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Crustacean zooplankton densities in northern temperate lakes are related to habitat temperature across a wide gradient in lake dissolved organic carbon and nutrient content

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Abstract

1. Lake crustacean zooplankton densities often are negatively correlated with terrestrial dissolved organic carbon (DOC) concentrations. These reductions in zooplankton with increased DOC are hypothesised to be linked to diminished resource quantity or lower resource quality as terrestrial material is low in essential nutrients and macromolecules. The impact of DOC on lake physics also potentially reduces available habitat for zooplankton as the warm and well-oxygenated epilimnion is shallower in lakes with high DOC concentrations. Our goal was to investigate these potential mechanisms to determine the influence of DOC on drivers of zooplankton densities in a survey of north temperate lakes.
2. We sampled crustacean zooplankton densities in 10 lakes that varied in mean DOC concentration from 6 to 27 mg L^{-1}. We also measured resource availability as chlorophyll concentration, resource quality as essential fatty acid (EFA) concentration and the stoichiometric ratio of carbon-to-phosphorus (C:P), and habitat availability as integrated habitat temperature and dissolved oxygen to determine the strongest predictor of zooplankton densities across lakes. In addition, we quantified zooplankton habitat use through Schindler trap profiles through the water column.
3. Zooplankton densities were most strongly related to integrated habitat temperature and were not closely related to measures of resource quantity or quality. Depth of the mix layer was negatively correlated with DOC concentration, yet there was no relationship between DOC concentration and zooplankton habitat use. Overall resource quantity and quality increased across the DOC gradient, as chlorophyll and EFA concentration were greatest in lakes with higher DOC.
4. Our results indicate the potential for physics-mediated responses between lake DOC and zooplankton density. As lakes with greater DOC concentrations have, on average, shallower mixed layers and colder habitats, zooplankton may either be constrained to a relatively smaller proportion of the catchment or experience reduced temperatures that may delay development or feeding rates.
5. Lake DOC concentrations are projected to increase under future climate scenarios, so accompanying changes in lake temperature profiles are likely to follow. These also may reduce food-web productivity, as shrinking mixed layers or colder

total water columns resulting from steeper thermoclines may reduce habitat availability or suitability for zooplankton communities.

KEYWORDS
dissolved organic carbon, lakes, resource quality, temperature, zooplankton

1 | INTRODUCTION

Increases in terrestrial dissolved organic carbon (DOC) concentration in lakes lead to complex responses by food webs. In some instances, zooplankton biomass or density may increase in lakes with greater DOC concentrations (Kelly et al., 2016; Minguez et al., 2019); however, other lake surveys and experiments have demonstrated sharp declines in both zooplankton and zoobenthos abundance and biomass with greater DOC (Craig et al., 2015; Kelly et al., 2014; Williamson et al., 2016). Hypothesised reasons for reduced invertebrate biomass include diminished habitat availability from a shallower thermocline, lower resource availability resulting from shading of primary producers, and/or reductions in resource quality as terrestrial resources may be deficient in important nutrients and macromolecules (Brett et al., 2009; Karlsson et al., 2009, 2015; Kelly et al., 2014; Taipale et al., 2014). As DOC concentrations in lakes are projected to increase globally as a consequence of climate change (de Wit et al., 2021; Meyer-Jacob et al., 2019), developing a better understanding of the mechanisms for variability in food web responses to higher DOC remains important.

Owing to its chromophoric nature, terrestrial DOC loading into lakes can alter the physical characteristics of the water column, and therefore zooplankton habitat availability. Lakes with greater DOC concentrations are characterised by having shallower mixed layer depth from increased light attenuation (Houser, 2006; Pérez-Fuentetaja et al., 1999). The shallower mixed layer often is accompanied by steeper thermo- and oxyclines, leading to a relatively warmer and well-oxygenated upper mixed layer, and a colder anoxic hypolimnion (Houser, 2006; Tanentzap et al., 2008). As zooplankton growth is maximised in warmer water, the reduction in the upper mixed layer as proportion of the water column may either reduce available habitat if zooplankton are reluctant to use cold hypolimnetic water, or reduce growth through physiological stress (Havens et al., 2015; Kelly et al., 2014; Vanderploeg et al., 2009). Past work on both zooplankton and benthic macroinvertebrates has observed strong relationships between either mixed layer depth or available oxygenated habitat, suggesting that this habitat reduction may be limiting the potential for secondary production (Craig et al., 2015; Kelly et al., 2014). However, for zooplankton it is unclear whether the reduction in mixed layer may limit production through either a habitat constraint or physiological responses.

Increases in DOC may influence zooplankton distributions in the water column in ways that could provide fitness benefits. Diel migration patterns by zooplankton often are observed in lakes, as zooplankton migrate to deeper and darker water during the day to avoid predation and then to shallower water at night to access food resources and warmer water (Bollens & Frost, 1991; Lampert, 1989). Zooplankton in lakes with high DOC concentrations may display reduced migration magnitudes, as the light attenuation from DOC provides a natural refuge even during the day (Wissel & Ramacharan, 2003). There may be significant physiological benefits of remaining in shallow water. For example, zooplankton that migrate into deeper waters may experience reductions in growth or productivity resulting from lower oxygen concentration or colder temperatures below the thermocline (Goto et al., 2012; Loose & Dawidowicz, 1994). Experiments also have noted that the benefits of using more of the water column as habitat for zooplankton are much greater when the temperature gradient between surface and deep water is small (Lampert et al., 2003; Winder et al., 2003), which may have implications for lakes undergoing a steepening thermocline caused by browning.

In addition to the changes in habitat suitability and habitat use brought about by increased DOC concentrations, higher DOC concentrations in lakes may influence resource quantity and quality. Early work exploring the relationships between DOC and primary production identified the potential for shading by terrestrial DOC to sharply decrease primary production across a set of lakes (Carpenter et al., 1998; Nürnberg & Shaw, 1998). However, more recent work has highlighted the inherent complexities in this relationship, as higher DOC concentration often is accompanied by DOC-associated nutrients that may contribute to greater primary production at intermediate DOC concentrations (Bergström et al., 2021; Seekell et al., 2015). The unimodal pattern may be further modulated based on lake and DOC characteristics, as lake size, DOC-to-nutrient ratios in the incoming load, and DOC chromophoricity may shift peaks in primary productivity across a DOC gradient (Kelly et al., 2018; Olson et al., 2020). Additionally, high DOC lakes may have greater volumetric algal biomass in the epilimnion compared to lower DOC lakes as a function of the increased nutrient concentrations (Nürnberg & Shaw, 1998); however, recent studies also have identified similar unimodal patterns between lake DOC and phytoplankton biomass (Bergström & Karlsson, 2019; Isles et al., 2021). As a result, resource availability for zooplankton may not necessarily be reduced under greater DOC loads.

Reductions in light availability and increases in nutrient concentrations associated with higher DOC concentrations also may lead to overall greater resource quality. More specifically, the variability in nutrients and light may alter algal stoichiometry and increase essential fatty acid (EFA) concentrations of available resources, both of which are key metrics that have been demonstrated to impact growth for zooplankton (Acharya et al., 2004; Bergström et al., 2022; Sterner & Elser, 2002). Low light availability may reduce carbon (C) fixation, and the non-homeostatic nature of phytoplankton allows for greater internal phosphorus (P) storage as lake P concentrations increase (Dickman et al., 2006). Increases in lipid-rich chloroplasts to deal with low light conditions or protection from UV stress also may increase the internal EFA concentration of individual phytoplankton (Guschina & Harwood, 2006; Sukenik et al., 1993; Wang & Chai, 1994). Finally, taxonomic changes may lead to greater resource quality in high DOC lakes. For example, Gutseit et al. (2007) demonstrated significant differences between low and high DOC lakes in EFA concentration likely to be a consequence of the dominance of an EFA-rich algal species. However, increased DOC-associated nutrient fertilisation in oligotrophic lakes also has been shown to increase densities of cyanobacteria, a group which is relatively deficient in nutrients and EFAs relative to other phytoplankton groups (Freeman et al., 2020). As a result, even if light limitation reduces resource availability, increases in resource quality may compensate to maintain zooplankton densities as DOC concentrations are greater (Hessen et al., 2002).

Despite past descriptions of reductions or increases in zooplankton production across gradients of terrestrial DOC concentration, we still lack an assessment of a potential suite of mechanisms for such variability. We sought to fill this gap by measuring zooplankton densities across a set of lakes that spanned broad gradients of DOC concentration, while simultaneously measuring habitat structure via thermal and oxygen profiles as well as mixing depth, habitat use by zooplankton, resource quantity and quality, and predator density. Our goal was to determine the best predictor of zooplankton density across lakes and therefore the most likely mechanism for variability in zooplankton density in response to variability in DOC concentrations. Our results suggest that previous hypotheses for reductions in zooplankton density across chemical characteristics such as DOC may be incomplete, as density was related to lake physical characteristics and not chemical properties, resource quantity or quality, nor predator density. These results will inform predictions for how zooplankton may respond to future environmental changes, including increases in terrestrial DOC concentrations or warming.

2 | METHODS

2.1 | Study sites

We conducted our lake survey at the University of Notre Dame Environmental Research Center (UNDERC) in Michigan, USA. A set of ten lakes that ranged in size from 0.75–67 ha were selected to span a gradient of DOC (~6–27 mg/L) and nutrient concentrations (mean total nitrogen [TN] range: 1,176–2,401 μg/L, mean total phosphorus [TP] range: 10.5–52.1 μg/L), and be representative of the diversity of physical and chemical properties of lakes in this region. Lake trophic status varied from meso-oligotrophic to dystrophic (Wetzel, 2001), with variations in catchment characteristics (e.g., adjacent wetland cover, lake:catchment area) contributing to many of the observed patterns in ecosystem characteristics. The lakes also varied in potential predation pressure on zooplankton, with the main planktivores being cyprinids, juvenile centrarchids and the invertebrate *Chaoborus* (for summary of lake characteristics, see Table 1).

