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Lake eutrophication and brownification downgrade availability and transfer of essential fatty acids for human consumption

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ABSTRACT

Fish are an important source of eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) for birds, mammals and humans. In aquatic food webs, these highly unsaturated fatty acids (HUFA) are essential for many physiological processes and mainly synthetized by distinct phytoplankton taxa. Consumers at different trophic levels obtain essential fatty acids from their diet because they cannot produce these sufficiently *de novo*. Here, we evaluated how the increase in phosphorus concentration (eutrophication) or terrestrial organic matter inputs (brownification) change EPA and DHA content in the phytoplankton. Then, we evaluated whether these changes can be seen in the EPA and DHA content of piscivorous European perch (*Perca fluviatilis*), which is a widely distributed species and commonly consumed by humans. Data from 713 lakes showed statistically significant differences in the abundance of EPA- and DHA-synthesizing phytoplankton as well as in the concentrations and content of these essential fatty acids among oligo-mesotrophic, eutrophic and dystrophic lakes. The EPA and DHA content of phytoplankton biomass (mg HUFA g^{-1}) was significantly lower in the eutrophic lakes than in the oligo-mesotrophic or dystrophic lakes. We found a strong significant correlation between the DHA content in the muscle of piscivorous perch and phytoplankton DHA content ($r = 0.85$) as well with the contribution of DHA-synthesizing phytoplankton taxa ($r = 0.83$). Among all DHA-synthesizing phytoplankton this correlation was the strongest with the dinoflagellates ($r = 0.74$) and chrysophytes ($r = 0.70$). Accordingly, the EPA + DHA content of perch muscle decreased with increasing total phosphorus ($r^2 = 0.80$) and dissolved organic carbon concentration ($r^2 = 0.83$) in the lakes. Our results suggest that although eutrophication generally increase biomass production across different trophic levels, the high proportion of low-quality primary producers reduce EPA and DHA content in the food web up to predatory fish. Ultimately, it seems that lake eutrophication and brownification decrease the nutritional quality of fish for human consumers.

1. Introduction

Freshwater and marine food webs are predominantly fueled by primary production of phytoplankton originating from a great diversity of different phylogenetic backgrounds (Thornton, 2012). In large and deep lakes as well as in marine systems, phytoplankton are the principal primary producers, whereas small and shallow lake ecosystems may also be reliant on littoral algal production (e.g. Reynolds, 2006; Karlsson and Byström, 2005; Lau et al., 2012; Vesterinen et al., 2016).

In addition to the basic photosynthetic process, i.e. conversion of energy from solar radiation to chemical energy supporting all higher trophic levels, phytoplankton also synthesize many essential biomolecules, such as fatty acids (FA), sterols and amino acids (Ahlgren et al., 1992; Volkman, 2003; Arts et al., 2009; Taipale et al., 2013). Consumers cannot produce many of these biomolecules *de novo* or convert them from other molecules (Vance and Vance, 2008). Therefore, most multicellular i.e. invertebrates and vertebrates rely on primary producers to obtain e.g. essential 'omega-3' (ω-3) and 'omega-6' (ω-6) polyunsaturated fatty acids (PUFA). The ω-3 and ω-6 FA cannot be interconverted from each other and thus both need to be obtained from the diet (Vance and Vance, 2008). Previous studies (Ravet and Brett, 2006) have shown that EPA (20:5ω-3) might be the most important essential fatty acid supporting somatic growth and reproduction of cladoceran zooplankton,

whereas DHA (22:6ω-3) appeared to be the most important for copepods and fish (Jonasdottir, 1994; Sargent et al., 1999). Cladoceran zooplankton have a very limited ability to convert C_{18} ω-3 (ALA; 18:3ω-3 or SDA; 18:4ω-3) FA to EPA (Von Elert, 2002; Taipale et al., 2011) and, thus they rely strongly on seston PUFA (Taipale et al., 2011). Calanoid copepods (e.g. *Eudiaptomus*) have a better ability to convert C_{18} ω-3 FA to EPA or DHA (Von Elert and Stampfl, 2000; Koussoroplis et al., 2014). However, this conversion has high energetic costs and, thus resource upgrading is minimal from zooplankton to fish. Therefore, fish need to obtain EPA and DHA from the diet or use energy for converting DHA from ALA. In aquaculture experiments juvenile and adult perch has been shown to be able to elongate and desaturate ALA into DHA when the diet did not contain any EPA or DHA (Henrotte et al., 2011).

For humans the uptake of ω-3 fatty acids, specifically EPA and DHA, from seafood and freshwater fish is very important for nutrition (Mozaffarian and Rimm, 2006). The precursor, α-linolenic acid (ALA, 18:3ω3), can be obtained from vegetable oils (e.g. olive oil, canola oil) and dairy products, but the bioconversion rate from ALA to EPA and DHA is inefficient in human body (conversion percentage 0.04–2.84%, Russell and Burgin-Maunder, 2012). EPA and arachidonic acid (ARA) are precursors of eicosanoids, which regulate the inflammatory and anti-inflammatory balance in humans (Simopoulos, 2002). The ω-3 and ω-6 PUFA can affect a wide range of physiological conditions (e.g. blood viscosity) and the incidence of a wide variety of diseases (e.g. cardiovascular diseases, diabetes, various cancers, kidney disease, Alzheimer's disease) (Pelliccia et al., 2013).

The content of EPA and DHA is very low or non-existent in terrestrial, e.g. plants, compared to aquatic primary producers e.g. algae (Hixson et al., 2015), and therefore algae are important sources of these highly unsaturated fatty acids (HUFA), not only for aquatic organisms, but also for many birds and mammals. In this way, algae are an essential link between the nutritional ecology of terrestrial and freshwater ecosystems. Biosynthesis of various PUFA by phytoplankton is influenced more by phylogeny-based traits than growth conditions (Taipale et al., 2013; Galloway and Winder, 2015), therefore, the nutritional quality of phytoplankton to zooplankton is highly variable and taxon dependent (Brett and Müller-Navarra, 1997; Brett et al., 2009a, 2009b). Diatoms (Bacillariophyceae), chrysophytes (Chrysophyceae), synurophytes (Synurophyceae), cryptophytes (Cryptophyceae), dinoflagellates (Dinophyceae) and raphidophytes (Raphidophyceae) can synthesize EPA and DHA, whereas green algae (Chlorophyceae, including Trebouxiophyceae and Conjugatophyceae) or cyanobacteria (Cyanophyceae) cannot produce these HUFA (Ahlgren et al., 1992; Guedes et al., 2011; Strandberg et al., 2015a).

Phytoplankton community structure is strongly influenced by the physical and chemical environment, in particular macro- and micronutrient availability, acidity/alkalinity, as well as the light and temperature conditions of lakes (Reynolds, 2006; Maileht et al., 2013), which all respond to environmental forcing, including anthropogenic pressures. Eutrophication due to excessive nutrient loading, especially phosphorus (P), from point and diffuse sources (industry, municipalities, water sewage treatment plants, agriculture and various other land use practices) is known to cause nuisance blooms of cyanobacteria in lakes (Schindler, 2012). Global warming and intensified stratification of lake waters may amplify the effect of nutrient loading in lakes (Kernan et al., 2010; Jeppesen et al., 2012; Anneville et al., 2015). In addition, brownification of surface waters has been observed in temperate and boreal regions of North America as well as Northern and Central Europe (e.g. Monteith et al., 2007; Couture et al., 2012; Räike et al., 2016). This phenomenon is caused by increased concentrations of colored terrestrial dissolved organic carbon (DOC), coupled with iron interactions (Weyhenmeyer et al., 2014), and it can profoundly impact the physical and chemical environment that phytoplankton encounter (Thrane et al., 2014; Seekell et al., 2015). Darker water color has been shown to favor cryptophytes and raphidophytes over cyanobacteria (e.g. Lepistö et al., 1994; Weyhenmeyer et al., 2004).

A previous study of Müller-Navarra et al. (2004) demonstrated that high total P concentration decreases the content of EPA and DHA in seston due to a proportional increase of cyanobacteria. Persson et al. (2007) added some clear-water lakes to the Müller-Navarra et al. (2004) data set, and reported a unimodal relationship between total phosphorus and EPA, thus, the highest EPA content were found in mesotrophic lakes. Both studies predicted that the growth and reproduction of cladoceran zooplankton would decrease with lake phosphorus concentration, but they did not measure the actual ω-3 or EPA content of zooplankton and/or higher food-web levels in eutrophic lakes (but see Ahlgren et al., 1996; Razavi et al., 2014). In addition, the effects of brownification on the essential fatty acid content of lake food webs from phytoplankton to piscivorous fish are poorly documented.

