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Spatiotemporal variability in chromophoric dissolved organic carbon in small, shallow lakes from discontinuous permafrost peatlands (Taiga Plains, Northwest Territories, Canada)

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Abstract

Lake browning has been widely projected for northern lakes affected by permafrost thaw, but the inherent heterogeneity in permafrost landscapes coupled with a paucity of data for many regions makes it challenging to develop circumpolar-scale assessments. This heterogeneity was evident in our analysis of surface water chemistry in 51 small, shallow (0.5–3 m) lakes in discontinuous permafrost peatlands of the Taiga Plains (Northwest Territories, Canada), which were distributed across three Level IV ecoregions (Cameron Uplands, South Mackenzie Plain, Tathlina Plain). A positive association between dissolved organic carbon (DOC) and true colour was only observed in the Cameron Uplands, while lakes in the Tathlina Plain had high concentrations of nonchromophoric DOC. Chromophoric DOC was the primary driver of variation in subfossil diatom (Bacillariophyceae) assemblages in sediment cores from a subset of 23 lakes, where small benthic Fragilariaceae that are known to be tolerant of low-light conditions were more abundant in highly coloured lakes. Only 2 of the 23 lakes exhibited increases in small benthic Fragilariaceae indicative of browning since ∼1850.

Key words: permafrost thaw, boreal peatlands, shallow lakes, dissolved organic carbon, paleolimnology

Introduction

Climate warming is accelerating permafrost degradation (Smith et al. 2022), resulting in substantial impacts on surface water quality and quantity through alterations in hydrological regimes, sediment loading, and biogeochemical cycles (Vonk et al. 2015; Spence et al. 2020). Of particular concern are the large reserves of organic carbon stored in permafrost peatlands that may be mobilized upon thaw, which must be accounted for in regional, national, and global assessments and prediction models (Harris et al. 2022). The nature and impacts of permafrost thaw exhibit high spatial heterogeneity across the globe related to the extent of permafrost development, ground ice content, topography, soils, and Quaternary legacies (Tank et al. 2020). Thus, it is critical to document and understand intrinsic variability across permafrost landscapes to better predict future trajectories of change.

The phenomenon of lake "browning", defined as an increase in chromophoric (i.e., coloured) dissolved organic carbon (DOC), has been identified as a priority area for permafrost lake research because of its significance for the global carbon cycle as well as lake ecosystem function (Vonk et al. 2015). High concentrations of coloured (or aromatic) DOC have been observed in lakes in permafrost thaw-affected catchments, indicating a potential link between permafrost degradation and lake browning (Wauthy et al. 2018). However, the spatiotemporal dynamics of DOC quantity and quality (i.e., origin, diagenetic condition, chemical composition) are complex and influenced by factors such as catchment vegetation, hydrological connections, water residence times, and in-lake production (Molot and Dillon 1997; Köhler et al. 2013; Pęczuła 2015; Kurek et al. 2023), all of which can change in response to permafrost thaw and climate warming. Furthermore, while a positive correlation between DOC and lake colour is usually assumed, exceptions have been documented where high concentrations of DOC have not corresponded to higher lake colour and light absorption properties. In these systems, often found in semi-arid regions with high rates of photobleaching (Curtis and Adams 1995; Anderson and Stedmon 2007; Saros et al. 2016; Osburn et al. 2017), an increase in DOC would not necessarily correspond to lake browning. A lack of correlation between DOC and lake colour has

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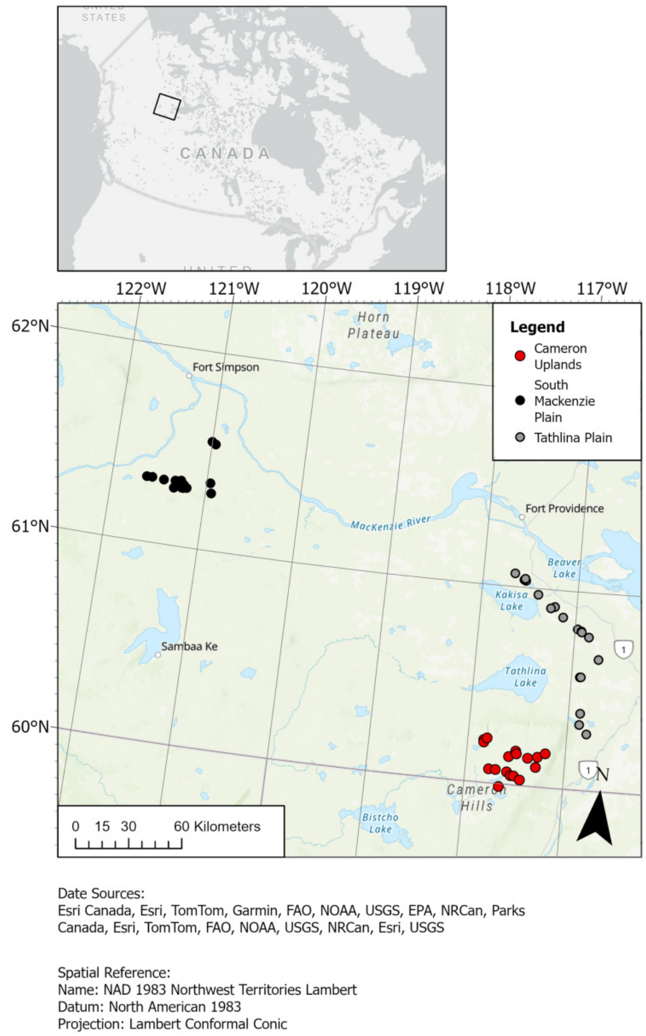
previously been documented for discontinuous permafrost peatland lakes in the Taiga Plains ecoregion of the southern Northwest Territories, Canada (Coleman et al. 2023). The Taiga Plains has experienced a rapid loss of permafrost in recent decades, which has converted forests into wetlands and enhanced hydrological connectivity in watersheds (Wright et al. 2022).

