Revisiting lakes within the Rideau Canal system (Ontario, Canada) to assess the impacts of multiple environmental stressors over the past ~25 years using diatom-based paleolimnology

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ABSTRACT

Diatom-based paleolimnological studies conducted ~25 years ago on five lakes (i.e., Big Rideau, Upper Rideau, Lower Rideau, Indian and Otter lakes) within the Rideau Canal system (Ontario, Canada) tracked extensive catchment disturbances related to canal construction (starting ca. 1828). Over the past three decades, these lakes have experienced additional environmental stressors including invasive zebra mussels and accelerated climate warming, warranting a paleolimnological re-assessment. We examine diatom compositional changes and visible range spectroscopy-inferred chlorophyll-*a* (VRS-Chla) trends over the past >200 years from sediment cores collected in 2019-2020 from these same lakes, with the aim of assessing environmental changes registered in these records since the original studies were undertaken ~25-30 years ago. Despite large-scale cultural disturbances, including extensive deforestation and flooding for canal construction, the most ecologically notable diatom changes in all sediment records occurred in the past ~25-30 years, and coincided with increases in VRS-Chla. During this recent period, small cyclotelloid and elongate planktonic diatoms increased in relative abundance, while large-celled *Aulacoseira* taxa declined. Exceptions to this trend include Upper Rideau Lake, where planktonic diatoms were scarce throughout the core and shifts occurred among benthic taxa, and Big Rideau Lake, which has a large littoral zone, where epiphytic diatoms became prominent in the past decade. These recent diatom changes could not be explained by nutrient enrichment, as measured total phosphorus (TP) concentrations have declined significantly since the 1970s. Increases in small planktonic taxa in some of the lakes also pre-date the ca. 1990 arrival of zebra mussels. We conclude that these recent changes were best explained by regional warming and declining wind speed resulting in new lake physical regimes. Such climate-driven changes are also consistent with the recent development of cyanobacterial blooms in these lakes, despite declining nutrient levels.

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INTRODUCTION

Lake ecosystems are being increasingly affected by multiple environmental stressors that collectively drive significant ecological changes. Among these, three major stressors - nutrient enrichment, invasive species, and climate warming - are of particular importance in understanding algal community dynamics (Litchman and de Tezanos Pinto, 2023), as they have profoundly influenced many temperate freshwater systems. These stressors can result in fundamental changes to lake properties and associated changes to nutrient and light resources, which can play critical roles in algal community dynamics (Rühland *et al.*, 2015; Bramburger and Reavie, 2016). Anthropogenic nutrient enrichment, long recognized as a widespread form of environmental pollution, can profoundly alter algal community composition and often promotes harmful cyanobacterial blooms (Smith *et al.*, 2006; Smith and Schindler, 2009; Hall and Smol, 2010). However, a growing number of studies are reporting increases in cyanobacterial blooms in remote lakes where nutrients have not increased and where favourable bloom-forming conditions are more closely related to warmer and longer open-water seasons and increased thermal stability (Paterson *et al*., 2017; Favot *et al*., 2019, 2024). Climate warming has impacted lake ecosystems by altering thermal stratification patterns, mixing regimes, and the timing and duration of open-water seasons, thereby influencing primary productivity and biogeochemical cycling (Hupfer and Lewandowski, 2008; Stainsby *et al*., 2011; Woolway and Merchant, 2019; Dusenge *et al*., 2019). In addition, the arrival of large populations of invasive benthic filter feeders, such as dreissenid mussels, has substantially altered Secchi depth (water clarity) and the availability of algal resources in some invaded lakes (Hecky *et al*., 2004). While other stressors, such as hydrological changes, morphological alterations, and contamination by pollutants, can also play notable roles, this study specifically focuses on nutrient enrichment, invasive species, and climate warming in shaping the ecological trajectories of our study lakes.

The Rideau Canal system in eastern Ontario (Canada) is a 202-km long inland waterway that consists of a series of rivers, lakes, and interconnecting locks/channels between the Ottawa River (Ottawa, Ontario) and Lake Ontario (Kingston, Ontario) (Fig. 1). To track the impacts of early-1800s canal construction and possible impacts from other extensive catchment disturbances (*e.g.*, shoreline development), several lakes within the Rideau Canal system were the subject of paleolimnological studies undertaken ~25-30 years ago (Christie and Smol, 1996; Karst and Smol, 2000; Forrest *et al*., 2002). Here, we revisit these same lakes (L. Opinicon, Big Rideau L., Indian L., Upper Rideau L. and Lower Rideau L.), using sediment cores collected in 2019 and 2020, to explore the effects of recent environmental stressors that have only become prominent since these earlier studies were published. These include the arrival of invasive zebra mussels, shoreline development, accelerated regional climate warming and reduced wind speed. A sixth lake (Otter Lake) is included as a reference system, situated within the region but external to the Rideau Canal system, thereby not affected by activities associated with canal construction.

We apply similar paleolimnological approaches to these recent ^{210}Pb-dated sediment cores to examine changes in diatom assemblage composition. In addition, we use a more recent paleolimnological method, visible range spectroscopy-inferred

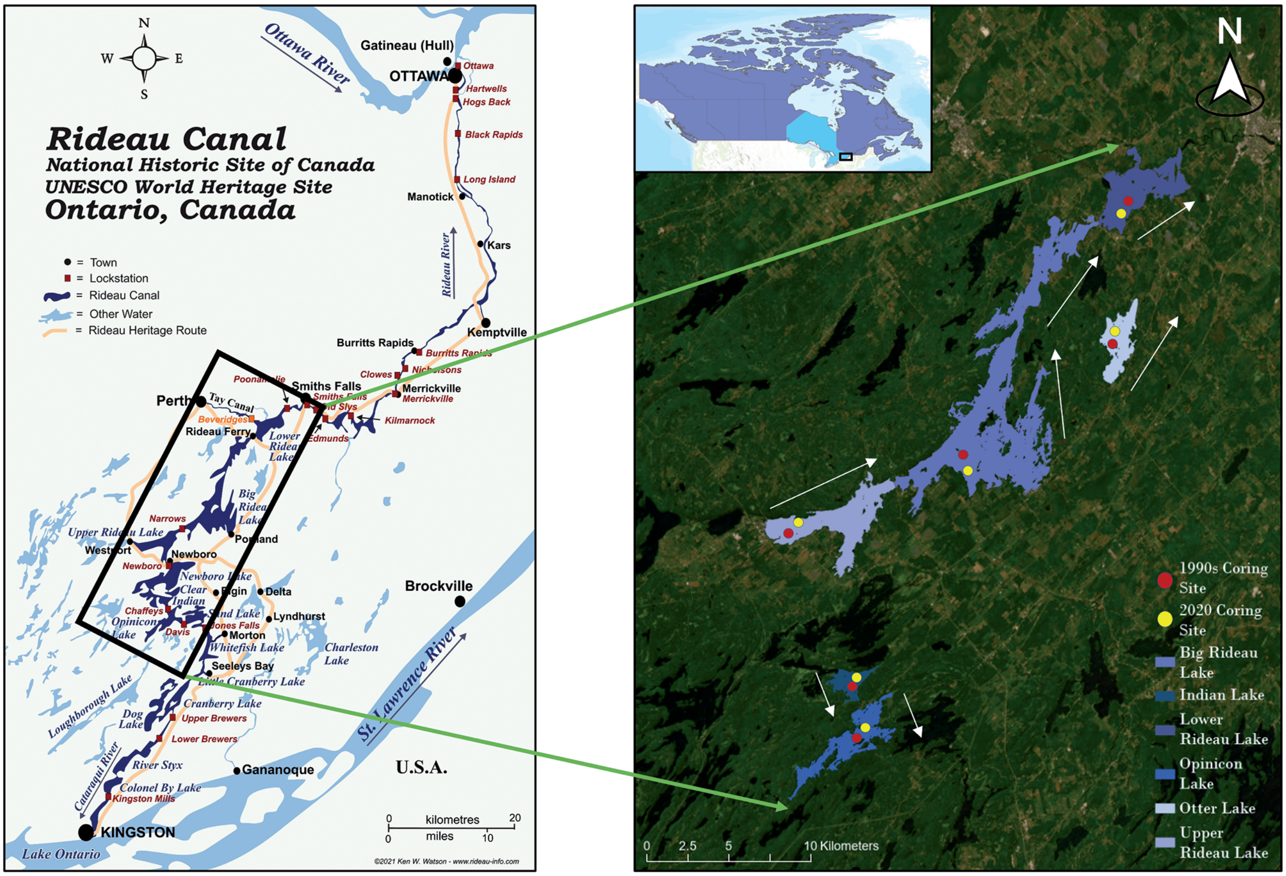

Fig. 1. Map (left) depicts the route of the Rideau Canal system between Ottawa and Kingston (ON, Canada) with a black box drawn around the six study lakes. On the right is a map developed using the ArcGIS Pro tool depicting the six study lakes and the locations of sediment cores retrieved in the 1990s (Christie and Smol, 1996; Karst and Smol, 2000; Forrest *et al*., 2002) and in 2019-2020 (this study). White arrows depict the direction of water flow. Map on left is from Ken Watson (https://www.rideau-info. com/canal/map-waterway.html), with permission.

chlorophyll-*a* (VRS-Chla), to infer trends in overall lake primary production (Michelutti *et al*., 2010; Michelutti and Smol, 2016). To compare trends with deeper lakes in the Rideau Canal system, we also include diatom-based paleolimnological and thermistor data from a recently published assessment of L. Opinicon, our shallowest of the canal study lakes (Balasubramaniam *et al*., 2023).

Site description

Development history

The primary purpose for building the Rideau Canal (constructed between 1827-1832) was to provide a secure military supply route for the transportation of supplies and troops between Montréal (Quebec) and Kingston (Ontario) (Raudzens, 1973). To provide steamboats with navigable depths, flooding of lakes and rivers within the Rideau Canal system during canal construction resulted in increased water depths of 2 to 3 m (Forrest, 2001). Currently, rule curves are followed to keep water levels within a ~1 m annual fluctuation (Forrest, 2001). During the early-1800s to the 1870s, much of the forested land in the Rideau Canal region was cleared for lumber, settlement, and agriculture (Legget, 1986). Cottage development along the Rideau Canal system began in the 1930s and has increased since the 1950s, contributing additional nutrients from land clearing, cottage activities and on-site sewage systems (Legget, 1986). Collectively, these activities would have resulted in increased soil erosion, runoff and nutrient loading.

