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Polyunsaturated Fatty Acid Content in the Muscles of Alien Fish Species of the Rybinsk Reservoir

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Abstract—The biochemical composition of the muscles of two fish species, European smelt *Osmerus eperlanus* and the Common (Caspian) kilka *Clupeonella cultriventris*, that were successively invaded and naturalized in the Rybinsk Reservoir in the second half of the 20th century, differs significantly in the fatty acid content. The sum content (mg/g) of eicosapentaenoic (20:5n-3) and docosahexaenoic (22:6n-3) polyunsaturated fatty acids in the muscle tissue of the kilka is almost four times higher than that in European smelt. Given that smelt and the kilka are similar in their ecological and morphological characteristics and do not differ significantly in the composition of their diet in the Rybinsk Reservoir, it is obvious that the observed differences primarily result from the phylogenetic aspect. The obtained data on the composition of the fatty acids of the invaders show that the replacement of one alien species with another (European smelt with the kilka) significantly changed the quality of production of an important link in the trophic web of the reservoir.

Keywords: European smelt *Osmerus eperlanus*, Common kilka *Clupeonella cultriventris*, alien species, polyunsaturated fatty acids, Rybinsk reservoir

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INTRODUCTION

Since the second half of the last century, biological invasions of alien species have become a global problem. More than that, the intensification of the invasive process is constant and observed everywhere and its pressure on native species and ecosystems is growing.

The main reasons for the intensification of the invasive process are climatic changes and human activities. Thus, in the case of climatic fluctuations in large Eurasian river basins, there were at least two successive changes in the direction of hydrobiont invasions over the past 50 years: from north to south, and then from south to north (Slynko et al., 2002, 2010; Popov, 2012). One of such cases is the fish invasion of the water bodies of the northern European invasion corridor (water bodies of the Volga basin). After the construction of canals and reservoirs (formation of lentic ecosystems) in the second half of the 20th century, two pelagic lake species, the smelt *Osmerus eperlanus* and the vendace *Coregonus albula*, distributed over this area from north to south. By the end of the 1970s these species reached the Saratov and Volgograd reservoirs, forming (especially in the Rybinsk reservoir) large self-reproducing populations (Yakovlev et al., 2001). By the beginning of the 21st century, the abundance of these species dropped sharply, and they were replaced in the pelagic zone by the southern invader, the Common (Caspian) kilka *Clupeonella cultriventris*. This replacement was clearly shown on the example of the Rybinsk Reservoir (Dgebuadze et al., 2008; Slynko and Kiyashko, 2012; Kiyashko et al., 2012) (Fig. 1).

Nowadays there is a large amount of data on the changes in the habitats, biodiversity, and food webs of ecosystems associated with the presence of the alien species. In particular, the approaches of production hydrobiology show that the invasion of a new species can either lead to a restructuring of food webs (changes in the direction of the flows of matter and energy), or to a safe invasion of the invader when it act as a native species from that same functional group (Crooks, 2002; Rodriguez, 2006; Gribben et al., 2013; Tassin and Kull, 2015). Much less attention has been paid to the consequences of invasions associated with indirect interactions, in particular, to the qualitative biochemical characteristics of alien species. Such

