

# Fatty Acid Composition and Contents of Seven Commercial Fish Species of Genus *Coregonus* from Russian Subarctic Water Bodies

Michail I. Gladyshev<sup>1,2</sup> · Nadezhda N. Sushchik<sup>1,2</sup> · Olesia N. Makhutova<sup>1,2</sup> · Larisa A. Glushchenko<sup>2</sup> · Anastasia E. Rudchenko<sup>2</sup> · Alexander A. Makhrov<sup>3</sup> · Elena A. Borovikova<sup>4</sup> · Yury Y. Dgebuadze<sup>3</sup>

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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<sup>-1</sup> 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<sup>-1</sup> wet weight, and for *C. lavaretus* from the Sobachye Lake, 16.61 mg g<sup>-1</sup> wet weight, respectively. Intra-genus variations of EPA + DHA contents of *Coregonus* species were from 1.87 to 17.60 mg g<sup>-1</sup> 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: migrational capability, 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.

**Keywords** Eicosapentaenoic acid · Docosahexaenoic acid · Anadromous fish · Freshwater fish · Planktivory · Benthivory

## 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 (PUFA) of the omega-3 (n-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 has been 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

✉ Michail I. Gladyshev  
glad@ibp.ru

<sup>1</sup> Institute of Biophysics of Siberian Branch of Federal Research Center “Krasnoyarsk Science Center” of Russian Academy of Sciences, Akademgorodok, 50/50, Krasnoyarsk 660036, Russia

<sup>2</sup> Siberian Federal University, Svobodny av. 79, Krasnoyarsk 660041, Russia

<sup>3</sup> A. N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences, Leninsky prospect, 33, Moscow 119071, Russia

<sup>4</sup> Institute for Biology of Inland Waters of Russian Academy of Sciences, Borok, Yaroslavl Region 152742, Russia

[10]. Some fish, especially freshwater species, have such low contents of EPA and DHA that it is impossible to obtain the recommended daily dose by eating these fish [e.g., 13, 14]. Thus, studies regarding PUFA contents of various fish species offer at least two benefits. First, 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 attainability of desirable healthy PUFA intakes [5, 15]. Second, 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 factors and ecological factors [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 as controlling FA contents of fish. For instance, pelagic-feeding species are regarded as richer in lipids, including EPA and DHA, than demersal fish [12, 18]. Piscivorous fish are believed to have relatively higher EPA and DHA content [14, 19]. Marine fish seem to be richer in PUFA, including EPA and DHA, than freshwater species [20, 21]. Fish from oligotrophic water bodies appeared to have comparatively higher PUFA contents [22]. However, at least one phylogenetic factor, species identity, may outweigh the ecological factors with regard to EPA and DHA contents in fish [13, 23, 24]. Indeed, in spite of any ecological factors, the maximum value of EPA and DHA content in species from, for example, 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 can variations of the PUFA contents be ascribed to 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 supplies for humans. The information about the taxon-specific limits also seems to be useful for fish aquaculture, especially for introducing 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 ( $\text{mg g}^{-1}$ ), 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 the Russian Subarctic. To our knowledge, this was the first attempt to determine taxon (genus)-specific limits of EPA and DHA contents in wild fish. In addition, we aimed to test common ideas concerning differences in EPA and DHA contents between planktivorous and benthivorous fish using congeneric species. 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 Khimreaktivsnab (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 by cautiously dissolving sodium in methanol. The solution was stored at 4 °C no more than a week prior to 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  $\text{mg mL}^{-1}$  and analysed by GC–MS. Methyl ester of nonadecanoic acid (Sigma-Aldrich, USA) was used as an internal standard, a stock solution of which in chloroform at concentration of 1  $\text{mg mL}^{-1}$  was prepared and stored at –20 °C.

### Aquatic Environments

All sampled water bodies (Table 1) were oligotrophic (except nearly mesotrophic Lake Onega) and had low water temperature, 6.5–15 °C. 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.

