Aquatic Sciences

RESEARCH ARTICLE

Contrasting responses of dimictic and polymictic lakes to environmental change: a spatial and temporal study

Zofia Ecaterina Taranu · Dörte Köster · Roland I. Hall · Theo Charette · Francine Forrest · Les C. Cwynar · Irene Gregory-Eaves

Abstract Although comparative analyses between dimictic and polymictic lakes have noted the key role of mixing regime in governing water quality, limnologists have historically focused on dimictic lakes, leaving polymictic lakes relatively understudied. In this study, we investigated whether the effects of agricultural development on water quality differed between dimictic and polymictic lakes in a naturally nutrient-rich region of Alberta, Canada. Through a spatial limnological analysis of 36 sites, we found that the relationship between surface water total phosphorus concentration and the percent of agriculture (% Agr) in the catchments differed between dimictic and polymictic lakes, where the proportion of variance explained was much more pronounced in the dimictic (79% explained) than in the polymictic systems (7% explained). Paleolimnological analyses of subfossil chironomids in surface sediment samples (0–1 cm) from 18 of the 36 study lakes, and in sediment core profiles from the dimictic and polymictic basins of a eutrophic lake, showed that water quality differed between mixis groups. We found that the surface sediment chironomid assemblages differed significantly between polymictic and dimictic lakes. Detailed analyses of the sediment cores demonstrated that the two basin types differed in their responses to land-use change through time, as only the dimictic basin showed a parallel increase in anoxia with increasing agricultural development. We suggest that in naturally-fertile landscapes, external nutrient loading exerts a more notable effect on dimictic lakes, whereas internal nutrient loading is more important in polymictic systems.

Keywords Eutrophication · Chironomid · Agriculture · Mixis · Anoxia

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Introduction

Although limnologists have long focused on deep, dimictic lakes, there is an increasing effort to study the more numerous shallow, polymictic lakes. Research conducted to date suggests that lake morphometry and mixing regime, which are themselves related (Hanna 1990), are factors that can influence water quality (Prepas and Trew 1983; Riley and Prepas 1985; Cornett 1989; Taranu and Gregory-Eaves 2008). Furthermore, shallow lakes are typically not as responsive to remediation efforts in comparison to deeper lakes owing to internal nutrient loading (Kalff 2002). In polymictic lakes, phosphorus that is released from the sediment in summer is made available to the trophogenic zone. In contrast, the metalimnion of stratified lakes slows or prevents the transport of phosphorus released from the

sediments to surface waters (Welch and Cooke 1995). A combination of wind resuspension, periodic anoxia on calm days, and macrophyte decomposition add to the rapid nutrient recycling in polymictic basins, and contribute to lagged responses (5–10 years or longer) when external nutrients are reduced. Lack of understanding of internal loading mechanisms, such a longevity and recovery rates, have rendered shallow lakes difficult to manage (Welch and Cooke 1995).

Empirical models and restoration techniques developed for deep, dimictic systems may not be directly transferable to shallower, polymictic systems. For example, Riley and Prepas (1985) demonstrated with a dataset from Alberta (Canada) that as surface water total phosphorus (TP) concentrations increased, the per unit increase in primary production (measured as chlorophyll *a* concentration; chl*a*) became increasingly disparate between dimictic and polymictic lakes. Thus, as both lake types became more eutrophic, the average summer chl*a* concentration in the polymictic lakes increased at a much faster rate than in the dimictic lakes ($\beta_{polymictic} = 19.9$ mg chl*a* m^{-3}/mg TP m^{-3} versus $\beta_{dimictic} = 9.9$ mg chl*a* m^{-3}/mg TP m^{-3}). They attributed this difference to the frequent recirculation of nutrients within polymictic lakes back into the euphotic zone, making them readily available for uptake by primary producers. More recently, in a meta-analysis of 358 lakes located in predominantly rural watersheds, Taranu and Gregory-Eaves (2008) showed that lake depth explained a significant fraction of the variation in TP concentration, in addition to diffuse nutrient loading from agricultural activities. Additionally, Trew (Alberta Environment; pers. comm.) noted that internal nutrient loading often far exceeds external loading in polymictic lakes of Alberta, Canada.

Unfortunately, few studies have compared the responses of dimictic and polymictic basins to changes in catchment land use (although see Moss et al. 2005; Langdon et al. 2006), despite growing recognition that lake depth and mixing regime can exert significant effects on water quality. To address this gap, here we compare how lakes that differ in thermal mixis vary in their response to land use across spatial and temporal gradients. Specifically, we conducted a study of 36 lakes in an agriculturally-active region of Alberta, Canada and performed both limnological and paleolimnological analyses to examine the effects of land-use change on the water quality of polymictic and dimictic lakes. Additionally, we assessed whether agricultural land use in the naturally-fertile landscapes of Alberta, Canada has a detectable impact on the water-quality of regional lakes. Eutrophic and hypereutrophic lakes are common in mid to southern Alberta (AENV 2007). Given that nutrient-rich soils and low-lying topographies are characteristic of this region, many authors have concluded

that the trophic status of these lakes is strongly influenced by the natural landscape (Blakney 1998; Blais et al. 2000; McEachern and Charette 2003/2004; Devito et al. 2005; Donahue 2006; Schindler et al. 2008). Several studies in Alberta and in a neighboring nutrient-rich region (Saskatchewan), however, have shown that lakes were responsive to agriculture and urbanization (Hall et al. 1999; Dixit et al. 2000; Blais et al. 2000; Quinlan et al. 2002; Schindler et al. 2008). Thus, we set out to evaluate whether agricultural development has had a detectable effect on the water quality of lakes with naturally high levels of nutrient loading from the catchment.

We applied two separate metrics of water quality to examine our study objectives: surface-water TP concentrations and qualitative inferences of bottom-water dissolved oxygen (DO) concentration. Contemporary TP data were used to indicate the present trophic state of lake surface waters. To infer past changes in bottom water DO concentration, we analyzed sub-fossil chironomid (Diptera: Chironomidae) larval head capsules; a well-established paleolimnological indicator of oxygen availability (Brodersen and Quinlan 2006). Both experimental and lake-survey studies have shown that different chironomid taxa survive under specific oxygen regimes (Quinlan et al. 1998; Little and Smol 2001; Brodersen et al. 2004, 2008). To date, applications of paleolimnological oxygen inference models based on chironomid assemblages have been restricted to dimictic lakes, which stratify following spring overturn and typically become progressively depleted in hypolimnetic oxygen throughout the summer. In polymictic systems, chironomids are generally not used to reconstruct DO as the periodic mixing in these lakes typically precludes the development of anoxia. Canadian Prairie polymictic lakes, however, are so productive that they show severe anoxia in both summer and winter (Barica 1987; Hall et al. 1999; pers. observ. and Meding and Jackson 2003).

In our contemporary spatial survey of 36 lakes, we examined whether the proportion of agricultural land in the catchment (% Agr) is correlated significantly with the summer average TP concentration of epilimnetic waters. Studies have suggested that polymictic and dimictic lakes behave differently, and so we tested the hypothesis that water quality of dimictic Albertan lakes is more strongly related to % Agr compared to polymictic Albertan lakes. Our prediction was that watershed activities (% Agr) would account for a greater amount of variability in lake water quality of dimictic lakes relative to polymictic Albertan lakes, as the water quality of the latter can be strongly influenced by internal nutrient loading (Alberta Environment; D. Trew, pers. comm.).

We recognize that several morphometric and landscape variables may influence the differential responses of

polymictic and dimictic lakes to agricultural activities, and thus we explored the influence of several additional variables. For example, studies have shown that the relationship between land cover (% Agr) and water quality is affected by the capacity of catchments to transport nutrients downstream (e.g. Fraterrigo and Downing 2008). Specifically, transport capacity likely depends on catchment size as phosphorus export is linearly related to CA (catchment area; Prairie and Kalff 1986). The volume of the receiving body of water is also an important variable, as incoming TP can become increasingly dilute in larger lakes. We, therefore, compared the relationship between TP and the CA: LV ratio between polymictic and dimictic lakes. Finally, we tested whether the effect of mean lake depth (Z_{mean}), a well-established modulator of water quality (e.g. Taranu and Gregory-Eaves 2008), varied between lake types.

In our paleolimnological analysis of sub-fossil chironomid assemblages, we first tested whether recently deposited chironomid communities in surficial sediments (0–1 cm) from 18 basins located along a modern land-use gradient were more responsive to agricultural catchment activity or to lake mixing regime. To examine how basins of different mixing regimes responded to a temporal gradient of human land use in the catchment, we then sampled a lake that possesses a dimictic and a polymictic basin (Moose Lake) and assessed water-quality trends through time, as inferred from the chironomid assemblages. By comparing two basins from the same lake, we controlled for possible confounding effects of differences in catchment characteristics and land use that occur between lakes, and thus isolated the key effect of interest: mixing regime.

Study area

A total of 36 lakes, located in the Boreal Plain and Grassland regions of the province of Alberta, Canada were sampled for the modern spatial survey (Table 1; Fig. 1). The catchments of these lakes are situated within a rolling-hill topography and underlain by layers of sandstone, silt-stone, shale, coal, and limestone (Mitchell and Prepas 1990; USGS 2007; AGS 2007). The catchments are situated along a pronounced gradient of agricultural disturbance (i.e. from 0 to 86% of catchment as agricultural land). Twenty-eight of the lakes were polymictic and eight were dimictic. The polymictic lakes had an average maximum depth (Z_{max}) of 8.8 m (range 4.0–18.3 m) and surface areas (SA) ranged from 50 to 9,350 ha (mean = 2,360 ha). In contrast, the dimictic lakes had an average Z_{max} of 28.0 m (range 15.5–40.0 m) and had generally smaller surface areas (range 490–3,150 ha; mean

1,460 ha). A biplot of lake SA versus Z_{max} illustrates that the dimictic and polymictic basins of this lake set have overlapping ranges in terms of SA, but that the lakes with the greatest SA are polymictic, whereas dimictic lakes have greater Z_{max} (Fig. 2). Many of the polymictic lakes of this study are not polymictic due to their shallow depths, but rather due to large SA.

