Available online at www.sciencedirect.com
ScienceDirect
Food Chemistry 104 (2007) 1353–1358
Food Chemistry
www.elsevier.com/locate/foodchem

Seasonal dynamics of fatty acid content of a common food fish from the Yenisei river, Siberian grayling, *Thymallus arcticus*

Nadezhda N. Sushchik [a], Michail I. Gladyshev [a,b,*], Galina S. Kalachova [a]

[a] *Institute of Biophysics, Akademgorodok, Krasnoyarsk 660036, Russia*
[b] *Siberian Federal University, Svobodny Avenue 79, Krasnoyarsk 660041, Russia*

Received 4 September 2006; received in revised form 12 December 2006; accepted 29 January 2007

Abstract

Seasonal variations of fatty acid contents in muscle tissue of one of the main food fish species in Siberian rivers, grayling, *Thymallus arcticus*, were studied over 3 years. Under a comparatively low range of water temperature variations, spawning appeared to be the main cause of seasonal changes in contents of quantitatively prominent and essential fatty acids in fish filets. In general, fish accumulated essential polyunsaturated fatty acids (PUFA), such as eicosapentaenoic (EPA) and docosahexaenoic (DHA), in their muscle tissue before reproductive seasons and then the PUFA seemed to be transferred into gonads during their formation. Hard roe of Siberian grayling had 3–4 times higher PUFA contents, than had that of the muscle tissue. The fish species, *T. arcticus*, was found to be a valuable source of the essential PUFA, including EPA and DHA, for human diet.

Keywords: Essential polyunsaturated fatty acids; Grayling; Seasonal dynamics

1. Introduction

Polyunsaturated fatty acids (PUFA) of the ω6, and especially of ω3, family are recognized essential biochemical components of human diet. These acids prevent cardiovascular, neural and some other diseases, and play a very important role in ontogenesis (e.g. Aktas and Halperin, 2004; Arts, Ackman, and Holub, 2001; Lauritzen, Hansen, Jorgensen, and Michaelsen, 2001; Silvers and Scott, 2002). Since ω3-PUFAs, such as eicosapentaenoic (20:5 ω3, EPA) and docosahexaenoic (22:6 ω3, DHA), are effectively synthesized only by aquatic organisms, humans can obtain these essential components by consuming marine and freshwater products. Food species of aquatic invertebrates and fish are known to differ in their fatty acid (FA) profiles. Apart from the species peculiarities, many organisms have seasonal variations of FA levels, and fish caught in different seasons may have different dietetic values (Gokce, Tasbozan, Celik, and Tabakoglu, 2004; McLean and Bulling, 2005; Ozyurt, Duysak, Akamca, and Tureli, 2005; Ozyurt and Polat, 2006; Ozyurt, Polat, and Ozkutuk, 2005; Rasoarahona, Barnathan, Bianchini, and Gaydou, 2005; Shirai, Suzuki, Tokairin, Ehara, and Wada, 2002a; Shirai, Terayama, and Takeda, 2002b; Varljen, Baticic, Sincic-Modric, Obersnel, and Kapovic, 2004). Thus, study of seasonal dynamics of FA composition of food fish is of importance for conclusions on their properties as a source of the essential components for humans.

Most of studies of the seasonal dynamics, cited above, have reported FA per cent levels in fish species. Evidently, the data on FA composition are very interesting from a biochemical point of view. Nevertheless, for conclusions on fish nutritive value, information on PUFA content is also required. For instance, in our previous study (Gladyshev, Sushchik, Gubanenko, Demirchieva, & Kalachova, 2007), cod was found to have a comparatively high per cent level of EPA + DHA (52%), while trout had comparatively

* Corresponding author. Address: Institute of Biophysics, Akademgorodok, Krasnoyarsk 660036, Russia. Tel.: +7 391 249 4517; fax: +7 391 243 3400.
E-mail address: glad@ibp.ru (M.I. Gladyshev).

0308-8146/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.foodchem.2007.01.050

low level of these PUFAs (26% of total FAs). However, the EPA + DHA content in cod was about 0.24 g/100 g of product, while the content in trout was about 0.59 g/100 g of product. Thus, as a matter of fact, trout appeared to be the most valuable food for EPA + DHA intake and, on the basis of the comparison of these PUFAs per cent levels only, an opposite and misleading conclusion could be reached.

