Ecology under lake ice

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Abstract

Winter conditions are rapidly changing in temperate ecosystems, particularly for those that experience periods of snow and ice cover. Relatively little is known of winter ecology in these systems, due to a historical research focus on summer "growing seasons." We executed the first global quantitative synthesis on under-ice lake ecology, including 36 abiotic and biotic variables from 42 research groups and 101 lakes, examining seasonal differences and connections as well as how seasonal differences vary with geophysical factors. Plankton were more abundant under ice than expected; mean winter values were 42.8% of summer values for chlorophyll *a*, 15.8% of summer phytoplankton biovolume, and 34.4% of summer zooplankton density. Dissolved nitrogen concentrations were typically higher during winter, and these differences were exaggerated in smaller lakes. Lake size also influenced winter-summer patterns for dissolved organic carbon (DOC), with higher winter DOC in smaller lakes. At coarse levels of taxonomic aggregation, phytoplankton and zooplankton community composition showed few systematic differences between seasons, although literature suggests that seasonal differences are frequently lake-specific, species-specific, or occur at the level of functional group. Within the subset of lakes that had longer time-series, winter influenced the subsequent summer for some nutrient variables and zooplankton biomass.

Introduction

Reduced ice cover on lakes and rivers worldwide (Magnuson et al. 2000; Benson et al. 2012) highlights an urgent need for research focused on under-ice ecosystem dynamics and their contributions to whole-ecosystem processes. Recently a global synthesis of summer lake temperature trends in lakes (O'Reilly et al. 2015) revealed that winter ice cover is a major force in determining the characteristics of summer warming trends, demonstrating the cascading effects between seasons. Cross-seasonal cascades can involve both abiotic and biotic variables, such as when winter ice characteristics influence spring and summer algal growth (e.g., Gerten & Adrian 2000; Straile 2002; Adrian et al. 2006; Blenckner et al. 2007). Consequently, in water bodies that freeze, the timing and physical characteristics of ice cover are likely to drive some of the most important biological changes for lakes overall (Salonen et al. 2009; Moore et al. 2009; Benson et al. 2012).

Marine research is ahead of freshwater research in studies of under-ice ecology, providing compelling evidence that winter conditions and changes in ice phenology play an important role in sea-ice system dynamics (Arrigo & Thomas 2004; Arrigo et al. 2008; Meier et al. 2014). The presence of ice in marine systems drives primary productivity that is critical for food webs (Lizotte 2001; Grebmeier 2012); for example, ice-associated algae in the Antarctic contribute 25-30% of total annual productivity for the region (Arrigo & Thomas 2004). But for lakes, there is very little information about the physics, geochemistry, and biology under ice, and this knowledge gap severely limits our ability to predict how changes in winter conditions will affect the ecology and productivity of inland waters. A recent study reported that only 2% of peer-reviewed freshwater literature has included under-ice lake processes (Hampton et al. 2015). The paucity of under-ice research in freshwater systems is especially surprising when one considers that half of the world's lakes periodically freeze, i.e. slightly more than 50 million lakes (Verpoorter et al. 2014). Also, the majority of lakes in the world are located between 60° and 66° N where annual ice cover duration currently averages more than 150 days (Weyhenmeyer et al. 2011).

The initial and highly influential model of the plankton ecology group (the PEG model; Sommer et al. 1986) hypothesized that winter in ice-covered lakes is a time of limited, if any, activity by primary or secondary producers. The widespread use of the term "growing season" to describe summer months in temperate lakes reflects the prevailing viewpoint of winter as an inactive period. In general, freshwater scientists have assumed that overall biological activity under lake ice is inconsequential or that under-ice primary producers resort to heterotrophy or dormancy, as has been observed in some studies (e.g., McKnight et al. 2000; Leppäranta 2015), particularly for high-latitude systems with heavy snow coverage. While the PEG model has since been revised (Sommer et al. 2012) with a call for additional winter work, areas of uncertainty range from the identity and activity of plankton to ecosystem-level processes such as whole-lake metabolism and greenhouse gas emissions. The lake studies that have included under-ice work strongly suggest that winter food webs and physical processes are both active and complex, but with few patterns that are readily generalizable (reviewed in Salonen et al. 2009; Bertilsson et al. 2013; Bruesewitz et al. 2015; Hampton et al. 2015).

Prior work indicates that winter under-ice conditions can be very similar to, or very different from, the ice-free summer conditions. Depending upon snow characteristics, ice can allow for up to 95% of photosynthetically active radiation (PAR) transmission

(Bolsenga & Verderploeg 1992), fueling winter algal blooms that rival those of summer (e.g., Jewson et al. 2009). In Lake Erie, phytoplankton growth and loss rates during winter can be similar to those of summer (Twiss et al. 2014). For certain lakes, the composition of phytoplankton communities is different under ice, dominated by smaller species (e.g., Wetzel 2001), or conversely dominated by large ice-associated filamentous diatoms (e.g., Katz et al. 2015; Beall et al. 2016), whereas other lakes do not appear to have distinct seasonal changes in phytoplankton community composition (Dokulil et al. 2014). Although zooplankton biomass generally appears to be lower under ice, changes in community composition can be highly variable across lakes (Dokulil et al. 2014). Even more scarce is information about nutrient and dissolved organic carbon concentrations under the ice that may help to drive many of these plankton dynamics (but see Özkundakci et al. 2016).

The pathways through which winter conditions may affect lake ecology throughout the year are similarly diverse. Winter ice conditions have been observed to alter phytoplankton biomass and composition in the subsequent ice-free season (Weyhenmeyer et al. 2008). For zooplankton, early emergence from diapause, synchronized with the timing of warming at the end of winter can be associated with higher summer density for zooplankton grazers (Gerten & Adrian 2000; Adrian et al. 2006). Such carry-over between seasons is not restricted to winter's influence on summer, of course, and there is evidence that under-ice zooplankton dynamics can depend in part on late summer zooplankton biomass (Dokulil et al. 2014). The diversity of responses found by under-ice studies suggests that a synthesis of existing knowledge is greatly needed and would help identify key next steps in winter limnology as well as promote productive collaborations (Hampton et al. 2015).

