Fatty acid composition and contents of seven commercial fish species of genus *Coregonus* from Russian Subarctic water bodies

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Abstract In several Russian northern lakes and rivers, Arctic cisco *Coregonus autumnalis*, least cisco *C. sardinella,* peled *C. peled,* tugun *C. tugun,* broad whitefish *C. nasus,* whitefish *C. lavaretus* and vendace *C. albula* were sampled in periods of officially permitted commercial fishery. Special attention was paid to contents (mg g^{-1} of wet weight) of eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) in muscle tissues (filets), which are essential for human nutrition. The highest values of EPA+DHA content in semi-anadromous fish and freshwater fish were recorded for *C. autumnalis* from the Yenisei River, 17.60 mg g^{-1} wet weight, and for *C. lavaretus* from the Sobachye Lake, 16.61 mg g^{-1} wet weight, respectively. Intra-genus variations of EPA+DHA contents of *Coregonus* species were from 1.87 to 17.60 mg g^{-1} wet weight. Since the congeneric species were genetically close to each other, the variations in EPA and DHA contents were thought to be caused primarily by ecological factors: capability to migrations, type of feeding and trophic status of aquatic ecosystems. In general, the majority of studied species appeared to be of a high nutritive value for humans, although unfavorable environmental conditions could considerably diminish this value.

Abbreviations

BFA Branched fatty acid(s)

CCA Canonical correspondence analysis

DHA Docosahexaenoic acid (22:6n-3)

EPA Eicosapentaenoic acid (20:5n-3)

FA Fatty acid(s)

FAME Fatty acid methyl ester(s)

GC-MS Gas chromatography - mass spectrometry

PL Phospholipids

PUFA Polyunsaturated fatty acid(s)

TAG Triacylglycerol(s)

Introduction

In recent decades, many extensive clinical and epidemiological studies have demonstrated a key importance of polyunsaturated fatty acids of omega-3 family, namely eicosapentaenoic acid (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3) for healthy functioning of human cardiovascular and neural systems [1– 4]. To prevent many cardiovascular diseases and psychiatric disorders, a personal daily consumption of 0.5 – 1 g of EPA+DHA was recommended by a number of national and international health organizations [5– 8]. The main food source of EPA and DHA for most humans is fish [9–12]. However, various fish species differ in EPA and DHA contents in edible biomass by more than two orders of magnitude [10]. Some fish species have too low contents of EPA and DHA and it is impossible to obtain the recommended daily dose by eating these fish [13, 14]. Thus, on the one hand, a continual improvement of databases on EPA and DHA contents in various fish species is necessary to provide individuals and public health officials with quantitative information on the desirable healthy intakes [5, 15]. On the other hand, it is important to comprehend causes of the great variations of EPA and DHA in fish biomass.

In general, two groups of factors can control fatty acid (FA) composition and contents in aquatic animals: phylogenetic and ecological [14, 16, 17]. Relative contributions of these two groups of factors to fish FA contents, including that of EPA and DHA, are not completely known yet. Among ecological factors, feeding habits (planktivorous, benthivorous, piscivorous), habitat (marine vs freshwater, pelagic vs. demersal and oligotrophic vs. eutrophic) and water temperature are regarded to control FA contents of fish. For instance, pelagic-feeding species are regarded to be richer in lipids, including EPA and DHA than demersal fish [12, 18]. Piscivorous fish are believed to have a higher EPA and DHA contents [14, 19]. Marine fish seem to be richer in polyunsaturated fatty acids (PUFA), including EPA and DHA, than freshwater species [20, 21]. Fish from oligotrophic water bodies appeared to have comparatively higher PUFA contents

[22]. However, phylogenetic factor, i.e., species identity, may overweight the ecological factors regarding the control of EPA and DHA contents in fish [13, 23, 24]. Indeed, in spite of any ecological factors, maximum value of contents of EPA and DHA in species from, let's say, order Salmoniformes are higher than that in order Cypriniformes [10]. Presumably, within each fish taxa (species, genus, …, order), there are genetically determined lower and upper limits of EPA and DHA contents, and only within these limits variations of the PUFA contents can be provided by ecological factors.

It is desirable to know the putative limits of EPA and DHA contents in fish taxa for many theoretical and applied purposes. For instance, we need to understand, how global challenges, climate warming, anthropogenic pollution, eutrophication or biological invasions, which cause changes of natural fish species composition, will affect PUFA supply for humans. The information about the taxon-specific limits also seems to be useful for fish aquaculture, especially for introducing of new species, potentially rich in EPA and DHA.

To determine the taxon-specific limits and to evaluate the contribution of ecological factors to EPA and DHA contents, it is necessary to quantify these contents as mass units, i.e., mg per g of fish biomass. Meanwhile, most published data are given in relative units, i.e. percent of total FA [25]. Nevertheless, to estimate the nutritive value of fish for humans, it is necessary to measure EPA and DHA contents in edible biomass (mg g^{-1}), rather than then percent [18, 24, 26–28].

Thus, the aim of our study was to evaluate variations of fatty acid composition and contents of EPA and DHA within commercially important species of genus *Coregonus* in water bodies of Russian Subarctic. To our knowledge, this was the first attempt to determine taxon (genus)-specific limits of EPA and DHA contents in wild fish. Besides, we aimed to test common ideas concerning differences in EPA and DHA contents between planktivorous and benthivorous fish using congeneric species. At last, we aimed to supplement existing data on EPA and DHA contents in fish with previously unexplored species.

