



RESEARCH LETTER

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Key Points:

- Ice-off is shifting earlier in the season at alpine lakes near the Continental Divide in Colorado, USA (> 3000 m elevation)
- Low spring snowfall, warm air temperatures, and high rainfall drive earlier ice-off
- Ice-off timing is linked to changes in hydrological, chemical, and biological lake properties

Supporting Information:

- Supporting Information S1

Correspondence to:

D. L. Preston,
daniel.preston@oregonstate.edu

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Climate regulates alpine lake ice cover phenology and aquatic ecosystem structure

Daniel L. Preston¹, Nel Caine^{2,3}, Diane M. McKnight^{2,4}, Mark W. Williams^{2,3}, Katherina Hell², Matthew P. Miller⁵, Sarah J. Hart³, and Pieter T. J. Johnson⁶

¹Department of Integrative Biology, Oregon State University, Corvallis, Oregon, USA, ²Institute of Arctic and Alpine Research, University of Colorado Boulder, Boulder, Colorado, USA, ³Department of Geography, University of Colorado Boulder, Boulder, Colorado, USA, ⁴Department of Civil, Environmental, and Architectural Engineering, University of Colorado Boulder, Boulder, Colorado, USA, ⁵U.S. Geological Survey, Utah Water Science Center, Salt Lake City, Utah, USA, ⁶Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, Colorado, USA

Abstract High-elevation aquatic ecosystems are highly vulnerable to climate change, yet relatively few records are available to characterize shifts in ecosystem structure or their underlying mechanisms. Using a long-term data set on seven alpine lakes (3126 to 3620 m) in Colorado, USA, we show that ice-off dates have shifted 7 days earlier over the past 33 years and that spring weather conditions—especially snowfall—drive yearly variation in ice-off timing. In the most well studied lake, earlier ice-off associated with increases in water residence times, thermal stratification, ion concentrations, dissolved nitrogen, pH, and chlorophyll *a*. Mechanistically, low spring snowfall and warm temperatures reduce summer stream flow (increasing lake residence times) but enhance melting of glacial and permafrost ice (increasing lake solute inputs). The observed links among hydrological, chemical, and biological responses to climate factors highlight the potential for major shifts in the functioning of alpine lakes due to forecasted climate change.

1. Introduction

The rate of climate warming is amplified at high elevations and alpine lakes are expected to be highly sensitive to projected change [Thompson *et al.*, 2005; Pepin *et al.*, 2015]. Because the low temperatures of alpine environments make snow and ice a prominent factor in controlling ecosystem structure and function [Jones, 2001; Fountain *et al.*, 2012], relatively small changes in climate have the potential to drive large shifts in hydrological, geochemical, and biological processes—a feature that is exacerbated by the minimal water storage capacity and sparse vegetation of thin alpine soils [Williams *et al.*, 2002; Beniston, 2003]. Furthermore, changes in atmospheric, terrestrial, and aquatic environments can become integrated in the ecosystem responses of lakes due to the transport of water through the catchment [Adrian *et al.*, 2009; Williamson *et al.*, 2009]. Alpine lakes thus offer valuable opportunities to understand and predict ecosystem responses to climate change.

Despite the importance of understanding how alpine lakes will respond to climate change, there exist few long-term records integrating hydrological, chemical, and biological aspects of ecosystem functioning for lakes at the highest elevations (>3000 m). Research performed in lower elevation aquatic systems has demonstrated that ice cover phenology can provide an integrated metric of climatic conditions [Brown and Duguay, 2010] and can control the length of the aquatic growing season, chemical interactions between water and the atmosphere, and hydrological lake characteristics [Ellis *et al.*, 1991; Smith and Lewis, 1992; Ohlendorf *et al.*, 2000; Striegl *et al.*, 2001; Austin and Colman, 2007]. While the duration of ice cover has decreased among lakes affected by long-term warming [Magnuson *et al.*, 2000], the magnitude and consistency of such effects remain less well understood in alpine systems. Previous studies examining ecosystem shifts of cold-region lakes have found similar responses to climate warming in some lake properties (e.g., earlier ice clearance and stratification, deeper thermoclines, and higher phytoplankton biomass), but in others they have diverged (e.g., nutrient concentrations, dissolved organic carbon, and major ions) [Schindler *et al.*, 1990; Winder and Schindler, 2004; Parker *et al.*, 2008]. Long-term records from high-elevation lakes are therefore useful to assess whether elevation can mediate the strength of effects and to work toward a more mechanistic understanding of how alpine lakes and the services they provide will be altered by climate change.

