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Earlier winter/spring runoff and snowmelt during warmer winters lead to lower summer chlorophyll-*a* in north temperate lakes

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Abstract

Winter conditions, such as ice cover and snow accumulation, are changing rapidly at northern latitudes and can have important implications for lake processes. For

example, snowmelt in the watershed—a defining feature of lake hydrology because it delivers a large portion of annual nutrient inputs—is becoming earlier. Consequently, earlier and a shorter duration of snowmelt are expected to affect annual phytoplankton biomass. To test this hypothesis, we developed an index of runoff timing based on the date when 50% of cumulative runoff between January 1 and May 31 had occurred. The runoff index was computed using stream discharge for inflows, outflows, or for flows from nearby streams for 41 lakes in Europe and North America. The runoff index was then compared with summer chlorophyll-*a* (Chl-*a*) concentration (a proxy for phytoplankton biomass) across 5–53 years for each lake. Earlier runoff generally corresponded to lower summer Chl-*a*. Furthermore, years with earlier runoff also had lower winter/spring runoff magnitude, more protracted runoff, and earlier ice-out. We examined several lake characteristics that may regulate the strength of the relationship between runoff timing and summer Chl-*a* concentrations; however, our tested covariates had little effect on the relationship. Date of ice-out was not clearly related to summer Chl-*a* concentrations. Our results indicate that ongoing changes in winter conditions may have important consequences for summer phytoplankton biomass and production.

KEYWORDS
chlorophyll-*a*, climate change, long-term data, phytoplankton biomass, snowmelt, stream discharge

1 | INTRODUCTION

Climate change has affected temperate lakes, both directly through inputs of thermal energy (O'Reilly et al., 2015) and indirectly through modifications to inputs of water and terrestrial materials from watersheds (Blenckner, 2005; Leavitt et al., 2009). Additionally, climate effects may occur during the well-studied, open-water growing seasons and the less-studied, winter season. Studies examining the effects of climate change on lakes have mainly focused on the direct effects on lake heat budgets and thermal structure during the summer at local to global scales (O'Reilly et al., 2015; Richardson et al., 2017; Torbick et al., 2016; Trumpickas et al., 2009; Woolway et al., 2017). Direct effects of meteorological forcing have also been studied during winter, particularly in relation to the declining duration of lake ice cover over the last several decades (Du et al., 2017; Fang & Stefan, 1998; Hodgkins et al., 2002; Johnson & Stefan, 2006; Robertson et al., 1992). Indirect effects of changing nutrient inputs and water volume from runoff on lake processes have been observed in the open water season, particularly with respect to changes in storms, drought events, and overall precipitation (Hayes et al., 2015; Stockwell et al., 2020; Vachon & del Giorgio, 2014; Williamson et al., 2016). For example, increased dissolved organic carbon inputs to lakes may alter the underwater light climate, thermal patterns, and phytoplankton productivity in lakes (Creed et al., 2018; Hongve et al., 2004; Kritzberg et al., 2020; Pilla et al., 2018; Read & Rose, 2013). However, the effects of changing terrestrial inputs into lakes during late winter and early spring have received little attention. Spring runoff is a major event of the annual hydrological

cycle in most drainage lakes at northern latitudes. In particular, the spring runoff delivers a large fraction of lakes' annual input of water and allochthonous nutrients, and warming winter temperatures are likely to have major effects on both the timing and magnitude of the spring runoff (Blöschl et al., 2017).

The strongest changes in the annual cycle of streamflow have occurred in watersheds where snow has a major effect on watershed hydrology. Warmer winter temperatures, greater volumes of rain versus snow, and earlier snowmelt have led to shifts in the seasonality of streamflow in such watersheds (Barnett et al., 2005; Stewart et al., 2004). Many temperate, Arctic, and boreal lakes receive the majority of their annual water and nutrient inputs through the winter/spring snowmelt pulse (Bouchard et al., 2013; Mielko & Woo, 2006; Pall et al., 2011; Rosenberg & Schroth, 2017; Sadro et al., 2018). Historically, spring melting of accumulated snow (often combined with rain) has led to a distinct spring peak in seasonal water and nutrient inputs. Under present and simulated future climatic conditions, more frequent winter rain and snowmelt events result in increased discharge during winter, reduced snowpack, and less runoff during the time of the traditional spring peak streamflow (Andréasson et al., 2004; Burns et al., 2007; Zion et al., 2011). The nutrient load in the runoff when the ground is still frozen or covered in snowpack is often less than that in runoff when the ground has thawed and is saturated (Mander et al., 2000; Pierson & Taylor, 1985; Shanley & Chalmers, 1999; Tiwari et al., 2018). As a result, changes in the amount and seasonality of nutrient loading, including available forms of nitrogen, phosphorus, and carbon, may affect lake productivity in subsequent seasons.

The timing of water and nutrient inputs to lakes during spring runoff often follows the loss of lake ice and coincides with increased light availability and water column mixing—factors expected to increase lake primary production. In contrast, a temporal mismatch between nutrient supply and the physical conditions conducive to planktonic primary production may develop if water and nutrients enter lakes earlier during winter. Low incoming solar radiation and deep mixing under isothermal conditions are expected to limit phytoplankton growth and nutrient uptake during winter in ice-free lakes. In addition, light availability in the water column is reduced in the presence of ice and snow cover (Bolsenga & Vanderploeg, 1992), and inverse stratification can promote nutrient inputs to pass through and be lost from the lake as a horizontal plume passing directly under the ice from inflows to the lake outlet (Cortés et al., 2017). Nutrients delivered during the winter are often assumed to remain available in the water column for later uptake by spring to summer phytoplankton blooms following the onset of stratification (Pierson et al., 2013). However, substantial biogeochemical changes to nutrients can occur under lake ice (Cavaliere & Baulch, 2018; Joung et al., 2017; Powers et al., 2017; Tan et al., 2018), which may affect their subsequent bioavailability to primary producers. In some conditions, substantial phytoplankton growth can occur during late winter under lake ice (Hampton et al., 2017; Salmi & Salonen, 2016), which may sequester allochthonous nutrients and then sink to the lake bottom, reducing the direct availability of nutrients in the subsequent summer season (Maier et al., 2019). Watershed-sourced nutrients associated with sediments may also become unavailable through settling and sedimentation of associated particles. Consequently, a great deal of uncertainty remains regarding the fate of nutrients entering lakes during winter.

We present the results of an analysis of 41 lakes from Europe and North America to address the following question: How does the timing and magnitude of winter/spring runoff affect summer lake phytoplankton biomass for lakes in which snow plays an important role in the hydrologic cycle? We hypothesized that climate warming leads to earlier and increased streamflow during the winter months and reduced phytoplankton biomass during summer because of lower nutrient concentrations and bioavailability. More specifically, we predicted that earlier winter/spring runoff (i.e., winter/spring center of volume [WSCV]) would be associated with lower lake chlorophyll-a (Chl-a) concentrations during the subsequent summer. Conversely, we predicted that lakes would have higher summer Chl-a in years with late spring runoff because nutrient inputs would more closely coincide with the onset of increased light, warming temperatures, and thermal stratification that promote phytoplankton growth in spring. In addition to the effects of snowmelt timing on summer Chl-a, we also tested the effects of snowmelt magnitude and duration (protractedness) on summer Chl-a and examined their relationship in the context of lake morphometry that underlie the relationship between runoff and phytoplankton biomass within a lake. We also examined the relationships between ice cover vs. WSCV and summer Chl-a. We focused on summer (rather than spring) Chl-a because summertime lake productivity is most relevant to lake users and the accumulation of toxic species, especially cyanobacteria.

2 | METHODS

To test our hypothesis, we compiled data on (1) summer Chl-a concentrations, as a proxy for phytoplankton biomass, in 41 lakes in Europe and North America and (2) associated streamflow to or from these lakes, which directly affects the timing and availability of nutrient inputs.

2.1 | Study lakes

Data were obtained from long-term monitoring programs through the Global Lake Ecological Observatory Network (GLEON; Table 1). All lakes froze at least occasionally and are in areas where snow accumulates (i.e., temperate lakes; Figure 1). We required a minimum of 5 years of lake Chl-a measurements (measured at least monthly during summer in the epilimnion or as a water column profile) and daily discharge data from an inlet, outlet, or nearby stream as a proxy for runoff. Most lakes, however, had longer records (average length 28 years; Table 1). We collected several variables to describe potential for differentiation in mixing patterns, nutrient cycling, and watershed characteristics for each lake when available. Variables included mean depth, surface area, maximum fetch, mean residence time, watershed area, latitude/longitude, temperature profiles of the entire water column or surface temperatures if profiles were not available, total phosphorus and dissolved organic carbon concentrations, and dates of ice-on and ice-out. These variables were used for covariate analyses (see classification and regression tree [CART] analysis below), or in the case of temperature, to define the summer period for each lake. The above variables were chosen because they were the most commonly measured characteristics that could potentially affect the relationship between WSCV and summer Chl-a.

2.2 | Index of summer Chl-*a*

To describe summer Chl-a, we first defined "summer" as the 90-day window around (1) the maximum epilimnetic water temperature for stratified systems where daily thermal profiles were available (epilimnetic depth calculated with the R package rLakeAnalyzer; Winslow et al., 2017), (2) the maximum mean water column temperature for unstratified systems where thermal profiles were available, or (3) the maximum surface temperature if only surface measurements were available. In cases where water temperature data were not available, we defined summer as the 90-day window around July 31 to encompass the period when data were collected most frequently.

