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The influence of season and levels of dietary lipid on growth performance and lipid composition in rainbow trout *Parasalmo mykiss* (Walbaum, 1792)

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ABSTRACT

We studied the growth performance and lipid composition of liver, muscles and visceral fat in rainbow trout *Parasalmo mykiss* (Walbaum, 1792) and the diets used in its cultivation during the spring-summer season. The differences in dietary lipid composition determined modifications in the biochemical composition of tissues of rainbow trout and had an effect on the weight and growth rate of the fish. Trophic and seasonal factors also had their influence on the studied parameters. The degree of influence depended on the functional characteristics of tissues and organs of rainbow trout.

Key words: season, diet, lipid, fatty acids, growth performance, rainbow trout.

Growth processes in aquatic organisms, especially at the early stages of their development, are largely determined by the trophic influence. Among the environmental factors, dietary composition and the degree of food availability forms exogenous heterogeneity of fish. Structural components of food are involved in plastic metabolism, and substrates for oxidation provide energy that requires for metabolic pathways of substances transformation.

Trophic chains are formed during the long process of coevolution, therefore biochemical composition of native feed objects is generally considered to be the most appropriate for normal growth and development of fish. In trout farms fishes are cultivated on artificial feed, and feedstock for its production must be as close as possible to the natural food of rainbow trout. However, intensive development of salmon aquaculture led to a deficit of the main lipid component in the feed – fish oil that was replaced by vegetable oils [Barlow, 2000; Tacon, 2004]. The presence of non-typical ingredients for the natural diet can have a significant effect on fish metabolism and, consequently, result in a change of functioning at all levels of organism organization (from the adaptive response to disease states).

The effects of various feed ingredients on the fish tissue composition and the growth performance are now actively investigated, and one of the most problematic issues is the lipid and fatty acids composition of the feeds [Bell et al., 2010; Pratoomyot et al., 2011; Yigit et al., 2012, etc.]. This kind of research is often conducted on rainbow trout [Hilton, Arkinson, 1982; Lee et al., 1992; Turchini, Francis, 2009; Randall et al., 2013]. In addition, aquaculture of rainbow trout is one of the promising areas in the economy of the North-West region of Russia, thus more scientific information is necessary for the successful development and profitability of local fisheries.

In the analysis of the processes of fish growth and development, besides the trophic factor, other factors must also be considered. The most significant environmental factor is the seasonal factor, including changes in temperature and the fish annual cycle. Impact of these factors on the lipid composition in visceral fat, muscle and liver of rainbow trout *Parasalmo mykiss* (Walbaum, 1792) was studied in this paper.

MATERIALS AND METHODS

Two genetically similar and homogeneous groups of juvenile rainbow trout aged 1+ (groups 1 and 2) were obtained from the commercial fish farm on Lake Ladoga (Republic of Karelia, Russia). Before the experiment groups 1 and 2 were fed diet 1. From March to June group 1 was fed commercial diet 1, while group 2 was fed diet 2. Diets 1 and 2 are commercial trout diets (characterized by the same feed conversion, 44 % crude protein) often used on fish farms in the North-West region of Russia. Experiment was conducted during the melting of snow and ice in northern lakes, when the stage of annual cycle of trout development changes from wintering to active feeding, and the frequency of feeding fish gradually increases (Table 1). Every third week of each month (March, April, May, June) 10 fish from each group were measured and fish tissues (liver, muscles and visceral fat) were sampled for the biochemical analysis.

The growth performance is shown in Table 1. Specific Growth Rate (SGR, %/day) was

Table 1

Water temperature, feeding frequency and growth performance of rainbow trout *Parasalmo mykiss* (Walbaum, 1792) fed two different diets

Month	March		April		May		June	
Fish groups	1	2	1	2	1	2	1	2
Number of fish, *n*	10	10	10	10	10	10	10	10
Diet	1	2	1	2	1	2	1	2
Feeding frequency, per week	2	2	4	4	7	7	14	14
Water temperature on the sampling date, °C	0		0.3		10.1		15.2	
Water temperature (averaged over the week preceding the sampling), °C	0		0.1		9.8		14.9	
Mean length of fish, cm	12.2 ± 0.5	12.4 ± 0.4	12.8 ± 0.5	12.5 ± 0.4	13.9 ± 0.3	13.4 ± 0.5	16.2 ± 0.6	15.0 ± 0.3
Mean weight of fish, g	21.2 ± 1.2	21.4 ± 0.9	24.6 ± 0.6	23.3 ± 0.7	33.0 ± 1.0	27.1 ± 0.9	75.1 ± 2.3	46.0 ± 1.4
Weight Increment, %			15.8	8.8	33.7	16.2	126.4	69.6
Specific Growth Rate, %/day			0.49	0.28	0.97	0.50	2.70	1.96

calculated as: $100 \times [\ln W_1 - \ln W_0] \times (\text{days})^{-1}$, and the Weight Increment (WI, %) was calculated as: $(W_0 - W_1) \times 100\ \%/W_0$, where W is the weight of the sampled fish in grams, W_0 and W_1 are the initial and the final mean weight of the fish in grams.

Total lipids (TL), total phospholipids (PL), triacylglycerols (TAG), cholesterol (Ch), cholesterol esters (ChE); individual PL – phosphatidylinositol (PI), phosphatidylserine (PS), phosphatidylcholine (PC), phosphatidylethanolamine (PE), sphingomyelin (SM), fatty acids of total lipid, total activity of lipase were investigated.

Total lipids of diets and tissue samples were extracted with chloroform : methanol (2 : 1, v/v) [Folch et al., 1957]. TL were fractioned by ascending thin-layer chromatography in the petroleum ether:diethyl ether:acetic acid solvent system (90 : 10 : 1 v/v) at room temperature [Stahl, 1965]. The position of the fractions was determined by standard mixes: phospholipid mixture (P3817 "Supelco", USA), cholesterol (C8667 "Sigma", USA), glyceryl trioleate (92860 "Sigma", USA) and cholesteryl palmitate (C78607 "Aldrich", USA). The concentration of the studied parameters was determined by spectrophotometry [Sidorov et al., 1972; Engelbrecht et al., 1974].