Lake descriptions

The Rideau Canal system is located within the physiographic region of the Great Lakes-St. Lawrence Lowlands (Fulton and Richard, 1987). The canal links 16 lakes within the Cataraqui River watershed (drainage area: 910 km^2) and the Rideau River watershed (drainage area: 3730 km^2) (Acres International Ltd., 1994) (Fig. 1). Of the six lakes selected for detailed paleolimnological analysis, L. Opinicon (detailed in Balasubramaniam *et al*., 2023), Big Rideau L., Lower Rideau L., Upper Rideau L., and Otter L. (canal reference), reside within the Rideau River watershed, whereas Indian L. is located within the Cataraqui watershed.

Big Rideau L. (coring location: 44°42'24.6 N, 76°14'5.0 W) is the largest (SA: 44.6 km^2) and deepest (Z_{mean} = 16.3 m; Z_{max} = 95 m) lake in the Rideau Canal system (Tab. 1) and thermally stratifies in the summer (Forrest, 2001). It is located next to the town of Portland in the townships of Tay Valley, Drummond/North Elmsley and Rideau Lakes (Fig. 1). The lake is currently oligo-mesotrophic with an eleven-year (2009-2019; May-June) mean total phosphorus (TP) concentration of 9.1 µg/L and an eight-year (2012-2020: May-June) mean Secchi transparency depth of 7.0 m.

Indian L. (coring location: 44°35'37 N, 76°19'09 W) is a small (SA: 2.7 km^2), moderately deep (Z_{mean} = 10.1 m; Z_{max} = 26 m) (Tab. 1) lake that thermally stratifies in the summer (Forrest, 2001). It is located in the upper reaches of the Cataraqui River watershed near Chaffey's Lock in the United Counties of Leeds and Grenville (Fig. 1). The lake is oligo-mesotrophic with an eleven-year (2009-2019: May-June) mean TP concentration of 10.6 µg/L and a five-year (2015-2019: May-June) mean Secchi transparency depth of 5.0 m.

Upper Rideau L. (coring location: 44°40'44.983 N, 76°22'26.634 W) is a relatively large (SA: 13.62 km^2), moderately deep (Z_{mean} = 8 m; Z_{max} = 23 m) (Tab. 1) lake that thermally stratifies in the summer (Christie and Smol, 1996). It is located next to the village of Westport in the United Counties of Leeds and Grenville (Fig. 1). The lake is mesotrophic with a ten-year (2010-2019: May-June) mean TP concentration of 16.6 µg/L and an eleven-year (2009-2019: May-June) mean Secchi transparency depth of 4.7 m.

Lower Rideau L. (coring location: 44°51'22.284 N, 76°07'20.758 W) is a relatively large (SA: 13 km^2), shallow (Z_{mean} = 2.8 m; Z_{max} = 23 m, in one deep area) (Tab. 1) lake and was identified as polymictic in the late-1990s (Forrest, 2001). The lake is located south-east of Smiths Falls, Ontario, within the townships of the Rideau Lakes and Drummond/North Elmsley (Fig. 1). The lake is oligo-mesotrophic with an eleven-year (2010-2020: May-June) mean TP concentration of 14.1 µg/L, and an eleven-year (2009-2019: May-June) mean Secchi transparency depth of 5.9 m.

Tab. 1. A selection of geographical, physical, and chemical data for the six Rideau Canal system study lakes. Physical data were obtained from Christie and Smol (1996), Karst and Smol (2000), and Forrest *et al.* (2002). Secchi depth and water chemistry data were based on samples collected for this study between September-October 2019/2020, the latter were analyzed by the National Laboratory for Environmental Testing (NLET) in Burlington, ON.

Parameter	Big Rideau L.	Indian L.	Lower Rideau L.	Upper Rideau L.	L. Opinicon	Otter L. (CR)
Latitude	44° 42' N	44° 35' N	44° 51' N	44° 40' N	44° 34' N	44° 47' N
Longitude	76° 14' W	76° 19' W	76° 07' W	76° 22' W	76° 19' N	76° 07' W
Mean depth (m)	16.3	10.1	2.8	8.1	4.9	10.0
Maximum depth (m)	95.0	26.0	23.0	22.0	9.2	37.0
Surface area (SA) (km^2)	44.6	2.7	13.0	13.6	7.8	6.0
Watershed area (W) (km^2)	128.5	359.0	478.9	155.0	598	46.6
SA:W	0.35	0.01	0.03	0.09	0.01	0.13
Average TP (µg/L)	11.6	10.2	13.0	8.0	11.3	8.6
TIN:TP	7.0	7.2	7.0	3.8	3.0	5.7
Average Secchi depth (m)	7.0	5.0	5.9	4.7	4.0	6.2

CR, canal reference; TP, total phosphorus; TIN, total inorganic nitrogen.

Otter L. (coring location: 44°47’07 N, 76°07’35 W) is a relatively small (SA: 6 km^2) and relatively deep (Z_{mean} = 10 m; Z_{max} = 37 m) (Tab. 1) lake that thermally stratifies in the summer (Forrest, 2001). It is not connected to the Rideau Canal system (our canal reference lake) and is located south of the community of Lombardy in the Township of Rideau Lakes, United Counties of Leeds and Grenville (Fig. 1). The lake is oligo-mesotrophic with a ten-year (2008-2017: May-June) mean TP concentration of 9.6 µg/L, and an eleven-year (2009-2019: May-June) mean Secchi transparency depth of 6.2 m.

METHODS

Sediment core collection

Sediment cores were collected from five lakes within the Rideau Canal system including Big Rideau L., Indian L., Lower Rideau L., Upper Rideau L. (September 2020), and L. Opinicon (October 2019), and from one canal reference lake that is external to the Rideau Canal system (Otter L., September 2020). Using bathymetric maps, the recent cores were retrieved using a Glew (1989) gravity corer from approximately the same locations as the earlier paleolimnological studies (Fig. 1). The cores were sectioned on site using a Glew (1988) extruder at 0.25 cm intervals for the first 5 cm followed by 0.5 cm intervals for the remainder of the core.

Limnological data

Water samples were collected at a depth of ~0.5 m on the same day and location where the sediment cores were retrieved. Water samples were kept in coolers and sent to the National Lab for Environmental Testing (NLET) in Burlington (Ontario) for detailed water chemistry analysis including major ions, TP and total nitrogen (TN: total Kjeldahl nitrogen (TKN) plus NO_3-/NO_2-). Mass ratios of TIN:TP were calculated to examine whether lakes were nitrogen or phosphorus limited using the thresholds of Bergström (2010). TP and Secchi depth data collected by citizen volunteers as part of Ontario’s Lake Partner Program (LPP) and the Rideau Valley Conservation Authority (RVCA) from 2002 to 2020 were compared to archived limnological measurements taken between the ~1970s and ~1980s from the Ontario Ministry of the Environment, Conservation and Parks (Sarah Baxter (MECP), Jan. 10, 2022, *personal communication*). For Indian Lake, archival limnological data were excluded from the comparative analysis due to the unavailability of TP data prior to 2002 and Secchi depth measurements prior to 1996. Other limnological variables (*e.g.*, nitrogen) were only measured sporadically, and therefore the data were not sufficient for temporal analysis. Given that the available TP and Secchi depth data for the remaining five lakes were not continuous, these data were organized into two time periods that centered on the periods before and after cores were collected for the studies by Forrest *et al.* (2002) [Big Rideau L. (1998), Lower Rideau L. (1999), Otter L. (2000)] and Christie and Smol (1996) [Upper Rideau L. (1991)]. TP and Secchi depth measurements comprised 2-3 samples taken during May/June, July/August, and September/October for each available year of data. A one-way analysis of variance (ANOVA) was used to assess whether there were significant differences between the two time periods and between individual months, for both TP and Secchi depth.

^{210}Pb radioisotopic dating

To establish core chronologies, 15-25 intervals were strategically selected from each sediment core and analysed for ^{210}Pb and ^{137}Cs activities using gamma spectrometry, following the methods outlined by Schelske *et al.* (1994). Core chronologies were based on unsupported concentrations of ^{210}Pb using ^{214}Pb as a proxy for background (supported) activities, and the constant rate of supply (CRS) model (Appleby, 2001) using ScienTissiME (http://www.scientissime.net/software). Trends in ^{137}Cs activities were examined as a potential independent chronological marker to corroborate ^{210}Pb dates. Dates for sediment intervals within the unsupported ^{210}Pb archive that were not examined with gamma spectroscopy were approximated through linear interpolation, whereas dates of interest beyond background ^{210}Pb concentrations (*e.g.*, canal construction) were extrapolated using third-order polynomial models (viewed cautiously as associated errors may be high).

Meteorological data

The long-term trends in regional mean annual air temperature (MAAT) and mean annual wind speed (MAWS) were examined using Environment Canada and Climate Change (ECCC) adjusted and homogenized climate data (Vincent *et al.,* 2020). Highly correlated MAAT (r = 0.96; p<0.001) data from two climate stations (ECCC, ID: 6104142, 6104725) (with climate records of at least 45 years) within ~50 km of the central area of the Rideau Lakes region (44°44 N, 76°14 W) were used to construct a composite temperature record by calculating the average temperature for each year of available data resulting in a 148-year record (from 1873 to 2021). There was a seven-year hiatus in the MAAT observations corresponding to World War II (1939-1945), as well as a six-year gap during the 1970s (1971-1976). These missing data were filled in using highly correlated temperature data from the nearby Brockville (ECCC, ID: 6100969, r = 0.82; p<0.001) and Hartington IHD (ECCC, ID: 6103367, r = 0.81; p<0.001) climate stations. MAWS data were only available from one climate station (ECCC, ID: 6104146; from 1969 to 2014) that was located within a ~50 km radius of all study lakes (*i.e.*, Kingston). A 30-year mean (1970-2000) of both the temperature and wind speed records were used as points of reference for comparison of overall trends through time. To highlight trends in MAAT and MAWS, locally estimated scatterplot smoothing (LOESS) with a span of 0.8 was applied to both temperature and wind speed data. A Mann-Kendall (MK) test was applied to the climate data to determine the significance of long-term monotonic trends using the “mk.test” function from the “Kendall” package (McLeod, 2016). MAAT data were standardized as Z-scores to facilitate comparison with PC1 sample scores, as presented in the Supplementary Figs.