In the Taiga Plains and other organic-covered terrains underlain by discontinuous permafrost, the permafrost is typically restricted to treed peat plateaus surrounded by a complex of collapsed scar wetlands (i.e., bogs and poor fens), channel fens, and small lakes (Wright et al. 2022). Peat plateaus act as run-off generators, while channel fens act as the main pathways for water to move through watersheds to the drainage outlet (Connon et al. 2014). The lakes have varying degrees of hydrological connectivity (Hayashi et al. 2004), including lakes connected by channel fens along hydrological cascades, and isolated lakes found within bogs or peat plateaus (Quinton et al. 2019; Olefeldt et al. 2021*a*). As permafrost thaws and peat plateaus collapse, bogs and fens can become more hydrologically interconnected, while the development of taliks (perennially unfrozen ground) can create new pathways for groundwater flow (Connon et al. 2018). This has implications for biogeochemical cycling in watersheds, including DOC transport and processing (Gordon et al. 2016; Olefeldt et al. 2021*a*; Wright et al. 2022). The continued degradation of permafrost may ultimately result in the drainage of wetlands and the reestablishment of forests on a permafrost-free landscape (Carpino et al. 2021; Disher et al. 2021).

Projections of widespread lake browning in thawing permafrost landscapes have significant implications for the global carbon cycle, but DOC dynamics in lakes are complex and highly influenced by hydrological regime. Permafrost degradation in discontinuous permafrost peatlands is driving significant hydrological and vegetative changes in watersheds, while thawing of organic permafrost soils can also release previously frozen organic carbon into lakes. The cumulative effects of these processes on lake DOC quantity and quality, and trajectories of change over time, must be better understood to evaluate the extent to which lake browning is likely to occur under future climate warming scenarios. Such efforts are challenged by the heterogeneity of permafrost landscapes and the paucity of data for many regions. In direct response to these challenges, our study examined the spatiotemporal patterns in DOC and colour for small lakes of the peatland-dominated Taiga Plains ecoregion. Our objectives were to (1) characterize spatial patterns in water chemistry in 51 small, shallow (0.5–3 m) lakes in the Cameron Uplands, Tathlina Plain, and South Mackenzie Plain Level IV ecoregions of the Taiga Plains (Fig. 1) and (2) assess the extent to which recent permafrost thaw may have resulted in lake browning using a diatom-based paleolimnological approach for a subset of 23 lakes. Insights generated through studies such as this one are foundational for improving estimates of the role that small permafrost peatland lakes play in global elemental cycles and landscape hydrological processes, which comprise ∼18% of northern lake areas (Olefeldt et al. 2021*b*).

Fig. 1. Map showing the locations of the 51 Taiga Plains study lakes within the southern Northwest Territories, Canada. Locator map shows the study region outlined by the black box. Data sources: Esri, TomTom, Food and Agriculture Organization of the United Nations, National Oceanic and Atmospheric Administration, U.S. Geological Survey, Natural Resources Canada, Northwest Territories, Esri Canada, Garmin, U.S. Environmental Protection Agency, Parks Canada. Spatial reference: North American Datum 1983 Northwest Territories Lambert Conformal Conic projection.



Materials and methods

Study site description

The Taiga Plains consists of more than a hundred thousand small (<10 ha) lakes and ponds, while peatlands of varying thickness cover more than 50% of the land area (Ecosystem Classification Group 2007). The study lakes are located within the southernmost part of the Taiga Plains in the Northwest Territories, distributed across the Taiga Plains High Boreal (HB) (Cameron Upland) and Taiga Plains Mid Boreal (MB) (South Mackenzie Plain, Tathlina Plain) Level III ecoregions (Ecosystem Classification Group 2007). The landscape is poorly drained, and characterized by stunted black spruce

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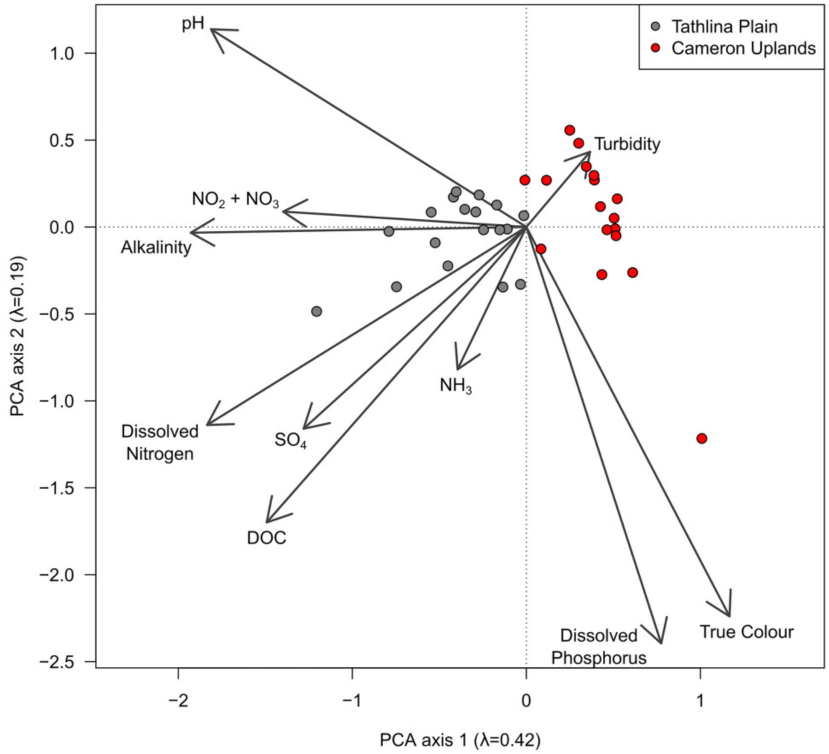
Fig. 2. Principal component analysis (PCA) of water chemistry variables in 35 small, shallow lakes in the Tathlina Plain (grey circles), and Cameron Upland (red circles) Taiga Plains Level IV ecoregions, southern Northwest Territories, Canada. DOC = dissolved organic carbon.



forests, treed bogs, horizontal fens, and peat plateaus. Dominant soil types are organic, organic cryosols, and gleysols in lowland regions, and brunisols and luvisols in upland areas. Deciduous and mixed-wood forest are found on hill slopes and outcrops of mineral soils. Climate is subarctic, with short, dry summers and long, cold winters. Lakes are typically ice-covered from November to May.

