ORIGINAL ARTICLE

Taxonomic and functional differences between winter and summer crustacean zooplankton communities in lakes across a trophic gradient

K. SHCHAPOV[1],*, P. WILBURN[2], A. J. BRAMBURGER[3], G.M. SILSBE[4], L. OLMANSON[5], C. J. CRAWFORD[6], E. LITCHMAN[7] AND T. OZERSKY[1]

[1]LARGE LAKES OBSERVATORY AND BIOLOGY DEPARTMENT, UNIVERSITY OF MINNESOTA DULUTH, DULUTH, 2205 E 5TH ST, MN 55812, USA, [2]NASA AMES RESEARCH CENTER-EXOBIOLOGY BRANCH, MOFFETT FIELD, CA 94035, USA, [3]WATERSHED HYDROLOGY AND ECOLOGY RESEARCH DIVISION, ENVIRONMENT AND CLIMATE CHANGE CANADA, 867 LAKESHORE RD, BURLINGTON, ON L7S 1A1, CANADA, [4]UNIVERSITY OF MARYLAND CENTER FOR ENVIRONMENTAL SCIENCE HORN POINT LABORATORY, 5475 LOVERS LN, MD 21613, USA, [5]DEPARTMENT OF FOREST RESOURCES, UNIVERSITY OF MINNESOTA, 1530 CLEVELAND AVENUE NORTH, ST. PAUL, MN 55108, USA, [6]U.S. GEOLOGICAL SURVEY EARTH RESOURCES OBSERVATION AND SCIENCE (EROS) CENTER INTEGRATED SCIENCE AND APPLICATIONS BRANCH 47914 252ND ST, SIOUX FALLS, SD 57198, USA AND [7]W. K. KELLOGG BIOLOGICAL STATION, MICHIGAN STATE UNIVERSITY, HICKORY CORNERS, 3700 E GULL LAKE DR, HICKORY CORNERS, MI 49060, USA

*CORRESPONDING AUTHOR. shcha001@umn.edu

Despite increasing interest in winter limnology, few studies have examined under-ice zooplankton communities and the factors shaping them in different types of temperate lakes. To better understand drivers of zooplankton community structure in winter and summer, we sampled 13 lakes across a large trophic status gradient for crustacean zooplankton abundance, taxonomic and functional community composition and C/N stable isotopes. Average winter zooplankton densities were one-third of summer densities across the study lakes. Proportionally, cladocerans were more abundant in summer than winter, with the opposite pattern for calanoids and cyclopoids. In green (eutrophic) lakes, zooplankton densities were higher under the ice than in brown (dystrophic) and blue (oligotrophic) lakes, suggesting better conditions for zooplankton in productive lakes during winter. Overall, zooplankton communities were more similar across lakes under the ice than during the open water season. Feeding group classification showed a decrease in herbivore abundance and an increase in predators from summer to winter. C/N stable isotope results suggested higher lipid content in overwintering zooplankton and potentially increased reliance on the microbial loop by winter zooplankton.

Our results show substantial variation in the seasonality of zooplankton communities in different lake types and identify some of the factors responsible for this variation.

KEYWORDS: zooplankton; seston; winter limnology; northern lakes; seasonality

INTRODUCTION

Increasing air temperatures associated with climate change are leading to a decrease in ice-cover extent and duration on many lakes (O'Reilly *et al.*, 2015; Sharma *et al.*, 2019). The decreasing lake ice cover significantly affects lake heat budgets, mixing regimes, light availability and various chemical and biological processes, both during winter and in the following open-water seasons (Salonen *et al.*, 2009; Ye *et al.*, 2019; Ozersky *et al.*, 2021). Additionally, changes in the timing of lake freezing and thawing may impact the life cycle of many aquatic species, including effects on timing of growth, reproduction and feeding behavior (Winder and Schindler, 2004; Stine *et al.*, 2009).

Predicting how lake ecosystems will respond to changes in winter conditions is difficult because, historically, the ice-covered period has received much less attention from ecologists than the open water period (Hampton *et al.*, 2017). Until recently, it was often assumed that winter is a time of dormancy and that winter processes have little effect on the open water period (Sommer *et al.*, 1986). However, previous studies suggest that life under the ice is active and that winter conditions can be important for regulating phytoplankton and zooplankton biomass and species composition in subsequent seasons (Weyhenmeyer *et al.*, 1999; Adrian *et al.*, 2006; Salonen *et al.*, 2009; Bertilsson *et al.*, 2013; Bruesewitz *et al.*, 2015; Hampton *et al.*, 2017; Wollrab *et al.*, 2021). Given that more than half of the lakes around the globe are covered with ice during the winter (Weyhenmeyer *et al.*, 2011) and the rapid shortening of the ice-cover period (Magnuson *et al.*, 2000; Blank *et al.*, 2009; Benson *et al.*, 2012), a better understanding of winter lake ecology is emerging as an important research priority.

Zooplankton are a key component in lake food webs and play an important role in cycling of nutrients and organic matter via grazing on phytoplankton. They are also an important food source for higher trophic levels. Open-water zooplankton abundance and community composition fluctuates seasonally depending on physical factors (temperature), as well as bottom-up (food availability) and top-down (predation) biological controls (Sommer *et al.*, 2012). Seasonal open-water studies have shown that zooplankton community succession is influenced by lake trophic status and differs between eutrophic and oligotrophic lakes (Sommer *et al.*, 1986; Vanni and Temte, 1990; Sommer *et al.*, 2012). However, relatively little is known about winter zooplankton communities, how they interact with lower and higher trophic levels and how lake trophic status affects winter zooplankton communities.

Lake trophic status may be broadly characterized using the lake color paradigm, which classifies lakes by water color based on concentrations of colored dissolved organic matter (CDOM) and total phosphorus (TP) into brown (dystrophic, high CDOM and low TP), green (eutrophic, low CDOM and high TP) and blue (oligotrophic, low CDOM and low TP) lakes (Williamson *et al.*, 1999; Webster *et al.*, 2008; Leech *et al.*, 2018). Bottom-up and top-down interactions between zooplankton, their food sources and visual predators vary along both CDOM and primary productivity gradients (Vinyard and O'Brien, 1976; Benndorf *et al.*, 2002; Wissel *et al.*, 2003; Yuan and Pollard, 2018). For example, Leech *et al.* (2018) showed that zooplankton biomass and community structure differ significantly between blue, brown, green and murky (high CDOM and TP) lakes with highest zooplankton abundance in green and murky lakes. Overall, the lake color paradigm offers a more holistic means of categorizing the lake environment for plankton communities and exploring zooplankton seasonal dynamic in diverse lake types beyond the more traditional oligotrophic/eutrophic classification.

Here, we examined seasonal patterns of the abundance, community structure and aspects of feeding ecology of crustacean zooplankton in 13 seasonally frozen north temperate lakes during summer and winter. Study lakes varied in trophic status and represented various color categories, including three green lakes, six blue lakes and four brown lakes. By comparing winter and summer zooplankton communities in diverse lake types, we sought to better understand plankton seasonal dynamics under different environmental conditions. Our main questions were: (1) how do environmental factors that may affect zooplankton communities differ within and between lakes in winter compared to summer; (2) how does zooplankton community composition, abundance and trophic structure vary between winter and summer in different lake types; and (3) to what extent do environmental factors in different lake types shape the zooplankton community in summer and winter seasons?

METHODS

Study sites

A total of 13 lakes (14 stations) in Minnesota and Wisconsin (Fig. 1, Table I) were sampled during the ice cover season in late winter and again during the summer stratified season. According to Minnesota Department of Natural Resources data (Lake Finder MN DNR, https://www.dnr.state.mn.us/lakefind/index.html), ice cover in the study region formed at the end of November and lasted until the end of April/beginning of May during the study years (2015 and 2018). We sampled lakes during academic spring breaks in 2015 (10 locations between 16 March and 20 March) and 2018 (four locations between 27 February and 1 March) when more time was available for planning and conducting research and when lakes ice was safe to operate on. Summer samples were collected in mid-summer, between 8 July and 23 July (10 locations in 2015 and four locations in 2018) when all lakes were stratified. Lakes were chosen to represent a range of physical, chemical and biological conditions in order to assess how winter and summer conditions differ in diverse north temperate lakes. The two Lake Superior stations included a moderate depth (47-m) site in the Apostle Islands region and a shallower (8-m) location in Chequamegon Bay (Fig. 1). Lakes LaSalle and Portsmouth are meromictic lakes with anoxic conditions below ca. 40 m depth. We categorized study sites according to the lake total phosphorus, dissolved organic carbon (DOC) and chlorophyll a concentrations into blue (oligotrophic), green (eutrophic) and brown (dystrophic) lakes (Williamson et al., 1999; Webster et al., 2008; Leech et al., 2018). Lakes in our study with integrated values of TP concentrations $\leq 1 \, \mu M \, L^{-1}$ (except for Portsmouth Lake), DOC $\leq 10 \, mg \, L^{-1}$ and chl $a \leq 5 \, \mu g \, L^{-1}$ were assigned to blue (oligotrophic) lakes. Meromictic Portsmouth Lake had integrated TP concentration of $1.2 \, \mu M \, L^{-1}$ due to elevated TP values in monimolimnion. Brown lakes had integrated values for TP > 0.5 but $\leq 1.3 \, \mu M \, L^{-1}$, DOC $> 10 \, mg \, L^{-1}$ and chl $a \leq 10 \, \mu g \, L^{-1}$. Green lakes had TP concentrations $\geq 1.3 \, \mu M \, L^{-1}$, DOC $\leq 20 \, mg \, L^{-1}$ and chl $a > 10 \, \mu g \, L^{-1}$ (Table I).

Sample collection

Sampling was conducted from the surface of the ice in February and March and from a small boat during the ice-free period in July. During both seasons, we collected water column temperature, dissolved oxygen, pH, total dissolved solids, fluorescent dissolved organic matter and conductivity profiles (Shchapov et al., 2021) using a YSI EXO2 multiparameter sonde (YSI In., Yellow Spring, OH, USA), water samples from different depths
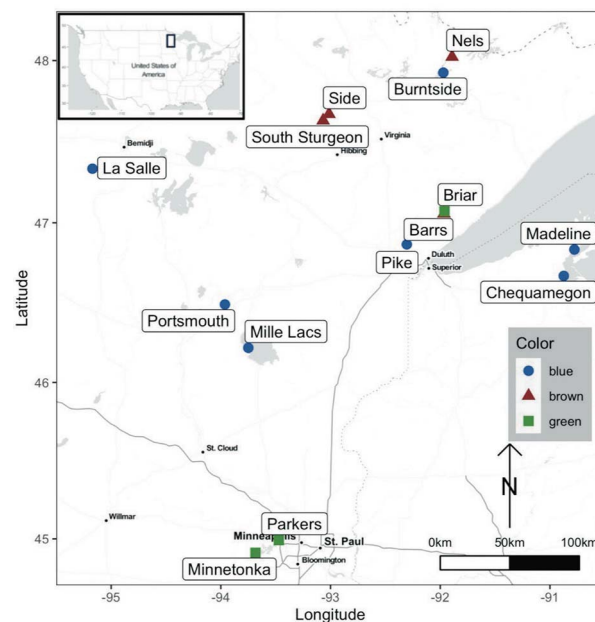
Fig. 1. Map of study locations. Lakes of different water color are indicated by different symbols.

for chemical analyses and zooplankton samples for determination of community composition and stable isotopes ($\delta^{13}C / \delta^{15}N$) analysis (SIA).

Several physical characteristics were measured during winter and summer periods. During the ice cover period, we visually estimated the percentage of snow cover on the ice. Average snow depth was determined from measurements of five locations within several meters from the sampling site. The thickness and properties of ice (layering) were recorded as well. Light attenuation through snow, ice and water was measured with either an LI-COR probe equipped with a quantum LI-192 cosine sensor (LI-COR Biosciences., NE, Lincoln, USA) or a submersible hyperspectral irradiance sensor (TriOS Ramses, Rastede, Germany). Light attenuation of ice was measured by paired measurements in air and by submersing the light sensor through the hole in the ice and placing it as close as possible to the underside of the ice. If any snow was present, measurements were repeated after carefully removing $\sim 1 \, m^2$ of snow. Light attenuation in the water column was determined from measurements of light levels at resolution of 0.5 m from water surface to depths of 5–10 m. The hole in the ice was covered by an opaque black plastic sheet to avoid light contamination during winter water column light attenuation measurements. We calculated the euphotic depth for each sampling location and period while accounting for light attenuation (Table II) by the water column as well as by snow and ice cover.

