

Lowered nutritional quality of plankton caused by global environmental changes

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Abstract

Global environmental changes are causing widespread nutrient depletion, declines in the ratio of dissolved inorganic nitrogen (N) to total phosphorus (DIN:TP), and increases in both water temperature and terrestrial colored dissolved organic carbon (DOC) concentration (browning) in high-latitude northern lakes. Declining lake DIN:TP, warming, and browning alter the nutrient limitation regime and biomass of phytoplankton, but how these stressors together affect the nutritional quality in terms of polyunsaturated fatty acid (PUFA) contents of the pelagic food web components remains unknown. We assessed the fatty acid compositions of seston and zooplankton in 33 lakes across south-to-north and boreal-to-subarctic gradients in Sweden. Data showed higher lake DIN:TP in the south than in the north, and that boreal lakes were warmer and browner than subarctic lakes. Lake DIN:TP strongly affected the PUFA contents—especially eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA)—in seston, calanoids, and copepods (as a group), but not in cladocerans. The EPA+DHA contents increased by 123% in seston, 197% in calanoids, and 230% in copepods across a lake molar DIN:TP gradient from 0.17 to 14.53, indicating lower seston and copepod nutritional quality in the more N-limited lakes (those with lower DIN:TP). Water temperature affected EPA+DHA contents of zooplankton, especially cladocerans, but not seston. Cladoceran EPA+DHA contents were reduced by ca. 6% for every 1°C increase in surface water. Also, the EPA, DHA, or EPA+DHA contents of *Bosmina*, cyclopoids, and copepods increased in lakes with higher DOC concentrations or aromaticity. Our findings indicate that zooplankton food quality for higher consumers will decrease with warming alone (for cladocerans) or in combination with declining lake DIN:TP (for copepods), but impacts of these stressors are moderated by lake browning. Global environmental changes that drive northern lakes toward more N-limited, warmer, and browner conditions will reduce PUFA availability and nutritional quality of the pelagic food web components.

KEYWORDS

boreal lakes, dissolved organic carbon, fatty acids, N:P stoichiometry, nitrogen deposition, phytoplankton, seston, subarctic lakes, warming, zooplankton

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1 | INTRODUCTION

Lakes are particularly common in high-latitude regions of the northern hemisphere (Lehner & Döll, 2004), where they provide habitats for diverse wildlife and important ecosystem services (Chapin et al., 2004). Yet, northern lakes are experiencing global environmental changes, such as climate warming and reduced atmospheric acid deposition (nitrogen [N] and sulfur [S]), that affect biogeochemical processes and catchment delivery of nutrients and carbon to lakes (Creed et al., 2018; Monteith et al., 2007; Simpson et al., 2014). These recent changes have caused widespread declines in N, phosphorus (P), and dissolved inorganic N to total P ratio (DIN:TP; Canham et al., 2012; Eimers et al., 2009; Isles et al., 2018), with concurrent increases in terrestrial colored dissolved organic carbon (DOC) concentrations, that is, browning, in many northern lakes (Isles et al., 2018, 2020; Larsen et al., 2011). Previous studies have implied that nutrient depletion and declines in lake DIN:TP ratio, coupled with browning, will intensify phytoplankton N-limitation (Isles et al., 2018, 2020), reduce phytoplankton biomass and impact their mineral and biochemical compositions (Bergström et al., 2020; Deininger et al., Faithfull, & Bergström, 2017), and affect the trophic support of phytoplankton for pelagic food webs (Deininger, Faithfull, Karlsson, et al., 2017). However, to what extent these changes in phytoplankton propagate to affect the nutritional quality of zooplankton, which are an important food web link to pelagic predators (e.g., fish), remains largely unknown (but see Keva et al., 2021).

Zooplankton growth and reproduction strongly depend on the nutritional quality measured in terms of polyunsaturated fatty acid (PUFA) contents of their diet (Brett et al., 2009; Müller-Navarra et al., 2000), although food quantity is also important particularly in oligotrophic systems (Persson et al., 2007). Long-chain (with ≥ 20 C) PUFA such as arachidonic acid (20:4 ω 6; ARA), eicosapentaenoic acid (20:5 ω 3; EPA), and docosahexaenoic acid (22:6 ω 3; DHA) are commonly accumulated in high amounts in zooplankton, fish, and other aquatic consumers, because of their importance for animal growth and physiological functions (Ahlgren et al., 2009; Brett et al., 2017; Brett & Müller-Navarra, 1997). Specifically, ARA and EPA are precursors of prostaglandins for regulating molting and reproduction (Ahlgren et al., 2009), and DHA is essential for functioning of cell membranes and neural tissue development (Ahlgren et al., 2009; Arts & Kohler, 2009). Algae are able to synthesize these long-chain PUFA *de novo* and contribute their main supply to aquatic food webs (Brett et al., 2017; Napolitano, 1999), although with different PUFA composition among algal taxa (Taipale et al., 2013). Apart from long-chain PUFA, the dietary contents of the 18C PUFA such as alpha-linolenic acid (18:3 ω 3; ALA) and linoleic acid (18:2 ω 6; LIN), which can be sourced from both algae and terrestrial organic matter (Napolitano, 1999; Taipale et al., 2015), are known to affect zooplankton fitness (Brett & Müller-Navarra, 1997; Peltomaa et al., 2017). Zooplankton such as herbivorous cladocerans are able to grow and reproduce with the presence of 18C PUFA but not long-chain PUFA in diet (e.g., green algae), although at a lower efficiency compared to cladocerans provided a diet with long-chain PUFA

(e.g., cryptophytes; Brett et al., 2009). However, the fitness of fish is strongly dependent on dietary long-chain PUFA availability, and they mainly retain ARA, EPA, and DHA (Ahlgren et al., 2009; Arts & Kohler, 2009; Sargent et al., 2003). The nutritional quality of seston for zooplankton is therefore shaped by all PUFA, while that of zooplankton for fish is set by zooplankton ARA, EPA, and DHA contents.

Zooplankton biomass has also been shown to be related to the availability of both 18C PUFA and long-chain PUFA in phytoplankton but not to the overall phytoplankton biomass (Gladyshev et al., 2010). This further supports the significant role of dietary PUFA for zooplankton development. Both cladocerans and copepods are common zooplankton groups in aquatic ecosystems worldwide, yet they generally differ in feeding strategy and fatty acid (FA) composition. For example, the opportunistic filter-feeding cladocerans have higher EPA but lower DHA requirements than do copepods, which are more active selective feeders (Ahlgren et al., 2009; Persson & Vrede, 2006). The dietary PUFA availability, therefore, affects the resource use, nutritional quality, and fitness of zooplankton (Brett et al., 2006, 2009; Taipale et al., 2014), which can in turn determine the trophic transfer efficiency in aquatic ecosystems (Müller-Navarra et al., 2000).

The diet of zooplankton, that is, seston, consists of varying amounts of phytoplankton, bacteria, and terrestrial organic matter, all of which differ in FA composition (Napolitano, 1999). Phytoplankton in northern lakes, especially those in regions with low atmospheric N deposition and low lake water DIN:TP ratio, are largely N-limited (Bergström, 2010; Bergström & Jansson, 2006; Isles et al., 2020). Previous studies have shown that lake DIN:TP ratio affects phytoplankton biomass, and that the response in phytoplankton biomass to changes in ambient nutrient concentration depends on the lake DOC concentration (Bergström & Karlsson, 2019; Deininger, Faithfull, & Bergström, 2017). Bacterial biomass and terrestrial organic matter concentration increase with increasing DOC concentration in lakes (Hessen, 1985; Thurman, 1985). Apart from the effects on phytoplankton biomass, declines in lake DIN:TP ratio and increases in lake DOC concentration have recently been shown to associate with reductions in long-chain PUFA contents of seston, by increasing the proportion of terrestrial organic matter and hampering phytoplankton development due to light and nutrient constraints (Bergström et al., 2020; Senar et al., 2019). Also, increased lake DOC aromaticity (higher specific ultraviolet absorbance) is associated with lower ω 3: ω 6 FA ratios of seston (Bergström et al., 2020), that is, reduced proportions of phytoplankton relative to proportions of terrestrial organic matter (Taipale et al., 2015). In contrast, reduced seston EPA in subarctic lakes is primarily related to reduced lake DIN:TP (Bergström et al., 2020), but whether this dependence exists in boreal lakes is unclear.