Sampling was conducted in accordance with the Bio-Ethics 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

**Table 1** Description of studied water bodies

Water body	Location	A or L <sup>a</sup>	$h_{av}^b$	$h_{max}^c$	$t^d$	pH	P <sup>e</sup>	N <sup>f</sup>	Chl <sup>g</sup>	References
The Yenisei River	69°28'N 86°01'E	3840	14	45	15	7.5	4	0.30	4	[30, 31] <sup>h</sup>
The Sobachye Lake	69°01'N 91°05'E	99	nd	162	6.5	nd	nd	nd	nd	[32] <sup>h</sup>
The Keret River	66°16'N 33°33'E	80	nd	nd	nd	6.8	5	0.22	nd	[33, 34]
The Bolshoie Krasnoie Lake	65°05'N 35°38'E	3	10	25	nd	7.2	nd	0.06	nd	[35–37]
Lake Onega	61°51'N 34°35'E	9720	30	120	11–16	7.5	10	0.25	5	[38]

nd no data

<sup>a</sup>A or L—surface area (A, km<sup>2</sup>) for lakes and length (L, km) for rivers

<sup>b</sup>Average depth ( $h_{av}$ , m)

<sup>c</sup>Maximum depth ( $h_{max}$ , m)

<sup>d</sup>Water temperature ( $t$ , °C) at periods of sampling

<sup>e</sup>Inorganic phosphorus (P,  $\mu\text{g L}^{-1}$  PO<sub>4</sub>-P)

<sup>f</sup>Inorganic nitrogen (N,  $\text{mg L}^{-1}$  NH<sub>4</sub>-N + NO<sub>3</sub>-N)

<sup>g</sup>Concentration of chlorophyll *a* of phytoplankton (Chl,  $\mu\text{g L}^{-1}$ )

<sup>h</sup>And our unpublished data



**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

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 are semi-anadromous fish, which feed in the Yenisei Gulf (the Kara Sea) and migrate in the river for spawning [40]. The 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, are semi-anadromous fish which feed in the Yenisei Gulf and migrate in the river for spawning. Least cisco from the Sobachye Lake are landlocked fish. The least cisco is primarily a 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 Lake Onega. In the Keret River, *C. lavaretus* is semi-anadromous fish, which feed in the

**Table 2** The basic biological and sampling information on *Coregonus* species from Russian Subarctic water bodies, 2016

Species name	Common name	Water body	<i>n</i> <sup>a</sup>	Month <sup>b</sup>	<i>L</i> <sup>c</sup>	<i>W</i> <sup>d</sup>	Food <sup>e</sup>	Reproduction <sup>f</sup>
<i>C. autumnalis</i>	Arctic cisco	Yenisei River	7	Sept	38.5 ± 1.0	650 ± 70	Crustaceans	Oct
<i>C. sardinella</i>	Least cisco	Yenisei River	8	Aug	20.1 ± 0.4	79 ± 5	Cladocerans	Oct–Nov
<i>C. peled</i>	Peled	Yenisei River	7	Aug	33.2 ± 0.6	534 ± 41	Detritus	Oct
<i>C. lavaretus</i>	Whitefish	Yenisei River	7	Aug	29.8 ± 0.9	340 ± 28	Chironomid larvae, mollusks	Oct–Nov
<i>C. tugun</i>	Tugun	Yenisei River	8	Aug	10.2 ± 0.1	10 ± 1	Chironomids larvae, cladocerans, copepods	Oct
<i>C. nasus</i>	Broad whitefish	Yenisei River	6	Aug–Sept	36.5 ± 5.1	872 ± 353	Mollusks, chironomid larvae	Oct–Nov
<i>C. sardinella</i>	Least cisco	Sobachye Lake	6	Sept	26.7 ± 0.4	163 ± 4	Cladocerans, copepods	Oct–Nov
<i>C. tugun</i>	Tugun	Sobachye Lake	7	Sept	13.7 ± 0.4	27 ± 2	Cladocerans, copepods, chironomid larvae	Oct
<i>C. nasus</i>	Broad whitefish	Sobachye Lake	7	Sept	41.0 ± 2.5	936 ± 207	Mollusks, amphipods, chironomid larvae	Oct–Nov
<i>C. lavaretus</i>	Whitefish	Sobachye Lake	7	Sept	44.9 ± 1.4	1303 ± 141	Mollusks, amphipods, chironomid larvae	Oct–Nov
<i>C. lavaretus</i>	Whitefish	Keret River	14	Sept–Oct	34.4 ± 0.8	348 ± 34	nd	Oct–Nov
<i>C. lavaretus</i>	Whitefish	Onega Lake	7	Aug	19.9 ± 0.3	66 ± 4	nd	Oct–Nov
<i>C. albula</i>	Vendace	Bolshoie Krasnoie Lake	8	Jun	19.8 ± 0.5	54 ± 4	nd	Nov–Dec

nd no data

<sup>a</sup>*n*—number of sampled individuals

<sup>b</sup>Month of catching

<sup>c</sup>*L*—total length, cm (mean ± SE)

