REVIEW AND SYNTHESIS

Ecology under lake ice

Stephanie E. Hampton,[1]* Aaron W. E. Galloway,[2] Stephen M. Powers,[1] Ted Ozersky,[3] Kara H. Woo,[1] Ryan D. Batt,[4] Stephanie G. Labou,[1] Catherine M. O'Reilly,[5] Sapna Sharma,[6] Noah R. Lottig,[7] Emily H. Stanley,[8] Rebecca L. North,[9] Jason D. Stockwell,[10] Rita Adrian,[11] Gesa A. Weyhenmeyer,[12] Lauri Arvola,[13] Helen M. Baulch,[9,14] Isabella Bertani,[15] Larry L. Bowman, Jr.,[16] Cayelan C. Carey,[17] Jordi Catalan,[18] William Colom-Montero,[12] Leah M. Domine,[19] Marisol Felip,[20] Ignacio Granados,[21] Corinna Gries,[8] Hans-Peter Grossart,[22,23] Juta Haberman,[24] Marina Haldna,[24] Brian Hayden,[25] Scott N. Higgins,[26] Jeff C. Jolley,[27] Kimmo K. Kahilainen,[28] Enn Kaup,[29] Michael J. Kehoe,[9,14] Sally MacIntyre,[30] Anson W. Mackay,[31] Heather L. Mariash,[32] Robert M. McKay,[33] Brigitte Nixdorf,[34] Peeter Nõges,[24] Tiina Nõges,[24] Michelle Palmer,[35] Don C. Pierson,[12] David M. Post,[16] Matthew J. Pruett,[1] Milla Rautio,[36] Jordan S. Read,[37] Sarah L. Roberts,[38] Jacqueline Rücker,[34] Steven Sadro,[39] Eugene A. Silow,[40] Derek E. Smith,[41] Robert W. Sterner,[3] George E. A. Swann,[38] Maxim A. Timofeyev,[40] Manuel Toro,[42] Michael R. Twiss,[43] Richard J. Vogt,[44] Susan B. Watson,[45] Erika J. Whiteford[46] and Marguerite A. Xenopoulos[44]

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 43.2% of summer values for chlorophyll *a*, 15.8% of summer phytoplankton biovolume and 25.3% 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.

Keywords

Aquatic ecosystem, data synthesis, freshwater, lake, limnology, long-term, plankton, seasonal, time series, winter ecology.

Ecology Letters (2017) **20**: 98–111

[1]*Center for Environmental Research, Education and Outreach, Washington State University, Pullman, WA, USA*

[2]*Oregon Institute of Marine Biology, University of Oregon, Charleston, OR, USA*

[3]*Department of Biology & Large Lakes Observatory, University of Minnesota Duluth, Duluth, MN, USA*

[4]*Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ, USA*

[5]*Department of Geography-Geology, Illinois State University, Normal, IL, USA*

[6]*Department of Biology, York University, Toronto, ON, Canada*

[7]*Center for Limnology, University of Wisconsin, Boulder Junction, WI, USA*

[8]*Center for Limnology, University of Wisconsin, Madison, WI, USA*

[9]*Global Institute for Water Security, University of Saskatchewan, Saskatoon, SK, Canada*

[10]*Rubenstein Ecosystem Science Laboratory, University of Vermont, Burlington, VT, USA*

[11]*Department of Ecosystem Research, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany*

[12]*Department of Ecology and Genetics, Uppsala University, Uppsala, Sweden*

[13]*Lammi Biological Station, University of Helsinki, Lammi, Finland*

[14]*School of Environment and Sustainability, University of Saskatchewan, Saskatoon, SK, Canada*

[15]*Water Center, Graham Sustainability Institute, University of Michigan, Ann Arbor, MI, USA*

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 (Moore *et al.* 2009; Salonen *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) hypothesised 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 generalisable (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 transmission (Bolsenga & Vanderploeg 1992), fuelling winter

[16]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA

[17]Department of Biological Sciences, Virginia Tech, Blacksburg, VA, USA

[18]CREAF, Consejo Superior de Investigaciones Científicas, Cerdanyola, Spain

[19]Department of Biology, University of St. Thomas, St. Paul MN, USA

[20]Department of Ecology, Universitat de Barcelona, Barcelona, Spain

[21]Centre for Research, Monitoring and Evaluation, Sierra de Guadarrama National Park, Rascafría, Spain

[22]Department of Experimental Limnology, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Stechlin, Germany

[23]Institute for Biochemistry and Biology, Potsdam University, Potsdam, Germany

[24]Centre for Limnology, Estonian University of Life Sciences, Tartu, Estonia

[25]Department of Biology, University of New Brunswick, Fredericton, NB, Canada

[26]IISD Experimental Lakes Area, Winnipeg, MB, Canada

[27]Columbia River Fisheries Program Office, U.S. Fish & Wildlife Service, Vancouver, WA, USA

[28]Department of Environmental Sciences, University of Helsinki, Helsinki, Finland

[29]Institute of Geology, Department of Isotope Paleoclimatology, Tallinn University of Technology, Tallinn, Estonia

[30]Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, CA, USA

[31]Department of Geography, University College London, London, UK

[32]National Wildlife Research Centre, Science and Technology Division, Environment and Climate Change Canada, Ottawa, ON, Canada

[33]Department of Biological Sciences, Bowling Green State University, Bowling Green, OH, USA

[34]Department of Freshwater Conservation, Brandenburg University of Technology Cottbus - Senftenberg, Bad Saarow, Germany

[35]Environmental Monitoring and Reporting Branch, Ontario Ministry of the Environment and Climate Change, Toronto, ON, Canada

[36]Department of Fundamental Sciences, Université du Québec à Chicoutimi, Chicoutimi, QC, Canada