The PUFA availability in aquatic food webs is also affected by temperature (Arts & Kohler, 2009). In cold environments, long-chain PUFA especially EPA and DHA are needed for maintaining cell membrane fluidity, that is, homeoviscous adaptation, of both phytoplankton and animals (Arts & Kohler, 2009). With climate warming, the availability of long-chain PUFA in aquatic food webs may decrease

due to lower demands for this adaptation (Arts & Kohler, 2009; Hixson & Arts, 2016). However, how warming interacts with declining lake DIN:TP and browning to affect the nutritional quality of seston and zooplankton is yet unexplored, although their combined effects on zooplankton potentially have strong implications for food web efficiency and fish production.

The above findings suggest that declines in lake DIN:TP ratio, combined with browning and/or warming, reduce the nutritional quality of seston for zooplankton. The FA composition of zooplankton can integrate and reflect changes in phytoplankton biomass and PUFA availability in seston that are induced by the global environmental changes. Here, we analyzed the FA compositions of seston and zooplankton collected from 15 subarctic and 18 boreal lakes which covered spatial gradients in lake DIN:TP ratio, DOC concentration, and temperature. We addressed the following questions:

- (i) How does seston nutritional quality in terms of the availability of 18C PUFA (i.e., ALA and LIN) and long-chain PUFA (i.e., ARA, EPA, and DHA) change across lake gradients in DIN:TP ratio, DOC concentration, and temperature?
- (ii) How do the effects of these lake gradients on seston PUFA contents propagate to affect the nutritional quality of zooplankton, and do copepods and cladocerans respond differently?
- (iii) Is lake DIN:TP ratio an overall more dominant environmental determinant than DOC concentration and temperature for nutritional quality of the pelagic food web components?

We predicted that, in the subarctic and boreal lakes, (i) seston PUFA contents (i.e., ALA, LIN, ARA, EPA, and DHA) increase with increasing lake DIN:TP ratio and decreasing DOC concentration and temperature (Bergström et al., 2020; Hixson & Arts, 2016); (ii) the changes in PUFA availability of zooplankton follow those of seston, but the FA responses differ among zooplankton taxa: copepod PUFA contents increase with increasing lake DIN:TP, as copepods are more N-dependent and able to selectively feed on PUFA-rich phytoplankton (Andersen & Hessen, 1991; Bergström et al., 2018), while cladoceran PUFA contents are more susceptible to alterations in lake DOC concentration and temperature because of their opportunistic filter-feeding behavior and because seston PUFA content decreases in warmer high-DOC lakes (Senar et al., 2019); and (iii) lake DIN:TP ratio is the major environmental control for PUFA availability in the plankton food chain, as declines in lake DIN:TP ratio are particularly prominent in northern lakes where phytoplankton is predominantly N-limited (Isles et al., 2018).

2 | MATERIALS AND METHODS

2.1 | Study sites and field sampling

We selected a total of 33 headwater lakes in the Swedish subarctic (15 lakes) and boreal regions (18 lakes), each with one region in the north and one in the south (Table S1; Figure S1). Selected regions

are Abisko (Subarctic-North; nine lakes), Jämtland (Subarctic-South; six lakes), Västerbotten (Boreal-North; nine lakes), and Värmland (Boreal-South; nine lakes). The subarctic lakes are located on the Swedish mountains and belong to the arctic/alpine ecoregion. The subarctic and boreal lakes are situated at 348–622 and 227–440 m above sea level, respectively, with no or little development in their catchments. The lakes covered gradients in lake DIN:TP ratio, DOC concentration, and temperature, both within and across regions. Swedish subarctic lakes generally have lower DOC concentrations than boreal lakes, due to smaller catchment inputs of terrestrial organic matter (Isles et al., 2020). A north-to-south increasing gradient in lake DIN:TP ratio exists in Sweden, because of the increasing atmospheric N deposition toward the south (Isles et al., 2018). The selected lakes were sampled three times between mid-June and mid-September in 2016 (Abisko, Värmland, and Västerbotten) or 2017 (Jämtland), once early in the open-water season soon after the onset of stratification, once in mid-summer, and once in late summer before circulation. Sampling dates differed among regions because of differences in ice-out, stratification, and circulation periods of the lakes. During the study period, lake DOC concentrations ranged 1.8–9.5 mg L⁻¹ in the subarctic lakes and 4.1–25.6 mg L⁻¹ in the boreal lakes. Ranges of surface water temperature were 7.9–18.7°C in the subarctic lakes and 9.7–25.4°C in the boreal lakes. Lake DIN:TP molar ratios ranged <0.1–9.9 and 0.2–57.2 in the northern and southern regions, respectively.

We used the methods in Bergström et al. (2018; 2020) for measurements of lake physicochemical characteristics and sampling of seston and zooplankton. The detailed methods for measuring water temperature, light extinction coefficient (K_d), spectral absorbance, specific ultraviolet absorbance (SUVA), DIN, total dissolved N (TDN), DOC, TP, and chlorophyll *a* are described in Text S1. Water samples for analysis of seston C concentration and fatty acid (FA) composition were collected from 0.5 to 1.0 m below surface and pre-filtered using a 50- μ m mesh net shortly after collection to remove zooplankton and detritus. Then, 120–420 ml of the filtrates was filtered through glass fiber filters (0.7 μ m pore size) that had been acid washed with 1.2 M HCl, rinsed with nano-filtered water, and pre-combusted at 550°C for 3 h. The seston filters were either oven-dried at 50°C (for C analysis) or freeze-dried (for FA analysis) and stored at -20°C. Crustacean zooplankton samples were collected by multiple hauling with a plankton net (100 μ m mesh size) in the water column from 1 m from lake bottom to the surface in order to obtain sufficient zooplankton amounts for subsequent FA analyses. They were then kept at 4°C in dark for ca. 16 h to allow gut content clearance, and afterward sorted to genus level. Major taxa present were (Calanoida) *Acanthodiptomus*, *Eudiaptomus*, *Heterocope*, *Mixodiptomus*, (Cyclopoida) *Cyclops*, *Megacyclops*, (Cladocera) *Bosmina*, and *Daphnia*, but other taxa such as (Cladocera) *Ceriodaphnia* and *Holopedium* were found occasionally. There were larger temporal and spatial variations in the presence of copepod genera compared to cladoceran genera; thus, we grouped the copepods into orders, that is, Calanoida and Cyclopoida, for subsequent analyses. In a few occasions, sorting to genus or order level was not

possible, and the zooplankton were sorted to copepods or cladocerans. Sorted samples were freeze-dried and stored at -20°C .

2.2 | Fatty acid analysis of seston and zooplankton

Methods for FA analysis of seston and zooplankton (or invertebrates) are reported in Bergström et al. (2020) and Grieve and Lau (2018), respectively. In brief, FA of the samples was extracted with 3:2 (v:v) hexane-isopropanol solution and methylated with 1:17:83 (v:v:v) trimethylsilyldiazomethane:isopropanol:dichloromethane. Internal standards used for analytical quality control and FA quantification were deuterium-labeled pentadecanoic acid (C/D/N Isotopes Inc.), deuterium-labeled methyl heptadecanoate (Sigma-Aldrich Sweden AB), and tridecane and octacosane. Concentrations of the resultant FA methyl esters were analyzed by a gas chromatography-mass spectrometry (GC-MS) (7890A GC, Agilent Technologies; Pegasus[®] High Throughput TOF-MS). The Supelco 37 Component FAME Mix (Sigma-Aldrich Sweden AB) and Bacterial Acid Methyl Ester BAME Mix (Sigma-Aldrich Sweden AB) were used to identify individual FA. Detailed descriptions of the capillary column and the GC-MS program are given by Bergström et al. (2020). Contents of individual FA in seston and zooplankton are reported as mg FA g^{-1} seston C and mg FA g^{-1} dry mass, respectively.

