

Abrupt changes in the physical and biological structure of endorheic upland lakes due to 8-m lake-level variation during the 20th century

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Abstract

Climate-induced variation in lake level can affect physicochemical properties of endorheic lakes, but its consequences for phototrophic production and regime shifts are not well understood. Here, we quantified changes in the abundance and community composition of phototrophs in Kenosee and White Bear lakes, two endorheic basins in the parkland Moose Mountain uplands of southeastern Saskatchewan, Canada, which have experienced > 8 m declines in water level since ~ 1900. We hypothesized that lower water levels and warmer temperatures should manifest as increased abundance of phytoplankton, particularly cyanobacteria, and possibly trigger a regime shift to turbid conditions due to evaporative concentration of nutrients and solutes. High-resolution analysis of sedimentary pigments revealed an increase in total phototrophic abundance (as β -carotene) concurrent with lake-level decline beginning ~ 1930, but demonstrated little directional change in cyanobacteria. Instead, significant increases in obligately anaerobic purple sulfur bacteria (as okenone) occurred in both lakes during ~ 1930–1950, coeval with alterations to light environments and declines in lake level. The presence of okenone suggests that climate-induced increases in solute concentrations may have favored the formation of novel bacterial habitats where photic and anoxic zones overlapped. Generalized additive models showed that establishment of this unique habitat was likely preceded by increased temporal variance of sulfur bacteria, but not phytoplankton or cyanobacteria, suggesting that this abrupt change to physical lake structure was unique to deep-water environments. Such climate-induced shifts may become more frequent in the region due to hydrological stress on lake levels due to warming temperatures across the Northern Great Plains.

Local and regional declines in lake levels are of great concern as human water use is expected to increase over the next century (Vörösmarty et al. 2000; Gaeta et al. 2014). In

addition to anthropogenic uses, lake levels may vary in response to perturbations in regional hydroclimate, particularly where evaporation rates exceed precipitation levels (Pham et al. 2009; Xiao et al. 2018). Such hydroclimate changes and subsequent lake-level declines are widespread in the Northern Great Plains, particularly in hydrologically managed endorheic basins which depend on spring snowmelt for water replenishment (van der Kamp et al. 2008; Pham et al. 2009; Sereda et al. 2011). In these regions, general circulation models (GCMs) forecast warmer temperatures and only modest changes in precipitation (Tanzeeba and Gan 2012; Asong et al. 2016; Zhou et al. 2018), potentially resulting in increased volatility of regional lake levels due to evaporative forcing. Resultant changes in regional water quality may include variation in nutrient, carbon, and major ion concentrations, proportion of littoral and pelagic habitats, phytoplankton community composition and production, and food-web dynamics including zooplankton and fish communities (Vinebrooke et al. 1998; Fischer and Öhl 2005; Hambright et al. 2008; Pham et al. 2009; Gal et al. 2013; Wigdahl

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et al. 2014; Vogt et al. 2018). Despite on-going variation in lake levels in the Canadian Prairie region (Fritz 1990; van der Kamp et al. 2008), little is known of the long-term effects of enhanced evaporative stresses on production, community composition, and stability of phototrophic assemblages.

Variation in lake levels also affects water-column heating and circulation, as well as the degree to which irradiance penetrates to stable environments such as lake bottoms or chemoclines (Zohary and Ostrovsky 2011). Changes in thermal stratification may be particularly noteworthy in shallow prairie and parkland systems where polymixis is common due to frequent high winds (Plancq et al. 2018), while variation in ionic content can affect chemical stratification (Hodgson et al. 1998). In addition, evaporative concentration of nutrients associated with lake-level decline may favor increased primary production, particularly under warm conditions (Vinebrooke et al. 1998; Zinabu 2002). As shallower ecosystems warm more quickly than deeper ones (Dröscher et al. 2009; Dibike et al. 2016), such conditions can promote blooms of planktonic algae and potentially-toxic cyanobacteria (Davis et al. 2009; Paerl and Paul 2012; Huisman et al. 2018; Hayes et al. 2019).

Large and disproportionate increases in cyanobacterial abundance can arise as an abrupt change, or “regime shift” (*sensu lato*) in some lake systems (Taranu et al. 2015; Bunting et al. 2016; Vogt et al. 2018). In some cases, there is increased temporal variance in the abundance or concentration of phytoplankton or cyanobacteria prior to the shift, marking a “critical slowing down” arising from changes in the strength of internal feedbacks due to environmental driver(s) (Scheffer et al. 2001; Scheffer and Carpenter 2003; Carpenter and Brock 2006; Dakos et al. 2015; Ratajczak et al. 2018). In lake systems, variation in primary production can rise because of prolonged gradual increases in nutrient influx (e.g., paradox of enrichment; Cottingham et al. 2000), after which the regime shift to prolific cyanobacteria is initiated by relative minor forcing that push lakes beyond critical thresholds (Dakos et al. 2015; Bunting et al. 2016). These transitions may become self-enforcing through positive feedback mechanisms and result in a transition to an alternate stable state that exhibits self-maintenance and hysteresis (Scheffer et al. 2001; Scheffer and Carpenter 2003; Dakos et al. 2015; Ratajczak et al. 2018). Additional environmental drivers which may result in a regime shift in lakes include changes in ice-cover duration, vertical-mixing regime, and water-column warming (Paerl and Paul 2012; Taranu et al. 2015); although, in theory, variation in lake level, chemical stratification, or ionic concentration could also induce a regime shift (Garcés et al. 1995; Hodgson et al. 1998). On the Northern Great Plains, changes in the interactions between the predominant air masses (Gulf, Pacific, Arctic) can cause increased evaporative concentration and salinity (Liu et al. 2008; Pham et al. 2009), variation in water-column mixing (polymixis to meromixis; Michels et al. 2007), and large changes (5–10 m) in lake level (van der

Kamp et al. 2008) that could all initiate a regime shift with large biological responses (Scheffer et al. 2001; Carpenter et al. 2011).

To date, little is known of whether changes in the physical status of lakes (deep/shallow, mixed/stratified, etc.) are recorded by temporal variation in primary production or whether such changes in physical conditions can initiate true regime shifts (Bunting et al. 2016; Taranu et al. 2018). Furthermore, it has been established that some regime shifts are not preceded by rising variance (Burthe et al. 2016; Ratajczak et al. 2018) and that rising variance in environmentally sensitive proxies does not invariably lead to a regime shift (Burthe et al. 2016), which makes the establishment of regime shifts very difficult without abundant a priori knowledge of the impacted system (Scheffer and Carpenter 2003; Dakos et al. 2015; Burthe et al. 2016). In this context, it may be useful to retroactively examine systems which have experienced substantial environmental changes to discover if any regime shifts occurred, either with or without an associated rise in variance of key proxies, such as biological production (Randsalu-Wendrup et al. 2016; Taranu et al. 2018). The establishment of past regime shifts, or transitions between alternate stable states, may provide critical insights on how nonlinear and abrupt changes in ecosystem response to environmental change may improve lake management and mitigation strategies (Bunting et al. 2016; Randsalu-Wendrup et al. 2016).

To better understand how lake-level variation may influence the temporal variability of lakes, we quantified historical changes in the production, composition, and variance of phototrophic assemblages in two proximal endorheic parkland lakes located in the Moose Mountain uplands of south-east Saskatchewan, Canada. Kenosee and White Bear lakes are presently unstratified (Plancq et al. 2018) and have experienced > 8 m declines in water level over the past century (Vance et al. 1997; Vinebrooke et al. 1998; van der Kamp et al. 2008). Analyses of historical changes in biomarker pigments from algae and phototrophic bacteria (cyanobacteria, purple sulfur bacteria) were used to: (1) quantify how phytoplankton abundance and community composition have varied in response to lake-level changes since ~ 1900; (2) determine if climate and lake-level change resulted in disproportionate increases in toxic cyanobacteria as is expected in warming, shallowing waters (Taranu et al. 2015; Bunting et al. 2016; Vogt et al. 2018) and (3) determine if any changes in lake physical structure (i.e., mixing regime, oxygenation, light penetration) due to historical lake-level variation are related to increased temporal variance of phytoplankton, such as seen in other prairie lakes which have undergone regime shifts (Carpenter et al. 2011; Bunting et al. 2016). Analysis of temporal patterns of primary producers may provide insights into the ecological effects of regional changes in lake levels (Dakos et al. 2015; Taranu et al. 2018) and will help forecast lake response to future

environmental change under a warmer and potentially more arid climate (Asong et al. 2016).

Materials and methods

Study sites

Kenosee Lake and White Bear Lake are located in the Moose Mountain Uplands of southeastern Saskatchewan, Canada (Fig. 1). These lakes are separated by ~ 2 km and share a humid, cold, continental climate (Köppen Dfb) with a mean annual temperature of 3.7°C and 427 mm yr^{-1} of precipitation during the 1981–2010 period (Estevan, Saskatchewan, station data; Environment and Climate Change Canada [ECCC]; https://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?searchType=stnProv&lstProvince=SK&txtCentralLatMin=0&txtCentralLatSec=0&txtCentralLongMin=0&txtCentralLongSec=0&stnID=2896&dispBack=0, accessed April 2021). Historical data suggest that while mean annual temperatures have increased by $\sim 2^{\circ}\text{C}$ over the past 80 yr, rainfall has increased only modestly and there has been little trend in snowfall (Supplemental Information Fig. S1; Homogenized Canadian Climate Station Data; ECCC; <https://www.canada.ca/en/environment-climate-change/service>

[s/climate-change/science-research-data/climate-trends-variability/adjusted-homogenized-canadian-data.html](https://climate-change/science-research-data/climate-trends-variability/adjusted-homogenized-canadian-data.html), accessed August 2021).

The two lakes are of similar size ($\sim 8\text{--}9\text{ km}^2$), although White Bear Lake is deeper ($Z_{\text{max}} = 15$ vs. 8 m) and drains a larger area (172 vs. 60 km^2) than Kenosee Lake (Table 1; Vance et al. 1997; van der Kamp et al. 2008). The catchments of Kenosee and White Bear lakes exhibit poor hydrological integration and neither lake has channelized inflows or outflows. Instead, wetlands, sloughs, and lakes in the Moose Mountain Uplands rely on complex subsurface connections of saline, carbonate-rich groundwater that is eventually discharged on the adjacent prairie surface $\sim 150\text{ m}$ below (Vance et al. 1997). Historically, Kenosee Lake spilled into White Bear Lake when water levels reached over 742 m above sea level (asl), but water conveyance between lakes has not been recorded since 1954 due to water-level low stands (see below) and the construction of a highway between the basins (Godwin et al. 2013).

Land use is similar within catchments of Kenosee and White Bear lakes, with $\sim 55\text{--}57\%$ cover by broadleaf deciduous forest primarily comprised of trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), green ash



Fig. 1. (A) Map of Kenosee and White Bear Lakes with marked coring locations. Coring depths are 7.6 and 9.2 m for Kenosee Lake and White Bear Lake, respectively. Map interpreted from photograph courtesy of the U.S. Geological Survey (Landsat 8 OLI/TIRS database). (B) The location of Kenosee and White Bear lakes in the Moose Mountain Uplands of southeast Saskatchewan in relation to the Province of Saskatchewan (SK) in Canada.

Table 1. Summary of physical and chemical characteristics of Kenosee and White Bear lakes. Surface area (km²) and max depth (m) were obtained from van der Kamp et al. (2008), while physical (Secchi depth), chemical (total phosphorus [TP], total nitrogen [TN], total organic carbon [TOC]), salinity, pH, and Chl *a* were measured once per month from Jun to Sep in 2016 (mean $\pm$ standard deviation).