For the paleolimnological analyses, we collected surface sediments (0–1 cm) from 15 of the 36 study lakes, which spanned a gradient of catchment land use (Table 1). We also conducted analyses of chironomid assemblages in sediment cores collected from two basins of Moose Lake, a lake that is well suited to explore temporal relationships between land use and water quality as it has undergone notable catchment development over the last century.

Moose Lake

Moose Lake is a relatively large lake, with four main bays. The deepest basin (Vezeau Bay) is ~20 m deep and dimictic, the main basin (Moose Main) is 12 m deep and polymictic, and the shallowest basin (Island Bay) is 3 m deep (Fig. 3; Mitchell and Prepas 1990). At the time of sounding (August 1962), the lake's mean residence time was 7.5 years, which corresponded to the lake surface at a geodetic elevation of 533.6 m. Mean elevation from 1950 to 2003 was 533.0 m ± 0.07 SE, and at the most recent sounding (2003), the lake level had decreased to 532.1 m and thus the current surface area and lake volume are estimated to be ~3,200 ha and ~160 $m^3 \times 10^6$, respectively.

The first trading post was established on the lake's northwest shore in 1789, but it took over a century (1907) for permanent settlement to commence (Mitchell and Prepas 1990). Settlement accelerated once more in 1912, and by 1928 the railroad had extended to the town of Bonnyville, located along the lake's shoreline. During the mid-1930s several fish-packing plants and mink farms were situated along the lake's shore. The first subdivision of land took place at Bonnyville Beach in 1945. By 1988, ~130 dwellings occupied the lake's shoreline, 37% of which were permanent residences. Agriculture is practiced in upland regions of the lake's catchment, predominantly along the northern and eastern shore of Vezeau Bay and the southern shores of the Main Basin (Fig. 3). Small livestock operations are common in the surrounding lake region (e.g. there are two operations at ~1.5 km south of Vezeau Bay). Currently, agricultural land occupies ~50% of the catchment and consists primarily of a mixture of forage crop (e.g. barley and oats) and livestock operations. Most of the nutrient load from the catchment originates from diffuse sources as urban lands represent <2% of the watershed

Table 1 A summary of the geographic, morphometric, and limnological data of our study lakes

Reference number	Lake name	Lake mixis	Z_{max} (m)	Z_{mean} (m)	Volume ($\times 10^6$ m³)	WRT (year)	LA (km²)	CA:LA	% Agr	[TP] (μg/L)	pH (range)
1	Lac Santé*	□	24.4	11.3	103	NA	9.1	NA	71.99	61.00	9.1
2	Sylvan*	□	18.3	9.6	412	100	42.8	2.4	57.31	19.53	8.8–9.0
3	Clear*	□	18.5	NA	NA	NA	NA	NA	High	24.00	8.7
4	Island	□	18.0	3.7	29.2	16	7.8	7.1	20.24	34.06	8.1–8.6
5	Baptiste South	□	15.5	5.6	56.5	6	5.1	56.8	16.56	57.05	7.6–8.8
6	Frog	□	19.4	NA	NA	NA	58.0	10.6	12.43	32.62	8.6–8.9
7	Ethel*	□	30.0	6.6	32.2	2.5	4.9	7.0	11.61	23.11	8.3–8.4
8	Long-Island*	□	13.0	7.4	NA	NA	2.6	NA	Low	27.50	8.2–8.3
9	Moore/Crane*	□	26.0	8.3	77.4	100	9.3	4.3	5.94	24.02	8.4–8.9
10	Wolf (2 basins)*	□	38.3	9.2	289	6	31.5	19.5	3.02	20.29	7.4–8.5
11	Touchwood	□	40.0	14.8	430	69.5	29.0	3.9	0.95	15.90	7.8–8.5
12	Marie*	□	26.0	14.0	484	47.5	34.6	11.2	0.00	13.16	7.5–8.5
13	Moose (2 basins)*	Δ	12.0	5.6	230	7.5	40.0	5.3	50.42	41.64	8.4–8.8
14	Skeleton (2 basins)*	Δ	17.0	6.5	51.4	61.5	7.9	3.6	8.54	33.47	8.4–8.8
15	Pine*	○	12.2	5.3	20.6	9	3.9	38.6	81.91	70.10	7.9–8.9
16	Big lake	○	0.8	NA	NA	NA	NA	NA	73.01	133.60	9.0
17	Buffalo	○	6.5	2.8	248	100	93.5	15.4	70.60	60.40	8.9–9.3
18	Saskatoon	○	4.0	2.6	19.3	100	7.5	4.3	68.91	893.18	8.9–9.1
19	Reesor	○	5.5	3.7	1.19	6	0.5	10.9	62.24	45.24	7.5–8.7
20	Gull*	○	8.0	5.4	437	100	80.6	2.6	59.04	40.25	9.0–10.1
21	Kehewin*	○	11.6	6.7	NA	NA	6.2	84.8	58.89	92.45	8.4–8.8
22	Garner	○	15.2	8.1	50.1	100	6.2	4.3	56.82	44.38	8.9–9.1
23	Wizard	○	11.0	6.2	14.8	13.5	2.5	12.0	46.97	50.00	7.7
24	Wabamun	○	11.0	6.3	513	100	81.8	3.2	44.10	30.02	7.9–9.6
25	Nakamun	○	8.0	4.5	15.8	21	3.5	12.7	39.36	119.17	7.8–9.5
26	Elkwater	○	8.4	3.5	8	6	2.3	11.1	34.32	47.22	8.1–8.3
27	Cooking	○	4.6	1.7	NA	NA	36.0	NA	29.62	458.75	8.6–9.2
28	Miquelon	○	6.0	2.7	23.8	100	8.7	4.1	29.02	128.41	9.3–9.4
29	Sandy	○	4.4	2.6	29.4	100	11.4	4.2	26.27	199.95	8.6–9.1
30	Winagami	○	4.7	1.7	80.7	1.5	46.7	4.7	24.77	62.75	8.3–8.9
31	Muriel	○	10.7	6.6	424	100	64.1	6.1	24.03	54.00	8.2–9.6
32	Thunder	○	6.1	3.0	21.1	100	7.0	2.9	19.68	41.10	8.3–8.7
33	North Buck	○	6.1	2.5	47.3	40.5	19.0	5.4	19.35	29.39	7.9–8.7
34	Tucker*	○	7.5	2.9	19	1.5	6.7	46.9	13.94	70.00	7.1–8.3
35	Long (near Boyle)*	○	9.0	4.3	29.3	7.5	5.8	14.5	4.27	51.20	8.3–8.4
36	Steele	○	6.1	3.2	20.9	2	6.6	38.6	3.80	146.88	7.8–8.4
37	Crimson	○	9.1	2.2	5.21	100	2.3	0.8	1.80	24.32	8.6–9.1
38	Gregoire	○	7.2	3.9	100	4	25.8	9.0	0.02	36.26	7.1–7.9

The subset of 18 basins cored for the paleolimnological analyses are indicated by an asterisk symbol

Lake mixis: *open square* dimictic basin; *open triangle* both dimictic and polymictic basins; *open circle* polymictic basin; Z_{max} maximum lake depth, Z_{mean} mean lake depth, *WRT* water residence time, *LA* lake area, CA: LA = catchment area to lake area ratio, *% Agr* catchment agricultural coverage, *TP* summer average total phosphorus concentration

(Mitchell and Prepas 1990). Although the CA: LV ratio of Moose Lake (0.92) is low relative to most lakes examined (lake-set mean CA: LV = 3.1), the estimated phosphorus loading (476 kg/year) from agricultural activities in the mid-1980s is notably greater that the regional mean (227 kg/year).

Materials and methods

Spatial limnological survey

To obtain an estimate of the percent of agricultural development in each catchment, we used a Geographical