We quantified the contents of different saturated FA, mono-unsaturated FA, bacteria-specific FA, and PUFA in the samples. However, we only focused on the 18C PUFA (i.e., ALA, LIN) and long-chain PUFA (i.e., ARA, EPA, and DHA), as they have been identified as most important FA for zooplankton fitness (Brett et al., 2009; Brett & Müller-Navarra, 1997; Peltomaa et al., 2017). Aquatic consumers with greater trophic reliance on algae than on terrestrial food resources generally have higher $\omega 3:\omega 6$ FA ratios (Lau et al., 2013, 2014; Taipale et al., 2015). Thus, we used the $\omega 3:\omega 6$ FA ratio

to indicate the relative contributions of autochthonous and allochthonous resources in seston and their relative trophic support for zooplankton.

2.3 | Data analysis

Lake DOC, TP, DIN:TP molar ratio, percentage chlorophyll *a* per seston C (%Chla), surface water temperature (at 0.5 m), and the FA data of seston and zooplankton were \log_{10} -transformed to approximate normal distribution and homoscedasticity. Absorbance at 250, 365, and 440 nm and K_d (all \log_{10} -transformed) were strongly and positively correlated with SUVA (linear regressions: $F_{1,31} = 46.23-224.83$, $R^2 = .60-.88$, all $p < .001$); thus, we used only SUVA to indicate the overall light availability and DOC aromaticity. We conducted redundancy analysis (RDA) to examine the regional and seasonal patterns in lake physicochemical characteristics (i.e., lake DOC, TDN, TP, DIN:TP, %Chla, SUVA, and temperature), and analyze whether region or season was the major contributor to total variation in these variables. Region and season were added as constraints and ANOVA-like permutation tests were used to assess whether these constraints and the RDA model were significant ($p < .05$). We also used nested ANOVA to compare lake physicochemical characteristics among regions and seasons (fixed factors), with individual lakes as a random factor nested within region. This nested ANOVA showed generally significant effects of both region and season on individual lake variables (Table S2). But the RDA indicated that region explained a much greater proportion of the total variation in lake variables than did season (Figure 1a,b), that is, larger differences in lake physicochemical characteristics were found among regions than among seasons. Hence, for all lake variables, we used the seasonal averages from individual lakes for subsequent statistical analyses.

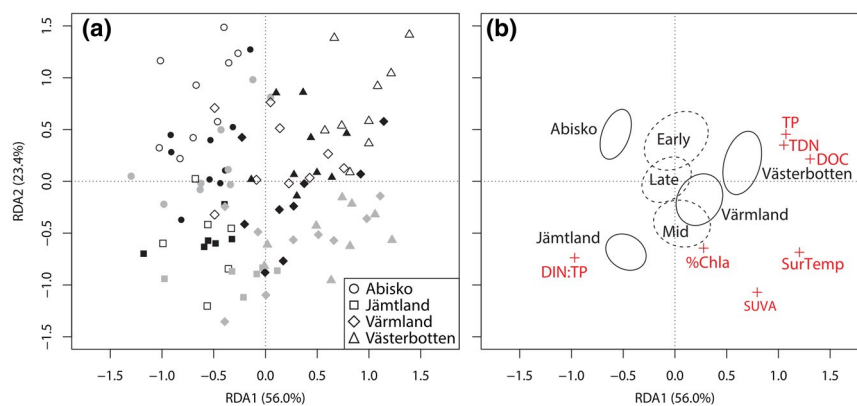


FIGURE 1 Redundancy analysis (RDA) of the lake physicochemical characteristics (eigenvalue = 3.373, adjusted $R^2 = .45$, $p < .001$). Region and season accounted for 37.6% and 7.8% of the total variance, respectively. Variance percentages explained by the RDA axes are indicated in parentheses. (a) Ordination of lake samples in early (white), mid (gray), and late summer (black); (b) lake physicochemical characteristics. Dissolved organic carbon (DOC) concentration, total phosphorus (TP) concentration, dissolved inorganic nitrogen to TP molar ratio (DIN:TP), percentage chlorophyll *a* per seston C (%Chla), and surface water temperature (SurTemp) were \log_{10} -transformed. SUVA is the specific ultraviolet absorbance, and TDN is total dissolved nitrogen. Ellipses indicate 95% confidence limits of group centroids for individual regions (solid lines) and seasons (broken lines)

We used stepwise multiple linear regressions with forward selection to assess whether lake DIN:TP, temperature, DOC concentration, and SUVA were significant determinants of individual PUFA, that is, ALA, LIN, ARA, EPA, and DHA, as well as EPA+DHA, of seston and zooplankton (i.e., individual orders or genera and whole group for both copepods and cladocerans, see below). We included EPA+DHA in the data analyses, as these two long-chain PUFA are of prime importance for growth, neural tissue development, and physiological functions of consumers including zooplankton and fish (Arts et al., 2001; Brett & Müller-Navarra, 1997). The model with the lowest corrected Akaike information criterion (AIC_c) was selected as the best model. Lake DIN:TP ratio has been shown as a major environmental predictor of long-chain PUFA contents in seston in Swedish subarctic lakes (Bergström et al., 2020). We tested the relationships of seston PUFA with lake DIN:TP ratio using exponential regressions, as these relationships based on our data from both subarctic and boreal lakes appeared nonlinear. The AIC_c of these exponential regressions were obtained for comparisons with the selected models from multiple linear regressions.

Linear regressions were used to test whether PUFA contents of the zooplankton taxa, that is, copepods and cladocerans, were associated with lake DIN:TP ratio. For copepods, we first conducted the regressions for individual orders, that is, calanoids and cyclopoids. When multiple samples (replicates) were collected for calanoids and/or cyclopoids in each lake and sampling occasion, the FA data were averaged by replicate and season. We also conducted regressions for copepods, and the PUFA data were sequentially averaged by replicate, order, and season. Cladocerans were sorted to genus, but there were relatively few samples for individual genera; thus, they were analyzed altogether as a group and their PUFA data were averaged by replicate, genus, and season before the regressions. Cladoceran PUFA was also regressed with surface water temperature, which was a main predictor of cladoceran PUFA based on the multiple regressions. The PUFA contents of cladocerans strongly depend on those of their diet (Brett et al., 2006), and the phytoplankton PUFA contents are expected to decrease with increasing water temperatures (Hixson & Arts, 2016).

Calanoids from Lake 5 (Värmland) and Lake 17 (Västerbotten), as well as the copepods from Lake 5 (Värmland) and Lake 8 (Värmland), had low EPA and DHA contents or ω 3: ω 6 FA ratios and were identified as outliers based on Grubb's test ($G = 2.93$ – 3.89 , all $p < .05$). These samples were from a single season (late summer for Lake 5, early summer for Lake 8, and mid-summer for Lake 17). Thus, they were excluded from the respective regressions (both multiple and simple linear regressions) for calanoids and copepods. We conducted RDA using the vegan package (Oksanen et al., 2019) in R (version 4.0.3; R Core Team, 2020) and nested ANOVA and regressions using JMP[®] (version 14.01; SAS Institute Inc.). Statistical significance level (α) was set at 0.05.

