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Seasonal distribution and fatty acid composition of littoral microalgae in the Yenisei River

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Abstract We studied fatty acid (FA) composition of littoral microalgae in the fast-flowing oligotrophic river, the Yenisei, Siberia, monthly for 3 years. Seasonal dynamics of species composition had similar patterns in all the studied years. In springs, a pronounced dominance of filamentous green algae occurred, in summer and autumn diatoms were abundant, and in late autumn and winter epilithic biofilms consisted primarily of cyanobacteria and detritus. In general, FA composition of the algal periphytic community was dominated by 16:0, 16:1ω7, 20:5ω3, 14:0, and 18:3ω3 throughout the studied period. Several groups of FAs, which had peculiar seasonal dynamics, were differentiated by statistical analysis based on a method of correlation graphs. The seasonal changes in FA composition could be partly explained by the seasonal succession of species composition of the community. Besides, we found that populations of both diatom and green algae grown in summer at a higher water temperature were lower in polyunsaturated fatty acids than those in spring, at a lower temperature. Hence, we suppose that the regular seasonal dynamics of FA composition of the studied littoral microalgae was driven both by changes in species composition and by temperature adaptations of the algal populations. The highest content of essential polyunsaturated FAs, eicosapentaenoic and docosahexaenoic acids, in the spring "psychrophilic" populations of diatoms could make them of the higher nutritive value for zoobenthic primary consumers.

Keywords Fatty acids · Riverine microalgae · Taxa composition · Temperature adaptations

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Introduction

Benthic periphytic algae are the major producers in rivers with high current velocities in temperate and Arctic climate zones. As a rule, the bottoms of such rivers are pebbly and covered with epilithic biofilms of benthic algae. Taxonomic composition and total biomass of algal periphyton communities have been shown to depend on major environmental variables, e.g., current velocity (Biggs et al. 1998; Passy 2002), bedrock types and hydrological conditions (Potapova 1996), geochemical parameters (Charles et al. 2006), nutrient concentrations and bioavailability (Bowman et al. 2005), and riparian vegetation conditions (Griffith et al. 2002). Studies addressing temporal variations in the river periphyton are relatively scarce (Soininen and Eloranta 2004; Stewart et al. 2005). Generally, the periphytic alga assemblages have often been considered as powerful indicators in assessing anthropogenic disturbance and pollution of lotic ecosystems, for instance, metal mining (Potapova 1996; Griffith et al. 2002).

As known, interactions at the aquatic producers–primary consumers interface often limit transfer of energy and matter in whole trophic chain due to profound differences in elemental and biochemical composition of biomass of photoautotrophs and animals. Studies of such interactions in pelagic ecosystems are focused on elemental and biochemical quality of phytoplankton as food for herbivorous zooplankton, that is, C/N/P stoichiometry and essential

polyunsaturated fatty acids (PUFA) of ω3 family. (e.g., Gulati and DeMott 1997). As a result, fatty acid (FA) composition of phytoplankton is comparatively well studied (e.g., Ahlgren et al. 1992; Thompson et al. 1992; Napolitano 1999). In contrast, the fatty acid data on periphytic algae are very scarce, and few works have been carried out only for stream communities (Napolitano 1994, 1999). In the available literature, the data on FA composition of algal periphyton of large rivers are absent.

We have previously shown that FA composition of freshwater phytoplankton strongly varied during a vegetation season due to succession of species composition (Sushchik et al. 2003a). We suppose that fatty acids of the riverine periphytic microalgae may also exhibit significant temporal variation resulting in changes in the food quality for the primary consumers.

The aim of the present work was to study seasonal dynamics of FA composition of littoral periphytic microalgae in the Yenisei River. We addressed several questions: (a) What fatty acid composition was characteristic of the riverine periphytic alga community presented in different seasons of the year? (b) Did seasonal changes in FA of the studied periphytic assemblages follow the same pattern during several studied years? (c) Were seasonal temperature changes involved in the control of FA composition in the periphyton?

Materials and methods

Study site and sampling Our approach to address these questions involved simultaneous analysis of algal taxa composition and fatty acids in periphytic assemblages in the Yenisei River. The Yenisei River is the largest river of Russia, it drains large catchment (2,650,000 km^2), and its average annual discharge is ca. 600 km^3. For a detailed description of the ecological features of the river, the reader is referred to Telang et al. (1991). Current velocity is up to 2 m s^{-1}, and the river has a relatively small bed width (ca. 500 m) but considerable depths and pebbly bottom. The sampling site (55°58′ N and 92°43′ E) is situated about 30 km downstream of the dam of Krasnoyarsk Hydroelectric Power Station, near the city of Krasnoyarsk (upstream). The catchment here is little affected by human activity. There are no canopy trees that shadow the station, and the sampling site has sufficient insolation to allow proper primary production. As a result of dam regulation, there is no ice cover at the station during winter because of water discharge from deeper layers of the reservoir. Water temperature was measured by a digital thermometer (Cole-Parmer, USA) and ranged between 5 and 10°C in summer–autumn and 0 and 5°C in winter–spring (Fig. 1). As a rule, in April–May, water level increased abruptly (up to 1–2 m) due to dam regulation, and large riparian