Based on the 1991–2020 Canadian Climate Normals (Environment and Climate Change Canada), the mean annual air temperature at Fort Simpson, the closest climate station for the South Mackenzie Plain lakes, is −2.3 °C, and the mean annual air temperature at Hay River, the closes climate station for the Tathlina Plain lakes, is −2.2 °C. Mean January temperature (the coldest month) is −23.6 °C in Fort Simpson and −21.4 °C in Hay River, while mean July temperature (the warmest month) is 17.7 °C in Fort Simpson and 16.6 °C in Hay River. Mean annual precipitation is 370.5 mm in Fort Simpson and 320.3 in Hay River, with 65% falling as rain. The HB Ecoregion falls within or just north of the MB Ecoregion at elevations of 300–700 m a.s.l., and the colder climate experienced at higher elevation is reflected in a higher proportion of organic terrain and peat plateaus. Climate data are sparse in the Taiga Plains HB Ecoregion, but climate models infer mean annual air temperatures of –2.0 to –4.5 °C, with mean January (the coldest month) temperatures of –24 to −28 °C, and mean July (the warmest month) temperatures of 15.5–17 °C (Ecosystem Classification Group 2007). Mean annual precipitation is modelled as 300–390 nm, with 55% falling as rain and 45% falling as snow (Ecosystem Classification Group 2007).

Permafrost is sporadic discontinuous (10%–50% of land area underlain by permafrost), occurring mainly as peat plateaus (Ecosystem Classification Group 2007). The region has warmed rapidly since 1948 (Vincent et al. 2015) and permafrost thaw has been accelerating (Wright et al. 2022). All our study lakes are distributed within or downstream of thawing discontinuous permafrost peatlands. A strong El Nino event in 1997/1998 resulted in a threshold loss of permafrost and increased the drainage efficiency of the landscape (Chasmer and Hopkinson 2017). Forest fire is an important driver of vegetation and permafrost dynamics in the region (Ecosystem Classification Group 2007; Gibson et al. 2018), although there was no evidence of recent burns at the study lakes at the time of sampling.

Field methods

Water chemistry surveys were conducted for lakes in the Cameron Upland and Tathlina Plain ecoregions in late July 2013. Lakes were accessed by helicopter equipped with pontoons, and water samples were collected in polyethylene bottles approximately 30 cm below the water surface. Lakes were sampled from the approximate centre of the lake, as the landscape has low relief, and the basins are relatively uniform. Bottles were rinsed three times with lake water prior to sample collection. Following collection, all water samples were kept cold and dark (stored in a fridge or cooler with ice packs)

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and delivered within 48 h to the Taiga Environmental Laboratory in Yellowknife where they were filtered and preserved for analysis within 10 business days. The Taiga Environmental Laboratory is accredited by the Canadian Association of Laboratory Accreditation. Lakes in the South Mackenzie Plain were accessed by helicopter equipped with pontoons in June 2018 as part of a previous study (Coleman et al. 2023). Lake depth estimates were taken using an acoustic depth sounder, although the shallow nature of the lakes combined with the soft substrate resulted in readings fluctuating by tens of centimeters, which is significant in these shallow systems.

Sediment cores were collected from a subset of 23 lakes in March (Tathlina Plain) and September (Cameron Upland) of 2012, and in June of 2018 (South Mackenzie Plain). The lakes were selected randomly or originally cored for other projects and re-purposed for this study (e.g., Coleman et al. 2015, 2019). Sediment cores from the Cameron Upland and Tathlina Plain were collected from the center of the lake using a Glew (1989) gravity corer with an internal diameter of 7.6 cm. Cameron Upland lakes were sampled from an inflatable raft in the open water season, while lakes in the Tathlina Plain were cored in winter using the ice as a stable platform. Cores were sectioned at 0.5 cm resolution using a Glew (1988) vertical extruder until 10 cm, 1 cm resolution from 10to 20 cm, and 2 cm resolution for the remainder of the core. Sediment cores from the South Mackenzie Basin were collected from the center of the lakes off the pontoons of a helicopter, using a Uwitec gravity corer (UWITEC, Mondsee, Austria) with an internal diameter of 8.6 cm and sectioned into 0.5 cm intervals using a modified Glew (1988) extruder. Sediment samples were placed directly into individual WhirlPak sample bags and kept frozen until analysis.

Laboratory methods

Water samples from lakes in the Cameron Upland and Tathlina Plain ecoregions were analyzed for ammonia (NH_3), nitrite (NO_2^-), nitrate (NO_3^-), dissolved nitrogen (DN), DOC, total organic carbon (TOC), dissolved phosphorus (DP), total alkalinity (alk), true colour (TColour), specific conductivity (Cond), total dissolved and suspended solids, turbidity, calcium (Ca), chloride (Cl), fluoride (F), magnesium (Mg), potassium (K), sodium (Na), and sulfate (SO_4) following standard methods (Clescari et al. 1998). Water samples from lakes in the South Mackenzie Plain were analyzed for DOC and true colour at York University (Coleman et al. 2023). DOC was analyzed using a Shimadzu-TOC5000 Series TOC-L analyzer (shimadzu.com) following the combustion catalytic oxidation method and nondispersive infrared detection. True color was measured using the platinum-cobalt method on a Genesys 10S UV-Vis spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA; American Public Health Association 2011).

Subfossil diatom analysis in sediment cores was performed as a "top-bottom" survey, where the uppermost sediment core interval was selected to represent recent conditions, and a bottom sediment core interval was selected to correspond to ~1850 (i.e., two intervals/time periods were analyzed per lake). Sediment core chronologies were established using ^{210}Pb dating (Appleby 2001), which we used to select the interval corresponding to ~1850. The South Mackenzie Plain lakes were dated for this study using the constant rate of supply model (Appleby and Oldfield 1978). Sediments were freeze-dried prior to radioisotopic analysis at Queen's University using an Ortec High Purity Germanium Gamma Spectrometer (Oak Ridge, TN, USA). Chronologies were established using ScienTissiME (Barry's Bay, ON, Canda). Certified reference materials were obtained from the International Atomic Energy Association (Vienna, Austria) for efficiency corrections. Sediment core dating methods/results for KAK-1 and TAH-7 (Tathlina Plain) can be found in Coleman et al. (2015), and sediment core dating methods/results for the Cameron Upland lakes can be found in Coleman et al. (2019).

Diatom slides were prepared from thawed, wet sediments following Battarbee et al. (2001) using the hydrogen peroxide method (South Mackenzie Plain) or the nitric acid method (Cameron Upland, Tathlina Plain) and mounted using Naphrax®. Diatom valves were identified using an Amscope B690C-PL or Leica DMRB light microscope equipped with differential interference contrast filters, viewed under an oil immersion lens at 1000 × magnification. Diatom valves were identified to the species level according to multiple reference texts (Krammer and Lange-Bertalot 1997, 1999, 2000; Fallu et al. 2002) and online databases (Guiry and Guiry 2021; Spaulding et al. 2021). Between 350 and 600 valves were counted per interval, except for the bottom sample of SC3 (29–29.5 cm; ~1891), where 240 valves were counted as diatom valves were broken and hard to identify.