[37]Office of Water Information, U.S. Geological Survey, Middleton, WI, USA

[38]School of Geography, University of Nottingham, Nottingham, UK

[39]Department of Environmental Science and Policy, University of California Davis, Davis, CA, USA

[40]Institute of Biology, Irkutsk State University, Irkutsk, Russian Federation

[41]Department of Biostatistics and Informatics, Colorado School of Public Health, Aurora, CO, USA

[42]Department of Aquatic Environment, Centre for Hydrographic Studies CEDEX, Madrid, Spain

[43]Department of Biology, Clarkson University, Potsdam, NY, USA

[44]Department of Biology, Trent University, Peterborough, ON, Canada

[45]Canada Centre for Inland Waters, Environment and Climate Change Canada, Burlington, ON, Canada

[46]Department of Geography, Loughborough University, Loughborough, UK

*Correspondence: E-mail: s.hampton@wsu.edu

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, synchronised 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 hypothesised that winter biomass and density of phytoplankton and zooplankton are significantly lower than that of summer, due to a low-light environment unfavourable 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. Furthermore, we hypothesise 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 towards synthesising 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 Supporting 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 seven 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
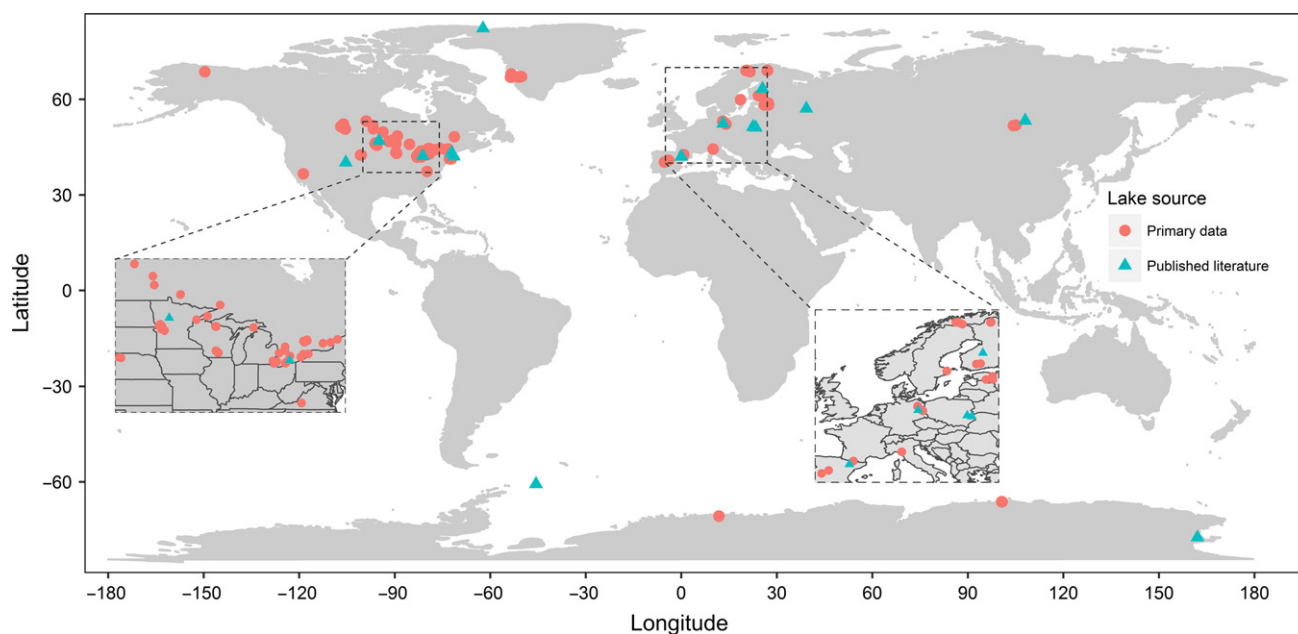
Figure 1 Map of lakes/sampling stations included in the full synthesis under-ice data set (i.e. 'primary data') and the published literature review. See Figure S2 for comparison of aggregated chl *a* between primary data and published literature samples.

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 Supporting Information).

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 analysed 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 (L mg C^{-1} m^{-1}), and colour (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 data set is available in the Knowledge Network for Biocomplexity (https://knb.ecoinformatics.org/, Hampton *et al*. 2016).

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.

