ARTICLE

Cladoceran diversity dynamics in lakes from a northern mining region: responses to multiple stressors characterized by alpha and beta diversity

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Abstract: The lakes surrounding the iron ore mining region of Schefferville, Quebec, Canada, sit within a landscape of historical disturbances, two of which have been relatively well documented over time: metal contamination and nutrient loading. Based on the analysis of sediment cores, we used cladoceran zooplankton subfossil assemblages from two lakes located in Schefferville to track both alpha and beta diversity over the last 100+ years. We showed that high metal concentrations were correlated with decreased cladoceran diversity, and that the site that experienced both direct wastewater input and atmospheric metal loading (Lake Dauriat) had the greatest declines in cladoceran richness. In both lakes, turnover in cladoceran assemblages was highest in the mining period. During the period of mine closures and improvement of wastewater treatment, some decreases in metal enrichment in the sediments and increases in cladoceran richness were observed in Lake Dauriat. Overall, a combined use of species richness and beta diversity metrics showed alpha and beta diversity are not always congruent, and that there are various ways to interpret scenarios of temporal beta diversity in northern freshwater systems.

Résumé : Les lacs entourant la région minière ferrifère de Schefferville (Québec, Canada) se trouvent dans un paysage marqué par des perturbations passées, dont deux sont relativement bien documentées dans le temps, à savoir la contamination par les métaux et l'apport de nutriments. À la lumière de l'analyse de carottes de sédiments, nous avons utilisé des assemblages de cladocères zooplanctoniques subfossiles provenant de deux lacs situés à Schefferville pour caractériser les diversités alpha et bêta au cours des 100 dernières années et plus. Nous démontrons que de fortes concentrations de métaux sont corrélées à une diversité de cladocères réduite et que le site ayant reçu des apports directs d'eaux usées et des apports atmosphériques de métaux (lac Dauriat) présente les plus fortes baisses de richesse des cladocères. Dans les deux lacs, le renouvellement des assemblages de cladocères était à son plus fort durant la période d'exploitation minière. Durant la période des fermetures de mines et de l'amélioration du traitement des eaux usées, certaines baisses de l'enrichissement en métaux dans les sédiments et augmentations de la richesse des cladocères ont été observées dans le lac Dauriat. Dans l'ensemble, l'utilisation combinée de mesures de la richesse spécifique et de la diversité bêta a permis de démontrer que les diversités alpha et bêta ne concordent pas toujours et qu'il y a différentes manières d'interpréter les scénarios de diversité bêta dans le temps dans les systèmes d'eau douce nordiques. [Traduit par la Rédaction]

Introduction

Perturbation of freshwater systems is of broad concern because of their importance in providing ecosystem services (Limburg 2009), their role as biodiversity hotspots (Strayer and Dudgeon 2010), and the prevalence of global water insecurity (Vörösmarty et al. 2010). Many studies have examined discrete changes in ecological communities in response to anthropogenic stressors (e.g., pre- and post-industrialisation comparison using historical and surface sediments in the field of paleolimnology; Dixit et al. 1999); however, it is also important to understand the processes by which communities change and the degree of temporal species turnover.

While many investigators have analysed alpha diversity trends (often measured as the number of species, or richness, in each lake), beta diversity is emerging as a more sensitive diversity metric as it characterizes the degree of change in species composition that may occur even without changes in the total number of species present. Of studies that have addressed alpha diversity responses to multiple stressors (e.g., Heugens et al. 2001), the impacts of multiple disturbances on local biodiversity patterns are often context-dependent, varying by the type of stressor and the local setting. For example, Yan et al. (2004) observed differential diversity responses in zooplankton communities across sites that were exposed to distinct combinations of metal contamination and acidification. Recent studies applying beta diversity metrics to evaluate responses to multiple stressors in aquatic systems have provided great insights. An illustrative example was conducted by Passy and Blanchet (2007), who examined algal community beta diversity responses to anthropogenic impacts (habitat degradation) and showed that spatial beta diversity was lower in degraded systems than in more pristine systems.

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2   Can. J. Fish. Aquat. Sci. Vol. 00, 0000

Fig. 1. Maps showing the location of (*a*) Schefferville in the Quebec landscape and (*b*) the two study lakes surrounding the town of Schefferville.
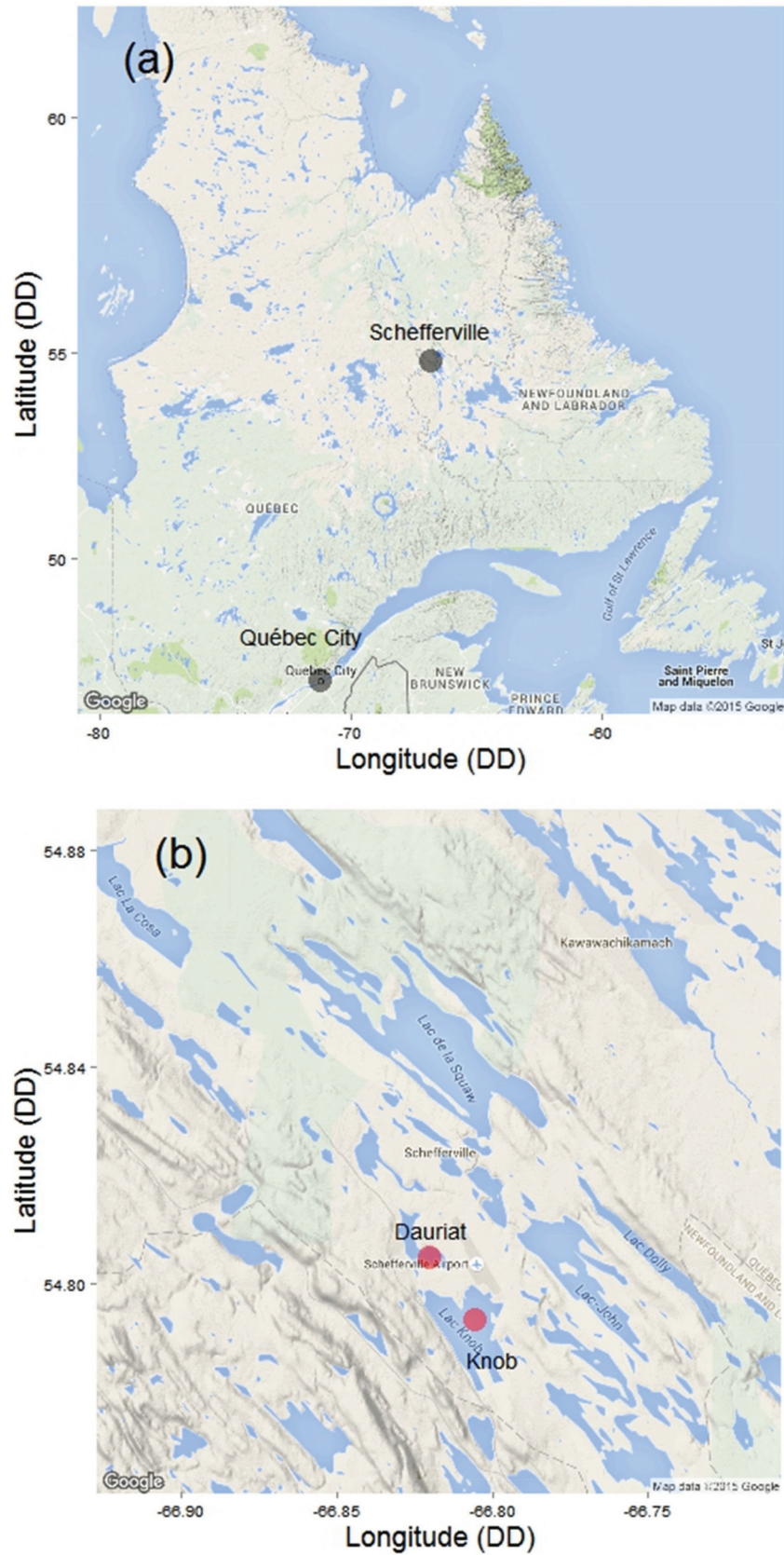
Table 1. Description of lake size characteristics and surrounding land use for each of the two study lakes.

Lake	Latitude	Longitude	Observed maximum depth (m)	Surface area (km²)	Surrounding land use
Dauriat	54°48′23.73″N	66°49′30.85″W	11	0.56	Town site; hedgerow around some of lake; used for raw sewage until 1975
Knob	54°37′29.13″N	66°48′30.77″W	5.2	2	Town site surrounding part of lake; drinking water source; flow through to Dauriat

The mining region surrounding Schefferville, Quebec, Canada, has a long history of multiple stressors from iron ore mining and the development of associated infrastructure. While many mining regions around the world have experienced large-scale acidification of their surface water bodies (such as the well-studied nickel-mining region of Sudbury–Killarney; Dillon et al. 1987), the sedimentary geology of the Labrador Trough has prevented acidification of aquatic systems around Schefferville (Aebischer et al. 2013, 2015). The sedimentary rock acts like a buffer, helping to neutralize the acidic effect that mining emissions would normally have on water bodies. Therefore, Schefferville presents a relatively unique system for studying the long term impacts of metal and nutrient contamination in the North, in the absence of acidification.

