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Zooplankton in northern lakes show taxon-specific responses in fatty acids across climate-productivity and ecosystem size gradients

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Abstract

Northern lakes are facing rapid environmental alterations—including warming, browning, and/or changes in nutrient concentrations—driven by climate change. These environmental changes can have profound impacts on the synthesis and trophic transfer of polyunsaturated fatty acids (PUFA), which are important biochemical molecules for consumer growth and reproduction. Zooplankton are a key trophic link between phytoplankton and fish, but their biochemical responses to environmental change are not well understood. In this study, we assess the trends in fatty acid (FA) composition of zooplankton taxa among 32 subarctic and temperate lakes across broad climate-productivity and ecosystem size gradients. We found that genus-level taxonomy explained most FA variability in zooplankton (54%), suggesting that environmental changes that alter the taxonomic composition also affect the FA composition of zooplankton communities. Furthermore, the FA responses and their underlying environmental drivers differed between cladocerans and copepods. Cladocerans, including widespread *Bosmina* spp. and *Daphnia* spp., showed pronounced responses across the climate-productivity gradient, with abrupt declines in PUFA, particularly eicosapentaenoic acid and arachidonic acid in warmer, browner, and more eutrophic lakes. Conversely, calanoid copepods had high and relatively stable PUFA levels across the gradient. In addition, all zooplankton taxa increased in stearidonic acid levels in larger lakes where PUFA-rich cryptophytes were more abundant. Overall, our results suggest that climate-driven environmental alterations pose heterogeneous impacts on PUFA levels among zooplankton taxa, and that the negative impacts of climate warming are stronger for cladocerans, especially so in small lakes.

Northern lakes are subject to a wide range of environmental alterations, including climate change, eutrophication, and browning (Schindler and Smol 2006; de Wit et al. 2007). In Arctic regions, climate warming is more than twice as fast as the global average (Allan et al. 2021), leading to higher mean water temperatures, shorter ice-cover duration, and thus longer growing seasons for biota (Rouse et al. 1997; Wrona et al. 2016). Warming also affects catchment processes and thereby indirectly influences lake ecosystems. For instance, in high-Arctic regions, accelerating permafrost thaws increase inputs of organic matter and nutrients to lakes (Kokelj et al. 2009; Vonk et al. 2015). Conversely, in the Arctic/alpine ecoregion of Sweden, lakes are suffering from nutrient declines during the last decades (Huser et al. 2018), which are concurrent to the warming-induced greening of tundra landscapes (Forbes et al. 2010; Myers-Smith and Hik 2018). At lower elevations and latitudes, lakes in forested catchments are undergoing long-term increases in water color (i.e., colored DOC, iron), referred to as "browning" (de Wit et al. 2007; Björnerås et al. 2017; Kritzberg 2017). While browning in northern lakes has been mainly caused by historical reductions in acid deposition (de Wit et al. 2007; Monteith et al. 2007), climate change also promotes browning via increases in catchment vegetation (Finstad et al. 2016; Kritzberg 2017) and due to climate-related changes in hydrology (Creed et al. 2018). Browning often comes with increased nutrient concentrations that stimulate primary production in

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Additional Supporting Information may be found in the online version of this article.

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nutrient-poor clear-water lakes (Seekell et al. 2015; Vonk et al. 2015; Creed et al. 2018), but also increases light attenuation that offsets the effect of nutrients and reduces whole-lake productivity (Karlsson et al. 2009; Creed et al. 2018). Overall, understanding the combined effects of warming, browning, and changes in nutrient concentrations is thus important for predicting food web responses in high-latitude lakes as a result of climate change.

Zooplankton are a key trophic link in lake food webs as they transfer energy, nutrients, and long-chain polyunsaturated fatty acids (LC-PUFA, i.e., PUFA with ≥ 20 carbon) from phytoplankton to fish (Lindeman 1942; Strandberg et al. 2015). Omega-3 LC-PUFA, such as eicosapentaenoic acid (20:5ω3, EPA), docosahexaenoic acid (22:6ω3, DHA), and the omega-6 arachidonic acid (20:4ω6, ARA), are essential for animal growth, reproduction, and a suite of physiological functions (Müller-Navarra et al. 2000; Ahlgren et al. 2009; Ilić et al. 2019). Saturated fatty acids (SAFA) and mono-unsaturated fatty acids (MUFA), in contrast, are mainly used for energy storage and membrane structure, and are less important for consumer growth and fitness (e.g., Goedkoop et al. 2007; Brett et al. 2009). EPA and DHA are synthesized de novo by certain micro-algae such as diatoms and cryptophytes, but not by chlorophytes and cyanobacteria (Ahlgren et al. 1990; Napolitano 1999). Warming, eutrophication and browning are expected to impair the production and transfer of LC-PUFA in aquatic food webs (Hixson and Arts 2016; Keva et al. 2021; Lau et al. 2021). This is partly explained by a reduced physiological demand of LC-PUFA (and increased demand of SAFA) by phytoplankton to adjust membrane fluidity to increasing temperatures according to homeoviscous adaptation (Hixson and Arts 2016; Holm et al. 2022). Furthermore, warming, eutrophication, and browning also induce shifts from PUFA-rich to PUFA-poor species in phytoplankton assemblages, for example the shift from a predominance of diatoms and cryptophytes in nutrient-poor colder waters to a predominance of chlorophytes and cyanobacteria in nutrient-rich and warmer conditions (Weyhenmeyer et al. 2013; Senar et al. 2019; Keva et al. 2021). Such a shift in autotrophic groups then generally lowers the bottom-up supply of LC-PUFA (Müller-Navarra et al. 2000; Keva et al. 2021), although there are exceptions (Hiltunen et al. 2015; Senar et al. 2019). Browning also promotes the importance of microbial heterotrophs (Ask et al. 2009; Berggren et al. 2014), which also tend to be devoid of LC-PUFA (e.g., Brett et al. 2009; Taipale et al. 2018). These changes in phytoplankton assemblages and PUFA production can negatively affect PUFA accumulation by zooplankton grazers and their nutritional quality (Gladyshev et al. 2011; Taipale et al. 2018; Lau et al. 2021), while also impeding zooplankton development (Sundbom and Vrede 1997; Müller-Navarra et al. 2000; Brett et al. 2009).

Cladocerans and copepods are common zooplankton taxa in freshwaters, including northern lakes. Cladoceran grazers are mostly generalist filter-feeders that do not actively select food particles (DeMott 1989; Sterner 1989) and that have parthenogenetic reproduction (Sommer et al. 1986). Copepods instead select which particles they ingest by their taste and shape (DeMott 1989; Sterner 1989), and only reproduce sexually, generally having lower growth rates and longer life cycles than cladocerans (Allan 1976). Copepods also tend to survive longer fasting periods than cladocerans (DeMott 1989), due to their ability to store lipids (fatty acid [FA]) (Hiltunen et al. 2015; Grosbois et al. 2017). Nevertheless, both copepods and cladocerans may avoid periods with adverse conditions via resting eggs (Gyllström and Hansson 2004), and via dormancy in copepod adults and copepodites (Dahms 1995; Gyllström and Hansson 2004). Cladocerans and copepods have different demands for LC-PUFA, that is, cladocerans generally require high EPA levels and slightly higher ARA levels than copepods, while copepods contain more DHA (e.g., Persson and Vrede 2006; Lau et al. 2012). These marked differences in feeding strategy, life histories, and FA requirements between cladocerans and copepods likely mediate their respective FA responses to environmental changes. For instance, the DHA concentrations in copepods and that of EPA in cladocerans (i.e., mg g DW^{-1}) decrease with increasing water temperature, which can be related to changes in the taxonomic composition of these groups and to their lower demand for LC-PUFA to maintain cell membrane fluidity at warmer conditions (Lau et al. 2021). Compared to cladocerans, the DHA and EPA concentrations in copepods are also more sensitive to declines in the nitrogen-to-phosphorus ratio in lake water (Lau et al. 2021), as copepods have a higher demand for nitrogen than do cladocerans. Yet, the taxon-specific FA responses among zooplankton to environmental change are still largely unknown.