Site	Kenosee Lake	White bear Lake
Surface area (km ²)	8	9
Drainage area (km ²)	60	172
Maximum depth (m)	8	15
Lake-level elevation (m asl)	741	729
TN ($\mu\text{g}\cdot\text{L}^{-1}$)	2048 $\pm$ 38	2533 $\pm$ 116
TP ($\mu\text{g}\cdot\text{L}^{-1}$)	27.50 $\pm$ 9.57	14.46 $\pm$ 10.41
TOC ($\text{mg}\cdot\text{L}^{-1}$)	26.75 $\pm$ 0.44	35.03 $\pm$ 1.97
Chl <i>a</i> ($\mu\text{g}\cdot\text{L}^{-1}$)	9.44 $\pm$ 4.41	8.40 $\pm$ 7.79
Salinity ($\text{g}\cdot\text{L}^{-1}$)	1.07 $\pm$ 0.03	1.84 $\pm$ 0.06
pH	8.58 $\pm$ 0.14	8.72 $\pm$ 0.07
Secchi depth (m)	1.84 $\pm$ 1.36	2.58 $\pm$ 1.07

(*Fraxinus pennsylvanica*), white birch (*Betula papyrifera*), and Manitoba maple (*Acer negundo*; Henderson et al. 2002), $\sim$ 21–27% cover by other water bodies, $\sim$ 9–10% by grasses and shrubs, and $<$ 1% agricultural cover (Agriculture and Agri-Food Canada 2013). The catchments of Kenosee and White Bear lakes have never been cleared. A portion of the catchment of White Bear Lake is encompassed by White Bear First Nations reserve created in 1875, while the remaining catchment area of both lakes became part of a Canadian federal forest reserve in 1894 and a Saskatchewan provincial park in 1931 (Henderson et al. 2002). Despite these designations and protections, significant recreational development has occurred on the shorelines of both lakes since the 1960s including the construction of cottages and golf courses. Monthly sampling during June–September 2016 showed that both lakes are currently hyposaline, alkaline, and mesotrophic (Table 1). Currently, both basins do not stratify, although nothing is known of the interannual variation in mixing intensity.

Lake-level history

Annual lake-level data for Kenosee and White Bear lakes were recorded by the Government of Canada (Historical Hydrometric Data; https://wateroffice.ec.gc.ca/mainmenu/historical_data_index_e.html, accessed April 2021) between 1964 and 2016. Values for White Bear Lake between 1910 and 1964 were obtained from Cullimore and Griffin (1979). While no data are available regarding Kenosee Lake's water-levels prior to 1964, a strong linear relationship between lakes levels since 1964 ($R^2 = 0.72$, $p < 0.0001$) suggest that both basins would have experienced similar degrees of lake-level variation during the early 20th century.

Paleolimnological analyses

Sediment cores were collected from deep-water sites from Kenosee and White Bear lakes using a Glew gravity corer (Glew 1989) in August 2016 (Fig. 1). The Kenosee Lake core was collected at $\sim$ 7.6 m depth (49°49.455'N, 102°18.882'W) and was $\sim$ 57 cm in length, while the White Bear Lake core was taken at $\sim$ 9.2 m depth (49°49.455'N, 102°18.882'W) and was $\sim$ 56-cm long. Both cores were sectioned on site at 0.5-cm intervals, stored in the dark on ice during transport, and refrigerated until analysis within 4 months of collection. Sediments from the top 40 cm of each core were freeze-dried (72 h, 0.1 Pa) for subsequent analyses of ²¹⁰Pb and ¹³⁷Cs activities, stable isotope content (carbon [C], nitrogen [N]), and pigment biomarker concentrations in the Institute of Environmental Change and Society at the University of Regina.

Sediment chronology was based on ²¹⁰Pb and ¹³⁷Cs activities quantified using gamma spectrometric analysis of 12 evenly spaced sections of each core (Appelby et al. 1986). Sediment age and mass accumulation rates ($\text{g cm}^{-2} \text{ yr}^{-1}$) were calculated using the constant rate of supply (CRS) model (Binford 1990). Sediment age-depth relationships were refined using shape-constrained additive models (SCAMs) with monotone decreasing P-splines via the *scam* package (Pya 2021) with generalized cross-validation smoothness parameter selection in R (R Core Team 2021).

Whole dried sediments were analyzed for stable isotope ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) and elemental content (N%, C%) by combustion using a Thermoquest Delta Plus isotope ratio mass spectrometer equipped with a Thermoquest NC2500 elemental analyzer (Savage et al. 2004). Carbon and nitrogen isotope values were standardized against international standards (Pee Dee Belemnite and atmospheric N₂, respectively) and expressed using standard ‰ notation. Elemental composition of whole sediments were estimated as % dry mass for N (N%) and C (C%) content, and were used to estimate C : N mass ratios.

High-performance liquid chromatography (HPLC) was used to quantify fossil pigment concentrations from alternate sediment sections in the Kenosee and White Bear cores following Leavitt and Hodgson (2001). Pigments were extracted from 15 to 100 mg of freeze-dried sediments by an 80 : 15 : 5 (by volume) solution of HPLC-grade acetone, methanol, and water. Extracts were filtered (0.22- μm pore) and evaporated under inert N₂ gas, before being redissolved into injection solution. Concentrations of fossil pigments were measured using an Agilent model 1260 HPLC calibrated with authentic pigment standards and using Sudan II as an internal reference. Pigment interpretation followed Leavitt and Hodgson (2001) with concentrations of chlorophyll *a* (Chl *a*) derivative pheophytin *a*, and β -carotene used as indicators of total phototroph abundance (Leavitt and Hodgson 2001). Other taxon-specific pigments included fucoxanthin (siliceous algae), diatoxanthin (primarily diatoms), alloxanthin

(cryptophytes), pheophytin *b* (chlorophytes), echinenone (total cyanobacteria), and canthaxanthin (Nostocales cyanobacteria). Lutein and zeaxanthin could not be separated and were combined as indicators of bloom-forming taxa (Leavitt and Hodgson 2001). In addition, okenone was used as an indicator of purple sulfur bacteria (Leavitt et al. 1989; Leavitt and Hodgson 2001). All pigment concentrations were expressed as nmoles pigment g^{-1} carbon (Leavitt et al. 1994). The ratio of Chl *a* to pheophytin *a* (Chl : pheo) was used as a metric of changes in preservation environment (Leavitt and Hodgson 2001), while the ratio of UVR-absorbing scytonemin derivatives to the sum of other carotenoids (alloxanthin, lutein-zeaxanthin, diatoxanthin) was used as an index of past exposure to UV irradiance (Leavitt et al. 1997).

Numerical analyses

Temporal trends in pigment and other geochemical proxies were estimated using generalized additive models (GAMs) using the *mgcv* package (Wood 2011, 2017; Simpson 2018). Specifically, pigment concentrations were estimated using a location-scale hierarchical GAM (HGAM) where both the mean and scale predictors used a global smooth of year and a factor smooth for each combination of the 2 lakes and

10 pigments for a total of 20 factors (model GS in Pedersen et al. 2019). The global smooth accounted for the common trend between both lakes and all pigments, while the factor smooth accounted for the deviations at the pigment and lake level from the global smooth. The model deviations were fit assuming a common smoothness parameter between lakes and pigments, but do not account for common trends between lakes or pigments separately. Both the global smooth and the factor smooth were fit using cubic regression splines. Finally, the scale predictor also accounted for the period of time represented by each core slice to account for changes in temporal averaging between adjacent samples. This was facilitated with the addition of a smooth of each sample's log-transformed temporal interval and by fitting the smooth with adaptive splines.

Pigment variances were extracted from pigment concentrations by calculating the product of the mean and shape estimates from the concentration HGAM. Credible intervals (95%) for the variance values were obtained by running 10,000 simulations and taking the 2.5% and 97.5% quantiles of the posterior distributions. Resultant pigment variances were also modeled using an HGAM under the same parameters as described above. In addition, Chl : pheo ratios and UV indexes were modeled individually using HGAMs with Gamma and Tweedie distributions, respectively. Both models used a smooth for year and lake, such that each lake had a different smoothness parameter (model I in Pedersen et al. 2019). In all models, observations were weighted by temporal resolution and the smoothness parameter was estimated using a restricted maximum likelihood approach (Simpson 2018). To identify periods of significant change, the first derivative of the estimated smooth trend was evaluated from the relevant model of each proxy (Bunting et al. 2016; Simpson 2018). Here, the first derivative of each proxy smooth was estimated using the *gratia* package in R (Simpson 2021). Periods of significant change were identified where the 95% credible interval on the estimated derivative excluded 0.

All statistical analyses were performed in the R statistical environment (R Core Team 2021). The *tidyr* and *dplyr* packages (Wickham 2021; Wickham et al. 2021) were used for data wrangling, while plots were created using the *ggplot2* and *cowplot* packages (Wickham et al. 2016; Wilke 2020). Code for analyses is available on GitHub at <https://github.com/simpson-lab/kenosee-white-bear>.

Results

Lake-level

Historical records suggested that both Kenosee and White Bear lakes experienced water-level variation of > 8 m since the early 20th century (Fig. 2). Taking the first common year of record (1964) as a benchmark, water levels in White Bear Lake were ~ 4 m higher between ~ 1910 and ~ 1930 before

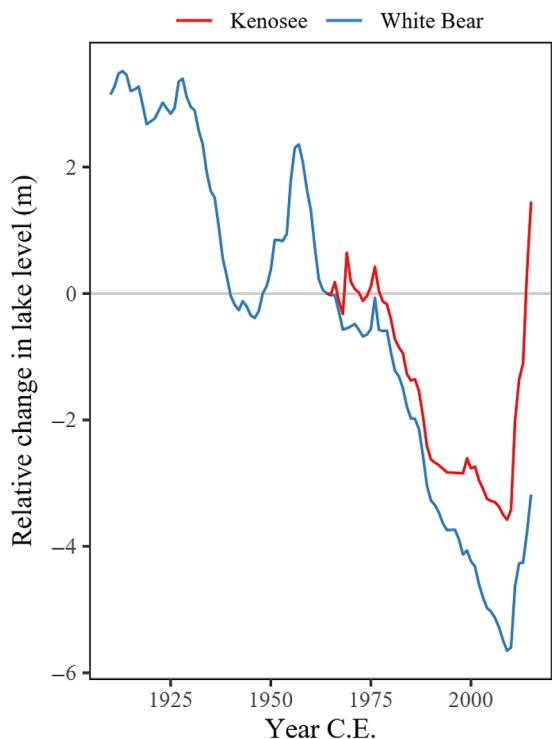


Fig. 2. Water levels of Kenosee Lake (red) and White Bear Lake (blue) relative to their levels in 1964. Data from 1964 to 2015 were obtained from the Government of Canada Water Office; data prior to 1964 for White Bear Lake were obtained from estimates from Cullimore and Griffin (1979).

declining toward a plateau by 1950. While lake levels rose ~ 2 m during the 1950s, values declined again to the late 1960s. The water levels of both lakes were stable until ~ 1975 when marked declines of up to 6 m and 3 m occurred in White Bear and Kenossee lakes, respectively. Water levels reached a minimum at ~ 2010 (-4 to -5.5 m) before rapidly rising by 2 m in White Bear Lake and 4 m in Kenossee Lake in recent years (Fig. 2). Given the strong

correlation between Kenossee and White Bear lake levels since 1964 ($R^2 = 0.72$, $p \leq 0.0001$), it is likely that Kenossee Lake experienced similar water-level fluxes prior to 1964. Together, these findings suggest that Kenossee and White Bear lakes have experienced water-level variations equivalent to $\sim 75\%$ and $\sim 55\%$ of their present depth, respectively, with only very recent increases toward historical benchmarks (Fig. 2).