However, the town of Schefferville is similar to many other communities developed around extractive industries, where the infrastructure needed to manage town and (in some cases) industrial wastewater has not necessarily kept pace with its rapid development. Indeed, wastewater treatment facilities were not installed in Schefferville until 1975, despite the founding of the town in the early 1950s (Adams 2007; Aebischer et al. 2015). Increased nutrient and metal inputs to surface water bodies have varied over time and across the Schefferville landscape (especially between the lakes within the town), arising not only from mining sites, but also from commercial infrastructure and residential development to support the mining sector (Lapèrierre et al. 2008; Aebischer et al. 2015).

Laperrière et al. (2008) were among the first to demonstrate the effect of mining and mining-related development on the aquatic structure and diversity of Lake Dauriat (previously named Lake Pearce). Their study emphasized that, while the majority of mining activities occurred between the mid-1950s and late 1970s, the legacy effects of these activities were still evident in Lake Dauriat, more than 20 years later. It is important to consider long term effects in the Schefferville region, as there was a resurgence of various mining activities in 2009 and 2011, though mining activities have now slowed again. As such, these focal lakes provide an opportunity to better understand the effects of metal pollution and increased nutrient inputs on cladoceran diversity in a boreal mining region without the compounding effect of acidification; especially as the interactions of ecosystem stressors may be reduced when one stressor (such as pH) has an omnibus effect (Burton and Johnston 2010).

Our study aims to quantify temporal and spatial patterns of alpha and beta diversity of cladoceran zooplankton in response to historical metal and nutrient disturbance in the Canadian boreal subarctic (Schefferville, Quebec, Canada). To do this, we focused on two lakes with different ecological histories with respect to metal contamination and nutrient loading. While one lake receives only metal loading from atmospheric sources (Lake Knob), the other lake receives both metals and nutrients via untreated wastewater loading (Lake Dauriat). The goals of our study were to (i) characterize the effect of metal contamination on cladoceran species richness and composition in the presence and absence of anthropogenic eutrophication and (ii) examine the extent to

Table 2. Mean and maximum sediment metal concentrations (ppm) along with sediment quality guidelines for the protection of aquatic life (for freshwater systems).

Metal	Dauriat mean	Dauriat maximum	Knob mean	Knob maximum	ISQG	PEL
Al	5 746	7 360	5 923	6 690	—	—
Fe	13 452	18 400	8 272	9 500	—	—
Mn	2 176	4 270	4 087	40 900	—	—
Zn	600	1 430	144	200	123	315
As	10	21	11	14	5.9	17
Cd	3	6	0.9	2	0.6	3.5
Co	64	121	37	124	—	—
Cr	67	85	72	93	—	—
Cu	159	348	35	52	35.7	197
Hg	3	8	0.9	0.9	0.2	0.5
Ni	105	226	81	158	—	—
Sb	5	5	5	5	—	—

Note: All concentrations are expressed in parts per million (ppm). ISQG refers to International Sediment Quality Guidelines for the Protection of Aquatic Life and is converted from $\mu g \cdot kg^{-1}$ dry mass (Canadian Council of Ministers of the Environment 2014). PEL refers to probable effect level, also converted from $\mu g \cdot kg^{-1}$ dry mass. Al = aluminum, Fe = iron, Mn = manganese, Zn = zinc, As = arsenic, Cd = cadmium, Co = cobalt, Cr = chromium, Cu = copper, Hg = mercury, Ni = nickel, Sb = antimony.

which patterns in cladoceran community species richness over time are congruent — or not — with temporal beta diversity.

We hypothesized that metal loading would decrease cladoceran species richness in these lakes both as metal-sensitive species are pushed toward tolerance limits and as a function of direct toxicity effects. However, there could be site specific differences in cladoceran response because the study lakes vary in their metal and nutrient loading histories. For example, greater water column production as a result of enhanced nutrient loading could lessen the impact of metal contamination, as cladocerans would have access to more food and the concentration of metals adsorbed onto any one phytoplankton cell would be diluted (Pickhardt et al. 2002). Additionally, the examination of temporal beta diversity (i.e., the turnover in assemblages, measured over multiple time points in a sediment record) to quantify cladoceran response to mining has the potential to help us understand different scenarios under which alpha and beta diversity patterns could be congruent.

Methods

Description of study site and field sampling

The Labrador Trough region, which straddles Quebec and Labrador (Fig. 1a), has long been part of the traditional territory of both the Naskapi and Innu (Innu–Montagnais) peoples (Boutet 2012). The Iron Ore Company of Canada (IOC) began ramping up mining operations in the region between 1939 and 1947 (Laperrière et al. 2008; Aebischer et al. 2015), and built the town of Schefferville in 1954. The first official shutdown of mining operations occurred between 1977 and 1982 (Laperrière et al. 2008; Aebischer et al. 2015). A timeline of both town development and mining activity in the region is shown in online Supplementary material, Fig. S1[1].

4

Can. J. Fish. Aquat. Sci. Vol. 00, 0000

Fig. 2. Heavy metal enrichment factors (EFs) and rarefied cladoceran species richness for Lake Dauriat (*a*) and Lake Knob (*b*). The metal EFs depicted represent total metal EFs of 10 heavy metals (Ag, Ba, Cd, Co, Cu, Fe, Hg, Mo, Ni, and Pb).
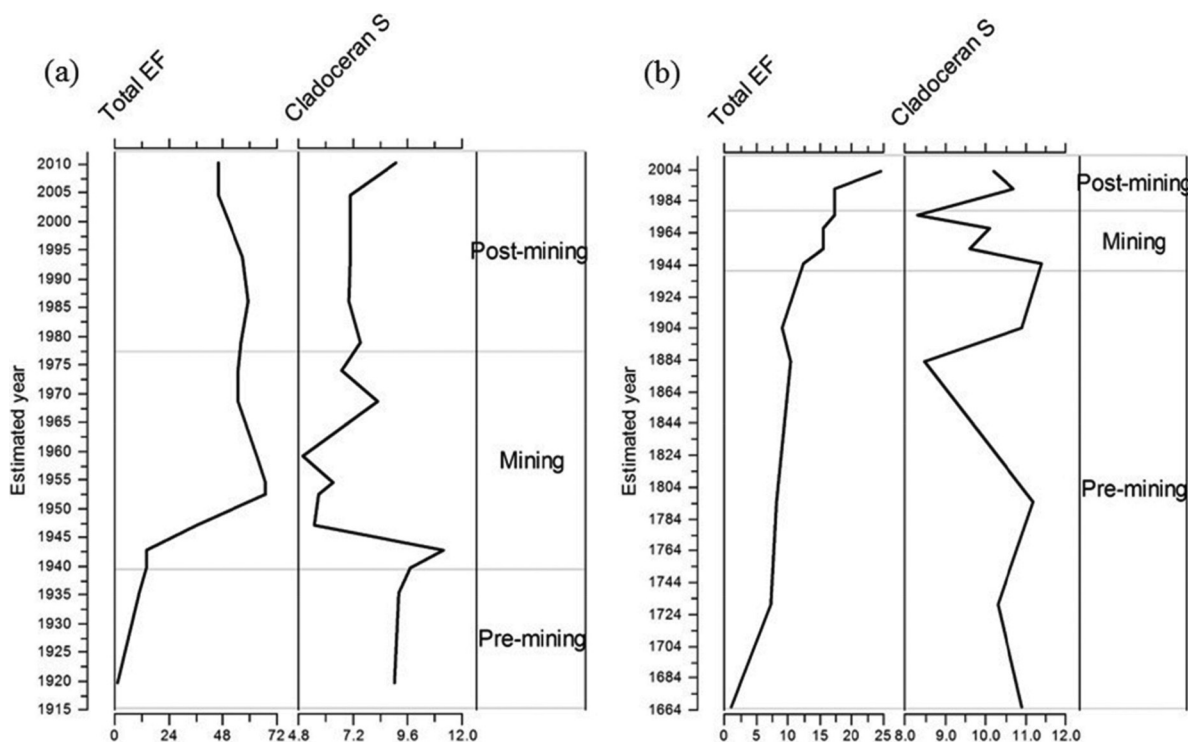
Our two study lakes, Lake Dauriat and Lake Knob, are situated within the town site of Schefferville (Fig. 1*b*; Table 1). Lake Knob is upstream (southeast) of the town site and serves as the drinking water source for Schefferville. A small outflow from Lake Knob connects it to Lake Dauriat, which is situated northwest and downstream of the town site. Lake Dauriat received raw sewage effluent from the town from 1954 until 1975 when a water treatment plant was built, and continues to receive both treated wastewater and surface runoff during rain events (note that historical records of sewage discharge volumes are not available). Laperrière et al. (2008) used sediment cores from Lake Dauriat in the centre of Schefferville to provide paleolimnological evidence of the negative effects of both mining activities and the discharge of sewage directly into this ecosystem. They found pronounced changes in diatom community composition and increases in diatom-inferred total phosphorus (DITP) from the 1940s to late 1970s (which partly overlapped with a monitoring record from the lake (Choulik and Moore 1992)), followed by partial recovery.