3 | RESULTS

Lake physicochemical characteristics significantly differed among regions and seasons (Tables S1 and S2; Figure 1a,b). The RDA

showed that region and season together explained ca. 38% and 8%, respectively, of the total variation in these lake variables, and that the first and second RDA axes (i.e., RDA1 and RDA2) accounted for the regional and seasonal differences, respectively (Figure 1a,b). The boreal lakes in Värmland and Västerbotten generally had higher surface water temperatures, %Chla, and concentrations of DOC, TDN, and TP but lower DIN:TP ratios than the subarctic lakes in Abisko and Jämtland (Figure 1b). Nested ANOVA indicated that lake DIN:TP ratios were higher in Jämtland (6.17 ± 1.17 ; mean \pm SE of seasonal averages from individual lakes) than in Abisko (2.57 ± 1.21) and Värmland (2.45 ± 1.38), and lowest in Västerbotten (0.47 ± 1.27) (Table S2). Lake DOC concentrations were higher in boreal Västerbotten (12.2 ± 1.1 mg L⁻¹) and Värmland (10.6 ± 1.1 mg L⁻¹) compared to in subarctic Abisko (5.3 ± 1.1 mg L⁻¹) and Jämtland (4.8 ± 1.1 mg L⁻¹; Table S2). SUVA was highest in Jämtland lakes (0.046 ± 0.003 L mg⁻¹ C cm⁻¹), intermediate in the boreal lakes (0.037 ± 0.003 and 0.042 ± 0.002 L mg⁻¹ C cm⁻¹ in Värmland and Västerbotten, respectively), and lowest in Abisko lakes (0.019 ± 0.003 L mg⁻¹ C cm⁻¹; Table S2). Surface water temperature of the lakes followed the decreasing order: Västerbotten ($17.8 \pm 1.1^\circ\text{C}$) > Värmland ($15.7 \pm 1.0^\circ\text{C}$) > Jämtland ($13.6 \pm 1.1^\circ\text{C}$) > Abisko ($11.6 \pm 1.0^\circ\text{C}$; Table S2). Lake DOC and TP concentrations were higher, while water temperature, DIN:TP ratio, %Chla, and SUVA were lower, in early or late summer than in mid-summer (Table S2). Lake TDN did not differ among seasons based on nested ANOVA. Thus, the lake physicochemical characteristics in early summer were more similar to those in late summer than in mid-summer (Figure 1b). Larger seasonal differences in the lake variables were detected between the subarctic regions (i.e., more distant apart along RDA2) than between the boreal regions (Figure 1b). Overall, the boreal lakes were warmer and had higher DOC concentrations than the subarctic lakes, while lakes in the south (Jämtland and Värmland) had higher DIN:TP ratios than lakes in the north (Abisko and Västerbotten).

Seston total FA contents in Abisko, Jämtland, Västerbotten, and Värmland lakes were 36.2 ± 7.3 , 47.0 ± 5.3 , 29.5 ± 5.5 , and 29.7 ± 3.5 mg FA g⁻¹ seston C, respectively (Table S3). There was a positive linear relationship between seston LIN content and lake DIN:TP ratio (Figure 2a). Seston ALA and ARA did not change with lake DIN:TP ratio (linear and exponential regressions: $F_{1,31} = 1.15$ – 2.46 , $R^2 = .04$ – $.07$, $p = .127$ – $.292$; Figure 2b). However, seston EPA, DHA, and EPA+DHA contents increased exponentially with increasing lake DIN:TP ratio (Figure 2c–e), inferring that the seston nutritional quality substantially increased as the lakes were less N-limited (cf. Bergström et al., 2020; Isles et al., 2020). Multiple linear regressions also showed that lake DIN:TP ratio was a major environmental determinant of all seston PUFA (Table S4). In particular, lake DIN:TP ratio was the only predictor in the best multiple regression models for seston DHA and EPA+DHA (Table S4). For seston EPA, DHA, and EPA+DHA, the exponential regressions using lake DIN:TP ratio alone always had lower AIC_c than did the best models from multiple linear regressions (Table S4; Figure 2c–e). Thus, we interpreted that the exponential models could describe the changes in these PUFA

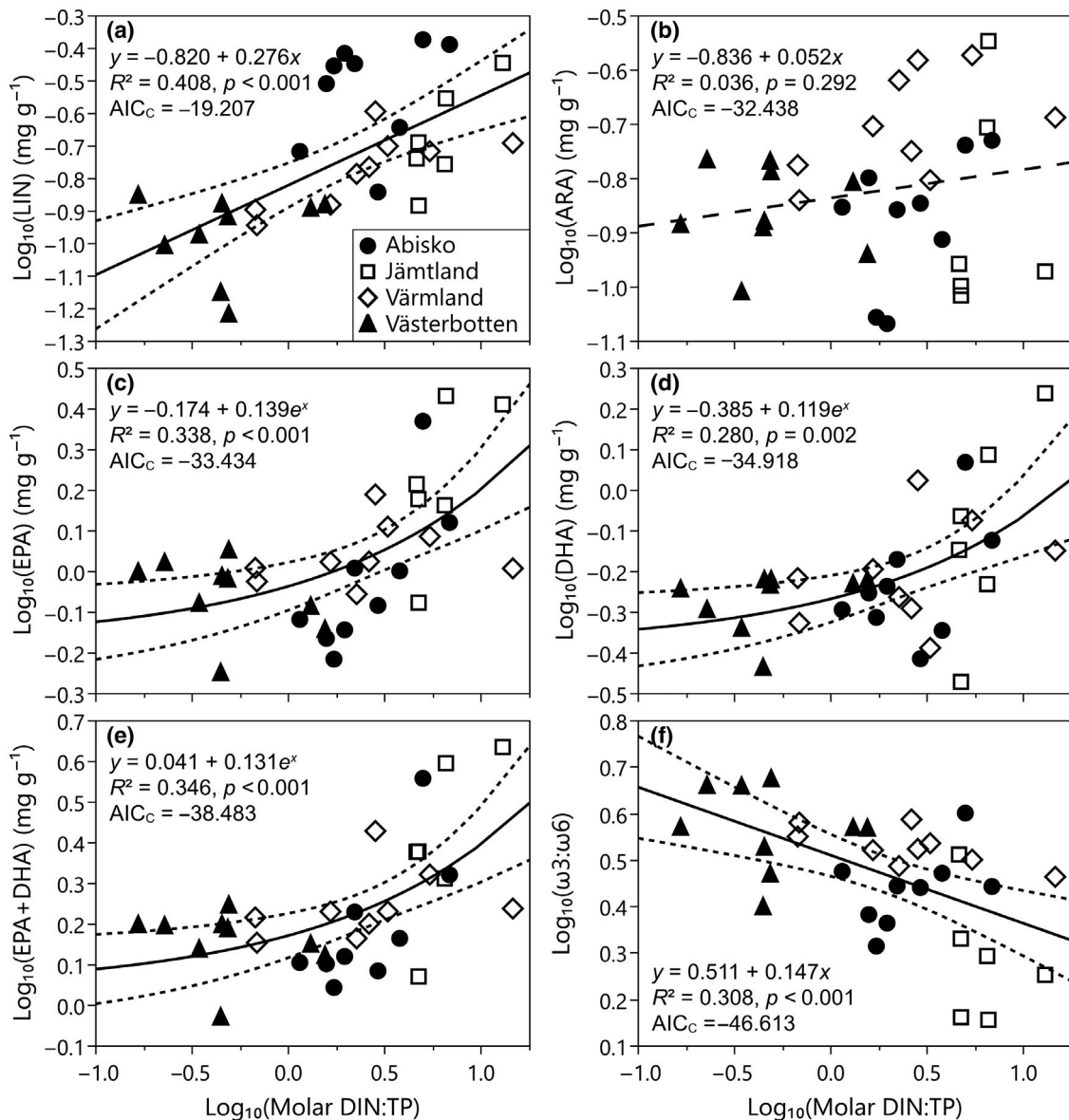


FIGURE 2 Regressions of seston fatty acid (FA) contents against the dissolved inorganic nitrogen to total phosphorus molar ratio (Molar DIN:TP) of the study lakes. (a) Linoleic acid; (b) arachidonic acid; (c) eicosapentaenoic acid; (d) docosahexaenoic acid; (e) total eicosapentaenoic acid and docosahexaenoic acid; (f) omega-3 to omega-6 FA ratio. AIC_c , corrected Akaike information criterion. Dotted lines indicate 95% confidence limits of significant regression models (solid lines). All data are seasonal means

