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Cladocera responses to ~200-year history of environmental stressors on Rideau Canal (Ontario, Canada) lakes

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Abstract

Five lakes within the Rideau Canal system (Ontario, Canada) were studied ~25 years ago using lake sediment cores for diatom analysis. More recently, new sediment cores were collected to assess limnological changes linked to more contemporary stressors, such as accelerated regional climate warming. However, long-term changes in the cladoceran assemblages remained unstudied in the earlier collections. Here, we reconstruct cladoceran assemblage dynamics over the past ~200 years to assess how this key intermediate trophic level has responded to multiple catchment disturbances and recent environmental change. The Rideau Canal was constructed in the early-1830s as a way to connect Ottawa to Kingston for military transport, but is now primarily used for recreational purposes. The construction of the canal resulted in many land-use changes including flooding, deforestation, and settlement, that likely impacted lakes within the system. Recently, environmental changes, including accelerated climate warming, zebra mussel invasions, and cyanobacterial blooms, are affecting these waterbodies. Despite relatively major changes recorded in diatom assemblages, only moderate shifts were observed in cladoceran assemblages during the period of canal construction. In contrast, the past ~25 years were characterized by increased dominance of *Bosmina* spp., a pattern widely associated with climate warming, along with declines in the relative abundance of most littoral cladoceran taxa. Overall, biological turnover in cladoceran assemblages was consistently lower than that observed for diatom assemblages across all lakes. These recent compositional changes are consistent with accelerated regional warming and associated limnological shifts, as well as reduced total phosphorus concentrations and altered food resources.

Key words: invertebrates; Canada; *Daphnia*; chydorids; *Bosmina*; zooplankton.

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INTRODUCTION

The Rideau Canal system of southern Ontario is a 202-km long waterway consisting of 24 lock stations, 52 dams, and multiple channels that connect the Ottawa River (Ottawa, Ontario) and Lake Ontario (Kingston, Ontario). Initially intended to transport military personnel and equipment, followed by a period of significant commercial transport, the canal system is now primarily used for recreational purposes (Bergman *et al.*, 2022). Over their history, the canal's watersheds have been subjected to a variety of anthropogenic stressors that have, both directly and indirectly, affected lake ecosystems. For example, the construction of the Rideau Canal (1826-1832) was one of the earliest, large-scale cultural disturbances in Canada that included wide-spread deforestation to provide timber for building the numerous locks and dams (CHPC, 1996), as well as extensive flooding that increased depths in many surrounding lakes by ~2-3 m to enable boat transport (Forrest *et al.*, 2002). The canal system is also one of the oldest cottage regions in Canada with most Rideau lakes having highly developed shorelines and multiple access points (Halseth and Rosenberg, 1994). More recently, the canal region has been impacted by the introduction of zebra mussels and increased regional anthropogenic climate warming (Balasubramaniam *et al.*, 2025).

Long-term environmental monitoring programs of aquatic ecosystems are rare, and when they are available, they are often implemented only after a stressor has exerted measurable impacts (Smol, 2019). In *lieu* of direct monitoring, paleolimnological approaches can be used to reconstruct background environmental conditions prior to the onset of human activities, thereby providing important context for evaluating the relative impacts of recent anthropogenic disturbances (Smol, 2019). In this study, Cladocera will be used as the primary biological indicator as they are key in aquatic food webs, occupying an intermediate trophic position between top-down (fish and invertebrate predators) and bottom-up (phytoplankton) regulators (Korosi and Smol, 2011). In addition, their chitinous remains are typically well preserved in most lake sediment records (Korhola and Rautio, 2001; Jeppesen *et al.*, 2011) and are easily identifiable based on distinctive morphological traits. Cladoceran species composition is influenced by multiple environmental factors that allow them to be effective indicators of habitat and trophic status (Nevalainen and Luoto, 2017), lake chemistry (DeSellas *et al.*, 2008), top-down interactions with predators

(Korosi *et al*., 2008), water-level changes (Wang *et al*., 2020), and climate warming (Thienpont *et al*., 2015).

Earlier paleolimnological studies of lakes near or within the Rideau Canal system focused on diatoms (Christie and Smol, 1996; Karst and Smol, 2000; Forrest *et al*., 2002) and chironomids (Little and Smol, 2000), with an overall goal to understand the ecological impacts of early 19th century canal construction and other extensive catchment disturbances (e.g., deforestation, flooding, and urbanization). Given that Cladocera were not included in previous paleoecological studies, insights into important food web dynamics were missing. Recently, these same lakes (Big Rideau, Indian, Lower Rideau, Upper Rideau, Opinicon, Otter) were re-cored to examine recent changes in diatoms and chlorophyll-*a* (Balasubramaniam *et al*., 2023, 2025) and chironomids (Lansing *et al*., 2025), since the earlier cores were collected ~25 years ago. Here, we explore long-term changes in cladoceran assemblages by revisiting Big Rideau L., Indian L., Upper Rideau L., and Lower Rideau L., with comparisons to recently published L. Opinicon, the shallowest of the study lakes (Graves *et al*., 2024). We use the same sediment cores collected in 2019 and 2020 by Balasubramaniam *et al*. (2023, 2025) and focus on the impacts associated with the construction of the Rideau Canal, as well as anthropogenic stressors that have emerged over the past ~25 years (zebra mussels, anthropogenic climate warming). The timing, magnitude, and nature of the cladoceran assemblage shifts are then compared among lake records as well as with the diatom profiles from these same lake cores (Balasubramaniam *et al*., 2025).

Site description

The construction of the Rideau Canal, completed in 1832, represented a major ecological disturbance to the region's aquatic systems. Canal development required the flooding of lakes to achieve navigable water depths for transportation (Forrest *et a*l., 2002), while extensive deforestation between the early 1800s and the 1870s occurred to support lumber, settlement, and agricultural expansion (Legget, 1986). Subsequent cottage development, beginning in the 1930s, further altered watershed conditions. Collectively, these activities have had lasting impacts on the physical, chemical, and biological characteristics of waterbodies within the Rideau Canal system.

The Rideau Canal system is situated within the Great Lakes-St. Lawrence Lowlands physiographic region (Fulton and Richard, 1987) and connects a network of 16 lakes spanning two major watersheds. Some lakes drain through the Cataraqui River watershed (drainage area: 910 km²), while others drain through the Rideau River watershed (drainage area: 3,730 km²). The Rideau River originates in Big Rideau Lake and flows northeast toward Ottawa, whereas the Cataraqui River originates in Newboro Lake and flows southwest toward Kingston (Parks Canada, 2025). Of the six lakes examined in this study, five are located within the Rideau River watershed, while Indian Lake lies within the Cataraqui River watershed. Otter Lake, however, is not part of the canal system, and was used as a reference site for stressors specifically associated with the construction of the Rideau Canal. The Rideau Canal system also spans distinct geological settings that may influence lake characteristics. Lower Rideau L. is situated on the Smiths Falls Limestone Plain, which is characterized by shallow soils and extensive limestone bedrock exposure (Watson, 2000; RVCA, 2014a; Parks Canada, 2025). In contrast, the remaining five study lakes are located on the Frontenac Axis, a geological ridge connecting the Canadian Shield to the north with the Adirondack Mountains to the south, and are underlain predominantly by granite, gneiss, and marble bedrock (Watson, 2000).

Big Rideau Lake

Big Rideau L. (44.7706° N, 76.2152° W) is the largest (surface area: 44.6 km²) and deepest (Z_{mean} = 16.3 m; Z_{max} = 95 m) lake in the Rideau Canal system (Fig. 1) and straddles both granitic and limestone bedrock (Forrest, 2001). It is currently oligo-mesotrophic to mesotrophic with an eleven-year (2009-2019: May-June) mean total phosphorus (TP) concentration of 9.1 µg L^{-1}, and a nine-year (2012-2020: May-June) mean Secchi transparency depth of 7.0 m (Tab. 1; Balasubramaniam *et al*., 2025).

Indian Lake

Indian L. (44.592° N, 76.327° W) is a small (surface area: 2.7 km²), relatively deep (Z_{mean} = 10.1 m; Z_{max} = 26 m), thermally stratified (Forrest, 2001) lake that is situated on Precambrian Shield bedrock (Fig. 1; Forrest, 2001). It is currently oligo-mesotrophic to mesotrophic with a ten-year (2010-2019: May-June) mean TP concentration of 10.6 µg L^{-1} and a five-year (2015-2019: May-June) mean Secchi transparency depth of 5.0 m (Tab. 1; Balasubramaniam *et al*., 2025).

Tab 1. Geographical, physical, and chemical data for the study lakes along the Rideau Canal, and Otter Lake. Chemical data and Secchi depth samples were collected by Balasubramaniam *et al.* (2023; 2025) in September/October 2019/2020, and analyzed by the National Laboratory for the Environmental Testing (NLET) in Burlington, ON. The physical data were from Christie and Smol (1996), Karst and Smol (2000), and Forrest *et al.* (2002).