Table I: Study lake characteristics, including color classification, size, depth, sampling depths, sampling dates, TP, DOC and chl a depth-integrated summer concentrations

Lake color	Lake, State	Lake Size, km^2	Site depth, m	Water sampling depths, m	Summer sampling date	Winter sampling date	$\int$ TP, μM L^{-1}	$\int$ DOC, mg L^{-1}	$\int$ Chl a, μg L^{-1}
Blue	Burntside, MN	28.9	26	0, 5, 14, 25	13 July 2015	19 March 2015	0.4	7.3	1.6
Blue	La Salle, MN	0.9	60.5	0, 7, 20, 35, 57	14 July 2015	20 March 2015	0.9†	6	2.3
Blue	Mille Lacs, MN	536.1	8.5	0.7	10 July 2015	18 March 2015	0.7	7.5	3.3
Blue	Pike, MN	2.0	13	0, 6, 12	8 July 2015	16 March 2015	0.7	10.5	2.5
Blue	Portsmouth, MN	0.5	93	0, 15, 25, 35, 80	10 July 2015	18 March 2015	1.8[a]	5.5	0.7
Blue	Superior (Chequamegon Bay), WI	82 102.6	8	0.75	9 July 2015	17 March 2015	0.2	6	0.7
Blue	Superior (Madeline Ice Road), WI	82 102.6	47	0, 15, 30, 45	9 July 2015	17 March 2015	0.3	1.7	1.2
Brown	Barrs, MN	0.52	6	0, 2, 3.75, 5	12 July 2015	16 March 2015	0.5	22	6.9
Brown	Nels, MN	0.7	8	0.7	13 July 2015	19 March 2015	0.5	14.5	1.9
Brown	Side, MN	1.5	10	0, 2, 4, 8	23 July 2018	2 March 2018	1.2	12.8	6.8
Brown	South Sturgeon	0.8	10	0, 2, 4, 8	23 July 2018	2 March 2018	1	38.5	0.8
Green	Briar, MN	0.3	5.5	0, 4.5	12 July 2015	16 March 2015	2.6	13	13.8
Green	Minnetonka	2.3	10	0, 2, 4, 8	16 July 2018	27 February 2018	5.1	19.2	58.1
Green	Parkers	0.4	10	0, 2, 4, 8	16 July 2018	27 February 2018	1.9	9.25	31.8

[a]Lakes LaSalle and Portsmouth are deep, meromictic lakes with high TP concentrations in the monimolimnion. The summer depth-integrated TP concentrations in the epilimnion are 0.5 μM L^{-1} (LaSalle) and 0.6 μM L^{-1} (Portsmouth).

Table II: Light attenuation coefficients for snow/ice and water column in winter and only for water column in summer along with snow and ice conditions for all lakes in wintertime. Nd—no data

Lake color	Lake, State	k_d snow	k_d ice	k_d water in winter	k_d water in summer	Snow depth, m	Ice thickness, m
Blue	Burntside, MN	Nd	2.7	0.4	0.5	0	0.6
Blue	LaSalle, MN	Nd	2.3	0.5	0.5	0	0.58
Blue	Mille Lacs, MN	Nd	2.6	0.3	0.6	0	0.65
Blue	Pike, MN	Nd	1.7	0.4	0.5	0	0.67
Blue	Portsmouth, MN	Nd	2.5	0.2	0.3	0	0.53
Blue	Superior (Chequamegon Bay), WI	Nd	3.4	0.2	0.3	0	0.52
Blue	Superior (Madeline Ice Road), WI	Nd	2.2	0.2	0.3	0	0.5
Brown	Barrs, MN	Nd	1.2	1.6	1.1	0	0.6
Brown	Nels, MN	Nd	5.8	1.2	1.2	0	0.58
Brown	Side, MN	20.2	2.5	0.8	0.7	0.36	0.62
Brown	South Sturgeon, MN	37.7	6.5	6	6.4	0.32	0.47
Green	Briar, MN	Nd	3.9	0.5	1	0	0.5
Green	Minnetonka, MN	7.6	0.9	0.8	1.4	0.2	0.68
Green	Parkers, MN	12.2	1.8	0.7	1.2	0.21	0.62

Water samples were collected for chl *a*, total phosphorus (TP), DOC and seston $\delta^{13}C/\delta^{15}N$ SIA with a 3.7 L Van Dorn water sampler at several discrete depths in each lake (Table I). At minimum, water was collected at lake surface (or immediately under the ice in winter) and 0.5 m above lake bottom. Water was collected into 2 L acid-washed bottles and stored in the dark until return to the lab for analyses.

Crustacean zooplankton samples were collected using zooplankton net tows (0.5 m mouth diameter, 64 μm mesh size, 1.5 m length), from 1.5 m above the lake bottom to the surface to determine the total abundance of zooplankton. We did not use flow meters on our nets, which could result in underestimates of zooplankton abundance due to net clogging and reduced net efficiency. Potential net clogging due to high biomass of phytoplankton can be a problem especially in deeper humic and eutrophic lakes (Mack *et al.*, 2012). However, we do not believe net clogging to be a major issue in our study due to relatively shallow depths of productive and humic lakes (Table I), and the high ratio (>4:1) of the net surface area to the net mouth area (Gannon, 1980). One sample from each sampling date was fixed with 90% ethyl alcohol upon collection and then transferred to 70% ethyl alcohol for storage until taxonomic identification and counting. A second zooplankton sample was cleaned from algae and debris and kept alive for ∼ 2 h in filtered lake water following collection to allow gut clearance; these zooplankton were then frozen for later determination of bulk C and N content and C/N stable isotope composition.

Lab analyses

DOC samples were filtered through pre-combusted Whatman GF/F filters into pre-combusted 40 mL amber glass vials. Concentrations of DOC were determined using a Shimadzu TOC-V autoanalyzer (Shimadzu Co., Kyoto, Japan). TP was determined using a potassium persulfate digestion method to convert phosphorus to orthophosphate (Murphy and Riley, 1962; Wetzel and Likens, 1991). Samples were then analyzed using a SEAL Analytical AQ400 autoanalyzer with US EPA119-A method for TP (Murphy and Riley, 1962). Phytoplankton abundance was estimated as chl *a* concentration. Chl *a* was filtered onto 0.2 μm nitrocellulose filters and extracted into 90% acetone solution (Welschmeyer, 1994). After an 18-h extraction period in the dark, extracts were analyzed using a Turner Designs 10-AU fluorometer (Turner Design, Sunnyvale, CA) using an excitation wavelength of 436 nm and emission of 680 nm.

Seston samples from different depths were filtered onto pre-combusted Whatman GF/F filters and frozen at −20°C. Afterward, filters were dried overnight and rolled in tin capsules for determination of bulk C and N content and C/N stable isotope composition. Bulk zooplankton samples for C and N stable isotopes analysis were kept at −20°C. Samples were freeze-dried, thoroughly homogenized and weighed into tin capsules. C/N SIA on seston and zooplankton samples was performed using Elemental Analysis—Isotope Ratio Mass Spectrometry (EA-IRMS) at the Large Lakes Observatory facilities. For both seston and bulk zooplankton SIA analysis we used acetanilide, B-2153 soil, B-2159 soil, caffeine and RM8548 standards and run them repeatedly after every 10 samples. The analytical errors calculated on seston replicates for $\delta^{13}C$ and $\delta^{15}N$ were 0.36‰ and 0.53‰, respectively.

Preserved zooplankton samples were subsampled using a Stempel pipette and transferred into a Bogorov chamber for counting. We counted and identified samples using

an Olympus SZH10 stereoscopic microscope (at $7\times$–$70\times$ magnification). Identification was based on the zooplankton key from Balcer *et al*. (1984) and Haney *et al*. (2013). Subsamples were identified and counted until at least 300 individuals were processed. We did not count or scan the whole sample for rare species due to relatively high zooplankton abundance, especially in samples collected during the summer season. We identified adult copepods and cladocerans to species level. Copepodites were distinguished between calanoids and cyclopoids only. Cladocerans were counted without age stage determinations. Nauplii were not separated by stage or taxonomic groups (cyclopoid vs. calanoid) and are included only in the total abundance analysis. They were excluded from community composition and feeding group analyses due to their high density and inability to separate them into those groups. Additionally, we assigned adult species to three feeding groups: herbivores, omnivores and predators based on information from Balcer *et al*. (1984) and Haney *et al*. (2013). We calculated abundance as individuals per liter (Ind. L^{-1}). Rotifers were present in our samples but were not counted or identified.

Data analysis

We used the R statistical computing environment (version 3.6.2) for analyses of our data (R Core Team 2017). All graphics were created using the ggplot2 package (Wickham, 2009).

The downwelling attenuation coefficient of PAR (K_D) in water was calculated using the Beer–Lambert Law. K_D of ice ($K_{D\ ICE}$) was calculated following Eq. 1, and where present the K_D of snow ($K_{D\ SNOW}$) was calculated following Eq. 2 where Z_{ICE} and Z_{SNOW} are the depth of ice and snow, respectively (m). To account for large seasonal differences in daily incident irradiance, euphotic depths are not calculated as the depth of 1% surface light but rather the depth where mean daily PAR is 1 μmol m^{-2} s^{-1} which corresponds to the approximate minimum light requirement of phytoplankton (Silsbe *et al*., 2016). Mean daily PAR in the summer and winter (485 and 90 μmol m^{-2} s^{-1}) was determined from remotely sensed PAR climatology (MODIS Aqua) for our region (90–95°W, 40–45°N). Euphotic depths in the summer and winter are calculated using Eq. 3 and 4, respectively.

$$K_{D\ ICE} = -\log\left(E_{z\ ICE}/E_0\right) \bullet Z_{ICE}^{-1} \qquad (1)$$

$$K_{D\ SNOW} = \left[-\log\left(E_{z\ ICE}/E_0\right) + K_{D\ ICE} \bullet Z_{ICE}\right]$$
$$\bullet\ Z_{SNOW}^{-1} \qquad (2)$$

$$Summer\ Z_{EU} = -\log\left(1/485\right) \bullet K_D^{-1} \qquad (3)$$

$$Winter\ Z_{EU} = -\log\left(1 \Big/ \left(90 \bullet \exp^{-K_{D\ ICE} \bullet Z_{ICE} - K_{D\ SNOW}}\right.\right.$$
$$\left.\left. \bullet\ Z_{SNOW}\right)\right) \bullet K_D^{-1} \qquad (4)$$

We calculated depth-integrated values for selected limnological parameters (chl *a*, DOC, and TP) using trapezoidal integration (Eq. 5).

$$DIV = \sum\left(ci + cb\right)/2 \times \left(db - di\right)/td, \qquad (5)$$

where DIV is the depth-integrated value for a particular variable, ci is the sample concentration value at depth i, cb the sample concentration value at depth below depth i, di the sample depth i, db the sample depth below depth i and td the station total depth.

To assess differences between seasons for environmental parameters and zooplankton community characteristics we used paired t-tests with adjusted *P*-values by using the Holm multiple testing correction. Zooplankton and environmental data were log10 transformed in order to meet the normality and equal variance assumptions for parametric t-tests. Pearson correlation tests were used to investigate the relationship between environmental parameters during winter and summer across all lakes. In order to assess the differences between lake types within or between seasons, we used 90% confidence interval (CI) overlap of log10-transformed values as a criterion of significant difference. We choose to use paired t-test and 90% CIs rather than repeated measures ANOVAs due to small number of observations in lakes grouped by color, the greater simplicity of the former approach and its relative conservativeness (Goldstein and Healy, 1995).