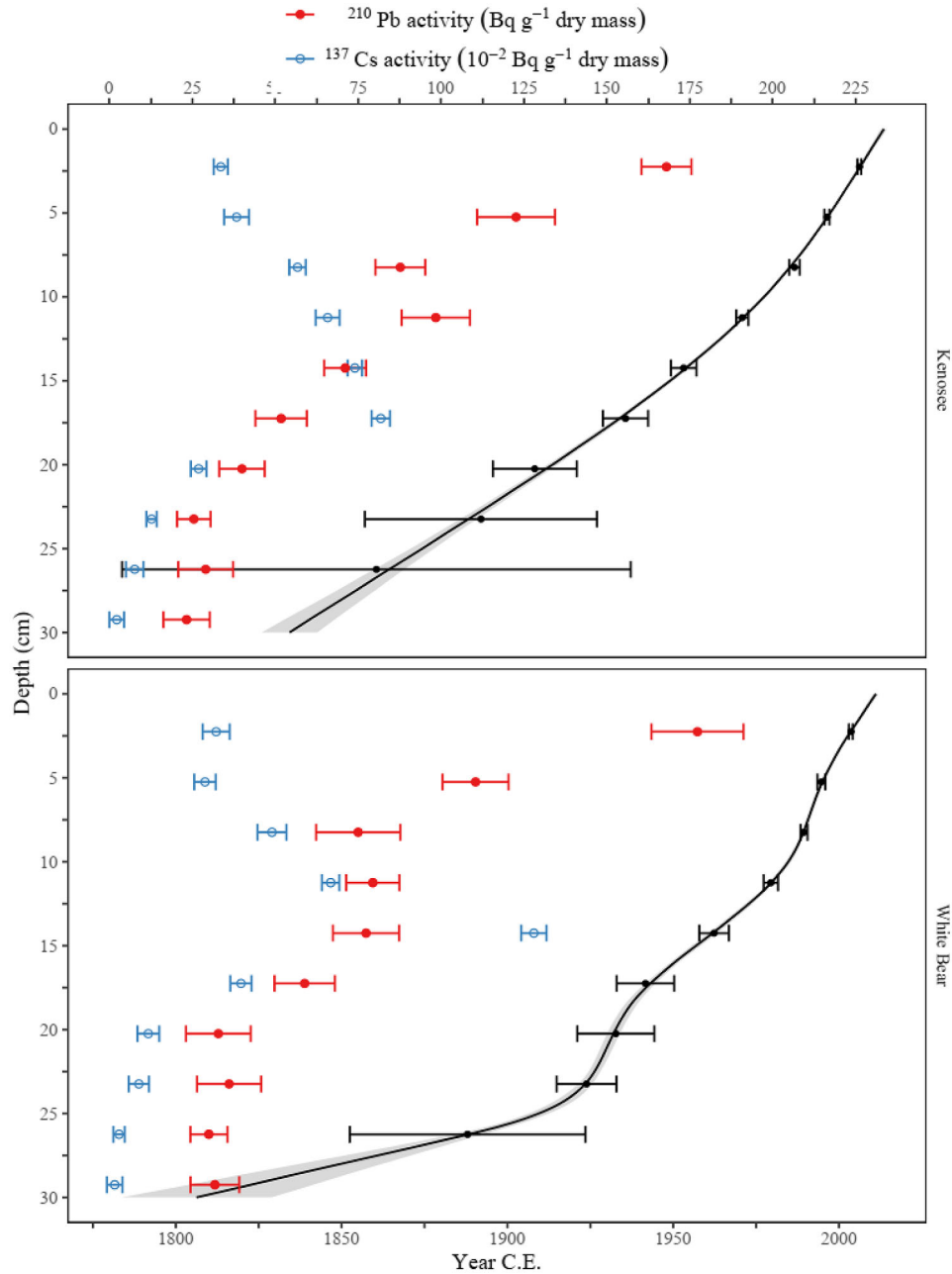


Fig. 3. Activities of ^{210}Pb and ^{137}Cs with associated error estimates (1σ) by core depth for Kenossee Lake and White Bear Lake. Age-depth relationships were estimated using SCAMs (shape-constrained additive models)-based CRS (constant rate of supply) models of ^{210}Pb activity in each core. Inferred dates are also presented with error ranges (1σ) by core depth for Kenossee Lake and White Bear Lake.

Sediment chronology

Activity of ^{210}Pb declined with sediment depth in the Kenosee and White Bear cores with little evidence of sediment mixing (Fig. 3). Activity profiles of ^{137}Cs were well defined in White Bear Lake sediments, with a clear maximum in ^{210}Pb -dated intervals corresponding to peak atmospheric nuclear testing in 1963 at 14 cm (Fig. 3). The ^{137}Cs peak was less well defined in Kenosee Lake, with a maximum at ~ 17 cm. Age-depth models suggested that bulk dry sediment accumulation rates were comparable between sites, whereas SCAMs based on the CRS models suggest that ages at ~ 30 cm were essentially the same; ~ 1830 and ~ 1810 for Kenosee and White Bear lakes, respectively (Fig. 3).

Geochemistry and stable isotopes

Geochemical trends in stable isotope values were generally similar in the cores from Kenosee and White Bear lakes (Fig. 4). In both cores, C and N content (% by mass) was low prior to ~ 1930 , but rose rapidly afterward to a transient

plateau ca. 1950–1975, before continuing to historical maxima in the most recently deposited sediments. The C : N ratios of both lakes exhibited an inverse relationship to C and N content, with stable values of ~ 18 prior to 1900, declining to a plateau before accelerating to a minimum after ca. 2000 (Fig. 4). Sedimentary $\delta^{13}\text{C}$ values were relatively stable and elevated at both sites before ~ 2000 ($\sim 15\text{‰}$), after which isotope values declined to $\sim -22.5\text{‰}$ in both lakes (Fig. 4). In contrast, trends in $\delta^{15}\text{N}$ were markedly different between lakes. In Kenosee Lake, $\delta^{15}\text{N}$ ratios decreased from $\sim 6\text{‰}$ to $\sim 4\text{‰}$ after approximately 1925 before returning to more enriched values after ~ 1960 (Fig. 4), whereas in White Bear Lake, $\delta^{15}\text{N}$ ratios continue to decline after ~ 1960 with depletions to $\sim 2\text{‰}$ in sediments deposited since ca. 2000 (Fig. 4).

Phototrophic pigments

Analysis of sedimentary carotenoid and chlorophyll pigments revealed significant changes in the composition, concentration, and variance of primary producers over the

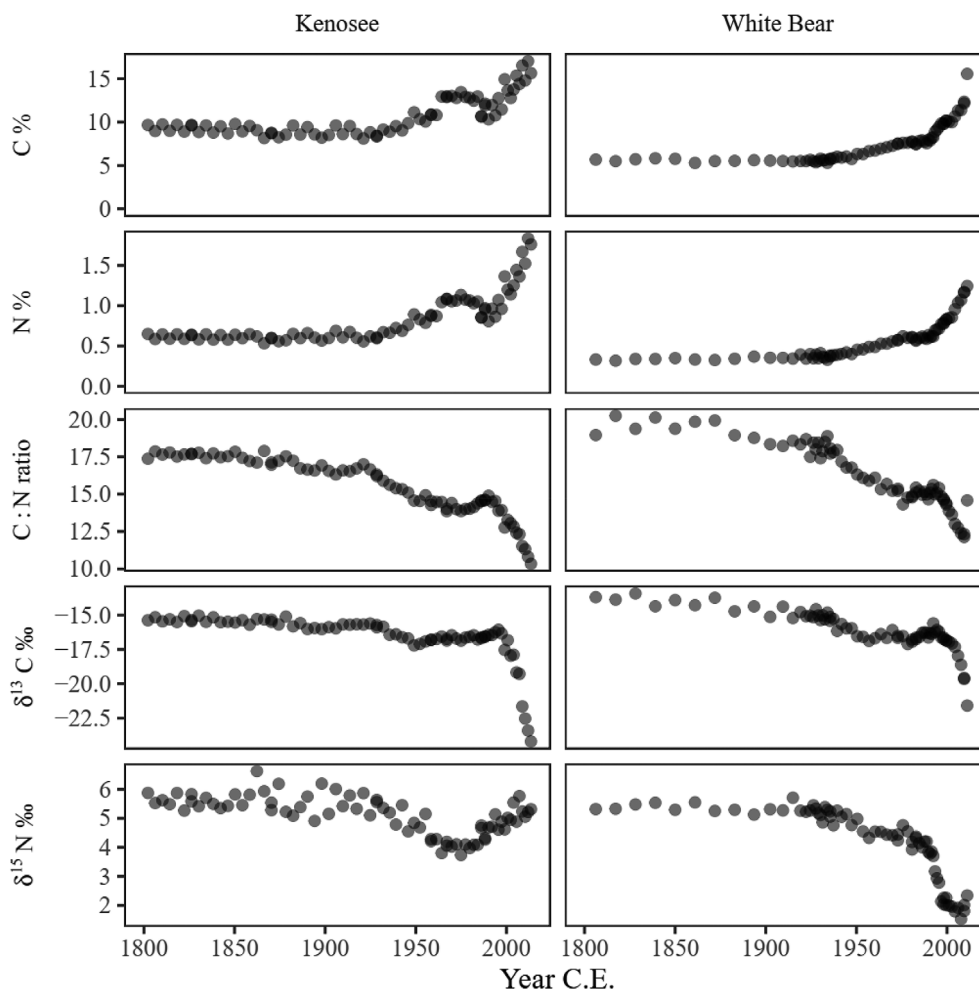


Fig. 4. Carbon (C%) and nitrogen (N%) content, C : N ratios, and stable isotope ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) plotted by year for Kenosee Lake and White Bear Lake.

past ~200 yr of Kenosee and White Bear lakes (Fig. 5). In these analyses, significant changes refer to periods of time when the slope (i.e., the first derivative) of pigment concentrations and variances are statistically significant from 0 (see the Methods section). In Kenosee Lake, concentrations of pigments indicative of siliceous algae (fucoxanthin), diatoms (diatoxanthin), cryptophytes (alloxanthin), chlorophytes (pheophytin *b*), and other bloom-forming taxa (lutein-zeaxanthin) were generally low, but did show periods of significant increase prior to ~1900. Abundances of chlorophytes (pheophytin *b*) increased significantly after ~1900, with the largest changes occurring after ~1930, concomitant with lake-level fall, whereas densities of diatoms (diatoxanthin),

cryptophytes (alloxanthin), and bloom-forming taxa (lutein-zeaxanthin) increased significantly across the 20th century with periods of minor declines centered at ~1975 and additional decreases in lake level (Figs. 2, 5). Trends in these phytoplankton were similar in White Bear Lake sediments, with the exception of a slightly delayed onset of significant increases at ~1930 (Fig. 5). In that lake, diatoxanthin exhibited distinctly high concentrations prior to 1900, but declined throughout the 20th century with statistically significant intervals of decline at ~1930 and ~1970 (Fig. 5).