Summer Chl-a index was calculated as the mean Chl-a concentration during the defined summer period. We calculated the index only if Chl-a was sampled at least three times during summer.

TABLE 1 Characteristics of lakes included in our analyses of the relationship between runoff timing and summer chlorophyll-*a*

| Lake	Location	Residence time (days)	Latitude	Longitude	Mean depth (m)	Surface area (km²)	Watershed area (km²)	Mean summer total phosphorus (µg/L)	Average dissolved organic carbon (mg/L)	Years of paired data
Annabessacook Lake[a]	Maine, USA	99	44.27	−69.98	6.4	5.7	216.3	49.2	NA	26
Bear Head Lake[a]	Minnesota, USA	NA	47.78	−92.08	3.7	2.7	8.4	46.6	6.9	8
Blue Chalk Lake[a]	Ontario, Canada	1610	45.20	−78.94	8.5	0.5	1.6	6.2	2.2	34
Lake Carlos[a]	Minnesota, USA	NA	45.95	−95.36	13.9	10.2	633.1	18.8	6.4	8
Lake Carmi	Vermont, USA	479	44.97	−72.88	4.0	5.7	31.2	31.5	NA	38
Lake Champlain	Vermont/New York, USA and Quebec, Canada	1205	44.54	−73.35	19.5	1126.6	21326.0	11.5	3.6	24
China Lake[a]	Maine, USA	562	44.44	−69.57	8.5	15.9	NA	32.3	NA	28
Chub Lake	Ontario, Canada	701	45.21	−78.98	8.9	0.3	3.1	8.6	6.3	35
Cobbosseecontee Lake	Maine, USA	341	44.25	−69.94	11.3	22.3	NA	25.1	NA	38
Cochnewagon Pond[a]	Maine, USA	730	44.23	−70.04	6.7	1.6	83.8	26.6	NA	37
Crosson Lake	Ontario, Canada	548	45.08	−79.03	9.2	0.6	5.8	9.4	5.0	35
Delavan Lake	Wisconsin, USA	1052	42.61	−88.60	7.6	7.0	99.7	124.4	NA	14
Dickie Lake	Ontario, Canada	573	45.15	−79.09	5.0	0.9	5.0	9.9	6.3	35
Lake Dunmore	Vermont, USA	429	43.91	−73.08	8.5	4.2	52.9	12.2	NA	26
Lake Mälaren/Ekoln sub-basin	Sweden	438	59.75	17.62	11.5	NA	2709.0	56.6	NA	53
Elk Lake[a]	Minnesota, USA	NA	47.19	−95.21	6.6	1.1	8.0	52.6	6.9	5
Lake Erken[a]	Sweden	3285	59.84	18.63	9.0	24.2	136.2	35.6	10.2	36
Lake Mälaren/Galten sub-basin	Sweden	25.55	59.45	16.17	3.4	61.0	8642.0	57.6	NA	37
Green Lake	Wisconsin, USA	5668	43.81	−89.00	33.6	29.5	218.2	80.2	NA	13
Harp Lake[a]	Ontario, Canada	1131	45.38	−79.13	13.3	0.7	5.4	6.3	NA	35
Harvey's Lake	Vermont, USA	932	44.29	−72.14	20.1	1.5	21.7	13.0	NA	29
Heney Lake	Ontario, Canada	434	45.13	−79.10	3.3	0.2	0.9	6.3	4.1	35
Long Lake	Maine, USA	388	44.04	−70.66	7.0	21.4	NA	6.7	NA	21
Maidstone Lake	Vermont, USA	2016	44.65	−71.65	14.0	3.1	12.6	6.6	NA	29
Lake Mendota[a]	Wisconsin, USA	1571	43.11	−89.42	12.7	39.9	604	139.3	NA	16
Oneida Lake[a]	New York, USA	239	43.20	−75.90	6.8	207.0	3738.8	30.7	NA	42
Otsego Lake[a]	New York, USA	1380	42.76	−74.89	25.0	16.4	191.7	4.5	NA	10
Plastic Lake	Ontario, Canada	1204	45.18	−78.82	7.9	0.3	1.3	4.7	2.6	35

(Continues)

TABLE 1 (Continued)

Lake	Location	Residence time (days)	Latitude	Longitude	Mean depth (m)	Surface area (km²)	Watershed area (km²)	Mean summer total phosphorus (µg/L)	Average dissolved organic carbon (mg/L)	Years of paired data
Red Chalk Lake[a]	Ontario, Canada	912	45.19	−78.95	16.7	0.4	5.9	5.9	3.9	35
Ridout Lake	Ontario, Canada	642	45.18	−78.98	6.7	0.5	NA	NA	4.0	8
Římov Reservoir[a]	České Budějovice, Czech Republic	74	48.85	14.49	15.6	1.8	489.0	23.6	5.1	36
Sabattus Pond[a]	Maine, USA	240	44.15	−70.11	4.3	8.0	81.8	42.4	NA	36
South Pond	Vermont, USA	NA	44.68	−72.53	NA	0.5	5.6	9.9	NA	27
Lake Sunapee[a]	New Hampshire, USA	1217	43.41	−72.04	11.4	16.6	116.8	6.5	NA	32
Ticklenaked Pond	Vermont, USA	146	44.19	−72.10	4.9	0.2	5.8	27.5	NA	15
Trout Lake[a]	Minnesota, USA	NA	47.87	−90.17	10.7	1.0	3.6	8.6	4.0	9
Upper Pleasant Pond	Maine, USA	NA	44.14	−69.89	3.0	3.2	NA	53.4	NA	34
Vänern	Västergötland/Dalsland/Värmland, Sweden	3577	58.88	12.69	27.0	5648	46830.0	8.3	NA	36
Võrtsjärv[a]	Estonia	365	58.28	26.03	2.8	270	3374.0	48.4	NA	35
Lake Willoughby	Vermont, USA	3136	44.75	−72.06	42.7	7.5	49.6	10.4	NA	24
Lake Winnipesaukee[a]	New Hampshire, USA	1825	43.71	−71.46	13.1	180.4	871.3	6.7	4.1	32

Note: "Years of paired data" indicates the number of years we calculated Chl-*a* index and WSCV.

Abbreviations: Chl-*a*, chlorophyll-a; NA, indicates that data were not available; WSCV, winter/spring center of volume.

[a]Indicates that ice-out dates were available and included in the analyses.
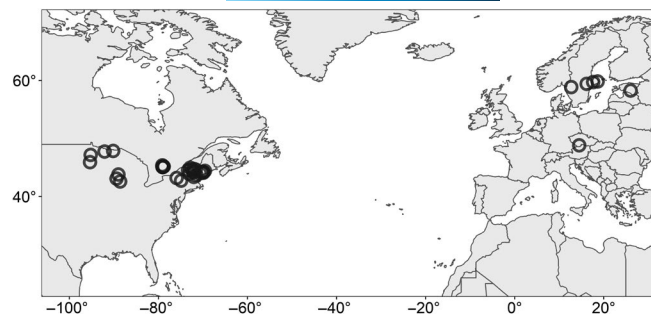
FIGURE 1 Locations of lakes used to test the hypothesis that years with earlier winter/spring runoff have lower summer chlorophyll-*a* (*N* =41)

Monthly measurements should capture the bulk of variation in Chl-*a* measurements in temperate lakes (Rusak et al., 2018). Where Chl-*a* profiles were measured for the whole water column or the epilimnion, we first took the water column or epilimnion mean Chl-*a* before averaging across dates. Chl-*a* was measured only in the epilimnion or at the surface in some lakes, and in those cases, only surface Chl-*a* was included in the Chl-*a* index. Because of the variability in Chl-*a* measurements among lakes, we only compared standardized WSCV to Chl-*a* within each lake before comparing slopes of relationships among lakes (see below for descriptions of regressions with *z*-scores). Within each lake data set, we only used data from one collection method if more than one method was used (i.e., we used the method with the most data).

2.3 | Indices of stream runoff timing and magnitude

Each study lake was paired with runoff from a gauged stream. Daily stream discharge data were used to calculate indices of snowmelt timing, duration, and magnitude. Where possible, gauged streams were chosen which fed (*n* = 10 lakes) or drained (*n* = 8) the study lakes. If no gauged streams were available, a nearby stream gauge was identified as a proxy for the timing of the snowmelt pulse (*n* = 14 lakes). Nearby streams ranged in distance from 7 to 55 km from the lake. We averaged values for multiple streams that directly fed lakes when data from multiple gauged streams were available (*n* = 9 lakes). Because we focused on relative changes in timing and magnitude rather than the absolute volume of water delivered to each lake, use of nearby streams provided a reasonable proxy for relative changes in runoff indices.

