

Landscape effects of climate, agriculture, and urbanization on benthic invertebrate communities of Canadian prairie lakes

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Abstract

Paleoecological analyses of fossil chironomid assemblages from eight lakes of the Qu'Appelle Valley, Saskatchewan, Canada, were used to quantify the relative influence of climate, resource use, and urbanization on benthic invertebrate communities 1850–1995. Fossil analyses inferred that Qu'Appelle lakes are naturally productive but that invertebrate communities were altered by agriculture and urbanization. In western lakes, rates of community change (chord distance per 5 yr) were low and nonsignificant ($P > 0.05$) prior to European settlement, but increased twofold after ~1930–1940. In contrast, uniformly significant rates of community change were recorded in eastern downstream lakes only after the 1960s. In both cases, high rates of change corresponded to alterations in the balance between deep-water (*Chironomus*) and littoral species (*Cladotanytarsus mancus* group, *Tanytarsus* s.lat. [s.l.]). Comparison of historical and fossil time series (~1920–1993) using variance partitioning analysis (VPA) explained up to 86.6% of past variations in chironomid community composition. Unexpectedly, climate (winter temperature) explained a significant ($P < 0.05$) and substantial (mean \pm SD, $n = 8$; $24.8 \pm 21.9\%$) amount of community variance at all sites except Round Lake. In contrast, land-use practices exhibited significant but less substantial ($6.7 \pm 6.1\%$, $n = 8$) impacts on zoobenthos of five lakes, whereas significant urban impacts ($3.6 \pm 7.5\%$, $n = 8$) were recorded only at two sites. Similarly, redundancy analysis showed that minimum winter or spring temperature significantly influenced the relative abundance of littoral taxa in seven lakes. Such strong effects of climate on benthic invertebrate communities contrast its weak effects on phytoplankton in these lakes and suggest that future environmental change may be expressed differentially among habitats.

As with many North American landscapes, prairie ecosystems have been subjected to multiple stresses, including

climate change, agricultural development, and urbanization. Consequently, surface waters in prairie landscapes are often

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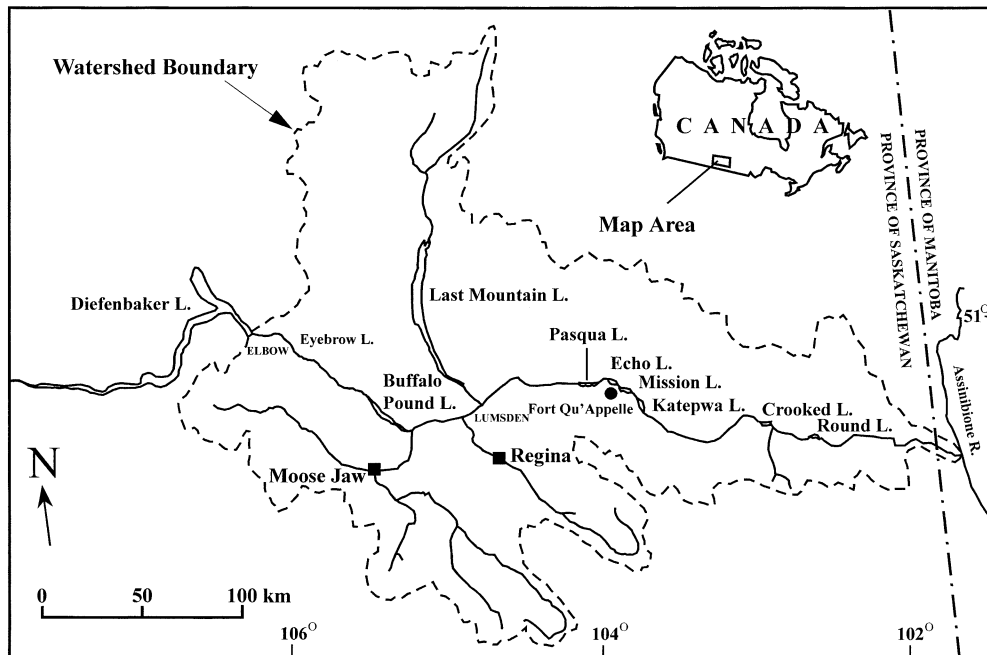


Fig. 1. Qu'Appelle River Valley drainage basin. The river flows from headwater Lake Diefenbaker through to Round Lake. Last Mountain Lake does not naturally receive water from the Qu'Appelle River, and sewage inputs from Moose Jaw and Regina first enter at Pasqua Lake.

degraded and exhibit elevated nutrient concentrations, low N:P ratios, blooms of toxic cyanobacteria, and periodic fish kills (Hammer 1971; Haertel 1976; Allan 1980; Chambers 1989). These patterns are particularly evident on a landscape basis, where lowland lakes draining upland agricultural areas are characterized by relatively high conductivity, nutrient content, and algal abundance, along with low water clarity relative to headwater systems (Soranno et al. 1999). Paleoecological analyses suggest that these changes in water quality result from a combination of agricultural practices and urbanization (Kitchell and Sanford 1992; Dixit et al. 2000) but that climatic influences account for only 5–10% of variance in algal communities during the 20th century (Hall et al. 1999a). Unfortunately, little is known of the response of benthic invertebrate communities to such multiple stressors, nor of how their responses might vary along a landscape gradient of point and nonpoint disturbances.

In lieu of monitoring data, paleolimnological analyses of fossil invertebrate communities can provide evidence of past trophic structure (Jeppesen et al. 1996), habitat alterations (Brodersen et al. 1998), secondary production (Hall and Yan 1997), microevolutionary processes (Hairston et al. 1999), and climate change (Lotter et al. 1999). In particular, analyses of fossil chironomids can identify changes in benthic conditions, including chemistry (oxygen, pH, salinity), habitat (macrophytes, substrates), and predation regime (reviewed in Walker 2001). Whereas algae are affected predominantly by short-term local factors (Allen et al. 1999), chironomids are more influenced by primary production (Berg and Hellenthal 1992), benthic oxygen (Little and Smol 2001; Quinlan and Smol 2001), water chemistry (Verschuren et al. 2000), and substrate conditions (Cogerino et al. 1995), factors that integrate environmental change over seasonal to

annual timescales (Walker et al. 1991; Walker 2001). Fortunately, with recent advances in variance partitioning techniques (Borcard et al. 1992; Hall et al. 1999a), it is now possible to quantify the statistical relationships to, and relative importance of, historical environmental change in relation to past invertebrate community variability.

The focus of this paper is to (1) document the changes that have occurred in the subfossil chironomid assemblages of prairie lakes in Canada following ancestral European settlement (~1890); (2) use variance partitioning analysis (VPA) to quantify the relative influences of climate, resource use, and urban factors on chironomid assemblages during the 20th century; and (3) determine whether lake position within the hydrologic landscape influences benthic community response to such multiple stressors.

Our analyses are based in the Qu'Appelle Valley, Saskatchewan, a watershed that supplies water to one-third of the population of the Canadian prairies (Hall et al. 1999a). Aquatic ecosystems of the Qu'Appelle Valley are important for fisheries, irrigation, livestock, and domestic water supply (Hammer 1971) but suffer from poor water quality, particularly in the eastern hypereutrophic lakes where blooms of potentially toxic *Microcystis* (Chambers 1989) and fishkills are common (Qu'Appelle Basin Study Board 1972).

Methods

Study area—The Qu'Appelle River is located in southern Saskatchewan, Canada, and extends from Lake Diefenbaker in the west to its eastern confluence with the Assiniboine River at the Saskatchewan–Manitoba border (Fig. 1). The Qu'Appelle Valley watershed contains seven major lakes and

Table 1. Selected mean characteristics of Qu'Appelle Valley lakes. Data averaged for 1994–2000 from Hall et al. (1999a,b), Dixit et al. (2000), Soranno et al. (1999), Graham (1997), and unpublished analyses. na, values not available; *, estimated using N:P ratios. Mean sediment parameters (mean \pm SD) were calculated for the period 1920–1993.