Data analysis

A principal component analysis (PCA) was conducted on water chemistry variables from the Cameron Uplands and Tathlina Plain lakes, to visualize relationships among limnological variables and assess regional variation in water chemistry. The PCA was scaled to a correlation matrix because of different units of measure (Borcard et al. 2011). PCA was run using the *rda* function in the package *vegan* for R (Oksanen et al. 2019). A biplot of scaling one was used to visualize environmental variables across different sites (Borcard et al. 2011). Scatterplots of DOC and true colour were plotted using functions in the *ggplot2* package (Wickham 2016). For each series separated by Level IV ecoregions, individual generalized additive models via restricted maximum likelihood (method REML) were plotted via *stat_smooth()*, developed using the *mgcv* package (Wood 2011).

To summarize the variation in sites by diatom relative abundance in the surface sediment intervals, the full diatom dataset was reduced to species found in any one site at >2% relative abundance. Following this, a PCA was conducted on Hellinger-transformed relative abundances and visualized using a scaling 2 biplot. The relationship with the water chemistry variables true colour and DOC was examined by passively plotting chemistry using the *envfit* function in *vegan* (Borcard et al. 2011). Note that this remains an indirect ordination, and the chemistry variables are not contributing to the separation of species or sites in the analysis. Finally, to

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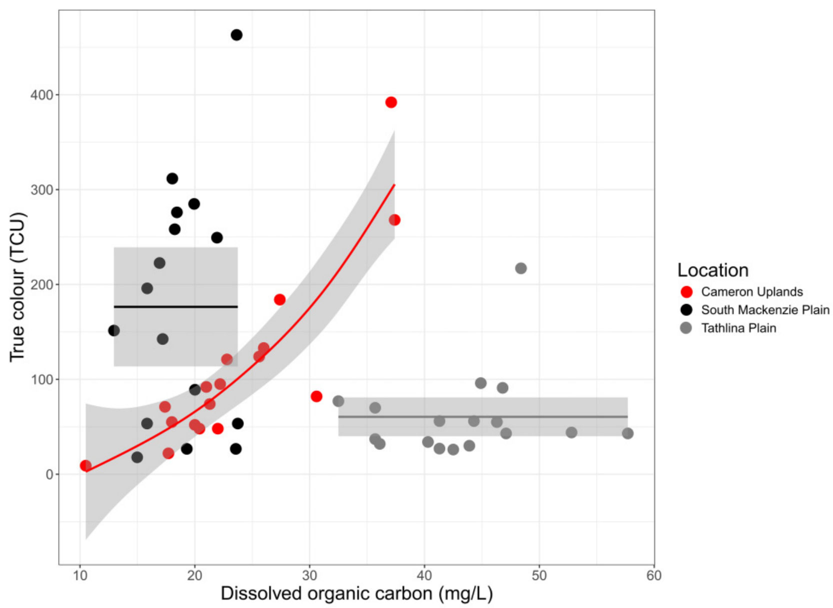
Table 1. Summary of surface area (in km^2), lake depth (m), and water chemistry parameters for lakes in the Cameron Uplands (17 lakes) and the Tathlina Plain (18 lakes) analyzed for this study.

	Cameron Uplands			Tathlina Plain			South Mackenzie Plain		
	Min	Max	Median	Min	Max	Median	Min	Max	Median
Surface area	0.11	0.91	0.26	0.01	1.58	0.07	0.1	7.1	0.3
Depth	0.5	3	n/a	0.5	2	n/a	0.5	2	n/a
pH	5.7	8	7	7.5	8.8	8.2	7.8	8.8	8.2
Alk	2.5	86.2	11.4	38.6	155	80.2	28	124	43
TP (filtered)	2	60	10	2	24	7.5	n/a	n/a	n/a
TP (unfiltered)	n/a	n/a	n/a	n/a	n/a	n/a	8	38	17
DN	0.4	1.1	0.7	0.9	2.3	1.5	0.5	1.5	0.8
DOC	10.5	37.4	22	32.5	57.7	44.1	13	23.7	18.4
TColour	9	392	82	26	217	49.5	18	463	174

Note: Results from the South Mackenzie Plain (15 lakes) published previously (Coleman et al. 2023) are shown for comparison (data available for download at http://hdl.handle.net/10315/39723). Alk = alkalinity (in mg/L $CaCO_3$); TP = total phosphorus (μg/L); DN = dissolved nitrogen (mg/L); DOC = dissolved organic carbon (mg/L), TColour = true colour (TCU).

Fig. 3. 1:1 plot of dissolved organic carbon and true colour (TCU—true colour unit) in lakes in the Cameron Uplands (red circles), South Mackenzie Plain (black circles), and Tathlina Plain (grey circles). Results of generalized additive models (line—model fit, grey ribbon—95% confidence interval) are shown for true colour as a function of dissolved organic carbon.