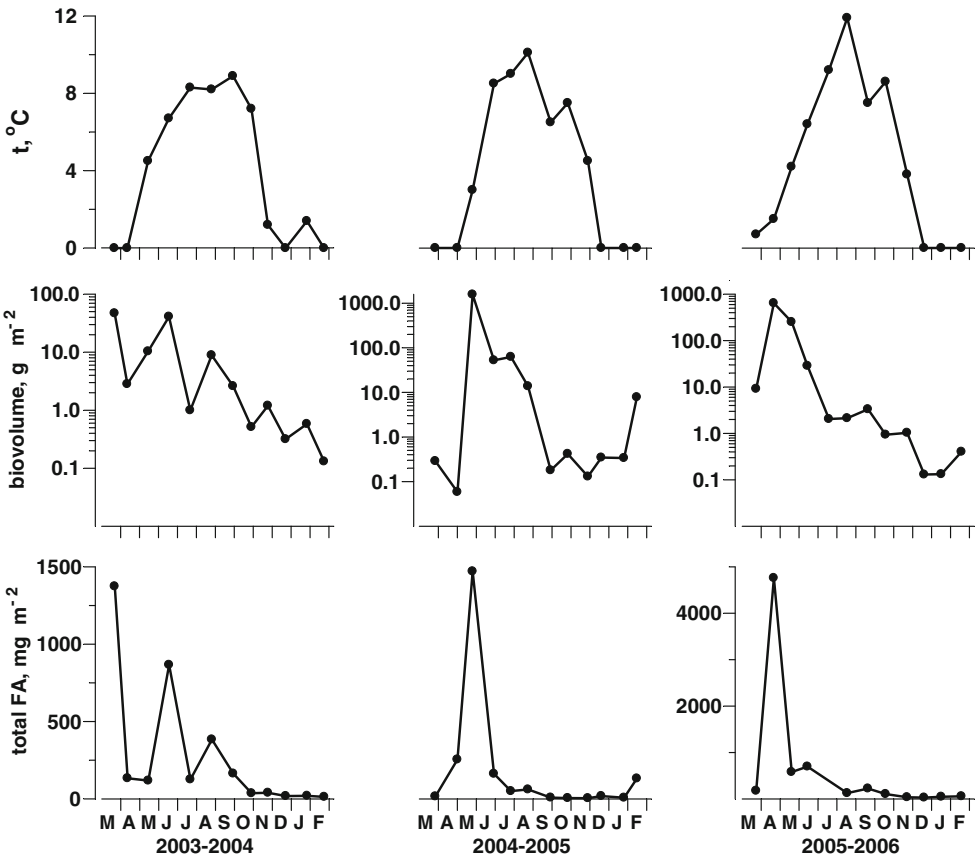

Fig. 1 Temperature of water, wet weight of periphytic algae, and total fatty acid content of periphyton in the littoral of the Yenisei River in the vicinity of Krasnoyarsk City (Siberia, Russia)

territories were flooded. Then, flow decreased until August, and the second weaker flood occurred in late summer. The flow in autumn and winter was relatively stable. Vascular plants from the river were described by Zotina (2008).

We sampled monthly from March 2003 to February 2006 in the littoral at about 0.5 m depth. Current velocity here was markedly lower than in the middle stream of the watercourse and varied between 0.2 and 0.5 m s^{-1} (Levadnaya 1986). The substrate comprised mostly cobbles (10–15 cm diameter) and pebbles (2–10 cm diameter). For periphyton (epilithic biofilms) sampling, a 1 dm^2 frame was placed in the bottom, the cobbles and pebbles which were inside the frame were withdrawn, and periphyton was collected by brushing it off from the surface of stones with a toothbrush and suspending it in a small volume of river water.

During the first studied year (from April 2003 to March 2004), three to four replicate samples were taken at sampling points lying 10 to 15 m apart. This allowed estimate variability that occurred due to local heterogeneity in algae distribution and accuracy of the sampling technique. From April 2004 to February 2006, we collected only one sample per month. Each sample in this period was taken as follows: the stones were withdrawn from three points lying 10 to 15 m apart and brushed off, and the suspensions were pooled together.

We occasionally observed separate colonies of some dominant algae in two dates of 2005, when epilithic biofilms were especially heavy in the littoral of the sampling site. This allowed us to collect such colonies from big cobbles, in addition to the common sampling procedure. In April and July 2005, colonies of *Ulothrix* species were taken, and in April 2005, *Didymosphenia* aggregations were taken. In each case, collected algae material was sufficient only for a single analytical run. The collected pieces of alga biomass were washed out with tap water in the lab and fixed for further fatty acid analysis.

Taxonomical and chemical analyses The periphyton samples were actively shaken for several minutes and immediately subsampled for taxonomic identification, counting of algae, size estimation and biovolume calculations, and fatty acid analyses. Aliquots for microscopical alga analysis were preserved with two drops of Lugol's iodine solution. The aliquots for fatty acid analysis were centrifuged at 2,500×*g* for 15 min, pellets were collected and placed in 5 mL of chloroform–methanol mixture (2:1 by volume), and a fixed volume of the internal standard solution (nonadecanoic acid) was added. The samples were kept at −20°C until their further analysis within a month.

Although epilithic biofilms appeared to comprise a complicated consortia that included algae, bacteria, and invertebrates, microscopical analysis showed that the studied periphyton mainly comprised eukaryotic and prokaryotic microalgae, and that bacteria and small ciliates were a small component (ca. 7–12% of total biovolume). Microalgae were counted and identified using a Fuchs–Rosenthal counting chamber (0.0032 mL volume) under an inverted microscope at ×400 magnification.

The number of diatom valves or cells counted varied among samples, ranging relatively evenly from about 100 to 2,500. Sizes were measured using an ocular micrometer, and appropriate geometrical shapes or their combinations were used to calculate median cell volume and then to convert cell numbers to volumes for each species of algae (Hillerbrand et al. 1999). Wet weight biomass was then calculated assuming a specific density of 1 g cm^{-3}.

For taxonomic identification, the following sources were generally used: Cyanophyceae (Elenkin 1949), Chlorophyceae (Moshkova and Hollerbach 1986), and Bacillariophyceae (Krammer and Lange-Bertalot 1986; Krammer and Lange-Bertalot 1991a, b). The relative abundances of particular alga taxa were assessed as percentages of their wet weight from the total wet weight of algae in a sample.

Laboratory FA analyses and comprehensive identification of fatty acids were described in detail elsewhere (Makhutova et al. 2003; Sushchik et al. 2003b). Briefly, lipids from periphyton samples were extracted with chloroform/methanol (2:1, *v*/*v*) three times simultaneously with mechanical homogenization with glass beads. Methyl esters of fatty acids (FAMEs) were prepared in a mixture of methanol–sulfuric acid (20:1, *v*/*v*) at 85°C for 2 h. FAMEs were then analyzed using a gas chromatograph–mass spectrometer (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, compared to those in the database (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 fatty acids was used.

Statistics Calculations of standard errors (SE) and Pearson product-moment correlations were carried out conventionally (Campbell 1967), using STATISTICA software, version 6.0 (StatSoft, Inc., USA).

We used the statistical method of correlation graphs to reveal possible regularities in seasonal dynamics of the FA composition of the studied periphyton. As a rule, intensive new vegetation of the riverine periphytic algae started in March. Hence, we used March as the starting point of an annual cycle and February as the final point; thereby, three whole annual cycles for periphyton growth and temporal succession were considered. For each annual cycle, the correlation coefficient matrix between percent contents of

all major fatty acids was calculated and three independent correlation matrixes were obtained. From each correlation matrix, only positive, high (>0.5), and statistically significant ($p<0.05$) coefficients were selected and presented in the correlation graph (Gladyshev et al. 2001; Kalachova et al. 2004). Then, all major fatty acids were depicted and the selected coefficients were presented as lines of different types indicating the correlation values between acids. Due to numerous correlations, several fatty acids jointed the distinct clusters. Other fatty acids did not correlate with each other and got separate position.