To quantify the timing of the snowmelt pulse, WSCV of streamflow was calculated for each lake. WSCV was the day of the year when 50% of the cumulative streamflow during a specified time window had been discharged from the watershed (Figure 2; Burns et al., 2007; Zion et al., 2011). Because all lakes in this study are in north temperate regions, we used January 1 to May 31 as the snowmelt window because this period provides a reasonable approximation of the span of the seasonal snow-covered and snowmelt period. To
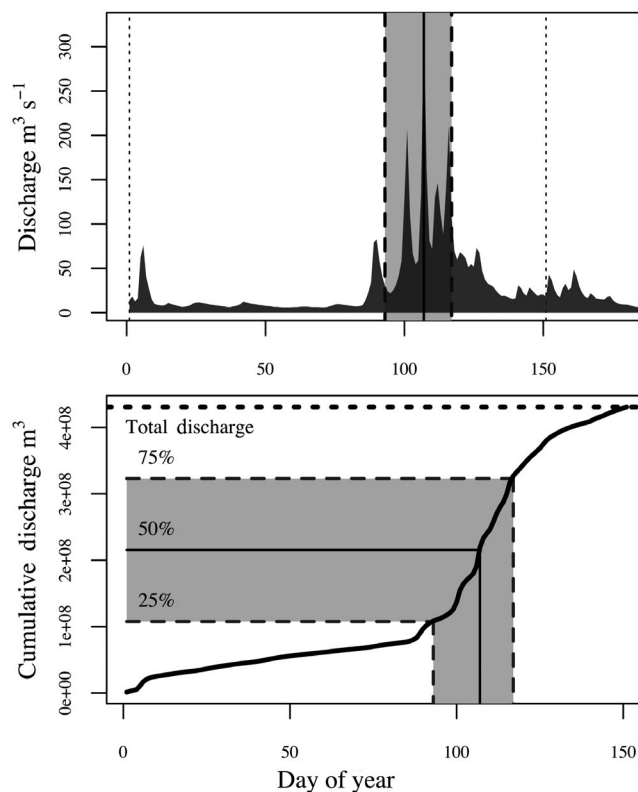
FIGURE 2 Metrics developed for runoff timing and magnitude for a sample year from a tributary to Lake Champlain in the context of average daily discharge (upper panel) and cumulative discharge during winter and spring (lower panel). In the upper panel, the dark, shaded region represents average daily discharge, and the region encompassed by the dotted lines is the period from January 1 to May 31. In the lower panel, the solid black line represents cumulative stream runoff for the defined spring window in 1 year. *y*-intercept of the horizontal, thick, dotted line represents total runoff delivered during this period. In both panels, the *x*-intercept of the vertical solid line represents the winter/spring center of volume (WSCV; day at which 50% of discharge has been delivered). The shaded area around the x-intercept represents the interquartile distance (IQD) between the dates of the 25th and 75th percentiles of discharge (measured in number of days)

quantify the magnitude of winter/spring runoff, the total cumulative runoff volume during the same January to May window was calculated for each year. To quantify the duration of winter/spring runoff, we used the interquartile distance (IQD), calculated as the number of days between the 25th and 75th percentile dates of cumulative runoff volume during the snowmelt window (Figure 2). All runoff indices were highly correlated whether the snowmelt window ended on May 31 or April 30. Therefore, our results were not sensitive to the choice of snowmelt window (Figures S1, S2, and S3).

2.4 | Comparison of runoff and phytoplankton indices

We used linear regression to test our hypothesis that earlier runoff corresponds to lower summer Chl-*a*. Prior to analyses, we detrended

the WSCV and Chl-*a* indices to better control for potential linear effects of other local changes over time, such as watershed land use not directly related to our research questions. Detrending ensured that our analyses primarily represented variations in the WSCV and Chl-*a* among years rather than trends occurring in the lakes over time. We also standardized all runoff and Chl-*a* indices to *z*-scores for each lake to make relative changes comparable among lakes of varying hydrologic and trophic status. We performed linear regressions on the detrended, standardized Chl-*a* index versus detrended, standardized WSCV for each lake using each year as an observation. We then took the slope from each lake and calculated the mean slope across all lakes and its 95% confidence interval to test for a statistically significant difference from zero using bootstrapping with 1000 iterations. Slope distributions were displayed using kernel density estimation (Läuter, 1988; Scott, 2015; Sheather & Jones, 1991). A positive mean slope and confidence interval that does not include zero indicated support for our hypothesis that earlier runoff corresponds with lower summer phytoplankton Chl-*a*. The same process was completed with detrended, standardized values for runoff magnitude versus Chl-*a*, runoff magnitude versus WSCV, and runoff duration versus WSCV. Additionally, we tested if the WSCV had become significantly earlier in our study lakes or if total runoff magnitude changed over time by calculating the mean slope and 95% confidence interval of WSCV and runoff magnitude *z*-scores (before detrending) versus year.

We examined the effects of several lake variables on the slope between Chl-*a* and runoff timing via a CART analysis (Breiman et al., 1984). In the CART analysis, we included lake thermal region (Maberly et al., 2020), mean lake depth, drainage ratio (ratio of watershed to lake surface area), mean summer total phosphorus concentration, and mean dissolved organic carbon concentration as predictor variables and the slope of Chl-*a* versus WSCV for each lake as the response variable. Mean residence time was discarded as a predictor variable because of its high correlation with mean depth ($r = 0.74$). Regression trees were built and pruned in the R packages rpart (Therneau & Atkinson, 2018) and rpart.plot (Milborrow, 2018). Missing data for predictor variables were accounted for using surrogate splits and the leaves were pruned to minimize cross-validation error (O'Reilly et al., 2015; Sharma et al., 2012). Data analysis and visualization were facilitated with R version 3.6.1 (R Development Core Team, 2019).

Relationships between ice cover and WSCV and the Chl-*a* index were explored in a subset of lakes where ice data were available. Ice-out date was strongly correlated with ice cover duration (average $r = 0.76$) for lakes where both were available ($N = 10$). We included only ice-out date in analyses because of the higher sample size ($N = 19$; Table 1). Note that Red Chalk, Blue Chalk, and Harp Lakes in Ontario, Canada, are in the same geographic region and ice-out date is estimated using a single sentinel lake. We analyzed the relationships of the WSCV with ice-out date and the Chl-*a* index with ice-out date as described above to calculate bootstrapped confidence intervals around mean slopes of these relationships. All indices were detrended and standardized (converted to *z*-scores within lakes). A

mean positive slope for the relationship between WSCV and ice-out would indicate that years with early runoff timing also have early ice-out. A mean positive slope for the relationship between Chl-*a* and ice-out would indicate that years with early ice-out have lower Chl-*a*.

We performed sensitivity analyses for each set of slopes that were tested by randomly leaving out four lakes and re-calculating the means and bootstrapped 95% confidence intervals with the slopes of the relationships in the remaining lakes. Simulations were repeated 1000 times for each relationship that was tested.

3 | RESULTS

Slopes for the standardized WSCV over years was mostly negative (80% of lakes; Figure 3A), indicating that runoff is generally becoming earlier over time. However, these data contained some notable outliers; therefore, the 95% confidence interval for the mean slope
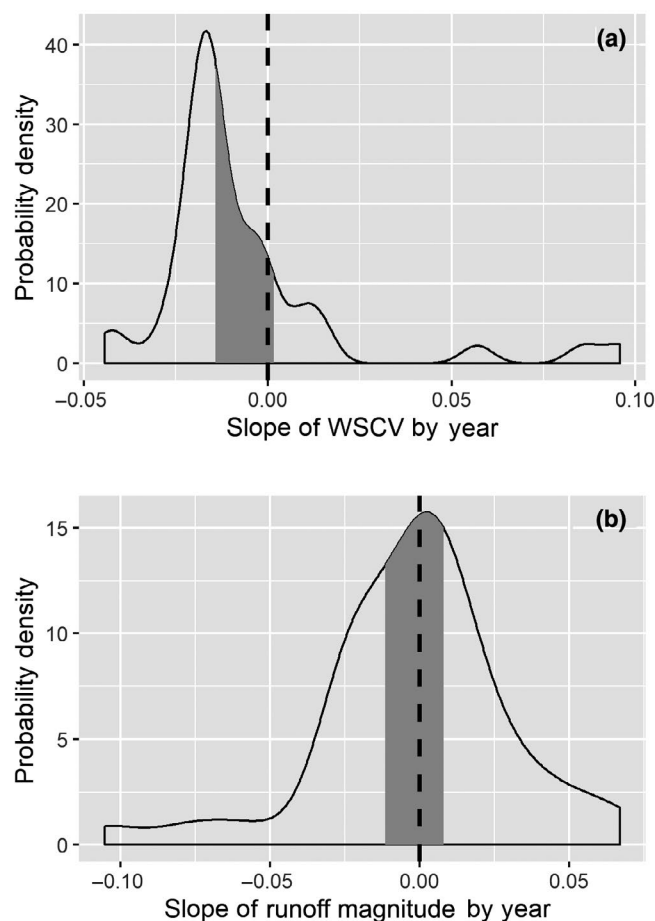
FIGURE 3 Slope distributions for all lakes of (a) runoff timing index (winter/spring center of volume [WSCV]) as a function of year and (b) total stream runoff magnitude as a function of year (before detrending) using kernel density estimation of trends over time. Negative slopes indicate that WSCV or magnitude are earlier over time. Dashed lines indicate slope of zero, and shaded regions represent the bootstrapped 95% confidence interval around the mean slope

extended slightly into the positive range (mean = −0.006; 95% confidence interval = [−0.015 to 0.002]). Means in this case are unitless z-scores.

Runoff magnitude did not change over time across our data set. The distribution of slopes of runoff volume versus year was centered close to zero (Figure 3B; mean = −0.022; 95% confidence interval = [−0.012 to 0.008]; 49% of lakes had negative slopes).

Earlier WSCV (detrended) generally corresponded with lower summer Chl-*a* (positive slope). A few lakes, however, had weak relationships or negative slopes of WSCV versus Chl-*a*, and confidence intervals around linear regressions were variable (Figure 4). However, when slopes for all lakes were plotted jointly, a majority of slopes were positive (63% of lakes; Figure 5A), indicating general support for our hypothesis. The mean slope of the Chl-*a* versus runoff timing relationship was significantly >0 (mean = 0.074; 95% confidence interval = [0.008–0.141]). These results are independent of other events in lakes over time (e.g., ongoing eutrophication) because Chl-*a* and runoff timing were detrended over time to minimize outside effects.

