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Selective transfer of polyunsaturated fatty acids from phytoplankton to planktivorous fish in large boreal lakes

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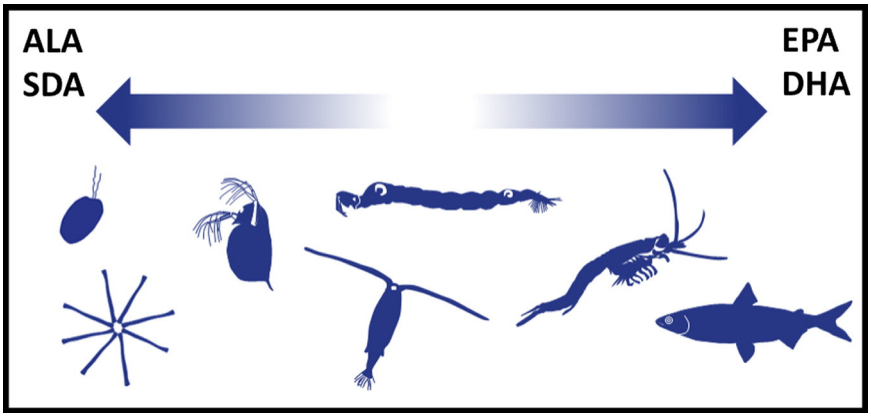
HIGHLIGHTS

- We analyzed the transfer of polyunsaturated fatty acid (PUFA) in pelagic food web
- The trophic transfer of PUFA along the food chain was selective
- Docosahexaenoic acid (DHA) was strongly enriched in the food chain
- DHA accounted for about 30% of total fatty acids in zooplanktivorous fish
- The proportion of C_{18} PUFA decreased with increasing trophic level

GRAPHICAL ABSTRACT



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ABSTRACT

Lake size influences various hydrological parameters, such as water retention time, circulation patterns and thermal stratification that can consequently affect the plankton community composition, benthic–pelagic coupling and the function of aquatic food webs. Although the socio-economical (particularly commercial fisheries) and ecological importance of large lakes has been widely acknowledged, little is known about the availability and trophic transfer of polyunsaturated fatty (PUFA) in large lakes. The objective of this study was to investigate trophic trajectories of PUFA in the pelagic food web (seston, zooplankton, and planktivorous fish) of six large boreal lakes in the Finnish Lake District.

Docosahexaenoic acid (DHA), eicosapentaenoic acid (EPA) and α-linolenic acid (ALA) were the most abundant PUFA in pelagic organisms, particularly in the zooplanktivorous fish. Our results show that PUFA from the n-3 family (PUFAn-3), often associated with marine food webs, are also abundant in large lakes. The proportion of DHA increased from ~4 ± 3% in seston to ~32 ± 6% in vendace (*Coregonus albula*) and smelt (*Osmerus eperlanus*), whereas ALA showed the opposite trophic transfer pattern with the highest values observed in seston (~11 ± 2%) and the lowest in the opossum shrimp (*Mysis relicta*) and fish (~2 ± 1%). The dominance of diatoms and cryptophytes at the base of the food web in the study lakes accounted for the high amount of PUFAn-3 in the planktonic consumers. Furthermore, the abundance of copepods in the large lakes explains the effective transfer

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of DHA to planktivorous fish. The plankton community composition in these lakes supports a fishery resource (vendace) that is very high nutritional quality (in terms of EPA and DHA contents) to humans.

1. Introduction

Large lakes are important ecosystems for maintaining biodiversity as well as providing a wide variety of ecosystem services for humans (Holmlund and Hammer, 1999; Krantzberg and deBoer, 2006; Vadeboncoeur et al., 2011). Commercial freshwater fisheries are usually focused on large lakes, which are also important for recreation and commercial navigation (Holmlund and Hammer, 1999; Krantzberg and deBoer, 2006). Lake size and morphometry have direct effects on several physicochemical parameters, such as vertical temperature gradients, water retention time and water circulation patterns, which together with catchment characteristics influence e.g. nutrient cycling, the trophic state, and food web structure. For example, plankton community composition (Lepistö and Rosenström, 1998), food chain length (Post et al., 2000) and carbon fluxes scale with lake size (Kortelainen et al., 2004; Brett et al., 2012). Although the ecological and hydrological processes of large lakes have been extensively studied (Nõges, 2008), research on the trophic transfer of polyunsaturated fatty acids (PUFA) through food webs of large lakes (surface area > 100 km^2) is very limited (Smyntek et al., 2008). Current knowledge on the composition and trophic dynamics of PUFA in freshwater lakes is almost entirely based on small or moderately sized lakes (Ahlgren et al., 1996; Kainz et al., 2004; Müller-Navarra et al., 2004; Ravet et al., 2010; Lau et al., 2012). In aquatic ecology, PUFA are attracting increasing attention because studies indicate that PUFA from the n-3 family (PUFAn-3) may limit consumer production (Müller-Navarra et al., 2004). Animals in general cannot synthesize PUFA de novo (Cook and McMaster, 2004), and must obtain these molecules from their diets to support somatic growth and reproduction (Tocher, 2003; Brett et al., 2009; Martin-Creuzburg et al., 2009).