of seston better. Based on these models, seston EPA increased from 0.8 to 1.9 mg FA g^{-1} seston C (i.e., +138%), DHA increased from 0.5 to 1.0 mg FA g^{-1} seston C (+100%), and EPA+DHA increased from 1.3 to 2.9 mg FA g^{-1} seston C (+123%), when the lake DIN:TP ratio increased from 0.17 to 14.53 (i.e., the range of seasonal averages of lake DIN:TP ratio from individual lakes; $\log_{10}(\text{DIN:TP}) = -0.78$ to 1.16 in Figure 2c–e). Seston $\omega 3:\omega 6$ FA ratio decreased linearly with increasing lake DIN:TP ratio, but the predicted value was still >2 when lake DIN:TP ratio was high (Figure 2f). This result suggests that the proportions of $\omega 3$ PUFA-rich phytoplankton in seston decreased as the lakes became less N-limited (i.e., with a higher DIN:TP ratio), but they were still higher compared to the proportions of terrestrial organic matter that was rich in LIN. The multiple regressions

showed that seston ALA and ARA contents increased while seston EPA decreased with increasing lake DOC concentrations (Table S4). In contrast, seston EPA increased, but seston ALA, ARA, and $\omega 3:\omega 6$ FA ratio decreased, with increasing SUVA that indicates lower light availability and higher DOC aromaticity of lake water (Table S4). Increasing surface water temperatures had negative effects on LIN and positive effects on ALA, ARA, and $\omega 3:\omega 6$ FA ratio of seston (Table S4).

Altogether there were 155 zooplankton samples from all study lakes and seasons, of which 128 samples were sorted to order (64 calanoid and 25 cyclopid samples) or genus level (23 *Bosmina* and 16 *Daphnia* samples; Table S5). Total FA contents ranged 35.9–107.4 mg FA g^{-1} dry mass in calanoids, 38.6–173.3 mg FA g^{-1} dry mass

in cyclopoids, 56.8–113.6 mg FA g⁻¹ dry mass in *Bosmina*, and 50.6–148.6 mg FA g⁻¹ dry mass in *Daphnia* (Table S3). The EPA contents were 0.7–4.8 mg FA g⁻¹ dry mass in calanoids, 0.9–6.0 mg FA g⁻¹ dry mass in cyclopoids, 0.4–3.7 mg FA g⁻¹ dry mass in *Bosmina*, and 1.0–8.5 mg FA g⁻¹ dry mass in *Daphnia* (Table S3). The DHA contents in calanoids, cyclopoids, *Bosmina*, and *Daphnia* were 5.0–28.5, 4.0–32.9, 0.1–3.0, and 0.3–8.6 mg FA g⁻¹ dry mass, respectively (Table S3). The EPA+DHA contributions in ω 3 PUFA were 60–99% in all zooplankton taxa. Of the total PUFA, EPA+DHA contributed 68%–93% in calanoids, 54%–88% in cyclopoids, 36%–59% in *Bosmina*, and 33%–73% in *Daphnia*.

The EPA, DHA, and EPA+DHA contents, and the ω 3: ω 6 FA ratios of calanoids and copepods increased with increasing lake DIN:TP ratio (Table S6; Figure 3a–h). Lake DIN:TP ratio alone explained 41%–63% of the variance in DHA, EPA+DHA, and ω 3: ω 6 FA ratios of calanoids and copepods (Figure 3c–h). However, calanoid and copepod ALA, LIN, and ARA did not change with lake DIN:TP ratio (linear regressions for calanoids: $F_{1,24} = 0.07\text{--}0.99$, $R^2 \leq .01\text{--}.03$, $p = .33\text{--}.79$; for copepods: $F_{1,29} = 2.04\text{--}2.78$, $R^2 \leq .01\text{--}.07$, $p = .15\text{--}.60$). The multiple regressions showed that calanoids were more EPA-rich in lakes with higher DIN:TP ratios and SUVA (Table S6), although the positive relationship of calanoid EPA with lake DIN:TP ratio alone was nonsignificant (Figure 3a). According to the linear regressions, calanoid DHA increased from 4.7 to 16.2 mg FA g⁻¹ dry mass (+245%), EPA+DHA increased from 6.3 to 18.7 mg FA g⁻¹ dry mass (+197%), and ω 3: ω 6 increased from 3.8 to 8.8 (+132%), along the lake DIN:TP ratio gradient (i.e., 0.17–14.53) (Figure 3c,e,g). Likewise, the copepod EPA increased from 1.5 to 3.0 mg FA g⁻¹ dry mass (+100%), DHA increased from 5.1 to 19.1 mg FA g⁻¹ dry mass (+275%), EPA+DHA increased from 6.7 to 22.1 mg FA g⁻¹ dry mass (+230%), and ω 3: ω 6 increased from 3.8 to 8.3 (+118%) on the same lake DIN:TP ratio gradient (Figure 3b,d,f,h). The nutritional quality of calanoids and copepods was, thus, higher in lakes with a higher DIN:TP ratio.

No significant relationships were found between cyclopoid PUFA contents or ω 3: ω 6 FA ratio and lake DIN:TP ratio (linear regressions: $F_{1,16} = 0.05\text{--}2.32$, $R^2 \leq .01\text{--}0.13$, $p = .15\text{--}.82$; Table S6; Figure 3a,c,e,g). The multiple regressions indicated that cyclopoid EPA and DHA contents were lower in lakes with warmer surface water (Table S6). The DHA and EPA+DHA of cyclopoids increased, but their ω 3: ω 6 FA ratio decreased, with increasing SUVA (Table S6). Copepods were richer in LIN, EPA, and EPA+DHA in lakes with higher DOC concentrations (Table S6). While in lakes with warmer surface water, copepods had lower DHA and EPA+DHA contents (Table S6), reflecting their lower nutritional quality.

The ARA content of cladocerans was positively correlated with lake DIN:TP ratio based on the multiple regressions (Table S7). The contents of other PUFA and the ω 3: ω 6 FA ratio of cladocerans did not change with lake DIN:TP ratio (linear regressions: $F_{1,26} = <0.01\text{--}3.29$, $R^2 \leq .01\text{--}.11$, $p = .08\text{--}.96$), but cladoceran ALA, EPA, EPA+DHA, and ω 3: ω 6 FA ratio decreased with increasing lake surface water temperature (Table S7; Figure 4a–d). Specifically, the EPA and EPA+DHA contents of cladocerans were reduced from 3.5 to 1.7 and from 5.5 to 2.8 mg FA g⁻¹ dry mass, respectively, when

the surface water increased from 10.1 to 21.7°C (Figure 4b; linear regression for cladoceran EPA: $\log_{10}(\text{EPA}) = 1.546 - 0.994(\log_{10}(\text{SurTemp}))$, $F_{1,26} = 4.08$, $R^2 = .14$, $p = .05$). Based on these models, the EPA and EPA+DHA contents of cladocerans decreased by 6.3% and 5.7%, respectively, for every 1°C increase in lake surface water temperature.

At the genus level, there was a marginally nonsignificant ($p = .06$) positive relationship between *Daphnia* EPA+DHA content and lake DIN:TP ratio, and *Bosmina* EPA content was higher in lakes with a higher DIN:TP ratio (Table S7). The multiple regressions showed a lower EPA+DHA content of *Bosmina* in lakes with warmer surface water (Table S7). Increasing SUVA had positive effects on LIN, ARA, EPA, and EPA+DHA of *Bosmina*, and on ALA and ω 3: ω 6 FA ratio of *Daphnia* (Table S7). The cladoceran ω 3: ω 6 FA ratio also increased with increasing SUVA (Table S7). Hence, these results showed that the cladocerans, especially *Bosmina*, had higher nutritional quality in darker lakes with higher DOC aromaticity. The nutritional quality of cladocerans was more affected by SUVA (i.e., light climate and DOC aromaticity) and water temperature than by lake DIN:TP ratio.