2.2 | Sample collection and processing

We sampled crustacean zooplankton (hereafter referred to as zooplankton) at discrete intervals in the water column of each lake to estimate densities as well as water column distribution (i.e., habitat use). Zooplankton samples were collected at the approximate deepest portion of each lake on three dates from May to July during the summer of 2013. Zooplankton were collected at approximately 00:00 hr and 12:00 hr for each date and were collected along depth profiles with a 15-L Schindler trap (Aquatic Research Instruments). Profile increments for sample collection were every 1 m for lakes <10 m and every 1.5 m for lakes ≥10 m. Schindler trap samples were fixed with a 70% ethanol solution and stored until enumeration. Zooplankton were identified to the following taxonomic classifications: *Daphnia* spp., *Holopedium*, *Diaphanasoma*, *Bosmina* and *Leptodora* using a Bogorov counting tray and stereo microscope. All individuals from each Schindler trap sample were counted.

Seston for both fatty acid and stoichiometric analysis were collected from each lake every 2 weeks from May to August 2013 for a total of six sample points. Differences in zooplankton feeding mode may allow them to be more or less selective. For example, *Daphnia* spp. have been observed to be rather non-selective filter-feeders compared to copepods or *Bosmina* (DeMott, 1986, 1988). However, even selective feeders still appear to assimilate allochthonous resources (Cole et al., 2011; Solomon et al., 2011), suggesting that the resource pool for zooplankton includes more than algal resources alone. As such, we analysed resource quality using bulk seston <80 μm, as it represents the total available food for zooplankton within the lake. Seston was collected from samples taken at the top, middle, and bottom of the upper mixed layer using a Van Dorn sampler and combined. Water was stored at 4°C until further processing (within 1 hr of collection). Lake water was pre-filtered through 80-μm mesh to remove zooplankton. For fatty acid characterisation, seston was concentrated by filtering 0.5–2 L of lake water onto precombusted GF/F filters (Whatman). Seston from 100–200 ml of lake water was captured on a separate set of precombusted G/F filters for measurement of C:P stoichiometry. Filters were stored at −80°C for subsequent fatty acid analysis. Filters used to measure seston C:P stoichiometry were dried at 60°C and stored in a drying oven until analysis.

Profiles of temperature, dissolved oxygen (DO) and photosynthetically active radiation (PAR) were taken at each lake during each visit using handheld sensors from the surface to the bottom at 0.5 m increments (Yellow Springs Instruments; LI-COR Biosciences).

TABLE 1 Morphological and limnological characteristics of study lakes.

Lake	Lake surface area (ha)	Maximum depth (m)	Mixed layer depth (m)	Surface temperature (°C)	Dissolved organic carbon ($mg\,L^{-1}$)	TP (mg/L)	TN (mg/L)	Water colour (a440)	Chlorophyll-*a* (mg/L)	Seston C (mg/L)
Bay	67.33	12.2	1.04 (0.22)	20.15 (1.04)	9.0 (1.4)	10.5 (1.3)	1,410.0 (290.0)	2.5 (0.1)	4.4 (0.2)	0.70 (0.09)
Brown	32.87	4.9	1.77 (0.23)	20.04 (0.86)	9.9 (0.7)	52.1 (24.2)	1,658.4 (213.2)	5.5 (0.4)	14.5 (1.9)	1.39 (0.13)
Cranberry	1.25	7.9	0.40 (0.06)	22.82 (1.02)	19.6 (1.1)	17.0 (2.4)	1,344.1 (250.9)	14.4 (1.0)	14.3 (1.4)	0.98 (0.12)
Deadwood	9.71	8.8	1.00 (0.17)	21.53 (1.21)	8.3 (0.6)	11.6 (1.5)	1,980.3 (366.7)	5.2 (0.5)	7.3 (1.3)	0.80 (0.23)
Hummingbird	0.75	7.6	0.30 (0.06)	17.83 (0.76)	27.2 (1.3)	21.1 (2.7)	940.8 (54.6)	23.0 (2.0)	16.6 (2.2)	1.85 (0.17)
Raspberry	4.62	6.1	1.56 (0.14)	18.97 (1.19)	6.8 (0.5)	16.2 (0.9)	1873.8 (341.6)	3.7 (0.3)	7.0 (0.3)	0.67 (0.13)
Reddington	1.23	16	0.28 (0.10)	21.16 (1.36)	16.8 (2.0)	19.3 (1.3)	1,829.3 (312.9)	16.4 (0.9)	9.6 (2.2)	1.09 (0.52)
Red Bass	10.92	6.7	0.83 (0.21)	22.72 (1.31)	18.6 (1.8)	20.1 (5.0)	1,081.1 (320.4)	17.5 (0.9)	15.2 (2.6)	1.28 (0.24)
Tuesday	0.91	14.9	0.68 (0.14)	20.30 (0.93)	11.7 (0.5)	27.7 (3.5)	1,129.7 (292.0)	5.9 (0.3)	11.8 (2.3)	1.24 (0.24)
West Long	4.86	14.0	1.41 (0.15)	19.35 (0.68)	6.5 (0.3)	15.6 (1.0)	439.3 (11.8)	3.5 (0.2)	6.3 (0.5)	0.60 (0.11)
Lake					***Choaborus* density (ind./L)**					**Piscivore present/absent**
Bay					0.8 (0.3)					Present
Brown					11.8 (7.8)					Present
Cranberry					2.2 (0.6)					Absent
Deadwood					1.5 (0.4)					Present
Hummingbird					4.2 (1.3)					Present
Raspberry					2.3 (1.1)					Present
Reddington					0.1 (0.1)					Absent
Red Bass					4.0 (1.5)					Present
Tuesday					2.1 (0.9)					Absent
West Long					1.3 (0.3)					Present

Note: All physical and water chemistry values are seasonal means of the integrated upper mixed layer (*SE*).

Mixed layer depth was calculated as the first depth at which there is a greater than 1° temperature change over a 1-m change in depth. Integrated water samples were taken from the upper mixed layer for analysis of water chemistry characteristics. Total nitrogen (following persulfate digestion) was analysed using a spectrophotometric method (Olsen, 2008), and TP (following persulfate digestion) was measured using a colorimetric assay (Menzel & Corwin, 1965). Chlorophyll-*a* was analysed using methanol extraction and a fluorometric method (Welschmeyer, 1994). DOC was analysed using a Shimadzu TOC-V total organic carbon analyser (Shimadzu Scientific Instruments). The majority of the DOC in lakes in this region is from terrestrial sources, and therefore we assumed that DOC concentration represented primarily terrestrial DOC concentration across our lakes (Wilkinson et al., 2013).

Chaoborus densities and food-web structure (presence/absence of piscivores) were used to evaluate the impact of predation on zooplankton abundances (Kelly et al., 2014). *Chaborus* densities were determined similar to zooplankton sampling through Schindler trap profiles. Samples were fixed with 70% ethanol, and all *Chaoborus* present were counted within each sample. From 2012 to 2018, fyke net and minnow trap surveys were conducted on each lake in our dataset as a part of the University of Notre Dame Environmental Research Center Aquatic Monitoring Program. Fyke nets ($n = 4$) were deployed for two to three nights each summer between 15 May and 15 August. We summarised these data to presence/absence of piscivores, where piscivores in these lakes included Largemouth Bass, Smallmouth Bass, Northern Pike, Muskellunge and Walleye. Lakes that were not part of the routine sampling programme (Deadwood, Red Bass and Reddington) were sampled in 2013 using similar methods to supplement the monitoring data.

2.3 | Fatty acid analysis

Seston fatty acids were extracted and analysed using methods outlined in Heissenberger et al. (2010). Freeze-dried samples (2–60 mg) were stored overnight in chloroform (2 ml) at −80°C. Lipids were extracted using a 2:1 chloroform: methanol solution (1 ml) after homogenisation with glass beads and the addition of NaCl (0.8 μl). After centrifugation, the organic lipid-containing layer was extracted with subsequent washes with chloroform, and evaporated with nitrogen gas (N_2) down to 0.5 ml. An aliquot (100 μl) of extracted lipids was dried and weighed (±1 μm) to obtain total lipid weight per sample. Remaining sample was evaporated to dryness using N_2, and then esterified with toluene (1 ml) and sulfuric acid (H_2SO_4) (2 ml, 1% v/v), and stored at 50°C for 15 hr. After incubation, potassium bicarbonate ($KHCO_3$) (2 ml, 2% v/v) and 1:1 Hexane:Methyl tert-butyl Ether (MTBE; 5 ml) were added and samples centrifuged. After centrifugation, the top layer was removed and evaporated using N_2, and then re-dissolved in hexane for analysis.

Fatty acid methyl esters (FAME) were analysed with a gas chromatograph (Thermo Scientific; detector: FID, carrier gas: Helium, oven: 140°C for 5 min, rising to 240°C at 4°C/min, holding at 240°C for 15 min, injector: 1 μl, 260°C), and identified with a 37 FAME standard mix (Supelco). Specific FAME concentrations were determined using a standard curve dilution of the FAME standard mix. Quantification of peak areas from the GC output was performed using XCALIBUR software (Thermo Scientific). Essential fatty acids (EFA) were characterised as 18:2ω6 (linoleic acid; LIN), 18:3ω3 (α-linolenic acid; ALA), 20:4ω6 (arachidonic acid; ARA), 20:5ω3 (eicosapentaenoic acid; EPA), and 22:6ω3 (docosahexaenoic acid; DHA). The EFA concentration in the seston was measured as volumetric concentration (μg EFA/L).

2.4 | Seston carbon and phosphorus concentration

For the determination of seston C and P content, all samples were combusted at 450°C for approximately 2 hr before analysis to remove excess organic C. Samples then were combined with 30 ml of milli-RO water, and analysed colorimetrically following persulfate digestion in a manner similar to lake TP samples. For seston C content, samples were analysed with a Carlo Erba elemental analyser.