Lake	Latitude (°N)	Longitude (°W)	Mean Depth (m)	Maximum Depth (m)	Surface Area (SA) (km²)	Watershed Area (W) (km²)	SA:W	TP (µg L^{-1})	Ca (mg L^{-1})	Secchi Depth (m)
Big Rideau L.	44.42	76.14	16.3	95.0	44.6	128.5	0.35	11.6	24.0	7.0
Indian L.	44.35	76.19	10.1	26.0	2.7	359.0	0.01	10.2	23.0	5.0
Upper Rideau L.	44.40	76.22	8.1	22.0	13.6	155.0	0.09	8.0	24.7	4.7
Lower Rideau L.	44.51	76.07	2.8	23.0	13.0	478.9	0.03	13.0	23.0	5.9
L. Opinicon*	44.34	76.19	4.9	9.2	7.8	598.0	0.01	11.3	23.3	4.0
Otter L. (CR)	44.47	76.07	10.0	37.0	6.0	46.6	0.13	8.6	31.7	6.2

CR, canal reference; TP, total phosphorus. *See Graves *et al.* (2024).

Upper Rideau Lake

Upper Rideau L. (44.682° N, 76.336° W) is a large (surface area: 13.62 km^2), relatively deep (Z_{mean} = 8 m; Z_{max} = 23 m) lake that thermally stratifies in the summer (Fig. 1; Christie and Smol, 1996). The surrounding bedrock is primarily composed of conglomerate sandstone, shale, and dolostone (RVCA, 2014b). The lake is mesotrophic with a ten-year (2010-2019: May-June) mean TP concentration of 16.6 µg L^{-1}and an eleven-year (2009-2019: May-June) mean Secchi transparency depth of 4.7 m (Tab. 1; Balasubramaniam *et al.*, 2025).

Lower Rideau Lake

Lower Rideau L. (44.8521° N, 76.1281° W) is a large (surface area: 13 km^2), shallow (Z_{mean} = 2.8 m; Z_{max} = 23 m, in one deep area), polymictic (Forrest, 2001) lake (Fig. 1). The underlying bedrock consists of Paleozoic quartz sandstone, some dolostone

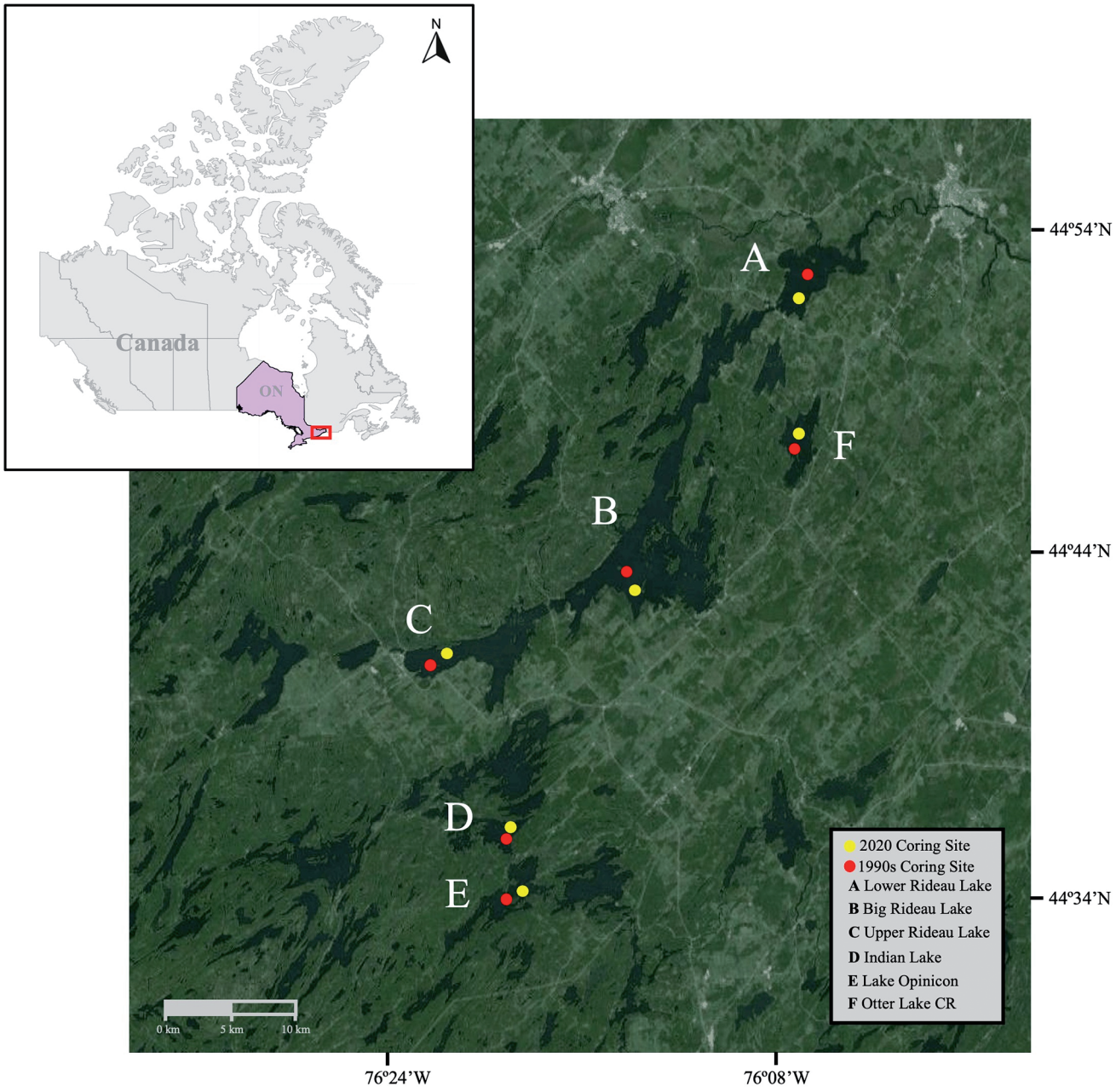

Fig. 1. Image of the study lakes Lower Rideau L., Big Rideau L., Upper Rideau L., Indian L., and L. Opinicon as well as the reference lake Otter L. (Ontario, Canada). The locations of the 1990s (Christie and Smol, 1996; Karst and Smol, 2000; Forrest *et al.*, 2002) and the 2020 (current study) sediment cores are labelled with red and yellow circles, respectively. Reference: image created in R using package *ggmap* (Kahle and Wickham, 2013). Inset: Map of Canada with the approximate location of the Rideau Canal (red box) within the province of Ontario (pink shading) developed using ArcGIS.

and possibly conglomerate (RVCA, 2014c). The lake is mesotrophic with an eleven-year (2010-2020: May-June) mean TP concentration of 14.1 µg L^{-1} and an eleven-year (2009-2019: May-June) mean Secchi transparency depth of 5.9 m (Tab. 1; Balasubramaniam *et al*., 2025).

Otter Lake (Reference)

Otter L. (45.8489° N, 76.4297° W) is a small (surface area: 6 km^2), relatively deep (Z_{mean} = 10 m; Z_{max} = 37 m), thermally stratified lake (Forrest, 2001) that is located outside the Rideau Canal system. It was chosen as a "reference" lake in this study as it was not affected by disturbances associated with canal construction and flooding (Fig. 1). It is currently oligo-mesotrophic with a ten-year (2008-2017: May-June) mean TP concentration of 9.6 µg L^{-1} and an eleven-year (2009-2019: May-June) mean Secchi transparency depth of 6.2 m (Tab. 1; Balasubramaniam *et al*., 2025).

METHODS

Sediment sample collection

Sediment cores were collected from the four lakes within the Rideau Canal system in 2020, including Big Rideau L., Indian L., Lower Rideau L., Upper Rideau L., as well as the reference lake (Otter L), as described in Balasubramaniam *et al*. (2025). In addition, our comparative analyses will incorporate the L. Opinicon sediment record, which was collected in 2019, drawing from recently published Cladocera data (Graves *et al.*, 2024). Given that a Global Positioning System (GPS) was not available for earlier core collections (1991 to 2000), bathymetric maps were used to retrieve the 2020 sediment cores at approximately the same location as the earlier paleolimnological studies (Fig. 1). The 2020 cores were collected using a Glew (1989) gravity corer and were sectioned on site using a Glew (1988) vertical extruder. Each sediment core was sectioned into 0.25 cm intervals for the first 5 cm followed by 0.5 cm intervals for the remainder of the core (Balasubramaniam *et al*., 2025). At the same time and location as the core collection, Secchi depth, coring depth, and surface water pH were recorded, and surface water samples were collected (at ~1 m) for water chemistry analyses. Water samples were sent to the National Lab for Environmental Testing (NLET) in Burlington (Ontario) where they were analyzed for ions (i.e., calcium, fluoride, chloride, magnesium, sodium, sulfate, potassium, silica) and TP. The sediment cores were freeze-dried prior to analyses.