<sup>d</sup>*W*—total weight, g (mean ± SE)

<sup>e</sup>Food items found in stomachs

<sup>f</sup>Months of reproductive period

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 a 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 a benthivore [40] (Table 2).

Vendace *Coregonus albula* (Linnaeus, 1758) in the Bolshoie Krasnoie Lake is a 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 samples were subdivided into two subsamples, for moisture and fatty acid analyses, respectively. To measure moisture, subsamples of ca. 1–2 g of wet weight were weighed, dried at 75 °C until constant weight, and weighed dry. The other sub-samples of muscle tissue were immediately weighed, placed into chloroform/methanol mixture (2:1, by vol.) and kept until further analysis at –20 °C. The samples were transported frozen to the laboratory in 1–2 weeks. Lipid analyses were done within 2 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<sub>2</sub>SO<sub>4</sub>, and chloroform and methanol were roto evaporated under vacuum at 35 °C. The extracted lipid was dissolved in 1 mL of hexane, then 0.2 mL of 3 M methanolic sodium methoxide solution was added, and the 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 to 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<sub>2</sub>SO<sub>4</sub>, and hexane was removed by roto-evaporating at 30 °C. The FAME were redissolved in 150–300 µL of hexane prior to 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 lipid extraction.

### Statistical Analysis

Kolmogorov–Smirnov one-sample test for normality  $D_{K-S}$ , 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 variation. *C. lavaretus* from the Sobachye Lake tended to have the lowest value of moisture,  $66.1 \pm 2.9\%$ , while *C. sardinella* from the Sobachye Lake tended to have the highest value,  $78.3 \pm 0.5\%$ . The difference between these values was statistically significant:  $P = 0.000129$  after the Kruskal–Wallis test.

In all samples, 70 FA were identified. However, for the following analysis, only 25 quantitatively prominent FA (mean level  $> 0.5\%$  at least in one fish species) were taken (Table 3). Thus, total sums of FA in Table 3 were lower than 100%.

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  $\Sigma 20:1$  and 18:4n-3 in the species (Fig. 2).

*C. autumnalis* from the Yenisei River tended to have minimal mean levels of 17:0, 20:4n-6 and 22:5n-6, but also tended to have maximum levels of  $\Sigma 20:1$  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  $\Sigma 20:1$ , 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. autumnalis* from the Yenisei River tended to have the highest content of total FA while *C. lavaretus* from the Keret River tended to have the lowest content of total FA, (Table 3). *C. lavaretus* from two other habitats, Lake Onega and the Yenisei River, like this species from the Keret River, had comparatively low content of total FA, while *C. lavaretus* from the Sobachye Lake had very high content of total FA (Table 3).

Mean contents of EPA + DHA in the studied congeneric species varied from  $1.87 \pm 0.06$  mg g<sup>-1</sup> wet weight in *C. lavaretus* from Lake Onega to  $17.60 \pm 3.63$  mg g<sup>-1</sup> 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,  $16.61 \pm 2.80$  mg g<sup>-1</sup> wet weight (Fig. 3). Thus, variations of average EPA and DHA contents between the congeneric species were ~ 10-fold, from 0.7 mg g<sup>-1</sup> of *C. lavaretus* from the Keret River to 9.9 mg g<sup>-1</sup> of *C. lavaretus* from the Sobachye Lake and from 1.1 mg g<sup>-1</sup> of *C. lavaretus* from Lake Onega to 9.0 mg g<sup>-1</sup> of *C. autumnalis* from the Yenisei River, respectively (Fig. 3). Meanwhile, variations of average percentages of EPA and DHA were ~ 4-fold only, from 6.3% of *C. tugun* from the Yenisei River to 12.1% of *C. lavaretus* from the Keret River and from 5.9% of *C. tugun* from the Yenisei River to 26.5% of *C. lavaretus* from the Keret River, respectively (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<sup>-1</sup> wet weight. Values of the contents of another species of this genus, published in available literature, fell