2.5 | Data analysis

We used multiple model comparisons to find the best predictor of zooplankton density across our set of survey lakes. We used average density taken from Schindler trap profiles as the response variable in zooplankton individuals/L. Zooplankton densities were standardised by lake depth to account for variability in the number of samples and the amount of water column sampled. We used linear models to find the predictor that explained the most variation in zooplankton density across lakes, with lake morphological, physical, chemical and resource quality measurements as independent variables. Specifically, we tested for relationships between zooplankton density and mixed layer depth, TP, Chl-*a*, EFA concentration, seston C:P, and *chaoborus* and fish densities. Water column temperature and DO were integrated from lake profiles to give a comprehensive predictor of thermal and oxygen conditions available to zooplankton. We used the 'integrate()' function in R to integrate temperature and DO from the surface to the last depth where zooplankton were measured in the water column of each lake. We used linear regression or multiple regression to test for the relationship between zooplankton community composition and environmental variables, with proportions logit-transformed before analysis. For all models, we used the seasonal averages for water chemistry and seston quality metrics (EFAs and C:P) taken from the integrated upper mixed layer of each lake. Variables in the models were log-transformed before analysis in order to meet normality assumptions when necessary, and all stoichiometric data were log-transformed according to Isles, 2020. All analyses were performed in the R statistical environment (R Core Team, 2020).

3 | RESULTS

3.1 | Limnological and plankton community characteristics

The lakes spanned a range of water chemistry characteristics and varied from oligotrophic to dystrophic to slightly eutrophic (Table 1). Lake DOC concentration was highly positively correlated to water colour (r = 0.96) and negatively correlated to average mixed layer depth (−0.76). Proxies of algal biomass also were highly correlated with terrestrial inputs, with greater chlorophyll concentrations in lakes with high DOC concentration (r = 0.75) and TP (r = 0.69), but not TN (r = 0.10). There was no strong correlation between lake DOC concentration and nutrient concentration across lakes (neither TP nor TN). Integrated lake temperatures were negatively related to lake depth (R^2 = 0.72, p = 0.002), and including lake DOC concentration improved model fit (R^2 = 0.91, $p < 0.001$). Integrated water temperature was not related to DOC alone. Integrated DO was negatively related to DOC concentration ($R^2 = 0.58$, $p = 0.01$), and including lake depth improved model fit (R^2 = 0.81, p = 0.002). Integrated DO was not related to lake depth alone. All lakes were anoxic near the sediments by the end of the sampling season. All lakes had *Chaoborus* present, with densities ranging from 0.13 to 11.81 individuals/L. Average zooplankton density ranged from 23 to 72 individuals/L across lakes and was dominated by copepods, as more than half of the lakes had greater than 50% of their communities as copepods compared to cladoceran zooplankton.

3.2 | Predictors of zooplankton density, community and habitat use

The best predictor of zooplankton density across survey lakes was integrated lake temperature (R^2 = 0.69, p = 0.002; Figure 1a). Temperature was a better predictor than integrated DO (Figure 1b), and average resource quality and quantity across lakes (Figure 1c–f; all $p > 0.05$). Zooplankton density did not correlate to any water chemistry characteristics of the survey lakes, including TN, TP, chlorophyll and DOC concentrations ($p > 0.05$). There also was no relationship between zooplankton density and food-web structure, including piscivorous fish presence/absence or invertebrate predators (for *chaoborus* density $R^2 = 0.22$, $p = 0.16$).

Zooplankton community composition was related to resource availability across lakes. On average, the proportion of the zooplankton community represented by copepods increased with increasing chlorophyll concentrations, although that increase was not statistically significant (R^2 = 0.37, p = 0.06). However, calanoids and cyclopoids responded differently, with average percentage cyclopoids increasing with increasing chlorophyll (R^2 = 0.56, p = 0.01; Figure 2a) and average percentage calanoids decreasing with increasing chlorophyll concentration but not significantly (R^2 = 0.23, p = 0.16; Figure 2b). The percentage of community represented by *Daphnia* did not significantly correlate with any resource quantity or quality predictors.

Zooplankton migration patterns varied between classic diel vertical migration (DVM) patterns, reverse DVM, or no observed migration while remaining either in the upper mixed layer or in the metalimnion (Figure 3; Supporting Information Figure S1). There was no significant relationship between lake characteristics and zooplankton migration pattern as evidenced by comparing the difference between mean day and night depth, and lake physical, chemical and food-web predictor variables ($p > 0.05$). Zooplankton on average were shallower in lakes with higher DOC concentrations, but again this relationship was not statistically significant ($r = -0.55$, $p = 0.09$; Figure 3). Zooplankton still used the entire water column even when the hypolimnion was anoxic. There was no relationship between predictor variables and mean night depth across lakes.

3.3 | Predictors of resource quantity and quality

Resource quantity and quality were positively related to lake chemical characteristics (Figure 4). Specifically, chlorophyll and EFA concentrations were both significantly positively related to lake DOC concentration ($R^2 = 0.56$, $p = 0.01$; $R^2 = 0.77$, $p < 0.001$; Figure 4a,b). This was influenced primarily by ALA, as ALA concentration increased with greater DOC concentration (r = 0.79, p = 0.006) and comprised the greatest proportion of the total EFA pool in seston across lakes (~25%–41% of total EFAs; Table 2). Concentrations of EPA also increased significantly with greater DOC (R^2 = 0.43, p = 0.04), but comprised a relatively lower proportion of the EFA pool (~15%–30% of total EFAs; Table 2). Concentrations of ARA and DHA comprised the lowest proportion of the total EFA pool (4%–21%; Table 2) and were not significantly related to any lake characteristics ($p > 0.05$). Average total EFA concentrations ranged from 2.3 to ~12.6 µg/L across all lakes with a mean of 5.4 µg/L. The concentration of EFAs per mg C of seston was not significantly related to any lake characteristic. Seston C:P ratios were negatively related to lake TP concentration (R^2 = 0.69, p = 0.002; Figure 4c). Average molar C:P ranged from 169 to 564 with a mean of 335 across all survey lakes.

4 | DISCUSSION

Zooplankton density was positively related to integrated water column temperature across our set of survey lakes. Despite predictions for reductions in resource quantity or quality, no measurement of those characteristics related significantly to zooplankton density. In fact, there was also no significant relationship between zooplankton density and lake DOC concentration, similar to what has been observed elsewhere (e.g., Kelly et al., 2014). This indicates that physical constraints on zooplankton also may be an important constraint on growth, and environmental changes may have indirect effects on zooplankton densities through these changes in lake physics. More

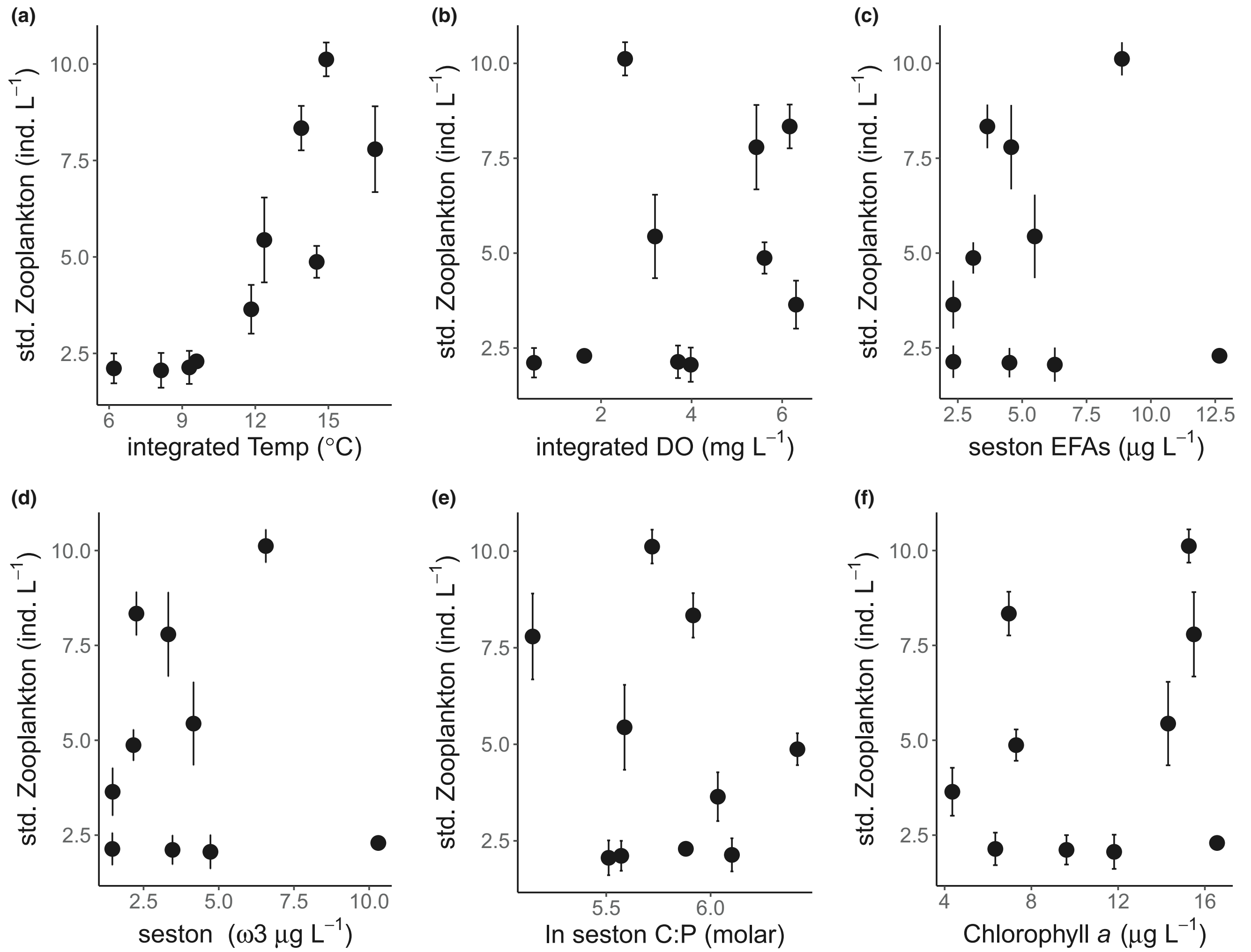

FIGURE 1 Relationships between lake depth-standardised zooplankton density and (a) integrated water temperature, (b) integrated dissolved oxygen, (c) seston essential fatty acid (EFA) concentration, (d) seston w3 FA concentration, (e) seston carbon-to-phosphorus ratio and (f) lake chlorophyll concentration. All points are seasonal means ± *SE*. [Correction added on 10 March 2023, after first online publication: In Figure 1(e) $\log_{10}$ is revised in this version].

specifically, large increases in DOC concentrations in small north-temperate lakes coupled with increases in global temperatures may decrease zooplankton density through increased stratification and reduced whole-water column temperature. Our results also indicate that the potential benefit of DOC fertilisation leading to higher resource availability for zooplankton, as seen in Kelly et al. (2016), may apply only over a limited range of DOC increases.