Thereby, the aim of our present work was to study seasonal dynamics of FA content in one of the most common food fish of the middle Yenisei river (Siberia, Russia), Siberian grayling. The Yenisei is the largest river in Russia, and the local population obtains the main part of their freshwater products from the river.

2. Materials and methods

2.1. Fish samples

The fish, *Thymallus arcticus* Pallas, was purchased in a local market in Krasnoyarsk city from the anglers' morning catch. Two-four fish specimens were transported to the laboratory and sampled on the same day. Muscle tissues (fillets) below the dorsal fin were taken as the samples. Pooled samples were prepared from two to four specimens, males and females, 17–24 cm in length. Although, age and sex differences in FA content evidently could occur, we regarded the fish as a whole food source, which was representative of the market and thus totally used by the local population, without any age or sex differences. Normally, samples were taken monthly, but some months were missed through technical causes. Besides the muscle tissue, in periods of spawning, also, hard roes were taken for analysis. Spawning of the grayling occurred in the spring (may be shifted to early summer) and in the autumn, but roe samples were taken on four dates only.

2.2. Analysis

To measure moisture content, fillets and eggs of about 5 g, of wet weight, were taken and dried to constant weight at 105 °C. Lipid extraction and pre-treatment, and chromato-mass-spectrometry (GC-MS) of methyl esters of fatty acids were the same as in our previous work (Gladyshev, Sushchik, Gubanenko, Demirchieva, and Kalachova, 2006). Briefly, lipids from samples were extracted with chloroform:methanol (2:1, v/v) three times, simultaneously, with mechanical homogenization of the tissues with glass beads. Before extraction, a fixed volume of an internal standard solution (19:0) was added to the samples. Methyl esters of fatty acids (FAMEs) were prepared in a mixture of methanol–sulphuric acid (20:1, v/v) at 90 °C for 2 h. FAMEs were then analysed using a GC-MS (model GCD Plus, Hewlett Packard, USA) equipped with a 30 m long × 0.32 mm internal diameter capillary column HP-FFAP. Peaks of FAMEs were identified by their mass spectra, comparing them to those in the data base (Hewlett–Packard, USA) and to those of available authentic standards (Sigma, USA). To determine double bond positions in monoenoic and polyenoic acids, GC-MS of dimethyloxazoline derivatives of FA were used (Makhutova, Kalachova, and Gladyshev, 2003).

2.3. Statistics

Calculations of standard errors (SE) and Student's *t*-test were carried out in the conventional way (Campell, 1967). Canonical correspondence analysis and one-linkage cluster analysis were carried out conventionally (Jeffers, 1981), using Euclidean distances. Prominent fatty acid contents (mg/g of wet weight) were used as the axes of multidimensional hyper-space. Calculations were carried out using STATISTICA software, version 6.0 (StatSoft Inc., Tulsa, OK, USA).

3. Results

In all the samples of muscle tissue, 59 acids were identified. Cluster analysis revealed no explicit trends in seasonal dynamics of the overall fatty acid contents: spring, summer, autumn and winter samples joined in small sporadic clusters (Fig. 1). To reveal acids with more or less explicit seasonal trends, canonical correspondence analysis (CCA) was carried out. Only 18 quantitatively prominent acids (Table 1) were included in CCA. Seasonal dynamics of quantitatively dominating acids and groups of biochemically important acids, those clustered close to each other in the two-dimensional space are depicted in seasonal graphs (Fig. 2) together with the total FA content (Fig. 3), except the data point of March, 2006.

A general tendency for seasonal dynamics of the fatty acids appeared to be as follows: (1) a 'spring' peak of con-

