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Special Section:
Winter limnology in a changing world

Key Points:
- Ice-off date has variable impacts on ecosystem properties across lake type and climatic zone
- Lakes with a short duration of ice have little ecological memory of ice-off date
- When lakes stratify immediately following ice-off, ice-off date impacts summer ecosystem properties

Supporting Information:
Supporting Information may be found in the online version of this article.

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A Comparison of Ecological Memory of Lake Ice-Off in Eight North-Temperate Lakes

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Abstract Ice-off dates on lakes are some of the longest phenological records in the field of ecology, and some of the best evidence of long-term climatic change. However, there has been little investigation as to whether the date of ice-off on a lake impacts spring and summer ecosystem dynamics. Here, I analyzed 274 years of long-term data from eight north temperate lakes in two climate zones to address whether lakes have ecological memory of ice-off in the subsequent summer. Five metrics were investigated: epilimnion temperatures, hypolimnion temperatures, hypolimnetic oxygen drawdown, water clarity, and spring primary productivity. The response of the metrics to ice-off date were variable across latitude and lake type. The northern set of lakes stratified quickly following ice-off, and early ice-off years resulted in significantly warmer hypolimnetic temperatures. Oxygen depletion in the hypolimnion was not impacted by ice-off date, likely because in late ice-off years the lakes did not fully mix. In the southern lakes, ice-off date was not correlated to the onset of stratification, with the latter being a more dominant control on hypolimnetic temperature and oxygen. The implications of these findings is that as ice-off date trends earlier in many parts of the world, the lakes that will likely experience the largest changes in spring and summer ecosystem properties are the lakes that currently have the longest duration of lake ice. In considering a future with warmer winters, these results provide a starting point for predicting how lake ecosystem properties will change with earlier ice-off.

Plain Language Summary Lake ice is disappearing around the world. This slow loss of winter is a clear sign of climate change, but does the date of ice-off impact spring and summer lake processes? Untangling a memory effect of ice-off from other factors, such as spring and summer weather, requires decades of monitoring data. Here, 274 years of lake records from eight lakes in two climate zones were analyzed to investigate whether lakes have ecological memory of ice-off. The response of lake temperature, oxygen concentrations, and water clarity to ice-off date were variable across latitude and lake size and type. It was found that when lakes stratify immediately following ice-off, bottom water conditions have ecological memory of the timing of ice-off. However, in lakes with a short duration of lake ice, this memory effect fades. The implication of this finding is that as ice-off date trends earlier in many parts of the world, the lakes that will likely experience the largest changes in spring and summer lake ecosystem properties are the lakes that currently have the longest duration of lake ice.

1. Introduction

The duration of lake ice is contracting for millions of lakes around the globe (Magnuson et al., 2000; Sharma et al., 2019). This is well documented in records of ice-off dates that have been collected for decades to centuries by citizens captivated by this momentous annual occurrence (Sharma et al., 2016). The transition from frozen to ice-free conditions has important societal significance (Knoll et al., 2019), but also immediate consequences to lake ecosystems, as ice controls a range of physical, chemical, and biological processes.

Ice is a physical barrier that limits energy input into lakes (Kirillin et al., 2012). Ice dampens wind energy and snow effectively blocks solar radiation from penetrating the water column. It also limits atmospheric exchange of gases, importantly oxygen. When a lake is frozen, the water column is typically inversely stratified with temperatures close to 0°C near the ice, and increasing to a maximum of 4°C at the bottom (Yang et al., 2021). In many lakes, the melting of snow and ice in the spring occurs relatively quickly. The transition from ice-covered to open water could be viewed as a disturbance to the system, as it rapidly changes the physical and chemical environment of a lake. Once ice free, wind energy will overcome the weak inverse-stratification and mix the water column. This mixing pumps oxygen into the hypolimnion

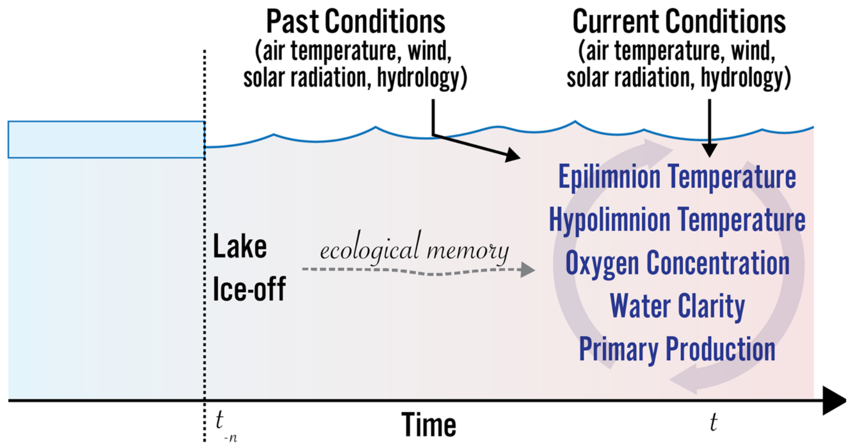

Figure 1. Conceptual figure considering the role of ice-off date in shaping current conditions in a lake. Ecosystem properties (water temperatures, oxygen concentration, water clarity, and primary production) are interconnected and influenced by both past and current conditions.

and delivers nutrients that have built up at depth to the surface. The combination of available sunlight and a delivery of nutrients into the epilimnion creates favorable conditions for phytoplankton growth (Adrian et al., 1999; Bleiker & Schanz, 1989; Sommer et al., 2012).

The timing of the transition to ice-free conditions has important ecological implications. In early ice-off years, earlier occurrences of spring phytoplankton blooms (Peeters et al., 2007) may contribute to higher annual primary productivity and shift carbon source-sink dynamics. Earlier oxygenation of the hypolimnion in the spring will halt anaerobic redox reactions (Cavaliere & Baulch, 2018) and there will be fewer occurrences of winter fish kills (Balayla et al., 2010; Shuter et al., 2012). The loss of lake ice will will have consequential impacts on lake ecosystems, but what is less clear is whether there is ecological memory of the date of ice-off in lakes.