European perch is a widely distributed and abundant fish in European lakes (Nesbo et al., 1999; Heibo et al., 2005). The perch is an omnivorous fish, generally having an ontogenetic dietary shift from zooplankton prey to benthic macroinvertebrates and finally to fish (Haakana et al., 2007; Estlander et al., 2010). An ontogenetic dietary shift to piscivory at a total length of 15–20 cm is especially frequent in large lakes with diverse fish fauna, where perch may opportunistically use a range of prey fish depending on their relative availability (Haakana et al., 2007; Hayden et al., 2014; Svanbäck et al., 2015). Large sized (>20 cm) perch are a common target of recreational and commercial inland fisheries in Europe due to their high value for human nutrition. In addition, there is an increasing interest also to develop aquaculture practices to increase the supply of large-sized perch for human consumption (Xu and Kestemont, 2002; Xu et al., 2001).

The increase in concentrations of nutrients, especially phosphorus (eutrophication), and DOC (brownification) are important factors changing the phytoplankton community structure of the lakes (Schindler, 2012; Maileht et al., 2013). We hypothesized that 1) the content of the essential fatty acids EPA and DHA in piscivorous perch is related to the abundance of EPA and DHA synthetizing algal taxa in lake phytoplankton communities, 2) lake eutrophication and brownification enhance the biomass growth of the non-EPA and non-DHA synthesizing phytoplankton taxa and 3) these changes affect the EPA and DHA content of piscivorous perch. We analyzed a large dataset of phytoplankton community composition from 713 boreal and subarctic lakes that were grouped into three lake type categories: oligo-mesotrophic (<35 μg P L^{-1}), eutrophic (>35 μg P L^{-1}) and dystrophic lakes (DOC > 15 mg C L^{-1}) and estimated the concentration and content of EPA and DHA of phytoplankton-origin in these lakes, based on phytoplankton monocultures. Finally, we analyzed the EPA and DHA content of European perch from 14 lakes including oligotrophic, eutrophic and dystrophic lakes. Our ultimate goal was to elucidate whether eutrophication or brownification of lakes impact the transfer of the essential fatty acids from algae to piscivorous fish and finally to human consumers.

2. Methods

2.1. Phytoplankton culturing

To study the diversity of ω-3 PUFAs and the ability of distinct freshwater phytoplankton taxa to synthesize EPA and DHA, we cultured and analyzed the ω-3 PUFA (18 ω-3, EPA and DHA) contents of 39 freshwater phytoplankton strains belonging to ten phytoplankton classes (Table 1). Phytoplankton strains were cultured at 18–20 °C under a 14 h:10 h or 16 h:8 h light:dark cycle with light intensity of 30–80 μmol m^{-2} s^{-1}. 1. Each strain was cultured in a medium specific to that strain (Table 1). Additionally, the diatom *Tabellaria* was cultured in two different media (Chu10 and Z8) and the euglenoid *Euglena gracilis* in a medium with organic substrates (EG) and without organic substrates (AF6, Table 1). Depending on the cell density, 0.5–3 ml of each culture was transferred into 100 ml of fresh media. Samples for fatty acid analyses were harvested by centrifuging (2000 rpm for 12 min) in the late phase of

Table 1
Class, order, species and the strain code information of the studied freshwater phytoplankton. Different media and light cycle, i.e. the light:dark period (h), light intensity (μmol m^{-2} s^{-1}) and temperature (°C) were used for different strains. Strains 14, 16 and 29 were not cultured, but collected from lakes during bloom conditions.

Class (groups)	Order	Species	Strain number	Strain	Medium	Light cycle	Light intensity	Temperature
Cyanophyceae (cyanobacteria)	Chroococcales	*Aphanothece* cf. *clathrata*	1	NIVA-CYA 369	MWC[a]	14:10	50	20
	Chroococcales	*Microcystis* sp.	2	NIVA-CYA 642	MWC[a]	14:10	50	20
	Chroococcales	*Snowella lacustris*	3	NIVA-CYA 339	MWC[a]	14:10	50	20
	Synechococcales	*Synechococcus elongatus*	4	UTEX LB 563	MWC[a]	14:10	50	20
	Nostocales	*Anabaena flos-aquae*	5	NIVA 138	MWC[a]	14:10	50	20
	Oscillatoriales	*Phormidium tenue*	6	NIVA-CYA 25	MWC[a]	14:10	50	20
	Oscillatoriales	*Planktothrix rubescens*	7	SCCAP K-576	MWC[a]	14:10	50	20
	Pseudanabaenales	*Limnothrix planktonica*	8	NIVA-CYA 107	MWC[a]	14:10	50	20
	Pseudanabaenales	*Pseudanabaena limnetica*	9	NIVA 276/11	MWC[a]	14:10	50	20
	Pseudanabaenales	*Pseudanabaena* sp.	10	SCCAP K-1230	MWC[a]	14:10	50	20
Cryptophyceae (cryptophytes)	Cryptomonadales	*Cryptomonas marssonii*	11	CCAP 979/70	DY-V[b]	16:8	30	20
	Cryptomonadales	*Cryptomonas ovata*	12	SCCAP K-1876	AF6[c]	16:8	30	20
	Pyrenomonadales	*Rhodomonas minuta*	13	CPCC[g] 344	L16[d]	14:10	30	18
Dinophyceae	Gonyaulacales	*Ceratium* sp.	14	Lake Köyhälampi	Lake Köyhälampi	–	–	15
(dinoflagellates)	Peridiniales	*Peridinium cinctum*	15	SCCAP K-1721	MWC[a]	14:10	70	20
Chrysophyceae (incl. Synurophyceae)	Synurales	*Mallomonas caudata*	16	Lake Horkkajärvi	Lake Horkkajärvi	–	–	20
(golden algae)	Synurales	*Synura* sp.	17	SCCAP K-1875	MWC[a]	16:8	30	20
Raphidophyceae	Chattonellales	*Gonyostomum semen*	18	LI21	MWC[a]	16:8	80	20
Diatomophyceae (diatoms)	Tabellariales	*Tabellaria* sp.	19	CCAP 1081/7	Chu 10[e]	14:10	40	18
	Tabellariales	*Tabellaria* sp.	20	CCAP 1081/7	Z8[f]	14:10	40	18
	Aulacoseirales	*Aulacoseira (Melosira) granulata*	21	CPCC 397	Chu 10[e]	14:10	40	18
	Thalassiosirales	*Cyclotella meneghiniana*	22	CCAC 0039	MWC[a]	14:10	40	18
	Fragilariales	*Asterionella formosa*	23	NIVA-BAC-3	MWC[a]	14:10	40	18
	Fragilariales	*Fragilaria crotonensis*	24	UTEX LB FD56	MWC[a]	14:10	40	18
	Fragilariales	*Diatoma tenuis*	25	CPCC 62	Chu 10[e]	14:10	40	18
	Fragilariales	*Synedra rumpens* var. *familiaris*	26	NIVA-BAC 18	MWC[1]	14:10	40	18
Euglenophyceae (euglenoids)	Euglenales	*Euglena gracilis*	27	CCAP[c] 1224/5Z	AF6[c]	16:8	40	20
	Euglenales	*Euglena gracilis*	28	CCAP[c] 1224/5Z	EG[g]	16:8	40	20
Chlorophyceae (green algae)	Chlamydomonadales	*Sphaerocystis* sp.	29	Lake Majajärvi	Lake Majajärvi			20
	Chlamydomonadales	*Eudorina* sp.	30	K-1771	MWC[a]	14:10	70	20
	Chlamydomonadales	*Chlamydomonas reindhardtii*	31	UWCC	MWC[a]	14:10	70	20
	Sphaeropleales	*Monoraphidium griffithii*	32	NIVA-CHL 8	MWC[a]	14:10	70	20
	Sphaeropleales	*Pediastrum* sp.	33	SCCAP K-1033	MWC[a]	14:10	70	20
	Sphaeropleales	*Acutodesmus* sp.	34	University of Basel	MWC[a]	14:10	70	20
	Sphaeropleales	*Selenastrum* sp.	35	SCCAP K-1877	MWC[a]	16:8	70	20
Trebouxiophyceae	Prasiolales	*Botryococcus* sp.	36	SCCAP K-1033	MWC[a]	14:10	70	20
Conjugatophyceae	Desmidiales	*Closterium* sp.	37	CPCC 288	Z8[f]	14:10	50	18
	Desmidiales	*Cosmarium reniforme*	38	SCCAP K-1145	MWC[a]	14:10	50	18
	Desmidiales	*Staurastrum* sp.	39	SCCAP K-1349	MWC[a]	14:10	50	18

[a] Guillard and Lorenzen, 1972; Guillard, 1975.
[b] Andersen et al., 1997.
[c] Watanabe et al., 2000.
[d] Lindström, 1983.
[e] Chu, 1942.
[f] Staub, 1961; Kótai, 1972.
[g] UTEX.

exponential growth, i.e., 2–3 weeks after the inoculation. Fatty acids of cultured phytoplankton were analyzed using a previously published protocol (Taipale et al., 2013).