Based on analyses of epiphytic lichens growing on trees in the area, as well as sediment cores taken from Lake Dauriat and a lake farther from the town (Lake Oksana), Aebischer et al. (2015) showed that the concentration of lead (Pb) decreased linearly (and significantly) with increased distance from both the Schefferville town site and active mining sites. This work demonstrated that lakes have received significant metal loading from both mining projects and the town itself, in addition to background loading of elements like Pb from distant sources via atmospheric deposition (e.g., leaded gasoline in the past, distant smelter activities). Furthermore, this same study used variations in stable isotope ratios for Pb, iron (Fe), and zinc (Zn) to define separate sources of metal loading to the Schefferville lakes. They found four distinct sources of metal loading: geogenic (occurring prior to mining in this region), town development (corresponding to the mining period), town development after the mining period (which, though also related to town development, had a distinct signature from that of development during the mining period), and long distance atmospheric transport. Note that the last

source provides important information about metal loading sources in the region in the absence of a full understanding of wind regime.

Field sampling occurred between 24–30 July 2012 and 4–14 September 2013. In July 2012, we collected an approximately 40 cm long (diameter = 6.5 cm) sediment core from each of Lakes Dauriat and Knob using a Maxi-Glew gravity corer, at the deepest observed part of each lake. We sectioned these cores at 0.25 cm intervals and froze the samples for transport back to the laboratory. The use of 0.25 cm intervals is common practice in paleolimnology (Smol 1992), particularly in studies from northern systems due to relatively lower sedimentation rates than in temperate systems. In September 2013, we used a gravity corer to collect a sediment core from the centre of each lake (observed Z_{max}). These cores were sectioned at 2 cm intervals and frozen. The 2012 cores were used for radiometric dating, heavy metal geochemistry, and isolation and enumeration of cladoceran subfossils. The 2013 cores were used for the isolation and enumeration of cladoceran ephippia.

Radiometric dating and heavy metal geochemistry

The 2012 cores from Lakes Dauriat and Knob served as references for chronology and geochemical analyses. We freeze-dried these cores and then measured magnetic susceptibility on each of the 0.25 cm sample slices by subsampling a constant volume. We then selected 15 evenly spaced intervals in each core for radiometric dating (^{210}Pb), and sent these to the GEOTOP facility at the University of Québec at Montreal. The selection of age models based on ^{210}Pb, radium (^{226}Ra), and cesium (^{137}Cs) activity is outlined in the online Supplementary material S2[1].

An additional 15 intervals were selected for geochemical analyses (again evenly spaced and adjacent to the 15 intervals selected for dating). These dried samples were analyzed at a commercial laboratory, Actlabs (Ancaster, Ontario, Canada). Using inductively coupled plasma-optical emission spectrometry (ICP-OES), concentrations of the following heavy metals were obtained for each interval: silver (Ag), aluminum (Al), barium (Ba), beryllium (Be),

Fig. 3. Relative abundance of Cladoceran assemblages over time in Lake Dauriat as expressed by percentage of the total Cladoceran assemblage. Only taxa with a relative abundance of at least 5% in at least one interval are shown (rare species excluded). Cladoceran taxa are: *Acroperus harpae* (*A. harpae*); *Alona affinis* (*A. affinis*); *Alona circumfimbria – Alona guttata* (*A. circumfimbria guttata*); *Alona quandrangularis* (*A. quandrangularis*); *Alona* spp.; *Alonella nana* (*A. nana*); *Chydorus gibbus* (*C. gibbus*); *Chydorus* cf. *sphaericus* (*C. sphaericus*); *Eurycercus* spp.; *Paralona piger* (*P. piger*); *Bosmina longirostris* (*B. longirostris*); *Eubosmina longispina* (*E. longispina*); and *Daphnia longispina* (*D. longispina*). Taxa are labelled as being found in either a littoral or pelagic habitat. Note that *Bosmina* spp. can be found in both open-water littoral as well as pelagic habitat. Black bars for *B. longirostris* and *E. longispina* represent the total number of individuals. Grey bars represent the fraction of that total that were determined from indistinguishable *Bosmina* spp., that were then split proportionally between the two species depending on the prevalence of individuals of each species in the sample. The mining period (1939–1977) is marked by dashed lines.
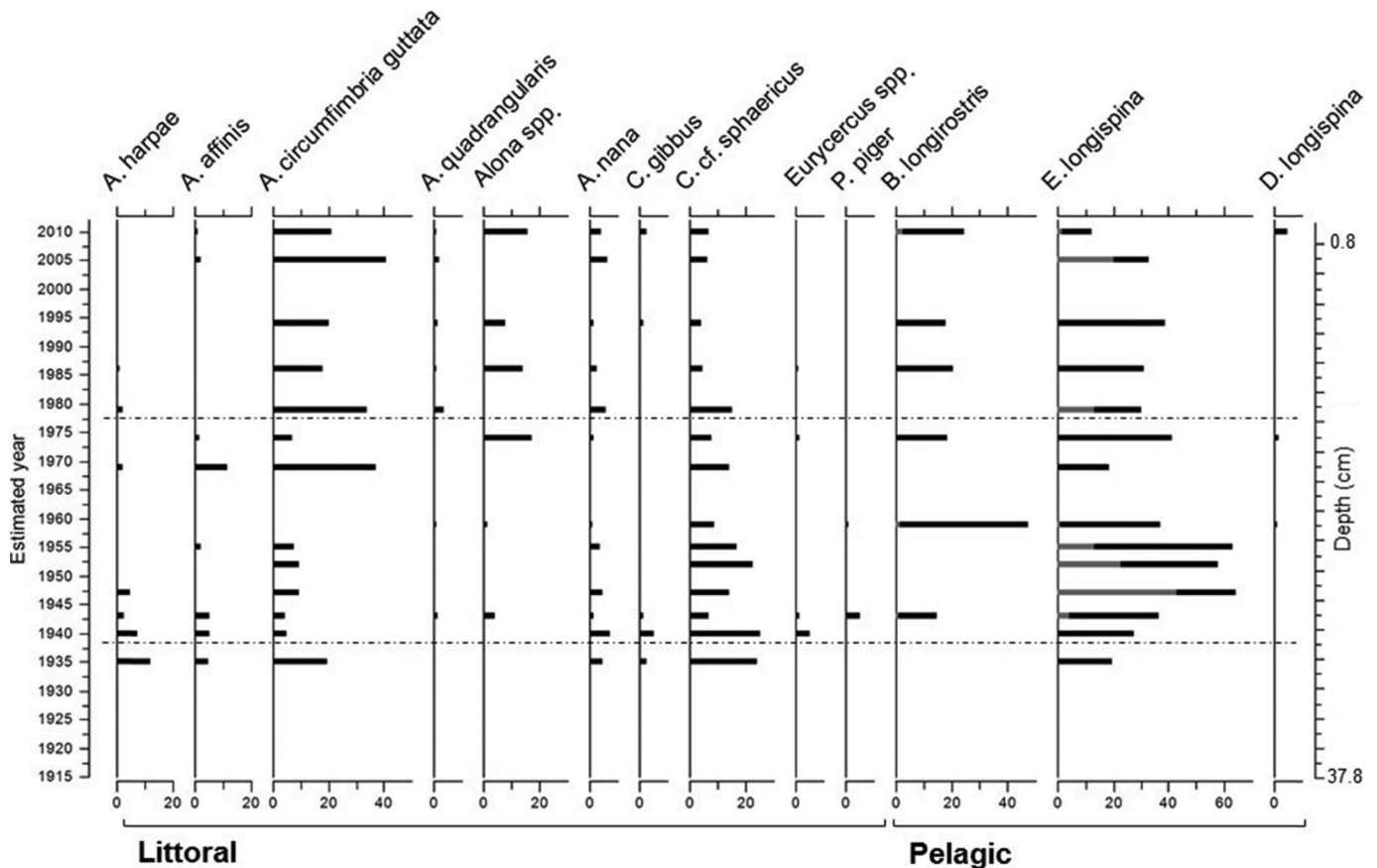
bismuth (Bi), calcium (Ca), cadmium (Cd), cobalt (Co), chromium (Cr), copper (Cu), Fe, gallium (Ga), mercury (Hg), potassium (K), lithium (Li), magnesium (Mg), manganese (Mn), molybdenum (Mo), sodium (Na), nickel (Ni), phosphorous (P), sulphur (S), antimony (Sb), scandium (Sc), strontium (Sr), tellurium (Te), titanium (Ti), uranium (U), vanadium (V), tungsten (W), yttrium (Y), Zn, and (zirconium) Zr. Hg concentrations were obtained through cold vapour Flow Injection Mass Spectrometry (FIMS). Total organic carbon (TOC) was quantified for these samples using a carbon–sulphur combustion analyzer.

Subfossil cladocera

For each interval selected, slides of cladoceran subfossils were prepared following a procedure adapted from Korhola and Rautio (2001). Approximately 0.1 g (this mass was increased for intervals with low subfossil abundance) of sediment was digested in 50 mL of potassium hydroxide (KOH) for 30 min at 65 °C. The solution was manually stirred every few seconds. The solution was removed from heat and 5 mL of 10% hydrochloric acid (HCl) was added to eliminate carbonates, before sieving through a 36 μm mesh. Sediments were washed for 15 min to remove any remaining dissolved organic matter, then transferred to a Falcon tube using as little water as possible for a total volume of 5–10 mL. Permanent slides were then prepared by pipetting 0.05 mL of

cleaned slurry material, which was then fixed with glycerine–safranin jelly. Kurek et al. (2010) established that a minimum of 70 to 100 individuals must be counted to reliably represent a cladoceran assemblage, though it was also noted that 50 individuals may be an appropriate count number in species-poor lakes to record the majority of taxa with relative abundance over 1% of the total assemblage (Kurek et al. 2010). As such, while we attempted to reach a minimum of 70 individuals per interval, some low abundance intervals were only counted to 50 individuals.