^{210}Pb dating

As described in detail in Balasubramaniam *et al.* (2025), ^{210}Pb gamma spectrometry techniques closely followed the methods outlined by Schelske *et al*. (1994). In brief, strategically selected intervals from the sediment cores (15-25 intervals) were prepared by weighing ~0.3 g of the freeze-dried material into plastic tubes at a height of ~2 cm. A chronology was established using the ScienTissiME package (http://www.scientissime.net/software; Scheer Software Solutions, Barry's Bay, ON, Canada), based on unsupported ^{210}Pb activity (total ^{210}Pb minus supported ^{210}Pb), and using ^{214}Pb as a proxy for background activities and the constant rate of supply (CRS) model (Appleby, 2001). In addition, ^{137}Cs trends were examined as a potential independent chronological marker to corroborate ^{210}Pb dates. Dates of interest beyond background ^{210}Pb (e.g., 1830 canal construction) were extrapolated using third-order polynomial regression models (these dates are viewed with caution as associated errors may be high). Further details of the CRS dating approach and results for these cores are reported in Balasubramaniam (2022) and Balasubramaniam *et al*. (2025).

Instrumental records

Trends in mean annual air temperature (MAAT) between 1873 and 2021 were obtained from Environment Canada and Climate Change (ECCC) for Kingston (ECCC, station ID: 6104142) and Lyndhurst Shawmere (ECCC, station ID: 6104725) using adjusted and homogenized climate data (Vincent *et al*., 2020). Using the same approach as Balasubramaniam *et al.* (2025), these two climate stations were chosen as they are within ~50 km of the central area of the Rideau Lakes region and the historical temperature data from both stations were highly correlated (r = 0.96; p<0.001). There was a seven-year hiatus in the MAAT observations which corresponds to World War II (1939-1945) and a six-year gap during the 1970s (1971-1976). Highly correlated temperature data from Brockville (ECCC, ID: 6100969, r = 0.82; p<0.001; Balasubramaniam *et al*., 2025) and Harrington IHD (ECCC, ID: 6103367, r = 0.81; p<0.001; Balasubramaniam *et al*., 2025) were used to supplement the Kingston record. MAAT was presented as anomalies data using the 1971-2000 average as the reference period and compared to trends in our paleolimnological proxies.

VRS-chlorophyll-*a* trends

Visible range spectroscopy-inferred chlorophyll-*a* (VRS Chl-*a*) analysis was used to examine trends in whole-lake primary production following methods described in Wolfe *et al.* (2006) and Michelutti *et al.* (2010) and is discussed in detail in Balasubramaniam *et al.* (2025). Briefly, a small amount of freeze-dried sediment from each interval was sieved through a 125-µm mesh, placed into glass cuvettes, and processed with a Model 6500 series Rapid Content Analyzer (FOSS NIRSystems, Inc.). Trends in Chl-*a* concentrations and its main diagenetic products were inferred from spectral absorbance values of wavelengths between 650-750 nm and using a log-transformed algorithm of standardized methods from Michelutti *et al*. (2010). To facilitate comparisons across our paleolimnological proxies and across records, long-term trends in VRS Chl-*a* concentrations were expressed as z-scores (standardized within sediment records to a mean of 0 and a standard deviation of 1).

Cladoceran analysis

For each sediment core, analysis was done at every 2 cm for cladoceran subfossil remains following methods described by Frey (1986) and Korhola and Rautio (2001). Briefly, ~0.2-g of freeze-dried sediment per interval was deflocculated in a 10% potassium hydroxide (KOH) solution at ~75°C for 30 min. Each sample was then passed through a sieve (38-µm) and rinsed with deionized water to remove small particles and KOH. Ethanol and safranin were used to preserve and stain the samples, respectively. One aliquot (100 µL each) of the concentrated remains was applied to a coverslip followed by glycerin jelly as a mounting medium to make permanent slides.

The identification of cladoceran subfossils generally followed Szerocyńska and Sarmaja-Korjonen (2007) and Korosi and Smol (2012a, 2012b). Cladoceran remains were identified under 200x or 400x magnification using a DMR2 microscope (Leica®

Microsystems, Wetzlar, Germany) and bright-field optics. All cladoceran remains including carapaces, headshields, and post-abdominal claws were counted and the most abundant remain was used to calculate the number of individuals per taxa. Coverslips were scanned in their entirety for all identifiable remains and a minimum of 70 individuals were enumerated for each interval (Kurek *et al.*, 2010) and expressed as percent relative abundance. We combined *Bosmina longirostris* and *Eubosmina longispina* into *Bosmina* spp. for analyses because of the lack of consistent visibility of the lateral headpore (position of lateral headpore is key for identification; Korosi and Smol, 2012a). *Daphnia* spp. included *Daphnia longispina* complex and *Daphnia pulex* complex. *Chydorus* spp. included *Chydorus brevilabris, Chydorus piger,* and *Chydorus gibbus.* As well, we combined *Alona affinis, Alona circumfimbriata, Alona quadrangularis,* and *Alona rustica* (only found in Big Rideau L.) into *Alona* spp., and *Alonella nana* and *Alonella excisa* into *Alonella* spp. for analyses.

For each sediment record, relative abundances of the most common taxa (greater than 2% in at least two intervals) were displayed stratigraphically using the *riojaPlot* package (Juggins, 2023) in R (version 4.3.1; R Development Core Team, 2024). The cladoceran taxa displayed in the stratigraphies were ordered by habitat (i.e., pelagic, littoral, and benthic). To quantitatively display the stratigraphic succession of cladoceran assemblages over time, taxa were organized from left to right in the stratigraphy based on increasing species scores from a canonical correspondence analysis (CCA) constrained to sediment core depth (Janssen and Birks, 1994). Cladocera stratigraphic zones were established through constrained incremental sum of squares (CONISS) cluster analysis (Grimm, 1991), with important zones identified by broken-stick analysis (Bennett, 1996) using the *vegan* package (Oksanen *et al*., 2015) in R (version 4.3.1, R Development Core Team, 2024). In addition, principal component analysis (PCA) biplots of cladoceran species abundances as arrows and core samples as numbers (core depths in cm) were generated for each sediment record to show the contribution and relationship of each species to PCA axes 1 and 2 and how species co-vary over time. PCA biplot ordinations were generated using the vegan package (Oksanen *et al*., 2015) in R (version 4.3.1, R Development Core Team, 2024) following species square-root transformation to stabilize variance (Legendre and Gallagher, 2001).

Comparison among paleo proxy trends and regional warming over past ~150 years

For each sediment record, a PCA was used to graphically summarize the major patterns in cladoceran assemblage variation over time, generated using the *vegan* package (Oksanen *et al*., 2015) in R (version 4.3.1, R Development Core Team, 2024) following species square-root transformation to stabilize variance (Legendre and Gallagher, 2001). The PCA axis 1 (PC1) sample scores were plotted against core depth/time for the cladoceran assemblages (this study) and compared to downcore PC1 sample scores derived from previously published diatom assemblages from the same cores (Balasubramaniam *et al*., 2023, 2025). The relationship between Cladocera and diatom PC1 sample scores were assessed using a Spearman rank correlation analysis. Detrended canonical correspondence analysis (DCCA), constrained to sediment age as the sole environmental variable, was used to estimate compositional turnover in cladoceran assemblages as beta diversity (scaled in standard deviation units) over time (*sensu* Smol *et al.*, 2005), providing a means to quantify and compare the magnitude of change in each record. Only data since the construction of the Rideau Canal were used (~200 years of the sediment record) to estimate species turnover. All data were analyzed equally by using square-root transformations of species-relative frequency data (to stabilize variances), detrending by segments, and no down-weighting of rare taxa. All DCCA analyses were conducted using CANOCO 5 (Šmilauer and Lepš, 2014).

RESULTS

^{210}Pb radioisotopic dating

A detailed summary of the ^{210}Pb dating of the sediment cores for Big Rideau L., Indian L., Upper Rideau L., Lower Rideau L., and Otter L. is provided in Balasubramaniam *et al*. (2025). Briefly, initial ^{210}Pb activities in Big Rideau L., Indian L., and Otter L. (~1200 Bq/kg; ~2400 Bq/kg; ~2000 Bq/kg, respectively) generally followed an exponential decline with sediment depth (Balasubramaniam *et al*., 2025). Upper Rideau L. and Lower Rideau L. had more vertical profiles before following a more typical exponential decay with depth (Balasubramaniam *et al.*, 2025). Indian L., Upper Rideau L., Lower Rideau L., and Otter L. had distinct ^{137}Cs peaks that were used to corroborate the ^{210}Pb chronology (Balasubramaniam, 2022).