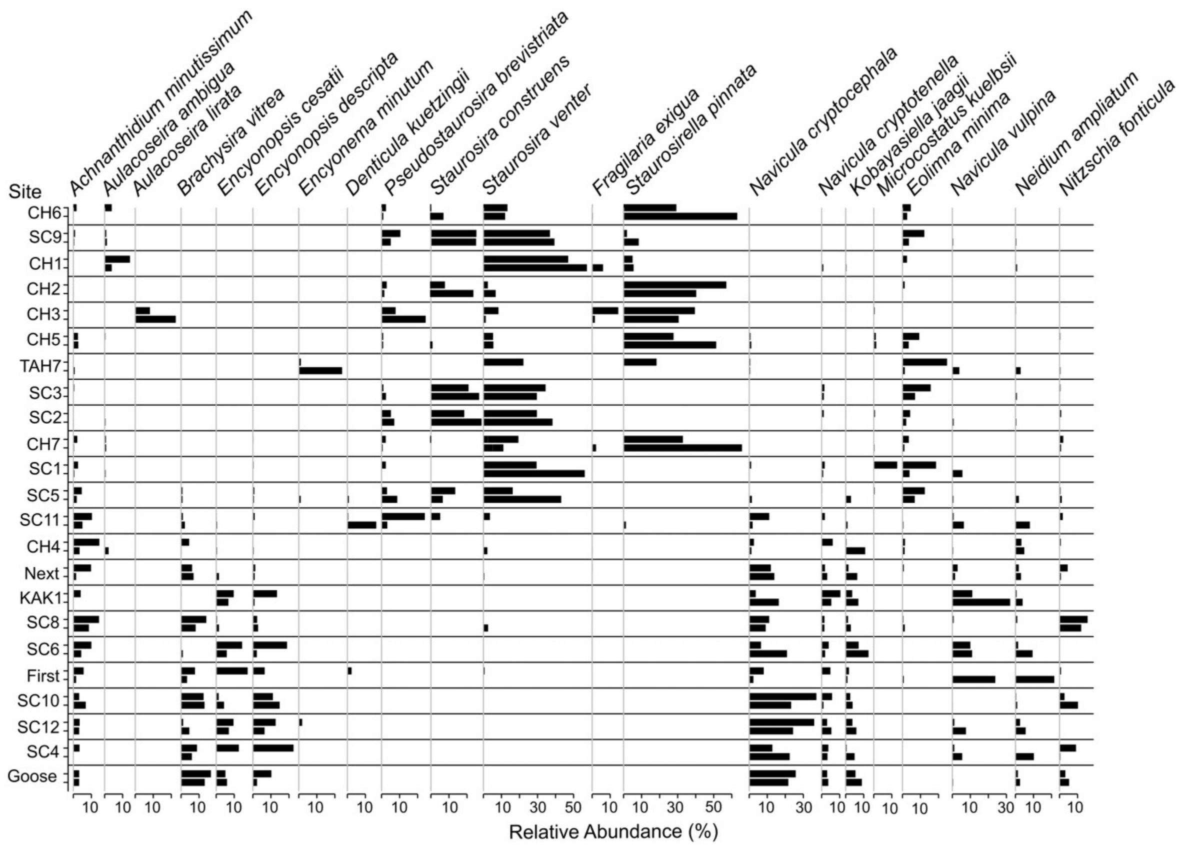
visualize change over time, the bottommost interval PCA axis 1 and 2 site scores were passively estimated using the *predict* function and displayed on a biplot.

Results

Water chemistry survey

PCA revealed a separation of Tathlina Plain and Cameron Upland lakes along PCA axis 1, where Tathlina Plain lakes had higher alkalinity, nitrogen (dissolved nitrogen, nitrate + nitrite, and ammonia), sulfate, and DOC (Fig. 2). Lakes of the Tathlina Plain also had notably smaller surface area relative to both the Cameron Uplands and South Mackenzie Plain (Table 1). There was a decoupling of DOC and true colour, where DOC was positively associated with total nitrogen and sulfate, while true colour was positively associated with dissolved phosphorus (DP) (Fig. 2). The relationship between DOC and true colour differed among the three Level IV ecoregions examined (Fig. 3). For lakes in the Cameron Uplands, the DOC gradient ranged from 10.5 to 37.4 mg/L, and true colour ranged from 9 to 392 true colour unit (TCU). True colour increased with DOC across the gradient (i.e., the two variables exhibited a statistically significant positive relationship) (Fig. 3). In contrast, there was no significant relationship between DOC and true colour in lakes from the Tathlina Plain and the South Mackenzie Plain (Fig. 3). Lakes in the Tathlina Plain had the highest DOC (32.5–57.7 mg/L) among the 51 study lakes, and comparatively lower true colour (26–271 TCU) (Table 1). Lakes in the South Mackenzie Plain exhibited a relatively narrow DOC range (13.0–23.7 mg/L) compared to the Tathlina Plain and Cameron Uplands lakes, while

Fig. 4. Relative abundance diagram displaying the most common (>10% in at least one sample) diatom taxa in a surface and bottom (∼1850) interval in small, shallow lakes from the Taiga Plains ecoregion. Lakes are ordered based on diatom principal component analysis axis 1 scores.



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true colour ranged from 17.8 to 463 TCU (Table 1). We note, however, that water samples from the South Mackenzie Plain lakes were analyzed in a different laboratory than lakes from the Tathlina Plain and Cameron Upland and collected at a different time (June 2018 vs. July 2013). Consequently, any comparisons drawn between the South Mackenzie Plain and the Tathlina Plain or Cameron Uplands should be considered with caution.

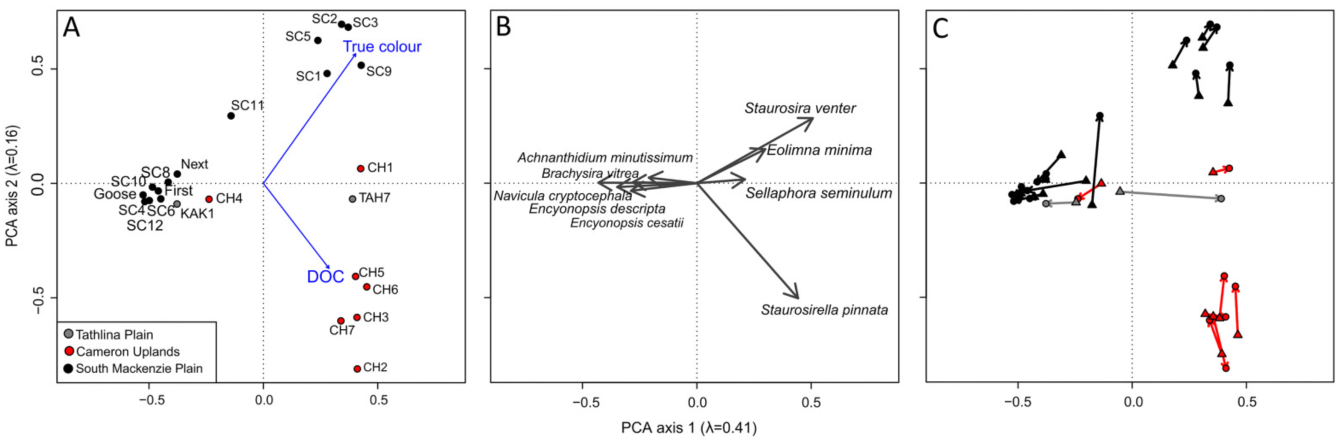
Subfossil diatom "top-bottom" survey

In total, 245 different diatom taxa were identified in the top and bottom sediments of the 23-lake subset. The assemblages in all lakes, in both top and bottom intervals, were dominated by benthic taxa (described in detail below), with the relative abundance of tychoplanktonic *Aulacoseira* spp. greater than 10% in only two sites, CH1 and CH3 (Fig. 4). The only lake with a notable proportion of the assemblage composed of planktonic species was Next Lake, where *Discostella pseudostelligera* made up ∼8% and *Pantocsekiella michiganiana* made up 7% of the assemblage. In all other lakes planktonic taxa were rare, with no site having abundances of centric or pennate plankters greater than 10% (Fig. 4).

