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Fasting or feeding: A planktonic food web under lake ice

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Abstract

1. Zooplankton can spend winter actively under the ice cover of lakes. However, dietary resources under lake ice are both quantitatively and qualitatively limited, and feeding might not be energetically rewarding for most zooplankton species. Many zooplankters are expected to fast throughout the winter, exhausting their previously accumulated fat storage. We hypothesised that only a fraction of the actively overwintering zooplankton contributes to an active food web under lake ice, leading to few trophic linkages within the planktonic community.
2. Zooplankton habitats and feeding were investigated under the ice of Lake Onego. Zooplankton habitats and migrations were studied by coupling zooplankton sampling around the clock to measurements of particle movement using an acoustic Doppler current profiler. Secondly, fatty acid-specific stable isotope compositions were used to determine whether and which zooplankton fatty acids ultimately came from the assimilation of under-ice seston.
3. The algal biomass was low under ice and mostly dominated by large diatoms. Copepods dominated the zooplankton community. Species present as late copepodite and adult instars were confined to the deeper layers, while nauplii occupied the surface layer. Diel vertical migration by *Cyclops* was the most tangible observation of persistent feeding under the ice. Previously accumulated fat storage represented most of zooplankton fatty acids, with few, yet detectable, fatty acids recently acquired by feeding under the ice.
4. Although some zooplankton taxa maintained feeding activity under the ice of Lake Onego, the food source available beneath the ice was not sufficiently rewarding to leave an isotopic imprint upon the dominant fatty acids of bulk zooplankton. The seston fatty acids that were passed on to zooplankton from feeding under ice were not provided by diatoms, although they made up most of the phytoplankton biovolume. Instead, the zooplankton food web was supported by mixotrophic phytoplankton (i.e. cryptophytes and chrysophytes) that represented <5% of the under-ice biovolume. Consequently, the planktonic food web under the ice of Lake Onego had few trophic linkages, and thereby low connectance.
5. Environmental conditions under the ice of Lake Onego do not depart significantly from those observed in lakes of similar latitudes. Therefore, low connectance food

webs could be relatively common under ice for lakes above 60° latitude. Our methodological approach is applicable to other lakes and could thus disclose the variability of under-ice food webs. This would provide a much more complete picture of annual dynamics of food webs in lakes that ice over.

KEYWORDS
CS-SIA, diel vertical migration, table isotope, winter limnology, zooplankton

1 | INTRODUCTION

The stillness of winter is a challenged paradigm: under the snow and ice covers of soils (Campbell et al., 2005), streams (Gabbud et al., 2019), or lakes (Salonen et al., 2009), biochemical and physiological activities, even if slowed down by thermodynamic constraints, can still persist at biologically significant rates. In lakes for instance, biovolumes of phytoplankton under the ice are on average one sixth of those measured during summer (Hampton et al., 2017). Zooplankton assemblages, although deprived of species that forego the harsh winter conditions in dormancy (Baumgartner & Tarrant, 2017), reach abundances during the iced season that are, on average, one quarter of those of summer (Hampton et al., 2017).

Actively overwintering under lake ice imposes several months of limited food resources, both quantitatively and qualitatively, upon zooplankton. Darkness under thick ice and snow cover hampers primary production (Bertilsson et al., 2013; Bolsenga & Vanderploeg, 1992). Detrital organic matter (from either autochthonous or allochthonous origins) and bacterial or protist cells (Bertilsson et al., 2013; Rautio et al., 2011) constitute the pool of available food sources for herbivorous zooplankton. Their poor nutritional quality might not be compensated for by the low amounts of mixotrophic motile phytoplankton that overcome light limitation to exist under ice (Campbell & Haase, 1981). Where and when light penetration through clear ice allows significant phototrophic growth, zooplankton could be partially relieved from quantitative food limitation. However, if the phytoplankton biomass under ice becomes dominated by large, colonial species (Katz et al., 2015; Maeda & Ichimura, 1973; Twiss et al., 2012; Vanderploeg et al., 1992), gape-limited herbivorous zooplankton will still encounter qualitative food limitation (Campbell & Haase, 1981). In both cases, feeding under ice might not be energetically rewarding for most zooplankton species.

The few studies that investigated crustacean feeding under lake ice suggested that copepod nauplii (Tereza et al., 2007), cladocerans (Rautio et al., 2011; Säwström et al., 2009), and some predatory copepods (Karlsson & Sawstrom, 2009) could maintain some foraging activities. However, extensive accumulation of fat storage before or around the onset of ice cover is a trait that is shared by many of the taxa that dominate zooplankton communities under ice (mainly copepods at copepodite and adult instars ; Grosbois et al., 2017; Mariash et al., 2011; Vanderploeg et al., 1998). Fat-replete zooplankton limit their swimming and feeding activities, likely as a way to *save for the future* (sensu Schneider et al., 2017). They typically migrate to greater depths (Baumgartner & Tarrant, 2017), where they exhaust their lipid reserves with no resupply from either phytoplankton or a bacterial/detrital carbon source for most of the ice season (Grosbois et al., 2017; Rautio et al., 2011). Thereby, only a fraction of the actively overwintering zooplankton might contribute to an active food web under lake ice, leading to few trophic linkages within the planktonic community.

This is the overall hypothesis we tested during late winter in Lake Onego (Russian Karelia). We first assumed that zooplankton vertical habitat would provide indirect evidence on whether and which zooplankton were feeding on under-ice algae. Indeed, the selection of vertical habitat by zooplankton arises from a trade-off between predation risk (light favours visual predators), temperature conditions (energetic constraints) and access to the algal resource (Lampert, 1989). We considered that non-feeding species would stay in the deeper, dark and warmest layers, where predation risks and energetic costs are limited. Feeding species spend time close to their potential food source either by selectively inhabiting the uppermost water layers, or by performing diel vertical migration, if the energetic value of the under-ice food sources balances the costs of migrating or staying in the coldest and sunlit layers. To this end, zooplankton habitats and migrations were studied by coupling frequent zooplankton sampling at different depth layers to measurements of particle movement under ice using an acoustic Doppler current profiler.

Secondly, we hypothesised that if the food sources available under ice are sufficiently nutritionally rewarding, they should support anabolic processes in zooplankton and not only direct catabolism (i.e. dietary carbon or compounds contribute to the synthesis of zooplankton biomass in winter). Due to the composite nature of seston (a mix of particles of many different origins, including detritus, heterotrophic microbes and different phytoplankton taxa), $\delta^{13}C$ alone does not resolve food web pathways at the seston–zooplankton interface (Bec et al., 2011; Perga et al., 2013). This is because a mismatch between seston and zooplankton $\delta^{13}C$ could indicate both that seston carbon is not transferred to the zooplankton biomass (no rewarding feeding) or that zooplankton are feeding selectively on algal particles whose $\delta^{13}C$ values differ from those of bulk seston (Grey et al., 2000). Different seston pools have different typical fatty acids (FA). For instance, omega-3 polyunsaturated FA indicate algal sources. However, the FA composition alone might also lead to ambiguous conclusions: typical FA for phytoplankton sources are likely to be found in zooplankton lipids in winter, although they might

have been accumulated before winter (Grosbois et al., 2017). In this study, we provide the first attempted study of FA-specific stable isotope compositions (SIA) under lake ice as a way to discriminate the isotope composition of different seston pools and to determine whether the FA in zooplankton biomass originated from the under ice seston FA.