**Table 3** Mean levels of fatty acids (mol% of the total) and total content of fatty acids (total FA, mg g<sup>-1</sup> of wet weight) of species of genus of species of genus *Coregonus*. Cases (fatty acids) with normal distribution are given in bold

Fatty acid	autY <sup>a</sup>	sarY <sup>b</sup>	peY <sup>c</sup>	lavY <sup>d</sup>	tugY <sup>e</sup>	nasY <sup>f</sup>	sarS <sup>g</sup>	tugS <sup>h</sup>	nasS <sup>i</sup>	lavS <sup>j</sup>	lavK <sup>k</sup>	lavO <sup>l</sup>	albB <sup>m</sup>
<b>14:0</b>	5.2	5.7	3.4	2.5	3.7	2.3	4.7	5.4	2.8	3.5	1.4 <sup>A</sup>	3.8	7.3 <sup>B</sup>
<b>15:0</b>	0.4	0.6 <sup>B</sup>	0.5	0.6 <sup>B</sup>	0.5	0.6	0.4	0.4	0.5	0.3 <sup>A</sup>	0.4	0.5	0.4
<b>16:0</b>	17.8	19.8	21.3	23.1	19.9	20.0	20.4	17.4	18.3	16.1 <sup>A</sup>	25.7 <sup>B</sup>	22.6	20.1
<b>16:1n-9</b>	0.2	0.3	0.7	0.4	0.5	0.5	0.4	0.6	0.4	0.2 <sup>A</sup>	0.3	0.9 <sup>B</sup>	0.7
<b>16:1n-7</b>	18.1	12.8	8.0	9.8	12.7	9.4	5.5	9.1	16.7	19.8 <sup>B</sup>	4.7	9.5	3.4 <sup>A</sup>
<b>15-17BFA</b>	0.7	1.5	2.5 <sup>B</sup>	1.6	1.3	2.2	1.3	1.4	1.6	0.9	0.4 <sup>A</sup>	1.3	1.5
16PUFA	1.8	1.4	1.3	1.1	1.9	1.0	0.8	1.3	3.2	4.4 <sup>B</sup>	0.3	0.6	0.2 <sup>A</sup>
<b>17:0</b>	0.1 <sup>A</sup>	0.3	0.7 <sup>B</sup>	0.5	0.6	0.6	0.3	0.3	0.4	0.3	0.3	0.7 <sup>B</sup>	0.3
18:0	2.0	2.6	3.6	3.8	5.2	4.1	3.0	3.5	5.6 <sup>B</sup>	1.8 <sup>A</sup>	3.3	3.4	2.9
<b>18:1n-9</b>	14.6	14.4	14.7	11.1	20.1 <sup>B</sup>	16.3	8.0	11.0	9.0	19.3	11.1	7.5 <sup>A</sup>	12.2
<b>18:1n-7</b>	5.3	4.7	4.0	4.2	5.5	5.5	2.4	4.0	6.1 <sup>B</sup>	4.2	3.5	4.6	1.9 <sup>A</sup>
<b>18:2n-6</b>	1.2	3.3	2.6	2.9	3.8	3.7	3.0	5.1 <sup>B</sup>	4.4	2.3	0.8 <sup>A</sup>	2.6	3.4
<b>18:3n-3</b>	0.8	2.5	4.6 <sup>B</sup>	2.2	4.4	3.0	2.9	4.5	2.2	1.4	0.4 <sup>A</sup>	4.4	3.0
18:4n-3	1.6	1.8	2.1	0.7	1.7	1.1	3.2	3.9 <sup>B</sup>	1.2	1.9	0.4 <sup>A</sup>	1.9	3.9 <sup>B</sup>
Σ20:1 <sup>n</sup>	5.1 <sup>B</sup>	2.7	0.9	0.9	0.9	1.7	0.8	0.5	1.0	1.0	1.5	0.3 <sup>A</sup>	0.7
20:2n-6	0.4	0.8 <sup>B</sup>	0.2 <sup>A</sup>	0.3	0.3	0.5	0.7	0.5	0.5	0.3	0.3	0.2 <sup>A</sup>	0.3
<b>20:4n-6</b>	0.5 <sup>A</sup>	1.0	2.7	3.0	1.5	2.6	2.9	2.4	1.8	1.5	2.5	4.3 <sup>B</sup>	2.5
20:3n-3	0.3	0.9	0.4	0.2	0.3	0.3	1.0 <sup>B</sup>	0.6	0.2	0.2	0.1 <sup>A</sup>	0.3	0.3
20:4n-3	1.2	1.4	0.9	0.4	0.6	0.5	1.9	1.9 <sup>B</sup>	0.5	0.7	0.3 <sup>A</sup>	0.8	1.7
<b>20:5n-3</b>	8.1	7.0	7.0	8.1	6.3 <sup>A</sup>	7.5	9.8	9.0	10.8	9.9	12.1 <sup>B</sup>	11.0	6.7
22:5n-6	0.1 <sup>A</sup>	0.5	1.0	0.6	0.3	0.6	1.6 <sup>B</sup>	0.9	0.3	0.3	0.4	0.8	1.5
22:4n-3	0.6	0.9 <sup>B</sup>	0.2	0.0 <sup>A</sup>	0.0	0.0	0.9	0.3	0.0	0.0 <sup>A</sup>	0.0	0.0	0.0
<b>22:5n-3</b>	2.2	2.1	1.7	2.0	1.3 <sup>A</sup>	2.0	2.6	2.7	2.4	2.2	2.9 <sup>B</sup>	2.4	1.5
<b>22:6n-3</b>	9.1	8.6	13.9	19.4	5.9 <sup>A</sup>	13.0	19.8	12.6	9.1	6.2	26.5 <sup>B</sup>	15.0	23.0
24PUFA	2.6 <sup>B</sup>	2.5	1.0	0.6	0.9	0.7	1.7	0.9	0.9	1.1	0.4 <sup>A</sup>	0.5	0.6
Total FA	100.3 <sup>B</sup>	58.7	15.4	9.7	44.0	11.8	11.3	23.6	32.3	95.3	5.9 <sup>A</sup>	6.6	10.5