Production of PUFA by algae is taxon-specific and the composition and availability of PUFA in food webs is determined by the community structure of the primary producers (Sushchik et al., 2004; Galloway and Winder, 2015; Strandberg et al., 2015). Although pelagic bacteria may be an important link in transferring carbon to zooplankton, bacteria contain only trace amounts of PUFA and thus the importance of the microbial loop in conveying PUFA to upper trophic level consumers is negligible (Taipale et al., 2014). The availability of PUFA to secondary consumers in the pelagic food web is not only determined by the taxonomic composition of producers but also by the community composition of the zooplankton (Persson and Vrede, 2006; Burns et al., 2011). Taxon-specific differences in fatty acid (FA) composition are much larger than intraspecific variation due to differences in the diet composition and/or environmental conditions (Hiltunen et al., 2015). Variation in phytoplankton and zooplankton community composition according to physical characteristics of lakes, allochthonous organic matter content and trophic state (Kortelainen, 1993; Lepistö and Rosenström, 1998) suggest that the FA in the pelagic food web of large lakes may differ from the more intensively studied smaller and shallower lakes (Müller-Navarra et al., 2004; Lau et al., 2012).

Most studies on trophic transfer of PUFA have been carried out at the phytoplankton–herbivore interface (e.g. Ravet et al., 2010; Burns et al., 2011; Gladyshev et al., 2011). Studies focusing on fish are much less common (Kainz et al., 2004). Compared to marine fish, freshwater fish typically contain less PUFAn-3 and are more enriched in PUFA from the n-6 family (PUFAn-6), leading to a lower n-3/n-6 ratio (Ahlgren et al., 1994; Ahlgren et al., 1996). The difference between the abundance of PUFAn-3 and PUFAn-6 between marine and freshwater fish presumably originates from concurrent differences in their diets. Even in large lakes, the majority of freshwater fish (up to 93% of species) utilize benthic resources in the littoral zone that are considered to be abundant in PUFAn-6 and have a low n-3/n-6 ratio (Vadeboncoeur et al., 2011; Lau et al., 2012). Extending the knowledge of the trophic transfer of PUFA to large lakes is also societally relevant due to the importance of commercial fisheries in these ecosystems (Holmlund and Hammer, 1999).

The aim of this study was to evaluate the significance of the commercially important vendace (*Coregonus albula*) as a source of eicosapentaenoic acid (EPA or 20:5n-3) and docosahexaenoic acid (DHA or 22:6n-3) for humans in this region, and to track the trophic transfer of PUFA in the pelagic food web of large lakes. Detailed understanding of the transfer patterns of these molecules from phytoplankton to fish is essential to identify and preserve the availability of EPA and DHA to higher trophic level consumers, including humans. Vendace is an obligate zooplankton specialist, and is therefore an excellent model to evaluate the composition and trophic transfer of PUFA in the pelagic ecosystem of large lakes (Viljanen, 1983; Northcote and Hammar, 2006).

2. Material and methods

The pelagic food web of large oligo-mesotrophic lakes (surface area > 100 km^2) were sampled for FA and stable isotope (SI) analyses in three seasons: spring, summer and autumn. The following members of the food web were sampled: seston (primary producers, bacteria and small heterotrophic flagellates), zooplankton (copepods, cladocerans, the opossum shrimp *Mysis relicta* and dipteran larvae *Chaoborus* spp.), and two highly zooplanktivorous fish species, vendace and smelt (*Osmerus eperlanus*). Vendace is a small-sized (total length 10–25 cm) and short-lived coregonid inhabiting large to medium-sized boreal lakes, mainly in northern Europe (Viljanen, 1983; Northcote and Hammar, 2006). Vendace is the most important species for freshwater fisheries in Finland accounting for over half of all inland fisheries; the value of the catch was estimated to be 6.5 million euros in 2012 (Anonymous, 2013). The species is abundant in oligo-mesotrophic lakes with low to moderate humic content and prefers well-oxygenated cooler water layers (Rask et al., 1999). Smelt were sampled opportunistically in spring and summer as a reference to check the similarity of the FA profile in another zooplanktivorous species. Although the data is presented the results are not discussed in detail due to the low sample number.

Total phosphorus concentrations of these lakes ranged between ~5 and 12 μg L^{-1}, and the chlorophyll *a* concentration between ~2 and 6 μg L^{-1} (Hiltunen et al., 2015; Strandberg et al., 2015). Dissolved organic carbon (DOC) concentration ranged from ~5 to 10 mg C L^{-1}, and correlated positively with water color (~15–57 mg Pt L^{-1}) and total nitrogen concentration (~230–640 μg L^{-1}). Seston (n = 21), zooplankton (n = 214) and planktivorous fish (vendace n = 71, and smelt n = 9) were collected for FA and stable isotope (SI) analyses from six lakes (eight sampling points) in the Vuoksi Lake District in Eastern Finland (Fig. 1). In five lakes (Lake Kallavesi, Lake Suvasvesi, Lake Paasivesi, Lake Orivesi and Lake Pyhäselkä) samples were collected during three seasons: spring (late May–early June), summer (late July–early August) and autumn (late September) in 2011. Lake Karjalan Pyhäjärvi was sampled only once in summer 2012. Details on the lakes can be found elsewhere (Hiltunen et al., 2015; Strandberg et al., 2015).

For seston FA analyses, lake water was pumped from the euphotic zone (0–4 m depth), sieved through a net (50 μm mesh size) to exclude zooplankton, and filtered through glass fiber filters (~0.7 μm; Whatman