2 | METHODS

2.1 | Study site

Lake Onego lies in the Karelian portion of Russia and is the second largest lake in Europe (9,700 km^2). It is dimictic and typically ice-covered from December to mid-April each year. This study was conducted between the 15 and 17 March 2017 in Petrozavodsk Bay (depth of 27 m) in the western part of the lake (61°48′26.8″N, 34°26′01.1″E). The waters are yellow-stained, oligo-mesotrophic with concentrations of dissolved organic carbon ranging from 9 to 27 mg C/L under the ice (Suarez et al., 2019). At the sampling dates, the lake was inversely stratified, with water temperatures ranging between 0 and 1°C (Figure 1). The ice was clear and allowed light penetration down to 1.7 m depth (photic depth). The warming, by solar radiation, of near-surface water from the freezing point towards the temperature of maximal density created daily convection. On our sampling days in Lake Onego, under-ice convection started after sunrise (7:00) to reach its maximum velocity (3 mm/s) 3 hours later (Bouffard et al., 2019). Under-ice convection developed during daytime down to the 10–15 m depth and was maintained until sunset (19:00) and finally slowed down and stopped around 21:00 (Bouffard et al., 2019). Daily convection entrained the phytoplankton below the photic depth, down to the 10–15m depths (Suarez et al., 2019). The chlorophyll *a* concentration was low: 0.3 ± 0.2 μg/L (mean ± *SD*) in the convective layer (Figure 1, Suarez et al., 2019). The diatom *Aulacoseira sp*. dominated the assemblage (>90% of total phytoplankton biovolume) while the remaining 10% comprised other diatoms (5%), the dinophyte *Peridium pusillum*, the Chrysophyceae *Mallomonas* sp. and the Cryptophyceae *Chroomonas* sp., *Cryptomonas* sp., and *Komma caudata* (5%) (Suarez et al., 2019).

2.1.1 | Zooplankton migration and depth selection under ice

An acoustic Doppler current profiler (ADCP; Nortek Signature 1,000 kHz with echo sounding mode) was frozen in the ice facing downward, and acoustic data were collected continuously over the 3 days of the study (sampling interval 4 Hz, vertical resolution 5 cm). The data were analysed for temporal and vertical changes in the intensity of the backscatter signal (mean volume backscattering strength [dB]) to determine the presence, timing, and movements of large particles under the ice. Given the frequency of the ADCP, the acoustic signal was best reflected to 480 μm particles with a lower

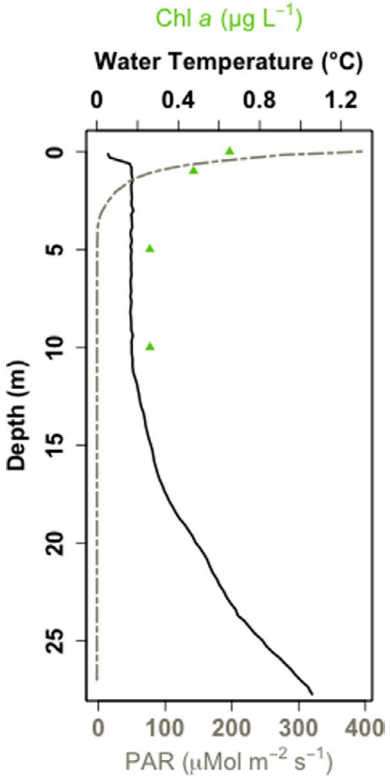

FIGURE 1 Vertical profiles of water temperature (solid black line), PAR (dashed line, both measured by a CTD75M from Sea and Sun [Trappenkamp, Germany]) and chlorophyll *a* (green points, chlorophyll a measurements after extraction on discrete water samples) for 17 March 2017 (at sampling time, data courtesy of E. Suarez and R. Zdorovennov) [Colour figure can be viewed at wileyonlinelibrary.com]

limit of 25 μm. The acoustic signal was converted into the mean volume backscattering strength using the sonar equation, thereby correcting for the attenuation of the acoustic signal with the distance from the emitter-receiver. Averaged vertical velocity of moving particles was inferred by following the space-time evolution of the peak in backscattering.

Because the ADCP provided no taxonomic resolution, zooplankton sampling was conducted using vertical trawls with a 64-μm mesh, 23-cm diameter closing net every 3 hr for 39 hr. The depth layers sampled were chosen according to the vertical thermal structure of the lake (i.e. 0–5, 5–10, and 10 m to the lake bottom 27 m). Samples were fixed with 4% formalin and counted using a stereomicroscope at the Northern Water Problems Institute of the Karelian Research Centre of the Russian Academy for Science. The organisms were identified to the species level, including instars where possible.

Potential selection of depth habitats by the four most abundant zooplankton taxa was tested using χ^2 tests of zooplankton concentrations in the depth layers averaged over a full 24 hr cycle. Observed concentrations along depths at midday (three sampling times from 9:00 to 14:30 on 16 March) and midnight (three sampling times from 21:00 to 03:00 in the nights of 15/16 March [night 1] and 16/17 March [night 2]) were compared to theoretical concentrations under the assumption of a uniform vertical distribution (theoretical value = average

concentration weighted by the thickness of the sampled layers). Changes in the depth habitats within times of day were tested, for the four dominant taxa, by bifactorial χ^2 tests, and the potential vertical dynamics were identified using the standardised residuals over time and depths for each taxon. All statistical analyses were conducted in R version 3.5.1 (The R Foundation for Statistical Computing).

2.2 | Fatty acid and FA-SI compositions of seston and zooplankton

2.2.1 | Sampling

Chlorophyll *a* concentrations were maximal in the morning, within the 0–2 m right underneath the ice (Suarez et al., 2019, Figure 1). Therefore, water intended for seston collection was sampled within the upper convective layer (pooled samples from 0.5 m below the ice and at 5 m depth) using a 2-L Niskin bottle on the last morning of the campaign. The water samples were filtered on pre-combusted glass fibre filters (Whatman GF/F, 0.7 μm nominal pore size; 1.5 L per filter). Zooplankton were collected under the ice by vertical trawls with a 64-μm mesh 23-cm diameter net over the whole water column. They were allowed to empty their guts for 4 hr in the dark. *Mysis* sp. that incidentally occurred in the zooplankton samples were removed. The seston and bulk zooplankton samples were frozen on site in liquid nitrogen and kept frozen until analysis.