In this study, we synthesize published and unpublished data to (1) quantify the FA changes of multiple zooplankton taxa in northern lakes across climate-productivity (i.e., temperature, nutrients, and water color) and lake-size gradients and (2) identify the key drivers for zooplankton FA variation. We predict that (1) genus-level taxonomy explains more of the zooplankton FA variation than do the environmental gradients, as zooplankton taxa differ in their requirements for long-chain PUFA that are independent of differences in habitat characteristics and food availability (Persson and Vrede 2006). We further predict (2) general increases in the proportion of SAFA with concurrent PUFA declines in all zooplankton taxa across the climate-productivity gradient, that is, toward warmer, browner, and more eutrophic conditions. This is because phytoplankton assemblages are expected to shift from the dominance of PUFA-rich cryptophytes and diatoms in cold oligotrophic lakes toward PUFA-deficient green algae and cyanobacteria in warmer nutrient-rich lakes (e.g., Keva et al. 2021), while browning promotes the relative importance of PUFA-deficient terrestrial organic matter and bacteria for zooplankton production (Berggren et al. 2014). We also predict that (3) lake area counteracts the effects of warming on zooplankton FA, as larger lakes support more diverse phytoplankton assemblages and favor the predominance of cryptophytes and diatoms compared to smaller lakes (Lau et al. 2017); accordingly, we predict that (4) levels of FA biomarkers for diatoms (EPA and 16:1ω7) and/or cryptophytes (stearidonic acid [18:4ω3, SDA]) in zooplankton are higher in larger lakes.

Materials and methods

Study sites and data compilation

We synthesized published and unpublished data of zooplankton FA in 32 Swedish lakes from 2002 to 2010 and 2020 to 2021 (Supporting Information Table S1). The combined dataset encompasses 100 samples of zooplankton FA collected between June and September across broad gradients in latitude (56.2–68.4°N), lake size (surface area: 0.11–68.4 km^2), and elevation (1–951 m a.s.l.) (Fig. 1; Table 1). We calculated mean FA values of zooplankton per taxon and per lake to avoid overrepresentation of data from lakes with multiple observations of the same taxon. This yielded 78 samples for statistical analysis. A majority of the FA data (71/100 samples) have been published in Johansson et al. (2016), Lau et al. (2012), and Persson and Vrede (2006), while 29/100 samples represent unpublished data (Supporting Information Table S1).

While the compilation of large data sets has a large scientific potential, the analysis of data from different sources also comes with inherent limitations. For this study, however, we have taken several steps to guarantee good comparability of data: First, we have been co-authors of all the studies from which data have been collected (*see* citations above), meaning we had access to the raw data and full control over the sampling and analytical procedures throughout. Second, we have selected common and easily identifiable FA to minimize the potential effects of methodological differences among datasets. Third, we have also checked that environmental gradients were temporally consistent (*see* details below). Finally, we strived to minimize possible effects of season, by selecting a vast majority of samples (89%) from the middle of the summer (July–August). All these measures were to maximize the data harmonization among the datasets while keeping a high number of samples that allowed us to test for different predictions.

For spatial analysis of the lake's environmental conditions, we calculated inter-annual means of climate and water chemistry data for the periods that include the years of zooplankton sampling (Supporting Information Table S1). Surface water samples (0.5 m) were analyzed for a suite of water chemistry variables using standardized methods and extracted from previous publications (Persson and Vrede 2006; Persson et al. 2008), as well as data from specific monitoring programs (Erken Laboratory, https://www.ieg.uu.se/erken-laboratory/lake-monitoring-programme/; or Swedish national and regional monitoring, https://miljodata.slu.se/MVM/Search; *see* also Fölster et al. 2014).

Absorbance at 420 nm (Abs$_{420}$), measured in a 5-cm cuvette, was used as a proxy for water color (SS-EN ISO 7887:2012). Water color measured as mg Platinum L^{-1} was back calculated to Abs$_{420}$ by dividing by 500 (Naturvårdsverket 1999), while Abs$_{430}$ was recalculated to Abs$_{420}$ by multiplying by 1.80 using established relationships for Swedish inland waters in our lab. Total phosphorus (TP) concentrations were analyzed using the SS-EN ISO 6878:2005 method (modified). Mean summer air temperature for the lakes (June–September) was extracted from the Climate Research Unit gridded Time Series dataset (version 4.06; Harris et al. 2020; https://crudata.uea.ac.uk/cru/data/hrg/), using the 2001–2011 and 2012–2021 periods for lakes sampled for zooplankton FA in 2002–2010 and 2020–2021, respectively (Supporting Information Table S1). Temperature data were obtained from grids of 0.5° latitude by 0.5° longitude, which are sufficiently large to cover not only the lakes, but also their catchments. Lake elevation was extracted from a GIS-elevation layer, while lake area was obtained from the Swedish lake register (Swedish Meteorological Institute, https://vattenwebb.smhi.se/svarwebb/) and, for the unregistered lakes, via manual areal measurements in the online map of the Swedish Land Survey (https://minkarta.lantmateriet.se/). Our selected inter-annual means of the environmental data (i.e., climate and water chemistry) were strongly correlated with those of the summer means from specific years of zooplankton sampling ($r = 0.85$–0.97), indicating that the among-lake climate-productivity gradient was consistent over the study period.

Methods for zooplankton FA sampling and analysis were similar among the datasets (Supporting Information Table S1). In brief, samples of zooplankton were collected in the summer by net hauls using 180- or 200-μm nets and freeze-preserved in the field using liquid nitrogen or dry ice. In the lab, samples were freeze-dried, sorted (generally to species or genus level), and stored at −20°C or −70°C under N_2. FAs were extracted using established methods such as the chloroform/methanol method (Tadesse et al. 2003), the hexane/isopropanol method (Eriksson and Pickova 2007) or the methanol/toluene/acetyl-chloride method (Grosbois et al. 2022), and immediately converted into FA methyl esters (FAME) using alkaline or acid transesterification (Supporting Information Table S1). FAME were quantified using GC-MS and/or GC-FID based on internal and external reference standards (Supporting Information Table S1). Among the FA identified in the various data sets (Supporting Information Table S1), we selected 16 common FA for our synthesis. Then, we recalculated percentages of each FA relative to the sum of these 16 FA, aiming to standardize the FA values among datasets (Supporting Information Table S2). These 16 FA are commonly and clearly identifiable by the different analytical methods (i.e., GC-MS, and/or GC-FID), and constituted 79–99% of all the FA in the original datasets.