Individual phospholipid fractions were analyzed using high-performance liquid chromatography ("Stayer", Akvilon, Russia). The mobile phase (eluent) was the solvent mixture of acetonitrile : methanol : phosphoric acid (918 : 30 : 30 : 17.5 v/v). The eluent flow rate was 1.0 ml/min. UF spectrometry at 206 nm was used for detection. Chromatograms were processed with the "Multichrom-Analytic, v. 1.5" software. The following standards were used to identify individual phospholipid fractions: phospholipid mixture for HPLC (Supelco), standard PS, PC, PI solutions (Sigma). Fatty acids were methylated with methanol [Tsyganov, 1971]. The fatty acid methyl esters (FAME) were analyzed by a gas chromatograph ("Crystal 5000", Chromatek, Russia) equipped with the flame ionization detector. Individual fatty acid was reported as weight percent of total fatty acids using mass response factors. The identification of fatty acid methyl esters was performed by external standards (all purchased from Sigma Chemical Co., USA). The values of fatty acids were presented as area percentage of total fatty acids. Total activity of lipase in tissues was determined by spectrophotometry with p-nitrophenyl laurate as the substrate [Pinsirodom, Parkin, 2001]. Total activity of enzymes was expressed as μmol p-nitrophenol/min/g.

The data were processed statistically; the two sample sets were compared using the Wilcoxon – Mann – Whitney test ($p \leq 0.05$). The data were analyzed by main-way Analysis of Variance (MANOVA) with two controllable factors (season and diet composition).

The research was carried out using the facilities of the Equipment Sharing Centre of the Institute of Biology, KarRC of RAS.

RESULTS AND DISCUSSION

According to the comparative analysis of lipid composition of the diets, diet 2 contained more storage lipids (triacylglycerols (TAG) and cholesterol esters (ChE)) than diet 1. It determined the prevalence of total lipids in diet 2 (Table 2). The amount of total phospholipids (PL) in the diets was similar, but the content of individual phospholipid components differed. The level of other structural components – cholesterol (Ch) in diet 2 was significantly lower compared to diet 1, which is probably due to the addition of vegetable oils in the production of diet 2. Rainbow trout belongs to predatory fish species and its natural feed is characterized by a high concentration of cholesterol. Cholesterol is a precursor for many bioactive substances and it forms the structural integrity of the biological membranes, providing normal functioning of the membrane-bound enzymes [Tocher et al., 2008]. Low level of this lipid fraction in the diet can lead to stunted growth and development of the fish [Yun et al., 2011].

Diet 1 was characterized by a relatively high content of saturated and long-chain $n-3$ ($C \geq 20$) polyunsaturated fatty acids (PUFA), which can denote using of fish oil as a source of the lipid component in its production [Bell et al., 2010]. High content of long-chain PUFA of $n-3$ family (such as eicosapentaenoic 20 : 5($n-3$) and docosahexaenoic 22 : 6($n-3$) acids) in the feed is necessary for the normal development and active growth of rainbow trout [Bell et al., 2010].

Table 2

Content of total lipids and their major fractions, individual phospholipids (% dry weight), and fatty acids (% total fatty acids) in the diets

Parameters	Diet 1	Diet 2
Total lipids	17.74 ± 1.3	25.60 ± 1.5[a]
Phospholipids	4.28 ± 0.4	4.50 ± 0.2
Triacylglycerols	13.18 ± 1.1	18.19 ± 2.0[a]
Cholesterol esters	0.40 ± 0.2	1.31 ± 0.5[a]
Cholesterol	1.88 ± 0.4	0.60 ± 0.3[a]
Phosphatidylinositol	0.04 ± 0.01	0.09 ± 0.02[a]
Phosphatidylserine	0.01 ± 0.0	0.01 ± 0.0
Phosphatidylethanolamine	1.45 ± 0.2	0.91 ± 0.3[a]
Phosphatidylcholine	2.50 ± 0.4	3.91 ± 0.4[a]
Sphingomyelin	0.02 ± 0.01	0.01 ± 0.0
16 : 0	20.11 ± 2.3	14.82 ± 1.1[a]
Σ saturated acids	33.91 ± 2.2	22.64 ± 0.9[a]
18 : 1(n−9)	19.87 ± 0.4	29.92 ± 0.6[a]
22 : 1(n−9)	0.66 ± 0.1	3.62 ± 0.3[a]
Σ monounsaturated fatty acids	27.39 ± 1.1	47.36 ± 2.3[a]
Σ (n−9) polyunsaturated fatty acids	0.64 ± 0.4	0.21 ± 0.2
18 : 2(n−6)	3.34 ± 0.6	11.80 ± 1.1[a]
20 : 4(n−6)	1.09 ± 0.2	0.41 ± 0.05[a]
Σ (n−6) polyunsaturated fatty acids	6.52 ± 0.7	13.52 ± 1.1[a]
Σ (n−4) polyunsaturated fatty acids	2.38 ± 1.3	0.51 ± 0.4
18 : 3(n−3)	0.89 ± 0.2	3.99 ± 0.3[a]
20 : 5(n−3)	15.56 ± 1.5	4.49 ± 0.3[a]
22 : 6(n−3)	7.44 ± 1.8	5.11 ± 1.2
Σ (n−3) polyunsaturated fatty acids	29.17 ± 1.2	15.67 ± 0.9[a]
Σ polyunsaturated fatty acids	38.7 ± 2.2	29.99 ± 1.3[a]

Note. Results are expressed as mean ± SD of three replicate analyses of different samples of each diet.
[a] – differences significant at $p \leq 0.05$, for the comparison between diet 1 and diet 2.

Diet 2 contained more monounsaturated fatty acids including erucic 22 : 1(n−9) acid, compared to diet 1 (see Table 2). At present, the question of the effect of high concentrations of erucic 22 : 1(n−9) acid in feed on the rainbow trout metabolism is debatable. According to one group of authors [Drew et al., 2007; Collins et al., 2012], erucic acid has no significant effect on the physiological and biochemical characteristics of the physiological state of the fish. According to other sources [Tucker, Hargreaves, 2004], increasing the content of erucic acid in the feed by more than 3 % can disrupt the growth and development of the organism up to the fish's death. Note that erucic acid level in the diet 2 was sufficiently close to said threshold.