Materials and Methods

Standards and Reagents

All organic solvents were of analytical grade and were purchased from Khimreactivsnab (Ufa, Russian Federation). Sodium of 99.8 % grade was purchased from Acros Organic - Thermo Fisher Scientific (Geel, Belgium). We prepared 3 M sodium methoxide solution cautiously dissolving sodium in methanol. The solution was stored at 4 ºC no more than a week prior usage. Standards of methyl esters of individual fatty acids (FAME) and their mixtures [29] were purchased from Sigma-Aldrich (USA). Solutions of the standard compounds were prepared in hexane at a concentration range of 0.5-5 mg mL^{-1} and analysed by GC-MS. Methyl ester of nonadecanoic acid (Sigma-Aldrich, USA) was used as an internal standard, which stock solution in chloroform at concentration of 1 mg mL^{-1} was prepared and stored at -20 ºC.

Aquatic Environments

All sampled water bodies (Table 1) were oligotrophic (except nearly mesotrophic Lake Onega) and had low water temperature. Dominant phytoplankton taxa were Bacillariophyta [31, 38, 39]. A map of the sampled water bodies is given in Fig. 1.

Fish Sampling

Fish of commercial sizes were obtained from local authorized fishers just after catching.

Following sampling was conducted in accordance with the BioEthics Protocol on Animal Care, approved by the Siberian Federal University. Species of genus *Coregonus*, collected in diverse water bodies, and numbers of samples are given in Table 2. Although feeding habits of these species were well known from literature, stomach contents of some specimens were taken for microscopic analyses to check their food items (Table 2).

Arctic cisco *Coregonus autumnalis* (Pallas, 1776) in the Yenisei River is semi-anadromous fish, which feed in the Yenisei Gulf (the Kara Sea) and migrate in the river for spawning [40]. Arctic cisco is a pelagic feeder, which eats zooplankton, planktobenthic invertebrates and small fish [40] (Table 2).

Least cisco *Coregonus sardinella* Valenciennes, 1848 were caught in the Yenisei River and in the Sobachye Lake. Least cisco from the Yenisei River, like Arctic cisco, is semi-anadromous fish, which feed in the Yenisei Gulf and migrate in the river for spawning. Least cisco from the Sobachye Lake is landlocked fish. Least cisco is primarily zooplanktivore [40] (Table 2).

Peled *Coregonus peled* (Gmelin, 1789) in the Yenisei River is planktivore-benthivore [40] (Table 2).

Whitefish *Coregonus lavaretus* (Linnaeus, 1758) were caught in the Yenisei River, in the Sobachye Lake, in the Keret River and in the Lake Onega. In the Keret River, *C. lavaretus* is semi-anadromous fish, which feed in in the White Sea. *C. lavaretus* in all the water bodies were benthivorous [40–43] (Table 2).

Tugun *Coregonus tugun* (Pallas, 1814) were caught in the Yenisei River and in the Sobachye Lake. Tugun is planktivorous-benthivorous species [40] (Table 2).

Broad whitefish *Coregonus nasus* (Pallas, 1776) were caught in the Yenisei River and in the Sobachye Lake. Broad whitefish is benthivore [40] (Table 2).

Vendace *Coregonus albula* (Linnaeus, 1758) in the Bolshoie Krasnoie Lake is planktivore [44, 45].

For biochemical analyses, samples of white muscle tissue of approximately 0.7-2 g, were taken 1 - 2 cm below the dorsal fin. When cutting the sample, we tried to avoid skin, red muscle and bones. The portion of muscle tissue was immediately weighed, placed into chloroform/ methanol mixture (2:1, by vol.) and kept until further analysis at −20 °C. The samples were transported to laboratory in 1-2 weeks under ice. Lipid analyses were done within two months after sampling.

Fatty Acid Analysis

Lipids were extracted with chloroform/methanol (2:1, by vol.) three times, when tissues were simultaneously homogenized with glass beads in a mortar [11]. The extracts were dried with anhydrous Na_2SO_4 and chloroform and methanol were roto evaporated under vacuum at 35 ºC. The extracted lipid was dissolved in 1ml of hexane, then 0.2 mL of 3 M methanolic sodium methoxide solution was added, and mixture was shaken vigorously for 1 min. Subsequently, the mixture was kept quiet at ambient temperature for 5 min, and finally 2.5 mL of hexane and 5 mL of a saturated solution of NaCl were added. Contents were mixed for 1 min, transferred in a separatory funnel, and the lower aquatic layer was discarded. The hexane layer was washed one more time with an aliquot of the solution of NaCl and twice with 5 mL of distilled water. The hexane solution of FAME was dried with anhydrous Na_2SO_4, and hexane was removed by roto-evaporating at 30 ºC. The FAME were redissolved in 150-300 µL of hexane prior chromatographic analysis.

A gas chromatograph equipped with a mass spectrometer detector (model 6890/5975C; Agilent Technologies, USA) and with a 30-m long, 0.25-mm internal diameter capillary HP-FFAP column was used for FAME analysis. Detailed descriptions of the chromatographic and mass-spectrometric conditions are given elsewhere [46]. The FAME were quantified according to the peak area of the internal standard, 19:0-FAME, which we added to samples prior to the lipid extraction.

Statistical Analysis

Kolmogorov-Smirnov one-sample test for normality $D_{K\text{-}S}$, standard errors (SE), Student's *t*-tests, one-way ANOVA with *post hoc* Tukey HSD test, Kruskal-Wallis test (in the absence of normal distribution) and canonical correspondence analysis (CCA) [47] were calculated conventionally, using STATISTICA software, version 9.0 (StatSoft Inc., Tulsa, OK, USA).

Results

Moisture content of studied species had a small range of variations. *C. lavaretus* from the Sobachye Lake tended to have the lowest value of moisture, 66.1 ± 2.9%, while *C. sardinella* from the Sobachye Lake tended to have the highest value, 78.3 ± 0.5%.