Results

Periphyton abundance and taxonomic composition A total of 64 taxa with a relative abundance >1% in at least one sample were identified in the Yenisei River samples. Of these, 43 taxa were diatoms, ten were green algae, seven were cyanobacteria, and one representative for each Chrysophyta, Xanthophyta, Dinophyta, and Euglenophyta was found. Some taxa were identified only to genus or family, e.g., Oscillatoriaceae. Two or three taxa dominating the periphyton community in each sampling date and their relative abundances (percent of the total wet weight) were presented in Table 1. Six taxa accounted more than >50% of the total biomass at least in one sample date: *Cocconeis placentula*, *Diatoma tenuis*, *Didymosphenia geminata*, *Gomphonema tenellum*, *Ulothrix zonata*, and *Ulotrix tenerrima*. Several species were frequently dominant, up to 12 among 36 dates: *C. placentula*, *D. geminata*, *U. zonata*, *Rhoicosphenia abbreviate*, *Gomphonema septum*, *G. tenellum*, and *Gomphonema ventricosum* (Table 1). Besides the taxa shown in Table 1, several other representatives of *Aulacoseira*, *Cymbella*, *Diatoma*, *Fragilaria*, *Gomphonema*, and *Navicula* genera were moderately abundant in the majority of the samples.

Total biomass of the littoral periphytic algae showed distinct and strong maximum in the spring months, with peak in 2004 being the highest—1,570 g m^{-2}. The periphyton accrual in 2005 was lower approximately by factor of 3 than that in the previous year. Note that in all the years studied the peak of periphyton biomass occurred when water temperatures were 0–4.5°C (Fig. 1). Moreover, daily average temperatures of air in March–April were lower than 5°C, which generally is accepted as a threshold for growth (Lindstrom et al. 2004). Then, second peaks (2003 and 2004) or relatively high levels (2005) of the algal biomass were observed in summer; however, they were significantly lower than those in spring. Strong decreases in periphyton biomass between the peaks were most probably related to flood events. In the late autumn and winter, levels of periphyton biomass ranged from 0.1 to 1.2 g m^{-2}.

Relative abundances of the major taxa found in the Yenisei littoral are shown in Fig. 2. Green algae were mainly the dominant group until May–June and mostly comprised of the filamentous species. They were especially abundant in 2004 with the highest annual peak of biomass (Figs. 1 and 2). As a rule, green algae peaked secondly in the middle or late summer. Both *Ulothrix* species occurred in periphyton samples from March until October, while *Palmella* sp. appeared in July and later, and *Microspora* sp. was found occasionally in January (Table 1). *Stigeoclonium tenue* was a typical representative of greens in most months, although its relative abundances were comparatively low. *D. tenuis*, species of *Gomphonema*, and *D. geminata* were the usual counterparts of the green algae that dominated in spring (Table 1). In general, the accrual of diatom biomass shifted a month or two later relative to that of green algae and occurred in early summer (Fig. 2). In this period, mostly colonial species dominated the diatom community, e.g., *Fragilaria capucina* and *Aulacoseira varians* (Table 1). From mid-summer until September, diatoms strongly dominated the periphyton community. Cyanobacteria became relatively abundant since late summer and even dominated in some later months of the annual cycles (Fig. 2). In 2004, *Chamaesiphon incrustans* markedly predominated periphytic cyanobacteria, while in other years there were representatives of the Oscillatoriaceae family (*Oscillatoria* sp., *Phormidium* sp., and unidentified species with very thin trichomes, 1–2 μm; Table 1).

Among the dominant diatom taxa (Table 1), some had distinct seasonal distribution, and others showed relatively uniform annual occurrence. For instance, *C. placentula*, *G. tenellum*, *R. abbreviate*, and *G. ventricosum* accounted for a significant part of the mature diatom assemblages in autumn and winter. *D. geminata* was highly abundant from May to September, while *Fragilaria arcus* in May and June, and *Cymbella ventricosa* was prominent in mid-summer. Thus, despite some interannual variations, the algal periphytic community of the littoral of the Yenisei River showed distinct and stable seasonal succession.

Fatty acids in periphytic biofilms In all samples collected for 3 years, 70 FAs were identified. Average annual percentages and ranges of prominent FAs (>0.1% of the total) are given in Table 2. Fatty acids of periphyton were dominated by the same FAs every year: 16:0, 16:1ω7, 20:5ω3, 14:0, and 18:3ω3 (Table 2). Evidently, the most dominant FAs of the Yenisei River periphyton were characteristic markers of diatoms (Brown et al. 1997; Napolitano 1999). The mean percentages of most FAs slightly varied between the studied years, except for

Table 1 Dominant species of periphytic microalgae and their percentages of the total biomass in the littoral of the Yenisei River in the vicinity of Krasnoyarsk City (Siberia, Russia), 2003–2006

