995
Moose Jaw pop., No.	1	1881	1995
Qu'Appelle Valley pop., No.	1	1881	1995
Total P load, Regina sewage, kg	1	1881	1995
Total N load, Regina sewage, kg	1	1881	1995
TN:TP; Regina sewage	1	1881	1995

Lake after its confluence with Moose Jaw River and Wasicana Creek and was mainly influenced by climatic controls (A. Banga pers. comm.). The site at Elbow measured discharge from Lake Diefenbaker into the Qu'Appelle drainage. This diversion is managed by Sask. Water Corp. and was considered resource use data in subsequent analyses.

Annual records of commercial fish harvest (1920–1992) and stocking (1924–1994) at Pasqua Lake were obtained from Fisheries Branch, SERM. Although commercial fisheries and stocking programs existed before 1920, data were not available.

Historical records of agricultural activity in the Qu'Appelle drainage were obtained from Census of Canada reports (Stat. Can. 1881–1991) for livestock biomass (kg live wt), field crop area, and total farmland area (ha; Table 3). Census data were available at 5- or 10-yr intervals since 1881. Annual estimates of agriculture variables were calculated by linear interpolation between census years. Livestock biomass was estimated from animal populations (ind.) and mean annual carcass weights (kg ind.⁻¹) for cattle and swine (1951–1995; K. Schmidt pers. comm.) and poultry (1961–1995; R. Shalla pers. comm.). Total livestock biomass was calculated from ratios of live:carcass weight for cattle (1.35), swine (1.72), and poultry (1.36). To estimate livestock

weight prior to onset of formal records, we used a 5-yr average of the earliest available weights.

Historical information concerning urban (Regina, Moose Jaw) and rural populations in the Qu'Appelle Valley (1881–1995) were obtained from Census of Canada reports (Stat. Can. 1881–1991). Annual population estimates were calculated by linear interpolation between census years.

Annual total P (TP) input (kg P yr⁻¹) from Regina's sewage was estimated (1881–1976) using monthly records of sewage volume at the central pump station (1938–1949, 1960–1995), mean TP concentration in raw sewage (1984–1993; 6.37 mg liter⁻¹), and P-removal efficiency of primary (8%; 1881–1914), secondary (25%; 1915–1976), or tertiary (84%; 1984–1995) treatment processes (Fries 1993). Because sewage volumes were not measured 1950–1959 or before 1938, we developed linear regression equations to estimate sewage volume from Regina's population. Preliminary analyses indicated that the relationship between sewage volume and population exhibited two distinct linear phases and that per capita sewage volumes increased from 83 to 152 × 10³ liters ind.⁻¹ yr⁻¹ after 1966. Sewage volumes 1881–1959 were estimated from regressions ($r^2 = 0.77$, $P < 0.001$, $n = 18$) developed for 1938 to 1949 and 1960 to 1965, where

Table 4. Explanatory variables used in variance partitioning analyses for various combinations of time periods and bioindicators (diatoms, pigments, chironomids). Variables are listed according to the variable categories of climate, resource use, or urban as described in the text. T_{\min} and T_{\max} —Mean minimum and mean maximum temperatures.

Variable category	post-1920	post-1950	post-1970
		Diatoms	
Climate	Spring evap., fall evap. Spring T_{\max} , winter T_{\max} Spring T_{\min} , summer T_{\min} Fall T_{\min}	Spring evap. Winter T_{\max} , spring T_{\min} Summer T_{\min} , fall T_{\min} Breakup date	Fall precip. Spring T_{\max} Fall T_{\min}
Resource use	Flow at Elbow Livestock Fieldcrops, farmland	Flow at Elbow Fish harvest Fieldcrops, farmland	Flow at Elbow Fish harvest, fish stocked Fieldcrops, farmland
Urban	Regina pop. TN load, TN:TP	Regina pop. TP load, TN load	Regina pop., QV pop. TP load, TN:TP
		Pigments	
Climate	Spring evap., spring T_{\max} Spring T_{\min} , winter T_{\min} Ice-free season	Spring evap. Spring T_{\min} , fall T_{\min} Winter T_{\min} Ice-free season	Annual precip. Winter T_{\max} , fall T_{\min} Winter T_{\min} Ice-free season
Resource use	Flow at Elbow Livestock, fieldcrops Farmland	Flow at Elbow Fish stocked Fieldcrops, farmland	Flow at Elbow Fish harvest, fish stocked Fieldcrops, farmland
Urban	Regina pop. Moose Jaw pop., QV pop. TN:TP	Regina pop. TN load, TN:TP	Regina pop., QV pop. TN:TP
		Chironomids	
Climate	Annual precip. Spring T_{\min} , summer T_{\min}	Annual precip.	None
Resource use	Fish harvest Livestock, fieldcrops, farmland	None	None
Urban	Moose Jaw pop., QV pop. TN load, TN:TP	QV pop.	None

sewage volume (MI) = $0.038 \times$ Regina population + 3,240.6.

Total N (TN) flux from sewage (kg N yr^{-1} ; 1881–1976) was also estimated from long-term records of sewage volume and mean TN concentration in effluent following primary ($31.9 \text{ mg liter}^{-1}$; 1890–1914) or secondary ($30.9 \text{ mg liter}^{-1}$; 1915–1976) treatment. TN flux following 1976 was calculated from annual measured sewage volumes and mean TN concentration after tertiary sewage treatment ($22.5\text{--}30.9 \text{ mg liter}^{-1}$). All sewage data were obtained from the Regina Wastewater Treatment Plant (Fries 1993; Dep. Public Works, City of Regina unpubl. data).

Field and laboratory methods—A sediment core 64-cm-long was retrieved from the deep-water region of Pasqua Lake in March 1995 using standard freeze-coring procedures (Leavitt et al. 1989). The frozen core was quartered lengthwise, cleaned by removing the outermost 5 mm with a wood-plane, and slowly thawed and dewatered in the dark. Upper sediments (0–15-cm depth) were sectioned into 5-mm intervals; deeper samples were sectioned every 1 cm. All samples were flushed with N_2 gas and frozen (-20°C) in the dark until analysis for fossils. Similar procedures were used to collect and process cores from all other sites.

Pasqua Lake sediments were freeze-dried (48 h, 0.01 Pa) and analyzed for ^{210}Pb content at 16 intervals over the length of the core. Analysis of ^{210}Pb was performed by Chalk River Laboratories (Atomic Energy of Can. Ltd.), using alpha spectrometry. Sediment age and mass accumulation rates ($\text{g cm}^{-2} \text{ yr}^{-1}$) were calculated using the constant rate of supply (CRS) model and the computer program of Binford (1990).

Microscope slides for diatom analyses were prepared using standard techniques described by Wilson et al. (1996), and coverslips were mounted onto glass microscope slides with Naphrax. At minimum, 500 diatom valves were identified and enumerated from each sample to determine species relative abundance (% diatom sum) using light microscopy ($1,000\times$ magnification, numerical aperture = 1.40). Diatom taxonomy followed Patrick and Reimer (1966a,b), Krammer and Lange-Bertalot (1986–1991), and Cumming et al. (1995).

Sedimentary pigments were extracted, filtered, and dried under N_2 gas following Leavitt et al. (1989). Carotenoid, chlorophyll, and derivative concentrations were quantified in each sediment sample using a Hewlett-Packard model 1050 high-performance liquid chromatograph (HPLC) following the reversed-phase procedure of Mantoura and Llewellyn (1983) as modified by Leavitt et al. (1989, 1999). Pigments