Cladocera trends

Across all study lakes, a total of 22 cladoceran species were identified and enumerated, 18 of which were common to all study lakes, whereas only two (*Disparalona acutirostris* and *Kurzia latissima*) were found in a subset of lakes (Upper Rideau L., Lower Rideau L., Otter L., and L. Opinicon), *Graptoleberis testudinaria* was found in a subset of lakes (Big Rideau L., Indian L., and Lower Rideau L.), and *Alona rustica* was only found in Big Rideau L.

Cladoceran assemblage changes

Biostratigraphical zones were established for each of the study lakes. Subzones of change that were of interest ecologically were also included (Fig. 2), although they were not deemed statistically significant by the broken-stick model. CONISS analysis identified two important stratigraphic zones in Big Rideau L., with the primary break occurring between core depths of 14 (ca. 1880) and 16 cm (ca. 1849) and a subzone between 2 cm (ca. 2010) and 4 cm (ca. 1999; Fig. 2a). In Indian L., the division occurred between depths 14 cm (ca. 1907) and 16 cm (ca. 1867) and a subzone between 4 cm (ca. 2002) and 6 cm (ca. 1987; Fig. 2b). The significant CONISS zone division in Upper Rideau L. occurred between 6 cm (ca. 2010) and 8 cm (ca. 2008) with a subzone between 22 cm (ca. 1876) and 24 cm (ca. 1838; Fig. 2c). Lower Rideau L. had a CONISS zone division between 48 cm (ca. 1829) and 50 cm, with a subzone between 16 cm and 18 cm (ca. 1966; Fig. 2d). The canal reference lake, Otter L., had a significant CONISS zone division between 10 cm (ca. 1960) and 12 cm (ca. 1951), with two subzones between 22 cm (ca. 1876) and 24 cm (ca. 1829) and the second occurring between 4 cm (ca. 1997) and 6 cm (ca. 1984; Fig. 2e).

For Cladocera species biplots, PCA axis one (PC1) accounts for 26-43% and PCA axis two (PC2) accounts for 13-18% of the total variance among the five study lakes (Fig. S1 a-e). The PCA biplots graphically illustrate which species (arrows) were most abundant at various times (numbers as core depth, in cm) in each sediment record (Fig. S1), aligning with the CONISS zones gener-

ated in Fig. 2. For example, in Big Rideau L., Indian L., Upper Rideau L., and Lower Rideau L., PC1 is positively related with taxa that are most abundant at the bottom of the cores (*Alona* spp., *A. harpae*, *Alonella* spp., *Pleuroxus* spp.), and in Indian and Upper Rideau lakes, *Daphnia* spp. were abundant (Fig. S1a-d). In Otter L., PC1 is positively related to species most abundant since the ~1990s (*Chydorus* spp., *Alonella excisa*, and *O. gracilis*) and negatively related to taxa abundant at the bottom of the core (*Alona* spp., *A. nana*, and *A. harpae*; Fig. S1e). In Big Rideau L., PC2 is positively related to *Alona affinis* around the period just before the construction of the canal and negatively related to taxa that are most abundant since ~1990s (*Bosmina* spp. and *Daphnia* spp.; Fig. S1a). In Indian L., Upper Rideau L., and Lower Rideau L., PC2 is positively and negatively related to taxa that are most abundant during the construction of the Rideau Canal (~1830; littoral taxa; Fig. S1b-d). In Otter L., PC2 is positively related to *Bosmina* spp. and *Eurycerus* spp. in the mid-1950s and negatively related to a variety of littoral taxa during the period following the construction of the Rideau Canal (mid-1800s; Fig. S1e).

Pre-canal construction disturbances (bottom of core to ~1830)

During the pre-canal period, cladoceran assemblages in the deeper lakes (Big Rideau L., Indian L., and Otter L.) were dominated by *Bosmina* spp., whereas Upper Rideau L. had approximately equal proportions of *Bosmina* spp. and littoral taxa. Meanwhile, Lower Rideau L. was dominated by littoral species. Big Rideau L. underwent a subtle decline in *Bosmina* spp. from 24 cm (~62%) to 16 cm (~43%; ca. 1849) with a concurrent increase in *Chydorus* spp. (~9% to ~25%; Fig. 2a). During this zone, *A. harpae, Alona* spp., and *Alonella* spp. all exhibited their highest relative abundances of the entire core. In Indian L., *Bosmina* spp. dominated the assemblage and remained relatively stable throughout most of this zone, with a subtle increase from 18 cm (~37%; ca. 1828) to 16 cm (~51%; ca. 1867) and a concurrent decline in *Daphnia* spp. (~33% to ~23%; Fig. 2b). *Chydorus* spp. increased in relative abundance during this zone, from ~1% at the bottom to ~13% at 16 cm (ca. 1867), with concurrent declines in *Alona* spp. from 17.5% (26 cm) to ~6% (16 cm). For Upper Rideau L., this zone was further divided into Zone 1a and 1b, with the former dominated by littoral species such as *Chydorus* spp. which remained around ~25-30% relative abundance, with a concurrent increase in *Bosmina* spp. from ~30% at the bottom of the core to ~40% at 24 cm (ca. 1828; Fig. 2c). In Lower Rideau L., from the bottom of the core to 50 cm there was a decrease in relative abundance of *Alona* spp. from ~38% to ~20%, *Chydorus* spp. increased from ~27% to ~36%, and *Bosmina* spp. increased from ~36% to 50% (Fig. 2d). In Otter L. (the reference lake), the zone was divided into Zone 1a and 1b (Fig. 2e). The majority of species were relatively stable in Zone 1a, with the exception of *Daphnia* spp. which declined from ~18% at the bottom of the core to ~9% at 24 cm (ca. 1829; Fig. 2e).

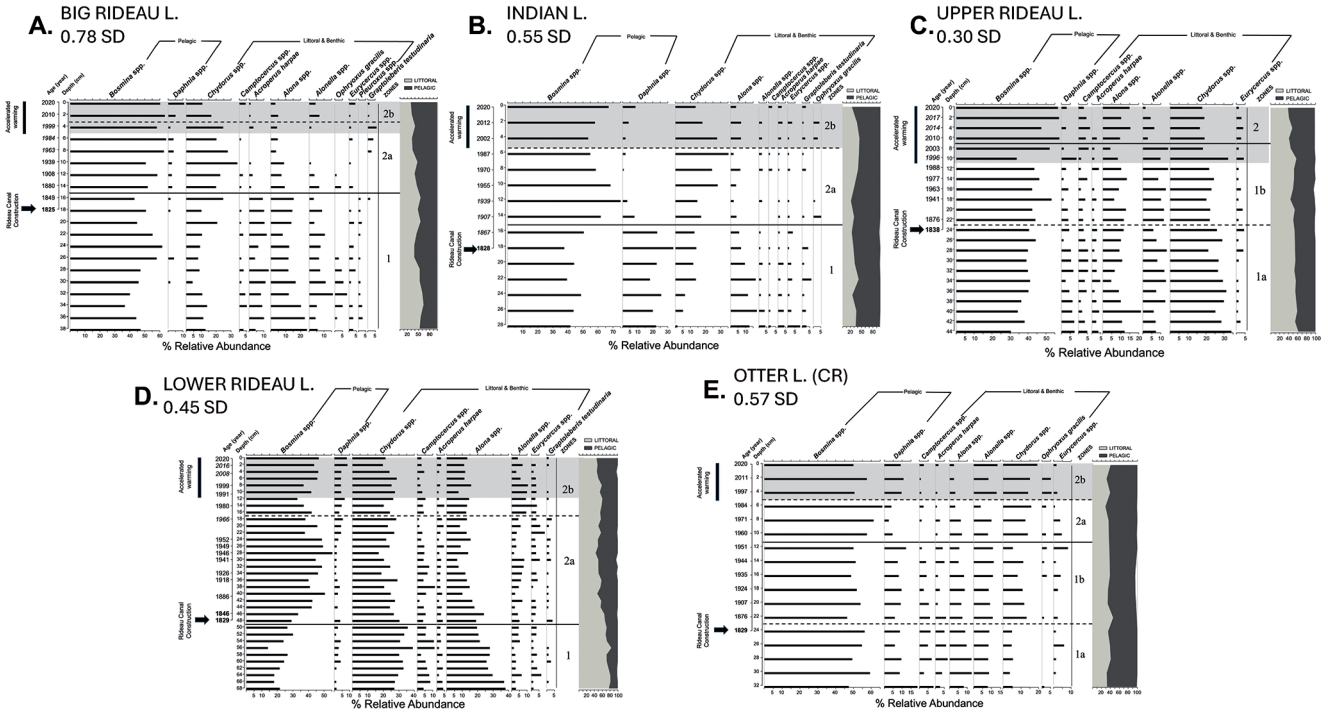

Fig. 2. Cladocera stratigraphic profiles showing the percent relative abundance of the most common taxa enumerated in the 2020 cores from Big Rideau L. **(A)**, Indian L. **(B)**, Upper Rideau L. **(C)**, Lower Rideau L. **(D)**, the canal reference (CR) lake Otter L. **(E)**.The figures are scaled by depth with the corresponding CRS-estimated ^{210}Pb dates presented as a secondary axis. Dates in bold have been extrapolated and are viewed with caution: italicized dates were interpolated. Cladocera are ordered from left to right based on their axis one species scores from a canonical correspondence analysis constrained to depth. Horizontal black lines depict significant zones (dashed lines are sub-zones) determined by constrained incremental sum of squares (CONISS). The ratio of benthic to pelagic sums are located on the right. The shaded grey area represents the period of recent accelerated warming.