Summer Chl-*a* increased with the magnitude of runoff. The mean slope of the linear regression for the effect of standardized, detrended runoff magnitude on the Chl-*a* index was significantly >0 (mean = 0.086; 95% confidence interval = [0.005–0.167]),

indicating that years with greater stream discharge volume tended to have higher Chl-*a* during the subsequent summer. The distribution of slopes demonstrated that a majority of lakes followed this trend (56% of lakes; Figure 5B), with some outliers having stronger relationships.

The duration of spring runoff as indicated by the IQD was negatively related to WSCV, indicating that years with earlier runoff had more protracted runoff (Figure 5C). The distribution of slopes for the relationship between IQD and WSCV was significantly <0 (mean = −0.272; 95% confidence interval = [−0.367 to −0.177]).

The WSCV was significantly positively related to runoff magnitude. In other words, years with later stream runoff also had a higher volume of stream discharge (Figure 5D; mean = 0.179; 95% confidence interval = [0.080–0.277]; 78% of lakes had positive slopes).

We found no significant factors that described variation among lakes in the WSCV versus Chl-*a* relationship. Drainage ratio, mean summer total phosphorus, and mean depth were significant in the original CART analysis but were removed during pruning and cross-validation. The influence of other lake variables tested was negligible, including lake thermal region, and average summer dissolved organic carbon.

The timing of ice-out was strongly related to WSCV, but not to Chl-*a*. The mean slope for the relationship between runoff timing
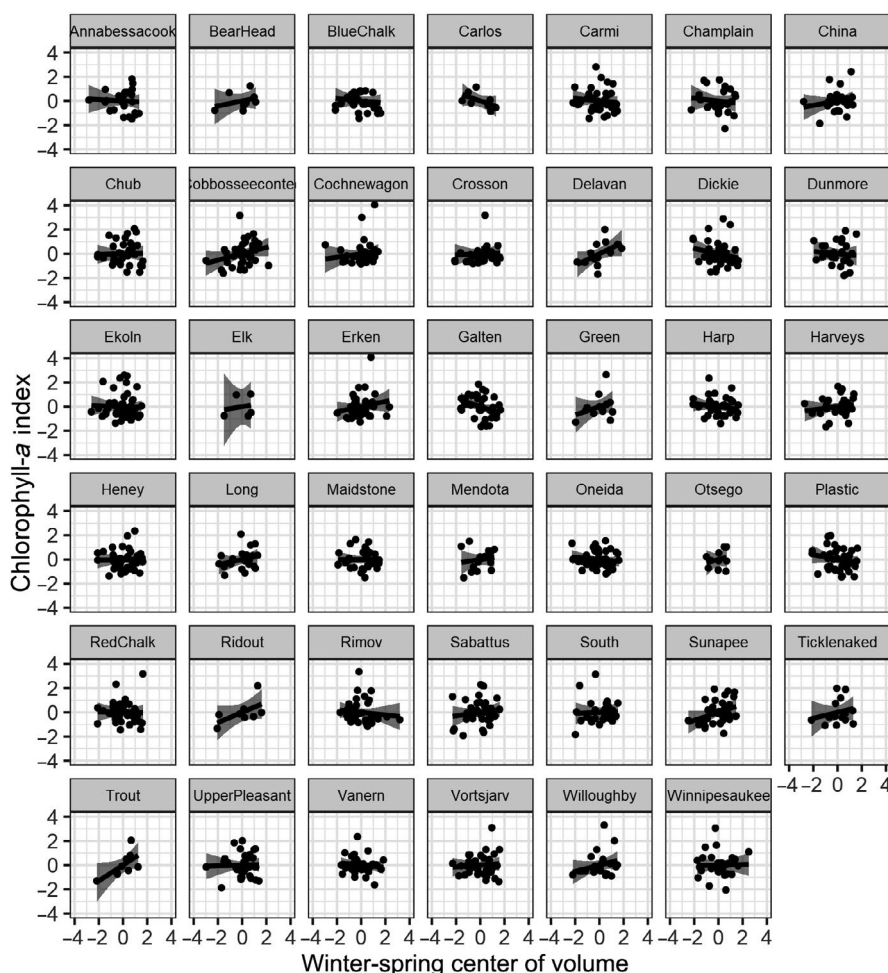
FIGURE 4 Relationships for chlorophyll-*a* (Chl-*a*) index by winter/spring center of volume (WSCV) for each lake. Indices were detrended and converted to *z*-scores. Negative values for *z*-scores indicate earlier WSCV or less Chl-*a*, indices of zero indicate years that matched mean conditions, and positive values indicate later WSCV or more Chl-*a*. Trend lines represent linear regressions, gray shading indicates regression confidence interval, and each point represents 1 year
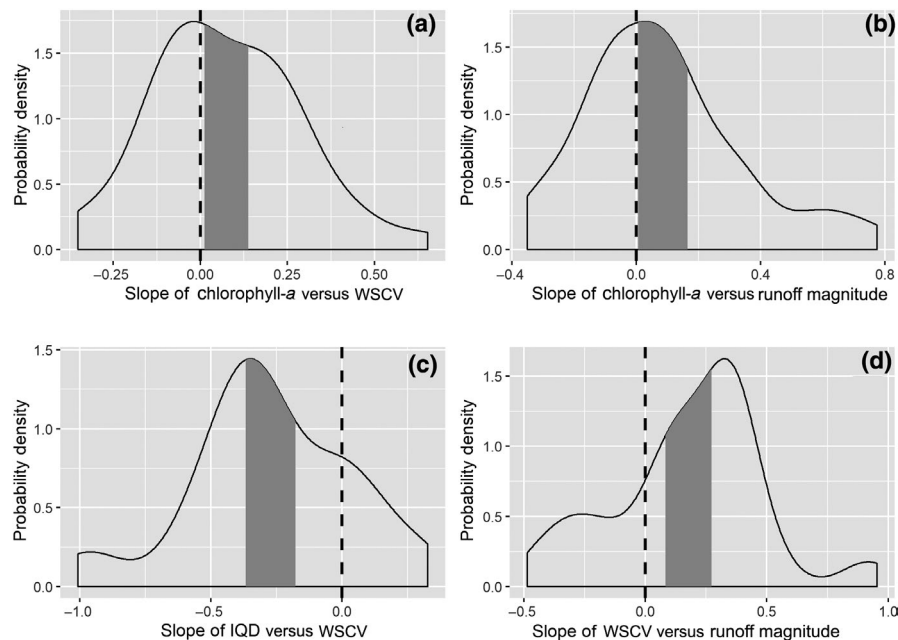
FIGURE 5 Slope distributions using kernel density estimation of relationships between detrended *z*-scores of variables. Dashed lines indicate slope of zero, and shaded regions represent the 95% confidence interval around the mean slope for each relationship. All relationships in this figure were statistically significant. (a) Positive slopes indicate that earlier winter/spring center of volume (WSCV) was associated with lower summer phytoplankton biomass. (b) Positive slopes indicate that winter/spring runoff magnitude has a positive effect on summer phytoplankton biomass. (c) Negative slopes of interquartile distance (IQD) of runoff versus WSCV indicate that years with earlier WSCV tend to also have more protracted runoff. (d) Positive slopes indicate that later WSCV corresponds with higher discharge magnitude

and ice-out date was significantly >0, indicating that years with early WSCV also had early ice-out (Figure 6A; mean = 0.623; 95% confidence interval = [0.419–0.828]; 89% of lakes had positive slopes). The confidence interval for the slope of the relationship between ice-out date and Chl-*a* included zero, indicating no significant relationship between Chl-*a* and ice-out date among lakes (Figure 6B; mean = 0.065; 95% confidence interval = [−0.051 to 0.181]; 53% of lakes had positive slopes).

Results of sensitivity analyses supported the results from the analysis of slope distributions (Table S.1). For example, the relationship between Chl-*a* and WSCV was significantly positive in 67% of simulations with four lakes missing and non-significant in the remaining 33% of simulations. The opposite hypothesis was not supported in any case (i.e., no mean slopes were negative in any of the 1000 simulations). Other relationships tested followed similar trends, where sensitivity analyses gave similar results to original data (Table S.1).

4 | DISCUSSION

Globally, most lakes are located in high-latitude regions (Verpoorter et al., 2014) where snowmelt has an influence on the timing of winter/spring runoff. Here, we supported the hypothesis that climate mediated changes in the timing of winter–spring runoff affects phytoplankton concentrations measured as Chl-*a* during the stratified period following spring runoff. We also found that years with earlier

runoff had lower winter/spring runoff volume, more protracted runoff, and earlier ice-out. Ice-out, although correlated with WSCV, was not related to summer Chl-*a*. Our results illustrate a previously underappreciated effect on lake biota by a climate change impact that is well documented in the hydrologic literature. Detecting a relationship between WSCV and summer Chl-*a* is difficult and required extensive data to detect a signal. Our hypotheses were based on the effects of runoff timing on nutrient availability, although we acknowledge that many other factors could regulate lake internal processes and are also well known to influence lake phytoplankton during the period of thermal stratification. We identified two primary mechanisms by which earlier winter/spring runoff can affect summer Chl-*a* concentrations. Both can affect the timing and availability of watershed-derived nutrients in lakes.