The correspondence analysis demonstrated a marked partitioning of the same species from different water bodies, e.g., *C. sardinella* from the Yenisei River and the Sobachye Lake, *C. tugun* from the Yenisei River and the Sobachye Lake, and *C. lavaretus* from the Keret River and the Yenisei River. (Fig. 2). Along Dimension 1, which represented the largest proportion of inertia, most overall differences in FA composition were found between *C. lavaretus* from the Keret River, on the one hand, and *C. autumnalis* and *C. lavaretus* from the Sobachye Lake, on the other hand (Fig. 2). These differences were mainly provided by contrast levels of 22:6n-3 and 16PUFA in the species (populations) (Fig. 2). Along Dimension 2, most differences were between *C. autumnalis* from the Yenisei River and *C. tugun* from the Sobachye Lake (Fig. 2).

These differences primarily were due to the contrast between levels of Σ20:1 and 18:4n-3 in the species (Fig. 2).

C. autumnalis from the Yenisei River tended to have the lowest mean levels of 17:0, 20:4n-6 and 22:5n-6, but the highest levels of Σ20:1 and 24PUFA (Table 3). *C. sardinella* from the Yenisei River tended to have the highest levels of 20:2n-6 (Table 3). *C. peled* from the Yenisei River tended to have the highest levels of 15-17BFA and 18:3n-3 (Table 3). *C. tugun* from the Yenisei River tended to have the lowest levels of 20:5n-3, 22:5n-3 and 22:6n-3, but the highest level of 18:1n-9 (Table 3). *C. sardinella* from the Sobachye Lake tended to have the highest levels of 22:5n-6 (Table 3). *C. tugun* from the Sobachye Lake tended to have the highest levels of 18:2n-6 (Table 3). *C. nasus* from the Sobachye Lake tended to have the highest levels of 18:0 and 18:1n-7 (Table 3). *C. lavaretus* from the Sobachye Lake tended to have the lowest levels of 15:0, 16:0 and 18:0, but the highest levels of 16:1n-7 and 16PUFA (Table 3). *C. lavaretus* from the Keret River tended to have the lowest level of 14:0, 15-17BFA, 18:2n-6, 18:3n-3, 18:4n-3, 20:3n-3, 20:4n-3 and 24PUFA but the highest level of 16:0, 20:5n-3, 22:5n-3 and 22:6n-3 (Table 3). *C. lavaretus* from Lake Onega tended to have the lowest level of 18:1n-9 and Σ20:1, but the highest levels of 16:1n-9 and 20:4n-6 (Table 3). *C. albula* from the Bolshoie Krasnoie Lake tended to have the lowest level of 16:1n-7, 16PUFA and 18:1n-7, but the highest levels of 14:0 (Table 3). *C. lavaretus* from the Keret River tended to have the lowest content of total FA, while *C. autumnalis* from the Yenisei River tended to have the highest content of total FA (Table 3).

Mean contents of EPA+DHA in the studied congeneric species varied from 1.87 ± 0.06 mg g^{-1} wet weight in *C. lavaretus* from Lake Onega to 17.60 ± 3.63 mg g^{-1} wet weight in *C. autumnalis* from the Yenisei River (Fig. 3). *C. lavaretus* from the Sobachye Lake also had very high content of EPA+DHA in biomass, 16.61 ± 2.80 mg g^{-1} wet weight (Fig. 3). Thus, variations of average EPA and DHA contents between the congeneric species were 10-fold (Fig. 3), while variations of average percentages of these PUFA were ~3-fold only (Table 3).

Discussion

Intra-genus variations of EPA+DHA contents of *Coregonus* species, revealed in this study, were from 1.87 to 17.60 mg g^{-1} wet weight. Values of the contents of another species of this genus, published in available literature, fell in the above range and varied from 3.1 mg g^{-1} wet weight in lake whitefish *C. clupeaformis* ([48], recalculated from dry weight using mean moisture content in Salmoniformes 72.5%) to 10.7 mg g^{-1} wet weight in European whitefish *C. macrophtalmus* ([14], recalculated from Table 5 of the source). Thus, in present study we expanded the lower and upper limits of intra-genus variations of EPA+DHA contents in wild *Coregonus* species. Moreover, to our knowledge, the highest values of EPA+DHA content in anadromous and freshwater fish, published in available literature, were 11.06 mg g^{-1} wet weight in Chinook salmon (*Oncorhynchus tshawytscha*) [49] and 11.07 mg g^{-1} wet weight in lake trout (*Salvelinus namaycush*) [50], calculated from Table 5 of the source), respectively. In our study, the maximum value for semi-anadromous species, *C. autumnalis*, was 17.60 mg g^{-1} wet weight, and for the landlocked *C. lavaretus* from the Sobachye Lake this value was 16.61 mg g^{-1} wet weight. Hence, in the present work, we expanded considerably the upper limit of EPA+DHA contents for anadromous freshwater fish.

The new maximum values of EPA+DHA content in the semi-anadromous *C. autumnalis* and the freshwater *C. lavaretus* are still lower than the maximum value of EPA+DHA content in marine fish, published in available literature, 25.6 mg g^{-1} wet weight in Sardine (*Sardinops sagax*) [28]. However, there are many unexplored freshwater fish species, especially in pristine cold oligotrophic Arctic lakes of Russia, and there might be found in future some species with extremely high content of EPA and DHA in their biomass. In any case, regarding present findings, the common point of view on higher PUFA contents in marine fish [20, 21, 51] should be taken with caution. Indeed, EPA+DHA contents in *C. autumnalis* and in *C. lavaretus* were considerably higher than that in a majority of marine fish, reviewed in [10]. The high nutritive value of freshwater fish for humans was revealed in this work. Thus, “more must be learned about the possible benefits of freshwater fish consumption in different areas of the world” [52, p. 1305].