Fig. 1 Lake mixis: *open square* dimictic basin; *open triangle* both dimictic and polymictic basins; *open circle* polymictic basin. Symbol colour scheme: *black* high Agr (50–100%), *grey* moderate Agr (10–49%), *white* low Agr (0–9%). Lakes not appearing on map: Clear (lat/long NA), Long-Island (54°51′N 113°89′W), and Gregoire (56°27′N 110°09′W) lakes. Surficial geology provided by Alberta Geological Survey. General map legend: *light grey* shale and ironstone partings; *grey* fine-grained, feldspathic sandstone with hard calcareous beds, laminated silstone and silty shale; *dark grey* Feldspathic sandstone, bentonitic mudstone, thick coal beds
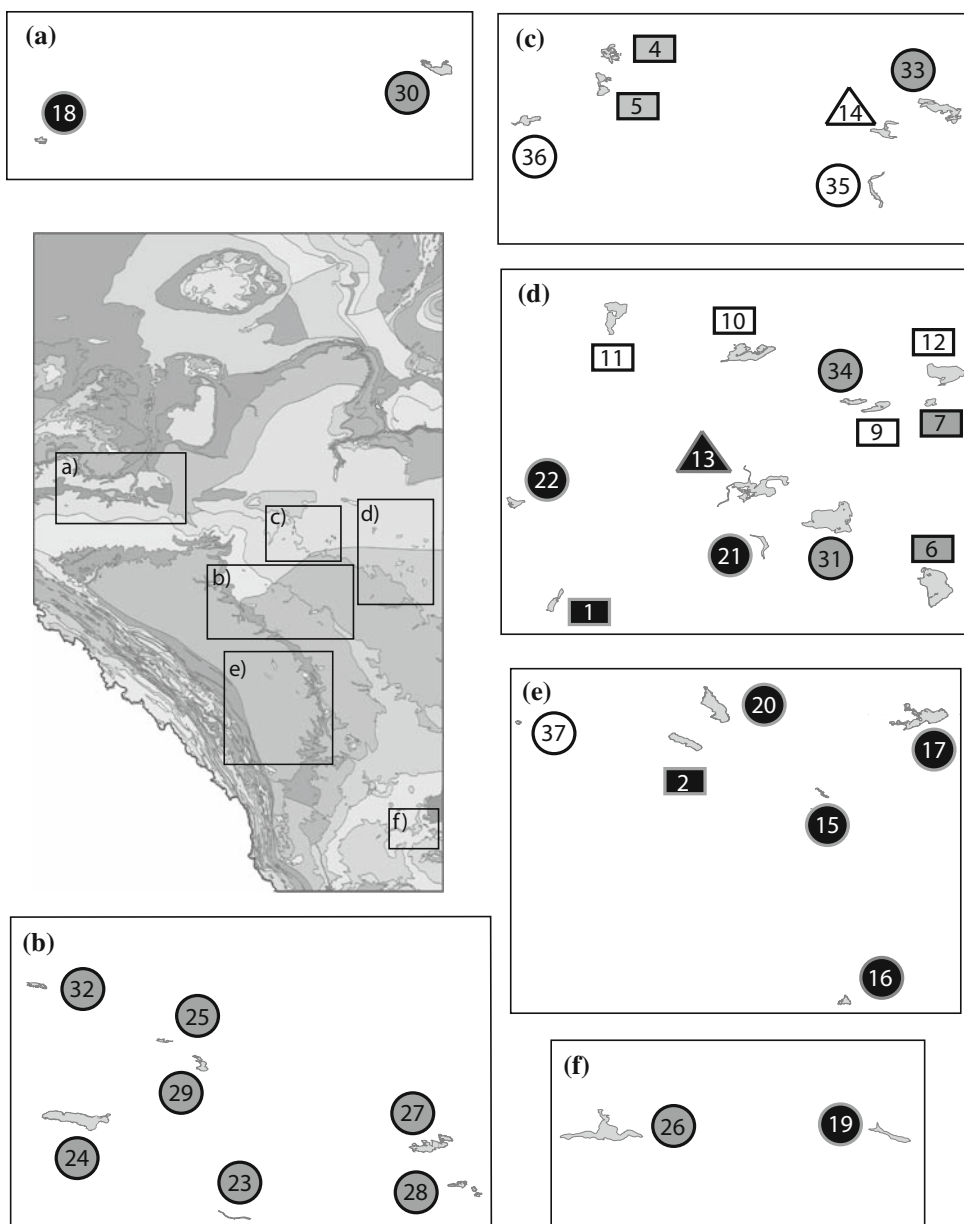
Information System (GIS; ESRI 1999) to quantify the coverage of different land use types (Table 1). Catchment boundaries for each lake were obtained from the Atlas of Alberta Lakes (Mitchell and Prepas 1990). Unpublished data on external and internal P loading for 20 of the 36 lakes in this set was made available by Alberta Environment (i.e. D. Trew, pers. comm.). This nutrient loading dataset was collected from the early 1980s to 1990 and all lakes ($n = 37$) were polymictic.

The average summer TP concentrations for each lake were based on long-term monitoring data provided by Alberta Environment (http://environment.alberta.ca/2024.html). Given that the GIS land-use database was updated between 2000 and 2006, we restricted our sites from a potential of 80 lakes to 36, for which lake monitoring data were available between 2000 and 2006. For each year within this recent time window, we averaged the TP concentrations from May to September. The mean of post-2000 summer averages was then used as a representative TP concentration for each lake. Natural log transformations were applied where the data distributions did not follow a Gaussian curve and were thus susceptible to violate statistical assumptions of the Least Square Regression technique.

We referred to the Atlas of Alberta lakes (Mitchell and Prepas 1990) to classify lakes according to their mixing regime. Lakes were categorized as either dimictic or polymictic depending on the shape of their temperature
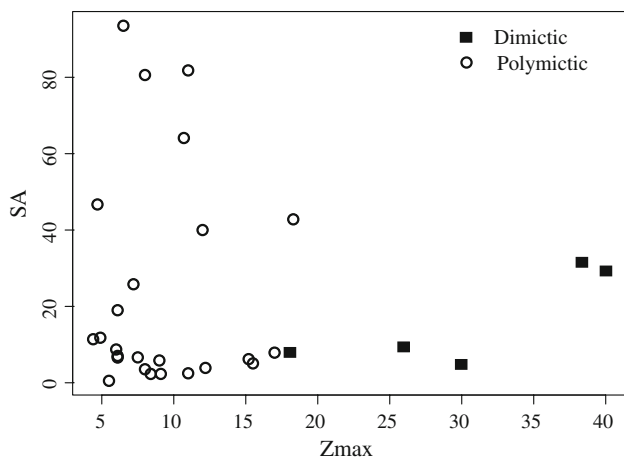
Fig. 2 Biplot of lake surface area (SA) versus maximum depth (Z_{max}) for dimictic lakes (*filled square*) and polymictic lakes (*open circle*) in Alberta

profiles in summer. These classifications were confirmed by field sampling during the summer of 2006 (from May to September), when temperature profiles were collected every 3 weeks.

Paleolimnological analyses

During the summers of 2005 and 2006, sediment cores were collected from 15 lakes of priority to Alberta Environment (a subset of the original 36 discussed above) at their deepest region with a gravity corer (Table 1; Glew 1988). Three of these lakes had multiple basins, which we

sampled separately, thus summing to a total sample size of 18 basins. Basins were selected to maximize the % Agr gradient within each mixis type (i.e., Agr range of dimictic basins: 0–72%; polymictic basins: 0–82%). All sediment cores were extruded at one-centimeter resolution. We examined surface sediments (top 1 cm) from each of these 18 basins and conducted a more detailed stratigraphic analysis of sediment cores collected from two basins from Moose Lake (one basin is dimictic and one is polymictic).

The Moose Lake sediment chronology was established by ^{210}Pb and [214]Bi radiometric dating at the University of Waterloo using an Ortec[©] Digital Gamma Ray Spectrometer. The ^{210}Pb and [214]Bi radioisotopic activities were measured on every second 1-cm sediment interval of each core from a known mass (0.2–1 g) of freeze-dried sediments for 47 h. Sediment ages were calculated using the constant-rate-of-supply (CRS) model (Binford 1990). Ages of sediment samples beyond the time limit for ^{210}Pb ages of approximately CE 1860 were estimated using a linear regression. To provide an independent control for the ^{210}Pb ages, ^{137}Cs was measured for the same sediment samples. The maximum activity of ^{137}Cs was assigned to the year of 1964, when the peak of worldwide ^{137}Cs fallout from nuclear weapons testing was recorded (Appleby et al. 1993).

All sediment samples were processed for chironomid analyses following standard techniques (Walker 2001). Briefly, homogenized sediment subsamples were deflocculated for 30 min in 10% KOH at 80°C. The wet weight of our sediment subsamples ranged between ~1.0 and

Fig. 3 Bathymetric and catchment land use map of Moose Lake. Sampling sites for the dimictic (X_v) and polymictic (X_M) basins are indicated by X_i, where i = V for Vezeau Bay and M for Main Bay. The catchment land use map displays agricultural land (*white*), forest (*dark grey*), water bodies (*light grey*), and wetlands (*black*). The bathymetric map has been modified from Mitchell and Prepas (1990)
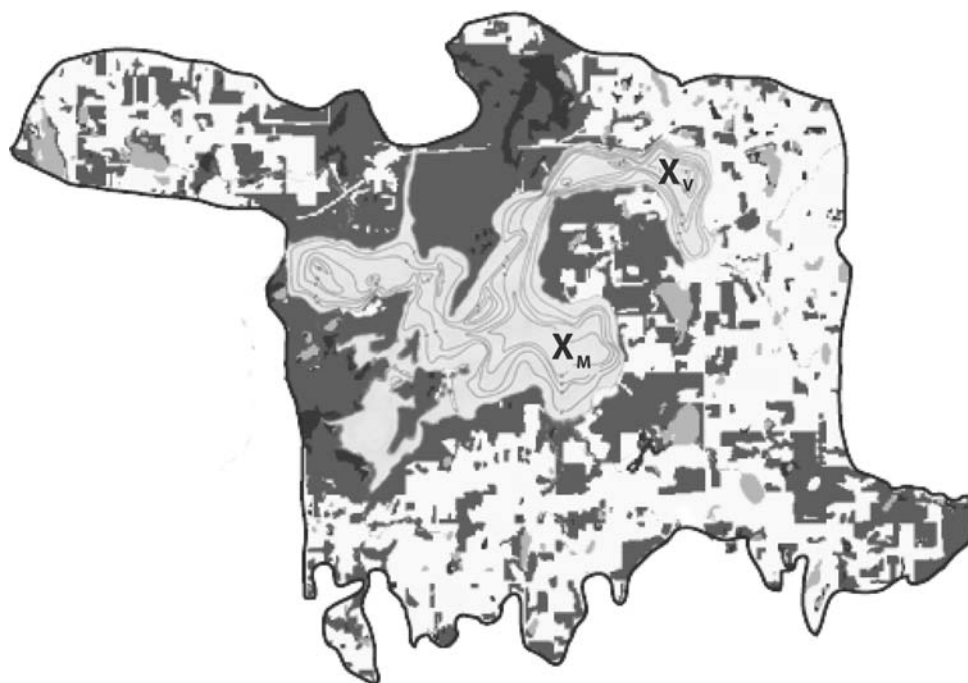
13.0 g in order to obtain a sufficient number of head capsules for a precise chironomid count (i.e. at least 50 head capsules per sample; Quinlan and Smol 2001a). The solutions were then sieved through a 100-μm mesh, rinsed with deionized water, and backwashed into a grooved Bogorov counting tray. Chironomid head capsules were picked under a dissecting microscope and permanently mounted onto slides using Entellan®. Specimens were identified to genus following Wiederholm (1983) and Oliver and Roussell (1983). We identified the first, underdeveloped instar of the tribe Chironomini as *Chironomi sp.1*. Quinlan and Smol (2001b) have suggested that this planktonic instar is reflective of productive, anoxic conditions. However, the head capsule of *Chironomi sp.1* is only lightly scleratized and therefore may be subject to differential preservation through a core. As a result, we have refrained from making interpretations based on *Chironomini sp. 1* in this study.