4.1 | Lower water temperature reduces zooplankton density

Zooplankton may experience significant fitness costs when faced with cold water temperatures that outweigh the influence of increased resource availability on growth. For example, Orcutt and Porter (1983) found that migrating zooplankton had higher growth rates when in warmer waters regardless of the amount of food available. Likewise, Loose and Dawidowicz (1994) observed reductions in most major life history parameters, including size, fecundity and growth rate for migrating versus non-migrating zooplankton, even when given more food. These reductions in life history parameters may be to the consequence of a combination of lower growth rates and extended development times as well as reductions in feeding rates for zooplankton that occur at lower temperatures (Clarke, 2006; DeLong et al., 2017; Loiterton et al., 2004). The physiological implications for migrating into colder temperatures indicates that migration strategies may serve no benefit for optimising growth by finding higher food availability in different habitat layers. Rather, maximum growth is achieved by remaining in the warmest conditions possible. Our results expand on this idea, as we demonstrate that water temperature variability in response to lake chemical changes also can be an important influence on zooplankton density across lakes, and improvements in resource quantity and/or quality may not always outweigh the effect of low water temperatures.

Across our lakes, integrated lake temperature was negatively related to lake depth. Deeper lakes in general have more water

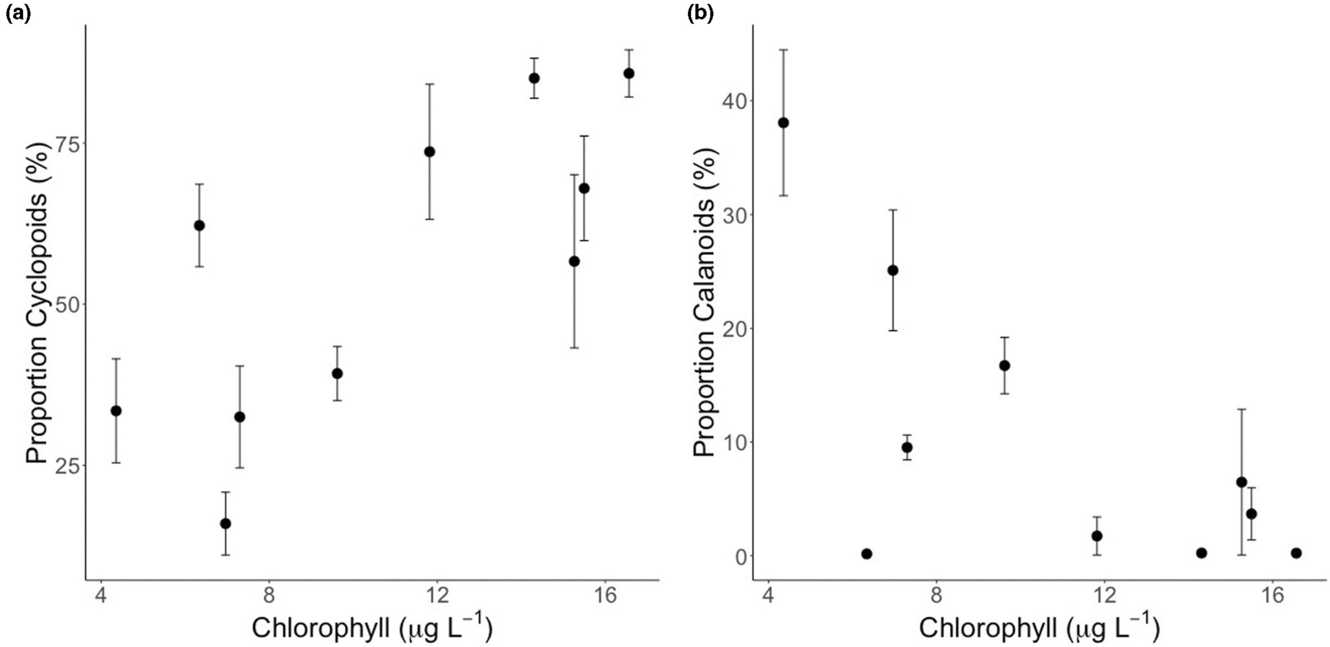

FIGURE 2 Relationships between average chlorophyll concentration and the percentage of zooplankton community as (a) cyclopoid copepods and (b) calanoid copepods. All points are seasonal means of percentage community composition ± *SE*.

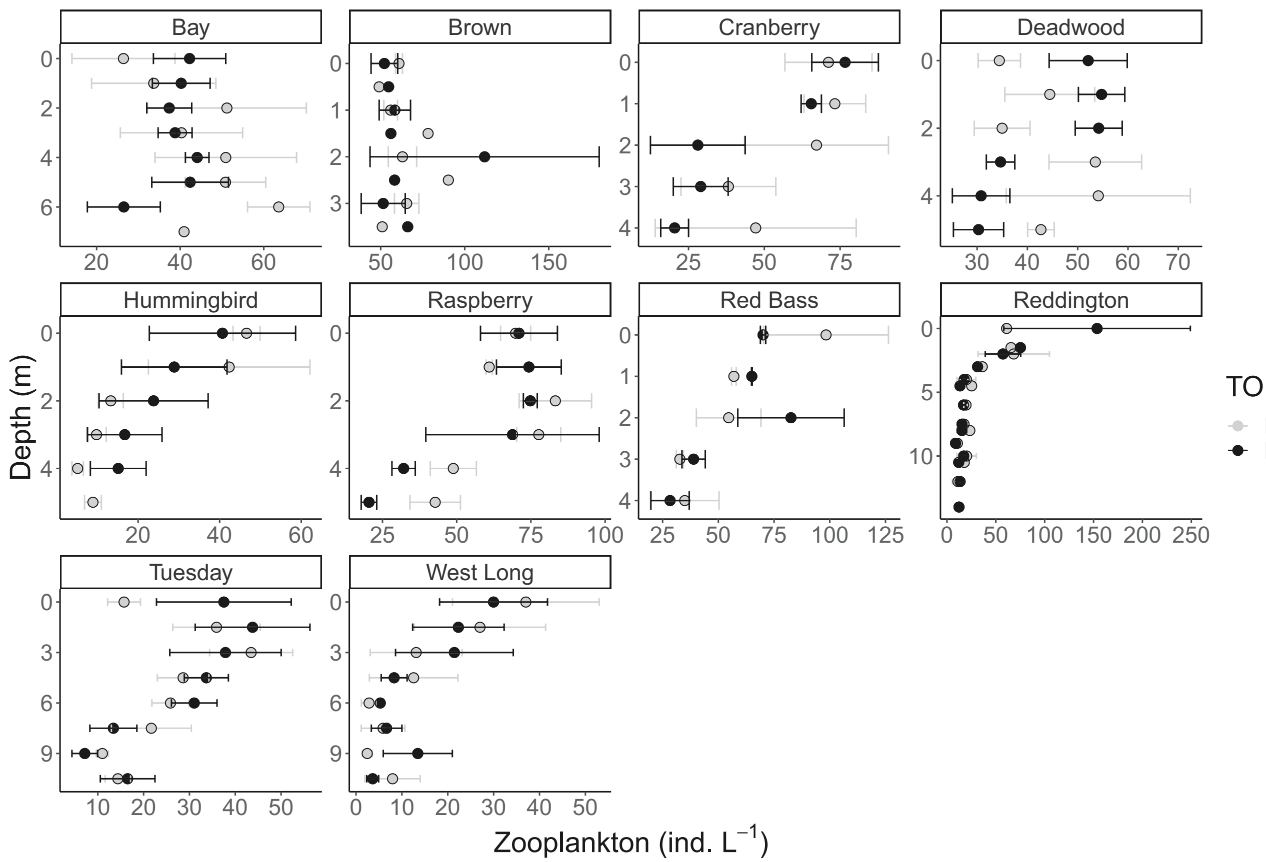

FIGURE 3 Depth profiles of zooplankton density across all survey lakes sampled at midday (grey points) and midnight (black points) visualising potential zooplankton movement resulting from diel vertical migration. Points are the average of sampling events throughout the growing season (n = 3) ± *SE*.

column below the thermocline compared to shallower lakes of similar chemistry. As a result, zooplankton density also was negatively correlated with lake depth ($r = 0.59$, $p = 0.07$). Lake DOC concentrations modulated this relationship as high DOC lakes were colder on average and therefore may have contributed to further reductions in zooplankton density in those lakes. Higher DOC in lakes has been demonstrated to not only reduce whole-water column temperature, but also diminish day-to-day variability in surface temperatures (Houser, 2006; Pilla et al., 2018). Our results suggest that the combination of depth and water colour is likely to be a significant driver of lake physics as well as food-web dynamics.