Since congeneric species were believed to be genetically close to each other, the above variations in EPA and DHA contents were likely caused primarily by ecological factors. Among the ecological factors, water temperature was often regarded as a driver of the PUFA contents in fish. The effect of water temperature was explained by a hypothesis of “homeoviscous adaptation”, which predicted a decrease of a degree of saturation of phospholipid FA with an increase of temperature to maintain an optimal cell membrane fluidity [53]. For instance, Arts et al. [54] found, that under a laboratory conditions an increase of water temperature from 12 to 19 ºC caused a decrease of DHA content in juvenile Atlantic salmon (*Salmo salar*) from 4.6 to 3.3 mg g^{-1} wet weight (recalculated from dry weight using mean moisture content in Salmoniformes 72.5%). There are also some data on higher PUFA contents in wild fish in cold waters compared to those in warm waters [55, 56]. However, other authors did not find any significant effect of water temperature on the PUFA levels in fish in a laboratory or in natural waters [18, 57–61] Moreover, in many works the putative peculiar role of EPA or DHA in the temperature adaptations of the cell membrane properties (fluidity, order, curvature and elastic stress) was not confirmed [53, 58, 62–64]. In any case, in our study water temperature in the subarctic water bodies was below 16 ºC and hardly contributed considerably to the observed differences in EPA and DHA contents between the studied species. Indeed, in the Yenisei River, or in the Sobachye Lake, *Coregonus* species, which dwelt together under the same temperature, had significantly different contents of these PUFA.

Another important ecological factor, which affects FA composition and content in fish biomass, is nutrition. Fish food chains in inland waters are known to base on autochthonous resources, microalgae, and, to some extent, on allochthonous (terrestrial) organic matter. Allochthonous resources are regarded to be of a high biochemical quality for consumers, including fish, especially in oligotrophic water bodies, where diatom, cryptophyte and dinoflagellate algae, rich in EPA and DHA, are dominant species [22, 65]. In our study, all water bodies were oligotrophic, diatom-dominated rivers and lakes, except the mesotrophic Lake Onega. It is worth to note, that *C. lavaretus* from Lake Onega had the lowest content of EPA and DHA in biomass. Hence, the above result seems to be in a good agreement with data of other authors on higher content of PUFA in fish from oligotrophic water bodies [22, 65]. Moreover, *C. lavaretus* from Lake Onega had the highest level of arachidonic acid 20:4n-6, which is regarded as marker of allochthonous (terrestrial) organic matter of the comparatively low nutritive value [31]. Thus, the lowest content of EPA+DHA of *C. lavaretus* from Lake Onega among the studied fish was likely determined by the low quality of its food sources.

Planktivorous (pelagic-feeding) fish are considered to have higher EPA and DHA contents than benthivorous (demersal) species [12, 18]. According to the above point of view, in our study, in the Yenisei River planktivorous *C. autumnalis* and *C. sardinella* tended to have higher EPA and DHA contents, than benthivorous *C. lavaretus* and *C. nasus*, while planktivorous-benthivorous *C. peled* and *C. tugun* had intermediate values. However, the high contents in *C. autumnalis* and *C. sardinella* may be explained by another cause, than the pelagic feeding only (see below). Moreover, in the Sobachye Lake, the planktivorous *C. sardinella* had the lowest EPA+DHA content, while the highest content was characteristic of the benthivorous *C. lavaretus*. Thus, planktivorous species of *Coregonus* genus did not necessary have a higher EPA and DHA contents compared to benthivorous species.

As mentioned above, marine fish are commonly regarded to be richer in PUFA content compared with freshwater fish [20, 21, 51]. In our study, the highest EPA and DHA contents were characteristic of the semi-anadromous *C. autumnalis*, which fed in the Yenisei Gulf of the Kara Sea and then migrated in the Yenisei River for spawning. Indeed, *C. autumnalis* had the highest level of sum of 20:1 fatty acids. These acids, namely 20:1n-9 and 20:1n-7, are known to be markers of marine copepods [66, 67]. Evidently, this species assimilated organic matter of marine origin, which seemed to be of very high nutritive value. For instance, marine planktonic copepods are extremely rich in lipids, which constitute up to 75% of their dry mass [68]. Moreover, *C. autumnalis* had the lowest proportion of the marker of low-quality terrestrial organic matter, 20:4n-6. Similarly, anadromous (marine) forms of another species of Salmoniformes, *Oncorhynchus nerka*, had considerable levels of Σ20:1 in their biomass, while in landlocked forms (kokanee) these FAs were nearly absent [24, 69]. In turn, levels of 20:4n-6 in the marine *O. nerka* were significantly lower, than that in kokanee [24, 69]. Thus, the migrating *C. autumnalis* had explicit markers of food of marine origin, while the contribution of low-quality terrestrial organic matter was considerably lower, than that in the land-locked river and lake fish species.

Another semi-anadromous species from the Yenisei River, *C. sardinella*, also tended to have higher level of Σ20:1 and lower level of 20:4n-6, than land-locked *C. sardinella* from the Sobachye Lake. However, the migratory species from the Keret River, *C. lavaretus*, did not have an explicitly higher level of Σ20:1, and lower level of 20:4n-6 than land-locked species. In addition, it should be noted that some 20:1 acids, e.g., 20:1n-13, are markers of mollusks [70]. Indeed, *C. nasus* from the Yenisei River, which consumed primarily mollusks, had a comparatively high level of Σ20:1.

What range of variations of EPA and DHA content in fish muscle tissues can be provided by feeding conditions? Species of the order Salmoniformes, Atlantic salmon (*Salmo salar*), reared in aquaculture using food of a low and high quality, i.e., based on vegetable and fish oil, respectively, had EPA+DHA content 3.2 mg g^{-1} and 7.0 mg g^{-1}, respectively [71]. Similarly, *Oncorhynchus mykiss*, reared in aquaculture using vegetable and fish oil, had EPA+DHA content 3.7 mg g^{-1} and 8.3 mg g^{-1}, respectively [72]. The above inter-species ranges of variations, provided by the changing of food composition in aquaculture, are evidently narrower, than the inter-genus ranges of variations of EPA+DHA content, revealed in our study. Thus, feeding conditions might not play the principal role in variations of EPA and DHA content in fish compared with the other ecological and phylogenetic factors. For instance, basing on the putative importance of food, Ahlgren et al. [65] supposed, that different fish species from the same ecosystem, with access to the same food items, should have similar FA content. However, in our study, the congeneric benthivorous fish species from the Sobachye Lake, *C. lavaretus* and *C. nasus*, had significantly different EPA and DHA contents.