The lowest and the highest means, which significantly ( $P < 0.05$ ) differ from each other after ANOVA post hoc Tukey HSD test (cases with normal distribution) or Kruskal–Wallis test, are labelled with letters A and B, respectively. Number of samples,  $n$ , for each species are given in Table 2

<sup>a</sup>autY—*C. autumnalis* from the Yenisei River

<sup>b</sup>sarY—*C. sardinella* from the Yenisei River

<sup>c</sup>peY—*C. peled* from the Yenisei River

<sup>d</sup>lavY—*C. lavaretus* from the Yenisei River

<sup>e</sup>tugY—*C. tugun* from the Yenisei River

<sup>f</sup>nasY—*C. nasus* from the Yenisei River

<sup>g</sup>sarS—*C. sardinella* from the Sobachye Lake

<sup>h</sup>tugS—*C. tugun* from the Sobachye Lake

<sup>i</sup>nasS—*C. nasus* from the Sobachye Lake

<sup>j</sup>lavS—*C. lavaretus* from the Sobachye Lake

<sup>k</sup>lavK—*C. lavaretus* from the Keret River

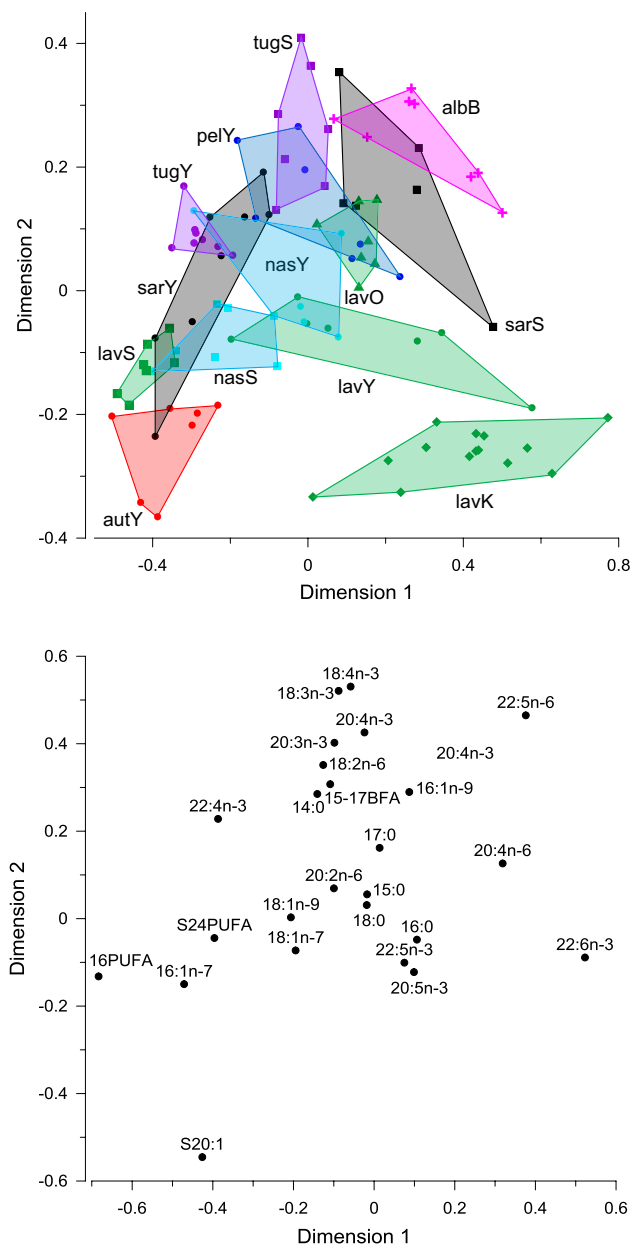
<sup>l</sup>lavO—*C. lavaretus* from Lake Onega

<sup>m</sup>albB—*C. albula* from the Bolshoie Krasnoie Lake

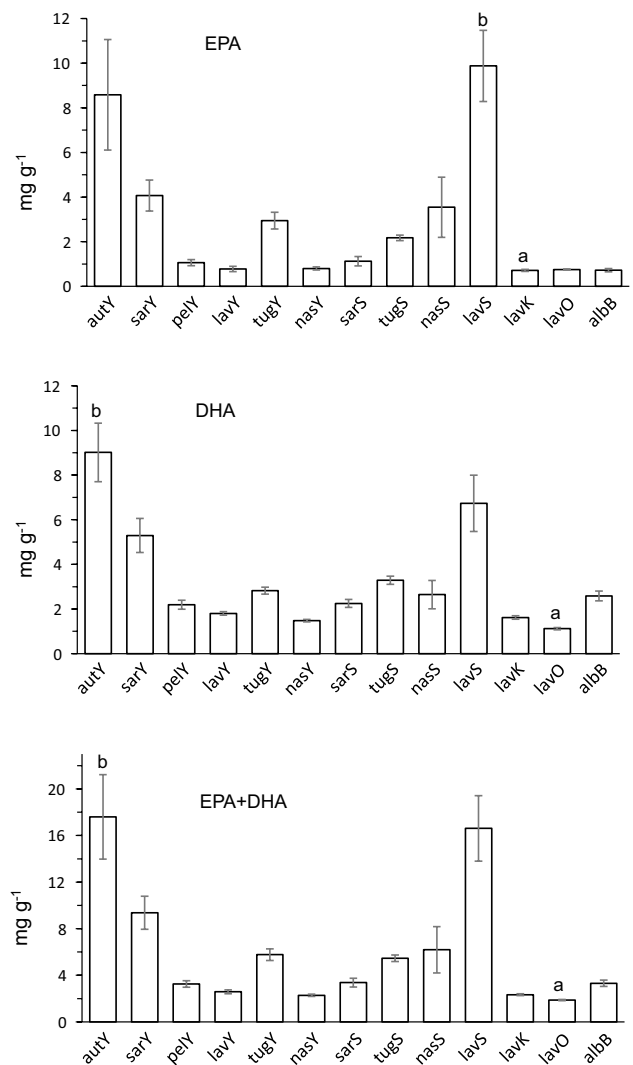
<sup>n</sup>Sum of 20:1n-11, 20:1n-9 and 20:1n-7

in the above range and varied from 3.1 mg g<sup>-1</sup> 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<sup>-1</sup> wet weight in European whitefish