Ecological memory is defined as the capability of the past states or experiences to influence present or future ecological responses (Padisak, 1992; Peterson, 2002). While any past event(s), either discrete or continuous, can impact ecological memory on an ecosystem, the concept of ecological memory is often discussed in relation to how ecosystems respond to ecological disturbances (Johnstone et al., 2016); for instance, how ecological memory shapes landscape dynamics after forest fires (Peterson, 2002), or how the severity of coral reef bleaching is influenced by past bleaching events (Hughes et al., 2019). To quantify ecological memory different components can be assessed, such as the length of the memory, the pattern of the memory, or the strength of the memory (Ogle et al., 2015). In northern lakes, ice-off can be viewed as a cyclical disturbance to lake ecosystems as the disappearance of ice rapidly changes the physical environment. Ice-off dates are some of the longest phenological records in the field of ecology, and are routinely used as a global indicator of climate change (Adrian et al., 2009; Woolway et al., 2020). But is the timing of ice-off an ecosystem property that conveys a lasting impact on lake ecosystems (Figure 1).

This intricate question can be explored in many ways, and it is difficult to separate the disappearance of lake ice with the co-occurrence of warmer air temperatures. Hutchinson marveled at the field of limnology for having so many unique systems to study (Hutchinson, 1964), with the drawback being, that whether the timing of ice-off conveys a lasting impact on a lake is likely highly system-dependent. The Great frozen Lakes of the world can retain lake ice so long into the summer that ice-off date is known to be a strong driver of summer temperatures (Austin & Colman, 2008). On the other hand, ice-off is likely a distant (and non-existent) memory for shallow, polymictic lakes that rapidly equilibrate with the atmosphere following ice-off (Adrian et al., 1999). To examine the influence of ice-off date requires many years of monitoring, as the combination of possible winter and spring meteorological conditions makes it difficult to isolate single drivers of ecosystem dynamics. Here, I analyze 274 years of long-term data from neighboring lakes to quantify the ecological memory of lake ice-off date on spring and summer ecosystem properties, and to understand if the ecological memory of ice-off is similar between two climatic zones.

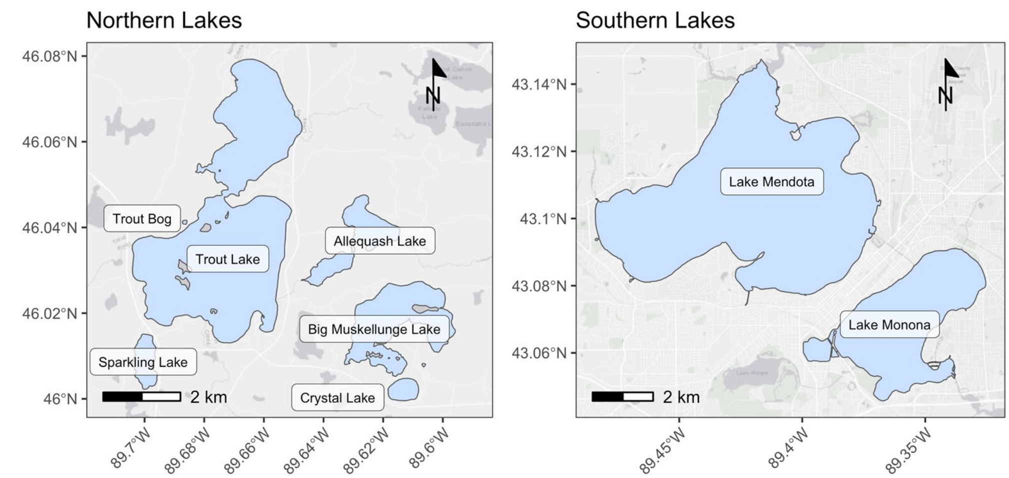

Figure 2. Northern and southern core study lakes of the North Temperate Lakes Long-Term Ecological Research program.

2. Methods

This analysis focuses on eight core study lakes of the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) program. Six lakes (Trout Bog, Allequash Lake, Sparkling Lake, Crystal Lake, Big Muskellunge Lake, and Trout Lake) are located in northern Wisconsin (Figure 2), surrounded by a mixed pine and northern hardwood forest, where mean annual air temperature is ~3.8°C. Allequash and Trout Lakes are drainage lakes, but the remaining lakes are seepage lakes, which receive water solely from groundwater and precipitation (Webster et al., 1996). All of the lakes are dimictic, with the exception of Allequash, which partially mixes during large wind events (Baines et al., 2000). Since 1980, the earliest ice-off date was March 19th, 2012, and the latest was May 16th, 1996. As Trout Lake is much larger than the other five lakes, it retains ice the latest into the spring. From 1982 to 2019, the mean spread in annual ice-off date between the six lakes was 7 days (median = 6, range = 2 to 23).

Two of the lakes (Lake Mendota and Lake Monona) are located in southern Wisconsin, in a predominantly agricultural and urban landscape, with mean annual air temperature ~8.0°C. Both lakes are drainage lakes, with minimal groundwater inflow. Since 1981, the earliest ice-off date was February 26th, 2002, and the latest was April 12th, 2014. Lake Monona always loses ice first, and the historical mean spread in annual ice-off date between the two lakes is 4 days (1982–2019, median = 2, range = 0–17). While the two regions have noticeably different climates, the largest and smallest differences in air temperatures both occur in the spring (Figure S1). The regions have the largest spread in average air temperature ~March 7th, and the smallest spread in average air temperatures ~May 25th (Figure S1), as recorded by meteorological stations in Madison, WI (southern lakes, USW00014837), and Minocqua, WI (northern lakes, UWC00475516).

The NTL-LTER has monitored the six northern lakes since 1981, and the southern lakes since 1995. This analysis begins with full years, starting in 1982 and 1996. Monitoring was biweekly during the ice-free season and every 6 weeks when the lakes were frozen. Especially in the southern lakes, data gaps exist following ice-on and preceding ice-off, due to hazardous conditions during freeze-up and thaw.

Water temperature and dissolved oxygen were sampled in the deepest part of the lake, at 1 m from the surface to within 1 m of the bottom using a YSI Pro-ODO meter, or a YSI Model 58 meter prior to 2011 (NTL-LTER, 2020d). Water clarity was recorded with a 20 cm Secchi disk on the same days, both without and with the aid of a plexiglass viewer (NTL-LTER, 2020f). For the southern lakes, the Secchi record with the viewer was used, as is it more robust, but for the northern lakes, the Secchi record without the viewer was used as it is the longer of the two datasets. In the northern lakes, chlorophyll-a samples were collected at 2 to 10 depths depending on the lake and analyzed spectrophotometrically (NTL-LTER, 2020a). Unfortunately, for the southern lakes, the chlorophyll record has an uncorrectable bias from 2002 to 2007. In lieu of chlorophyll, I analyzed phytoplankton biomass in Lake Mendota and Monona (unavailable for northern lakes)

Table 1
Lake Characteristics and Relationships Between Ecosystem Metrics (See Table Footnotes) and Ice-Off Groupings