For the data analysis, we used individual FA, and FA groups that provided information that was relevant to the research questions we addressed: groups of SAFA, MUFA, and PUFA were used to indicate overall changes in zooplankton FA composition across the climate-productivity and lake-size gradients. Individual LC-PUFA (i.e., EPA, ARA, DHA) were used because of their importance for the physiology and fitness of

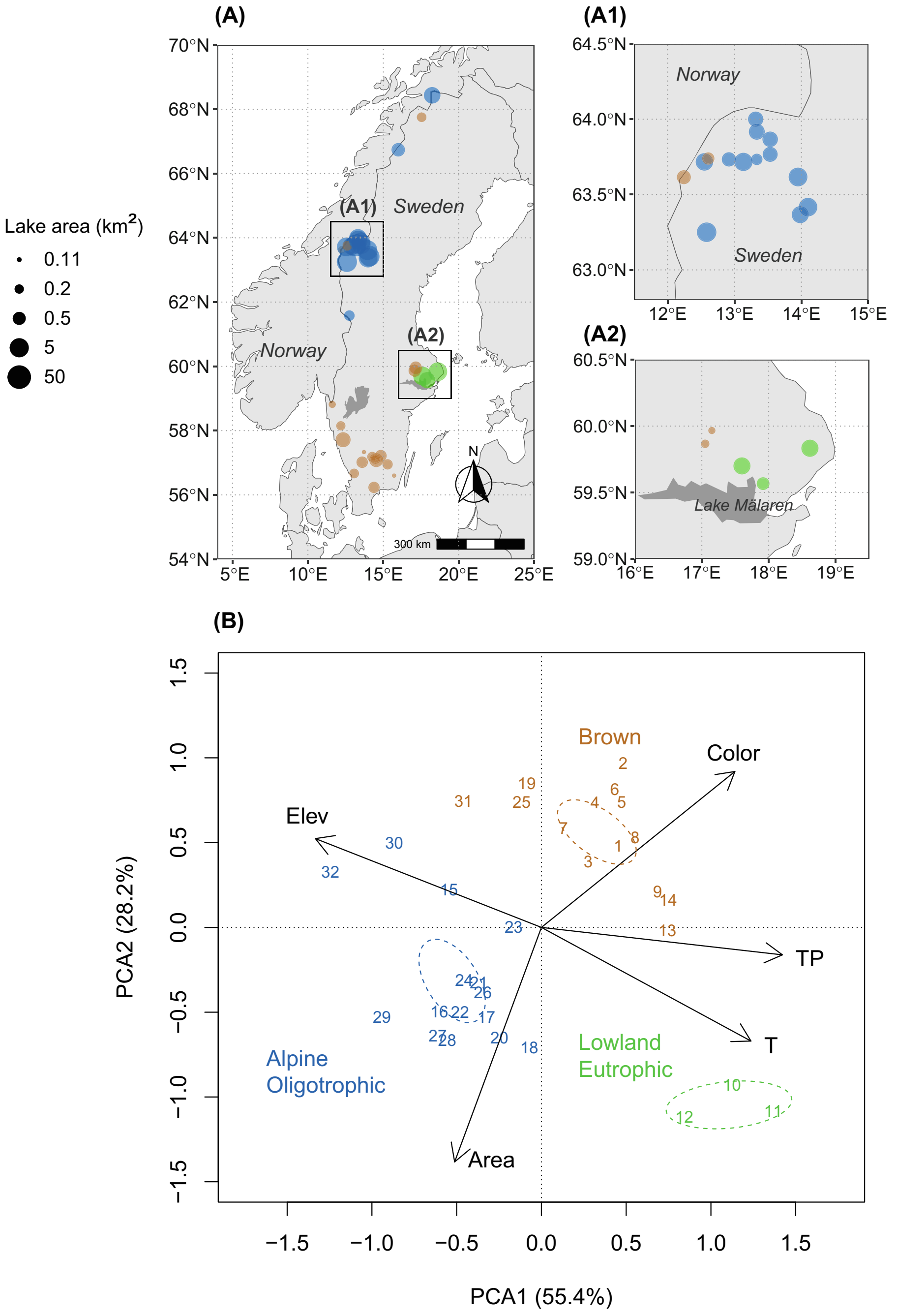

Fig. 1. (**A**) Locations of the 32 study lakes. Lake area is represented by the size of the circle and panels (A1) and (A2) show a higher resolution of the annotated regions. (**B**) Principal component analysis (PCA) of the lakes' physicochemical variables (color, water color; area, lake area; Elev, elevation; T, temperature; TP, total phosphorus). Ellipses indicate 95% confidence limits of group centroids for individual lake types classified by *k*-means clustering. Lakes are numbered based on an increasing order of their latitudes. Individual lake names and numbers are shown in Supporting Information Fig. S3.

organisms. We also included individual FA biomarkers for different algal groups—that is, 16:1ω7*c* *cis*-palmitoleic acid for diatoms and 18:4ω3 SDA for cryptophytes (Taipale et al. 2013)—to indicate changes in algal resource use by zooplankton across the gradients. The ratio between omega-3 and omega-6 FA (ω3/ω6) was additionally used to reflect the overall trophic support by algae vs. terrestrial organic matter for zooplankton (Hixson et al. 2015; Taipale et al. 2015). Zooplankton FA composition may vary with their total lipid content (e.g., Hiltunen et al. 2015; Grosbois et al. 2017). Yet, zooplankton lipid content data are not available from the individual studies, so we are unable to test for the zooplankton response in lipid content

Table 1. Geographic and physicochemical characteristics of the different lake types. Area, lake area; Color, absorbance at 420 nm; TP, total phosphorus concentration; T, mean annual air temperature; N = number of lakes.

Lake type	Latitude (°N)	Longitude (°E)	Elevation (m a.s.l.)	Area (km^2)	TP (μg P L^{-1})	Color (Abs$_{420}$ 5 cm^{-1})	T (°C)	N
Alpine Oligotrophic	61.6–68.4	12.5–18.2	296–952	0.41–65	< 1.0–8.0	<0.005–0.03	6.8–12.8	15
Brown	56.2–63.8	11.6–17.1	55–697	0.11–2.64	3.7–21.7	0.04–0.51	8.1–15.5	14
Lowland Eutrophic	59.6–59.8	17.6–17.9	1–11	4.8–23	28.9–42.3	0.03–0.15	15.9	3

across the climate-productivity and lake-size gradients, as well as its associated effects on the zooplankton FA.

Data analyses

FA percentage data were logit-transformed prior to multivariate analysis for normal-distribution approximation. The ω3/ω6 ratio, along with all environmental variables, including TP, water color, and mean annual temperature, were $\log_{10}$-transformed-prior to analysis. The study lakes differed in elevation, but elevation was not included as an explanatory variable of zooplankton FA composition due to high collinearity with TP ($r = -0.70$; Supporting Information Fig. S1) and temperature ($r = -0.71$; Supporting Information Fig. S1), which both are mechanistic drivers of FA availability in seston (zooplankton food) (e.g., Müller-Navarra et al. 2000; Hixson and Arts 2016).