PCA axis 1 explained 41% of the variation in the diatom taxa of the surface sediments. *Eolimna minima*, *Staurosira venter*, *Sellaphora seminulum*, and *Staurosirella pinnata* had positive PCA axis 1 species scores, and were associated with the lakes that had higher DOC and/or colour, variables which were plotted passively (Figs. 5A and 5B). *Navicula cryptocephala*, *Encyonopsis descripta*, *Encyonopsis cesatii*, *Achnanthidium minutissimum*, and *Brachysira vitrea* had negative PCA axis 1 species scores, and were associated with lakes that had lower DOC/colour (Figs. 5A and 5B). PCA axis 2 explained 16% of the variation in diatom taxa. Lakes with negative PCA axis 1 scores (low DOC/colour) exhibited very little variation along PCA axis 2 (Fig. 5A). For lakes with positive PCA axis 1 scores (higher DOC/colour), variation along PCA axis 2 was driven by *Nepenthes minima*, and *Staurosira venter* (positive PCA axis 2 species scores) in coloured lakes of the South Mackenzie Plain (Figs. 5A and 5B), where colour and DOC are uncoupled (Fig. 3), and *Staurosirella pinnata* in high DOC lakes in the Cameron Uplands (Figs. 5A and 5B), where DOC is positively correlated with true colour (Fig. 3).

In the lower DOC/colour lakes (negative PCA axis 1 site scores), the change in diatom assemblage between ∼1850 and present-day was primarily toward more negative PCA axis 1 site scores (Fig. 5C), associated with an increase in epiphytic diatom taxa (Fig. 5B). An exception to this trend was seen in TAH-7 (Tathlina Plain) and SC11 (South Mackenzie Plain) (Fig. 5C). TAH-7 exhibited a shift from negative to positive PCA axis 1 scores, associated with movement in ordination space toward lakes with higher DOC and/or colour. SC11 exhibited a shift to positive PCA axis 2 scores, and a slight shift

Fig. 5. (A) Principal component analysis (PCA) biplot of site scores showing variation in diatom taxa in surface sediments of lakes in the Taiga Plains ecoregion of the southern Northwest Territories, Canada. Blue arrows represent passively fitted environmental variables; (B) PCA biplot of species scores for the taxa with the highest score-loading values (>0.2 on either axis); (C) PCA site scores for surface sediments (as circles) with passively plotted site scores from bottom (~1850) intervals (triangles). Arrows represent the direction of change in diatom assemblages between 1850 and present-day. DOC, dissolved organic carbon.



to more positive PCA axis 1 scores, predominantly tracking an increase in *N. minima* and *Staurosira venter* that characterized coloured lakes in the South Mackenzie Plain (Figs. 5A and 5B). For lakes with positive PCA axis 1 site scores (higher DOC and/or colour), the change in diatom assemblage between ~1850 and present-day was primarily toward increased PCA axis 2 site scores, except for CH2 that shifted toward more negative PCA axis 2 site scores associated with an increase in *Staurosirella pinnata* (Fig. 5C).

Discussion

Spatial patterns in DOC and lake colour

This study documented notable variation in DOC characteristics between three Level IV ecoregions within the Taiga Plains ecozone, reflected in the relationship between DOC concentration and true colour (a proxy for aromatic, chromophoric DOC). Lakes in the Cameron Uplands exhibited a positive correlation between true colour and DOC, a common pattern for north temperate regions (Pace and Cole 2002; Seekell et al. 2015; Bartels et al. 2016). In contrast, DOC and true colour were uncorrelated in lakes in the Tathlina Plain and South Mackenzie Plain. Lakes in the South Mackenzie Plains spanned a relatively lower DOC range (~13–24 mg/L) compared to lakes in the Tathlina Plain (~32–58 mg/L).

The properties of lake DOC reflect the major DOC sources, as well as transport pathways and degradation processes. Water residence time is often a strong predictor of lake DOC characteristics, as it is integrative of several intrinsic (e.g., in-lake degradation of DOC) and extrinsic (e.g., aquatic-terrestrial linkages) controls (Kellerman et al. 2014; Catalan et al. 2016; Pugh et al. 2021; Kurek et al. 2023). Increasing rainfall (spatially and temporally) may enhance the transport of allochthonous DOC to lakes, while diminishing in-lake preferential degradation of the chromophoric (aromatic) DOC fraction (Kellerman et al. 2014; Pugh et al. 2021; Kurek et al. 2023). Surficial geology, local relief, and catchment vegetation determine the delivery of aromatic terrestrially derived DOC to lakes, with the proportion of peatlands in the watershed as a particularly strong predictor of aromatic DOC (Sepp et al. 2019; Pugh et al. 2021; Kurek et al. 2023). Subsurface water inputs may also be a significant source of DOC to boreal lakes, with the amount and quality of groundwater DOC contributions reflecting the composition of the soils and nature of the subsurface flow paths (Olefeldt et al. 2013; Einarsdottir et al. 2017).

The drivers of lake DOC properties explained above account for the variation in DOC commonly documented across broad gradients of latitude, permafrost, ecozones, and treeline ecotones (Stolpmann et al. 2021; Kurek et al. 2023). In this study, however, we documented substantial differences in three regions that appear quite similar in terms of broad characteristics. Study lakes across all three Taiga Plains ecoregions were small and shallow (<2–3 m), situated in low-relief terrain within sporadic discontinuous permafrost peatlands, and experienced similar subarctic climates. The Tathlina Plain has been described as containing large expanses of flat, poorly drained terrain, with glacial and organic deposits underlain by Devonian limestone, which may distinguish it from the Cameron Upland and South Mackenzie Plain (Ecosystem Classification Group 2007). The Tathlina Plain lakes were also notably smaller than the Cameron Uplands and South Mackenzie Plain, which may potentially reflect differences in water balance, surface water contributions, and/or water residence time. Similarly, the Cameron Upland, while still characterized as low-relief in peatland-dominated areas, has more gentle relief than was observed in the Tathlina Plain and in the areas of the South Mackenzie Plain where the study lakes were located. The Cameron Upland lakes were also less alkaline than lakes in the South

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Mackenzie Plain and Tathlina Plain. Further study is needed to uncover the localized drivers of DOC within ecozones, but our results demonstrate that heterogeneity within ecozones can lead to pronounced impacts on lake DOC.