Lake	Area (km ²)	Volume (m ³ \times 10 ⁶)	Mean depth (m)	Conductivity (μ S cm ⁻¹)	pH	Dissolved			DOC (mg C L ⁻¹)	Water residence (yr ⁻¹)	Sediment accumulation (mm yr ⁻¹)	Depth-age correlation (r ²)	Organic matter content (%)
						Dissolved nitrogen (μ g L ⁻¹)	phosphorus (μ g L ⁻¹)	Chl (μ g L ⁻¹)					
Buffalo Pound	29.1	87.5	3.0	480	8.4	500	185	6	8.0	0.7	2.9 \pm 0.1	0.97	11.8 \pm 0.7
Last Mountain	226.6	1,807.2	7.9	2,050	9.1	580	130	11	11.5	12.6	3.9 \pm 0.0	1.00	21.5 \pm 3.0
Pasqua	20.2	120.8	5.8	2,100	8.5	1,850*	270	25	na	0.7	5.7 \pm 0.1	0.98	20.1 \pm 3.1
Mission	12.5	122.1	9.8	1,200	8.5	na	na	16	na	0.7	3.7 \pm 0.1	0.99	18.3 \pm 2.8
Echo	7.7	62.9	8.2	1,200	8.5	na	na	24	na	0.4	4.3 \pm 0.1	0.99	16.6 \pm 1.7
Katepwa	16.2	233.2	14.3	1,150	8.5	760	285	13	10.5	1.3	4.1 \pm 0.0	1.00	17.9 \pm 3.1
Crooked	15.0	120.9	7.9	1,350	9.1	1,050	600	22	10.5	0.5	5.2 \pm 0.1	0.99	13.9 \pm 1.4
Round	10.9	83.9	7.6	na	na	na	na	na	na	na	3.6 \pm 0.1	0.97	11.8 \pm 0.6

two reservoirs (Table 1). Lake Diefenbaker was formed by inundation of a dry valley in 1968, whereas Buffalo Pound Lake was deepened following dam construction in 1952 (Hall et al. 1999b). Last Mountain Lake occupies an adjacent valley that flows into the Qu'Appelle River. Pasqua Lake is the first lake to receive domestic sewage from the cities of Moose Jaw and Regina. Pasqua Lake is also the first of four closely situated lakes, termed the Fishing Lakes, which also include Echo, Mission, and Katepwa Lakes. The town of Fort Qu'Appelle (population 3,931; Statistics Canada 1991) is located between Echo and Mission Lakes. Crooked Lake and Round Lake are situated approximately 75 and 90 km downstream, respectively, from the Fishing Lakes.

The Qu'Appelle Valley originated as a glacial meltway during the retreat of Pleistocene ice sheets and is a wide, deep valley within which the much smaller present-day river flows. The landscape is of low relief, characterized by flat stretches and small rolling hills. Most Qu'Appelle lakes were formed at locations where alluvial fans from glacial tributaries restricted the flow of the Qu'Appelle River (Hammer 1971). The Qu'Appelle watershed was formerly a parkland and mixed-grass prairie but has been largely converted to agricultural fields and pastures (Hall et al. 1999a). The dry climate consists of cold winters (avg. -18.3°C in January) and warm summers (avg. 18.3°C in July), and lakes are ice-covered for 4–5 months (Hammer 1971; Hall et al. 1999a).

Qu'Appelle Valley lakes (Table 1) are mesotrophic to hypereutrophic (mean chlorophyll *a* [Chl *a*] 6–25 $\mu\text{g L}^{-1}$, dissolved P 130–600 $\mu\text{g L}^{-1}$), with N-limited algal production (N:P < 5:1, by mass; Hall et al. 1999a; Soranno et al. 1999). All lakes are alkaline (pH 8.2–9.1) and slightly saline (conductivity 480–2,050 $\mu\text{S cm}^{-1}$). Most of the natural lakes are of moderate size (770–2,910 ha), with the exception of Last Mountain Lake (22,660 ha), are shallow (maximum depth: 5.5–30.8 m), and exhibit weak thermal stratification.

The Qu'Appelle drainage has undergone dramatic changes over the last century, with conversion of 95% of grassland to field crops and pasture (since \sim 1890), growth of urban centers and sewage efflux (after 1930), fisheries and hydrologic management (since \sim 1900), and long-term climatic warming (Hall et al. 1999a). Previous paleoecological research has demonstrated that these lakes are naturally productive because of high P loading (Allan et al. 1980) but that water quality declined after the onset of agriculture and intensive urbanization, particularly in sites directly downstream from sewage outfalls (Hall et al. 1999a; Dixit et al. 2000). Analysis of fossil pigments and diatoms further suggests that sewage effects were rapidly filtered out within the Fishing Lakes chain, and that downstream Crooked and Round Lakes exhibited little response to urbanization (Hall et al. 1999a; Dixit et al. 2000). At Buffalo Pound and Pasqua Lakes, past chironomid assemblages were characteristic of productive lakes with low concentrations of oxygen in deep waters (Warwick 1982; Hall et al. 1999a,b).

Field and laboratory methods—Lake sediments were collected from the deep-water regions of Last Mountain, Pasqua, Echo, Mission, Katepwa, Crooked, and Round Lakes in March 1995 using standard freeze coring techniques (Hall et al. 1999a). Sediments from Buffalo Pound were collected

in July 1996 using a gravity corer. Lake Diefenbaker was not analyzed herein because its history was not sufficiently long (<30 yr) to allow variance partitioning analyses comparable to those at other sites (see below). All cores were sectioned at 0.5-cm intervals from 0–15 cm and at 1.0-cm intervals thereafter. Freeze corers were cleaned, thawed, and dewatered in a dark cold room before being sectioned (Hall et al. 1999a), whereas the gravity core was sectioned at lake-side. Geochronologies, which were used to estimate fossil assemblage ages for comparison with concomitant historical data, were established using ^{210}Pb analyses and the constant rate of supply calculations (details in Hall et al. 1999a,b).

For chironomid analyses, 1–9 g wet mass of sediment were deflocculated in 10% KOH for 2–3 d at room temperature then were washed through a 95- μm sieve. Sediments retained on the mesh were sorted for chironomid head capsules at $\times 20$ –60 magnification using a dissecting microscope. Head capsules were mounted onto glass microscope slides using Euparal[®] mounting medium and were identified to the lowest possible taxonomic designation with reference to Wiederholm (1983), Walker (1988), and Oliver and Rousel (1983). Where possible, sediment intervals were subsampled further if sufficient chironomid remains were not found (<40 head capsules). In some instances, adjacent intervals were pooled if resampling failed to yield sufficient remains.

Numerical methods—All numerical analyses were based on chironomid taxa that had a relative abundance of >2% in at least one sample in any lake. Long-term patterns of chironomid community change were summarized using principal components analysis (PCA). All lakes were included in the PCA ordinations to allow quantitative comparison of chironomid changes among sites (Dixit et al. 2000). Ordinations were scaled to focus on intersample distances and were centred by species using CANOCO 4.0 for Windows (ter Braak and Smilauer 1998).

Rates of change of chironomid communities were quantified using chord distance per 5 yr (Hall et al. 1999a). Prior to calculating rates of change, chironomid data were interpolated at linear 5-yr intervals. All start dates were standardized to 1990 because pooling of surface sediment samples otherwise resulted in inconsistent time series lengths. Confidence limits (95%) for rates of change were estimated from fossil data using randomizations with 1,000 Monte Carlo permutations.