2.2.2 | Lipid extraction and FA separation

Seston filters and zooplankton samples were analysed for their FA composition in the Stable Isotope and Organic Geochemistry Laboratories at the Institute of Earth Surface Dynamics, University of Lausanne (Switzerland) using adapted procedures (Spangenberg et al., 2006, 2014). All solvents used for lipid extraction and FA separations were of a quality suitable for chromatography and were glass-distilled shortly before use. Anhydrous sodium sulfate and hydrochloric acid (HCl, 35% w/w) were of analytical grade or higher purity. To avoid cross-contamination and to minimise background signal, all glassware used for sample handling was thoroughly washed, rinsed with deionised water and heated (480°C, > 4 hr) before use. All the samples were frozen at −20°C for 2 days, freeze-dried and, stored at −20°C for lipid extraction. The dried filters were cut into pieces using organic-solvent cleaned forceps and scissors before lipid extraction. An aliquot of internal standard solution containing a defined amount of deuterated carboxylic acids (D_{23}*n*-$C_{12:0}$, lauric acid, D_{39}*n*-$C_{20:0}$, arachidic acid, Cambridge Isotopes Laboratories, Tewksbury, MA, U.S.A.) in dichloromethane was added to each sample, for identification and quantification of FA. Total lipids were then extracted using vortexing and sonication in solvents of decreasing polarity: 2 × methanol, 2 × methanol/dichloromethane, 2 × dichloromethane). The extracts were combined and the solvent removed via gentle evaporation under a clean nitrogen flow. The carboxylic acids were obtained by hydrolysis with 10% KOH/MeOH at room temperature for > 16 hr. The non-saponifiable lipids were separated with several hexane aliquots. The fraction containing the acid lipids was acidified with 1 N HCl to pH < 1, and the FA extracted with hexane and methylated (boron trifluoride/methanol solution) to provide FA methyl esters (FAMEs). The FAMEs were stored at −20°C until analysis.

2.2.3 | Chemical characterisation and quantification of FAs

Chemical characterisation of FAMEs was performed by gas chromatography/mass spectrometry (GC/MS) using an Agilent (Palo Alto, U.S.A.) 6890 GC connected to an Agilent 5973 mass selective detector operating at 70 eV (source 230°C and quadrupole 150°C) in the electron ionisation mode (emission current 1 mA, multiple ion detection over m/z 20 to 550), and helium as carrier gas. The FAMEs were analysed with the fused silica HP-FFAP (50 m × 0.20 mm; length × inner diameter) coated with 0.33 μm nitroterephthalic acid modified polyethylene glycol stationary phase. Samples were injected splitless at 230°C. After an initial period of 2 min at 100°C, the column was heated to 240°C (held 26 min) at 5°C/min, then to 245°C (held 4 min). These GC conditions were optimised for good separation of unsaturated FAs.

Due to their very low concentrations of FA, the seston samples (15 in total) were pooled by three for further analyses, permitting at least triplicate runs. The FAMEs of the merged seston filter samples ($n = 5$) and the zooplankton ($n = 6$) were next analysed with another fused silica column and GC temperature programs to permit the detection of long chain FAs (i.e. PUFAs). An Agilent HP-ULTRA 2 (50 m × 0.32 mm i.d.) coated with 0.17 μm 5% phenylmethylsilicone stationary phase. Samples were injected splitless at 320°C. After an initial period of 2 min at 100°C, the column was heated to 310°C (held 20 min) at 4°C/min.

Compound identification was based on comparison with standards, GC retention time, and MS fragmentation patterns. The PUFA isomers were assigned by comparison of retention time and MS spectra with those obtained from the GC/MS chromatogram of the Supelco 37 FAME mixture. Quantification of the FA was done by comparison of the peak area of the FA with that of the internal standards. Potential shifts due to the different unsaturation degree of analytes and internal standards were checked periodically by injection of the Supelco FAME mix (procedure validated previously, Bellworthy et al., 2019). The differences between the ratio of certificate concentrations of saturated FA and PUFA (i.e. 16:0/20:5ω3, 18:0/20:5ω3, 20:0/20:5ω3, 16:0/22:6ω3, 18:0/22:6ω3, 20:0/22:6ω3) and those obtained from the peak area of the GC/MS were <5%. One blank sample was run for every six samples throughout the analytical procedure. The absence of any measurable recovered extract from the blanks indicates that no detectable laboratory contamination was introduced to the seston filter and zooplankton samples during the analytical procedure.

2.2.4 | Carbon isotope analysis of FAs

The compound-specific stable carbon isotope analysis of the FA was done using a GS/combustion/isotope ratio MS (IRMS) with an Agilent 6,890 GC instrument coupled to a Thermo Fisher Scientific (Bremen, Germany) Delta V Plus IRMS instrument via a combustion interface III under a continuous helium flow. GC separation was performed with the HP-FFAP column and temperature programme used for GC/MS. The stable isotope compositions were reported in the δ notation as variations of the molar ratio R of the heavy (^{i}E) to light isotope (^{j}E) of element E (i.e. ^{13}C/^{12}C) relative to an international standard:

$$\delta^{i}E_{\text{sample / standard}} = \frac{R(^{i}E/^{j}E)_{\text{sample}}}{R(^{i}E/^{j}E)_{\text{standard}}}$$

For carbon stable isotope ratios (δ^{13}C), the standard is the Vienna Pee Dee Belemnite limestone. For calibration, the previously determined C isotopic compositions (by elemental analysis/IRMS) of the deuterated carboxylic acids added as internal standards were used. For quality control, the repeatability and intermediate precision of the GC/combustion/IRMS analysis and the performance of the GC and combustion interface were evaluated every 5 runs by injection of a carefully prepared mixture of FAMEs reference materials (Spangenberg et al., 2014), methyl icosanoate (δ^{13}C −25.38‰) from the Biogeochemical Laboratories at Indiana University, U.S.A., and duplicate analyses of the FAME fractions of Lake Onego samples. The standard deviation for repeatability of the δ^{13}C values ranged between ±0.05 and ±0.5‰, depending on the concentration (m/z 45 peak size between 15,000 mV and <500 mV). The isotopic shift due to the carbon introduced by methylation was corrected using the following mass balance equation (Spangenberg et al., 1998):

$$\delta^{13}C_{FA} = \left((n+1) * \delta^{13}C_{FAME} - \delta^{13}C_{MeOH} \right) / n.$$

where $\delta^{13}C_{FAME}$ and $\delta^{13}C_{MeOH}$ are the δ^{13}C values of the measured FAME and methanol used during methylation, respectively. Delta $^{13}C_{FA}$ represents the δ^{13}C value of the given FA prior to methylation, and *n* is the number of carbon atoms in the (nonmethylated) FA.