To assess differences in oxygen concentrations of the profundal zone of each basin type and to remove potential confounding effects of differences in the littoral zone, we first analyzed the full chironomid assemblages (i.e. both littoral and profundal taxa) and then proceeded to analyze the profundal-only taxa (as discussed further below). The separation of littoral versus profundal taxa was based on a review of the Chironomidae literature (Wiederholm 1983; Pinder 1995; Brodersen and Lindegaard 1997; Clerk et al. 2000, 2004; García-Berthou and Moreno-Amich 2000; Little and Smol 2000; Little et al. 2000; Nocentini et al. 2001; Quinlan and Smol 2001b; Heiri and Lotter 2003; Millet et al. 2003; Massaferro et al. 2005). The relative abundances of the profundal-only taxa were then recalculated based on the sum of all profundal taxa (i.e. when the littoral taxa were excluded from all counts).

To draw inferences of bottom-water DO availability from the chironomid assemblages, we synthesized the results from previous experimental and field-based research (Quinlan et al. 1998; Brodersen et al. 2008) to develop a qualitative DO inference diagram that could be applied to both polymictic and dimictic lakes (Fig. 4). Our simplified diagram orders profundal chironomid taxa along a gradient of their relative oxygen optima as determined by their weighted average (WA) values from the Quinlan and Smol (2001b) transfer function, which have been further supported by experimental determinations of oxygen optima and consumption rates (Brodersen et al. 2004, 2008). Specifically, in this simplified model, we ordered four profundal chironomid taxa (*Chironomus*, *Procladius*, *Sergentia* and *Heterotrissocladius*) according to decreasing tolerance of anoxia, with *Chironomus* having the highest tolerance of anoxia (and lowest oxygen consumption rate), and *Heterotrissocladius* having the lowest tolerance of anoxia (Fig. 4).
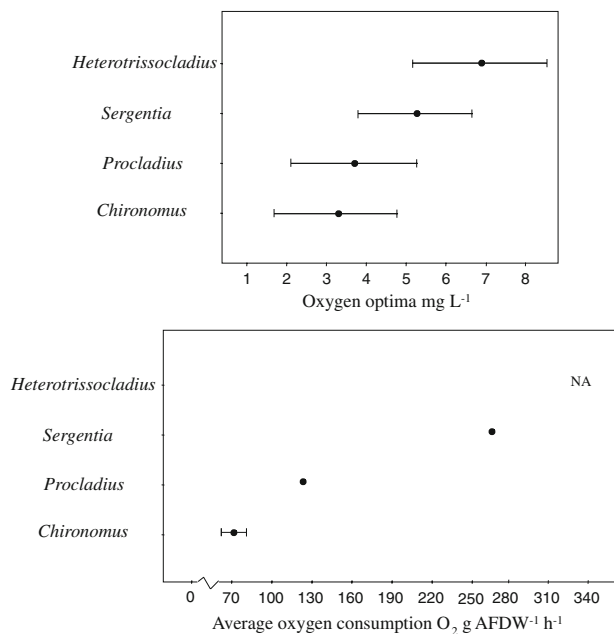

Fig. 4 Simplified oxygen optima diagram; **a** weighted average (WA) oxygen optima (*filled circle*) and tolerance values (*horizontal bars*) (in mg/L) as presented in Quinlan and Smol (2001b), and **b** oxygen consumption rates (*filled circle*) (in $\mu mol\ O_2\ g\ AFDW^{-1}h^{-1}$) as presented in Brodersen et al. (2008), where *AFDW* ash free dry weight and *h* hours. Given that our taxonomy is at the genus level, the oxygen consumption value presented for the *Chironomus* taxa is the average and standard deviation of the three *Chironomus* species values presented in Brodersen et al. (2008). *NA* no data available

Statistical analysis

All correlation analyses were conducted using the open-source software R (R Development Core Team 2007). To explore the chironomid compositional turnover (i.e. gradient length) and to determine assemblage differences between lakes of different mixing regimes and agricultural impacts, we conducted a detrended correspondence analysis (DCA) and principal component analysis (PCA), respectively, of the surface-sediment chironomid assemblages from 18 Albertan basins. We used the computer program CANOCO v. 4.53 to run both the DCA and PCA (ter Braak and Smilauer 2004). We also conducted a DCA and PCA of the sediment samples from the two basins of Moose Lake to assess differences in the temporal patterns of change of profundal chironomid assemblages between the basins. Finally, assemblage similarities within and between sites and/or sediment core depths were assessed using the analysis of similarity test (ANOSIM) of the PRIMER software package (Clarke and Warwick 2001) on Bray–Curtis similarity coefficients (Bray and Curtis 1957), where samples from each surface sediment site or from each core interval were assigned to different groups (i.e. dimictic or polymictic). This software creates a similarity matrix, where each

matrix entry represents the Bray–Curtis coefficient between every pair of sites and/or between every pair of downcore intervals, and from which one can then test the null hypothesis of no differences between groups. The analysis output provides an ANOSIM R statistic value, which was obtained from 999 random permutations of the group labels between the samples and demonstrates the probability that the null hypothesis is true. The R statistic ranges from -1 to 1, and approaches the value of one when all sites within one group (e.g. dimictic) are more similar to each other than any sites from the other group (e.g. polymictic). R will approach zero if the null hypothesis of equivalent similarities between and within groups cannot be rejected.

Results

Spatial limnological survey

A modest but significant linear correlation was found between TP and % Agr when all 36 lakes were analyzed ($r = 0.42$; $p = 0.011$). To address whether diffuse nutrient loading from agriculture is a more important determinant of water quality in dimictic than in polymictic lakes, we separated the 36 lake-set according to lake mixing regime. From this analysis, we noted a much stronger relationship between TP and % Agr among the dimictic basins ($r = 0.89$; $p = 0.003$; $n = 8$) relative to that among the polymictic basins ($r = 0.26$; $p = 0.174$; $n = 28$) (Fig. 5a). This difference in correlation coefficients is not an artifact of sample size, as ten randomized sub-samples of the polymictic lake set to a sample size equivalent to that of the dimictic lake set ($n = 8$ lakes) consistently resulted in weak and non-significant correlations. Furthermore, the difference in correlation strength is not likely due to the range of % Agr represented in each lake mixis group, as both datasets covered approximately the same disturbance range (polymictic lakes: 0.02–86.34% Agr; dimictic lakes: 0.95–72% Agr). We did, however, note important differences in TP and chl$a$ concentrations between the two lake sets; both parameters were significantly greater in the polymictic lakes compared to the dimictic lakes (Mann–Whitney Test: $U > U_{0.05(2),6,17}$ for both TP and chl$a$ between the lake categories; Fig. 5b).

Given that internal P loading increases when deep summertime mixing events are more pronounced (Larsen et al. 1981), we evaluated differences in euphotic TP concentration due to lake morphometry (Z_{mean}) and mixis. We detected a significant relationship between TP and Z_{mean} ($r = -0.56$; $p = 0.001$) when all lakes were included in the analysis. Separating the lake set according to mixis regime resulted in a weaker relationship for the polymictic lakes ($r = -0.40$; $p = 0.05$) in comparison to the dimictic lakes ($r = -0.97$; $p = 0.004$). Given that the
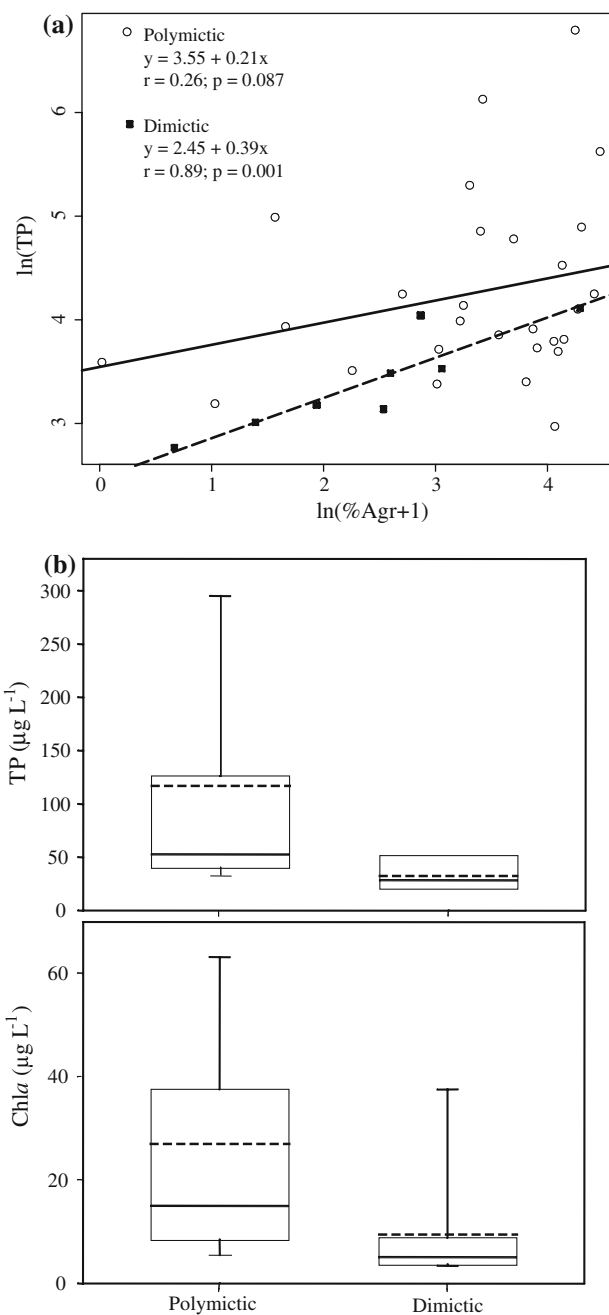

Fig. 5 a Scatterplot showing the relationship between total phosphorus concentration (ln(TP)) and percent agriculture cover (ln(%Agr + 1)) in lake catchments for dimictic lakes (*black closed squares*) and polymictic lakes (*open circle*) in Alberta. **b** Box and whisker plots comparing TP and chl$a$ concentrations between polymictic and dimictic lakes of Alberta. *Solid and dashed horizontal lines* indicate the medians and means, respectively. The rectangle delimits the 25 and 75 percentiles, and the *whiskers* represent the 10th and 90th percentiles. Mann–Whitney tests for TP ($U > U_{0.05(2),8,28}$) and chl$a$ ($U > U_{0.05(2),7,10}$) concentrations were both significant ($p < 0.05$)

polymictic lakes in our lake set are likely mixed due to their large surface areas rather than shallow depths, it was also necessary to take SA into account. We expected that

lakes with small SA: Z_{max} ratios (i.e. primarily dimictic lakes) would have lower TP, whereas lakes with larger ratios would have larger TP values. We found that the lakes with low SA: Z_{max} values did indeed have much lower TP concentrations, but no significant relationships between these two variables were detected.