4 | DISCUSSION

Our results showed that lake N:P stoichiometry strongly affected the nutritional quality, especially the long-chain PUFA availability, of seston, calanoids, and copepods. Although surface water temperature was not a significant determinant of seston PUFA availability, warmer surface water resulted in lower EPA+DHA contents of both copepods and cladocerans. Also, the DHA contents in the DHA-dependent cyclopoids and copepods, and the EPA contents in the EPA-dependent cladocerans (Ahlgren et al., 2009; Persson & Vrede, 2006), were lower at warmer conditions. Seston EPA contents decreased in the more DOC-rich lakes, but the EPA and EPA+DHA contents of copepods in these lakes were higher. Contents of ARA and EPA of calanoids, DHA and EPA+DHA of cyclopoids, and ARA, EPA, and EPA+DHA of *Bosmina* also increased in lakes with higher SUVA that reflects lower light availability and higher DOC aromaticity. Overall, these results indicate the taxon-specific responses of zooplankton FA to global environmental changes, and that zooplankton PUFA content will generally decrease upon declining lake DIN:TP ratio (for copepods) and warming (for both copepods and cladocerans), but the negative effects of these stressors on zooplankton PUFA are moderated by lake browning.

The seston EPA and DHA contents exhibited strong exponential relationships with the water N:P stoichiometry of the study lakes, where phytoplankton were primarily N- or NP-limited (Bergström et al., 2020; Deininger, Faithfull, Karlsson, et al., 2017; Isles et al., 2020). Upon increases in lake DIN:TP ratio, the phytoplankton biomass could have been stimulated to enrich the long-chain PUFA availability in seston (Bergström et al., 2020). Our results support the positive relationships of seston EPA, DHA, and other PUFA with lake DIN:TP ratio and phytoplankton biomass (i.e., percent chlorophyll *a* per seston C) previously observed in Swedish subarctic lakes

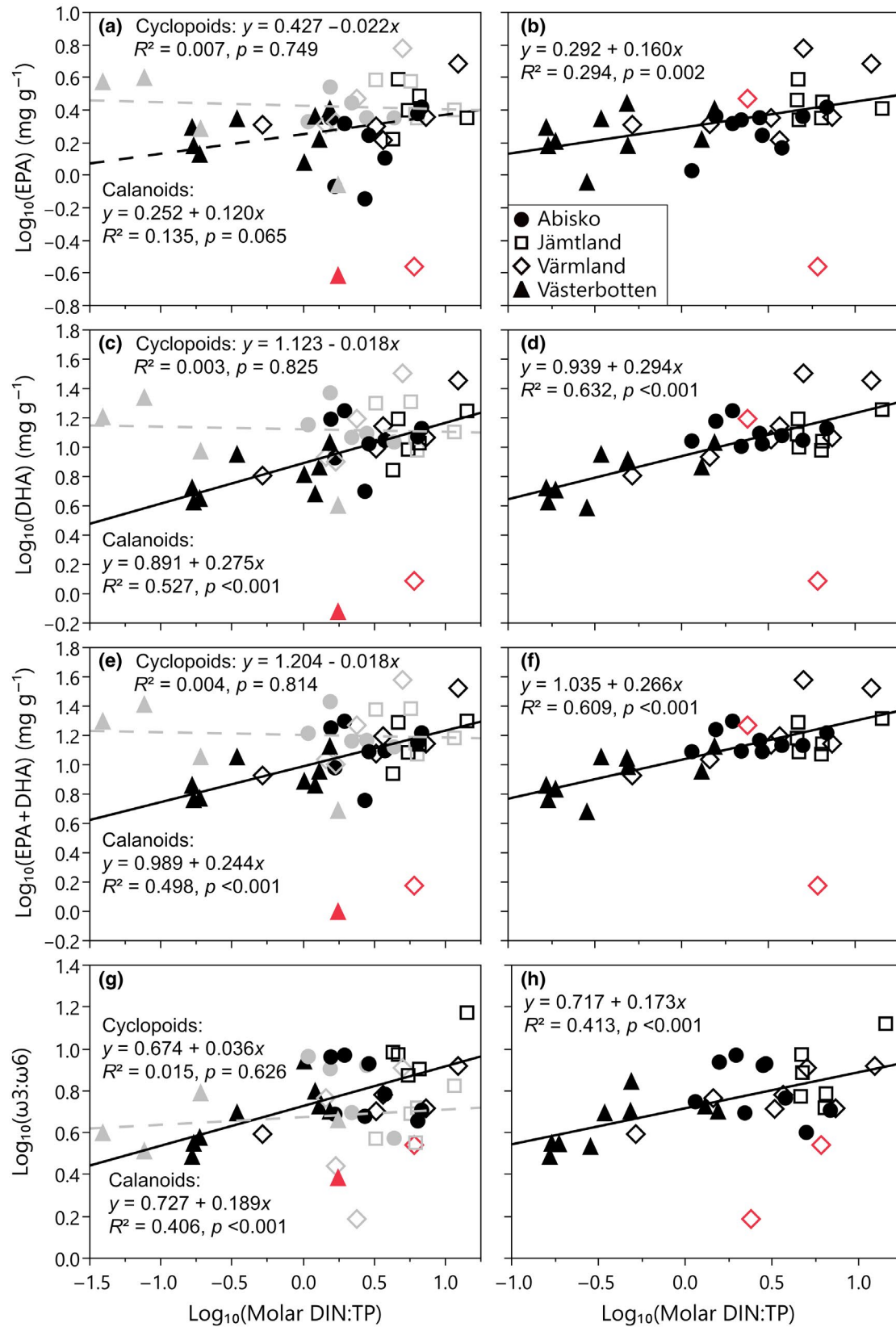


FIGURE 3 Linear regressions of copepod fatty acid (FA) contents against the dissolved inorganic nitrogen to total phosphorus molar ratio (Molar DIN:TP) of the study lakes. Regressions were analyzed for calanoids and cyclopoids separately (black and gray symbols, respectively; a, c, e, g) and for all copepods (b, d, f, h). (a, b) Eicosapentaenoic acid; (c, d) docosahexaenoic acid; (e, f) total eicosapentaenoic acid and docosahexaenoic acid; (g, h) omega-3 to omega-6 FA ratio. Red symbols indicate outliers of calanoids (a, c, e, g) and copepods (b, d, f, h) excluded from the regressions. Broken lines are nonsignificant models, that is, $p > .05$. All data are seasonal means