2.2.5 | Analyses of FA and FA-SIA results

Results were analysed with regard to the known biomarker properties of FA: the saturated FA 14:0, 16:0, and 18:0 were considered as generic markers of both living and detrital organic matter (Boschker et al., 2005). The mono-unsaturated 16:1ω7 can be found in high abundances in both diatoms and Gram-negative bacteria (Taipale et al., 2015) and was therefore regarded as a potential biomarker for both. Source-specific biomarkers included odd- (15:0 and 17:0) and branched-chain FA (15:0i, 15:0a, 17:0i, 17:0a) as markers for Actinobacteria (further referred as to bacterial FA, see Grosbois et al., 2017, for a synthesis). The PUFA 18:3ω3, 20:4ω6, 20:5ω3, and 22:6ω3, typical of many of the algal taxa present at the sampling dates (i.e. diatoms, cryptophytes, chrysophytes, and dinophytes), were considered as generic markers for phytoplankton, while the FA 18:4ω3, absent from diatoms, is a marker highly specific to cryptophytes and chrysophytes (Taipale et al., 2013).

3 | RESULTS

3.1 | Zooplankton movements under ice

The backscattering echo showed upward and downward synchronised movements from particles of sizes comparable with

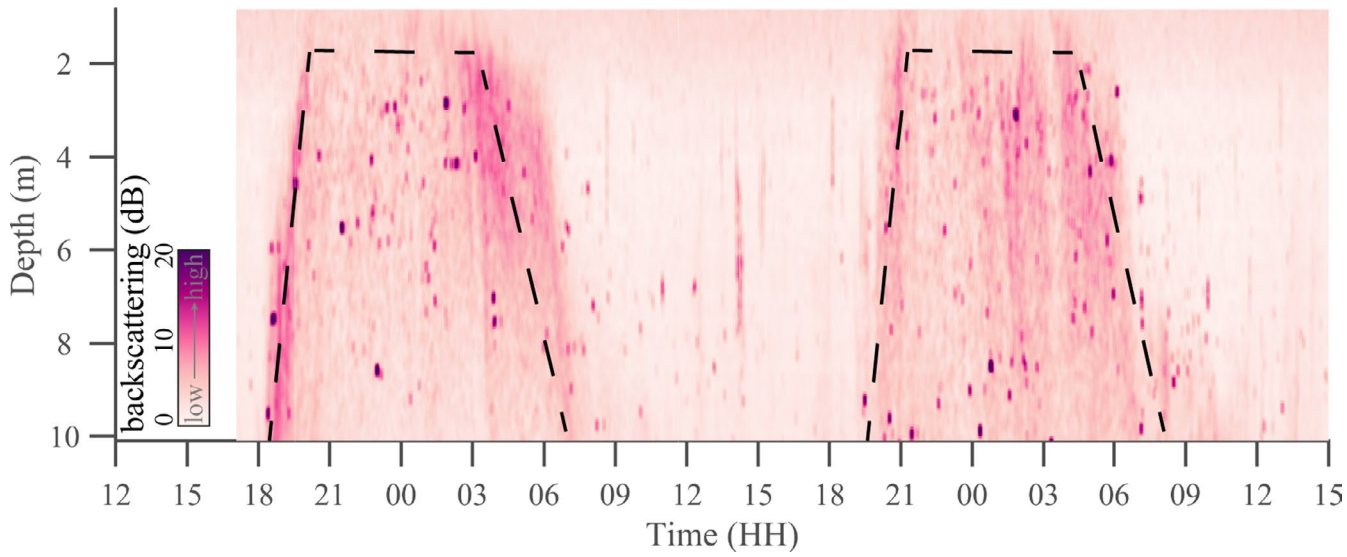

FIGURE 2 Mean volume backscattering strength (dB) from the downward-looking ADCP from 15 to 17 March 2017. The dashed line highlights depths of elevated backscattering over time (i.e. vertical movements) [Colour figure can be viewed at wileyonlinelibrary.com]

crustacean zooplankton (Figure 2). Upward movements from at least the 10 m depth up to the 2 m depth occurred between 18:00 and 21:00 for both monitored days, and the reverse downward movements occurred between 5:00 and 8:00 the following morning. The vertical displacement corresponded to a mean vertical velocity of 5.7 ± 0.4 mm/s.

3.2 | Zooplankton composition, taxonomic depth habitats, and changes in time

Altogether, 21 zooplankton taxa (12 crustacean and nine rotiferan taxa, Figure S1) were observed, but four copepod taxa represented >90% of total abundances. The average abundance of zooplankton was 0.500 ind/L (*SD* = 0.238 ind/L). The nauplii of indistinct Cyclopoida species contributed up to 35% of the community, while the calanoid *Eudiaptomus gracilis*, exclusively at the late copepodite and adult stages, represented 30% of the total abundance. *Cyclops* spp. from different copepodite stages (CIV and V mainly) contributed 15% and *Megacyclops gigas* at the adult and late copepodite stages contributed approximately 10%. All four dominant zooplankton taxa showed a significant selection for a depth layer (Table 1). Cyclopoid nauplii were more concentrated in the convective layer, above the 10m depths, while *E. gracilis* was found preferentially below the 10-m depth. *Cyclops* copepodites were more abundant at intermediate depths, in 5 and 10 m. *Megacyclops gigas* was more concentrated below the 5-m depth.

The vertical distribution of *E. gracilis* and *M. gigas* did not change much between midday and midnight (Figure 3b, d; Figure S1b, d). Cyclopoid nauplii were more abundant in the uppermost layer at midday (Figure 3a) although the changes in the standard residuals over the time of the day did not show any clear diel dynamics (Figures S1, 2a). The vertical distribution of copepodite stages of *Cyclops* sp. was the most dependent on the time of day, with higher concentrations in the 0–5-m depth layer for both studied nights and a maximum concentration in the intermediate depth layer during the day (Figure 3c, Figure S1 2c). Changes in the standard residuals over time suggest that *Cyclops* copepodites moved down from the uppermost (0–5 m) to the intermediate depth layer (5–10-m) between 6:00 and 9:00 and back up in between 18:30 and 21:00, a timing and vertical range that matched those detected by the ADCP.