The content of essential fatty acids (linoleic 18 : 2(n−6) and linolenic 18 : 3(n−3) acids) in diet 2 was significantly higher than in diet 1. Elongation and desaturation of fatty acids take place in the body of rainbow trout. PUFA can be synthesized from essential acids, however, PUFA synthesis in the fish's organism is insufficient [Thanuthong et al., 2011]. The lack of long-chain polyunsaturated fatty acids in diet 2 could bring to growth inhibition in the respective group. Thus, we found Weight Increase of fish in group 1, which were fed with relatively high levels of eicosapentaenoic 20 : 5(n−3) and docosapentaenoic 22 : 6(n−3) acids, from 16 % in April to 126 % in June; for the second group of fish the weight increase was two times smaller (see Tables 1, 2).

A significant effect of trophic factor on levels of total lipids in muscle and liver was noted. The content of total lipids in group 2 was higher than in group 1 (Tables 3, 4). Variation

Table 3

Content of total lipids and their major fractions, individual phospholipids (% dry weight), fatty acids (% of total fatty acids), total activity of lipase (mol/g tissue/min) in the muscles of rainbow trout *Parasalmo mykiss* (Walbaum, 1792)

Month	March		April		May		June	
Fish groups	1	2	1	2	1	2	1	2
Total lipids	11.7 ± 0.8	12.7 ± 0.8[a]	11.5 ± 0.9	12.5 ± 0.9[a]	11.4 ± 0.7	12.6 ± 0.9[a]	11.5 ± 0.8	12.8 ± 0.6[a]
Phospholipids	4.6 ± 1.1	4.8 ± 0.5	4.5 ± 1.0	4.8 ± 0.6	4.5 ± 0.4	4.8 ± 0.3	4.0 ± 0.3[d]	4.4 ± 0.2[d]
Triacylglycerols	5.1 ± 1.7	6.1 ± 1.1[a]	5.1 ± 0.5	6.0 ± 0.6[a]	5.0 ± 0.5	6.1 ± 0.4[a]	5.5 ± 0.6	6.7 ± 0.4[a]
Cholesterol esters	0.5 ± 0.4	0.4 ± 0.1	0.4 ± 0.2	0.3 ± 0.5	0.3 ± 0.2	0.3 ± 0.1	0.3 ± 0.2	0.2 ± 0.1
Cholesterol	1.5 ± 0.6	1.4 ± 0.1	1.5 ± 0.5	1.4 ± 0.1	1.5 ± 0.1	1.4 ± 0.2	1.7 ± 0.1[d]	1.5 ± 0.1
Cholesterol / Phospholipids	0.32 ± 0.1	0.29 ± 0.0	0.34 ± 0.2	0.30 ± 0.1	0.35 ± 0.0	0.30 ± 0.0	0.42 ± 0.1[d]	0.36 ± 0.0[d]
Phosphatidylinositol	0.38 ± 0.3	0.19 ± 0.1[a]	0.39 ± 0.1	0.20 ± 0.1[a]	0.39 ± 0.1[c]	0.21 ± 0.0[a]	0.45 ± 0.1[d]	0.32 ± 0.0[a,d]
Phosphatidylserine	0.12 ± 0.04	0.05 ± 0.1[a]	0.11 ± 0.0	0.05 ± 0.0[a]	0.11 ± 0.0	0.04 ± 0.0[a]	0.10 ± 0.0	0.03 ± 0.0[a]
Phosphatidylethanolamine	1.5 ± 0.1	1.3 ± 0.3[a]	1.5 ± 0.1[b]	1.2 ± 0.2[a,b]	1.5 ± 0.2	1.0 ± 0.2[a,c]	0.9 ± 0.1[d]	0.7 ± 0.1[a,d]
Phosphatidylcholine	2.6 ± 0.3	3.2 ± 0.3[a]	2.6 ± 0.3	3.3 ± 0.3[a]	2.8 ± 0.2	3.4 ± 0.3[a]	2.8 ± 0.3	3.4 ± 0.3[a]
Sphingomyelin	0.01 ± 0.0	0.03 ± 0.0[a]	0.01 ± 0.0	0.02 ± 0.0[a]	0.01 ± 0.0	0.02 ± 0.0[a]	0.01 ± 0.0	0.02 ± 0.0[a]
16 : 0	19.4 ± 2.4	15.4 ± 1.3[a]	20.1 ± 2.5	16.6 ± 03[a]	20.5 ± 0.6	14.8 ± 0.3[a,c]	19.6 ± 0.6	9.8 ± 0.3[a,d]
Σ saturated acids	29.8 ± 2.5	22.9 ± 1.0[a]	29.9 ± 2.1	24.0 ± 0.3[a]	30.2 ± 0.5	21.3 ± 0.3[a,c]	30.7 ± 0.6	15.5 ± 0.2[a]
18 : 1(n−9)	15.7 ± 4.0	23.5 ± 1.7[a]	13.7 ± 1.2[b]	19.4 ± 0.9[a,b]	12.3 ± 0.9[c]	21.7 ± 1.7[a,c]	12.2 ± 0.5	20.7 ± 1.6[a]
22 : 1(n−9)	1.1 ± 0.3	2.8 ± 0.3[a]	1.2 ± 0.2	2.2 ± 0.3[a,b]	1.0 ± 0.1	3.0 ± 0.2[a,c]	1.0 ± 0.1	2.6 ± 0.2[a]
Σ monounsaturated fatty acids	30.4 ± 3.7	40.8 ± 2.0[a]	28.6 ± 1.6	34.6 ± 1.3[a,b]	25.0 ± 1.0[c]	41.2 ± 2.0[a,c]	25.6 ± 0.9	43.2 ± 1.0[a]
Σ (n−9) polyunsaturated fatty acids	0.7 ± 0.5	0.4 ± 0.2[a]	0.5 ± 0.1	0.3 ± 0.03	0.5 ± 0.03	0.3 ± 0.02	0.4 ± 0.1	0.2 ± 0.01[a]
18 : 2(n−6)	3.7 ± 0.7	7.5 ± 0.5[a]	3.7 ± 0.5	6.2 ± 0.3[a]	3.9 ± 0.5	7.0 ± 0.2[a]	4.1 ± 0.3	9.8 ± 0.1[a,d]
20 : 4(n−6)	0.99 ± 0.1	0.62 ± 0.1[a]	1.16 ± 0.2[b]	1.16 ± 0.3[b]	1.13 ± 0.1	0.58 ± 0.1[c]	1.02 ± 0.1	0.51 ± 0.04
Σ (n−6) polyunsaturated fatty acids	7.0 ± 0.7	9.8 ± 0.4[a]	6.6 ± 0.5	9.4 ± 0.4[a]	6.2 ± 0.3[c]	9.0 ± 0.1[a]	6.8 ± 0.4	12.9 ± 0.3[a,d]
Σ (n−4) polyunsaturated fatty acids	1.2 ± 0.5	0.5 ± 0.1[a]	1.2 ± 0.2	0.5 ± 0.04[a]	1.2 ± 0.2	0.5 ± 0.02[a]	1.4 ± 0.1	0.5 ± 0.02[a]
18 : 3(n−3)	0.9 ± 0.2	2.4 ± 0.2[a]	0.9 ± 0.1	1.9 ± 0.2[a,b]	0.8 ± 0.1	2.0 ± 0.1[a]	1.1 ± 0.1	2.1 ± 0.01[a]
20 : 5(n−3)	6.7 ± 0.4	4.8 ± 0.2[a]	7.3 ± 0.3[b]	4.9 ± 0.4[a,b]	7.4 ± 0.5	3.5 ± 0.3[a]	8.6 ± 0.1[d]	3.6 ± 0.2[a,d]
22 : 6(n−3)	18.7 ± 0.6	15.0 ± 0.8[a]	20.8 ± 0.7[b]	21.9 ± 1.1[b]	20.1 ± 1.0	22.2 ± 1.5[a]	19.7 ± 1.1	25.6 ± 0.6[a,d]
Σ (n−3) polyunsaturated fatty acids	30.0 ± 1.0	24.9 ± 1.1[a]	33.0 ± 1.2[a,b]	30.7 ± 1.1[a,b]	36.7 ± 1.0[c]	28.3 ± 1.1[a,c]	34.6 ± 1.1	31.4 ± 0.6[d]
Σ polyunsaturated fatty acids	39.8 ± 1.4	36.3 ± 1.1[a]	41.5 ± 1.3	41.4 ± 1.5[b]	44.8 ± 1.1[c]	37.5 ± 1.7[a,c]	43.7 ± 0.8	43.3 ± 0.4
Total activity of lipase	0.11 ± 0.0	0.13 ± 0.0	0.15 ± 0.0	0.22 ± 0.1	0.24 ± 0.0	0.25 ± 0.1	0.33 ± 0.0	0.28 ± 0.1