Similar to Hall et al. (1999a), variance partitioning using redundancy analysis (RDA) was used to explore the relationships between changes in fossil chironomid communities and categories of concomitant historical data, including climate (C), urbanization (U), and resource use (R; agriculture, fisheries). Details of historical data and their sources are presented in Hall et al. (1999a). Briefly, annually resolved climate data consisted of seasonal evaporation (net, gross; mm), precipitation (mm), and air temperature (minimum, maximum; $^{\circ}\text{C}$), as well as ice thaw and freeze dates (calendar day of year: DOY) for the Red River at Winnipeg, Manitoba (east of the Qu'Appelle Valley), and discharge volume (10^6 L yr^{-1}) of the Qu'Appelle River at Lumsden, Saskatchewan (Fig. 2). Average climatic conditions were calculated for spring (Apr–May), summer (Jun–Aug), fall (Sep–Oct), and

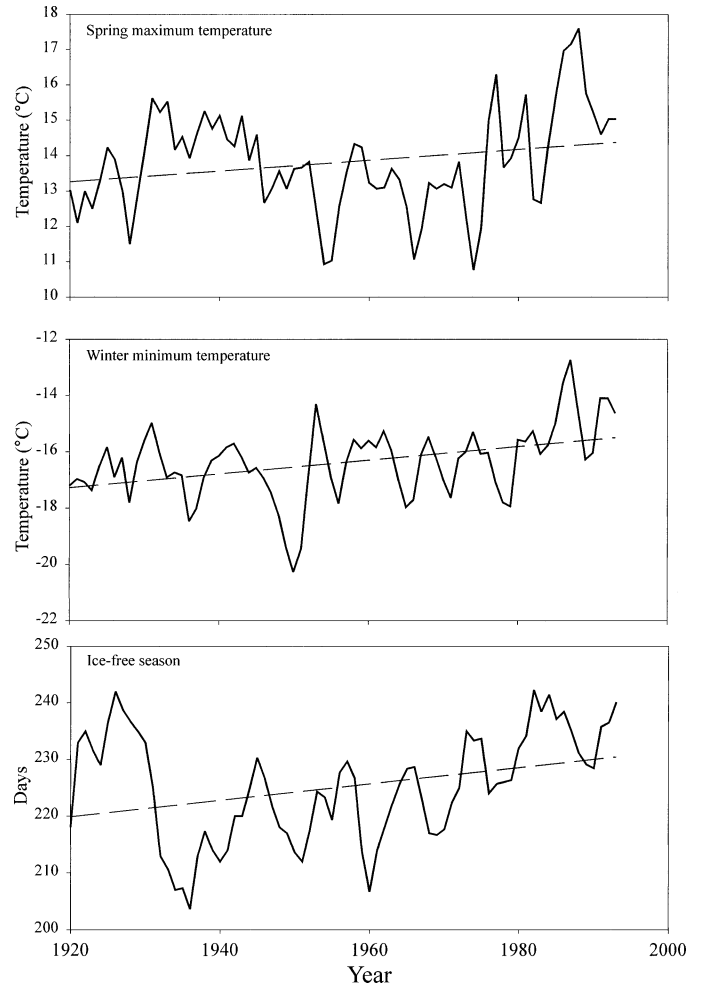


Fig. 2. Climatic variation in the Qu'Appelle River drainage basin, 1920–1993, for selected variables. Mean annual observations of air temperature from Indian Head, Saskatchewan, were used to estimate annual patterns in seasonal climatic change. See text and Hall et al. (1999a) for further description. The solid line represents a 3-yr moving average of the data to illustrate subdecadal trends. The dashed line represents a simple linear regression of the data to illustrate a long-term trend.

winter (Nov–Mar) using arithmetic means (temperature) or sums (precipitation, evaporation) of average monthly data based on daily observations. Resource-use variables included discharge volume (10^6 L yr^{-1}) from Lake Diefenbaker measured at Elbow, Saskatchewan, livestock biomass (tons, t), area of field crops and total farmland (ha), and commercial fish harvest (t) and stocking (no. of fish). For Buffalo Pound, annual maximum and minimum lake levels (m, above sea level) and annual fluctuation in lake depth (m) also were used as resource variables. Annual extraction of water from Buffalo Pound (10^6 L yr^{-1}) was included as a resource variable for Buffalo Pound and downstream lakes. For Qu'Appelle lakes downstream of Regina and Moose Jaw (Pasqua to Round Lakes), urban variables included populations of Regina and Moose Jaw, the rural population of the catchment, total P (TP) and total N (TN) input (kg) from Regina's sewage, and the TN:TP ratio of Regina's sewage.

Table 2. Species codes for chironomid taxa retained for principal components analysis (>2% in one sample).

Taxon	Code	Taxon	Code
1. <i>Chironomus</i>	CHIRON	13. <i>Stictochironomus</i>	STICTO
2. <i>Chironomini</i> sp. 1	CHRSP1	14. <i>Xenochironomus</i>	XENOCH
3. <i>Cladopelma</i>	CLADOP	15. <i>Cladotanytarsus mancus</i> group	CLDTNY
4. <i>Cryptochironomus</i>	CRYPTC	16. <i>Microspectra</i> type	MICROP
5. <i>Cryptotendipes</i>	CRYPTE	17. <i>Tanytarsus</i> s.l.	TANYSL
6. <i>Dicotendipes</i>	DICROT	18. <i>Procladius</i>	PROCLD
7. <i>Endochironomus</i>	ENDOCH	19. Tribe Pentaneurini	PENTAN
8. <i>Glyptotendipes</i>	GLYPTO	20. <i>Tanypus</i>	TANYPU
9. <i>Microtendipes</i>	MICROT	21. <i>Corynoneura/Thienemanniella</i>	CORYTH
10. <i>Parachironomus</i>	PARACH	22. <i>Cricotopus/Orthocladius</i>	CRICOR
11. <i>Paratendipes</i>	PARATE	23. <i>Nanocladius</i>	NANOCL
12. <i>Polypedilum</i>	POLYPE	24. <i>Psectrocladius</i> subgenus <i>Psectrocladius</i>	PSECTP

Upstream and side-valley lakes (Buffalo Pound, Last Mountain) had only rural population as an urban variable. An unweighted three-point moving average was used to smooth all historical time series prior to analyses, as described by Hall et al. (1999a).

VPA of fossil chironomid communities was performed on time series spanning 1920–1993. Significant variables within each explanatory category were selected using the methodology of Hall et al. (1999a). In summary, variables were retained only if they explained a significant ($P = 0.05$) amount of variance in the fossil chironomid data based on

RDAs constrained to that variable alone. Subsequent RDAs were performed constrained to all significant variables within a category, and explanatory variables with the highest variance inflation factor (VIF) were sequentially eliminated until all VIFs were <5 (Hall et al. 1999a). Analyses were conducted using RDAs because preliminary analysis of gradient length ($\ll 2$ SD) using detrended correspondence analysis showed that linear methods of ordination were more appropriate than unimodal techniques (Birks 1995).

Ordinations using RDA were used to further investigate the relationship between climate change during the 20th century and variations in fossil composition. As with PCA, an RDA with all lakes was used to identify overall climate–species relationships during 1920–1993, whereas lake-specific analyses were conducted to identify variability in forcing relationships among sites. Significant climatic variables were identified and included as detailed above for VPA.

Results

Subfossil chironomid taxa (32) were found in sediments from the eight natural lakes; 24 were retained after eliminating rare taxa (see Table 2 for taxon codes). PCA of data from all lakes explained 54.7% of historical variation along the first PC axis and 15.6% along the second axis (Fig. 3). Taxon scores showed an agglomeration of littoral taxa within the center of the ordination and clear separation of taxa characteristic of deep-water habitats (primarily *Procladius*, *Chironomus*) or littoral substrates (*Cladotanytarsus mancus* group, *Paratendipes*, *Cricotopus/Orthocladius*, *Endochironomus*).

Buffalo Pound Lake—Historical changes in chironomid communities at Buffalo Pound Lake have been described by Hall et al. (1999b). Briefly, fossil chironomid assemblages over the past ~200 years were indicative of productive conditions (*Chironomus*) and dense macrophyte habitats (*Glyptotendipes*, *Cricotopus/Orthocladius*). Trends from ~1780 to ~1930 involved gradual declines in *Endochironomus*, *Glyptotendipes* and *Cricotopus/Orthocladius* and increases in *Chironomus*, *Chironomini* sp. 1, and predaceous *Procladius*

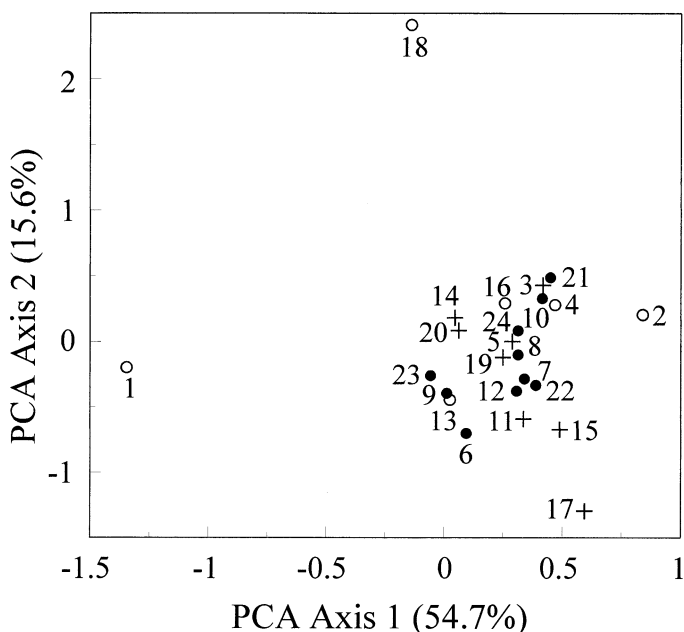


Fig. 3. Taxon scores in a principal components analysis (PCA) of fossil chironomid data in sediment cores from the natural lakes of the Qu'Appelle River Valley (Buffalo Pound and more eastern lakes), including taxa that appeared in at least one sample with a relative abundance of >2%. Taxon codes are given in Table 2. Solid circles, taxa commonly associated with aquatic macrophytes (Brodersen 1998); crosses, other littoral taxa; open circles, taxa indicative of deep-water habitat (Sæther 1979).