The cultured strains represent the most abundant taxa across boreal and temperate zone, including e.g. Northern and Central Europe (Maileht et al., 2013). These taxa form on average 74% of the total phytoplankton biomass in the long term monitoring data collected from Finnish lakes (phytoplankton database of Finnish Environment Institute). For genera which we were not able to culture we used the average fatty acid values of the class, since fatty acids profiles are similar within the class (Strandberg et al., 2015a; Galloway and Winder, 2015).

2.2. Phytoplankton derived ω-3, EPA and DHA in different lake types

Carbon content of phytoplankton was analyzed with a Carlo-Erba Flash 1112 series element analyzer (Carlo-Erba, Milan, Italy). We used content (μg mg C^{-1}) of Σω-3, EPA and DHA of each cultured phytoplankton strain to calculate phytoplankton-derived average concentrations (μg FA L^{-1}) of these PUFA in three different lake types based on phytoplankton carbon biomass (μg C L^{-1}) obtained with quantitative microscopic counts (Wetzel and Likens, 2000). Furthermore, the content (μg FA mg C^{-1}) of each PUFA/HUFA category in one lake was based on cumulative sum of each phytoplankton genus (Table 2):

$$\sum_{i=a}^{n} f(i) = \frac{PUFA_a * CBM_a}{TCBM} + \frac{PUFA_b * CBM_b}{TCBM} + \dots + \frac{PUFA_n * CBM_n}{TCBM},$$

where *PUFA* denotes the content of PUFA (μg ω-3, EPA or DHA in mg C) and *CBM* the carbon biomass (μg C L^{-1}) of each phytoplankton genus ($a, b, \dots, n$) (see Table 1), and *TCBM* denotes the total carbon biomass (μg C L^{-1}) of the corresponding lake sample. If the PUFA content for a specific genus was not obtained by culturing, to calculate the PUFA content of

Table 2
Physico-chemical parameters with mean and range in parenthesis: number (No) of lakes and samples, lake area, maximum depth, total phosphorus (TP), dissolved organic carbon (DOC), chlorophyll a (Chla) content, phytoplankton biomass and water temperature, in the three lake types.

Lake type	No. of lakes	No. of samples	Lake area (km^2)	Maximum depth (m)	TP (µg L^{-1})	DOC (mg L^{-1})	Chla (µg L^{-1})	Phytoplankton biomass (mg C L^{-1})	Temperature (°C)
Oligo-mesotrophic	570	2102	75 (0.3–1377)	19 (1–93)	14 (3–34)	8 (4–15)	9 (1–60)	0.16 (0.01–2.70)	19 (7–26)
Eutrophic	90	346	31 (0.4–261)	6 (1–67)	69 (36–180)	10 (6–15)	42 (9–110)	1.08 (0.15–5.01)	20 (11–26)
Dystrophic	53	99	20 (0.4–85)	12 (1–41)	20 (6–33)	18 (16–31)	13 (1–42)	0.21 (0.02–1.12)	19 (7–27)

the remaining genera, the average content of each PUFA at phytoplankton class were used instead.

In order to evaluate differences in phytoplankton composition and ω-3 PUFA synthesized in different type of lakes, we used 2547 phytoplankton community composition samples from 713 lakes with variable total phosphorus (TP, 3–180 µg L^{-1}) and dissolved organic carbon (DOC, 4–31 mg C L^{-1}) concentration (phytoplankton and water quality databases of the Finnish Environment Institute). The data represent summer period (July–August) in lakes from southern to northern Finland (Table 2). The lakes were sampled at 0–2 m or 0–4 m depth from 2000 to 2015. Data consisted only of lakes larger than 30 ha with maximum depth ≥ 2 m. Lakes were classified into three groups according to their TP and DOC concentration representing oligo-mesotrophic (TP < 35 µg P L^{-1}, DOC <15 mg C L^{-1}), eutrophic (TP ≥ 35 µg P L^{-1}, DOC < 15 mg C L^{-1}) and dystrophic lakes (TP < 35 µg P L^{-1}, DOC ≥ 15 mg C L^{-1}) (Vollenweider, 1968). Lakes with both high concentration of TP and DOC (TP ≥ 35 µg P L^{-1} and DOC > 15 mg C L^{-1}) were excluded from the data as well as the lakes which did not belong to the same nutrient or DOC category throughout the study period to evaluate eutrophication and brownification impact separately. Since there were only few actual DOC measurements, DOC concentrations were calculated using the equation based on the relationship between water color (Hazen units) and DOC = 0.0872 ∗ color + 3.55 (Kortelainen, 1993). Differences in phytoplankton composition as well as the concentration and content of phytoplankton Σ ω-3 PUFA, EPA and DHA among the three lakes types were analyzed using one-way ANOVA and pairwise comparison with Tukey's HSD test.

2.3. Sampling of perch

Among the 713 lakes involved in the phytoplankton study (Table 2), 14 lakes representing the three lake types (oligo-mesotrophic, eutrophic and dystrophic) were sampled in 2013 for European perch with a total length range of 230–365 mm (Table 3). These large sized perch are typically piscivorous and 6–12 years old (Heibo et al., 2005; Svanbäck et al., 2015). The average total length of the prey fish of large perch is generally <10 cm (range 2–15 cm) (Amundsen et al.,

2003, Hayden et al., 2014). Prey species usually consist of small perch, ruffe (*Gymnocephalus cernuus*), bleak (*Alburnus alburnus*), vendace (*Coregonus albula*) and smelt (*Osmerus eperlanus*) (Haakana et al., 2007, Kahilainen, unpublished) that are all, except ruffe, zooplanktivorous at total length <10 cm. Lipids were extracted from perch dorsal muscle tissue (fillet) using previously published methods and fatty acid methyl esters were run with a GC-MS (Shimadzu) (Taipale et al., 2013). The EPA, DHA and total ω-3 content of perch muscle tissue was analyzed from either fresh or freeze-dried (−70 °C, 48 h) samples. The results are presented as mg FA g^{-1} (wet weight) in perch muscle. For freeze–dried samples the ratio of dry weight to wet weight (0.2) was used for conversion (Ahlgren et al., 1996).

The comparison of EPA and DHA in perch muscle between different lake types were tested with ANOVA and pairwise comparison with Tukey's HSD test. The relationship between EPA and DHA content of dorsal muscle of perch were analyzed against phytoplankton ω-3, EPA and DHA content and proportion of phytoplankton groups within community as well as total phosphorus (TP) and dissolved organic carbon (DOC) concentration of the lakes was analyzed with linear regression analysis. For the analysis, cyanobacteria, green algae and desmids were classified as non-EPA and non-DHA synthetizing phytoplankton. Accordingly, cryptophytes, dinoflagellates, chrysophytes (incl. synurophytes), diatoms, raphidophytes and euglenoids were classified as EPA synthetizing phytoplankton, and cryptophytes, dinoflagellates, chrysophytes and euglenoids as DHA-synthetizing phytoplankton. The ω-3, EPA and DHA content of phytoplankton in the specific lakes during the period 2000–2013 (June to August), covering the life-time of perch, were used in analyses (n = 2–10 per lake, except Lake Vaattojärvi n = 1). Statistical analyses were conducted with IBM SPSS Statistics 20 (IBM Corp., Armonk, NY, USA). For a significant relationship, we used a p-value of <0.05.