Note. Results are expressed as mean ± SD. Superscript letters denote significant differences between groups of fishes as determined by Wilcoxon − Mann − Whitney test ($p \leq 0.05$): [a] − for the comparison of fish groups 1, 2, [b] − for the comparison of the indices in March and April, [c] − for the comparison of the indices in April and May, [d] − for the comparison of the indices in May and June.

Table 4

Content of total lipids and their major fractions, individual phospholipids (% dry weight), fatty acids (% of total fatty acids), total activity of lipase (mol/g tissue/min) in the liver of rainbow trout *Parasalmo mykiss* (Walbaum, 1792)

Month	March		April		May		June	
Fish groups	1	2	1	2	1	2	1	2
Total lipids	13.8 ± 1.0	14.8 ± 0.9[a]	13.9 ± 0.7	14.4 ± 1.3	14.7 ± 0.9	14.6 ± 0.4	14.0 ± 0.3	14.9 ± 0.4[a]
Phospholipids	10.8 ± 1.6	9.7 ± 1.4	10.5 ± 0.5	9.7 ± 0.9	11.0 ± 0.8	8.8 ± 1.2[a]	9.6 ± 0.6[d]	7.9 ± 0.4[a,d]
Triacylglycerols	0.9 ± 0.1	2.6 ± 0.9[a]	1.0 ± 1.1	3.1 ± 0.9[a,b]	1.1 ± 0.7	3.0 ± 0.5[a]	1.0 ± 1.4	3.0 ± 0.5[a]
Cholesterol esters	0.5 ± 0.2	0.5 ± 0.4	0.5 ± 0.3	0.5 ± 0.2	0.4 ± 0.2	0.5 ± 0.2	1.2 ± 0.2[d]	1.2 ± 0.2[d]
Cholesterol	1.6 ± 0.1	1.9 ± 0.6	1.9 ± 0.6	2.1 ± 0.4	2.2 ± 0.3	2.3 ± 0.6	2.2 ± 0.5	2.5 ± 0.2
Cholesterol / phospholipids	0.14 ± 0.0	0.20 ± 0.1	0.17 ± 0.1	0.24 ± 0.1	0.20 ± 0.1	0.26 ± 0.1	0.30 ± 0.1[d]	0.31 ± 0.0[d]
Phosphatidylinositol	0.55 ± 0.1	0.28 ± 0.1[a]	0.55 ± 0.1	0.32 ± 0.1[a]	0.64 ± 0.1[c]	0.47 ± 0.0[a,c]	0.70 ± 0.1[d]	0.51 ± 0.1[a,d]
Phosphatidylserine	0.43 ± 0.3	0.40 ± 0.1	0.40 ± 0.1	0.31 ± 0.1[b]	0.36 ± 0.1	0.29 ± 0.0	0.30 ± 0.1[d]	0.24 ± 0.1[d]
Phosphatidylethanolamine	4.18 ± 0.4	2.46 ± 0.7[a]	3.73 ± 0.5[b]	2.43 ± 0.5[a]	3.66 ± 0.3	1.61 ± 0.2[a,c]	2.59 ± 0.5[d]	1.40 ± 0.4[a,d]
Phosphatidylcholine	5.18 ± 0.8	6.22 ± 0.4[a]	5.36 ± 0.3	6.30 ± 0.7[a]	5.89 ± 0.5	6.31 ± 0.4[a]	5.98 ± 0.3	6.34 ± 0.4[a]
Sphingomyelin	0.04 ± 0.0	0.08 ± 0.0[a]	0.04 ± 0.0	0.09 ± 0.0[a]	0.07 ± 0.0[c]	0.09 ± 0.0	0.08 ± 0.0	0.09 ± 0.0
16 : 0	22.4 ± 2.2	16.7 ± 1.1[a]	30.9 ± 2.1[b]	18.5 ± 0.5[a,b]	33.7 ± 2.4	20.3 ± 1.2[a]	31.5 ± 1.3[d]	24.0 ± 2.2[a,d]
Σ saturated acids	44.8 ± 3.5	33.7 ± 2.5[a]	45.8 ± 2.2	32.1 ± 0.6[a]	49.8 ± 2.9[c]	31.8 ± 1.0[a]	52.3 ± 2.2	25.8 ± 3.0[a,d]
18 : 1(n−9)	13.5 ± 1.9	19.7 ± 1.7[a]	17.7 ± 0.7[b]	15.4 ± 0.8[b]	12.6 ± 1.6[c]	17.2 ± 0.5[a,c]	12.5 ± 0.4	27.0 ± 1.5[a,d]
22 : 1(n−9)	1.4 ± 0.5	1.7 ± 0.2	1.0 ± 0.3	1.4 ± 0.1	0.7 ± 0.1[c]	1.1 ± 0.3	0.5 ± 0.1	1.6 ± 0.4[a,d]
Σ monounsaturated fatty acids	31.0 ± 3.3	34.6 ± 2.8[a]	32.4 ± 2.1	34.0 ± 0.5	28.8 ± 2.2	36.9 ± 1.5[a,c]	24.4 ± 1.2[d]	41.9 ± 1.6[a,d]
Σ (n−9) polyunsaturated fatty acids	0.4 ± 0.1	0.2 ± 0.0[a]	0.4 ± 0.1	0.2 ± 0.0[a]	0.5 ± 0.2	0.2 ± 0.0[a]	0.6 ± 0.2	0.3 ± 0.0[a]
18 : 2(n−6)	3.0 ± 0.4	5.1 ± 0.3[a]	3.1 ± 0.6	5.2 ± 0.3[a]	3.1 ± 0.4	5.2 ± 0.2[a]	3.1 ± 0.2	6.0 ± 0.6[a,d]
20 : 4(n−6)	1.7 ± 0.7	1.5 ± 0.1	1.6 ± 0.2	1.4 ± 0.2	1.6 ± 0.4	1.4 ± 0.2	1.5 ± 0.2	1.0 ± 0.1[d]
Σ (n−6) polyunsaturated fatty acids	5.5 ± 0.6	7.8 ± 0.3[a]	5.5 ± 0.7	7.9 ± 0.4[a]	5.6 ± 0.6	7.9 ± 0.6[a]	5.7 ± 0.6	8.3 ± 1.0[a]
Σ (n−4) polyunsaturated fatty acids	0.8 ± 0.2	0.5 ± 0.03	0.8 ± 0.4	0.5 ± 0.03	0.9 ± 0.3	0.5 ± 0.04	1.1 ± 0.2	0.6 ± 0.1
18 : 3(n−3)	0.8 ± 0.2	1.5 ± 0.2[a]	0.9 ± 0.1	1.5 ± 0.1[a]	0.8 ± 0.1	1.6 ± 0.1[a]	0.9 ± 0.1	1.6 ± 0.1[a]
20 : 5(n−3)	1.8 ± 1.6	5.6 ± 0.5[a]	1.1 ± 0.2[b]	6.0 ± 0.2[a]	2.3 ± 0.7	5.7 ± 0.9[a]	2.2 ± 0.5	5.7 ± 0.8[a]