	Area (ha)	Max depth (m)	Hypo depth range	Summer epi temp[a]	Summer hypo temp[b]	Hypo oxygen drawdown[c]	Spring water clarity[d]	Spring primary production[e]
Northern Lakes (1982–2019)								
Trout Bog	1.0	8.0	6–8 m	–	↑ 0.07 °C	NA	–	–
Allequash Lake	164.2	8.0	6–8 m	–	*↑ 3.02 °C	↑ 10.5 days	*↑ 1.35 m	↓ 4.25 g/L
Sparkling Lake	63.7	20.0	15–21 m	–	*↑ 1.30 °C	–	↑ 1.50 m	–
Crystal Lake	37.5	20.4	16–21 m	–	–	–	↑ 1.10 m	↓ 2.35 g/L
Big Muskellunge Lake	363.4	21.3	15–22 m	–	*# ↑ [f] 0.79 °C	↓ 10.5 days	–	–
Trout Lake	1,565.1	35.7	25–36 m	–	*↑ 1.48 °C	*↓ 11.5 days	↑ 0.6 m	↓ 2.15 g/L
Southern Lakes (1996–2019)								
Lake Monona	1,359.8	22.5	15–23 m	–	–	↓ 5.5 days	↑ 1.4 m	↓ 5.41 mg/L
Lake Mendota	3,961.2	25.3	20–26 m	–	↑ 0.83 °C	↓ 10.0 days	–	–

Note. Hypo = Hypolimnion and Epi = Epilimnion. An upward directional arrow is shown if the early ice-off median > average ice-off median > late ice-off median, and vice versa for a downward arrow. Significance between the early and late ice-off group (Dunn's test, $p < 0.05$) is denoted by an asterisk (*).
[a]Mean water temperature between July 1st and Sep 1st from 0 to 2 m. [b]Mean water temperature between July 1st and Sep 1st across hypolimnetic depth range (Column 3). [c]Earliest date of oxygen saturation <40% at a specific depth in the hypolimnion. See Figure 8 for depths. [d]Maximum recorded secchi depth between ice-off and July 1st. [e]Northern Lakes: Maximum recorded surface (≤5 m) chlorophyll concentration between ice-off and July 1st. Southern Lakes: Maximum recorded integrated phytoplankton biomass between ice-off and July 1st. [f]Sig. Difference between early and late ice-off groups, but average ice-off group had the highest median (See Figure 5).

(NTL-LTER, 2020e). Composite sample depths are 0–8 m for Lake Mendota and 0–2 m for Lake Monona. Data from 2012 to 2013 in Crystal Lake were removed due to an artificial mixing experiment that took place over those 2 years.

Years were grouped based on quartile dates of ice-off for each individual lake (NTL-LTER, 2020b; 2020c). The categories were "early ice-off": 0–25th percentile, "average ice-off": 25–75th percentile, and "late ice-off": 75–100th percentile. The span of days encompassed by the "average ice-off" grouping ranged from 13 days in Big Muskellunge, Trout Bog, Trout Lake, and Lake Mendota to 16 days in Lake Monona. The onset of stratification was also calculated using linear interpolation between the first spring temperature profile with a density difference of 0.1 g kg^{-1} and the preceding profile (Gray et al., 2020; Wilson et al., 2020). Uncertainties in onset of stratification are given as the date range between the two profiles. Stratification groupings into "early," "average," and "late" were calculated in the same way as ice-off groupings using the linearly interpolated stratification onset date.

Five lake metrics were examined to gauge the impact of lake ice-off date on ecosystem state. (1) Eplimnetic temperature; from 0 to 2 m. (2) Hypolimnetic temperature; with depth ranges unique to each lake (Table 1). Mean summer water temperatures was calculated from July 1st to September 1st. (3) Oxygen drawdown in the hypolimnion; calculated as the first date following ice-off that oxygen saturation at a specific depth was <40%. The depths used were 4 m above the lake bottom for the deep lakes, and 6 m for Trout Bog and Allequash Lake. (4) Spring water clarity; assessed as the maximum Secchi disk depth between ice-off and July 1st. (5) Spring primary production. Two proxies were used: maximum surface (≤5 m) chlorophyll concentration in the northern lakes, and maximum phytoplankton biomass in the southern lakes between ice-off and July 1st. Significant differences between groupings ($p \leq 0.05$, adjusted using Bonferroni correction) were evaluated using a Kruskal-Wallis test (non-parametric analog to a one-way ANOVA), followed by a post-hoc Dunn's test for pairwise multiple comparisons (Kassambara, 2021). However, the number of years in each grouping are small, and p-values should not be considered the sole metric for evaluation. Therefore, we also considered there to be a difference between early, average, and late ice-off groupings when the early ice-off median > average ice-off median > late ice-off median, and vice versa.