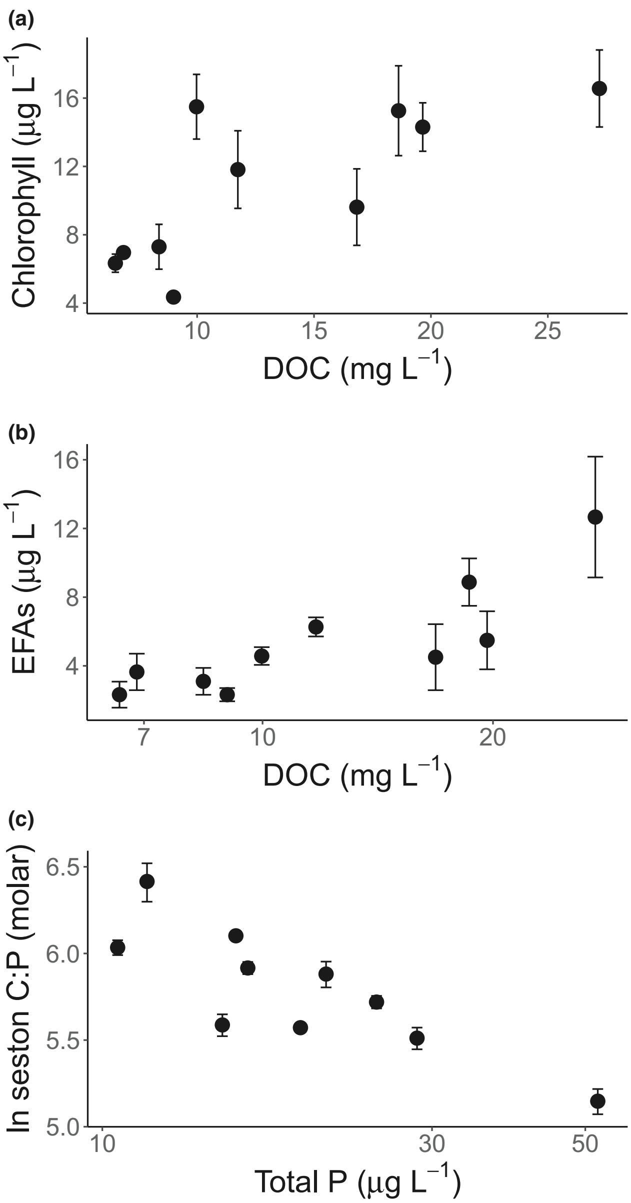

FIGURE 4 Relationships with the best predictors of proxies for resource quantity and quality across survey lakes. (a) Lake chlorophyll and lake dissolved organic carbon (DOC) concentration, (b) seston essential fatty acid (EFA) concentration and lake DOC concentration, and (c) seston carbon-to-phosphorus ratio and lake TP. All points are the average of sampling events throughout the growing season ± *SE*. [Correction added on 10 March 2023, after first online publication: In Figure 4(c) $\log_{10}$ is revised in this version].

We did not observe strong patterns between lake DOC concentration and zooplankton density directly, yet DOC-mediated reductions in water column temperature may be responsible for lower densities in high DOC lakes. Chromophoric terrestrial DOC increases light attenuation through the water column, and results in a shallower mixed layer depth, a steeper thermocline and lower water column temperatures as a whole (Houser, 2006; Read & Rose, 2013; Solomon et al., 2015). Past work has offered reductions in habitat depth resulting from shallower mixed layer depths as a possible reason for lower zooplankton productivity in high DOC lakes (Kelly et al., 2014). However, experiments that have attempted to isolate the impact of mixing depth have not been able to fully explain variability in zooplankton biomass, but only in zooplankton distributions throughout the water column (Cantin et al., 2011). Other studies have highlighted the potential for high productivity when the mixed layer was expanded, but ultimately lower overall biomass as hypolimnetic predator refuge for zooplankton is more limited and predation-related mortality increased (Sastri et al., 2014). Our characterisation of vertical migration patterns show whole-water column use by zooplankton even in some lakes with high DOC concentrations and lower water column temperatures. Therefore, it is unlikely that the impact of DOC on zooplankton in lakes is purely a consequence of habitat limitation based on space, but in part the result of physiological growth limitation when more than just the upper mixed layer is used. Across our set of lakes, there also were instances of high zooplankton density constrained almost entirely to the upper mixed layer (e.g., Reddington Lake). In this case, low predator density may allow for a lack of migration, but owing to high DOC concentrations the benefit of remaining in the warm upper mixed layer is reduced by a shallower epilimnion resulting in overall lower whole-water column densities.

The influence of temperature on zooplankton in our lakes is highlighted especially for Hummingbird Lake which has the greatest chlorophyll concentration and EFA concentration, but the lowest zooplankton density. Seston C:P and *Chaoborus* densities also were not as high as other lakes with greater zooplankton densities. Although resource quantity and quality were high on average, Hummingbird Lake had the greatest DOC concentration and therefore a relatively cold water column compared to other lakes (third lowest integrated temperature). The presence of planktivores (both *Choaborus* and fish) lead to the zooplankton using most of the water column via migration unlike similarly high DOC lakes (i.e., Reddington Lake). As a result, the zooplankton migrate through and spend significant time within a cold hypolimnion which comprises a relatively large proportion of the total water column. These cold temperatures may reduce growth and development (Goto et al., 2012; Loose & Dawidowicz, 1994). We do not have sufficient data to test this mechanism directly, yet the lack of high density despite abundant high-quality resources suggest that this may be possible.

TABLE 2 Resource quality measurements for all survey lakes. [Correction added on 10 March 2023, after first online publication: In Table 2 last column $\log_{10}$ is revised in this version].

Lake	EFA (µg/L)	EFA (µg/mg C)	LIN (µg/L)	ALA (µg/L)	ARA (µg/L)	EPA (µg/L)	DHA (µg/L)	ln C:P molar
Bay	2.32 (0.38)	5.35 (0.35)	0.73 (0.12)	0.94 (0.13)	0.11 (0.11)	0.32 (0.21)	0.20 (0.20)	6.02 (3.68)
Brown	4.57 (0.51)	3.18 (0.31)	1.00 (0.20)	1.43 (0.23)	0.71 (0.22)	1.18 (0.34)	0.23 (0.15)	5.13 (3.07)
Cranberry	5.48 (1.69)	4.48 (0.68)	1.32 (0.33)	1.96 (0.53)	0.42 (0.27)	1.02 (0.45)	0.75 (0.34)	5.55 (3.62)
Deadwood	3.09 (0.78)	4.24 (0.50)	0.85 (0.32)	0.74 (0.19)	0.37 (0.19)	0.58 (0.29)	0.53 (0.18)	6.33 (4.90)
Hummingbird	12.66 (3.51)	8.62 (0.86)	2.09 (0.40)	4.58 (1.47)	1.08 (0.49)	3.01 (0.86)	1.89 (0.49)	5.87 (3.62)
Raspberry	3.65 (1.06)	19.66 (1.36)	0.93 (0.31)	0.79 (0.21)	0.71 (0.20)	0.89 (0.33)	0.31 (0.20)	5.86 (3.72)
Reddington	4.51 (1.92)	9.67 (1.03)	1.04 (0.31)	1.24 (0.37)	0.38 (0.38)	1.21 (0.51)	0.61 (0.42)	5.57 (NA)[a]
Red Bass	8.88 (1.38)	5.59 (0.40)	2.06 (0.27)	2.73 (0.43)	1.21 (0.33)	2.04 (0.52)	0.80 (0.47)	5.70 (3.29)
Tuesday	6.26 (0.55)	5.27 (0.38)	1.37 (0.32)	1.15 (0.08)	0.17 (0.17)	2.00 (0.29)	1.56 (0.54)	5.48 (3.43)
West Long	2.32 (0.75)	3.56 (0.46)	0.75 (0.13)	0.80 (0.22)	0.11 (0.11)	0.44 (0.28)	0.21 (0.21)	6.11 (NA)[a]

Note: EFA and C:P are seasonal means ± *SE*. Stoichiometric data presented as log-transformed according to Isles, 2020.

Abbreviations: ALA, α-linolenic acid; ARA, arachidonic acid; C:P, carbon-to-phosphorus ratio; DHA, docosahexaenoic acid; EFA, essential fatty acid; EPA, eicosapentaenoic acid; LIN, linoleic acid.

[a]Only one particulate P sample due to sample loss.

4.2 | Variability in zooplankton habitat-use patterns

Observations of zooplankton habitat use in our set of lakes highlights the variability in distribution strategies and water column use. For example, some lakes are characterised by whole-water column use while other lakes appear to have zooplankton mostly constrained to the upper mixed layer. Previous assessments of zooplankton habitat use and migration strategies have described many different potential drivers of observed population distributions across all taxa, including food availability, predator presence or abundance, and density-dependence (Dodson, 1990; Lampert, 2005; Larsson & Lampter, 2012; Leibold, 1990; Sanful et al., 2017). Lampert (2005) and Lampert et al. (2003) suggest that vertical migration follows an optimal strategy in the absence of predation, with zooplankton choosing an environment that adequately trades off food availability in deeper waters with greater temperatures for growth in the epilimnion. Some studies posit that migration patterns should exclusively follow thermal optima regardless of any food-quantity tradeoffs (Orcutt & Porter, 1983), whereas others suggest migration patterns regulated primarily by either fish or invertebrate predators (Loose & Dawidowicz, 1994). We did not uncover any combination of lake, resource quantity or quality, or food-web characteristics that were significantly related to zooplankton distribution throughout the water column that would provide direct evidence for specific drivers of habitat-use strategy. We did observe shallower zooplankton during the day in high DOC lakes, suggesting that increased water colour may provide increased refuge from predators or UV stress (Weidel et al., 2017; Williamson et al., 2020). Regardless of the mechanism driving a specific response in habitat use across our set of survey lakes, we observe both whole-water column use and constrained epilimnetic habitat use by zooplankton across the gradient of DOC concentration (i.e., DVM and no migration). As a result, the interaction of cold water column temperatures and shallow epilimnion may reduce zooplankton densities either through reducing fitness from physiological thermal costs or reductions in available habitat. Both mechanisms could therefore contribute to the strong negative relationship between areal zooplankton productivity and abundance and DOC concentration seen elsewhere (Kelly et al., 2014; Leach et al., 2019; Nova et al., 2021).