Period of canal construction and other anthropogenic impacts (ca. 1830 – ca. 1990s)

Immediately following the completion of the Rideau Canal in 1832, the Big Rideau L. Cladocera record registered an increase in the relative abundances of *Bosmina* spp. from ~43% at 15 cm (ca. 1849) to ~64% at 6 cm (ca. 1984; Fig. 2a). The relative abundances of *Chydorus* spp. peaked (~34%) at 10 cm (ca. 1939) but then declined to ~20% at 6 cm (ca. 1984). Several littoral species, including *Camptocercus* spp., *A. harpae*, *Alonella* spp., *Ophryoxus gracilis,* and *Pleuroxus* spp., declined to 0% relative abundance during this zone. *Alona* spp. declined from ~18% at 16 cm (ca. 1849) to ~5% at 6 cm (ca. 1984). In Indian L., *Chydorus* spp. increased from ~15% at 14 cm (ca. 1907) to ~35% at 6 cm (ca. 1987), whilst *Bosmina* spp. declined from ~70% at 12 cm (ca. 1939) to ~50% at 6 cm (ca. 1987; Fig. 2b), with a concurrent decline in littoral species (such as *Camptocercus* spp., *Alona* spp., *Eurycercus* spp., and *Graptoleberis testudinaria*). *Daphnia* spp. declined markedly from 23% at 16 cm (ca. 1867) to 0% at 10 cm (ca. 1955), with a slight reappearance at ~2% at 6 cm (ca. 1987). In Upper Rideau, L. *Bosmina* spp. declined from ~41% at 18 cm (ca. 1941) to ~34% at 10 cm (ca. 1996), *Chydorus* spp., *Daphnia* spp., and other littoral species remained relatively stable until ca. 1996 where some littoral species such as *Camptocercus* spp., *A. harpae*, and *Alona* spp. began to decline (Fig. 2c). In Lower Rideau L., the earlier assemblages underwent subtle declines in littoral species including *Alona* spp. that declined from ~20% relative abundance at 48 cm, to ~15% at 18 cm (Fig. 2d). Concurrently, *Bosmina* spp. increased briefly to ~55% relative abundance at 28 cm (ca. 1946), before declining to ~38% at 18 cm (ca. 1966; Fig. 2d). *Daphnia* spp. increased from ~1% abundance at 34 cm (ca. 1926) to ~5% at 18 cm (ca. 1966) whereas *Chydorus* spp. underwent a subtle increasing trend towards the middle of the zone with a subsequent decline towards the end of the zone. In the reference lake, Otter L., the Cladocera assemblage saw an increase in *Chydorus* spp. between Zone 1a and Zone 1b and the assemblages remained stable through the remainder of Zone 1b (Fig. 2e). In Zone 2a, *Chydorus* spp. increased further from ~5% at 12 cm (ca. 1951) to ~15% at 6 cm (ca. 1984) and *Bosmina* spp. increased from 50% to ~66% during the same time period. Concurrently, *Daphnia* spp. declined from ~12% at 12 cm (ca. 1951) to ~4% at 6 cm (ca. 1984) and *Eurycercus* spp. declined from ~8% to ~1%.

Recent accelerated climate warming (~1990s – present)

In Big Rideau L., *Bosmina* spp. continued to dominate the most recent sediments but there was a notable increase in *Daphnia* spp. (Fig. 2a), doubling in relative abundance to 10% in the uppermost interval (ca. 2021). Meanwhile, many littoral species declined, particularly *Chydorus* spp. (Fig. 2a). Likewise, in Indian L., *Bosmina* spp. continued to dominate the assemblage during Zone 2b, increasing from ~53% at 4 cm (ca. 2002) to ~67% at 0 cm (ca. 2021). *Daphnia* spp. that had previously declined sharply with canal construction increased above trace abundances during this zone, reaching ~9% by 0 cm (ca. 2021; Fig. 2b). *Chydorus* spp. began to decline during this period from ~28% at 4 cm (ca. 2002) to ~13% at 0 cm (ca. 2021), whereas other littoral species remained in low abundances during this period of accelerated warming. Similar to Big Rideau and Indian lakes, relative abundances of *Bosmina* spp. in Upper Rideau L. increased during the most recent period of the record from ~34% at 10 cm (ca. 1996) to ~57% at 0 cm (ca. 2021; Fig. 2c). However, relative abundances of *Daphnia* spp. declined from ~8% in ca. 1996 and this taxon was not observed in the samples from 6 cm (ca. 2010) to 2 cm (ca. 2017), but by 0 cm returned in trace abundance of ~3% (Fig. 2c). Littoral taxa showed minor fluctuations in relative abundance except for *Alonella* spp. which declined from ~10% in ca. 1996 to ~1% at the surface (Fig. 2c). In Lower Rideau L., *Bosmina* spp. remained dominant, increasing from ~33% at 12 cm to ~47% at 0 cm, whereas *Daphnia* spp. remained stable at ~4% until 2 cm (ca. 2016), increasing thereafter to ~8% (Zone 2b; Fig. 2d). *Chydorus* spp. and *Alonella* spp. remained in relatively high abundances, decreasing slightly in the upper three intervals. Cladoceran assemblages in Otter L. (reference lake) also underwent compositional changes over the past few decades (Zone 2b) including a decrease in *Bosmina* spp. beginning in ca. 1984 with a change in relative abundance from ~66% to 50% by 0 cm (Fig. 2e). During this recent period of warming, *Daphnia* spp. relative abundance in Otter L. doubled from ~5% at 6 cm (ca. 1984) to ~10% at 0 cm, together with increases in *Chydorus* spp. from ~14% at 4 cm (ca. 1997) to ~19% at 0 cm, and *Alonella* spp. from ~4% at 6 cm (ca. 1984) to ~13% at 0 cm. The remainder of the littoral species remained relatively stable.

Comparison among paleo proxy trends and regional warming over past ~150 years

The main cladoceran trends in the study lakes' sediment records, summarized using PC1 sample scores (Fig. 3 a-e), tracked similar temporal responses to diatoms (PC1 sample scores; Fig. 3 a-e). PCA axis 1 explained between 32 and 58% of the total variance in the cladoceran assemblages over time within the lakes (Fig. 3 a-e). All of the Cladocera PC1 samples scores (Fig. 3 a-e) were significantly correlated to the diatom PC1 sample scores (Big Rideau L.: r = 0.829, $p<0.001$; Indian L.: r = 0.659, $p = 0.02$; Upper Rideau L.: r = 0.732, $p = 0.002$; Lower Rideau L.: r = 0.498, $p=0.04$; Otter L.: r = 0.615, $p = 0.04$). In Big Rideau and Indian lakes (Fig. 3 a,b), PC1 scores recorded declining scores from the ~1860s and then increases from the ~1990s to present, corresponding to the time of increased accelerated warming in the region (Fig. 3f). VRS Chl-*a* for Big Rideau and Indian lakes (Fig. 3a,b) followed similar trends, with increases around the time of canal construction (ca. 1832), subsequent declines to the mid 1900s (~1940 for Big Rideau L. and ~1930 for Indian L.), and both trends showing increases to the top of the cores, corresponding with the period of accelerated warming (Fig. 3f) and increases in *Daphnia* spp., *Bosmina* spp., and declines in littoral species (Fig. 2a,b). The PC1 scores from Upper Rideau L. (Fig. 3c) remained relatively stable until the ~1990s where they declined to the top of the core. Similar to the PC1 trends in Upper Rideau L., the VRS Chl-*a* trend remained stable to ca. 1990, after which it rapidly increased to the top of the core, corresponding with the period of acerated warming (Fig. 3f) and increases in *Bosmina* spp., declines in *Daphnia* spp., and fluctuations in littoral species (Fig. 2c). In both Lower Rideau and Otter lakes (Fig. 3d,e), an increasing trend in the PC1 scores to the ~1990s were noted, where the scores sharply increased to the top of the core, corresponding with the period of accelerated warming (Fig. 3f). The VRS Chl-*a* trend in Lower Rideau L. (Fig. 3d) declined from the bottom of the core through to the ~1960s, whereas Otter L. (Fig. 3e) remained relatively stable until ~1840s where it declined slightly. In both Lower Rideau and Otter lakes, an increasing trend in VRS Chl-*a* was observed from ~1990s to the top of the core which corresponded with the period of accelerated warming (Fig. 3f) and the continued dominance in *Bosmina* spp. (Fig. 2 d,e).