It is well known, that contents of lipids (total fatty acids) in fish tissues are highly variable and depend on feeding and reproduction season [14, 19, 73]. In our study, content of total FA, which tightly correlated with total lipid content in fish [65] varied significantly. Since all species were sampled before spawning season, these variations were believed to be caused primarily by food availability in particular aquatic ecosystems. It is worth to note, that all fish were obtained in the periods of officially permitted commercial fishery. The EPA and DHA content in fish is the indicator of their nutritive value for humans. Therefore, the measuring of the nutritive value in the period of commercial fishery seemed to be reasonable.

In our study, a considerable discrepancy between levels (percentages) of PUFA and their content in mass units in fish biomass was found, like in many other studies [14, 24, 26– 28]. Indeed, *C. lavaretus* from the Keret River had the highest EPA and DHA levels, 12.1% and 26.5%, respectively, while it had one of the lowest content of EPA+DHA, 2.33 mg g^{-1} wet weight. This phenomenon might be explained by a difference between PUFA contents in polar lipids, phospholipids (PL) and neutral lipids, triacylglycerols (TAG). The functionally important EPA and DHA are known to contain mostly in PL, which are structural lipids of cell membranes and their constant proportions are essential for muscle tissue functioning [74]. Thus, a high proportion of EPA and DHA seem to be maintained in fish muscles even under unfavorable feeding conditions. Meanwhile, under favorable feeding conditions, fish accumulate storage lipids, TAG, which are relatively poor in PUFA and contain mainly saturated and monounsaturated FA [18, 75]. Therefore, fatty fish with high total lipid (total FA) contents have high EPA and DHA contents in mass units, but levels (percent of total FA) of these PUFA are ‘diluted’ by the other FAs in TAG. Hence, our study confirmed, that the nutritive value of fish species for humans should be estimated basing on mass units, mg per g of consumed tissues, rather than on the basis of total FA percentage.

In the present work, the data on EPA and DHA contents in seven species of the genus *Coregonus* were obtained for the first time except the only report for *C. lavaretus* [76]. Majority of these species in most studied water bodies appeared to be the valuable food source for humans, i.e., they could provide the recommended daily personal doze of EPA and DHA. However, environmental conditions of the species habitats should be taken in account in future works, since some ecological factors could diminish the species (genus)-specific contents of the essential PUFA in fish biomass.

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Compliance with Ethical Standards

Conflict of interest All authors have no conflicts of interest.

References

1. Hibbeln JR, Nieminen LRG, Blasbalg TL, Riggs JA, Lands WEM (2006) Healthy intakes of n-3 and n-6 fatty acids: estimations considering worldwide diversity. Am J Clin Nutr 83:1483S–1493

2. McNamara RK, Carlson SE (2006) Role of omega-3 fatty acids in brain development and function: Potential implications for the pathogenesis and prevention of psychopathology. Prostaglandins, Leukotrienes Essent Fatty Acids 75: 329–349

3. Adkins Y, Kelley DS (2010) Mechanisms underlying the cardioprotective effects of omega-3 polyunsaturated fatty acids. J Nutr Biochem 21:781–792

4. De Caterina R (2011) n–3 Fatty acids in cardiovascular disease. N Engl J Med 364:2439–2450

5. Harris WS, Mozaffarian D, Lefevre M, Toner CD, Colombo J, Cunnane SC, Holden JM, Klurfeld DM, Morris MC, Whelan J (2009) Towards establishing dietary reference intakes for eicosapentaenoic and docosahexaenoic acids. J Nutr 139:804S–819S

6. Kris-Etherton P.M., Grieger J.A., Etherton T.D. (2009) Dietary reference intakes for DHA and EPA. Prostaglandins, Leukotrienes and Essential Fatty Acids 81: 99–104.

7. Casula M, Soranna D, Catapano AL, Corrao G (2013) Long-term effect of high dose omega-3 fatty acid supplementation for secondary prevention of cardiovascular outcomes: A meta-analysis of randomized, double blind, placebo controlled trials. Atheroscler Suppl 14:243–251

8. Nagasaka R, Gagnon C, Swist E, Rondeau I, Massarelli I, Cheung W, Ratnayake WMN (2014) EPA and DHA status of South Asian and white Canadians Living in the National Capital Region of Canada. Lipids 49:1057–1069

9. Robert SS (2006) Production of eicosapentaenoic and docosahexaenoic acid-containing oils in transgenic land plants for human and aquaculture nutrition. Mar Biotechnol 8:103–109

10. Gladyshev MI, Sushchik NN, Makhutova ON (2013) Production of EPA and DHA in aquatic ecosystems and their transfer to the land. Prostaglandins Other Lipid Mediators 107:117–126

11. Gladyshev MI, Makhutova ON, Gubanenko GA, Rechkina EA, Kalachova GS, Sushchik NN (2015) Livers of terrestrial production animals as a source of long-chain polyunsaturated fatty acids for humans: An alternative to fish? Eur J Lipid Sci Technol 117: 17–1421

12. Tacon AGJ, Metian M (2013) Fish matters: importance of aquatic foods in human nutrition and global food supply. Rev Fish Sci 21:22–38

13. Kwetegyeka J, Mpango G, Grahl-Nielsen O (2008) Variation in fatty acid composition in muscle and heart tissues among species and populations of tropical fish in lakes Victoria and Kyoga. Lipids 43:1017–1029