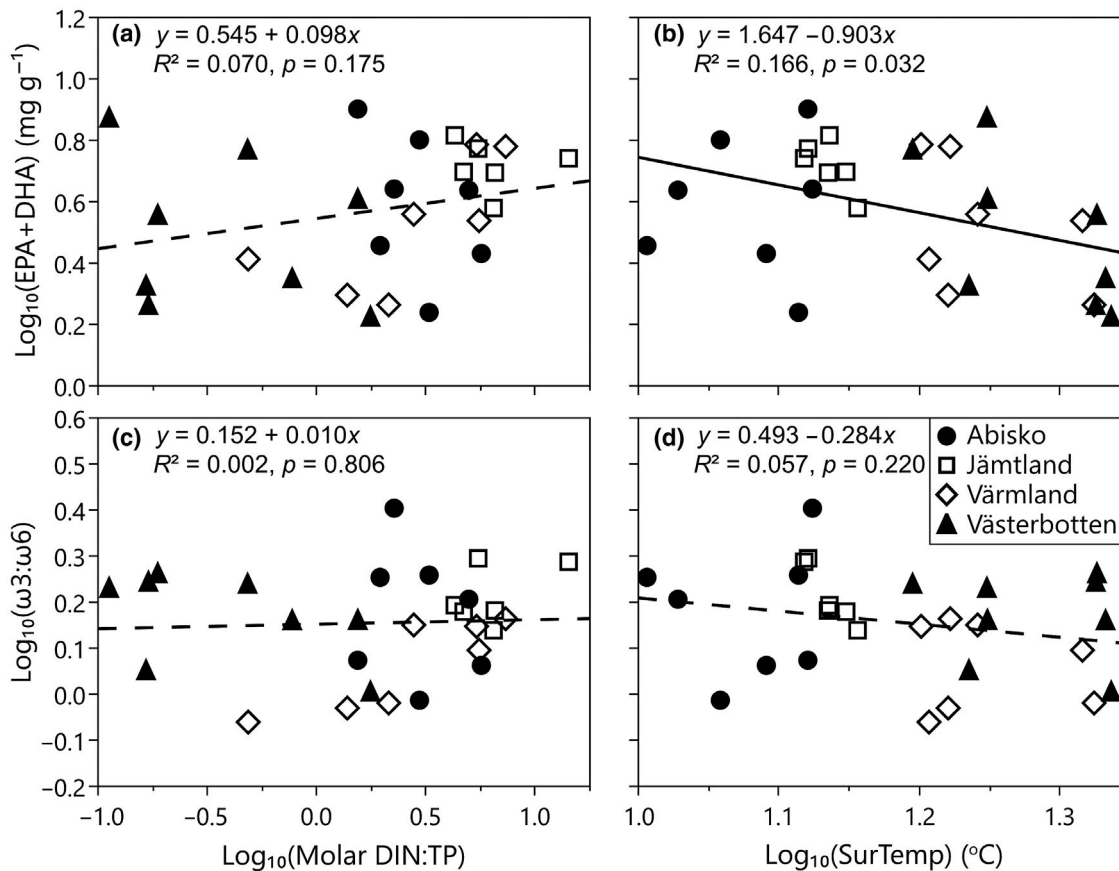


FIGURE 4 Linear regressions of cladoceran fatty acid (FA) contents against the dissolved inorganic nitrogen to total phosphorus molar ratio (Molar DIN:TP) and the surface water temperature (SurTemp) of the study lakes. (a, b) Total eicosapentaenoic acid and docosahexaenoic acid; (c, d) omega-3 to omega-6 FA ratio. Broken lines are nonsignificant models, that is, $p > .05$. All data are seasonal means

in Abisko and Jämtland (Bergström et al., 2020). However, our study, with more lakes (especially in boreal regions) and extended gradients in lake physicochemical characteristics, indicates that these relationships are nonlinear. Upon declines in lake DIN:TP ratio, the lakes with originally high DIN:TP ratio (Jämtland) showed faster decreases in seston EPA and DHA than the lakes with lower DIN:TP ratio (Abisko and Värmland). However, when the lake DIN:TP ratio fell below certain levels, the seston EPA and DHA contents remained low and did not continue to decrease (i.e., the Västerbotten-lake scenario). In particular, when lake DIN:TP ratio was 3.3 ($\log_{10}(\text{DIN:TP}) \approx 0.5$), the threshold below which phytoplankton shift from NP- to N-limitation based on bioassay experiments (Bergström, 2010; Bergström et al., 2020; Isles et al., 2020), the predicted seston EPA and DHA contents were 1.15 and 0.65 mg FA g⁻¹ seston C, respectively. Our estimate of seston EPA is close to the predicted value for solely subarctic lakes and the EPA level (i.e., ca. 1 mg FA g⁻¹ seston C) that can severely hinder zooplankton growth and reproduction (Bergström et al., 2020; Müller-Navarra et al., 2000). Among the 20 lakes with a lake DIN:TP ratio below 3.3, in total 18 lakes (i.e., 90%) had seston EPA contents <1.15 mg FA g⁻¹ seston C and 13 lakes (i.e., 65%) had seston EPA contents ≤ 1.0 mg FA g⁻¹ seston C. A recent estimate showed that 63% of the pristine lakes (i.e., those with minimal agricultural land use and development in catchments) in Sweden had lake DIN:TP

ratios below 3.3 (Isles et al., 2018). Upscaling our results to the whole of Sweden indicates at least 40% of Swedish pristine lakes currently have a lake DIN:TP ratio below 3.3 and a seston EPA content below 1.0 mg FA g⁻¹ seston C. Thus, our results suggest that nutrient depletion and declines in lake DIN:TP ratio will induce N-limitation of phytoplankton and promote reductions in seston nutritional quality to critically low levels that hinder pelagic trophic transfer. Low EPA and DHA availability at the trophic base, as a consequence of N-limitation of phytoplankton, is likely widespread in northern lakes.

It is evident that the impacts of intensified N-limitation (i.e., declining lake DIN:TP ratio) on seston had resulted in reduced nutritional quality of zooplankton, especially calanoids and copepods. Hence, there would be a lower EPA and DHA supply from these zooplankton taxa to fish that heavily depend on these PUFA for growth, reproduction, and physiological functions (Ahlgren et al., 2009; Arts & Kohler, 2009; Sargent et al., 2003). However, fish also have a strong trophic reliance on benthic prey in subarctic and boreal lakes (Karlsson et al., 2009; Lau et al., 2017), where the EPA and DHA contents of fish are not necessarily linked to those of zooplankton (Keva et al., 2021). Fish may adapt to nutritional quality changes in zooplankton by shifting to use benthic prey resources (Lau et al., 2017). Yet, the shift from pelagic to benthic prey resources indirectly supports the negative effects of declining lake DIN:TP ratio

on zooplankton EPA and DHA availability and the associated impairment of the pelagic trophic transfer of essential biochemical nutrients to fish.

The $\omega 3:\omega 6$ FA ratios of calanoids and copepods decreased with decreasing lake DIN:TP ratio, reflecting the reduced trophic support from phytoplankton, or alternatively the increased diet contribution from allochthonous organic matter (Lau et al., 2012, 2014; Taipale et al., 2015), as the lakes became more N-limited. Lower phytoplankton biomass has been found in northern lakes with a lower lake DIN:TP ratio (Bergström & Jansson, 2006), and this change in phytoplankton biomass is not necessarily associated with significant changes in phytoplankton community composition (Deininger, Faithfull, & Bergström, 2017). However, in this study, the negative correlation between lake DIN:TP ratio and seston $\omega 3:\omega 6$ FA ratio suggests a potentially greater biomass reduction of $\omega 6$ PUFA-rich phytoplankton (e.g., chrysophytes; Taipale et al., 2013, 2020) compared to $\omega 3$ PUFA-rich phytoplankton in the more N-limited lakes (e.g., cryptophytes) (see also Deininger, Faithfull, & Bergström, 2017). Nevertheless, copepods and especially calanoids have stronger preferences for phytoplankton (over allochthonous organic matter) than do cladocerans in northern lakes (Berggren et al., 2015). The acquisition of dietary EPA and DHA by copepods was probably constrained by low phytoplankton quantity and reduced seston EPA and DHA availability in the more N-limited lakes. Also, copepods have stronger dependence on N and have a higher body N:P ratio than do cladocerans (Andersen & Hessen, 1991; Bergström et al., 2018). Phytoplankton are more N-limited in lakes with a low DIN:TP ratio, and therefore, seston N:P decreased with decreasing lake DIN:TP ratio (Pearson correlation between \log_{10} -transformed seston N:P molar ratio and lake DIN:TP molar ratio: $R = .60, p < .001$). These results together imply that copepod performance and nutritional quality will be increasingly constrained by both low seston N:P ratio and reduced EPA and DHA availability of seston upon declines in lake DIN:TP ratio.