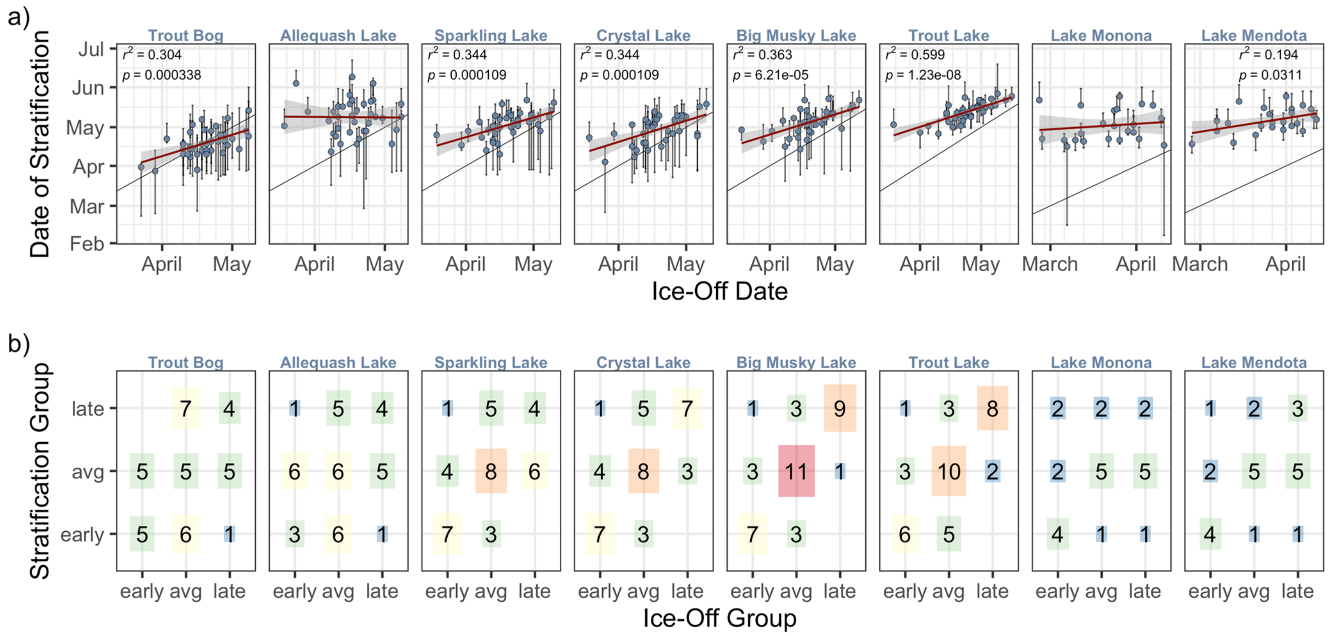

Figure 3. (a) Ice-off date versus onset of stratification. Uncertainty in stratification date is shown as the date of manual observation before and after stratification. Linear regression (red line) p-values, and r^2 values are noted. The black line is the 1:1 line. (b) Ice-off and stratification groupings. Colored boxes reflect the number of years that fell into each of the groupings: early 0–25th percentile, avg 25–75th percentile, and late 75–100th percentile.

3. Results

In total, 274 years-long records of lake characteristics were analyzed to explore the sustained influence of lake ice-off date on spring and summer ecosystem properties. The date of ice-off and the onset of stratification were highly correlated (linear regression $r^2 = 0.30$ to 0.60, $p \leq 0.05$) in the northern lakes, with the exception of Allequash Lake (Figure 3a). During late ice-off years, the onset of stratification happened immediately following ice-off, and in some cases, preceded ice-off. In the southern lakes, the date of ice-off was weakly correlated with the onset of stratification in Lake Mendota ($r^2 = 0.19$), but uncorrelated in Lake Monona. The number of days between ice-off and stratification was longer in the southern lakes. When grouped by ice-off and stratification dates, there were very few years when ice-off was early and stratification was late, and vice-versa across all eight lakes (Figure 3b).

Epilimnetic temperatures in all eight lakes warmed earlier in earlier ice-off years, as would be expected (Figure S2). However, any temperature margin gained in March or April, was quickly lost by mid-May. Trout Lake, the largest of the northern study lakes, retained a difference in epilimnetic temperatures the longest, until early June. Mean epilimnetic temperatures from July 1st to September 1st showed no significant differences between early and late ice-off years (Figure S3). Time-series of hypolimnetic temperatures for all eight lakes show a varying response to the date of ice-off (Figure 4). In the northern lakes, years with early ice-off had warmer summer (July 1st to September 1st) hypolimnia than years with late ice-off, and significantly so in Allequash, Sparkling, Big Muskellunge, and Trout Lakes (Figure 5). In the larger lakes, Crystal, Big Muskellunge, and Trout Lakes, average ice-off years were closer in temperature to early ice-off years. In the southern lakes, ice-off date had no significant influence on summer hypolimnetic temperatures (Figure 6). Time-series reveal that while hypolimnetic temperatures in Lake Monona and Mendota warm earlier in early ice-off years, this difference is overcome by May (Figure 4).

Hypolimnetic temperatures were also compared to the date of stratification. In the southern lakes, Lake Monona and Mendota, a late onset of stratification typically resulted in a warmer summer hypolimnion (Figure 7). In the northern lakes, this relationship was only seen weakly in Allequash Lake. In Trout Bog, Crystal, Big Muskellunge, and Trout Lakes, late stratification often resulted in a colder than average summer hypolimnion. In the northern lakes, ice-off date appears to be a stronger driver of hypolimnetic temperatures, versus the southern lakes, where onset of stratification is more influential than ice-off date.