Research that builds a knowledge base about the processes occurring over nearly half the annual cycle for approximately half of the world's lakes is a worthy challenge, with potentially global repercussions. Here we explore differences between winter and summer conditions both across and within lakes, focusing on dynamics of phytoplankton, zooplankton, nutrients, and dissolved organic carbon. We address two overarching questions on under-ice ecology: 1) What is the magnitude and direction of ecological change from winter to summer; and 2) For which variables and to what extent are winter and summer seasons connected, i.e., what is the influence of winter conditions on the following summer season, and the influence of summer conditions on the following winter? We hypothesized that winter biomass and density of phytoplankton and zooplankton are significantly lower than that of summer, due to a low-light environment unfavorable for emergence or growth (e.g., Vincent & Vincent 1982; Cáceres & Schwalbach 2001; Jewson et al. 2009), low temperature (e.g., Özkundakci et al. 2016), or nutrient limitation (e.g., O'Brien et al. 1992; Özkundakci et al. 2016), and that these differences would be modified by geophysical characteristics of lakes. Further, we hypothesize that lake conditions can carry over across seasons, as suggested in the revised PEG model (Sommer et al. 2012; Domis et al. 2013), such that an understanding of winter conditions will improve understanding of summer conditions, and vice versa. The presence of seasonal carry-over would indicate that winter is not simply a "reset" that leads back to similar spring ice-out conditions year after year, and would suggest revisions to current field and laboratory approaches currently focused on "growing season" dynamics.

Methods

Data Acquisition

Data were acquired from both an initial literature review to provide baseline expectations for ecological patterns and, much more comprehensively, from a collation of primary data.

Literature review. As an initial step toward synthesizing knowledge, we compiled under-ice data for chlorophyll *a* (chl *a*) concentration from a literature survey. We found 14 papers for which data would be readily compared to those solicited from primary data contributors (based on criteria in Supplemental Information). From these papers, we compiled data from 17 lakes (Fig. 1), extracting data from text, tables, or from figures. For the literature review effort, we were unable to compare ice-on (winter) and ice-off (summer) data, as only 7 of the lakes in these papers also included biological data during the summer season.

Primary data collation. The scientific community was solicited for data on physical, chemical, and biological variables of lakes and reservoirs (hereafter together called "lakes") during ice cover. We used an open call for participation through electronic mailing lists and professional networks, and then interacted extensively with data contributors. In total, we collated winter under-ice and summer observations between 1940 and 2015 for 101 lakes at 135 unique sampling locations across wide gradients of latitudes, production, and trophic status (Fig. 1). For the Laurentian Great Lakes, most sampling stations were located nearshore or in bays.

Contributors of primary data used a structured template to report values from winter periods when the lake had complete ice cover (hereafter "winter"), and summer periods when the lake was completely open and, in dimictic systems, stratified (hereafter "summer"). For 10 lakes that were polymictic or lack reliable summer stratification, summer data are from a representative open water period chosen by the primary data contributors, usually midsummer. We asked researchers to provide data aggregated from the photic zone, for each lake and season. Across all lakes, the median sample depth during winter was 2.0 m, and the mean ratio of sample depths (winter:summer) was 1.01. We did not include winter data from those years that did not have ice cover (e.g., Müggelsee sometimes does not freeze). Each seasonal value used in our analysis was computed by the individual data providers (Box S1; Fig. S1). The number of within-season sampling events was reported by researchers for 71% of our compiled seasonal averages; of these, 64% of the winter averages and 79% of the summer averages were based on 3 or more sampling events. When a lake had multiple sampling stations, the stations were generally treated independently. Exceptions were cases where researchers specified multiple stations that were functionally similar and could be pooled in aggregate. After pooling the functionally similar stations, the majority of lakes (84 of 101 lakes) did not retain multiple distinct stations for analyses (see SI).

Data availability differed among lakes and variables. For several major variables, paired winter and summer observations were present in at least 30 stations, often over 10 years. All stations had at least one variable with both winter and summer data, and the variable-specific sample sizes and periods of record are in Table S1. The median period of record for most variables was 2-3 years. Variables included water temperature (107 unique stations with paired winter-summer data), chlorophyll *a* (chl *a* as μg L^{-1}; 118 stations), total phosphorous (TP as μg L^{-1}; 106 stations), total dissolved phosphorus (TDP as μg L^{-1}; 72 stations), total nitrogen (TN as μg L^{-1}; 75 stations), total dissolved nitrogen (TDN as μg L^{-1}; 73 stations), TN:TP (atomic ratio; 74 stations), TDN:TDP (atomic ratio; 66 stations), and dissolved organic carbon (DOC as mg L^{-1}; 81 stations). Our reported values for TDP and TDN are conservative, because not all researchers performed the digestion step. Nonetheless, because common nutrient methods were usually used at a given lake, our approach still captures the relative difference between seasons (winter-summer), except in lakes where the dissolved organic fraction varies substantially between seasons. In addition, 36 stations had data for total zooplankton density (individuals L^{-1}). Group-specific zooplankton counts (proportion of total abundance) for calanoid, cyclopoid, *Daphnia*, rotifer, other cladoceran, and unspecified other zooplankton were also available. Methodology for zooplankton data collection differs across programs to a degree that complicates comparisons across lakes for rotifers and unspecified other zooplankton, such that those data were not analyzed here and total zooplankton densities were accordingly adjusted as well. Subsequent references to zooplankton density include *Daphnia*, other cladocerans, cyclopoid and calanoid copepods for all 36 stations. For phytoplankton biovolume mm^{-3} L^{-1}, there were data for 17 stations. Group-specific phytoplankton counts (proportion of total abundance) for chlorophyte, cryptophyte, cyanophyte, bacillariophyte, dinoflagellate, and other phytoplankter were available at 17 stations. Specific ultraviolet absorbance (SUVA, L mg C^{-1} m^{-1}), and color (platinum units) were also available at some stations. Although we solicited benthic data, only a few researchers provided data for any type of benthic variable, suggesting a widespread lack of benthic winter sampling. The lake-specific averages for winter and summer conditions, by variable, are shown in Table S2. For chl *a*, TP, TDP, TN, TDN, DOC, and zooplankton density, more than 25% of stations had a period of record ≥10 years. The complete dataset is available in the Knowledge Network for Biocomplexity (https://knb.ecoinformatics.org/).

Data analysis

We approached data analysis in two ways. The first approach was to quantify the average winter-summer differences across all lakes in the data set, identifying major physical features of lakes that affect the magnitude of observed winter-summer differences. The second approach was to examine univariate seasonal dynamics within lakes, including winter-summer differences and winter-summer correlations, using the subset of lakes where longer-term (≥10 years) time series were available.

<u>Winter-summer differences across lakes.</u> We calculated the mean winter value and the mean summer value for every station and variable, and examined mean winter-summer differences across all lakes in the data set. Magnitude, direction and significance of differences between winter and summer were determined using linear mixed effect (LME) modeling with year as a random intercept (Bates et al. 2015). For the multivariate plankton compositional data, we used permutational analysis of variance (PERMANOVA; Anderson 2001) from the vegan package in R ("adonis" function, Oksanen et al. 2016; R Core Team 2016) on sites that had complete cases for both winter and summer communities. To discern major physical variables correlated with the magnitude and sign of winter-summer differences, we used a regression tree approach (rpart package in R, Therneau et al. 2015, with applications from Breiman et al. 1984). We used the variable-specific average winter-summer difference as the response variable; the candidate explanatory variables were lake

area, lake maximum depth, latitude (absolute), and elevation. Trees were cross-validated and pruned using the complexity parameter value which minimized the cross-validated error. Mean winter-summer difference and standard error of the difference were calculated for each branch of the regression trees. We also used a regression tree approach to analyze average winter-summer difference in plankton community composition as a matrix response (mvpart package in R, Therneau et al. 2014), for both the crustacean zooplankton community and the phytoplankton community data. Candidate explanatory variables included the same four variables as previous trees, as well as winter-summer difference in water temperature and, for zooplankton, the summer chl *a*.

