Poor nutritional quality of primary producers and zooplankton driven by eutrophication is mitigated at upper trophic levels

Sami Johan Taipale1 | Anne-Mari Ventelä2 | Jaakko Litmanen1 | Lauri Anttila2

1Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland
2Pyhäjärvi Institute, Ruukkipuisto, Kauttua, Finland

Correspondence
Sami Johan Taipale, Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland.
Email: sami.taipale@jyu.fi

Funding information
This research was supported by the Academy of Finland research grant 333564, awarded to Sami J. Taipale and by the foundation of Kalatalouden ja merenkulun koulutuksen edistämissäätiö, awarded to Lauri Anttila.

Abstract
Eutrophication and rising water temperature in freshwaters may increase the total production of a lake while simultaneously reducing the nutritional quality of food web components. We evaluated how cyanobacteria blooms, driven by agricultural eutrophication (in eutrophic Lake Köyliöjärvi) or global warming (in mesotrophic Lake Pyhäjärvi), influence the biomass and structure of phytoplankton, zooplankton, and fish communities. In terms of the nutritional value of food web components, we evaluated changes in the ω-3 and ω-6 polyunsaturated fatty acids (PUFA) of phytoplankton and consumers at different trophic levels. Meanwhile, the lakes did not differ in their biomasses of phytoplankton, zooplankton, and fish communities, lake trophic status greatly influenced the community structures. The eutrophic lake, with agricultural eutrophication, had cyanobacteria bloom throughout the summer months whereas cyanobacteria were abundant only occasionally in the mesotrophic lake, mainly in early summer. Phytoplankton community differences at genus level resulted in higher arachidonic acid, eicosapentaenoic acid (EPA), and docosahexaenoic acid (DHA) content of seston in the mesotrophic than in the eutrophic lake. This was also reflected in the EPA and DHA content of herbivorous zooplankton (Daphnia and Bosmina) despite more efficient trophic retention of these biomolecules in a eutrophic lake than in the mesotrophic lake zooplankton. Planktivorous juvenile fish (perch and roach) in a eutrophic lake overcame the lower availability of DHA in their prey by more efficient trophic retention and biosynthesis from the precursors. However, the most efficient trophic retention of DHA was found with benthivorous perch which prey contained only a low amount of DHA. Long-term cyanobacterial blooming decreased the nutritional quality of piscivorous perch; however, the difference was much less than previously anticipated. Our result shows that long-term cyanobacteria blooming impacts the structure of plankton and fish communities and lowers the nutritional quality of seston and zooplankton, which, however, is mitigated at upper trophic levels.

KEYWORDS
benthic invertebrates, freshwater food web, ontogenetic diet shift, perch, phytoplankton, polyunsaturated fatty acids

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2022 The Authors. Ecology and Evolution published by John Wiley & Sons Ltd.
1 | INTRODUCTION

Globally, freshwater ecosystems are challenged by land use and many factors connected to climate warming, such as changing precipitation, eutrophication (as an increase in total phosphorus) (Hasler, 1947), and water browning (an increase of DOC) (Karlslund et al., 2009; Leech et al., 2018; O’Reilly et al., 2003). In the boreal zone, lake water temperature and precipitation are increasing, which may increase nitrogen (N), phosphorus (P), and dissolved organic carbon (DOC) loading, especially from agricultural and peatland-dominated catchments (Lathrop et al., 2019; Ruosteenoja et al., 2016). Changing environmental conditions affect ecosystem function and phytoplankton, zooplankton, and fish community structure (Havens, 2008; Jeppesen et al., 2010, 2012; Keva et al., 2021; Sukenik et al., 2015; Ventélä et al., 2016). At the same time, these conditions also impact the nutritional value of the phytoplankton and thus the production and the transfer of essential biomolecules through food webs (Lau et al., 2021; Müller-Navarra et al., 2004; Taipale et al., 2016, 2019).

The ω-3 and ω-6 polyunsaturated fatty acids (PUFA) have been found to have many physiologically necessary functions in all animals including humans (Arts et al., 2009; Simopoulos, 2000). Because animals cannot synthesize ω-3 and ω-6 PUFA de novo, they need to obtain these molecules from their diet. Therefore, short-chain ω-3 and ω-6 PUFA of α-linolenic acid (ALA, 18:3ω3) and linoleic acid (LA, 18:2ω6) are usually considered essential fatty acids (EFA) or “essential nutrients” for animals (Parrish, 2009). However, eicosapentaenoic acid (EPA, 20:5ω3), docosahexaenoic acid (DHA, 22:6ω3), and arachidonic acid (ARA, 20:4ω6) are physiologically most important for consumers (Hulbert & Abbott, 2012; Parrish, 2009; Stanley-Samuelson et al., 1988). Therefore, they may be called physiologically essential or semi-essential PUFA (Taipale et al., 2019).

In marine and freshwater ecosystems, green algae and cyanobacteria are classified as non-EPA and non-DHA-synthesizers, while golden algae, dinoflagellates, cryptophytes, diatoms, and raphidophytes are primary producers of EPA and DHA (Ahlgren et al., 1992; Jónasdóttir, 2019; Taipale et al., 2013; Taipale, Vuorio, et al., 2016). However, EPA- and DHA-synthesizing phytoplankton taxa can also be found abundantly in eutrophic lakes (Lepistö & Rosenström, 1998). A clear decline in the nutritional quality of seston can be seen in hyper-eutrophic lakes (Müller-Navarra et al., 2004; Taipale et al., 2019). Therefore, it is important to monitor the abundance of EPA- and DHA-synthesizing phytoplankton taxa (cryptomonads, golden algae, diatoms, dinoflagellates, raphidophytes, euglenoids) throughout the summer to understand the nutritional quality of phytoplankton. Agricultural eutrophication has been the main reason for increased cyanobacteria blooms in boreal and temperate lakes (Jørgensen & Rast, 2001). However, the growing abundance of cyanobacteria in the recent past is related to climate change and especially due to the increased temperature of lakes (Deng et al., 2016; Elliot, 2012; Paerl & Huisman, 2008; Pätynen et al., 2014; Rasconi et al., 2017). Previous studies have shown that a decrease in the nutritional quality of phytoplankton is mainly attributed to the changes by the phytoplankton community structure, but also because the nutritional value of phytoplankton cells decreases by eutrophication (Keva et al., 2021; Lau et al., 2021; Taipale et al., 2019).

Herbivorous zooplankton is a key link in connecting phytoplankton and planktivorous fish and thus the nutritional value of zooplankton is important for the growth of fish fry (Taipale et al., 2018). However, individual zooplankton taxa differ by their nutritional value (Kratina & Winder, 2015). This is because cladocerans usually accumulate EPA whereas copepods are rich in DHA (Brett et al., 2009; Hiltunen et al., 2016; Smyntek et al., 2008; Taipale et al., 2011). Moreover, zooplanktons are generally inefficient in their ability to biosynthesize ALA to EPA and DHA. Thus, they are strongly dependent on the fatty acid quality in their diet (Elert et al., 2003; Koussoroplis et al., 2014; Taipale et al., 2011). Herbivorous cladoceran (Daphnia and Bosmina) is a keystone species in most lake ecosystems (Bergquist et al., 1985; Kerfoot et al., 1988; Lynch & Shapiro, 1981). It can detect high nutritional quality patches and can selectively feed on high nutritional quality particles (Hartmann & Kunkel, 1991; Schatz & McCauley, 2007). Moreover, fatty acid-based modeling has shown that seston microbial (including algae) composition does not necessarily match with assimilated diet (Taipale et al., 2019). This is because herbivorous zooplankton (Daphnia and Bosmina) favors high nutritional quality diet (Galloway et al., 2014; Taipale et al., 2019). Cyanobacteria blooms may lead to poorer energy flow in aquatic food webs because they poorly support zooplankton somatic growth and reproduction (Bednarska et al., 2014; Elert et al., 2003; Peltomaa et al., 2017; Porter & McDonough, 1984). They can also be linked to the upper trophic level only by certain zooplankton taxa (e.g., Chydorus; Tönno et al., 2016). Environmental changes (e.g., eutrophication, browning, global warming) have been shown to have different impacts on the nutritional value of zooplankton (Keva et al., 2021; Lau et al., 2021; Senar et al., 2019). As a result, it appears that the lower nutritional value of phytoplankton does not always affect higher trophic levels. However, a recent study of productivity and temperature gradient in sub-arctic lakes showed that the zooplankton community changed from the Calanoid (Eudiaptomus graciloides) dominated community towards herbivorous cladocerans (Daphnia and Bosmina), resulting in a decrease in the EPA and DHA content of zooplankton community (Keva et al., 2021). Environmental changes and especially eutrophication have been known to change the structure of fish communities (Keva et al., 2021). It is well documented that cyprinid fish, e.g., roach (Rutilus rutilus) and bream (Abramis brama), are ultimate winners...
in the eutrophication in boreal lakes, whereas vendace (Coregonus albula) and burbot (Lota lota) are known to be losers (Tammi et al., 1999). However, it is not well known how dependent different fish species are on the EPA and DHA content of their prey. The ability of freshwater fish to biosynthesize longer-chain PUFA from their precursors is reportedly better than with marine fish (Sargent et al., 2021). Nevertheless, there is a paucity of studies with different freshwater fish species are lacking. Eutrophication and browning impact on the EPA and DHA content of fish muscle are contradicting (Ahlgren et al., 1996; Keva et al., 2019; Strandberg et al., 2016; Taipale, Vuorio, et al., 2016). However, some fish species could seemingly mitigate the low nutritional quality of their prey. Ahlgren et al. (1996) found that EPA and DHA content of roach is higher in oligotrophic lakes than in eutrophic lakes, whereas they did not find a similar difference in the perch, which is in contrast to our previous finding with piscivorous perch (Taipale, Vuorio, et al., 2016). Chaguaceda et al. (2020) recently reported that the content of ARA, EPA, and DHA are strongly regulated over ontogeny in perch muscles based on their FA profiles and compound-specific stable isotopes (Scharnweber et al., 2021). However, it is not clear how the low availability of DHA, caused by cyanobacteria blooming driven by eutrophication or climate change, impact EPA and DHA content of fish at different trophic levels.