TABLE 1 Pearson's residuals (observed-theoretical/sqrt[theoretical]) from the χ^2 test of vertical distribution of the concentrations of the four dominant taxa, over a full diel cycle (16 March 2017). All tests were significant $p < 0.001$

Depth layers	Cyclopoid Nauplii	*E. gracilis*	*Cyclops* sp.	*M. gigas*
0–5 m	22	−115	−50	−50
5–10 m	4	−55	149	34
10 m-bottom	−26	170	−99	15

3.3 | Fatty acid and FA-SI composition of the seston and zooplankton

3.3.1 | Fatty acid composition

The concentrations of total seston FA in the water were low (40 μg/L), as could be expected from the limited phytoplankton biomass. The sum of the FA biomarkers that we retained for the study represented 78 and 80% of total FA concentrations in, respectively, seston and zooplankton. Even-chain saturated FA biomarkers and 16:1ω7 made up to 75% of the total seston FA (Figure 4a), the 16:0 and 18:0 FA alone representing 60%. Bacterial FA contributed to 3% of total seston FA. Phytoplankton-derived FA contributed to < 1%, the 18:4ω3 and 18:4ω3 being the only FAs specific to phytoplankton that could be recovered in measurable amounts (long-chain PUFA were virtually absent). The total FA composition of zooplankton was quite different from that of seston (Figure 4b). In zooplankton, the even-chain saturated FA biomarkers and 16:1ω7 made up to 52% of total FA, with a comparatively higher contribution of 16:1ω7 and 14:0, and a lower share of 18:0 as compared to seston. Phytoplankton derived FAs contributed a much larger share of total FA in both bulk zooplankton (24%). Contrary to seston, long-chain PUFA (20:5ω3, 20.4ω6 and 22:6ω3) contributed half of the phytoplankton-derived FA, while 18:4ω3 and 18:4ω3 each contributed 6%. As for seston, bacterial FA contributed a low share of total zooplankton FA (<2%).

Fatty acid SIA

The variability of FA $\delta^{13}C$ was large, spanning over a 10‰ range in both the seston and zooplankton samples, and attested to diverse FA origins (Figure 5). The generic, even-chain saturated FA, 16:1ω7, and bacterial FA in seston (i.e. FA that contributed up to 77% of total FA) had $\delta^{13}C$ values tightly clustered at −29.5‰ (*SD* = 0.85‰; Figure 5a). By contrast, the biomarker FA for cryptophytes/chrysophytes (i.e. 18:4ω3) had a $\delta^{13}C$ value that was 8‰ lower than the generic and bacterial FA biomarkers (mean −37.4‰, *SD* = 0.6‰). The generic phytoplankton biomarker 18:3ω3, that is typically abundant in all the phytoplankton taxa observed under the ice of Lake Onego (i.e. diatoms, cryptophytes, and chrysophytes), had highly variable $\delta^{13}C$ values spreading in between these two extremes.

The similar $\delta^{13}C$ values for the generic, 16:1ω7 and bacterial FA matched the $\delta^{13}C$ values expected for the terrestrial-derived organic matter in a boreal landscape (Karlsson et al., 2003; Lajtha & Michener, 1994). The water colour, the high dissolved organic carbon content, and the low algal biomass under the ice of Lake Onego imply that the organic matter pool may be loaded by detrital, terrestrial organic matter. However, part of the 16:1ω7 and 18:3ω3 in seston came from the diatoms, and their $\delta^{13}C$ values suggested that the diatom biomass under ice could exhibit a $\delta^{13}C$ value that cannot be distinguished from that of the terrestrial endmember (i.e. the isotopic value representative for the terrestrial organic matter). This would imply taxon-specific $\delta^{13}C$ values

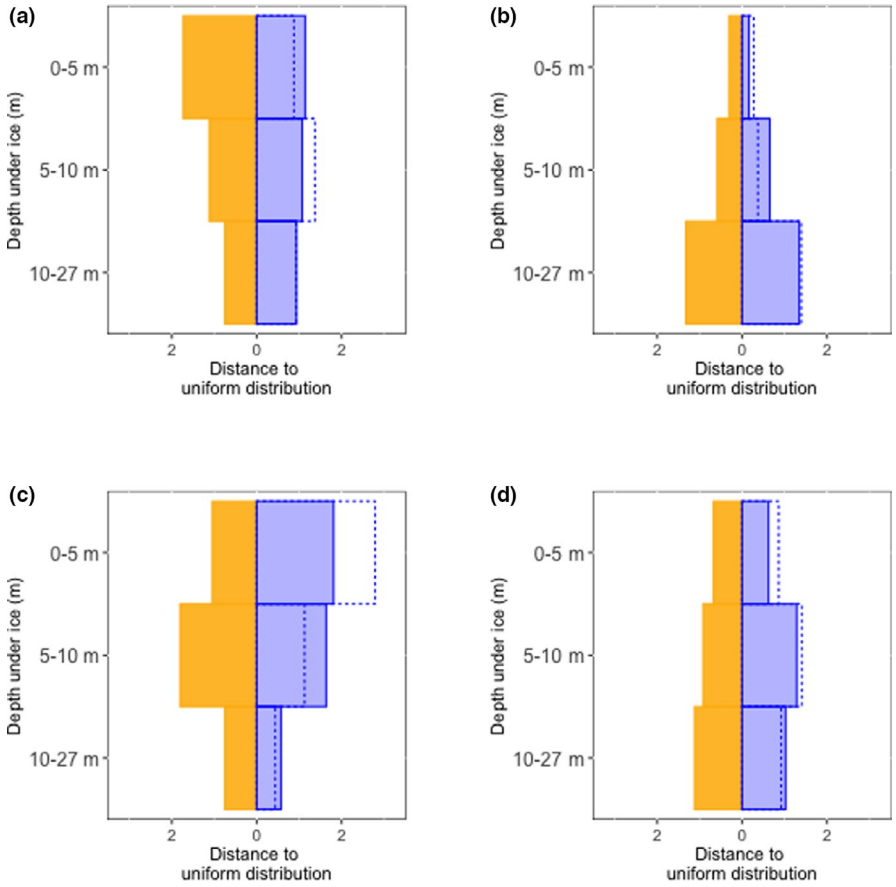

FIGURE 3 Vertical distribution of the four dominant taxa in Lake Onego between 15 and–17 March 2017 at midday (yellow) and midnight (blue fill for night 1, dotted blue line for night 2). The taxa are ordered according to their decreasing contribution to the total water column assemblage, and the data are the ratio between the observed concentration for a given depth layer and theoretical concentration expected for a vertically uniform distribution (i.e. distance to uniform distribution). (a) Cyclopoida nauplii, (b) *Eudiaptomus gracilis* (adults and copepodites), (c) *Cyclops* copepodites, (d) *Megacyclops gigas* (adults and copepodites) [Colour figure can be viewed at wileyonlinelibrary.com]

for the co-existing phytoplankton taxa, which would not be surprising considering the known differences in cell size and physiology between diatoms and chrysophytes/cryptophytes (Vuorio et al., 2006). We therefore considered the average $\delta^{13}C$ value for the generic, 16:1ω7 and bacterial FA as an endmember encompassing the isotopic signals of the terrestrial, detrital organic matter and diatoms, while the $\delta^{13}C$ value for the 18:4ω3 was regarded as an unambiguous endmember of the isotopic signal of chrysophytes and cryptophytes (Figure 5).