Here we used a long-term data set from the Green Lakes Valley near the Continental Divide in Colorado, USA (Figure 1), to examine the hydrological, chemical, and biological responses of alpine lakes (3126 to 3620 m) to climate conditions. By analyzing 33 years of data on ice phenology, local climate, and hydrology, we examine

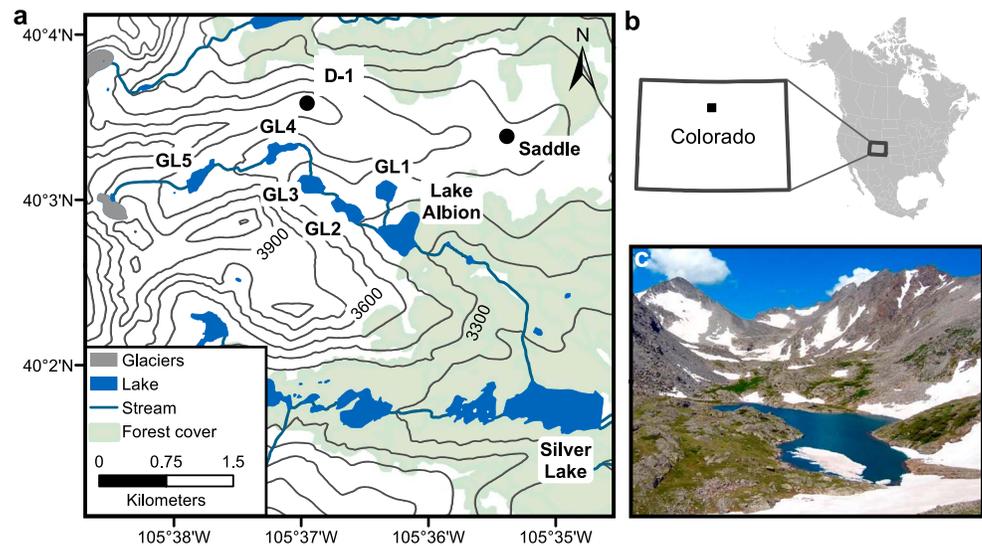


Figure 1. (a) Study site showing Silver Lake, Lake Albion, Green Lake 1 (GL1), Green Lake 2 (GL2), Green Lake 3 (GL3), Green Lake 4 (GL4), and Green Lake 5 (GL5) adjacent to Niwot Ridge in the Colorado Front Range, USA. The locations of the D1 and Saddle climate stations are also indicated on the map. (b) The upper right inset shows the location of the Niwot Ridge Long-Term Ecological Research site within Colorado, USA. (c) Green Lake 4 is shown in the lower right inset (Photo: Niwot-LTER).

how the timing of ice clearance at seven alpine lakes has shifted over time and test hypotheses about which climate drivers—including air temperature, snowfall, and rainfall—most influence the timing of ice clearance. We then use 13 to 15 years of data on lake water chemistry and lake phytoplankton from the most well studied lake (Green Lake 4) to examine how variation in ice phenology and underlying climate drivers are linked to changes in lake ecosystem properties.

2. Data and Methods

2.1. Study Site

The Green Lakes Valley lies approximately 6 km east of the continental divide in Colorado, USA, and has been studied extensively as part of the Niwot Ridge Long Term Ecological Research Program (see *Bowman and Seastedt* [2001] for an overview). Seven alpine paternoster lakes lie within or just below the Valley: Silver Lake (3126 m), Lake Albion (3345 m), Green Lake 1 (3425 m), Green Lake 2 (3400 m), Green Lake 3 (3450 m), Green Lake 4 (3550 m), and Green Lake 5 (3620 m) [Caine, 2001]. In addition to rain and snowmelt, the source waters of the lakes include groundwater and talus springs [Liu *et al.*, 2004] and meltwater from the nearby Arikaree Glacier and from permafrost that has been detected in much of the upper valley [Williams *et al.*, 2006; Caine, 2010].