14. Vasconi M, Caprino F, Bellagamba F, Busetto ML, Bernardi C, Puzzi C, Moretti VM (2015) Fatty acid composition of freshwater wild fish in subalpine lakes: a comparative study. Lipids 50:283–302

15. Chuang L-T, Bulbul U, Wen P-C, Glew RH, Ayaz FA (2012) Fatty acid composition of 12 fish species from the Black Sea. J Food Sci 77:C512–C518

16. Makhutova ON, Sushchik NN, Gladyshev MI, Ageev AV, Pryanichnikova EG, Kalachova GS. 2011. Is the fatty acid composition of freshwater zoobenthic invertebrates controlled by phylogenetic or trophic factors? Lipids 46:709–721

17. Lau DCP, Vrede T, Pickova J, Goedkoop W (2012) Fatty acid composition of consumers in boreal lakes – variation across species, space and time. Freshwater Biol 57:24–38

18. Litzow MA, Bailey KM, Prahl FG, Heintz R (2006) Climate regime shifts and reorganization of fish communities: the essential fatty acid limitation hypothesis. Mar Ecol Prog Ser 315:1–11

19. Sushchik NN, Gladyshev MI, Kalachova GS (2007) Seasonal dynamics of fatty acid content of a common food fish from the Yenisei River, Siberian grayling, *Thymallus arcticus*. Food Chem 104:1353–1358

20. Garg ML, Wood LG, Singh H, Moughan PJ (2006). Means of delivering recommended levels of long chain n-3 polyunsaturated fatty acids in human diets. J Food Sci 71:R66–R71

21. Rubio-Rodriguez N, Beltran S, Jaime I, de Diego SM, Sanz M, Carballido JR (2010) Production of omega-3 polyunsaturated fatty acid concentrates: a review. Innovative Food Sci Emerging Technol 11:1–12

22. Taipale SJ, Vuorioc K, Strandberg U, Kahilainen KK, Jarvinen M, Hiltunen M, Peltomaa E, Kankaala P (2016) Lake eutrophication and brownification downgrade availability and transfer of essential fatty acids for human consumption. Environ Int 96:156–166

23. Ahlgren G, Vrede T, Goedkoop W (2009) Fatty acid ratios in freshwater fish, zooplankton and zoobenthos - are their specific optima? In: Arts MT, Kainz M, Brett MT (eds) Lipids in aquatic ecosystems. Springer, New York

24. Gladyshev MI, Lepskaya EV, Sushchik NN, Makhutova ON, Kalachova GS, Malyshevskaya KK, Markevich GN (2012) Comparison of polyunsaturated fatty acids content in filets of anadromous and landlocked sockeye salmon *Oncorhynchus nerka*. J Food Sci 77:C1306–C1310

25. Hixson SM, Sharma B, Kainz MJ, Wacker A, Arts MT (2015) Production, distribution, and abundance of long-chain omega-3 polyunsaturated fatty acids: a fundamental dichotomy between freshwater and terrestrial ecosystems. Environ Rev 23: 414–424

26. Gladyshev MI, Sushchik NN, Gubanenko GA, Demirchieva SM, Kalachova GS (2007) Effect of boiling and frying on the content of essential polyunsaturated fatty acids in muscle tissue of four fish species. Food Chem 101:1694–1700

27. Gladyshev MI, Artamonova VS, Makhrov AA, Sushchik NN, Kalachova GS, Dgebuadze YY (2017) Triploidy does not decrease contents of eicosapentaenoic and docosahexaenoic acids in filets of pink salmon Oncorhynchus gorbuscha. Food Chem 216:66–69

28. Huynh MD, Kitts DD (2009) Evaluating nutritional quality of pacific fish species from fatty acid signatures. Food Chem 114:912–918

29. Popova ON., Haritonov AY, Sushchik NN, Makhutova ON, Kalachova GS, Anzhelika A. Kolmakova AA, Michail I. Gladyshev MI (2017) Export of aquatic productivity, including highly unsaturated fatty acids, to terrestrial ecosystems via Odonata. Sci Total Environ 581–582:40–48

30. Gladyshev MI, Gribovskaya IV, Adamovich VV (1993) Disappearance of phenol in water samples taken from the Yenisei River and the Krasnoyarsk reservoir. Water Res 27:1063–1070, doi:10.1016/0043-1354(93)90071-O

31. Gladyshev MI, Kolmakova OV, Tolomeev AP, Anishchenko OV, Makhutova ON, Kolmakova AA, Kravchuk ES, Glushchenko LA, Kolmakov VI, Sushchik NN (2015) Differences in organic matter and bacterioplankton between sections of the largest Arctic river: Mosaic or continuum? Limnol Oceanogr 60:1314–1331

32. Pichugin MY (2009) The development of an artificial hybrid and revealing elements of reproductive isolation between sympatric forms of Dryagin's char and *Salvelinus alpinus* complex (Salmonidae) from Sobachye mountain lake (Taimyr). J Ichthyol 49:236–248

33. Leonov AV, Filatov NN, Zdorovennov RE, Zdorovennova GE (2006) Mathematical modeling of the ecosystem functioning conditions in the Chupa estuary of the White Sea: transformation of organogenic substances and bioproductivity of the marine environment. Water Resour 33:543–567

34. The White Sea and its watershed under influences of climate and anthropogenic impacts. (2007) Filatov N, Terzhevik A (eds). Karelian Research Center of the RAS, Petrozavodsk (in Russian)

35. Gritsevskaya GL, Kyabeleva GK, Nikolayeva LA, Semenov VN (1972) Hydrology and hydrochemistry of Solovetsky lakes. Proceedings of SevNIORH 6:5–44 (in Russian)

36. Savina EA (1991) Evaluation of degree of water pollution of surface waterbodies of the Solovetsky archipelago. In: Boyarsky PV (ed) Unknown Solovkee. Russian Scientific Research Institute of Cultural and Natural Heritage, Moscow (in Russian).