22 : 6(n−3)	11.6 ± 2.2	10.2 ± 0.9	11.8 ± 0.6	10.9 ± 0.9	12.1 ± 0.6	9.5 ± 0.5[a,c]	12.2 ± 1.1	8.8 ± 2.0[a]
Σ (n−3) polyunsaturated fatty acids	14.9 ± 5.5	20.1 ± 1.1[a]	15.7 ± 0.8	21.7 ± 0.8[a]	15.0 ± 1.0	21.7 ± 0.4[a]	17.1 ± 1.7	22.2 ± 0.6[a]
Σ polyunsaturated fatty acids	24.2 ± 5.7	31.7 ± 0.6[a]	21.8 ± 1.4	33.9 ± 0.6[a]	21.3 ± 2.4	31.4 ± 1.2[a]	23.3 ± 0.7	32.3 ± 1.6[a]
Total activity of lipase	0.07 ± 0.0	0.07 ± 0.0	0.07 ± 0.0	0.07 ± 0.0	0.06 ± 0.0	0.07 ± 0.0	0.06 ± 0.0	0.07 ± 0.0

N o t e. Results are expressed as mean ± SD. Superscript letters denote significant differences between groups of fishes as determined by Wilcoxon − Mann − Whitney test ($p \leq 0.05$): [a] − for the comparison of fish groups 1, 2, [b] − for the comparison of the indices in March and April, [c] − for the comparison of the indices in April and May, [d] − for the comparison of the indices in May and June.

of total lipid content in muscle and liver was minor during the season because the level of PL and ChE decreased, whereas the concentration of TAG and cholesterol increased. The decrease in the concentration of total lipids in adipocytes from March to May was observed (Table 5), which can be due to energy consumption to support the vital functions of trout in the period of low digestive activity during the wintering. In June fish began to feed actively (see Table 1) and contents of total lipid in the visceral fat increased, as well as the lipids stored in adipocytes [Yíldíz et al., 2006]. We also observed seasonal variations in the concentration of total lipids in visceral fat caused by changes in the level of triacylglycerols, which are the dominant lipid fraction in the tissue. Total activity of lipase in adipocytes was gradually declining from March to May and seriously decreased in June (see Table 5). Reverse seasonal correlation between TAG and total activity of lipase in the visceral fat may suggest that storage lipids in this tissue are primarily oxidized during the winter, and consumption of the organism stores is reduced as the water temperature increases in the spring-summer season. The effect of trophic factor on TAG content in muscles was 30 % ($p < 0.05$), in contrast to the seasonal factor, which had no significant effect on this parameter (Table 6). This fact may be due to intensive feeding of trout that happened only in June. In early spring period (March – April) the absence of TAG accumulation in muscles was probably related to low feeding rate, whereas in May and June it can be the consequence of increased total lipase activity. Different directions of seasonal changes of lipase activity in muscles and visceral fat occurred due to specific functional characteristics of these tissues. Muscles carry out motor activity and, additionally, together with visceral fat, have the storage function. Fish become the most active after the melting of ice on the lake. Also, fish growth performance increased two times from April to June in both groups (see Table 2). It was associated with the activation of anabolism structural components, which requires more energy. TAG levels in liver did not depend on the season (see Table 6), since lipids are normally not stored in this tissue during the feeding period. Total activity of lipase in liver was significantly lower than in other tissues and did not depended on the seasonal or trophic factor.