In contrast to the copepod PUFA patterns, the cladoceran EPA and DHA contents did not change with lake DIN:TP ratio, although the availability of these PUFA in seston was higher when the lakes were less N-limited. This could be linked to the increased P constraint on performance and PUFA accumulation of cladocerans in lakes with a higher DIN:TP ratio where seston N:P was also higher. Cladocerans (e.g., *Daphnia*) are P-rich (Andersen & Hessen, 1991; Bergström et al., 2018) and their somatic growth and EPA accumulation have been found negatively correlated with seston N:P ratio (Müller-Navarra et al., 2000). Furthermore, cladocerans have strong demands for $\omega 3$ PUFA especially EPA for growth and are characterized by high $\omega 3:\omega 6$ FA ratios (Ahlgren et al., 2009; Brett et al., 2009; Taipale et al., 2015). The seston $\omega 3:\omega 6$ FA ratio, however, was lower in lakes with higher DIN:TP ratio in this study. We conjecture that the low seston $\omega 3:\omega 6$ FA ratio, combined with the enhanced P constraint linked to an elevated lake DIN:TP ratio, negatively affected cladocerans fitness and their PUFA accumulation in these lakes.

Zooplankton from different taxonomic levels (cyclopoids, *Bosmina*, and copepods and cladocerans) commonly showed a

decreasing trend in EPA, DHA, and/or EPA+DHA contents toward lakes with warmer surface water. Temperature was a major predictor of these PUFA in cladocerans, but it was less important compared to lake DIN:TP ratio on copepod PUFA contents. In warmer conditions, the lower PUFA contents in zooplankton could be the result of reduced diet quality and reduced PUFA demands for maintaining cell membrane fluidity, that is, homeoviscous adaptation (Hixson & Arts, 2016; Senar et al., 2019). Warming and/or shorter ice cover duration are expected to enhance phytoplankton biomass in northern lakes (Keva et al., 2021; Weyhenmeyer et al., 2013) and the resultant phytoplankton community may become less or more taxonomically diverse (Lau et al., 2020; Weyhenmeyer et al., 2013), and will potentially increase the abundance of cyanobacteria which are unable to synthesize long-chain PUFA (Keva et al., 2021; Weyhenmeyer et al., 2013). Warming may also reduce the nutritional quality of individual phytoplankton taxa, such as diatoms and cryptophytes, which are rich in long-chain PUFA, as their need for homeoviscous adaptation is lower in a warmer environment (Hixson & Arts, 2016). The global analysis by Hixson and Arts (2016) indicated a 3.3% reduction in EPA and a 11.1% reduction in DHA in phytoplankton for every 1°C increase in water temperature. Similar impacts of increasing temperature on seston EPA and DHA contents were not detected by the multiple regressions in this study, likely because the warmer boreal lakes (i.e., Västerbotten and Värmland lakes) also had a lower DIN:TP ratio than the subarctic lakes (i.e., Abisko and Jämtland lakes), and the negative effects of warming could have been masked by those of lake DIN:TP ratio declines on phytoplankton PUFA contents. For all zooplankton taxa in this study, EPA and DHA together contributed high proportions in total $\omega 3$ (60%–99%) and total PUFA (33%–73%). Based on the estimates by Hixson and Arts (2016), it is reasonable that the EPA and EPA+DHA contents of cladocerans were reduced by ca. 6% with every 1°C increase in our study lakes (i.e., their EPA and EPA+DHA reduced by $\geq 49\%$ across the 10–22°C water temperature gradient). Gladyshev et al. (2011) also found a $>97\%$ decrease in the EPA+DHA content (i.e., from 171.7 to ≤ 3.8 mg FA g⁻¹ C) of zooplankton in northern lakes along a summer water temperature gradient of 2–28°C. Thus, our results indicate that warming, either alone or combined with declining lake DIN:TP ratio, will result in food quality reductions of zooplankton for higher consumers in northern lakes. As climate change is causing increases in global lake surface water temperatures and is predicted to impair long-chain PUFA production by phytoplankton (Hixson & Arts, 2016; O'Reilly et al., 2015), the nutritional quality of lake zooplankton is potentially also decreasing worldwide.

Browning, as reflected by increasing lake DOC concentrations and aromaticity (i.e., SUVA), might have moderated the negative effects of declining lake DIN:TP ratio and increasing temperature on the nutritional quality of zooplankton. *Bosmina*, cyclopoids, and copepods were richer in EPA, DHA, or EPA+DHA in lakes with a high DOC concentration or SUVA. Hiltunen et al. (2015) also found increased long-chain $\omega 3$ PUFA concentrations (particularly EPA) in different copepod and cladoceran taxa in lakes with higher DOC concentrations, and our results might be linked to the browning-induced

shifts in dominant taxa and biomass of phytoplankton (Deininger, Faithfull, & Bergström, 2017). Browning can substantially shift the phytoplankton community in northern lakes from dominance within non-flagellated taxa (e.g., chlorophytes to cyanobacteria that are poor in both EPA and DHA) in eutrophic lakes ($TP \geq 30 \mu\text{g L}^{-1}$; Senar et al., 2019) or from dominance from non-flagellated taxa to flagellated taxa (e.g., chlorophytes to cryptophytes that are rich in both EPA and DHA) in oligotrophic or mesotrophic lakes ($TP < 30 \mu\text{g L}^{-1}$; Deininger, Faithfull, & Bergström, 2017; Hiltunen et al., 2015). Browning also has contrasting effects on phytoplankton biomass in low-DOC (positive) and high-DOC lakes (negative; Bergström & Karlsson, 2019). Copepods generally contain abundant DHA, which can be related to the development of vast sensory receptors and their capability in active prey capture and selective feeding (Persson & Vrede, 2006). It is possible that copepods selectively fed on the long-chain PUFA-rich phytoplankton (e.g., cryptophytes), resulting in their higher EPA, DHA, or EPA+DHA contents in the study lakes with higher DOC concentrations. Also, some intermediate consumers such as heterotrophic flagellates are able to assimilate low-quality food, for example, allochthonous organic matter and phytoplankton (e.g., chlorophytes) that lack long-chain PUFA, and upgrade them during anabolism to high-quality compounds including EPA and DHA (Hiltunen et al., 2017; Klein Breteler et al., 1999). Trophic upgrading by these consumers could have made them valuable food sources that provide necessary biochemical nutrients for zooplankton in the browner lakes (Hiltunen et al., 2017; Klein Breteler et al., 1999).

In conclusion, our results imply that reduced lake DIN:TP ratio and intensified N-limitation of phytoplankton in northern lakes, which are mainly driven by widespread declines in N deposition (Isles et al., 2018), will reduce the nutritional quality in particular the long-chain PUFA contents of seston, calanoids, and copepods. As the lake DIN:TP ratio drops to 3.3 or below, the seston EPA and DHA contents will fall to critically low levels that will severely affect zooplankton performance. Warming will also reduce zooplankton nutritional quality, and it is relatively more important than declining lake DIN:TP ratio to affect PUFA contents of cladocerans. Declines in lake DIN:TP ratio and warming in combination possibly will reduce the long-chain PUFA supply from zooplankton to planktivorous predators (e.g., fish), potentially impairing their fitness. Increasing lake DOC concentrations, which may have positive or negative effects on phytoplankton biomass depending on the original lake DOC concentration, will reduce overall EPA and DHA contents in seston. However, browning seems to moderate the negative impacts of declining lake DIN:TP ratio and warming on zooplankton PUFA, likely via community shifts in phytoplankton (toward dominance by long-chain PUFA-rich taxa) or via trophic upgrading of low-quality C to higher quality compounds by intermediate consumers. Our results have strong relevance for subarctic and boreal lakes globally, such as in North America and Northern Europe, where phytoplankton N-limitation, lake browning, and warming caused by changes in climate and reduced atmospheric acid deposition are also common (Creed et al., 2018; Monteith et al., 2007; Simpson et al., 2014). Overall, our results suggest that global environmental changes that drive

northern lakes toward more N-limited, warmer, and browner conditions will reduce the nutritional quality of pelagic food web components in terms of their PUFA availability, leading to lower trophic transfer efficiency and lake productivity.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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