Winter-summer differences across lakes
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) modelling 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 minimised 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 analyse 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, whereas for others the overall average represents only 1 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 y_t represents the sequence of winter and summer values, 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 eqn 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 eqn 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: (1) correlations between winter and the previous summer season (summer$_{t-1}$), or summer-into-winter *(SW)* correlations; and (2) 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 (Fig. S2), although still significantly lower than that of summer (13.6 ± 2.84 μg L^{-1}, $P < 0.0001$,
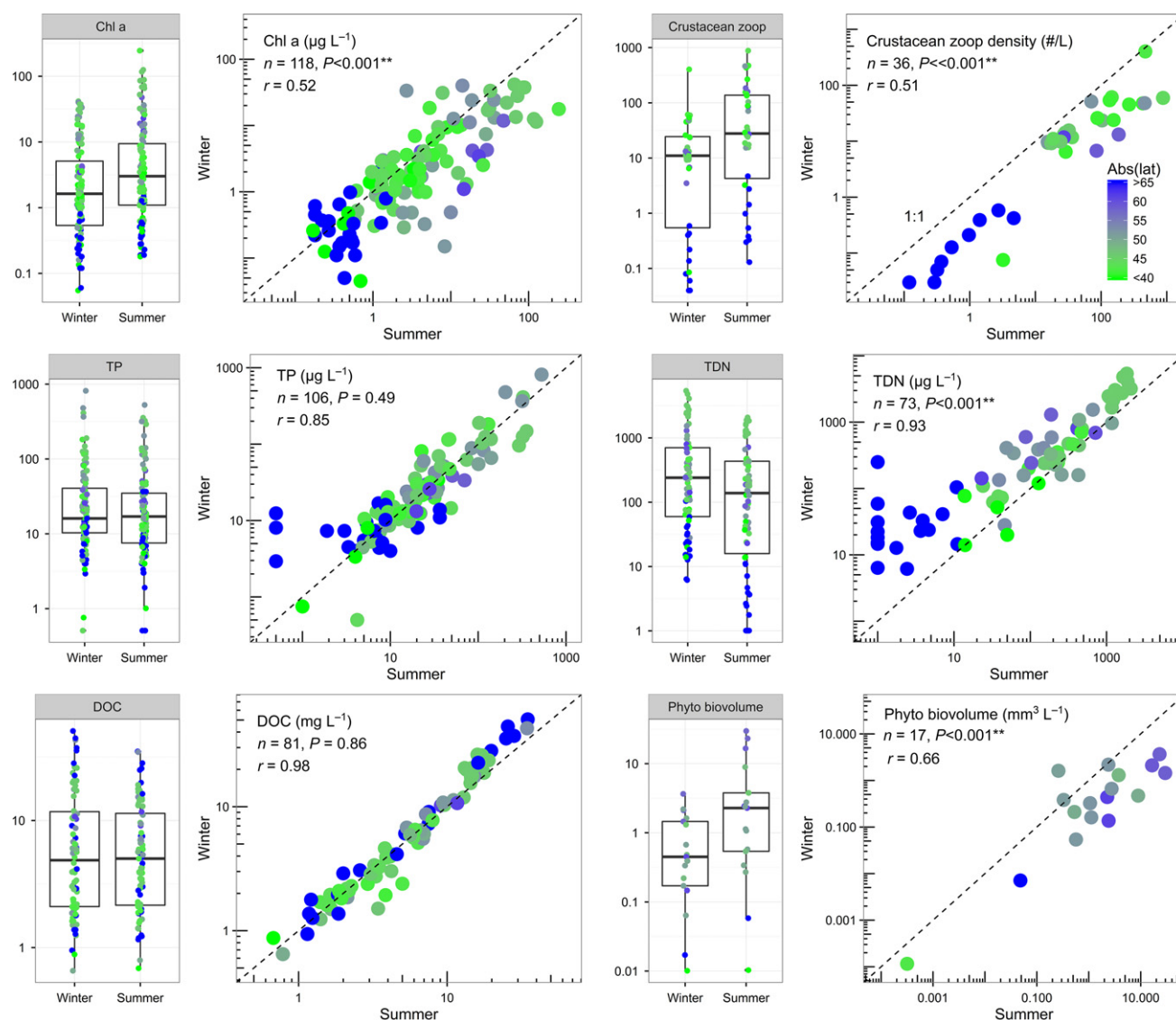
Figure 2 Average ice-on (winter) vs. ice-off (summer) conditions across lakes for major limnological variables. Boxplots show all reported available ice-on and ice-off data. Each point represents the cross-year average from one sampling location; colour indicates latitude (absolute). Scatterplots show the paired ice-on-ice-off values at each location. *P*-values are from lme models. Scales are logarithmic.

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 ($\pm$ 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 ($\pm$ 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 seven shallowest lakes (< 2.10 m) had 2070 µg L^{-1} higher TDN on average in winter than summer, seven 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, whereas the 59 deeper lakes (> 5.2 m) showed winter TDN values 123 µg

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

Variable	No. winter obvs	No. paired obvs	Fitted difference (± higher in winter)	SE of difference	Intercept (typical summer value)	SE 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
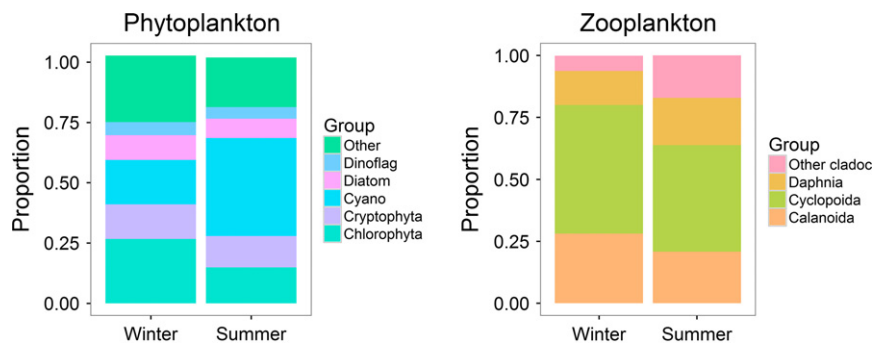
Figure 3 Average community composition for major phytoplankton and crustacean zooplankton groups during the winter and summer seasons, expressed as a proportion of total density.

L^{-1} higher than summer on average (tree R^2 = 0.722, Fig. S7). TN was also higher during winter ($P < 0.001$, LME-fitted difference of +161 μg 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 R^2 = 0.538, Fig. S7). Regression trees demonstrated that larger (≥ 0.373 km^2) lakes had 0.145 mg L^{-1} lower DOC in winter compared to summer, whereas smaller (< 0.373 km^2), 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 four of four 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 three 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

Table 2 Summary of winter-summer differences and winter-summer correlations from univariate time series of individual lakes

Variable	No. of time series	Seasonal difference present (% of time series)		Sign of summer-winter slope* (% 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

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 three lakes reported both variables with sufficient data to include in our time series analysis, such that patterns are not readily compared between these variables.
*Sign of the summer-winter slope determined using detrended data and AIC selection.