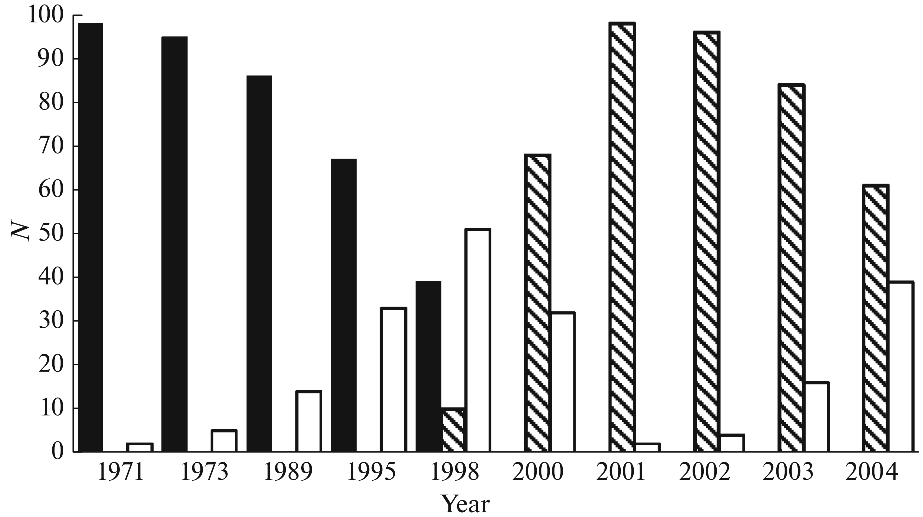

Fig. 1. Dynamics of the fish population (*N*, % of total biomass) in the pelagic zone of the Rybinsk Reservoir at the end of the 20th–beginning of the 21st centuries, according to the control catches by the pelagic trawl of the staff of the Papanin Institute for Biology of Inland Waters of the Russian Academy of Sciences (according to: Dgebuadze et al., 2008): (■) European smelt *Osmerus eperlanus*; (▧), Common kilka *Clupeonella cultriventris*; (□), other fish species.

interactions can have a significant impact not only on the recipient ecosystem, but also on adjacent ecosystems.

In this regard, it is of particular interest to consider cases with the replacement of a native species or an alien species by an invader of the same trophic level, but with different qualitative biochemical characteristics. One of such differences is the content of physiologically and biochemically important substances, in particular, polyunsaturated fatty acids (PUFAs) of the omega-3 (n-3) family, namely eicosapentaenoic (20:5n-3, EPA) and docosahexaenoic (22:6n-3, DHA) acids.

EPA and DHA are essential components of the nutrition of many vertebrates, including fish, as well as humans. EPA is a biochemical precursor for the synthesis of endohormones (lipid mediators)—prostaglandins, thromboxanes, and leukotrienes, which regulate inflammatory and allergic reactions, pain syndrome, and the state of the cardiovascular system. DHA regulates the synthesis of endohormones and is also the main component of phospholipids in the cell membranes of nerve tissues, including the cerebral cortex and retina (SanGiovanni and Chew, 2005; McNamara and Carlson, 2006; Adkins and Kelley, 2010; Wall et al., 2010; Norris and Dennis, 2012; Calder, 2018). Thus, proper dietary intake of EPA and DHA (~1 g per person per day) ensures the prevention of cardiovascular diseases and neural disorders (Plourde and Cunane, 2007; Harris et al., 2009; Kris-Etherton et al., 2009; Phang et al., 2011; Casula et al., 2013; Nagasaka et al., 2014; Calder, 2018; Bernasconi et al., 2021). The main food source of EPA and DHA for humans is fish (Robert, 2006; Adkins and Kelley, 2010; Tacon and Metian, 2013; Gladyshev et al., 2013, 2015b; Tocher et al., 2019).

However, it is well-known that not all fish species can serve as a real food source of PUFAs, since many of them contain too little of these biologically active substances in their edible biomass (Kwetegyeka et al., 2008; Gladyshev and Sushchik, 2019). Indeed, the content of PUFAs in the muscle tissue of different fish species can differ by more than 200 times, and the reasons for such a large variability are different (Gladyshev et al., 2013, 2018). It is believed that the content of EPA and DHA in fish is controlled by genetic (taxonomic identity) and environmental factors, including feeding patterns (Ahlgren et al., 2009; Tacon and Metian, 2013; Vasconi et al., 2015; Gladyshev et al., 2018). As for the differences in the content of PUFAs caused by different taxonomic identity in the above-mentioned alien species, European smelt and the Common kilka, we failed to find any information on their fatty acid composition in the literature. However, there is data on significant differences in the content of EPA and DHA in other representatives of the families Osmeridae and Clupeidae which include the species under consideration (Gladyshev et al., 2018).

The aim of the work is to compare the composition (% of the total amount) and content (mg/g wet weight) of fatty acids (FA) in the muscle tissue of two alien species in the Rybinsk Reservoir, the Common kilka and European smelt, and also to calculate the accumulation of PUFAs (sums EPA and DHA), which could potentially be recovered from the reservoir's pelagic fish production.