Since European perch (Perca fluviatilis) have three ontogenetic dietary stages, it is an ideal fish species to evaluate eutrophication's impact on the nutritional value of the same species at different trophic levels. Perch fry eats zooplankton, from which it gradually moves to the benthos and on to fish food (Estlander et al., 2010, 2012; Haakana et al., 2007; Rask, 1986). Previously, it was found that the piscivorous (length > 20 cm) perch of oligo- and mesotrophic lakes contain more EPA and DHA than perch in eutrophic lakes (Gladyshev et al., 2018; Taipale, Vuorio, et al., 2016). Chaguaceda et al. (2020) suggested strong regulation of EPA and DHA in perch muscle.

Here, (H1), we hypothesized that long-term cyanobacteria blooms by agricultural eutrophication increases the biomass of phytoplankton, zooplankton, and fish communities, but also changes the structure of plankton and fish communities. We assumed that long-term cyanobacterial bloom decreases the biomass of EPA- and DHA-synthesizing phytoplankton taxa, favors small cladoceran over copepods, and increases the number of cyprinids over percids fish.

Secondly, we hypothesized (H2) that the nutritional quality of seston is decreased by lake trophic status (Keva et al., 2021; Lau et al., 2021; Müller-Navarra et al., 2004; Taipale, Vuorio, et al., 2016). We also assumed that this decrease in the nutritional quality of primary producers is reflected at different trophic levels via changes in the nutritional quality of their prey. Finally, we assumed (H3) that consumers try to compensate for their lower nutritional quality of prey by more efficient trophic retention and biosynthesis of physiological essential PUFA.

### 2 | MATERIALS AND METHODS

#### 2.1 | Study area

The research material was collected during the summer of 2017 from mesotrophic Lake Pyhäjärvi and eutrophic Lake Köyliönjärvi, which are both located in southwest Finland, as shown in Table 1. Weather conditions are similar for these two lakes, which can be seen in equal surface temperature during the 2000s (PERMANOVA: Pseudo-F_{1,157} = 0.33, p = .578). However, these two lakes differ in their productivity (PERMANOVA: Pseudo-F_{1,129} = 190.4, p = .001) and nutrients (PERMANOVA for TP and TN: Pseudo-F_{1,185} = 475/622, p = .001) based on measurements between 2000 and 2017 (Hertta database, Finnish Environmental Centre). Based on total phosphorus and chlorophyll concentration, Lake Köyliönjärvi can be considered a eutrophic or hyper-eutrophic lake, whereas Lake Pyhäjärvi can be considered to be a mesotrophic lake (Bengtsson et al., 2012). Moreover, Lake Köyliönjärvi is a shallow lake (mean depth 3 m) with the deepest point of 13 m, whereas the mean depth of Lake Pyhäjärvi is 5 m, with the deepest point being 26 m. Both lakes suffer from an overly high nutrient load from their catchments. Lake Köyliönjärvi usually experiences large cyanobacterial blooms in summer, which temporarily declined in the 1990s due to fish removal (Savolainen et al., 2000). Lake Pyhäjärvi has been subjected to a variety of water protection measures since the 1980s, thereby decelerating the lake's eutrophication development (Ventelä et al., 2007, 2016). In the 2000s, climate change affected the phytoplankton community, and cyanobacteria blooms have become more frequent in Lake Pyhäjärvi (Deng et al., 2016). This development will

| Parameter          | Unit  | Mesotrophic Lake Pyhäjärvi | Eutrophic Lake Köyliönjärvi |
|--------------------|-------|----------------------------|-----------------------------|
| Total phosphorus   | µg P/L | 19 ± 5.2                   | 22 ± 7.0                    |
| Total nitrogen     | µg N/L | 422 ± 50                   | 422 ± 76                    |
| Chlorophyll        | µg/L  | 7.5 ± 3.6                  | 8.0 ± 3.1                   |
| Turbidity          | FNU   | 2.4 ± 1.1                  | 2.4 ± 0.7                   |
| Secchi Depth       | m     | 2.5 ± 0.6                  | 2.3 ± 0.2                   |
| Temperature        | °C    | 18.4 ± 2.6                 | 17.0 ± 1.9                  |

#### MATERIALS AND METHODS

The research material was collected during the summer of 2017 from mesotrophic Lake Pyhäjärvi and eutrophic Lake Köyliönjärvi, which are both located in southwest Finland, as shown in Table 1. Weather conditions are similar for these two lakes, which can be seen in equal surface temperature during the 2000s (PERMANOVA: Pseudo-F_{1,157} = 0.33, p = .578). However, these two lakes differ in their productivity (PERMANOVA: Pseudo-F_{1,129} = 190.4, p = .001) and nutrients (PERMANOVA for TP and TN: Pseudo-F_{1,185} = 475/622, p = .001) based on measurements between 2000 and 2017 (Hertta database, Finnish Environmental Centre). Based on total phosphorus and chlorophyll concentration, Lake Köyliönjärvi can be considered a eutrophic or hyper-eutrophic lake, whereas Lake Pyhäjärvi can be considered to be a mesotrophic lake (Bengtsson et al., 2012). Moreover, Lake Köyliönjärvi is a shallow lake (mean depth 3 m) with the deepest point of 13 m, whereas the mean depth of Lake Pyhäjärvi is 5 m, with the deepest point being 26 m. Both lakes suffer from an overly high nutrient load from their catchments. Lake Köyliönjärvi usually experiences large cyanobacterial blooms in summer, which temporarily declined in the 1990s due to fish removal (Savolainen et al., 2000). Lake Pyhäjärvi has been subjected to a variety of water protection measures since the 1980s, thereby decelerating the lake's eutrophication development (Ventelä et al., 2007, 2016). In the 2000s, climate change affected the phytoplankton community, and cyanobacteria blooms have become more frequent in Lake Pyhäjärvi (Deng et al., 2016). This development will
be further accelerated in future based on the modeling (Pätynen et al., 2014).

2.2 | Phytoplankton and zooplankton community and fatty acid sampling

Throughout the summer months (June–August) of 2017, the water quality (Secchi-depth, water temperature, turbidity, chlorophyll-a, total phosphorus, phosphate phosphorus, and total nitrogen), and community composition of phyto- and zooplankton, and their fatty acid composition and content, were monitored. A sample of 0–5 m water column was taken with a tube sampler (model: Sormunen, volume 6.3 L) to analyze quantitatively the community composition of the phyto- and zooplankton. Plankton community samples were analyzed by the commercial laboratory Lounais-Suomen ympäristötutkimus Oy, where certified persons counted phytoplankton and zooplankton samples. Physico-chemical water samples were taken with a Limnos tube sampler (volume 2.6 L) and analyzed by the Lounais-Suomen ympäristötutkimus Oy lab. The sample points in the lakes were selected to be in line with the environmental monitoring program of the Finnish Environmental Institute, in order to utilize the water quality material found in the Hertta database (www.syke.fi/avoin_tieto). In total, the summer sampling campaign included six samples for Lake Pyhäjärvi and five samples for Lake Köylönjärvi.

Polyunsaturated fatty acids (PUFA) of seston (phytoplankton) available for herbivorous zooplankton were studied by pre-filtering seston with a 50 µm sieve and then filtering a specific amount of water through GF/F filter paper (Whatman). Sampled herbivorous cladoceran was majorly (>95%) Daphnia and Bosmina and contained random (<5%) Chydorus, Ceriodaphnia, or Diaphanosoma. It was used to estimate the nutritional quality of diet for planktivorous perch since herbivorous cladoceran (especially Daphnia together with Bosmina) is the major prey for planktivorous perch (Estlander et al., 2010; Ruohonen, 2006). The zooplankton sample was collected horizontally with a 50 µm plankton net and main genera were picked up with microscope glass. Surface water (0–2 m water column) was sampled with a tube sampler (model: Sormunen, volume 6.3 L) for the fatty acid composition and content analysis of seston.

2.3 | Zoobenthos community and fatty acid sampling

In addition to seasonal phyto- and zooplankton sampling, zoobenthos was sampled once in the littoral zone depth of 2–3 m in late summer 2017. In both study lakes, a similar sampling procedure for one sample point was carried out with an Ekman grab. The samples were filtered by a 500 µm screen to remove the fine material and then all macroscopic zoobenthos were picked up in the laboratory. Chironomidae larvae were the only abundant group in both lake samples. According to earlier studies (not published), in Lake Pyhäjärvi at least, Chironomidae larvae form a significant part of the diet for bentivorous perch.

2.4 | Fish community and fatty acid sampling

Fish community structure and biomasses were obtained from the national fish monitoring database (Hertta/Koekalastusrekisteri) managed by the Natural Resources Institute Finland. This study covered the years 2012, 2015, 2017, and 2020 for eutrophic Lake Köylönjärvi. Similarly, 2009, 2012, 2015, and 2019 were covered for mesotrophic Lake Pyhäjärvi. Briefly, NORDIC multimesh survey nets (Appelberg et al., 1995) were used for gillnet sampling. Gillnet sampling followed random stratified sampling, including nets in pelagic, metalimnetic, and benthic gillnets (Olin et al., 2016), whereas gillnet sampling was done yearly during July and August. The annual number of gillnet nights were 40 for eutrophic Lake Köylönjärvi and 56 for mesotrophic Lake Pyhäjärvi. To compare fish biomasses between lakes, we used BPUE (wet mass per unit effort = kg fish per gillnet night) (Rask et al., 2020) of individual fish species. To compare the structure of perch communities in these two lakes we used CPUE (number of fish per gillnet night) of the perch group (diet group). The perch community was divided into categories including its ontogenetic diet shift (Estlander et al., 2010; Estlander, et al., 2012), planktivorous (length: <15 cm), bentivorous (15–19 cm), and piscivorous (>19 cm). These categories relate to the main diet but planktivorous fish may also feed on benthic invertebrates, and bentivorous perch feeds on smaller fish (Amundsen et al., 2003; Estlander et al., 2010, 2012).