Month	2003–2004	Percent	2004–2005	Percent	2005–2006	Percent
March	*Gomphonema tenellum* Kütz.	36.0	*Rhoicosphenia abbreviate*	46.3	*Ulothrix zonata*	49.9
	Ulothrix zonata Kütz.	29.2	*Cocconeis placentula*	22.5	*Diatoma tenuis*	17.8
	Gomphonema ventricosum Greg.	7.3	*Gomphonema septum*	9.8	*Didymosphenia geminata*	10.8
April	*Ulothrix zonata*	33.1	*Rhoicosphenia abbreviate*	43.6	*Ulothrix zonata*	47.1
	Gomphonema septum Mogh.	28.1	*Gomphonema septum*	19.4	*Didymosphenia geminata*	18.9
	Cocconeis placentula Ehr.	8.5	*Ulotrix tenerrima*	16.3	*Diatoma tenuis*	14.8
May	*Didymosphenia geminata* (Lyngb.) M.Schmidt	19.3	*Ulothrix zonata*	90.0	*Ulothrix zonata*	87.6
	Fragilaria arcus (Ehr.) Kütz.	16.5	*Diatoma tenuis* (Lyngb) Ag.	8.4	*Fragilaria arcus*	4.0
	Gomphonema ventricosum	14.0				
June	*Fragilaria construens* (Ehr.) Grun	20.3	*Diatoma tenuis*	58.3	*Fragilaria arcus*	19.3
	Fragilaria capucina Desm.	15.7	*Cymbella stuxbergii*	14.1	*Aulacoseira varians* Ag.	18.8
	Aulacoseira islandica O. Mull	11.2	*Ulothrix zonata*	13.5	*Ulothrix zonata*	15.4
July	*Cymbella ventricosa* Kütz.	23.4	*Ulothrix zonata*	93.0	*Didymosphenia geminata*	36.2
	Ulothrix zonata	10.1	*Didymosphenia geminata*	3.0	*Cymbella ventricosa*	19.3
	Navicula sp.	10.1			*Palmella* sp.	11.8
August	*Didymosphenia geminata*	57.2	*Didymosphenia geminata*	40.1	*Cymbella stuxbergii*	16.6
	Cymbella stuxbergii Cl.	16.6	*Cymbella stuxbergii*	14.5	*Didymosphenia geminata*	15.6
	Navicula sp.	3.1	*Rhoicosphenia abbreviate*	14.1	*Palmella* sp.	15.5
September	*Didymosphenia geminata*	30.3	*Cocconeis placentula*	37.4	*Didymosphenia geminata*	35.3
	Gomphonema septum	15.2	*Navicula* sp.	29.9	*Rhoicosphenia abbreviate*	14.1
	Cymbella stuxbergii	10.8	*Gomphonema ventricosum*	10.5	*Ulothrix zonata*	10.4
October	*Gomphonema septum*	25.1	*Ulothrix tenerrima*	55.6	*Gomphonema ventricosum*	47.8
	Gomphonema ventricosum	17.7	*Cocconeis placentula*	13.3	*Gomphonema longiseps* Ehr.	12.4
	Rhoicosphenia abbreviate (Kütz.) Grun.	11.9	*Chamaesiphon incrustans* Grun.	11.1	*Cocconeis placentula*	7.7
November	*Rhoicosphenia abbreviate*	27.4	*Chamaesiphon incrustans*	49.9	*Gomphonema septum*	36.1
	Gomphonema septum	20.1	*Cocconeis placentula*	25.5	*Cocconeis placentula*	18.2
	Gomphonema tenellum	19.4	*Rhoicosphenia abbreviate*	17.0	*Rhoicosphenia abbreviate*	17.7
December	*Cocconeis placentula*	53.5	*Navicula* sp.	37.7	*Oscillatoriaceae*	40.9
	Aulacoseira islandica	12.3	*Chamaesiphon incrustans*	28.1	*Gomphonema lanceolatum* Ehr.	23.5
	Gomphonema tenellum	8.0	*Cocconeis placentula*	13.5	*Gomphonema tenellum*	13.5
January	*Cocconeis placentula*	27.4	*Microspora* sp.	44.5	*Gomphonema tenellum*	42.1
	Gomphonema ventricosum	14.4	*Cocconeis placentula*	21.8	*Chamaesiphon incrustans*	21.1
	Cocconeis sp.	12.7	*Rhoicosphenia abbreviate*	18.4	*Rhoicosphenia abbreviate*	16.4
February	*Cocconeis placentula*	29.7	*Ulothrix zonata*	25.9	*Gomphonema tenellum*	61.8
	Gomphonema tenellum	25.8	*Gomphonema ventricosum*	22.1	*Achnanthes* sp.	12.7
	Rhoicosphenia abbreviate	20.4	*Cymbella stuxbergii*	15.8	*Cocconeis placentula*	7.5

16:1ω7, 16:4ω3, 18:4ω3, and long-chain saturated acids. Among the studied years, the average level of 16:1ω7 was the lowest in 2004–2005, and the levels of 16:1ω3 and 18:4ω3 were markedly lower in 2003–2004, while the percentages of 18:0, 20:0, 22:0, 24:0, and 26:0 significantly decreased in 2005–2006. The epilithic biofilms evidently contained some bacteria. As a result, bacterial fatty acid biomarkers, iso and anteiso odd-numbered chain FAs (Napolitano 1999), were also found, although at comparatively low levels (Table 2). Besides this, some ciliates and other protozoa can be found in periphytic community, and these organisms can also provide for some FA. Their contribution in the total FA may coarsely be estimated by the content of 22:6ω3, 20:4ω6, 22:5ω6, and 18:1ω9. Percentages of these FAs were comparatively low in all the years studied (Table 2). Hence, namely microalgae likely

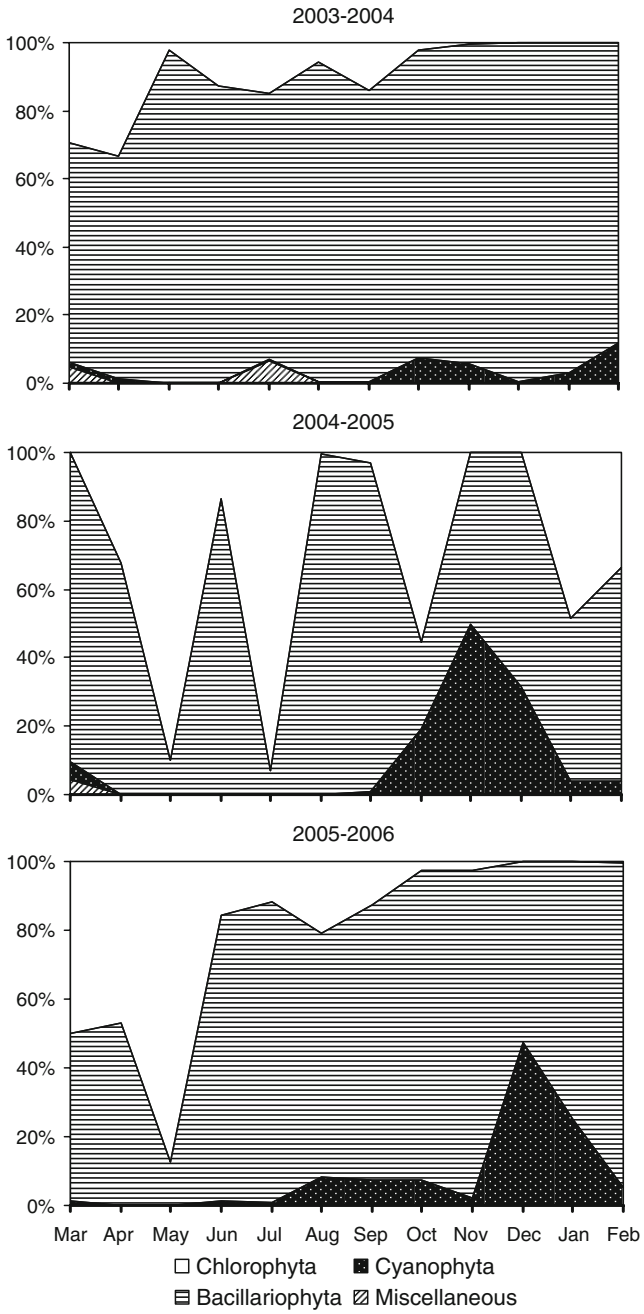

Fig. 2 Taxa composition of algae and cyanobacteria (percent of total wet weight) in periphyton in the littoral of the Yenisei River in the vicinity of Krasnoyarsk City (Siberia, Russia)

supplied the most FAs contained in periphytic biofilms of the Yenisei littoral.