To assess whether lake volume and catchment area modulate the effect of agricultural P loading (i.e. whether large lakes located in small catchments have lower TP concentration), we examined the relationship between TP and the ratio of CA: LV. Within the polymictic and dimictic lakes sets we detected a positive relationship between TP and CA: LV, but with the low sample size of the dimictic lake set, we did not detect a significant relationship (polymictic lakes: $r = 0.54$; $p = 0.006$; $n = 25$; dimictic lakes: $r = 0.62$; $p = 0.26$; $n = 6$). These results suggest that the effect of agriculture on downstream lakes may be obscured in lakes with large CA: LV.

External versus internal P loading

We examined a subset of 20 polymictic Alberta lakes for which we had internal and external P loading data (unpublished AENV 1990) to establish whether the agricultural P load was significant and to evaluate whether internal P loading was related to basin morphometry. Within the 20 lake dataset, however, we identified two outliers in terms of TP concentration (Saskatoon Lake = 815 μg TP/L, average of subset excluding Saskatoon Lake = 72 μg TP/L ± 58 SD) and internal P load (Winagami Lake = 15,005 kg, average of subset excluding Winagami Lake = 2,134 kg ± 1,781 SD) and thus these were removed from further analyses. To determine the contribution of agricultural load to the total loading from the catchment, we correlated external load and Agr load and found a significant relationship ($r = 0.79$; $p < 0.001$). We then tested the relationship between Agr load and % Agr and found a significant, positive correlation ($r = 0.75$; $p < 0.001$). Finally, given the importance of CA and LV in modulating TP concentrations, we examined their effects on internal P loading in polymictic lakes. We found significant quadratic relationships between internal P loading and LV ($r = 0.87$; $p = 0.00005$), SA ($r = 0.87$; $p = 0.00004$) and CA ($r = 0.82$; $p = 0.0004$), with peak internal loading at mid-range values. However, internal loading was linearly related to Z_{max} ($r = 0.40$; $p = 0.07$), which suggests that the deeper, polymictic basins are more likely to become strongly stratified on calm summer days and experience increased anoxia.

Paleolimological analysis: surface sediments

To assess whether differences in bottom water oxygen concentrations exist between polymictic and dimictic lakes

in Alberta, we compared the sub-fossil chironomid communities from the surface (0–1 cm) sediment samples of 18 lake basins located along a modern gradient of catchment land use. To determine whether chironomid abundance followed a unimodal or linear distribution, we conducted a Detrended Correspondence Analysis (DCA), with detrending by segments. The first DCA axis gradient length was less than 1.5 SD, indicating that a linear PCA model was preferable over a unimodal CA model (ter Braak and Prentice 1988; Birks 1995). A PCA of the full chironomid assemblages (i.e. littoral and profundal chironomid taxa) from the 18-basin dataset partitioned the sites between dimictic and polymictic mixing regimes. The first PCA axis alone explained 63% of the variation in chironomid taxa and distinguished polymictic sites dominated by the profundal *Chironomus* taxa (i.e. predominantly *Chironomus plumosus*) from dimictic basins dominated by a variety of littoral taxa (Fig. 6). Furthermore, the PCA axis-1 scores of the dimictic basins were significantly different from the polymictic axis-1 scores (t test: $t = -2.16$; p value $= 0.01$), thus we have interpreted the first axis as a synthetic variable for basin mixing regime. We also found a statistically significant difference in the full chironomid assemblages between the two mixis types based on our ANOSIM analysis (Global $R = 0.3$; $p < 0.003$), demonstrating that the similarity in taxa relative abundances was greater among sites of the same mixing regime than between lakes of different mixing regimes. The relative abundance of *Chironomus*, for example, was significantly higher in the polymictic basins than in the dimictic basins (Mann–Whitney test: $U > U_{0.05(2),7,13}$; $p < 0.05$) and the chironomid community was significantly more diverse in the dimictic basins than in the polymictic basin (Mann–Whitney test of Shannon–Wiener index was significant at $\alpha = 0.002$). Even after correcting for differences in count size among sites, using rarefaction techniques, the dimictic basins were more species rich (Mann–Whitney test significant at $\alpha = 0.002$).

In this study, we suggest that differences in the relative abundances of littoral taxa are not a mere artifact of differences in lake morphometry, as the proportion of littoral to profundal area was comparable between lake types. Furthermore, lake water residence time for the polymictic basins (range 1.5 to >100 years; mean 51.9 years) was not significantly different (Mann–Whitney test $U' < U_{(2),0.05,7,25}$) from that of the dimictic basins (range 2.5 to >100 years, mean 35.4 years). Instead, we suggest that differences within the littoral environment (such as macrophyte cover and turbidity) may account for the observed differences in littoral taxa relative abundances.

To draw inferences of profundal oxygen concentrations from the chironomid assemblages, we restricted our analyses to the profundal-only taxa as differences in littoral habitat between lakes of different mixing (discussed above)
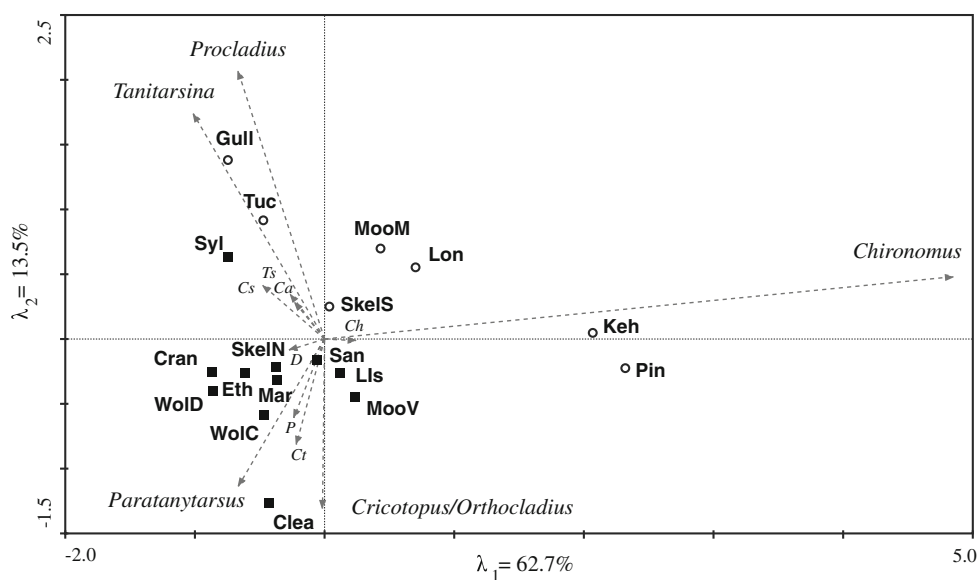
Fig. 6 Principal Component Analysis (PCA) of the surface sediment chironomid assemblages from 18 Albertan basins, with dimictic basins indicated as *closed squares* and polymictic basins as *open circles*. *Arrows* indicate dominant (≥5% in ≥5 sites) chironomid taxa. Taxa codes: *Ch = Chironomini sp.1, Cs = Cladotanytarsus, Ca = Cladopelma, Ct = Corynoneura/Thienemaniella, D = Dicrotendipes, P = Polypedilum, Ts = Tanytarsus*. Lake codes: *San* Lac Santé, *Syl* Sylvan Lake, *Clea* Clear Lake, *Moo V* Moose Lake, Vezeau Bay, *Ske N* Skeleton Lake, North Basin; *Eth* Ethel Lake, *LIs* Long-Island Lake, *Cran* Crane Lake, *Wol C* Wolf Lake, Central Basin; *Wol D* Wolf Lake, Deep Basin; *Mar* Marie Lake, *Pin* Pine Lake, *Keh* Kehewin Lake, *Gull* Gull Lake, *Moo M* Moose Lake, Main Basin; *Tuc* Tucker Lake, *Ske S* Skeleton Lake, South Basin; *Lon* Long Lake

could obscure patterns in relative abundance data (although full relative abundance plots are presented in Appendix Figs. 9, 10, 11). When analyzing profundal-only data, Quinlan and Smol (2001a) noted a stabilization of the taxon percent abundances as count sizes reached 15–20 head capsules (h.c.) per sample. As such, a minimum count of 20 h.c. for such analyses is suggested, which we achieved in all but one lake (Wolf Lake-Deep Basin = 18.5 h.c.).

When focusing solely on profundal taxa, we noted that the oxygen-requiring *Heterotrissocladius* and *Sergentia* taxa were only present in the assemblages of the dimictic basins, most of which had little to no agricultural activity in their catchments (Fig. 7). Lake depth, however, also likely plays a role in the occurrence of these deep-water taxa. *Heterotrissocladius*, for example, tends to be found in the profundal zone of deeper temperate lakes where oxygen is available and water temperature is colder. It is, thus, not surprising that *Heterotrissocladius* was found solely in the dimictic basins of this lake set (Fig. 7), and that the relative abundance of this taxon had a weak, positive relationship with Z_{max} ($r = 0.7$; $p = 0.3$; $n = 4$). Trophic variables, however, explain more of the variation in the distribution of *Heterotrissocladius*. Specifically, we found that the relative abundance of *Heterotrissocladius* decreased as lake TP increased ($r = -0.78$; $p = 0.037$). Referring to our simplified oxygen optima diagram (Fig. 4), these results suggest that the dimictic basins are located at the higher end

of the gradient of oxygen availability. The profundal chironomid taxa of the polymictic basins, however, were exclusively composed of *Chironomus* and *Procladius* and, thus, indicated qualitatively lower oxygen availability. In general, relative abundance of *Chironomus* was positively correlated to TP ($r = 0.72$; $p = 0.0005$) and negatively related to Z_{max} ($r = -0.61$; $p = 0.006$) across all 18 sites. *Procladius*, however, was neither related to TP nor Z_{max}.