Perch individuals for fatty acid analysis were caught in the late summer of 2017. Perches from mesotrophic Lake Pyhäjärvi were received from professional fishers who used open-water seine fishing and gillnets for catching fish. Perch fry were also netted from a pier. Perch in Lake Köylönjärvi were caught using the Nordic gillnet series. Due to the rapid development of young fish, the young-of-the-year perch were caught within two weeks, from both lakes, to ensure the comparison between the lakes was relevant. Fry were caught on September 12 in Lake Köylönjärvi and September 2 and 11 in Lake Pyhäjärvi. The length, weight, and sex of each fish were determined (Table S1). Age was determined mainly by using gill-covering bone, operculum, and, in some cases, a more precise determination was made by examining scales. Samples for fatty acid analysis were taken from the dorsal muscles and stored at −20°C until they were freeze-dried within one month from sampling. The research material covered a total of 48 fish in Lake Pyhäjärvi and 37 fish in Lake Köylönjärvi (Table S1). In addition to perch, five individuals of small roach (<10 cm) were obtained from both lakes to estimate if PUFA content of omnivorous fish and potential diet for piscivorous perch differ in their PUFA content.
2.5 | Fatty acid analysis

Lipids were extracted from the freeze-dried seston, cladocera, Chironomidae, and fish samples in Kimax borosilicate tubes with chloroform-methanol (2:1) mixture. Fatty acids were methylated using mild sulfuric acid. Methyl esterified samples were analyzed on a Shimadzu GC-MS-QP2010 Ultra (Nishinokyo-Kuwabara-Cho, Kioto, Japan) with helium as carrier gas. Column was Zebron ZB-FAME column (35 m × 0.25 mm × 0.20 μm). The temperature of the injector was 270°C and we used a splitless injection mode (for one min). Temperatures of the interface and ion source were 250 and 220°C, respectively. Phenomenex® (Torrance, California, USA) ZB-FAME column (30 mx0.25 mmx0.20 μm) with 5 m Guardian was used with the following temperature program: 50°C was maintained for one min, then the temperature was increased at 10°C/min to 130°C, followed by 7°C/min to 180°C, and 2°C/min to 200°C. This temperature was held for three minutes, and finally, the temperature increased 10°C/min to 260°C. The total program time was 35.14 min and the solvent cut time was nine minutes. Fatty acids were identified by the retention times (RT) and using specific ions which were also used for quantification (Taipale, Hiltunen, et al., 2016). Fatty acid concentrations were calculated using calibration curves based on known standard solutions (15, 50, 100, and 250 ng) of a FAME standard mixture (GLC standard mixture 566c, Nu-Chek Prep, Elysian, MI, USA) and using recovery percentage of internal standards. The Pearson correlation coefficient was >0.99 for each individual fatty acid calibration curve. Additionally, we used 1,2-dinonadecanoyl-sn-glycero-3-phosphatidylcholine (Larodan, Malmö, Sweden) and free fatty acid of C23:0 (Larodan, Malmö, Sweden) as internal standards and to calculate the recovery percentages. The fatty acid content of seston (<50 μm) was calculated based on phytoplankton carbon as described by Taipale et al. (2019). Otherwise, fatty acid content was calculated based on the dry weight of zooplankton, zoobenthos, or fish muscle.

Trophic retention of ARA, EPA, and DHA by zooplankton, Chironomidae, roach, and different ontogenetic stages of perch were calculated by the following equation (referred to as accumulation factor by Hessen & Leu, 2006):

\[ \text{Trophic retention} = \frac{(\text{FA}_{\text{diet}}/\text{FA}_{\text{consumer}})}{1} - 1, \text{ where FA}_{\text{diet}} \text{ represents ARA, EPA, and DHA content (μg mg/C) of diet and FA}_{\text{consumer}} \text{ cites their content in the consumers.} \]

The average diet composition for each consumer was taken from previous studies. For herbivorous zooplankton, we used seston, 0+ perch, and roach. For planktivorous perch, we used herbivorous cladocera, whereas for benthivorous perch, we used 20% of herbivorous zooplankton and 80% of Chironomidae. We used 0+ perch and roach for piscivorous perch (Estlander et al., 2010; Ruohonen, 2006).

2.6 | Bulk stable isotope analysis and trophic position

Approximately 0.6–1.2 mg of freeze-dried seston, zooplankton, benthic invertebrates, or fish muscle sample was weighted and encapsulated to tin cups. The $^{15}$N/$^{14}$N was measured using a Carlo Erba Flash 1112 series elemental analysis connected to a Thermo Finnigan Delta Plus Advantage isotope ratio mass spectrometer in continuous flow mode. Isotopic data are presented in standard delta notation with units per mil (‰) and relative to the Vienna Pee Dee Belemnite (VPDB) international standard. Precision and accuracy were determined through repeated measurements of an internal working standard that was found to be 0.2 and 0.3, respectively.

Trophic level (TL) of consumers (herbivorous cladocera (Daphnia and Bosmina), Chironomidae, roach, and perch) was determined by using $\delta^{15}$N values (Post et al., 2002).

\[ \text{TL}_{\text{consumer}} = \lambda + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}})/\Delta^{15}\text{N}, \]

where $\lambda$ refers to the trophic position of the baseline organism, $\delta^{15}$N-consumer nitrogen stable isotope value of a given consumer, and $\delta^{15}$N-baseline nitrogen stable isotope values of baseline organism (seston in our case) in study lake. $\Delta^{15}$N is a trophic fractionation factor that was set 3.4‰ per trophic level according to Post (2002). Perch were divided into planktivorous (TL < 3.6), benthivorous (TL 3.6–3.9), and piscivorous (TL > 3.9) categories based on trophic levels.

2.7 | Estimating the herbivorous cladoceran diet

We used the measured cladoceran FA profiles to estimate relative cladoceran diet compositions (%). We used Quantitative Fatty Acid Signature Analysis in R (QFASAR) (Bromaghin, 2017; Iverson et al., 2004) with $\chi^2$ distance measure (Stewart et al., 2014), which is the most accurate current fatty acid-based method for herbivorous cladoceran diet estimation (Litmanen et al., 2020). The diets were estimated with an FA profile library formed of homogeneous diet feeding experiments consisting of dinoflagellates, golden algae, cryptophytes, diatoms, green algae, euglenoids, cyanobacteria, actinobacteria, and microbes sustaining on (terrestrial) particulate organic matter/detritus (Galloway et al., 2014; Litmanen et al., 2020). The standard deviation for the diet estimates was produced with 100 sample bootstrapping in QFASAR (Table S2). The estimation was conducted with R Statistical Software v. 3.6.1 (R Core Team, 2019).

2.8 | Statistical analysis

We used PERMANOVA ( Primer 7) analysis and Bray-Curtis similarity to compare phytoplankton, zooplankton, and fish community structure at class, genus, or species level, using lake trophic status (mesotrophic or eutrophic) and month as factors. We used the same approach to compare fatty acid composition and content of essential fatty acids in phytoplankton (seston), herbivorous cladoceran, benthic invertebrates, and perches. PERMANOVA with Euclidean distance as resemblance matrix was used for univariate analysis (Anderson et al., 2017). Non-metric multidimensional scaling NMDS
was used to separate communities’ structure, fatty acid composition, and content of essential fatty acids (Primer 7). The correlations between MDS1 and MDS2 and variables were analyzed with Spearman correlation analysis. Hierarchical Cluster analysis was used to create similarity groups in NMDS. We used bubble plots to illustrate the total biomass of phytoplankton, zooplankton, and fish communities in NMDS.

3 | RESULTS

3.1 | Water quality and phytoplankton community

Total phosphorus, nitrogen, chlorophyll, and turbidity were significantly higher in eutrophic Lake Köyliönjärvi than in mesotrophic Lake Pyhäjärvi and lake trophic status explained 66% of the difference (Tables 1 and 2). When using two factor analysis, trophic status explained 62% of the variance (PERMANOVA: Pseudo-\(F_{1,13} = 71.3, p = .001\)) and month explained 9% of the variation of phosphorus, nitrogen, chlorophyll, and turbidity (PERMANOVA: Pseudo-\(F_{1,13} = 40.6/2.9, p = .001/0.045\)). The temperature of surface water was equal in both lakes and whereas Secchi depth was higher in the mesotrophic Lake Pyhäjärvi than in the eutrophic Lake Köyliönjärvi during the open water season 2017 (Table 2).

Cyanobacteria, diatoms, and green algae were percentually the three most abundant taxa in eutrophic Lake Köyliönjärvi, whereas cyanobacteria and diatoms were percentually the most common classes in Lake Pyhäjärvi. The contribution of dinoflagellates during summer months was significantly higher in Lake Pyhäjärvi than in Lake Köyliönjärvi, but otherwise, the lakes did not differ in their phytoplankton composition at class level (see Table 2). However, the contribution of DHA-synthesizing taxa (cryptophytes, dinoflagellates, golden algae) was higher in the mesotrophic lake (24.3 ± 12% of all) than in the eutrophic lake (6.8 ± 7.7%). Total phytoplankton biomass was higher in eutrophic Lake Köyliönjärvi than in mesotrophic Lake Pyhäjärvi (see Figure 1). However, comparison at class level showed that only biomas of green algae was higher in eutrophic Lake Köyliönjärvi than in mesotrophic Lake Pyhäjärvi, whereas diatom biomass was higher in the mesotrophic Lake Pyhäjärvi than in the eutrophic Lake Köyliönjärvi (refer to Figure 1, Table 2). Due to the higher biomass of diatoms in the eutrophic Lake Köyliönjärvi, the biomass of EPA-synthesizing taxa was also higher, whereas the biomass of DHA-synthesizing taxa did not differ between lakes (Table 2). According to the PERMANOVA, each lake explained 51% of the variation in phytoplankton biomasses at class level but explained only 36% of variation at the genus level (Table 2).