To elucidate the fatty acid composition of particular epilithic algae in natural conditions, three samples of separate algal colonies were taken when they were occasionally found out. Their fatty acid analysis revealed a huge difference between *Ulothrix* and *Didymosphenia* samples and general similarity of the *Ulothrix* samples collected in April and July 2005 (Table 3). Dominant FAs of *Ulothrix* were 18:4ω3, 16:0, 16:4ω3, and 18:3ω3. However, the percentages of saturated FA in July were markedly higher than those in April at the expense of PUFAs. The Main FAs in *Didymosphenia*-like colonies were 20:5ω3, 16:0, 16:1ω7, and 16:4ω1 (Table 3). The ratio of 16:1ω7 to 16:0 was close to 1, which is typical for diatoms. Note that the diatom colony had relatively high percentage of 22:6ω3, while the colonies of greens were rich in 22:5ω3. Green and diatom algae have weak capacity to synthesize C22 PUFAs. Hence, C22 PUFA in periphyton probably reflected the input of organic matter of some protists and rotifers which might be habitably related with particular alga colonies.

Correlation graphs To consider peculiar seasonality of FA composition, correlation coefficients between percentages of all prominent FA (Table 2) were calculated in each annual cycle (started from March and finished in February). All fatty acids and all significant positive correlations between them were presented as correlation graphs (Figs. 3, 4, and 5). The statistical parameters for the lowest correlation coefficients were the same in each year: $r=0.58$, $t > t_{st}$, $p<0.05$ at $\nu=10$. In each correlation graph, several FA groups which significantly positively correlated to each other were revealed.

In the 2003–2004 annual cycle, there were two large groups (clusters) of FAs (Fig. 3). One of them was formed by saturated straight and branched acids and 18:3ω3 and 16:3ω3. Monoenoic and dienoic C18 acids were comparatively weaker related with the group. The second included polyunsaturated FA of a various chain length and 16:1ω7. The knot group of this cluster was formed by eicosapentaenoic acid and C16 acids of ω4 and ω1 families. Several other PUFAs and saturated 14:0 did not join any cluster (Fig. 3).

In the next year, three distinct FA groups at the correlation graph (Fig. 4) were revealed. The FA components of the largest cluster were almost the same as in the previous year. The stronger correlations between C15, C16, and C17 saturated acids were remarkable for this cluster. The cluster of PUFAs which was generally analogous to the previous one (Figs. 3 and 4, *2*) contained the same knot of 20:5ω3 and ω4 and ω1 C16 acids and strongly joined 18:3ω6 and 20:4ω3. Unlike 2003–2004, acid 16:1ω7 separated from the second cluster, while acid 14:0 joined. The main peculiarity of the graph of 2004–2005 was the united group of 16:4ω3, 18:4ω3, and 22:5ω3. Previously, the acid 16:4ω3 had separate position (Fig. 3), while the two latter acids were weakly related to the second cluster.

The group of saturated FA and C18 monoenoic and dienoic acids was the most prominent in the correlation

Table 2 Fatty acid composition (percent of the total) of periphytic biofilms in the littoral of the Yenisei River in the vicinity of Krasnoyarsk City (Siberia, Russia)

FA	2003–2004		2004–2005		2005–2006	
	m	min–max	*m*	min–max	*m*	min–max
12:0	0.4	0.1–0.7	0.5	0.0–0.8	0.3	0.0–0.5
14:0	5.4	3.6–7.8	6.3	4.2–10.4	6.3	3.1–10.9
i15:0	0.4	0.2–0.7	0.4	0.0–0.6	0.4	0.1–0.8
ai15:0	0.3	0.1–0.5	0.4	0.0–1.2	0.3	0.1–0.9
15:0	0.8	0.3–1.5	1.0	0.2–3.1	0.5	0.2–1.1
16:0	23.0	16.4–31.0	23.3	13.9–42.1	21.6	14.5–32.1
16:1ω7	18.0	7.3–31.4	15.6	4.3–30.3	19.5	7.2–29.5
i17:0	0.3	0.1–0.7	0.2	<0.1–0.5	0.2	<0.1–1.0
16:2ω7+ω6	0.4	0.2–0.9	0.5	<0.1–1.0	0.4	0.2–0.6
ai17:0	0.2	0.1–0.4	0.1	<0.1–0.4	0.2	<0.1–0.4
16:2ω4	1.7	0.1–2.7	1.9	0.5–3.9	2.0	0.8–3.0
17:0	0.5	0.1–0.8	0.3	<0.1–1.0	0.2	<0.1–0.5
16:3ω4	1.7	0.5–2.5	1.9	0.7–3.2	1.6	0.9–2.4
16:3ω3	1.4	0.2–3.8	1.7	0.2–4.5	1.3	0.4–2.2
16:4ω3	1.1	0.4–2.3	2.0	<0.1–11.0	1.8	0.5–8.2
16:4ω1	2.4	0.2–5.5	2.4	<0.1–4.8	2.3	0.8–4.5
18:0	4.2	1.1–7.9	3.3	0.9–8.4	2.1	0.5–4.8
18:1ω9	4.5	2.0–6.2	4.6	1.1–11.6	3.9	1.8–5.3
18:1ω7	2.8	0.7–4.9	2.3	<0.1–4.8	2.5	0.6–3.4
18:2ω6	3.7	1.4–7.5	3.9	1.6–7.5	3.5	2.4–5.4
18:3ω6	0.5	<0.1–1.0	0.4	<0.1–0.7	0.6	0.2–1.1
18:3ω3	5.7	1.3–12.3	5.4	1.7–8.9	6.0	1.8–10.0
18:4ω3	2.2	1.0–4.8	3.8	0.1–17.8	3.3	0.5–14.1
20:0	0.6	0.1–1.2	0.4	<0.1–1.1	0.2	<0.1–0.4
20:3ω6	0.2	<0.1–0.3	0.1	<0.1–0.4	0.1	0.0–0.2
20:4ω6	0.5	<0.1–0.8	0.5	<0.1–1.0	0.6	0.3–1.1
20:4ω3	0.3	<0.1–0.6	0.3	<0.1–0.5	0.4	0.1–0.7
20:5ω3	11.4	3.3–20.3	10.1	0.3–23.8	11.9	4.3–18.0
22:0	0.7	0.1–1.2	0.5	<0.1–0.9	0.4	0.2–0.9
22:5ω6	0.1	<0.1–0.8	0.1	<0.1–0.2	0.2	<0.1–0.7
22:5ω3	0.6	0.2–1.0	0.7	<0.1–2.6	0.9	0.3–2.9
24:0	0.7	<0.1–3.0	0.7	<0.1–1.5	0.3	0.2–0.6
22:6ω3	0.8	0.2–1.7	0.9	<0.1–2.0	1.1	0.3–1.7
26:0	0.4	<0.1–2.3	0.2	<0.1–2.0	<0.1	<0.1