In Kenosee Lake, concentrations of pigments from cyanobacteria (echinenone and canthaxanthin) were relatively elevated at ~1800 and rose significantly to ~1850 before

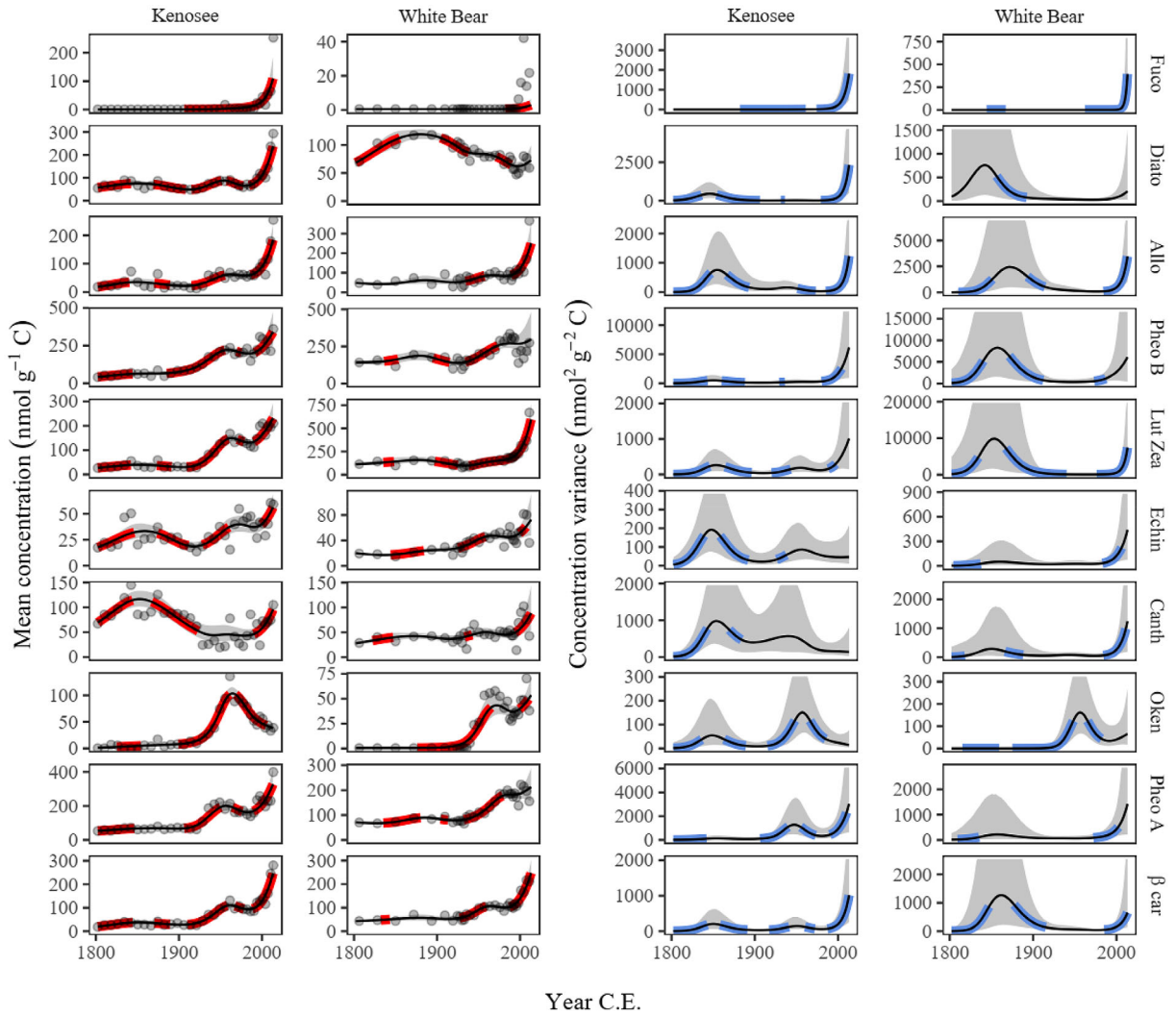


Fig. 5. Mean concentrations (left) and concentration variances (right) of fossil pigments by year in sediments from Kenosee Lake and White Bear Lake. Pigment mean concentrations and concentration variances are fitted with hierarchical generalized additive models (HGAMs). In all plots, solid lines are the fitted model trends, gray shading represents 95% confidence intervals of the trends, and emboldened sections of the trends represent significant changes in pigment mean concentration or concentration variance. Fuco = fucoxanthin (siliceous algae), Diato = diatoxanthin (primarily diatoms), Allo = alloxanthin (cryptophytes), Pheo B = pheophytin *b* (chlorophytes), Lut Zea = lutein-zeaxanthin (chlorophytes and cyanobacteria pigments, i.e., “bloom-forming” taxa), Echin = echinenone (total cyanobacteria), Canth = canthaxanthin (Nostocales cyanobacteria), Oken = okenone (purple sulfur bacteria), Pheo A = pheophytin *a* (total production), β car = β -carotene (total production).

declining significantly to 1900 (Fig. 5). Abundance of total cyanobacteria (echinenone) then rose significantly from ~ 1930 to 1950 alongside falls in lake level (Figs. 2, 5). In contrast, potentially N_2 -fixing colonial cyanobacteria (canthaxanthin) declined throughout the early 20th century, reaching stable and relatively low concentrations between ~ 1930 and 2000 before rising significantly after ~ 2000 (Fig. 5). Concentrations of both pigments were low in White Bear Lake prior to 1900, despite periods of significant increases during this time, and slowly rose over the 20th century, with significant increases in echinenone at ~ 1930 –1950 alongside declines in lake level (Figs. 2, 5). In both lakes, concentrations of okenone from obligately anaerobic purple sulfur bacteria were negligible prior to ~ 1900 , but increased substantially during the early 20th century and reached maxima at ~ 1950 , a period of stable water levels at both sites (Figs. 2, 5). Thereafter, concentrations of okenone declined significantly in Kenosee lake during periods of lake-level increase (~ 1950 –1970) and subsequent decline (~ 1970 –2010) (Figs. 2, 5). These declines in okenone concentration did not reach pre-1900 minimum values. In White Bear Lake, concentrations of okenone

plateaued during ~ 1950 –2000 despite substantial lake-level changes, before rising significantly thereafter (Figs. 2, 5). In addition, overall biomarkers of total phototroph production (pheophytin *a*, β -carotene) were relatively stable before ~ 1900 , but increased significantly between ~ 1900 and 1950 in Kenosee Lake and between ~ 1930 and 1970 in White Bear Lake (Fig. 5). Maximum values of these pigments occurred in both lakes after ~ 2000 , coeval with recent increases in lake levels (Figs. 2, 5).

Temporal trends in variance of primary producers were similar in Kenosee and White Bear lakes sediments (Fig. 5). At both sites, variance of diatoms (diatoxanthin), cryptophytes (alloxanthin), and green algae (pheophytin *b*, lutein) was elevated during the mid-19th century, centered at ~ 1840 –1860, before declining significantly to low values by 1900 (Fig. 5). Variance measures of these phytoplankton remained low through the period of lake-level variation during the 20th century before increasing significantly after ~ 2000 (Figs. 2, 5). In Kenosee Lake, variance in cyanobacterial abundance (echinenone, canthaxanthin) increased significantly prior to ~ 1850 then significantly declined to low values by 1900

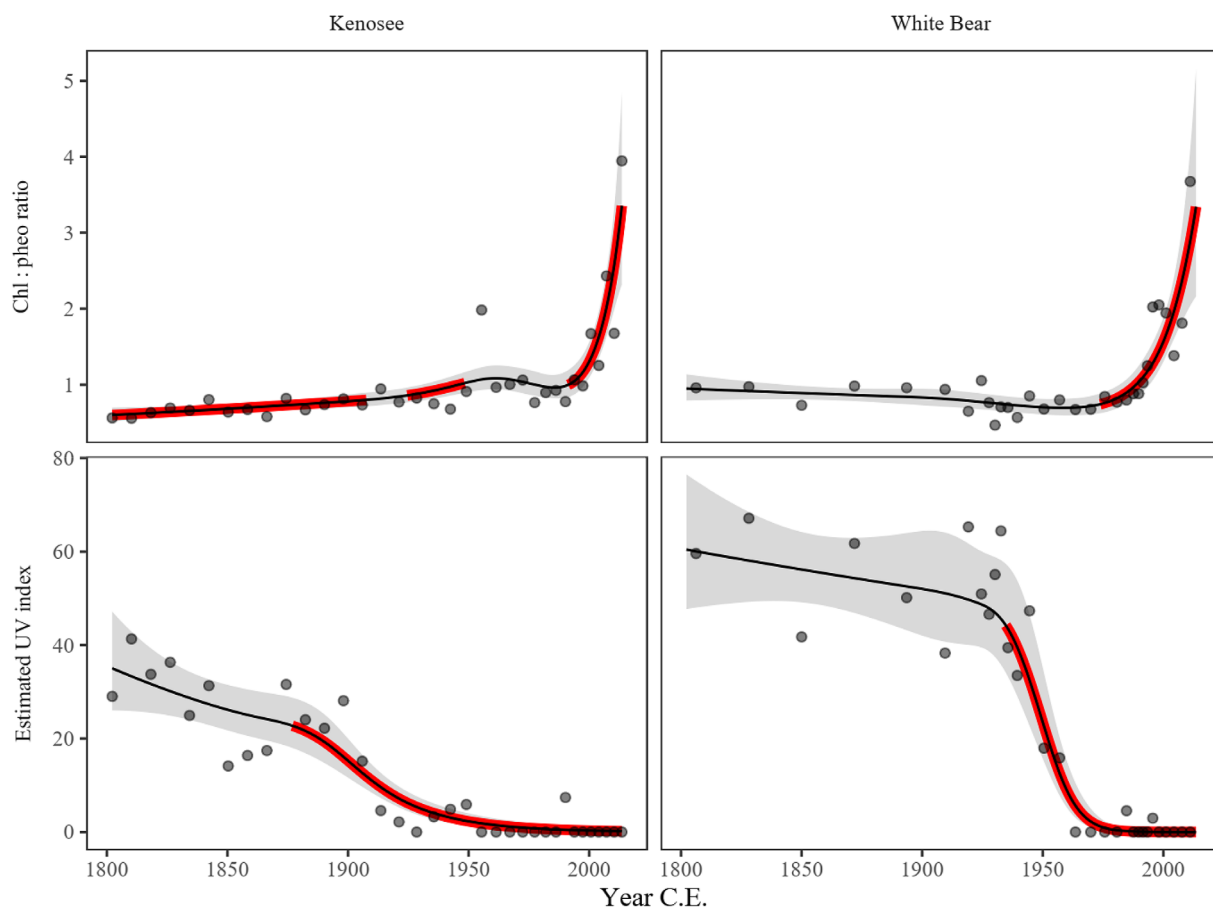


Fig. 6. Precursory Chl *a* to derivative pheophytin *a* (Chl : pheo) ratios and estimated UV index values plotted by year for Kenosee Lake and White Bear Lake. In all plots, solid lines are the fitted model trends, gray shading represents 95% trend confidence intervals, and emboldened sections represent periods of significant change.

(Fig. 5). In White Bear Lake, 19th century changes in variance of these pigments were much less marked, although still significant increases in cyanobacterial variance were recorded up to ~1850 (Fig. 5). Similarly, variance in purple sulfur bacteria (okenone) differed between lakes before ~1900, with slightly elevated values in Kenosee in the mid-19th century, but consistently low variance in White Bear Lake during the same interval (Fig. 5). Changes in okenone variance were more coherent between lakes after ~1900, rising significantly between ~1930 and ~1950 during the period of lake-level decline (Figs. 2, 5). These peaks in okenone variance were short-lived and declined significantly to ~1975, a period of substantial lake-level variation. In contrast to other pigments, variation in okenone time series did not rise again during late 20th century periods of lake-level decline, nor did it increase significantly when lakes refilled after ~2010 (Figs. 2, 5). Finally, there were few common patterns of historical change in variation of total primary producers (pheophytin *a*, β -carotene), with a higher amount of significant variance changes across the 20th century in Kenosee Lake and more significant changes during the 19th century at White Bear Lake (Fig. 5). In both basins, variance of these pigments rose significantly after ~2000 (Figs. 2, 5).

Analysis of changes in preservation environment (as Chl : pheo ratios) suggested that there was little variation in sedimentary pigment preservation in either lake until the most recently deposited sediments (Fig. 6). Although changes in Chl : pheo ratios were significant in Kenosee Lake for the first 150 yr of the record, these changes were minor relative to those seen after ~2000. Reconstruction of the UVR index suggested that phytoplankton were exposed to relatively high levels of UV radiation during the 19th century, but that exposure declined significantly through the 20th century, culminating in minimum values in the recent sediments of both lakes (Fig. 6).