2.2. Data Collection

From 1981 to 2014, the date of ice clearance in the spring for the seven lakes within the Green Lakes Valley has been recorded (Table S1 in the supporting information). These data include the earliest date at which each lake became completely ice free. To examine local drivers of ice-off timing, we used daily precipitation totals and air temperature means (1981 to 2014) from a climate station (D1), that is, ~350 m from GL4 at an elevation of 3749 m (Figure 1). Daily precipitation values were converted into snow and rain based on an empirically derived snow probability function [Dai, 2008] (supporting information). To obtain daily lake water residence times, we divided the total volume of GL4 by the 24 h stream discharge that was measured at the outlet of the lake from June to August of each year [Monsen *et al.*, 2002]. From 1998 to 2013, we collected water samples for chemical analysis approximately every 1 to 2 weeks from GL4 during the ice-free period (~June to September, depending on year). We collected samples from the inlet, the outlet, as well as 0 m, 3 m, and 9 m in depth at the center of the lake and measured lake temperature and water chemistry using standardized protocols [Williams *et al.*, 1996] (see supporting information and <http://snobear.colorado.edu/Seiboldc/kiowa.html> for details). Chlorophyll *a* samples were collected from 2000 to 2014 (excluding 2003 and 2012) and were filtered

within 12 h (0.7 μm), extracted with hot ethanol or acetone, and analyzed with fluorescence spectroscopy to quantify chlorophyll *a* content [see Flanagan *et al.*, 2009] (supporting information). We identified phytoplankton (primarily to genus) and conducted cell counts for samples from 2000 to 2007 (Table S2).

2.3. Analyses

To determine whether ice-off dates have shifted earlier in all seven lakes, we used a linear mixed effects model (LME) with fixed effects of lake elevation and of year, a random intercept term for lake identity, and ice-off date (days from 1 April) as the response variable. To account for possible temporal autocorrelation, we examined autocorrelation function plots and used Akaike information criterion values to compare models with different autoregressive and moving average terms (supporting information) [Cowpertwait and Metcalfe, 2009]. The two lowest elevation lakes are sometimes drained partially in the winter (Silver Lake and Lake Albion). To ensure ice-off trends were not strongly influenced by artificial changes in water level, we also analyzed the ice-off data without these two lakes (supporting information).

To examine climate drivers of ice cover phenology, we first identified the temporal period over which each climate variable affected ice-off date at each individual lake with linear models and exploratory model selection (supporting information). We found that the timing of associations between the climate variables and ice-off was consistent across the seven lakes, with April through June being the most relevant period for snowfall, rainfall, and temperature. We next calculated climate variable indices using the sum of each climate variable over the April to June period, allowing us to capture all variability within the 3 month period (relative to using mean values which would potentially lose information). To determine which climate variables best predicted ice-off among all seven lakes we compared the model fits of four models containing either each climate variable alone or all three climate variables together (Table S3). In addition to the climate variables, each model included a random intercept term for lake identity and a fixed effect of lake elevation.

Lastly, to examine how ice-off timing was linked to lake ecosystem structure in Green Lake 4, we used linear models (LM) with ice-off date as the predictor and yearly summer means for each lake variable as the response (log transformed if needed to improve normality). Responses included hydrological, chemical, and biological variables and were meant to capture representative yearly values, incorporating variation in time (\sim June to September) and space (depth and location within the lake). In this way our analysis asked how changes in ice-off date, and corresponding variation in the length of the summer growing season, covaried with other changes in lake hydrology, water chemistry, and biology. In our analysis, ice-off date was treated as an integrator of multiple climate factors; as such, we did not expect that ice-off was necessarily driving all the patterns in lake ecosystem properties but that climate drivers were affecting multiple components of the lake in a consistent manner.