Means (*m*) and minimum and maximum (min–max) values for 3 years are given, for each sampling started in March and finished in February

graph of 2005–2006 (Fig. 5). The group of PUFA had comparatively weaker and fewer relations; therefore, several subgroups of this cluster were further considered separately. Like in the previous years, there was the typical subgroup that contained the knot of ω4 and ω1 C16 acids and 20:5ω3 (Fig. 5, *2*). The next subgroup included C18, C20, C22 PUFA, 16:1ω7, and 14:0 (Fig. 5, *4*). The highest correlations were found in the third subgroup of 16:4ω3, 18:4ω3, and 22:5ω3 (Fig. 5, *3*), like in 2004–2005. In contrast to the previous years, both 16:3ω3 and 18:3ω3 acids were separated from the large group of saturated acids and were slightly related through 16:4ω3 with the majority of PUFA.

Annual dynamics of FA groups formed in the correlation graphs are shown in Fig. 6. If some correlation groups were absent, the dynamics of separate acids, which formed knots in other correlation graphs, were given, e.g., 16:4ω3. First, in all correlation graphs the group based on saturated FA and C18 monoenoic and dienoic acids occurred and its percent content of the total increased in late autumn and winter (Fig. 6). The percentage of this group was also high in March 2004, corresponding to the late start of spring vegetation growth and low periphyton biomass (Figs. 1 and 6). Second, the group including C20 and C22 and ω4 and ω1 C16 PUFA also constantly presented in all correlation graphs. Its maximum percentages were observed in early

Table 3 Fatty acid composition (percent of the total) of algal colonies isolated from hard substrates in the littoral of the Yenisei River in the vicinity of Krasnoyarsk City (Siberia, Russia)

FA	*Ulothrix*		*Didymosphenia*
	April 2005	July 2005	April 2005
12:0	0.1	0.2	0.1
14:0	3.1	7.2	3.9
i15:0	0.0	0.2	0.2
ai15:0	0.0	0.1	0.2
15:0	0.1	0.4	0.7
16:0	17.0	23.2	21.1
16:1ω7	2.2	1.5	19.1
16:2ω7+ω6	0.2	0.3	0.2
16:2ω4	0.3	0.0	2.5
17:0	0.1	0.2	0.1
16:3ω4	0.3	0.1	2.4
16:3ω3	3.5	2.6	0.2
16:4ω3	15.3	12.3	0.8
16:4ω1	0.8	0.1	4.5
18:0	0.5	1.4	2.6
18:1ω9	0.7	1.6	2.8
18:1ω7	1.5	2.4	1.3
18:2ω6	2.7	4.0	1.5
18:3ω6	0.3	0.4	0.0
18:3ω3	14.3	11.7	1.6
18:4ω3	20.6	14.8	2.9
20:0	0.0	0.2	0.1
20:4ω6	0.2	0.2	0.2
20:4ω3	0.3	0.4	0.5
20:5ω3	6.6	3.4	25.0
22:0	0.4	0.7	0.2
22:5ω3	2.7	2.2	1.2
24:0	0.1	0.2	0.3
22:6ω3	0.3	0.0	2.3
SFA	21.5	34.0	29.4
MFA	7.9	9.9	23.8
PUFA	68.9	53.5	46.6

SFA sum of saturated acids, *MFA* sum of monounsaturated acids, *PUFA* sum of polyunsaturated fatty acids

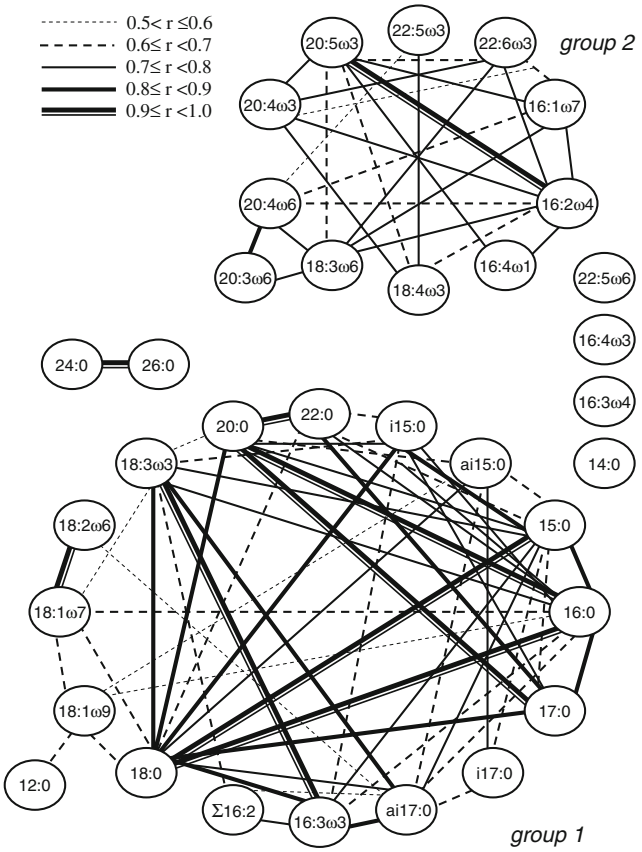

Fig. 3 Correlation graph of percentages (of the total sum) of fatty acids in periphyton in the Yenisei River, March 2003–February 2004. *r* the correlation coefficients which are statistically significant ($n=12$, $p<0.05$)

spring or summer (Fig. 6). The third group containing 16:4ω3 and 18:4ω3 was distinct only in the two latter years. In 2003–2004, FA 18:4ω3 joined the united group of PUFA, while 16:4ω3 had separate position (Fig. 3). Hence, we presented here the dynamics of 16:4ω3 for 2003 and groups 3 for 2005 and 2006 in the same block (Fig. 6). The maximum percentages of these FA were observed in early spring (March–April), preceding the peak of the large PUFA group 2. In 2004 and 2005, this group reached 35–40%.

Besides EPA and ω4 and ω1 C16 PUFA, saturated 14:0 and monounsaturated 16:ω7 acids are often considered as diatom markers in aquatic trophic studies. We showed and analyzed their seasonal dynamics (Fig. 6, last panel), in contrast to PUFA markers. At least one of these two acids had separate position, i.e., peculiar seasonal dynamics in each annual cycle: 14:0 in 2003, 16:1ω7 in 2004, and both in the separate subgroup 4 in 2005 (Fig. 6). It is interesting to remark that seasonal maxima of these FA took place in mid- or late summer, after the peak of the PUFA group 2. Thus, four groups of FA (or sometimes single FA) could be indicated, which showed peculiar repeatable dynamics during three annual cycles. Some interannual variability in composition and dynamics of each group was likely related to the interannual fluctuations in species composition and abundances.