Discussion

Kenosee and White Bear lakes have experienced lake-level variability of > 8 m during the last century (Fig. 2), likely reflecting rising regional temperatures, increased evaporation, and complex interactions between Arctic, Gulf, and Pacific air masses which affect regional snowpack, spring runoff, and groundwater availability (Bonsal et al. 2006; Pomeroy et al. 2007; Liu et al. 2008; van der Kamp et al. 2008; McCullough et al. 2012). Lake-level decline was marked by coeval increases in primary production beginning ca. 1930, including elevated abundance of total phytoplankton, diatoms, cryptophytes, and chlorophytes (Fig. 5), concomitant increases in sedimentary C and N content (Fig. 4) and bulk sedimentation rates (Fig. 3). However, despite increasing temperatures and loss of over 50% of lake depth, neither total nor colonial diazotrophic cyanobacteria increased substantially during the 20th century relative to prior levels (Fig. 5). Instead,

fossil concentrations of okenone from anaerobic purple sulfur bacteria increased in both lakes during ~1930–1950 (Fig. 5), showing that light penetrated to anoxic habitats during this interval (Pfennig 1978; Leavitt et al. 1989). While variance in total primary production did not increase substantially prior to the development of illuminated anoxic habitats during intervals of stable and low lake level, temporally coherent and significant increases in okenone variance occurred during lake-level declines between ~1930 and 1950 suggesting that the development of illuminated and anoxic habitats in both Kenosee and White Bear lakes may represent a regime shift with respect to bacteria and physical lake structure (Scheffer et al. 2001; Dakos et al. 2015). These patterns are consistent with the establishment of bacterial plates within transient chemoclines following lake-level decline and evaporative concentrations of solutes in deep waters (Leavitt et al. 1989; Vinebrooke et al. 1998; Pham et al. 2009). This novel physical lake structure does not appear to represent an alternate stable state, as subsequent and substantial changes in lake-level restricted the anoxic and illuminated environments and suggests that any possible regime shift was transient and lacked hysteresis (Dakos et al. 2015; Ratajczak et al. 2018). Regardless, these abrupt changes in lake level, mixing, oxygenation, light penetration, and biotic structure may become more common in the Northern Great Plains, where future climate change is expected to increase evaporative forcing by 2050 due to a ~5°C warming and only a modest (< 5%) increase in precipitation (Asong et al. 2016; Sauchyn et al. 2020).

Climate forcing of upland lakes

Lake levels at Kenosee Lake and White Bear Lake declined > 8 m since 1910 (Fig. 2). While extraordinary relative to many boreal lakes, such large excursions are common in the Northern Great Plains (Fritz 1990; van der Kamp et al. 2008) due to water deficits (precipitation-evaporation) ranging -20 to -60 cm yr⁻¹ (Pham et al. 2009; Haig et al. 2020, 2021), and pronounced shifts in the relative importance of winter air masses that control the hydrodynamics of snow accumulation and melting (Bonsal et al. 2006; Pomeroy et al. 2007; Liu et al. 2008). In the Canadian Prairie region, > 70% of annual precipitation falls as summer rain, but up to 80% of regional runoff is derived from spring snow melt (Akinremi et al. 1999). This snowmelt recharges surface and intermediary-depth aquifers (van der Kamp and Maathuis 1991) that can also contribute water to some prairie and parkland lakes (Shaw and Prepas 1990). In general, regional precipitation is regulated by a complex interplay between air masses from the Arctic, Pacific Ocean, and Gulf of Mexico (Bryson and Hare 1974) that is additionally influenced by the El Niño-Southern Oscillation, North Atlantic Oscillation, and Pacific Decadal Oscillation climate systems (Trenberth and Hurrell 1994; Hurrell 1995; Mantua et al. 1997). Paleoclimate and modeling analyses reveal that centennial- and continental-scale variation in these air masses

affect the position of the winter jetstream and, in turn, the precipitation supply which creates decadal-scale changes in runoff, lake level, and salinity (Fritz 1990; Michels et al. 2007; Liu et al. 2008; McCullough et al. 2012). Relationships between runoff and lake level are further complicated by the presence of numerous shallow water bodies within lake catchments (Fig. 1) that variously “fill and spill” depending on antecedent meteorological conditions (Coles and McDonnell 2018; Haig et al. 2021). Finally, land-use practices can alter lake levels by channelizing surface flow, removing wetlands, extracting for human use, modifying forests, or through agricultural irrigation (Fang et al. 2007; Mao and Cherkauer 2008).

Patterns of hydrology in White Bear and Kenosee lakes (Fig. 2) are consistent with known variability in regional climate and land-management practices (Vance et al. 1997; Vinebrooke et al. 1998). For example, stable elevated lake levels were recorded in White Bear Lake until onset of the prolonged prairie droughts of the 1920s and 1930s when blocking high pressure cells reduced the influx of moisture from the Gulf of Mexico (Bonsal et al. 2006). Lake levels recovered briefly during the 1950s before declining again to a plateau until the early 1970s. These events correspond to rapid changes between arid and pluvial conditions during the 1950s and 1960s (Henderson et al. 2002). After ~1970, lake levels declined continuously until the early 21st century, reflecting a both 0.95 cm yr⁻¹ decline in prairie winter precipitation during this interval (Akinremi et al. 1999; Henderson et al. 2002) and local water management practices which included water extraction for nearby golf courses and the construction of a highway that restricted flow between adjacent waterways, including Kenosee and White Bear lakes (Godwin et al. 2013). Finally, sudden recent increases in lake level of 2–4 m may reflect changes in the supply of moisture into the region, similar to the step-change increase in precipitation and runoff in nearby Manitoba during the 1990s (McCullough et al. 2012; Dumanski et al. 2015). In this case, delays in lake-level response (Fig. 2) may arise because antecedent arid conditions created substantial hydrological sinks in both lakes’ catchments by lowering water levels in many small water bodies (Fig. 1). The presence of empty hydrological sinks decoupled precipitation and runoff until the sinks were filled and regained a steady state (“fill and spill”) exchange of influx and outflow of water (Coles and McDonnell 2018; Haig et al. 2021), although further local research is needed to validate this mechanism.

Phototroph response to lake-level declines

Analysis of chemically stable algal and cyanobacterial pigments revealed similar increases in primary production in Kenosee and White Bear lakes during the 20th century (Fig. 5). Specifically, when analyzed using GAMs, mean concentrations of biomarkers for diatoms (diatoxanthin), cryptophytes (alloxanthin), chlorophytes (pheophytin *b*, lutein), total

cyanobacteria (echinenone), and all primary producers (pheophytin *a*, β -carotene) increased significantly from ~1930 until the 21st century, although onset of eutrophication was delayed in White Bear Lake, compared to signals from Kenosee Lake (Fig. 5). Elevated lake production is consistent with trends seen in lowland lakes throughout the Canadian Prairies and normally reflect substantial changes in land use and nutrient influx (Leavitt et al. 2006; Pham et al. 2008; Maheaux et al. 2016). In contrast, catchments of upland Kenosee and White Bear lakes have not been subject to extensive modification, beyond shoreline development, suggesting that more extensive algal growth arose because of marked lake-level declines after ~1930 and ~1975 (Fig. 2). Although speculative, we note that shallow lakes are usually more productive than deeper basins of given size (Jeppesen et al. 2014) due to a higher fraction of profundal sediments in contact with warm surface waters and consequently elevated rates of internal nutrient loading (Søndergaard et al. 2013). Furthermore, phytoplankton production in prairie lakes can increase when evaporation concentrates epilimnetic nutrients and other solutes (Oduor and Schagerl 2007; Wissel et al. 2011; Vogt et al. 2018).

Historical variation in geochemical and isotopic sediment features were generally comparable in Kenosee and White Bear lakes and were consistent with pigment inferences of increased lake production after ~1930 (Figs. 3, 4). Specifically, variation in C and N content were inversely correlated with White Bear Lake water levels ($R^2_{\text{adj}} = 0.76, 0.89$), whereas C : N mass ratios varied with lake level until the ~2010 minimum. Similarly, bulk sedimentation in White Bear Lake, and to a lesser extent Kenosee Lake, exhibited marked acceleration during intervals of declining lake level in the 20th century, with more modest rates of accumulation between ~1940 and 1970 when lake levels were generally stable beyond a transitory 2 m change during the 1950s (Fig. 3). Together, these patterns are consistent with increased deposition of organic matter resulting from elevated autochthonous primary production (Meyers and Teranes 2001), as recorded by coeval declines in C : N ratios from values characteristic of terrestrial plants (C : N ~20–25) to those associated with autochthonous organic matter (C : N ~8–12; Gu et al. 2006; Woodward et al. 2012). Depleted $\delta^{13}\text{C}$ values in both lakes are also consistent with elevated in situ primary production during the 20th century, reflecting increased photosynthetic uptake of isotopically depleted CO_2 from respired in situ sources (Meyers and Teranes 2001; Woodward et al. 2012) as seen in other eutrophied prairie lakes (Bunting et al. 2016).

Unlike most biogeochemical proxies, late 20th century measures of nitrogen cycling (as $\delta^{15}\text{N}$) differed between Kenosee and White Bear lakes, with sedimentary enrichment at the former site and depletion at the latter (Fig. 4). In general, historical patterns of $\delta^{15}\text{N}$ were correlated strongly with concentrations of okenone from purple sulfur bacteria ($R^2_{\text{adj}} = 0.79, p < 0.0001$), taxa known to fix nitrogen in

illuminated anaerobic habitats (Madigan 1995). We infer that cyanobacteria did not contribute substantially to fixed N pools (c.f., Hayes et al. 2019), as concentrations of canthaxanthin from potentially diazotrophic cyanobacteria (Leavitt and Hodgson 2001; Hayes et al. 2019) were uncorrelated to historical variation in $\delta^{15}\text{N}$ values (Figs. 3, 5). Thus, while it is possible that enhanced shoreline development since the 1960s (e.g., cottages and golf courses) may have added isotopically enriched N from fertilizers or wastes (Botrel et al. 2014), the absence of common patterns in $\delta^{15}\text{N}$ of the lakes since the 1960s is more consistent with differential supply of fixed N from diazotrophic purple sulfur bacteria.

Historical variation in Nostocales cyanobacteria (canthaxanthin) did not show a close correspondence to either observed changes in lake levels (Fig. 2) or other sediment proxies of lake production (Figs. 3–5), despite cyanobacterial preference for warm, nutrient-rich, shallow conditions (Paerl and Paul 2012; Vogt et al. 2018), their presence in the current phytoplankton (Bos et al. 2019), and fossil concentrations which were similar those in other regional eutrophic lakes (Leavitt et al. 2006; Bunting et al. 2016; Maheaux et al. 2016). For example, Nostocales were most abundant in Kenosee Lake during the 19th century and declined to stable low values until the 2000s, whereas this group varied little over the past 200 yr in White Bear Lake until recent years (Fig. 5). While we currently lack a definitive mechanistic explanation for either the 19th century maximum in Kenosee Lake, or the marked difference with nearby White Bear Lake, anecdotally low water levels during the late 19th century (Henderson et al. 2002) may have favored anthropogenic eutrophication either from initial settler recreational activities, or cultural use of the lakes by regional First Nations. Although further research is required to resolve the reasons for elevated cyanobacteria during the 19th century, the absence of marked increases in Nostocales during the 20th century contrasts sharply with other lakes that similarly underwent pronounced eutrophication and/or regime shifts (Scheffer et al. 2001; Carpenter and Brock 2006; Bunting et al. 2016).

Preferential increases in eukaryotic phytoplankton (diatoms, cryptophytes, and chlorophytes) over cyanobacteria during the past 200 yr appears to have reduced the mean exposure of phototrophs to UV radiation (Fig. 6). In general, changes in UVR exposure were unrelated to observed lake levels. Significant declines in UVR indices occurred earlier (late 1800s) in Kenosee Lake than in White Bear Lake (~ 1930), similar to timing of significant increases in biomarkers from eukaryotic phytoplankton and declines in lake level (Figs. 2, 5, 6). We infer that reduced UVR exposure arose from progressive, but slightly asynchronous, eutrophication of both lakes, as declines in lake level should have increased mean UVR exposure. Similar declines in UVR exposure are recorded elsewhere in lakes undergoing cultural eutrophication (Stevenson et al. 2016).