For testing zooplankton FA responses across the environmental gradients for cladoceran and copepod taxa, we first grouped the cladoceran grazers *Bosmina* spp. Baird, 1845 and *Daphnia* spp. O.F. Müller, 1785, based on their similar feeding ecology and FA compositions (Fig. 2A) and their presence in all study lake types (Fig. 2; Supporting Information Fig. S2B). Similarly, we pooled calanoid copepods from the family Diaptomidae (i.e., *Eudiaptomus* spp. Kiefer, 1932, *Arctodiaptomus laticeps* (G.O. Sars, 1863), and *Mixodiaptomus laciniatus* (Lilljeborg in Guerne & Richard, 1889)) into copepod grazers. The filter-feeding cladocerans *Ceriodaphnia* spp. Dana 1853 and *Holopedium gibberum* Zaddach, 1855 as well as the predatory cladocerans *Bythotrephes longimanus* Leydig, 1860, and *Polyphemus pediculus* (Linnaeus, 1758) and the predatory copepods *Heterocope* spp. G.O. Sars, 1863 were present in relatively few lakes at either ends of the gradient (Supporting Information Fig. S2B). Principal component analysis (PCA) was used to assess the environmental gradients based on the lakes' geographic and physicochemical data, including TP, water color, mean air temperature, lake elevation, and lake area. The first PCA axis (PC1) was strongly and positively correlated with temperature, water color, and TP ($r > 0.7$; Supporting Information Fig. S1), and explained 55.4% of the total variance in lake abiotic variables (Fig. 1B; Supporting Information Fig. S3). Thus, we used PC1 scores as a climate-productivity index (CPI), that is a surrogate for simultaneous effects of eutrophication, browning, and warming that are typical in northern lakes (e.g., Hayden et al. 2017; Keva et al. 2021). The CPI was then used for univariate analysis to test for zooplankton FA responses.

We classified lake types based on the physicochemical variables using k-means clustering and the Calinski–Harabasz criterion to determine the optimal number of partitions. K-means clustering yielded an optimum of three lake groups ($k = 3$, calinski = 39.9) that we identified as Alpine Oligotrophic, Brown, and Lowland Eutrophic lakes (Fig. 1). The Alpine Oligotrophic lakes are cold, low in nutrients and color, and encompass a broad range in size (Fig. 1; Table 1; Supporting Information Fig. S4). The Brown lakes are generally warmer, small (< 2 km^2) and with intermediate nutrient concentrations, while the Lowland Eutrophic lakes have the highest TP concentrations and low to intermediate water color, with temperatures similar to those of the Brown lakes (Fig. 1; Table 1; Supporting Information Fig. S4).

The effects of environmental variables and genus on FA variation of zooplankton were tested using redundancy analysis (RDA) with forward selection. Zooplankton genus, temperature, water color, TP, and lake area were used as explanatory variables. We selected the best model based on the lowest Akaike information criterion (AIC). Similarly, the RDA was applied separately for cladoceran (*Bosmina* and *Daphnia*) and copepod grazers (Diaptomids: *Arctodiaptomus*, *Eudiaptomus*, and *Mixodiaptomus*), excluding genus as an explanatory variable. Therefore, to avoid bias, the other genera were excluded from the analysis of genus-specific FA responses across the environmental gradients.

Highly covaried variables were identified with variance inflation factors > 2.5 (O'Brien 2007), leaving only one of the collinear variables for subsequent analysis. The statistical significance of the selected independent variables in the RDA was determined using permutation tests (n.perm = 999) on their marginal effects at $\alpha = 0.05$. Differences in the FA composition among zooplankton groups were tested using PERMANOVA, and the multivariate homogeneity of group dispersions in FA variation was tested using the "betadisper" function in R. Linear regressions were used to investigate the changes in FA of copepod and cladoceran groups (i.e., including predators and rare taxa along the gradients) across the CPI and lake-size gradients. To simplify visualization, we present regressions of physiologically important FA (i.e., DHA, EPA, ARA) and other FA that correlated with CPI and lake area gradients in either copepods or cladocerans ($r > 0.5$, $p < 0.05$). Multivariate analyses were performed using the vegan package version 2.6-4 (Oksanen et al. 2022)

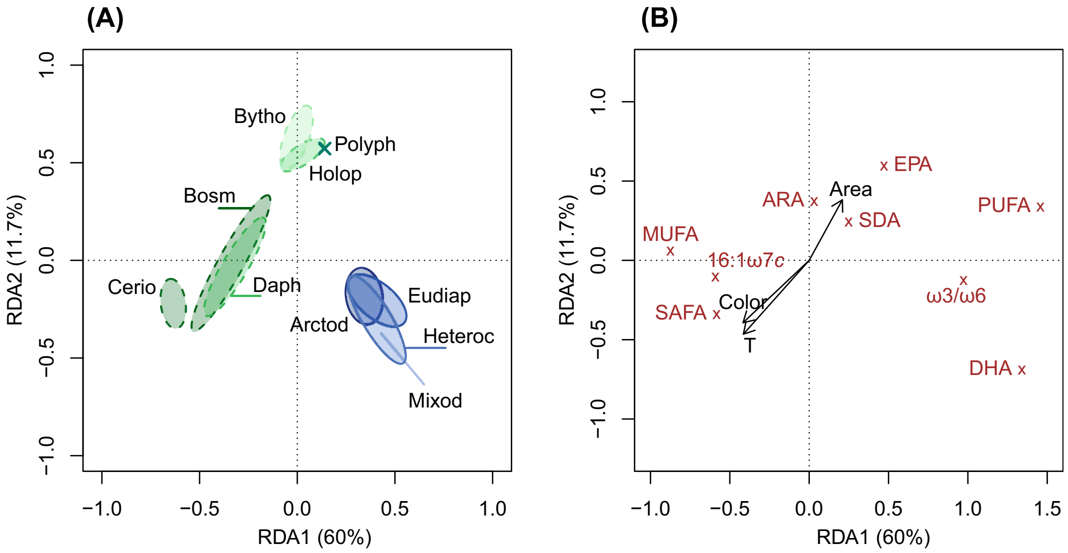

Fig. 2. Redundancy analysis (RDA) of zooplankton FA compositions. (**A**) Ordination of different taxonomic groups: Bosm, *Bosmina* ($n = 12$); Cerio, *Ceriodaphnia* ($n = 4$); Daph, *Daphnia* ($n = 18$); Holop, *Holopedium* ($n = 10$); Bytho, *Bythotrephes* ($n = 5$); Polyph, *Polyphemus* ($n = 1$); Arctod, *Arctodiaptomus* ($n = 7$); Eudiapt, *Eudiaptomus* ($n = 9$); Mixod, *Mixodiaptomus* ($n = 2$); Heteroc, *Heterocope* ($n = 11$). Ellipses indicate 95% confidence limits of group centroids for individual taxa with $n > 2$, with dashed borders and green colors for cladocerans and solid borders and blue colors for copepods. For *Polyphemus* ($n = 1$), the ellipse collapses into a single point, and for *Mixodiaptomus* ($n = 2$), the ellipse collapses into a line. (**B**) Eigenvectors of the physicochemical variables (area, lake area; color, water color; T, temperature) and the FA classes (SAFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, poly-unsaturated fatty acids; SDA, stearidonic acid; 16:1ω7*c*, *cis*-palmitoleic acid; EPA, eicosapentaenoic acid; ARA, arachidonic acid; DHA, docosahexaenoic acid; ω3/ω6, omega-3/omega-6 ratio). Variance explained (%) by the RDA axes are indicated in parentheses.

and all analyses were performed using R version 4.2.0 (R Core Team 2022).

Results

The study lakes encompassed a broad range of environmental conditions from ultra-oligotrophic to eutrophic (mean TP < 1.0–$42.3\ \mu$g P L^{-1}), clear-water to brown colored (< 0.005–0.51 Abs$_{420}$), and with summer (June–September) mean temperatures ranging from 6.8°C to 15.9°C (Table 1).