3. Results

3.1. Content of ω-3 PUFA by freshwater phytoplankton

A detailed screening of ω-3 PUFA content in 39 freshwater phytoplankton taxa, from ten phylogenetically different groups, showed

Table 3
Location (latitude, Lat and longitude, Long), mean (minimum-maximum) values of morphometric, physical and chemical characteristics, maximum depth (Zmax), mean depth (Zmean), chlorophyll a (Chla), total phosphorus (TP), total nitrogen (TN) and dissolved organic carbon concentration (DOC) of the lakes (Jun–Aug 2000–2013, n > 5), from which perch were sampled, and range of total length (TL), wet weight, and number of sampled fish (n). Lakes Karjalan Pyhäjärvi, Kermajärvi, Kuorinka, Ylinen and Ätäskö are oligo-mesotrophic lakes, Aalisjärvi, Pasmajärvi, Rattosjärvi and Vaattojärvi are eutrophic lakes, and Harkkojärvi, Hattujärvi, Koitere, Mekrijärvi and Nuorajärvi are dystrophic lakes.

Lake	Lat (°N)	Long (°E)	Area (km^2)	Zmax (m)	Zmean (m)	Chla (µg L^{-1})	TP (µg P L^{-1})	TN (µg N L^{-1})	DOC (mg C L^{-1})	TL (mm)	Weight (g)	n
Ätäskö	62.05	29.98	14	8.0	3.5	15 (4.3–27)	27 (19–41)	660 (350–940)	11 (7.9–21)	246–365	186–686	10
Harkkojärvi	62.96	31.04	4.4	10	3.5	11 (9.4–12)	21 (17–23)	427 (400–440)	18 (18–19)	245–365	155–641	6
Hattujärvi	62.98	31.18	5.1	9.0	3.3	6.7 (3.4–16)	21 (16–30)	389 (340–410)	16 (15–19)	237–334	155–471	5
Karjalan Pyhäjärvi	61.8	29.88	248	27	8.0	3.1 (1.0–8.6)	5.9 (3.0–14)	241 (190–540)	4.7 (4.0–5.7)	255–322	200–460	9
Ylinen	62.6	30.22	3.7	35	12	2.8 (2.7–2.9)	4.0 (3.0–5.0)	380 (360–400)	6.4 (6.2–6.6)	232–310	165–385	5
Kermajärvi	62.43	28.72	86	56	10.1	4.4 (2.5–6.7)	6.7 (4.0–12)	393 (290–470)	5.7 (4.9–6.6)	267–363	239–643	6
Koitere	63.05	30.85	164	46	6.7	5.8 (1.0–19)5	10 (6.0–17)	319 (260–430)	11 (8.8–19)	265–343	199–402	10
Kuorinka	62.62	29.42	13	32	10.5	1.2 (1.0–2.1)	2.9 (1.5–7.0)	183 (160–210)	3.9 (3.6–4.4)	266–332	232–399	9
Mekrijärvi	62.77	30.97	8.2	3.0	1.8	15 (12–17)	25 (22–26)	650 (600–670)	22 (19–24)	243–323	157–369	10
Nuorajärvi	62.68	31.12	40	12	3.3	8.4 (4.2–13)	21 (17–26)	414 (360–540)	19 (12–35)	264–287	189–277	9
Vaattojärvi	67.2	24.14	2.3	4.5	1.8	7.6 (2.3–14)	30 (27–32)	502 (410–560)	16 (13–21)	235–288	174–296	5
Rattosjärvi	66.85	24.88	4.1	6.8	2.1	22 (13−31)	38 (22–51)	540 (360–740)	12 (11–13)	230–262	156–222	5
Pasmajärvi	67.11	24.37	8.4	4.1	1.6	24 (15–59)	39 (31–52)	743 (550–1100)	12 (9.2–16)	232–288	156–323	5
Aalisjärvi	67.00	24.55	6.0	6.0	3.2	13 (12–14)	35.5 (35–36)	425 (370–480)	13.6 (13.1–14)	244–303	177–387	5

great variation in the contribution and content of ω-3 PUFA with different carbon chain lengths (Fig. 1). Cyanobacteria (excluding the genera *Aphanothece* and *Synechococcus*), green algae and desmids were rich in C_{18} ω-3 PUFA, but all these did not contain C_{20} or C_{22} ω-3 HUFA, e.g. EPA or DHA. In green algae and desmids C_{16} ω-3 PUFA contributed $9 \pm 5\%$ of all FA. Cyanobacteria had the lowest content of all ω-3 PUFA (14 ± 9 μg FA mg C^{-1}). The contribution of ω-3 PUFA of total FA was the lowest in diatoms whose major FA was 16:1ω7. EPA was the major ω-3 PUFA in diatoms and contributed $16 \pm 12\%$ of total FA. The highest contribution of ω-3 PUFA among phytoplankton classes was found in cryptophytes, dinoflagellates, and chrysophytes (incl. synurophytes). We found the highest content of EPA in the raphidophyte *Gonyostomum semen* (28 ± 1 μg FA mg C^{-1}), cryptophytes (23 ± 11 μg FA mg C^{-1}), diatoms (20 ± 15 μg FA mg C^{-1}), and dinoflagellates (14 ± 13 μg FA mgC^{-1}). In euglenoids the EPA content was <1 μg FA mg C^{-1}. The highest DHA contents were observed in dinoflagellates (27 ± 10 μg FA mg C^{-1}), cryptophytes (10 ± 4 μg FA mg C^{-1}) and chrysophytes (7 ± 2 μg FA mg C^{-1}). Additionally, low DHA contents were found in euglenoids (3 ± 1 μg DHA mg C^{-1}), and in raphidophytes and diatoms (<1 μg DHA mg C^{-1} in both).

3.2. Phytoplankton composition and phytoplankton-derived ω-3 PUFA in different lake types

Phytoplankton composition differed among the three lake types (Fig. 2). Diatoms and chrysophytes were the most abundant phytoplankton classes in oligo-mesotrophic lakes. Their proportions were $23 \pm 24\%$ and $22 \pm 10\%$ of the total phytoplankton biomass, respectively. Cyanobacteria were the major phytoplankton class in eutrophic lakes, alone constituting $41 \pm 27\%$ of the phytoplankton biomass. In oligo-mesotrophic and dystrophic lakes the proportion of cyanobacteria was only $13 \pm 12\%$ and $5 \pm 9\%$ of the phytoplankton biomass, respectively. Raphidophytes and diatoms were the two major phytoplankton classes in dystrophic lakes constituting $36 \pm 29\%$ and $21 \pm 21\%$ of the biomass, respectively. In eutrophic lakes the total phytoplankton biomass was ca. 6-fold higher than in oligo-mesotrophic and dystrophic lakes (Fig. 2).
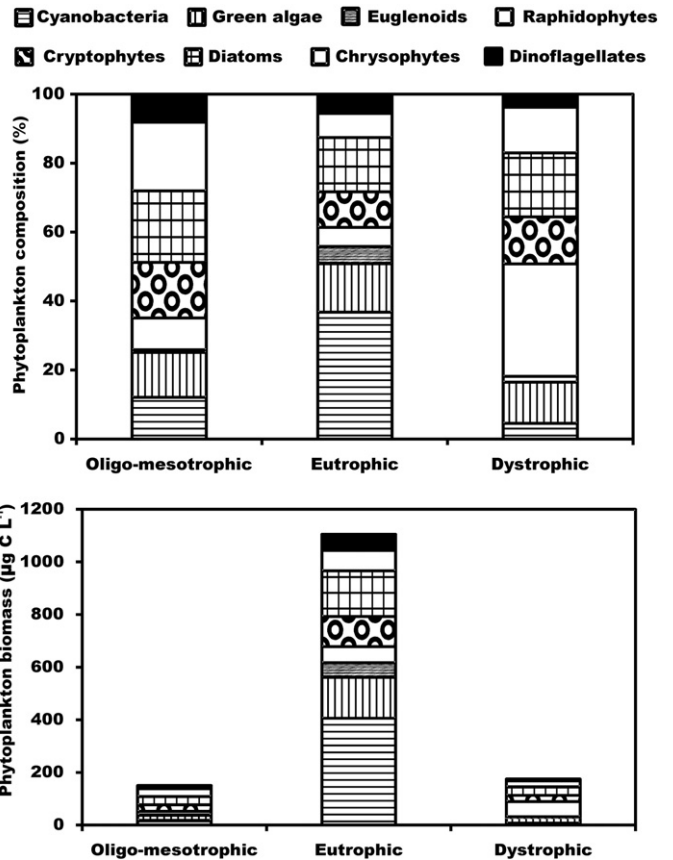
Fig. 2. Phytoplankton community structure (%) and biomass (μg C L^{-1}) of major phytoplankton classes in oligo-mesotrophic, eutrophic and dystrophic lakes.