Concentrations of most fossil pigments increased significantly after ~ 2000 in both Kenosee and White Bear lakes

(Fig. 5), concomitant with 2–4 m increases in lake level (Fig. 2). In part, these changes reflect post-depositional pigment transformation, as indicated by rapid changes in Chl : pheo ratios in sediments deposited since ~ 2000 (Fig. 6). Such first-order decay is observed in sediments of other prairie lakes (Patoine and Leavitt 2006), but is usually restricted to labile pigments with oxygen- or N-rich functional groups (e.g., Chl *a*, fucoxanthin, and peridinin) rather than less-substituted hydrocarbons (e.g., β -carotene, alloxanthin, diatoxanthin, lutein-zeaxanthin, etc.; Cuddington and Leavitt 1999; Leavitt and Hodgson 2001). Given that chemically stable pigments also increased markedly toward the surface of the core, we infer that both Kenosee and White Bear lakes may be undergoing modern eutrophication, possibly reflecting increased nutrient transfer from the landscape due to increased runoff and subsequent lake-level rise (McCullough et al. 2012; Tanzeeba and Gan 2012; Asong et al. 2016). Furthermore, elevated concentrations of stable phototrophic biomarkers (e.g., ubiquitous β -carotene) in recent sediments from both study lakes are also consistent with documented water quality problems in both Kenosee and White Bear Lakes since 2000, including the formation of algal blooms (Godwin et al. 2013; Bos et al. 2019).

Evidence of possible regime shifts in upland lakes

Declines in regional lake level between ~ 1930 and ~ 1950 resulted in the formation of illuminated, anoxic, deep-water habitats that were ideal for the proliferation of obligately anaerobic purple sulfur bacteria (Pfennig 1978) in both Kenosee and White Bear lakes (Fig. 5). The development of such bacterial populations between ~ 1930 and 1950 prerequisites either the illumination of anoxic lake sediments (Jørgensen and Postgate 1982; Maheaux et al. 2016) or the formation of strong seasonal or semi-permanent chemoclines resulting from concentrating solutes associated with climate-mediated lake-level decline (Züllig and Rheineck 1985; Leavitt et al. 1989). We infer that permanent meromictic conditions were not established in either Kenosee Lake or White Bear Lake as there were few concomitant changes in the preservation of labile pigments as okenone concentrations increased (Fig. 6), total okenone concentrations were much lower than those seen in fully meromictic systems (Züllig and Rheineck 1985; Leavitt et al. 1989; Vinebrooke et al. 1998), and peak concentrations of okenone in Kenosee Lake were twofold greater than those in White Bear Lake (Fig. 5), as would be expected given the greater illumination of sediments in the shallower lake following lake-level declines (Table 1; Fig. 6). Alternatively, the observation that both lakes are currently hyposaline (Table 1), despite recent increases in lake level (Fig. 2), suggests that salt concentrations were substantially higher during the lake-level low-stands of the 20th century. As shown in other regional lakes, declines in lake level due to evaporative forcing and reduced runoff are associated with higher deep-water salt concentrations that favor establishment

of meromictic conditions in even shallow prairie lakes (Garcés et al. 1995; van der Kamp et al. 2008; Pham et al. 2009).

Alongside increases in pigment concentrations, variance of okenone time series also rose significantly, beginning at ~ 1930 and reaching maximum values at ~ 1950 (Fig. 5). Rising variance has been considered as a predictor of a regime shift in some lake systems undergoing eutrophication (Carpenter and Brock 2006; Bunting et al. 2016), although some work suggests that regime shifts can occur without preceding increases in variance, or that rising variance does not always result in a regime shift (Burthe et al. 2016; Ratajczak et al. 2018). As well, it has been noted that rising variance can also be indicative of changes in the variability of environmental forcing agents (e.g., climate, nutrient flux, etc.), independent of the occurrence of regime shifts (Dakos et al. 2015; Burthe et al. 2016). In our case, as pigment variances were calculated from pigment mean concentrations, an increase or decrease in the latter will result in the change in the former, making it difficult to assess the validity of any possible regime changes. Furthermore, differences in temporal averaging of core sediments (yr cm^{-1}) due to physical compression of deposits also makes it difficult to evaluate whether rising variance is truly antecedent to the peak okenone concentrations, despite our attempts to weight samples by temporal resolution in HGAM analyses (see the Methods section). Taken together, these observations suggest that further research is needed to determine how sedimentary records may be used to record changes in variance as a means of distinguishing between abrupt ecosystem changes, regime shifts, or true alternative stable states (Taranu et al. 2018). Regardless, we note that the marked rise in okenone is an unambiguous marker for the establishment of a novel, illuminated, anoxic environment, and that the coeval rise in variance of okenone ca. 1930–1950, but not algal or cyanobacterial pigments, is consistent with potential establishment of an abrupt change in the deep-water environment (Fig. 5). Further research is needed to evaluate these possibilities, including analysis of variance in potential forcing functions, addition of limnological proxies to complement paleolimnological knowledge, and other factors influencing variance (c.f., Bunting et al. 2016).

Periods of illuminated deep-water anoxic habitats appear to have been ephemeral or unstable in both Kenosee and White Bear lakes (Fig. 5). Therefore, in these cases, rising variance does not appear to signal lake transition to an alternate stable state nor represent the establishment of internal feedback mechanisms that favor hysteresis between states (Scheffer et al. 2001; Dakos et al. 2015; Ratajczak et al. 2018). Instead, the $> 8\text{-m}$ rise and fall of lake levels appears to have resulted in a series of novel phototroph communities whose composition reflected extant hydroclimate and lake-level conditions (McCullough et al. 2012; Asong et al. 2016), physical processes such as mixing and light penetration (Garcés et al. 1995; Hodgson et al. 1998), and landscape influences on nutrient supply (Taranu et al. 2015; Bunting et al. 2016). As well,

despite evidence of warming temperatures and increased nutrient concentrations during the 20th century, there was little evidence of increased cyanobacterial populations until after the large concentrations of okenone had abated in the latter half of the century (Fig. 5). These findings are in stark contrast to many studies that highlight increased cyanobacterial production under warm and nutrient-rich conditions such as those present at Kenosee and White Bear lakes (Paerl and Paul 2012; Vogt et al. 2018). We speculate that intervals of reduced mixing, anoxia, or even weak meromixis may have favored internal nutrient supply from sediments that sustained cyanobacteria through the last half of the 20th century (Fig. 5). However, we also note that continued lake-level declines may have eventually restricted anoxic, illuminated habitats and sulfur bacterial growth after 1950, possibly due to the influence of high regional winds (Plancq et al. 2018). This hypothesis is consistent with the more pronounced declines in okenone in shallower Kenosee Lake compared to deeper White Bear Lake (Fig. 5).

Conclusions

Kenosee and White Bear lakes have experienced $> 8\text{ m}$ declines in lake level over the last century due to increased temperature and evaporations rates, combined with variations in climate systems that regulate introduction of moist oceanic air and precipitation (Akinremi et al. 1999; Bonsal et al. 2006; Michels et al. 2007; Pham et al. 2009). Quantification of historical changes in sedimentary stable isotopes, geochemistry, and biomarker pigments suggests that both lakes began to eutrophy during the early 20th century, coeval with documented declines in lake levels (Fig. 2). By the mid-20th century, declines in lake levels and increased solute concentrations allowed the development of illuminated anoxic habitats that allowed expansion of obligately anaerobic purple sulfur bacteria (Züllig and Rheineck 1985; Leavitt et al. 1989). However, despite evidence of eutrophication in biomarkers from eukaryotic phytoplankton, Kenosee and White Bear lakes did not exhibit substantial increases in colonial cyanobacteria, nor the significant increases in temporal variation of primary producers typical of lakes undergoing nutrient-driven regime shifts (Taranu et al. 2015, 2018; Bunting et al. 2016). Instead, the establishment of anoxic habitats for photosynthetic sulfur bacteria was recorded by rising variance only in their biomarker okenone, and suggests that only deep-water habitat and taxa, rather than the entire ecosystem, underwent a transition to a novel structure. Overall, it appears that rising variance of okenone did not constitute either an alternate state change or true regime shift (sensu Burthe et al. 2016; Ratajczak et al. 2018), but instead illustrates that climate-induced changes in lake-level can result in abrupt variation in lake structure that reconfigures deep-water habitats and biological communities (Fig. 5). Given that GCMs predict that the northern Great Plains region will rapidly become more arid in

coming century (Tanzeeba and Gan 2012; Asong et al. 2016; Sauchyn et al. 2020), we anticipate the development of similar deep-water and biotic assemblages in other regional lakes.

Data Availability Statement

Data from this study is open and available on github at <https://github.com/simpson-lab/kenosee-white-bear>.

References

- Agriculture and Agri-Food Canada. 2013. Annual crop inventory. Ottawa, Ontario, Canada. <https://open.canada.ca/data/en/dataset/ba2645d5-4458-414d-b196-6303ac06c1c9>
- Akinremi, O. O., S. M. McGinn, and H. W. Cutforth. 1999. Precipitation trends on the Canadian prairies. *J. Climate* **12**: 2996–3003.
- Appelby, P. G., P. J. Nolan, D. W. Gifford, M. J. Godfrey, F. Oldfield, N. J. Anderson, and R. W. Battarbee. 1986. ^{210}Pb dating by low background gamma counting. *Hydrobiologia* **143**: 21–17. doi:10.1007/BF00026640
- Asong, Z. E., M. N. Khaliq, and H. S. Wheeler. 2016. Projected changes in precipitation and temperature over the Canadian Prairie Provinces using the Generalized Linear Model statistical downscaling approach. *J. Hydrol.* **539**: 429–446. doi:10.1016/j.jhydrol.2016.05.044
- Binford, M. W. 1990. Calculation and uncertainty analysis of ^{210}Pb dates for PIRLA project lake sediment cores. *J. Paleolimnol.* **3**: 253–267. doi:10.1007/BF00219461
- Bonsal, B. R., T. D. Prowse, C. R. Duguay, and M. P. Lacroix. 2006. Impacts of large-scale teleconnections on freshwater-ice break/freezing-up dates over Canada. *J. Hydrol.* **330**: 340–353. doi:10.1016/j.jhydrol.2006.03.022
- Bos, J. S., L. Nanayakkara, M. Hurlbert, and K. Finlay. 2019. Citizen science for Saskatchewan lakes: A pilot project. *Lake Reserv. Manag.* **35**: 77–89. doi:10.1080/10402381.2018.1538172
- Botrel, M., I. Gregory-Eaves, and R. Maranger. 2014. Defining drivers of nitrogen stable isotopes ($\delta^{15}\text{N}$) of surface sediments in temperate lakes. *J. Paleolimnol.* **52**: 419–433. doi:10.1007/s10933-014-9802-6
- Bryson, R. A., and F. K. Hare. 1974. *Climates of North America*. Elsevier.
- Bunting, L., P. R. Leavitt, G. L. Simpson, B. Wissel, K. R. Laird, B. F. Cumming, A. St. Amand, and D. R. Engstrom. 2016. Increased variability and sudden ecosystem state change in Lake Winnipeg, Canada, caused by 20th century agriculture. *Limnol. Oceanogr.* **61**: 2090–2107. doi:10.1002/lno.10355
- Burthe, S. J., and others. 2016. Do early warning indicators consistently predict nonlinear change in long-term ecological data? *J. Appl. Ecol.* **53**: 666–676.
- Carpenter, S. R., and W. A. Brock. 2006. Rising variance: A leading indicator of ecological transition. *Ecol. Lett.* **9**: 311–318. doi:10.1111/j.1461-0248.2005.00877.x
- Carpenter, S. R., E. H. Stanley, and M. J. Vander Zanden. 2011. State of the world's freshwater ecosystems: Physical, chemical, and biological changes. *Annu. Rev. Environ. Res.* **36**: 75–99. doi:10.1146/annurev-environ-021810-094524
- Coles, A. E., and J. J. McDonnell. 2018. Fill and spill drives runoff connectivity over frozen ground. *J. Hydrol.* **558**: 115–128. doi:10.1016/j.jhydrol.2018.01.016
- Cottingham, K. L., J. A. Rusak, and P. R. Leavitt. 2000. Increased ecosystem variability and reduced predictability following fertilization: Evidence from palaeolimnology. *Ecol. Lett.* **3**: 340–348. doi:10.1046/j.1461-0248.2000.00158.x
- Cuddington, K., and P. R. Leavitt. 1999. An individual-based model of pigment flux in lakes: Implications for organic biogeochemistry and paleoecology. *Can. J. Fish. Aquat. Sci.* **56**: 1964–1977. doi:10.1139/f99-108
- Cullimore, D. R., and D. Griffin. 1979. Data collection relevant to White Bear Lake water quality status, 24. Regina Water Research Institute, Univ. of Regina.
- Dakos, V., S. R. Carpenter, E. H. van Nes, and M. Scheffer. 2015. Resilience indicators: Prospects and limitations of early warnings of regime shifts. *Phil. Trans. R. Soc. B* **37**: 20130263. doi:10.1098/rstb.2013.0263
- Davis, T., D. Berry, G. Boyer, and C. Gobler. 2009. The effects of temperature and nutrients on the growth and dynamics of toxic and non-toxic strains of *Microcystis* during cyanobacteria blooms. *Harmful Algae* **8**: 715–725. doi:10.1016/j.hal.2009.02.004
- Dibike, Y., T. Prowse, B. Bonsal, and H. O'Neil. 2016. Implications of future climate on water availability in the western Canadian river basins. *Int. J. Climatol.* **37**: 3247–3263. doi:10.1002/joc.4912
- Dröscher, I., A. Patoine, K. Finlay, and P. R. Leavitt. 2009. Climate control of spring clear-water phase through the transfer of energy and mass to lakes. *Limnol. Oceanogr.* **54**: 2469–2480. doi:10.4319/lo.2009.54.6_part_2.2469
- Dumanski, S., J. W. Pomeroy, and C. J. Westbrook. 2015. Hydrological regime changes in a Canadian Prairie basin. *Hydrol. Process.* **29**: 3893–3904. doi:10.1002/hyp.10567
- Fang, X., A. Minke, J. Pomeroy, T. Brown, C. Westbrook, X. Guo, and S. Guangul. 2007. A review of Canadian Prairie hydrology: Principles, modelling and response to land use and drainage change. Center for Hydrology Report, 2. Univ. of Saskatchewan.
- Fischer, P., and U. Öhl. 2005. Effects of water-level fluctuations on the littoral benthic fish community in lakes: A mesocosm experiment. *Behav. Ecol.* **16**: 741–746. doi:10.1093/beheco/ari047
- Fritz, S. C. 1990. Twentieth-century salinity and water-level fluctuations in Devils Lake, North Dakota: Test of a diatom-based transfer function. *Limnol. Oceanogr.* **35**: 1771–1781. doi:10.4319/lo.1990.35.8.1771
- Gaeta, J. W., G. G. Sass, and S. R. Carpenter. 2014. Drought-driven lake level decline: Effects on coarse woody habitat