The first and second axes of the PCA explained 55.4% and 28.2%, respectively, of the total variation in lake environmental conditions (Fig. 1). PC1 (which was used as CPI) was strongly and positively correlated with water color, TP, and temperature ($r = 0.72$–0.90, $p < 0.001$), and negatively correlated with elevation ($r = -0.85$, $p < 0.001$) (Fig. 1; Supporting Information Fig. S1). PC2 was instead negatively correlated with lake area ($r = -0.88$, $p < 0.001$) and positively correlated with water color ($r = 0.58$, $p < 0.001$) (Fig. 1; Supporting Information Fig. S1).

Genus explained most of the variation in FA composition among zooplankton (54.1%) according to the RDA (Table 2, model A), with a distinct separation between cladoceran and copepod genera that was characterized by high MUFA and high DHA, respectively (Fig. 2). The RDA also identified temperature, lake area, and water color as significant explanatory variables of the zooplankton FA composition (Fig. 2B; Table 2, model A), but only contributing to 8.0%, 2.5%, and 1.0% of the variation, respectively. High temperature and water color were associated with high SAFA levels in zooplankton, while larger lake areas were associated with higher levels of PUFA, such as SDA, EPA, and ARA (Fig. 2B).

Bosmina and *Daphnia* did not differ in FA composition (PERMANOVA, $F_{1,28} = 0.599$, $p = 0.543$) and showed highly similar responses across the environmental gradients (Fig. 2; Supporting Information Fig. S2). A separate RDA conducted for cladoceran grazers (i.e., *Bosmina* and *Daphnia*) selected temperature, lake area, and water color as the main explanatory variables (Table 2, model B), which explained 58% of the FA variation. Temperature alone explained the highest portion of cladoceran grazers' FA variation (28.0%) (Table 2, model B). Lake area and water color explained 4.1% and 3.5% of the FA variation of cladoceran grazers, respectively, although permutation tests showed that their effects on cladoceran FA were not significant (Table 2, model B). Increasing temperature and water color were associated with higher SAFA in the cladocerans, at the expense of lower PUFA, particularly EPA, while larger lake area was associated with higher SDA and higher ω3/ω6 (Fig. 3A,B).

The separate RDA for copepod grazers (i.e., *Eudiaptomus*, *Mixodiaptomus*, and *Arctodiaptomus*) selected water color and lake area in the best model, which explained 57% of the copepod FA variation (Table 2, model C). For copepod grazers, the lake area explained slightly more of the FA variation (22.5%) than did water color (18.9%). Increasing lake area was associated with higher SDA, but lower EPA and DHA, in copepod grazers

Table 2. Best redundancy analysis (RDA) models of the effects of taxonomic group and/or environmental variables on the zooplankton FA composition. Independent variables used for RDA forward selection were taxonomy (at genus level; model A), and temperature, TP, water color, lake area (models A–C). Marginal effects of the selected independent variables were tested using 999 permutations.

Independent variables	df	F	p Values	% variation (marginal)	R^2 (model)	AIC
(A) All taxa						
Genus	9	18.9	**0.001**	54.1	0.79	−60.97
Temperature	1	25.12	**0.001**	8.0		
Color	1	7.98	**0.003**	2.5		
Lake area	1	3.32	**0.035**	1.0		
Residuals	65					
(B) Cladoceran grazers						
Temperature	1	16.61	**0.001**	28.0	0.58	−18.77
Lake area	1	2.43	0.10	4.1		
Color	1	2.08	0.132	3.5		
Residuals	25					
(C) Copepod grazers						
Lake area	1	7.91	**0.002**	22.5	0.57	−21.72
Color	1	6.65	**0.002**	18.9		
Residuals	15					

(Fig. 3C,D). Responses of copepod grazers across the climate-productivity gradient differed from those of cladoceran grazers, as increasing water color was associated with an increase in EPA and a decrease in MUFA in copepod grazers (Fig. 3B,D).

Univariate regressions of selected FA also showed that the cladoceran and copepod groups (including all taxa) differed in their FA response with increasing CPI (Fig. 4). Cladocerans showed strong declines in PUFA (from 60% to 7%), among the 16 selected FA, mainly due to declines in EPA (from 23% to 0%), ARA (from 10% to 1%) and DHA (from 3% to 0%), and concurrent increases in MUFA (from 15% to 32%) and SAFA (from 25% to 61%) across the increasing CPI gradient. Copepods also increased in SAFA (from 33% to 38%) in response to increasing CPI. Conversely, copepods showed increases in EPA (from 9% to 17%), ARA (from 2% to 6%) and marginally significant decreases in MUFA (from 13% to 7%) as CPI increased (Fig. 4), while there were no trends in DHA and PUFA.

With increasing lake area (from 0.1 to 65 km^2), cladoceran EPA increased from 8% to 16%, whereas copepods decreased in DHA (27% to 17%), EPA (16% to 9%) and ARA (5% to 2.6%) (Fig. 5). Copepod EPA and ARA were negatively correlated with water color (EPA, $r = 0.81$, $p < 0.001$; ARA, $r = 0.82$, $p < 0.001$; $n = 29$). However, DHA in copepods was not correlated with either CPI (Fig. 4; $r = -0.11$, $p = 0.57$, $n = 29$) or water color ($r < 0.01$, $p = 0.98$, $n = 29$).

The cryptophyte biomarker SDA increased from 2% to 9% in cladocerans and from 1% to 12% in copepods with increasing lake area (Fig. 5A), but decreased in cladocerans with increasing CPI (from 10% to < 1%; Supporting Information Fig. S5). In contrast, $16{:}1\omega 7c$ decreased in cladocerans with increasing lake area (from 10% to 5%), and increased at higher CPI (from 2% to 12%) (Supporting Information Fig. S5). The share of $16{:}1\omega 7c$ in copepods was stable across gradients in lake area and CPI (Supporting Information Fig. S5).

Discussion

Our analysis of a large data set of different lake types across environmental gradients shows that the effects of environmental change on zooplankton FA composition are highly dependent on their taxonomy. In line with prediction (1), genus-level taxonomy explained a major share of FA variation in zooplankton (54%) despite the wide range of environmental conditions addressed (Table 1). This implies that the effects of environmental change on zooplankton FA composition are strongly mediated by zooplankton community assembly (Bergström et al. 2022). However, we also found contrasting FA responses between the major zooplankton groups, that is, cladocerans and copepods, across the environmental gradients (Figs. 3–5). This is best exemplified by the dramatic decrease in cladoceran PUFA with increasing CPI (from 60% to 20%), which supports prediction (2), compared to the stable share of PUFA in copepods (ca. 60%) (Fig. 4B). This suggests that decreases in the nutritional quality of cladocerans with climate change have potentially negative consequences for lake food webs. We found that lake size contributed to changes in zooplankton FA, which could be related to higher trophic support of PUFA-rich algae (i.e., cryptophytes) for zooplankton in larger lakes, as depicted by the increase in the cryptophyte FA biomarker (SDA) in both cladocerans and copepods (Fig. 5A, supporting predictions (3) and (4)). This finding was further corroborated by the positive relationship between cryptophyte-relative biovolume in phytoplankton and lake size for a large set of lakes across the whole of Sweden (Supporting Information