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 generalisations 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 generalisable 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 (43.2% 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 & 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
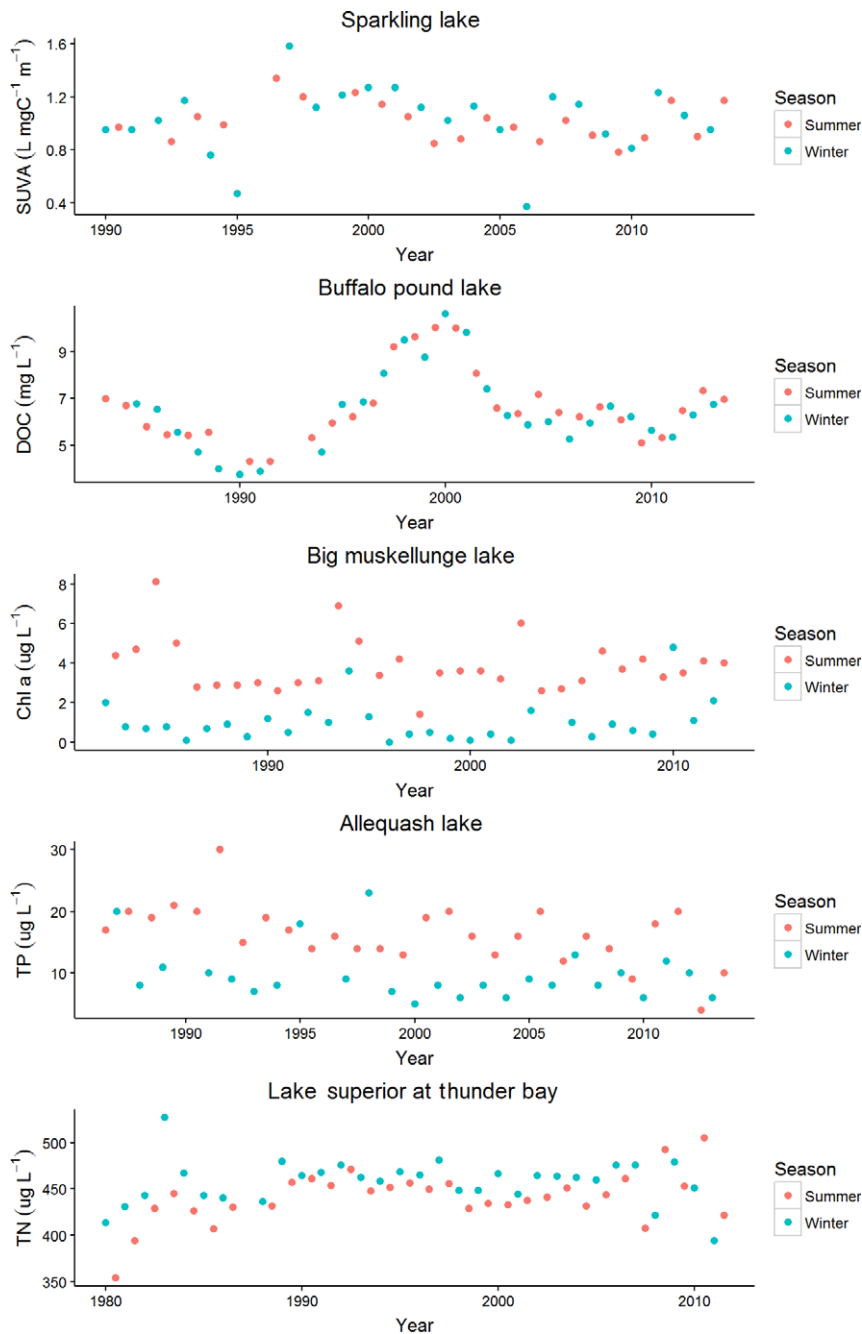
Figure 4 Example time series that demonstrate the temporal patterns encountered for different lakes and variables. Panel 1: first-order autoregressive structure, specific ultraviolet absorbance (SUVA) in Sparkling Lake, Wisconsin, USA; 2: first-order autoregressive structure with moving average, DOC 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.

(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 & Salonen 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 characterise 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 generalised 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 generalisations 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 remain unknown. Previous studies indicate that many if not all lakes do harbour 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 characterised 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 & Adrian 2009) it has been shown that different phytoplankton communities were favoured 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-fourth 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-oxidising 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), whereas cyclopoids may prey on other zooplankton (Ventura & Catalan 2008). Furthermore, 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 characterised 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 fuelled 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. Furthermore, a variety of rotifers are well known to proliferate under ice (e.g. Pennak 1968; Melnik *et al.* 2008; Dokulil & Herzig 2009; Virro *et al.* 2009). 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 (Bondarenko *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). Furthermore, 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), whereas winter DOC was variable but often more similar to that of summer. The higher concentrations of dissolved N likely reflect winter nutrient mineralisation (Cornett & Rigler 1979; Nürnberg *et al.* 1986; Catalan 1992) providing continued N inputs, whereas 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 metres 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 mineralisation and nitrification dominate winter N cycles in shallow lakes, whereas the higher water volume:surface area ratios in deeper lakes may limit N mineralisation 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 km^2) had lower DOC in winter, whereas smaller lakes (< 0.373 km^2) 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, 2012; Blenckner *et al.* 2007). Similarly, the severity of winter influenced spring nutrient concentrations in Lake Peipsi (Blank *et al.* 2009). Altogether such seasonal connections strongly favour 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 not 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, palaeolimnology 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 reorganisation 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). 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 a need for accurate downscaled 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.