Paleolimnological analysis: temporal trends at Moose Lake

To further determine the effects of lake mixing regime, we compared temporal changes in chironomid communities in sediment cores from two separate basins of Moose Lake that differ in mixing regime. Prior to European settlement (~1900), the two basins of Moose Lake had similar trajectories in profundal chironomid assemblages (Fig. 8a, b). By mid-1950s, however, we identified the start of a diverging trend between the two basins (Fig. 8c). In the dimictic basin (Vezeau Bay), the relative abundance of *Chironomus* remained fairly constant (50–70%) throughout most of the core, with the exception of a temporary increase at ~CE 1900 coincident with arrival of European settlers, indicating a brief rise in oxygen stress (Fig. 8a). Since the mid 1960s there has been a gradual increase in relative abundance of *Chironomus* coupled with a decrease in *Procladius* (i.e. indicating a slight shift towards the anoxic

Fig. 7 Relative abundance of profundal chironomid taxa from the upper sediments (0–1 cm) of the 18 central Alberta study basins. Within each type of lake mixis, the lakes are ordered according to decreasing catchment land use (i.e. Lac Santé and Pine Lake have the greatest coverage of agriculture in their catchments). Dimictic basins are indicated by *black bars* and polymictic basins by *grey bars*
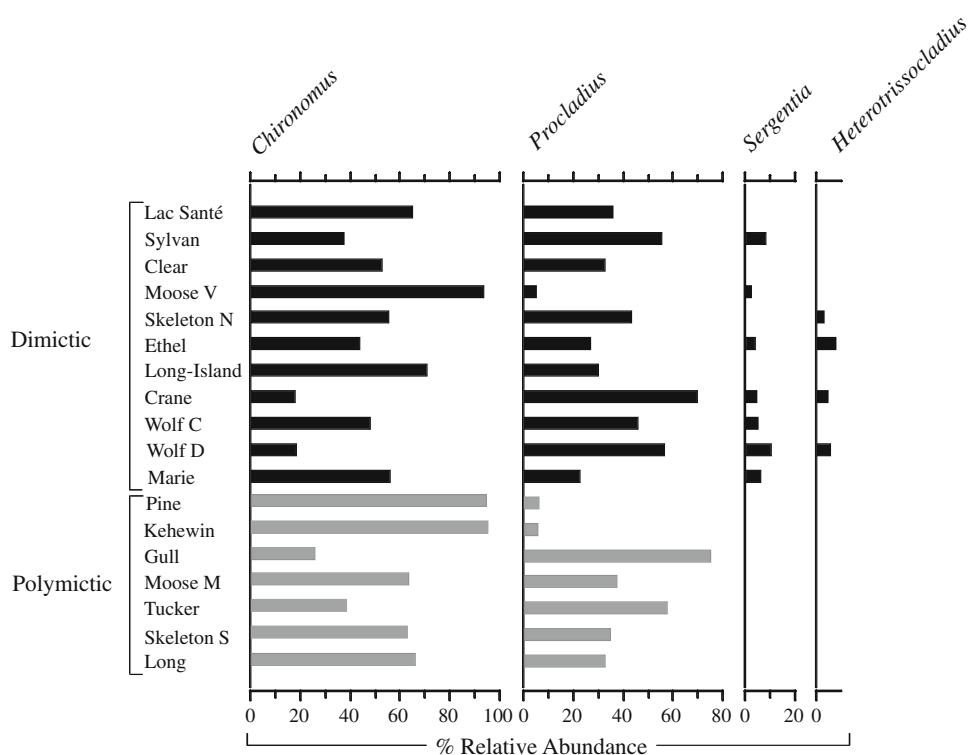
end of the spectrum). The polymictic basin (Moose Main) likewise had fairly constant values of *Chironomus* (75–80%), but in contrast to the dimictic basin, experienced a slight decrease in *Chironomus* (to ~60%) and an increase in *Procladius* (to ~40%) from the mid 1970s onwards (Fig. 8b). Given that the flux of chironomids in each core has been relatively constant through time, we suggest that anoxia has never been severe enough to completely inhibit chironomid production.

Discussion

The integration of information from three separate analyses (i.e. the spatial limnological survey, the surface sediment samples and the temporal trends of the Moose Lake paleo-record) identified a clear and strong role of lake mixis in regulating nutrient concentrations and the response of lake biota to external nutrient loading. Our findings are also in accordance with Brodersen et al. (1998), who suggested that dividing lake sets according to lake mixis would increase the predictive strength of chironomid inference models.

Contemporary relationship between land use and water quality

The limnological spatial survey is the first line of evidence that we provided to highlight how polymictic and dimictic lakes differed in their responses to external P loads. Our results, as well as those of previous studies in the region (Prepas and Trew 1983; Riley and Prepas 1984, 1985; Trew Alberta Environment, pers. comm.), show that internal loading is high in regional polymictic basins. We suggest that this effect greatly masks increases in external loading from the catchments of polymictic lakes. In theory, the intercept of the relationship between TP and % Agr represents the average or expected TP concentration of the lake set when the % Agr is zero, or likewise, where all nutrient loading is solely background and/or internal. The significant correlation between Agr load and % Agr further indicates that when % land cover is low the actual nutrient load from farmland is likewise reduced. The significantly higher intercept we observed in our polymictic lake set relative to the dimictic lake set (Fig. 5a) is consistent with earlier work by Trew (Alberta Environment, pers. comm.) who found that internal loading was on average 12.9 times greater than external loading across 36 polymictic lakes in Alberta.

Internal nutrient load in the polymictic lakes of the region is due, at least in part, to the elevated primary production (Fig. 5b) and anoxia that develops both in summer (pers. observ.) and winter (Meding and Jackson 2003). We have also shown through our empirical analyses that lake morphometry is a significant determinant of internally-loaded P during summer months for the subset of 18 polymictic lakes examined. Studies in European shallow lakes have shown that anoxia is not a prerequisite for the release of phosphorus from the sediments (Søndergaard

Fig. 8 Paleolimnological profiles of the relative abundances of the profundal-only chironomid taxa (%), the flux of chironomid head capsules (no./cm^2 × year) for the total profundal and littoral taxa, and the ^{210}Pb activity data (dpm/g) of the dimictic (**a**) and polymictic (**b**) basins of Moose Lake, Alberta. Note: we have not plotted the flux of chironomid capsules in the surface sample of each basin because of the large errors associated with these estimates. **c** displays the PCA axis 1 scores of the dimictic and polymictic profundal chironomid assemblages through time. For all three panels, the date of European settlement in the catchment is ca. CE 1910
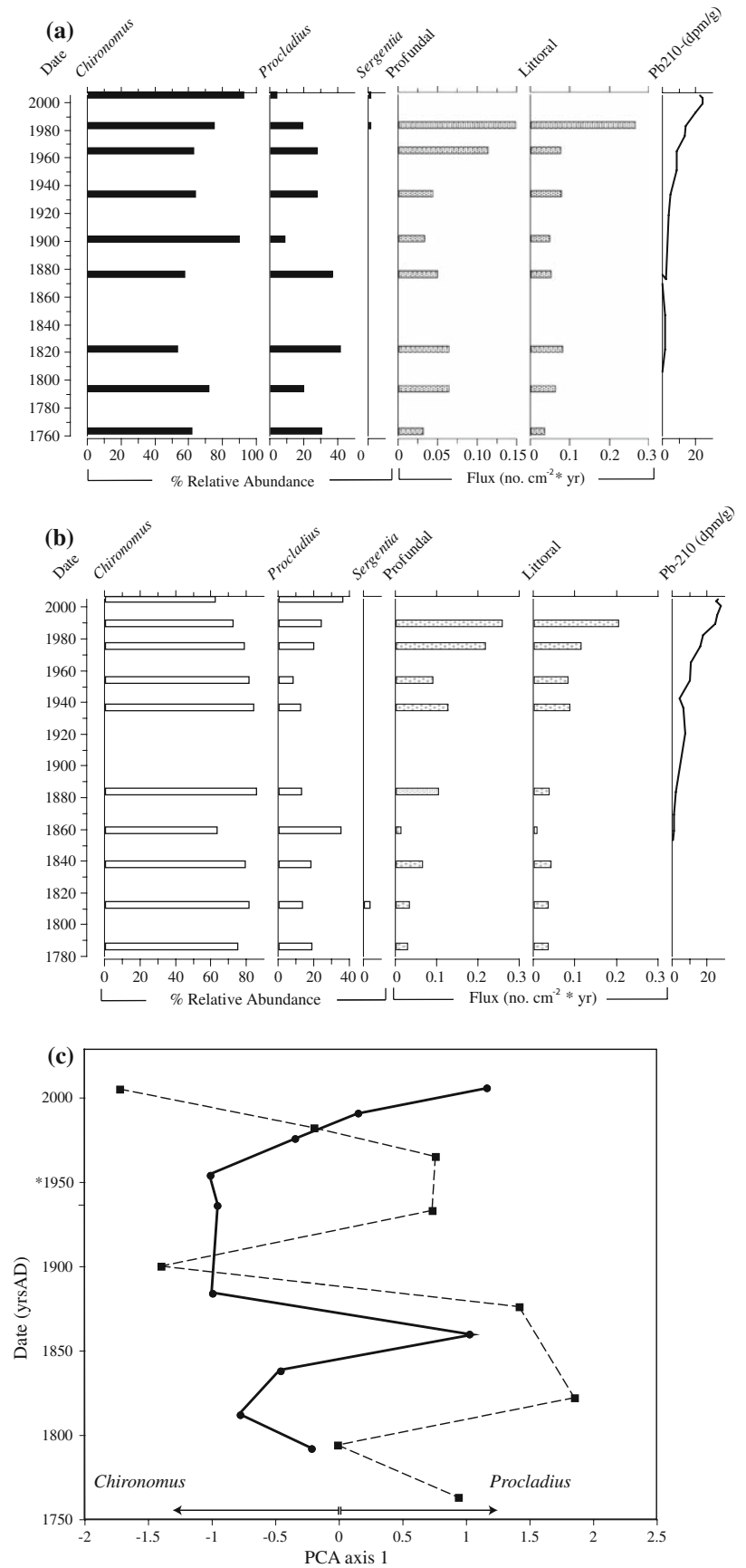
et al. 2003). Wind-driven turbulence and changes in pH and sulfur concentrations in sediments are all additional factors that can influence the transmittance of phosphorus to the overlying water column in shallow lakes (Søndergaard et al. 2003). Although dimictic lakes can also develop anoxic deep waters that promote internal P recycling, the nutrient-rich hypolimnic water is only brought to the photic zone during spring and fall turnover, and thus the opportunity for a positive feedback with algal production is more limited.