The proportion of phytoplankton not containing EPA and/or DHA (cyanobacteria, green algae and desmids) of the total phytoplankton biomass was significantly higher (ANOVA, $F_{2,710} = 104.9$, p < 0.001) in
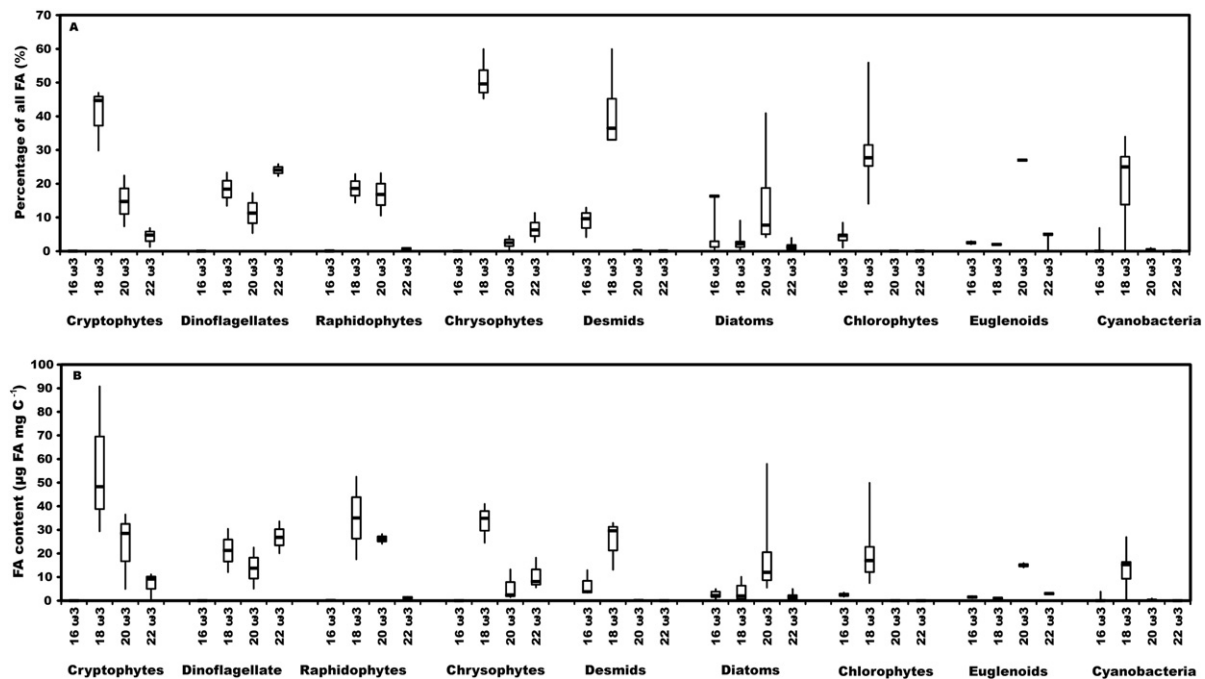
Fig. 1. Polyunsaturated fatty acid composition (%) and content (μg FA mg C^{-1}) of 16, 18, 20 and 22 ω-3 PUFA in the major phytoplankton groups in cultures. The box plots represent medians with 25 and 75 percentiles and the bars minimum and maximum values.

eutrophic lakes than in oligo-mesotrophic or dystrophic lakes (Fig. 3). The concentration of Σ ω-3 PUFA on volumetric basis (µg FA L^{-1}) was significantly higher in the eutrophic lakes than in the oligo-mesotrophic or dystrophic lakes (ANOVA, $F_{2,710} = 272.7$, p < 0.001, Fig. 3) whereas ω-3 PUFA content of the phytoplankton biomass (µg FA mg C^{-1}) was the highest in dystrophic lakes (ANOVA, $F_{2,710} = 19.5$, p < 0.01, Fig. 3).

Even though the EPA concentration was the highest in eutrophic lakes (ANOVA, $F_{2,710} = 85.1$, p < 0.001, Fig. 3), the contribution of EPA-synthesizing phytoplankton of all phytoplankton (cryptophytes, chrysophytes, diatoms, dinoflagellates, raphidophytes; ANOVA, $F_{2,710} = 66.9$, p < 0.001) and the content of EPA (ANOVA, $F_{2,710} = 30.1$, p < 0.001) were lower in the eutrophic lakes than in the oligo-mesotrophic lakes. Similarly, the concentration of DHA was higher in eutrophic lakes than in the dystrophic or oligo-mesotrophic lakes (ANOVA, $F_{2,710} = 173.7$, p < 0.001), but the contribution of DHA-synthesizing phytoplankton (ANOVA, $F_{2,710} = 37.3$, p < 0.001) and the content of DHA (ANOVA, $F_{2,710} = 21.7$, p < 0.001) was higher in oligo-mesotrophic lakes than in eutrophic or dystrophic lakes.

3.3. Variation of EPA and DHA in perch muscle

In perch muscle 41 ± 3% of all FA consisted of ω-3 PUFA. DHA was the most abundant ω-3 FA (34 ± 3% of all FA), whereas the proportion of EPA and C$_{18}$ ω-3 PUFA was lower (7 ± 1% and 1 ± 0.3% of all FA, respectively). The average content (± SD) of EPA and DHA in perch muscle was 0.28 ± 0.08 mg g^{-1} and 1.46 ± 0.40 mg g^{-1}, respectively. The DHA content of perch muscle was strongly related to the proportion of DHA synthesizing phytoplankton (dinoflagellates, cryptophytes, chrysophytes, euglenoids) in phytoplankton biomass (R^2 = 0.69) or phytoplankton DHA content (R^2 = 0.73) during the approximate growth period of perch (from the year 2000 to 2013) in the lakes (Fig. 4 AB). The residuals of the latter regression equation did not correlate with 18 ω-3 PUFA content of phytoplankton (r = 0.22, p = 0.46). Among the DHA containing phytoplankton classes, the relationship was strongest with dinoflagellates and chrysophytes (Pearson correlation: r = 0.74 and r = 0.70, respectively, p < 0.01 in both). The DHA content in predatory perch muscle was generally 2–3 times higher compared with that in the phytoplankton biomass.

EPA in perch muscle did not correlate significantly with the sum contribution of all EPA-synthesizing groups (cryptophytes, dinoflagellates, raphidophytes, chrysophytes and diatoms; r = 0.27, p > 0.05) or with the EPA content of any phytoplankton group. The percentage of cyanobacteria and generally non-EPA and non-DHA containing phytoplankton groups (cyanobacteria, green algae) of the total phytoplankton correlated negatively with the content of EPA or DHA in perch muscle (r = −0.76 to −0.82, p < 0.01).

The content of EPA + DHA in perch muscle (mg g^{-1}) had a strong negative relationship with the concentration of total phosphorus (µg L^{-1}) in the lakes (Fig. 4C). Along with increasing DOC concentration the EPA + DHA content in perch muscle also decreased; DOC explained a large part of the variation (83%), when the eutrophic lakes were removed from perch data (Fig. 4D).

3.4. Availability of EPA and DHA in perch from different types of lakes for human consumption

In predatory perch muscle the EPA + DHA content (mean ± SD mg g^{-1}) differed significantly among oligo-mesotrophic, eutrophic and dystrophic lakes (ANOVA $F_{2, 11} = 63.7$, p < 0.01) being the highest in oligo-mesotrophic lakes (2.2 ± 0.2 mg EPA + DHA g^{-1}), but also clearly higher in dystrophic lakes (1.7 ± 0.1 mg EPA + DHA g^{-1}) than in eutrophic lakes (1.2 ± 0.1 mg EPA + DHA g^{-1}). All lake types differed significantly from each other (Tukey's HSD tests, p < 0.05). A schematic illustration of 18 ω-3 (ALA + SDA), EPA and DHA content in phytoplankton and perch (mg g^{-1}) and the potential transfer routes of these essential fatty acids in oligo-mesotrophic, eutrophic and dystrophic lakes are presented in the Fig. 5. A daily intake of 250–500 mg EPA and DHA has been recommended to lower the risk of mortality due to coronary heart disease (CHD) (Mozaffarian and Rimm, 2006, Kris-Etherton et al., 2009). Based on our results, the required human daily dose of EPA and DHA of 250 mg would mean consumption of 112 g perch fillet from oligo-mesotrophic lake, or 145 g of perch fillet from dystrophic lake, in contrast to 217 g of perch fillet from eutrophic lake.