Concentrations of cholesterol esters in muscles and visceral fat in both groups decreased by June (see Tables 3, 5), and it was associated with the use of ChE, a reserve source of cholesterol, which is required for membranes construction during fish growth. ChE concentration in liver also decreased from March to May, but increased in June (see Table 4), which may be due to higher exogenous Ch input and activation of internal synthesis [Merayo, 1996].

Although the feeds differed considerably in cholesterol content (see Table 2), we did not observe any significant effect of the trophic factor on this index in muscles and visceral fat. Presumably, the two fish groups did not differ in the content of steroid components in tissues because their level in cells was kept constant, and potential lack of exogenous Ch input in group 2 was balanced by its synthesis within the organism.

All the investigated organs and tissues of rainbow trout from both groups demonstrated seasonal variations in the content of structural components: a slight rising in Ch content from March to May and its significant increase in June; a reduction in PL concentrations in visceral fat, muscles and liver from May to June (see Tables 3–5). These modifications were also responsible for the change in Ch/PL ratio – one of the main indicators of the functional condition of biological membranes. The increase of this index during the study period was apparently due to the adaptive response of biomembranes to a reduction in their fluidity with a rise in the ambient temperature [Henderson, Tocher, 1987].

Declining of the total phospholipid concentration in trout tissues was mainly due to the reduction in the content of phosphatidylethanolamine (PE) and phosphatidylethanolserine (PS), which are metabolically interlinked, and comprise high amounts of unsaturated fatty acids, which dilute the membrane lipid bilayer [Hazel, 1979; Zehmer, Hazel, 2005]. In contrast, phosphatidylcholine (PC) concentration in fish muscles grew slightly during the study period (see Table 3); the same trend was also observed for phosphatidylinositol (PI). Changes in concentrations of individual PL in rainbow trout tissues from March to June must

Table 5

Content of total lipids and their main fractions (% dry weight), fatty acids (% total fatty acids), total activity of lipase (mol/g tissue/min) in the visceral fat of rainbow trout *Parasalmo mykiss* (Walbaum, 1792)

Month	March		April		May		June	
Fish groups	1	2	1	2	1	2	1	2
Total lipids	72.5 ± 2.8	77.5 ± 2.2[a]	61.3 ± 3.1[b]	67.7 ± 2.9[b]	59.3 ± 1.7[c]	57.1 ± 2.1[c]	66.6 ± 2.9[d]	66.3 ± 2.3[a,d]
Phospholipids	21.9 ± 3.7	19.3 ± 4.0	20.1 ± 2.2	18.2 ± 0.7[b]	19.6 ± 2.1	17.4 ± 1.5[c]	17.3 ± 2.2[c]	15.3 ± 1.0[d]
Triacylglycerols	44.4 ± 3.5	52.3 ± 2.0[a]	35.1 ± 1.7[b]	43.6 ± 2.5[a,b]	29.6 ± 1.4[c]	34.3 ± 2.2[a,c]	44.5 ± 1.8[d]	45.8 ± 1.7[d]
Cholesterol esters	2.6 ± 1.9	2.5 ± 1.7	2.5 ± 1.5	2.4 ± 1.1	2.5 ± 0.9	2.8 ± 1.1	1.7 ± 0.7[d]	1.2 ± 0.4[a,d]
Cholesterol	3.6 ± 1.1	3.4 ± 1.5	3.6 ± 0.3	3.5 ± 0.6	3.6 ± 0.3	3.6 ± 0.1	4.1 ± 0.1[d]	4.0 ± 0.2[d]
Cholesterol / phospholipids	0.16 ± 0.05	0.25 ± 0.0[a]	0.17 ± 0.0	0.27 ± 0.1[a]	0.18 ± 0.0	0.32 ± 0.1[a,c]	0.23 ± 0.0[d]	0.40 ± 0.1[a,d]
16 : 0	17.2 ± 0.9	14.2 ± 0.2[a]	16.1 ± 0.4[b]	13.9 ± 0.5[a]	15.9 ± 1.0	12.6 ± 0.2[a]	18.3 ± 0.9[a,d]	11.9 ± 0.2[a]
Σ saturated acids	29.3 ± 0.8	22.6 ± 0.5[a]	27.8 ± 0.7[b]	23.4 ± 0.5[a]	27.3 ± 0.7	20.2 ± 0.4[a,c]	31.5 ± 1.2[d]	18.0 ± 0.5[a,d]
18 : 1(n −9)	21.2 ± 1.0	26.6 ± 1.0[a]	22.9 ± 0.8	25.9 ± 0.6[a]	22.2 ± 0.7	24.8 ± 1.1[a]	17.5 ± 0.6[d]	24.9 ± 0.5[a]
22 : 1(n −9)	1.9 ± 0.3	3.9 ± 0.3[a]	2.4 ± 0.7	3.8 ± 0.2[a]	2.2 ± 0.3	4.1 ± 0.5[a]	1.7 ± 0.2	4.0 ± 0.3[a]
Σ monounsaturated fatty acids	43.0 ± 1.7	47.4 ± 0.4[a]	44.6 ± 0.4	47.7 ± 1.1[a]	43.7 ± 0.7	48.8 ± 0.2[a]	37.1 ± 1.2[d]	50.6 ± 0.5[a,d]
Σ (n −9) polyunsaturated fatty acids	0.6 ± 0.1	0.3 ± 0.1[a]	0.6 ± 0.2	0.3 ± 0.0[a]	0.6 ± 0.1	0.2 ± 0.0[a]	0.6 ± 0.1	0.2 ± 0.0[a]
18 : 2(n −6)	5.8 ± 0.3	8.2 ± 0.4[a]	6.1 ± 0.5	8.2 ± 0.5[a]	6.3 ± 0.3	8.3 ± 0.1[a]	6.4 ± 0.4	12.0 ± 1.1[a,d]
20 : 4(n −6)	0.63 ± 0.1	0.44 ± 0.2[a]	0.65 ± 0.1	0.39 ± 0.1[a]	0.72 ± 0.1[c]	0.36 ± 0.0[a]	0.74 ± 0.0	0.29 ± 0.0[a]
Σ (n−6) polyunsaturated fatty acids	8.4 ± 0.3	10.3 ± 0.2[a]	8.9 ± 0.6	10.4 ± 0.4[a]	9.0 ± 0.6	10.3 ± 0.1[a]	8.5 ± 0.2	13.9 ± 1.1[a,d]
Σ (n −4) polyunsaturated fatty acids	1.5 ± 0.2	0.7 ± 0.3[a]	1.5 ± 0.3	0.7 ± 0.1[a]	1.4 ± 0.2	0.5 ± 0.1[a]	1.7 ± 0.1[d]	0.5 ± 0.0[a]
18 : 3(n −3)	1.3 ± 0.1	2.5 ± 0.1[a]	1.2 ± 0.1	2.4 ± 0.2[a]	1.2 ± 0.1	2.5 ± 0.1[a]	1.2 ± 0.2	3.1 ± 0.2[a,d]
20 : 5(n −3)	5.0 ± 0.6	4.3 ± 0.3[a]	4.5 ± 1.0	4.2 ± 0.5	5.0 ± 0.6	4.7 ± 0.4	5.7 ± 0.3[d]	3.3 ± 0.4[a,d]
22 : 6(n −3)	6.2 ± 1.3	7.3 ± 0.5[a]	6.3 ± 1.3	7.2 ± 0.5[a]	7.1 ± 0.2[c]	7.2 ± 0.2	7.0 ± 0.7	7.6 ± 0.6[a,d]
Σ (n−3) polyunsaturated fatty acids	16.4 ± 2.4	17.9 ± 0.8[a]	16.0 ± 0.9	7.3 ± 1.1[a]	17.5 ± 0.5[c]	17.9 ± 0.3	20.0 ± 1.2[d]	17.5 ± 1.0[a]
Σ polyunsaturated fatty acids	27.7 ± 2.5	30.0 ± 0.7[a]	27.6 ± 1.9	28.9 ± 1.1	29.0 ± 1.5[c]	31.0 ± 0.3	31.4 ± 1.2[d]	31.4 ± 1.0
Total activity of lipase	0.66 ± 0.1	0.65 ± 0.1	0.64 ± 0.2	0.62 ± 0.0	0.47 ± 0.1	0.49 ± 0.1	0.35 ± 0.1	0.32 ± 0.1