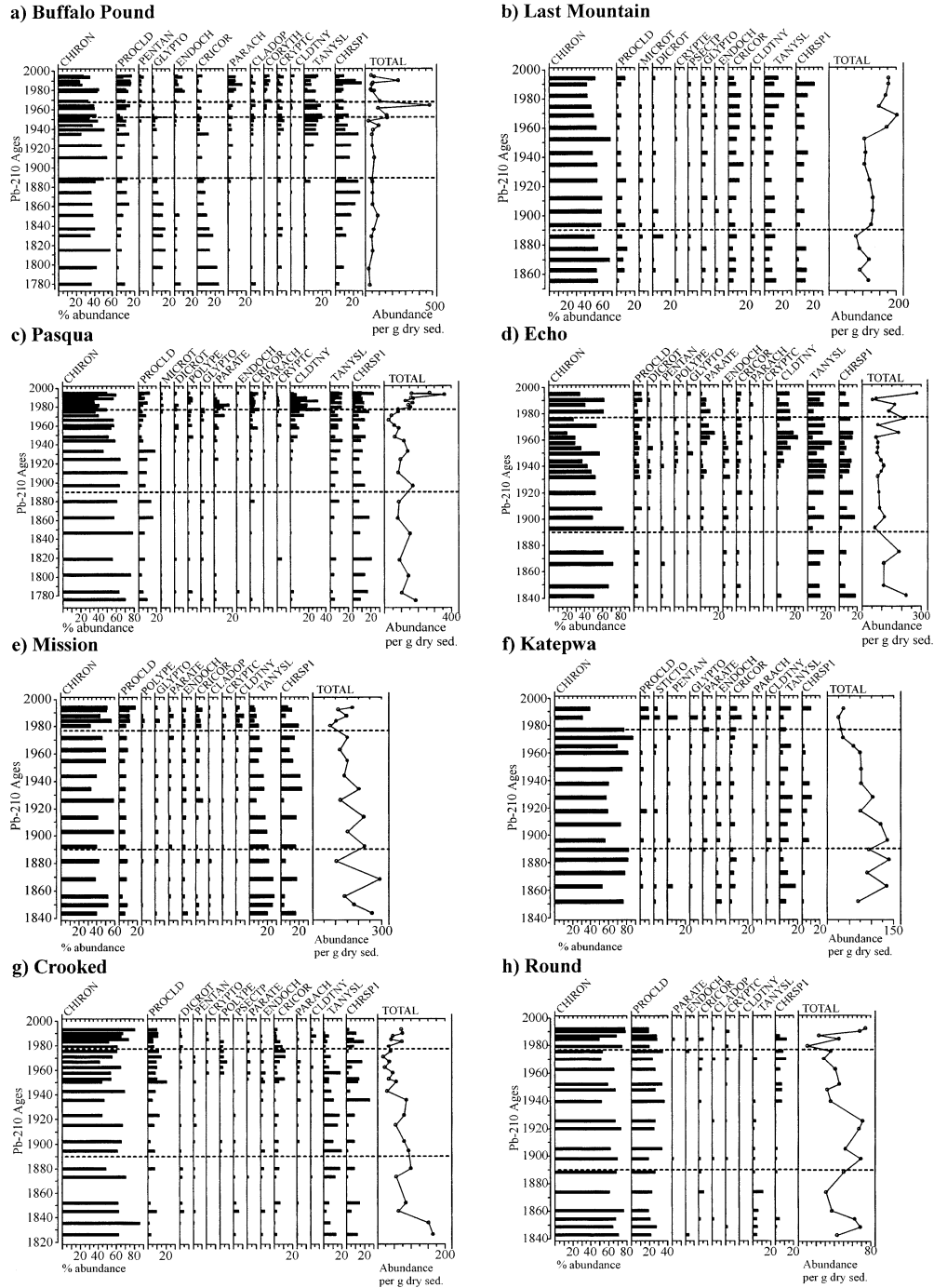


Fig. 4. Fossil chironomid profiles in Qu'Appelle Valley lakes, ca. 1800–1995. All taxa are percent relative abundance, TOTAL is individuals g^{-1} dry mass of sediment. Taxa are arranged from left to right in order of increasing PCA axis 1 score; sites are arranged west (a) to east (h). Lowermost dashed line represents the onset of agriculture (1890); uppermost dashed line is the start of tertiary sewage treatment, except at Last Mountain (no sewage) and Buffalo Pound Lakes (top, water diversion 1969; middle, impoundment 1952).

(Fig. 4a). Chironomid communities from ~1930 to ~1980 also included relatively high abundances of *Tanytarsus* s.l., whereas littoral taxa were slightly more common in post-1980 assemblages. Absolute concentrations of most chironomids increased after lake impoundment in 1952 and re-

mained high until ~1968, when water was introduced from Lake Diefenbaker. Although variable, ca. post-1968 densities were similar to those of the preimpoundment era.

When considered in context of community change throughout the Qu'Appelle Valley drainage, PCA ordination

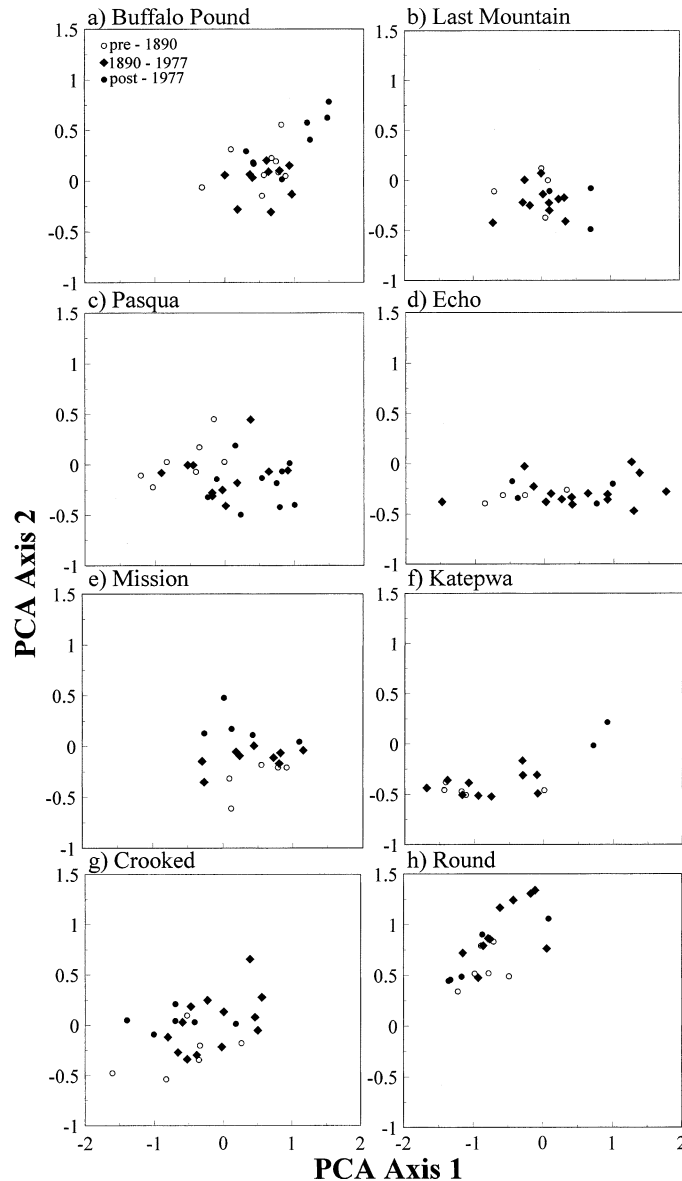


Fig. 5. PCA sample scores of fossil assemblages from Qu'Appelle Valley lakes, ca. 1800–1995. Presettlement communities (open circle) are distinguished from those arising after sewage treatment (solid circle) or in the intervening period (solid triangle). Sites are arranged west (a) to east (h).

of Buffalo Pound chironomid assemblages showed that taxonomic composition varied only subtly as a consequence of initial agricultural activities (~1890), lake impoundment (1952), or water diversion (1968; Fig. 5a).