STATEMENT OF AUTHORSHIP

SEH conceived of the project idea. SEH, AWEG and KHW initiated the project and provided oversight during data collection, integration and aggregation. SEH, EHS and TO served on the steering committee. KHW, AWEG and SGL led QA/QC on the submitted data sets. SMP, TO, RDB, CMO, SS, NRL, EHS, RLN, JDS, RA and GAW performed exploratory analyses and helped determine scope and structure of manuscript. SMP, SEH and SGL performed final analyses and designed figures and tables. All other listed authors aggregated data for submission to this project and contributed to interpretation of results and final manuscript text.

REFERENCES

Adrian, R., Walz, N., Hintze, T., Hoeg, S. & Rusche, R. (1999). Effects of ice duration on plankton succession during spring in a shallow polymictic lake. *Freshw. Biol.*, 41, 621–634.

Adrian, R., Wilhelm, S. & Gerten, D. (2006). Life-history traits of lake plankton species may govern their phenological response to climate warming. *Glob. Change Biol.*, 12, 652–661.

Adrian, R., O'Reilly, C.M., Zagarese, H., Baines, S.B., Hessen, D.O., Keller, W. et al. (2009). Lakes as sentinels of climate change. *Limnol. Oceanogr.*, 54, 2283–2297.

Adrian, R., Gerten, D., Huber, V., Wagner, C. & Schmidt, S.R. (2012). Windows of change: temporal scale of analysis is decisive to detect ecosystem responses to climate change. *Mar. Biol.*, 159, 2533–2542.

Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecol.*, 26, 32–46.

Arrigo, K.R. & Thomas, D.N. (2004). Large scale importance of sea ice biology in the Southern Ocean. *Antarct. Sci.*, 16, 471–486.

Arrigo, K.R., van Dijken, G. & Pabi, S. (2008). Impact of a shrinking Arctic ice cover on marine primary production. *Geophys. Res. Lett.*, 35, L19603.

Bashenkhaeva, M.V., Zakharova, Y.R., Petrova, D.P., Khanaev, I.V., Galachyants, Y.P. & Likhoshway, Y.V. (2015). Sub-Ice Microalgal and Bacterial Communities in Freshwater Lake Baikal, Russia. *Microb. Ecol.*, 70, 751–765.

Bates, D., Maechler, M., Bolker, B. & Walker, S.C. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.*, 67, 1–48.

Beall, B.F.N., Twiss, M.R., Smith, D.E., Oyserman, B.O., Rozmarynowycz, M.J., Binding, C.E. et al. (2016). Ice cover extent drives phytoplankton and bacterial community structure in a large north-temperate lake: implications for a warming climate. *Environ. Microbiol.*, 18, 1704–1719.

Benson, B.J., Magnuson, J.J., Jensen, O.P., Card, V.M., Hodgkins, G., Korhonen, J. et al. (2012). Extreme events, trends, and variability in Northern Hemisphere lake-ice phenology (1855–2005). *Clim. Change.*, 112, 299–323.

Bertilsson, S., Burgin, A., Carey, C.C., Fey, S.B., Grossart, H.-P., Grubisic, L.M. et al. (2013). The under-ice microbiome of seasonally frozen lakes. *Limnol. Oceanogr.*, 58, 1998–2012.

Blank, K., Haberman, J., Haldna, M. & Laugaste, R. (2009). Effect of winter conditions on spring nutrient concentrations and plankton in a large shallow Lake Peipsi (Estonia/Russia). *Aquat. Ecol.*, 43, 745–753.

Blenckner, T., Adrian, R., Livingstone, D.M., Jennings, E., Weyhenmeyer, G.A., George, D.G. et al. (2007). Large-scale climatic signatures in lakes across Europe: a meta-analysis. *Glob. Change Biol.*, 13, 1314–1326.

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

Bondarenko, N.A., Timoshkin, O.A., Röpstorf, P. & Melnik, N.G. (2006). The under-ice and bottom periods in the life cycle of *Aulacoseira baicalensis* (K. Meyer) Simonsen, a principal Lake Baikal alga. *Hydrobiologia*, 568, 107–109.

Bondarenko, N.A., Belykh, O.I., Golobokova, L.P., Artemyeva, O.V., Logacheva, N.F., Tikhonova, I.V. et al. (2012). Stratified distribution of nutrients and extremophile biota within freshwater ice covering the surface of Lake Baikal. *J. Microbiol.*, 50, 8–16.

Breiman, L., Friedman, J., Olshen, R. & Stone, C. (1984). *Classification and Regression Trees*. Wadsworth, Belmont.

Bruesewitz, D.A., Carey, C.C., Richardson, D.C. & Weathers, K.C. (2015). Under-ice thermal stratification dynamics of a large, deep lake revealed by high-frequency data. *Limnol. Oceanogr.*, 60, 347–359.

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Science & Business Media, Springer-Verlag, New York, USA.

Cáceres, C.E. & Schwalbach, M.S. (2001). How well do laboratory experiments explain field patterns of zooplankton emergence? *Freshw. Biol.*, 46, 1179–1189.

Callieri, C. & Stockner, J.G. (2002). Freshwater autotrophic picoplankton: a review. *J. Limnol.*, 61, 1–14.

Carey, C.C., Hanson, P.C., Lathrop, R.C. & Amand, A.L.S. (2016). Using wavelet analyses to examine variability in phytoplankton seasonal succession and annual periodicity. *J. Plankton Res.*, 38, 27–40.

Catalan, J. (1992). Evolution of dissolved and particulate matter during the ice-covered period in a deep, high-mountain lake. *Can. J. Fish Aquat. Sci.*, 49, 945–955.

Catalan, J., Ventura, M., Brancelj, A., Granados, I., Thies, H., Nickus, U. *et al.* (2002). Seasonal ecosystem variability in remote mountain lakes: implications for detecting climatic signals in sediment records. *J. Paleolimnol.*, 28, 25–46.