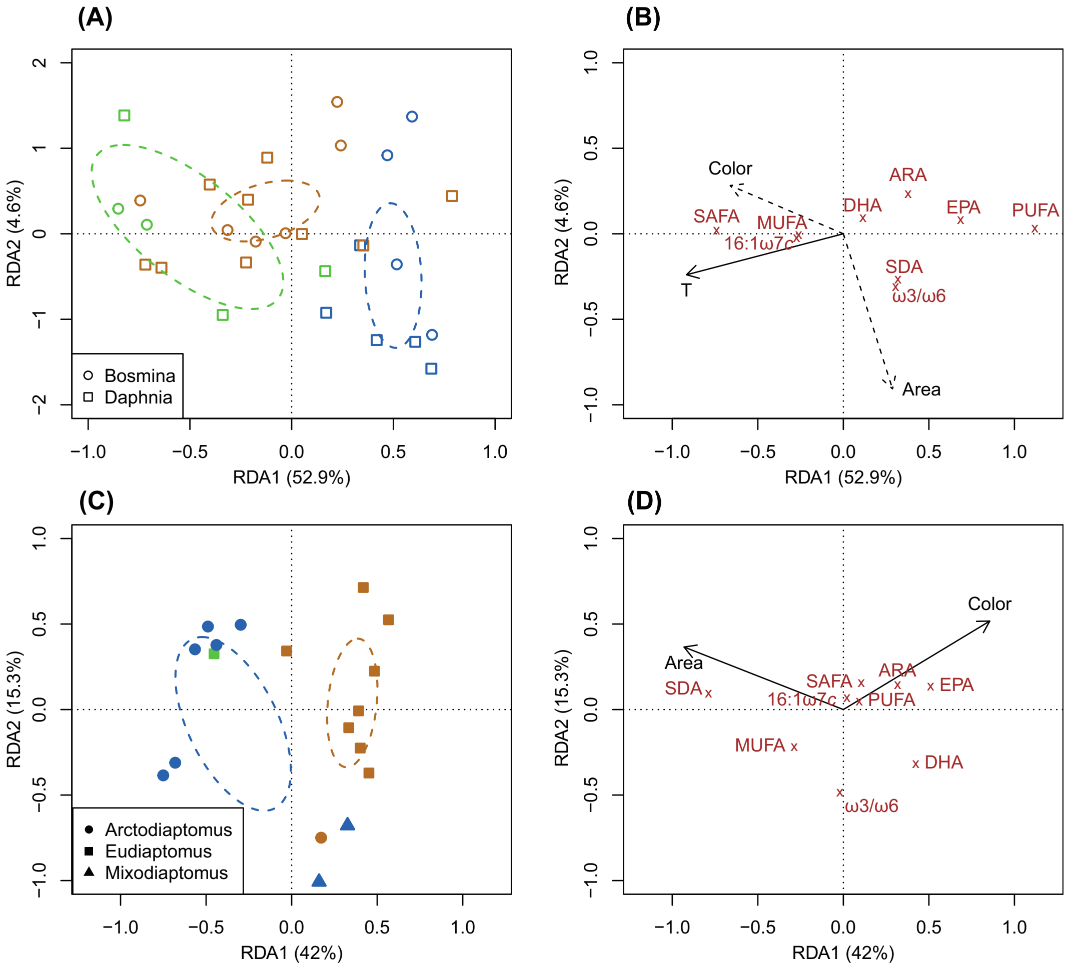

Fig. 3. Redundancy analysis (RDA) of FA compositions of cladoceran grazers ($n = 29$) (**A**, **B**) and copepod grazers ($n = 18$) (**C**, **D**). Panels (**A**) and (**C**) show the ordination of zooplankton samples colored by lake type (Alpine Oligotrophic in blue, Brown in brown, and Lowland Eutrophic in green). Ellipses indicate 95% confidence limits of group centroids for individual lake types with $n > 2$. Panels (**B**) and (**D**) show the eigenvectors of the explanatory environmental variables and the zooplankton FA composition (abbreviations are the same as in Fig. 2). Dash arrows show variables selected by forward selection that are non-significant. Variance explained (%) by the RDA axes are indicated in parentheses.

Fig. S6). Therefore, we infer that the negative effects of climate change on zooplankton nutritional quality for fish are stronger in smaller lakes.

Underlying drivers of FA composition in copepods and cladocerans differed

Temperature explained most of the FA variation of cladoceran grazers, while both lake area and water color explained most of the FA composition in copepod grazers (Figs. 3B,D, 4). These findings agree with a spatial study in the Swedish subarctic and boreal lakes, where Lau et al. (2021) found that the EPA concentrations in cladocerans were most responsive to temperature gradients, whereas the EPA and ARA concentrations in calanoid copepods also responded to the specific ultraviolet absorbance of water (i.e., a proxy for water color and DOC aromaticity; Weishaar et al. 2003) (Fig. 3B,D). Warming and browning may thus not only affect zooplankton FA composition in northern lakes (Hiltunen et al. 2015; Keva et al. 2021), but have different impacts on cladocerans and copepods. Lau et al. (2021) also found that the nitrogen (N) to phosphorus (P) ratio was an important predictor for copepod FA, as copepods have a higher demand for nitrogen than cladocerans. Atmospheric N deposition has been historically higher in southern than in northern and central Sweden (Ferm et al. 2019), resulting in a latitudinal gradient in lake N : P ratios (Elser et al. 2009) (Fig. 1). Therefore, we do not exclude the possibility that differences in lake water N : P ratios may explain some of the FA variation in copepods in our dataset.

Effects of the climate-productivity gradient

In line with prediction (2), cladocerans decreased in PUFA, but increased in MUFA and SAFA in warmer, browner, and/or more eutrophic lakes (Fig. 4). The observed decrease in PUFA was mostly attributed to EPA, ARA, and DHA, which together led to drastic