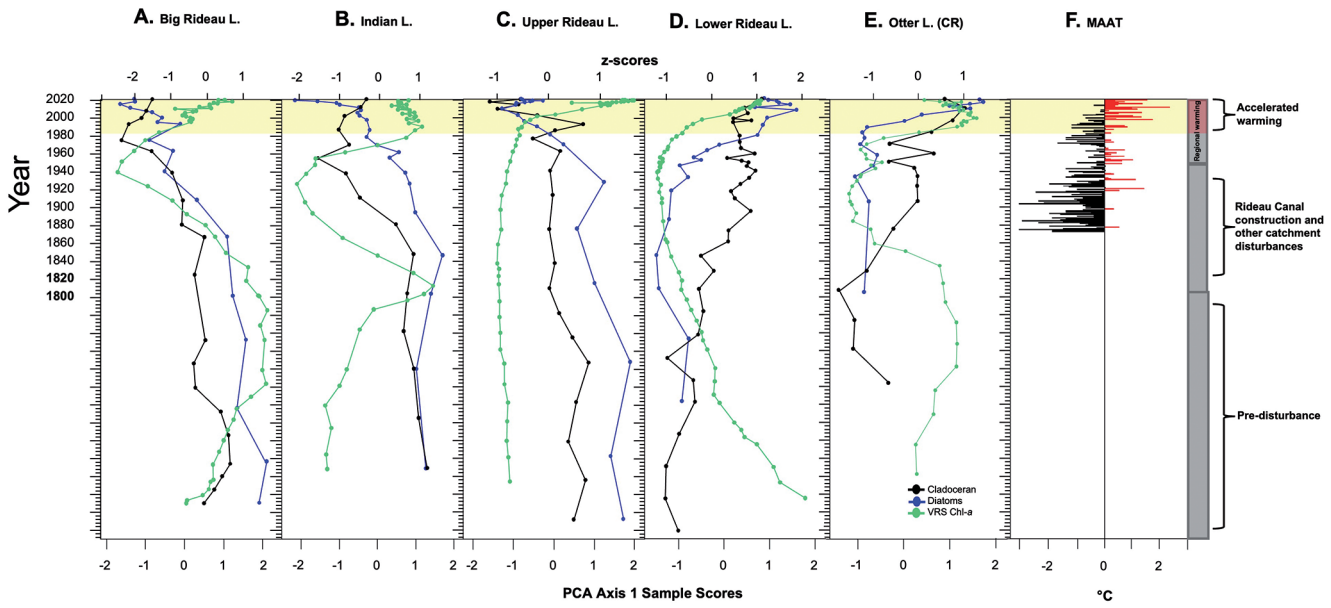

Fig. 3. Comparison of the Cladocera and diatom assemblage changes summarized by principal component analysis axis one sample scores (PC1) and the VRS Chl-*a* concentrations presented as z-scores in Big Rideau L. **(A)**, Indian L. **(B)**, Upper Rideau L. **(C)**, Lower Rideau L. **(D)**, and the canal reference (CR) lake, Otter L. **(E)**. Cladoceran, diatoms, and VRS Chl-*a* are represented by the black, blue, and green line respectively. Mean annual air temperature (MAAT), presented as anomalies, from the Kingston, Ontario and Lyndhurst Shawmere, Ontario weather stations where the negative anomalies (black bars) are values below the baseline mean (1971-2000) and positive anomalies (red bars) are values above the mean (**F**).

The biological turnover of the cladoceran assemblages (estimated by DCCAs) in the six study lakes ranged from 0.30-0.78 SD (Tab. 2; Fig. 2) with no clear indication that lake depth had an effect. While two of the shallower canal-impacted lakes in this study, Upper Rideau L. (Z_{mean} = 8.0 m) and Lower Rideau L. (Z_{mean} = 2.8 m), had relatively low beta-diversity values (0.30 SD and 0.45 SD, respectively), shallow L. Opinicon (Z_{mean} = 4.9 m) had a relatively high compositional turnover (0.70 SD). Of the deeper lakes, Indian L. (Z_{mean} = 10.1 m) had a compositional turnover of 0.55 SD, whereas Big Rideau L. (Z_{mean} = 16.3 m), the deepest lake in the system, had the greatest amount of compositional change with a beta-diversity value of 0.78 SD (Tab. 2). The relatively deep reference lake, Otter L. (Z_{mean} = 10.0 m), had a comparatively low compositional turnover value of 0.57 SD (Fig. 4C). For each study lake, Cladocera assemblage compositional turnover was lower than for the diatom assemblages (Tab. 2), which is expected as there is a higher number of diatom taxa compared to Cladocera taxa.

The 148-year composite temperature anomalies record representing the Rideau Lakes region indicates that conditions were generally cooler between 1873 to 1920, as evidenced by bars being predominantly below the 1971-2000 mean (Fig. 3f). From the 1920s onward, MAAT anomalies were frequently above the baseline mean, particularly since the late 1990s when the highest temperatures were recorded and were consistently above the mean (Fig. 3f).

DISCUSSION

Over the past ~200 years, the Rideau Canal study lakes have experienced several catchment disturbances related to the construction of the canal (flooding and deforestation) and historical land-use changes (settlement, nutrient enrichment, cottage development). More recently, the Rideau lakes region has experienced accelerated climate change that is known to exacerbate other stressors (Smol,

Tab. 2. Detrended canonical correspondence analysis (DCCA) for both diatoms and cladocerans. Scores are based on data from post-Rideau Canal construction (1820).

Lake	Cladoceran B.D. (SD units)	Diatoms B.D. (SD units)
Big Rideau L.	0.78	1.20
Indian L.	0.55	1.00
Upper Rideau L.	0.30	0.71
Lower Rideau L.	0.45	1.05
L. Opinicon*	0.70	1.10
Otter L. (CR)	0.57	1.05

CR, canal reference lake; B.D., beta diversity; SD, standard deviation. *See Graves *et al.* (2024).

2010, 2019). Below, we discuss the impact of these multiple environmental stressors on the cladoceran assemblages and make comparisons to recently published diatom trends from the same lakes (Balasubramaniam *et al*., 2025).

Baseline conditions: pre-Rideau Canal construction

The prevalence of *Bosmina* spp. during the pre-canal period in all cladoceran records, together with the presence of *Daphnia* spp. (although to differing degrees across lakes), suggest that baseline conditions in the study lakes were naturally mesotrophic. For example, during periods of high production (such as when TP values are high), *Daphnia* spp. were found to have a positive relationship with TP values (Urabe *et al.*, 1997; Labaj *et al*., 2021), although this relationship is usually indirect as increased TP can positively impact the quality and quantity of food resources (Scheuerell *et al*., 2002). The pelagic *Bosmina* spp. were the main cladocerans in the deeper lakes (Big Rideau L., Indian L., and Otter L.), whereas in shallower lakes (Upper Rideau L. and Lower Rideau L.), *Bosmina* spp. co-dominated the assemblages with a several littoral species. *Bosmina* species, unlike *Daphnia*, possess the ability to migrate both horizontally and vertically (Adamczuk, 2012). *Daphnia* species, which are often the ideal prey for planktivorous fish, are restricted to the limnetic zones of lakes as they are limited by their filter-feeding strategies. Conversely, *Bosmina*, which are often avoided by planktivorous fish (Adamczuk, 2012), can move throughout the water body and are adapted to feed upon smaller and less abundant food.

The pre-canal diatom records from these lakes support the cladoceran interpretations that the lakes are naturally productive. For example, *Aulacoseira* taxa (*A. ambigua, A. granulata,* and *A. subartica*), which were an important component of the assemblages during the pre-canal period (Balasubramaniam *et al*., 2025), have been found across a range of TP concentrations but are commonly reported in mesotrophic conditions (Reavie and Smol, 2001; Cumming *et al*., 2015; Duda *et al.*, 2023). In addition, the prevalence of these large-celled taxa suggests the lakes experienced periods of strong water column mixing, as these conditions would keep these taxa from sinking out of the photic zone (Padisák *et al*., 2003; Ptacnik *et al*., 2003). The prevalence of the benthic fragilarioid taxa during this early part of the record is consistent with colder conditions, longer periods of ice coverage, and shorter growing seasons (Lotter and Bigler, 2000; Douglas and Smol, 2010; Rühland *et al.*, 2015; Balasubramaniam *et al*., 2025). Collectively, the composition of Cladocera and diatom assemblages indicate that the pre-canal conditions of the Rideau lakes were naturally mesotrophic, well-mixed, and experienced shorter growing seasons (Christie and Smol, 1996: Karst and Smol, 2000; Forrest *et al*., 2002; Balasubramaniam *et al.*, 2025).