Discussion

We found significant and regular temporal variations in both algal taxa composition and biomass and the FA

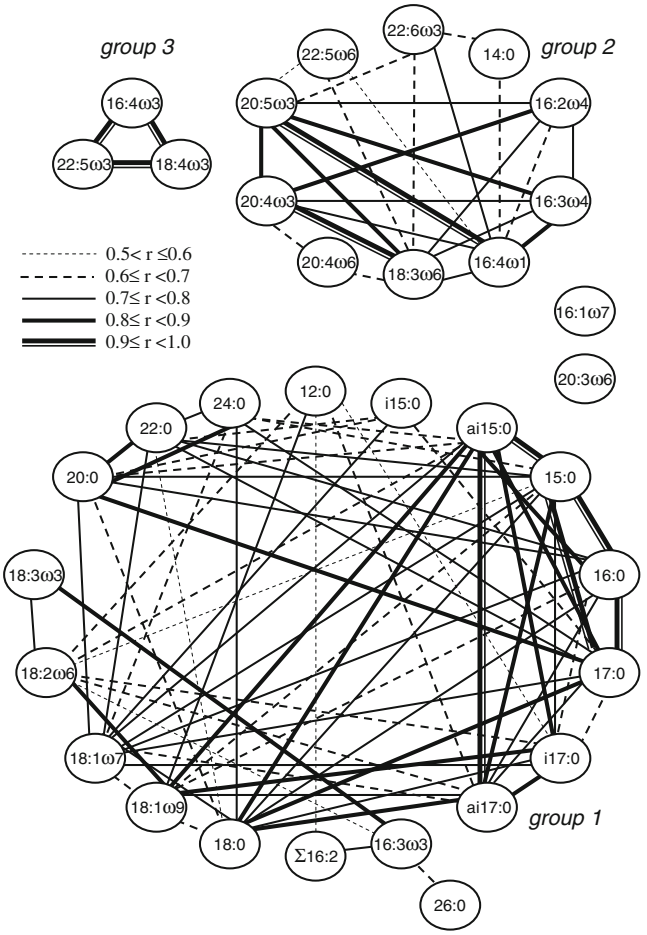

Fig. 4 Correlation graph of percentages (of the total sum) of fatty acids in periphyton in the Yenisei River, March 2004–February 2005. Abbreviations and number of samples in the analysis are the same as in Fig. 3

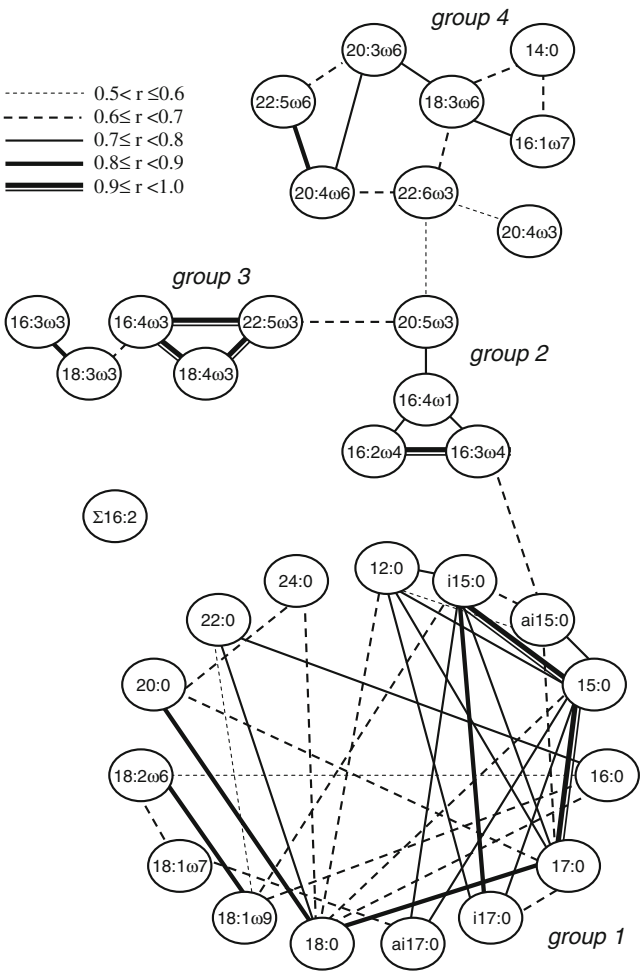

Fig. 5 Correlation graph of percentages (of the total sum) of fatty acids in periphyton in the Yenisei River, March 2005–February 2006. Abbreviations and number of samples in the analysis are the same as in Fig. 3

composition of periphyton of the Yenisei River. Correlation graph analysis was used to elucidate potential factors which determined FA dynamics of the studied riverine periphyton. Periphytic FAs were divided into several correlation groups which probably originated from peculiar taxa or were specifically controlled by environmental factors. We supposed that the FA composition reflected temperature adaptations of dominant species and/or temperature-dependent changes in the species composition of the higher taxa.

Taxa abundance and dominance The seasonal successions of the alga taxa were similar in all studied years, although the values of the biomass peaks strongly varied among the growth seasons (Fig. 1). Briefly, three different algal seasonal assemblages can be distinguished during a year: (a) filamentous green algae accompanied with diatoms at the start of the growth season, (b) diverse summer diatom community, and (c) cyanobacterial thin-trichome species with diatom species of relatively small cell size in late autumn and winter. Similarly, differences between alga communities in early, mid-summer, and autumn have been earlier reported for Finland boreal rivers (Soininen and Eloranta 2004). The temporal succession of periphytic alga communities in the Yenisei littoral was likely related to seasonal variation of hydrological and physicochemical conditions, e.g., periods of snow melting and flood resulting in subsidies of nutrients, temperature, grazing by zoobenthic organisms, and others. At present, we could not explicitly estimate specific contributions of these factors in the seasonal succession of periphyton. On the other hand, we observed significant interannual differences in the absolute abundance of particular alga taxa, for instance, the filamentous green algae.