- and fishes. *Can. J. Fish. Aquat. Sci.* **71**: 315–325. doi:[10.1139/cjfas-2013-0451](https://doi.org/10.1139/cjfas-2013-0451)
- Gal, G., M. Skerjanec, and N. Atanasova. 2013. Fluctuations in water level and the dynamics of zooplankton: A data-driven modelling approach. *Freshw. Biol.* **58**: 800–816. doi:[10.1111/fwb.12087](https://doi.org/10.1111/fwb.12087)
- Garcés, B. L. V., K. Kelts, and E. Ito. 1995. Oxygen and carbon isotope trends and sedimentological evolution of a meromictic and saline lacustrine system: The Holocene Medicine Lake basin, North American Great Plains, USA. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **117**: 253–278. doi:[10.1016/0031-0182\(94\)00136-V](https://doi.org/10.1016/0031-0182(94)00136-V)
- Glew, J. R. 1989. A new trigger mechanism for sediment samplers. *J. Paleolimnol.* **2**: 241–243.
- Godwin, B., V. Wittrock, and J. Thorpe. 2013. Ecosystem based surface water quantity management plan for Moose Mountain Provincial Park. Saskatchewan Research Council Publication No. 13413-1E13, Regina, Saskatchewan.
- Gu, B., A. D. Chapman, and C. L. Schelske. 2006. Factors controlling seasonal variations in stable isotope composition of particulate organic matter in a softwater eutrophic lake. *Limnol. Oceanogr.* **51**: 2837–2848. doi:[10.4319/lo.2006.51.6.2837](https://doi.org/10.4319/lo.2006.51.6.2837)
- Haig, H. A., N. M. Hayes, G. L. Simpson, Y. Yi, B. Wissel, K. Finlay, K. R. Hodder, and P. R. Leavitt. 2021. Application of isotope mass balance models to assess spatial variability in lake hydrology on the Northern Great Plains, Canada. *J. Hydrol. X* In review. **6**: 100046.
- Haig, H. A., N. M. Hayes, G. L. Simpson, Y. Yi, B. Wissel, K. R. Hodder, and P. R. Leavitt. 2020. Comparison of isotopic mass balance and instrumental techniques as estimates of basin hydrology in seven connected lakes over 12 years. *J. Hydrol. X* **6**: 100046. doi:[10.1016/j.hydroa.2019.100046](https://doi.org/10.1016/j.hydroa.2019.100046)
- Hambright, K. D., T. Zohary, W. Eckert, S. S. Schwartz, C. L. Schelske, K. R., and P. R. Leavitt. 2008. Exploitation and destabilization of a warm, freshwater ecosystem through engineered hydrological change. *Ecol. App.* **18**: 1591–1603. doi:[10.1890/07-0931.1](https://doi.org/10.1890/07-0931.1)
- Hayes, N. M., A. Patoine, H. A. Haig, G. L. Simpson, V. J. Swarbrick, E. Wiik, and P. R. Leavitt. 2019. Spatial and temporal variation in nitrogen fixation and its importance to phytoplankton growth in phosphorus-rich lakes. *Freshw. Biol.* **64**: 269–283. doi:[10.1111/fwb.13214](https://doi.org/10.1111/fwb.13214)
- Henderson, N., E. Hogg, E. Barrow, and B. Dolter. 2002. Climate change impacts on the island forests of the Great Plains and the implications for nature conservation policy: The outlook for Sweet Grass Hills (Montana), Cypress Hills (Alberta-Saskatchewan), Moose Mountain (Saskatchewan), Spruce Woods (Manitoba) and Turtle Mountain (Manitoba-North Dakota). *Prairie Adaptation and Research Collaborative*, Univ. of Regina.
- Hodgson, D. A., S. W. Wright, P. A. Tyler, and N. Davies. 1998. Analysis of fossil pigments from algae and bacteria in meromictic Lake Fidler, Tasmania, and its application to lake management. *J. Paleolimnol.* **19**: 1–22. doi:[10.1023/A:1007909018527](https://doi.org/10.1023/A:1007909018527)
- Huisman, J., G. A. Codd, H. W. Paerl, B. W. Ibelings, J. M. Verspagen, and P. M. Visser. 2018. Cyanobacterial blooms. *Nat. Rev. Microbiol.* **16**: 471–483. doi:[10.1038/s41579-018-0040-1](https://doi.org/10.1038/s41579-018-0040-1)
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic oscillation: Regional temperatures and precipitation. *Science* **269**: 676–679. doi:[10.1126/science.269.5224.676](https://doi.org/10.1126/science.269.5224.676)
- Jeppesen, E., and others. 2014. Climate change impacts on lakes: An integrated ecological perspective based on a multi-faceted approach, with special focus on shallow lakes. *J. Limnol.* **73**: 84–107. doi:[10.4081/jlimnol.2014.844](https://doi.org/10.4081/jlimnol.2014.844)
- Jørgensen, B. B., and J. R. Postgate. 1982. Ecology of the bacteria of the sulphur cycle with special reference to anoxic-oxic interface environments. *Philos. Trans. R. Soc. Lond. B* **298**: 543–561. doi:[10.1098/rstb.1982.0096](https://doi.org/10.1098/rstb.1982.0096)
- van der Kamp, G., D. Keir, and M. Evans. 2008. Long-term water level changes in closed-basin lakes of the Canadian prairies. *Can. Water Resour. J.* **33**: 23–38. doi:[10.4296/cwrj3301023](https://doi.org/10.4296/cwrj3301023)
- van der Kamp, G., and H. Maathuis. 1991. Annual fluctuations of groundwater levels as a result of loading by surface moisture. *J. Hydrol.* **127**: 137–152. doi:[10.1016/0022-1694\(91\)90112-U](https://doi.org/10.1016/0022-1694(91)90112-U)
- Leavitt, P. R., R. Brock, C. Ebel, and A. Patoine. 2006. Landscape-scale effects of urban nitrogen on a chain of freshwater lakes in central North America. *Limnol. Oceanogr.* **51**: 2262–2277. doi:[10.4319/lo.2006.51.5.2262](https://doi.org/10.4319/lo.2006.51.5.2262)
- Leavitt, P. R., S. R. Carpenter, and J. F. Kitchell. 1989. Whole-lake experiments: The annual record of fossil pigments and zooplankton. *Limnol. Oceanogr.* **34**: 700–717. doi:[10.4319/lo.1989.34.4.0700](https://doi.org/10.4319/lo.1989.34.4.0700)
- Leavitt, P. R., and D. A. Hodgson. 2001. Sedimentary pigments, p. 95–325. *In* J. P. Smol, H. J. B. Birks, and W. M. Last [eds.], *Tracking environmental change using lake sediments*, Volume 3: Terrestrial, algal, and siliceous indicators. Kluwer Academic Publishers.
- Leavitt, P. R., D. E. Schindler, A. J. Paul, A. K. Hardie, and D. W. Schindler. 1994. Fossil pigment records of phytoplankton in trout-stocked alpine lakes. *Can. J. Fish. Aquat. Sci.* **51**: 2411–2423. doi:[10.1139/f94-241](https://doi.org/10.1139/f94-241)
- Leavitt, P. R., R. D. Vinebrooke, D. Donald, J. P. Smol, and D. W. Schindler. 1997. Past ultraviolet radiation environments in lakes derived from fossil pigments. *Nature* **388**: 457–459. doi:[10.1038/41296](https://doi.org/10.1038/41296)
- Liu, J., R. E. Stewart, and K. Szeto. 2008. Water vapor fluxes over the Canadian Prairies and the Mackenzie River Basin, p. 109–125. *In* M. Woo [ed.], *Cold region atmospheric and hydrologic studies*. Springer.
- Madigan, M. T. 1995. Microbiology of nitrogen fixation by anoxygenic photosynthetic bacteria, p. 915–928. *In* R. E. Blankenship, M. T. Madigan, and C. T. Bauer [eds.], *Anoxygenic photosynthetic bacteria*. Advances in