Due to differences in the available period of record, the overall winter average can represent 30+ years for some lakes and variables, while for others the overall average represents only one year of data. We expected that variation in sample size might create noise that could obscure differences (Type 2 error), but not suggest differences that do not exist (Type 1 error).

Winter-summer differences within lakes. For time series that were available, we examined within-lake differences between winter and summer. For this we used only time series that had ≥10 winter values, meaning at least 10 years of data and 20 values overall. To allow a robust examination of winter-summer correlations (below), we used contiguous portions of each time series, allowing no more than 1 data gap. Before examining differences, every time series was detrended using a 7-point moving average filter (3.5 years) to account for longer-term trends, and we confirmed that no significant linear trends remained after filtering. With each detrended time series, summer-winter differences were examined using a simple seasonal model

$$y_t = b_{ice} * D + b_0 + e \qquad (1)$$

where b_{ice} is the coefficient describing the winter-summer difference, D is a dummy variable (1 in winter, 0 in summer) that employs the b_{ice} coefficient, b_0 is the intercept (representing the mean summer value), and e is the error term. We then compared the seasonal model (2 parameters) to the simple intercept model (1 parameter, b_0, representing the overall mean) using the Akaike Information Criterion corrected for small sample sizes (AIC_c) (Burnham & Anderson 2002). If the seasonal model differed from the simple intercept model by $\Delta AIC_c \geq 2$, we interpreted this result to mean that the time series showed a seasonal difference. Detailed diagnostic plots including raw and detrended time series are provided in Figure S4 for one example lake (Big Muskellunge Lake, chl *a*). For 194 of the 238 available time series (82%), residuals from eq. 1 were not autocorrelated at lag 1 according to the Box-Ljung test, and this is demonstrated by the partial autocorrelation plot of the detrended+deseasoned data (Fig. S4). For the other 44 time series, we added a first-order autocorrelated error structure to eq. 1. The percent of time series having winter values greater than summer values, or vice versa, was tabulated by variable.

Winter-summer correlations within lakes. Using the same univariate, contiguous, moving-average detrended time series as above (those with >10 winter values), we examined temporal correlations between winter and summer. These included: i) correlations between winter and the previous summer season (summer_{t-1}), or summer-into-winter *(SW)* correlations; and ii) correlations between winter and the subsequent summer (summer_{t+1}), or winter-into-summer *(WS)* correlations. We determined the sign of seasonal correlations, if present, using a simple model of the detrended data

$$Y_{winter,\,t} = b_{SW} * Y_{summer,t-1} + b_0 + e \qquad (2)$$

where t is the index of the time series and b_{SW} is the slope of the relationship between winter and the previous summer. If this *SW* correlation model did not show AIC_c improvement >2 AIC_c units compared to the intercept model (1 parameter, b_0, representing the overall mean), the time series was interpreted as not seasonally correlated. We then separately evaluated the corresponding *WS* correlation model, $Y_{summer,\,t+1} = b_{WS} * Y_{winter,t} + b_0 + e$, also using AIC_c. A minority of these *SW* and *WS* correlation models produced autocorrelated residuals, and to these we added a first-order autocorrelated error structure, although this modification did not change the model selection nor the sign of b_{SW} or b_{WS} for any time series. Here a positive *WS* correlation indicates that high summer values follow high winter values, or low summer values follow low winter values. Alternatively, a negative *WS* correlation indicates anti-persistence, such that low summer values follow high winter values, or high summer values follow low winter values. As examples, we illustrate the presence/absence of winter-summer correlations for every chl *a* time series, including *SW* correlations (Fig. S5) and *WS* correlations (Fig. S6). The percent of time series having positive/negative *SW* correlations or positive/negative *WS* correlations was tabulated by variable (Table S5).

Results

Seasonal differences across lakes

Indicators of plankton biomass were lower in the winter than during the summer. Across lakes and latitude, average winter chlorophyll *a* (± SE) (5.87 ± 0.88 μg L^{-1}, Fig. 2) in the primary data ranged much more widely than in those from our literature survey (Supplemental Fig. S2), although still significantly lower than that of summer (13.6 ± 2.84

μg L^{-1}, $p<0.0001$, Table 1). Using the regression tree approach, the shallowest lakes (max depth < 2.93 m, n = 13 lakes) showed greatest disparity in chlorophyll, with summers higher than winters by 52.3 ± 18.2 μg L^{-1}(R^2 for chl *a* tree = 0.330). Under-ice phytoplankton biovolume averaged about 1/6th that of the summer average (n=17, $p<0.001$ by LME, Table 1). However, at our coarse level of taxonomic aggregation, phytoplankton community composition did not differ significantly between winter and summer when examined across all lakes (PERMANOVA, p=0.77; Fig. 3). Across lakes, average zooplankton density (± SE) was significantly lower under ice (27.8 ± 11.2 individuals L^{-1}) than during summer (110 ± 30.8 individuals L^{-1}; $p<0.001$), and winter crustacean zooplankton community composition differed significantly from that of summer (PERMANOVA; p=0.05), with cladocerans generally more abundant in summer (Fig. 3). Regression trees did not provide further insights into plankton community shifts, differentiating only two lakes out of 17, and are not discussed further here. The complete list of summary statistics, for every variable, is shown in Table S3. The PERMANOVA statistical outputs are in Table S4.

Dissolved N concentrations tended to be higher during winter, and seasonal differences were more prominent for dissolved N than for dissolved P. Across lakes, average (± SE) TDN was approximately 2-fold higher under ice (707 ±129 μg L^{-1}, Fig. 2) than in summer (375 ± 62.2 μg L^{-1}; $p<0.001$ by lme). The pattern of higher winter TDN appeared particularly pronounced as maximum depth decreased. Regression trees showed that the 7 shallowest lakes (< 2.10 m) had 2070 μg L^{-1} higher TDN on average in winter than summer, 7 lakes of intermediate depths (5.20 < max depth > 2.10 m) had TDN winter values that were 758 μg L^{-1} higher than summer on average, while the 59 deeper lakes

(>5.2m) showed winter TDN values 123 μg L^{-1} higher than summer on average (tree R2 = 0.722, Fig. S7). TN was also higher during winter ($p<0.001$, LME-fitted difference of +161μg L^{-1}), likely as a reflection of higher dissolved N, which typically accounted for the majority of the N pool (winter TDN:TN= 0.807 compared to summer TDN:TN= 0.592). Winter and summer did not differ significantly for TP or TDP according to LME models ($p>0.2$). DOC concentrations did not differ seasonally ($p=0.863$ by LME). Interestingly, these DOC patterns clearly varied with lake area and elevation (tree R2 = 0.538, Fig. S7). Regression trees demonstrated that larger (>= 0.373 km2) lakes had 0.145 mg L^{-1} lower DOC in winter compared to summer, while smaller (< 0.373 km2), low elevation (< 366 m) lakes (n=19) had 6.69 mg L^{-1} higher DOC in winter, and similarly small lakes at higher elevations also had 0.810 mg L^{-1} higher DOC in winter. Regression tree analyses did not produce significant models for plankton density or phosphorus variables.