VRS chlorophyll-*a* analyses

Visible reflectance spectroscopy-inferred chlorophyll-*a* (VRS-Chla), which incorporates its isomers and main diagenetic products, was used to assess trends in whole lake primary production following the methods described by Michelutti *et al.* (2010) and Wolfe *et al.* (2006) and reviewed in Michelutti and Smol (2016). A small amount of freeze-dried sediment collected from each interval across all sediment cores were sieved through a 125 µm mesh (to prevent the influence of particle size) and placed in glass cuvettes. Samples were then processed with a

Model 6500 series Rapid Content Analyzer (FOSS NIRSystems, Inc.) and the spectral absorbances of wavelengths between 650 and 700 nm were analyzed to infer changes in chlorophyll-*a* concentrations based on the updated algorithm originally published in Michelutti *et al*. (2010). Specifically, sediment chlorophyll-*a* concentrations were inferred using log transformed data from Michelutti *et al*. (2010) with the equation: Chlorophyll-*a* + derivatives = EXP(0.83784*LN(peak area 650-700 nm) + (-2.48861)). VRS-Chla data were standardized as Z-scores, with each record normalized to a mean of zero and a standard deviation of one.

Diatom analyses

Diatom samples were prepared for analyses using methods outlined in Rühland and Smol (2002) as a general guide. For each sediment core, approximately 18-22 sediment intervals were analysed for diatoms, with particular attention to the post-1995 assemblages. A minimum of 350 diatom valves were enumerated per sedimentary interval and were identified to the lowest taxonomic level possible (often to variety) using primarily Krammer and Lange-Bertalot (1986-1991), Camburn and Charles (2000), and the Diatoms of North America online source (Spaulding *et al.,* 2019) as the main taxonomic guides and AlgaeBase for currently accepted taxonomic names. The diatom data are presented as percent relative abundances of the total number of valves counted for each sedimentary interval. An index of chrysophyte cysts (C) to diatom valves (D) was also calculated for each interval and expressed as a percentage using the formula C:D% = (# of cysts / (# of cysts + # of diatom valves)) x 100 (Cumming *et al.,* 1993). For comparison purposes, it is important to note that the planktonic diatom grouping applied in the Karst and Smol (2000) and the Forrest *et al*. (2002) study included *Aulacoseira* Thwaites taxa; this grouping was not applied in the Christie and Smol (1996) study. Considering the ecophysiological differences between heavier, large-celled *Aulacoseira* taxa and other planktonic taxa (Rühland *et al*., 2015), we treated *Aulacoseira* taxa as a separate group in this study.

The relative abundances of the most common diatom taxa (2.5% relative abundance in at least two intervals) were displayed stratigraphically using the C2 program and were ordered from left to right based on the species scores of a canonical correspondence analysis (CCA) constrained to sample depth (Janssen and Birks, 1994). Diatom stratigraphic zones were identified using constrained incremental sum of squares (CONISS) (Grimm, 1991) using the 'rioja' package (Juggins, 2017). The number of important stratigraphical zones was identified by broken stick analyses (Bennett, 1996) using the 'vegan' package (Oksanen *et al*., 2015). To simplify the graphical display and highlight diatom trends, selected taxa were grouped together if they were from the same genera and/or displayed similar trends over time (see Supplementary Materials). However, all statistical analyses were performed on the ungrouped diatom data, and diatom taxa that occurred in greater than 1% relative abundance in at least two sedimentary intervals were included in these analyses.

To enable comparisons in the timing and magnitude of change across all records, the major patterns of variation in the diatom assemblages from each sediment core were summarized with principal component analysis (PCA) axis one (PC1) and axis 2 (PC2) sample scores, using the 'vegan' package in R (Oksanen *et al.,* 2015). Prior to analysis, diatom relative abundances were square root transformed to downweight the influence of dominant taxa. The effective number of taxa was also calculated to examine changes over time in the Hill's N2 diversity index (Hill, 1973), where N2 is the number of "very abundant" taxa in a sample (Birks, 2012).

The relationships between diatom trends (*i.e.*, PC1 and PC2 sample scores, benthic fragilarioid sum, planktonic sum, *Aulacoseira* sum, Hill's N2), VRS-Chla and regional instrumental records (MAAT and MAWS) were assessed with a Spearman rank correlation analysis using the "Hmisc" package (R Core Team, 2015; Harrell, 2019). To match the temporal resolution between the paleolimnological and instrumental data, air temperature and wind speed data were averaged to match the period of accumulation for each sedimentary interval based on ^{210}Pb dates (Sorvari *et al*., 2002; Rühland *et al.,* 2013; Hadley *et al.,* 2019).

RESULTS

Limnological data

The direction of change in water quality measurement between archival data (~1975-1995) and recent data (~1996-2020) were generally consistent across all study lakes (Fig. 2: note that archival data do not exist for Indian Lake), including shallow L. Opinicon (presented in Fig. 2 of Balasubramaniam *et al*., 2023). TP concentrations were significantly higher ($p<0.05$) in the archival time period across all months in Big Rideau L. and Lower Rideau L., and two of the three months for Upper Rideau L. and Otter L., whereas Secchi depth measurements were significantly lower ($p<0.001$) across all months in Big Rideau L., Lower Rideau L., and Otter L., and for May/June in Upper Rideau L. (Fig. 2). Mass ratios of TIN:TP ranged from 3.0 to 7.1 (Tab. 1), suggesting that all but one of the study lakes are phosphorus-limited (*i.e.*, DIN:TP > 3.4; Bergström 2010), where the TIN:TP ratio in L. Opinicon (3.0) suggests N and P co-limitation.

^{210}Pb radioisotopic dating

Graphical displays of the ^{210}Pb dating results including gamma activity profiles, age-depth plots (with associated errors) and sediment accumulation rates for the five sediment cores are reported in *Fig. S1*, and for L. Opinicon in Balasubramaniam *et al*. (2023). 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 (*Fig. S1a-b, e*), whereas the upper few centimeters in Lower Rideau L. and Upper Rideau L. had more vertical profiles, before following a typical exponential decay with depth (*Fig. S1c-d*). Using the Binford Rule (Binford, 1990) option available in the ScienTissiME program, equilibrium depth was reached at 13.25 cm (CRS date: 1892.9±18.9), 15.25 cm (CRS date: 1894.5±15.4), 34.25 cm (CRS date: 1927.27±15.7), 22.25 cm (CRS date: 1876.9±17.6), and 23.25 cm (CRS date: 1851.3±16.8) for Big Rideau L., Indian L., Lower Rideau L., Upper Rideau L., and Otter L., respectively.

Instrumental climate records

MAAT within the Rideau Lakes region (composite data from nearby climate stations) increased significantly (Mann-Kendall

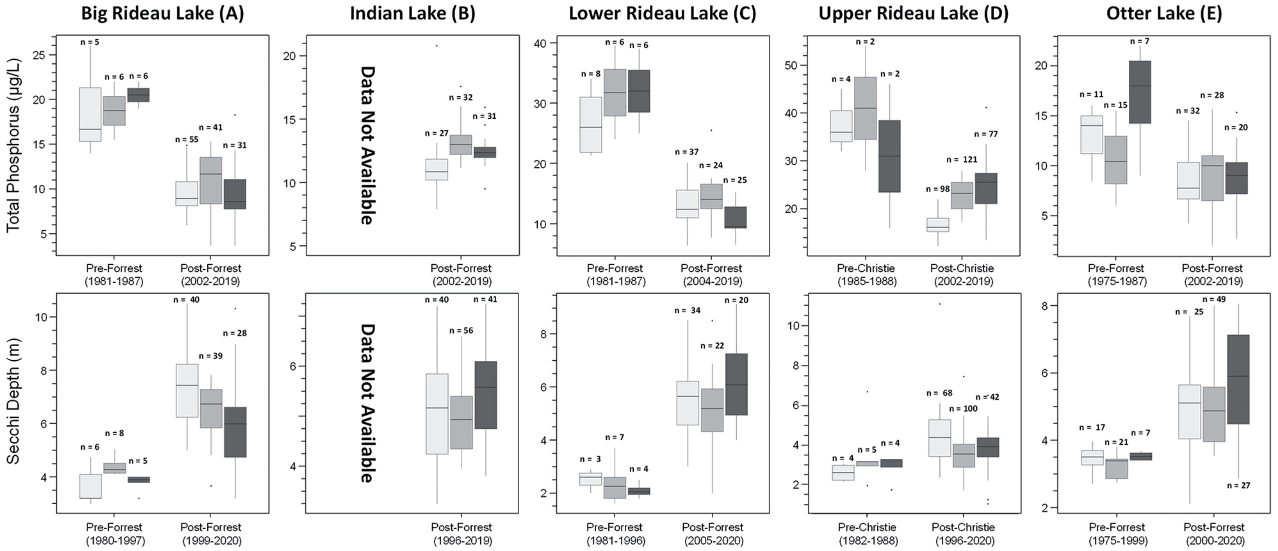

Fig. 2. Box and whisker plots comparing total phosphorus (TP) concentrations and Secchi depths between two time periods [before and after the previously published records in Christie and Smol (1996), Karst and Smol (2000) and Forrest *et al.* (2002)] for Big Rideau L. (A), Indian L. (B), Lower Rideau L. (C), Upper Rideau L. (D), and Otter L. (canal reference lake) (E). Note that TP and Secchi depth data for Indian Lake were not available for the earlier time period. The horizontal lines within the box and whisker plots represent the median values, and the vertical lines depict the range for the months of May/June, July/August, and September/October.

test, $p<0.001$), with an increase of ~1.97°C over the past 148 years (1873-2021) (Fig. 3a). By the end of the 1930s, MAAT increased above the 30-year mean (1970-2000) and remained relatively steady until the 1990s. Temperatures notably increased thereafter, particularly from the mid-2000s to present day when temperatures were the highest on record (Fig. 3a). MAWS was variable but showed a significant declining trend over the 46-year (1969-2014) record (Mann-Kendall test, $p<0.01$), with an overall decline of 2.15 km/h (Fig. 3b).