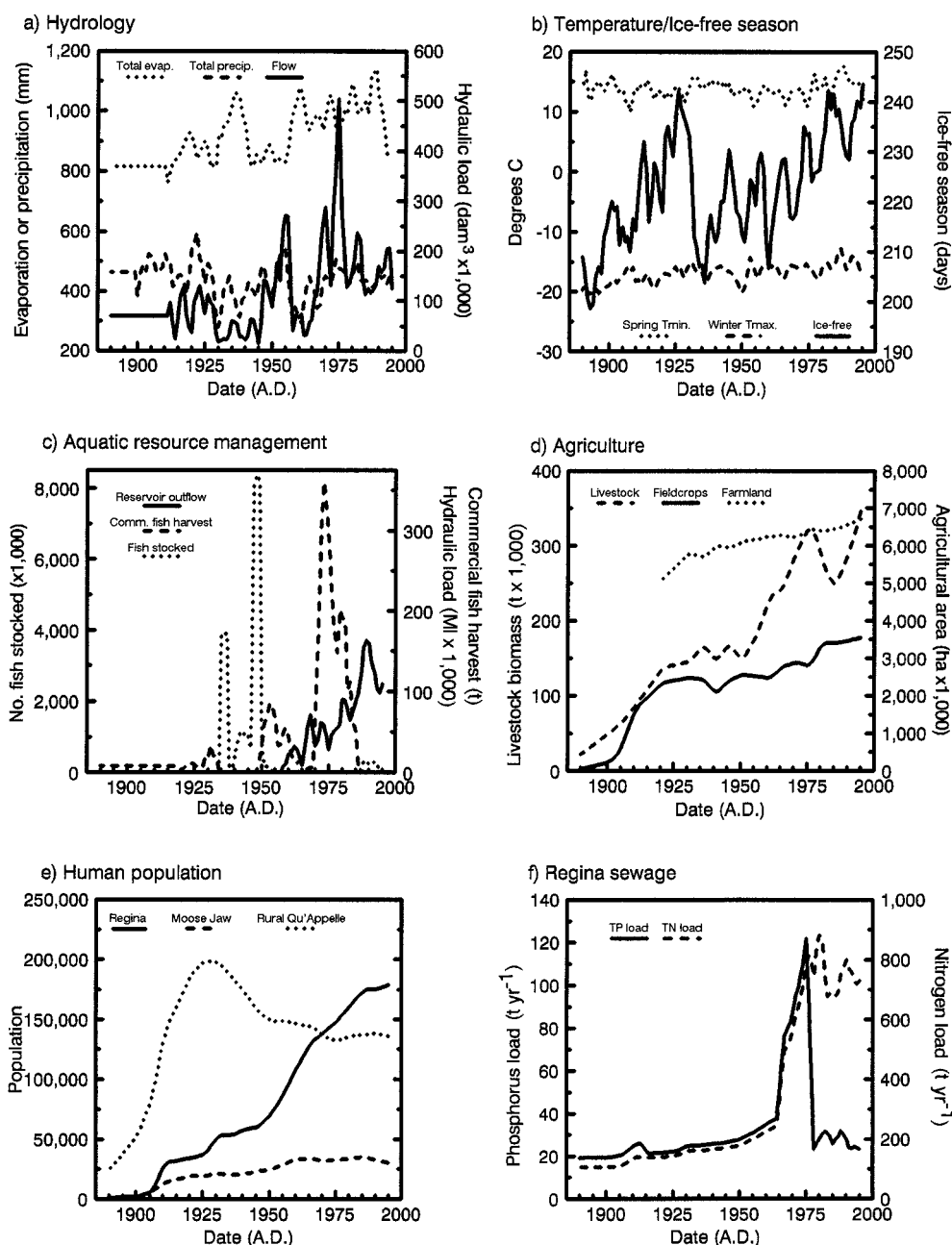


Fig. 2. Long-term data for the Qu'Appelle drainage basin. Historical records include climatic variables: (a) hydrological balance and (b) temperature and ice-free growing season; resource use variables: (c) aquatic resource management, and (d) agriculture; and urban factors: (e) human population, and (f) nutrients from sewage. Further details given in methods and Table 3.

identified included carotenoids characteristic of total algae (β -carotene), cryptophytes (alloxanthin), siliceous algae and dinoflagellates (fucoxanthin), mainly diatoms (diatoxanthin), cyanobacteria (echinenone), filamentous cyanobacteria (canthaxanthin, myxoxanthophyll), and N_2 -fixing cyanobacteria (aphanizophyll). Isomeric carotenoids from green algae (lutein) and cyanobacteria (zeaxanthin) were inseparable on our HPLC system and are presented together. Similarly, carotenoids from *Aphanizomenon* (aphanizophyll), *Anabena* (4-keto-myxoxanthophyll), and the Oscillatoriaceae (oscillaxan-

thin) were incompletely resolved and were presented as aphanizophyll. Chlorophyll *b* and *a*-phorbins (Chl *a*, pheophytin *a*) were used to independently quantify changes in chlorophytes and total algae, respectively. Pheophorbide *a*, a derivative of chlorophyll *a* produced during ingestion of algae by aquatic grazers, provided a measure of herbivory (Daley 1973; Carpenter and Bergquist 1985). All pigment concentrations were expressed as nmol pigment g^{-1} organic matter, following estimation of organic content by weight loss on ignition at 500°C (Dean 1974).

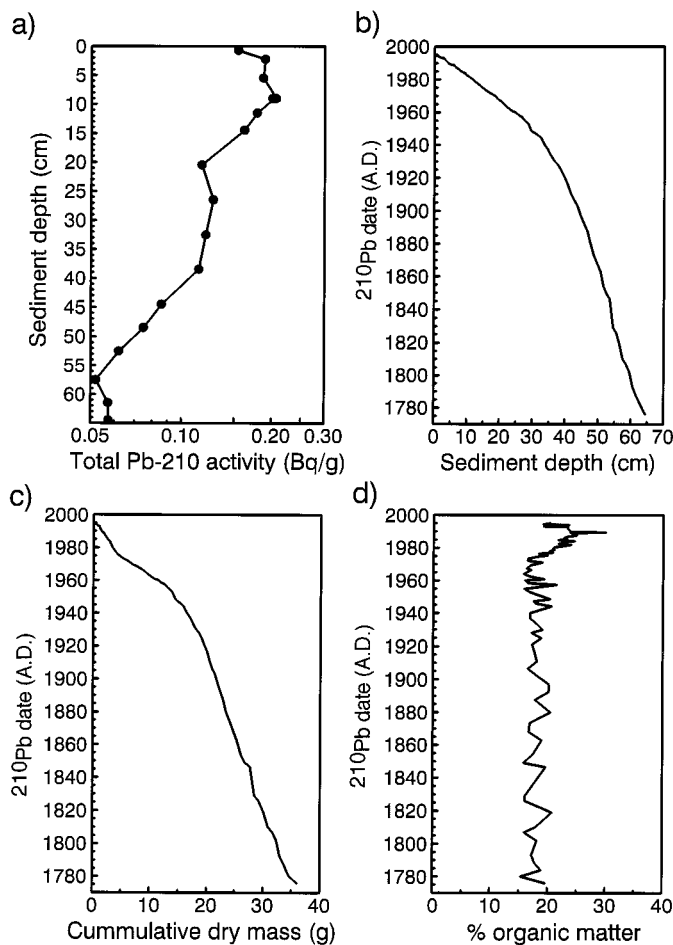


Fig. 3. ^{210}Pb radiometric dating and loss-on-ignition analysis of Pasqua Lake sediment core. [a.] Sediment depth vs. total ^{210}Pb activity (Bq g^{-1} dry wt). [b.] Estimated age vs. sediment depth. [c.] Estimated age vs. cumulative dry mass of sediment (g dry wt). [d.] Estimated age vs. organic matter content (% of dry wt).

Chironomid remains were isolated from sediments after deflocculation in warm 8–10% KOH. Head capsules retained on 95- μm Nitex mesh were sorted at 50 \times magnification using a Nikon dissecting microscope, and mounted in Euparal onto microscope slides. Chironomid remains were identified to genus at 100–1,000 \times magnification with reference to Wiederholm (1983), Walker (1988), and Oliver and Roussel (1983). In some instances, larger taxonomic groupings were necessary (e.g., *Cricotopus/Orthocladius*).

Numerical analyses—All numerical analyses of diatom and chironomid assemblages were based on percent abundances and included 30 diatom taxa with $\geq 1\%$ abundance and 18 chironomid taxa with $\geq 2\%$ abundance in at least one sample. Numerical analyses included the 13 most abundant pigments listed above.

Temporal patterns of community change (ca. 1776–1994) were explored with independent principal components analysis (PCA) of fossil diatom, pigment, and chironomid assemblages. PCA ordinations were scaled by Euclidean distance and centered by species, using CANOCO version 3.12

(ter Braak 1990). Unlike diatom and chironomid assemblages, pigment abundances required $\log_{10}(x + 1)$ transformation to provide normal error distribution (Jongman et al. 1995).

Rate of change of community composition was estimated for diatom and chironomid percentage data as chord distance per 5 yr and for $\log_{10}(x + 1)$ -transformed pigment concentrations as Euclidean distances per 5 yr. Chord and Euclidean distances are dissimilarity coefficients that are appropriate for estimating rates of change from percentage and abundance data, respectively (Lotter et al. 1995). In addition to the 13 pigments listed above, peridinin, chlorophyll *c*, and UV-radiation absorbing pigments (Leavitt et al. 1997) were included in rate of change computations. Species data were interpolated at linear 5-yr intervals before calculating rates of change. In all cases, 95% confidence limits were estimated from fossil data using Monte Carlo simulations with 1,000 permutations.