To visualize differences between winter and summer in terms of zooplankton abundance and species composition, we used nonmetric multidimensional scaling (NMDS) from the *vegan* package in R (Oksanen *et al*., 2018). Community similarity was calculated using the Bray–Curtis dissimilarity metric (*betadisper* function in vegan), generated from species abundance data. Species abundance data was fourth-root transformed in order to reduce the influence of the most abundant taxa (Clarke and Warwick, 2001). We also used permutational multivariate analysis of variance (PERMANOVA; *adonis* function in vegan) to test for significant differences in zooplankton community composition between winter and summer seasons. In order to identify the species that contributed most to the dissimilarity between seasons, we used similarity percentage analysis (SIMPER; *vegan* package; Oksanen *et al*., 2018). We set a 40% similarity threshold within groups. Additionally, we examined the

relationship between zooplankton species abundance and environmental variables (using *envfit* function in *vegan*) for each season among different lake types.

RESULTS

Environmental variables

Snow, ice and light conditions varied between seasons across all lakes (Fig. 2a; Table II). Among sampled lakes, only four had snow on the ice surface during sampling in 2018, with snow depth ranging between 20 and 36 cm. Lakes sampled in 2015 did not have snow accumulation on ice surface due to lower snow amounts in the study region in 2015 compared to 2018 (Weekly Snow Depth and Rank Maps MN DNR, https://www.dnr.sta te.mn.us/climate/snowmap/index.html). Ice thickness varied between 47 and 67 cm across all study locations. Lake euphotic depths differences between seasons were significant ($P = 0.0002$), with higher values in summer (10.9 ± 7.1 SD m) than in winter (6.6 ± 6 m). Blue lakes, on average, had the highest euphotic depth (16.7 ± 5.2 m) in summer and a relatively high value (11.3 ± 4.5) in winter. Green lakes had low euphotic depths during winter (3 ± 1.8 m) with about 2 m change between seasons. Brown lake euphotic depths were substantially lower in winter (0.8 ± 1.1 m) compared to summer (5.1 ± 3.2 m). Light attenuation results (Table II) among lakes showed that snow and ice absorb and reflect most of the incoming light in winter. This is especially evident for lakes sampled during winter 2018, when ice was covered with snow. We found that, across all lakes, water column k_d values were significantly higher (df = 13, $P = 0.03$) in summer (1.1 ± 1.6) than in winter (1 ± 1.5).

Most of the water chemistry parameters were significantly different between winter and summer (Fig. 2b–d). The exception were depth-integrated DOC values which were not significantly different between seasons (df = 13, $P = 0.4$) with winter values of 16.3 ± 23.4 and 12.3 ± 9.3 mg L^{-1} in summer. However, high DOC brown lakes seemed to have larger summer-winter variation in DOC concentrations compared to blue and green lakes (Fig. 2b). The 90% confidence intervals for winter DOC values in brown lakes (10.5–93.3 mg L^{-1}) showed significant difference to DOC values in blue lakes (2.3–5.5 mg L^{-1}), and no difference with green lakes (5.6–17 mg L^{-1}). Summer DOC 90% CIs indicate similar results to winter (Table S1). Total phosphorus (TP) concentrations were significantly higher (df = 13, $P = 0.03$) in summer compared to winter with average values across all lakes of 0.8 ± 0.7 μM L^{-1} in winter and 1.3 ± 1.3 μM L^{-1} in summer (Fig. 2c). We found that TP

90% CIs were overlapping across all lake types in winter, while in summer green lakes (1.2–6.9 μM L^{-1}) were slightly overlapping with brown lakes (0.4–1.3 μM L^{-1}) but were significantly different (0.3–1 μM L^{-1}) from blue lakes. Depth-integrated chl *a* concentrations were significantly lower in the winter compared to the summer (df = 13, $P = 0.03$,) with average values of 1.4 ± 1.4 and 9.1 ± 16.4 μg L^{-1}, respectively (Fig. 2d). According to 90% CIs, winter chl *a* values were only significantly different between green (1.6–4.5 μg L^{-1}) and brown (0–1.6 μg L^{-1}) lake types, but not with blue (0.6–1.9 μg L^{-1}) lakes. In summer, green lakes differed significantly (8.7–100 μg L^{-1}) from brown (0.8–7.1 μg L^{-1}) and blue (0.9–2 μg L^{-1}) lake types. Overall, seasonal differences in chl *a* concentrations in green and brown lakes were more pronounced than in blue lakes.

Zooplankton communities and abundance

Total zooplankton and nauplii densities varied between seasons (Fig. 3). Zooplankton density (adult and copepodites) ($\pm$SD) was significantly different (df = 13, $P < 0.001$) between summer and winter with values of 14.1 ± 14 and 4.6 ± 4.9 Ind L^{-1}, respectively (Fig. 3a). Green lakes on average had the highest total zooplankton density (9.8 Ind L^{-1}) compared to brown (5.3 Ind L^{-1}) and blue (1.9 Ind L^{-1}) lakes in winter. In summer zooplankton densities increased across all lakes with the highest density again in green (34.6 Ind L^{-1}), then brown (13.2 Ind L^{-1}) and blue (5.9 Ind L^{-1}) lakes. Winter 90% CIs for total zooplankton densities overlapped and were not significantly different between all lake types (Table S1), while summer CIs showed that green lakes differ significantly (13.5–76.2 Ind L^{-1}) from blue (2.5–8.2 Ind L^{-1}), but not brown (4–27.2 Ind L^{-1}) lakes. Nauplii density did not change significantly (df = 12, $P = 0.06$) between seasons, with average values 14.3 ± 28.7 Ind L^{-1} in winter and 12.8 ± 11.2 Ind L^{-1} in summer (Fig. 3c). Blue lakes had lower average nauplii densities in winter (2.1 ± 1.9 Ind L^{-1}) than summer (8.4 ± 6.6 Ind L^{-1}), while green (41.3 ± 56.2 Ind L^{-1}) and brown (12 ± 13.2 Ind L^{-1}) lakes on average had higher nauplii densities under the ice compared to the open-water period (27 ± 15.2 and 9.9 ± 6.8 Ind L^{-1}, respectively). For both seasons, we found that nauplii 90% CIs overlapped for all lake types and were not significantly different (Table S1).

The absolute and relative abundances of main zooplankton groups changed between seasons and among sampled lakes (Fig. 4). The density of calanoid copepods was not significantly different (df = 11, $P = 0.7$) between winter and summer across lakes, averaging 1.6 ± 2.7 and 1.8 ± 2.5 Ind L^{-1}, respectively (Fig. 4a). However, the
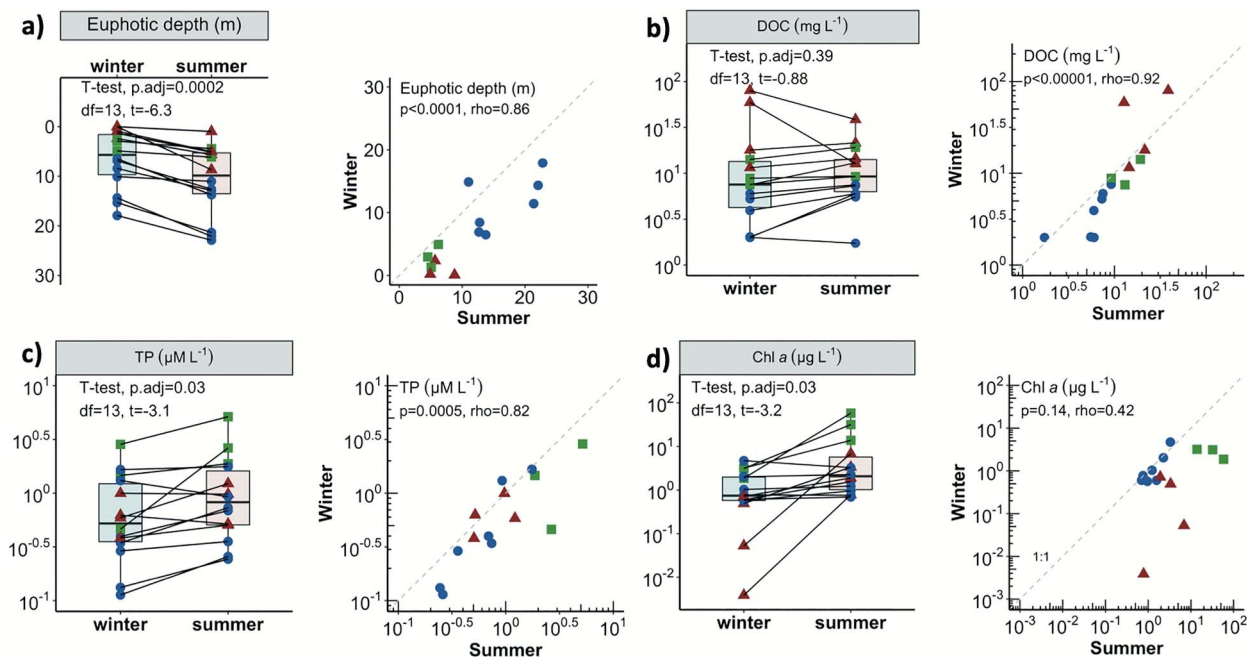
Fig. 2. Depth-integrated water chemistry variables (b, c, d) and euphotic depth (a) in summer and winter for all lakes. Boxplots represent data recorded across all lakes in winter and summer; winter and summer values for individual lakes are connected by black lines. Scatterplots show the paired winter and summer lake data for each variable; *P*- and rho-values are from Pearson correlation tests. Each lake is represented by different shape and color; blue circles indicate blue lakes, brown triangles indicate brown lakes, green squares show green lakes. Scales for chemistry variables are logarithmic.

relative abundance of calanoids varied greatly between seasons with relatively more calanoids under the ice ($32.6 \pm 24.2\%$) than in summer ($19.7 \pm 24.5\%$) (Fig. 4d). Cyclopoid average density was not significantly different (df = 13, $P = 0.08$) between summer and winter with higher values in summer (3.4 ± 5.1 Ind L^{-1}) than in winter (1.4 ± 1.7 Ind L^{-1}) (Fig. 4b). Cyclopoids were relatively more abundant in winter ($52.6 \pm 24.6\%$) compared to summer ($32.1 \pm 24.3\%$) (Fig. 4e). Cladoceran average density was significantly different (df = 10, $P = 0.006$) between seasons with higher values in summer (5.2 ± 8.5 Ind L^{-1}) compared to winter (0.8 ± 1.4 Ind L^{-1}) (Fig. 4c). The relative abundance of cladocerans also was higher in summer ($48.2 \pm 32.2\%$) than in winter ($14.8 \pm 13.1\%$) (Fig. 4f). Among all lakes, green lakes had the highest relative abundance of cladocerans in winter ($20.7 \pm 4.8\%$). In the summer, the highest cladoceran percentage was in brown lakes ($52.8 \pm 12.3\%$). Our 90% CI analysis for main zooplankton groups densities showed that only cyclopoids in blue lakes during winter were significantly different from brown lakes (Table S1).