37. Natural environments of the Solovetsky archipelago in a changing climate. (2007) Shvartsman YuG, Bolotov IN (eds). Ural Branch of the Russian Academy of Science,Yekaterinburg (in Russian)

38. Lake Onega. Atlas. (2010) Filatov NN (ed). Karelian Research Centre of the RAS, Petrozavodsk (in Russian)

39. Annals of nature recorded by Federal Institution “Nature Reserves of Taimyr” (2016) Issue 3. Norilsk (in Russian)

40. Vyshegorodcev AA (2000) Fishes of the Yenisei. Nauka, Novosibirsk (in Russian)

41. White Sea biological resources and problems of their rational exploitation. Part II (1995) Scarlato OA (ed). Zoological Institute of the RAS, St.-Petersburg (in Russian)

42. Bioresources of Lake Onego. (2008) Kukharev VI, Lukin AA (eds). Karelian Research Centre of the RAS, Petrozavodsk (in Russian)

43. Sterligova OP, Ilmast NV, Savosin DS (2016) Cyclostomata and fish of freshwater of Karelia. Karelian Scientific Center of RAS, Petrozavodsk (in Russian)

44. Rusakova SA (1972) Feeding of vendace of the Goreloye Lake and the Bolshoie Krasnoie Lake. Proceedings of SevNIORH 6:85–89 (in Russian)

45. Borovikova EA, Alekseeva YaI, Schreider MJ, Artamonova VS, Makhrov AA (2013) Morphology and genetics of the ciscoes (Actinopterygii: Salmoniformes: Salmonidae: Coregoninae: *Coregonus*) from the Solovetsky Archipelago (White Sea) as a key to determination of the taxonomic position of ciscoes in Northeastern Europe. Acta Ichthyol Piscatoria 43:183–194

46. Gladyshev MI, Sushchik NN, Gubanenko GA, Makhutova ON, Kalachova GS, Rechkina EA, Malyshevskaya KK (2014) Effect of the way of cooking on contents of essential polyunsaturated fatty acids in filets of zander. Czech J Food Sci 32:226–231

47. Legendre P, Legendre L (1998) Numerical Ecology. Elsevier Science, Amsterdam

48. Wagner T, Jones ML, Ebener MP, Arts MT, Brenden TO, Honeyfield DC, Wright GM, Faisal M (2010) Spatial and temporal dynamics of lake whitefish (*Coregonus clupeaformis*) health indicators: Linking individual-based indicators to a management-relevant endpoint. J Great Lakes Res 36:121–134

49. Cladis DP, Kleiner AC, Freiser HH, Santerre CR (2014) Fatty acid profiles of commercially available finfish fillets in the United States. Lipids 49:1005–101

50. Neff MR, Bhavsar SP, Braekevelt E, Arts MT (2014) Effects of different cooking methods on fatty acid profiles in four freshwater fishes from the Laurentian Great Lakes region. Food Chem 164:544–550

51. Guler GO, Aktumsek A, Cakmak YS, Zengin G, Citil OB (2011) Effect of season on fatty acid composition and n-3/n-6 ratios of zander and carp muscle lipids in Altinapa Dam Lake. J Food Sci 76:C594–C597

52. Philibert A, Vanier C, Abdelouahab N, Chan HM, Mergler D (2006) Fish intake and serum fatty acid profiles from freshwater fish. Am J Clin Nutr 84:1299–1307

53. Arts MT, Kohler CC (2009) Health and condition in fish: the influence of lipids on membrane competency and immune response. ? In: Arts MT, Kainz M, Brett MT (eds) Lipids in aquatic ecosystems. Springer, New York

54. Arts MT, Palmer ME, Skiftesvik AB, Jokinen IE, Browman HI (2012) UVB radiation variably affects n-3 fatty acids but elevated temperature reduces n-3 fatty acids in juvenile Atlantic salmon (*Salmo salar*). Lipids 47:1181–1192

55. Wall R, Ross RP, Fitzgerald GF, Stanton C (2010) Fatty acids from fish: the anti-inflammatory potential of long-chain omega-3 fatty acids. Nutr Rev 68:280–289

56. Pethybridge HR, Parrish CC, Morrongiello J, Young JW, Farley JH, Gunasekera RM, Nichols PD (2015) Spatial patterns and temperature predictions of tuna fatty acids: tracing essential nutrients and changes in primary producers. PLoS ONE 10(7): e0131598

57. Gokce MA, Tasbozan O, Celik M, Tabakoglu S S (2004). Seasonal variations in proximate and fatty acid compositions of female common sole (*Solea solea*). Food Chem 88:419–423

58. Laurel BJ, Copeman LA, Parrish CC (2012) Role of temperature on lipid/fatty acid composition in Pacific cod (*Gadus macrocephalus*) eggs and unfed larvae. Mar Biol 159:2025–2034

59. Murzina SA, Nefedova ZA, Falk-Petersen S, Ripatti PO, Ruokolainen TR, Pekkoeva SN, Nemova NN (2013) Lipid status of the two high latitude fish species, *Leptoclinus maculatus* and *Lumpenus fabricii*. Int J Mol Sci 14:7048–7060

60. Wijekoon MPA, Parrish CC, Mansour A (2014) Effect of dietary substitution of fish oil with flaxseed or sunflower oil on muscle fatty acid composition in juvenile steelhead trout (Oncorhynchus mykiss) reared at varying temperatures. Aquaculture 433:74–81

61. Gribble MO, Karimi R, Feingold BJ, Nyland JF, O'Hara TM, Gladyshev MI, Chen CY (2016) Mercury, selenium and fish oils in marine food webs and implications for human health. J Mar Biol Assoc U K 96:43–59

62. Stillwell W, Wassall SR (2003) Docosahexaenoic acid: membrane properties of a unique fatty acid. Chem Phys Lipids 126:1–27

63. Dymond MK (2015) Mammalian phospholipid homeostasis: Homeoviscous adaptation deconstructed by lipidomic data driven modelling. Chem Phys Lipids 191:136–146

64. Dymond MK (2016) Mammalian phospholipid homeostasis: evidence that membrane curvature elastic stress drives homeoviscous adaptation in vivo. J R Soc Interface 13: 20160228.