Cladoceran remains typically preserved in lake sediments are the chitinized body parts: carapaces, post-abdomens, post-abdominal claws, head shields, and mandibles (Korhola and Rautio 2001). For each species or species group, subfossil remains were counted and the most frequently occurring subfossil was used to calculate species abundance for each interval. However, there were some cases where we were unable to resolve subfossils to the species level. For example, in some samples we found *Bosmina* spp. carapaces and head shields with their pore location covered and therefore could not resolve these individuals to species. In these cases, we split the aggregated count between *Bosmina longirostris* and *Eubosmina longispina* based on the proportion of individuals from these species that had already been accurately identified in that sample. In the same way, carapaces of large *Alona* species that could not be

Fig. 4. Relative abundance of Cladoceran assemblages over time in Lake Knob as expressed by percentage of the total Cladoceran assemblage. Only taxa with a relative abundance of at least 5% in at least one interval are shown (rare species excluded). Cladoceran taxa are as in Fig. 3. Bar colour and setup of the figure is the same as Fig. 3.
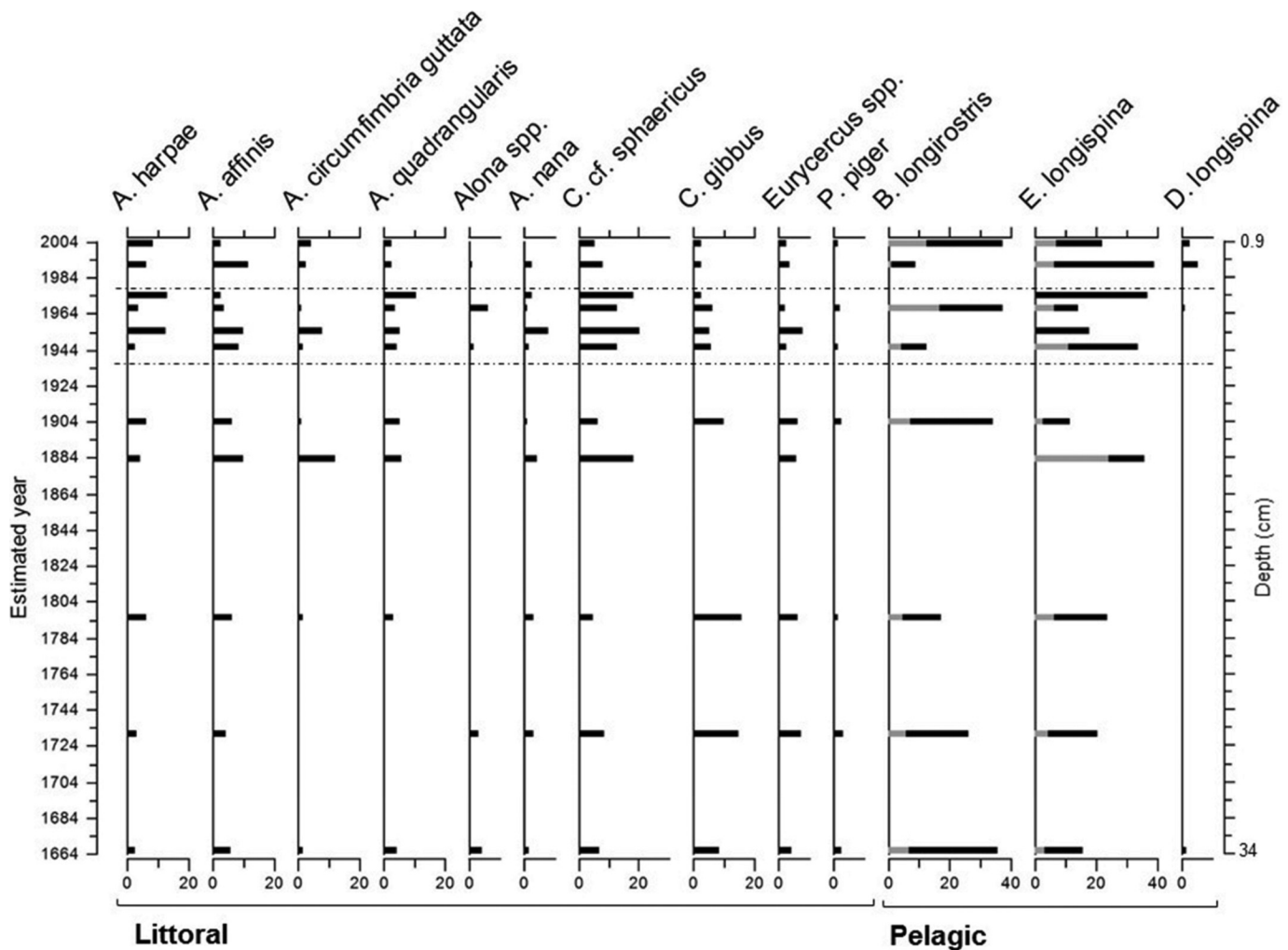
separated were split between *Alona affinis* and *Alona quadrangularis*. Poorly preserved *Chydorus* spp. individuals were also split proportionately between the identified chydoriids (Chydoridae) in a sample. Identifications were based on the following taxonomic guides: Frey (1959 and 1962), Megard (1967), Sweetman and Smol (2006), Szeroczynska and Sarmaja-Korjonen (2007), and Korosi and Smol (2012*a*, 2012*b*).

Statistical analyses

Taxa richness

All statistical analyses were completed in R version 3.1.2 (R Core Team 2014). We calculated rarefied taxon richness for each interval to determine richness standardized by the minimum number of individuals counted in any of the intervals, using rarefy() in vegan (Oksanen et al. 2015).

Beta diversity

We quantified temporal beta diversity between each time interval within each lake core, computing temporal beta diversity directionally such that the oldest time point was compared to the second oldest time point, the second oldest time point compared to the third oldest, and so on. We used the R function TBI() (Legendre 2015) to produce a measure of assemblage differentiation between each of the intervals based on the relative abundance of taxa recorded at each interval. We used the percentage

difference option in the TBI() function, which computes dissimilarity using the quantitative (not presence–absence) form of the Sørensen index, also called a Bray–Curtis index (Legendre 2015). We also extracted the proportion of total temporal beta diversity that was explained either by the loss or gain of species' abundance (Legendre and Salvat 2015) to better understand the mechanisms behind the temporal differentiation of assemblages. For example, a comparison where total temporal beta diversity was explained mostly by a loss component would mean that the assemblage change occurring between time intervals at that point is mostly the result of individual species experiencing decreased relative abundance.

Linear mixed effect models

To test the effect of metal loading on cladoceran taxa richness, we employed a mixed effect modelling approach to allow lake identity to be included as a random factor in the model. This meant that we pooled the data from both lakes to test the relationship between metals and cladoceran assemblages. The response variables considered for these models were rarefied taxa richness, as well as the first principal component (PC1) scores from a principal components analysis (PCA) of the cladoceran relative abundance data. We Hellinger-transformed relative abundance values for the cladoceran assemblages and performed a PCA using rda() in vegan. We used scores() (vegan) to extract the "site"

Fig. 5. Cladoceran resting stages extracted from sediment intervals from Lake Dauriat (*a*) and Knob (*b*). The sediment core number is specified at the top of each panel. "Specimen_type" refers to the type of resting stage material observed in the samples: "CAS_1" refers to an empty casing that would have held a single diapause egg; "CAS_2" refers to an empty casing that would have held two diapause eggs; "CAS_X" refers to an empty casing that would have held more than two eggs; "CAS_und" refers to a casing where it could not be determined whether it would have held one or two eggs; "EPH_1" refers to a casing with one egg present; "EPH_2" refers to a casing with two eggs present; "EPH_X" refers to a casing with multiple eggs present. No comment is made on the viability of the observed eggs. Gaps between histogram bars represent intervals where no resting stages were found in the sediment cores. [Colour online.]

scores for the first principal axis for this PCA, though these represent scores for each individual interval (lake–time combination) as opposed to individual sites.

The explanatory variables for these models were either a total metal enrichment factor (EF) or the PC1 from a PCA of heavy metal concentrations. We calculated an EF for each heavy metal using the following formula (from Bhuiyan et al. 2010):

$$\frac{([\text{Element}]_{\text{Sample X}}/[\text{Al}]_{\text{Sample X}})}{([\text{Element}]_{\text{Background}}/[\text{Al}]_{\text{Background}})}$$

where each element's EF is calculated with reference to Al concentrations, and "Background" refers to the oldest interval in a core. After calculating each element's individual EF, we then summed the EFs to result in total EFs, keeping the background EF as a constant. We performed a PCA on heavy metal data for the following elements: Ag, Al, arsenic (As), Ba, Be, Bi, Ca, Cd, Co, Cr, Cu, Fe, Ga, Hg, K, Li, Mg, Mn, Mo, Na, Ni, P, Pb, S, Sb, Sc, Sr, Te, V, Y, Zn, and Zr (standardized by Al). We again extracted "site" scores from the PCA to represent scores for each individual sample (interval).

