



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 synthesized 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.

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1. Introduction

Freshwater and marine food webs are predominately 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 (20:5 ω -3) might be the most important essential fatty acid supporting somatic growth and reproduction of cladoceran zooplankton,

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whereas DHA (22:6 ω -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 C₁₈ ω -3 (ALA; 18:3 ω -3 or SDA; 18:4 ω -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 C₁₈ 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, 18:3 ω 3), 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-Maunders, 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; Rälke 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 synthesizing 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 $\mu\text{g P L}^{-1}$), eutrophic (>35 $\mu\text{g P L}^{-1}$) 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 $\mu\text{mol m}^{-2} \text{s}^{-1}$. 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

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