Constrained and partial canonical ordinations (ter Braak 1988) were used to evaluate the relationships between three categories of explanatory variables (climate, resource use, urban activity) and changes in fossil assemblages in Pasqua Lake. Variance partitioning (Borcard et al. 1992) uses direct gradient analysis [e.g., canonical correspondence analysis (CCA) or redundancy analysis (RDA)] to estimate the fraction of variance in community composition explained by categories of measured variables (e.g., environmental, temporal, or spatial factors). Variance partitioning with three categories of explanatory variables has been used previously with ecological data (Qinghong and Bråkenhielm 1995) and is based on standard ordination methods (Lotter et al. 1995).

Five steps were required to partition variance in fossil data among climate (*C*), resource use (*R*), and urban (*U*) categories. First, canonical ordination with no covariables was used to measure the total amount of variance (as sum of canonical eigenvalues) in the fossil assemblages attributable to all explanatory variables ($C + R + U$) and the total unexplained variance [$100 - (C + R + U)$]. Second, a series of partial canonical ordinations was used to calculate variance explained by the unique effects of each category (*C*, *R*, or *U*). In this step, ordinations of individual explanatory categories were run with the remaining two categories as covariables. Third, a series of partial canonical ordinations were used to calculate the pure effects plus first-order interactions for each set of predictors ($C + CR$, $C + CU$, $R + CR$, $R + UR$, $U + CU$, $U + UR$). In each trial, one category of explanatory variables was paired with one of the remaining categories acting as a covariable. Fourth, first-order interaction terms (CR , UR , CU) were calculated by subtracting appropriate terms generated during steps 2 and 3 [e.g., $CU = (C + CU) - C$]. Finally, the second-order interaction (CRU) was calculated as the difference between 100% and the sum of variance captured in the first, second, and fourth steps ($CRU = 100 - C - R - U - CR - CU - UR - \text{unexplained}$).

Redundancy analysis (RDA) was used to partition variance in fossil assemblages because exploratory detrended correspondence analysis (DCA) suggested that fossil assemblages varied along environmental gradients in a linear rather than unimodal fashion (ter Braak 1986). Computations were performed using CANOCO v. 3.12 (ter Braak 1990). RDA

was performed with percent abundances of diatom and chironomid taxa or pigment concentrations after smoothing with an unweighted three-point running mean. Because our interests were to investigate controls of long-term biological changes rather than interannual variability, historical data were also smoothed using a 3-yr running mean.

Variance partitioning requires similar numbers of historical variables within each explanatory category to avoid bias in analyses (Borcard et al. 1992). We developed and used objective a priori criteria to ensure similar numbers of statistically significant variables per category (Table 3). First, we restricted climate data to annual and seasonal values for winter (November–March), spring (April–May), summer (June–August), and fall (September–October). We then selected only explanatory variables that accounted for significant amounts of variance in fossil data (critical $\alpha = 0.05$), based on a series of RDAs constrained to a single explanatory variable at a time (ter Braak 1990). Significant variables were assigned to one of the explanatory categories (Table 3). Finally, we performed a series of RDAs on each category, sequentially eliminating the explanatory variable with the highest variable inflation factor (VIF) until all VIFs were <20 (Hall and Smol 1996). This step eliminated collinearity among variables within each category (ter Braak 1990) and resulted in similar numbers of variables per category (Table 4). Three-way partitions were performed independently on fossil time-series beginning in 1890, 1920, 1950, and 1970 to investigate how the relative importance of explanatory categories varied with the duration of study. The resource use category included variables related to aquatic resource management (fisheries and hydrology) and terrestrial land use (agriculture), because aquatic communities are often strongly regulated by changes in food-web dynamics, hydrology as well as land use (e.g., Kitchell 1992). We further partitioned variance due to resource use into agriculture and aquatic categories to more clearly define relative impacts of each and to improve management strategies.

Results

Historical data—Most climate variables were highly variable during the last century (Fig. 2a,b). For example, annual precipitation and evaporation (mm yr^{-1}) varied unpredictably, although evaporation was generally highest during the 1930s and 1950–1990 and was in excess of precipitation in all years. Discharge volume of the Qu'Appelle River at Lumsden was characterized by high interannual variation, with above-average flow 1950–1957 and 1970–1995 (Fig. 2a). Peak river flow occurred in 1974, due to regional spring flooding (Kenney 1990). Despite high interannual variability, mean maximum winter temperatures rose $>2^\circ\text{C}$ during the

20th century (Fig. 2b). The most marked trend in climate data was a substantial increase in duration of the ice-free season during 1900–1930 and 1935–1995. Since 1935, the ice-free season has increased by ~ 30 d (Fig. 2b), continuing a trend that originated ca. 1860 (Rannie 1983).

Historical records indicated substantial changes in aquatic resource management since 1920 (Fig. 2c). Fish stocking peaked during the 1940s, with 22.6 million walleye fry added to Pasqua Lake in 1948. Commercial fish harvest in Pasqua Lake increased after 1950 and peaked 1970–1985, with annual catches of up to 400 t. Since completion of Lake Diefenbaker in 1969, discharge of nutrient-poor water into the Qu'Appelle River increased regularly, with maximum discharges since the late 1980s (Fig. 2c).

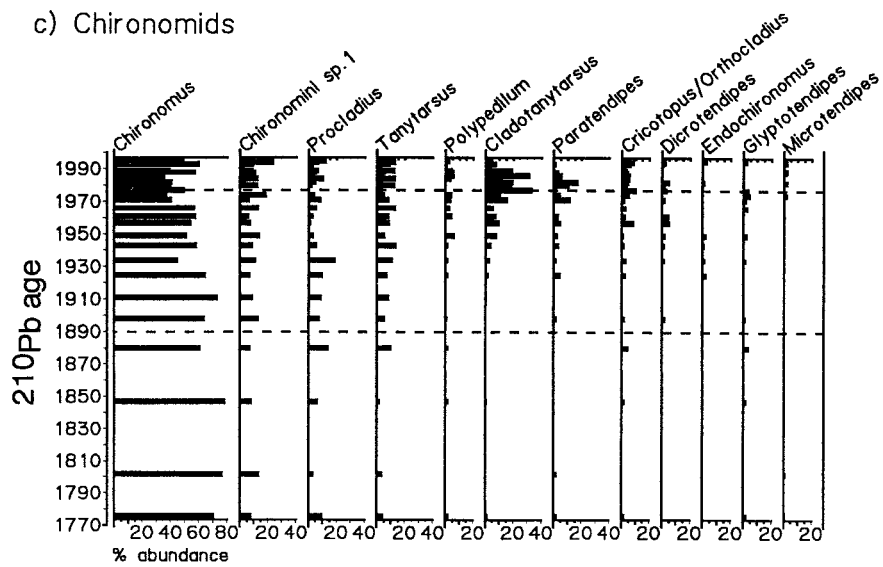
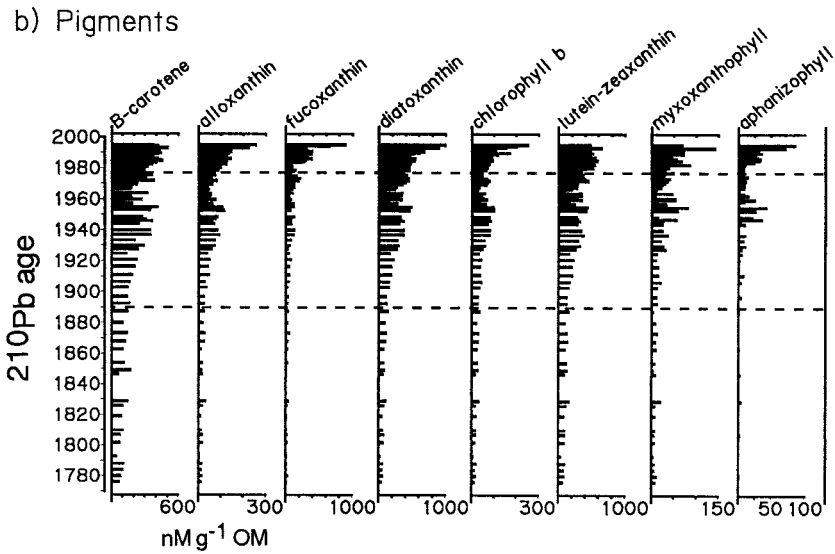
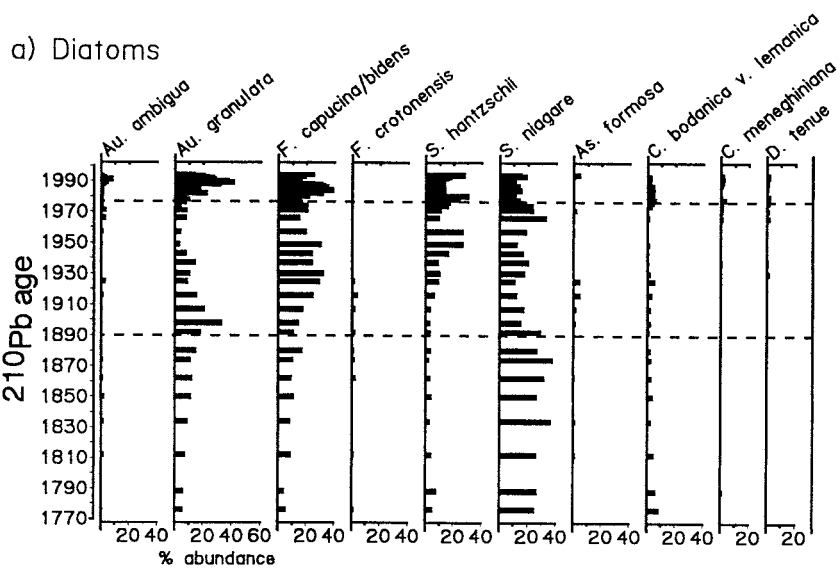
Terrestrial resource use changed dramatically since 1900 (Fig. 2d). Agricultural activities increased rapidly during the early 1900s, especially 1905–1925 following construction of the trans-national railway and incorporation of Saskatchewan as a province (1905). The area of cereal crops increased exponentially from 1890 to 1915, but declined during droughts of the 1930s and WW2 (Fig. 2d). Since 1945, field-crop area has increased at constant rates. In general, the biomass of livestock increased steadily since 1900, although temporal variability has been higher since 1950 than previously.