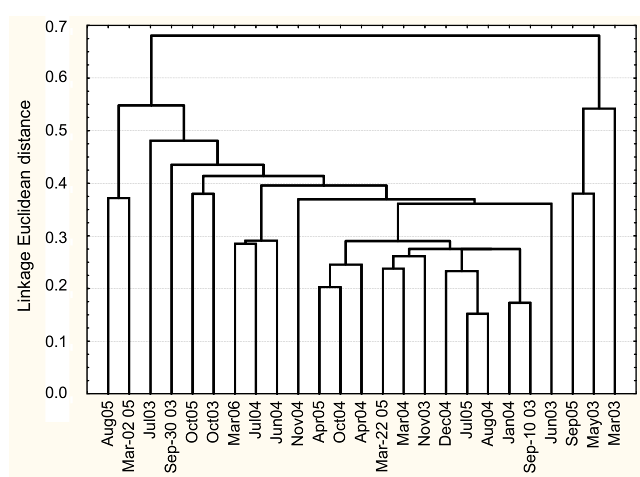

Fig. 1. Dendrogram of the cluster analysis of seasonal dynamics (March 2003–March 2006) of the contents (mg/g of wet weight) of 59 fatty acids in muscle tissue of Siberian grayling *Thymallus arcticus*, from the Yenisei river near Krasnoyarsk city (Siberia, Russia). The ordinate axis represents Euclidean distances in 59-dimension hyper-space.

Table 1
Contents (mg/g of wet weight) of quantitatively prominent fatty acids in muscle tissue of Siberian grayling *Thymallus arcticus*, from the Yenisei river near Krasnoyarsk city (Siberia, Russia)

	2003								2004									2005							2006
	Mar	May	Jun	Jul	Aug	Sep	Oct	Nov	Jan	Mar	Apr	Jun	Jul	Aug	Oct	Nov	Dec	Mar	Mar	Apr	Jul	Aug	Sep	Oct	Mar
14:0	0.34	0.25	0.12	0.28	0.13	0.10	0.14	0.20	0.08	0.15	0.11	0.11	0.08	0.08	0.13	0.12	0.10	0.16	0.17	0.15	0.08	0.19	0.34	0.17	0.15
16:0	2.28	2.05	1.58	1.52	1.23	1.76	1.61	1.58	1.16	1.39	1.29	1.10	0.98	1.09	1.35	1.05	1.09	1.61	1.53	1.46	1.09	1.56	2.05	1.52	1.19
16:1[a]	1.00	0.52	0.24	0.72	0.30	0.60	0.30	0.40	0.23	0.37	0.42	0.20	0.18	0.16	0.32	0.17	0.20	0.30	0.30	0.29	0.15	0.38	0.74	0.39	0.27
16:2ω4	0.12	0.06	0.03	0.09	0.03	0.07	0.03	0.04	0.02	0.03	0.04	0.03	0.02	0.02	0.03	0.02	0.02	0.02	0.03	0.04	0.01	0.05	0.08	0.04	0.03
16:3ω4	0.08	0.06	0.03	0.10	0.03	0.07	0.03	0.04	0.02	0.03	0.03	0.01	0.01	0.01	0.02	0.02	0.03	0.02	0.03	0.04	0.01	0.04	0.08	0.04	0.03
18:0	0.35	0.30	0.27	0.24	0.26	0.28	0.28	0.29	0.21	0.30	0.30	0.29	0.22	0.24	0.25	0.46	0.23	0.30	0.29	0.21	0.28	0.34	0.28	0.27	0.27
18:1ω9	1.20	1.04	0.39	0.89	0.55	0.91	0.51	0.73	0.54	0.67	0.74	0.35	0.39	0.40	0.71	0.35	0.48	0.64	0.64	0.66	0.44	0.56	1.01	0.70	0.41
18:1ω7	0.33	0.25	0.14	0.21	0.16	0.20	0.17	0.20	0.17	0.14	0.20	0.08	0.11	0.10	0.14	0.04	0.12	0.19	0.18	0.13	0.11	0.18	0.30	0.14	0.08
18:2ω6	0.29	0.13	0.06	0.11	0.06	0.11	0.05	0.06	0.05	0.07	0.08	0.07	0.05	0.04	0.10	0.07	0.05	0.14	0.09	0.23	0.07	0.14	0.16	0.11	0.07
18:3ω3	0.45	0.19	0.11	0.17	0.11	0.18	0.08	0.09	0.08	0.09	0.12	0.04	0.07	0.08	0.18	0.09	0.08	0.21	0.12	0.16	0.13	0.26	0.25	0.19	0.13
18:4ω3	0.13	0.09	0.03	0.11	0.05	0.12	0.03	0.05	0.03	0.03	0.04	0.01	0.03	0.03	0.07	0.05	0.04	0.11	0.05	0.06	0.04	0.08	0.12	0.07	0.04
20:1ω9	0.04	0.05	0.01	0.03	0.03	0.04	0.02	0.04	0.02	0.03	0.04	0.00	0.02	0.02	0.05	0.02	0.02	0.04	0.04	0.05	0.02	0.03	0.05	0.04	0.02
20:4ω6	0.19	0.18	0.12	0.14	0.13	0.16	0.13	0.16	0.09	0.13	0.14	0.10	0.10	0.12	0.15	0.12	0.16	0.20	0.17	0.15	0.18	0.23	0.21	0.17	0.13
20:4ω3	0.08	0.06	0.03	0.05	0.04	0.06	0.04	0.04	0.03	0.03	0.04	0.03	0.02	0.04	0.06	0.03	0.04	0.08	0.05	0.05	0.04	0.07	0.08	0.05	0.03
20:5ω3	1.02	0.78	0.60	0.92	0.79	0.78	0.70	0.71	0.72	0.69	0.85	0.46	0.44	0.62	0.81	0.56	0.64	0.64	0.56	0.77	0.72	0.96	1.04	0.92	0.41
22:5ω6	0.09	0.10	0.05	0.07	0.06	0.10	0.07	0.07	0.03	0.04	0.05	0.06	0.04	0.06	0.08	0.06	0.08	0.14	0.08	0.07	0.07	0.16	0.13	0.10	0.07
22:5ω3	0.38	0.27	0.14	0.26	0.27	0.27	0.25	0.27	0.34	0.28	0.40	0.16	0.17	0.24	0.29	0.06	0.30	0.27	0.20	0.27	0.26	0.34	0.31	0.34	0.20
22:6ω3	2.20	2.37	1.38	1.57	1.76	1.80	2.28	1.77	1.73	1.63	2.05	1.39	1.10	1.86	1.94	1.67	2.10	2.92	1.58	2.01	1.92	2.85	2.45	2.35	1.21
Total[b]	11.40	9.33	5.62	8.02	6.30	8.40	6.97	7.07	5.85	6.43	7.43	4.86	4.27	5.46	7.08	5.26	6.01	8.46	6.47	7.27	5.91	8.97	10.30	8.06	4.98