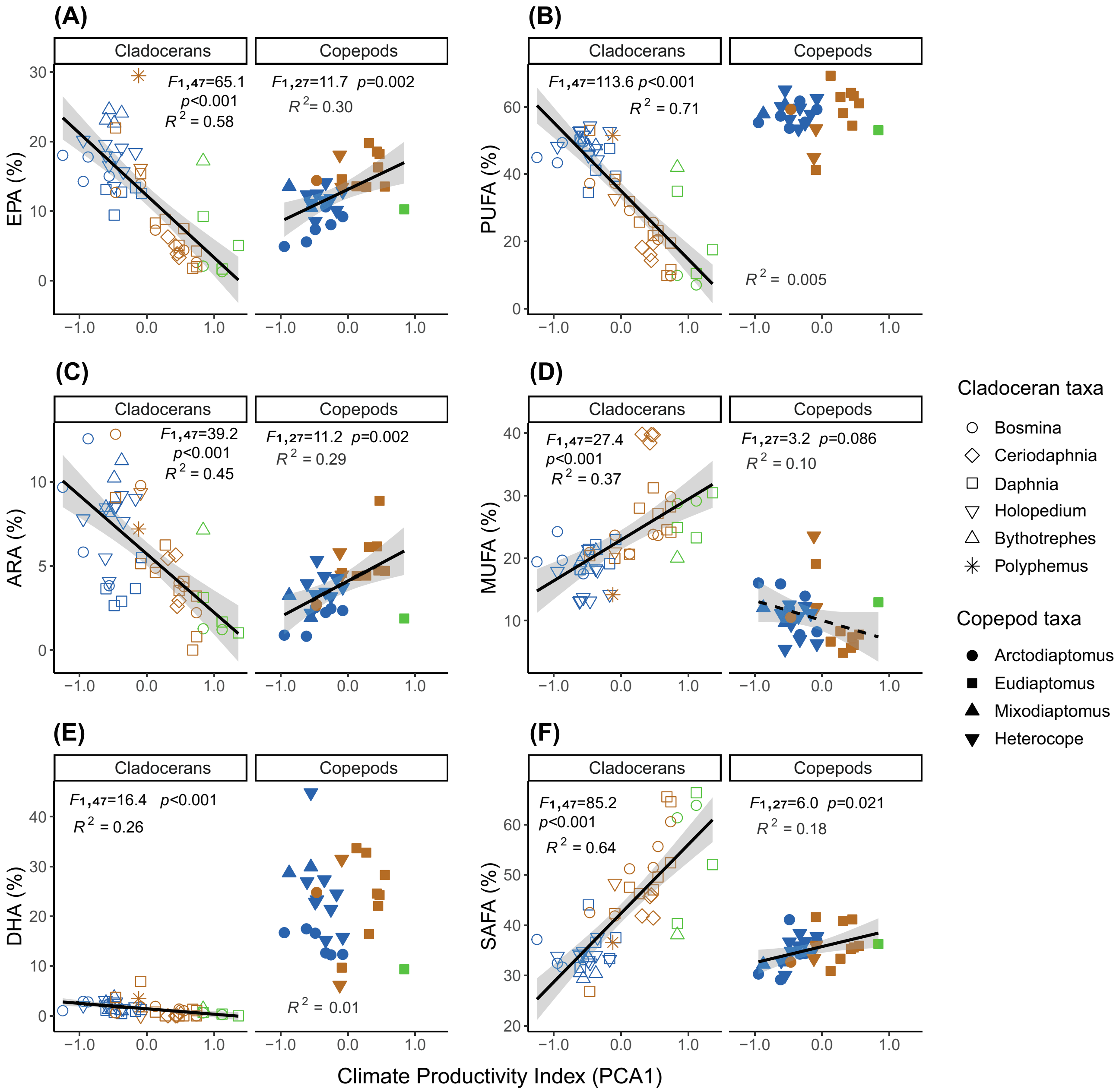

Fig. 4. Linear regressions of selected FA (**A–C**) and FA groups (**D–F**) in cladocerans ($n = 49$) and copepods ($n = 29$) as a function of climate-productivity index (PC1; *see* text) for the different lake types: Alpine Oligotrophic (blue), Brown (brown), and Lowland Eutrophic (green). Solid and dashed lines represent regression models (± SE in shades) with $p < 0.05$ and $0.05 < p < 0.1$, respectively. R^2 is shown for all models, while F and p values for significant models only.

decreases from ca. 40% to 2% LC-PUFA in response to increasing CPI (Fig. 4). Lau et al. (2021) found a similar, yet more moderate decrease in EPA + DHA concentrations of cladocerans with increasing temperature, which may be due to their narrower latitude and elevation gradient (60–68°N, 227–590 m a.s.l.) than in our study (56–68°N, 1–952 m a.s.l.). The steep declines in EPA and ARA in cladocerans in our study likely resulted from differences in the dietary seston composition (DeMott 1989; Sterner 1989). Warming- and browning-induced increases in nutrient concentrations can promote blooms of green algae and cyanobacteria (Taipale et al. 2019; Keva et al. 2021), which are devoid of LC-PUFA such as EPA and ARA (Ahlgren et al. 1990; Napolitano 1999). Browning additionally increases the trophic support of bacterial production and terrestrially derived detritus for zooplankton (Berggren et al. 2014), both of which lack LC-PUFA (Brett et al. 2009; Taipale et al. 2018). We hypothesize that cladoceran grazers incorporate such dietary FA changes due to their largely non-selective feeding (Brett et al. 2009; Taipale et al. 2015, 2018), and thereby become highly sensitive to ongoing warming, browning, and eutrophication in northern lakes.

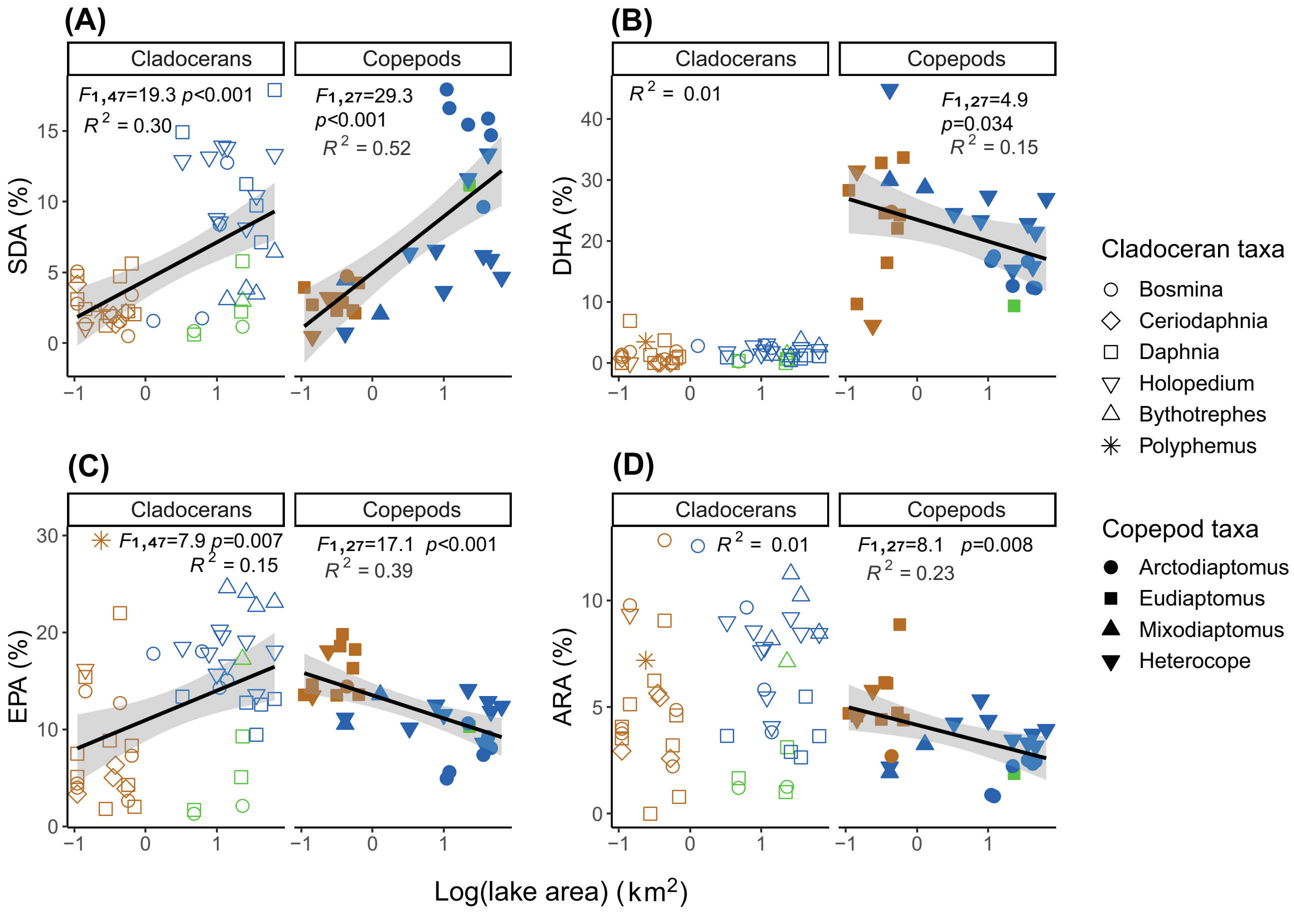

Fig. 5. Linear regressions of selected FA with lake area in cladocerans ($n = 49$) and copepods ($n = 29$). Color codes show the different lake types: Alpine Oligotrophic (blue), Brown (brown), and Lowland Eutrophic (green). Solid lines represent regression models (± SE in shades) with $p < 0.05$. R^2 is shown for all models, while F and p values for significant models only.