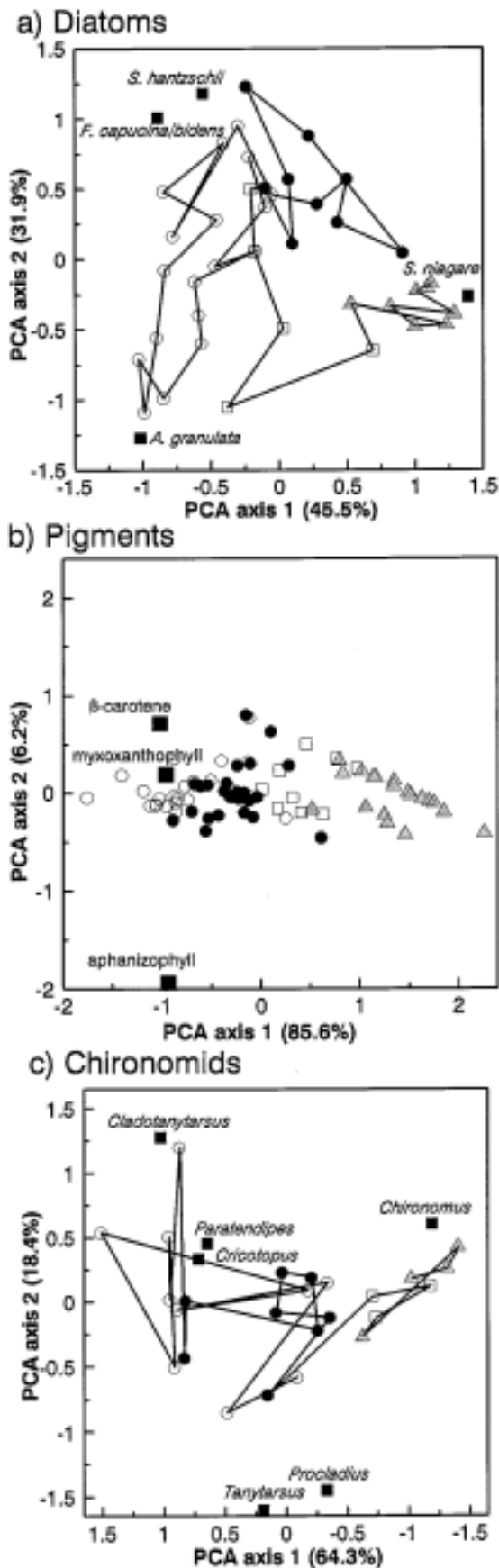
The first Census of the Qu'Appelle district in 1881 indicated that human populations were initially low (5,241) and predominantly of indigenous origin (88%; Stat. Can. 1881). By 1900 the human population had reached $\sim 50,000$ (Fig. 2e). Rural population expanded from 1900 to 1930 as Europeans settled available farmland but declined thereafter as a result of drought, war, changing agricultural practices, and increasing urbanization. The cities of Regina and Moose Jaw were established in 1882 but grew slowly until Regina was incorporated as the provincial capitol in 1905. The population of Regina increased substantially after 1945, while that of Moose Jaw has remained relatively constant since 1950 (Fig. 2e).

Nutrient inputs from sewage were low following initial establishment (1910) but increased rapidly following expansion (1950–1970) of Regina's wastewater collection system (Fig. 2f). Installation of tertiary sewage treatment in 1977 reduced TP flux to levels characteristic of 1930s, although TN inputs have remained at an historical maximum.

Sediment accumulation rate— ^{210}Pb activity in Pasqua Lake sediments declined with depth, but in a nonmonotonic fashion (Fig. 3a). Abrupt changes in ^{210}Pb concentrations at depths of 39, 21, and 10 cm suggest that sediment accumulation rates were not constant and that CRS models were most appropriate for determining sediment age (Appleby and

Fig. 4. Temporal changes in biological community composition as reflected in the sediment core from Pasqua Lake, based on (a) percent abundances of common diatom taxa, (b) concentrations (nmol g^{-1} organic matter) of the most abundant chlorophyll and carotenoid pigments, and (c) percent abundances of common chironomid taxa. Pigments include β -carotene (all plants), alloxanthin (cryptophytes), fucoxanthin (chromophytes), diatoxanthin (diatoms), chlorophyll *b* (chlorophytes), lutein-zeaxanthin (chlorophytes + cyanobacteria), myxoxanthophyll (filamentous cyanobacteria), and aphanizophyll (N_2 -fixing cyanobacteria). Dashed lines indicate the onset of European-style agriculture in 1890 and the onset of tertiary sewage treatment in Regina in 1977.





Oldfield 1983; Blais et al. 1995). Despite changes in sediment accumulation, the ^{210}Pb chronology demonstrated that sediments from Pasqua Lake included the pre-European era (Fig. 3b). Similar results were recorded from all other sites. An abrupt transition from upper black organic-rich sediments to lower tan-gray carbonate-rich sediments occurred at the 46-cm level in the Pasqua Lake core. Based on ^{210}Pb dating, this transition occurred at 1890 ± 0.9 yr (SD), coincident with the onset of European-style agriculture within the Qu'Appelle drainage (Fig. 2d). The rate of sediment accumulation was relatively constant until ~ 1945 but increased thereafter (Fig. 3b,c). The organic content of Pasqua Lake sediments was unchanged until ca. 1970 ($17.8\% \pm 3.9$ SD), at which time values increased to a maximum ($23.4\% \pm 2.0$ SD) in the 1980s (Fig. 3d).

Diatoms—Diatoms were well preserved, abundant, and composed of taxa characteristic of productive conditions at all levels of the Pasqua Lake core (Fig. 4a). Pre-European assemblages had high abundances of the eutrophic taxa *Stephanodiscus niagarae*, *Aulacoseira granulata*, and *Fragilaria bidens/capucina*. Species composition changed shortly after the onset of European settlement ca. 1890, as *S. niagarae* declined and *A. granulata* increased. Highly eutrophic *Stephanodiscus hantzschii* increased sharply during ca. 1930–1960. Since the 1960s, diatom communities have been highly variable, with rapid shifts in the relative dominance of the four common taxa: *A. granulata*, *F. capucina/bidens*, *S. hantzschii*, and *S. niagarae*.