4. Discussion

In freshwater and marine systems the physiologically important ω-3 PUFA, EPA and DHA, are mainly synthesized by phytoplankton. Our analysis of ten major freshwater phytoplankton groups showed that EPA and DHA are primarily synthesized (>1 µg FA mg C^{-1}) by only five (cryptophytes, dinoflagellates, raphidophytes, chrysophytes and diatoms) and four (cryptophytes, dinoflagellates, chrysophytes and euglenoids) phytoplankton groups. Since phytoplankton groups have the distinct ability to synthesize EPA and DHA, the physico-chemical factors influencing phytoplankton composition are important factors regulating the overall synthesis of EPA and DHA in lake ecosystems. Although, on ecosystem level i.e. volumetric basis, the concentration of phytoplankton-originated EPA and DHA was higher in eutrophic lakes than in the oligo-mesotrophic or dystrophic lakes, the highest DHA content of phytoplankton was observed in oligo-mesotrophic lakes. The significant relationship between DHA content in phytoplankton and predatory perch muscle strongly indicate the importance of taxonomic
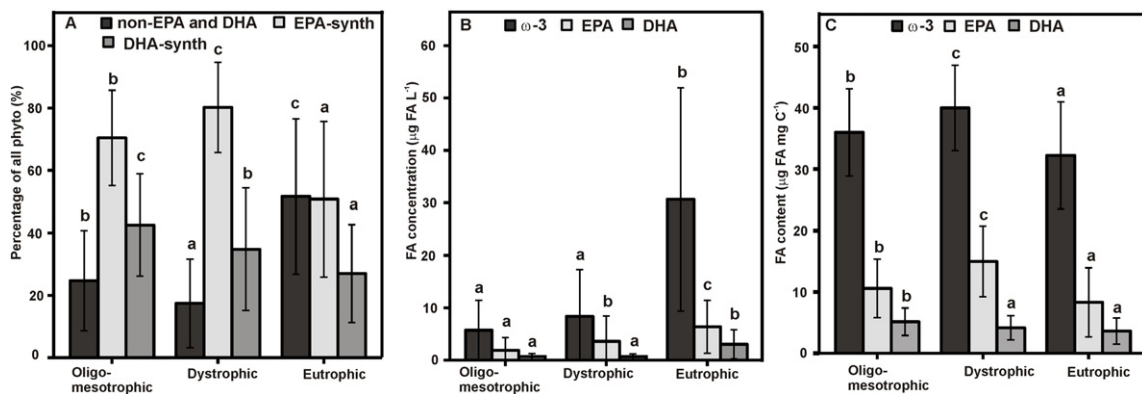

Fig. 3. (A) Average proportion ± SD (n = 713 lakes, June–August 2000–2015) of non-EPA and non-DHA synthesizing (green algae, desmids, cyanobacteria), EPA-synthesizing (EPA-synth; cryptophytes, dinoflagellates, chrysophytes, diatoms, raphidophytes) and DHA-synthesizing (DHA-synth; cryptophytes, dinoflagellates, chrysophytes, euglenoids) taxa within phytoplankton community and (B) the estimated concentration (µg FA L^{-1}) and (C) content (µg FA mg C^{-1}) of EPA, DHA and other ω-3 PUFA in phytoplankton of oligo-mesotrophic, eutrophic and dystrophic lakes. Different letters indicate significant (p < 0.05) differences between the lake types (p > 0.05, c > b > a) in specific fatty acid group.
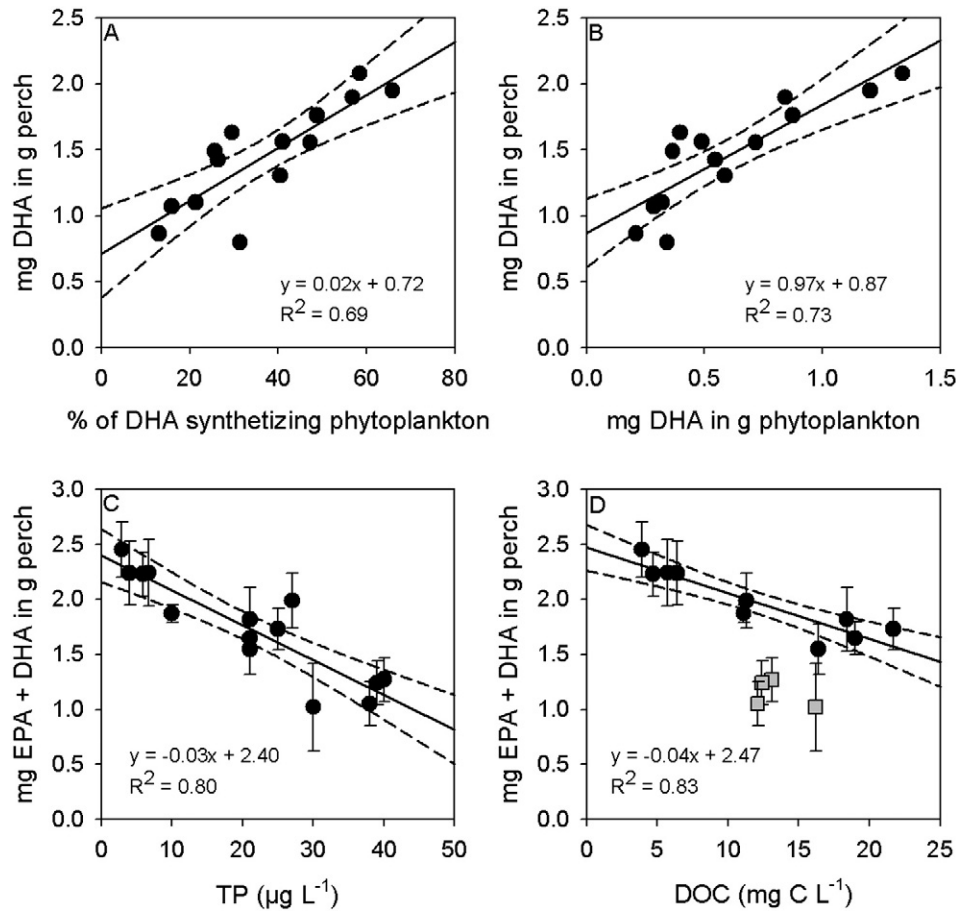
Fig. 4. (A) DHA content (mg DHA in g muscle) of perch (total length >23 cm) muscle related to the proportion of DHA synthesizing phytoplankton (cryptophytes, dinoflagellates, chrysophytes, euglenoids) and (B) DHA content of phytoplankton (mg DHA in g wet weight) in the lakes. (C) EPA and DHA content in perch muscle related to total phosphorus (TP) and dissolved organic carbon (DOC) concentration of the lakes. The regression between perch EPA + DHA content and lake DOC concentration does not include the lakes with TP >30 μg L^{-1} (marked as 'gray squares'). Regression equations with R^2 and lines with 95% confidence limits are also shown. All linear regressions were significant (p < 0.05).

composition of the food-web base on biochemical quality and transfer of essential micronutrients to higher trophic levels i.e. determines the nutritional quality of top consumers. Eutrophication (anthropogenic or climate induced) or brownification strongly influence the phytoplankton community composition and the capacity of algae to produce and transfer physiologically important EPA and DHA to higher trophic levels in aquatic food webs. Although eutrophic lakes are producing high quantity of plankton and fish, the essential fatty acids are 'diluted' in a large biomass. Such process has also important implications to nutritional recommendations.

High biomasses and surface blooms of cyanobacteria are typical consequences of eutrophication, and are especially caused in inland waters by phosphorus loading (Ptacnik et al., 2008; Maileht et al., 2013; Carvalho et al., 2013). Low content of EPA and DHA in phytoplankton was actually prevailing in many European and North-American lakes before the period of efficient sewage treatment (Galloway and Winder, 2015). Restricted availability of EPA and DHA by cyanobacteria-dominated phytoplankton has been shown to yield poor somatic growth in zooplankton (Müller-Navarra et al., 2004; Persson et al., 2007). In the 14 boreal lakes of this study, the contribution of dinoflagellates and chrysophytes among the DHA synthesizing taxa correlated strongly with the DHA content of perch muscle. Our results also confirm that dinoflagellates, which are known to contain high amounts of DHA (>24% of all FA; Ahlgren et al., 1992), are a crucial source of DHA in freshwater food webs.