MATERIALS AND METHODS

Sample Collection

The study material was collected in the Rybinsk Reservoir (upper reaches of the Volga River). Fish were caught with a pelagic trawl (vertical opening during trawling is 1.5 m; horizontal opening, 12 m; mesh size in codend is 5 mm). Samples were taken from 20 specimens of the Common kilka (October 19, 2019) and from 12 specimens of European smelt (October 2020). The used methods of field collection of fish muscle tissue samples, sample preparation for chromatographic analysis of fatty acid composition are described in detail elsewhere (Gladyshev et al., 2020). For biochemical analysis, cuts of muscle tissue (0.7–2.0 g) were taken from under the dorsal fin of each fish specimen. The muscle samples were placed in a mixture of chloroform: methanol (2 : 1 by volume, 2–3 mL) and stored at −20°C. Samples were delivered to the laboratory in thermally insulated containers with refrigerant within 1–2 weeks after collection and were analyzed within 3 months.

Fatty Acid Analysis

The lipid fraction from fish muscles was extracted with a mixture of chloroform and methanol in a ratio of 2 : 1; the procedure was described in detail elsewhere (Gladyshev et al., 2020). Briefly: extraction was carried out from the flesh sample in three-stages by portions of a mixture of chloroform and methanol (5–7 mL each) with simultaneous mechanical homogenization with glass beads. The resulted portions of the extracting mixture were combined and filtered through a layer of anhydrous Na_2SO_4 and the solvents were removed on a rotary vacuum evaporator. The lipids were dissolved in 0.8 mL NaOH methanol solution (8 g/L) and placed in a water bath at 90°C for 10 min; the lipids were esterified by adding an excess of 3% solution of H_2SO_4 for 12 min at the same temperature. The obtained fatty acid methyl esters (FAMEs) were extracted from the mixture by twice successive addition of 2.5 mL of hexane and then washed twice with 5 mL of saturated solution of NaCl. The hexane solution containing FAMEs was dried by passing through a layer of anhydrous Na_2SO_4, and hexane was evaporated on a rotary vacuum evaporator. Previous to chromatographic analysis, FAMEs were again dissolved in a small volume of hexane.

FAMEs were analyzed on a gas chromatograph with a mass spectrometric detector (model 6890/5975C, Agilent Technologies, USA) with helium as the carrier gas, split-injection, and an HP-FFAP capillary column (30 m long and 0.25 mm inner diameter). The following temperature conditions were used: isothermal period 120°C for 3 min, rise to 180°C at a rate of 5°C/min, 10 min isothermal period, second rise to 220°C at a rate of 3°C/min, 5 min isothermal period, final rise to 230°C at a rate of 10°C/min and keeping this temperature for 30 min; temperature of the injection port and interface was 230°C; detector ionization energy, 70 eV; scanning was performed in the range of 45–500 atomic units. Fatty acid peaks were identified by the obtained mass spectra by comparing them with those available in the NIST-2005 database (Agilent Technologies, USA), as well as by comparing the retention time with that of the standards (Supelco, USA). The quantitative content of fatty acids in the samples was determined by the peak value of the internal standard, nonadecanoic acid methyl ester 19:0 (Sigma-Aldrich, USA), a fixed amount of which was added to the samples prior lipid extraction.

Calculation of Fish Production and PUFAs Accumulation

The production of the studied species (F, g/(m^3 × yr.)) was calculated as for pelagic planktivorous fish based on the literature data on the production of zooplankton prey during the growing season (Lazareva and Sokolova, 2015) according to the generally accepted formula[1]: $F = P(1/k_2)k_3$, where P is zooplankton production, g/(m^3 yr.); k_2 is feed coefficient; k_3 is an indicator of the use of food resources by fish. The numerical values of k_2 and k_3 for the Rybinsk Reservoir[2] are 8.00 and 0.45, respectively.

The accumulation of PUFA in fish biomass (E, mg/(m^3 yr.)) was calculated according to the formula: $E = F(C_{sm.}N_{sm.} + C_{sp.}N_{sp.} + C_{others}N_{others})$, where $C_{sm.}$,$C_{sp.}$, and C_{others} are PUFA content (sum of EPA + DHA (mg/g wet weight) in European smelt, Common kilka , and other pelagic fish of the Rybinsk Reservoir, respectively); $N_{sm.}$, $N_{sp.}$, and N_{others}, are the proportion of European smelt, Common kilka, and other pelagic fish, respectively, in the biomass of pelagic fish in the Rybinsk Reservoir. Values of $C_{sm.}$ and $C_{sp.}$ were determined in this study; the value of C_{others} (2.8 mg/g) was taken from literature data as an average for fish of the orders Cypriniformes and Perciformes (Gladyshev, 2021), since representatives of these orders made up the bulk of "other" fish in the period (1971–2004) for which the calculations were made (Dgebuadze et al., 2008). Values of $N_{sm.}$, $N_{sp.}$, and N_{others} for 1971–2004