NMDS output showed that phytoplankton community structure varied greatly between the two lakes but varied more, during summer months, in mesotrophic Lake Pyhäjärvi than in eutrophic Lake Köyliönjärvi (Figure 1c). Moreover, similarity analysis (SIMPER) showed that the dissimilarity of phytoplankton communities at the genus level between the lakes was relatively high (89.4%). Cyanobacteria genus of *Dolichospermum* and *Microcystis* and diatom genera of *Aulacoseira* were more abundant taxa in eutrophic Lake Köyliönjärvi than in mesotrophic Lake Pyhäjärvi, whereas *Aphanizomenon* (Cyanobacteria) was more abundant in the mesotrophic than in the eutrophic lake. The closer comparison of EPA- and DHA-synthesizing phytoplankton genus (SIMPER: Average dissimilarity = 78.7%) showed that *Aulacoseira, Acanthoceras, Uroglena, Rhodomonas, Cryptomonas, and Ceratium* were more abundant in eutrophic Lake Köyliönjärvi (explaining 61.1% of dissimilarity). Whereas *Dinobryon, Tabellaria, Fragilaria, Rhizosolenia,* and *Gymnodinium* were more abundant in mesotrophic Lake Pyhäjärvi (explaining 15.4% of dissimilarity).

3.2 | Zooplankton community

NMDS output revealed changes in the zooplankton community structure between the lakes but also by the season (see Figure 2c). Two-factor PERMANOVA of zooplankton biomasses at genus level showed the following statistical difference between the lakes (PERMANOVA (lake/month): Pseudo-\(F_{1,11} = 4.3/3.3, p = .017/0.09\)). Lake and month accounted for 21% and 32% of all variation, respectively. According to the similarity analysis, most of the difference between the lakes (SIMPER: average dissimilarity 67.8%) was explained by the genus of the *Chydorus, Eudiaptomus,* and Mesocyclops, which were more abundant in the eutrophic than in the mesotrophic lake. However, *Bosmina* was more abundant in the mesotrophic than in the eutrophic lake. Nevertheless, herbivorous cladoceran was the most abundant zooplankton group in both lakes (Figure 2a), of which *Chyrodus, Daphnia,* and *Bosmina* were the most abundant genus. *Eudiaptomus graciloides* was the only abundant herbivorous calanoid in both lakes and were the second-most abundant zooplankton group with predator cyclopoids in both lakes. *Megacylops, Mesocyclops,* and *Thermocyclops* were all abundant in mesotrophic Lake Pyhäjärvi whereas *Megacylops* did not occur in the eutrophic Lake Köyliönjärvi. Predator cladoceran (*Leptodora kindtii*) was the only zooplankton group which differed statistically significantly between lakes being more abundant in eutrophic Lake Köyliönjärvi than in mesotrophic Lake Pyhäjärvi (Table 2, Figure 2b).

3.3 | Benthic and fish communities

Our benthic invertebrate sampling was not quantitative, but our sampling in two lakes showed differences in the presence of various benthic invertebrates. Meanwhile, we found only Chironomidae in eutrophic Lake Köyliönjärvi, while our sampling of mesotrophic Lake Pyhäjärvi resulted in finding several individuals of *Asellus aquaticus,* *Ephemeroptera, Oligochaeta,* Megaloptera, and Plecoptera.

Figure 3a showed that the Total BPUE (kg fish per gillnet night) and CPUE (number of fish per gillnet night) in 2012–2020 was higher in eutrophic Lake Köyliönjärvi than in mesotrophic Lake Pyhäjärvi.


Table 2: Statistical results for PERMANOVA between mesotrophic and eutrophic lakes. % cites to the contribution, FA% to fatty acid profile, concentration to µg FA mg/L, %, QFASA to the contribution of fatty acid-based diet estimates.

| Component                          | DF1 | DF2 | Pseudo-F | P(perm) | Difference             |
|------------------------------------|-----|-----|----------|---------|------------------------|
| Total nitrogen                     | 1   | 13  | 23.8     | 0.003   | Mesotrophic < eutrophic |
| Total phosphorus                   | 1   | 13  | 15.2     | 0.003   | Mesotrophic < eutrophic |
| Chlorophyll a                      | 1   | 13  | 31.6     | 0.001   | Mesotrophic < eutrophic |
| Turbidity                          | 1   | 13  | 87.9     | 0.001   | Mesotrophic < eutrophic |
| Secchi depth                       | 1   | 13  | 179.5    | 0.001   | Mesotrophic < eutrophic |
| Temperature                        | 1   | 13  | <0.001   | 1       | Mesotrophic = eutrophic |
| Dinoflagellates (%)                | 1   | 11  | 3.9      | 0.04    | Mesotrophic > eutrophic |
| DHA-synth. taxa (%)                | 1   | 11  | 8.5      | 0.023   | Mesotrophic > eutrophic |
| Total phytoplankton biomass        | 1   | 10  | 9.3      | 0.0018  | Mesotrophic < eutrophic |
| Diatoms (biomass)                  | 1   | 10  | 9.3      | 0.005   | Mesotrophic > eutrophic |
| Green algae (biomass)              | 1   | 10  | 526      | 0.002   | Eutrophic > mesotrophic |
| Phytoplankton biomass (class)      | 1   | 10  | 9.3      | 0.023   | Mesotrophic < eutrophic |
| Phytoplankton biomass (genus)      | 1   | 11  | 6.2      | 0.003   | Mesotrophic < eutrophic |
| EPA-synth. taxa (biomass)          | 1   | 11  | 12.2     | 0.002   | Mesotrophic > eutrophic |
| DHA-synth. taxa (biomass)          | 1   | 11  | 0.002    | 0.95    | Mesotrophic = eutrophic |
| Predatory cladoceran               | 1   | 11  | 3.5      | 0.042   | Mesotrophic < eutrophic |
| BPUE                               | 1   | 7   | 23.2     | 0.035   | Mesotrophic < eutrophic |
| CPUE                               | 1   | 7   | 28.3     | 0.036   | Mesotrophic < eutrophic |
| Roach (biomass)                    | 1   | 7   | 48.1     | 0.033   | Mesotrophic < eutrophic |
| Perch (BPUE)                       | 1   | 7   | 0.27     | 0.641   | Mesotrophic = eutrophic |
| Seston (FA%)                       | 1   | 12  | 22       | 0.002   | Mesotrophic > eutrophic |
| Herbivorous cladoceran (FA%)       | 1   | 12  | 4.4      | 0.001   | Mesotrophic < eutrophic |
| Chironomidae larvae (FA%)          | 1   | 5   | 20.5     | 0.004   | Mesotrophic > eutrophic |
| Roach (FA%)                        | 1   | 8   | 3.2      | 0.059   | Mesotrophic = eutrophic |
| Perch (FA%; all sizes together)    | 1   | 93  | 7.7      | 0.001   | Mesotrophic = eutrophic |
| Perch, young of the year (FA%)     | 1   | 22  | 13.4     | 0.001   | Mesotrophic > eutrophic |
| Perch, planktivorous (FA%)         | 1   | 22  | 6.5      | 0.003   | Mesotrophic = eutrophic |
| Perch, benthivorous (FA%)          | 1   | 26  | 11.2     | 0.001   | Mesotrophic > eutrophic |
| Perch, piscivorous (FA%)           | 1   | 13  | 3.1      | 0.024   | Mesotrophic > eutrophic |
| Sestonic EPA (concentration)       | 1   | 25  | 0.025    | 0.864   | Mesotrophic = eutrophic |
| Sestonic DHA (concentration)       | 1   | 25  | 49.6     | 0.001   | Mesotrophic > eutrophic |
| Golden algae (%, QFASA)            | 1   | 10  | 10.2     | 0.024   | Mesotrophic > eutrophic |
| Crypto (%, QFASA)                  | 1   | 10  | 13.3     | 0.013   | Mesotrophic > eutrophic |
| tPOM microbes (%, QFASA)           | 1   | 10  | 6.2      | 0.034   | Mesotrophic < eutrophic |
| Dinoflagellates (%, QFASA)         | 1   | 10  | 2.1      | 0.169   | Mesotrophic > eutrophic |

(Table 2) Lake trophic status explained 83% and 79% of the variation in BPUE and CPUE, respectively. The percids were found to contribute (BPUE%) 20.6 ± 6.1% and 55.3.6 ± 5.0% of total BPUE in eutrophic Lake Köyliönjärvi and mesotrophic Lake Pyhäjärvi, respectively. Conversely, the contribution of cyprinids was higher in Lake Köyliönjärvi (66.3 ± 3.2%) than in Lake Pyhäjärvi (18.6 ± 6.5%). Roach (Rutilus rutilus) was the main (BPUE% = 42 ± 4%) fish species in Lake Köyliönjärvi and its biomass was statistically higher (Table 2) than in Lake Pyhäjärvi. Correspondingly, perch (Perca fluviatilis) was the main (BPUE% = 39 ± 7%) fish species in the Lake Pyhäjärvi; however, the BPUE of perch did not differ between lakes (Table 2). According to the SIMPER (average dissimilarity between lakes = 50.7%, Table 2) and NMDS (Figure 3c), bleak, smelt, whitefish, and ruffe were more prevalent (BPUE%) in mesotrophic Lake Pyhäjärvi, whereas pike, pikeperch, bream, and white bream were more prevalent in eutrophic Lake Köyliönjärvi. The abundance of different ontogenetic groups of perches did not differ statistically between the lakes due to the high variation in mesotrophic Lake Pyhäjärvi (refer to Figure 3b). However, planktivorous perch contributed 91 ± 3% of all perch (CPUE%) in eutrophic
Lake Köyliönjärvi, but 75 ± 17% of all perch in Lake Pyhäjärvi. Moreover, benthivorous perch contributed 20 ± 15% of all perch in Lake Pyhäjärvi, but only 6 ± 3% of all perch in Köyliönjärvi. The contribution of piscivorous perch to overall perches was similar in both lakes (~3–5%).