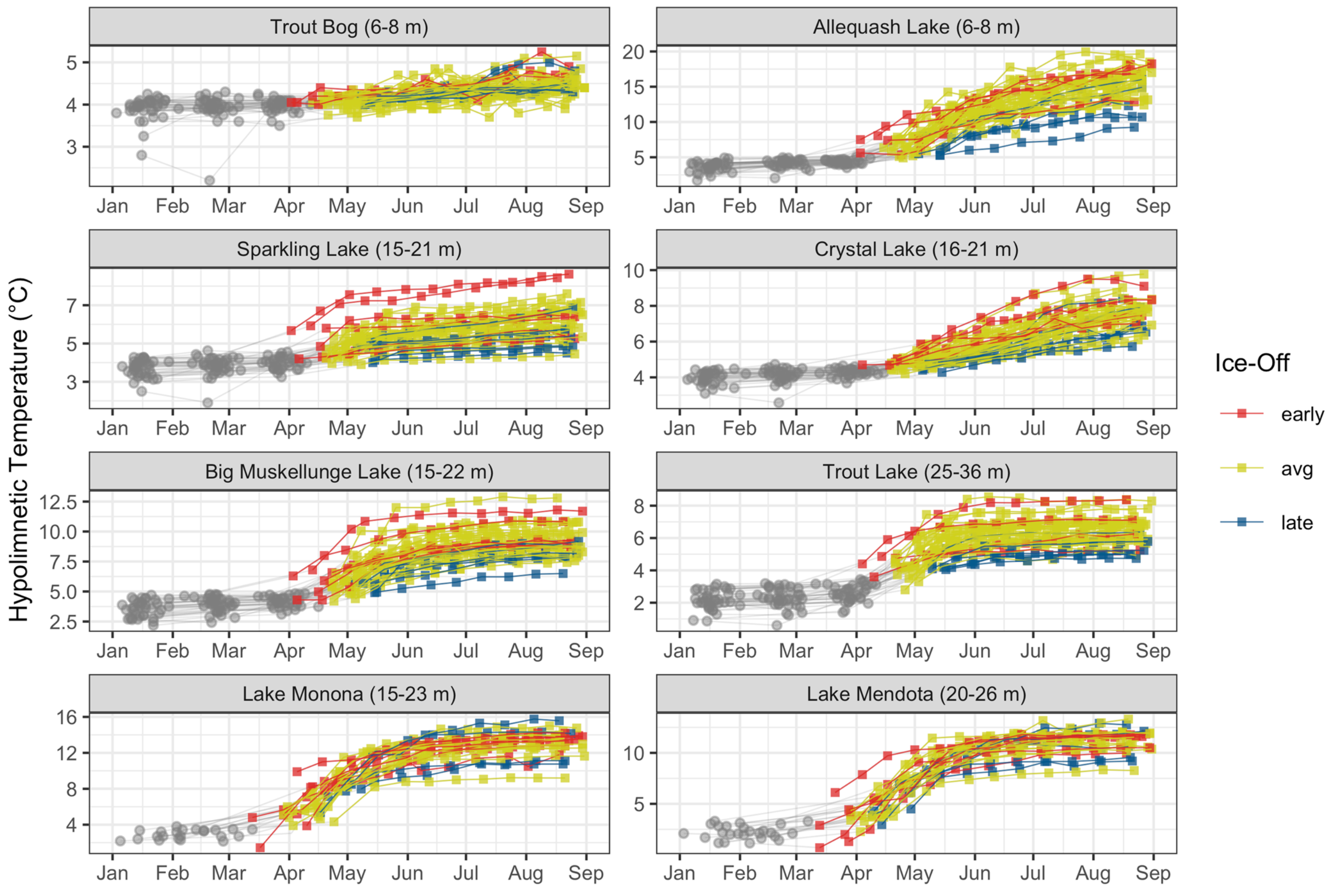

Figure 4. Hypolimnetic temperatures in the eight study lakes grouped by ice-off date. Northern lake data are from 1982 to 2019. Southern lake data are from 1996 to 2019. Gray dots represent observations taken when the lake was ice-covered. In some early ice-off years, such as 2012, poor ice conditions on the southern lakes prevented under-ice sampling and the first observation of the year was taken after ice-off.

The relationship between ice-off date and dissolved oxygen drawdown in the hypolimnion was variable amongst the lakes. Trout Bog was not considered in the analysis of hypolimnetic oxygen as the hypolimnion is rarely oxygenated in the spring. In Trout Lake, early ice-off years had significantly earlier hypolimnetic oxygen drawdown (11.5 days) than late ice-off years (Figure 5 and Table 1). The same pattern was evident (but not significant) in Big Muskellunge (10.5 days), Monona (5.5 days), and Mendota (10.0 days). Allequash Lake was the only lake where later ice-off resulted in earlier loss of oxygen in some years (Figure 5 and Table 1). In Sparkling, Crystal, Monona, and Mendota there was no consistent relationship between the three ice-off groupings. When plotted as time-series, the northern lakes (excluding Trout Bog) reached a higher maximum oxygen saturation in early ice-off years (Figure 8). In the southern lakes, ice-off date did not influence hypolimnetic oxygen saturation. In Lake Monona and Mendota, date of stratification was a strong control on the onset of hypoxia (Figures S4 and S5), with early stratification years having significantly earlier hypolimnetic oxygen drawdown than late ice-off years, by 18.5 and 20 days, respectively.

The only significant difference in maximum spring Secchi depth between early and late ice-off was found in Allequash Lake (1.35 m). However, Secchi depth was also higher in early ice-off years in Sparkling, Crystal, Trout, and Monona (Table 1). The relationships between ice-off date and chlorophyll concentrations were likewise variable amongst lakes, but generally mirrored Secchi depth trends (Figures 5 and 6). Although not significant, Allequash, Crystal, Trout, and Monona had lower chlorophyll or phytoplankton biomass in early ice-off years.

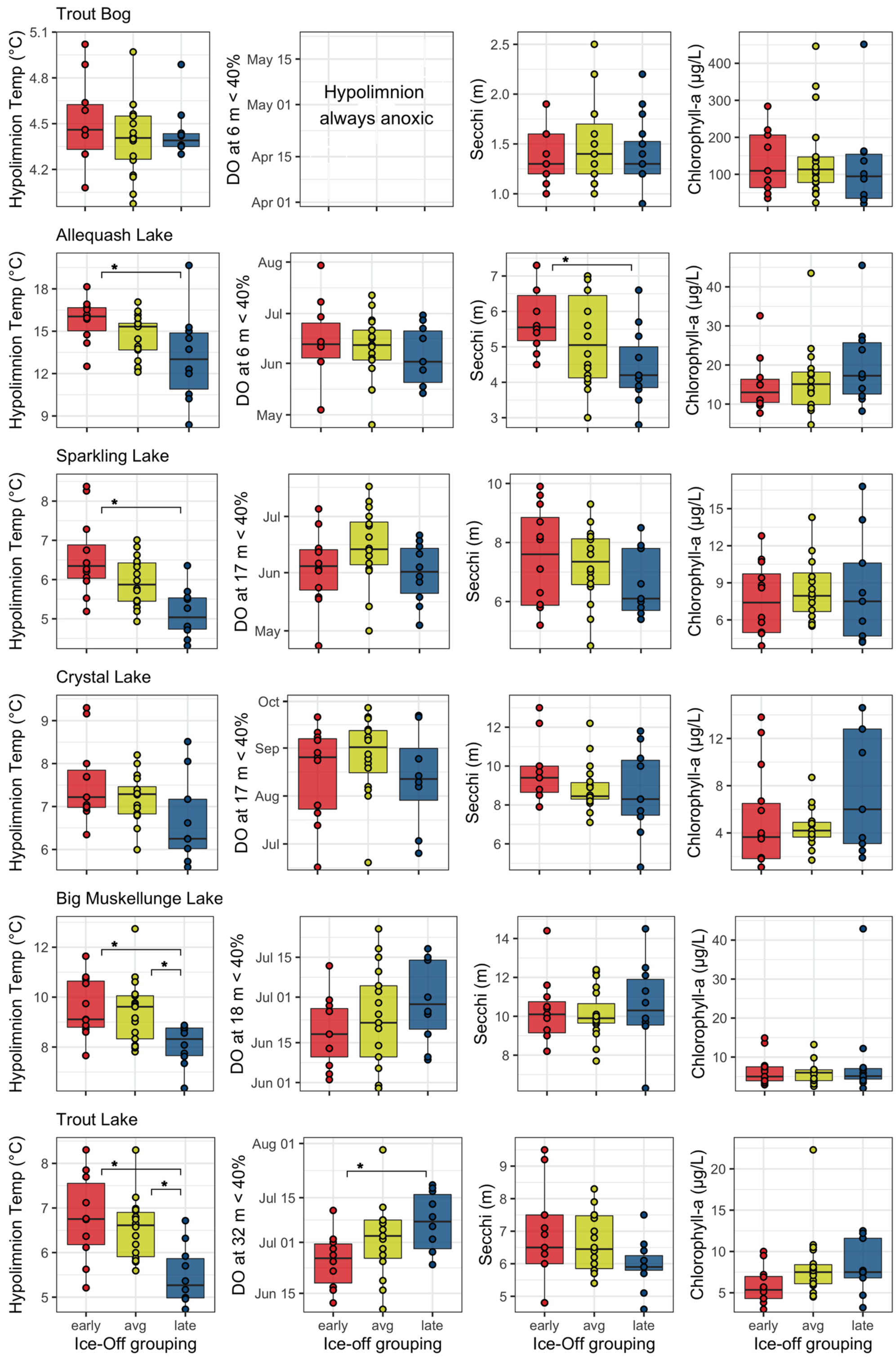

Figure 5. Boxplots of mean summer hypolimnetic temperatures, hypolimnetic oxygen depletion, maximum spring secchi depth, and maximum spring surface chlorophyll concentrations in six northern study lakes grouped by ice-off date. Ecosystem metric dates and depth ranges are described in Table 1. Significance between any two groups (Dunn's test, $p < 0.05$) is denoted by an asterisk.