Our study is the first one to quantify EPA and DHA content of *Mallomonas* and *Synura*, which are abundant genera among

chrysophytes in boreal lakes, together with *Uroglena* and *Dinobryon* (Eloranta, 1995; Lepistö and Rosenström, 1998; Lepistö, 1999; Järvinen et al., 2013). The succession of chrysophytes starts in late spring or early summer in Finnish lakes with *Synura* as one typical species, followed by *Dinobryon* and *Mallomonas* in the summer (Eloranta, 1995). The analysis of >300 Finnish lakes by Eloranta (1995) showed that chrysophytes belong to the most characteristic phytoplankton groups in Finnish lakes, but they are generally less abundant in brown-colored forest lakes, eutrophic lakes and acid clearwater lakes (Eloranta, 1995). Our results, based on results of >700 Finnish lakes, confirm the negative relationship between chrysophyte abundance and eutrophication, and water color/brownification. Chrysophytes prefer oligotrophic conditions (e.g. Maileht et al., 2013; Järvinen et al., 2013), but their abundance typically increases along trophic state until the level of mesotrophy or slight eutrophy (Eloranta, 1995). In Finnish lakes, the chrysophyte maxima and chrysophyte species richness is the highest during summer from June to August when *Mallomonas* typically strongly contributes to the chrysophyte biomass (Eloranta, 1995).

We focused on screening EPA or DHA synthesizing phytoplankton strains, and did not evaluate the consumability aspect of distinct phytoplankton for herbivorous consumers (size, shape, taste, digestability, toxicity; DeMott, 1986, 1995; DeMott and Moxter, 1991). Some freshwater dinoflagellates (e.g., *Peridinium bipes*, *P. willei*, and *Ceratium hirundinella*) are too large (>50 μm) to be consumed by herbivorous zooplankton. The large-sized *Ceratium* is more common in eutrophic lakes than in the oligo-mesotrophic or dystrophic lakes, where dinoflagellates are typically represented by small-sized taxa (e.g. Willén,
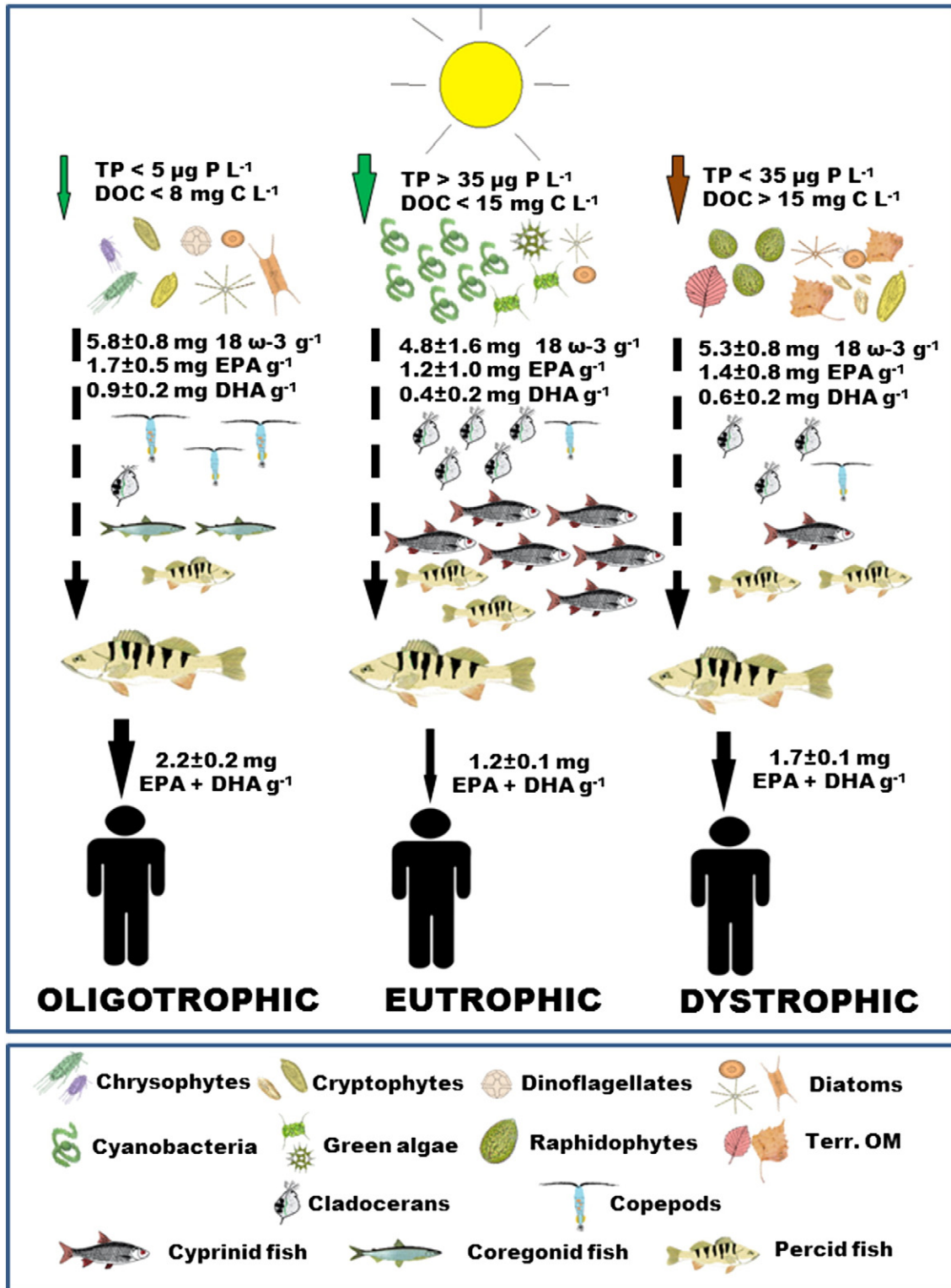
Fig. 5. Schematic approximation of the routes of ω-3 fatty acids across lake food webs via perch to human nutrition from oligotrophic (including mesotrophic), eutrophic and dystrophic lakes. Phosphorus (TP) and dissolved organic carbon (DOC) concentration influence phytoplankton biomass and composition. Phytoplankton biomass can be 5-fold greater in eutrophic lakes than in oligo-mesotrophic or dystrophic lakes, but due to the high contribution of non-EPA and non-DHA synthesizing taxa within phytoplankton community, phytoplankton 18 ω-3 FA (ALA + SDA), EPA and DHA content (mg g^{-1} wet weight) is lower in eutrophic lakes than in oligotrophic or dystrophic lakes. The ω-3 FA is transferred via herbivorous zooplankton and planktivorous fish to piscivorous fish (in this case large perch). TP and DOC concentration influence also zooplankton and fish biomasses and community structure. In boreal eutrophic lakes the total fish biomass can be ca. 2.6-fold (percid fish biomass 1.9-fold) greater than that in oligo-mesotrophic lakes (see Olin et al., 2002). However, the EPA and DHA content in individual perch is the highest in the oligo-mesotrophic lakes. Thus, a person should eat 1.9 and 1.5 times more perch from eutrophic and dystrophic lakes, respectively, compared with those from oligotrophic lakes to achieve the daily recommended intake of EPA and DHA. EPA and DHA content in phytoplankton and perch (>20 cm) are based on the results from the studied 14 lakes (see Table 3, Terr. OM = terrestrial organic matter).

2003). Herbivorous fish have been observed to feed directly on large-sized (50–60 μm) *Peridinium* in Lake Kinneret (Zohary et al., 1994), but there is no evidence of their direct consumption in boreal lakes. In general, herbivory is rare in boreal lake fish and absent in the feeding guild of perch (e.g. Haakana et al., 2007; Estlander et al., 2010; Svanbäck et al., 2015). The raphidophyte *Gonyostomum semen* contains substantial amounts of EPA, and can form high biomasses in brown-water (dystrophic) lakes. However, due to their grazing resistance for most zooplankton taxa (Lebret et al., 2012), the transfer of *Gonyostomum* produced EPA to higher trophic levels seems to be poor. Even though diatoms formed the highest proportion of phytoplankton biomass among all EPA and DHA synthetizing taxa, the sum of EPA and DHA content in perch did not correlate significantly with the contribution of diatoms in the lakes. The result suggests that zooplankton may not efficiently utilize filamentous and colony forming diatoms (e.g. *Aulacoseira, Asterionella, Tabellaria, Diatoma, Fragilaria*), which often formed the bulk of the diatom biomass (56 ± 23% of all diatoms) in the lakes. Altogether, our results indicate that not all phytoplankton synthesized EPA and DHA is transferred equally to higher trophic levels.