[1] Procedure for determining the consequences of a negative impact of construction, reconstruction, and structural repairs of construction facilities, the introduction of new technological processes and the implementation of other activities on the state of aquatic biological resources and their habitats and the development of measures to eliminate the consequences of negative impacts on the state of aquatic biological resources and their habitats aimed at restoring their disturbed state. Approved by the Order of the Federal Agency for Fishery No. 238 dated May 06, 2020. (https://legalacts.ru/doc/prikaz-rosrybolovstva-ot-06052020-n-238-ob-utverzhdenii-metodiki/).

[2] The same source.

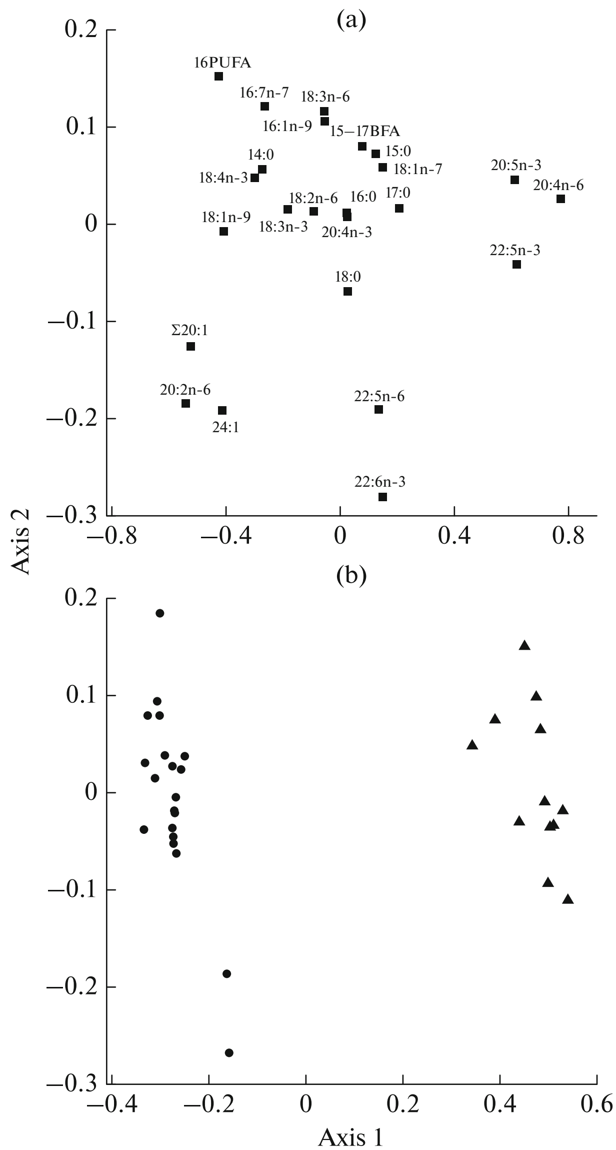

Fig. 2. Results of the canonical multivariate correspondent analysis of fatty acid levels in the biomass (muscle tissue) of the Common kilka *Clupeonella cultriventris* and European smelt *Osmerus eperlanus* from the Rybinsk Reservoir: (a) fatty acids, (b) fish: (●) kilka, (▲) smelt. The proportion of explained dispersion (inertia) along axis 1 is 89.3, along axis 2 is 5.3%; $\chi^2 = 458.3$, number of degrees of freedom, 713. BFA, branched fatty acids; PUFA, polyunsaturated fatty acids.

were taken from the literature data (Dgebuadze et al., 2008) (Fig. 1).

Statistical Analyses

The Kolmogorov–Smirnov test was used to test the normality of the distribution, and the Student's *t*-test was used to compare mean values in independent samples. Canonical multivariate correspondence analysis (Legendre and Legendre, 1998) was used to compare fatty acid composition. Calculations and data visualization were performed using the STATISTICA 9.0 software package (StatSoft, Inc., USA).