Cloern, J.E., Alpine, A.E., Cole, B.E. & Heller, T. (1992). Seasonal changes in the spatial distribution of phytoplankton in small, temperate-zone lakes. *J. Plankton Res.*, 14, 1017–1024.

Cornett, R.J. & Rigler, F.H. (1979). Hypolimnetic Oxygen Deficits: their Prediction and Interpretation. *Science*, 205, 580–581.

Dokulil, M.T. & Herzig, A. (2009). An analysis of long-term winter data on phytoplankton and zooplankton in Neusiedler See, a shallow temperate lake, Austria. *Aquat. Ecol.*, 43, 715–725.

Dokulil, M.T., Herzig, A., Somogyi, B., Vörös, L., Donabaum, K., May, L. *et al.* (2014). Winter conditions in six European shallow lakes: a comparative synopsis. *Estonian J. Ecol.*, 63, 111–129.

Domis, L.N.D.S., Elser, J.J., Gsell, A.S., Huszar, V.L.M., Ibelings, B.W., Jeppesen, E. *et al.* (2013). Plankton dynamics under different climatic conditions in space and time. *Freshw. Biol.*, 58, 463–482.

Felip, M. & Catalan, J. (2000). The relationship between phytoplankton biovolume and chlorophyll in a deep oligotrophic lake: decoupling in their spatial and temporal maxima. *J. Plankton Res.*, 22, 91–106.

Gerten, D. & Adrian, R. (2000). Climate-driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic Oscillation. *Limnol. Oceanogr.*, 45, 1058–1066.

Granin, N.G., Jewson, D.H., Gnatovskii, R.Y., Levin, L.A., Zhdanov, A.A., Gorbunova, L.A. *et al.* (2000). Turbulent mixing under ice and the growth of diatoms in Lake Baikal. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen*, 27, 812–2814.

Grebmeier, J.M. (2012). Shifting patterns of life in the pacific arctic and sub-arctic seas. *Annu. Rev. Mar. Sci.*, 4, 63–78.

Hampton, S.E., Moore, M.V., Ozersky, T., Stanley, E.H., Polashenski, C.M. & Galloway, A.W.E. (2015). Heating up a cold subject: prospects for under-ice plankton research in lakes. *J. Plankton Res.*, 37, 277–284. fbv002

Hampton, S.E., Labou, S.G., Woo, K.H. and others. (2016). Winter and summer comparison of biological, chemical, and physical conditions in seasonally ice-covered lakes. *Knowledge Network for Biocomplexity*, doi:10.5063/F12V2D1V.

Hawes, I. (1985). Factors controlling phytoplankton populations in maritime antarctic lakes. In *Antarctic Nutrient Cycles and Food Webs* (eds Siegfried, P.W.R., Condy, D.P.R., Laws, D.R.M.). Springer, Berlin, Heidelberg, pp. 245–252.

Jewson, D.H., Granin, N.G., Zhdanov, A.A. & Gnatovsky, R.Y. (2009). Effect of snow depth on under-ice irradiance and growth of *Aulacoseira baicalensis* in Lake Baikal. *Aquat. Ecol.*, 43, 673–679.

Karlsson, J. & Säwström, C. (2009). Benthic algae support zooplankton growth during winter in a clear-water lake. *Oikos*, 118, 539–544.

Katz, S.L., Izmest'eva, L.R., Hampton, S.E., Ozersky, T., Shchapov, K., Moore, M.V. *et al.* (2015). The "*Melosira* years" of Lake Baikal: winter environmental conditions at ice onset predict under-ice algal blooms in spring. *Limnol. Oceanogr.*, 60, 1950–1964

Kelley, D.E. (1997). Convection in ice-covered lakes: effects on algal suspension. *J. Plankton Res.*, 19, 1859–1880.

Kirk, J.T.O. (2011). *Light and Photosynthesis in Aquatic Ecosystems*. 3rd edn. Cambridge University Press, New York, USA.

Kozhova, O.M. & Izmest'eva, L.R. (1998). *Lake Baikal: Evolution and Biodiversity*. 2nd edn. Backhuys Publishers, Leiden, Netherlands

Larsson, P. & Wathne, I. (2006). Swim or rest during the winter – what is best for an alpine daphnid? *Archiv für Hydrobiologie*, 167, 265–280.

Lee, R.F., Hagen, W. & Kattner, G. (2006). Lipid storage in marine zooplankton. *Mar. Ecol. Prog. Ser.*, 307, 273–306.

Lepistö, A., Futter, M.N. & Kortelainen, P. (2014). Almost 50 years of monitoring shows that climate, not forestry, controls long-term organic carbon fluxes in a large boreal watershed. *Glob. Change Biol.*, 20, 1225–1237.

Leppäranta, M. (2010). Modelling the formation and decay of lake ice. In *The Impact of Climate Change on European Lakes, Aquatic Ecology Series*. (ed George, G.). Springer, Netherlands, pp. 63–83.

Leppäranta, M. (2015). Freezing of Lakes. *Freezing of Lakes and the Evolution of their Ice Cover*. Springer, Berlin Heidelberg, pp. 11–50.

Livingstone, D.M. & Adrian, R. (2009). Modeling the duration of intermittent ice cover on a lake for climate-change studies. *Limnol. Oceanogr.*, 54, 1709–1722.

Lizotte, M.P. (2001). The contributions of sea ice algae to antarctic marine primary production. *Am. Zool.*, 41, 57–73.

Mackay, A.W., Ryves, D.B., Morley, D.W., Jewson, D.H. & Rioual, P. (2006). Assessing the vulnerability of endemic diatom species in Lake Baikal to predicted future climate change: a multivariate approach. *Glob. Change Biol.*, 12, 2297–2315.