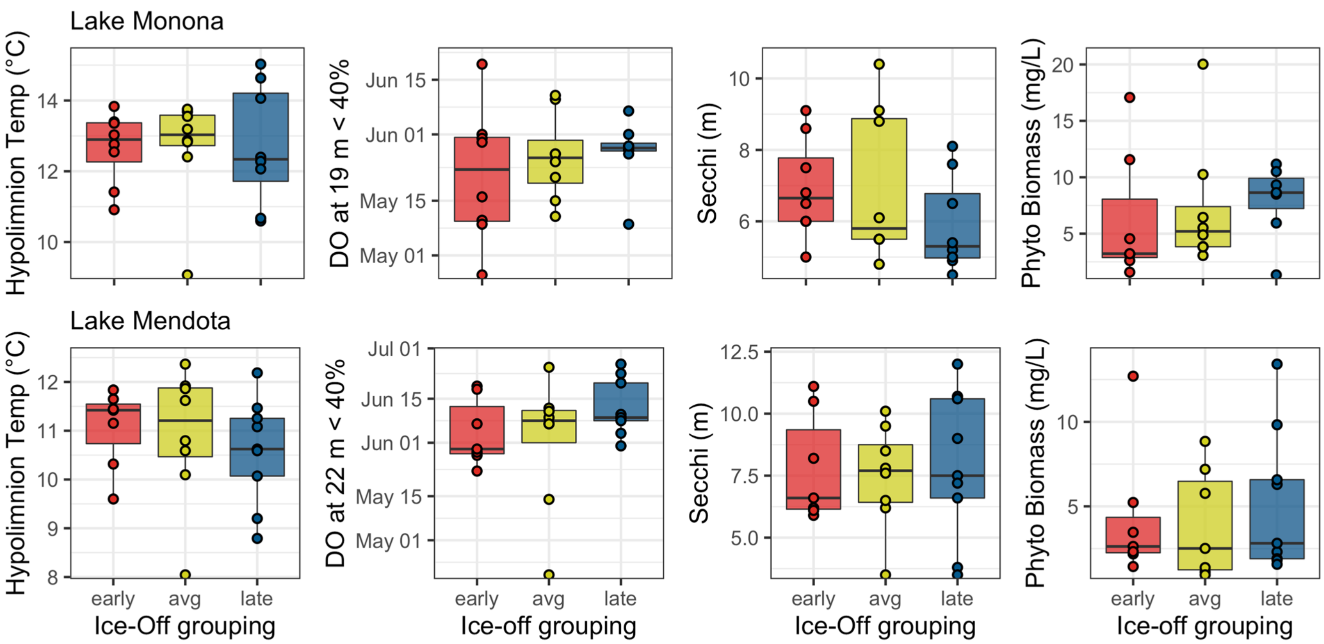

Figure 6. Boxplots of mean summer hypolimnetic temperatures, hypolimnetic oxygen depletion, maximum spring secchi depth, and maximum spring phytoplankton biomass in two southern study lakes grouped by ice-off date. Ecosystem metric dates and depth ranges are described in Table 1. No groups showed significant differences.

4. Discussion

Spring mixing plays a critical role in reducing the ecological memory of ice-off in these dimictic lakes. When ice-off is early and the window of time before the onset of stratification widens, the variability in atmospheric conditions, namely air temperature and wind, become more important factors in heat gain (Winslow et al., 2017) than the timing of ice-off. Once stratified, the epilimnion continues to rapidly warm, while temperature gains in the hypolimnion slow due to limited heat exchange with the epilimnion (Magee et al., 2016). The finding that summer epilimnion temperatures are not impacted by ice-off date is not new, and it has been shown both for these lakes and the region that surface water temperatures correlate with air

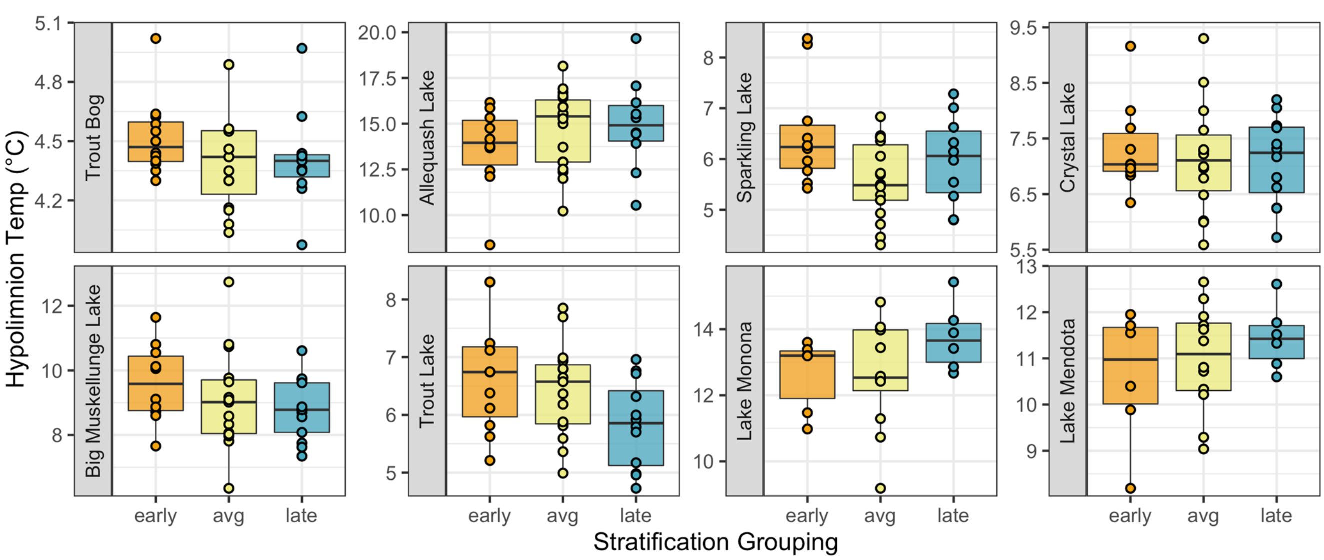

Figure 7. Boxplots of mean hypolimnetic temperature from June 1 to September 1, grouped by date of stratification. Northern lake data are from 1982 to 2019. Southern lake data are from 1995 to 2019. No groups showed significant differences.