RESULTS

According to the obtained results, the composition of fatty acids in the muscle tissues of the Common kilka and European smelt differs significantly (Fig. 2). On axis 1, which reflects the main share of dispersion in the multidimensional space between 24 FAs, the greatest differences can be traced between minor acids 20:2n-6 and ∑20:1, on the one hand, and 20:4n-6, on the other. There were also significant differences in the levels of acids that significantly contribute to the total amount of fatty acids, namely, 16:1n-7, 18:1n-9, 18:3n-3, 18:4n-3, and 20:5n-3 (Table). The total amount of FAs in the kilka was significantly higher than in smelt (Table 1). The content of EPA + DHA in the kilka muscles was significantly higher than that in the smelt (Student's *t*-test, $p < 0.001$; 7.67 ± 0.46 versus 1.99 ± 0.15 mg/g, respectively). Thus, for the calculations of the PUFA accumulation in fish biomass, the following values were determined: $C_{sp.} = 7.67$ mg/g and $C_{sm} = 1.99$ mg/g.

Fish production in the pelagic zone of the reservoir underwent twofold changes in the 1970s–1980s and remained almost unchanged in 1995–2004. At the same time, the accumulation of PUFAs in fish biomass in the 2000s almost doubled compared to the previous period (Fig. 3).

DISCUSSION

European smelt invaded into the Rybinsk Reservoir in the early 1940s, at the very beginning of it's the formation (Poddubnyi, 1971). The species quickly formed a large population, which number began to decline only by the end of the 1990s due to the global warming (Gerasimov and Ivanova, 2015). The Common kilka was first discovered in the Rybinsk Reservoir in 1993, and by the beginning of the 2000s, it began to dominate in the fish population of the pelagic zone of the reservoir (Fig. 1). The number of both species varied significantly throughout the years after the invasion. However, since the end of the 1990s, the kilka is the dominant species (Gerasimov and Karabanov, 2015).

Both species inhabit the pelagic zone and are planktivores. However, based on the data on the content and ratio of fatty acids, it can be assumed that they differ in their feeding spectra. Indeed, significantly higher proportions of fatty acids ∑20:1 were found in the kilka biomass. These acids also were found in the seston of the Rybinsk Reservoir and can be considered as markers of planktonic copepods (Makhutova et al., 2008). Also, the kilka biomass was characterized by significantly higher levels of 18:3n-3, a marker of green algae and cyanobacteria, and 18:4n-3, a marker of chrysophyte and cryptophyte algae (Ahlgren et al., 1992; Desvilettes et al., 1997). On the contrary, the biomass of European smelt showed a significantly higher level of arachidonic acid 20:4n-6, which is considered as a marker of allochthonous organic matter of terrestrial origin (Gladyshev et al., 2015a).

The smelt biomass also contained a higher percentage of EPA, which is often regarded as a marker of diatoms (Dijkman and Kromkamp, 2006). However, a high level of EPA in the smelt muscles was complemented by relatively low values of 16:1n7, 16PUFA, and 14:0, which are also markers of diatoms (Dijkman and Kromkamp, 2006) and, more than that, it is important to note that the sum of FAs in the kilka that reflects the favorable nutritional conditions (Ahlgren et al., 1996), was almost an order of magnitude higher than in smelt (Table 1). Precisely the low content of total amount of FAs in the smelt biomass results in significantly lower content of EPA (mg/g wet weight) in it in comparison to the kilka (despite the high percentage level of EPA in the smelt).

Probably, at a low level of the total FAs in the smelt, most of the FAs were used to obtain energy via the β-oxidation process, while the physiologically important EPA was retained in the phospholipids of cell membranes and its share (% of the total FA) increased accordingly. More favorable nutritional conditions for the kilka are also confirmed by a significantly higher level of oleic acid 18:1n-9 in it (Table 1). Among other fatty acids oleic acid is known to be most intensively used for catabolism, being a characteristic component of storage lipids (Tocher, 2003). The important role of oleic acid as an energy fuel for the muscle tissues of fish during swimming has also been shown (McKenzie et al., 1998).

Thus, according to the analysis of marker FAs, the base of the Commom kilka trophic chain consists of cyanobacteria and green, cryptophyte, and chrysophyte algae, which are largely utilized through copepods, while allochthonous organic matter is relatively more represented in the smelt trophic chain.