Diatom assemblage trends

Big Rideau Lake

In Big Rideau Lake, CONISS clustering analysis identified four biostratigraphical zones of which three were deemed significant by a broken stick model (Fig. 4a). Zones 1A and 1B (pre-industrial era to ca. 1925) were dominated by benthic fragilarioid taxa (*i.e.*, *Staurosirella pinnata* (Ehrenberg) D.M. Williams and Round, *Pseudostaurosira brevistriata* (Grunow) D.M. Williams and Round, *Staurosira construens* Ehrenberg). The transition from Zone 1A to Zone 1B is characterized by a decrease in the relative abundance of *P. brevistriata* and a concurrent increase in the relative abundance of *Aulacoseira subarctica* (O. Müller) E.Y. Haworth, coinciding with the period of canal construction (1827-1832). In Zone 2 (ca. 1925 to ca. 2005), there was a pronounced diatom shift with the relative abundances of *A. subarctica*, *Fragilaria crotonensis* Kitton and the *Pantocsekiella* group becoming prominent in the assemblage for the first time in the sediment record (Fig. 4a). Concurrently, previously abundant *S. pinnata*, *P. brevistriata*, *S. construens*, and the *Navicula sensu lato* (*s.l.*) group declined markedly. Zone 3 (ca. 2005 to ca. 2020) was

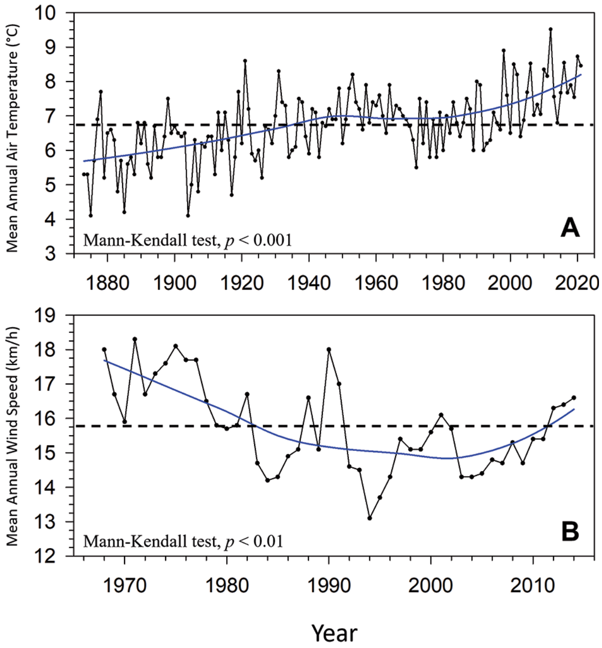

Fig. 3. Mean annual air temperature (MAAT) from 1873 to 2021 (A) and mean annual wind speed (MAWS) from 1968 to 2014 (B) recorded at climate stations within a ~50 km radius of the central area of the Rideau Lakes region (ECCC station ID: MAAT - 61041412, 6104725, 6100969, 6103367; MAWS - 6104146). A LOESS smoother (span=0.8) was applied to improve trend visualization (blue lines) and the horizontal dashed lines represent the 1970-2000 averages of MAAT and MAWS.

characterized by notable increases in the relative abundances of a suite of epiphytic diatoms including *Diploneis, Cocconeis*, *Achnanthes* (*s.l.*), and *Amphora* taxa. Similarly, indicators of increased lake nutrient availability, including small-celled planktonic *Stephanodiscus parvus* Stoermer and Håkansson (eutrophic) and elongate *F. crotonensis* (meso-eutrophic), increased abruptly in Zone 3. Concurrent with these increases, *A. subarctica* and the *Pantocsekiella* group abruptly declined. The C:D index generally displayed consistent values of 8-10% throughout the majority of the sediment record (Fig. 4a).

Indian Lake

CONISS clustering analysis and the broken stick model identified three significant biostratigraphical zones for the Indian Lake record (Fig. 4b). Zone 1 (pre-industrial era to ca. 1860) was characterized by the co-dominance of *A. subarctica*, *Aulacoseira ambigua* (Grunow) Simonsen, elongate planktonic taxa, [*F. crotonensis*, *Tabellaria flocculosa* (Roth) Kützing str. III (*sensu* Koppen 1975)] along with benthic fragilarioid taxa (*S. pinnata*, *S. construens*, and *P. brevistriata*) (Fig. 4b). The transition to Zone 2 (ca. 1860 to ca. 2010) was marked by a notable decline in the relative abundances of all benthic fragilarioid taxa, fluctuations in *F. crotonensis*, and the rise of the centric planktonic *Pantocsekiella* group for the first time above trace relative abundances in the record, while tychoplanktonic *Aulacoseira* taxa continued to dominate (Fig. 4b). The transition to Zone 3 (ca. 2010) marks the largest diatom compositional change within the record with a pronounced shift to planktonic diatom taxa dominance including increases in the relative abundances of *F. crotonensis*, the *Pantocsekiella* group, and *T. flocculosa* str. III and concurrent declines in *A. subarctica* and *A. ambigua* (Fig. 4b). The C:D index was at its highest near the bottom of the core and remained generally stable for the majority of the core aside from two peaks observed at the transition from Zone 2 to Zone 3 (Fig. 4b).

Lower Rideau Lake

In Lower Rideau Lake, CONISS clustering analysis and the broken stick model identified three significant biostratigraphical zones (Fig. 4c). Assemblages in Zone 1 (pre-industrial era to ca. 1850) were dominated by both benthic fragilarioid (*P. brevistriata*, *S. construens*, and *S. pinnata*) and, to a lesser extent, *Aulacoseira* taxa (*Aulacoseira granulata* (Ehrenberg) Simonsen, *A. ambigua*) (Fig. 4c). Zone 2 (ca. 1850 to ca. 1975) was characterized by a marked increase in *A. granulata* and *A. ambigua* relative abundances that corresponds well with the construction of the Rideau Canal (1827-1832). Benthic fragilarioid taxa continued to dominate the assemblage, although collectively their relative abundances slightly declined from Zone 1 to Zone 2. Albeit in trace relative abundances, *F. crotonensis* and the *P. comensis*/*ocellata* group were observed for the first time in Zone 2 (Fig. 4c). In Zone 3 (ca. 1975 to ca. 2020), the diatom assemblage underwent a marked shift in composition where planktonic taxa (*F. crotonensis*, *P. comensis*/*ocellata* group) became prominent for the first time in the record. Concurrently, epiphytic *C. placentula* and *Staurosira venter* (Ehrenberg) Cleve and J.D. Möller became increasingly prominent (Fig. 4c). The relative abundances of *A. granulata* and *A. ambigua*, which were among the most abundant taxa in Zone 2, declined considerably at the transition between Zone 2 and Zone 3, while benthic fragilarioid taxa continued to be prominent members of the assemblage. The cyst:diatom (C:D) index gradually increased from the bottom of the core, peaking at the close of Zone 2, followed by a declining trend towards the surface intervals (Fig. 4c).

Upper Rideau Lake

In Upper Rideau Lake, CONISS clustering analysis identified four biostratigraphical zones of which two were deemed significant by the broken stick model (Fig. 4d). Of the five diatom profiles studied, Upper Rideau L. was the only record where planktonic diatoms were not registered above trace relative abundances. Benthic fragilarioid taxa dominated the earlier portion of Zone 1 (pre-industrial era to ca. 1976), particularly *S. construens* and *S. pinnata*, with lower relative abundances of *P. brevistriata*. A short-lived increase in *A. granulata* occurred towards the end of Zone 1A, while the transition to Zone 1B was marked by an increase in the relative abundances of *A. granulata* and *Navicula s.l.* taxa, and a decline in *P. brevistriata* that approximately corresponded with the construction of the Rideau Canal (1827-1832). Zone 2 (ca. 1976 to ca. 2020) was characterized by an increase to dominance by *S. pinnata* with a concurrent decline in the previously dominant *S. construens*. *A. granulata* declined to near trace abundances while the *Navicula* (*s.l.*) group increased, reaching peak relative abundances ca. 1995. The transition to Zone 2B (ca. 2000) was characterized by the complete disappearance of *A. granulata* and a rise in *S. venter* and the *Achnanthes* (*s.l.*) group. The C:D index was low for most of the record aside from a slight increase within Zone 2 (Fig. 4d).

Otter Lake (canal reference lake)

In Otter Lake (outside of the Rideau Canal system), CONISS clustering analysis identified three biostratigraphical zones of which two were deemed significant by the broken stick model (Fig. 4e). Diatom assemblages in Zone 1A (ca. 1839 to ca. 1965) were co-dominated by *A. subarctica*, *A. ambigua* and *Stephanodiscus medius* Håkansson/*parvus* group. The transition to Zone 1B was marked by a notable increase in the relative abundances of the *P. comensis*/*gordonensis* group with a concurrent and gradual decline in *A. subarctica* and an abrupt decline in *T. flocculosa* str. III near the close of the zone. The most pronounced change in the record occurred at the transition from Zone 1B to Zone 2 (ca. 2007 to ca. 2020), marked by a shift to distinctly higher relative abundances of the *P. comensis/gordonensis* group and *F. crotonensis*, and an equally pronounced decline in previously dominant *A. subarctica* and *A. ambigua*. There was no consistent pattern observed in the C:D index, with peak values reached at both the bottom of the record and near the close of Zone 1B (ca. 2000), with the index fluctuating between ~15-30% for the majority of the record (Fig. 4e).

Summary and comparison of paleo proxy and climate trends

Response to canal construction

Diatom assemblage trends summarised using PCA sample scores (Fig. 5a-e), and as trends in the sums of planktonic, *Aulacoseira*, and benthic fragilarioid taxa (Fig. 6a-c), show varied responses to the impact of canal construction. In Big Rideau L. and shallow L. Opinicon, PC2 samples scores deviate notably from the zero line at around the time of canal construction (Fig. 5a-e), associated with declines in the relative abundances of benthic fragilarioid taxa and *A. ambigua*, respectively. However, the response to canal construction is clearer at the species-grouping level, where canal construction had notable impacts on all five diatom records (Fig. 6). In particular, canal construction coincided with a sharp shift in dominance from benthic fragilarioid taxa to *Aulacoseira* taxa in Big Rideau L., Indian L., Lower Rideau L., and Upper Rideau L., whereas in shallow L. Opinicon (Balasubramaniam *et al*., 2023), the opposite shift was observed (Fig. 6b,c). The number of "very abundant" taxa (Hill's N2 diversity) during the period of widespread catchment disturbance following canal construction varied across records, with minimal changes in Big Rideau L. and Upper Rideau L., an overall decline in Indian L. and L. Opinicon, and a general increase in Lower Rideau L. (*Fig. S2*).