3. Results

3.1. Ice-Off Trends and Climate Drivers

Ice-off dates in the Green Lakes Valley advanced by \sim 7 days over 33 years (Figure 2a). Ice-off dates fell primarily in May and June for the lower elevation lakes and in July for the higher elevation lakes (Figure 2b). Based on a linear mixed effects model, year had a significant negative effect on ice-off date (LME, $\beta = -0.211$, $SE = 0.095$, $p = 0.028$), while elevation had a positive effect, with higher elevation lakes clearing ice later in the season than lower elevation lakes (LME, $\beta = 0.11$, $SE = 0.027$, $p = 0.009$; Figure 2b). The results were similar, but with a stronger relative effect of elevation, when we removed the two lowest elevation lakes from the analysis (supporting information).

By analyzing the relationships between local climate data and ice phenology, we found that snowfall, rainfall, and air temperature over the April to June period were linked to ice-off timing among all seven lakes. A model including all three climate variables performed better than models with each of the three variables alone, although spring snowfall was the most strongly linked variable to ice-off timing (Table S3). The model with all three climate variables indicated that increases in spring snowfall strongly delayed ice-off ($\beta = 0.084$, $SE = 0.0069$, $p < 0.0001$; Figure 3a), while warmer air temperatures ($\beta = -0.014$, $SE = 0.0043$, $p = 0.0012$; Figure 3b) and higher rainfall ($\beta = -0.057$, $SE = 0.026$, $p = 0.029$; Figure 3c) both accelerated ice-off. The 2 years with the lowest spring snowfall (2002 and 2012) corresponded to the 2 years with the earliest ice-off dates on record (Figure 3a), reflecting the importance of spring snowfall in driving ice-off variation.

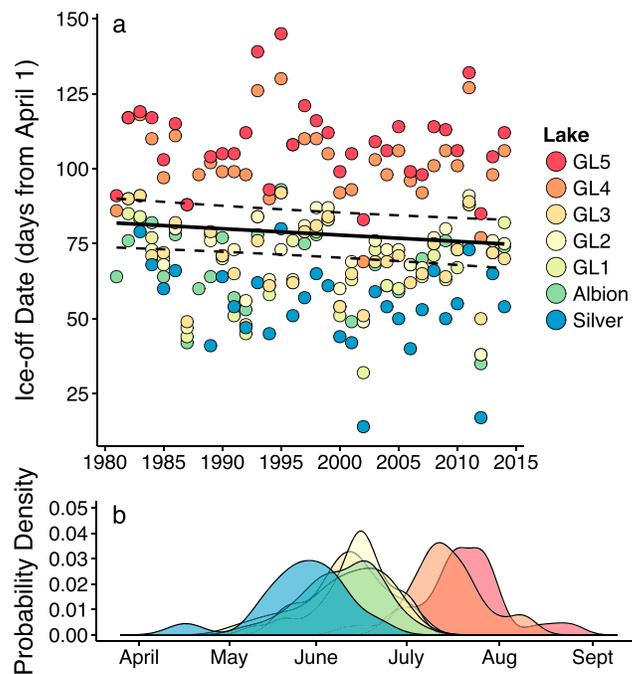


Figure 2. (a) Ice-off dates from 1981 to 2014 for the seven lakes within the Green Lakes Valley in Colorado, USA. The black linear regression line with 95% confidence band corresponds to a linear mixed effects model with fixed effects of year and of elevation and a random intercept for lake identity. The legend at right lists the lake from lowest elevation (Silver–3126 m) to highest elevation (GL5–3620 m). (b) The probability distribution of ice-off timing for each of the seven lakes over the course of the season. The colors correspond to lake identities in Figure 2a.

and most of the major ions, including Ca^{2+} , Mg^{2+} , Na^+ , K^+ , Cl^- , and SO_4^{2-} (Figures 4e–4j and supporting information). In contrast, NO_3^- and Si, both of which can be biologically regulated, showed no relationship with ice-off date at GL4 (Figures 4k and 4l). Total dissolved nitrogen correlated negatively with ice-off (LM, $r^2 = 0.34$, $p = 0.021$; Figure 4m), dissolved organic carbon showed a marginal negative relationship (LM, $r^2 = 0.29$, $p = 0.083$; Figure 4o), whereas total dissolved phosphorus was not significantly correlated with ice-off (LM, $r^2 = 0.010$, $p = 0.703$; Figure 4n).