Across all lakes, we identified 21 distinct species in summer compared to 14 species in winter. Our data showed that the average number of species per lake in winter (4.4 ± 1.7 spp.) was significantly (df = 13, $P = 0.01$) lower than in summer (6.6 ± 2.6 spp.) (Fig. 3d). We used NMDS

ordination to visualize differences in zooplankton communities in winter and summer across study lakes (Fig. 5). Multivariate homogeneity of group dispersions analysis showed greater dispersion around the median for summer zooplankton communities (0.43) than for those in winter (0.35), suggesting that zooplankton communities are more similar among lakes in winter than in summer. Ordination of the Bray–Curtis dissimilarity matrix of all zooplankton species revealed that winter and summer communities differed significantly in their composition (permANOVA $P = 0.0096$). Differences between green, brown and blue lakes were significant as well (permANOVA $P < 0.001$). SIMPER analysis showed that densities of *Daphnia longiremis* (11.4%), *Bosmina longirostris* (9.8%), *Leptodiaptomus sicilis* (9.5%), *Diacyclops thomasi* (8.1%) and *Skistodiaptomus oregonensis* (8.2%) contributed the most to dissimilarity between winter and summer seasons, together accounting for ~47% of the community difference between seasons. Altogether, on average, these species constituted >90% of the total zooplankton abundance across all lakes in winter, while in summer, they contribute about 68% of total abundance. Chl *a*, TP and TN were the strongest environmental covariates with multivariate dissimilarity trends for zooplankton communities in summer and winter (Fig. 5). In summer (Fig. 5c), chl *a* ($R^2 = 0.49$, $P = 0.0166$) concentration and TP ($R^2 = 0.54$, $P = 0.0085$)
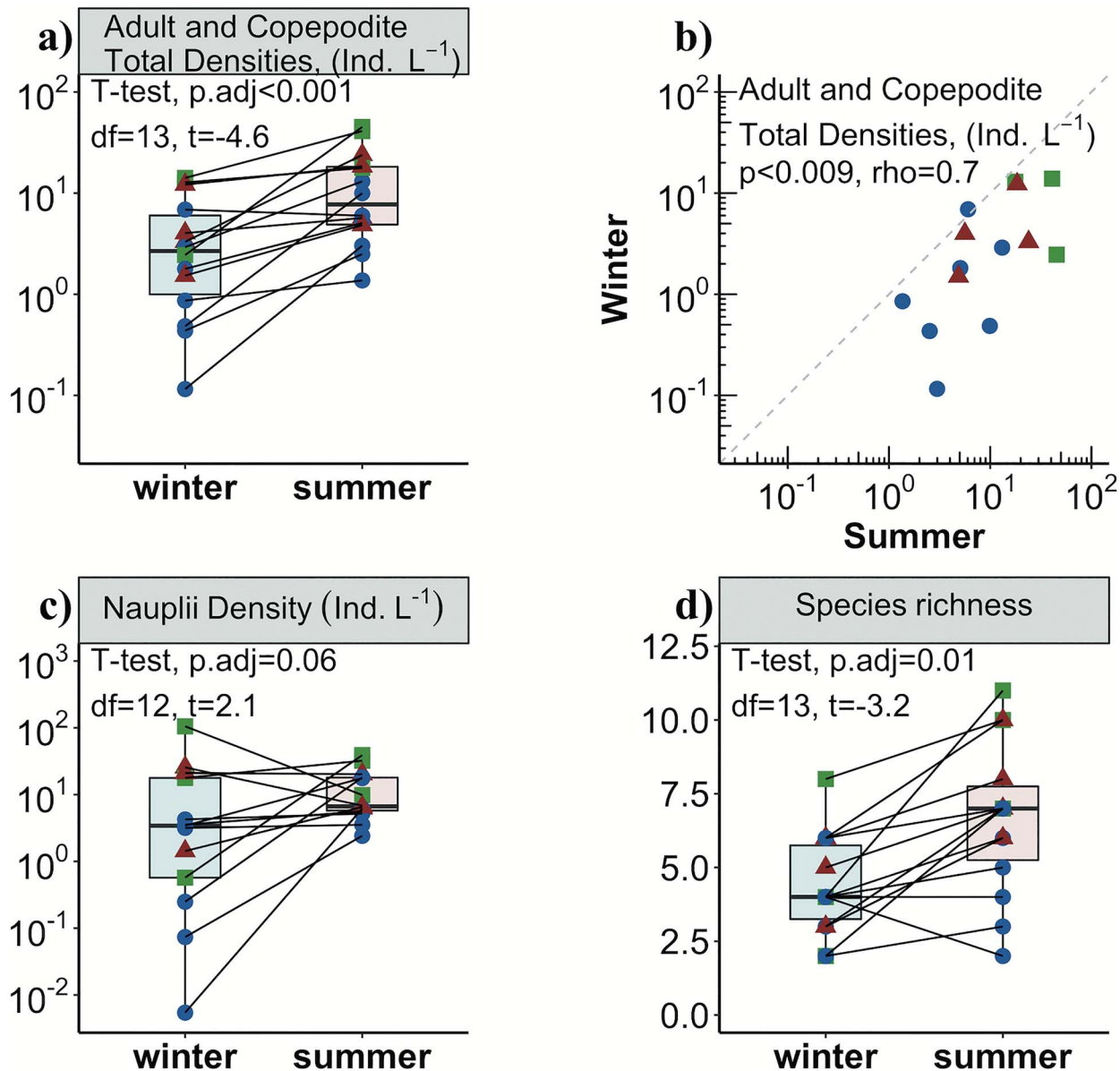
Fig. 3. Zooplankton abundance based on adult and copepodite counts (a and b) and only on nauplii numbers (c). Paired t-test results with adjusted *P*-values shown for abundance data. Scatterplot show the paired winter and summer zooplankton data for total zooplankton count; correlation coefficients (rho) and *P*-values are from Spearman rank correlation test. Each lake is represented by different shape and color; round blue points indicate blue lakes, brown triangles indicate brown lakes and green squares show green lakes. Scales for density are logarithmic.

increased in the direction of green lakes. Both vectors also pointed away from *Holopedium gibberum*, *B. longirostris* and *Limnocalanus macrurus* and toward *S. pygmaeus*, *Onychodiaptomus birgei*, *O. sanguineus*, *L. siciloides*, *S. oregonesis*, *D. pulicaria*, *D. parvula*, *D. retrocurva*, and *Mesocyclops edax*. In winter (Fig. 5b), the community dissimilarities no longer trended with chl *a* or TP but instead gained correlation with TN (R² = 0.59, *P* = 0.0078). The TN vector did not trend with a specific lake type. It appeared to point away from *B. longirostris* and *L. sicilis* and toward *Alona*,

S. pygmaeus, *Acanthocyclops vernalis*, *S. oregonensis*, *Tropocyclops prasinus mexicanus* and *D. longiremis*.

The absolute densities and relative abundances of different zooplankton feeding groups varied in lakes of different types between winter and summer (Fig. 6). The average density of herbivores was significantly higher in summer than in winter with values in summer equal 6.91 ± 8.9 and in winter 2.1 ± 3.6 Ind L⁻¹ (Fig. 6a). The relative abundance of herbivores was also higher in summer (67.3 ± 24%) than in winter (47 ± 24.5%).
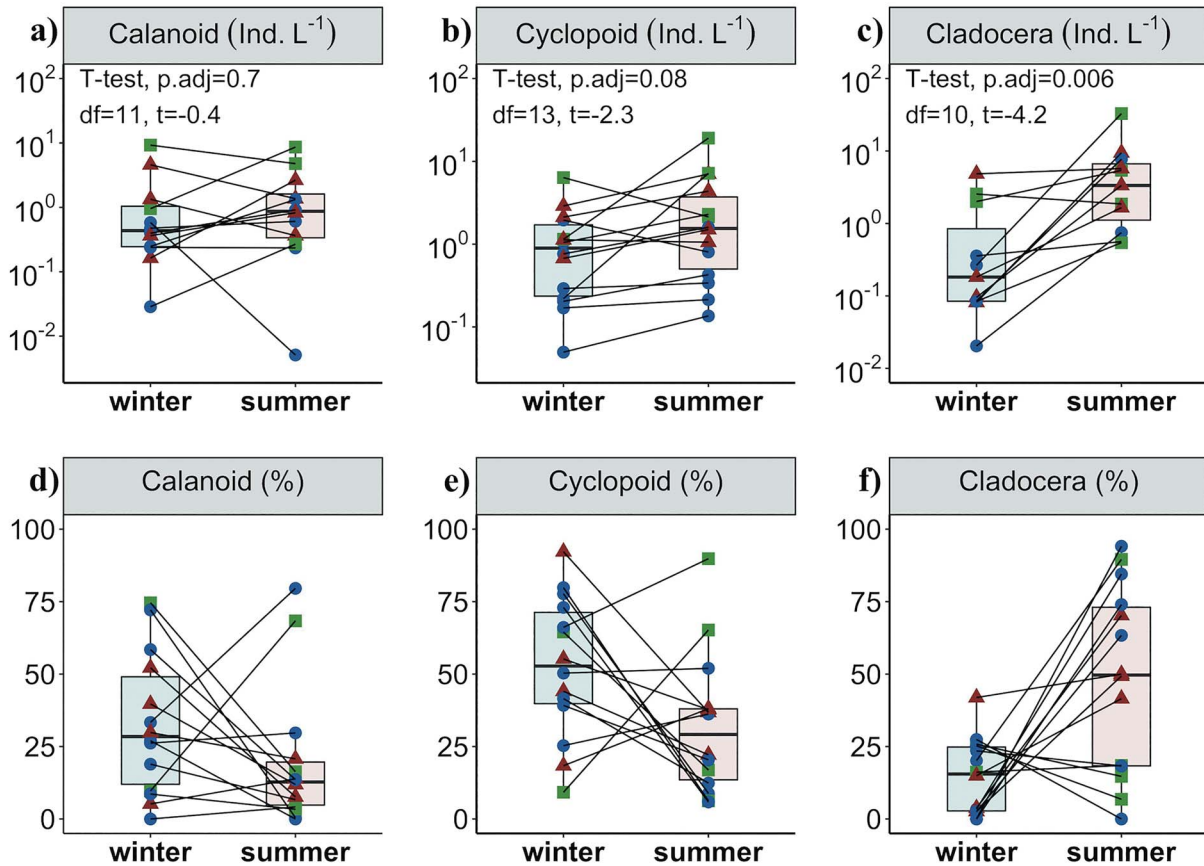
Fig. 4. Zooplankton taxonomic groups densities (a–c) and percentage abundance (d–f) based on the number of adult individuals between summer and winter seasons across all sampled lakes. Paired t-test results with adjusted *P*-values shown for abundance data. Each lake is represented by different shape and color; round blue points indicate blue lakes, brown triangles indicate brown lakes and green squares show green lakes. Scales for density are logarithmic.

Interestingly, in some lakes (Parkers, LaSalle, Side and Portsmouth) the relative abundance of herbivores was lower in summer compared to winter (Fig. 6b). The average density of predatory zooplankton across all lakes was not significantly different between winter and summer with values 1.21 ± 1.5 and 3.06 ± 5.2 Ind L^{-1}, respectively (Fig. 6d). However, the relative abundance of predators across all lakes was higher in winter ($49.1 \pm 22.1\%$) compared to summer ($29 \pm 25.5\%$) (Fig. 6e).

Seston and zooplankton C and N stable isotope values showed divergent interseasonal patterns (Fig. 7). Depth-integrated seston δ^{13}C was not significantly different between seasons with average values ($\pm$SD) for summer equal $-30.3 \pm 1.8‰$ and winter $-31.7 \pm 2.7‰$ (Fig. 7a). On the other hand, zooplankton δ^{13}C values were significantly more depleted during the winter ($-36.1 \pm 4.4‰$) than in summer ($-31.3 \pm 4.6‰$) (Fig. 7d). Seston δ^{15}N signatures were significantly more enriched in winter

($4.7 \pm 4.7‰$) compared to summer ($1.3 \pm 2.6‰$) (Fig. 7b). Average zooplankton δ^{15}N values followed a similar pattern to seston and also were significantly more enriched in winter ($8.8 \pm 3.6‰$) compared to summer ($5.3 \pm 4.1‰$) (Fig. 7e). Seston carbon to nitrogen (C/N) ratio did not differ significantly between winter (8.8 ± 2.6) and summer (8.2 ± 2.8), while zooplankton C/N ratio were significantly higher in winter (5.8 ± 1.1) than in summer (3.8 ± 1.4) (Fig. 7c and f).