Trends in VRS-Chla were comparable in Big Rideau L. and Indian L., where they gradually increased from the bottom of the sediment core until the period of canal construction (*Fig. S3*). In contrast, VRS-Chla in Lower Rideau L. and L. Opinicon showed a steady decline from the bottom of the core to ca. 1950s-1960s. In Upper Rideau L., VRS-Chla trends remained notably stable until the late-1980s, thereafter increasing sharply.

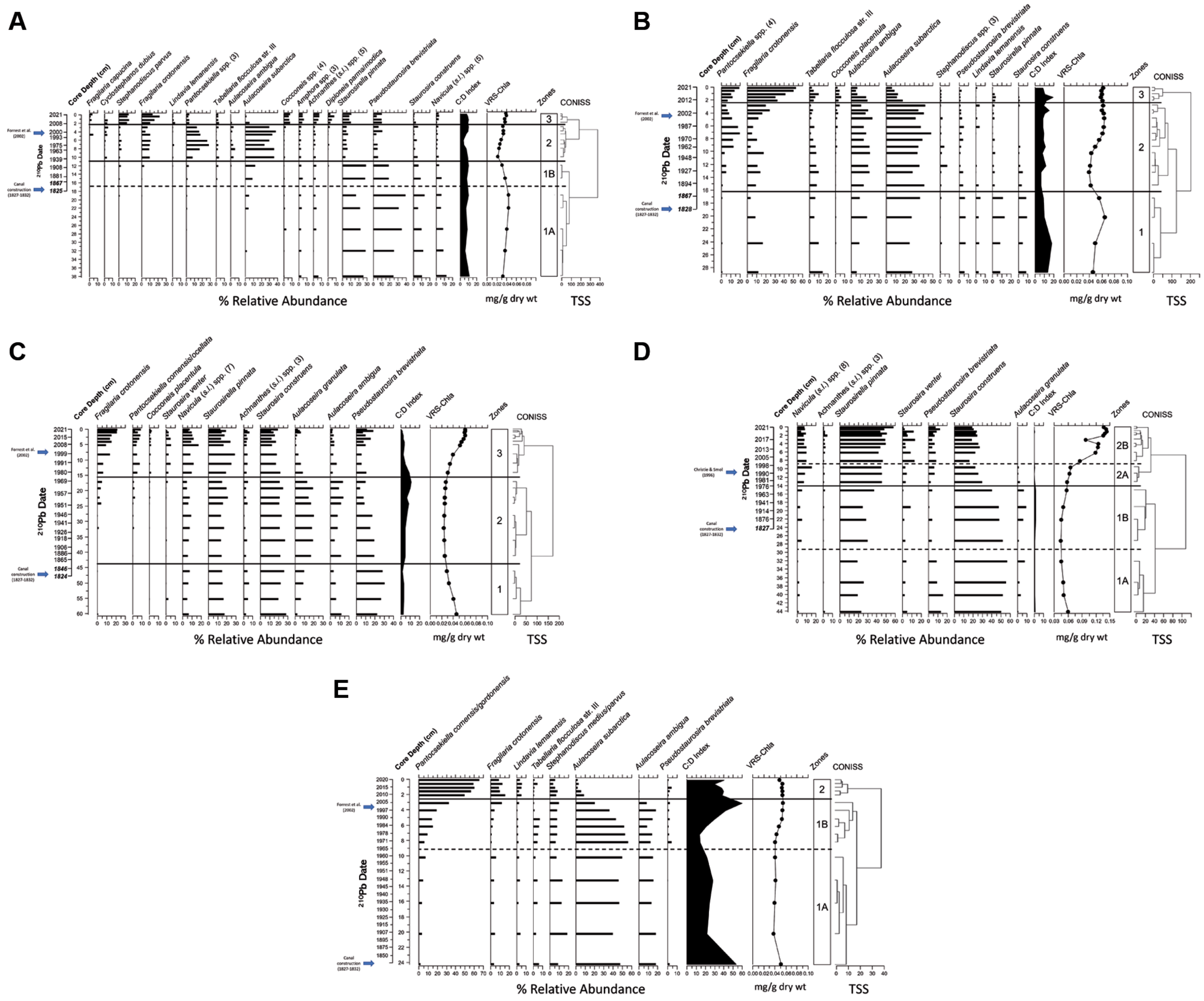

Fig. 4. Diatom stratigraphic profiles showing the percent relative abundances of the most common diatom taxa enumerated in the sediment cores from Big Rideau L. (A), Indian L. (B), Lower Rideau L. (C), Upper Rideau L. (D), and the canal reference lake, Otter L. (E). The figures are scaled by core depth with the corresponding CRS-estimated ^{210}Pb dates presented as a secondary axis. Diatom taxa were ordered from left to right based on canonical correspondence analysis (CCA) axis 1 species scores. Horizontal lines depict zones determined by constrained incremental sum of squares (CONISS), with the dendrogram displayed on the far right, where TSS is the total sum of squares. Dates in bold and italicized font represent extrapolated age estimates that correspond to the construction of the Rideau Canal (~1830); these early dates should be viewed with caution as the associated errors are potentially high. A ratio of chrysophyte cysts to diatom valves (C:D index) and trends in VRS-Chla concentrations are also displayed. Numbers in brackets following diatom names indicate the number of taxa in that grouping. Key historical dates (*e.g.*, canal construction, date of previous paleolimnological study) are highlighted with blue arrows.

Recent ecological changes: 1990s-2020s

The most pronounced diatom changes summarized by PC1 and PC2 sample scores were registered in the most recent decades (ca. 1980s to 2020) in all sediment cores including the canal reference, Otter L. (Fig. 5a-f). With the exception of Upper Rideau L. and Big Rideau L., this shift was characterized by a pronounced increase in the relative abundances of planktonic diatoms, often occurring for the first time in the sediment record, with a concurrent decline in *Aulacoseira* (Indian L., Lower Rideau L., Otter L.) and benthic taxa (L. Opinicon) (Fig. 6). The Upper Rideau L. diatom record deviated from this trend as planktonic taxa remained below trace abundances throughout the core, and this most recent diatom response was characterized by a sharp shift among benthic diatom taxa (Fig. 4d). Big Rideau L. also differed, in that the most recent (ca. 2005) compositional shift included a pronounced decline in the relative abundances of *Pantocsekiella* taxa and *A. subarctica* and an increase in planktonic *S. parvus* and *Cyclostephanos dubius* (Hustedt) Round together with a variety of epiphytic taxa (Fig. 4a). During this most recent period, Hill's N2 diversity notably increased in Big Rideau L., Lower Rideau L. and L. Opinicon but notably decreased in Indian L., with little change in Upper Rideau L. and Otter L. where the effective number of taxa were generally lower (*Fig. S2*).

Since the middle of the 20th century, VRS-Chla showed an increasing trend across most of the study lakes (*Fig. S3*), with further increases exceeding the mean (*i.e.*, Z-score = 0) in the post-1980s (Indian L., Otter L.) and post-2000 (Big Rideau L., Lower Rideau L., Upper Rideau L.) sediments. Although remaining above the mean of the record, VRS-Chla for Otter L. showed a moderate declining trend post-2000. VRS-Chla in L. Opinicon increased post-1960s but remained relatively stable and did not exceed the mean thereafter.

Comparisons between trends in diatom assemblage composition (PC1, PC2 sample scores) and composite regional MAAT data (as Z-scores) displayed significant correlations ($p<0.05$) in five of the six study lakes (*Tab. S1*, *Fig. S4*), which was notably strong for the canal reference, Otter L. (rho = 0.89, $p<0.001$: *Fig S4f*). VRS-Chla trends showed strong and significant correlations with regional MAAT trends for Big Rideau L., Upper Rideau L., Lower Rideau L., and Otter L. (*Tab. S1*). The cumulative relative abundances of planktonic and *Aulacoseira* species, as well as VRS-Chla displayed significant correlations in four of the six study lakes (*Tab. S1*). PC2 samples scores displayed significant correlations with MAAT in Big Rideau L., Upper Rideau L., whereas the benthic fragilarioid sum and Hill's N2 diversity were only significantly correlated to MAAT in Lower Rideau L. and Big Rideau L., respectively (*Tab. S1*).

DISCUSSION

The six lakes examined in our Rideau Canal system study have undergone notable diatom compositional changes in at least the past ~200 years. However, despite major catchment disturbances following canal construction (1827- 1832), the most ecologically significant shifts registered across all sediment cores occurred during the past three decades, evidenced through changes in diatom composition, diatom diversity, and trends in VRS-Chla. Based on an assessment of several potential environmental stressors (nutrient changes, zebra mussel invasion, climate change), we use a weight-of-evidence approach to explain this recent reorganization of diatom communities over the past few decades.