*C. macrophthalmus* ([14], recalculated from Table 5 of the source). Thus, in the present study we expanded the lower and upper limits of intra-genus variations of EPA + DHA contents in wild *Coregonus* species. Moreover, to our



**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 (green 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 ( $\text{mg g}^{-1}$  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. The lowest and the highest means, which significantly ( $P < 0.05$ ) differ from each other after the Kruskal–Wallis test, are labelled with letters a and b, respectively. Number of samples,  $n$ , for each species are given in Table 2

knowledge, the highest values of EPA + DHA content in anadromous and freshwater fish, published in available literature, were 11.06 mg g<sup>-1</sup> wet weight in Chinook salmon (*Oncorhynchus tshawytscha*) [49] and 11.07 mg g<sup>-1</sup> 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<sup>-1</sup> wet weight, and for the landlocked *C. lavaretus* from the Sobachye Lake this value was 16.61 mg g<sup>-1</sup> wet weight. Hence, in the present work, we expanded considerably the upper limit of EPA + DHA contents for anadromous and 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<sup>-1</sup> wet weight in Sardine (*Sardinops sagax*) [28]. Meanwhile, many freshwater fish species, especially in pristine cold oligotrophic Arctic lakes of Russia, which may have very high content of EPA and DHA, are as yet unexplored. 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 those 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 and especially conspecific fish 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 °C caused a decrease of DHA content in juvenile Atlantic salmon (*Salmo salar*) from 4.6 to 3.3 mg g<sup>-1</sup> 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 °C 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 be based on autochthonous resources, microalgae and, to some extent, on allochthonous (terrestrial) organic matter. Autochthonous 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 noting 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 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 causes other than only pelagic feeding (see below). Moreover, in 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 the 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 [31]. Similarly, anadromous (marine) forms of another species of Salmoniformes, *Oncorhynchus nerka*, had considerable levels of  $\Sigma 20:1$  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 a higher level of  $\Sigma 20:1$  and a 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  $\Sigma 20:1$ , and lower level of 20:4n-6 than land-locked species. In addition, it should be noted that some 20:1 acids are markers of mollusks [70]. Indeed, *C. nasus* from the Yenisei River, which consumed primarily mollusks, had a comparatively high level of  $\Sigma 20:1$ .

Comparing anadromous (semi-anadromous) and land-locked conspecific fish, it should be taken in account that land-locked populations may have a higher capacity of biosynthesis (conversion) of long-chain PUFA, EPA and DHA from short-chain n-3 precursor FA compared to that of anadromous populations [71, 72]. For instance, this putative ability might partly explain the higher EPA + DHA content of land-locked *C. lavaretus* from the Sobachye Lake vs. the lower content of migratory *C. lavaretus* from the Keret River.

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 based on vegetable and fish oil, had EPA + DHA content 3.2 and 7.0 mg g<sup>-1</sup>, respectively [73]. Similarly, *Oncorhynchus mykiss*, reared in aquaculture using vegetable and fish oil, had EPA + DHA content 3.7 and 8.3 mg g<sup>-1</sup>, respectively [74]. 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, based 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, 75]. 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 noting 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, 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, as 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 contents of EPA + DHA, 2.33 mg g<sup>-1</sup> 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 be contained mostly in PL, which are structural lipids of cell membranes, and their constant proportions are essential for muscle tissue functioning [76]. Thus, a high proportion of EPA and DHA seems 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, 77]. 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 based on mass units, mg per gram of consumed tissues, rather than on the basis of total FA percentage.

Total FA content, as the proxy of total lipid content [65], seemed to have a considerable effect on EPA + DHA content in fish species. Indeed, *C. lavaretus* from the Sobachye Lake had the highest total FA content and also the highest EPA + DHA content among the studied populations. In turn, *C. lavaretus* from Lake Onega, the Keret River and the Yenisei River had considerably lower total FA contents and accordingly lower EPA + DHA contents.

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* [78]. A majority of these species in most of the studied water bodies appeared to be valuable food sources for humans regarding their high EPA and DHA content. However, environmental conditions of the species habitats should be taken into 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.

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