3.4 | Food web structure based on fatty acids

According to the two-factor PERMANOVA analysis (PERMANOVA (lake/species): Pseudo-$F_{1,12145} = 6.2/124.3$, $p = .001$), lake type explained only 0.5% and species (organism) 84% of FA variation,
when all fatty acid profiles of seston, zooplankton, benthic invertebrates, roach, and perch were placed in the same analysis. This same phenomenon can also be seen in NMDS output (see Figure 4). Comparison of fatty acid profiles of seston (≤50 µm) between lakes showed statistical difference but lake type explained only 19% of the variation (Table 2). The dissimilarity of fatty acid profiles (SIMPER: 15.9%) was explained by the fatty acids of 18:0, 14:0, 16:1ω7c, 16:0, and ALA which together contributed 65% of the
difference between lakes. Fatty acid profiles of herbivorous cladoceran (Daphnia, Bosmina) also differed between lakes and lake types and explained 29% of the variation (Table 2). According to the SIMPER, the dissimilarity between lakes was 19.2% and fatty acids of 14:0, ALA, EPA, 18:1ω7, and 16:1ω7 altogether explained 47% of the variation. Additionally, the contribution of DHA in herbivorous zooplankton was much higher in the mesotrophic than in the eutrophic lake. Fatty profiles of Chironomidae also differed significantly between lakes and the trophic status of a lake explained 85% of the variation (Table 2). The dissimilarity of fatty acid profiles of Chironomidae between lakes was 14.7% (SIMPER) and EPA, 16:1ω7, 18:1ω9, 16:0, and LIN explained most (63.9%) of the differences between lakes. The fatty acid profile of roach did not differ (P(MC) = 0.058) between lakes, whereas fatty acid profiles of perches differed between lakes (Table 2), but lake trophic status explained only 8% of the variation. Moreover, age, length, and ontogenic stage explained 34%, 86%, and 25%, respectively of variation in fatty acid profiles of all perch. A comparison of three ontogenic diet groups of perch showed a statistical difference between the two lakes in all groups. Trophic status of each lake explained 39% of the variation in fatty acid profiles of the young-of-the-year and planktivorous perch and 56% in benthivorous perch, but only 7% of the variation of piscivorous perch (Table 2). Dissimilarity (SIMPER) of fatty acid profiles of different ontogenetic group perch was only 7–11%. These differences can be observed in the NMDS output as well (Figure 4b, Figure S1).

3.5 | The content of polyunsaturated fatty acids in the food web components

Sestonic concentration (µg FA/L) of DHA was equal in both lakes whereas the concentration of EPA was higher in the mesotrophic lake than in the eutrophic lake (Table 2). The content (µg FA/mg/C) of individual ω-3 and ω-6 PUFA showed different patterns across trophic levels and between lake types (Figure 5). Seasonal variation of food web components in the content of individual ω-3 and ω-6 PUFA was greater in the mesotrophic lake as compared to the eutrophic lake (see SD bars in Figure 5). The content of SDA (stearidonic acid), EPA, DHA, LIN, and ARA in seston (<50 µm phytoplankton) of the mesotrophic Lake Pyhäjärvi exceeded their content in the seston of eutrophic Köyliönjärvi (Pairwise PERMANOVA; Table S3, Figure 5).

Similarly, herbivorous cladoceran was found to contain more SDA, EPA, DHA, and ARA in mesotrophic Lake Pyhäjärvi than in eutrophic Lake Köyliönjärvi, whereas Chironomidae larvae contained more ALA, EPA, DHA, LIN, and ARA in the mesotrophic lake than in the eutrophic lake. Roach had equal content of all ω-3 and ω-6 PUFA in both lakes. The young-of-the-year and planktivorous perch in the mesotrophic lake contained more ALA, SDA, and LIN than the eutrophic lake perch. Additionally, the ARA content of the young-of-the-year was also higher in the mesotrophic lake. Both benthivorous and piscivorous perch in the mesotrophic lake contained more SDA and EPA than in the eutrophic lake. Moreover, LIN, ALA, and DHA content of piscivorous perch in the mesotrophic lake exceeded levels found in the eutrophic lake. When comparing EPA + DHA content of different age perches between the lakes, EPA + DHA content was higher in the mesotrophic than in eutrophic lake in the age groups of 2’–6’ (PERMANOVA (lake/species): Pseudo-F1/12/93 = 36.8/32.1, p = .001; Table S4, Figure 6).

3.6 | Trophic retention of polyunsaturated fatty acids in mesotrophic and eutrophic lakes

Evaluation of ω-3 and ω-6 PUFA content of different trophic levels showed that the ALA, SDA, EPA, and ARA content was the highest in herbivorous cladocerans whereas LIN content was highest in the Chironomidae larvae, and DHA content was the highest in the young-of-the-year perch. Calculations of trophic retention of ARA, EPA, and DHA between Daphnia and Bosmina and seston showed high retention of all these biomolecules in both lakes in relation to other consumers (Figure 7, Table S5). Moreover, trophic retention of these biomolecules was more efficient by Daphnia and Bosmina in the eutrophic lake than in the mesotrophic lake. Chironomidae larvae retained efficiently EPA, but not DHA or ARA from their diet and did not differ between the mesotrophic and the eutrophic lakes. Planktivorous roach and perch retained efficiently DHA, but not EPA or ARA from their diet in both lakes. Trophic retention of DHA was higher in the planktivorous roach and perch in the eutrophic lake than in the mesotrophic lake. We found that the highest trophic retention of DHA for benthivorous perch in the eutrophic lake was 2–3 times higher than in the mesotrophic lake. Piscivorous perch have a similar amount of EPA, DHA, and ARA with their prey and thus did not retain EPA, DHA, or ARA from their diet.

3.7 | Trophic position of consumers based δ15N value of primary producers

The δ15N value of primary producers was 2.7 ± 1.0‰ in mesotrophic Lake Pyhäjärvi and 4.6 ± 0.9‰ in eutrophic Lake Köyliönjärvi during sample summer months. Based on these primary producer values, the trophic position values for herbivorous cladoceran were 1.5 ± 0.1 (δ15N = 6.2 ± 0.5‰) and 2.2 (δ15N = 8.7‰) for mesotrophic and eutrophic lakes, respectively. For Chironomidae larvae, values were 2.1 ± 0.1 (δ15N = 8.2 ± 0.4‰) in the mesotrophic lake and 1.8 (δ15N = 7.3‰) in the eutrophic lake. Roach trophic position was 3.3 ± 0.1 (δ15N = 11.0 ± 0.3‰) in the mesotrophic lake and 3.5 ± 0.1 (δ15N = 10.9 ± 0.2‰) in the eutrophic lake. The trophic position of planktivorous, benthivorous, and piscivorous perch was 3.3 ± 0.1 (δ15N = 10.4 ± 0.5‰), 3.7 ± 0.1 (δ15N = 12.0 ± 0.5‰), and 4.1 ± 0.1 (δ15N = 13.2 ± 0.4‰) for the mesotrophic lake, and 3.5 ± 0.1 (δ15N = 13.1 ± 0.3‰), 3.8 ± 0.1 (δ15N = 14.2 ± 0.1‰), and 4.1 ± 0.1 (δ15N = 15.1 ± 0.3‰) for the eutrophic lake.

The comparison of DHA accumulation at different trophic levels between mesotrophic eutrophic lakes showed great differences at first
The ω-3 (ALA, SDA, EPA, and DHA) and ω-6 (LIN and ARA) polyunsaturated fatty acid content of food web components (seston <50 µm, herbivorous cladoceran, Chironomidae larvae, roach of 10–15 cm, four categories of perch) in mesotrophic Lake Pyhäjärvi and in eutrophic Lake Köyliönjärvi. Star cites to statistical difference at 0.05 level. 0+ = the young-of-the-year perch.

3.8 Evaluation of herbivorous cladoceran diet and transfer of EPA and DHA

The herbivorous cladoceran diets estimated with a fatty acid-based method (QFASAR χ²) differed between the two lakes (Figure S2). Dinoflagellates, cryptophytes, and microbes on tPOM formed >75% of herbivorous cladoceran diet in the eutrophic lake, whereas the diets in mesotrophic Lake Pyhäjärvi also included golden algae and diatoms. Lake type accounted for 50% of the difference, and the month explained 28% of the difference between lakes (PERMANOVA (lake/month): Pseudo-F 1/2,10 = 14.5/4.0, P(perm) = 0.011/0.025).

The contribution of golden algae in the diet of herbivorous cladoceran was statistically significantly higher in the mesotrophic lake, whereas cryptophytes and microbes on tPOM were more abundant in the diet of cladoceran in the eutrophic lake (Table 2).

Pearson regression analysis showed significant positive relation only between EPA content of herbivorous cladoceran and seston, but...
not with any other \( \omega-3 \) or \( \omega-6 \) PUFA (Figure S3). Moreover, the EPA content of herbivorous cladoceran was best explained by the contribution of assimilated cryptophytes, golden algae, dinoflagellates, and diatoms, whereas DHA content was best explained by the contribution of dinoflagellates and golden algae (Figure S3).