The first mechanism is related to changes in the delivery and mixing of runoff-derived nutrients entering a lake and results from the interaction of runoff with the physical structure of the water column. If snowmelt occurs during mid-winter when lakes are ice covered with stable inverse stratification (Kirillin et al., 2012), a significant fraction of near 0°C snowmelt inputs will enter the lake as a shallow under-ice plume that does not readily mix into the denser water below. Under these conditions, the effective residence time of these nutrient inputs will be reduced, and a substantial fraction can flow out of the lake without effectively mixing into the water column (Cortés et al., 2017). By contrast, if snowmelt and increased runoff occur later in winter after solar heating and convective mixing have destabilized the under-ice water column (Kirillin et al., 2012) or
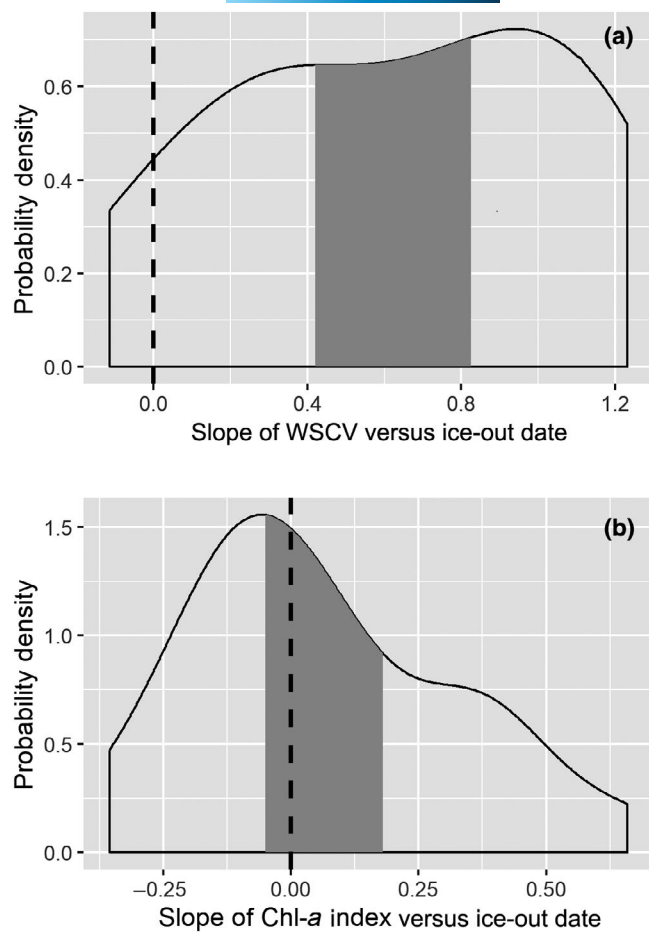
FIGURE 6 Slope distributions using kernel density estimation of relationships between detrended *z*-scores of variables. Dashed lines indicate slope of zero, and shaded regions represent the 95% confidence interval around the mean slope for each relationship. (a) Positive slopes indicate that earlier winter/spring center of volume (WSCV) was associated with earlier ice-out date. (b) Overlap of the 95% confidence interval with zero indicates no significant relationship between Chl-*a* and ice-out date among lakes

after the loss of ice cover, a much higher fraction of nutrients may be retained because nutrients are more effectively mixed through-out the water column and become available to support epilimnetic production (Roberts et al., 2018). Furthermore, if a lake becomes sufficiently anoxic under the ice-covered period, under-ice snowmelt inputs deliver oxygen to the water column, reducing the likelihood of anoxia and associated geochemical transformations, particularly in shallow lakes with low residence times (Joung et al., 2017). Because anoxia mediates both sediment phosphorus release (Joung et al., 2017) and denitrification (Cavaliere & Baulch, 2018; Powers et al., 2017), reductions in anoxia will also reduce nutrient availability.

The second mechanism by which changes in runoff timing may affect summer Chl-*a* is related to changes in the bioavailability of nutrients that enter the lake during winter, which can be affected by many internal lake processes. If highly bioavailable allochthonous materials are delivered during a period when light and low tempera-ture limit growth, the potential of these nutrients to support the

growth of phytoplankton may be reduced. In this case, more nutri-ents could be used by bacteria or physically removed from the water column by adsorption to sinking particles. Less is known about this potential mechanism, although biological activity continues through-out the winter under ice (Bertilsson et al., 2013; Bižić-Ionescu et al., 2014; Grosbois & Rautio, 2018; Katz et al., 2015; Hampton et al., 2017; McKay et al., 2015) and some effects on the bioavailability of nutrients are likely.

The spring phytoplankton bloom is also an important biological mediator of the fate of nutrients that enter a lake system, and the timing and magnitude of the spring bloom will affect the availability of nutrients during summer. The spring bloom is expected to happen earlier over time with climate change (Peeters et al., 2007). If the ice cover permits sufficient light penetration when winter runoff en-ters a lake, substantial phytoplankton growth occurs prior to ice-off (Pernica et al., 2017; Salmi & Salonen, 2016) so that earlier WSCV would lead to an early spring phytoplankton bloom. Diatoms would likely dominate such a bloom (Goedkoop & Johnson, 1996; Poister & Armstrong, 2003). Large diatoms tend to take up nutrients and sink out of the water column, thereby reducing nutrient availabil-ity (Lund, 1959; Naselli-Flores et al., 2020; Reynolds, 2006; Zohary et al., 2020).

When earlier nutrient inputs during winter lead to an earlier phy-toplankton bloom, the differential response of phytoplankton and zooplankton to water temperature can affect trophic interactions that will further increase the effect of an early phytoplankton bloom on nutrient availability. Phytoplankton tend to be less limited by low temperatures compared to crustacean zooplankton and especially microzooplankton (Berger et al., 2010, 2014; Winder et al., 2012). An early phytoplankton bloom that occurs when zooplankton are still temperature-limited will reduce nutrient availability because nutrients fixed in the phytoplankton biomass sink out of the eu-photic zone and are less likely to be recycled by zooplankton grazing (Sommer et al., 2012).

Despite the complexity of processes regulating nutrient avail-ability, our results indicate that the timing of the spring flood has an impact on subsequent summer Chl-*a* as we originally hypothe-sized. Our hypothesis that earlier runoff results in lower summer Chl-*a* was supported, and we also found several other significant relationships to watershed hydrology that mediate the relationship between runoff and summer lake phytoplankton biomass. Years with earlier runoff timing were also years with lower runoff vol-ume in the winter and spring, more protracted runoff, and earlier ice loss, all factors that would reduce nutrient loading and nutrient availability. In contrast, years with later runoff also tended to have higher runoff volume, which would lead to larger nutrient loads. These interrelated changes in hydrology all potentially have impli-cations for how summer phytoplankton biomass may change with climate change.

Watershed hydrology, however, is not the only climate-related factor affecting summer Chl-*a*. For example, summer stratification plays a role in nutrient availability (Welch & Cooke, 1995). In deep lakes, the strength of summer stratification affects the mixing of

hypolimnetic nutrients across the thermocline (Langenberg et al., 2003), while in shallow lakes the strength and duration of stratification can control the development of hypolimnetic hypoxia and subsequent release of nutrients from lake sediments (Wilhelm & Adrian, 2008). Changing climate is expected to affect stratification dynamics in both shallow (Robertson et al., 2018) and deep lakes (Hondzo & Stefan, 1993; Robertson & Ragotzkie, 1990). Increased frequency of intense storms is another factor mediated by climate that may influence summer productivity (Stockwell et al., 2020). Large storms may disrupt plankton communities through effects on lake thermal structure, while also delivering large pulses of external nutrients (Jennings et al., 2012).

Aquatic primary production has increased over time with increased nutrient loading in many regions with changing land use and increased development (O'Neil et al., 2012; Paerl et al., 2018). Independent of climate related changes to the timing of nutrient delivery to lakes, the effect of internal loading processes may be more pronounced in lakes whose watershed are subjected to anthropogenic eutrophication, where larger pools of legacy nutrients in sediments are available for release (Robertson et al., 2018; Sharpley et al., 2013; Stackpoole et al., 2019). In pristine lakes, external nutrient loads such as those delivered during the spring flood may be an important proximate source of nutrients for summer plankton communities. However, our method of detrending over time only accounts for linear effects that progressed in one direction over time (e.g., increasing eutrophication) and does not account for non-linear effects or interactive effects of changing environmental conditions. Other non-linear effects may add additional noise to our data set.

When considering the interaction of runoff timing and summer Chl-*a*, we expected that the effects related to physical mixing and nutrient bioavailability would be most important. We also expected that the strength of the relationship would be related to water residence times (and thereby mean depth in our data set) because lakes with a short residence time have a larger fraction of the water column replaced during the spring flood. However, we did not find residence time or mean depth to be a significant influence in this respect, which illustrates the complexity of the physical relationships regulating nutrient availability. For example, in Emerald Lake, a mountain lake in the Sierra Nevada of California, USA, summer phytoplankton biomass tends to be higher in years with shallow snowpacks that begin melting earlier rather than wet years with large snowpacks that begin melting late. Years with shallow snowpack have lower overall discharge, and result in alpine lakes warming earlier and reaching higher maximum temperatures. These lakes also have elevated summer nutrient concentrations because of reduced snowmelt dilution, and consequently higher phytoplankton biomass than years with deep snowpacks (Sadro et al., 2018). This example is contrary to our original hypothesis—earlier runoff led to enhanced summer Chl-*a*—and demonstrates that our results can be limited to certain lake types (i.e., our study was limited to north temperate lakes).