The first two PCA axes captured 77.4% of variance in diatom communities and identified three distinct periods with broadly different diatom assemblages (Fig. 5a). These communities were used subsequently to define water-quality eras for comparison with other fossil groups (see below). The first distinct diatom assemblage existed from the base of the core (ca. 1776) until ca. 1890 and encompassed the pre-settlement era. These communities were characterized by high abundances of *S. niagarae*. The tight cluster of assemblages ca. 1776–1890 suggested that species composition of diatom communities was more stable than at any time afterward. Pre-settlement communities were followed by a brief transition period (1900–1930) before a second distinct grouping formed with high percent abundances of *S. hantzschii* (1930–1976). Finally, the composition of modern assemblages (1977–1994) has been variable, with *S. hantzschii*, *A. granulata*, and *F. capucina/bidens* alternating as co-dominants concomitant with tertiary sewage treatment. The uppermost sediments ordinate near communities from 1925 to 1943, suggesting that present-day diatom assem-

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Fig. 5. Principal components analysis (PCA) ordinations of sample scores and selected species scores from (a) diatom percent abundances, (b) fossil pigment concentrations ($\log_{10}[x + 1]$), and (c) chironomid percent abundances. Lines join adjacent sediment core samples. \triangle —Samples deposited between ca. 1776 and 1890; \square —1891–1930; \bullet —1931–1976; \circ —1977–1993. \blacksquare —Species scores of selected taxa and pigments.

blages remain distinctly different from pre-settlement communities.

Pigments—Fossil algal pigments provided information on biomass changes of the major algal groups in Pasqua Lake since ca. 1776 (Fig. 4b). The presence of myxoxanthophyll (from filamentous cyanobacteria) and aphanizophyll (N_2 -fixing cyanobacteria) at all levels in the core suggests that bloom-forming cyanobacteria were regular features of algal communities in Pasqua Lake throughout the past 200 yr. Concentrations of these pigments were as high before European settlement as they were immediately afterward. Early agricultural activities (1890–1920) were associated with only small increases (~50%) in fossil pigment concentrations. However, concentrations of most algal pigments increased 2–4-fold during 1930–1960. In particular, carotenoids from cyanobacteria (echinenone, canthaxanthin, myxoxanthophyll, aphanizophyll) were 300–400% more abundant, consistent with degraded water quality. Pigment concentrations declined ca. 1960–1976, but were high and variable 1977–1995.

Analysis of fossil pigment concentrations using PCA ordination also separated pre-settlement algal communities from more recent fossil assemblages (Fig. 5b). The first PCA axis captured 85.6% of the variance in pigment concentrations and separated samples according to inferred total algal biomass (as β -carotene). The second axis accounted for only 6.2% of the variance but generally separated samples with exceptionally high abundances of N_2 -fixing cyanobacteria. Pre-settlement samples (ca. 1776–1890) were characterized by low inferred algal abundance and were distinct from assemblages of the other diatom-defined eras. Following a transition period (ca. 1891–1930) inferred algal abundances increased further, often with relatively high biomass of N_2 -fixing cyanobacteria (1931–1976). Sediments deposited since 1977 were inferred to have the highest algal biomass of the historical sequence, although concentrations of pigments from bloom-forming cyanobacteria were somewhat reduced.

Chironomids—Chironomid assemblages of the past 200 years were composed mainly of the genus *Chironomus*, a taxon characteristic of deep-water habitats with low oxygen availability (Nagell and Landahl 1978; Saether 1979; Fig. 4c). In pre-settlement assemblages, more than 70% of all chironomids belonged to *Chironomus*. Relative abundances of *Chironomus* declined ca. 1900–1930 due to a decline in absolute fossil density rather than reciprocal increases in littoral taxa such as *Procladius*, *Tanytarsus* s. lat. (Fig. 6). Absolute abundances of most chironomids, including deep-water (*Chironomus*, *Chironomini* sp. 1) and littoral (*Procladius*, *Tanytarsus*) taxa, continued to decline ca. 1930–1977 (Fig. 6). During the mid-1970s, *Chironomus* abundances reached historical minima, although the macrophyte-associated *Cladotanytarsus* and *Paratendipes* (Beattie 1982) increased as early as 1930 (Figs. 4c, 6). Fossil chironomid concentrations increased sharply after 1970 (Fig. 6), although taxonomic composition has been highly variable.

High temporal variability of chironomid communities was evident from PCA ordination (Fig. 5c). The first PCA axis

separated samples along a gradient of *Chironomus* abundance and captured 64.3% of total variance. The second PCA axis accounted for a further 18.4% of variance and separated samples based on differences in relative proportions of *Procladius*–*Tanytarsus* and *Cladotanytarsus*–*Paratendipes*. Pre-settlement communities (ca. 1776–1890) were distinct from later assemblages due to elevated *Chironomus* abundance. Since ca. 1890 chironomid assemblages have been unpredictable, despite reduced abundances of *Chironomus* and increases in littoral taxa (Fig. 5c). However, unlike pigment- and diatom-based PCA, chironomid communities during ca. 1931–1976 were not clearly distinguished from the most recent era (1977–1994).

Rate of change—Temporal patterns of community change were broadly similar among all fossil groups since ca. 1776 (Fig. 7). Rates of diatom and chironomid community change were low and non-significant ($P < 0.05$) before the onset of European-style agriculture in 1890, but increased after 1890 and have remained significant to the present. Both fossil assemblages have been characterized by high rates of change since the 1930s and by extreme rates since the mid-1970s. Although algal pigments were more variable in the pre-settlement era than were diatoms and chironomids, variability in fossil pigments also increased from the 1930s to the 1990s (Fig. 7b).

Variance partitioning—Variance partitioning analyses may have been sensitive to missing historical data. We attempted to partition variance for the entire post-settlement period (1890–1994); however, historical records did not extend back to 1890 for some climate (precipitation, evaporation, hydrology) and all fisheries data (Table 3). Although missing values were extrapolated 10–30 years from the earliest available records, analyses of post-1890 time series will underestimate true historical variance in explanatory categories and are not presented or discussed further. Instead, post-1920 data sets included the longest continuous historical records, generally explained the greatest amount of variance in fossil assemblages, and were considered the most reliable of the partitioning analyses (Fig. 8). Comparison of post-1920, post-1950, and post-1970 analyses permitted identification of how the relative importance of control variables varied through time.

Historical changes in climate, resource use, and urban activities all explained significant ($P < 0.05$) amounts of variance in the composition of fossil assemblages, although the relative importance of each category depended on the fossil group and period of study (Fig. 8). In most cases, historical variables accounted for 71–97% of the total variance in fossil diatom, pigment, and chironomid assemblages between ca. 1920 and 1994, suggesting that few important explanatory variables were missed in our analysis (Borcard et al. 1992). However, fossil assemblages differed in whether variance was better explained by direct effects (diatoms, chironomids) or higher order interactions (pigments).

Significant amounts of variance in fossil community composition could be explained by a small subset of the 83 original historical variables (Table 4). Following removal of collinear historical variables, fossil diatoms, pigments, and