Analyses of chlorophyll *a* data revealed additional links to variation in ice-off dates. Chlorophyll *a* concentrations decreased with ice-off date (LM, $r^2 = 0.29$, $p = 0.056$; Figure 4p). In the years with the latest ice-off, summer chlorophyll concentrations were $< 0.5 \mu\text{g/L}$, indicating relatively low phytoplankton production, whereas they were 5 times higher in 2002, which had an ice-off date of ~ 2 months earlier. We note, however, that the trend in chlorophyll *a* was strongly affected by two points that represent the earliest (2002) and latest (2011) ice-off years (see supporting information for additional discussion of chlorophyll *a* data).

4. Discussion

Our results demonstrate consistent links between local climate, ice cover phenology, and multiple aquatic ecosystem properties in alpine lakes above 3000 m near the Continental Divide in Colorado, USA. Within the most well studied lake, ice cover phenology was associated with shifts in lake characteristics, including hydrological, chemical, and biological properties. Such patterns were driven, both directly and indirectly, by the climatic factors that shape hydrology throughout the catchment, highlighting how lakes integrate wider scale ecosystem change. These results indicate that future aquatic ecosystem shifts may be predicted based on the seasonal timing of changes in temperature and precipitation at the highest elevations.

3.2. Hydrological, Chemical, and Biological Properties

Years with earlier ice-off dates at Green Lake 4 showed consistent changes in lake hydrology and water temperatures during the ice-free period. Hydraulic residence times in summer correlated negatively with ice-off date, such that years with early ice-off had a longer residence time (LM, $r^2 = 0.57$, $p < 0.001$; Figure 4a). Residence time differed by ~ 75 days between the earliest to the latest ice-off years (Figure 4a). Earlier ice-off years also had a $\sim 4^\circ\text{C}$ warmer mean and maximum surface water temperatures and an increase in the temperature difference between the surface and 9 m (LM, $r^2 = 0.68$, $p < 0.001$; Figure 4b). GL4 does not stratify in all years; however, in the earliest ice-off years we observed a difference in temperature between the epilimnion and hypolimnion of 3 to 4°C .

Ice-off date was also consistently linked to summer water chemistry, being negatively correlated with pH (LM, $r^2 = 0.35$, $p = 0.011$; Figure 4c), conductivity (LM, $r^2 = 0.45$, $p = 0.004$)