DISCUSSION

Our objectives were to compare winter and summer zooplankton communities across diverse north temperate lakes. We found that, across all study lakes, winter zooplankton abundance was approximately one third of the open water period densities (Fig. 3). However, zooplankton were still active under the ice, and high nauplii
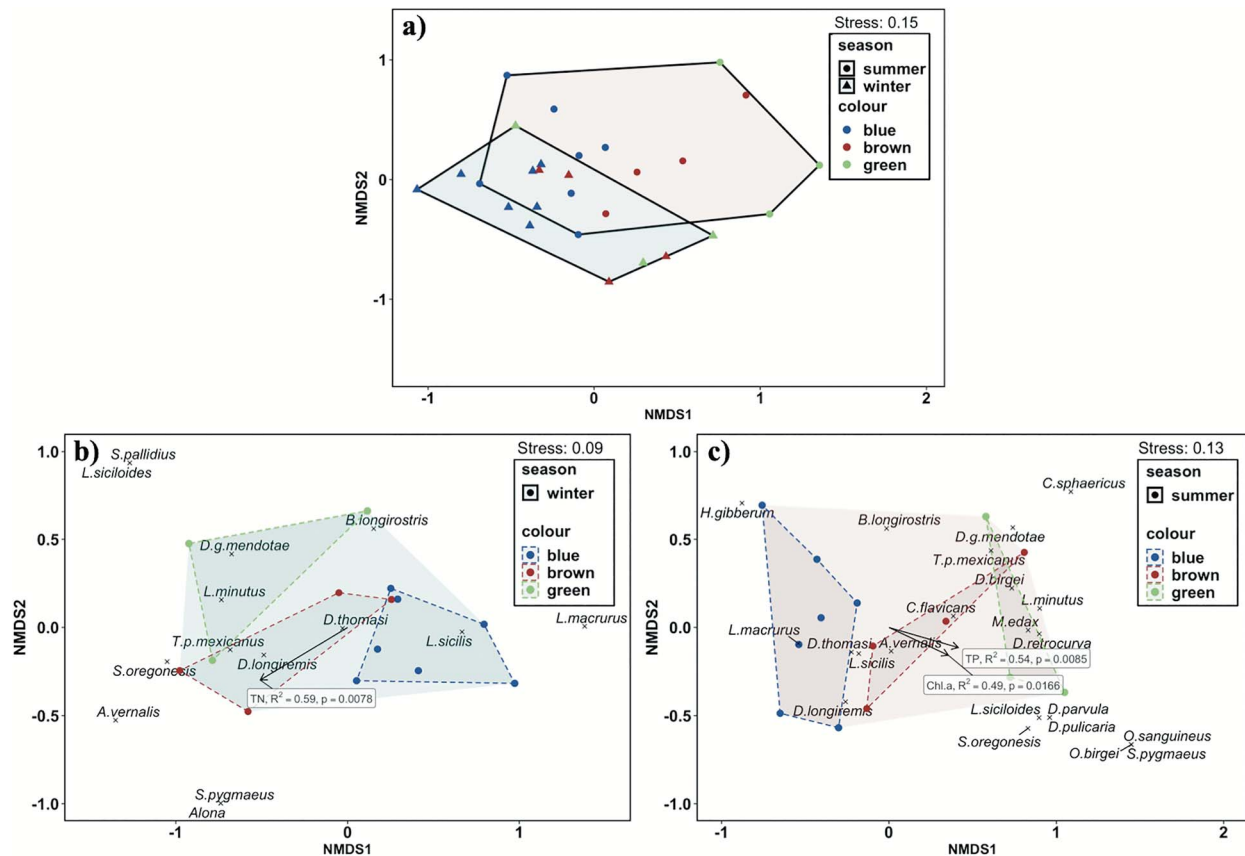
Fig. 5. NMDS of the Bray–Curtis dissimilarity plot for zooplankton species across all lakes in winter (polygon filled with blue color) and summer (polygon filled with red color) (plate a); only in winter (plate b), and only in summer (plate c). Blue-edged polygons represent blue lakes (oligotrophic), brown-edged polygons represent brown lakes (high DOC) and green-edged polygons show green lakes (eutrophic). Vectors on plates b and c represent correlations ($P < 0.05$) between environmental variables and the distribution of zooplankton species.

densities indicate potential reproduction by copepods. We also observed interesting patterns of seasonal change in zooplankton community structure. Zooplankton communities were more similar across our study lakes during winter than in summer (Fig. 5). In addition, we found that calanoid and cyclopoid copepods dominated zooplankton numbers under the ice, while cladocerans were dominant in the summer (Fig. 4). Feeding group classification and stable isotope analysis suggested that herbivory was a more important energy pathway in the summer, whereas predation may be more important under the ice. It is important to emphasize that all our study lakes were sampled only once in winter and once in summer. Thus, our results represent a snapshot of late winter and mid-summer conditions for the study lakes and do not consider successional patterns, which may lead to significant intraseasonal changes in zooplankton communities (e.g. Sommer *et al.* 2012), but are poorly understood for the under-ice period. Although limited to one sampling date in each season, our study offers new information

about zooplankton abundance, community composition and trophic structure under the ice across diverse northern lakes, a topic rarely represented in the limnological literature.

Large seasonal variations in environmental conditions

Our results show large winter to summer changes in environmental parameters relevant to zooplankton, as well as differences in how winter–summer conditions change in lakes of different trophic status (Fig. 2). In all our study lakes, euphotic depth was lower in winter than in summer, mainly due to presence of ice and snow cover (Fig. 2a). However, water column light attenuation coefficients show that the water columns of study lakes were clearer in winter than summer (Table II). Ice characteristics and the presence of snow can have large impacts on light conditions in the water column beneath. For example, snow-covered (<10 cm) ice with impurities
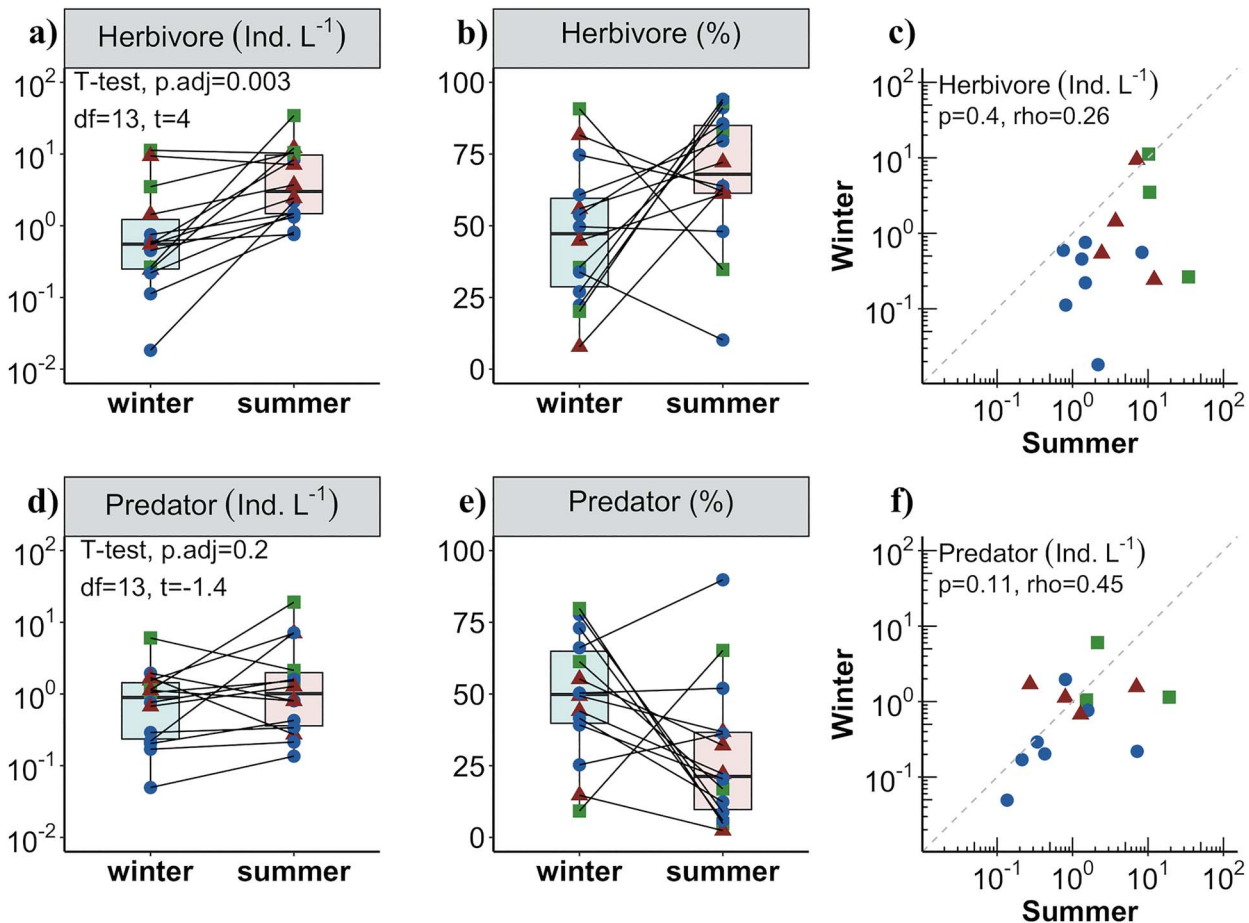
Fig. 6. Boxplots represent zooplankton herbivore and predator feeding groups densities and percentage abundance based on the number of adult individuals in summer and winter across all lakes; paired t-test results with adjusted *P*-values showed for abundance data. Scatterplots show the paired winter and summer zooplankton data for herbivore and predator feeding groups; correlation coefficients (rho) and *P*-values are from Spearman rank correlation test. Each lake is represented by different shape and color; round blue points indicate blue lakes, brown triangles indicate brown lakes and green squares show green lakes. Scales for density are logarithmic.

and gas bubbles can reduce PAR to <10% of surface values, and snow deeper than 13.5 cm has been found to reduce light below levels required for phytoplankton growth (Bolsenga and Vanderploeg, 1992; Leppäranta, 2014; Pernica *et al.*, 2017). In the four study lakes that had appreciable snow cover (range 20–36 cm), ice and snow cover substantially reduced light penetration (to 2.4–3% of surface irradiance immediately under the ice). The total amount of solar radiation reaching Earth's surface at the latitude of our study is 2-fold higher in July than in March, further impacting the light environment in lakes during winter. Thus, lower light conditions in winter can reduce phytoplankton biomass, contributing to the lower zooplankton abundances and changes in trophic structure that we observed in winter (see next sections). However, in the absence of deep snow, light levels can still be relatively high during winter, supporting winter-period primary production. According to Gosselin *et al.*

(1985), sea algae showed photosynthetic activity at light level of 7.6 µmol m^{-2} s^{-1} and algae biomass increased at light intensity of > 20 µmol m^{-2} s^{-1}. In our study, 11 out of 14 sampling locations had winter light intensities equal to or above those thresholds.