We tested the relationship between metal loading and enrichment on cladoceran taxa richness with the models outlined in Supplementary S3[1], using lmer() in the R package lme4 (Bates et al. 2015). We then assessed each model via Akaike information criteria AICc() from the package AICcmodavg (Mazerolle 2015). Because the observations from our two cores have the potential to be significantly autocorrelated (samples are from the same cores but different time points), we used the method outlined in Simpson and Anderson (2009) to test for autocorrelation amongst our intervals. In particular, we constructed linear models using gls() in nlme (Pinheiro et al. 2015), including one model with the Continuous AR(1) correlation structure (based on year estimates for each interval). We then used an ANOVA to test for significant differences between the linear model without the autocorrelation structure included and the model with the autocorrelation structure included.

Exploratory study of cladoceran ephippia in sediment cores

We were interested in whether additional information regarding temporal cladoceran dynamics could be gleaned from examining ephippial cases and diapause resting stages left in the sediment record. Using the 2013 sediment cores, we completed a preliminary study of cladoceran ephippia isolated from the sediment. We sieved wet sediments from 2 cm intervals (~10 g at a time) from one core from each lake, examined sediments under a dissecting scope, and manually removed all observed ephippia. We noted whether each ephippia removed was an empty casing or whether it still contained eggs. For the latter, we noted whether the ephippia contained (or would have contained) one, two, or more eggs.

Results

Geochemical loading to the two study lakes

Dauriat and Knob lakes showed contrasting histories in terms of metal loading and other abiotic drivers (see raw plots in Fig. S4[1] for details). Metal loading to Lake Dauriat varied greatly over time, with Fe, Al, Cu, Co, and Ni showing both pronounced peaks and troughs during both pre-mining and mining time periods. Metal concentrations in Lake Dauriat sediments generally exceeded both International Quality Guidelines for the Protection of Aquatic Life as well as probable effect levels (Canadian Council of Ministers of the Environment 2014) (Table 2). The temporal variation in specific metals measured from the Lake Dauriat core, combined with relatively constant background levels of other elements (such as As, Cd, Hg, and Zn), resulted in considerable variation in the scores from the first axis of the PCA of metal concentrations. Metal enrichment in the Lake Dauriat record peaked in the 1950s–1960s, followed by a second peak in the 1980s when compared to historical conditions (Fig. 2*a*). Metal loading in Lake Knob was less pronounced despite the presence of the regional metal stressors (Fig. 2*b*). The majority of heavy metals measured in Lake Knob remained fairly constant over time with the exception of Mn, which showed peaks in recent intervals. Metal concentrations in the Lake Knob sediments generally exceeded levels from International Quality Guidelines for the Protection of Aquatic Life, but did not always exceed probable effect levels.

Biodiversity

Across the two lakes, we enumerated a total of 37 taxa. However, many of these taxa were relatively rare. Once we removed taxa that did not make up at least 5% of a sample's assemblage in at least one interval in two lakes, we were left with 14 taxa (Figs. 3 and 4). In Lake Dauriat, cladoceran species richness showed considerable fluctuations over time, with a fairly extensive reduction in rarefied richness in the 1960s (Fig. 2*a*). Species richness then increased, but only the most recent sediment interval came close to the pre-mining values. In comparison to Lake Dauriat, cladoceran species richness trends from Lake Knob were relatively stable, even during the mining period (Fig. 2*b*). Species richness in the Lake Knob record was highest at the start of extraction activities, followed by fluctuations in richness during and after the mining period. Estimated sedimentation rates were considered constant over time in both Lake Knob and Lake Dauriat because of the selection of a Constant Initial Concentration age model and, as such, cladoceran species richness could not be correlated with estimates of sedimentation rate.

The community assemblages of the two lakes were different and remained so over time. In Lake Dauriat, bosminids (*B. longirostris* and *E. longispina*) maintained their relative abundance throughout the mining period, whereas taxa such as *Alona circumfimbria* and *Alona* spp. became much more abundant after the main mining period (Fig. 3). In Lake Knob, *B. longirostris* and *E. longispina* were also quite abundant, with other species present in low relative abundance throughout the core profile (Fig. 4). *Chydorus* cf. *sphaericus* was found in intervals throughout the Lake Dauriat and Lake Knob records, although it was generally more abundant during the mining period in both lakes. In comparing both records using PCA, we observed that the earliest Lake Dauriat assemblages (1920–1930s) were most similar to the Lake Knob assemblages, with more recent Lake Dauriat assemblages differing substantially from Lake Knob given the prevalence of *Alona* spp., and *A. circumfimbria*. Lake Knob assemblages tended to be characterized by taxa such as *A. affinis* and *Acroperus harpae*. The PCA also demonstrated that there was less variation in cladoceran assemblages over time in the Lake Knob record relative to that of Lake Dauriat. Furthermore, we found a noticeable difference in the resting egg bank of
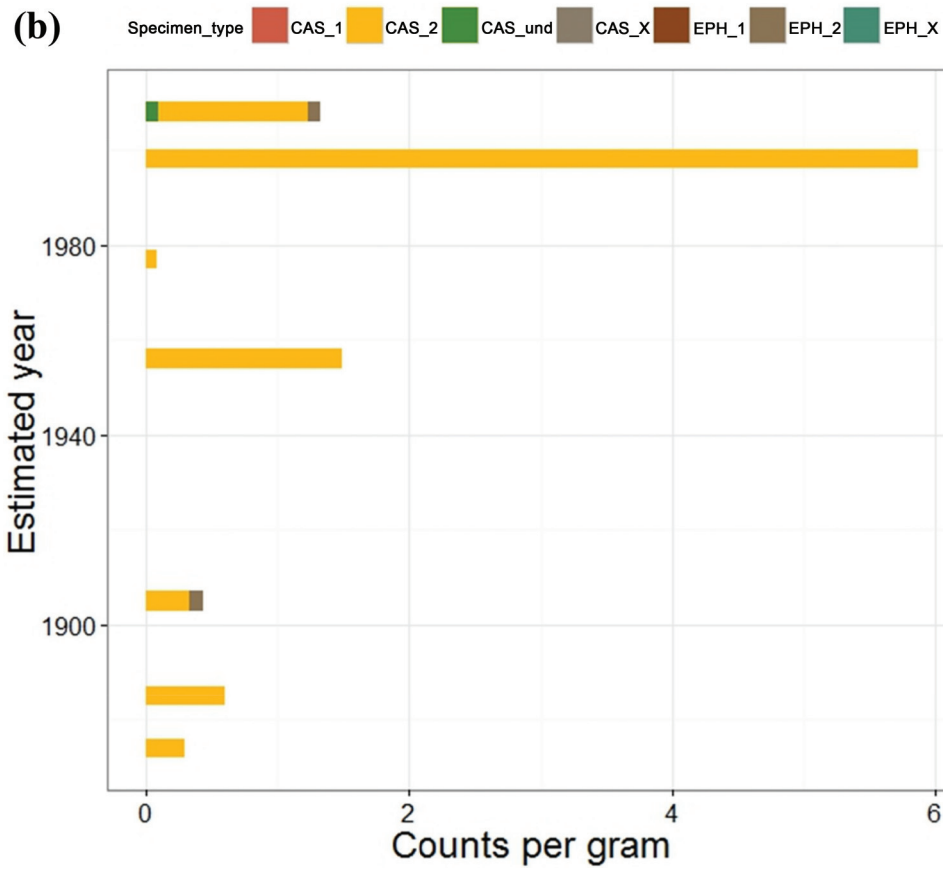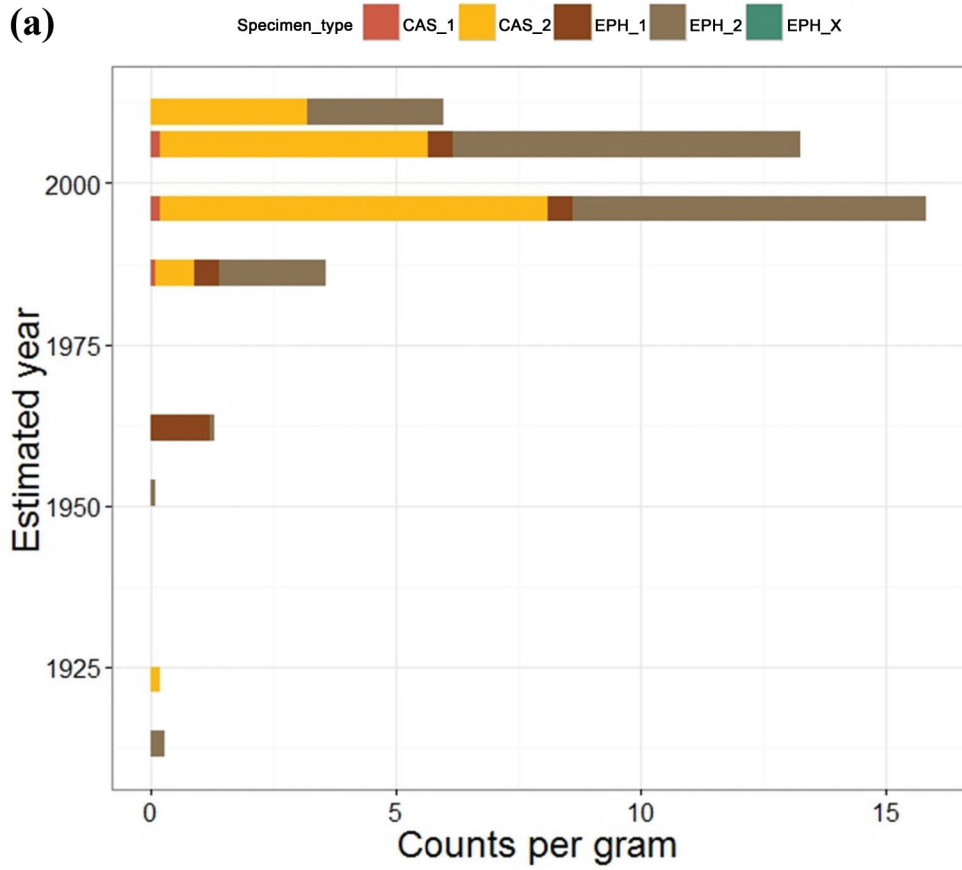
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8