Winter-summer differences within lakes

In general, within-lake differences between summer and winter were consistent with differences observed across lakes. For example, chl *a* was lower in winter at 17 of the 34 sites (50%) that met our longer-term data criteria (Table 2). The summary statistics for each individual time series are in Table S5. Phytoplankton density was also lower in winter compared to summer in 4 of 4 sites. Similarly, zooplankton densities were significantly lower during winter at 10 of 11 sites (91%); the one exception was a bog lake, Trout Bog (USA), which had a relatively low summer zooplankton density and no detectable winter-summer difference. For nutrients, patterns again differed between N and P. Over 70% of the sites had higher winter TDN (11 of 14) and TN (21 of 30), whereas only 14% of sites had higher winter TDP (2 of 14) and 21% had higher TP (7 of 33). Allequash Lake (Fig. 4) provides an example where TP concentration was lower during winter. DOC was lower during winter at 6 of 26 sites (23%), and higher in winter at 3 sites including Trout Bog, USA, with no differences between winter and summer at the other 17 sites (65%). Three variables lacked differences between summer and winter values at >50% of sites (TP, TDP, DOC).

Winter-summer correlations within lakes

From a total of 238 time series for different lakes and variables (Table S5), after accounting for trends, our AIC-based approach detected 94 time series (39%) with some form of correlation between winter and the previous summer, or between winter and the following summer. Several individual variables had seasonal correlations in ≥33% of the available time series, including chl *a*, phytoplankton density, TDN, TN, and TDP (Table 2). Negative correlations outnumbered the positive correlations, suggesting seasonal anti-persistence. Positive seasonal correlations were absent for chl *a*, zooplankton density, DOC, TP, TDN, and TDP. For chl *a*, negative winter-into-summer (*WS*) correlations (26% of time series) and summer-into-winter (*SW*) correlations (32%) were both relatively common. For TDN, negative *SW* correlations outnumbered negative *WS* correlations (43% vs. 0%), suggesting summer carry over. Overall, the frequency of these winter-summer negative correlations ranged widely among variables.

Discussion

This global synthesis of under-ice ecology underscores the importance of winter conditions for lake ecology throughout the year. Using multiple approaches, our cross-lake synthesis revealed several clear differences between winter and summer conditions, offering generalizations about winter ecology that have been difficult to infer from prior studies involving one or a few lakes. We also provide new evidence that interseasonal connections are common for several ecological and biogeochemical variables, linking winter to both the previous and subsequent summers. Among our clearest results, primary producers (algae) and consumers (zooplankton) are typically less abundant under ice than in summer, but they maintain substantial populations in winter. Arguably, this may be interpreted as evidence of high winter productivity, and we explore the possibility below. Also clear was the result that winter dissolved nitrogen was consistently higher than summer. While crustacean zooplankton composition showed some general seasonal differences, we found no generalizable differences in phytoplankton community composition between winter and summer at the coarse level of taxonomic aggregation used here. As long-term climate change alters thermal regimes across globally distributed lakes in both summer (O'Reilly et al. 2015) and winter (Magnuson et al. 2000), it is increasingly important to understand how under-ice physical and ecological conditions influence ecology throughout the year. Overall, this work represents an important step towards understanding winter ecology in lakes broadly, as well as the connections to year-round dynamics and whole-lake functionality.

Our results indicate seasonal differences in chl *a*, plankton biomass and biovolume, and dissolved nitrogen between winter and summer, both across and within lakes. Despite lower under-ice values, particularly for the shallowest lakes, on average chl *a* was relatively high (42.8% of summer chl *a*) given the shorter photoperiod and variable physical conditions of winter. Indeed, winter levels exceeded those of summer in multiple cases such as Lake Simcoe (Canada), Lake Scharmüetzelsee (Germany), and Fish Lake (USA) which all had more than 10 years of winter data. Previous under-ice lake studies have reported chlorophyll values as high as 154 μg L -1 (Twiss et al. 2012). Conversely some lakes have undetectable chlorophyll levels under ice (e.g., Hawes 1985). While the available winter limnology literature provides evidence that lakes can support an abundance of algae under ice - as demonstrated by genetic (e.g., Bashenkhaeva et al. 2015), pigment (e.g., Catalan et al. 2002), and cell count (e.g., Phillips & Fawley 2002; Katz et al. 2015) data - it is also important to remember that estimates of algal biomass or primary productivity based on chlorophyll can be skewed seasonally. Intracellular pigment content can change with temperature and light conditions (Kirk 2011), such that smaller seasonal differences in chlorophyll could in part be due to light adaptation leading to increased cellular pigment concentrations.

In general, light can be the limiting factor for photosynthesis under ice, with ice conditions and overlying snow producing spatially (e.g., Cloern et al. 1992, Arrigo and Thomas 2004) and temporally (e.g., Tanabe et al. 2008; Bruesewitz et al. 2015) heterogeneous transmission of light and altered spectral distribution (Roulet & Adams 1986). The timing and characteristics of winter precipitation, wind, temperature variation, and solar radiation influence variability in under-ice light conditions, including the formation of clear congelation ice which can have higher light transmittance than lake water (Leppäranta 2010). When light is sufficient for photosynthesis, the under-ice environment can be hospitable for algal growth; complex under-ice convection can keep nutrients and algae mixed in the photic zone (Kelley 1997; but see Vehmaa & Solonen 2009), and in Lake Baikal the ice itself can provide a vast habitat for attached algae to maintain access to light (Timoshkin 2001; Bondarenko et al. 2012). In relatively dark conditions with low primary production, we might anticipate lower oxygen conditions, greater winter accumulation and subsequent contributions of greenhouse gases to the atmosphere, smaller algal and grazer populations available to initiate population growth at ice-out (Sommer et al. 2012), and less ice-associated algae sloughing off to feed the benthos as summer begins (Bondarenko et al. 2006). Because increased intracellular chlorophyll content may be an adaptation to low light conditions, exhibited by many but not all (Felip & Catalan 2000) phytoplankton, we recommend measuring primary productivity directly, if that is the variable of interest, or measuring both cell density and community composition in order to characterize plankton biomass and identity.