Along with light, phosphorus availability is important for ecosystem productivity as this element can be a limiting factor for phytoplankton and, consequently, zooplankton production (Hanson and Peters 1984; Schindler *et al.*, 2016). Overall, depth-integrated TP values were higher in summer than during the ice-covered period across most study lakes (Fig. 2c), likely due to lower concentrations of particulate P (in phytoplankton and suspended detritus). Lakes that had higher TP concentrations in summer (green lakes) also had higher TP concentrations in winter, which might be due to high concentartions of inorganic P, indicating their greater potential to support winter phytoplankton production if light is not limiting.
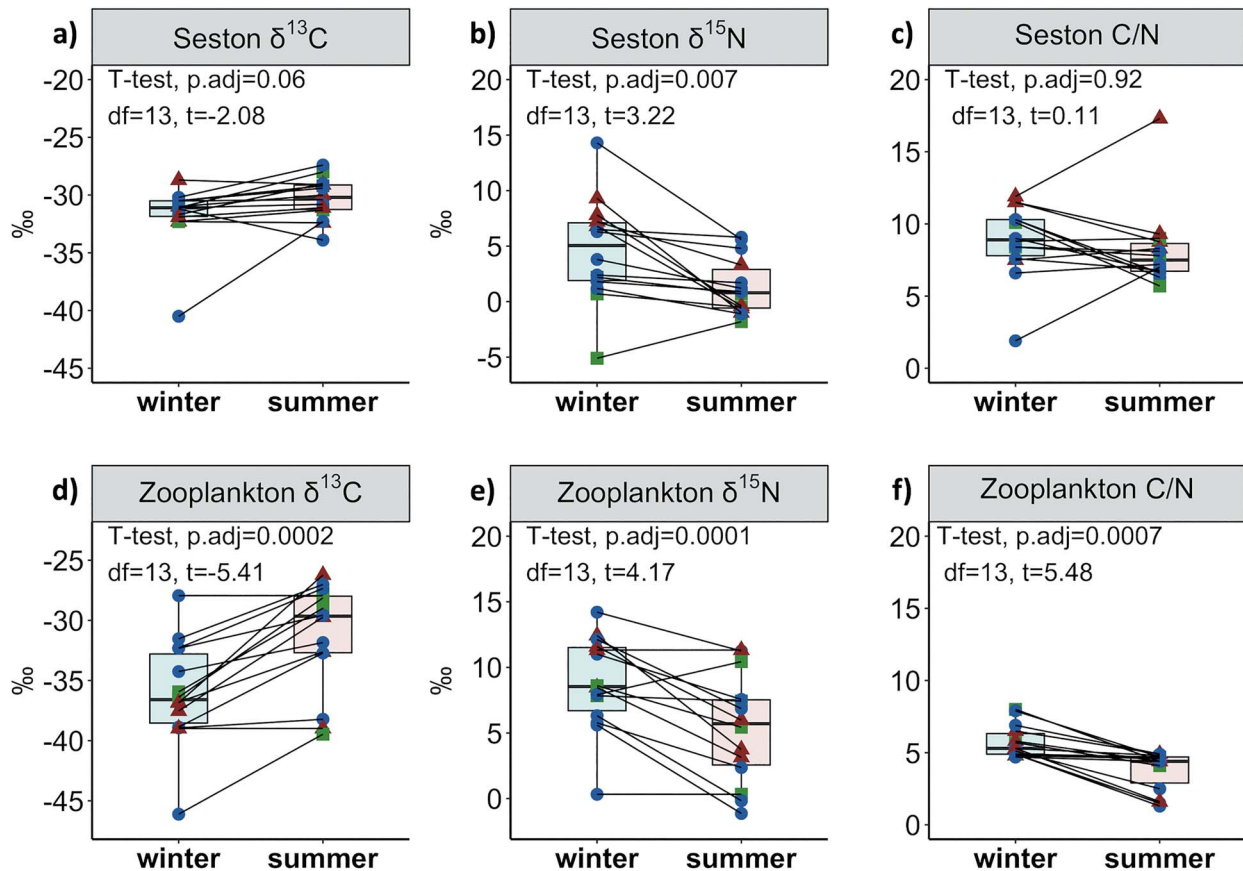
Fig. 7. Depth-integrated SIA data for seston (top panel—a, b and c) and bulk zooplankton (bottom panel—d, e and f) in the winter and summer across all lakes. Each lake is represented by different shape and color; round blue points indicate blue lakes, brown triangles indicate brown lakes and green squares show green lakes. Results of paired t-test with adjusted *P*-values showed on the top of each boxplot.

Chl *a* concentrations (Fig. 2d), used as a proxy for phytoplankton biomass, were almost universally lower in winter compared to summer (with exception of large, shallow, oligo-mesotrophic Lake Mille Lacs). The lower values of chl *a* during the ice-cover period are likely due to reduced light conditions, low temperatures and potentially high grazing pressure by zooplankton and low rates of water column mixing, which reduce nutrient replenishment to the upper, illuminated water layer of ice covered lakes (Bengtsson, 2011; Bertilsson *et al.*, 2013). While chl *a* concentrations were lower in winter ($1.4 \pm 1.4\ \mu g\ L^{-1}$) than summer ($9.1 \pm 16.4\ \mu g\ L^{-1}$) in all but one lake, green lakes retained relatively higher chl *a* concentrations in winter ($2.7 \pm 0.7\ \mu g\ L^{-1}$) compared to other lake types. The observed, moderately high chl *a* values in productive lakes during the ice-covered period suggest that nutrient limitation of phytoplankton may still be important during winter, despite reduced light availability. Overall, these results show that more productive lakes in summer also have higher phytoplankton biomass in winter. Hampton *et al.* (2017) found a similar pattern, with a strong correlation between winter and summer chl *a* concentrations across 101 lakes. Interestingly, in addition to having higher winter chl *a* concentrations, green lakes also showed the greatest cumulative average change in chl *a* between winter and summer (92.1% change), followed by brown lakes (90.1% change). In contrast, relatively little change in chl *a* concentrations occurred between seasons in blue lakes (0.3% change). The relative stability of phytoplankton abundance, measured here as chl *a* concentrations, in blue lakes may potentially be explained by persistent year-round nutrient limitation, or higher top-down pressure from wintertime zooplankton grazing.

Although pelagic primary consumers mainly depend on phytoplankton production (Hessen *et al.*, 1989; Bern, 1994; Brett *et al.*, 2009), zooplankton can also utilize other energy sources such as terrestrial DOC (Carpenter *et al.*, 2005; Kankaala *et al.*, 2010). Allochthonous C usually is a poor C source for zooplankton due to low nutrition content in organic matter of terrestrial origin (Brett *et al.*, 2009; Galloway *et al.*, 2014). However, poor-quality C can be upgraded by bacterial action and transferred to higher

trophic levels through the microbial loop (Bec *et al.*, 2003; Martin-Creuzburg *et al.*, 2005; Säwström *et al.*, 2009). The concentrations of DOC in our study were higher in brown lakes during winter (42.1 ± 32.8 mg L^{-1}) compared to summer (21.8 ± 11.8 mg L^{-1}), while in green and blue lakes, DOC was slightly higher in summer than under the ice (Fig. 2b). Seasonal changes in DOC concentrations can be explained by the lake's size and watershed features, climate conditions, loading rates of allochthonous material along with photodegradation losses (Wetzel, 2001; Pace and Cole, 2002; Vachon *et al.*, 2016; Hampton *et al.*, 2017). The higher concentration of DOC in brown lakes during winter may be due to the combined effects of extensive terrestrial input from the surrounding watershed prior to the ice-cover period (Wetzel, 2001; Raymond and Saiers, 2010) and low light conditions under the ice resulting in reduced photodegradation and assimilation of DOC (Farjalla *et al.*, 2009; Vachon *et al.*, 2016). The high DOC in brown lakes, where winter phytoplankton concentrations are especially low, may play an important role for overwintering zooplankton through its assimilation and trophic upgrading via the microbial loop (Rautio *et al.*, 2011).

Seasonal changes in zooplankton abundance and community composition

Total adult and copepodite densities (hereafter referred to as total zooplankton) across all lakes were lower during the ice-cover period than during open water and constituted 32% of summer zooplankton numbers. Other studies also report reduction in zooplankton numbers during the ice-covered period. For instance, Hampton *et al.* (2017) showed that, across 36 lakes, winter zooplankton abundance was roughly 25% of summer values and other studies have also demonstrated between 1.2- and 38-fold (9.4-fold on average) decrease in zooplankton densities (Jensen, 2019; Kalinowska *et al.*, 2019; Kalinowska and Karpowicz, 2020). In our study, green lakes had the highest average zooplankton density in both seasons, followed by brown, and then blue lakes (Fig. 3a and b). As with phytoplankton, the most significant change in average zooplankton density between winter and summer was in green lakes (71.8% reduction), then followed by blue (67.1%) and brown (60.2%) lakes. While winter and summer changes are similar across all lake types, it appears that green (eutrophic) lakes can provide better conditions for zooplankton under the ice. The presence of abundant *Daphnia* spp. (many of which had full guts and eggs in brood pouches) and high number of nauplii in green lakes during winter provides additional support for this. Cladocerans like *Daphnia* spp. typically undergo diapause and are rare in lakes during the ice-covered period because of low temperatures and low phytoplankton biomass. However, in systems with enough food under the ice, *Daphnia* can still be active and reproduce (Tsugeki *et al.*, 2009; Hamrová *et al.*, 2011; Mariash *et al.*, 2017).

Nauplii abundance, which is indicative of reproduction by copepods, showed equal or even higher densities under the ice than in summer for some lakes (Fig. 3c). We found the highest nauplii counts in one green (105 Ind L^{-1}) and brown (25.6 Ind L^{-1}) lake during the winter, while in summer, maximum nauplii densities reached 39 and 20.2 Ind L^{-1} in green and brown lakes, respectively. Thus, our results show that zooplankton remain active under the ice and can even maintain high reproductive activity in some lakes. Alternatively, as seen in previous studies for some cyclopoid copepods (Elgmork, 2006; Wærvågen and Nilssen 2010), high nauplii abundance under the ice might be partly explained by the presence of overwintering nauplii cohorts.

Zooplankton species composition was different between winter and summer, with higher species diversity during the summer. Across all lakes, we found 21 species during the open water season compared to 14 species under the ice. We found nine zooplankton species that appeared only during the summertime and were absent or below the detection limit under the ice. Among those species, a few had a relatively high abundance in some lakes during summer and accounted for 12% of multivariate dissimilarity between two seasons (*Diaphanosoma birgei*, *M. edax* and *H. gibberum*). When we compared winter–summer diversity for different lake types, we found that blue lakes showed less change between winter (eight species) and summer (10 species) compared to green (9 vs. 18 spp.) and brown (10 vs. 14 spp.) lakes.

Our results showed that zooplankton communities were more similar across lakes during winter than during the open water period (Fig. 5). Butts and Carrick (2017) similarly reported greater similarity among phytoplankton communities during the winter in a study of seven diverse lakes in Michigan. Their explanation was that the harsh winter conditions (low light and temperature, stable water column) provided a selective advantage to specific groups of phytoplankton (e.g. mixotrophic flagellates) regardless of lake trophic status. Likewise, we believe that the same increased similarity of environmental conditions during winter is responsible for the greater zooplankton community similarity across lakes and lake types in winter compared to summer. Additional studies of lake communities in winter are needed to determine whether our findings and those of Butts and Carrick (2017) are generally true about the way pelagic communities reorganize across seasons.

Along with changes in species composition, we also observed changes in coarse-level taxonomic and feeding

group composition across seasons and lake types (Figs 4 and 6). Calanoid and cyclopoid copepods dominated during the ice-cover period across all lakes, while the relative and absolute abundances of cladocerans were higher in summer across all lakes. These results agree with other studies, which also show the dominance of copepods during the winter ice cover (Rautio *et al.*, 2000, Rautio *et al.*, 2011; Hampton *et al.*, 2017, Perga *et al.*, 2021). That is likely due to the ability of copepods to accumulate fat reserves before winter and use them throughout the ice-covered period (Mariash, 2012; Grosbois *et al.*, 2017). Cladocerans, such as *Daphnia*, have lower ability to accumulate storage lipids (Smyntek *et al.*, 2008) and have growth and reproduction optima at temperatures above 15°C (Lynch and Ennis, 1983; Gliwicz *et al.*, 2001), which helps explain their lower densities under the ice. Nevertheless, our results showed that cladocerans (mainly *Daphnia* spp.) were still present under the ice in many of our study lakes, constituting on average 21% of total zooplankton abundance.

It is important to mention that zooplankton densities and species composition among different lake types also can be affected by fish predation. It has been shown that planktivorous fish can reduce the number of large-size zooplankton in eutrophic and hypertrophic lakes (Auer *et al.*, 2004), while in brown lakes, crustacean zooplankton densities are less affected by fish (Wissel et al., 2003). Although most studies of lacustrine zooplankton–fish interactions were conducted in summer, several from fall, winter and spring showed high predation pressure on zooplankton by fish in different lake types (Vanni *et al.*, 1990; Jeppesen *et al.*, 1997, Jeppesen *et al.*, 2004, Hansson *et al.*, 2007). Therefore, fish can have a strong top-down effect on zooplankton and must be incorporated in future seasonal studies to better understand the complete picture of lake trophic interactions.

Seasonal changes in zooplankton trophic structure

Among feeding groups, during the ice-covered period, we observed high relative abundance of predators (52% of total abundance) (Fig. 6). In contrast, during the open water season, all lakes on average were dominated by herbivorous zooplankton (67.5%) with predators (28.5%) following next. The elevated relative abundance of predators among all lake types in our study suggests that predatory zooplankton may be better adapted to survive periods of low phytoplankton biomass under the ice. These changes in densities of different feeding groups are likely related to food availability, specifically higher phytoplankton availability in the summer and, possibly,

greater importance of the microbial loop in winter which may support predatory species during that time. Zooplankton classified as predators are often omnivorous and this flexibility in diet might also help explain their dominance during winter. For example, some cyclopoid copepod species can alter their feeding behavior from herbivory to carnivory in environments with low primary production, and also change their feeding strategies at different life stages (Lampert, 1978; Santer, 1993).