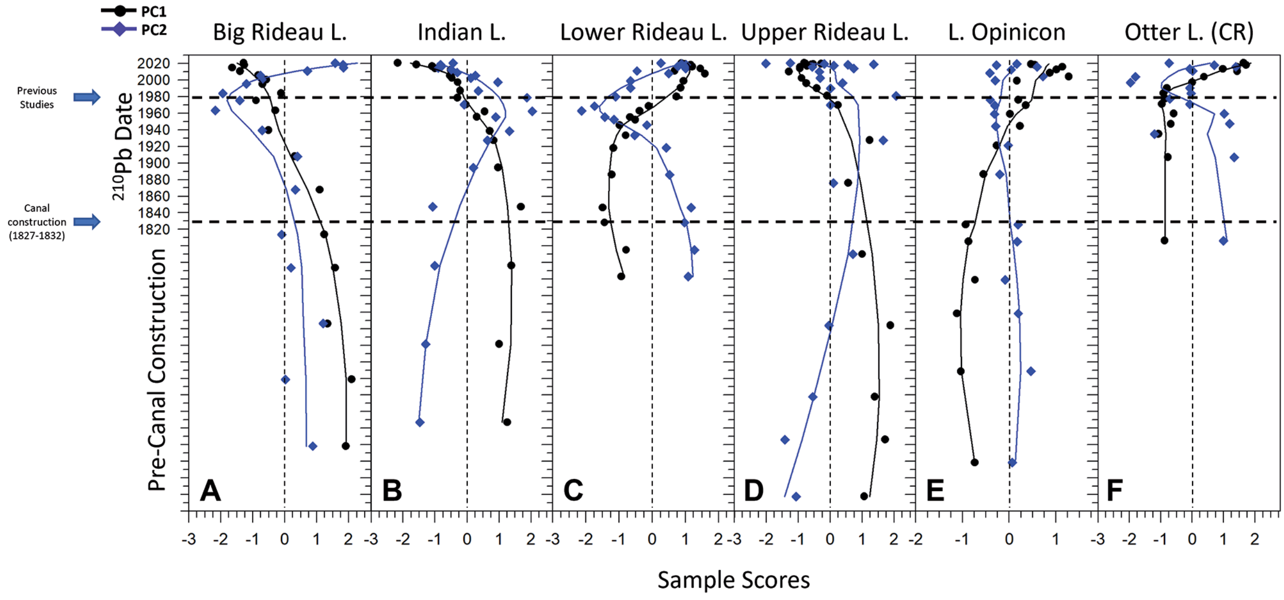

Fig. 5. Principal component analysis (PCA) axis one (black circles) and axis two (blue diamonds) samples scores scaled by CRS-estimated ^{210}Pb dates for Big Rideau L. (A), Indian L. (B), Lower Rideau L. (C), Upper Rideau L. (D), L. Opinicon (E), and Otter L. (F). Trends in PC1 (black line) and PC2 (blue line) sample scores were highlighted using LOESS with a span of 0.8. Key dates (*e.g.*, canal construction, previous paleolimnological studies) are highlighted with blue arrows. Dates in bold and italicized font represent extrapolated age estimates that correspond to the construction of the Rideau Canal (~1830); these dates are viewed with caution as the associated errors are potentially high. The arrow labeled "Previous Studies" represents the top of cores from previous studies/cores, where the position of the arrow and the associated dashed line represent an average of the corresponding years across these studies.

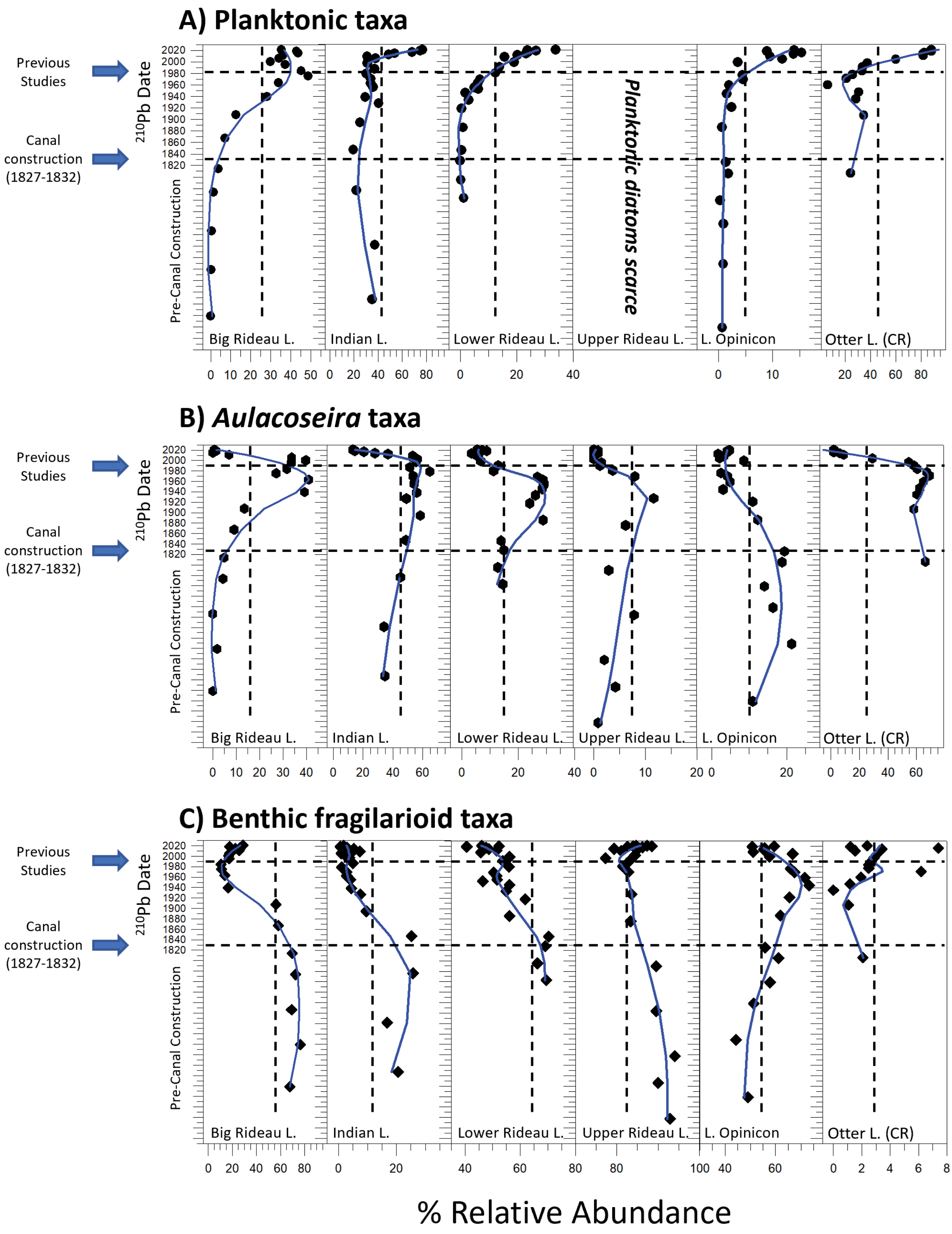

Fig. 6. Trends in the sum of A) planktonic, B) *Aulacoseira*, and C) benthic fragilarioid taxa plotted as % relative abundance and scaled by CRS-estimated ^{210}Pb dates for all study lakes. Trends in the planktonic diatom sum for Upper Rideau Lake are not included as planktonic diatoms were scarce in this record (MRA of entire record = 0.72%). Vertical dashed lines represent the mean % relative abundances over the span of the record. Trends were highlighted using LOESS with a span of 0.8 (blue solid lines). Key dates (*e.g.* canal construction and previous paleolimnological studies) are highlighted with blue arrows. Dates in bold and italicized font represent extrapolated age estimates that correspond to the construction of the Rideau Canal (~1830); these dates are viewed with caution as the associated errors are potentially high. The arrow labeled "Previous Studies" represents the top of cores from previous studies/cores, where the position of the arrow and the associated dashed line represent an average of the corresponding years across these studies.

Past lake conditions: pre-Rideau Canal construction

Prior to the construction of the Rideau Canal, the pre-disturbance diatom assemblages across all study lakes were dominated by a diverse group of benthic fragilarioid and heavily silicified *Aulacoseira* taxa (Figs. 4 and 6). Benthic fragilarioid taxa are opportunistic generalists as they have a wide range of ecological tolerances and can live in a variety of limnological conditions, often outcompeting other diatom taxa when conditions are relatively inhospitable (*e.g.*, low light availability, shorter growing seasons) (Smol and Douglas, 2007). High abundances of these taxa during this early period were notable in Big Rideau L., Indian L., Lower Rideau L., Upper Rideau L., and L. Opinicon (Figs. 4 a-d and 6c; Balasubramaniam *et al*., 2023), which likely reflects colder conditions with longer periods of ice cover and shorter growing seasons (Lotter and Bigler, 2000; Douglas and Smol, 2010; Rühland *et al.*, 2015). High relative abundances of *Aulacoseira* taxa in the pre-disturbance assemblages of most of our records are likely indicative of strong water column mixing that helps these heavily-silicified taxa maintain a competitive position within the photic zone (Padisák *et al*., 2003; Ptacnik *et al*., 2003). The *Aulacoseira* taxa common to our study lakes are often associated with mesotrophic conditions but are found across a range of TP concentrations (optima range from 8.8 µg/L - 25.7 µg/L; Reavie and Smol, 2001; see Supplementary Material; Cumming *et al*., 2015; Duda *et al*., 2023). Planktonic diatoms were scarce during this early period, but the occurrence of taxa indicative of moderate TP concentrations, such as *F. crotonensis* (9.6-18 µg/L; see Supplementary Material; Reavie and Smol, 2001; Cumming *et al*., 2015; Duda *et al*., 2023) and *S. medius*/*parvus* (16 - 28 µg/L; see Supplementary Material; Reavie and Smol, 2001; Cumming *et al*., 2015) in Indian L. and Otter L., respectively, also suggest somewhat naturally productive conditions. Collectively, the pre-disturbance diatom assemblages suggest that these lakes were relatively productive, well-mixed and experienced longer periods of ice cover, in agreement with previous paleolimnological studies (Christie and Smol, 1996: Karst and Smol, 2000; Forrest *et al*., 2002).

Past lake conditions: post-Rideau Canal (1827-1832) to ~1990

With canal construction, regions along the Rideau Canal system were flooded to create navigable depths for steamboat transport, resulting in a water level increase of ~2-3 m in several nearby lakes and rivers (Forrest *et al*., 2002). Extensive flooding and the submergence of terrestrial ecosystems can mobilize bioavailable nutrients, which contribute to increased nutrient inputs to freshwater systems (Jayarathne *et al*., 2016). In addition, the procurement of timber for canal construction led to widespread deforestation and promoted settlement, agriculture, and industrial activities, further intensifying land clearance (Christie and Smol, 1996; Karst and Smol, 2000; Forrest *et al*., 2002). Forest clearance is considered one of the key drivers of soil erosion (Boardman and Poesen, 2006), often a contributing factor to increased nutrient run-off. In addition, extreme hydrological events such as flooding during the period of canal construction may have temporarily increased flushing rate (Talbot *et al*., 2018). The various effects of canal construction on our impacted lakes were clearly registered in the diatom records. For example, an increase in the relative abundances of *A. ambigua*, *A. granulata*, and *A. subarctica* (most notably in Indian L. and Lower Rideau L.) is consistent with increased nutrient inputs and/or a well-mixed water column during this period of severe catchment disturbance. In one of our impacted lakes (Indian L.), *Stephanodiscus* taxa also became prevalent at this time, in agreement with higher nutrient inputs. These diatom compositional changes are similar to changes reported in earlier paleolimnological studies from these lakes that also concluded that the effects of flooding and canal construction led to moderately higher nutrients (Christie and Smol, 1996; Karst and Smol, 2000; Forrest *et al*., 2002). However, in shallow, macrophyte-dominated L. Opinicon, flooding resulted in considerable expansion of the littoral zone (Karst and Smol, 2000), evidenced by marked declines in the relative abundance of *Aulacoseira* taxa and increases in benthic diatom taxa (Balasubramaniam *et al*., 2023).