4 | DISCUSSION

In this study, we found a clear impact of agricultural eutrophication on the structure of plankton and fish communities, but the effect on the nutritional value of food web components varied at different trophic levels. Presumably, total phytoplankton biomass was four times higher in the lake with agricultural eutrophication than in the mesotrophic lake. The increase in phytoplankton biomass caused by eutrophication is well documented in temperate and boreal lakes (Taipale et al., 2019; Taipale, Vuorio, et al., 2016; Vollenweider et al., 1974). Cyanobacteria were abundant throughout the summer months in the eutrophic lake; however, since cyanobacteria (Aphanizomenon) were abundant for a short period during early summer in the mesotrophic lake, the average cyanobacteria biomass for the whole summer period did not differ between lakes. However, mesotrophic and eutrophic lakes differ in their cyanobacteria species composition due to the different TP thresholds for different species (Vuorio et al., 2020). Seasonal succession of different phytoplankton species was higher in the mesotrophic lake than in the agricultural eutrophic lake. However, lakes did not differ by the contribution or the biomass of EPA-synthesizing phytoplankton taxa, but only in the DHA-synthesizing taxa. This was also evidenced in the higher DHA content per phytoplankton carbon in the mesotrophic lake than in the eutrophic lake, as previously found for boreal lakes (Taipale et al., 2019). Even though phytoplankton communities in mesotrophic and eutrophic lakes did not differ at class level, seston fatty acid profiles (<50 \( \mu \)m) were found to differ between the lakes, reflecting changes in the available phytoplankton diet for herbivorous zooplankton. Moreover, the contribution and the content of ARA, EPA, and DHA in seston was higher in the mesotrophic lake than in the eutrophic lake, as found in prior studies (Lau et al., 2021; Müller-Navarra et al., 2004; Taipale, Vuorio, et al., 2016). Fatty acid biomarkers for golden algae and dinoflagellates in <50 \( \mu \)m seston suggested a higher availability of these algae for herbivorous zooplankton in the mesotrophic lake than in the eutrophic lake.

Considering our hypothesis, calanoids (Eudiaptomus graciloides) was equally abundant in both lakes and the biomass of herbivorous cladoceran or calanoids did not differ between lakes, suggesting that they obtained enough essential biomolecules for sustaining such a high biomass; this observation is also congruent with previous findings (Havens & Beaver, 2011). Here, we focused on herbivorous cladoceran (Daphnia and Bosmina) whose nutritional value was higher in the mesotrophic lake than in the eutrophic lake throughout the summer months. This was mainly attributed to the differences in the feeding behavior between lakes. Herbivorous cladoceran (Daphnia and Bosmina) assimilated more golden algae and dinoflagellates in <50 \( \mu \)m seston suggested a higher availability of these algae for herbivorous zooplankton in the mesotrophic lake than in the eutrophic lake.

![FIGURE 7](https://example.com/figure7.png)

FIGURE 7  Trophic retention of EPA (a), DHA (b), and ARA (c) relating to the content of their diet. Star (*) indicates the statistical difference between mesotrophic and eutrophic lakes. See Table S3 for PERMONAVA results.
because it is too large for herbivorous cladoceran (Santer, 1996), it is unclear what dinoflagellate species *Daphnia* and *Bosmina* were actually feeding on.

Diatoms were relatively common taxa in both lakes, but *Daphnia* and *Bosmina* did not consume them in high proportion, which may be the result of their filamentous form or low nutritional quality due to the growth stage (Diekmann et al., 2009; Jónasdóttir, 1994; Jónasdóttir & Kierboe, 1996). In contrast, *Daphnia* and *Bosmina* fed on cryptophytes in both lakes; these are both common in eutrophic lakes and form a superior diet for herbivorous zooplankton (Lepistö & Rosenström, 1998; Peltomaa et al., 2017; Taipale, Galloway, et al., 2016). According to our fatty acid-based diet estimates, herbivorous cladoceran (*Daphnia* and *Bosmina*) did not feed directly on cyanobacteria in either lake, thus confirming previous findings that cyanobacteria is a dead-end in the energy flow and biomolecule transfer (Porter & McDonough, 1984). However, we did not study the diet of *Chydorus* which has been previously shown to feed on cyanobacteria (Tönno et al., 2016). Nevertheless, microbes on tPOM/detritus were the main dietary component of herbivorous cladoceran in the eutrophic lake, which is consistent with the previous finding that a microbial food chain on decaying cyanobacteria bloom is the main link between cyanobacteria and zooplankton (Kluivver et al., 2012; Ventelä et al., 2002). Therefore, even though zooplankton do not directly feed on cyanobacteria, their decay seems to support a high biomass of edible microbes for zooplankton.

Though it seems unlikely, it is often mentioned in the extant literature that *Daphnia* and *Bosmina* are able to detect high nutritional quality patches (Schatz & McCauley, 2007) and can select high nutritional quality particles (Hartmann & Kunkel, 1991). In this study, we found that they overcame relatively poor availability of EPA- and DHA-synthesizing phytoplankton taxa in the eutrophic lake, as we measured higher trophic retention of EPA and DHA by herbivorous zooplankton (*Daphnia* and *Bosmina*) in the eutrophic than in the mesotrophic lake. Unfortunately, we were unable to compare the impact of the lake's trophic status on the DHA content of herbivorous calanoids (*Eudiaptomus*). Calanoids feed selectively on high-quality algae, preferably on dinoflagellates with high DHA content (Kleppel, 1993). Nevertheless, results in the phytoplankton and zooplankton interface were congruent with our hypotheses that lake trophic status can decrease the nutritional value of phytoplankton and herbivorous zooplankton.

Chironomidae larvae were found to contain very small amounts of DHA, but high amounts of EPA, which supports previous findings in many benthic invertebrates (Ahlgren et al., 2009; Goedkoop et al., 2000; Strandberg et al., 2020; Vesterinen et al., 2021). Our result showed that eutrophication and long-term cyanobacteria blooming affect the nutritional value of *Chironomidae* larvae whose EPA and DHA content was dramatically lowered in the eutrophic lake. This negative impact on the nutritional value was even greater with *Chironomidae* larvae than when found with herbivorous zooplankton. However, the EPA content of *Chironomidae* larvae can differ greatly among different species (Makhatova et al., 2017), and thus, the lower EPA and DHA content of *Chironomidae* larvae in the eutrophic lake could be attributed to different species. This is supported by the fact that *Chironomidae* larvae differ in their trophic position between lakes. Altogether, our results indicate that *Chironomidae* larvae were unable to biosynthesize EPA from ALA, which is opposite to Strandberg et al. (2020) laboratory experiment with *Chironomus* larvae.

Our data covered four different years of fish community data in the 2000s; cyprinid fish species were found to be more abundant in eutrophic Köyliönjärvi than in mesotrophic Lake Pyhäjärvi. Correspondingly, whitefish, vendace, and smelt were more abundant in mesotrophic Lake Pyhäjärvi than in eutrophic Lake Köyliönjärvi. However, in contrast to our hypothesis, the abundance of perch did not differ between lakes and perch can seemingly achieve higher biomasses in the eutrophic than in the oligo- or mesotrophic lakes (Keva et al., 2021).

Long-term cyanobacteria blooming by agricultural eutrophication has a different impact on the nutritional value of fish at different trophic levels. Our results showed that lowered EPA and DHA content of herbivorous zooplankton (*Daphnia* and *Bosmina*) did not reflect in the EPA or DHA content of young-of-the-year or planktivorous perch and roach. However, it is possible that planktivorous fish fed on DHA-rich *Eudiaptomus*, thus obtaining DHA (Sarvala et al., 1998; Vesterinen et al., 2021). Therefore, we were unfortunately unable to analyze *Eudiaptomus* from both lakes. Nevertheless, we found lower ARA content of the young-of-the-year perch in the eutrophic lake than in the mesotrophic lake. Altogether, it seems that juvenile perch and roach successfully biosynthesized DHA from short-chain ω-3 PUFA, as found previously with one- and two-year-old perch in aquaculture circumstances (Henrotte et al.,
Moreover, the strong regulation of EPA and DHA in perch dorsal muscle was recently found in a mesotrophic lake (Chaguaceda et al., 2020). However, trout fries are not able to biosynthesize DHA from precursors (Taipale et al., 2018; Wirth et al., 1997). Therefore, even freshwater fish species differ in their ability to biosynthesize DHA from ALA (Ishikawa et al., 2019; Sargent, et al., 1999). Altogether, it is clear that DHA plays a key role in the early-stage development of fish fry (Mourente et al., 1991). It also seems that juvenile perch preferred DHA biosynthesis over biosynthesis of ARA from LIN, since biosynthesis of ARA and DHA use the same enzymatic processes (Nielsen et al., 2019).

The high contribution of ALA and SDA in perch has been related to their planktivorous stage (Chaguaceda et al., 2020). The same fatty acids were also characteristic of the young-of-the-year in both lakes and of perch relating to 1- to 2-year-old in the eutrophic lake. Most of the one- to two-year-old perch in the mesotrophic lake already cluster together with benthivorous perch, which may suggest that the same ages/size perch were in the different ontogenetic stages in the mesotrophic and eutrophic lake. The EPA + DHA content was lower in the benthivorous perch in the eutrophic than in the mesotrophic lake. Nevertheless, DHA content alone did not differ between lakes, which is why it is possible that during the low availability of DHA in their diet, they biosynthesized DHA from ALA as was recently suggested based on the compound-specific isotope data (Scharnweber et al., 2021).