4.3 | Resource quantity and quality did not correlate with zooplankton density

We did not observe any strong relationships between zooplankton density and measurements of resource quantity or quality. Specifically, there was no systematic pattern between density and chlorophyll concentration, seston C:P or seston EFA concentration. The prevalence of resource quantity and quality limitation for zooplankton in lakes is highly variable and context-dependent, with past studies highlighting the importance of both quantity over quality and *vice versa* (DeMott et al., 2004; Demott & Müller-Navarra, 1997; Elser et al., 2001; Hessen et al., 2002). Kelly et al. (2016) observed increases in zooplankton density in response to improvements in resource quantity and quality from increases in DOC to one half of an experimental lake. However, the increases in DOC and resulting changes in resources were relatively subtle compared to the large gradient of DOC concentrations observed here. Additionally, other studies have demonstrated relationships between DOC and zooplankton, mediated by changes in phytoplankton taxonomic composition and digestibility (Bergström et al., 2021; Senar et al., 2019; Strandberg et al., 2020). Our results suggest that physiological limitations through reduced temperatures also may be an important consideration for diminished zooplankton production with increased lake DOC concentration.

No patterns emerged between resource quantity and quality and zooplankton density, yet we did observe patterns between zooplankton community composition and resource availability. In general, copepod representation increased in lakes with higher chlorophyll concentrations. More specifically, cyclopoids made up a greater proportion of the community while calanoids declined in more productive lakes. This may be caused by the selectivity of different groups, as calanoids tend to be more selective in resource acquisition compared to cyclopoids (Berggren et al., 2015). Zooplankton groups also have different resource constraints, with some groups requiring more EPA versus DHA, or more P versus N (for cladocerans and copepods, respectively). However, variation in community composition can be highly context-dependent, with variability in zooplankton communities being explained by environmental characteristics, lake spatial arrangement, and/or inter- and intraspecific interactions among and within groups (Symons et al., 2014). Community composition may be highly seasonal (Fu et al., 2021), as we observed declines in cyclopoid representation throughout the summer in some lakes with corresponding increases in cladocerans and/or calanoids. As such, although the patterns across lakes are strong, we lack sufficient data to fully understand specific mechanisms for community structure.

We observed strong relationships between lake characteristics and resource quality for zooplankton. The EFA concentration in the seston was positively related to DOC concentration, which was likely to have been a product of increased phytoplankton biomass as the amount of EFAs per unit C did not change with environmental variables. Higher DOC has been demonstrated to increase phytoplankton biomass and therefore EFA availability, with the added nuance that some of this shift may reduce trophic EFA transfer if undigestible groups dominate under higher DOC and nutrient conditions (Strandberg et al., 2020). This is in contrast to other studies which have demonstrated reductions in EFA availability resulting from shifts in phytoplankton community composition with higher low-PUFA cyanobacterial groups (Senar et al., 2019). As these studies suggest, phytoplankton community composition has the potential to influence EFAs for zooplankton; however, we lack the data to fully investigate whether any shifts in phytoplankton groups contributed to the patterns seen here. Nutrient concentration did impact seston C:P stoichiometry, with greater TP concentrations contributing to lower C:P on average as would be expected based on non-homeostasis of phytoplankton (Sterner & Elser, 2002). Other recent work has indicated that N limitation can contribute to reductions in fatty acid availability, specifically lower EPA, DHA and $\omega 3$ concentration at lower lake N:P (Lau et al., 2021). We did not observe this same pattern, perhaps as a result of the relatively high N concentrations relative to P across our study lakes.

4.4 | Global change may lead to context-dependent responses in zooplankton density

According to our survey, widespread increases in terrestrial DOC loading combined with climate warming may reduce zooplankton densities in lakes with similar geomorphological characteristics. Increases in DOC concentrations have been observed and are predicted to continue in freshwater ecosystems across the Northern Hemisphere as a result of climate change and recovery from acidification (Meyer-Jacob et al., 2019; Monteith et al., 2007; Weyhenmeyer & Karlsson, 2009). Further increases in DOC concentration may impact lake thermal profiles, as reductions in transparency may decrease thermocline depth and warm the upper mixed layer, while simultaneously cooling hypolimnetic waters (Houser, 2006; Pérez-Fuentetaja et al., 1999; Pilla et al., 2018). Additionally, climate warming is predicted to increase overall lake temperatures, including surface and hypolimnetic water (Edlund et al., 2017; Winslow et al., 2017), yet some lake surveys have observed cooling hypolimnetic waters resulting from increased strength of stratification after warming (Niedrist et al., 2018). These patterns suggest that although climate warming may increase zooplankton densities if whole-water column temperatures increase, there is a potential for increases in global temperatures to non-intuitively reduce zooplankton densities if bottom layers cool and whole-lake temperatures decline, despite warmer upper mixed layers. This is especially true if temperature and DOC concentrations increase simultaneously, causing a steeper thermocline and reductions in lake temperatures experienced by zooplankton. Whole-lake experimentation has identified positive resource-mediated responses of zooplankton density to increased DOC (Kelly et al., 2016), yet results from Williamson et al. (2020) and those presented here suggest that habitat-related variables, especially lake temperatures, should be considered when trying to predict zooplankton responses to future global change.

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DATA AVAILABILITY STATEMENT

Data for zooplankton densities, resource quality and environmental parameters are available upon request. Catch data for fish across survey lakes is available in the University of Notre Dame Environmental Research Center Aquatic Monitoring Program database (10.25390/caryinstitute.7438598.v6).

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REFERENCES

Acharya, K., Kyle, M., & Elser, J. J. (2004). Biological stoichiometry of daphnia growth: An ecophysiological test of the growth rate hypothesis. *Limnology and Oceanography*, *49*, 656–665. https://doi.org/10.4319/lo.2004.49.3.0656

Berggren, M., Bergström, A.-K., & Karlsson, J. (2015). Intraspecific autochthonous and Allochthonous resource use by zooplankton in a humic Lake during the transitions between winter, summer and fall. *PLoS One*, *10*, e0120575. https://doi.org/10.1371/journal.pone.0120575

Bergström, A.-K., Deininger, A., Jonsson, A., Karlsson, J., & Vrede, T. (2021). Effects of nitrogen enrichment on zooplankton biomass and N:P recycling ratios across a DOC gradient in northern-latitude lakes. *Hydrobiologia*, *848*, 4991–5010. https://doi.org/10.1007/s10750-021-04689-5

Bergström, A.-K., & Karlsson, J. (2019). Light and nutrient control phytoplankton biomass responses to global change in northern lakes. *Global Change Biology*, *25*, 2021–2029. https://doi.org/10.1111/gcb.14623

Bergström, A.-K., Lau, D. C. P., Isles, P. D. F., Jonsson, A., & Creed, I. F. (2022). Biomass, community composition and N:P recycling ratios of zooplankton in northern high-latitude lakes with contrasting levels of N deposition and dissolved organic carbon. *Freshwater Biology*, *67*, 1508–1520. https://doi.org/10.1111/fwb.13956

Bollens, S. M., & Frost, B. W. (1991). Diel vertical migration in zooplankton: rapid individual response to predators. *Journal of Plankton Research*, *13*, 1359–1365. https://doi.org/10.1093/plankt/13.6.1359

Brett, M. T., Kainz, M. J., Taipale, S. J., & Seshan, H. (2009). Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 21197–21201. https://doi.org/10.1073/pnas.0904129106

Cantin, A. C., Beisner, B. E. B. E., Gunn, J. M. G. M., Prairie, Y. T. P. T., & Winter, J. G. W. G. (2011). Effects of thermocline deepening on lake plankton communities. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*, 260–276. https://doi.org/10.1139/F10-138

Carpenter, S. R., Cole, J. J., Kitchell, J. F., & Pace, M. L. (1998). Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in experimental lakes. *Limnology and Oceanography*, *43*, 73–80. https://doi.org/10.4319/lo.1998.43.1.0073

Clarke, A. (2006). Temperature and the metabolic theory of ecology. *Functional Ecology*, *20*, 405–412.

Cole, J. J., Carpenter, S. R., Kitchell, J., Pace, M. L., Solomon, C. T., & Weidel, B. (2011). Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 1975–1980.