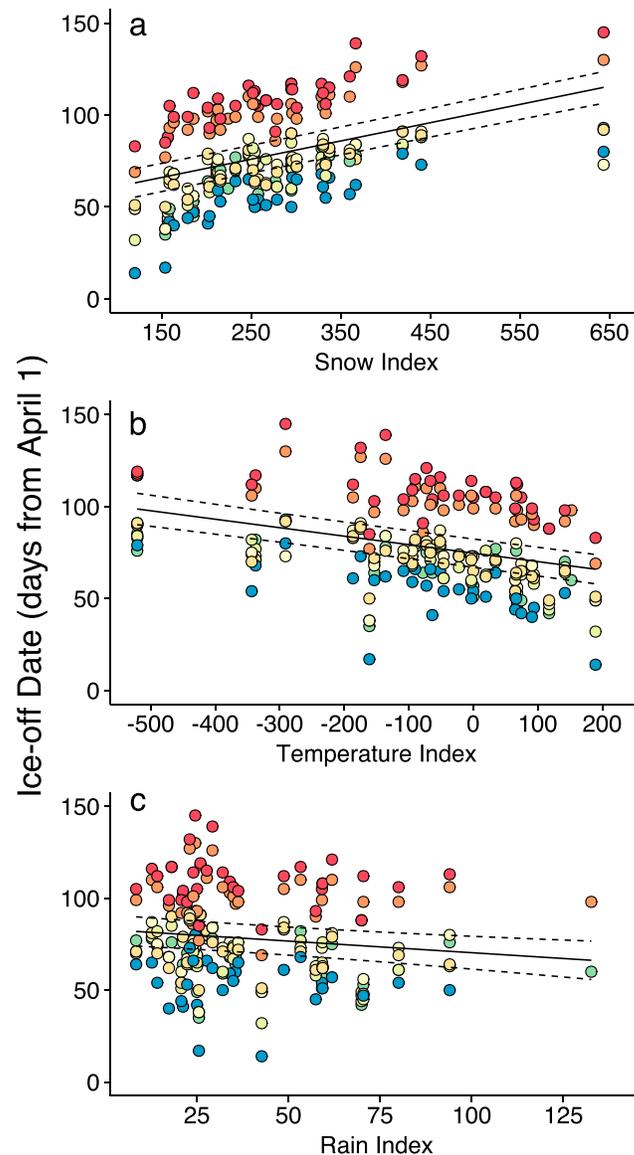


Figure 3. Correlations between ice-off dates for the seven lakes in the Green Lakes Valley and (a) spring snowfall, (b) spring air temperature, and (c) spring rainfall. Colors correspond to lake identities in Figure 2. The climate indices are the sums of total daily snowfall (mm), total daily rainfall (mm), or mean daily temperatures ($^{\circ}\text{C}$) from the period of 1 April to 30 June of each year (1981 to 2014). Climate data are from the D1 climate station adjacent to Green Lake 4. The regression lines and 95% confidence bands correspond to coefficients from a linear mixed effects model with fixed effects of each climate variable and of lake elevation and a random intercept for lake identity.

evidence for increases in average annual temperatures and especially summer temperatures [Clow, 2010; McGuire et al., 2012]. Climate forecasts for the mountain regions of Colorado predict an increase in temperature of 3 to 5°C over the next 50 years under a moderate emissions scenario [Lukas et al., 2014]. While future changes in total precipitation are less certain, forecasted warming will drive shifts from spring snow to rain that should accelerate direct effects of increased air temperatures on ice cover phenology.

Yearly variation in the timing of ice-off at Green Lake 4 was linked to multiple aspects of lake ecosystem functioning, including summer hydraulic residence times and the potential for lake stratification. Years with early ice-off were associated with longer residence times in summer because spring snowfall, which is closely

The directional shift toward earlier timing of ice-off among lakes in the Green Lakes Valley is relatively consistent with records from other lake and river ecosystems at lower elevations [Hodgkins et al., 2002; Duguay et al., 2006; Prowse et al., 2007]. The observed rate of change in ice-off timing over the last three decades in our study (2.1 days/decade) is faster than long-term averages (over ~ 150 years) from the Northern Hemisphere [Magnuson et al., 2000] but is similar to several studies that examined trends in the latter portion of the twentieth century, as we do here [Jensen et al., 2007; Benson et al., 2012]. These studies suggest that rates of change in ice phenology have increased over the last four decades relative to earlier periods, likely in conjunction with more rapid rates of climate warming.

Our results indicate that the net effect of climate change on lake ice cover in the Green Lakes Valley will depend on the magnitude of warming, changes in total precipitation, and the relative proportions of snow versus rain in the spring and early summer. Snowfall had the strongest effect in driving variation of ice-off timing likely because it insulates the ice layer from warming air temperatures, reduces solar radiation from reaching the ice by increasing albedo, and minimizes the accumulation of sediments on the ice surface that decrease albedo [Duguay et al., 2003]. Although we did not detect statistically significant long-term trends in our April to June climate indices, which were highly variable between years (see supporting information and Figure S4), within the Green Lakes Valley there has been