Lake impacts during the post-Rideau Canal construction era (ca. early 1800s to mid-1990s)

The construction of the canal (1827 to 1832) led to multiple catchment disturbances that impacted our study lakes, most notably, widespread flooding resulting in increased lake depths and surface areas in all study sites, together with an increase in nutrient runoff into these systems. The pronounced change in surrounding hydrology and lake morphometry was clearly registered in all the cladoceran records (except the reference site, Otter Lake) by an overall increase in pelagic taxa (e.g., *Bosmina* spp. and *Daphnia* spp.), consistent with the increase in the availability of pelagic habitats. The increase in *Chydorus* spp. (specifically *Chydorus brevilabris*) in Big Rideau L. and Indian L. during the period of canal construction suggests an increase in nutrients, as these taxa have been reported to increase during periods of eutrophic or hypertrophic conditions (Bos and Cumming, 2003). By the 1860s, approximately two-thirds of the Rideau region had been clear-cut to support agriculture and settlement (CHPC, 1996). Subsequent cottage development, which began in the 1930s and expanded substantially after the 1950s (CHPC, 1996), contributed to soil erosion, collectively increasing nutrient runoff into the lakes (Christie and Smol, 1996; Karst and Smol, 2000; Forrest *et a*l., 2002; Balasubramaniam *et al*., 2025). Initial increases in *Chydorus* spp. during the late 1880s to early 1900s in Big Rideau and Indian lakes support this conclusion, as this taxon has been reported to become prevalent during periods of increased nutrients (Bos and Cumming, 2003; Laird *et al*., 2023). During this period of heavy catchment disturbance, the diatom records showed changes that were consistent with the cladoceran assemblages. Across the study lakes, but most notably in Indian L. and Lower Rideau L., increases in *A. ambigua, A. granulata,* and *A. subarctica* point to increased nutrient inputs and a well-mixed water column (Balasubramaniam *et al*., 2025). Additionally, following canal construction, benthic fragilarioid taxa generally declined across lakes which is likely a consequence of the extensive flooding (Balasubramaniam *et al*., 2025). An increase in total suspended solids (TSS) likely occurred at this time as the high-flow rate event of the flooding transported large amounts of sediment and debris in the waterbodies (Talbot *et al*., 2018). The increase in TSS would also impact light penetration in the waterbodies and therefore the amount of light reaching the benthic fragilarioid taxa, further contributing to their decline (Balasubramaniam *et al*., 2025). Increases in TSS can also negatively impact the cladoceran communities. For example, particulates can interfere with the filtering mechanisms of *Daphnia* spp. (Kirk, 1991), whereas *Bosmina* spp. are generally less affected, providing a competitive advantage over *Daphnia* spp. in high TSS environments (Jiang *et al*., 2010; Pinto *et al*., 2023).

In the mid- to late-1900s, nutrient inputs into the lakes notably declined following a reduction in agricultural activities (Warren, 1997), a reduction in the usage of phosphate-based detergents (McGucken, 1989), improvements in residential septic systems (Forrest *et al.*, 2002), and the establishment of secondary forests (Forrest *et al*., 2002). One of the clearest responses to these changes in nutrient reductions was registered in Big Rideau L., where declines in the relative abundance of the higher nutrient indicator, *Chydorus* spp., were observed between the 1940s to 1980s. However, the remainder of the study lakes did not exhibit this same trend in declining *Chydorus* spp. Big Rideau L. is the largest and deepest out of the study lakes with the highest surface area to watershed area ratio (~35%; Tab. 1). Because of this large SA:WA ratio, the nutrient inputs into the lake were likely diluted in relation to the other study lakes with smaller SA:WAs (Forrest *et al*., 2002; Balasubramaniam, 2022). Consequently, once nutrient loading decreased further during the mid-1900s, concentrations in Big Rideau L. may have fallen below levels capable of sustaining *Chydorus* spp., particularly in conjunction with declining VRS Chl-*a* values. Indian and Otter lakes displayed a different pattern, showing declines in *Daphnia* spp. from approximately the 1940s to the 1980s, while *Chydorus* spp. in both systems remained stable or increased slightly. The reduction in *Daphnia* spp. may also be consistent with nutrient declines. During this interval, both lakes exhibited their lowest VRS Chl-*a* values, which likely reduced

food availability for larger cladocerans (DeMott and Kerfoot, 1982). Additionally, decreased nutrient concentrations may have increased water clarity, thereby enhancing visual predation pressure on *Daphnia* spp.

In the shallower, macrophyte-dominated systems (Upper Rideau L., L. Opinicon), flooding during canal construction may have further increased the extent of the littoral zones of these lakes, leading to notable increases in cladoceran littoral taxa (L. Opinicon is discussed in detail in Graves *et al*., 2024) and epiphytic diatoms (Karst and Smol, 2000; Balasubramanium *et al.*, 2023, 2025). The littoral zone of Upper Rideau L. is currently estimated to cover ~53% of the lake, despite it being a relatively deep system (Z_{max} = 22.0 m, Z_{mean} = 8 m). This agrees with the cladoceran assemblage being comprised evenly of littoral species and pelagic *Bosmina* spp. and may explain the relatively low biological turnover (Tab. 2). The extensive macrophyte coverage in Upper Rideau L. provides cladocerans with complex habitats and a variety of food sources, particularly for *Chydorus* spp. (Tremel *et al.*, 2000; Basińska *et al.*, 2014). The high abundance of *Chydorus* spp. and the strong representation of a variety of other littoral taxa suggest that macrophytes were important in this shallow system from the beginning of the record to the late 1980s. Similarly in Balasubramaniam *et al.* (2025), planktonic diatom taxa were scarce throughout the Upper Rideau L. sediment record, with the observed assemblage shifts occurring primarily among benthic taxa. The large macrophyte abundance in both Upper Rideau L. and L. Opinicon suggest a clear-water equilibrium, as the macrophytes can utilize nutrients and indirectly suppress algal activity (Scheffer *et al*., 1993). Comparatively, in the deeper study lakes that do not possess the same extensive littoral zones, higher biological turnover values were observed (Tab. 2). These deeper lakes may have been impacted by the increase in TSS following the flooding of the canal as TSS can reduce the light penetration in the water column (Talbot *et al*., 2018) and thus negatively impact both the macrophyte and algal communities living within the benthic zones. This was also recorded in the diatom assemblages, where Balasubramaniam *et al*. (2025) tracked declines in the relative abundances of benthic fragilarioid taxa across the study lakes.

Although activities associated with canal construction, particularly flooding, would not have affected the reference lake (Otter L.), it did not escape the impacts of deforestation as the region was clear cut to provide timber for the damming the waterways. As a result, Otter L. also likely experienced increased nutrient loading from soil erosion, agriculture run-off, and cottage development. Nonetheless, Otter L. had the lowest historic TP values compared to the other study lakes (Tab. S1). During this period, there was an increase in *Chydorus* spp. where the relative abundance doubles from previous numbers and continues to increase to ca. 1984. Although TP values were likely lower in Otter L. compared to the other lakes, the occurrence of *Fragilaria crotonensis* and *Stephanodiscus medius/parvus* in the diatom record, which both have moderate TP requirements (Reavie and Smol, 2001; Cumming *et al.*, 2015; Duda *et al*., 2023), indicate that the lake had naturally productive conditions and likely enough nutrient enrichment to provide a competitive advantage to *Chydorus* spp.

Recent period: past ~25 years (1990s-present)

The near-synchronous change in cladoceran assemblage composition across lakes, starting in the early 1990s, was characterized by a general shift from *Chydorus* spp. to greater abundances of pelagic *Bosmina* spp. and *Daphnia* spp. This period occurred during a time of multiple environmental stressors, including the introduction of zebra mussels, cyanobacterial blooms, and recent accelerated warming (Balasubramaniam *et al*., 2025). Below, we examine whether the assemblage changes can be explained by these stressors, and make comparisons to the diatom records from these same cores (Balasubramaniam *et al*., 2025).