Last Mountain Lake—Fossil assemblages from Last Mountain Lake contained taxa characteristic of productive, anoxic conditions (*Chironomus*, *Chironomini* sp. 1, *Procladius*) throughout the past ~150 yr (Fig. 4b). Although relative abundances fluctuated slightly for littoral taxa such as *Dicrotendipes*, *Glyptotendipes*, *Cricotopus/Orthocladius*, *Endochironomus*, and *Tanytarsus* s.l., there were few discernible patterns beyond slight declines in *Chironomus* and *Procladius* after ~1930. Similarly, absolute chironomid densities increased slightly after ~1890 and again after ~1970,

mainly because of *Chironomus*, *Chironomini* sp. 1, *Tanytarsus* s.l., and *Cricotopus/Orthocladius*.

Ordination of the Last Mountain Lake communities confirmed that the composition of fossil assemblages varied little through time (Fig. 5b). In general, the most recent assemblages clustered away from presettlement communities, reflecting a higher relative abundance of *Chironomini* sp. 1 and *Tanytarsus* s.l.

Pasqua Lake—Preagricultural chironomid communities in Pasqua Lake (Fig. 4c) were similar to those of Buffalo Pound and Last Mountain Lake, with high relative abundances of *Chironomus*, *Chironomini* sp. 1, and *Procladius* (see Hall et al. 1999a). From ~1890 to ~1977, abundances of littoral and macrophyte-associated taxa increased (*Para-*

tendipes, *Cladotanytarsus mancus* group), while deep-water taxa declined (*Chironomus*, *Procladius*), particularly after 1930. *Chironomus* reached a historical minimum in the mid-1970s, while *Paratendipes* and *Cladotanytarsus mancus* group increased to their greatest relative abundances. These latter community changes were short-lived, and fossil composition reverted to that characteristic of the 1940s in the most recent sediments. Overall, changes in absolute chironomid density mirrored variations in the relative abundances of deep-water taxa.

PCA of Pasqua Lake fossil assemblages demonstrated that presettlement communities were distinctly different from those occurring after ~1890 (Fig. 5c). The large spread in PCA axis 1 scores reflects declines in *Chironomus* from ~70% of fossil sum to less than 40% during the 20th century. Fossil assemblages deposited after 1977 were usually discrete from those of presettlement sediments, although the 1995 sample was situated close to pre-~1890 assemblages.

Echo Lake—Presettlement assemblages in Echo Lake were composed mainly of *Chironomus*, similar to patterns recorded at Pasqua Lake (Fig. 4d). Additionally, declines in *Chironomus* after ~1890 were paralleled by increases in littoral taxa such as *Paratendipes* and, after ~1930, *Cladotanytarsus mancus* group. Both littoral groups reached their maxima during the ~1960s. However, unlike in Pasqua Lake, abundances of *Chironomus* after ~1977 were highly variable and did not correspond to other major changes in fossil taxonomic composition. Absolute abundances declined following the onset of agriculture ca. 1890, mainly reflecting loss of deep-water *Chironomus*, and remained low until the 1960s after which they increased twofold.

PCA mainly recorded the large changes in the relative abundance of *Chironomus*, from a maximum of ~85% at ~1895 to ~20% during the mid-1960s (Fig. 5d). Unlike upstream Pasqua Lake, communities recorded after ~1977 were not consistently different from those seen in preagricultural times.

Mission Lake—Presettlement chironomid assemblages in Mission Lake were composed principally of profundal *Chironomus* and littoral *Tanytarsus* s.l., with lesser abundances of *Procladius* and Chironomini sp. 1 (Fig. 4e). Unlike upstream Pasqua and Echo Lakes, postsettlement communities did not record consistent declines in the relative abundance of *Chironomus* nor increases in those of littoral taxa. Similarly, only small increases in the relative abundances of *Procladius* and *Cladotanytarsus mancus* group were recorded after 1977. Instead, relative abundances of *Tanytarsus* s.l. declined continuously after maxima during the presettlement era. Analysis of fossil concentration profiles showed that preagricultural assemblages were variable and declined after ~1930, reaching minimum values during the past 20 yr.

PCA of chironomid relative abundances clearly distinguished preagricultural communities from more recent assemblages (Fig. 5e). Similarly, faunal communities have been distinctive since onset of tertiary sewage treatment in 1977. However, unlike most upstream lakes, both preagricultural and recent communities were distinguished along

the second PCA axis, reflecting changes in littoral *Tanytarsus* s.l., *Procladius*, and *Cladotanytarsus mancus* group.

Katepwa Lake—Similar to Mission Lake, pre-1890 fossil assemblages from Katepwa Lake were dominated by profundal *Chironomus* and littoral *Tanytarsus* s.l. (Fig. 4f). Few directional changes in community composition were recorded following the onset of widespread agriculture ca. 1890. Instead, declines in *Chironomus* relative abundance were mirrored by reciprocal increases in *Tanytarsus* s.l. and Chironomini sp. 1 until the 1970s. After ~1977, *Chironomus* relative abundance declined twofold concomitant with increases in most other taxa. Total fossil densities declined following the onset of European-style agriculture and again after 1960, mainly because of loss of *Chironomus*.

Ordination of PCA sample scores from Katepwa Lake did not consistently distinguish presettlement and later communities (Fig. 5f). Although only two samples were recovered from post-1977 sediments, ordinations suggested that recent community composition is unique in the past 200 yr.

Crooked Lake—Preagricultural chironomid communities were composed mainly of *Chironomus*, with lesser abundances of Chironomini sp. 1 and *Tanytarsus* s.l. (Fig. 4a). Overall, taxonomic composition varied little until the ~1960s, when relative abundances of littoral *Polypedilum*, *Paratendipes*, and *Cricotopus/Orthocladius* all increased. However, these patterns were short-lived, with relative abundances of littoral taxa declining in favor of *Chironomus* during the ~1980s. Overall, fossil concentrations declined irregularly from maximal densities in the early 19th century to minima during the ~1960s and ~1970s, before increasing ~200% after 1977.

PCA ordination of Crooked Lake fossil assemblages did not clearly separate presettlement, recent (post-1977), and intervening assemblages (Fig. 5g). As in upstream Mission and Katepwa Lakes, there was a tendency for preagricultural assemblages to cluster along the second PC axis, reflecting fluctuations in the relative abundance of *Chironomus*, Chironomini sp. 1, and *Tanytarsus* s.l.

Round Lake—Historical trends in chironomid composition were only weakly developed in Round Lake fossil assemblages (Fig. 4h). Presettlement communities were composed mainly of *Chironomus* and *Procladius*, similar to other lakes. Relative abundance of *Tanytarsus* s.l. declined after ~1890, whereas Chironomini sp. 1 increased slightly between ~1940 and ~1990. Absolute abundances of chironomids varied irregularly throughout the core, with elevated densities during the 1850s, 1900–1940, and the 1990s.

PCA ordination demonstrated that communities during the 20th century were characterized by high relative abundances of *Procladius* compared to other Qu'Appelle lakes (Fig. 5h). However, ordinations did not identify periods of distinct community composition.