Phytoplankton biovolume was lower under ice than in the summer on average, consistent with chl *a* values, when all lakes were considered together. However, we did not detect systematic seasonal differences in phytoplankton community composition that could be generalized among all lakes. The lack of detectable difference does not imply that algal communities in each lake did not change from season to season; rather, this result suggests that generalizations about "winter" or "summer" taxa are difficult to make at the coarse level of taxonomic grouping we used. Moreover, it is rare for monitoring programs to quantify picoplankton, which constitute substantial portions of algal communities in summer and winter (Callieri & Stockner 2002; Bondarenko et al. 2012), such that their contributions to our results are unknown. Previous studies indicate that many if not all lakes do harbor relatively distinct winter and summer algae, frequently with differences occurring at species level (Kozhova & Izmest'eva 1998; Dokulil et al. 2014; Özkundakci et al. 2016), division level (Carey et al. 2016), or by functional traits (Özkundakci et al. 2016) with winter assemblages characterized by taxa that are more tolerant to cold and low-light conditions. Despite constraints by cold temperature, light limitation or altered mixing under the ice, winter species diversity has been found to be rather high (Salonen et al. 2009). Moreover, for Müggelsee, a lake located in a geographical transition phase of becoming ice-free more frequently with current and projected climate warming (Livingstone and Adrian 2009) it has been shown that different phytoplankton communities were favored across a gradient of mild to strong winter severity, associated with the key functional traits of motility, nutritional mode (autotrophy, heterotrophy, mixotrophy) and the ability to form resting stages (Özkundakci et al. 2016).

As algal communities adjust to ice cover, seasonal shifts in higher trophic levels such as zooplankton would also be anticipated. In this study, average winter zooplankton density declined to roughly one third that of summer - lower but still substantial enough to suggest that many of these relatively short-lived grazers actively feed and reproduce under ice. In the absence of live primary producers or residual producer biomass, presence of zooplankton under the ice can be explained by the consumption of other carbon sources such as chemolithotrophs (e.g., methane-oxidizing bacteria), or detritus. For example, planktonic heterotrophs and phototrophs, and benthic algae under the ice can provide alternative diet sources throughout winter for zooplankton in some lakes (Karlsson & Säwström 2009; Rautio et al. 2011; Hampton et al. 2015), while cyclopoids may prey on other zooplankton (Ventura & Catalan 2008). Further, as in marine systems (Lee et al. 2006), some freshwater grazers may be able to use lipid stores accumulated in prior seasons; lipid percentage in zooplankton samples collected from a lake in northern Finland varied from over 60% in early winter to approximately 20% in late winter (Syväranta & Rautio 2010).

The composition of crustacean zooplankton differed across seasons, with summer characterized by more cladocerans such as *Daphnia*. These taxa are generally associated with greater presence in summer months, with temperature and photoperiod offering cues for hatching, and growth fueled by higher temperature and food availability (Adrian et al. 2006). Even so, as we observed for phytoplankton, it seems likely that many differences between summer and winter zooplankton community composition may be lake-specific, species-specific or better captured by functional trait grouping. Many zooplankton are strict diapausing species that disappear from the water column into sediments during winter (Nilssen & Elgmork 1977; Ventura & Catalan 2005; Larsson & Wathne 2006), but several copepod species in high-latitude lakes of Europe and Canada have been shown to reach peak density in mid-winter (Rigler et al. 1974; Rautio et al. 2000; Scharfenberger et al. 2013) undergoing diapause during summer. Further, a variety of rotifers are well known to proliferate under ice (e.g., Pennak 1968; Dokulil & Herzig 2009; Virro et al. 2009; Melnik et al. 2008). Other studies also report persisting populations of *Daphnia* under the ice (Snow 1972; Larsson & Wathne 2006; Slusarczyk 2009) but data are still somewhat scarce. Our study suggests that when aggregating species to coarse taxonomic groups we may see some expected differences, but will miss out on the complexity of plankton composition, dynamics and functionality illustrated in the few detailed single-lake winter studies. It is not necessarily the overall abundance or biomass of major taxonomic groups which differ between seasons or change with global warming – but the species per se and the relative species composition (reviewed in Adrian et al. 2009). While this is well known for summer, information on species and functional trait composition during winter is indeed scarce. Given that the ice itself provides a vast potential substrate for attached algae and an associated community of metazoans (Bonderenko et al. 2012), and that common sampling methods do not target this microhabitat, a major advance in winter limnology would be the broader assessment of primary producers at this ice-water interface where some lakes have shown extraordinarily high algal biomass and activity (e.g. Timoshkin 2001; Bondarenko et al. 2012; Twiss et al. 2012). Further, shifts from autotrophy to mixotrophy and heterotrophy clearly occur in some communities under ice (e.g. Rhode 1955, Özkundakci et al. 2016), and examining how this trait varies from winter to summer likely will yield important insights for ecosystem-level carbon cycles.

TDN and TN were higher under ice based on both our cross-lakes approach (Table 1) and a within-lakes time series approach (Table 2), while winter DOC was variable but more similar to that of summer. The higher concentrations of dissolved N likely reflect winter nutrient mineralization (Cornett & Rigler 1979; Nürnberg et al. 1986, Catalan 1992) providing continued N inputs, while dissolved N uptake may be lower under winter conditions due to low temperature and light, and possibly less denitrification. More specifically, these results indicate that within the first few meters of the water column, dissolved N accumulates disproportionately under ice relative to P, especially in shallower lakes according to the regression tree analysis. A possible explanation is that benthic N mineralization and nitrification dominate winter N cycles in shallow lakes, whereas the higher water volume:surface area ratios in deeper lakes may limit N mineralization per unit volume and perhaps increase the role of pelagic uptake by phytoplankton. While the cross-lakes approach (Table 1) suggested that winter DOC was similar to summer on average, the regression tree analysis indicated DOC was unique among our variables, with opposing patterns in two distinct lake groups. More specifically, larger lakes (>0.373 km2) had lower DOC in winter, while smaller lakes (<0.373 km2) had higher DOC in winter, especially those occurring at lower elevation (<366 m). These smaller, lower elevation lakes also tended to have higher DOC overall, possibly resulting in especially dark conditions under ice. The dynamics of DOC can be influenced by multiple interacting factors such as lower terrestrial carbon input during cold winters (Lepistö et al. 2014), sustained benthic metabolism, uptake of DOC by bacteria (Tulonen et al. 1994), and photodegradation (Wetzel 2001), but few studies have partitioned DOC sources and processing during winter. DOC dynamics under ice clearly represent a key area for future research.