The carbon isotopic composition of individual FA in zooplankton differed markedly from that of seston, and only a few FA had $\delta^{13}C$ values that matched those of the two endmembers (Figure 5b). Three of the six bacterial FA (15:0i and a, and 17:0) had $\delta^{13}C$ values that fell within the detrital-diatom endmember while 18:3ω4 and 18:3ω3 had $\delta^{13}C$ close to the cryptophyte/chrysophyte endmember. However, the generic FA, the 16:1ω7, and the phytoplankton-derived FA of 20 or more C atoms had $\delta^{13}C$ values clustered around −34‰, that is a value that fell in between the two endmembers.

4 | DISCUSSION

Our study provides clear evidence of a planktonic food web persisting under the ice of Lake Onego in late winter. However, in this energy-limited cold environment, the planktonic food web had few trophic linkages. The low algal biomass under the ice of lake Onego resulted in a low total FA concentration in total seston. Under clear ice, the large filamentous diatom species *Aulacoseira* sp. can develop but its growth becomes quickly light-limited by the coloured nature of the waters and the depth of convection that entrains the cells well below the photic depth (Suarez et al., 2019). Although dominating the biomass, *Aulacoseira* sp. might not provide adequate food for zooplankton. Firstly, the edibility of these large colonial algae is limited because of the gape limitation of most filter-feeder zooplankton (Infante & Litt, 1985; Kerfoot & Kirk, 1991) and the average length of filaments was 250 μm when sampled (Suarez et al., 2019). Secondly, eicosapentaenoic acid (20:5ω3), which is a typical biomarker for diatoms, along with an indicator of good food quality (Gulati & De Mott, 1997), was only detected in trace amounts in the seston, suggesting that the diatom biomass was particularly poor in lipids and PUFA at our sampling period. The lipid content of *Aulacoseira*sp. varies from low concentrations in reproductive cells in the beginning of algal development under ice to abundant lipid reserves in larger vegetative cells as ice break up in lakes (Jewson et al., 2010). The low fat and 20:5ω3 content of the under-ice seston might indicate that we caught *Aulacoseira* while it was still in its reproductive stage. As a result of low total phytoplankton biomass, potential dilution with terrestrial and detrital organic matter, as well as the low fat content of *Aulacoseira* under the ice of Lake Onego, seston lacked the diatom FA fingerprint (14:0, 16:0, 16:1ω7, 20:5ω3) in spite of their dominance in phytoplankton under ice. Zooplankton dietary resources

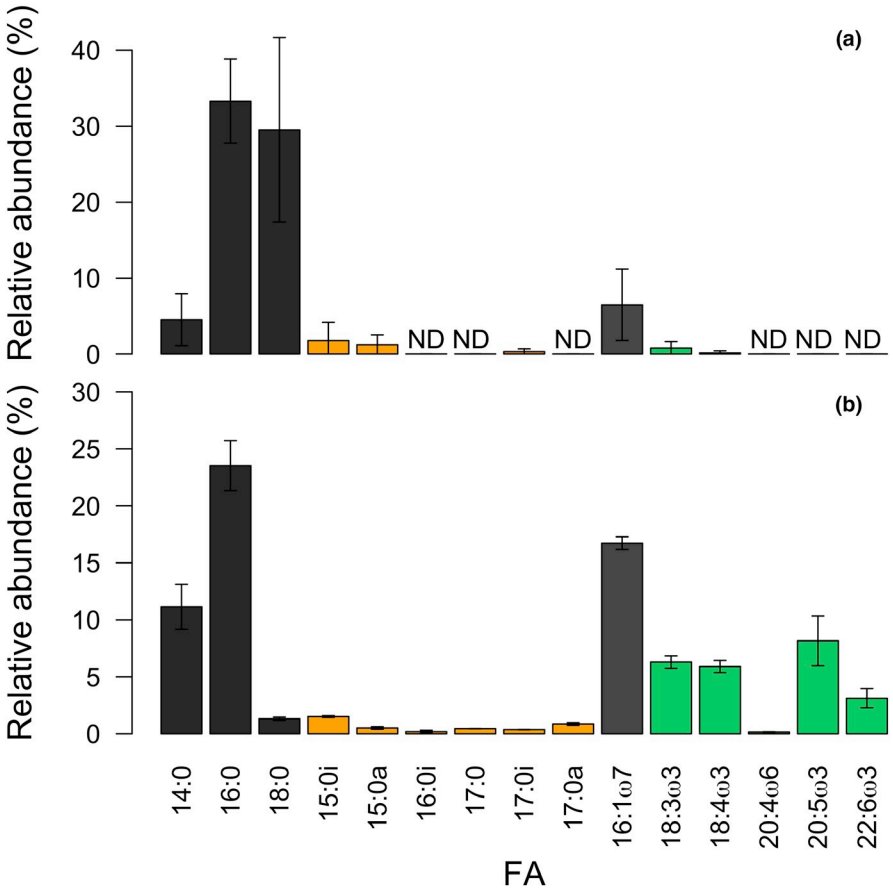

FIGURE 4 Average contribution (mean ± *SD*) of selected fatty acids (FA) to (a) seston and (b) bulk zooplankton. Generic FA are indicated in black, typical FA for Actinobacteria in orange, the 16:1ω7 in grey and typical phytoplankton FA in green. ND = not detected [Colour figure can be viewed at wileyonlinelibrary.com]

were, as expected, quantitatively and qualitatively limited under the ice of Lake Onego.

In contrast, the diatom FA fingerprint (14:0, 16:0, 16:1ω7, 20:5ω3) was strong in the FA composition of zooplankton, revealing that diatoms are a major dietary resource for zooplankton in Lake Onego. However, the $\delta^{13}C$ values of these diatom biomarker FA in zooplankton were not consistent with those of the corresponding FA in seston under ice, when present. Instead, most of the biomarker FA in zooplankton (representing ≈75% of total FA), amongst which all the diatom fingerprint FA occurred, showed similar $\delta^{13}C$ values, falling between the diatom-terrestrial and the cryptophyte–chrysophyte endmembers present under ice. It is unlikely that the intermediate isotope composition of the major zooplankton FA resulted from mixed feeding on the two dietary sources present in seston under ice. Indeed, the monounsaturated and PUFA of more than 20C were virtually absent from the seston, and the potential precursor that could lead to the bioconversion to long-chain FA was also quite limiting (i.e. 18:3ω3, Gulati & De Mott, 1997). The intermediate and similar isotope composition of these FA in bulk zooplankton is probably inherited from the fat storage accumulated during the previous productive season. Both the FA and FA $\delta^{13}C$ in zooplankton point to a key role for diatoms in constituting the fat storage that enables zooplankton to overwinter but not as the main dietary resource for zooplankton during the iced-over season in Lake Onego.