[a] ω7 + ω9.
[b] For all 59 identified acids.

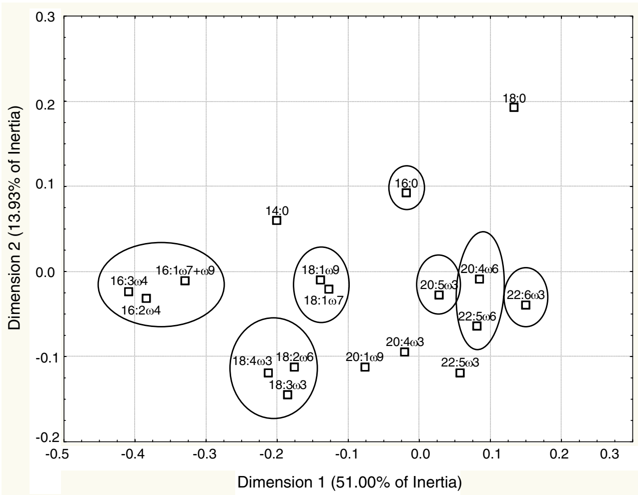

Fig. 2. Results of canonical correspondence analysis of seasonal dynamics (March 2003–March 2006) of contents (mg/g of wet weight) of 18 quantitatively prominent fatty acids in muscle tissue of Siberian grayling *Thymallus arcticus*, from the Yenisei river near Krasnoyarsk city (Siberia, Russia), represented in a two-dimensional space, reproducing 64.9% of total inertia.