Landscape patterns chironomid change—Comparison among lakes revealed several landscape patterns of change in species densities. First, *Tanytarsus* s.l. (Fig. 6a) exhibited a strong longitudinal trend, with increased density of this taxon

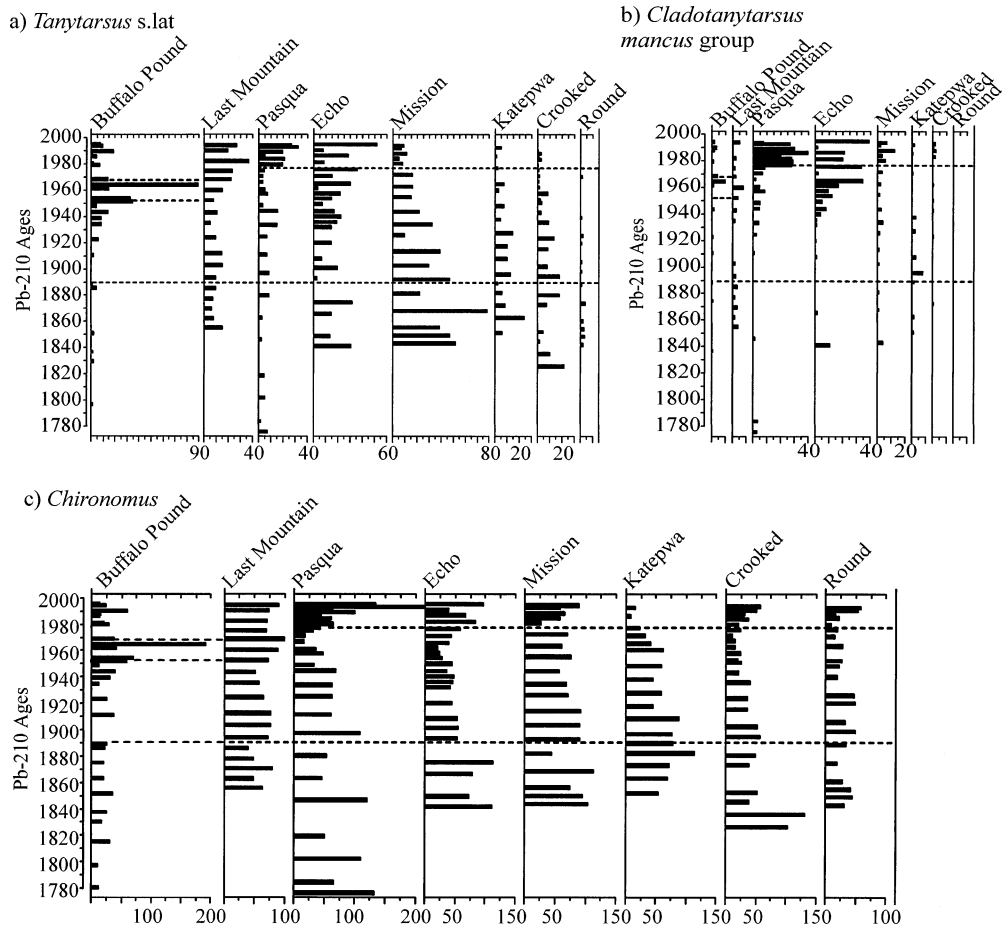


Fig. 6. Absolute abundances (remains g^{-1} dry mass) of (a) *Tanytarsus* s.l., (b) *Cladotanytarsus mancus* group, and (c) *Chironomus* from selected Qu'Appelle Valley lakes. Sites are arranged west to east. Dashed lines as in Fig. 3.

after 1980 in sites west of Echo Lake, while fossil concentrations declined in sediments from more eastern lakes (Mission, Katepwa, Crooked, Round). In contrast, concentrations of *Cladotanytarsus mancus* group increased substantially after ~1940 in lakes immediately downstream from sewage outfalls (Fig. 6b), whereas no significant pattern was seen in upstream Last Mountain and Buffalo Pound Lakes or in eastern Crooked and Round Lakes. Finally, densities of *Chironomus* generally declined during the 20th century in Qu'Appelle lakes subject to sewage inputs (Fig. 6c), although the timing of the historical minimum was earlier in midreach (1960–1970s) than downstream basins (1970–1980s). Concentrations of *Chironomus* fossils also increased after ~1977 in lakes receiving sewage. Neither pattern was observed at headwater sites, Buffalo Pound, and Last Mountain Lakes.

Rates of community change—Rates of community change have been greater in the most recently deposited sediments than at any other point in the past 200 yr for lakes located along the central axis of the Qu'Appelle River valley (Fig. 7). In general, lakes west of the town Fort Qu'Appelle show lower rates of change prior to ~1940, whereas east of the town site, maximum variation is expressed only after ~1960. In contrast, Last Mountain Lake, which lies in a side chain

of the Qu'Appelle drainage (Fig. 1), exhibits the highest degree of temporal variability in chironomid community composition during the 19th century.

Variance partitioning analysis of community change—Combined changes in climate (*C*), resource use (*R*), and urbanization (*U*) explained substantial amounts of variation (24.8–86.6%) in past chironomid assemblages at all sites except easternmost Round Lake (Fig. 8). No landscape pattern was noted for either total variance explained or the effects of individual historical categories. At least one climate variable was retained in the VPA of the seven lakes with significant variance explained, compared to five lakes in which resource-use variables were significant, and only two lakes with significant urban effects (Table 3). No variance was explained in Round Lake, a site with little directional change in chironomid community composition and high baseline variability in absolute fossil densities (Fig. 4h). We infer that poor correlations did not arise from imprecise chronologies because accumulation rates, burial depth age relationships (Table 1), and ^{210}Pb profiles (not shown) were similar to those of other Qu'Appelle lakes.

Overall, climate was the strongest single explanatory category in the VPA of Qu'Appelle fossil chironomid com-

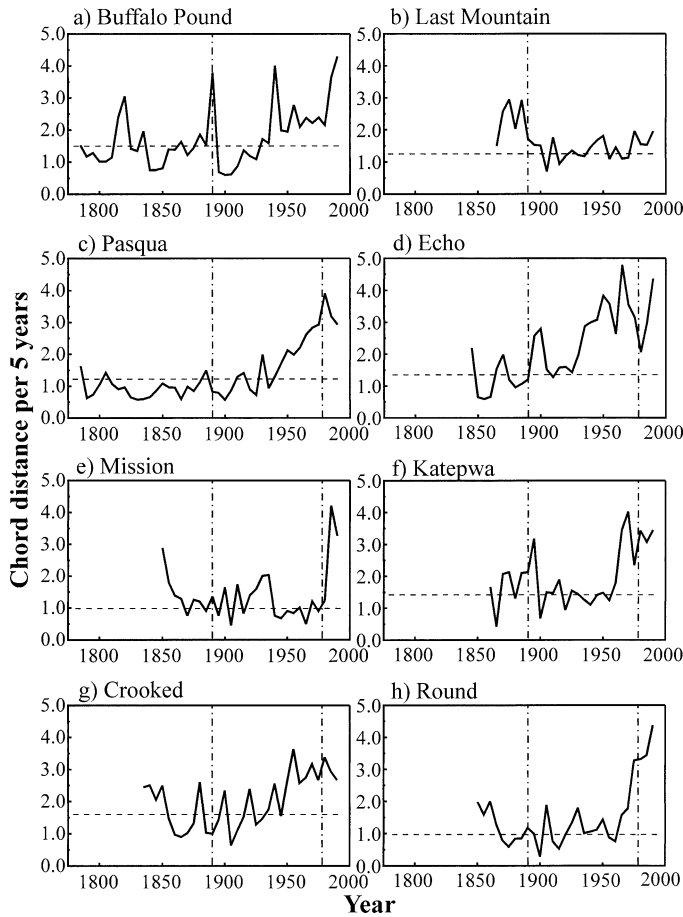


Fig. 7. Rates of community change (chord distance per 5 yr) in Qu'Appelle Valley lakes from ~1800–1990 based on chironomid percent abundances. Horizontal dotted lines represent 95% confidence limits based on Monte Carlo permutation tests with 1,000 iterations. Vertical dashed lines represent European arrival (1890) and initiation of sewage treatment (1977). Sites are arranged west (a) to east (h).