In revising the PEG model, Sommer et al. (2012) speculate that winter activity should have effects on phytoplankton and zooplankton in the subsequent season; indeed, we found evidence for strong winter-summer linkage for some lakes and variables. In lakes that had longer time series, such as the Laurentian Great Lakes, northern Wisconsin lakes, northern Europe lakes, and Canadian lakes, the influence of winter conditions on the following summer's value differed among variables. Winter and summer were often negatively related, such that high winter values were associated with low values from the adjacent summer, or low winter values were associated with high values from the adjacent summer (Fig. S5, Fig. S6, Table S5). Among variables in our analysis, these negative cross-seasonal relationships were particularly frequent for zooplankton density and chl *a*, although several other variables also had negative winter-summer correlations in >20% of the available time series. In the case of chl *a*, one explanation for antagonistic winter-summer dynamics is that high winter production may reduce the pelagic nutrient pool, strengthening P limitation or Si limitation in the following summer, in turn reducing summer production. For zooplankton, one possible explanation for negative winter-summer correlations could be that high prior zooplankton abundance or composition reduces the availability of readily-ingestible phytoplankton at the beginning of the next season. Many studies have suggested that overwintering populations can boost summer populations and vice versa (e.g. Sommer et al. 2012). A clear next step would be to examine temporal trends at the population level for zooplankton. Overall, evidence is increasing among independent studies for the prevalence of carryover between seasons. Coherent responses in algal and zooplankton phenology associated with conditions related to the winter North Atlantic Oscillation, which determines winter weather conditions across large parts of Europe, provide well studied examples (Weyhenmeyer et al. 1999; Gerten & Adrian 2000; Straile et al. 2003; Blenckner et al. 2007; Straile et al. 2012). Similarly, the severity of winter influenced spring nutrient concentrations in Lake Peipsi (Blank et al. 2009). Altogether such seasonal connections strongly favor previous calls to “close the loop” (Salonen et al. 2009) and study the full annual cycle in order to understand lake dynamics, particularly as lake temperature rises worldwide (O’Reilly et al. 2015). Though winter conditions often present logistical challenges to field sampling, we should dismiss opportunities that are within reach and could greatly increase our basic understanding of winter ecology.

Implications

We are losing ice without a deep understanding of what ecological processes are at stake. Our synthesis demonstrates that under-ice environments in lakes are biologically dynamic, and that in some cases understanding winter can help to predict summer conditions, highlighting the importance of expanding our knowledge of under-ice dynamics. Climate change is already altering lake conditions by increasing summer water temperatures (O'Reilly et al. 2015) and decreasing winter ice duration (Magnuson et al. 2000; Benson et al. 2012; Shuter et al. 2013). While our study identifies some of these basic patterns across and within lakes, how climate change will influence seasonal differences and connections, as well as the nature of any feedbacks associated with these potential changes, remains unclear. Long-term changes in lake ice already have been associated with shifts in the timing of under-ice phytoplankton blooms (Adrian et al. 1999; Blenckner et al. 2007). Here, paleolimnology may offer useful insights into how lakes responded during periods of warming, through the analysis of microfossils in sedimentary records. For example, Smol et al. (2005) show that global warming over the past 150 years has resulted in wide-scale reorganization of circumpolar lake ecosystems through shortening of the winter season, with highest changes in beta-diversity occurring at the most northern latitudes. Over longer timescales, declining winter ice conditions, inferred from chrysophyte cysts, suggest that European Pyrenees lakes gradually warmed from the early Holocene to c. 4000 years ago (Pla & Catalan 2005). While in ancient lakes such as Baikal, we can look to previous warm periods such as the Last Interglacial (125,000 years ago) which reveal a decline in ice-associated diatoms, but greater abundance in species that require either strong mixing conditions or extended summer stratification (Rioual & Mackay 2005).

Effects of shortening ice duration may present the most straight-forward scenarios to consider. Predicting the influence of climate change on other ice characteristics, such as clarity, may be a more difficult task. Observed and anticipated shifts in precipitation, wind, and solar radiation patterns associated with climate change are heterogeneous across and within regions, and can greatly alter the under-ice environment by changing the amount of incident light that penetrates the ice. Surface snow accumulation of as little as 10 cm can reduce light penetration to levels insufficient for photosynthesis and convective mixing that influences algal suspension as well as nutrient concentrations in the photic zone (Granin et al. 2000; Mackay et al. 2006; Jewson et al. 2009; Salmi & Salonen 2016). As with many aspects of climate change, the extremes and the timing of shifts, in addition to average changes, are important (reviewed in Adrian et al. 2012).

Conclusion

Our results suggest two principles that should motivate future work: 1) knowledge of under-ice conditions within lake ecosystems may help to refine expectations of how lake conditions, dynamics and functionality will unfold over the next season; 2) under-ice observations, and measures of seasonal connectivity or dis-connectivity between seasons, may enhance our ability to detect and understand ecological responses to lake warming, especially when monitoring is sustained over the long-term. Both of these ideas are testable, but only in the presence of long-term paired winter-summer lake data. Thus, while most lakes can be expected to experience shorter winter ice duration and longer summers, our capability to predict the ecosystem-wide impacts is constrained by our limited knowledge of under-ice ecology and also accurate down-scaled climate predictions that allow us to anticipate under-ice physical conditions. However, as our study demonstrates, lake conditions are not the simple result of weather conditions during the current season but can also depend upon external and internal forces operating on the ecosystem in previous seasons. Our capacity to predict effects of warming waters and shortening ice duration on lake ecosystems, and the resources they provide to society, will depend in part on our ability to rapidly accumulate more knowledge of winter ecology and its influence on ecological processes throughout the year. In the future, we predict that there will be no more “off-seasons” for freshwater ecologists.

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Table 1. Winter-summer differences expressed across lakes. Linear mixed models were used, with a random intercept for year.

Variable	# winter obvs	# paired obvs	Fitted difference (+=higher in winter)	s.e. of difference	Intercept (typical summer value)	s.e. of intercept	p-value of difference	p-value of intercept
chl *a* (µg/L)	119	118	-5.06	0.661	9.13	0.612	<<0.001	<<0.001
phyto biovolume (mm^3/L)	17	17	-12.8	1.85	14.7	1.31	<<0.001	<<0.001
crustacean zoop density(no./L)	36	36	-41.8	5.82	54.8	4.15	<<0.001	<<0.001
DOC (mg/L)	82	81	-0.0559	0.324	5.53	0.418	0.863	<<0.001
TDN (µg/L)	78	73	262	44.0	300	38.8	<<0.001	<<0.001
TDN:TDP (as atoms)	71	66	27.5	40.6	161	29.6	0.498	<<0.001
TDP (µg/L)	73	72	3.97	3.18	11.8	2.83	0.213	<<0.001
TN (µg/L)	76	75	161	23.1	552	23.7	<<0.001	<<0.001
TN:TP (as atoms)	75	74	24.0	6.44	88.3	4.89	<<0.001	<<0.001
TP (µg/L)	107	106	-1.35	1.95	27.1	1.98	0.488	<<0.001
water temp (°C)	113	107	-15.1	0.19	16.2	0.202	<<0.001	<0.001

Table 2. Summary of winter-summer differences and winter-summer correlations from univariate time series of individual lakes. Correlations for summer-into-winter (*SW*) and winter-into-summer (*WS*) are both shown. Zooplankton groups are referenced here as counts L^{-1} (calculated from reported proportion of total zooplankton density). Note that for chl *a* and phytoplankton density only 3 lakes reported both variables with sufficient data to include in our time series analysis, such that patterns are not readily compared between these variables.