In contrast to the analysis of marker FAs that reflect assimilated food, studies of the feeding spectra of the kilka and smelt by classical methods (analysis of the content of the alimentary tract, that is, not assimilated, but ingested food) showed that these species in the Rybinsk Reservoir practically do not differ in terms of the main food objects. *Bosmina* sp., *Leptodora kindtii*, *Daphnia* sp., and *Bythotrephes longimanus* formed the basis of the smelt feeding in the summer periods until the 1970s. In spring, the smelt feeds on copepods (Copepoda) and chironomid larvae (Chironomidae). Large individuals of older ages (which have practically disappeared since the 1970s) consumed larvae and juveniles of fish, including individuals of their own species (Ivanova, 1982; Gerasimov and Ivanova, 2015). From 2000 to 2009 the food composition of the kilka almost did not change. The main food objects

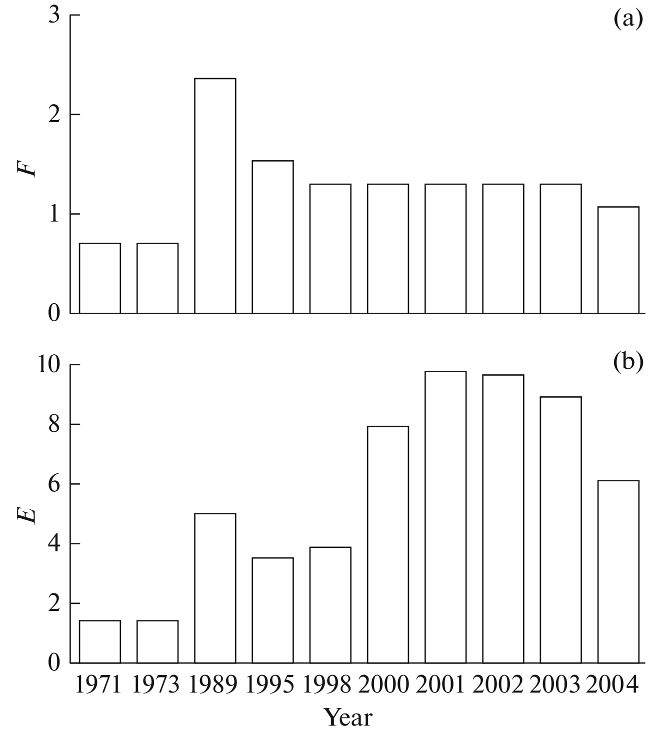

Fig. 3. Dynamics of production (F, g/(m^3 yr.)) of the fish population of the pelagic zone of the Rybinsk Reservoir (a) and accumulation (E, mg/(m^3 yr.)) of polyunsaturated fatty acids (EPA + DHA) in fish biomass (b) at the end of the 20th—beginning of the 21st centuries.

were water fleas (Cladocera: *Bosmina* sp., *Daphnia* sp., *Bythotrephes longimanus*, and *Leptodora kindtii*), followed by copepods (*Heterocope* sp., *Eudiaptomus* sp., and common species of Cyclopoida) (Kiyashko et al., 2012). Thus, according to the visual analysis of the contents of the alimentary tract, there were no significant differences in the nutrition of European smelt and the Common kilka in the Rybinsk Reservoir. Obviously, due to the existing discrepancies in the assessment of the feeding spectra of the kilka and smelt in the Rybinsk Reservoir, they require further study.

For the first time the content of the sum of EPA + DHA (mg/g) in muscle tissue (edible biomass) of two species (*C. cultriventris* and *O. eperlanus*) has been determined. It turned out, that the content of these PUFAs in the biomass of the Common kilka is almost four times higher than that in European smelt. As noted above, according to the meta-analysis data (Gladyshev et al., 2018), the content of EPA and DHA in fish biomass is most affected by phylogenetic (belonging to a certain taxonomic group) factors, while ecological and morphological factors are only of secondary importance. Considering that European smelt and the Common kilka are quite similar in their ecological and morphological parameters (small pelagic fish feeding mainly on plankton), it is obvious

Table 1. Means ($M \pm m$) of the proportion (% of the total amount) and the sum (mg/g wet weight) of fatty acids in muscle tissue of the Common kilka *Clupeonella cultriventris* (n = 20) and European smelt *Osmerus eperlanus* (n = 12) from the Rybinsk Reservoir and significance of differences in means (p) according to the Student's t-test