The greater TP and chl*a* variability observed in the polymictic lakes is indicative of differences in factors such as lake morphometry and fetch. Furthermore, given the sensitivity of mixis patterns in polymictic lakes to meteorological conditions, different weather from year to year has the potential to increase the complexity, and thus, variability of productivity in polymictic lakes. At a given point along the polymictic to dimictic mixing gradient, however, lake depth impedes mixing of phosphorus from the hypolimnion to the surface waters. When this takes places, external P loading becomes the primary source of nutrients in dimictic lakes, while an internal feedback loop supplies phosphorus throughout the summer in polymictic systems (Schaffner and Oglesby 1978; Fee 1979). Given the importance of lake depth, we evaluated differences in euphotic TP that were due to lake morphometry and mixis (i.e. the relationship between TP and Z_{mean}). We observed a strong negative relationship between TP and Z_{mean}, where for every unit increase in Z_{mean}, TP decreases three and fourfold in dimictic and polymictic lakes, respectively. This is in accordance with the gradual switch in primary P source, from internal to external P loading, as one moves along the polymictic to dimictic continuum as depth increases.

Similar to the results reported herein, a meta-analysis of 358 temperate lakes also revealed that lake morphometry explained a significant fraction of the residual variation remaining in TP across lakes after accounting for the proportion of agriculture in the lakes' catchments (Taranu and Gregory-Eaves 2008). The study showed that shallow lakes had higher TP concentrations than deeper lakes under equivalent agricultural development. Thus, our modern limnological survey results are consistent with both local and international studies.

Paleolimnological analyses

Ecological processes associated with lake mixing regime and their sensitivity to land-use change are reflected in the chironomid assemblages preserved in the sediment. We found a strong dichotomy in the proportion of littoral chironomid taxa between polymictic and dimictic lakes, where the relative abundances of littoral taxa were lower in the polymictic lakes (Fig. 6). Previous chironomid studies of polymictic lakes have generally found that littoral taxa

(having higher oxygen and temperature optima) dominated the sedimentary assemblages because of greater littoral habitat availability relative to the dimictic lakes (Dall et al. 1984; Brodersen et al. 1998). Most of our polymictic lakes differ from earlier study sites, however, in that they are relatively deep but susceptible to mixing in summer because of their large surface areas. As such, the portion of littoral to profundal area in polymictic lakes is comparable to those of dimictic lakes of this region, and thus the relative abundances of littoral taxa would not necessarily be more abundant in the polymictic lakes. Furthermore, no significant differences in water residence time were detected between the polymictic and dimictic basins of our lake set (Mann–Whitney test $U' < U_{\alpha(2),0.05,7,25}$). In addition, it seems unlikely that chironomids are reflecting a strong air temperature difference between the polymictic and dimictic lakes as most polymictic sites are located in the southern range of our lake set and, as such, one would expect the polymictic lakes to have a slightly warmer micro-climate. Yet the relatively low relative abundance of littoral chironomids in our polymictic lakes (which have warmer temperature optima; Heiri et al. 2003; Walker and Cwynar 2006) suggests the opposite trend. Instead, we suggest that the differences in relative abundances of littoral taxa are likely related to the relatively high turbidity and low macrophyte densities in the polymictic sites. It is well known that macrophytes provide critical habitat and refuge for littoral chironomid taxa (Pinder 1986; Brodersen et al. 2001). Based on an earlier Albertan limnological study by Jackson (2003), we can infer that the turbidity in our polymictic lakes (modeled using Jackson's 2003 predictive equation) support lower macrophyte densities than in our dimictic lakes (i.e., lower littoral chironomid habitat) and in addition, the Secchi depths of the polymictic lakes were significantly shallower than those of the dimictic lakes (Mann–Whitney test $U' < U_{\alpha(2),0.001,12,26}$).

The analysis of profundal-only chironomid taxa from the surface sediments revealed a trend that is consistent with the observation of higher TP concentrations in polymictic lakes; namely, oxygen-requiring taxa (i.e. *Heterotrissocladius* and *Sergentia*) were exclusively present in deeper, lower productivity, dimictic lakes (Fig. 7). The dominant taxon in the more productive, polymictic lakes was *Chironomus*, a genus that is known to be an important indicator of chronic anoxia and capable of surviving under anaerobic conditions as a result of higher hemoglobin concentration in the larval bodies (Curry 1965; Nagell and Landahl 1978). This suggests that these polymictic basins are more susceptible to anoxia. *Chironomus* is also a genus that is capable of withstanding pronounced environmental variation in trophic state better than other taxa, and thus retains a competitive advantage in fluctuating environments, such as the stochastic mixing of polymictic systems (Woodward

and Shulmeister, 2006). Not surprisingly, we observed that *Chironomus* was strongly correlated to TP and Z_{max} across all 18 sites, whereas *Procladius* was not related to TP or Z_{max}.

Based on detailed monitoring of both the polymictic and dimictic lakes, we know that both lake types experience profundal anoxia in summer. This phenomenon is generally more unusual in polymictic lakes, but not unexpected in eutrophic to hypereutrophic lakes, where short periods of wind stagnation and heightened decompositional activity in summer can result in rapid development of bottom water anoxia at the sediment-water interface (Papst et al. 1980; Osgood 1988; Taranu 2008). Meding and Jackson (2003) have also demonstrated that during the winter season, when Albertan lakes are ice-covered, their oxygen decay rates are significantly and positively related to phosphorus concentrations. Given that phosphorus and chl*a* concentrations were significantly greater in the polymictic study lakes, the available oxygen would be expected to be consumed more rapidly and lead to more extensive winter anoxia relative to the dimictic lakes. Thus, although both lake types experience oxygen stress, we found that disparities in the severity of anoxia between both basin types were related to differences in TP concentrations and internal P loading.

There are numerous variables, not measured in this study, that likely exert an important control on the chironomid community composition. Profundal anoxia due to elevated productivity in Albertan polymictic lakes is at such an extreme range, however, that it is likely the most important limiting factor to chironomid growth, survival and diversity. For example, in a within-lake oxygenation study, Dinsmore and Prepas (1997) demonstrated that in a neighboring Albertan lake (Amisk Lake), the chironomid assemblage of the oxygenated basin was affected by DO concentrations, rather than temperature.

Our time-series data further strengthens the conclusions that the nutrient-rich polymictic lakes are less responsive to land-use changes than the dimictic lakes. The widespread increase in land use in the catchment of Moose Lake, which began with the settlement of Europeans in the catchment at the turn of the 20th century, is reflected in the chironomid profiles as a qualitative increase in oxygen stress in the dimictic basin (Fig. 8a). The chironomid stratigraphy of the polymictic basin from Moose Lake, on the other hand, indicated an opposite trend of a slight alleviation in the severity of oxygen stress (Fig. 8b).

The results presented herein build upon a growing literature to suggest that the response of chironomid communities to land-use change depends on lake typology. Consistent with our findings, Little and Smol (2000) reported a muted response in chironomid assemblages from a polymictic lake to large-scale land use changes associated with the construction of a canal system. This same

construction activity, however, had a pronounced effect on the trophic state of a neighboring deep lake, as inferred by diatom assemblages (Christie and Smol 1996). Karst and Smol (2000) also noted that although deep lakes of the surrounding area demonstrated an increase in diatom-inferred TP concentration (DI-TP), this same polymictic lake had only a minor change in DI-TP, which the authors attributed to a macrophyte-maintained equilibrium. Langdon et al. (2006) likewise observed distinct responses in the chironomid community to land-use changes across different lake types. The contrasting responses between lakes of different mixing regime are even more compelling when one compares these to studies where multiple basins within the same lake are studied. Francis (2001), for example, demonstrated that three deep, dimictic basins within the same lake had similar temporal trends of increased inferred oxygen stress and eutrophication. Our study is unique, however, in that we showed that basins from the same lake but with different mixing regimes showed contrasting responses to land-use change.

In a companion analysis of the diatom record of Moose Lake (based on the same sediment core as this study), Köster et al. (2008) found that changes in diatom species composition in the dimictic basin were correlated to climatic change up until the time of European land settlement. After this time, climate could not explain variations in the diatom assemblages (Köster et al. 2008). In the polymictic basin, however, changes in the diatom assemblages were correlated with climate over the entire length of the record. As historical data from a nearby lake (Cold Lake, Alberta) shows that ice break-up dates have come earlier over the last 50 years (Komex International Ltd 2003), we suggest that this climate change may have alleviated to some degree winter anoxia, which is heightened in polymictic lakes. Similar to the Köster et al. (2008) diatom results, we also observed a strong correlation between the Cold Lake climate variables (i.e. total precipitation (mm) and mean temperature (°C) from 1953 to 2005) and the PCA axis 1 scores from the profundal taxa analysis of the polymictic basin of Moose Lake ($r = 0.99; p = 0.011$ and $r = 0.9; p = 0.097$, respectively).

Our findings, which show the differential responses between lake mixis types to land use, regional climate and internal loading, are supported by numerous previous studies (e.g. Gerten and Adrian 2001; George et al. 2004; Mooij et al. 2005). The overriding effect of climate on the dynamics of the polymictic basin of Moose Lake is also consistent with observations made by Schindler et al. (1996) who stated that polymictic lakes are more sensitive to climatic changes because of their large surface area: volume ratios and generally smaller mean depths. Kangur et al. (2007) also demonstrated that water level and temperature were important variables in governing eutrophication signals in a large, shallow European lake.