65. Ahlgren G, Sonesten L, Boberg M, Gustafsson I-B (1996) Fatty acid content of some freshwater fish in lakes of different trophic levels - a bottom-up effect? Ecol Freshw Fish 5:15–27

66. Graeve M, Albers C, Kattner G (2005) Assimilation and biosynthesis of lipids in Arctic Calanus species based on feeding experiments with a 13C labelled diatom. J Exp Mar Biol Ecol 317:109– 125

67. Kattner G, Hagen W (2009) Lipids in marine copepods: latitudinal characteristics and perspectives to global warming. In: Arts MT, Kainz M, Brett MT (eds) Lipids in aquatic ecosystems. Springer, New York

68. Lee RF, Hagen W, Kattner G (2006) Lipid storage in marine zooplankton. Mar Ecol Prog Ser 307:273–306

69. Ozawa A, Satake M, Fujita T (1993) Comparison of muscle lipid composition between marine and landlocked forms of sockeye salmon (*Oncorhynchus nerka*). Comp Biochem Physiol B 106:513–516

70. Makhutova ON, Protasov AA, Gladyshev MI, Sylaieva AA, Sushchik NN, Morozovskaya IA, Kalachova GS (2013) Feeding spectra of bivalve mollusks *Unio* and *Dreissena* from Kanevskoe Reservoir, Ukraine: are they food competitors or not? Zool Stud 52: Art. No. 56

71. Torstensen BE, Froyland L, Ornsrud R, Lie O (2004) Tailoring of a cardioprotective muscle fatty acid composition of Atlantic salmon (*Salmo salar*) fed vegetable oils. Food Chem 87:567–580

72. Stone DAJ, Oliveira ACM, Plante S, Smiley S, Bechtel P, Hardy RW (2011) Enhancing highly unsaturated omega-3 fatty acids in phase-fed rainbow trout (*Oncorhynchus mykiss*) using Alaskan fish oils. Aquacult Nutr 17: E501–E510

73. Sushchik NN, Rudchenko AE, Gladyshev MI (2017) Effect of season and trophic level on fatty acid composition and content of four commercial fish species from Krasnoyarsk Reservoir(Siberia, Russia). Fish Res187:178–187

74. Mairesse G, Thomas M, Gardeur J-N, Brun-Bellut J (2006) Effects of geographic source, rearing system, and season on the nutritional quality of wild and farmed *Perca fluviatilis*. Lipids 41:221–229

75. Benedito-Palos L, Calduch-Giner JA, Ballester-Lozano GF, Perez-Sanchez J (2013) Effect of ration size on fillet fatty acid composition, phospholipid allostasis and mRNA expression patterns of lipid regulatory genes in gilthead seabream (*Sparus aurata*). Br J Nutr 109:1175–1187

76. Suomela J-P, Lundén S, Kaimainen M, Mattila S, Kallio H, Airaksinen S (2016) Effects of origin and season on the lipids and sensory quality of European whitefish (*Coregonus lavaretus*). Food Chem 197:1031–1037

Figure Captions

Fig 1 Map of sample sites (pointed by arrows): KR – the Keret River; BKL – the Bolshoie Krasnoie Lake (situated in the Bolshoy Solovetsky Island in the White Sea), SL – the Sobachye Lake

Fig 2 Canonical correspondence analysis of levels of fatty acids (% of total) in species of genus *Coregonus*: autY – *C. autumnalis* from the Yenisei River (red circles); sarY – *C. sardinella* from the Yenisei River (black circles); pelY – *C. peled* from the Yenisei River (blue circles); lavY – *C. lavaretus* from the Yenisei River (green circles); tugY – *C. tugun* from the Yenisei River (violet circles); nasY – *C. nasus* from the Yenisei River (light-blue circles); sarS – *C. sardinella* from the Sobachye Lake (black squares); tugS – *C. tugun* from the Sobachye Lake (violet squares); nasS – *C. nasus* from the Sobachye Lake (light-blue squares); lavS – *C. lavaretus* from the Sobachye Lake (green squares); lavK – *C. lavaretus* from the Keret River (green diamonds); lavO – *C. lavaretus* from Lake Onega (orange triangles); albB – *C. albula* from the Bolshoie Krasnoie Lake (rose crosses). Dimension 1 and Dimension 2 represented 48.1% and 15.5% of inertia, respectively

Fig 3 Mean content (mg·g^{-1} wet weight) of eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) and their sum (EPA+DHA) in species of genus *Coregonus*: autY – *C. autumnalis* from the Yenisei River; sarY – *C. sardinella* from the Yenisei River; pelY – *C. peled* from the Yenisei River; lavY – *C. lavaretus* from the Yenisei River; tugY – *C. tugun* from the Yenisei River; nasY – *C. nasus* from the Yenisei River; sarS – *C. sardinella* from the Sobachye Lake; tugS – *C. tugun* from the Sobachye Lake; nasS – *C. nasus* from the Sobachye Lake; lavS – *C. lavaretus* from the Sobachye Lake; lavK – *C. lavaretus* from the Keret River; lavO – *C.*

lavaretus from Lake Onega; albB – *C. albula* from the Bolshoie Krasnoie Lake. Bars represent standard error. Means labelled with the same letter are not significantly different at $P < 0.05$ after Kruskal-Wallis test