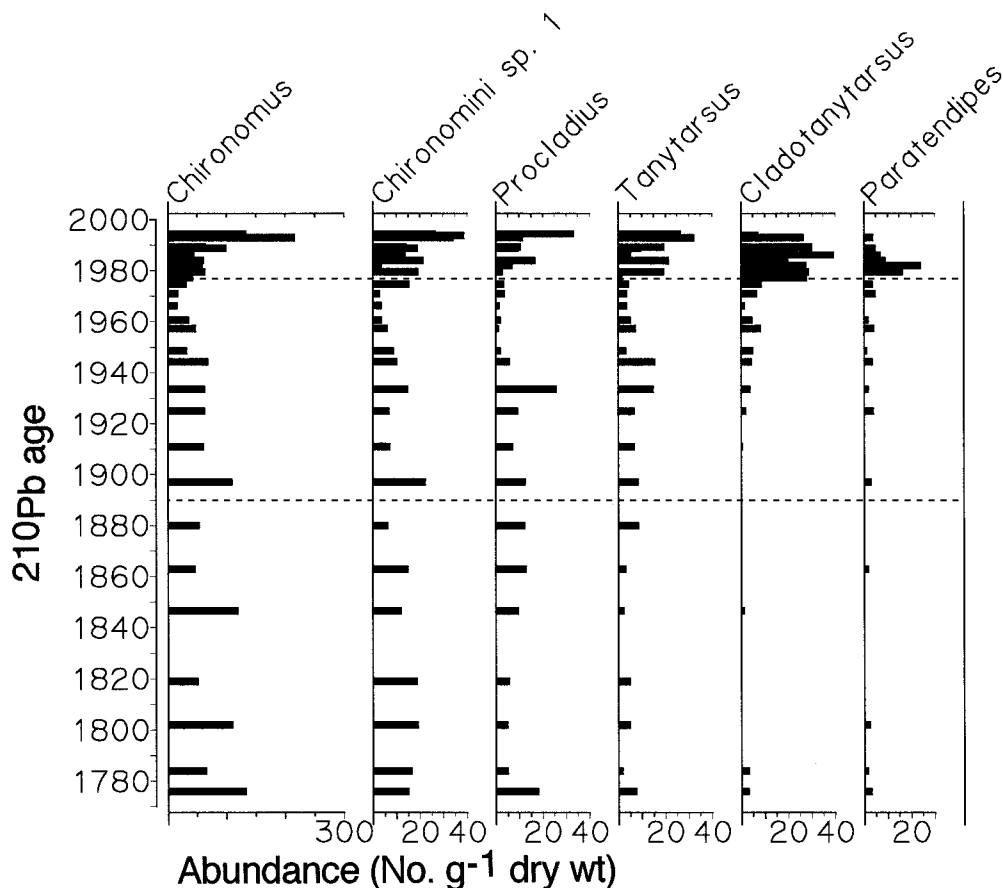


Fig. 6. Temporal changes in concentrations of chironomid remains in the Pasqua Lake sediment core. Dashed lines indicate the onset of European-style agriculture in 1890 and the onset of tertiary sewage treatment in Regina in 1977.

chironomids were significantly correlated with 14, 13, and 11 variables, respectively. The total number of explanatory variables was relatively constant for time-series originating in 1920 and 1950, but declined for post-1970 analyses. Urban population, sewage characteristics, livestock biomass, crop area, and temperature or evaporation had consistently important influence on fossil communities since 1920 (Table 4).

Variance partitioning analysis was sensitive to the length of time encompassed by historical data, as well as the specific fossil assemblage. For example, the ability to explain variance in fossil diatom community composition improved steadily as the duration of study declined from 74 to 24 yr (Fig. 8). In contrast, the ability to explain changes in fossil chironomid composition declined to insignificance during the same period, while the explanatory power of historical data remained relatively constant in analyses of fossil pigments. Similarly, direct effects of explanatory categories (*C*, *U*, *R*) on fossil diatoms or pigments accounted for 29–45% of fossil variance, regardless of the period of study (Fig. 8a,b), whereas main effects accounted for 56% of variance in fossil chironomid assemblages in post-1920 analyses, but only 11% and 0% in post-1950 and post-1970 partitions, respectively (Fig. 8c).

Resource use was usually the single most important ex-

planatory category for fossil diatoms and pigments regardless of the duration of study (14–25%) and was also important in post-1920 analyses of chironomid assemblages (19%). The combined effects of resource use and urban activities independent of climate (*R*, *U*, *RU*), accounted for 38% of the total variance in fossil algal assemblages since 1920 (Fig. 8a,b). In contrast, direct effects of climate independent of human activities (*C*) accounted for only 4–10% of variance in fossil algal assemblages.

To investigate which resource variables were most closely correlated with biotic changes during the periods of complete historical data (1920–1994), we further partitioned the variance explained by resource-use into that attributable to agriculture, aquatic resource use, and their joint effects (Table 5). Agriculture accounted for substantially more variance (12.3–14.5%) than did aquatic resource use (1–6.6%) for all fossil assemblages ca. 1920–1994. Since 1950, most variance in algal communities has been attributable to the joint effects of agriculture and aquatic resources (8–12.9%), whereas changes in chironomid communities were statistically unrelated to either factor. Analyses of the post-1970 data suggested that recent aquatic resource use has influenced diatom communities more strongly than has agriculture, but that fossil pigment composition remained strongly

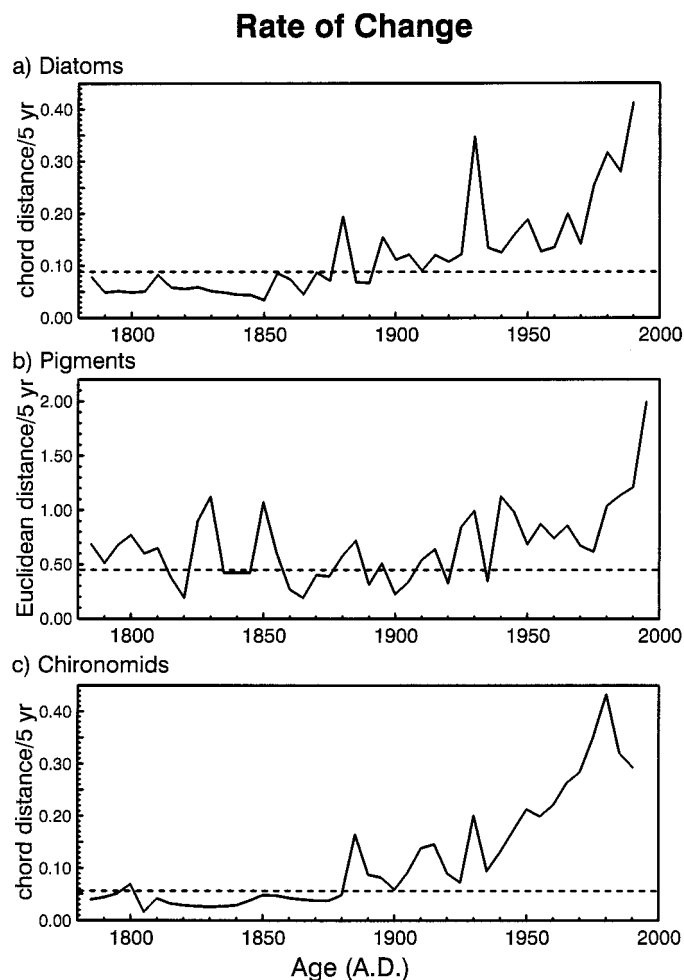


Fig. 7. Rates of community change (chord or Euclidean distance per 5 yr) in Pasqua Lake, ca. 1775–1990 based on (a) diatom percent abundances, (b) algal pigment concentrations [$\log(x + 1)$], and (c) chironomid percent abundances. Dashed lines indicate 95% C.L. based on Monte Carlo tests with 1,000 random permutations.

correlated with the joint influence of agriculture and aquatic resource use (Table 5).

Landscape analysis of past algal biomass—Pasqua Lake is the first site downstream of the cities of Regina and Moose Jaw and may be especially sensitive to urbanization (Fig. 1). To evaluate the importance of landscape position on past changes in total algal abundance, fossil profiles of ubiquitous β -carotene were constructed for the six natural lakes of the Qu'Appelle Valley (Fig. 9). When fossil concentrations were expressed relative to mean levels during the pre-agricultural era (ca. 1776–1890), the increase in inferred algal abundance was greatest in Pasqua Lake. Although pigment concentrations increased concomitant with European style land-use ~1890, β -carotene concentrations greatly increased ca. 1930–1960 and again after 1977, concomitant with tertiary sewage treatment in Regina. Although Pasqua Lake showed the most striking increases in fossil β -carotene relative to pre-agricultural values (>400%), smaller increases (50–75%) also occurred in the downstream Fishing Lakes (Fig.

9). In general, inferred increases in algal abundance were lower downstream of Pasqua Lake and in upstream Last Mountain Lake, which does not receive municipal sewage from Regina (Fig. 1).

Discussion

History of water-quality change—The composition of fossil algal and invertebrate communities demonstrated that Pasqua Lake has been productive throughout the past 200 yr (Fig. 4). Pre-European fossil assemblages included pigments from filamentous and N_2 -fixing cyanobacteria (myxoxanthophyll, aphanizophyll), diatoms characteristic of eutrophic lakes in western Canada (*S. niagarae*, *A. granulata*, *F. capucina/bidens*; Cumming et al. 1995), and chironomids (*Chironomus*) tolerant of low oxygen tensions (Vincent, 1980). Principal components (Fig. 5) and rate of change analyses (Fig. 7) suggested that these communities varied little during the century prior to European-style agriculture. Our findings are consistent with documentation of high concentrations of bioavailable non-apatite P in pre-settlement sediments (Allan et al. 1980) and regular hypolimnetic anoxia in Qu'Appelle lakes during the past 100 yr (Hammer 1973).