More locally, the few century-scale paleolimnological records from Alberta, which have all come from polymictic lakes, have shown enhanced eutrophication trends since ∼CE 1960, but these were all sites where urbanization has provided a substantial proportion of the nutrient signal (Blais et al. 2000; Schindler et al. 2008). In a neighboring study region (Saskatchewan), a series of paleolimnological studies did report a significant interaction between water-quality indicators and agriculture in a series of polymictic lakes (Hall et al. 1999; Dixit et al. 2000; Quinlan et al. 2002), but climate was a much stronger predictor of chironomid community changes (i.e. explained on average four times more variance) than agriculture (Quinlan et al. 2002). These earlier regional studies provide evidence that when the nutrient load is strong enough (i.e. when both agriculture and urban activities are present simultaneously), even polymictic lakes will show eutrophication trends.

Conclusion

Our findings indicate that processes related to a lake's morphometry are important in governing the response of lake water quality and ecological changes to land use. Collectively, our data suggests that dimictic lakes situated in naturally nutrient-rich landscapes are responsive to changes in land use across spatial and temporal gradients. Our analyses of polymictic basins, however, indicate that other factors can have an overriding influence on the chironomid assemblages and that external, non-point loading has not yet exerted a detectable effect in these polymictic systems. We propose that shorter ice-cover seasons, together with an overriding influence of internal loading, may be driving the changes in these polymictic lakes. Given that droughts are forecasted to be more intense in this region in the near future, which could alter lake mixing regime, defining the response of lake types to land-use changes is important for effective management.
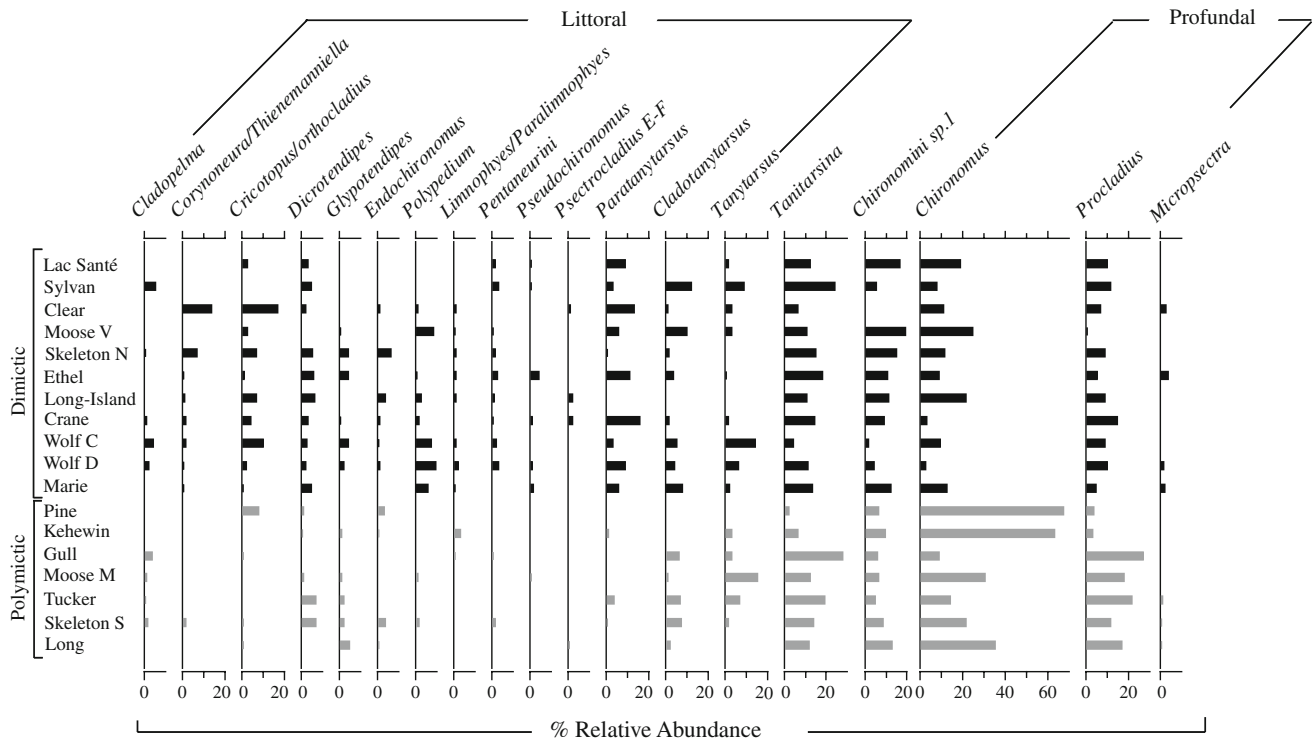
Appendix

See Figs. 9, 10, 11

Fig. 9 Chironomid relative abundances of the complete community from the top core intervals of 18 Albertan Basins. Taxa listed comprise at least 2% of the assemblage in at least two basins

Fig. 10 Relative abundances of the complete community from downcore chironomid assemblages of the dimictic basin (Moose V) of Moose Lake. Taxa listed comprise at least 2% of the assemblage in at least two sample intervals
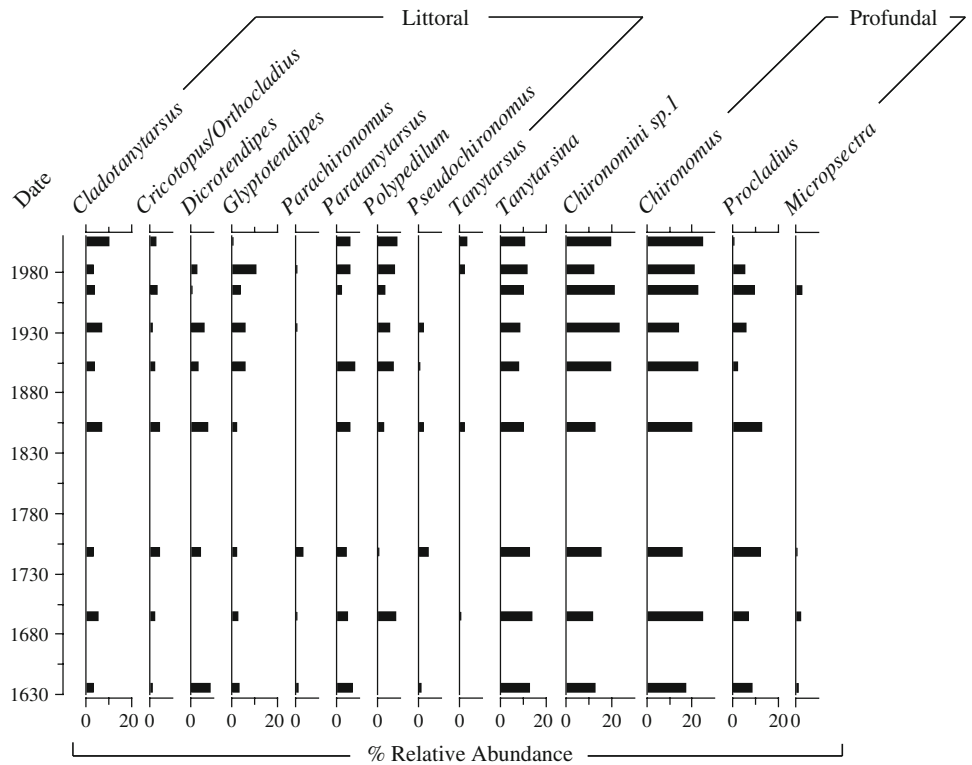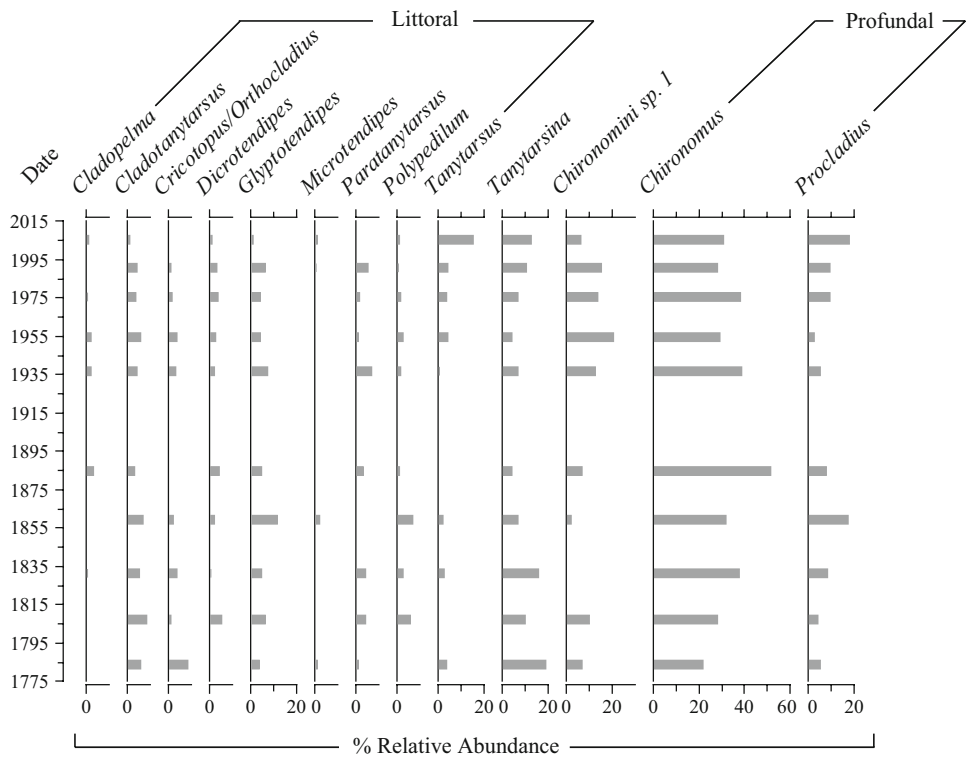

Fig. 11 Relative abundances of the complete community from downcore chironomid assemblages of the polymictic basin (Moose M) of Moose Lake. Taxa listed comprise at least 2% of the assemblage in at least two sample intervals

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