Zebra mussel invasion

The introduction of the invasive zebra mussels (*Dreissena polymorpha*) into the Rideau Canal system was first reported in the mid-1990s (Watson, 2000), with populations increasing until ~2013 and declining markedly thereafter (Martel and Madill, 2018). In many freshwater systems, the high algal filtering rates of zebra mussels have led to modifications in bottom-up control through declines in algal biomass, increases in water clarity (Hecky *et al*., 2004), and the consumption of both organic and inorganic matter (Newell, 2004), all of which indirectly impact cladoceran communities (Thorp and Casper, 2003). The presence of zebra mussels also tends to favour phytoplankton taxa with lower nutrient preferences (Fishman, 2010), and reduce phytoplankton biomass overall (MacIsaac *et al*., 1995; Caraco *et al*., 1997; Bastviken *et al*., 1998). In systems with zebra mussel invasions, large-bodied pelagic Cladocera, particularly *Daphnia* species, often decline in abundance (David *et al*., 2009; Armstrong and Cumming, 2025) while smaller-bodied taxa (such as pelagic *Bosmina* and littoral *Chydorus* species) may become increasingly dominant as they are better competitors in nutrient-poor conditions when there is lower food abundance available (DeMott and Kerfoot, 1982; Reissing *et al*., 2015). In our dataset, however, the abundance of small-bodied littoral *Chydorus* spp. did not increase in any of the Rideau study lakes. Rather, both small-bodied *Bosmina* spp. and large-bodied *Daphnia* spp. increased in the majority of the lakes (Big Rideau L., Indian L., Lower Rideau L., and Otter L.). These trends suggest that zebra mussel invasions in the Rideau Lakes were most likely not driving factors in the cladoceran assemblage change.

Nutrient changes

Like many lakes in Ontario (Yan *et al*., 2008; Rühland *et al.*, 2010; Rahman *et al*., 2025), the six Rideau study lakes have experienced declines in TP concentrations over the past few decades (MECP, *unpublished data*; Balasubramaniam *et al.*, 2025; Tab. S1). Declining food resources may be linked to the continued dominance of *Bosmina* spp. in recent cladoceran assemblages, despite an increase in *Daphnia* spp. relative abundances in the study lakes. When food resources shift to smaller sizes and are less nutrient dense, *Bosmina* spp. may outcompete larger-bodied *Daphnia* spp. (DeMott and Kerfoot, 1982). Declining TP concentrations can also impact the overall health of the cladocerans, but *Bosmina* spp. are more disturbance tolerant (Jiang *et al.*, 2014), and their TP requirements are much lower than *Daphnia* spp. (Schulz and Sterner, 1999; Reissig *et al.*, 2015). In the diatom records from these same sediment cores, the shift from *Aulacoseira* and/or benthic fragilarioid taxa to small planktonic cyclotelloid taxa that have similarly low TP optima (Duda *et al*., 2023) is consistent with recent nutrient declines in our Rideau lakes (Balasubramaniam *et al*., 2025). Both the cladoceran and diatom records suggest nutrient changes alone cannot explain the assemblage changes and the switch in life strategies, and other environmental factors played a role.

Cyanobacterial blooms

Despite a significant decrease in TP concentrations over the past ~40-50 years (MECP, *unpublished data*), cyanobacterial blooms

have been reported in a number of the Rideau lakes during the current period of accelerated warming including in Lower Rideau L. (2015), Upper Rideau L. (2012, 2015, 2016, 2020), and Otter L. (2020) (MECP, unpublished data). In aquatic ecosystems, cyanobacteria can alter competitive outcomes by affecting species differently (Gliwicz and Lampert, 1990) and can reduce biodiversity through multiple inhibitory effects on zooplankton (Paerl and Otten, 2013). Based on the size efficiency hypothesis (Brooks and Dodson, 1965), which states that large-bodied zooplankton herbivores are better competitors for phytoplankton than smaller-bodied because of their higher filtering efficiency and stronger ability to ingest larger particles, *Daphnia* species are usually the superior competitors (DeMott and Kerfoot, 1982). However, during periods of cyanobacterial blooms, *Bosmina* species and other smaller-bodied cladoceran tend to outperform *Daphnia* species (Jiang *et al.*, 2014) as large cyanobacterial filaments/colonies can interfere with cladoceran filtering apparatuses (Gilbert, 1990). In addition to mechanically affecting filtering processes, cyanobacteria are a poorer food option for Cladocera as they lack essential lipids found in "high quality" algae (Martin-Creuzburg *et al*., 2008). However, *B. longirostris* is known to co-exist with toxic blue-green algae (Jiang *et al*., 2013), as this species is resistant to certain strains of cyanobacteria (i.e., *Microcysits aeruginosa* and *Anabaena flosaquae*) that can be toxic to some cladocerans (Fulton, 1988). The shift from *Daphnia* spp. to *Bosmina* spp. during the last two decades in Upper Rideau L. occurs during the period of reported cyanobacterial blooms on that lake (MECP, *unpublished data*) and aligns with the expected increase in small-bodied cladoceran species (Jiang *et al*., 2014). However, all other study lakes registered an increase in large-bodied *Daphnia* spp. which is counter to expected cladoceran response to cyanobacteria blooms.

Recent accelerated climate warming

The Rideau Canal region, like other lake regions around the world, has experienced increasing air temperatures over the past century, with a steepening of that trend since the ~1990s (Fig. 3f). Increased regional air temperatures, longer ice-free periods, enhanced thermal stratification, and higher primary production, can indirectly affect cladoceran assemblage composition (Jeppesen *et al*., 2014; Thienpont *et al*., 2015). For example, *Daphnia* species tend to thrive during warmer periods when there is an increase in open-water conditions and algal plankton production (Sommer *et al.*, 1986; Berger *et al*., 2007; DeSellas *et al*., 2011) and increased nutrient cycling (Abgeti and Smol, 1995). In regions with mild winters and early springs, *Daphnia* species can experience an early proliferation because of the increased temperatures and an abundance of high-quality resources (George and Hewitt, 2006), which can also give *Daphnia* species an advantage over macroinvertebrate predators (Neill, 1981). In our Rideau lakes records, *Daphnia* spp. are increasing in relative abundance, but smaller-bodied, pelagic *Bosmina* spp. remain dominant in the assemblages. Given that TP concentrations have been declining since the 1970s in all lakes and the lakes are currently oligo-mesotrophic (Christie and Smol, 1996; Karst and Smol, 2000; Forrest *et al*., 2002; Balasubramaniam *et al*., 2023; Balasubramaniam *et al*., 2025), the prominence of *Bosmina* spp. in our sediment records suggests an increase in small-sized food availability and lower nutrient density in these systems, as noted above. During periods of increased temperatures, smaller-bodied Cladocera are favoured as they have relatively low energy requirements (Moore and Folt, 1993; Daufresne *et al.*, 2009) and can be sustained by nutrient-poor food (DeMott and Kerfoot, 1982). Under these warming conditions, there is often a general shift to more pelagic-dominated zooplankton opposed to diverse littoral communities (Kattel *et al.*, 2008). This has been seen in nearby Algonquin Park, where both cottage-impacted lakes and reference lakes saw a trend towards declining species diversity and an increase in small, efficient grazers, namely bosminids (DeSellas *et al.*, 2025). The general increasing trend in *Bosmina* species observed in our records during periods of recent warming has been reported in lakes across Canada as a response to climate-associated limnological changes such as longer ice-free periods, higher primary production, and longer open-water seasons (Jeziorski *et al*., 2015; Hargan *et al*., 2016; Armstrong and Kurek, 2019; Laird *et al*., 2023).

In the diatom record (Balasubramaniam *et al*., 2025), the study lakes showed an increase in the relative abundance of planktonic diatom taxa, which were generally concurrent with declines in *Aulacoseira* taxa and/or fragilarioid taxa. The changes within the diatom assemblages discussed in Balasubramaniam *et al*. (2025) were also more pronounced than those recorded in the earlier paleolimnology studies (Christie and Smol, 1996; Karst and Smol, 2000; Forrest *et al*., 2002). While the cladoceran assemblages have changed significantly across the Rideau Canal study lakes, the responses are not as pronounced compared to that of diatom assemblages. The muted response in cladocerans compared to diatoms has been shown in other multi-proxy paleolimnological studies (Smol *et al*., 2005; Thienpont *et al*., 2015; Valleau *et al*., 2020) and may be because of the higher number of diatom taxa compared to cladoceran.

CONCLUSIONS

Lakes within the Rideau Canal system have experienced various catchment disturbances. Building on the earlier diatom-based paleolimnological studies, the compositional changes in cladoceran assemblages were examined, with the largest assemblage changes occurring since the ~1990s. The most pronounced shift in the cladoceran assemblages, when considered alongside regional meteorological data and VRS Chl-*a*, is likely related to regional climate warming. These data show that the study lakes, which experienced extensive catchment disturbances in the 19th century, are now changing rapidly in response to recent climate warming and related limnological changes. Ongoing research should explore further multi-proxy studies to help gain insight into the trophic status-related changes occurring within these waterbodies.

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Online supplementary material:

Tab. S1. Historic and current total phosphorus water chemistry.

Fig. S1. Principal component analysis (PCA) biplots of cladoceran relative abundances.

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