N o t e. Results are expressed as mean ± SD. Superscript letters denote significant differences between groups of fishes as determined by Wilcoxon−Mann−Whitney test ($p \leq 0.05$): [a] − for the comparison of fish groups 1, 2, [b] − for the comparison of the indices in March and April, [c] − for the comparison of the indices in April and May, [d] − for the comparison of the indices in May and June.

Table 6

Effect of diet and season on lipid composition in tissues of rainbow trout *Parasalmo mykiss* (Walbaum, 1792)

Parameters	Visceral fat		Muscles		Liver	
	diet	season	diet	season	diet	season
1	2	3	4	5	6	7
Total lipids		37.9 17.9	13.3 16.7		8.1 6.0	36.5 19.8
Phospholipids		11.1 3.4	7.3 9.1	20.7 8.6	5.9 6.9	
Triacylglycerols	28.3 30.9	30.1 13.1	30.2 37.9		10.6 10.5	12.4 4.9
Cholesterol esters		11.4 3.9	8.5 16.6	29.4 16.8	11.3 13.5	
Cholesterol		17.3 4.7		13.5 5.1	10.9 10.1	23.9 9.5
Cholesterol / phospholipids	6.4 6.81	35.3 12.6		19.5 6.2	22.4 30.0	11.3 3.5
Phosphatidylinositol			8.0 9.4	10.5 4.1		31.7 14.1
Phosphatidylserine			5.1 4.8	12.1 3.9		27.2 9.0
Phosphatidylethanolamine			19.9 21.6	11.3 4.4	15.5 16.5	11.8 3.2
Phosphatidylcholine			14.9 16.0	27.0 11.1		
Sphingomyelin			19.2 19.6	8.5 2.9		
16 : 0	67.0 190.8	5.4 5.1	58.7 111.9		24.19 64.9	15.3 13.7
Σ saturated acids	75.1 329.0	3.5 5.1	76.9 255.3		34.9 101.6	10.0 9.7
18 : 1(n−9)	17.5 38.54	20.4 14.9	64.8 192.0	8.4 8.3	38.1 99.3	12.2 10.5
22 : 1(n−9)	66.4 275.9	10.7 14.8	80.5 470.3	18.0 22.5	22.5 26.5	14.9 5.8
Σ monounsaturated fatty acids	56.2 249.7	4.5 6.6	77.7 555.4	4.5 10.7	18.2 59.7	8.4 9.2
Σ (n−9) polyunsaturated fatty acids	84.3 412.3	6.2 7.8	76.1 243.1		49.1 105.6	8.9 13.5
18 : 2(n−6)	67.1 309.1	11.7 17.9	75.3 1037.1	13.7 63.1	54.3 155.7	12.1 11.6
20 : 4(n−6)	67.6 164.3		18.2 91.3			25.7 34.1
Σ (n−6) polyunsaturated fatty acids	58.1 202.2	17.4 20.2	73.3 729.8	14.7 48.7	25.6 61.5	13.6 10.9
Σ (n−4) polyunsaturated fatty acids	83.1 144.6	10.1 15.6	79.5 158.4	8.3 9.4	54.3 99.7	6.5 13.6

Finising Table 6

1	2	3	4	5	6	7
18 : 3(n−3)	88.5	3.0	83.0	5.9	42.3	21.9
	1245.6	13.9	1300.9	31.0	219.1	37.8
20 : 5(n−3)	19.7		65.1	5.2	5.6	6.4
	20.1		306.3	8.2	8.6	3.2
22 : 6(n−3)	40.3	10.6		15.9	7.4	5.8
	111.4	3.0		14.7	19.9	5.1
Σ (n−3) polyunsaturated fatty acids			50.8	14.2	6.4	8.1
			168.2	15.7	16.4	6.9
Σ polyunsaturated fatty acids	5.9	17.1	40.2	11.3	7.9	8.0
	5.3	5.1	88.6	8.3	20.4	6.9
Total activity of lipase	7.2	77.2		62.4		
	35.6	213.4		153.6		

Note. Data shown in the table represents statistically significant results (MANOVA, $p \leq 0.05$). The numerator – the degree of influence of the factor (% of total dispersion) on lipid parameters in tissues of rainbow trout; the denominator – indicator of F-criterion.

have been due to modifications of membrane viscosity which were an adaptive reaction to increased water temperature [Fodor et al., 1995].