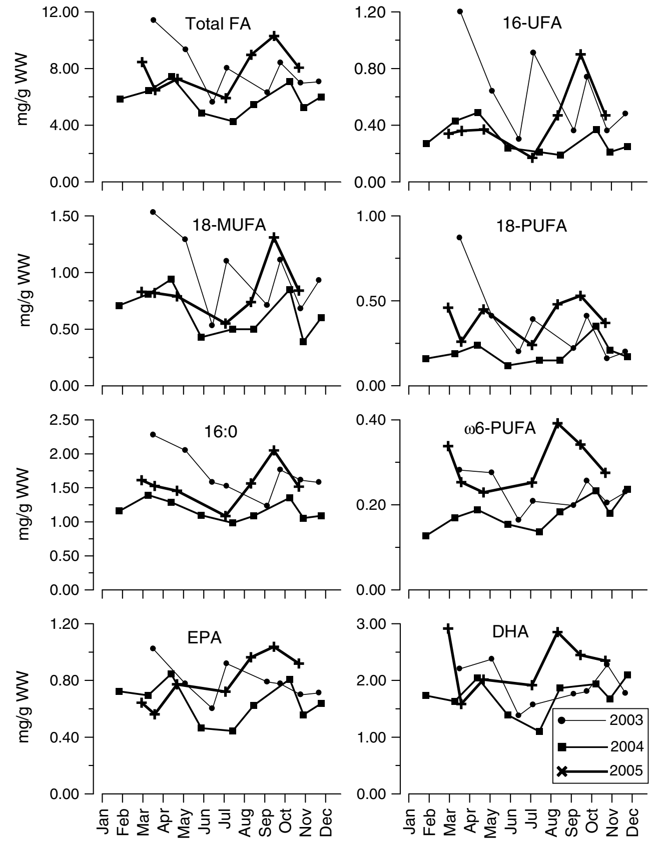

Fig. 3. Seasonal dynamics (March 2003–October 2005) of contents (mg/g of wet weight) of quantitatively dominating acids and sums of biochemically related acids, those clustered close to each other in the two-dimensional space (see Fig. 2). 18-MUFA (monounsaturated fatty acids) – sum of 18:1ω9 and 18:1ω7; 16-UFA (unsaturated fatty acids) – sum of 16:1ω7, 16:2ω4 and 16:3ω4; 18-PUFA (polyunsaturated fatty acids) – sum of 18:2ω6, 18:3ω3 and 18:4ω3; ω6 PUFA – sum of 20:4ω6 and 22:5ω6, EPA (eicosapentaenoic acid), DHA (docosahexaenoic acid). Data on muscle tissue of Siberian grayling *Thymallus arcticus*, from the Yenisei river near Krasnoyarsk city (Siberia, Russia).

tents before and during spawning; (2) a ‘summer’ decrease after spawning; an ‘autumn’ peak before and during spawning; (3) a ‘winter’ decrease after spawning. As a matter of fact, these peaks and decreases cannot be attributed strictly to the calendar months, nor to spring, summer, autumn and winter times of the year, since the spawning fluctuated between years from spring to early summer and from late summer to autumn. These fluctuations were probably caused by inter-annual climatic variations and inter-annual peculiarities of water discharge from the upstream dam of the Krasnoyarsk hydroelectric power station.

The quantitatively dominating fatty acids can be separated into two groups with peculiar seasonal dynamics. The first group included those acids, strictly or mainly, obtained by fish from diet: the cluster of 16-UFA (16:1ω7 + ω9, 16:2ω4, 16:3ω4), the cluster of 18-PUFA (18:2ω6, 18:3ω3, 18:4ω3) and EPA (20:5ω3) (Fig. 2). This group had an additional summer peak in 2003, probably caused by very favourable feeding conditions, and comparatively smooth summer decrease in the other years (Fig. 3). The second group included acids, mainly synthesized by fish: palmitic acid (16:0) and DHA (22:6ω3) (Fig. 2). These acids had a pronounced ‘summer’ minimum (Fig. 3). Acids of the cluster of 18-MUFA (18:1ω9, 18:1ω7) and of the cluster of ω6-PUFA (20:4ω6, 22:5ω6) (Fig. 2), originating from both of these sources, had both the above tendencies in their seasonal dynamics in different years (Fig. 3).

The moisture content in muscle tissue was, on average, 77.4 ± 0.2%. In roe, the moisture was 62.6 ± 0.3% and differed significantly from that of muscle tissue, $t = 37.2$, $p < 0.001$.

The same 59 fatty acids were identified in roe samples. Contents of the quantitatively prominent 18 acids in roe are given in Table 2. Average contents of each quantitatively prominent acid in roe and in muscle tissue were compared using the Student’s *t*-test. Average contents of all the acids, except 16:2ω4 and 16:3ω4, and the total FA content were significantly higher in roe, than in muscle tissue (Table 2).