Fatty acid profiles and δ15N of piscivorous perch differed from two other ontogenetic stages, thus confirming their different feeding behavior and higher trophic position. Our result showed that agricultural eutrophication and long-term cyanobacterial blooming has the greatest impact on the nutritional value of fish at upper trophic levels. The EPA and DHA content of the dorsal muscle of perch were higher in the mesotrophic lake than in the eutrophic lake, which agrees with our hypothesis. However, EPA + DHA content of piscivorous perch in the eutrophic lake was almost two times higher than the previous finding in piscivorous perches from four eutrophic boreal lakes (Taipale, Vuorio, et al., 2016). Since both eutrophication and browning (an increase of DOC) have negative relationships with EPA + DHA content of piscivorous perch, it is possible that eutrophication and browning have an additive negative impact on the perch nutritional value (Strandberg et al., 2016; Taipale, Vuorio, et al., 2016). In contrast to planktivorous and benthivorous perch, piscivorous perch has similar DHA content as their prey and trophic retention of DHA by piscivorous perch was lower in the eutrophic lake in comparison to the mesotrophic lake. However, it is also possible that large size females allocate dietary DHA to their gonad development and other crucial tasks (Keva et al., 2019).

### 5 | CONCLUSIONS

In conclusion, our monitoring process throughout the summer months revealed that cyanobacteria blooming lasted much longer in the eutrophic lake suffering agricultural eutrophication when compared with the mesotrophic lake disturbed by global warming. The lakes differed in the biomass and structure of phytoplankton, zooplankton, and fish communities. Phytoplankton communities of these two lakes were found to differ at the genus level, resulting in differences in the nutritional value of seston and herbivorous zooplankton. However, the lowered nutritional value of prey did not decrease the EPA or DHA content of planktivorous perch or roach. Therefore, they seemingly compensated for the lowered nutritional value of prey by biosynthesizing EPA and DHA from their precursors. Despite compensated EPA and DHA content of planktivorous fish, piscivorous perch feeding on them were found to have lower EPA + DHA content in the eutrophic lake. Our study here emphasizes that long-term cyanobacterial blooming by agricultural eutrophication can have varied consequences on the nutritional value of food web components at different trophic levels.

### ACKNOWLEDGEMENTS

We thank technician Nina Honkanen for helping with stable isotope measurements and technicians Emma Pajunen and Mervi Koistinen for helping with fatty acid analysis. Additionally, we thank Tapio Putko for helping in Lake Köyliöjärvi sampling.

### CONFLICT OF INTEREST

None.

### AUTHOR CONTRIBUTION

Sami Johan Taipale: Formal analysis (supporting); Funding acquisition (supporting); Methodology (lead); Writing – original draft (lead).
Anne-Mari Ventelä: Supervision (equal); Writing – review & editing (supporting).
Jaakko Litmanen: Methodology (supporting); Writing – review & editing (supporting).
Lauri Anttila: Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (equal); Writing – review & editing (supporting).

### SUBMISSION DECLARATION

This work is original, has not been previously published, and is not under consideration for publication elsewhere.

### DATA AVAILABILITY STATEMENT

Phytoplankton, zooplankton, and fish data are available at Open access interfaces for environmental data at the Finnish Environmental Centre (www.syke.fi) and fatty acid data are available for download from Dryad (doi:10.5061/dryad.1c59z3x1).

### ORCID

Sami Johan Taipale: https://orcid.org/0000-0001-7510-7337
Jaakko Litmanen: https://orcid.org/0000-0003-2828-3885
Lauri Anttila: https://orcid.org/0000-0002-4530-9912

### REFERENCES

Ahlgren, G., Gustafsson, I., & Boberg, M. (1992). Fatty acid content and chemical composition of freshwater microalgae. *Journal of Phycology*, 28, 37-50.
Jónasdóttir, S. H. (1994). Effects of food quality on the reproductive success of Acartia tonsa and Acartia hudsonica: Laboratory observations. Marine Biology, 121(1), 67–81. https://doi.org/10.1007/BF00349475

Jónasdóttir, S. H. (2019). Fatty acid profiles and production in marine phytoplankton. Marine Drugs, 17, 151.

Jónasdóttir, S. H., & Kierboe, T. (1996). Copepod recruitment and food composition: Do diatoms affect hatching success? Marine Biology, 125(4), 743–750.

Jørgensen, S. E., & Rast, W. (2001). Lakes and reservoirs: Water quality: The impact of eutrophication. UNEP-IETC/IIEC.

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

Kerfoot, W. C., Levitan, C., & DeMott, W. R. (1988). Daphnia-phytoplankton interactions: Density-dependent shifts in resource quality. Ecology, 69, 1804–1825. https://doi.org/10.2307/1941159

Keva, O., Taipale, S. J., Hayden, B., Thomas, S. M., Vesterinen, J., Kankaala, P., & Kahlilainen, K. K. (2021). Increasing temperature and productivity change biomass, trophic pyramids and community-level omega-3 fatty acid content in subarctic lake food webs. Global Change Biology, 27, 282–296. https://doi.org/10.1111/gcb.15387

Keva, O., Tang, P., Käkelä, R., Hayden, B., Taipale, S. J., Harrold, C., & Kahlilainen, K. K. (2019). Seasonal changes in European whitefish muscle and invertebrate prey fatty acid composition in a subarctic lake. Freshwater Biology, 64, 1908–1920. https://doi.org/10.1111/fwb.13381

Kleppel, G. S. (1993). On the diets of calanoid copepods. Marine Ecology Progress Series, 99, 183. https://doi.org/10.3354/meps099183

Koussoroplis, A., Nussbaumer, J., Arts, M. T., Guschina, I. A., & Kainz, M. J. (2014). Famine and feast in a common freshwater calanoid: Effects of diet and temperature on fatty acid dynamics of Eudiaptomus gracilis. Limnology and Oceanography, 59, 947–958.

Kratina, P., & Winder, M. (2015). Biotic invasions can alter nutritional composition of zooplankton communities. Oikos, 124, 1337–1345. https://doi.org/10.1111/oik.02240

Lathrop, R. C., Kasprzak, P., Tarvainen, M., Ventelä, A., Keskinen, T., Koschel, R., & Robertson, D. M. (2019). Seasonal epilimnetic temperature patterns and trends in a suite of lakes from Wisconsin (USA), Germany, and Finland. Inland Waters, 9, 471–488. https://doi.org/10.1080/20442401.2019.1637682

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

Leech, D. M., Pollard, A. I., Labou, S. G., & Hampton, S. E. (2018). Fewer blue lakes and more murky lakes across the continental US: Implications for planktonic food webs. Limnology and Oceanography, 63, 2661–2680. https://doi.org/10.1002/lno.10967

Lepistö, L., & Rosenström, U. (1998). The most typical phytoplankton taxa in four types of boreal lakes. Hydrobiologia, 369, 89–97.

Litmanen, J. J., Perälä, T. A., & Taipale, S. J. (2020). Comparison of Bayesian and numerical optimization-based diet estimation on herbivorous zooplankton. Philosophical Transactions of the Royal Society B, 375, 20190651. https://doi.org/10.1098/rstb.2019.0651

Lynch, M., & Shapiro, J. (1981). Predation, enrichment, and phytoplankton community structure 1. Limnology and Oceanography, 26, 86–102. https://doi.org/10.4319/lo.1981.26.1.0086

Makhotova, O. N., Borisova, E. V., Shulepina, S. P., Kolmakova, A. A., & Sushchik, N. N. (2017). Fatty acid composition and content in chironomid species at various life stages dominating in a saline Siberian lake. Contemporary Problems of Ecology, 10, 230–239. https://doi.org/10.1134/S1995425517030064

Mourente, G., Tocher, D. R., & Sargent, J. R. (1991). Specific accumulation of docosahexaenoic acid (22:6n–3) in brain lipid during development of juvenile turbot Scophthalmus maximus L. Lipids, 26, 871–877. https://doi.org/10.1007/BF020535970

Müller-Navarra, D. C. C., Brett, M. T., Park, S., Chandra, S., Ballantyne, A. P., Zorita, E., & Goldman, C. R. (2004). Unsaturated fatty acid content in seston and tropho-dynamic coupling in lakes. Nature, 427, 69–72. https://doi.org/10.1038/nature02210

Nielsen, B. L. H., Getterup, L., Jørgensen, T. S., Hansen, B. W., Hansen, L. H., Mortensen, J., & Jepsen, P. M. (2019). n-3 PUFA biosynthesis by the copepod Acapyclops royoi documented using fatty acid profile analysis and gene expression analysis. Biology Open, 8, bio038331.

Olin, M., Tialinen, J., Kurkilähti, M., Rask, M., & Lehtonen, H. (2016). An evaluation of gillnet CPUE as an index of perch density in small forest lakes. Fisheries Research, 173, 20–25. https://doi.org/10.1016/j.fishres.2015.05.018

O’Reilly, C. M., Alin, S. R., Plisnier, P., Cohen, A. S., & McKee, B. A. (2003). Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. Nature, 424, 766–768. https://doi.org/10.1038/nature01833

Paerl, H. W., & Huisman, J. (2008). Blooms like it hot. Science, 320, 57–58. https://doi.org/10.1126/science.1155398

Parrish, C. C. (2009). Essential fatty acids in aquatic food webs. In M. T. Arts, M. T. Brett, & M. J. Kainz (Eds.), Lipids in aquatic ecosystems (pp. 309–326). Springer.

Pätynen, A., Elliott, J. A., Kiuru, P., Sarvala, J., Ventelä, A., & Jones, R. (2014). Modelling the impact of higher temperature on the phytoplankton of a boreal lake. Boreal Environment Research, 19, 66–78.

Peltonaa, E. T., Aalto, S. L., Vuorio, K. M., & Taipale, S. J. (2017). The importance of phytoplankton biomolecule availability for secondary production. Frontiers in Ecology and Evolution, 5, 128. https://doi.org/10.3389/fevo.2017.00128

Porter, K. G., & McDonough, R. (1984). The energetic cost of response to blue-green algal filaments by cladocerans 1. Limnology and Oceanography, 29, 365–369. https://doi.org/10.4319/lo.1984.29.2.0365

Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology, 83(3), 703–718. https://doi.org/10.1890/0012-9658(2002)083[703:USITPT]2.0.CO;2

R Core Team (2019). R: A language and environment for statistical computing (version 3.5. 2, 2018). R Foundation for Statistical Computing. There is no corresponding record for this reference.