Projections of lake browning are often predicated on the assumption that lake colour increases with increasing DOC, an assumption that is generally well supported for many north temperate lake regions (Seekell et al. 2015; Bouchard et al. 2017). However, exceptions have been documented in the Yukon Flats, low Arctic Greenland, the Boreal Plains of Alberta, and elsewhere (Anderson and Stedmon 2007; Johnston et al. 2020; Pugh et al. 2021; Cotner et al. 2022; Kurek et al. 2023). These regions are often characterized as less connected to surface flow paths, leading to the accumulation of high concentrations of autochthonous and heavily photodegraded allochthonous DOC in hydrologically isolated lakes with longer water residence times. It has been estimated that approximately one-quarter of total circumpolar lake area is in arid, low relief regions, and these lakes have been historically underrepresented in studies on north temperate lake DOC dynamics (Johnston et al. 2020). In this study, we identified the Tathlina Plain as another circumpolar region exhibiting a pattern of lakes with high concentrations (30–60 mg/L) of predominantly nonchromophoric DOC. Future study is needed to determine if lakes of the Tathlina Plain have similar characteristics to the Yukon Flats and parts of Greenland, including longer water residence times and DOC quality characterized as authochthonous or degraded allochthonous.

The Taiga Plains is undergoing rapid landscape transformation because of climate warming and permafrost thaw. Permafrost thaw has enhanced the overall connectivity of discontinuous permafrost peatland watersheds and created new subsurface flow paths (Connon et al. 2014, 2018). Increases in subsurface and surface flows could increase the supply of fresh allochthonous DOC to lakes, which may contribute to lake browning. This could include a re-distribution of water previously held in long-term storage by thermokarst wetlands impounded by permafrost, which would be released by thaw (Haynes et al. 2018). Assessments of long-term changes in lake DOC characteristics in discontinuous permafrost peatlands is essential for understanding landscape carbon cycling with ongoing climate change.

Temporal changes in chromophoric DOC as inferred by diatoms

Diatom assemblages were dominated by benthic taxa that appeared to be responding primarily to light availability/quality in the benthic zone, with the first PCA axis (the primary direction of variation) separating epiphytic diatoms from benthic diatom assemblages that are tolerant of low light conditions. *Achnanthidium minutissimum*, *B. vitrea*, *N. cryptocephala*, *E. descripta*, and *E. cesatii* were associated together in lakes with lower chromophoric DOC. Many of these species are epiphytic (Michelutti et al. 2002, 2007; Bouchard et al. 2017), and as such, their dominance in the lakes with lower chromophoric DOC is likely reflecting greater growth of aquatic macrophytes and/or mosses resulting from increased light availability to the benthic zone. This corresponded to our field observations, where aquatic mosses were visible at the sediment-water interface in the sediment cores we collected from many of these lakes. *Brachysira vitrea*, *N. cryptocephala*, and *Encyonopsis* spp. have also previously been found to be associated with benthic mosses in an assessment of diatom ecology across different lake substrate types in Goose Lake, a lake with low chromophoric DOC located at the Scotty Creek Research Station (Coleman et al. 2023). *Achnanthidium minutissimum* is widely regarded as a benthic cosmopolitan taxon and it was also the most abundant taxon in periphytic biofilm samples from the Old Crow Flats in the Yukon, Canada (Mohammed et al. 2021).

Small benthic Fragilariaceae (*Staurosirella pinnata*, *Staurosira venter*) and small *Navicula* species sensu lato (*S. seminulum*, *N. minima*), in contrast, were associated with higher DOC and/or coloured lakes. Small benthic Fragilariaceae species are opportunistic, generalist taxa that are ubiquitous across wide environmental gradients, and are often abundant in harsh, low light conditions where other diatom taxa are less competitive (Lotter and Bigler 2000; Smol et al. 2005; Rühland et al. 2008, 2015; Griffiths et al. 2021; Kahlert et al. 2022; Weckström et al. 2023). Low light conditions can occur associated with prolonged lake ice cover (Lotter and Bigler 2000; Rühland et al. 2015), in waters with high suspended solids (Karst-Riddoch et al. 2005), and in lakes with elevated chromophoric DOC (Pienitz and Smol 1993; Pienitz et al. 1999; Ruhland et al. 2003; Coleman et al. 2023). The association of small benthic Fragilariaceae with lakes that have higher chromophoric DOC documented in this study, a verification of the findings in Coleman et al. (2023) with a larger lake set, indicates that these taxa have potential as paleoecological indicators of brownification in small, shallow lakes of discontinuous permafrost peatlands in the Taiga Plains.

Between 1850 and present-day, the epiphyte-dominated lakes shifted primarily toward more negative PCA axis 1 scores, associated with higher abundances of epiphytic diatom taxa. Warming air temperatures and increased length of the open water season can promote the development of more abundant and complex benthic vegetation (Smol and Douglas 2007; Weckstrom et al. 2023). Therefore, the trend toward more negative PCA axis 1 scores may be tracking regional warming (Vincent et al. 2015). Similar increases in epiphytic diatom abundance and diversity have been documented in association with climate warming across the northern hemisphere (Smol et al. 2005). Lakes SC11 (South Mackenzie Plain) and TAH-7 (Tathlina Plain) are clear exceptions to the trend toward more epiphytic taxa, where diatom assemblage changes since ~1850 may instead be indicative of lake browning.