To further investigate seasonal changes of zooplankton trophic dynamics, we used C and N stable isotope analysis of seston and bulk zooplankton (Fig. 7). Stable isotopes of C are often used to identify the source of organic matter in seston and zooplankton (France, 1995). Across all sampled lakes, we found that seston C stable isotope values ranged in summer between -27.4 and -33.9‰, while in winter they ranged from -28.7 to -40.5‰. Among sampled lakes, meromictic Lake LaSalle had the most depleted $\delta^{13}C$ depth-integrated value -40.5‰ in winter. This outlier value might be explained by the effect of anoxic conditions below the 40 m depth and the development of methanogenic bacteria, which usually have a depleted $\delta^{13}C$ signature (Deines *et al.*, 2009). We found small seasonal variation in seston $\delta^{13}C$ among blue and brown lakes. This may be explained by low phytoplankton production in blue lakes and high concentrations of allochthonous organic matter in brown lakes despite the season (Yoshii *et al.*, 1999; Grey *et al.*, 2000; Gu et al., 1999, 2011). In green lakes, the difference between winter and summer was slightly higher (1.7‰), but still low. The slightly enriched values of seston $\delta^{13}C$ in green lakes during summer $(-29.5 \pm 1.7$‰) might suggest higher phytoplankton production rates during the summer compared to winter (McCusker *et al.*, 1999).

Stable isotopes of N can provide information about the trophic position of consumers or their reliance on tissue catabolism during starvation (Vander Zanden and Rasmussen, 2001). In our study, we observed higher values of seston $\delta^{15}N$ in winter than in summer for all lakes. Notably, this was evident in brown lakes where winter $\delta^{15}N$ ranged between 6.8 and 9.3‰, while in summer $\delta^{15}N$ values were much lower and ranged between -0.6 and 3.3‰. High $\delta^{15}N$ values of seston might suggest low efficiency of N recycling under the ice in low productivity brown lakes (Karlsson *et al.*, 2004). Alternatively, high abundance of heterotrophic protists and low phytoplankton biomass in winter seston samples of brown lakes may be a source of elevated $\delta^{15}N$ values since heterotrophic protists rely more on the microbial loop and have a correspondingly elevated trophic position (Tranvik, 1992; Karlsson and Säwström, 2009). Similarly, zooplankton $\delta^{15}N$ values were also higher in winter compared to summer across all

lakes. This enrichment may indicate zooplankton starvation (and hence tissue catabolism, which is reflected in enriched δ^{15}N) or higher prevalence of carnivory during the ice-covered period (Adams and Sterner, 2000). The seasonal enrichment of zooplankton δ^{15}N ($\pm$SD) was especially large in low productivity blue (5 ± 3.8‰ change) and brown (4 ± 4.5‰ change) lakes. This observation is in accordance with our results on feeding groups, where the percentage abundance of predators is highest in blue and brown lakes during the wintertime (Fig. 6). The N stable isotope results suggest the possible importance of the terrestrial organic matter, which may be trophically upgraded through the additional trophic step of the bacteria-heterotrophic protist link and potentially subsidize zooplankton communities under the low food conditions in winter. Additional research is needed to better understand pelagic trophic dynamics during the ice cover season and the role of winter-active zooplankton in coupling the classic and microbial food webs.

CONCLUSION

Ongoing climate change is reducing the duration of the ice-cover period while prolonging the open-water season on north temperate lakes (Sharma *et al.*, 2020). This may impact lake food webs and energy flow among trophic levels (Wollrab *et al.*, 2021). Zooplankton are a crucial component in the energy transfer from bacteria and phytoplankton to fishes in lakes. Therefore, it is important to understand how seasonal changes alter zooplankton communities in lakes of different trophic status, how zooplankton will be affected by the shortening of ice cover, and how these changes will modify energy transfer from the base of the food web to long-lived consumers. Our study represents only one sampling date in winter and summer across diverse lakes and potentially might demonstrate different seasonal successional patterns among zooplankton communities. Nonetheless, this study provides new insights into seasonal zooplankton dynamics across lakes of different trophic states. We showed that zooplankton communities in all lakes are still active under the ice despite low phytoplankton biomass. We found that zooplankton community composition changed dramatically but predictably between seasons. Finally, feeding group and stable isotope analyses suggest changes in the food sources that support zooplankton during the winter. Nonetheless, many questions about winter in lakes remain. Year-round limnological studies that examine community and trophic dynamics across the entire food web (from bacteria to fish) are needed to improve prediction of what the future holds for our changing lakes.

DATA ARCHIVING

Original data for this study are available online via the Data Repository for University of Minnesota (DRUM; Shchapov *et al.*, 2021). They include CTD profiles, water chemistry parameters and zooplankton abundance and community composition data.

SUPPLEMENTARY DATA

Supplementary data is available at *Journal of Plankton Research* online.

ACKNOWLEDGEMENTS

FUNDING

REFERENCES

Adams, T. S. and Sterner, R. W. (2000) The effect of dietary nitrogen content on trophic level 15N enrichment. *Limnol. Oceanogr.*, **45**, 601–607.

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

Auer, B., Elzer, U. and Arndt, H. (2004) Comparison of pelagic food webs in lakes along a trophic gradient and with seasonal aspects: influence of resource and predation. *J. Plankton Res.*, **26**, 697–709.

Balcer, M. D., Korda, N. L. and Dodson, S. I. (1984) *Zooplankton of the Great Lakes: a guide to the identification and ecology of the common crustacean species*, The University of Wisconsin Press, Madison, WI.

Bec, A., Desvilettes, C., Véra, A., Lemarchand, C., Fontvieille, D. and Bourdier, G. (2003) Nutritional quality of a freshwater heterotrophic flagellate: trophic upgrading of its microalgal diet for *Daphnia hyalina*. *Aquat. Microb. Ecol.*, **32**, 203–207.

Bengtsson, L. (2011) Ice-covered lakes: environment and climate-required research. *Hydrol. Process.*, **25**, 2767–2769.

Benndorf, J., Böing, W., Koop, J. and Neubauer, I. (2002) Top-down control of phytoplankton: the role of time scale, lake depth and trophic state. *Freshwater Biol*, **47**, 2282–2295.

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

Bern, L. (1994) Particle selection over a broad size range by crustacean zooplankton. *Freshwater Biol*, **32**, 105–112.

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

Blank, K., Haberman, J., Haldna, M. and 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.

Bolsenga, S. J. and 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**, 95–104.

Brett, M. T., Kainz, M. J., Taipale, S. J. and Seshan, H. (2009) Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. *Proc. Natl. Acad. Sci. U. S. A.*, **106**, 21197–21201.

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

Butts, E. and Carrick, H. J. (2017) Phytoplankton seasonality along a trophic gradient of temperate lakes: convergence in taxonomic composition during winter ice-cover. *Northeastern Nat*, **24**, 167–187.

Carpenter, S. R., Cole, J. J., Pace, M. L., Van de Bogert, M., Bade, D. L., Bastviken, D. and Kritzberg, E. S. (2005) Ecosystem subsidies: terrestrial support of aquatic food webs from 13C addition to contrasting lakes. *Ecology*, **86**, 2737–2750.

Clarke, K. R. and Warwick, R. M. (2001) A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Mar. Ecol. Prog. Ser.*, **216**, 265–278.

Deines, P., Wooller, M. J. and Grey, J. (2009) Unravelling complexities in benthic food webs using a dual stable isotope (hydrogen and carbon) approach. *Freshwater Biol*, **54**, 2243–2251.

Elgmork, K. (2006) A monograph of life history strategies of the freshwater, planktonic copepod *Cyclops scutifer* GO SARS 1863 (with 19 figures and 8 tables). *Arch Hydrobiol, Suppl*, **151**, 301–352.

Farjalla, V. F., Amado, A. M., Suhett, A. L. and Meirelles-Pereira, F. (2009) DOC removal paradigms in highly humic aquatic ecosystems. *Environ. Sci. Pollut. Res.*, **16**, 531–538.

France, R. L. (1995) Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. *Limnol. Oceanogr.*, **40**, 1310–1313.

Galloway, A. W., Taipale, S. J., Hiltunen, M., Peltomaa, E., Strandberg, U., Brett, M. T. and Kankaala, P. (2014) Diet-specific biomarkers show that high-quality phytoplankton fuels herbivorous zooplankton in large boreal lakes. *Freshwater Biol*, **59**, 1902–1915.

Gannon, J. E. (1980) Towards improving the use of zooplankton in water quality surveillance of the St. Lawrence Great Lakes. *Can Tech Rep Fish Aquat Sci*, **976**, 87–109.

Gliwicz, M. Z., Slusarczyk, A. and Slusarczyk, M. (2001) Life history synchronization in a long-lifespan single-cohort daphnia population in a fishless alpine lake. *Oecologia*, **128**, 368–378.

Goldstein, H. and Healy, M. J. (1995) The graphical presentation of a collection of means. *J R Statist Soc: A*, **158**, 175–177.

Gosselin, M., Legendre, L., Demers, S. and Ingram, R. G. (1985) Responses of sea-ice microalgae to climatic and fortnightly tidal energy inputs (Manitounuk Sound, Hudson Bay). *Can. J. Fish. Aquat. Sci.*, **42**, 999–1006.

Grey, J., Jones, R. I. and Sleep, D. (2000) Stable isotope analysis of the origins of zooplankton carbon in lakes of differing trophic state. *Oecologia*, **123**, 232–240.

Grosbois, G., Mariash, H., Schneider, T. and Rautio, M. (2017) Under-ice availability of phytoplankton lipids is key to freshwater zooplankton winter survival. *Sci. Rep.*, **7**, 1–11.

Gu, B., Alexander, V. and Schell, D. M. (1999) Seasonal and interannual variability of plankton carbon isotope ratios in a subarctic lake. *Freshwater Biol.*, **42**, 417–426.

Gu, B., Schelske, C. L. and Waters, M. N. (2011) Patterns and controls of seasonal variability of carbon stable isotopes of particulate organic matter in lakes. *Oecologia*, **165**, 1083–1094.

Hampton, S. E., Galloway, A. W., Powers, S. M., Ozersky, T., Woo, K. H., Batt, R. D., Labou, S. G., O'Reilly, C. M. *et al.* (2017) Ecology under lake ice. *Ecol. Lett.*, **20**, 98–111.

Hamrová, E., Mergeay, J. and Petrusek, A. (2011) Strong differences in the clonal variation of two Daphnia species from mountain lakes affected by overwintering strategy. *BMC Evol. Biol.*, **11**, 231.

Haney, J. F., Aliberti, M. A., Allan, E., Allard, S., Bauer, D. J., Beagen, W., Bradt, S., Carlson, B. *et al.* (2013) *An image-based key to the zooplankton of North America: version 5.0*, University of New Hampshire Center for Freshwater Biology, Durham, NH 03824 USA. (cfb.unh.edu) Accessed 2019.

Hanson, J. M. and Peters, R. H. (1984) Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. *Can. J. Fish. Aquat. Sci.*, **41**, 439–445.

Hansson, L. A., Nicolle, A., Brodersen, J., Romare, P., Anders Nilsson, P., Brönmark, C. and Skov, C. (2007) Consequences of fish predation, migration, and juvenile ontogeny on zooplankton spring dynamics. *Limnol. Oceanogr.*, **52**, 696–706.

Hessen, D. O., Andersen, T. and Lyche, A. (1989) Differential grazing and resource utilization of zooplankton in a humic lake. *Arch Hydrobiol*, **114**, 321–347.

Jensen, T. C. (2019) Winter decrease of zooplankton abundance and biomass in subalpine oligotrophic Lake Atnsjøen (SE Norway). *J Limno*, **78**, 348–363.