Can. J. Fish. Aquat. Sci. Vol. 00, 0000

(a)

Specimen_type ☐ CAS_1 ☐ CAS_2 ☐ EPH_1 ☐ EPH_2 ☐ EPH_X

(b)

Specimen_type ☐ CAS_1 ☐ CAS_2 ☐ CAS_und ☐ CAS_X ☐ EPH_1 ☐ EPH_2 ☐ EPH_X

Fig. 6. Beta diversity for (left) Lake Dauriat (DAR) and (right) Lake Knob (KB), shown over time. Each temporal beta diversity point represents a comparison between two intervals, and the year midpoint of that comparison is shown on the *y* axis. "Total_beta" refers to total temporal beta diversity computed between time intervals. "Species_loss" refers to the loss of Cladoceran abundance on a taxa by taxa basis. The mining period (1939–1977) is shaded.
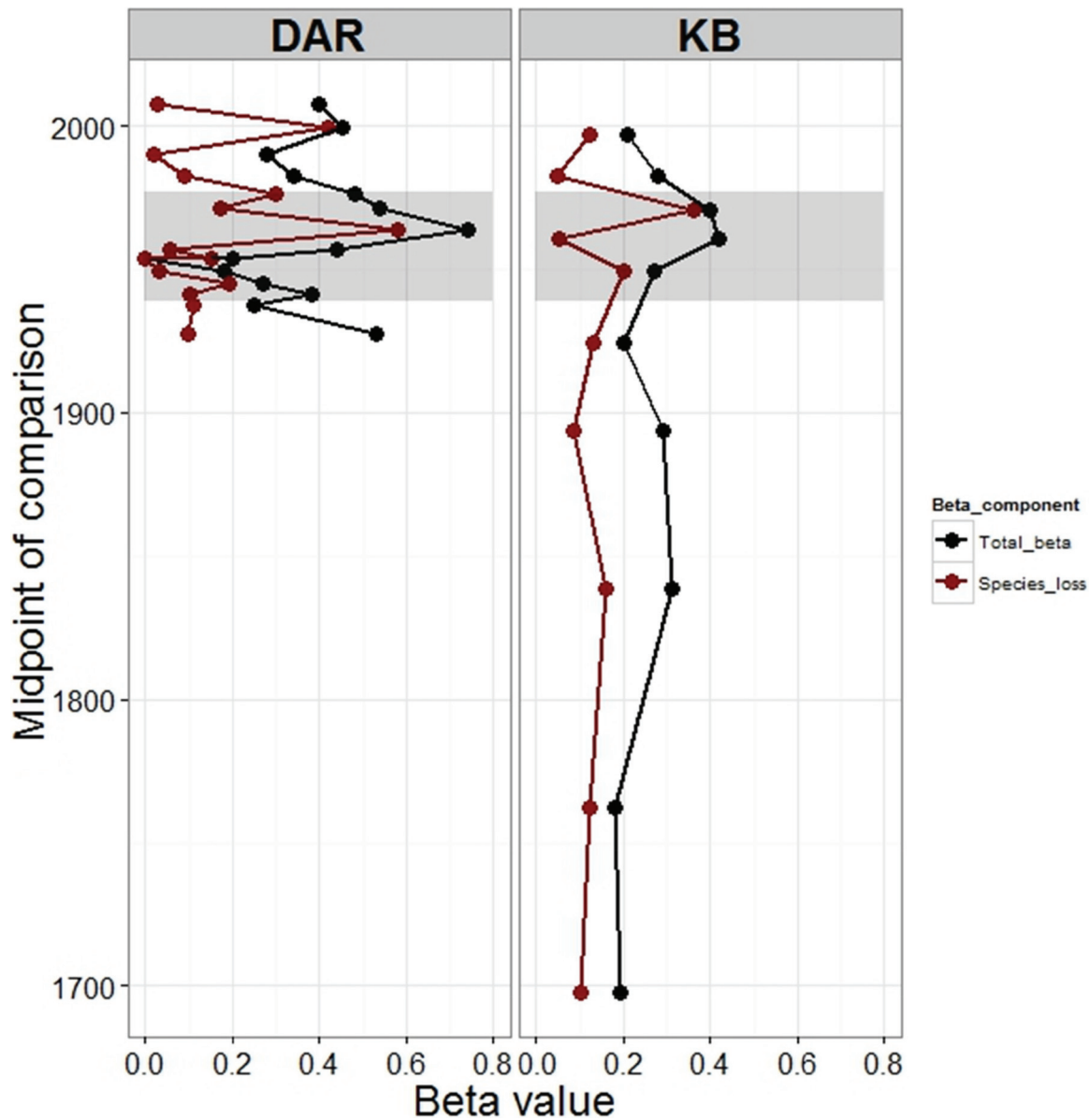
Lake Dauriat compared to Lake Knob in our preliminary analysis, whereby there was a greater ratio of unhatched:empty cladoceran ephippial cases in Lake Dauriat relative to Lake Knob (Fig. 5). The abundance of both intact ephippia and cases was also generally higher in Lake Dauriat. The most pronounced changes in temporal beta diversity were observed in the Lake Dauriat record compared to Lake Knob (Fig. 6). However, beta diversity peaked during the period of mining and town construction in both lake records (from the late 1930s to the 1970s). In both Lakes Dauriat and Knob, changes in total beta diversity were largely explained by a loss of species (i.e., the loss component which measures the changes in abundance on a species by species basis).

Cladoceran response to metal loading

The best fit model for the relationship between cladoceran species richness and metal loading was the simple linear model of $Clad\_S_i \sim Metal\ EF_i + \varepsilon$ without lake included as a random factor

(lowest AIC as well as the highest explained variation (Adj. R^2 = 0.69) amongst the null linear models); Table 3; Fig. 7a). The second lowest AIC values were from the model $Clad\_S_{ij} \sim Metal\ EF_i + Lake_j + \varepsilon$, with lake included as a random factor (Fig. 7b). For both of these models, the slope for the mixed effect model was significantly different from zero, as indicated by the range of upper and lower confidence intervals (i.e., did not include zero; varied between −0.05 and −0.08). Although we found that measurements of adjoining sediment intervals were autocorrelated (ϕ = 0.6), we failed to detect a significant difference based on an ANOVA of the linear model run with autocorrelated structure, and the model run without accounting for this autocorrelation. The set of models with cladoceran richness as a response and metal PC1 as an explanatory variable had higher AIC and ower Adj. R^2 values than the models with metal EF as an explanatory variable (Table 3). Linear models with cladoceran PC1 as a response variable ex-

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10

Can. J. Fish. Aquat. Sci. Vol. 00, 0000

Table 3. Mixed-effect model summaries and model assessment in order of decreasing plausibility.

Model	Random factor	AIC value	Adj. R^2 (for linear models)
Clad_$S_{ij} \sim$ Metal_EF$_i + \varepsilon$	None	85	0.69
Clad_$S_{ij} \sim$ Metal_EF$_i$ + Lake$_j + \varepsilon$	Lake (varying intercept)	88	—
Clad_$S_{ij} \sim$ Metal_EF$_i$ + Lake$_j + \varepsilon$	Lake (varying intercept + slope)	94	—
Clad_$S_{ij} \sim$ Metal_PC1$_i + \varepsilon$	None	100	0.51
Clad_$S_{ij} \sim$ Metal_PC1$_i$ + Lake$_j + \varepsilon$	Lake (varying intercept)	102	—
Clad_$S_{ij} \sim$ Metal_PC1$_i$ + Lake$_j + \varepsilon$	Lake (varying intercept + slope)	107	—

Note: The formula (as used as input in lme4) is shown along with the AIC value for each model. Only models with high amounts of explained variation are shown.