		Seasonal difference present (% of time series)		Sign of summer-winter slope* (% of time series)				
Variable	# of time series	winter> summer	winter< summer	SW pos	SW neg	WS pos	WS neg	Any pos or neg
chl *a*	34	9	50	0	32	0	26	47
phyto density	4	0	100	25	0	25	0	50
crustacean zooplankton density	11	0	91	0	18	0	9	18
DOC	26	12	23	0	15	0	4	19
TDN	14	79	7	0	43	0	0	43
TDP	14	14	0	0	21	0	14	36
TN	30	70	3	0	33	3	10	47
TP	33	21	21	0	18	0	12	30
water temp	20	0	100	5	0	5	5	15

* Sign of the summer-winter slope determined using detrended data and AIC selection.

Figures

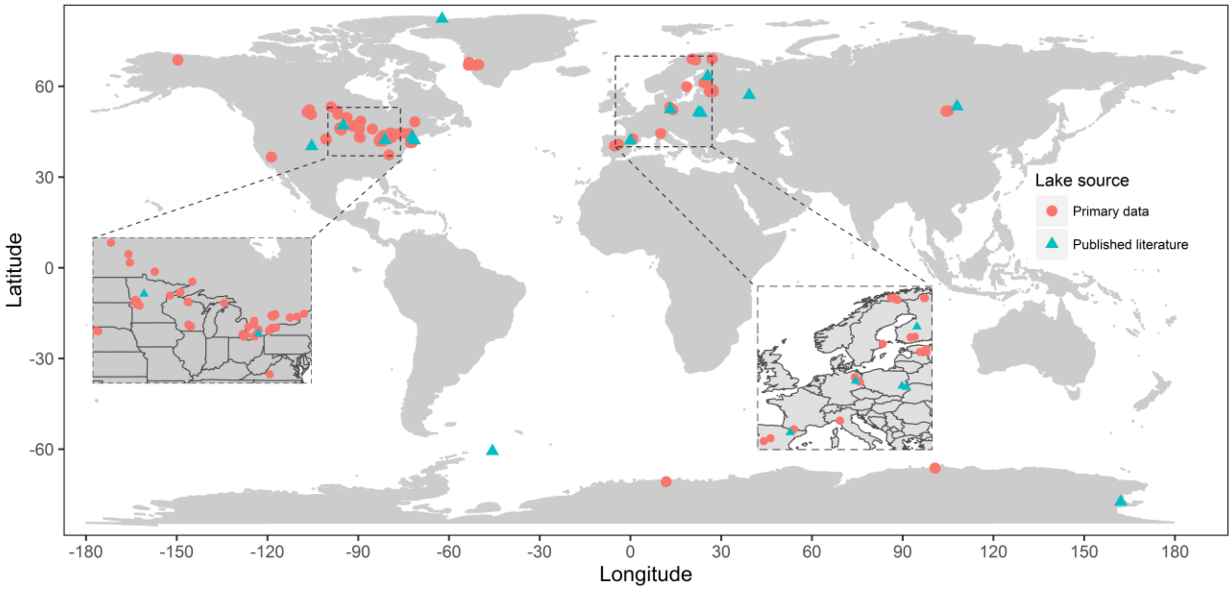

Figure 1. Map of lakes/sampling stations included in the full synthesis under-ice dataset (i.e., “primary data”) and the published literature review. See Figure S2 for comparison of aggregated chl *a* between primary data and published literature samples.