Fatty acid	Common kilka	European smelt	p
14:0	2.61 ± 0.09	1.35 ± 0.06	<0.01
15:0	0.40 ± 0.01	0.51 ± 0.01	<0.01
16:0	19.79 ± 0.34	20.20 ± 0.42	>0.05
16:1n-9	0.52 ± 0.02	0.46 ± 0.03	>0.05
16:1n-7	6.49 ± 0.26	3.52 ± 0.20	<0.01
15-17BFA*	1.47 ± 0.04	1.69 ± 0.06	<0.01
16PUFA**	1.16 ± 0.07	0.39 ± 0.04	<0.01
17:0	0.53 ± 0.01	0.78 ± 0.02	<0.01
18:0	4.06 ± 0.17	4.11 ± 0.12	>0.05
18:1n-9	31.88 ± 0.56	11.17 ± 0.31	<0.01
18:1n-7	3.73 ± 0.08	4.99 ± 0.15	<0.01
18:2n-6	1.60 ± 0.04	1.28 ± 0.03	<0.01
18:3n-6	0.16 ± 0.01	0.15 ± 0.01	>0.05
18:3n-3	4.09 ± 0.10	2.68 ± 0.11	<0.01
18:4n-3	2.50 ± 0.08	1.24 ± 0.08	<0.01
∑20:1	0.35 ± 0.01	0.07 ± 0.02	<0.01
20:2n-6	0.13 ± 0.01	0.02 ± 0.01	<0.01
20:4n-6	1.38 ± 0.04	6.57 ± 0.18	<0.01
20:4n-3	0.43 ± 0.01	0.43 ± 0.02	>0.05
20:5n-3	7.33 ± 0.15	23.93 ± 0.53	<0.01
22:5n-6	0.71 ± 0.04	0.87 ± 0.06	<0.05
22:5n-3	0.39 ± 0.02	1.28 ± 0.07	<0.01
22:6n-3	5.99 ± 0.49	7.38 ± 0.50	>0.05
24:1	0.29 ± 0.02	0.10 ± 0.02	<0.01
Total amount of fatty acids	60.3 ± 4.70	6.3 ± 0.50	<0.01

$M \pm m$, mean value and its error; n, number of samples; * branched fatty acids; ** polyunsaturated fatty acids.

that the observed differences in the content of EPA and DHA result primarily from the phylogenetic component, which confirms the conclusions of the earlier meta-analysis. It should also be noted that the previously studied closely related species of representatives of the families of the kilka and the smelt also had differences in the content of EPA + DHA, coinciding with the trend established in our work: the Pacific herring *Clupea harengus pallasi* was characterized by values of 4.68–16.8 mg/g (Gladyshev et al., 2007; Huynh and Kitts, 2009), while the rainbow smelt *Osmerus mordax* was characterized by a lower value of 4.21 mg/g (Cladis et al., 2014).

It has been repeatedly noted that the creation of artificial reservoirs leads to the formation of new habitats, in particular pelagic zones. However, the formation of new communities in such habitats is often cannot be fully covered by the animal populations of the rivers on which the reservoir was created (Fernando and Holčíck, 1982; Slynko and Kiyashko, 2012). In this case, the alien species play an important role in the creation of a real lentic ecosystem on the base of the lotic one (Kudersky, 1974). In the case of the Rybinsk Reservoir, invasion and even domination of alien species (European smelt at the beginning and then the Common kilka) into the pelagic zone of the reservoir did not lead to serious destructive consequences neither for native species nor for the ecosystem as a whole. The obtained data on the composition of the fatty acids of the invaders showed that the replacement of one alien species with another (smelt with kilka) significantly changed the quality of production of an important link in the trophic web of the reservoir. It is quite obvious that it is necessary to study the impact of these changes on other organisms of aquatic and near-water ecosystems, in particular, the Common kilka consumers.

In recent decades, the assessment of biological production of aquatic ecosystems, including fish production, covers not only its quantity, but also its quality (Taipale et al., 2016; Gladyshev, 2018). The main indicator of fish quality is the content of EPA and DHA in them (Taipale et al., 2016; Gladyshev and Sushchik, 2019). Of course, fish, along with PUFAs, is also a source of other valuable nutrients for humans: proteins (amino acids), trace elements, and vitamins. However, the contribution of fish as a source of protein to the total consumption of plant and animal proteins by humans is only 6% (Tacon and Metian, 2013), while the proportion of fish EPA + DHA in global dietary intake exceeds 97% (Gladyshev et al., 2015b). Therefore, the quality of fish production should be assessed by the content of PUFAs. From this point of view, the Common kilka is a more valuable product for human nutrition than European smelt.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of Interests. The authors declare that they have no conflicts of interest.

Statement on the Welfare of Animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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