Only few, minor FA in bulk zooplankton had $\delta^{13}C$ values that matched those measured in contemporary under-ice seston (<15% of zooplankton total lipids): the 18:4ω3 and 18:3ω3 with an isotopic signal typical for the cryptophyte–chrysophyte endmember (12% of zooplankton total lipids), and the bacterial FA 15:0a and 15:0i, 17:0a with a terrestrial-diatomic isotopic signal (<3% of zooplankton total lipids). This study relies on a couple of sampling days but the relative slow turnover of zooplankton fatty-acids (2–3 weeks at optimal growing temperatures and probably longer at near freezing temperatures; Arts et al., 2009) guarantees that these results are not a snapshot but, instead, integrate most of the iced-over period. These FA were therefore passed on to zooplankton through recent feeding under ice. The consistency of the $\delta^{13}C$ values of the cryptophyte–chrysophyte biomarker (18:4ω3) and of the generic phytoplankton biomarker (18:3ω3) in zooplankton reveals that cryptophytes and chrysophytes, although accounting for only 5% of the total phytoplankton biovolume, were the sole supply of newly acquired algal FA to zooplankton under ice. Therefore, at the level of bulk zooplankton, FA-SIA indicated there was sufficient feeding activity to allow some of the under-ice seston FA to be passed on to zooplankton. However, this dietary source was not sufficiently rewarding to leave an isotopic imprint upon the dominant FA in zooplankton (ubiquitous FA such as 16:0 or 18:0, or physiologically important FA such as long-chain PUFA), which were instead representative of fats stored before the iced-over season.

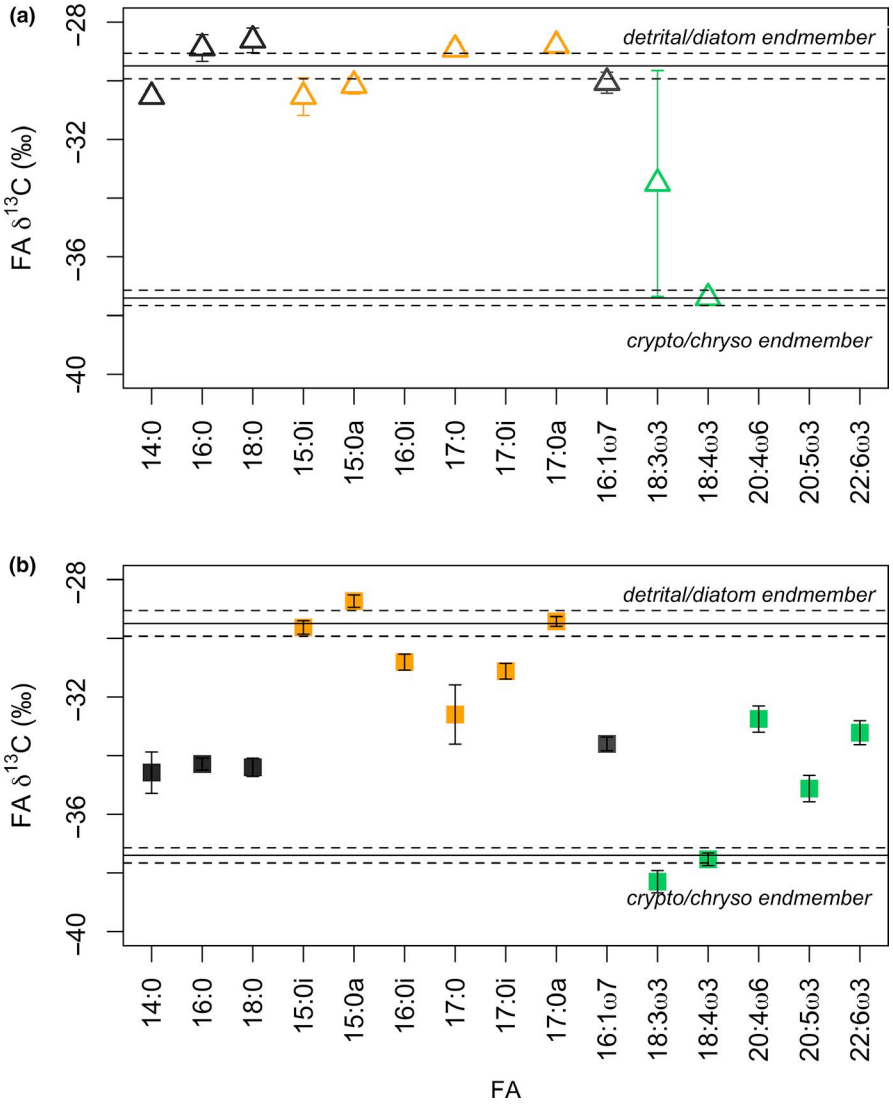

FIGURE 5 Delta ^{13}C values of the individual fatty acids (FA) in (a) seston and (b) zooplankton. Generic FA are indicated in black, typical FA for Actinobacteria in orange, the 16:1ω7 in grey and typical phytoplankton FA in green. The solid and continuous lines indicate the mean (± *SD* in dashed lines) of the $\delta^{13}C$ values of the detrital–diatom endmember and of the $\delta^{13}C$ of the cryptophyte and chrysophyte biomass [Colour figure can be viewed at wileyonlinelibrary.com]

Because zooplankton samples were not sorted by taxon prior to the biomarker analyses, information provided by FA-SIA is only valid at the level of the bulk community. However, data on vertical habitats and migration provide useful hints on which zooplankton taxa were feeding. *Eudiaptomus gracilis* and *M. gigas* usually overwinter in *active dormancy* at late copepodite and adult stages, as they do not have the ability to produce diapausing eggs (Krylov et al., 1996; Santer et al., 2000). In Lake Onego, they preferentially occupied the deeper layers below 10 and 5 m, respectively, at all times of day. The instars at which these two species were present have the capacity to store fats from the previous productive season, allowing them to fast for several weeks. In active diapause, they can retain the capacity to feed on algae, detritus, or nauplii, but at lower rates than non-diapausing stages (Krylov et al., 1996; Santer et al., 2000). Their deep position in the water column suggests that if feeding, their dietary source would be limited to the phytoplankton brought deep down in the water column through convective entrainment and sedimentation. In contrast to later instars, copepod nauplii preferentially occupied the uppermost layer under ice, where rotifer abundances were also 10 times higher than those of crustaceans (Perga et al., 2020). Although data on nauplii feeding are scarce, the nature and size range of nauplii prey items are expected to differ from copepodite and adult stages, targeting small algal cells, microzooplankton and detritus (Vogt et al., 2013). Nauplii might be the node in the food web by which both algal (i.e. mainly cryptophytes and chrysophytes) and the few detrital FAs are channelled to crustacean zooplankton, either by direct grazing or through predation on microzooplankton. Last, the ADCP survey highlighted that some zooplankton performed normal diel vertical migration within the uppermost 10-m depth layer, while the net sampling identified *Cyclops* sp. (<5 m at night, and >5 m during the day) as the most likely vertical migrant. *Cyclops*, which was present at CIV and CV stages, stayed within the convective layer and moved upward to the surface layer at night. *Cyclops*, from later instars to adult stages, is an efficient predator (Adrian & Frost, 1993), preying on algal cells, bacteria but also rotifers and nauplii (Meyer et al., 2017). Diel vertical migration implies that the energetic cost of swimming up and down to avoid visual predators is balanced by the gain in dietary energy (Lampert, 1989). Fatty acid SIA performed at the taxonomic level could lead to unambiguous conclusions regarding whether nauplii and *Cyclops* copepodites were the taxa that