Although the Big Rideau L. diatom record registered an increase in the relative abundance of *A. subarctica* together with declines in benthic *P. brevistriata* during this period of major watershed disturbances, this shift was relatively minor compared to the other study lakes, likely a result of its high volume contributing to a dilution effect on incoming nutrient inputs (Forrest *et al*., 2002). Larger, deeper lakes often possess greater chemical resistance due to dilution in comparison to smaller, shallower lakes, so that a lake's ability to resist chemical perturbations can be influenced by a lake's volume. Similar dilution effects have been reported in other studies of larger, deeper lakes in Ontario in response to increased nutrient inputs (Nelligan *et al*., 2016; Paterson *et al*., 2017). Big Rideau L. also recorded shifts that were distinct from the other impacted lakes. For example, a pronounced mid-20th century compositional shift from benthic diatom dominance to higher relative abundances of a variety of more open water taxa (*A. subarctica*, *Pantocsekiella* taxa, *F. crotonensis*) overshadowed the response to canal construction (Fig. 4a), suggesting significant limnological diatom habitat changes. To date, there is no clear indication of what environmental changes would have triggered this interesting compositional shift in Big Rideau L.

The relative abundances of benthic fragilarioid taxa generally declined across the study lakes following canal construction (Fig. 6c), likely because of the physical consequences associated with extensive flooding. As expected, shallow L. Opinicon was a clear exception to this trend (Fig. 6c) as flooding doubled its length and expanded its already extensive macrophyte-dominated littoral zone (discussed in Balasubramaniam *et al.,* 2023), thereby offering additional habitat for benthic species (Karst and Smol, 2000). In the deeper study lakes, the displacement of benthic fragilarioid taxa through flooding could perhaps be explained by the direct removal of algae due to shear stress associated with increased water velocity, or by the mobilization of lakebed sediments leading to algal abrasion (Bona *et al*., 2012) and increased total suspended solids (TSS). Considering the extent at which flooding had taken place during canal construction, the physical removal of bottom-dwelling taxa may be a likely explanation for the decrease in benthic fragilarioid taxa observed in the impacted lakes. In general, TSS would also increase in aquatic systems following a flooding event, as these high-flow events transport large amounts of suspended sediment and debris (Talbot *et al*., 2018). An increase in TSS would also reduce light penetration deeper within the water column, negatively affecting the environment for bottom-dwelling benthic taxa, potentially contributing to the observed decline in our sediment records.

Lakes that were impacted by flooding during canal construction would be expected to experience increased flushing rates that may affect whole lake primary production. Declines in VRS-Chla were notable in Big Rideau L., Indian L., L. Opinicon, while trends in the remaining lakes were relatively stable or continued a declining trend that began prior to the onset of canal construction (*Fig. S3*). The impact of increased flushing rates has been associated with a reduction in algal biomass in other lake systems (*i.e.*, a dilution effect) (Peierls *et al*., 2012). Furthermore, an increase in primary production requires sufficient light penetration within the water column, where the previously mentioned increase in TSS likely hindered light penetration (Talbot *et al*., 2018). Thus, the combination of increased flushing rates and TSS may explain the declining trend in VRS-Chla concentrations in some of our sediment records.

Recent lake conditions: ~1990-2020

Although there was variability across records, increases in the relative abundances of planktonic diatom taxa, particularly since the ~1990s, were generally concurrent with marked declines in *Aulacoseira* and/or benthic fragilarioid taxa (Figs. 4a-c,e and 6). However, diatom compositional shifts in response to post-1990s environmental stressors in Big Rideau L. included the distinct arrival of a variety of epiphytic diatom taxa, whereas in Upper Rideau L., compositional shifts occurred among a variety of benthic diatom taxa as planktonic taxa were not observed at any point in the sediment record. Much like shallow L. Opinicon (Balasubramaniam *et al*., 2023), a considerable portion of Upper Rideau L. is littoral (53%) (MECP, unpublished data) despite being a relatively deep lake. Following canal construction, the already extensive littoral zone of Upper Rideau L. had likely expanded due to extensive flooding (Christie and Smol, 1996) and may be a plausible factor for the continued lack of planktonic taxa post-1995. The diatom changes observed in the past few decades in our study lakes showed a general continuation of the most recent trends reported in the earlier paleolimnological records (Christie and Smol, 1996; Karst and Smol, 2000; Forrest *et al*., 2002) but are now much more pronounced. The potential environmental drivers for these most recent diatom compositions shifts will be discussed below.

Can nutrient changes help explain the recent shift in diatom composition?

Currently, the six study lakes are oligotrophic to mesotrophic with TP concentrations (September 2020) ranging from 8 to 13 µg/L (Tab. 1), and TIN:TP ratios suggest that most of lakes are P-limited. The significant decline in TP concentrations observed during the past ~50 years (Fig. 2, see Balasubramaniam *et al*., 2023 for L. Opinicon) was likely associated with reductions in agricultural activities in the watershed since the 1950s (Warren, 1997), reduced use of phosphate-based detergents (McGucken, 1989), improved soil nutrient retention of secondary growth forests, as well as improvements in residential septic systems (Forrest *et al*., 2002). The recent shift from *Aulacoseira* and/or benthic fragilarioid taxa to higher relative abundances of planktonic diatoms (Big Rideau and Upper Rideau lakes were exceptions) included small *Pantocsekiella* taxa that are commonly found in relatively low nutrient lakes (Hadley *et al*., 2013), as well as *F. crotonensis* (Figs. 4 and 6a). *F. crotonensis* is often considered a sign of potential nutrient enrichment (Walker, 1993) and in many calibration studies is reported to prefer mesotrophic conditions (17.6 - 18 µg/L; Reavie *et al*., 1995; Cumming *et al*., 2015). However, in a set of 450 relatively low nutrient lakes in Ontario (Duda *et al*., 2023), *F. crotonensis* was one of the most common taxa (n=224; max=46.1%) with a somewhat lower TP optimum of 9.6 µg/L. Moreover, recent increases in the relative abundances of *F. crotonensis* have been reported in diatom records from mesotrophic Ontario lakes experiencing declines in TP (Rühland *et al*., 2010; Hawryshyn *et al*., 2012). The continued prominence of *F. crotonensis* in these P-limited lakes, during periods of significant decline in TP, supports the observation that this taxon may have a broad range of TP requirements (Rimet *et al*., 2009).

Although it is clear from available monitoring data that our study lakes have experienced significant declines in TP concentrations over the past few decades (Fig. 2), the recent decrease in the relative abundances of *Aulacoseira* and/or benthic fragilarioid taxa with concurrent increases in planktonic diatoms reflects an ecologically important shift in diatom life strategy that cannot be entirely explained by a decline in nutrients. For example, in hundreds of Ontario lakes with TP concentrations similar to our lakes (Duda *et al*., 2023), *A. subarctica* and *A. ambigua* were some of the most common (n=232 and 346, respectively) and abundant (maximum occurrence = 36% and 59%, respectively) taxa observed, with TP optima (8.8 µg/L and 9.4 µg/L, respectively) that, from a strictly trophic status perspective, would be ideally suited to thrive in our study lakes. The small *Pantocsekiella* taxa that increased in the past few decades in Indian L., Lower Rideau L., and Otter L., are also commonly observed in oligotrophic to mesotrophic lakes throughout Ontario (Werner *et al*., 2005; Rühland *et al*., 2010; Hawryshyn *et al*., 2012; Hadley *et al*., 2013; Duda *et al*., 2023). This suggests that increases in a variety of planktonic diatoms and the decline in *Aulacoseira* taxa during the past ~30 years is unlikely to be strictly a function of nutrient changes.

Can the invasion of zebra mussels help explain the recent shift in diatom composition?

Zebra mussels (*Dreissena polymorpha*) were first reported in the Rideau Canal system in the early- to mid-1990s, likely introduced via small recreational boats according to both unpublished and published reports (Watson, 2000). A 26-year monitoring record of zebra mussels on the Rideau River indicated that peak abundances were observed between 2001 to 2005, with declining numbers thereafter (Martel and Madill, 2018). Zebra mussels are efficient filter feeders that can affect the amount and quality of primary production within aquatic systems and are associated with increased water clarity and considerable declines in phytoplankton abundances (Strayer, 2010). Initial increases in the relative abundances of *Pantocsekiella* taxa from ca. 1970 to ca. 1980 observed in the Otter L., Indian L., and Lower Rideau L. sediment records clearly pre-date the arrival of zebra mussels. These changes were also reported in earlier paleolimnological records retrieved several decades prior to the invasion of these dreissenid mussels (Forrest *et al*., 2002). Additionally, relatively small, pelagic diatoms would be the most susceptible to grazing by zebra mussels (Naddafi *et al*., 2007), but these are the very taxa that increased the most following their introduction. The increase in elongate planktonic *F.*

crotonensis is also counter to what would be expected, as this is a low-light adapted taxon (Hartig and Wallen, 1986) that has generally been observed to decline with zebra mussel invasions (Fishman *et al*., 2010). Therefore, recent increases in planktonic *Pantocsekiella* taxa and *F. crotonensis* could not have been triggered by the arrival of zebra mussels and associated changes in lake properties.

An increase in light penetration with the invasion of zebra mussels, however, can promote increased macrophyte growth, thereby providing new habitats suitable for epiphytic diatoms (Zhu *et al*., 2006). Big Rideau L. registered an interesting shift in diatom composition within the time frame of the zebra mussel invasion that is distinct from the other sediment records. Since the early-2000s, a variety of epiphytic diatom taxa became prominent for the first time in the sediment record (Fig. 4a), consistent with deeper Secchi depth readings since 1999 (Fig. 2a). The pronounced decline in both *Pantocsekiella* taxa and *A. subarctica* concurrent with the recent increase in epiphytic diatom taxa suggests that in the past ~10-15 years, macrophyte beds in Big Rideau L. may be more prominent than in the past. Although not as pronounced a change as observed in Big Rideau L., the shift among benthic fragilarioid taxa observed in Upper Rideau L. starting in the late-1990s also occurs at approximately the same time as the arrival of zebra mussels (Figs. 4d and 6c) and a deepening of Secchi depth (Fig. 2d). Although zebra mussel monitoring data within the Rideau Canal system are relatively scarce, peak mussel abundances in the Rideau River (Martel and Madill, 2018) occurred during approximately the same period as the recent diatom shifts recorded in the Big Rideau and Upper Rideau sediment records. However, despite sharp declines in zebra mussel abundance in the Rideau Lakes over recent years, epiphytic and benthic taxa continue to dominate the diatom assemblages of these lakes, suggesting that zebra mussels played a limited role (if any) in affecting recent changes in diatom assemblage composition.