Magnuson, J.J., Robertson, D.M., Benson, B.J., Wynne, R.H., Livingstone, D.M., Arai, T. *et al.* (2000). Historical trends in lake and river ice cover in the Northern Hemisphere. *Science*, 289, 1743–1746.

McKnight, D.M., Howes, B.L., Taylor, C.D. & Goehringer, D.D. (2000). Phytoplankton dynamics in a stably stratified antarctic lake during winter darkness. *J. Phycol.*, 36, 852–861.

Meier, W.N., Hovelsrud, G.K., vanOort, B.E.H., Key, J.R., Kovacs, K.M., Michel, C. *et al.* (2014). Arctic sea ice in transformation: a review of recent observed changes and impacts on biology and human activity. *Rev. Geophys.*, 52, 2013RG000431

Melnik, N.G., Lazarev, M.I., Pomazkova, G.I., Bondarenko, N.A., Obolkina, L.A., Penzina, M.M. *et al.* (2008). The cryophilic habitat of micrometazoans under the lake-ice in Lake Baikal. *Fundamental and Applied Limnology/Archiv für Hydrobiologie*, 170, 315–323.

Moore, M.V., Hampton, S.E., Izmest'eva, L.R., Silow, E.A., Peshkova, E.V. & Pavlov, B.K. (2009). Climate change and the world's "Sacred Sea"—lake baikal, siberia. *Bioscience*, 59, 405–417

Nilssen, J.P. & Elgmork, K. (1977). Cyclops abyssorum. Life-cycle dynamics and habitat selection [lowland lake Lonavatn, western Norway]. *Memorie dell'Istituto Italiano di Idrobiologia, Dott. Marco de Marchi Verbania Pallanza*, 34, 197–238.

Nürnberg, G.K., Shaw, M., Dillon, P.J. & McQueen, D.J. (1986). Internal phosphorus load in an oligotrophic precambrian shield lake with an anoxic hypolimnion. *Can. J. Fish Aquat. Sci.*, 43, 574–580.

O'Brien, W.J., Hershey, A.E., Hobbie, J.E., Hullar, M.A., Kipphut, G.W., Miller, M.C. *et al.* (1992). Control mechanisms of arctic lake ecosystems: a limnocorral experiment. *Hydrobiologia*, 240, 143–188.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B. *et al.* (2016). vegan: Community Ecology Package. R package version 2.4-0

O'Reilly, C.M., Sharma, S., Gray, D.K., Hampton, S.E., Read, J.S., Rowley, R.J. *et al.* (2015). Rapid and highly variable warming of lake surface waters around the globe. *Geophys. Res. Lett.*, 42, 2015GL066235

Özkundakci, D., Gsell, A.S., Hintze, T., Täuscher, H. & Adrian, R. (2016). Winter severity determines functional trait composition of phytoplankton in seasonally ice-covered lakes. *Glob. Change Biol.*, 22, 284–298.

Pennak, R.W. (1968). Field and experimental winter limnology of three colorado mountain lakes. *Ecology*, 49, 505–520.

Phillips, K.A. & Fawley, M.W. (2002). Winter phytoplankton community structure in three shallow temperate lakes during ice cover. *Hydrobiologia*, 470, 97–113.

Pla, S. & Catalan, J. (2005). Chrysophyte cysts from lake sediments reveal the submillennial winter/spring climate variability in the northwestern Mediterranean region throughout the Holocene. *Clim. Dyn.*, 24, 263–278.

R Core Team. (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rautio, M., Sorvari, S. & Korhola, A. (2000). Diatom and crustacean zooplankton communities, their seasonal variability and representation in the sediments of subarctic Lake Saanajärvi. *J. Limnol.*, 59, 81–96.

Rautio, M., Mariash, H. & Forsström, L. (2011). Seasonal shifts between autochthonous and allochthonous carbon contributions to zooplankton diets in a subarctic lake. *Limnol. Oceanogr.*, 56, 1513–1524.

Rhode, W. (1955). Can plankton production proceed during winter darkness in subarctic lakes? *Verh. Int. Ver. Limnol.*, 12, 117–122.

Rigler, F.H., MacCallum, M.E. & Roff, J.C. (1974). Production of Zooplankton in Char Lake. *J. Fish. Res. Bd. Can.*, 31, 637–646.

Rioual, P. & Mackay, A.W. (2005). A diatom record of centennial resolution for the Kazantsevo Interglacial stage in Lake Baikal (Siberia). *Global and Planetary Change, Progress towards reconstructing past climate in Central Eurasia, with special emphasis on Lake Baikal*, 46, 199–219.

Roulet, N.T. & Adams, W.P. (1986). Spectral distribution of light under a subarctic winter lake cover. *Hydrobiologia*, 134, 89–95.

Salmi, P. & Salonen, K. (2016). Regular build-up of the spring phytoplankton maximum before ice-break in a boreal lake. *Limnol. Oceanogr.*, 61, 240–253.

Salonen, K., Leppäranta, M., Viljanen, M. & Gulati, R.D. (2009). Perspectives in winter limnology: closing the annual cycle of freezing lakes. *Aquat. Ecol.*, 43, 609–616.

Scharfenberger, U., Mahdy, A. & Adrian, R. (2013). Threshold-driven shifts in two copepod species: testing ecological theory with observational data. *Limnol. Oceanogr.*, 58, 741–752.

Shuter, B.J., Minns, C.K. & Fung, S.R. (2013). Empirical models for forecasting changes in the phenology of ice cover for Canadian lakes. *Can. J. Fish Aquat. Sci.*, 70, 982–991.

Slusarczyk, M. (2009). Extended lifespan traded for diapause in Daphnia. *Freshw. Biol.*, 54, 2252–2262.