Lake TAH-7 experienced a shift from negative PCA axis 1 scores (epiphyte-dominated lakes) to positive scores (Fragilariaceae-dominated lakes). A high-resolution paleolimnological assessment of diatom assemblage changes has previously been published for TAH-7 (Coleman et al. 2015). The study revealed a shift from large *Navicula* taxa to *Encyonema minutum* following a fire event circa 1850 (inferred based on a peak in macroscopic charcoal), followed by a decrease in *E. minutum* and increases in small *Navicula* and small benthic Fragilariaceae taxa (Coleman et al. 2015). The increase

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in small *Navicula* and small benthic Fragilariaceae taxa corresponded to δ^{13}C depletion, lending additional support to an inference that increases in these taxa was tracking lake browning (Korosi et al. 2015). Forest fires are known to accelerate permafrost degradation in the Taiga Plains (Gibson et al. 2018). The browning signal indicated by diatom assemblage changes in TAH-7 may potentially be the result of new hydrological pathways created by the degradation of permafrost following the fire, leading to a trajectory of increased aromatic DOC inputs.

Lake SC11 shifted mainly along PCA axis 2, the secondary axis of variation that separated diatom assemblages in high DOC/coloured lakes in the Cameron Hills (negative PCA axis 2 scores, dominance by *Staurosirella pinnata*) from coloured lakes in the South Mackenzie Plain (positive PCA axis 2 scores, dominance by *N. minima*, and *Staurosira venter*). SC11 shifted toward increased PCA axis 2 scores, associated with increases in *N. minima* and *Staurosira venter.* There has not been any high-resolution paleolimnological study of SC11, which would be needed to ascertain the timing of the change and assess any potential linkages to fire or permafrost thaw. The increase in PCA axis 2 scores in SC11 was also documented in all the Fragilariaceae-dominated lakes from the South Mackenzie Plain, and three of the six Fragilariaceae-dominated lakes from the Cameron Uplands. The possible reasons for shifts among the small benthic Fragilariacae and small *Navicula sensu lato* taxa are unclear and would require additional investigation into diatom autoecology/biogeography in small permafrost peatland lakes of the Taiga Plains.

Subfossil diatom ecology studies for Arctic and subarctic lakes in North America have focused mainly on treeline ecotones (Pienitz and Smol 1993; Pienitz et al. 1995*a*, 1995*b*; Rühland et al. 2003), which do not account for variation in species-environment relationships across lakes within discontinuous permafrost peatlands. An understanding of local ecological context can be critical for the application and interpretation of (paleo)ecological indicators, especially for generalist taxa like small benthic Fragilariaceae. This study leveraged sample archives and was not specifically designed for a quantitative assessment of geographic and environmental controls on diatom species assemblages, which would have required a larger sample size and consistent methodology for water chemistry analysis. We would also recommend future study to investigate the interaction of chromophoric DOC with water depth, as we interpret the association between benthic diatoms and chromophoric DOC as a response to the quality of the light environment in the benthic zone, which in these shallow (<2–3 m) lakes would also be modulated by changes in lake depth. The Taiga Plains experienced a drought in 2023–2024, with water levels down ~0.5–1 m (J. Korosi, unpublished data, 2024). The application of diatoms within a multi-proxy paleolimnological study could provide further context for disentangling the effects of multiple drivers on species assemblage changes, such as the example for TAH-7 where lignin-derived phenols and stable isotopes of carbon provided additional insights into changes in carbon cycling that corroborate the diatom-inferred decrease in water clarity (Coleman et al. 2015; Korosi et al. 2015). Further study could also investigate whether a DOC-inference model using visible–near-infrared spectroscopy (e.g., Rouillard et al. 2011) can be developed for Taiga Plains lakes, one that is able to distinguish between chromophoric and nonchromophoric DOC.

Conclusions

We documented substantial differences in DOC quality between small, shallow lakes in three ecoregions of the Taiga Plains that are similar in terms of landscape type (discontinuous permafrost peatlands) and climate. Only one of the three ecoregions exhibited a positive correlation between DOC and lake colour. We identified the Tathlina Plain as another circumpolar region where lakes are characterized by high concentrations (30–60 mg/L) of predominantly nonchromophoric DOC, a class of lakes that is underrepresented in the scientific literature. Variation in DOC quality among Taiga Plains ecoregions was reflected in the algal community, where diatom (Bacillariophyceae) assemblages were primarily structured along a gradient of DOC/colour. Epiphytic diatom taxa were dominant in lakes with low chromophoric DOC while small benthic Fragilariaceae were dominant in lakes with high chromophoric DOC. Rather than a direct influence of DOC, the relationship with diatom assemblages likely reflects the influence of chromophoric DOC on light penetration to the benthic zone, where benthic Fragilariaceae are more tolerant of low-light conditions in these conditions. Variation in DOC quality across the study lakes, combined with its primary significance in structuring diatom assemblages, indicates that biogeochemical cycling of DOC may be a key mechanism of past and future ecological responses to climate warming and permafrost thaw.

Increases in epiphytic diatoms between ~1850 and present-day were observed in most of the lower DOC/colour lakes, except for two lakes that exhibited changes in diatom assemblages that implied lake browning had occurred. Increases in epiphytic diatoms are likely tracking factors such as a longer open-water season, warmer waters, and enhanced nutrients, which would increase the growth of aquatic macrophytes and mosses. Of the two lakes that underwent lake browning based on interpretation of diatom changes, one had a temporal association between the onset of browning and a fire event that may have accelerated permafrost degradation. This suggests that there is a mechanism by which permafrost thaw may lead to lake browning, but our study does not provide evidence that lake browning has been pronounced and widespread in lakes of the Taiga Plains. Gaps in our understanding of diatom autoecology prevent us from being able to make inferences about potential browning trends in lakes that already had high baseline colour.

This study leveraged samples that had been previously collected for other purposes and was not explicitly designed to tease apart the influence of landscape factors on DOC spatiotemporal dynamics, or on factors such as water depth that may modulate the relationship between chromophoric DOC and light penetration to the benthic zone. However, the clear, region-specific spatial differences in lake DOC that we documented, combined with evidence that DOC is a strong driver of benthic algal communities across space and time,

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highlights a need to unravel the complexity in DOC in permafrost landscapes, to better understand the potential for thaw to contribute to lake browning across the circumpolar north. Furthermore, our study inferred changes in lake colour in the context of other limnological responses to climate warming (e.g., growing season, temperature, nutrients, water depth), highlighting the need to consider multiple ecosystem drivers when interpreting the responses of biological communities.

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Data availability

Data generated or analyzed during this study is available in the York University online repository (YorkSpace), https://hdl.handle.net/10315/42896.

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Competing interests

The authors declare there are no competing interests.

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