We set out to evaluate the relationship between the timing of winter/spring runoff and summertime Chl-*a* concentration across a large set of lakes because a relationship that may appear weak within a single lake, due to potential confounding factors, may be more consistently observed across many lakes and attributed to a common factor that impacts all of them. Despite the complexity of processes regulating summer chlorophyll concentration, some of which are only weakly affected by the timing of runoff, we found evidence that ongoing changes in the seasonality of the hydrologic inputs to lakes have effects that extend into the period of summer stratification. We do not propose that changes in the timing of winter spring runoff will override other factors that could regulate summer Chl-*a* concentrations, such as warmer summer epilimnetic temperatures or stronger thermal stratification (Berger et al., 2006; Winder & Sommer, 2012). Rather, we consider changes in the timing of runoff a potential mediating effect on summer lake productivity, and one that has not been fully explored. Given the large number of lakes that could be affected, our findings warrant further investigations that include data collection specifically designed to evaluate the flow-paths and bioavailability of nutrients entering lakes during winter.

DATA AVAILABILITY STATEMENT

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REFERENCES

Andréasson, J., Bergström, S., Carlsson, B., Graham, L. P., & Lindström, G. (2004). Hydrological change – climate change impact simulations for Sweden. *AMBIO: A Journal of the Human Environment*, *33*(4), 228–234. https://doi.org/10.1579/0044-7447-33.4.228

Barnett, T. P., Adam, J. C., & Lettenmaier, D. P. (2005). Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature*, *438*(7066), 303–309. https://doi.org/10.1038/nature04141

Berger, S. A., Diehl, S., Kunz, T. J., Albrecht, D., Oucible, A. M., & Ritzer, S. (2006). Light supply, plankton biomass, and seston stoichiometry in a gradient of lake mixing depths. *Limnology and Oceanography*, *51*(4), 1898–1905. https://doi.org/10.4319/lo.2006.51.4.1898

Berger, S. A., Diehl, S., Stibor, H., Sebastian, P., & Scherz, A. (2014). Separating effects of climatic drivers and biotic feedbacks on seasonal plankton dynamics: No sign of trophic mismatch. *Freshwater Biology*, *59*(10), 2204–2220. https://doi.org/10.1111/fwb.12424

Berger, S. A., Diehl, S., Stibor, H., Trommer, G., & Ruhenstroth, M. (2010). Water temperature and stratification depth independently shift cardinal events during plankton spring succession. *Global Change Biology*, *16*(7), 1954–1965. https://doi.org/10.1111/j.1365-2486.2009.02134.x

Bertilsson, S., Burgin, A., Carey, C. C., Fey, S. B., Grossart, H.-P., Grubisic, L. M., Jones, I. D., Kirillin, G., Lennon, J. T., Shade, A., & Smyth, R. L. (2013). The under-ice microbiome of seasonally frozen lakes.

Limnology and Oceanography, *58*(6), 1998–2012. https://doi.org/10.4319/lo.2013.58.6.1998

Bižić-Ionescu, M., Amann, R., & Grossart, H.-P. (2014). Massive regime shifts and high activity of heterotrophic bacteria in an ice-covered lake. *PLoS One*, *9*(11), e113611. https://doi.org/10.1371/journal.pone.0113611

Blenckner, T. (2005). A conceptual model of climate-related effects on lake ecosystems. *Hydrobiologia*, *533*(1–3), 1–14. https://doi.org/10.1007/s10750-004-1463-4

Blöschl, G., Hall, J., Parajka, J., Perdigão, R. A. P., Merz, B., Arheimer, B., Aronica, G. T., Bilibashi, A., Bonacci, O., Borga, M., Čanjevac, I., Castellarin, A., Chirico, G. B., Claps, P., Fiala, K., Frolova, N., Gorbachova, L., Gül, A., Hannaford, J., … Živković, N. (2017). Changing climate shifts timing of European floods. *Science (New York, N.Y.)*, *357*(6351), 588–590. https://doi.org/10.1126/science.aan2506

Bolsenga, S. J., & Vanderploeg, H. A. (1992). Estimating photosynthetically available radiation into open and ice-covered freshwater lakes from surface characteristics; a high transmittance case study. *Hydrobiologia*, *243–244*(1), 95–104. https://doi.org/10.1007/BF00007024

Bouchard, F., Turner, K. W., MacDonald, L. A., Deakin, C., White, H., Farquharson, N., Medeiros, A. S., Wolfe, B. B., Hall, R. I., Pienitz, R., & Edwards, T. W. D. (2013). Vulnerability of shallow subarctic lakes to evaporate and desiccate when snowmelt runoff is low. *Geophysical Research Letters*, *40*(23), 6112–6117. https://doi.org/10.1002/2013GL058635

Breiman, L., Friedman, J. H., Olshen, R. A., & Stone, C. J. (1984). *Classification and regression trees*. Wadsworth.

Burns, D. A., Klaus, J., & McHale, M. R. (2007). Recent climate trends and implications for water resources in the Catskill Mountain region, New York, USA. *Journal of Hydrology*, *336*(1–2), 155–170. https://doi.org/10.1016/J.JHYDROL.2006.12.019

Cavaliere, E., & Baulch, H. M. (2018). Denitrification under lake ice. *Biogeochemistry*, *137*(3), 285–295. https://doi.org/10.1007/s10533-018-0419-0

Cortés, A., MacIntyre, S., & Sadro, S. (2017). Flowpath and retention of snowmelt in an ice-covered arctic lake. *Limnology and Oceanography*, *62*(5), 2023–2044. https://doi.org/10.1002/lno.10549

Creed, I. F., Bergström, A.-K., Trick, C. G., Grimm, N. B., Hessen, D. O., Karlsson, J., Kidd, K. A., Kritzberg, E., McKnight, D. M., Freeman, E. C., Senar, O. E., Andersson, A., Ask, J., Berggren, M., Cherif, M., Giesler, R., Hotchkiss, E. R., Kortelainen, P., Palta, M. M., … Weyhenmeyer, G. A. (2018). Global change-driven effects on dissolved organic matter composition: Implications for food webs of northern lakes. *Global Change Biology*, *24*(8), 3692–3714. https://doi.org/10.1111/gcb.14129

Du, J., Kimball, J. S., Duguay, C., Kim, Y., & Watts, J. D. (2017). Satellite microwave assessment of Northern Hemisphere lake ice phenology from 2002 to 2015. *The Cryosphere*, *11*(1), 47–63. https://doi.org/10.5194/tc-11-47-2017

Fang, X., & Stefan, H. G. (1998). Potential climate warming effects on ice covers of small lakes in the contiguous U.S. *Cold Regions Science and Technology*, *27*(2), 119–140. https://doi.org/10.1016/S0165-232X(97)00027-X

Goedkoop, W., & Johnson, R. K. (1996). Pelagic-benthic coupling: Profundal benthic community response to spring diatom deposition in mesotrophic Lake Erken. *Limnology and Oceanography*, *41*(4), 636–647. https://doi.org/10.4319/lo.1996.41.4.0636

Grosbois, G., & Rautio, M. (2018). Active and colorful life under lake ice. *Ecology*, *99*(3), 752–754. https://doi.org/10.1002/ecy.2074

Katz, S. L., Izmest'eva, L. R., Hampton, S. E., Ozersky, T., Shchapov, K., Moore, M. V., Shimaraeva, S. V., & Silow, E. A. (2015). The "Melosira years" of Lake Baikal: Winter environmental conditions at ice onset predict under-ice algal blooms in spring. *Limnology*

and Oceanography, 60(6), 1950–1964. https://doi.org/10.1002/lno.10143

Hampton, S. E., Galloway, A. W. E., Powers, S. M., Ozersky, T., Woo, K. H., Batt, R. D., Labou, S. G., O'Reilly, C. M., Sharma, S., Lottig, N. R., Stanley, E. H., North, R. L., Stockwell, J. D., Adrian, R., Weyhenmeyer, G. A., Arvola, L., Baulch, H. M., Bertani, I., Bowman, L. L., … Xenopoulos, M. A. (2017). Ecology under lake ice. Ecology Letters, 20(1), 98–111. https://doi.org/10.1111/ele.12699

Hayes, N. M., Vanni, M. J., Horgan, M. J., & Renwick, W. H. (2015). Climate and land use interactively affect lake phytoplankton nutrient limitation status. Ecology, 96(2), 392–402. https://doi.org/10.1890/13-1840.1

Hodgkins, G. A., James, I. C., & Huntington, T. G. (2002). Historical changes in lake ice-out dates as indicators of climate change in New England, 1850–2000. International Journal of Climatology, 22(15), 1819–1827. https://doi.org/10.1002/joc.857

Hondzo, M., & Stefan, H. G. (1993). Regional water temperature characteristics of lakes subjected to climate change. Climatic Change, 24(3), 187–211. https://doi.org/10.1007/BF01091829

Hongve, D., Riise, G., & Kristiansen, J. F. (2004). Increased colour and organic acid concentrations in Norwegian forest lakes and drinking water? A result of increased precipitation? Aquatic Sciences - Research across Boundaries, 66(2), 231–238. https://doi.org/10.1007/s00027-004-0708-7

Jennings, E., Jones, S., Arvola, L., Staehr, P. A., Gaiser, E., Jones, I. D., Weathers, K. C., Weyhenmeyer, G. A., Chiu, C.-Y., & De Eyto, E. (2012). Effects of weather-related episodic events in lakes: An analysis based on high-frequency data. Freshwater Biology, 57(3), 589–601. https://doi.org/10.1111/j.1365-2427.2011.02729.x

Johnson, S. L., & Stefan, H. G. (2006). Indicators of climate warming in Minnesota: Lake ICE covers and snowmelt runoff. Climatic Change, 75(4), 421–453. https://doi.org/10.1007/s10584-006-0356-0