4. Discussion

According to our data, spawning was the main cause of the seasonal variations of contents of many fatty acid species in muscle tissue of Siberian grayling. In general, before spawning, in early spring and late summer, fish accumulated essential fatty acids in their muscles. We analyzed muscle tissue only, while the accumulation is known often to take place in other tissues and organs, e.g. in liver (Rodriguez et al., 2004; Saito et al., 2005). Nevertheless, according to our data, the pre-spawning accumulation was conspicuous also in the muscle tissue. Moreover, in another work, we have revealed a high content of storage lipids – triacylglycerols (TAG) in muscle tissues of Siberian

Table 2
Contents (mg/g of wet weight) of quantitatively prominent fatty acids in hard roe and muscle tissue (means from Table 1) of Siberian grayling *Thymallus arcticus*, from the Yenisei river near Krasnoyarsk city (Siberia, Russia)

	Roe					Muscles	t
	Sep 2003	Mar 2005	Jun 2005	Mar 2006	Mean ± SE	Mean ± SE	
14:0	0.77	0.63	0.41	0.75	0.64 ± 0.08	0.16 ± 0.01	**5.68
16:0	5.11	6.26	3.90	5.96	5.31 ± 0.53	1.44 ± 0.07	**7.27
16:1[a]	1.42	1.63	0.85	2.08	1.50 ± 0.26	0.37 ± 0.04	**4.34
16:2ω4	0.06	0.11	0.03	0.16	0.09 ± 0.03	0.04 ± 0.01	1.67
16:3ω4	0.01	0.02	0.01	0.10	0.04 ± 0.02	0.04 ± 0.00	0.01
18:0	0.98	1.42	0.73	1.58	1.18 ± 0.20	0.28 ± 0.01	**4.57
18:1ω9	2.52	3.98	1.87	2.76	2.78 ± 0.44	0.64 ± 0.05	**4.83
18:1ω7	0.60	1.01	0.51	0.61	0.68 ± 0.11	0.16 ± 0.01	**4.68
18:2ω6	0.23	0.71	0.30	0.39	0.41 ± 0.11	0.10 ± 0.01	*2.89
18:3ω3	0.31	1.03	0.46	0.93	0.68 ± 0.18	0.15 ± 0.02	*3.05
18:4ω3	0.21	0.40	0.33	0.25	0.30 ± 0.04	0.06 ± 0.01	**5.54
20:1ω9	0.15	0.21	0.11	0.23	0.17 ± 0.03	0.03 ± 0.00	**5.10
20:4ω6	0.75	1.36	0.71	0.83	0.91 ± 0.15	0.15 ± 0.01	**4.99
20:4ω3	0.17	0.41	0.25	0.26	0.27 ± 0.05	0.05 ± 0.00	**4.46
20:5ω3	3.07	4.54	1.78	3.26	3.16 ± 0.56	0.72 ± 0.03	**4.32
22:5ω6	0.26	0.46	0.27	0.33	0.33 ± 0.05	0.08 ± 0.01	**5.36
22:5ω3	0.73	1.62	0.47	1.06	0.97 ± 0.25	0.26 ± 0.02	*2.87
22:6ω3	5.73	11.84	5.70	7.14	7.60 ± 1.45	1.92 ± 0.09	**3.91
Total[b]	24.55	39.58	19.65	30.53	28.58 ± 4.29	6.64 ± 0.32	**5.10

SE – standard error, t – Student's test for the degree of freedom d.f. = 27.
[a] ω7 + ω9.
[b] For all 59 identified acids.
* $p < 0.01$.
** $p < 0.001$.

grayling (Sushchik, Gladyshev, Kalachova, Makhutova, and Ageev, 2006). Other authors have also reported a high content of TAG in dorsal fillets of some other fish species (Shirai et al., 2002a). Our studies were focussed on the muscle tissue because it is the main part of fish used for human consumption.

Fatty acids, which were accumulated in fillets of Siberian grayling, then seemed to be transferred to gonads during their formation, as was revealed by some other authors for another fish species (Gokce et al., 2004; Luzzana et al., 1996). Indeed, contents of all important fatty acids were significantly higher in roe than in muscles (Table 2). We analyzed muscle tissue of pooled samples, both males and females, but took the results into account only for the comparison hard roe of females. Nevertheless, male gonads (soft roe) during the formation are also believed to take many fatty acids from the other fish tissues. Thus, during and after spawning, the contents of essential fatty acids in muscle tissue decreased.