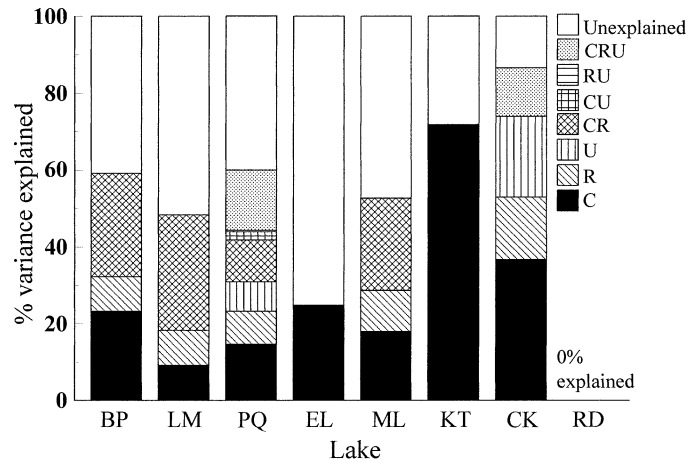


Fig. 8. Variance partitioning analysis of fossil chironomid assemblages in Qu'Appelle Valley lakes as percent fossil variance explained (1920–1993) by climate (C), urban (U), and resource-use factors (R). CU, CR, and UR represent first-order interactions, whereas CUR represents a second-order interaction. Lakes are arranged west to east and are Buffalo Pound (BP), Last Mountain (LM), Pasqua (PQ), Echo (EL), Mission (ML), Katepwa (KT), Crooked (CK) and Round (RD).

munities (Fig. 8). The unique effects of climate explained up to 71.8% of variation in past chironomid communities (mean $24.8 \pm 21.7\%$, $n = 8$), whereas interactive effects of climate with other categories (CR, CU, CUR) were also usually substantial ($15.3 \pm 13.7\%$). Seasonal temperatures were the most common climatic variable retained in VPAs (six of eight lakes), including winter minimum temperature (four lakes), spring maximum temperature, and summer and fall minimum temperatures (two each; Table 3). Duration of ice cover was also a significant predictor of past chironomid change at three lakes.

Resource-use was the second most important explanatory category in most VPAs. Although the unique effects of resource-use ($6.7 \pm 6.1\%$) were usually lower than those of climate, resource–climate interactions (CR + CUR) were substantial in analyses of five lakes. Overall, resource-related

Table 3. Explanatory variables retained in variance partitioning analysis for ~1920–1993 time period. T_{max} and T_{min} , mean maximum and minimum temperatures, respectively.

Lake	Climate*	Resource use	Urban
Buffalo Pound	Annual gross evaporation, spring T_{max} , fall T_{min} , winter T_{min}	Fish stocking, field crops Flow at Elbow	None
Last Mountain	Summer T_{min} , winter T_{min}	Livestock, field crops	None
Pasqua	Annual precipitation, spring T_{min} , summer T_{min}	Fish harvest, field crops, farmland	Moose Jaw population, TN:TP
Echo	Fall T_{min}	None	None
Mission	Duration of ice-free season	Fish harvest	None
Katepwa	Winter T_{min} , duration of ice-free season	None	None
Crooked	Spring precipitation, spring T_{max} , winter T_{min} , duration of ice-free season	Livestock, farmland, flow at Elbow	Qu'Appelle Valley population, TN, TN:TP
Round	None	None	None

* Winter (Nov–Mar), spring (Apr–May), summer (Jun–Aug), fall (Sep–Oct) from Hall et al. (1999a).

effects (*R*, *CR*, *UR*, *CUR*) were similar among sites in which the resource category was retained ($21.8 \pm 18.3\%$). Overall, area of crops or farms (three lakes) and fisheries management practices (three lakes) were the main explanatory variables within the resource-use category (Table 3).

Historical patterns of urbanization explained significant amounts of variance in chironomid communities in Pasqua and Crooked Lakes only (Fig. 8). Although Crooked Lake is separated from Pasqua Lake by four other systems, urbanization and its interaction with other categories (*U*, *CU*, *RU*, *CRU*) contributed to >25% of the explained variance at both sites. Urban variables retained in VPA included Moose Jaw and rural population, mass of sewage N from Regina, and N:P ratios of effluent (Table 3).

Redundancy analyses of climatic effects—Ordinations using RDA of climatic data and fossil assemblages from all lakes identified spring minimum temperature as the most important factor influencing overall chironomid community composition. Ordinations of individual lakes further demonstrated that changes in relative abundance of littoral taxa were associated with variations in minimum spring or winter temperatures in all lakes but Mission (ice-free season) and Round (no predictor). However, although littoral taxa were more abundant under warm conditions in most lakes, relative percentage of littoral species declined with increased temperature in shallow Crooked and Buffalo Pound Lakes.

Discussion

History of water quality and invertebrate community change—Analysis of benthic invertebrate communities demonstrated that all Qu'Appelle lakes were productive throughout the past 150–200 yr. Prior to the advent of European-style agriculture ca. 1890, fossil chironomid assemblages were composed of 40–80% hemoglobin-containing *Chironomus* (aka 'bloodworm'), a reliable indicator of low oxygen content in hypolimnetic waters (Little and Smol 2001; Quinlan and Smol 2001). In general, relative abundances of *Chironomus* were 10–20% lower in headwater Buffalo Pound and Last Mountain Lakes than in downstream sites, consistent with modern limnological surveys that show western lakes are less productive than eastern sites (Soranno et al. 1999) and with the hypothesis that chironomid densities increase with lake productivity until anoxia eventually limits benthic colonization (Warwick 1982; Little et al. 2000). Prevalence of *Chironomus* also agrees with fossil evidence for abundant bloom-forming cyanobacteria and eutrophic diatoms prior to modern land-use practices (Hall et al. 1999a; Dixit et al. 2000), with high sedimentary content of nonapatite P (Allan et al. 1980), and with explorers' journals stating that Qu'Appelle lakes were green-colored during the 18th and 19th centuries. Together, these analyses demonstrate that, despite polymixis, Qu'Appelle lakes were naturally eutrophic, with regular deep-water anoxia.

Native zoobenthos composition was not altered uniformly by the establishment of European-style agricultural practices within the Qu'Appelle Valley ca. 1890 (Fig. 5). Ordinations using PCA suggested that preagricultural communities were distinctive only at Pasqua and Mission Lakes but that their

unique nature arose from changes in deep-water *Chironomus* (PCA axis 1) and littoral *Tanytarsus* s.l. (PCA axis 2), respectively. Similarly, rates of community change did not increase significantly after onset of agriculture in any lake (Fig. 7). Thus, although absolute chironomid densities declined following the onset of widespread farming in the Fishing Lakes and Crooked Lake (Fig. 4), these changes did not greatly alter community composition. These patterns are consistent with analyses of fossil pigments and diatoms from these (Hall et al. 1999a,b) and other prairie lakes (Hickman and Klarer 1981; Vinebrooke et al. 1998; Blais et al. 2000) that show little effect of grassland conversion to agriculture on algal communities and water quality. However, our results contrast with other paleoecological investigations, which demonstrate that deforestation and concomitant agricultural development profoundly alter lake chemistry and biotic composition (e.g., Siver et al. 1999). Further research will be required to determine whether such differences reflect variation among regions in baseline lake productivity, catchment sensitivity to disturbance, climatic regime, or other factors.

Chironomid communities have exhibited highly significant ($P < 0.05$) rates of change within Qu'Appelle lakes since at least 1975 (Fig. 7). In general, high rates of variation reflect changes in the absolute abundance of deep-water *Chironomus* and littoral *Tanytarsus* s.l. and correspond to periods of rapid diatom community change and elevated abundance of colonial cyanobacteria (Hall et al. 1999a; Dixit et al. 2000; Hall et al. unpubl. data). Similar variations in other prairie lake communities during the 1970s have been attributed to regional climatic change (Vinebrooke et al. 1998; see below) or intensified land use (Blais et al. 2000). Although the period of most rapid community change also corresponds to onset of tertiary sewage treatment at Regina and Moose Jaw (ca. 1977), several observations suggest that recent instability of chironomid communities does not result exclusively from the effects of urban waste. First, VPA suggests that there was no significant direct relationship between sewage treatment practices and invertebrate assemblages in six of eight lakes. Second, elevated rates of community change preceded the start of tertiary treatment in six lakes. Finally, community variability was also maximal since 1980 in Buffalo Pound Lake, a site without direct sewage inputs. Instead, we suggest that recent increases in algal production (Dixit et al. 2000) and invertebrate community variation reflect regional climate change, as recorded east (Schindler et al. 1996) and west (Vinebrooke et al. 1998) of the Qu'Appelle drainage.