Joung, D. J., Leduc, M., Ramcharitar, B., Xu, Y., Isles, P. D. F., Stockwell, J. D., Druschel, G. K., Manley, T., & Schroth, A. W. (2017). Winter weather and lake-watershed physical configuration drive phosphorus, iron, and manganese dynamics in water and sediment of ice-covered lakes. Limnology and Oceanography, 62(4), 1620–1635. https://doi.org/10.1002/lno.10521

Kirillin, G., Leppäranta, M., Terzhevik, A., Granin, N., Bernhardt, J., Engelhardt, C., Efremova, T., Golosov, S., Palshin, N., Sherstyankin, P., Zdorovennova, G., & Zdorovennov, R. (2012). Physics of seasonally ice-covered lakes: A review. Aquatic Sciences, 74(4), 659–682. https://doi.org/10.1007/s00027-012-0279-y

Kritzberg, E. S., Hasselquist, E. M., Škerlep, M., Löfgren, S., Olsson, O., Stadmark, J., Valinia, S., Hansson, L.-A., & Laudon, H. (2020). Browning of freshwaters: Consequences to ecosystem services, underlying drivers, and potential mitigation measures. Ambio, 49(2), 375–390. https://doi.org/10.1007/s13280-019-01227-5

Langenberg, V. T., Sarvala, J., & Roijackers, R. (2003). Effect of wind induced water movements on nutrients, chlorophyll-a, and primary production in Lake Tanganyika. Aquatic Ecosystem Health & Management, 6(3), 279–288. https://doi.org/10.1080/14634980301488

Läuter, H. (1988). Silverman, B.W.: Density estimation for statistics and data analysis. Chapman & Hall, London – New York 1986, 175 pp., £12 [Book Review]. Biometrical Journal, 30(7), 876–877. https://doi.org/10.1002/bimj.4710300745

Leavitt, P. R., Fritz, S. C., Anderson, N. J., Baker, P. A., Blenckner, T., Bunting, L., Catalan, J., Conley, D. J., Hobbs, W. O., Jeppesen, E., Korhola, A., McGowan, S., RÜhland, K., Rusak, J. A., Simpson, G. L., Solovieva, N., & Werne, J. (2009). Paleolimnological evidence of the effects on lakes of energy and mass transfer from climate and humans. Limnology and Oceanography, 54(6part2), 2330–2348. https://doi.org/10.4319/lo.2009.54.6_part_2.2330

Lund, J. W. G. (1959). Buoyancy in relation to the ecology of the freshwater phytoplankton. British Phycological Bulletin, 1(7), 1–17. https://doi.org/10.1080/00071615900650031

Maberly, S. C., O'Donnell, R. A., Woolway, R. I., Cutler, M. E. J., Gong, M., Jones, I. D., Merchant, C. J., Miller, C. A., Politi, E., Scott, E. M., Thackeray, S. J., & Tyler, A. N. (2020). Global lake thermal regions shift under climate change. Nature Communications, 11(1), 1–9. https://doi.org/10.1038/s41467-020-15108-z

Maier, D. B., Diehl, S., & Bigler, C. (2019). Interannual variation in seasonal diatom sedimentation reveals the importance of late winter processes and their timing for sediment signal formation. Limnology and Oceanography, 64(3), 1186–1199. https://doi.org/10.1002/lno.11106

Mander, Ü., Kull, A., Kuusemets, V., & Tamm, T. (2000). Nutrient run-off dynamics in a rural catchment: Influence of land-use changes, climatic fluctuations and ecotechnological measures. Ecological Engineering, 14(4), 405–417. https://doi.org/10.1016/S0925-8574(99)00064-6

McKay, R. M. L., Prášil, O., Pechar, L., Lawrenz, E., Rozmarynowycz, M. J., & Bullerjahn, G. S. (2015). Freshwater ice as habitat: Partitioning of phytoplankton and bacteria between ice and water in central European reservoirs. Environmental Microbiology Reports, 7(6), 887–898. https://doi.org/10.1111/1758-2229.12322

Mielko, C., & Woo, M. (2006). Snowmelt runoff processes in a headwater lake and its catchment, subarctic Canadian Shield. Hydrological Processes, 20(4), 987–1000. https://doi.org/10.1002/hyp.6117

Milborrow, S. (2018). rpart.plot: Plot "rpart" models: An enhanced version of "plot.rpart". https://cran.r-project.org/package=rpart.plot

Naselli-Flores, L., Zohary, T., & Padisák, J. (2020). Life in suspension and its impact on phytoplankton morphology: An homage to Colin S. Reynolds. Hydrobiologia, 848(1), 7–30. https://doi.org/10.1007/s10750-020-04217-x

O'Neil, J. M., Davis, T. W., Burford, M. A., & Gobler, C. J. (2012). The rise of harmful cyanobacteria blooms: The potential roles of eutrophication and climate change. Harmful Algae, 14, 313–334. https://doi.org/10.1016/j.hal.2011.10.027

O'Reilly, C. M., Sharma, S., Gray, D. K., Hampton, S. E., Read, J. S., Rowley, R. J., Schneider, P., Lenters, J. D., McIntyre, P. B., Kraemer, B. M., Weyhenmeyer, G. A., Straile, D., Dong, B. O., Adrian, R., Allan, M. G., Anneville, O., Arvola, L., Austin, J., Bailey, J. L., … Zhang, G. (2015). Rapid and highly variable warming of lake surface waters around the globe. Geophysical Research Letters, 42(24), 10773–10781. https://doi.org/10.1002/2015GL066235

Paerl, H. W., Otten, T. G., & Kudela, R. (2018). Mitigating the expansion of harmful algal blooms across the freshwater-to-marine continuum. Environmental Science & Technology, 52(10), 5519–5529. https://doi.org/10.1021/acs.est.7b05950

Pall, P., Vilbaste, S., Kõiv, T., Kõrs, A., Käiro, K., Laas, A., Nõges, P., Nõges, T., Piirsoo, K., Toomsalu, L., & Viik, M. (2011). Fluxes of carbon and nutrients through the inflows and outflow of Lake Võrtsjärv, Estonia. Estonian Journal of Ecology, 60(1), 39–53. https://doi.org/10.3176/eco.2011.1.04

Peeters, F., Straile, D., Lorke, A., & Livingstone, D. M. (2007). Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate. Global Change Biology, 13(9), 1898–1909. https://doi.org/10.1111/j.1365-2486.2007.01412.x

Pernica, P., North, R. L., & Baulch, H. M. (2017). In the cold light of day: The potential importance of under-ice convective mixed layers to primary producers. Inland Waters, 7(2), 138–150. https://doi.org/10.1080/20442041.2017.1296627

Pierson, D. C., Samal, N. R., Owens, E. M., Schneiderman, E. M., & Zion, M. S. (2013). Changes in the timing of snowmelt and the seasonality of nutrient loading: Can models simulate the impacts on freshwater trophic status? Hydrological Processes, 27(21), 3083–3093. https://doi.org/10.1002/hyp.9894

Pierson, D. C., & Taylor, C. H. (1985). Influence of snowcover development and ground freezing on cation loss from a wetland watershed during spring runoff. Canadian Journal of Fisheries and Aquatic Sciences, 42(12), 1979–1985. https://doi.org/10.1139/f85-245

Pilla, R. M., Williamson, C. E., Zhang, J., Smyth, R. L., Lenters, J. D., Brentrup, J. A., Knoll, L. B., & Fisher, T. J. (2018). Browning-related decreases in water transparency lead to long-term increases in surface water temperature and thermal stratification in two small lakes. *Journal of Geophysical Research: Biogeosciences*, 123(5), 1651–1665. https://doi.org/10.1029/2017JG004321

Poister, D., & Armstrong, D. E. (2003). Seasonal sedimentation trends in a mesotrophic lake: Influence of diatoms and implications for phosphorus dynamics. *Biogeochemistry*, 65(1), 1–13. https://doi.org/10.1023/A:1026087808168

Powers, S. M., Baulch, H. M., Hampton, S. E., Labou, S. G., Lottig, N. R., & Stanley, E. H. (2017). Nitrification contributes to winter oxygen depletion in seasonally frozen forested lakes. *Biogeochemistry*, 136(2), 119–129. https://doi.org/10.1007/s10533-017-0382-1

R Development Core Team. (Ed.). (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://doi.org/10.1007/978-3-540-74686-7

Read, J. S., & Rose, K. C. (2013). Physical responses of small temperate lakes to variation in dissolved organic carbon concentrations. *Limnology and Oceanography*, 58(3), 921–931. https://doi.org/10.4319/lo.2013.58.3.0921

Reynolds, C. S. (2006). *The ecology of phytoplankton*. Cambridge University Press. https://doi.org/10.1017/CBO9780511542145

Richardson, D., Melles, S., Pilla, R., Hetherington, A., Knoll, L., Williamson, C., Kraemer, B., Jackson, J., Long, E., Moore, K., Rudstam, L., Rusak, J., Saros, J., Sharma, S., Strock, K., Weathers, K., & Wigdahl-Perry, C. (2017). transparency, geomorphology and mixing regime explain variability in trends in lake temperature and stratification across northeastern North America (1975–2014). *Water*, 9(6), 442. https://doi.org/10.3390/w9060442

Roberts, D. C., Forrest, A. L., Sahoo, G. B., Hook, S. J., & Schladow, S. G. (2018). Snowmelt timing as a determinant of lake inflow mixing. *Water Resources Research*, 54(2), 1237–1251. https://doi.org/10.1002/2017WR021977

Robertson, D. M., & Ragotzkie, R. A. (1990). Changes in the thermal structure of moderate to large sized lakes in response to changes in air temperature. *Aquatic Sciences*, 52(4), 360–380. https://doi.org/10.1007/BF00879763