The trophic factor had no significant effect on individual phospholipids level in liver, except for PE (see Table 6). The concentration of this component was higher both in liver of group 1 and in the diet in which they were cultivated (see Tables 2, 4).

Compared to liver, the content of individual PL fractions in muscles was more dependent on the fish dietary. During the period of intensive feeding (May – June), PI content in muscles increased, especially in group 2. In the diet for group 2 PI content dominated (see Tables 2, 3). The high degree of influence of feed on sphingomyelin (SM) content in muscle (see Table 6) was observed because, according to some literary sources, SM enters fish organisms exclusively in food composition [Tocher, 2003].

We did not report the values of individual PL in visceral fat because analysis of their content in this tissue revealed significant prevalence of PC, whereas other fractions were present there in trace amounts.

The trophic factor significantly influenced the fatty acids distribution in muscles and visceral fat (see Table 6). Reduction in saturated (SFA) and monounsaturated (MUFA) fatty acids in storage tissues from March to May must be the evidence of intensive consumption of organism's stores to sustain the fish through the winter. The fatty acids are predominantly used as oxidation substrates [Weber et al., 2003]. In May, when fish began active feeding, total saturated FA increased and MUFA content decreased in storage tissues in group 1, whereas in group 2 the content of saturated fatty acids decreased and content of MUFA raised, apparently in agreement with the fatty acid profiles of the feeds [Skonberg et al., 1994].

The trophic factor significantly influenced the content of erucic 22 : 1(n−9) acid in visceral fat and muscles (see Table 6). This acid accumulated in fish tissues from March to June (see Tables 3–5) which can be associated with an increase in fish feeding frequency in the end of the study period, and possibly indicative of the absence or decreased activity of the enzymes involved in its metabolism. According to the literature, the use of the feed, containing a sufficiently high level of erucic acid, can lead to stunted growth of fish [Yigit et al., 2012]. In our studies we demonstrated that the growth rate of fish, which consumed the feed 2 with a high content of erucic acid, was significantly lower than that of the fish which consumed the diet with a lower level of this acid (see Tables 1, 2).

The effect of the diet was especially vivid in the analysis of impact of the investigated factors on non-typical fatty acids content in fish tissues, and which concentrations in the diets were also minor: 14 : 1(n−9), 16 : 1(n−9), 17 : 0, 18 : 4(n−3), etc. We found the high le-

vel of influence of the trophic factor on these acids in fish tissues (see Table 6). Seasonal variations in fatty acids, which content in tissues was less than 1 %, was mainly determined by their accumulation. It was associated with the beginning of the fish feeding period and increased frequency of feeding fish [Hua, Bureau, 2009]. These modifications are another evidence of dominant impact of trophic factor on fatty acid spectrum of tissues [Villalta et al., 2008]. The fatty acids content in the storage tissues was more determined by the composition of diets than in fish liver, in agreement with previous studies by other authors [Csengeri et al., 1986].

The level of $n-6$ PUFA in all investigated tissues depended mainly on the content of linoleic 18 : 2($n-6$) acid, which dominates in this family. Linoleic 18 : 2($n-6$) acid content in the storage tissues from both groups increased by June (see Tables 3, 5), which was probably related to the intensive nutrition of fish in this period. Effect of food on the content of linoleic 18 : 2($n-6$) acid in all tissues was significant (see Table 6), because the level of this acid depends on exogenous input [Bell et al., 2010].

We did not found seasonal variations in content of another essential acid – 18 : 3($n-3$) linolenic, in trout tissues. Apparently, the concentration of this acid remained nearly constant throughout the study period due to the maintenance of its particular physiologically required level in the fish cells. All tissues from group 2 contained more linolenic 18 : 3($n-3$) acid than in group 1, with a rise in June. That is probably the consequence of different levels of this acid in the corresponding diets and active fish feeding in summer months.

The content of arachidonic 20 : 4($n-6$) acid in visceral fat and muscles depended on the diet composition, and its content in liver – on the change of the season (see Table 6). These discrepancies are probably related to the functional characteristics of tissues. Visceral fat and muscle are the main storage tissues. The reason could be the high degree of influence of the trophic factor. J. Y. Bae together with colleagues [2004] studied the influence of dietary arachidonic 20 : 4($n-6$) acid on the growth performance of eel. They established that arachidonic 20 : 4($n-6$) acid content in the diet must be at least 0.7 % for normal fish growth and development. We observed that arachidonic 20:4(n−6) acid level in the diet at 0.4 % inhibited fish growth rate and weight (see Tables 1, 2).

The diets did not differ in content of docosahexaenoic 22 : 6($n-3$) acid (DHA), but its composition had a significant impact on the level of this acid in visceral fat and liver. DHA content in muscles and visceral fat was much lower in group 1 as compared to group 2. According to some studies [Villalta et al., 2008], the concentration of docosapentaenoic 22 : 6($n-3$) acid in Senegal sole is inversely proportional to the dietary eicosapentaenoic 20 : 5($n-3$) acid. Indeed, we saw in this study that eicosapentaenoic 20 : 5($n-3$) acid concentration in diet 1 was 3 times higher than in diet 2 (see Table 2).

CONCLUSIONS

Lipid composition of rainbow trout tissues was determined by the functions of the tissues. The lipid composition of storage tissues mainly depended on the fish dietary, whereas the lipid composition of the liver, the latter being a metabolically active organ, was more dependent on the season. Changes in the content of lipid components in muscle and visceral fat together with seasons change were associated with increased activity of fish feeding. The differences in the growth performance in the two groups of fish in the period of the study, was probably due to the diet composition.

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