Despite the eutrophic nature of Pasqua Lake, analyses of fossil communities inferred that water quality has substantially declined as a result of human activities within the watershed (Figs. 4, 5). Analyses of fossil diatoms, pigments, and chironomids identified ca. 1930–1960 as a period of greatly reduced water quality characterized by elevated algal biomass (β -carotene), near-historical maxima of pigments indicative of nuisance blooms of cyanobacteria (myxoxanthophyll, aphanizophyll), and abundant *S. hantzschii*, one of the most reliable diatom indicators of lake eutrophy (Hall and Smol 1992). Declining concentrations of *Chironomus* fossils (Fig. 6) during that era likely resulted from elevated biological oxygen consumption during decomposition of phytoplankton and organic pollution from Regina's sewage (Doyle unpubl. rep.). During this period, ~70% of N and P in the Qu'Appelle River leading to Pasqua Lake originated from municipal wastes (Peters 1973), taste and odor problems were common, and quality of surface water was reported as insufficient for crop irrigation or consumption by humans or livestock (Doyle unpubl. rep.).

Fossil analyses suggested that water quality in Pasqua Lake may have improved ca. 1960–1970 (Figs. 4, 5), when the abundance of *S. hantzschii*, cyanobacteria, and total algal biomass declined (Fig. 4), yet fossil chironomid abundances remained low (Fig. 6). Unfortunately, the mechanisms producing this change remain obscure, as nutrient flux in sewage increased 5-fold, livestock production doubled, and river discharge was relatively constant (Fig. 2).

Installation of tertiary sewage treatment in Regina substantially reduced TP inputs to the Qu'Appelle drainage since 1977 (Fig. 2f; Munro 1986) but did not improve water quality over levels during 1930–1960. Recent fossil communities have been extremely variable (Fig. 7) with continued high abundance of total algae, nuisance cyanobacteria, and eutrophic diatoms (*S. hantzschii*, *A. granulata*, *F. capucina/bidens*). While increased concentrations of *Chirono-*

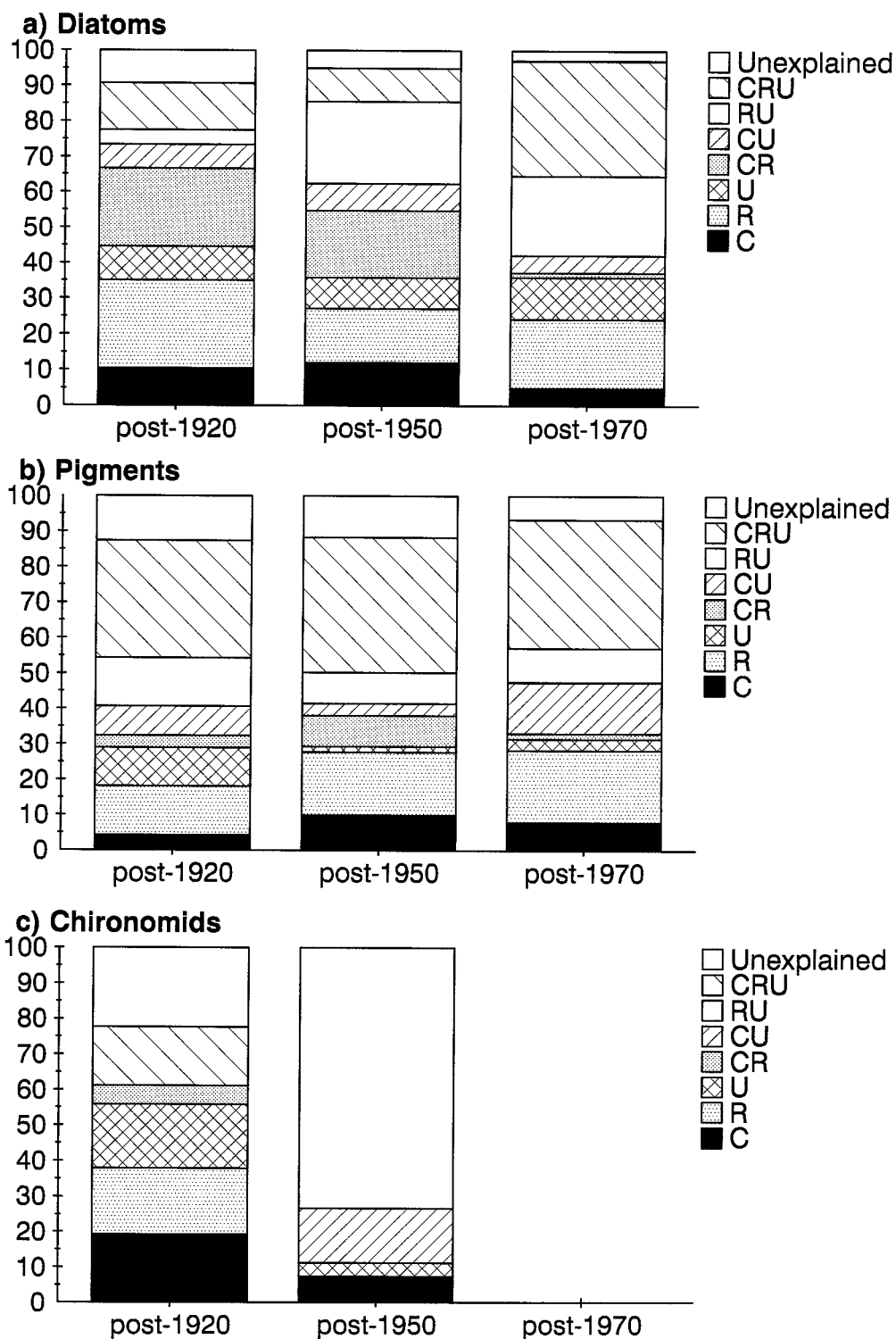


Fig. 8. Effects of climate (C), resource use (R), and urban factors (U) on fossil assemblages of (a) diatoms, (b) pigments, and (c) chironomids from Pasqua Lake determined using variance partitioning analyses with partial canonical ordination. Variance partitioning results for ca. 1920–1993, 1950–1993, and 1970–1993.

Table 5. Relative influence of agriculture (A), aquatic resource use (B), and the joint influence of both factors (A + B) on each fossil assemblage. Number of variables included in predictor categories are indicated in parentheses.

Indicator group	Time period	% of total variance (No. of variables)		
		A	B	A + B
Diatoms	post-1920	14.5 (3)	6.6 (1)	3.6
	post-1950	3.0 (2)	4.1 (2)	8.0
	post-1970	2.7 (2)	13.4 (3)	3.2
Pigments	post-1920	12.3 (3)	1.0 (1)	0.6
	post-1950	3.7 (2)	1.3 (2)	12.9
	post-1970	4.6 (2)	4.3 (3)	11.5
Chironomids	post-1920	14.5 (3)	4.9 (1)	-0.7
	post-1950	0 (0)	0 (0)	0
	post-1970	0 (0)	0 (0)	0

mus are consistent with reductions in the extent or duration of deep-water anoxia (Fig. 6), the rise of littoral and macrophyte-associated chironomid taxa suggests that aquatic macrophytes have become more abundant since 1977. Similar slow responses to sewage diversion have been documented in other basins impacted by agricultural and urban activities (Kitchell 1992). Overall, it is evident that recent algal and chironomid communities have remained distinctly different from those that existed before European settlement.

Similar trends in pigment and diatom assemblages strongly suggest that changes in water quality, rather than diagenetic events, produced the historical changes recorded in the fossil record. Interpretation of fossil pigment signals in surface sediments (<10 yr old) can be problematic because elevated concentrations of pigments arising from increased algal abundance cannot be reliably distinguished from patterns produced by incomplete in situ degradation (Leavitt 1993; Leavitt and Findlay 1994). Pigment degradation occurs most intensely in the water column, but residual pigment molecules can continue to degrade in surface sediments (e.g., Leavitt and Carpenter 1990a, b) particularly when exposed to elevated oxygen content (Hurley and Armstrong 1991). Similarly, elevated pigment concentrations ca. 1930–1960 (Fig. 4b) could have resulted from greater algal production or from enhanced preservation under increased anoxia (Leavitt 1993). However, the observation that morphological fossils are less susceptible to changes in oxygen than are pigments (Bendz and Lindqvist 1978), yet provide a similar history of water-quality change, suggests that all fossil communities are responding more directly to environmental controls than post-depositional artifacts.