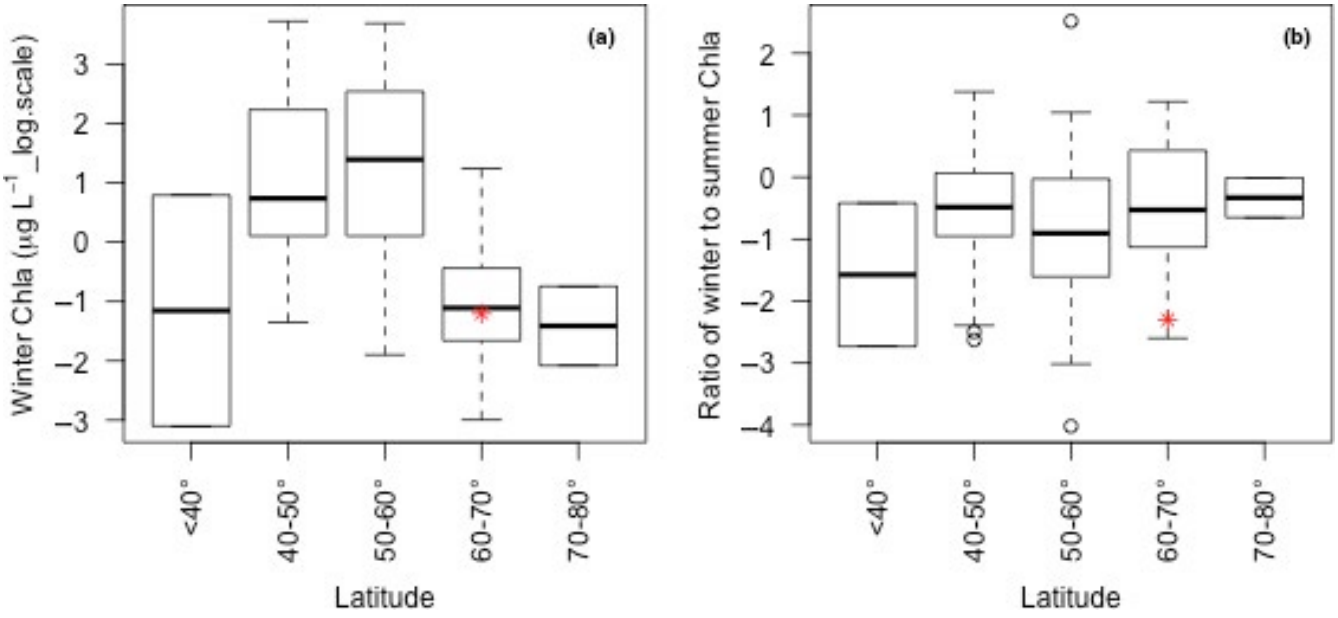

FIGURE 6 Boxplots of (a) average chlorophyll *a* concentrations measured under ice, and (b) of the ratio of winter to summer concentrations for lakes of different latitudinal ranges (data retrieved from Hampton et al., 2017). The red star represents the data measured for Lake Onego during this study [Colour figure can be viewed at wileyonlinelibrary.com]

assimilated the FA from under-ice seston, if the technical difficulty in collecting pure samples of sufficient dry weight for FA-SIA can be overcome for such small taxa.

In conclusion, the algal biomass under the ice of Lake Onego in late winter was low. Despite quantitative and qualitative food limitation, feeding was still sufficiently energetically rewarding for some taxa, probably the species that persisted at nauplii (indistinct cyclopoids) and copepodite (*Cyclops* sp.) stages. Diel vertical migration by *Cyclops* was the most tangible observation of the persistence of an under-ice planktonic food web. Compound-specific SIA detected the transfer of under-ice dietary resources to the total crustacean biomass through a subtle signal which would have been missed by any bulk stable isotope or FA analysis. However, almost half of the crustacean zooplankters (*E. gracilis* and *M. gigas*), resting at greater depths, might not contribute to the food web under ice. Most of zooplankton FA were derived from previously acquired fat storage, and only <15% of zooplankton FA had been freshly acquired and conveyed by the under-ice food web. Those recently assimilated algal-derived FA that left an imprint upon the zooplankton FA were not provided by the diatoms growing under ice, despite their dominance in the phytoplankton. Instead, the minor fraction of mixotrophic Crytophytes and Chrysophytes seemed to play a disproportionately large role in maintaining the crustacean food web. Consequently, the planktonic food web under ice had, as expected, few trophic linkages, and thereby low connectance.

Algal biomass under the ice of Lake Onego during this study (0.3 µg/L) was well below the average concentration (5.8 µg/L) computed for 118 stations in the synthesis by Hampton et al. (2017), and was also one order of magnitude lower than the chlorophyll *a* concentrations measured in summer in Lake Onego (3 µg/L, Tekanova & Syarki, 2015). However, when accounting for the latitudinal range of lakes within the dataset of Hampton et al. (2017), the chlorophyll *a* concentration measured in Lake Onego during winter 2017 corresponded to those expected for lakes above 60° latitude (median value = 0.3 µg/L, Figure 6a). The estimated ratio of winter to summer chlorophyll *a* fell within the lowermost range of observed ratios for the corresponding latitudes (Figure 6b), as a likely consequence of the light limitation of photosynthesis by the coloured nature of the waters of Lake Onego. Observed zooplankton densities in Lake Onego (0.5 ind/L) were also highly comparable to those compiled for lakes of similar latitudes by Hampton et al. (2017), although the sample size was more limited (0.03–0.5 ind/L for a set of 10 lakes). Thus, although low, the algal biomasses and zooplankton concentrations measured in March 2017 under the ice of Lake Onego are quite representative of lakes beyond 60° latitude. Since the environmental conditions under the ice of Lake Onego do not depart significantly from lakes of similar latitudes, low connectance food webs could be relatively common under ice for lakes beyond 60° latitude.

The methodology developed here is the first of its kind and therefore few studies exist with which to compare our results. We developed a reproducible approach which is adapted to the field constraints inherent in iced-over conditions. Replicating this approach in other ice-covered lakes will disclose the variability of under-ice food webs. This would provide a much more complete picture of annual dynamics of food webs in lakes that ice over.

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DATA AVAILABILITY STATEMENT

All data (zooplankton counts, FA and FA-δ^{13}C) are available on Zenodo (https://doi.org/10.5281/zenodo.3958639) under https://doi.org/10.5281/zenodo.3958639.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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