Robertson, D. M., Ragotzkie, R. A., & Magnuson, J. J. (1992). Lake ice records used to detect historical and future climatic changes. *Climatic Change*, 21(4), 407–427. https://doi.org/10.1007/BF00141379

Robertson, D. M., Siebers, B. J., Diebel, M. W., & Somor, A. J. (2018). Water-quality response to changes in phosphorus loading of the Winnebago Pool Lakes, Wisconsin, with special emphasis on the effects of internal loading in a chain of shallow lakes. *Scientific Investigations Report*, https://doi.org/10.3133/sir20185099

Rosenberg, B. D., & Schroth, A. W. (2017). Coupling of reactive riverine phosphorus and iron species during hot transport moments: Impacts of land cover and seasonality. *Biogeochemistry*, 132(1–2), 103–122. https://doi.org/10.1007/s10533-016-0290-9

Rusak, J. A., Tanentzap, A. J., Klug, J. L., Rose, K. C., Hendricks, S. P., Jennings, E., Laas, A., Pierson, D., Ryder, E., Smyth, R. L., White, D. S., Winslow, L. A., Adrian, R., Arvola, L., de Eyto, E., Feuchtmayr, H., Honti, M., Istvánovics, V., Jones, I. D., … Zhu, G. (2018). Wind and trophic status explain within and among-lake variability of algal biomass. *Limnology and Oceanography Letters*, 3(6), 409–418. https://doi.org/10.1002/lol2.10093

Sadro, S., Sickman, J. O., Melack, J. M., & Skeen, K. (2018). Effects of climate variability on snowmelt and implications for organic matter in a high-elevation lake. *Water Resources Research*, 54(7), 4563–4578. https://doi.org/10.1029/2017WR022163

Salmi, P., & Salonen, K. (2016). Regular build-up of the spring phytoplankton maximum before ice-break in a boreal lake. *Limnology and Oceanography*, 61(1), 240–253. https://doi.org/10.1002/lno.10214

Scott, D. W. (2015). *Multivariate density estimation: Theory, practice, and visualization* (2nd ed.). Wiley. https://doi.org/10.1002/9781118575574

Shanley, J. B., & Chalmers, A. (1999). The effect of frozen soil on snowmelt runoff at Sleepers River. Vermont. *Hydrological Processes*, 13(12–13), 1843–1857. https://doi.org/10.1002/(SICI)1099-1085(199909)13:12/13<1843:AID-HYP879>3.0.CO;2-G

Sharma, S., Legendre, P., Boisclair, D., & Gauthier, S. (2012). Effects of spatial scale and choice of statistical model (linear versus tree-based) on determining species–habitat relationships. *Canadian Journal of Fisheries and Aquatic Sciences*, 69(12), 2095–2111. https://doi.org/10.1139/cjfas-2011-0505

Sharpley, A., Jarvie, H. P., Buda, A., May, L., Spears, B., & Kleinman, P. (2013). Phosphorus legacy: Overcoming the effects of past management practices to mitigate future water quality impairment. *Journal of Environmental Quality*, 42(5), 1308–1326. https://doi.org/10.2134/jeq2013.03.0098

Sheather, S. J., & Jones, M. C. (1991). A reliable data-based bandwidth selection method for kernel density estimation. *Journal of the Royal Statistical Society: Series B (Methodological)*, 53(3), 683–690. https://doi.org/10.1111/j.2517-6161.1991.tb01857.x

Sommer, U., Adrian, R., De Senerpont Domis, L., Elser, J. J., Gaedke, U., Ibelings, B., Jeppesen, E., Lürling, M., Molinero, J. C., Mooij, W. M., van Donk, E., & Winder, M. (2012). Beyond the Plankton Ecology Group (PEG) model: Mechanisms driving plankton succession. *Annual Review of Ecology, Evolution, and Systematics*, 43(1), 429–448. https://doi.org/10.1146/annurev-ecolsys-110411-160251

Stackpoole, S. M., Stets, E. G., & Sprague, L. A. (2019). Variable impacts of contemporary versus legacy agricultural phosphorus on US river water quality. *Proceedings of the National Academy of Sciences of the United States of America*, 116(41), 20562–20567. https://doi.org/10.1073/pnas.1903226116

Stewart, I. T., Cayan, D. R., & Dettinger, M. D. (2004). Changes in snowmelt runoff timing in western North America under a business as usual' climate change scenario. *Climatic Change*, 62(1–3), 217–232. https://doi.org/10.1023/B:CLIM.0000013702.22656.e8

Stockwell, J. D., Doubek, J. P., Adrian, R., Anneville, O., Carey, C. C., Carvalho, L., De Senerpont Domis, L. N., Dur, G., Frassl, M. A., Grossart, H.-P., Ibelings, B. W., Lajeunesse, M. J., Lewandowska, A. M., Llames, M. E., Matsuzaki, S.-I., Nodine, E. R., Nõges, P., Patil, V. P., Pomati, F., … Wilson, H. L. (2020). Storm impacts on phytoplankton community dynamics in lakes. *Global Change Biology*, 26(5), 2756–2784. https://doi.org/10.1111/gcb.15033

Tan, Z., Yao, H., & Zhuang, Q. (2018). A small temperate lake in the 21st century: Dynamics of water temperature, ice phenology, dissolved oxygen, and chlorophyll a. *Water Resources Research*, 54(7), 4681–4699. https://doi.org/10.1029/2017WR022334

Therneau, T., & Atkinson, B. (2018). *rpart: Recursive partitioning and regression trees*. https://cran.r-project.org/package=rpart

Tiwari, T., Sponseller, R. A., & Laudon, H. (2018). Extreme climate effects on dissolved organic carbon concentrations during snowmelt. *Journal of Geophysical Research: Biogeosciences*, 123(4), 1277–1288. https://doi.org/10.1002/2017JG004272

Torbick, N., Ziniti, B., Wu, S., & Linder, E. (2016). Spatiotemporal lake skin summer temperature trends in the northeast United States. *Earth Interactions*, 20(25), 1–21. https://doi.org/10.1175/EI-D-16-0015.1

Trumpickas, J., Shuter, B. J., & Minns, C. K. (2009). Forecasting impacts of climate change on Great Lakes surface water temperatures. *Journal of Great Lakes Research*, 35(3), 454–463. https://doi.org/10.1016/J.JGLR.2009.04.005

Vachon, D., & del Giorgio, P. A. (2014). Whole-Lake CO_2 dynamics in response to storm events in two morphologically different lakes. *Ecosystems*, 17(8), 1338–1353. https://doi.org/10.1007/s10021-014-9799-8

Verpoorter, C., Kutser, T., Seekell, D. A., & Tranvik, L. J. (2014). A global inventory of lakes based on high-resolution satellite imagery. *Geophysical Research Letters*, 41(18), 6396–6402. https://doi.org/10.1002/2014GL060641

Welch, E. B., & Cooke, G. D. (1995). Internal phosphorus loading in shallow lakes: Importance and control. *Lake and Reservoir Management*, *11*(3), 273–281. https://doi.org/10.1080/07438149509354208

Wilhelm, S., & Adrian, R. (2008). Impact of summer warming on the thermal characteristics of a polymictic lake and consequences for oxygen, nutrients and phytoplankton. *Freshwater Biology*, *53*(2), 226–237. https://doi.org/10.1111/j.1365-2427.2007.01887.x

Williamson, C. E., Overholt, E. P., Brentrup, J. A., Pilla, R. M., Leach, T. H., Schladow, S. G., Warren, J. D., Urmy, S. S., Sadro, S., Chandra, S., & Neale, P. J. (2016). Sentinel responses to droughts, wildfires, and floods: Effects of UV radiation on lakes and their ecosystem services. *Frontiers in Ecology and the Environment*, *14*(2), 102–109. https://doi.org/10.1002/fee.1228

Winder, M., Berger, S. A., Lewandowska, A., Aberle, N., Lengfellner, K., Sommer, U., & Diehl, S. (2012). Spring phenological responses of marine and freshwater plankton to changing temperature and light conditions. *Marine Biology*, *159*(11), 2491–2501. https://doi.org/10.1007/s00227-012-1964-z

Winder, M., & Sommer, U. (2012). Phytoplankton response to a changing climate. *Hydrobiologia*, *698*(1), 5–16. https://doi.org/10.1007/s10750-012-1149-2

Winslow, L., Read, J., Woolway, R., Brentrup, J., Leach, T., & Zwart, J. (2017). *rLakeAnalyzer: Lake physics tools*. https://cran.r-project.org/package=rLakeAnalyzer

Woolway, R. I., Dokulil, M. T., Marszelewski, W., Schmid, M., Bouffard, D., & Merchant, C. J. (2017). Warming of Central European lakes and their response to the 1980s climate regime shift. *Climatic Change*, *142*(3–4), 505–520. https://doi.org/10.1007/s10584-017-1966-4

Zion, M. S., Pradhanang, S. M., Pierson, D. C., Anandhi, A., Lounsbury, D. G., Matonse, A. H., & Schneiderman, E. M. (2011). Investigation and Modeling of winter streamflow timing and magnitude under changing climate conditions for the Catskill Mountain region, New York, USA. *Hydrological Processes*, *25*, 3289–3301. https://doi.org/10.1002/hyp.8174

Zohary, T., Flaim, G., & Sommer, U. (2020). Temperature and the size of freshwater phytoplankton. *Hydrobiologia*, *848*(1), 143–155, https://doi.org/10.1007/s10750-020-04246-6

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.