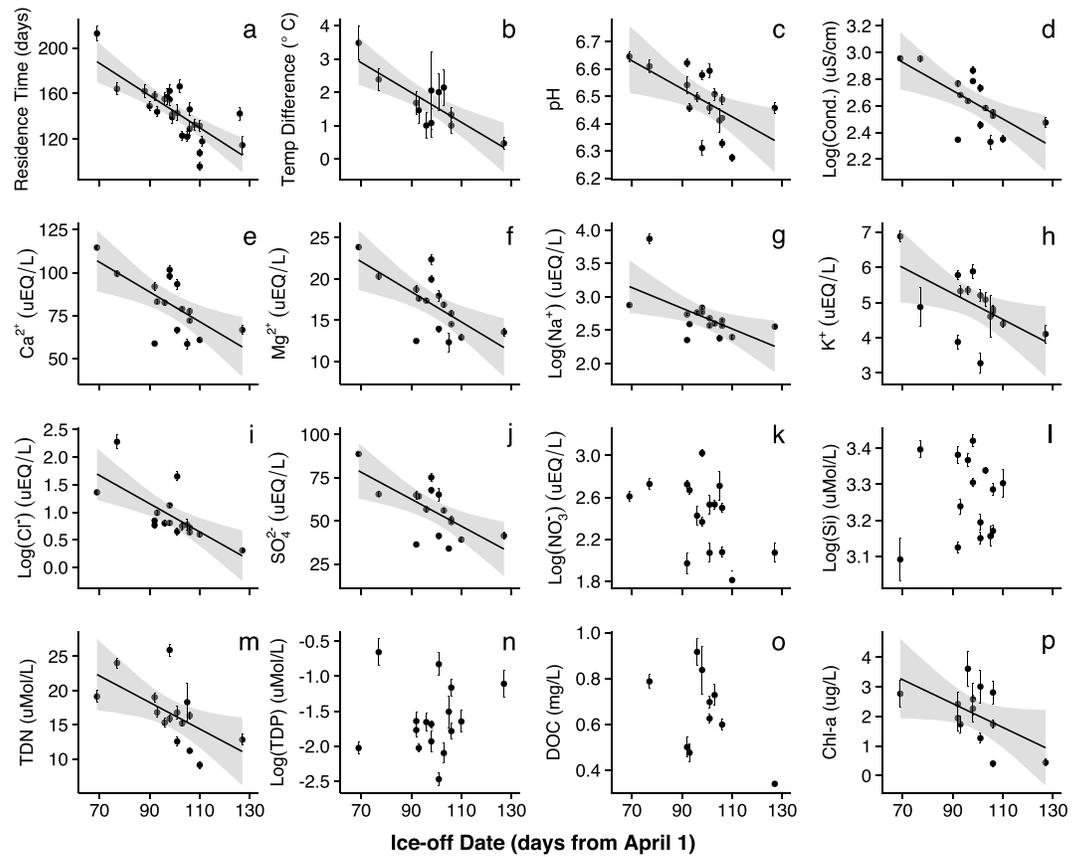


Figure 4. Correlations of ice-off dates at Green Lake 4 with (a) lake water residence times, (b) differences in water temperatures between the surface and 9 m depth, (c) pH, (d) log-transformed conductivity, (e) calcium, (f) magnesium, (g) log-transformed sodium, (h) potassium, (i) log-transformed chloride, (j) sulfate, (k) log-transformed nitrate, (l) log-transformed silica, (m) total dissolved nitrogen, (n) log-transformed total dissolved phosphorus, (o) dissolved organic carbon, and (p) chlorophyll *a*. Error bars correspond to one standard error around summer means from the ice-free period. Plots with regression lines and 95% confidence bands indicate statistically significant linear regressions.

linked to ice-off timing, is a strong predictor of the magnitude of runoff through the catchment in June, July, and August [Williams *et al.*, 2006]. Years with heavy spring snowfall result in a high volume of summer snow melt which reduces lake residence times (see Figure S5). This yearly variation in summer lake residence times is also linked to the timing of peak discharge, which is shifting earlier in the high mountain areas of Colorado [Clow, 2010]. We also observed a negative correlation between the difference in lake water temperature between the surface and 9 m and the timing of ice-off, likely caused by a combination of higher summer air temperatures warming the surface water and longer residence times extending the period for the lake surface to warm [Winder and Schindler, 2004; Peeters *et al.*, 2007]. Taken together, the linkages between a long ice-free period, increased residence times, and a greater probability of stratification may amplify the changes observed in lake chemistry and biota.