Fig. 7. Relationship between cumulative metal enrichment factor and rarefied Cladoceran species richness for the two Schefferville lakes ($n_{interval}$ = 27) using (a) a linear model and (b) mixed effect model with lake as a random factor. For the linear model, the blue line represents Lake Dauriat and the red line Lake Knob (Adj. R^2 = 0.7). For the mixed effect model, the slope of the overall line is −0.071, whereas the upper and lower confidence intervals for this model are −0.0 and −0.08, respectively. [Colour online.]
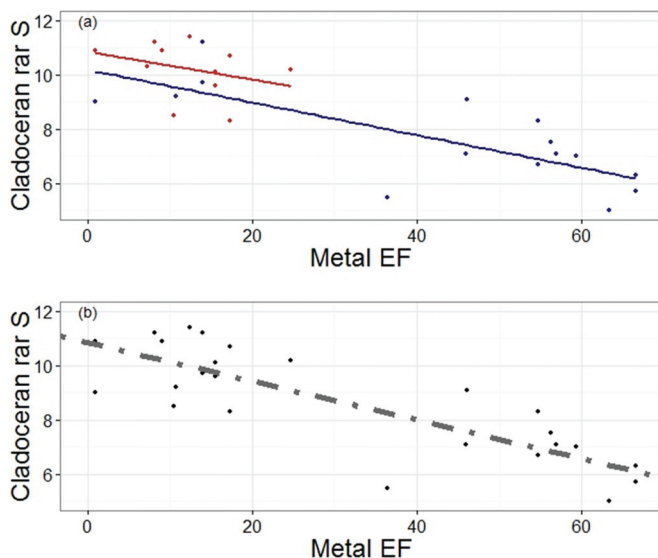
plained very low amounts of variation (Adj. R^2 = 0.09 with metal EF as an explanatory variable; Adj. R^2 = 0.02 with metal PC1 as an explanatory variable).

Discussion

A common approach across the Quebec landscape has been a focus on restoration of sites post-mine closure, as opposed to proactive planning for the mitigation of effects on biodiversity (Hamilton et al. 2015). An improved understanding of biodiversity responses to mining in the Schefferville landscape over time could contribute to more proactive planning in the future. Both Lake Dauriat and Lake Knob are situated within the limits of the same town site and are exposed to the same sources of atmospheric metal deposition. Despite this similarity, peaks in heavy metals and metal enrichment varied between the lakes, with Lake Dauriat experiencing higher sediment metal concentration enrichment values compared to background conditions (where T = 0, bottom of sediment core). Based on isotopic analyses, Aebischer et al. (2015) have recently shown that the sediments of Lake Dauriat indicate pollution sources arising from mining activities, as well as municipal waste and sewage. However, the extent of metal enrichment derived from mining sources in both focal lakes appears to be ecologically important, even in Lake Knob where atmospheric deposition dominated, as numerous sediment intervals had metal concentrations above quality guidelines for aquatic

life. Consistent with our hypothesis, we found that periods of higher metal loading were associated with decreased cladoceran richness in both lakes. This relationship was most evident in Lake Dauriat which received both metal and nutrient inputs, though we do not have evidence for a strong lake effect in our study. Secondly, we determined that the contribution of loss and gain components to temporal beta diversity differed over time and between lakes. To further advance our knowledge of responses to metal contamination, we explored the interpretation of alpha richness and temporal beta diversity trends together.

The approach taken by this study was to use paleolimnology to examine biodiversity dynamics over time. The field of paleolimnology has been championed as an ideal way to study biodiversity dynamics (Gregory-Eaves and Beisner 2011). Furthermore, based on recent studies by Levi et al. (2014) and Winegardner et al. (2015), we now have evidence that paleolimnological approaches can draw similar conclusions regarding environmental and spatial drivers of diversity as studies using a contemporary ecological approach. However, this is not always the case: Kurek et al. (2011) used paleolimnology to show that environmental factors were more important than spatial variables in cladoceran communities of lakes in Ontario, Canada. More of these kinds of comparative studies are needed to understand the context dependency of such results.

Alpha richness and temporal beta diversity can be interpreted relative to each other in a number of ways to provide new insight based on our observation of cladoceran assemblages in response to multiple stressors. This is because high temporal beta diversity indicates strong gain or loss components individually or in combination. Thus, if the gain component of beta diversity (pseudo species replacement) dominated during a stressful event, then temporal beta diversity (increasing) would not track alpha diversity (decreasing due to a metal stress; Fig. 8a). However, if the dominant explanatory component of temporal beta diversity was loss, then reductions in alpha richness should occur, as species are lost between intervals (including via reduced abundance, which make species extirpations more likely demographically; Fig. 8b). Conversely, if the dominant explanatory component of temporal beta diversity was a strong taxa gain component, this could be associated with either no net change of richness between intervals (if species abundance for those already present increased, as opposed to new species being added), or an increase in richness as new species colonized the lake over time (Fig. 8c). In our study, temporal beta diversity was highest during time periods of maximum (or near maximum) metal enrichment, while cladoceran alpha richness was declining. Consideration of alpha richness and beta diversity in this way is important, as it improves understanding of biodiversity trends that can be masked when only considering alpha diversity.

Metal contamination had an overarching effect on local cladoceran species richness in our study lakes. A simple linear negative relationship between cladoceran species richness and metal enrichment factor was the most robust model and is consistent with the sensitivity of zooplankton to increased heavy metal concentrations in many laboratory toxicity studies (e.g., Biesinger and

Fig. 8. Three hypothetical assemblages (Scenarios A, B, C) of eight species (A–H) (relative abundance) at each of three time points (1, 2, and 3) show ways in which patterns observed using cladoceran richness may or may not be congruent with those observed using temporal beta diversity. Beta diversity is further represented by either a loss component (hashed bar) or gain component (solid bar). Scenarios A and B represent assemblages where species richness has decreased over time (for the context of this study, we will assume that this decrease over time is related to a negative linear relationship with metal contamination), whereas Scenario C shows an assemblage where species richness has stayed constant over time, despite changes in the relative abundance of individual species. In Scenario A, metal tolerant species are able to take advantage of niches opened up in high metal conditions, thus contributing to an increased gain component in temporal beta diversity because these metal tolerant species gain in abundance on an individual basis. Under this scenario, the conclusions drawn about the effect of metal contamination in a system would be different if observing species richness (decreasing) or temporal beta diversity (high gain component). Scenario B demonstrates an example where both species richness and temporal beta diversity show congruent patterns, where cladoceran species richness decreases with higher metal concentrations, resulting in a high loss component making up total temporal beta diversity, as species themselves are lost and remaining species experience losses in abundance. Finally, Scenario C shows a situation where cladoceran richness may increase or stay the same with increased metal concentrations; this is further echoed by an increase in abundance on a species by species basis in terms of temporal beta diversity. As such, individual species show gains in abundance, and species richness either stays constant or increases. [Colour online.]

Christensen 1972; Bossuyt and Janssen 2005, among others). Reduced cladoceran species richness due to metal contamination from mining and smelting is a common occurrence across aquatic systems, from the subarctic to temperate regions. While the acute toxicity responses of aquatic invertebrates to different metals can vary in magnitude (Canadian Council of Ministers of the Environment 2014), the negative effects on cladoceran diversity and abundance have been demonstrated using paleolimnological studies across many different types of metal mining. For example, extreme increases in As and other heavy metals from gold mining and roasting activities at Yellowknife's Giant Mine in the Northwest Territories, Canada, resulted in a functional absence of cladocerans from nearby lakes during mining operations (Thienpont et al. 2016). In another example, smelting of Cu, Zn, and silver sulphide in Flin Flon, Manitoba, Canada, resulted in significant decreases in cladoceran abundance in surrounding lakes (Doig et al. 2015). In the region around Sudbury, Ontario, Canada, Ni mining and the accompanying acidification and metal contamination has also resulted in severe reductions in invertebrate communities, with cladocerans slower to recover than copepod species (Keller et al. 2002; Yan et al. 2004). Indeed, the extent of mining, processing (e.g., smelting, roasting, etc.), and associated activities (construction, waste discharge, etc.) might be more important to cladoceran diversity than the actual metal type itself, as mining activities introduce a whole suite of multiple stressors to a system.

Despite the potential for interaction between multiple stressors in the Schefferville system, nutrient loading in Lake Dauriat did not appear to mitigate or exacerbate the effect of metal contamination, as we did not find strong support for lake-specific declines in richness to metal enrichment. This is interesting, as local knowledge and the lithology of the Lake Dauriat cores indicates an anoxic period from the 1950s to 1970s. During this period, one might have expected metal deposition in Lake Dauriat to have had an amplified impact on biodiversity because eutrophication and subsequent deep water anoxia may have altered redox reactions within the sediments. This would make metals in the sediments more soluble and enable more diffusion into overlying waters (e.g., Jacobs and Emerson 1982), thus exposing cladoceran repeatedly to, or to a more toxic form of, metal contamination. However, in our study, the simple relationship between metal concentration and cladoceran richness appears to be the most supported model. In addition, while changes in sedimentation rates may also have affected these results, we do not believe that these results are artefactual (as per Smol 1981) because the best age model for Lake Dauriat was one where sedimentation rate was held relatively constant. Even when a different age model was used (i.e., Constant Rate of Supply), we still failed to find a significant effect of sedimentation rates on cladoceran species richness. In future, it would be helpful to conduct a chironomid analysis of sediment records from Lakes Dauriat and Knob to gain some insight into the sever-

ity and spatial extent of hypolimnetic anoxia. With more information on the nutrient loading stressor (i.e., volume of sewage inputs; not available for this site), it might also be possible more accurately characterize the extent of multiple stressors in Lake Dauriat.