Many authors have reported pronounced changes in fatty acid composition of muscle tissues of fish in reproductive seasons (Gokce et al., 2004; Shirai et al., 2002a), as in our study. Nevertheless, the seasonal changes in lipids of aquatic animals could also be due to temperature and food (McLean and Bulling, 2005; Ozyurt et al., 2005; Shirai et al., 2002b). We also found that acids, strictly or mainly obtained by fish from diet, including EPA, had peculiar seasonal dynamics, with summer peaks, probably caused by favourable feeding conditions. Water temperature in the studied section of the Yenisei river varied comparatively slightly, from about 0 °C in winter to 10 °C in summer, and seemed to provide no explicit effect on FAs (Fig. 3).

Dynamics of DHA in our study differed from those of EPA, as in some other studies (Ozyurt et al., 2005; Rasoarahona et al., 2005). This difference may have occurred because EPA was primarily obtained by the grayling from food, while a significant part of the DHA could be synthesized by the grayling species (Ahlgren, Carlstein, & Gustafsson, 1999; Sushchik et al., 2006). Content of DHA in grayling food, zoobenthos, in the Yenisei river was previously found to be very low (Sushchik et al., 2006). DHA was the dominant fatty acid in the grayling muscle tissue and roe; its content, on average, exceeded that of the other quantitatively important dominant FA, 16:0 (Tables 1 and 2).

Average contents of the essential PUFAs, EPA and DHA, of Siberian grayling were practically the same as those of European grayling, *Thymallus thymallus* L. (Ahlgren, Blomqvist, Boberg, and Gustafsson, 1994; Ahlgren et al., 1999). Moreover, the contents of EPA and DHA in grayling were about twice higher than those of many common freshwater fish, such as roach, bream, carp, tench, perch and burbot (Ahlgren et al., 1994).

5. Conclusions

Siberian grayling, *T. arcticus*, is a valuable source of the essential PUFAs, including EPA and DHA, for human diet. During reproduction periods, normally in spring and autumn, contents of PUFA in muscle tissue (dorsal filets) of the grayling decrease, and fatty acids are probably directed to gonad lipids. Hard roe of Siberian grayling has significantly higher essential PUFA contents, than has muscle tissue, and the roe is also a very valuable product for human nutrition.

Acknowledgements

We used GS-MS of the Joint Equipment Unit of Krasnoyarsk Scientific Centre of the Siberian Branch of the Russian Academy of Sciences. The work was supported by award No. REC-002 of the U.S. Civilian Research & Development Foundation for the Independent States of the Former Soviet Union (CRDF), grant of Russian Foundation for Basic Research (RFBR) No. 03-04-48055 and by a personal grant of the Russian Science Support Foundation for young Candidates of Science (Ph.D).

References

Ahlgren, G., Blomqvist, P., Boberg, M., & Gustafsson, I. B. (1994). Fatty acid content of the dorsal muscle – an indicator of fat quality in freshwater fish. *Journal of Fish Biology, 45*, 131–157.

Ahlgren, G., Carlstein, M., & Gustafsson, I.-B. (1999). Effects of natural and commercial diets on the fatty acid content of European grayling. *Journal of Fish Biology, 55*, 1142–1155.

Aktas, H., & Halperin, J. A. (2004). Translational regulation of gene expression by ω-3 fatty acids. *Journal of Nutrition, 134*, 2487S–2491S.

Arts, M. T., Ackman, R. G., & Holub, B. J. (2001). "Essential fatty acids" in aquatic ecosystems: a crucial link between diet and human health and evolution. *Canadian Journal of Fisheries and Aquatic Sciences, 58*, 122–137.

Campell, R. C. (1967). *Statistics for biologists*. Cambridge: University Press.

Gladyshev, M. I., Sushchik, N. N., Gubanenko, G. A., Demirchieva, S. M., & Kalachova, G. S. (2006). Effect of way of cooking on content of essential polyunsaturated fatty acids in muscle tissue of humpback salmon (*Oncorhynchus gorbuscha*). *Food Chemistry, 96*, 446–451.

Gladyshev, M. I., Sushchik, N. N., Gubanenko, G. A., Demirchieva, S. M., & Kalachova, G. S. (2007). Effect of boiling and frying on the content of essential polyunsaturated fatty acids in muscle tissue of four fish species. *Food Chemistry, 101*, 1694–1700.

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

Jeffers, J. (1981). *An introduction to system analysis: With ecological application*. Moscow: Mir (Translated from English).