Rasconi, S., Winter, K., & Kainz, M. J. (2017). Temperature increase and fluctuation induce phytoplankton biodiversity loss—Evidence from a multi-seasonal mesocosm experiment. Ecology and Evolution, 7, 2936–2946. https://doi.org/10.1002/ece3.2889

Rask, M. (1986). The diet and diet feeding activity of perch, Perca fluviatilis L., in a small lake in southern Finland. Annales Zoologici Fennici, 23, 49–56.

Rask, M., Malinen, T., Olin, M., Peltonen, H., Ruuhijärvi, J., Vesala, S., & Hietala, J. (2020). Responses of the fish community in a eutrophicated lake to long-term food web management assessed by multiple sampling methods. Hydrobiologia, 847, 4559–4573. https://doi.org/10.1007/s10750-020-04243-9
Ruohoneno, T. (2006). Ahvenen ja hauen kasvu, ravinto ja ravinnonkulutuksen arviointi Säkylän Pyhäjärvesä vuosina 2002 ja 2004 – loppuraportti. D4213/3516/2001, hanke 134170. University of Helsinki.

Ruosteenoja, K., Jylhä, K., & Kääränen, M. (2016). Climate projections for Finland under the RCP forcing scenarios. Geophysica, 51, 17–50.

Santer, B. (1996). Nutritional suitability of the dinoflagellate Ceratium furcoides for four copepod species. Journal of Plankton Research, 18, 323–333.

Sargent, J., Bell, G., McEvoy, L., Tocher, D., & Estevez, A. (1999). Recent developments in the essential fatty acid nutrition of fish. Aquaculture, 177, 191–199.

Salonen, S., & Vuorio, K. (2000). Restoration of the eutrophicated Koeylojenajärvi (SW Finland) through fish removal: Whole-lake vs. mesocosm experiences. Boreal Environment Research, 5, 39–52.

Scharnweber, K., Chaguaceda, F., & Eklöv, P. (2021). Fatty acid accumulation in feeding types of a natural freshwater fish population. Oecologia, 196, 1–11. https://doi.org/10.1007/s00442-021-04913-y

Schatz, G. S., & McCauley, E. (2007). Foraging behavior by Daphnia in stoichiometric gradients of food quality. Oecologia, 153, 1021–1030. https://doi.org/10.1007/s00442-007-0793-0

Senar, O. E., Creed, I. F., Strandberg, U., & Arts, M. T. (2019). Browning reduces the availability—but not the transfer—of essential fatty acids in temperate lakes. Freshwater Biology, 64, 2107–2119.

Simopoulos, A. P. (2000). Human requirement for N-3 polysaturated fatty acids. Poultry Science, 79, 961–970. https://doi.org/10.1093/ps/79.7.961

Smyntek, P. M., Teece, M. A., Schulz, K. L., & Storch, A. J. (2008). Taxonomic differences in the essential fatty acid composition of groups of freshwater zooplankton relate to reproductive demands and generation time. Freshwater Biology, 53, 1768–1782. https://doi.org/10.1111/j.1365-2427.2008.02001.x

Stanley-Samuelson, D. W., Jurenka, R. A., Cripps, C., Blomquist, G. J., & de Renobales, M. (1988). Fatty acids in insects: Composition, metabolism, and biological significance. Archives of Insect Biochemistry and Physiology, 9, 1–33. https://doi.org/10.1002/arch.940090102

Stewart, C., Iverson, S., & Field, C. (2014). Testing for a change in diet using fatty acid signatures. Environmental and Ecological Statistics, 21, 775–792. https://doi.org/10.1007/s10651-014-0280-9

Strandberg, U., Palviainen, M., Eronen, A., Piirainen, S., Laurén, A., Akkanen, J., & Kankaala, P. (2016). Spatial variability of mercury and polysaturated fatty acids in the European perch (Perca fluviatilis) – Implications for risk-benefit analyses of fish consumption. Environmental Pollution, 219, 305–314. https://doi.org/10.1016/j.envpol.2016.10.050

Strandberg, U., Vesterinen, J., Ilo, T., Akkanen, J., Melanen, M., & Kankaala, P. (2020). Fatty acid metabolism and modifications in Chironomus riparius. Philosophical Transactions of the Royal Society B-Biological Sciences, B375, 20190643. https://doi.org/10.1098/rstb.2019.0643

Sukenik, A., Quesada, A., & Salmaso, N. (2015). Global expansion of toxic and non-toxic cyanobacteria: effect on ecosystem functioning. Biodiversity and Conservation, 24, 889–908. https://doi.org/10.1007/s10531-015-0905-9

Taipale, S. J., Galloway, A. W., Aalto, S. L., Kilhainen, K. K., Strandberg, U., & Kankaala, P. (2016). Terrestrial carbohydrates support freshwater zooplankton during phytoplankton deficiency. Scientific Reports, 6, 1–15. https://doi.org/10.1038/srep30897

Taipale, S. J., Hiltunen, M., Vuorio, K., & Peltomaa, E. (2016). Suitability of phytosterols alongside fatty acids as chemotaxonomic biomarkers for phytoplankton. Frontiers in Plant Science, 7, 212. https://doi.org/10.3389/fpls.2016.00212

Taipale, S. J., Kahilainen, K. K., Holtgrieve, G. W., & Peltomaa, E. T. (2018). Simulated eutrophication and browning alters zooplankton nutritional quality and determines juvenile fish growth and survival. Ecology and Evolution, 8, 2671–2687. https://doi.org/10.1002/ece3.3832

Taipale, S. J., Kainz, M. J., & Brett, M. T. (2011). Diet-switching experiments show rapid accumulation and preferential retention of highly unsaturated fatty acids in Daphnia. Oikos, 120, 1674–1682. https://doi.org/10.1111/j.1600-0706.2011.19415.x

Taipale, S. J., Strandberg, U., Peltomaa, E., Galloway, A. W., Ojala, A., & Brett, M. T. (2013). Fatty acid composition as biomarkers of fresh-water microalgae: Analysis of 37 strains of microalgae in 22 genera and in seven classes. Aquatic Microbial Ecology, 71, 165–178. https://doi.org/10.3354/ame01671

Taipale, S. J., Vuorio, K., Aalto, S. L., Peltomaa, E., & Tirola, M. (2019). Eutrophication reduces the nutritional value of phytoplankton in boreal lakes. Environmental Research, 179, 108836. https://doi.org/10.1016/j.envres.2019.108836

Taipale, S. J., Vuorio, K., Strandberg, U., Kahilainen, K. K., Järvinen, M., Hiltunen, M., Peltomaa, E., & Kankaala, P. (2016). Lake eutrophication and brownification downgrades availability and transfer of essential fatty acids for human consumption. Environment International, 96, 156–166. https://doi.org/10.1016/j.envint.2016.08.018

Tammi, J., Lappalainen, A., Mannio, J., Rask, M., & Vuorenmaa, J. (1999). Effects of eutrophication on fish and fisheries in Finnish lakes: a survey based on random sampling. Fisheries Management and Ecology, 6, 173–186. https://doi.org/10.1046/j.1365-2400.1999.00152.x

Tönns, I., Agasild, H., Köiv, T., Freiberg, R., Nõges, P., & Nõges, T. (2016). Algal diet of small-bodied crustacean zooplankton in a cyanobacteria-dominated eutrophic lake. PLoS One, 11(4), e0154526. https://doi.org/10.1371/journal.pone.0154526

Vesterinen, J., Keva, O., Kahilainen, K. K., Strandberg, U., Hiltunen, M., Kankaala, P., & Taipale, S. J. (2021). Nutritional quality of littoral macroinvertebrates and pelagic zooplankton in subarctic lakes. Limnology and Oceanography, 66, S81–S97.

Ventelä, A., Amsinck, S. L., Kauppila, T., Johansson, L. S., Jeppesen, E., Kirkkala, T., Søndergaard, M., Weckström, J., & Sarvala, J. (2016). Ecosystem change in the large and shallow Lake Säkylän Pyhäjärvi, Finland, during the past–400 years: Implications for management. Hydrobiologia, 778, 273–294.

Ventelä, A., Tarvainen, M., Helminen, H., & Sarvala, J. (2007). Long-term management of Pyhäjärvi (southwest Finland): eutrophication, restoration–recovery? Lake and Reservoir Management, 23, 428–438. https://doi.org/10.1080/07438140709354028

Vesterinen, J., & Sarvala, J. (2002). The effect of small zooplankton on the microbial loop and edible algae during a cyanobacterial bloom. Freshwater Biology, 47, 1807–1819. https://doi.org/10.1046/j.1365-2427.2002.00924.x

Vollenweider, R. A., Munawar, M., & Stadelmann, P. (1974). A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. Journal of the Fisheries Board of Canada, 31, 739–762. https://doi.org/10.1139/f74-100

Vuorio, K., Järvinen, M., & Kotamäki, N. (2020). Phosphorus thresholds for bloom-forming cyanobacterial taxa in boreal lakes. Hydrobiology, 847, 4389–4400. https://doi.org/10.1007/s10750-019-04161-5

Willén, E. (2003). Dominance patterns of planktonic algae in Swedish forest lakes. In L. Naselli-Flores, J. Padisák, & M. T. Dokuill (Eds.), Phytoplankton and equilibrium concept: The ecology of steady-state
assemblages. Developments in hydrobiology (Vol. 172, pp. 315–324). Springer. https://doi.org/10.1007/978-94-017-2666-5_25

Wirth, M., Steffens, W., Meinelt, T., & Steinberg, C. (1997). Significance of docosahexaenoic acid for rainbow trout (Oncorhynchus mykiss) larvae. Lipid/Fett, 99(7), 251–253.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.