Jeppesen, E., Jensen, J. P., Søndergaard, M., Fenger-Grøn, M., Bramm, M. E., Sandby, K., Møller, P. H. and Rasmussen, H. U. (2004) Impact of fish predation on cladoceran body weight distribution and zooplankton grazing in lakes during winter. *Freshwater Biol*, **49**, 432–447.

Jeppesen, E., Jensen, J. P., Søndergaard, M., Lauridsen, T., Pedersen, L. J. and Jensen, L. (1997) Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia*, **342-343**, 151–164.

Kalinowska, K., Napiórkowska-Krzebietke, A., Bogacka-Kapusta, E. and Stawecki, K. (2019) Comparison of ice-on and ice-off abiotic and biotic parameters in three eutrophic lakes. *Ecol Res*, **34**, 687–698.

Kalinowska, K. and Karpowicz, M. (2020) Ice-on and ice-off dynamics of ciliates and metazooplankton in the Łuczański canal (Poland). *Aquat Ecol*, **54**, 1121–1134.

Kankaala, P., Taipale, S., Li, L. and Jones, R. I. (2010) Diets of crustacean zooplankton, inferred from stable carbon and nitrogen isotope analyses, in lakes with varying allochthonous dissolved organic carbon content. *Aquat Ecol*, **44**, 781–795.

Karlsson, J., Jonsson, A., Meili, M. and Jansson, M. (2004) δ15N of zooplankton species in subarctic lakes in northern Sweden: effects of diet and trophic fractionation. *Freshwater Biol*, **49**, 526–534.

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

LakeFinder. *Minnesota Department of Natural Resources*. Accessed June 11, 2021. https://www.dnr.state.mn.us/lakefind/index.html Accessed June 11 2021.

Lampert, W. (1978) Climatic conditions and planktonic interactions as factors controlling the regular succession of spring algal bloom and extremely clear water in Lake Constance: with 4 figures in the text. *Verh – Int Ver Theor Angew Limnol*, **20**, 969–974.

Leech, D. M., Pollard, A. I., Labou, S. G. and Hampton, S. E. (2018) Fewer blue lakes and more murky lakes across the continental US: implications for planktonic food webs. *Limnol. Oceanogr.*, **63**, 2661–2680.

Leppäranta, M. (2014) *Freezing of lakes and the evolution of their ice cover*, Springer-Verlag, Berlin Heidelberg.

Lynch, M. and Ennis, R. (1983) Resource availability, maternal effects, and longevity. *Exp. Gerontol.*, **18**, 147–165.

Mack, H. R., Conroy, J. D., Blocksom, K. A., Stein, R. A. and Ludsin, S. A. (2012) A comparative analysis of zooplankton field collection and sample enumeration methods. *Limnol Oceanograp: Methods*, **10**, 41–53.

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

Mariash, H. (2012) Seasonal feeding strategies of subarctic zooplankton. *Biol Res Univ Jyväskylä*, **241**, 37.

Mariash, H. L., Cusson, M. and Rautio, M. (2017) Fall composition of storage lipids is associated with the overwintering strategy of *Daphnia*. *Lipids*, **52**, 83–91.

Martin-Creuzburg, D., Bec, A. and Von Elert, E. (2005) Trophic upgrading of picocyanobacterial carbon by ciliates for nutrition of *Daphnia magna*. *Aquat. Microb. Ecol.*, **41**, 271–280.

McCusker, E. M., Ostrom, P. H., Ostrom, N. E., Jeremiason, J. D. and Baker, J. E. (1999) Seasonal variation in the biogeochemical cycling of seston in Grand Traverse Bay, Lake Michigan. *Org. Geochem.*, **30**, 1543–1557.

Murphy, J. A. M. E. S. and Riley, J. P. (1962) A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta*, **27**, 31–36.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B. *et al.* (2018) *Vegan: community ecology package*. R package version 2.5–2, https://CRAN.R-project.org/package=vegan.

O'Reilly, C. M., Sharma, S., Gray, D. K., Hampton, S. E., Read, J. S., Rowley, R. J., Schneider, P., Lenters, J. D. *et al.* (2015) Rapid and highly variable warming of lake surface waters around the globe. *Geophys. Res. Lett.*, **42**, 10–773.

Ozersky, T., Bramburger, A. J., Elgin, A. K., Vanderploeg, H. A., Wang, J., Austin, J. A., Carrick, H. J., Chavarie, L. *et al.* (2021) The changing face of winter: lessons and questions from the Laurentian Great Lakes. *Eur. J. Vasc. Endovasc. Surg.*, **126**, e2021JG006247. 10.1029/2021JG006247.

Pace, M. L. and Cole, J. J. (2002) Synchronous variation of dissolved organic carbon and color in lakes. *Limnol. Oceanogr.*, **47**, 333–342.

Perga, M. E., Syarki, M., Spangenberg, J. E., Frossard, V., Lyautey, E., Kalinkina, N. and Bouffard, D. (2021) Fasting or feeding: a planktonic food web under lake ice. *Freshwater Biol*, **66**, 570–581.

Pernica, P., North, R. L. and Baulch, H. M. (2017) In the cold light of day: the potential importance of under-ice convective mixed layers to primary producers. *Inland Waters*, **7**, 138–150.

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

Rautio, M., Sorvari, S. and 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.

Raymond, P. A. and Saiers, J. E. (2010) Event controlled DOC export from forested watersheds. *Biogeochemistry*, **100**, 197–209.

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

Santer, B. (1993) Potential importance of algae in the diet of adult *Cyclops vicinus*. *Freshwater Biol*, **30**, 269–278.

Säwström, C., Karlsson, J., Laybourn-Parry, J. and Granéli, W. (2009) Zooplankton feeding on algae and bacteria under ice in Lake Druzhby, East Antarctica. *Polar Biol*, **32**, 1195–1202.

Schindler, D. W., Carpenter, S. R., Chapra, S. C., Hecky, R. E. and Orihel, D. M. (2016) Reducing phosphorus to curb lake eutrophication is a success. *Environ. Sci. Technol.*, **50**, 8923–8929.

Sharma, S., Blagrave, K., Magnuson, J. J., O'Reilly, C. M., Oliver, S., Batt, R. D., Magee, M. R., Straile, D. *et al.* (2019) Widespread loss of lake ice around the Northern Hemisphere in a warming world. *Nat Clim Change*, **9**, 227–231.

Sharma, S., Meyer, M. F., Culpepper, J., Yang, X., Hampton, S., Berger, S. A., Brousil, M. R., Fradkin, S. C. *et al.* (2020) Integrating perspectives to understand lake ice dynamics in a changing world. *Eur. J. Vasc. Endovasc. Surg.*, **125**, e2020JG005799.

Shchapov, K., Ozersky, T. and Wilburn, P. (2021) *Winter and summer zooplankton community and environmental parameters data of thirteen lakes located in Minnesota and Wisconsin*. Retrieved from the Data Repository for the University of Minnesota, https://doi.org/10.13020/ja8f-q670.

Silsbe, G. M., Behrenfeld, M. J., Halsey, K. H., Milligan, A. J. and Westberry, T. K. (2016) The CAFE model: a net production model for global ocean phytoplankton. *Global Biogeochem. Cycles*, **30**, 1756–1777.

Smyntek, P. M., Teece, M. A., Schulz, K. L. and Storch, A. J. (2008) Taxonomic differences in the essential fatty acid composition of groups of freshwater zooplankton relate to reproductive demands and generation time. *Freshwater Biol*, **53**, 1768–1782.

Sommer, U., Adrian, R., De Senerpont Domis, L., Elser, J. J., Gaedke, U., Ibelings, B., Jeppesen, E., Lürling, M. *et al.* (2012) Beyond the Plankton Ecology Group (PEG) model: mechanisms driving plankton succession. *Annu. Rev. Ecol. Evol. Syst.*, **43**, 429–448.

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

Stine, A. R., Huybers, P. and Fung, I. Y. (2009) Changes in the phase of the annual cycle of surface temperature. *Nature*, **457**, 435–440.

Tranvik, L. J. (1992) Allochthonous dissolved organic matter as an energy source for pelagic bacteria and the concept of the microbial loop. *Hydrobiologia*, **229**, 107–114.

Tsugeki, N. K., Ishida, S. and Urabe, J. (2009) Sedimentary records of reduction in resting egg production of *Daphnia galeata* in Lake Biwa during the 20th century: a possible effect of winter warming. *J. Paleo.*, **42**, 155–165.

Vachon, D., Lapierre, J. F. and DEL Giorgio, P. A. (2016) Seasonality of photochemical dissolved organic carbon mineralization and its relative contribution to pelagic CO2 production in northern lakes. *Eur. J. Vasc. Endovasc. Surg.*, **121**, 864–878.

Vander Zanden, M. J. and Rasmussen, J. B. (2001) Variation in δ15N and δ13C trophic fractionation: implications for aquatic food web studies. *Limnol. Oceanogr.*, **46**, 2061–2066.

Vanni, M. J. and Temte, J. (1990) Seasonal patterns of grazing and nutrient limitation of phytoplankton in a eutrophic lake. *Limnol. Oceanogr.*, **35**, 697–709.

Vinyard, G. L. and O'brien, W. J. (1976) Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). *J. Fish. Res. Board Can.*, **33**, 2845–2849.

Wærvågen, S. B. and Nilssen, J. P. (2010) Life histories and seasonal dynamics of common boreal pelagic copepods (Crustacea, Copepoda) inhabiting an oligotrophic Fennoscandian lake. *J Limnol*, **69**, 311.

Webster, K. E., Soranno, P. A., Cheruvelil, K. S., Bremigan, M. T., Downing, J. A., Vaux, P. D., Asplund, T. R., Bacon, L. C. *et al.* (2008) An empirical evaluation of the nutrient-color paradigm for lakes. *Limnol. Oceanogr.*, **53**, 1137–1148.

"Weekly Snow Depth and Rank Maps". *Minnesota Department of Natural Resources*. Accessed June 11, 2021. https://www.dnr.state.mn.us/climate/snowmap/index.html.

Welschmeyer, N. A. (1994) Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnol. Oceanogr.*, **39**, 1985–1992.

Wetzel, R. G. (2001) *Limnology: lake and river ecosystems*, Academic Press, San Diego.

Wetzel, R. G. and Likens, G. E. (1991) Inorganic nutrients: nitrogen, phosphorus, and other nutrients. In *Limnological analyses*, Springer, New York, NY, pp. 81–105.

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

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

Wickham, H. (2009) Elegant graphics for data analysis. *Fortschr. Med.*, **35**, 10–1007.

Williamson, C. E., Morris, D. P., Pace, M. L. and Olson, O. G. (1999) Dissolved organic carbon and nutrients as regulators of lake ecosystems: resurrection of a more integrated paradigm. *Limnol. Oceanogr.*, **44**, 795–803.

Winder, M. and Schindler, D. E. (2004) Climatic effects on the phenology of lake processes. *GCB Bioenergy*, **10**, 1844–1856.

Wissel, B., Boeing, W. J. and Ramcharan, C. W. (2003) Effects of water color on predation regimes and zooplankton assemblages in freshwater lakes. *Limnol. Oceanogr.*, **48**, 1965–1976.

Wollrab, S., Izmest'yeva, L., Hampton, S. E., Silow, E. A., Litchman, E. and Klausmeier, C. A. (2021) Climate change–driven regime shifts in a planktonic food web. *Proc Am Soc Zool*, **197**, 281–295.

Ye, X., Anderson, E. J., Chu, P. Y., Huang, C. and Xue, P. (2019) Impact of water mixing and ice formation on the warming of Lake superior: a model-guided mechanism study. *Limnol. Oceanogr.*, **64**, 558–574.

Yoshii, K., Melnik, N. G., Timoshkin, O. A., Bondarenko, N. A., Anoshko, P. N., Yoshioka, T. and Wada, E. (1999) Stable isotope analyses of the pelagic food web in Lake Baikal. *Limnol. Oceanogr.*, **44**, 502–511.

Yuan, L. L. and Pollard, A. I. (2018) Changes in the relationship between zooplankton and phytoplankton biomasses across a eutrophication gradient. *Limnol. Oceanogr.*, **63**, 2493–2507.