In contrast to cladocerans, PUFA and DHA in copepods were not affected across the climate-productivity gradient, which does not support prediction (2) and is similar to the findings by Gladyshev et al. (2015), who showed lower PUFA differences in copepods compared to cladocerans in warm and cold lakes. Furthermore, the magnitude of increase in SAFA across the CPI gradient was seven times lower in copepods than in cladocerans (Fig. 4). These findings suggest that copepods have a strong ability to regulate FA composition irrespective of changes in environmental conditions and seston composition, either by selective feeding on available PUFA-rich food sources (DeMott 1989; Sterner 1989) and/or by internal FA metabolism (Ravet et al. 2010). Copepod grazers are also able to feed on microfauna in the pelagic (e.g., ciliates and protozoans) (Karlsson et al. 2007; Kunzmann et al. 2019) and on meiofauna in benthic habitats in winter (Muschiol et al. 2008), when they spend their copepodite stages in surficial sediments (Goedkoop and Johnson 1996). Trophic upgrading by microfauna and meiofauna, that is, the conversion of dietary precursor FA to LC-PUFA, may, therefore, contribute to PUFA-enrichment of food resources for copepods (Martin-Creuzburg et al. 2005). Alternatively, predatory copepods (e.g., *Heterocope*) may benefit from the selective accumulation of LC-PUFA in food webs (Persson and Vrede 2006; Strandberg et al. 2015).

Our finding that both EPA and ARA in copepods moderately increased across the CPI gradient, particularly with increasing water color, contrasted with the observed EPA and ARA decreases in cladocerans (Fig. 4). Johansson et al. (2016) showed for seven of our lakes (lakes 1, 3–8; Supporting Information Fig. S3) that the increase in EPA and ARA accumulation in the copepod *Eudiaptomus gracilis* was related to the intensity and duration of blooms of the flagellate *Gonyostomum semen*. With two additional lakes (total $N = 9$), we similarly found positive correlations of copepod EPA and ARA with the relative biovolume of *G. semen* in phytoplankton (Supporting Information Fig. S7A,D). *G. semen* is rich in EPA (Gutseit et al. 2007; Taipale et al. 2013), but most cladocerans are unable to feed on *G. semen* due to its large cell size and trichocyst defense mechanisms (Johansson et al.

2013). Copepod grazers such as *E. gracilis* can feed on and obtain abundant EPA from *G. semen* at high rates (Johansson et al. 2013). Therefore, more flexible feeding strategies and the capability to feed more selectively and on larger particles likely make copepods less susceptible than cladocerans to climate-induced changes in seston composition and food quality.

The role of lake size

Our results revealed that lake size had a strong effect on zooplankton FA composition. The cryptophyte biomarker SDA increased by ca. 10%–15% in both copepod and cladoceran grazers across our lake-size gradient from 0.11 to 65 km^2, supporting prediction (4). These findings were reinforced by positive correlations between SDA and the relative biovolume of cryptophytes in phytoplankton in a subset of our study lakes ($N = 17$) (Supporting Information Fig. S7H) and by the increases in relative biovolume of cryptophytes in phytoplankton with increasing lake area for 102 monitoring lakes across Sweden (Supporting Information Fig. S6). Cryptophytes are rich in LC-PUFA, including DHA and EPA (Ahlgren et al. 1990; Napolitano 1999). However, the increased trophic support from cryptophytes did not necesarily result in higher LC-PUFAs in zooplankton. For instance, in copepods, LC-PUFAs (i.e., EPA, DHA, and ARA) moderately decreased concurrently with lake size (by 10%, 7%, and 3%, respectively) (Figs. 3B, 4), which does not align with expected increases in LC-PUFA in phytoplankton (Supporting Information Fig. S7C,F). These results may be partly influenced by the increase in EPA and ARA with increasing CPI and water color, as the browner lakes were generally smaller than, the clear-water lakes in our study (Table 1; Supporting Information Fig. S1, S4). However, the decrease in DHA in copepods was independent from the CPI and water color, and may thus be a direct effect of lake area on FA regulation. Relative decreases of LC-PUFA have been linked to increases in 18C-PUFA as lipid stores in copepods prior to overwintering (Hiltunen et al. 2015; Grosbois et al. 2017). Thus, the observed decreases of LC-PUFA and increases of SDA in copepods with increasing lake area could be related to the higher investment in energy storage in larger and relatively cooler lakes. Based on the current correlative results, however, we are unable to unravel the mechanisms (e.g., dietary, metabolic, or life-history processes) that underlay the observed effects of lake size on copepod LC-PUFA. Yet, our findings of higher phytoplankton food quality in larger lakes—through the predominance of cryptophytes— suggest that lake size moderates the negative impacts of climate change on zooplankton food quality for fish.

Implications for lake food webs

Our results show that warming, eutrophication, and browning drastically decrease LC-PUFA, that is, the nutritional quality, of cladocerans in northern lake food webs. This decrease of LC-PUFA in cladocerans, combined with increases in cladoceran predominance over copepods (Hayden et al. 2017; Bergström et al. 2022), potentially underlie the observed decreases in LC-PUFA content of zooplankton communities in northern lakes that are warmer, browner, and more eutrophic (Keva et al. 2021). Because LC-PUFA are key for trophic transfer efficiency in aquatic food webs (Müller-Navarra et al. 2000; Ahlgren et al. 2009) and fish productivity (Taipale et al. 2018), our results imply that climate change likely impairs the pelagic trophic transfer efficiency in northern lakes. Our results also show that PUFA in both cladocerans and copepods combined were highest in Alpine Oligotrophic lakes. This highlights the importance of Alpine Oligotrophic lakes for providing high-quality food for higher trophic levels, while also pinpointing their susceptibility to environmental change, particularly if such lakes are small. Rapid climate change in the Arctic/alpine landscape (Schindler and Smol 2006; Allan et al. 2021) thus likely compromises the biochemical food quality of zooplankton and has strong repercussions for the Arctic/alpine lake food webs.

Conclusion

Our study shows that both ecological and phylogenetic differences among zooplankton taxa underlie their contrasting, taxon-specific FA responses to environmental change. These responses are modulated by lake size, whereby smaller lakes likely are more susceptible to simultaneous warming, browning, and eutrophication due to the lower abundances of PUFA-rich phytoplankton taxa such as cryptophytes. These taxon-specific FA responses, in conjunction with expected zooplankton-community shifts towards more sensitive cladoceran taxa will reduce the zooplankton food quality and, ultimately, the trophic transfer of high-quality PUFA to planktivorous fish in northern lakes, which are expected to become warmer, browner, and/or more eutrophic in the face of global change.

Data availability statement

Raw data for this paper are publicly available on DiVA portal (https://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-523761).

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Conflict of Interest

None declared.

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