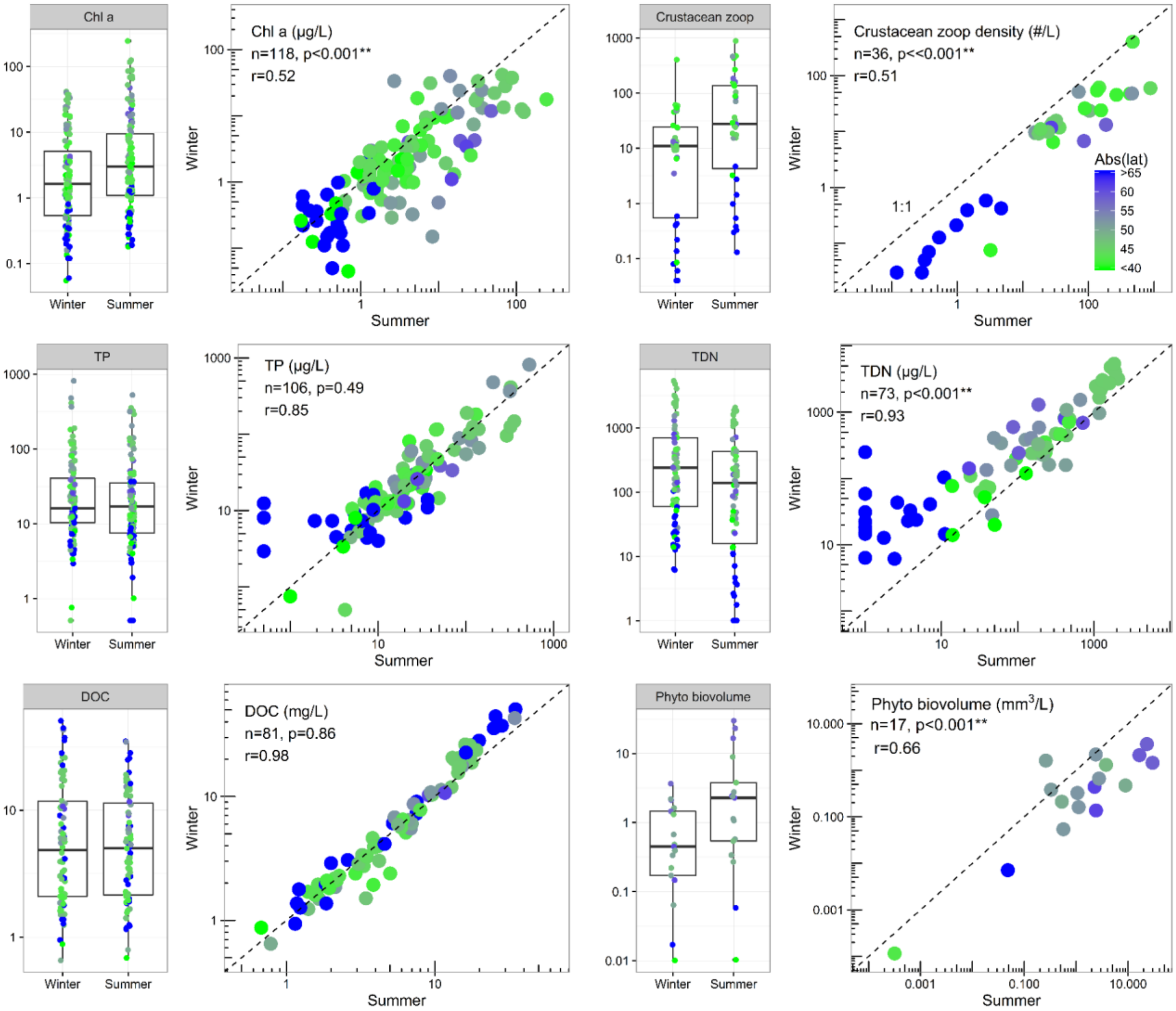

Figure 2. Average ice-on (winter) versus ice-off (summer) conditions across lakes for major limnological variables. Boxplots show all reported available ice-on and ice-off data. Each point represents the cross-year average from one sampling location; color indicates latitude (absolute). Scatterplots show the paired ice-on-ice-off values at a given each location. P-values are from lme models. Scales are logarithmic.

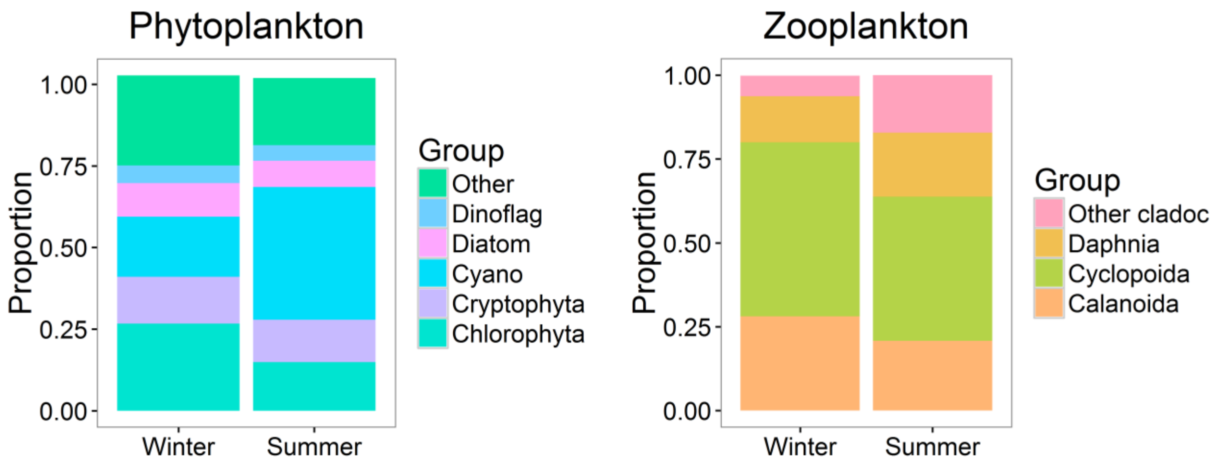

Figure 3. Average community composition for major phytoplankton and crustacean zooplankton groups during the winter and summer seasons, expressed as a proportion of total density.

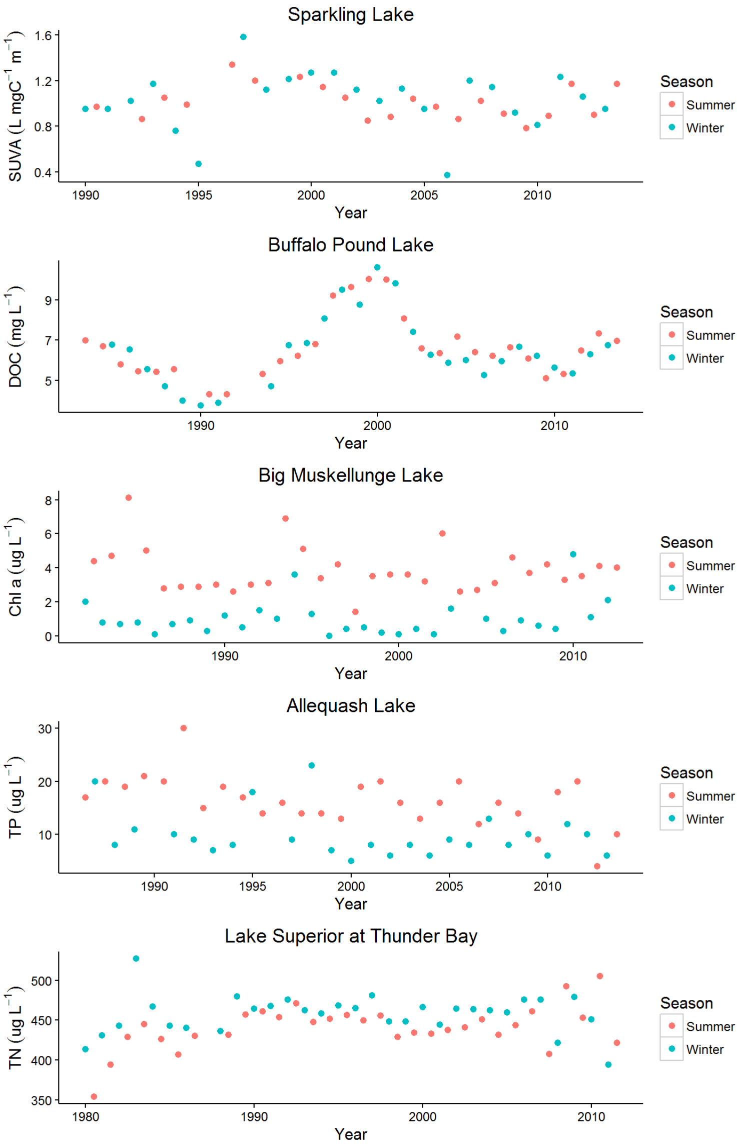

Figure 4. Example time series that demonstrate the temporal patterns encountered for different lakes and variables. Panel 1: first order autoregressive structure, SUVA in Sparkling Lake, Wisconsin, USA; 2: first order autoregressive structure with moving average, DOC in Buffalo Pound Lake, Saskatchewan, Canada; 3: seasonal difference, chl *a* in Big Muskellunge Lake, Wisconsin, USA; 4: seasonal difference with moving average, TP in Allequash Lake, Wisconsin, USA; 5: seasonal difference with first order autocorrelation structure and moving average, TN in Lake Superior at Thunder Bay, Ontario, Canada.