Smol, J.P., Wolfe, A.P., Birks, H.J.B., Douglas, M.S.V., Jones, V.J., Korhola, A. *et al.* (2005). Climate-driven regime shifts in the biological communities of arctic lakes. *PNAS*, 102, 4397–4402.

Snow, N.B. (1972). The effect of season and animal size on the caloric content of daphnia pulicaria forbes 1,2. *Limnol. Oceanogr.*, 17, 909–912.

Sommer, U., Gliwicz, Z.M., Lampert, W. & Duncan, A. (1986). The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch. Hyrobiologia*, 106, 433–471.

Sommer, U., Adrian, R., Domis, L.D.S., Elser, J.J., Gaedke, U., Ibelings, B. *et al.* (2012). Beyond the plankton ecology group (PEG) model: mechanisms driving plankton succession. *Annu. Rev. Ecol. Evol. Syst.*, 43, 429–448.

Straile, D. (2002). North Atlantic Oscillation synchronizes food-web interactions in central European lakes. *Proc. Biol. Sci.*, 269, 391–395.

Straile, D., Livingstone, D.M., Weyhenmeyer, G.A. & George, D.G. (2003). The response of freshwater ecosystems to climate variability associated with the North Atlantic Oscillation. In: *The North Atlantic Oscillation: climatic Significance and Environmental Impact* (eds. Hurrell, J.W., Kushnir, Y., Ottersen, G. & Visbeck, RTIN). American Geophysical Union, Washington, D.C., pp. 263–279

Straile, D., Adrian, R. & Schindler, D.E. (2012). Uniform temperature dependency in the phenology of a keystone herbivore in lakes of the Northern Hemisphere. *PLoS ONE*, 7, e45497.

Syväranta, J. & Rautio, M. (2010). Zooplankton, lipids and stable isotopes: importance of seasonal, latitudinal, and taxonomic differences. *Can. J. Fish Aquat. Sci.*, 67, 1721–1729.

Tanabe, Y., Kudoh, S., Imura, S. & Fukuchi, M. (2008). Phytoplankton blooms under dim and cold conditions in freshwater lakes of East Antarctica. *Polar Biol.*, 31, 199–208.

Therneau, T., Atkinson, B., Ripley, B., Oksanen, J. & De'ath, G. (2014). mvpart: Multivariate partitioning. R package version 1.6-2

Therneau, T., Atkinson, B. & Ripley, B. (2015). rpart: Recursive Partitioning and Regression Trees. R package version 4.1-10

Timoshkin, O.A. (2001). Lake Baikal: diversity of fauna, problems of its immiscibility and origin, ecology and "exotic" communities. *Index of Animal Species Inhabiting Lake Baikal and Its Catchment Area*. Nauka Publishers, Novosibirsk, Russia, pp. 74–113.

Tulonen, T., Kankaala, P., Ojala, A. & Arvola, L. (1994). Factors controlling production of phytoplankton and bacteria under ice in a humic, boreal lake. *J. Plankton Res.*, 16, 1411–1432.

Twiss, M.R., McKay, R.M.L., Bourbonniere, R.A., Bullerjahn, G.S., Carrick, H.J., Smith, R.E.H. *et al.* (2012). Diatoms abound in ice-covered Lake Erie: an investigation of offshore winter limnology in Lake Erie over the period 2007 to 2010. *J. Great Lakes Res.*, 38, 18–30.

Twiss, M.R., Smith, D.E., Cafferty, E.M. & Carrick, H.J. (2014). Phytoplankton growth dynamics in offshore Lake Erie during mid-winter. *J. Great Lakes Res.*, 40, 449–454.

Vehmaa, A. & Salonen, K. (2009). Development of phytoplankton in Lake Pääjärvi (Finland) during under-ice convective mixing period. *Aquat. Ecol.*, 43, 693–705.

Ventura, M. & Catalan, J. (2005). Reproduction as one of the main causes of temporal variability in the elemental composition of zooplankton. *Limnol. Oceanogr.*, 50, 2043–2056.

Ventura, M. & Catalan, J. (2008). Incorporating life histories and diet quality in stable isotope interpretations of crustacean zooplankton. *Freshw. Biol.*, 53, 1453–1469.

Verpoorter, C., Kutser, T., Seekell, D.A. & Tranvik, L.J. (2014). A global inventory of lakes based on high-resolution satellite imagery. *Geophys. Res. Lett.*, 41, 2014GL060641

Vincent, W.F. & Vincent, C.L. (1982). Factors controlling phytoplankton production in lake vanda (77°S). *Can. J. Fish Aquat. Sci.*, 39, 1602–1609.

Virro, T., Haberman, J., Haldna, M. & Blank, K. (2009). Diversity and structure of the winter rotifer assemblage in a shallow eutrophic northern temperate Lake Võrtsjärv. *Aquat. Ecol.*, 43, 755–764.

Wetzel, R.G. (2001). *Limnology: Lake and River Ecosystems*. Gulf Professional Publishing, Academic Press, San Diego.

Weyhenmeyer, G.A., Blenckner, T. & Pettersson, K. (1999). Changes of the plankton spring outburst related to the North Atlantic Oscillation. *Limnol. Oceanogr.*, 44, 1788–1792.

Weyhenmeyer, G.A., Westöö, A.-K. & Willén, E. (2008). Increasingly ice-free winters and their effects on water quality in Sweden's largest lakes. *Hydrobiologia*, 599, 111–118.

Weyhenmeyer, G.A., Livingstone, D.M., Meili, M., Jensen, O., Benson, B. & Magnuson, J.J. (2011). Large geographical differences in the sensitivity of ice-covered lakes and rivers in the Northern Hemisphere to temperature changes. *Glob. Change Biol.*, 17, 268–275.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.