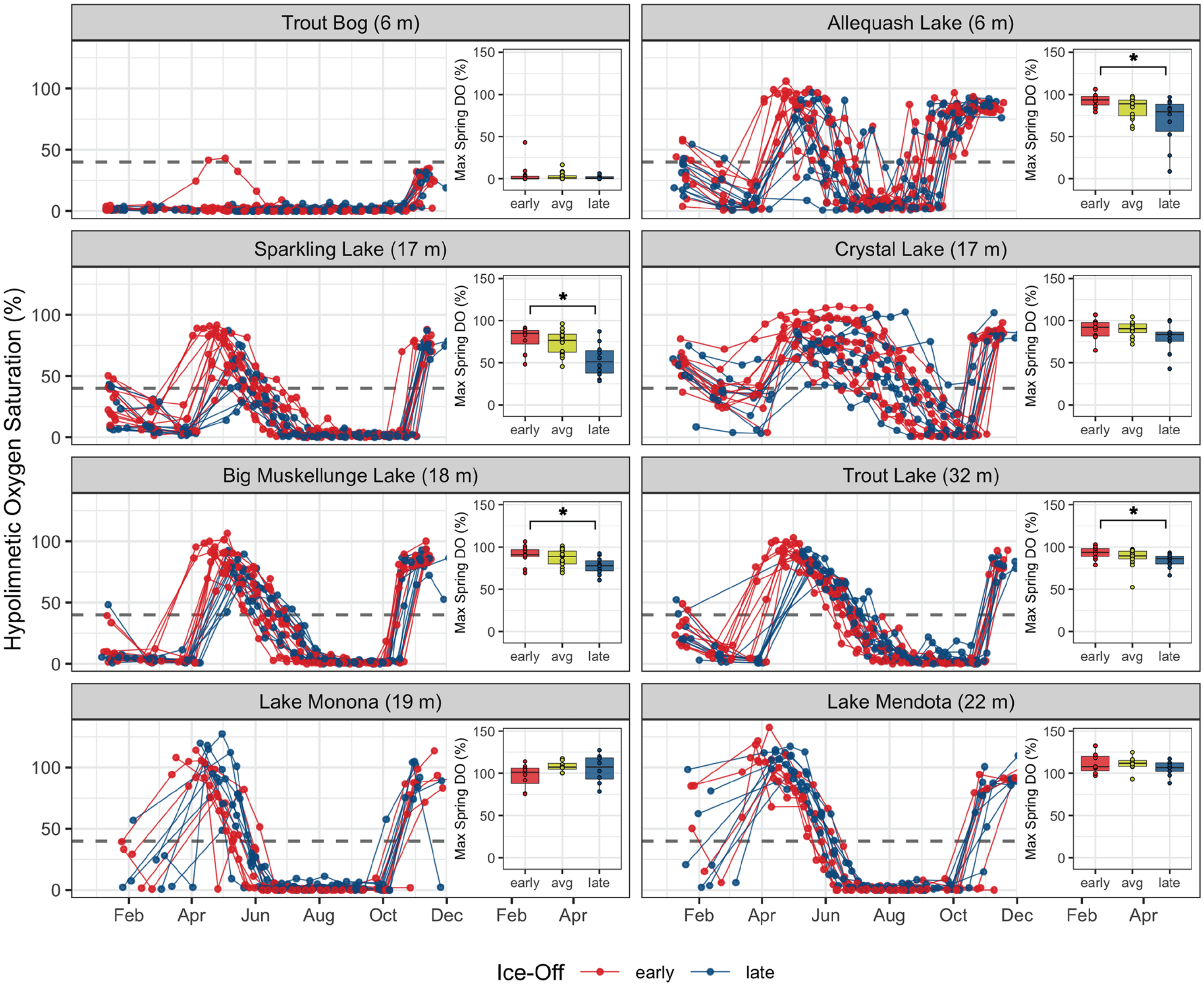

Figure 8. Time-series of oxygen saturation in the hypolimnion in the eight study lakes in early (red) and late (blue) ice-off years. 40% oxygen saturation is denoted by the dashed line. Northern lake data are from 1982 to 2019. Southern lake data are from 1996 to 2019. Insets show boxplots of maximum spring oxygen saturation in the three ice-off groupings. Significance between any two groups (Dunn's test, $p < 0.05$) is denoted by an asterisk.

temperatures (Winslow et al., 2015, 2017). Large lakes warm more slowly than small lakes, but in this region only lakes with an extremely large thermal mass (e.g., Lake Superior) would retain an ecological memory effect of lake ice-off on summer epilimnion temperature (Austin & Colman, 2008).

The ecological memory of lake ice on hypolimnetic temperatures was noticeably divergent between the two climate zones (northern vs. southern Wisconsin). In the northern study lakes, there was ecological memory of lake ice on hypolimnetic temperatures. In these dimictic lakes, following ice-off, the water column mixes and becomes isothermal near 4°C, after which the entire water column warms until the onset of stratification (Boehrer & Schultze, 2008). In late ice-off years, many of the northern lakes stratified immediately following ice-off, and there was little heat gain. In some cases, the onset of stratification has been documented to take place before ice-off (N. Lottig pers. comm.), likely a result of low snow cover that regulates light penetrating into the water column (Pernica et al., 2017). In these years, lakes may not fully mix, and the hypolimnion remains cold throughout the summer. In Trout and Sparkling Lake, hypolimnion temperatures barely reached 6°C in late ice-off years. In early ice-off years, the lakes were able to gain more heat in the hypolimnion before the onset of stratification, and although spring weather conditions played a larger role in heat gain, early ice-off years had significantly warmer summer hypolimnia in four of the six lakes.

In the southern lakes, ice-off was sufficiently independent of the onset of stratification that ice-off date did not impart any memory effect on summer hypolimnion temperatures (Figure 6). Unlike the northern lakes, where late stratification took place in years with late ice-off and therefore little heat gain, late stratification in the southern lakes allowed Lake Monona and Mendota to gain more heat than in years with early stratification (Figure 7). A modeling study of Lake Mendota found that the midsummer temperature difference between the epilimnion and hypolimnion was highly correlated with spring turnover date (Magee et al., 2016). This suggests an ecological memory of spring climate in these lakes, but not specifically ice-off date.