Twice higher transfer efficiency of ω-3 PUFA (18–22 carbon) than bulk carbon from phytoplankton to zooplankton has been previously observed in a eutrophic reservoir (Gladyshev et al., 2011). Because fatty acid turnover is relatively rapid in herbivorous zooplankton (six days in cladocerans; Taipale et al., 2011), zooplankton EPA and DHA content can vary greatly during and between seasons (Gladyshev et al., 2006; Taipale et al., 2009; Ravet et al., 2010). Therefore, the long-term availability of EPA and DHA, as calculated here from average phytoplankton community composition, seems to be important for higher trophic levels. The strong correlation between the DHA content in phytoplankton and perch muscle suggests high transfer efficiency of this essential fatty acid in the food chain presumably via zooplankton and planktivorous fish to piscivorous perch. Planktivorous fish, such as vendace and smelt, have been shown to enrich DHA from their zooplankton prey (Linko et al., 1992; Strandberg et al., 2015b). Alternatively, perch may also bioconvert shorter-chain ω-3 FA to DHA, as this process occur in the feeding experiments (Henrotte et al., 2011). However, since phytoplankton DHA content explained 73% of perch DHA content, it seems that DHA is obtained with high affinity from the diet and it is intensively enriched in the food web (Strandberg et al., 2015b). One could speculate that some proportion, e.g. one third, of DHA could have been originated from short-chain ω-3 PUFA in phytoplankton, which was elongated in the food chain (zooplankton – planktivorous fish) or by perch. However, we did not get direct or indirect evidence for this because the residuals in the regression equation between DHA content of phytoplankton and perch muscle did not correlate significantly with the 18 ω-3 PUFA content of phytoplankton. More studies in natural environments are needed to evaluate the importance of 18 ω-3 PUFA as a source for EPA and DHA in predatory fish. Our results suggest that lake primary production of EPA and DHA synthetizing phytoplankton taxa will set up a general framework for the abundance of these PUFA for the whole food web. Thus, for better understanding the synthesis of EPA and DHA, taxon-specific productivity measurements are needed instead of measuring bulk primary production (Dijkman et al., 2009).

Eutrophication and brownification will alter the fish community structure in lakes, where oligotrophic lakes are salmonid, mesotrophic and dystrophic lakes percid dominated and eutrophic lakes cyprinid dominated systems (Brucet et al., 2013). These changes are also generally followed by decrease in body size as well as increase in density and biomass of fish (Olin et al., 2002; Arranz et al., 2016). Changes in fish community composition and structure, will also change the prey fish availability and selection of piscivorous perch, where vendace and smelt are important in oligotrophic lakes, percids (ruffe, perch) in mesotrophic and dystrophic lakes and cyprinids (roach, bleak) in eutrophic lakes (Haakana et al., 2007, Kahilainen, unpublished). The DHA content of the dorsal muscle tissue of perch decreased significantly with

increasing total phosphorus and DOC concentrations in the lakes. Ahlgren et al. (1996) observed that the content of EPA and DHA in the cyprinid fish, roach (*Rutilus rutilus*), were lower in eutrophic lakes than in oligotrophic lakes. Recently, also Razavi et al. (2014) observed decreasing EPA contents in planktivorous bighead carp (*Hypophthalmichthys nobilis*) with increasing eutrophy in Chinese reservoirs. In contrast to the results of our study, Ahlgren et al. (1996) did not observe differences in perch EPA and DHA contents between oligotrophic and eutrophic lakes. These authors concluded that piscivorous fish probably have more constant FA composition than herbivorous-omnivorous fish. We found higher variation in perch EPA and DHA content among lakes along an eutrophication gradient, most likely due to higher number of lakes sampled, than in the study of Ahlgren et al. (1996). Also brownification alone seems to lower DHA accumulation in the food web, which can be seen when the four eutrophic dystrophic lakes were excluded from the perch data. Terrestrial detritus and bacteria do not contain essential fatty acids and cannot support consumers' demands for EPA and DHA for somatic growth and reproduction (Brett et al., 2009a; Taipale et al., 2014). Thus, the detritus-based microbial food chain cannot compensate for the attenuated primary production due to light extinction by colored DOC in dystrophic lakes. Accordingly, negative effects of brownification have been shown on the growth of young perch (Rask et al., 2014) and on fish productivity, in general (Karlsson et al., 2015).

Our study clearly show that EPA + DHA content of perch decrease with increasing phosphorus concentration of the lakes. However, the effects of eutrophication on EPA + DHA availability for human consumption can be regarded ambiguous because eutrophication is generally followed by greater fish yields. For example, a strong positive correlation between total phosphorus concentration (<20–>80 μg TP L^{-1}) and commercial yield of perch was found in the long-term data of the large temperate lakes Upper Constance (Eckmann et al., 2006) and Geneva (Dubois et al., 2008), although several other factors like changes in fishing intensity and climatic conditions also influenced. Olin et al. (2002) studied the relative biomass change (biomass per unit effort) of fish communities in 36 boreal lakes along a phosphorus gradient (11–130 μg TP L^{-1}) using Nordic multi-mesh gill nets according to the current European standard. They found 2.6-times greater total fish biomass in boreal eutrophic lakes (31–50 μg TP L^{-1}) compared with oligo-mesotrophic lakes (11–30 μg TP L^{-1}). For perch, the biomass difference between these lake types was 1.9-fold, which was opposite to the difference in EPA + DHA content in perch muscle (1.8-fold) in the respective lake types observed in our study. Assuming similar changes for the whole fish community, the 1.9–2.6 fold increase in fish biomass does not mean equal increase in EPA + DHA content, but rather 'dilution' of these essential fatty acids to a larger fish biomass. Thus, despite increase in fish yield, the quality fish for human consumption becomes poorer along with eutrophication (see also Ahlgren et al., 1996; Razavi et al., 2014).

Our results show that perch from eutrophic or dystrophic lakes contain less EPA and DHA, which should be taken into account in the recommendation of fish consumption recommendations for daily dose of EPA and DHA uptake (Fig. 5). However, the doubling of daily fish consumption recommendations i.e. from circa 100 g to 200 g may not be feasible at single daily meal level. A recent study, covering lakes from subarctic Europe to southern South America (Kosten et al., 2012), has revealed an increase in the percentage of cyanobacteria in total phytoplankton biomass, reflecting eutrophication. Similarly, DOC concentrations in lakes are increasing in the boreal and temperate regions (e.g. Couture et al., 2012; Räike et al., 2016). Both eutrophication and brownification alter food webs from phytoplankton to top consumers and these effects are expected to strengthen with climate change (Jeppesen et al., 2000, 2010). Our results here, using extensive phytoplankton data and a common piscivore, European perch, provide new evidence on how eutrophication and brownification downgrade the biochemical quality of aquatic food webs from primary producers to predatory consumers.

5. Conclusions

The results of this study showed that EPA and DHA contents vary in the dorsal muscle tissue of piscivorous perch (>20 cm) among oligo-mesotrophic, eutrophic and dystrophic lakes. An adult human would need to eat 1.8 times more perch from eutrophic lakes and 1.5 times more from dystrophic lakes than that from oligo-mesotrophic lakes to gain the recommended daily intake of EPA and DHA from perch fillets. This is due to the fact that nutrient increase (eutrophication) and DOC increase (brownification) both change phytoplankton composition and favor phytoplankton taxa which do not synthesize EPA + DHA or have low PUFA:C-ratio. Our study showed for the first time a link between the DHA content in piscivorous perch and the contribution and content of phytoplankton-derived DHA in seston. Our results also suggests that not all phytoplankton-derived EPA and DHA is transferred equally to higher trophic levels, and emphasizes the importance of the role of dinoflagellates and chrysophytes that are sensitive to eutrophication and to some extent also to brownification. Therefore, even a moderate increase of nutrients and dissolved organic carbon may decrease the transfer of DHA in aquatic food webs.

Acknowledgements

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