Causes of community change—It is inherently difficult to interpret the causes of change in fossil assemblages, particularly when there are multiple stressors that can interact on differing timescales. Fortunately, the development of VPA protocols allows some measure of objectivity in quantifying the relation between environmental and biological time series (Borcard et al. 1992; Hall et al. 1999a). Although we recognize that VPA potentially suffers from the same numeric difficulties as other multivariate and correlation-based analyses (lag effects, lurking variables, nonsense correla-

tions), comparison of VPA among lakes and fossil indicators can help reduce the possibility of spurious results.

Variance partitioning identified climatic variability as the strongest correlate of benthic invertebrate community change since 1920. When considered over all lakes, climate and its interactions with other factors (*C*, *CU*, *CR*, *CUR*) accounted for $40.1 \pm 20.9\%$ of past variation in chironomid assemblages, even at sites known to be eutrophic because of urban sewage (Fishing Lakes; Hall et al. 1999a; Dixit et al. 2000). In particular, factors related to the severity of winter climate (fall and winter minimum temperature, duration of ice cover; Shuter et al. 1983) were significant predictors of community variance at six of eight sites. We note with interest that summer temperature was retained in only two analyses, despite the wide use of fossil chironomid communities in paleoclimatic reconstructions of mean summer thermal conditions (e.g., Walker et al. 1991; Lotter et al. 1999). Instead, RDA suggested that the mechanism of community change at many sites involved increased winter or spring minimum temperatures that favored higher abundances of littoral taxa. Unfortunately, these analyses cannot determine whether the beneficial effects of warming and reduced ice cover increased littoral abundance (cf., Magnuson et al. 2000) or whether warm conditions promoted deep-water anoxia (Babin and Prepas 1985) and declines in the relative abundance of profundal species. Winter anoxia is common in these (Hammer 1971) and other prairie lakes (Barica and Mathias 1979; Baird et al. 1987) and could be an important control of chironomid community structure.

Significant effects of climate variability on benthic invertebrate communities contrasts with previous analyses, suggesting that climatic change has little direct effect on algal community composition in these lakes (Hall et al. 1999a). Earlier analyses of Pasqua Lake fossils, as well as unpublished VPA from the remaining Qu'Appelle lakes (Hall et al. unpubl. data), demonstrate that the unique effects of climate explain only $6.0 \pm 2.3\%$ of historical variance in algal pigment or diatom assemblages at all sites (Hall et al. 1999a). In contrast, climate alone explained up to 71.8% of past variance in chironomid communities, averaging 24.8% in all Qu'Appelle lakes and 28.4% in those with significant explained variance. Because both diatoms (Smol and Cumming 2000) and chironomids (Walker et al. 1995; Lotter et al. 1999) are sensitive indicators of climatic change, and because planktonic diatoms predominate in Qu'Appelle lakes (e.g., Dixit et al. 2000), we infer that differences in results of VPA of past flora and fauna may reflect differential effects of climate on biota in benthic and planktonic habitats.

Stimulation of lake production by urbanization and agriculture might have interacted with climate change to influence chironomid abundance and taxonomic composition. We note with interest that interactions of climate and human explanatory categories (*CU*, *CR*, *CUR*) were substantial at five lakes (12.6–30.1% of variance), particularly headwater systems where ~50% of explained fossil variance was attributable to combined effects of climate and humans. Although these interactions do not infer factor interactions (as in analyses of variance), such covariance is consistent with fossil diatom and pigment evidence of lake eutrophication beginning at ~1930 and of twofold increases in sediment

deposition rates in these and other prairie ecosystems (Vinebrooke et al. 1998; Hall et al. 1999a; Dixit et al. 2000). According to VPA, these human effects included farming, sewage, and hydrologic factors known to regulate lake production. Thus, because climate records demonstrate rising winter temperatures and declining ice cover since 1920 (Magnuson et al. 2000), we speculate that strong interactions of climate and land use could reflect a change in mechanisms controlling chironomid communities, from climatic factors early in the 20th century to more recent human effects. Similar shifts in control mechanisms are known from geochemical studies (e.g., Vitousek et al. 1997; Carpenter et al. 1998).

Landscape patterns of invertebrate community change— There is increasing evidence that lake chemistry and biology, as well as their responsiveness to human activities and climate, depend on lake position within a hydrologic landscape (Kratz et al. 1997; Magnuson et al. 1998; Rusak et al. 1999; Soranno et al. 1999). For example, lake water conductivity, alkalinity, nutrient content, and algal biomass increase in a downstream direction within the Qu'Appelle and other agricultural drainages, whereas water transparency declines (Soranno et al. 1999). Analyses of algal chlorophyll and pelagic invertebrate densities also indicate strong spatial patterns of temporal coherence among biotic communities within Qu'Appelle lakes (Rusak and Leavitt unpubl. data), similar to those seen in boreal landscapes (e.g., Rusak et al. 1999; Baines et al. 2000).

Analysis of fossil chironomid densities also revealed landscape patterns of taxonomic change (Fig. 6). For example, absolute densities of littoral *Tanytarsus* s.l. declined from west to east following the onset of European-style agriculture, especially since 1990. Because this fossil group includes diverse genera, such as *Paratanytarsus* and *Corynocera*, ecological interpretations of the causes of such landscape patterns are difficult. However, because this group encompasses littoral taxa, we speculate that its losses reflect a decline in the quality of the nearshore habitat. Consistent with this hypothesis, recent *Tanytarsus* s.l. densities are lowest in eastern lakes, sites with elevated phytoplankton biomass (Soranno et al. 1999), and low densities of submerged macrophytes (Chambers 1989). Similarly, we note that landscape patterns of *Cladotanytarsus mancus* group are consistent with a strong positive response of this taxon to sewage inputs, with greatly enhanced densities after 1940 in Pasqua Lake being rapidly attenuated in subsequent basins (cf. Dixit et al. 2000). Van den Berg et al. (1997) noted that *Cladotanytarsus* was negatively associated with submerged macrophytes because of a greater extent of anoxia at the sediment–water interface within macrophyte beds. Therefore, recent changes in *Cladotanytarsus mancus* group might reflect changes in nearshore habitat of submerged macrophytes. Finally, although landscape patterns were less strongly developed for deep-water *Chironomus*, abundance of this taxon declined through the 20th century, then increased in most lakes concomitant with diatom community change and increased cyanobacterial abundance after 1980 (Dixit et al. 2000; Hall et al. unpubl. data). Together, these taxonomic changes translated into landscape patterns of community variability within the central Qu'Appelle chain,

with western lakes (Buffalo Pound, Pasqua, Echo) exhibiting uniformly significant rates of change after ~1940, whereas eastern sites showed increased variability only after ~1960 (Fig. 7). We attribute this pattern to landscape differences in lake sensitivity to climate change or land use (cf., Webster et al. 2000), rather than urbanization, because both Pasqua and Echo Lakes receive sewage, yet exhibit rates of community change similar to those seen in Buffalo Pound Lake.

Unexpectedly, VPA of fossil chironomid communities did not support the hypothesis that zoobenthos were organized along landscape gradients. For example, the importance of climate as an explanatory variable was equally strong in headwater and downstream lakes, likely reflecting the uniformly cold and dry regional climate (Hall et al. 1999a). Similarly, the effects of resource-use on zoobenthos alternated strong and weak along the central lake chain. The most intriguing result was that urban effects were strongly expressed both in Pasqua Lake and in Crooked Lake, a site >75 km downstream and separated by three intervening lakes. As shown by Dixit et al. (2000), the effects of sewage effluent on lake production were rapidly eliminated within the Fishing Lakes chain. Similarly, Hall et al. (1999a, unpubl. data) could demonstrate little change in algal abundance in Crooked Lake as a result of sewage inputs. Presently, we have no convincing explanation for the disjunct effects of urbanization, other than to suggest that they may reflect either a lurking variable (e.g., local land development) or a nonsense correlation. Overall, consistent patterns of community change in response to climatic factors (Table 3) suggest that happenstance correlations were rare in our study.

We have used highly resolved time series of fossil chironomid communities from eight prairie lakes to quantify historical changes in benthic invertebrate communities and to identify probable cause of community variation. Our analyses demonstrate that lakes of the Qu'Appelle Valley drainage are naturally productive. Furthermore, we show that variability in winter climate has been a significant control for benthic community composition at most sites during the 20th century, unlike planktonic algal communities, which have responded more directly to human activities (Hall et al. 1999a). This latter result is particularly exciting because it suggests that future climatic change could be expressed differentially among habitats or trophic levels within lakes.

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