Craig, N., Jones, S. E., Weidel, B. C., & Solomon, C. T. (2015). Habitat, not resource availability, limits consumer production in lake ecosystems. *Limnology and Oceanography*, *60*, 2079–2089. https://doi.org/10.1002/lno.10153

de Wit, H. A., Stoddard, J. L., Monteith, D. T., Sample, J. E., Austnes, K., Couture, S., Fölster, J., Higgins, S. N., Houle, D., Hruška, J., Krám, P., Kopacek, J., Paterson, A. M., Valinia, S., Van Dam, H., Vuorenmaa, J., & Evans, C. D. (2021). Cleaner air reveals growing influence of climate on dissolved organic carbon trends in northern headwaters. *Environmental Research Letters*, *16*, 104009. https://doi.org/10.1088/1748-9326/ac2526

DeLong, J. P., Gibert, J. P., Luhring, T. M., Bachman, G., Reed, B., Neyer, A., & Montooth, K. L. (2017). The combined effects of reactant kinetics and enzyme stability explain the temperature dependence of metabolic rates. *Ecology and Evolution*, *7*, 3940–3950. https://doi.org/10.1002/ece3.2955

Demott, W., & Müller-Navarra, D. (1997). The importance of highly unsaturated fatty acids in zooplankton nutrition: Evidence from experiments with daphnia, a cyanobacterium and lipid emulsions. *Freshwater Biology*, *38*, 649–664. https://doi.org/10.1046/j.1365-2427.1997.00222.x

DeMott, W. R. (1986). The role of taste in food selection by freshwater zooplankton. *Oecologia*, *69*, 334–340. https://doi.org/10.1007/BF00377053

DeMott, W. R. (1988). Discrimination between algae and artificial particles by freshwater and marine copepods. *Limnology and Oceanography*, *33*, 397–408. https://doi.org/10.4319/lo.1988.33.3.0397

DeMott, W. R., Edington, J. R., & Tessier, A. J. (2004). Testing zooplankton food limitation across gradients of depth and productivity in small stratified lakes. *Limnology and Oceanography*, *49*, 1408–1416. https://doi.org/10.4319/lo.2004.49.4_part_2.1408

Dickman, E. M., Vanni, M. J., & Horgan, M. J. (2006). Interactive effects of light and nutrients on phytoplankton stoichiometry. *Oecologia*, *149*, 676–689. https://doi.org/10.1007/s00442-006-0473-5

Dodson, S. (1990). Predicting diel vertical migration of zooplankton. *Limnology and Oceanography*, *35*, 1195–1200. https://doi.org/10.4319/lo.1990.35.5.1195

Edlund, M. B., Almendinger, J. E., Fang, X., Hobbs, J. M. R., VanderMeulen, D. D., Key, R. L., & Engstrom, D. R. (2017). Effects of climate change on Lake thermal structure and biotic response in northern wilderness lakes. *Water*, *9*, 678. https://doi.org/10.3390/w9090678

Elser, J. J., Hayakawa, K., & Urabe, J. (2001). Nutrient limitation reduces food quality for zooplankton: Daphnia response to Seston phosphorus enrichment. *Ecology*, *82*, 898–903. https://doi.org/10.2307/2680208

Freeman, E. C., Creed, I. F., Jones, B., & Bergström, A.-K. (2020). Global changes may be promoting a rise in select cyanobacteria in nutrient-poor northern lakes. *Global Change Biology*, *26*, 4966–4987. https://doi.org/10.1111/gcb.15189

Fu, H., Özkan, K., Yuan, G., Johansson, L. S., Søndergaard, M., Lauridsen, T. L., & Jeppesen, E. (2021). Abiotic and biotic drivers of temporal dynamics in the spatial heterogeneity of zooplankton communities across lakes in recovery from eutrophication. *Science of the Total Environment*, *778*, 146368. https://doi.org/10.1016/j.scitotenv.2021.146368

Goto, D., Lindelof, K., Fanslow, D. L., Ludsin, S. A., Pothoven, S. A., Roberts, J. J., Vanderploeg, H. A., Wilson, A. E., & Höök, T. O. (2012). Indirect consequences of hypolimnetic hypoxia on zooplankton growth in a large eutrophic lake. *Aquatic Biology*, *16*, 217–227. https://doi.org/10.3354/ab00442

Guschina, I. A., & Harwood, J. L. (2006). Lipids and lipid metabolism in eukaryotic algae. *Progress in Lipid Research*, *45*, 160–186. https://doi.org/10.1016/j.plipres.2006.01.001

Gutseit, K., Berglund, O., & Graneli, W. (2007). Essential fatty acids and phosphorus in seston from lakes with contrasting terrestrial dissolved organic carbon content. *Freshwater Biology*, *52*, 28–38. https://doi.org/10.1111/j.1365-2427.2006.01668.x

Havens, K. E., Pinto-Coelho, R. M., Beklioğlu, M., Christoffersen, K. S., Jeppesen, E., Lauridsen, T. L., Mazumder, A., Méthot, G., Alloul, B. P., Tavşanoğlu, U. N., Erdoğan, Ş., & Vijverberg, J. (2015). Temperature effects on body size of freshwater crustacean zooplankton from Greenland to the tropics. *Hydrobiologia*, *743*, 27–35. https://doi.org/10.1007/s10750-014-2000-8

Heissenberger, M., Watzke, J., & Kainz, M. J. (2010). Effect of nutrition on fatty acid profiles of riverine, lacustrine, and aquaculture-raised salmonids of pre-alpine habitats. *Hydrobiologia*, *650*, 243–254. https://doi.org/10.1007/s10750-010-0266-z

Hessen, D. O., Færøvig, P. J., & Andersen, T. (2002). Light, nutrients, and P:c ratios in algae: Grazer performance related to food quality and quantity. *Ecology*, *83*, 1886–1898. https://doi.org/10.1890/0012-9658(2002)083[1886:LNAPCR]2.0.CO;2

Houser, J. N. (2006). Water color affects the stratification, surface temperature, heat content, and mean epilimnetic irradiance of small lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 2447–2455.

Isles, P. D. F. (2020). The misuse of ratios in ecological stoichiometry. *Ecology*, *101*, e03153. https://doi.org/10.1002/ecy.3153

Isles, P. D. F., Creed, I. F., Jonsson, A., & Bergström, A.-K. (2021). Trade-offs between light and nutrient availability across gradients of dissolved organic carbon Lead to spatially and temporally variable responses of Lake phytoplankton biomass to Browning. *Ecosystems*, *24*, 1837–1852. https://doi.org/10.1007/s10021-021-00619-7

Karlsson, J., Bergström, A. K., Bystrom, P., Gudasz, C., Rodriguez, P., & Hein, C. (2015). Terrestrial organic matter input suppresses biomass production in lake ecosystems. *Ecology*, *96*, 2870–2876.

Karlsson, J., Byström, P., Ask, J., Ask, P., Persson, L., & Jansson, M. (2009). Light limitation of nutrient-poor lake ecosystems. *Nature*, *460*, 506–509. https://doi.org/10.1038/nature08179

Kelly, P. T., Craig, N., Solomon, C. T., Weidel, B. C., Zwart, J. A., & Jones, S. E. (2016). Experimental whole-lake increase of dissolved organic carbon concentration produces unexpected increase in crustacean zooplankton density. *Global Change Biology*, *22*, 2766–2775. https://doi.org/10.1111/gcb.13260

Kelly, P. T., Solomon, C. T., Weidel, B. C., & Jones, S. E. (2014). Terrestrial carbon is a resource, but not a subsidy, for lake zooplankton. *Ecology*, *95*, 1236–1242. https://doi.org/10.1890/13-1586.1

Kelly, P. T., Solomon, C. T., Zwart, J. A., & Jones, S. E. (2018). A framework for understanding variation in pelagic gross primary production of Lake ecosystems. *Ecosystems*, *21*, 1364–1376. https://doi.org/10.1007/s10021-018-0226-4

Lampert, W. (1989). The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology*, *3*, 21–27. https://doi.org/10.2307/2389671

Lampert, W. (2005). Vertical distribution of zooplankton: Density dependence and evidence for an ideal free distribution with costs. *BMC Biology*, *3*, 10. https://doi.org/10.1186/1741-7007-3-10

Lampert, W., McCauley, E., & Manly, B. F. J. (2003). Trade–offs in the vertical distribution of zooplankton: Ideal free distribution with costs? *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *270*, 765–773. https://doi.org/10.1098/rspb.2002.2291

Larsson, P., & Lampter, W. (2012). Finding the optimal vertical distribution: Behavioural responses of Daphnia pulicaria to gradients of environmental factors and the presence of fish. *Freshwater Biology*, *57*, 2514–2525. https://doi.org/10.1111/fwb.12024

Lau, D. C. P., Jonsson, A., Isles, P. D. F., Creed, I. F., & Bergström, A. (2021). Lowered nutritional quality of plankton caused by global environmental changes. *Global Change Biology*, *27*, 6294–6306. https://doi.org/10.1111/gcb.15887

Leach, T. H., Winslow, L. A., Hayes, N. M., & Rose, K. C. (2019). Decoupled trophic responses to long-term recovery from acidification and associated browning in lakes. *Global Change Biology*, *25*, 1779–1792. https://doi.org/10.1111/gcb.14580

Leibold, M. A. (1990). Resources and predators can affect the vertical distributions of zooplankton. *Limnology and Oceanography*, *35*, 938–944. https://doi.org/10.4319/lo.1990.35.4.0938

Loiterton, B., Sundbom, M., & Vrede, T. (2004). Separating physical and physiological effects of temperature on zooplankton feeding rate. *Aquatic Sciences*, *66*, 123–129. https://doi.org/10.1007/s00027-003-0668-3

Loose, C. J., & Dawidowicz, P. (1994). Trade-offs in diel vertical migration by zooplankton: The costs of predator avoidance. *Ecology*, *75*, 2255–2263. https://doi.org/10.2307/1940881

Menzel, D., & Corwin, N. (1965). The measurement of total phosphorous in seawater based on the liberation of organically bound fractions by persulfate oxidation. *Limnology and Oceanography*, *10*, 280–282.