A fundamental process with regard to solute transport through the catchment in dry and warm years is the melting of glacial ice and permafrost [Williams *et al.*, 2006; Barnes *et al.*, 2014]. The same climate factors that influence ice cover phenology also affect rates of glacial and permafrost thawing, which have been increasing in the past three decades in the Green Lakes Valley and surrounding areas [Hoffman *et al.*, 2007; Caine, 2010]. Meltwater from these sources is a primary vector of nitrogen and rock weathering products (e.g., calcium, magnesium, and sulfate) that are transported into lakes, particularly in autumn months [Williams *et al.*, 2006; Mast *et al.*, 2011; Slemmons and Saros, 2012; Barnes *et al.*, 2014]. As a result, years with early ice-off lead to greater inputs of late season ions into the lake. Concurrently, low rates of summer stream flow in dry and warm years further serve to concentrate solutes, both in-stream above the lake, and within the lake itself. Similar associations between thawing permafrost and increases in lake ions have been observed in northern Canada [Kokelj *et al.*, 2009], suggesting this may be a general response of lake chemistry to warming in areas where permafrost is present (but see Lewis *et al.* [2015]).

Observed links between ice-off timing and lake chemistry are also the result of climate-driven changes in the relative importance of solute input rates relative to in-lake processes. The lake water chemistry responses that did not show a significant correlation with ice cover are solutes that are affected by in-lake biological processes. For instance, silica, nitrate, and total dissolved phosphorus have all been shown to become depleted by phytoplankton production in Green Lake 4 [Gardner *et al.*, 2008; Flanagan *et al.*, 2009; Bowman *et al.*, 2014]. Additionally, much of the dissolved organic carbon in Green Lake 4 during runoff is terrestrial in origin; however, after peak snowmelt, the residence time of water in Green Lake 4 increases and dissolved organic carbon (DOC) becomes more autochthonous in origin (i.e., derived from in-lake phytoplankton and microbial sources) [Hood *et al.*, 2003; Miller and McKnight, 2010]. As such, earlier ice-out is correlated with earlier snowmelt, reducing lake flushing, increasing the residency time of water in the lake, decreasing the importance of some terrestrial inputs, but increasing the importance of within-lake processes.

We suggest that the decoupling of the aforementioned water chemistry parameters (i.e., silica, nitrate, phosphorus, and DOC) with ice-off timing is due to changes in hydrologic connectivity that occur after ice clearance at Green Lake 4. A number of lake water chemistry parameters, including sodium, potassium, chloride, silica, and total dissolved phosphorus, did not behave similarly in 2002 and 2012, the two earliest ice-off years that corresponded with widespread droughts in Colorado [Pielke *et al.*, 2005; Castle *et al.*, 2014]. These 2 years had the two lowest spring precipitation totals in the last three decades but differed strongly in summer precipitation; in 2002, the drought persisted into the summer months, whereas 2012 was the second wettest summer in the data set. The rain events in 2012, which occurred after an extremely dry spring, may have effectively “reset” some lake parameters by flushing out phytoplankton (decreasing its role in producing DOC and taking up silica, phosphorus, and nitrogen) and increasing delivery rates of other solutes from the terrestrial environment. Similar biological controls on lake phosphorus and silica, and variation driven by climate, have been observed in European lakes [Blenckner *et al.*, 2007].

5. Conclusions

Our results suggest that shifts in the timing and/or magnitude of snowfall will interact with forecasted temperature increases to drive the net effects of future climate on alpine lakes in Colorado. The fact that hydrological, chemical, and biological properties responded in a covarying manner highlights the need for additional interdisciplinary approaches to understanding effects of climate change on high-elevation aquatic systems, especially given the importance of alpine lakes to downstream ecosystem processes and services (e.g., provisioning of drinking water).

Acknowledgments

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