- photosynthesis and respiration book series (AIPH, volume 2). Springer.
- Maheaux, H., P. R. Leavitt, and L. Jackson. 2016. Asynchronous onset of eutrophication among shallow prairie lakes of the Northern Great Plains, Alberta, Canada. *Glob. Change Biol.* **22**: 271–283. doi:[10.1111/gcb.13076](https://doi.org/10.1111/gcb.13076)
- Mantua, N., S. Hare, Y. Zhang, J. W. Wallace, and W. R. Francis. 1997. A pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* **78**: 1069–1079. doi:[10.1175/1520-0477\(1997\)078%3C1069:APICOW%3E2.0.CO;2](https://doi.org/10.1175/1520-0477(1997)078%3C1069:APICOW%3E2.0.CO;2)
- Mao, D., and K. A. Cherkauer. 2008. Impacts of land-use change on hydrologic responses in the Great Lakes region. *J. Hydrol.* **374**: 71–82. doi:[10.1016/j.jhydrol.2009.06.016](https://doi.org/10.1016/j.jhydrol.2009.06.016)
- McCullough, G. K., S. B. Page, R. H. Hesslein, M. P. Stainton, H. J. Kling, A. G. Salki, and D. J. Barbera. 2012. Hydrological forcing of a recent trophic surge in Lake Winnipeg. *J. Great Lakes Res.* **38**: 95–105. doi:[10.1016/j.jglr.2011.12.012](https://doi.org/10.1016/j.jglr.2011.12.012)
- Meyers, P. A., and J. L. Teranes. 2001. Sediment organic matter, p. 239–270. *In* W. M. Last and J. P. Smol [eds.], *Tracking environmental change using Lake sediments, volume 2: Physical and geochemical methods*. Kluwer Academic Publishers.
- Michels, A., K. R. Laird, S. E. Wilson, D. Thomson, P. R. Leavitt, R. J. Oglesby, and B. F. Cumming. 2007. Multi-decadal to millennial-scale shifts in drought conditions on the Canadian Prairies over the past six millennia: Implications for future drought assessment. *Glob. Change Biol.* **13**: 1295–1307. doi:[10.1111/j.1365-2486.2007.01367.x](https://doi.org/10.1111/j.1365-2486.2007.01367.x)
- Oduor, S. O., and M. Schagerl. 2007. Temporal trends of ion contents and nutrients in three Kenyan Rift Valley saline-alkaline lakes and their influence on phytoplankton biomass, p. 59–68. *In* R. D. Gulati, E. Lammens, N. de Pauw, and E. van Donk [eds.], *Shallow lakes in a changing world*. Springer.
- Paelr, H. W., and V. J. Paul. 2012. Climate change: Links to global expansion of harmful cyanobacterial blooms. *Nat. Rev. Microbiol.* **16**: 471–483. doi:[10.1016/j.watres.2011.08.002](https://doi.org/10.1016/j.watres.2011.08.002)
- Patoine, A., and P. R. Leavitt. 2006. Century-long synchrony of algal fossil pigments in a chain of Canadian prairie lakes. *Ecology* **87**: 1710–1721. doi:[10.1890/0012-9658](https://doi.org/10.1890/0012-9658)
- Pedersen, E. J., D. L. Miller, G. L. Simpson, and N. Ross. 2019. Hierarchical generalized additive models in ecology: An introduction with mgcv. *PeerJ* **7**: e6876. doi:[10.7717/peerj.6876](https://doi.org/10.7717/peerj.6876)
- Pfennig, N. 1978. General physiology and ecology of photosynthetic bacteria, p. 3–18. *In* R. K. Clayton and W. R. Sistrom [eds.], *The photosynthetic bacteria*. Plenum Press.
- Pham, S. V., P. R. Leavitt, S. McGowan, and P. Peres-Neto. 2008. Spatial variability of climate and land-use effects on lakes of the northern Great Plains. *Limnol. Oceanogr.* **53**: 728–742. doi:[10.4319/lo.2008.53.2.0728](https://doi.org/10.4319/lo.2008.53.2.0728)
- Pham, S. V., P. R. Leavitt, S. McGowan, B. Wissel, and L. Wassenaar. 2009. Spatial and temporal variability of prairie lake hydrology as revealed using stable isotopes of hydrogen and oxygen. *Limnol. Oceanogr.* **54**: 101–118. doi:[10.4319/lo.2009.54.1.0101](https://doi.org/10.4319/lo.2009.54.1.0101)
- Plancq, J., B. Cavazzin, S. Juggins, H. A. Haig, P. R. Leavitt, and J. L. Toney. 2018. Assessing environmental controls on the distribution of long-chain alkenones in the Canadian prairies. *Org. Geochem.* **117**: 43–55. doi:[10.1016/j.orggeochem.2017.12.005](https://doi.org/10.1016/j.orggeochem.2017.12.005)
- Pomeroy, J., D. Gray, T. Brown, N. Hedstrom, W. Quinton, R. Granger, and S. Carey. 2007. The cold regions hydrological model: A platform for basing process representation and model structure on physical evidence. *Hydrol. Process.* **21**: 2650–2667. doi:[10.1002/hyp.6787](https://doi.org/10.1002/hyp.6787)
- Pya, N. 2021. SCAM: Shape constrained additive models. <https://cran.r-project.org/package=scam>
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing.
- Randsalu-Wendrup, L., D. J. Conley, J. Carstensen, and S. C. Fritz. 2016. Paleolimnological records of regime shifts in lakes in response to climate change and anthropogenic activities. *J. Paleolimnol.* **56**: 1–14. doi:[10.1007/s10933-016-9884-4](https://doi.org/10.1007/s10933-016-9884-4)
- Ratajczak, Z., and others. 2018. Abrupt change in ecological systems: Inference and diagnosis. *Trends Ecol. Evol.* **33**: 513–526. doi:[10.1016/j.tree.2018.04.013](https://doi.org/10.1016/j.tree.2018.04.013)
- Sauchyn, D. J., D. Davidson, and M. Johnston. 2020. Prairie Provinces, chapter 4. *In* F. J. Warren, N. Lulham, and D. S. Lemmen [eds.], *Canada in a changing climate: Regional perspectives report*. Government of Canada.
- Savage, C., P. R. Leavitt, and R. Elmgren. 2004. Distribution and retention of effluent nitrogen in surface sediments of a coastal bay. *Limnol. Oceanogr.* **49**: 1503–1511. doi:[10.4319/lo.2004.49.5.1503](https://doi.org/10.4319/lo.2004.49.5.1503)
- Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends Ecol. Evol.* **18**: 648–656. doi:[10.1016/j.tree.2003.09.002](https://doi.org/10.1016/j.tree.2003.09.002)
- Scheffer, M., S. R. Carpenter, J. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* **413**: 591–596. doi:[10.1038/35098000](https://doi.org/10.1038/35098000)
- Sereda, J., M. Bogard, J. Hudson, D. Helps, and T. Dessouki. 2011. Climate warming and the onset of salinization: Rapid changes in the limnology of two northern plains lakes. *Limnologia* **41**: 1–9. doi:[10.1016/j.limno.2010.03.002](https://doi.org/10.1016/j.limno.2010.03.002)
- Shaw, R. D., and E. E. Prepas. 1990. Groundwater-lake interactions: II. Nearshore seepage patterns and the contributions of groundwater to lakes in central Alberta. *J. Hydrol.* **119**: 121–136. doi:[10.1016/0022-1694\(90\)90038-Y](https://doi.org/10.1016/0022-1694(90)90038-Y)
- Simpson, G. L. 2018. Modelling palaeoecological time series using generalised additive models. *Front. Ecol. Evol.* **6**: 149. doi:[10.3389/fevo.2018.00149](https://doi.org/10.3389/fevo.2018.00149)

- Simpson, G. L. 2021. Gratia: Graceful 'ggplot'-based graphics and other functions for GAMs fitted using 'mgcv'. <https://cran.r-project.org/package=gratia>.
- Søndergaard, M., R. Bjerring, and E. Jeppesen. 2013. Persistent internal phosphorus loading during summer in shallow eutrophic lakes. *Hydrobiologia* **710**: 95–107. doi:10.1007/s10750-012-1091-3
- Stevenson, M. A., S. McGowan, N. J. Anderson, R. H. Foy, P. R. Leavitt, Y. R. McElearney, D. R. Engstrom, and S. Pla-Rabés. 2016. Impacts of forest plantation management on primary production in upland lakes from north-west Ireland. *Glob. Chang. Biol.* **22**: 1490–1504. doi:10.1111/gcb.13194
- Tanzeba, S., and T. Gan. 2012. Potential impact of climate change on the water availability of South Saskatchewan River Basin. *Clim. Change* **112**: 355–386. doi:10.1007/s10584-011-0221-7
- Taranu, Z. E., S. R. Carpenter, M. E. Perga, T. Ives, V. Frossard, Z. Thoma, J. P. Jenny, and J. C. Vermaire. 2018. Can we detect ecosystem critical transitions and early warning signals of catastrophic shifts from paleo-ecological records? *Ecosphere* **9**: e02438. doi:10.1002/ecs2.2438
- Taranu, Z. E., and others. 2015. Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the Anthropocene. *Ecol. Lett.* **18**: 375–384. doi:10.1111/ele.12420
- Trenberth, K. E., and J. W. Hurrell. 1994. Decadal atmosphere-ocean variations in the Pacific. *Clim. Dyn.* **9**: 303–319. doi:10.1007/BF00204745
- Vance, R. E., W. M. Last, and A. J. Smith. 1997. Hydrologic and climatic implications of a multidisciplinary study of late Holocene sediment from Kenosee Lake, southeastern Saskatchewan, Canada. *J. Paleolimnol.* **18**: 365–393. doi:10.1023/A:1007948909342
- Vinebrooke, R., R. Hall, P. R. Leavitt, and B. F. Cumming. 1998. Fossil pigments as indicators of phototrophic response to salinity and climatic change in lakes of western Canada. *Can. J. Fish. Aquat. Sci.* **55**: 668–681. doi:10.1139/cjfas-55-3-668
- Vogt, R. J., S. Sharma, and P. R. Leavitt. 2018. Direct and interactive effects of climate, meteorology, river hydrology, and lake characteristics on water quality in productive lakes of the Canadian prairies. *Can. J. Fish. Aquat. Sci.* **75**: 47–59. doi:10.1139/cjfas-2016-0520
- Vörösmarty, C. J., P. Green, J. Salisbury, and R. B. Lammers. 2000. Global water resources: Vulnerability from climate change and population growth. *Science* **289**: 284–288. doi:10.1126/science.289.5477.284
- Wickham, H. 2021. Tidy: Tidy messy data. <https://cran.r-project.org/package=tidy>
- Wickham, H., R. François, L. Henry, and K. Müller. 2021. Dplyr: A grammar of data manipulation. <https://cran.r-project.org/package=dplyr>
- Wickham, H., and others. 2016. ggplot2: Elegant graphics for data analysis. <https://cran.r-project.org/package=ggplot2>
- Wigdahl, C. R., J. E. Saros, S. C. Fritz, J. R. Stone, and D. R. Engstrom. 2014. The influence of basin morphometry on the regional coherence of patterns of diatom-inferred salinity in lakes of the northern Great Plains (USA). *Holocene* **24**: 603–613. doi:10.1177/0959683614523154
- Wilke, C. O. 2020. Cowplot: Streamlined plot theme and plot annotations for 'ggplot2'. <https://cran.r-project.org/package=cowplot>
- Wissel, B., R. N. Cooper, P. R. Leavitt, and S. V. Pham. 2011. Hierarchical regulation of pelagic invertebrates in lakes of the northern Great Plains: A novel model for inter-decadal effects of future climate change. *Glob. Change Biol.* **17**: 172–185. doi:10.1111/j.1365-2486.2010.02291.x
- Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. B* **73**: 3–36. doi:10.1111/j.1467-9868.2010.00749.x
- Wood, S. N. 2017. Generalized additive models: An introduction with R, 2nd ed. Chapman Hall.
- Woodward, C. A., A. P. Potito, and D. W. Beilman. 2012. Carbon and nitrogen stable isotope ratios in surface sediments from lakes of western Ireland: Implications for inferring past lake productivity and nitrogen loading. *J. Paleolimnol.* **47**: 167–184. doi:10.1007/s10933-011-9568-z
- Xiao, K., and others. 2018. Evaporation from a temperate closed-basin lake and its impact on present, past, and future water level. *J. Hydrol.* **561**: 59–75. doi:10.1016/j.jhydrol.2018.03.059
- Zhou, X., G. Huang, X. Wang, and G. Cheng. 2018. Dynamically-downscaled temperature and precipitation changes over Saskatchewan using the PRECIS model. *Clim. Dyn.* **50**: 1321–1334. doi:10.1007/s00382-017-3687-9
- Zinabu, G. M. 2002. The effects of wet and dry seasons on concentrations of solutes and phytoplankton biomass in seven Ethiopian rift-valley lakes. *Limnologia* **32**: 169–179. doi:10.1016/S0075-9511(02)80006-8
- Zohary, T., and I. Ostrovsky. 2011. Ecological impacts of excessive water level fluctuations in stratified freshwater lakes. *Inland Waters* **1**: 47–59. doi:10.5268/IW-1.1.406
- Züllig, H., and S. Rheineck. 1985. Pigmente phototropher Bakterien in Seesedimenten und ihre Bedeutung für die Seenforschung. *Swiss J. Hydrol.* **47**: 87–126. doi:10.1007/BF02551937

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Conflict of Interest

None declared.

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