Can regional climate warming help explain the recent shift in diatom composition?

Regional climate change can be a potential trigger for the most recent diatom compositional shifts observed in our Rideau lakes sediment records, and in association with recent reports of cyanobacterial blooms in Lower Rideau, Upper Rideau, and Indian lakes. For example, increases in air temperature, longer ice-free periods and declines in wind speed can lead to fundamental changes in lake water properties and resource availability that can, in turn, have substantial indirect effects on diatom assemblage composition (Rühland *et al*., 2008, 2015), and promote the proliferation of bloom forming cyanobacteria (Paerl and Huisman, 2008; Favot *et al.* 2019, 2024). These climate-mediated changes in limnological conditions include a longer growing season (Futter, 2003), with earlier and longer summer stratified periods (Stainsby *et al*., 2011; Woolway *et al.,* 2022), declines in the duration/strength of water column mixing (Elçi, 2008), and attendant changes in light and nutrient availability (Winder and Sommer, 2012). This is consistent with limited monitoring data for the Rideau Lakes region, where water column measurements and lake ice observations for L. Opinicon from 1984 to 2010 indicate longer and stronger periods of thermal stratification and a decline in the duration of ice cover by ~12.7 days over this period (Conboy and English, 2010; Balasubramaniam *et al*., 2023). Compared to larger and heavier diatoms, these conditions often favour small, centric (*e.g.*, *P. comensis*, *P. ocellata*) and elongate planktonic taxa (*e.g.*, *F. crotonensis*) whose high surface-area to volume ratios reduce sinking velocities (Padisák *et al*., 2003), enable more efficient nutrient uptake (Behrenfeld, 2021) and light harvesting (Round *et al*., 1990; Ptacnik *et al*., 2003). With warming, these ecophysiological traits provide these planktonic taxa the ability to outcompete large-celled diatoms such as *Aulacoseira* taxa, which require turbulent water column mixing to maintain a beneficial position within the photic zone (Rühland *et al*., 2015). These climate-mediated changes in lake thermal regimes are consistent with the recent (post- ~1990) marked increase in the relative abundances of planktonic diatom taxa, and the equally pronounced declines in *Aulacoseira* and benthic fragilarioid taxa registered in our sediment records. These diatom life strategy shifts were particularly evident in Indian L., Lower Rideau L., and Otter L., and corresponded with the highest temperatures recorded in the region (Fig. 3a, *Fig. S4*) as well as significant declines in MAWS (Fig. 3b).

In contrast to the other lakes within the Rideau Canal system, planktonic diatoms were notably scarce throughout the entire record in Upper Rideau L. Upper Rideau L. has similar morphometric characteristics to shallow L. Opinicon, and both lakes have extensive macrophyte-dominated littoral zones. However, in L. Opinicon, planktonic diatoms have recently become established in the sediment record in response to accelerated regional warming (Balasubramaniam *et al*., 2023). In general, warmer temperatures will support the growth of emergent macrophytes, leading to increased vegetation cover (Hossain *et al*., 2017). Considering benthic diatoms are often associated with macrophytes, the lack of notable abundances of planktonic diatoms in Upper Rideau L. and a decline in *Aulacoseira granulata* (the only non-benthic taxon in this record) may suggest an increased amount of littoral area relative to pelagic/open-water habitat, leading to increased benthic diatom taxa dominance (Fig. 6c). As noted above, it is possible that the presence of zebra mussels may have further intensified macrophyte growth via increased light penetration.

The most recent diatom compositional shift registered in Big Rideau L. (ca. 2005) includes notable increases in the relative abundances of planktonic *F. crotonensis* and small, centric *S. parvus*, both of which have been commonly associated with nutrient enrichment and mesotrophic conditions (Cumming *et al*., 2015; Reavie and Cai, 2019). The clear increase in *S. parvus* relative abundances ca. 2005 is interesting as this is a period when TP concentrations were at their lowest (Fig. 2), suggesting that their recent rise is not a signal of nutrient enrichment in Big Rideau L. *Stephanodiscus* taxa distinctly bloom in the epilimnion immediately following ice-out in spring when water column mixing is vigorous (Stoermer and Håkansson, 1984; Bradbury, 1988; Interlandi *et al*., 1999) and the first flux of nutrients (phosphorus and silica) from hypolimnetic waters are circulated to the photic zone (Bradbury, 1988), even in oligotrophic lakes (Reavie *et al*., 2014). Tentatively, a stronger snow melt and longer periods of isothermal mixing in spring resulting in an intense and short-lived increase in nutrient replenishment throughout the water column from the bottom of the lake (Bradbury, 1988; Morabito *et al*., 2001; Interlandi *et al*., 1999; Yu *et al*., 2010; Westover *et al*., 2021) may have been sufficient to support the spring growth of eutrophic taxa such as *S. parvus*. However, such trends are difficult to interpret without data on seasonal trends in diatom composition, snow melt, lake ice and spring mixing.

Substantial declines in regional wind speed (Fig. 3b) together with regional forest regrowth since the mid-20th century (Crowder and Conboy, 2010) were likely key factors facilitating changes in the mixing patterns and thermal properties of our study lakes. Atmospheric stilling (the decline of near-surface terrestrial wind speed) is a phenomenon that has been observed worldwide in recent decades (McVicar *et al*., 2012), including within the Rideau Canal system (Fig. 4b). Wind speed is one of the most important drivers of physical processes within lakes, where even modest reductions may cause substantial changes to stratification and mixing dynamics and has been associated with increased epilimnetic temperatures of inland lakes (Woolway and Merchant, 2019; Woolway *et al*., 2022). The forested area of the Rideau lakes region, which was once completely stripped of trees for agriculture and development, had been left to regrow unimpeded for the past ~70 years (Crowder and Conboy, 2010). The return of these dense forests likely played an important role in sheltering the study lakes from wind exposure, thereby reducing the strength and depth of vertical mixing. Declines in regional wind speed over the past ~50 years (Fig. 3b) combined with the recent regrowth of forests in the Rideau lakes region would have likely promoted extended periods of thermal stratification and weakened turbulent mixing, further promoting the shift towards higher abundances of planktonic diatom taxa in these lakes.

Cyanobacterial blooms have been reported in recent years in several of our study lakes including Lower Rideau L. (2015), Upper Rideau L. (2012, 2015, 2016, 2020), and Otter L. (2020) (MECP, unpublished data), despite significant declines in measured TP concentrations over the past ~40-50 years (Fig. 2). Increased nutrients in aquatic systems typically stimulates the occurrence of cyanobacterial algal blooms (Heisler *et al*., 2008), often resulting in a shift in phytoplankton community composition towards dominance by cyanobacteria (Watson *et al*., 1997). However, more recently, increases in cyanobacterial bloom formation have been associated with rising temperatures (Paerl and Huisman, 2008), even in the absence of nutrient increases (Favot *et al*., 2019; Smol, 2019). Bloom-forming cyanobacteria generally grow better at higher temperatures as most have temperature optima above 25°C (Visser *et al*., 2016), often exceeding the temperature optima of phytoplankton species such as diatoms (Lürling *et al*., 2013) and green algae (Joehnk *et al*., 2008). Perhaps more importantly, rising temperatures promote and strengthen the vertical stratification of lakes, thereby reducing vertical mixing. Bloom-forming cyanobacteria can exploit these conditions as they have intracellular gas vesicles that regulate their buoyancy (certain benthic, periphytic and epilithic cyanobacteria species do not possess these intracellular gas vesicles), combined with reduced vertical water column mixing, they can form dense surface blooms (Walsby *et al*., 1997). In turn, dense surface blooms can locally increase water temperatures (Ibelings *et al*., 2003) through the intense absorption of light by their photosynthetic pigments (Paerl and Huisman, 2008). The recent occurrence of cyanobacterial blooms observed in some of our study lakes is in agreement with longer and warmer open water periods and periods of thermal stratification which has been reported in numerous studies in the past few years (*e.g.*, Favot *et al*., 2019). The conditions conducive to the formation and proliferation of algal blooms align with those facilitating the observed shifts in diatom assemblage composition that we document here.

CONCLUSIONS

Using similar paleolimnological approaches, in 2019 and 2020, we revisited several lakes in the Rideau Canal system that were the focus of paleolimnological assessments conducted ~25-30 years ago (Christie and Smol, 1996; Karst and Smol, 2000; Forrest *et al*., 2002). Building on these earlier studies, which initially suggested that climate warming may have already been a factor behind recent increases in small, centric planktonic taxa, the analyses of sediment cores collected in 2019 and 2020 show that the trajectory of this trend has continued at an accelerated pace, consistent with regional meteorological records. Air temperatures are projected to continue to rise with longer and warmer ice-free periods, as well as longer and stronger periods of thermal stratification, all of which will have consequences throughout the food web. Such changes may further promote late-summer cyanobacterial blooms, which are already present in most of the study lakes. Additional paleolimnological reassessments of these same lakes using invertebrate indicators (research in progress) will provide more holistic assessments of ecosystem change, and further help decipher the roles of multiple stressors in these rapidly changing ecosystems.

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Online supplementary material:

Tab. S1. The results of Spearman rank correlation analysis between MAAT trends and paleo-proxy (diatom and VRS-Chla) data.

Fig. S1. Results of 210Pb dating using gamma spectrometry.

Fig. S2. Trends in Hill's N2 diversity index.

Fig. S3. Trends in visible range spectroscopy-inferred chlorophyll-a (VRS-Chla) concentrations (expressed as Z-scores) scaled by CRS-estimated 210Pb dates.

Fig. S4. Comparison between mean annual air temperature (MAAT) data and principal component analysis (PCA).