Identifying mechanisms that regulate community change—Variance partitioning identified resource use and urbanization as the strongest correlates of biological change in Pasqua Lake (Fig. 8). The combined effects of resource use and urban activities (*R*, *U*, *RU*), independent of climate, accounted for 37–38% of total variance in fossil assemblages since 1920. In particular, analysis of algal community change since 1920 demonstrated that the long-term influence of resource use on algae was mediated mainly through changes

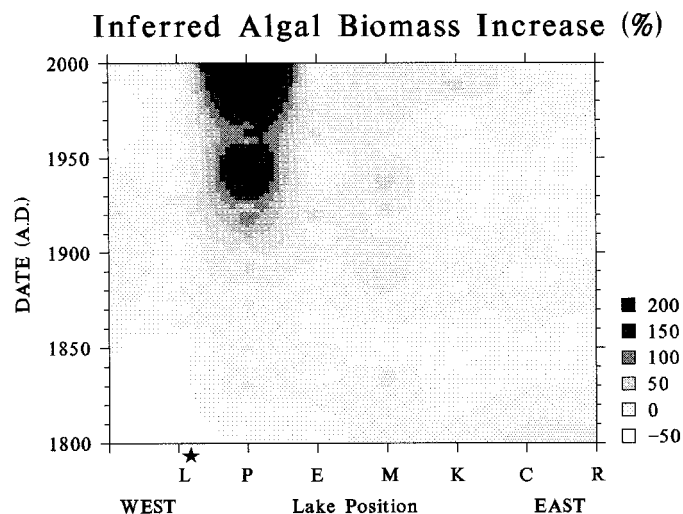


Fig. 9. Inferred changes in total algal biomass relative to mean pre-agricultural values in natural lakes of the Qu'Appelle Valley. Lakes arranged on a landscape gradient from west to east (see Fig. 1). Municipal sewage enters the system below Last Mountain Lake (*). Dark areas indicate large increases in total algal biomass, inferred as fossil β -carotene. Inferred increases in algal biomass plotted using a distance-weighted least-squares smoothing function (Wilkinson 1989). Lakes include Last Mountain (L), Pasqua (P), Echo (E), Mission (M), Katepwa (K), Crooked (C), and Round (R).

in terrestrial practices involving livestock or crops (Tables 4, 5). While the effects of climatic variables on biotic assemblages were also important, climate impacts were mediated by human activity, as demonstrated by the high proportion of variance attributable to factor interactions (i.e., *CU*, *CR*, *CRU*) rather than to direct effects (*C*; Fig. 8).

Landscape-level paleoecology confirmed the importance of urban factors in regulating water quality in Pasqua Lake (Fig. 9). Concentrations of β -carotene in sediments of Pasqua Lake increased sharply after ca. 1930, and peaked during the 1970s (Fig. 4) when Regina's population and sewage nutrient inputs were greatest (Fig. 2e,f). β -carotene is the most chemically stable of the algal carotenoids and provides the most reliable index of changes in total algal standing crop (Leavitt and Carpenter 1990a,b; Leavitt and Findlay 1994). Consequently, analysis of fossil β -carotene in other Qu'Appelle lakes indicated that the greatest increases in algal abundance occurred in Pasqua Lake and that the magnitude of change declined in both upstream and downstream lakes. These patterns are consistent with mass balance budgets during the 1970s which estimated that >60% of TP in the Qu'Appelle basin was derived from Regina sewage which enters the valley upstream of Pasqua Lake (Qu'Appelle Basin Study Bd. 1972).

Variance partitioning explained a high proportion of variance in algal communities (71–97%; Fig. 8), indicating that few important explanatory variables were missed by our analyses (Borcard et al. 1992). High explained variance also suggests that any inaccuracies in sediment chronology did not seriously alter relationships among environmental factors and biotic responses. Unexpectedly, little variance was explained by post-1950 and post-1970 partitions of chironomid

assemblages (11% and 0%, respectively). We hypothesize that the absence of significant explanatory variables indicates that short-term fluctuations in chironomid community composition were regulated by factors other than those included in our analyses (e.g., macrophyte abundance, oxygen tension, sediment contamination), such as has been demonstrated for living populations (Vincent 1980). We infer that low explained variance did not result from shorter time-series and low sample size in post-1950 analyses, because diatom analyses with similar sample size and shorter time-series (post-1970, $n = 15$) to those of chironomids (post-1950, $n = 14$) explained substantially more variance (97% vs. 27%; Fig. 8).

Management of prairie lakes—Variance partitioning and landscape analyses of century-long historical and fossil records allow formulation of specific recommendations for prairie lake managers. First, fossil analyses demonstrated that Pasqua Lake is a naturally eutrophic lake and should not be managed for low productivity. Second, despite high baseline production, present water quality in Pasqua Lake is considerably worse than before European settlement, with high total algal biomass, nuisance cyanobacteria, and poor oxygen content reducing deep-water fish habitat. Consequently, water-quality improvements are possible, as indicated by the return of abundant *Chironomus* populations and greater inferred deep-water oxygen availability since 1977 (Figs. 4c, 6; Warwick 1980). However, recent increases in littoral macrophyte-associated chironomids (e.g., *Cladotanytarsus*, *Cricotopus*; Beattie 1982) suggest that aquatic weeds are currently more abundant than at any other time in the past 200 yr. Managers must consider that further water-quality improvements may lead to a new state characterized by abundant macrophytes, such as seen in shallow European lakes in agricultural basins (e.g., Mortensen et al. 1994).

Third, management strategies should further investigate the role of sewage inputs, agriculture, and reservoir hydrology on water quality. For example, variables reflecting nutrient export from Regina's sewage (Regina population, TP and TN fluxes, TN:TP), cropland area, livestock biomass, and discharge volume from Lake Diefenbaker consistently accounted for significant variance in fossil pigments, diatoms, and chironomids (Table 4). Although climate variables related to the length of the ice-free season were also important (ice-free days, T_{\max} and T_{\min} in spring and fall), these factors cannot be regulated.

Fourth, nutrient abatement programs should reduce N inputs to Qu'Appelle lakes. Fossil data show that inferred algal abundance and water quality has not substantially improved in Pasqua Lake since 1977, despite tertiary sewage treatment which reduced P loading to levels of the 1930s (Figs. 2, 4). Although high interannual variability in recent plankton composition is symptomatic of lake recovery following sewage diversion (e.g., Kitchell 1992), P control alone has not substantially reduced inferred algal abundance even after 20 yr (Fig. 4). Not surprisingly, several lines of evidence suggest that P supply does not limit algal growth in Qu'Appelle lakes. For example, P-chlorophyll models greatly underestimate algal biomass as Chl *a* (Chambers 1989), as occurs in other subsaline prairie lakes (Campbell and Prepas 1986).

As well, bottle bioassays during 1994–1996 regularly demonstrate algal growth limitation by N or N + P, but not by P alone (Graham 1997). Finally, low N:P ratios (<5:1, by atom; Table 2) favor N₂-fixing cyanobacteria, consistent with overall limitation of algal growth by N availability (Tilman et al. 1986). Presently, tertiary sewage treatment does not reduce N inputs from Regina, and export of N to the Qu'Appelle Valley drainage at a historical maximum (Fig. 2f). Installation of modern N-removal systems should greatly improve water quality in Pasqua Lake, once initial blooms of N₂-fixing cyanobacteria have abated.

Finally, managers must recognize that the most effective method of water-quality control will likely vary with position of the lake within the catchment. Landscape analysis demonstrated that urban impacts were greatest in Pasqua Lake, but diminished with distance from sewage inputs (Fig. 9). Consequently, reduction of municipal nutrient flux may only improve water quality in Pasqua and adjacent Fishing Lakes. Downstream lakes (Katepwa, Round, Crooked) are presently the most productive within the Qu'Appelle (Table 2), experience extensive cyanobacterial blooms during May–September (Hammer 1971; Graham 1997), and have exhibited whitefish kills during the past 150 yr (Hammer 1973). Given that European-style land use has had comparatively little impact on inferred total algal abundance in these eastern lakes, it seems unlikely that urban sewage treatment will effectively improve their water quality.

In conclusion, paleoecological analyses have demonstrated that algal and invertebrate communities in prairie lakes are subject to significant impacts of human land-use practices that obscure the effects of climatic change. Cropland area, livestock biomass, and urban nitrogenous wastes were especially potent controls of algal abundance and water quality, particularly in mid-drainage lakes that receive sewage inputs. However, the combination of variance partitioning and landscape analysis of fossil records suggests that the precise management strategy will vary with lake position within the drainage basin.

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