Meyer-Jacob, C., Michelutti, N., Paterson, A. M., Cumming, B. F., Keller, W. B., & Smol, J. P. (2019). The browning and re-browning of lakes: Divergent lake-water organic carbon trends linked to acid deposition and climate change. *Scientific Reports*, *9*, 16676. https://doi.org/10.1038/s41598-019-52912-0

Minguez, L., Sperfeld, E., Berger, S. A., Nejstgaard, J. C., & Gessner, M. O. (2019). Changes in food characteristics reveal indirect effects of lake browning on zooplankton performance. *Limnology and Oceanography*, *65*, 1028–1040. https://doi.org/10.1002/lno.11367

Monteith, D. T., Stoddard, J. L., Evans, C. D., de Wit, H. A., Forsius, M., Høgåsen, T., Wilander, A., Skjelkvåle, B. L., Jeffries, D. S., Vuorenmaa, J., Keller, B., Kopácek, J., & Vesely, J. (2007). Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature*, *450*, 537–540. https://doi.org/10.1038/nature06316

Niedrist, G. H., Psenner, R., & Sommaruga, R. (2018). Climate warming increases vertical and seasonal water temperature differences and inter-annual variability in a mountain lake. *Climatic Change*, *151*, 473–490. https://doi.org/10.1007/s10584-018-2328-6

Nova, C. C., Rocha, A. M., Branco, C. W. C., & Bozelli, R. L. (2021). New insights on the relation between zooplankton and humic substances in tropical freshwater ecosystems. *Anais da Academia Brasileira de Ciências*, *93*, e20190409. https://doi.org/10.1590/0001-3765202120190409

Nürnberg, G. K., & Shaw, M. (1998). Productivity of clear and humic lakes: Nutrients, phytoplankton, bacteria. *Hydrobiologia*, *382*, 97–112. https://doi.org/10.1023/A:1003445406964

Olsen, K. K. (2008). Multiple wavelength ultraviolet determinations of nitrate concentration, method comparisons from the Preakness brook monitoring project, October 2005 to October 2006. *Water, Air, and Soil Pollution*, *187*, 195–202. https://doi.org/10.1007/s11270-007-9508-8

Olson, C. R., Solomon, C. T., & Jones, S. E. (2020). Shifting limitation of primary production: Experimental support for a new model in lake ecosystems. *Ecology Letters*, *23*, 1800–1808. https://doi.org/10.1111/ele.13606

Orcutt, J. D., & Porter, K. G. (1983). Diel vertical migration by zooplankton: Constant and fluctuating temperature effects on life history parameters of Daphnia1. *Limnology and Oceanography*, *28*, 720–730. https://doi.org/10.4319/lo.1983.28.4.0720

Pérez-Fuentetaja, A., Dillon, P. J., Yan, N. D., & McQueen, D. J. (1999). Significance of dissolved organic carbon in the prediction of thermocline depth in small Canadian shield lakes. *Aquatic Ecology*, *33*, 127–133. https://doi.org/10.1023/A:1009998118504

Pilla, R. M., Williamson, C. E., Zhang, J., Smyth, R. L., Lenters, J. D., Brentrup, J. A., Knoll, L. B., & Fisher, T. J. (2018). Browning-related decreases in water transparency Lead to long-term increases in surface water temperature and thermal stratification in two Small Lakes. *Journal of Geophysical Research. Biogeosciences*, *123*, 1651–1665. https://doi.org/10.1029/2017JG004321

R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Read, J. S., & Rose, K. C. (2013). Physical responses of small temperate lakes to variation in dissolved organic carbon concentrations. *Limnology and Oceanography*, *58*, 921–931.

Sanful, P. O., Aikins, S., & Hecky, R. E. (2017). Depth distribution of zooplankton in relation to limnological gradients under different stratification and interannual regimes in a deep, tropical crater lake. *Annales de Limnologie – International Journal of Limnology*, *53*, 293–307. https://doi.org/10.1051/limn/2017015

Sastri, A. R., Gauthier, J., Juneau, P., & Beisner, B. E. (2014). Biomass and productivity responses of zooplankton communities to experimental thermocline deepening. *Limnology and Oceanography*, *59*, 1–16. https://doi.org/10.4319/lo.2014.59.1.0001

Seekell, D. A., Lapierre, J.-F., & Karlsson, J. (2015). Trade-offs between light and nutrient availability across gradients of dissolved organic carbon concentration in Swedish lakes: Implications for patterns in primary production. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 1663–1671. https://doi.org/10.1139/cjfas-2015-0187

Senar, O. E., Creed, I. F., Strandberg, U., & Arts, M. T. (2019). Browning reduces the availability—But not the transfer—Of essential fatty acids in temperate lakes. *Freshwater Biology*, *64*, 2107–2119. https://doi.org/10.1111/fwb.13399

Solomon, C. T., Carpenter, S. R., Clayton, M. K., Cole, J. J., Coloso, J. J., Pace, M. L., Vander Zanden, M. J., & Weidel, B. C. (2011). Terrestrial, benthic, and pelagic resource use in lakes: Results from a three-isotope Bayesian mixing model. *Ecology*, *92*, 1115–1125.

Solomon, C. T., Jones, S. E., Weidel, B. C., Buffam, I., Fork, M. L., Karlsson, J., Larsen, S., Lennon, J. T., Read, J. S., Sadro, S., & Saros, J. E. (2015). Ecosystem consequences of changing inputs of terrestrial dissolved organic matter to lakes: Current knowledge and future challenges. *Ecosystems*, *18*, 376–389. https://doi.org/10.1007/s10021-015-9848-y

Sterner, R., & Elser, J. (2002). *Ecological stoichiometry: The biology of elements from molecules to the biosphere*. Princeton University Press.

Strandberg, U., Hiltunen, M., Rissanen, N., Taipale, S., Akkanen, J., & Kankaala, P. (2020). Increasing concentration of polyunsaturated fatty acids in browning boreal lakes is driven by nuisance alga Gonyostomum. *Ecosphere*, *11*, e03189. https://doi.org/10.1002/ecs2.3189

Sukenik, A., Zmora, O., & Carmeli, Y. (1993). Biochemical quality of marine unicellular algae with special emphasis on lipid composition. II. *Nannochloropsis* Sp. *Aquaculture*, *117*, 313–326. https://doi.org/10.1016/0044-8486(93)90328-V

Symons, C. C., Pedruski, M. T., Arnott, S. E., & Sweetman, J. N. (2014). Spatial, environmental, and biotic determinants of zooplankton community composition in Subarctic Lakes and ponds in Wapusk National Park, Canada. *Arctic, Antarctic, and Alpine Research*, *46*, 159–190. https://doi.org/10.1657/1938-4246-46.1.159

Taipale, S. J., Brett, M. T., Hahn, M. W., Martin-Creuzburg, D., Yeung, S., Hiltunen, M., Strandberg, U., & Kankaala, P. (2014). Differing Daphnia magna assimilation efficiencies for terrestrial, bacterial, and algal carbon and fatty acids. *Ecology*, *95*, 563–576. https://doi.org/10.1890/13-0650.1

Tanentzap, A. J., Yan, N. D., Keller, B., Girard, R., Heneberry, J., Gunn, J. M., Hamilton, D., & Taylor, P. A. (2008). Cooling lakes while the world warms: Effects of forest regrowth and increased dissolved organic matter on the thermal regime of a temperate, urban lake. *Limnology and Oceanography*, *53*, 404–410. https://doi.org/10.4319/lo.2008.53.1.0404

Vanderploeg, H. A., Ludsin, S. A., Ruberg, S. A., Höök, T. O., Pothoven, S. A., Brandt, S. B., Lang, G. A., Liebig, J. R., & Cavaletto, J. F. (2009). Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. *Journal of Experimental Marine Biology and Ecology*, *381*, S92–S107. https://doi.org/10.1016/j.jembe.2009.07.027

Wang, K. S., & Chai, T. (1994). Reduction in omega-3 fatty acids by UV-B irradiation in microalgae. *Journal of Applied Phycology*, *6*, 415–422. https://doi.org/10.1007/BF02182158

Weidel, B. C., Baglini, K., Jones, S. E., Kelly, P. T., Solomon, C. T., & Zwart, J. A. (2017). Light climate and dissolved organic carbon concentration influence species-specific changes in fish zooplanktivory. *Inland Waters*, *7*, 210–217. https://doi.org/10.1080/20442041.2017.1329121

Welschmeyer, N. A. (1994). Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnology and Oceanography*, *39*, 1985–1992. https://doi.org/10.4319/lo.1994.39.8.1985

Wetzel, R. (2001). *Limnology: Lake and River Ecosystems*, 3rd ed. Academic Press.

Weyhenmeyer, G. A., & Karlsson, J. (2009). Nonlinear response of dissolved organic carbon concentrations in boreal lakes to increasing temperatures. *Limnology and Oceanography*, *54*, 2513–2519. https://doi.org/10.4319/lo.2009.54.6_part_2.2513

Wilkinson, G. M., Pace, M. L., & Cole, J. J. (2013). Terrestrial dominance of organic matter in north temperate lakes: Organic matter composition in lakes. *Global Biogeochemical Cycles*, *27*, 43–51. https://doi.org/10.1029/2012GB004453

Williamson, C. E., Overholt, E. P., Pilla, R. M., Leach, T. H., Brentrup, J. A., Knoll, L. B., Mette, E. M., & Moeller, R. E. (2016). Ecological consequences of long-term browning in lakes. *Scientific Reports*, *5*, 18666. https://doi.org/10.1038/srep18666

Williamson, C. E., Overholt, E. P., Pilla, R. M., & Wilkins, K. W. (2020). Habitat-mediated responses of zooplankton to decreasing light in two Temperate Lakes undergoing long-term Browning. *Frontiers in Environmental Science*, *8*, 73. https://doi.org/10.3389/fenvs.2020.00073

Winder, M., Boersma, M., & Spaak, P. (2003). On the cost of vertical migration: Are feeding conditions really worse at greater depths? *Freshwater Biology*, *48*, 383–393. https://doi.org/10.1046/j.1365-2427.2003.00995.x

Winslow, L. A., Read, J. S., Hansen, G. J. A., Rose, K. C., & Robertson, D. M. (2017). Seasonality of change: Summer warming rates do not fully represent effects of climate change on lake temperatures. *Limnology and Oceanography*, *62*, 2168–2178. https://doi.org/10.1002/lno.10557

Wissel, B., & Ramacharan, C. W. (2003). Plasticity of vertical distribution of crustacean zooplankton in lakes with varying levels of water colour. *Journal of Plankton Research*, *25*, 1047–1057. https://doi.org/10.1093/plankt/25.9.1047

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