The stark contrast between hypolimnetic temperature controls in the northern and southern lakes suggests that with respect to hypolimnetic water temperatures, lakes only have an ecological memory of ice-off date where the spring mixing period is very short. However, this would include a large swath of the world's lakes that currently freeze (Sharma et al., 2019), including north-temperate and southern boreal lakes, mountain lakes (Flaim et al., 2020), and lakes with a large thermal mass (Austin & Colman, 2008); keeping in mind that at certain latitude, northern lakes become cold-monomictic (Lewis, 1993) and may only stratify intermittently (Welch et al., 1982).

I had hypothesized that warmer water temperatures seen in early ice-off years would result in a more rapid depletion of hypolimnetic oxygen depletion. However, a significant association between ice-off date and hypolimnetic oxygen concentrations was only found in Trout Lake (Figure 5). This result is in part due to the fact that in the northern lakes, years with late ice-off were less likely to fully mix to 100% saturation (Figure 8). This aligns with the observation that in late ice-off years the water column can stratify prior to ice-out due to radiative energy penetrating a snow-free ice-cover. Therefore, in these lakes, ice-off does play an important role in summer hypolimnetic oxygen availability, but any early onset of oxygen depletion in early ice-off years is offset by less water column mixing in late ice-off years, resulting in no ecological memory of lake ice-off date on hypolimnetic oxygen concentration in many of the lakes.

In the southern lakes, the period of time between ice-off and summer stratification meant that the lakes always fully mix, and ice-off date had little effect on oxygen replenishment in the water column (Figure 8). However, the onset of stratification did play a strong role in the timing of hypolimnetic oxygen depletion (Figures S4 and S5). Early stratification resulted in a significantly earlier drawdown of hypolimnetic oxygen in the southern lakes, and a similar, although insignificant, relationship in the northern lakes (Figure S4). Many predict that warming atmospheric temperatures will lead to an earlier onset of summer stratification (Woolway et al., 2020) and a longer duration of hypolimnetic summer anoxia (Fang & Stefan, 2009). While keeping in mind the uncertainty associated with the date of stratification in NTL-LTER data, my findings support this. In the NTL-LTER study lakes, as atmospheric temperatures warm, both lake ice-off and hypolimnetic oxygen depletion will take place earlier in the year, but these two ecosystem shifts are only linked through atmospheric air temperatures and there is not a direct effect of ice-off on summer oxygen depletion.

While the metrics of hypolimnetic temperature and dissolved oxygen suggest some ecological memory of ice-off date in the northern study lakes, the metrics of spring water clarity and primary productivity do not show any consistent trend among lakes. Although drivers of water clarity on north-temperate Wisconsin lakes have been extensively studied (Lisi & Hein, 2019; Lottig et al., 2014; Rose et al., 2017), these studies do not examine the potential influence of lake ice on summer water clarity. Even a study on the drivers of the spring clear water phase in Lake Mendota did not examine ice-off date as a driver of water clarity (Matsuzaki et al., 2020). It may be that these studies also did not find any causal link of clarity to ice conditions, and therefore did not include lake ice in their models.

Based on phenological literature documenting the potential for trophic mismatch between phytoplankton and their primary consumers in warm springs (Winder & Schindler, 2004), I hypothesized that early ice-out would result in the lowest water clarity because zooplankton emergence might not coincide with the spring phytoplankton bloom. Overall, there was little evidence of this, and in some cases, like Trout Lake, early ice-off resulted in some of the clearest years on record (Figure 5). Chlorophyll concentrations and phytoplankton biomass patterns were similarly unique to each lake. Overall, these results suggest that spring phytoplankton blooms and water clarity are driven by a suite of complex factors, and the effect of ice-off cannot be seen in 40 years of data (Warner et al., 2018). It may be that an effect of ice-off would be noticeable at the phyla/division level as different phytoplankton groups have been found to be more sensitive to spring mixing conditions (Adrian et al., 1999; Berger et al., 2010; Kienel et al., 2017). Spring phytoplankton productivity may also be shaped by phytoplankton dynamics preceding ice loss (Twiss et al., 2012; Wilhelm et al., 2014), which would likely be shaped by available light beneath the ice cover (Bertilsson et al., 2013; Jewson et al., 2009). Contrasting the memory effects on hypolimnetic conditions that were found, any epilimnetic biological memory effect of ice-off date is likely soon forgotten as community dynamics begin to be structured by weather conditions (Adrian et al., 1999). Future work detailing the depth of the stratification would be useful in identifying epilimnetic extent and possible habitat changes based on the timing of ice-off.

This analysis was structured around five ecosystem metrics, two of which are considered physical metrics (epilimnion and hypolimnion temperature), two of which are driven by both physical and biological processes (hypolimnetic oxygen concentration, and water clarity), and one that is considered a biological metric (phytoplankton biomass/chlorophyll). The finding of ecological memory effects on physical metrics and not biological metrics is likely related to the tendency of biological variables in these lakes to be much more variable than physical metrics. Across the NTL-LTER lakes, biological variables have more frequent extremes driven by short-term dynamics (Batt et al., 2017), and a memory signal of lake ice might not be observable given the stochastic nature of lake biology. More complex modeling that incorporates additional variables that structure ecosystem dynamics such as snow thickness, mixing depth, nutrient and carbon concentrations, and hydrology would be the next step in searching for a memory effect of lake ice on spring and summer lake biological properties. Higher-frequency measurements (i.e., daily), might also reveal short-term memory effects that cannot be identified with biweekly sampling.

This analysis revealed variable impacts of the timing of ice-off on ecosystem properties across lake type and climatic zone. Even within a climate zone, there was large variation in the impact of ice-off date, which suggests lake-specific factors cannot be overlooked. The most consistent signal of an ecological memory effect of lake ice was on hypolimnetic water temperatures in the northern suite of lakes. Warmer hypolimnia will increase biological processing rates, structure fish habitat, and may leave lakes more susceptible to mixing events due to weaker water column stability. As ice-off date trends earlier in many parts of the world (Sharma et al., 2019), the lakes that will likely experience the largest changes in spring and summer lake ecosystem properties are dimictic lakes that currently have the longest duration of lake ice. In considering a future with warmer winters (Sharma et al., 2020), quantifying the ecological memory of lake ice provides a starting point for predicting how lake ecosystem properties will change with earlier ice-off.

Data Availability Statement

The data on which this article is based are available in NTL-LTER (2020a–2020e).

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