Lauritzen, L., Hansen, H. S., Jorgensen, M. H., & Michaelsen, K. F. (2001). The essentiality of long chain $n-3$ fatty acids in relation to development and function of the brain and retina. *Progress in Lipid Research, 40*, 1–94.

Luzzana, U., Serrini, G., Moretti, V. M., Grimaldi, P., Paleari, M. A., & Valfre, F. (1996). Seasonal variations in fat content and fatty acid composition of male and female coregonid 'bondella' from Lake Maggiore and landlocked shad from Lake Como (Northern Italy). *Journal of Fish Biology, 48*, 352–366.

Makhutova, O. N., Kalachova, G. S., & Gladyshev, M. I. (2003). A comparison of the fatty acid composition of *Gammarus lacustris* and its food sources from a freshwater reservoir, Bugach, and the saline Lake Shira in Siberia, Russia. *Aquatic Ecology, 37*, 159–167.

McLean, C. H., & Bulling, K. R. (2005). Differences in lipid profile of New Zealand marine species over four seasons. *Journal of Food Lipids, 12*, 313–326.

Ozyurt, G., Duysak, O., Akamca, E., & Tureli, C. (2005). Seasonal changes of fatty acids of cuttlefish *Sepia officinalis* L. (Mollusca: Cephalopoda) in the north eastern Mediterranean Sea. *Food Chemistry, 95*, 382–385.

Ozyurt, G., & Polat, A. (2006). Amino acid and fatty acid composition of wild sea bass (*Dicentrarchus labrax*): a seasonal differentiation. *European Food Research and Technology, 222*, 316–320.

Ozyurt, G., Polat, A., & Ozkutuk, S. (2005). Seasonal changes in the fatty acids of gilthead sea bream (*Sparus aurata*) and white sea bream (*Diplodus sargus*) captured in Iskenderun Bay, eastern Mediterranean coast of Turkey. *European Food Research and Technology, 220*, 120–124.

Rasoarahona, J. R. E., Barnathan, G., Bianchini, J.-P., & Gaydou, E. M. (2005). Influence of season on the lipid content and fatty acid profiles of three tilapia species (*Oreochromis niloticus, O. macrochir and Tilapia rendalli*) from Madagascar. *Food Chemistry, 91*, 683–694.

Rodriguez, C., Acosta, C., Badia, P., Cejas, J. R., Santamaria, F. J., & Lorenzo, A. (2004). Assessment of lipid and essential fatty acids requirements of black seabream (*Spondyliosoma cantharus*) by comparison of lipid composition in muscle and liver of wild and captive adult fish. *Comparative Biochemistry and Physiology B, 139*, 619–629.

Saito, H., Seike, Y., Ioka, H., Osako, K., Tanaka, M., Takashima, A., et al. (2005). High docosahexaenoic acid levels in both neutral and polar lipids of a highly migratory fish: *Thunnus tonggol* (Bleeker). *Lipids, 40*(9), 941–953.

Shirai, N., Suzuki, H., Tokairin, S., Ehara, H., & Wada, S. (2002a). Dietary and seasonal effects on the dorsal meat lipid composition of Japanese (*Silurus asotus*) and Thai catfish (*Clarias macrocephalus* and hybrid *Clarias macrocephalus* and *Clarias galipinus*). *Comparative Biochemistry and Physiology A, 132*, 609–619.

Shirai, N., Terayama, M., & Takeda, H. (2002b). Effect of season on the fatty acid composition and free amino acid content of the sardine *Sardinops melanostictus*. *Comparative Biochemistry and Physiology B, 131*, 387–393.

Silvers, K. M., & Scott, K. M. (2002). Fish consumption and selfreported physical and mental health status. *Public Health Nutrition, 5*, 427–431.

Sushchik, N. N., Gladyshev, M. I., Kalachova, G. S., Makhutova, O. N., & Ageev, A. V. (2006). Comparison of seasonal dynamics of the essential PUFA contents in benthic invertebrates and grayling *Thymallus arcticus* in the Yenisei river. *Comparative Biochemistry and Physiology B, 145*, 278–287.

Varljen, J., Baticic, L., Sincic-Modric, G., Obersnel, V., & Kapovic, M. (2004). Composition and seasonal variation of fatty acids of *Diplodus vulgaris* L. from the Adriatic Sea. *Journal of the American Oil Chemists Society, 81*, 759–763.