While the response of cladoceran diversity to metal enrichment was similar in both lakes, there are some key differences with respect to biotic and abiotic lake characteristics. The magnitude of metal contamination was much higher in Lake Dauriat, and it experienced more drastic reductions in taxon richness. Additionally, the preliminary investigation of the cladoceran resting egg banks showed other potential differences. For example, we found evidence for a greater ratio of unhatched:empty cladoceran ephippial cases in the resting egg bank of Lake Dauriat than in Lake Knob. A dominance of empty cases could indicate a greater hatching success from Lake Knob sediments with less severe contamination, although other mechanisms cannot be ruled out (e.g., poorer preservation of eggs in Lake Knob). Reduced hatching success in the presence of multiple stressors (metal contamination and eutrophication in Lake Dauriat) is supported by Rogalski (2015), who found that metal contamination negatively affected the hatching of *Daphnia* ephippia from lake sediments. More experimental work could be insightful to evaluate the support for different potential mechanisms, and might elucidate eco-evolutionary dynamics via the rapid adaptation of cladoceran species to metal stressors (e.g., Turko et al. 2016).

Community composition in our two study lakes showed a similar response to those observed in other mining regions. The dominance of *B. longirostris* and *E. longispina* observed in both lakes is similar to reports from other metal-contaminated lakes in northern Russia and eastern Canada (Lukin et al. 2003; Korosi et al. 2013; Labaj et al. 2015). Bosminid dominance has generally been attributed more to their heightened ability to withstand acidification, with some indications for a tolerance of metals (Doig et al. 2015). We also observed a consistent presence of *Chydorus* cf. *sphaericus*, a species that is generally associated with macrophytes and mud (Chen et al. 2010) or moderately acidified waters (Belyaeva and Deneke 2007). Our results indicated that this species can also survive some degree of metal contamination without accompanying acidification, but this remains to be verified experimentally. On the other hand, *Holopedium gibberum* has commonly been observed in metal-contaminated and acidified lakes of the Ni mining region of Sudbury (Canada; Valois et al. 2011). However, Yan et al. (2004) found that *H. gibberum* was twice unsuccessful in colonizing a previously acidified and metal-contaminated Sudbury lake, even after remediation through liming. While we also observed *H. gibberum* in one of our samples from Lake Knob (during the mining period), it was present only at very low relative abundance (less than 5% of the total assemblage), suggesting that it is not tolerant of the disturbance conditions in our focal lakes. It is also important to note that *H. gibberum* is historically rare in the region
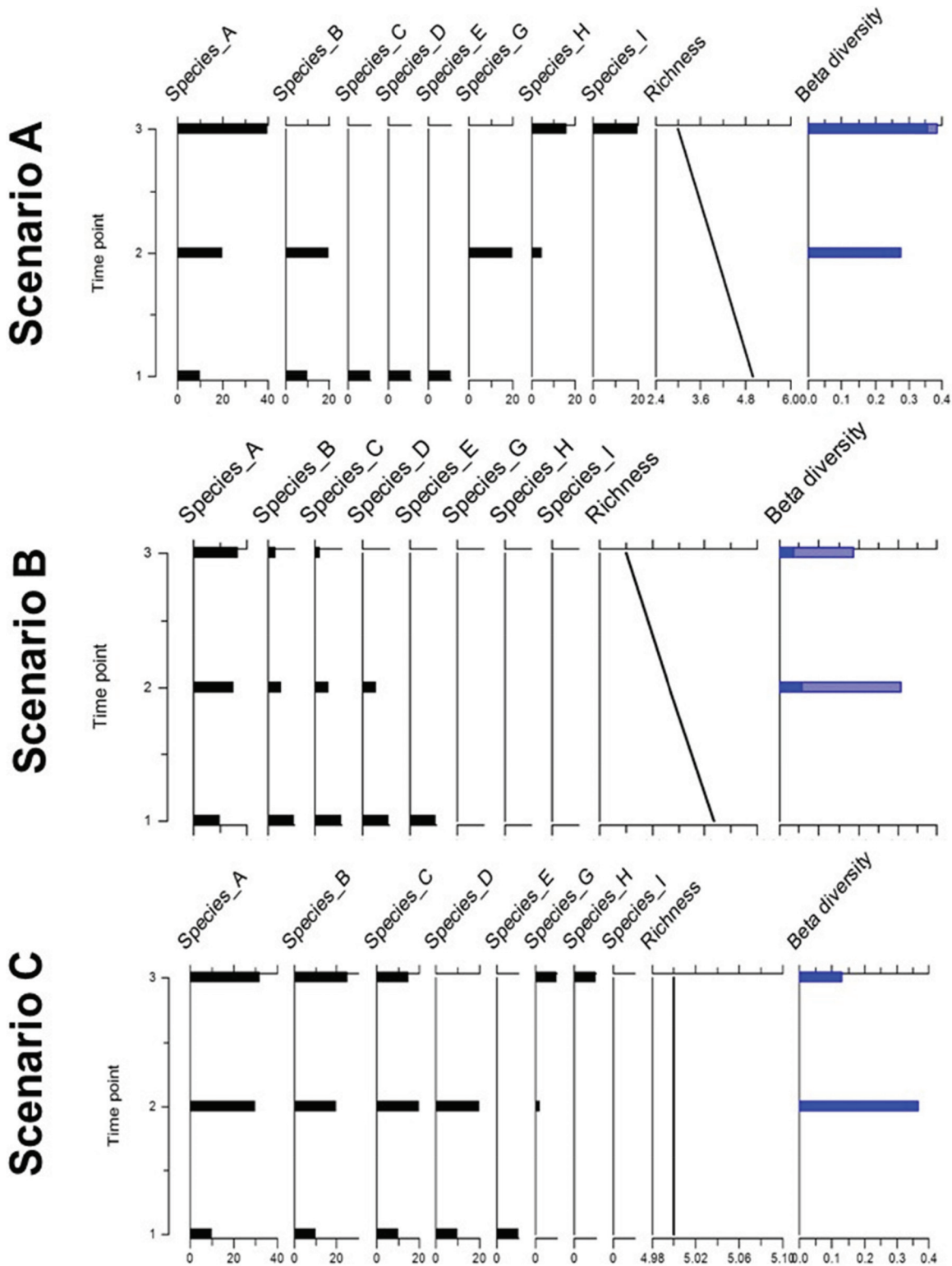
and generally not broadly distributed across northern Quebec (at least in historical research; Carter et al. 1980). Here again, experimental research would help to elucidate the tolerance of this taxon to heavy metal and acidification stressors.

Temporal beta diversity varied throughout both cores and consistently showed peaks during the mining period. These peaks were mostly attributable to loss in abundance on a taxon-by-taxon basis in both lakes, with one exception in Lake Knob. In Lake Knob, two incidences of higher total beta diversity occurred during the mining period (during the 1960s and 1970s): the first explained predominantly by taxa gain, and the second predominantly by taxa loss. Both taxa gain and loss in this case were mainly related to changes in *Bosmina* spp. taxa. This switching in explanatory components can be explained by (*i*) a lag in cladoceran taxon response or (*ii*) the creation of new niches for metal- and disturbance-tolerant taxa during early mining activities in Lake Knob, before metal-sensitive taxa were affected. As mining activities continued, however, increasing disturbance should have re-

duced relative abundance of non-metal tolerant species and perhaps also of generalist taxa as observed in Lake Dauriat. This taxa loss would have sustained a high temporal beta diversity. Such "switching" between dominance of taxa loss and gain components in temporal beta diversity has been demonstrated in at least one other study of mollusc communities (Legendre and Salvat 2015). Thus, variation in the main explanatory component of temporal beta diversity provides insight into community richness dynamics as we observed for Lake Knob.

In a review of freshwater ecosystems subjected to a wide variety of anthropogenic stressors, Niemi et al. (1990) documented 150 case studies where aquatic assemblages (from plankton to fish) exhibited resilience to a disturbance. They found that the majority of these trended towards biological recovery in less than three years, as long as (i) the disturbance or stressor did not physically alter aquatic habitat, (ii) there were no residual pollutants remaining from the disturbance, and (iii) the system was not isolated, thus precluding recolonization. In our study, cladoceran communities in Lake Knob changed relatively little prior to the mining period. For Lake Dauriat, the majority of assemblage turnover occurred during the mining period due to reductions in taxa richness associated with increased metal contamination. However, the cladoceran assemblages in Lake Dauriat have not returned to their pre-mining state even though mining activities were terminated in this region by the early 1980s. We suggest that the lack of recovery could be because lake sediments are still metal-enriched and continue to release metals to the water column. Climate change is an unlikely mechanism for the observed assemblage shifts, as temperature records show very little change over the study period (Environment and Climate Change Canada 2015). Alternatively, species assemblages may take longer to recover in a multiple stressor situation, as in Lake Dauriat, if adaptation to one stressor results in an increased susceptibility to other stressors (Moe et al. 2013).

Our study quantified historical patterns in cladoceran species richness and turnover in two northern lakes that were exposed to differences in metal contamination and eutrophication. Understanding both the effect of metal loading on cladoceran assemblage richness in this region, as well as their propensity for turnover over time, is important because the extent of mining continues to vary from year to year. As such, biological assemblages that might be considered "recovered" post-mining may still be exposed to evolving stressor combinations via legacy effects and the addition of new stressors. The strength of our study is in our use of a temporal beta diversity lens to quantify cladoceran turnover over a 100–300 year period across a major perturbation event. Cladoceran communities were considerably dynamic, despite a linear negative relationship with metal contamination.

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14

Can. J. Fish. Aquat. Sci. Vol. 00, 0000

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