Most algae that dominated in littoral periphyton of the Yenisei River are common representatives of running waters of the moderate climate zone worldwide. For instance, a strong dominance of *D. geminata* has been

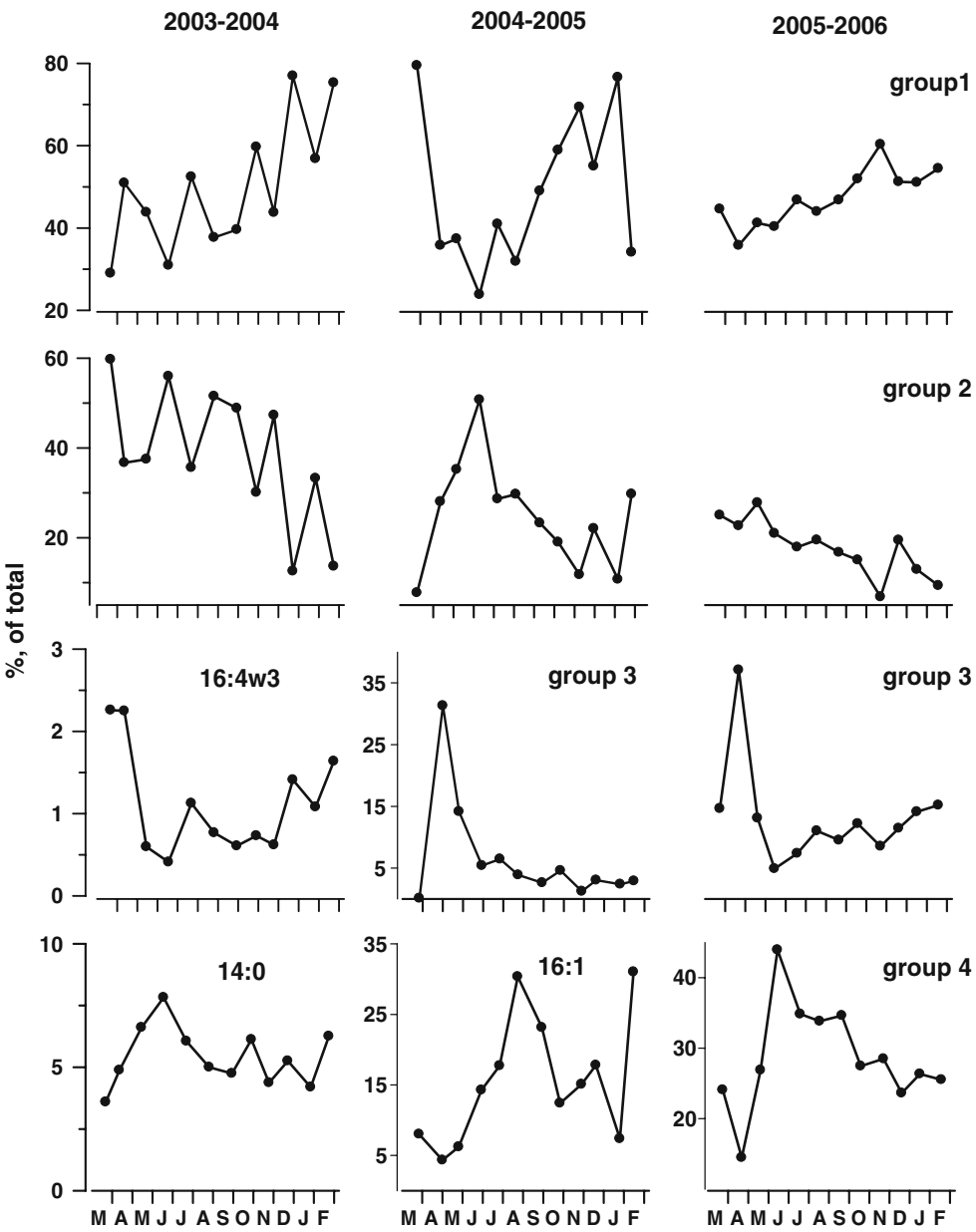

Fig. 6 Sums of percentages (of the total) of FA belonging to similar correlation groups in the graphs for periphyton of the Yenisei River. Numbers of the groups correspond to those in Figs. 3, 4, and 5

reported for the Carpathian mountain rivers (Kawecka and Sanecki 2003); *C. placentula*, *F. capucina*, *Cymbella*, and *Aulacoseira* species have been reported to be abundant in Canadian and Finland fast-flowing rivers (Soininen and Eloranta 2004; Stewart et al. 2005), while *U. zonata* have sporadically formed masses in New Zealand rivers and Colorado rocky mountain streams (Biggs et al. 1998; Niyogi et al. 1999). A number of diatom, green, cyanobacteria species, which were characteristic of periphyton in the Yenisei River, widely occurred in running waters of the geographically close Kolyma mountains at north-eastern Siberia (Potapova 1996). *D. tenuis*, which distinctly dominated diatoms of the Yenisei in spring, has previously been found in rather cold systems, e.g., in a Canadian arctic river (Stewart et al. 2005) and in north-eastern Siberian rivers (Potapova 1996). In contrast, dominance of *Gomphonema* species, that is *G. tenellum* and *G. ventricosum*, was typical for the rivers with higher temperatures in South New Zealand and in the northern and eastern mountain regions of the USA (Jowett and Biggs 1997; Fore and Grafe 2002). Occurrence of these species in the Yenisei River, mostly in summer and autumn when temperature increases, conforms to the above data. The dominance of the common species in Yenisei is in a good agreement with the hypothesis of Kilroy et al. (2007) that in disturbed systems like the fast-flowing rivers the endemic algal taxa are rather rare. However, we did not find any literature data on mass occurrence of *G. septum*, which was one of the distinct dominant species in the Yenisei River.

Total biomass of the littoral periphyton greatly varied between the years in spring peaks while its levels were relatively similar in late summer, autumn, and winter (Fig. 1). We can compare the values of spring accrual of the alga biomass with the data of Bowman et al (2005) for Canadian oligotrophic rivers and Potapova (1996) for Kolyma mountain rivers. In the Canadian rivers, the maximum recorded algal wet weight was up to 20 g m^{-2}. However, the periphytic communities in these rivers mostly comprised diatoms (Bowman et al. 2005). Total algal wet weight reached up 350 g m^{-2} in the watercourses of Kolyma Basin and up to 480 g m^{-2} in the coastal rivers (Potapova 1996), being well comparable with that in our study. Nevertheless, we found higher algal biomass compared to other cited works likely due to a strong dominance of the green filamentous algae. Long filamentous *Ulothix* species are common in watercourse habitats with lower flow velocities, near 0.3–0.5 m s^{-1} (Biggs et al. 1998), and may form very thick mats. We studied the littoral part of the river where the flow velocity decreased substantially. This provided a good habitat for these algae.

The periphytic biofilms in the late autumn and winter contained a greater part of detritus, revealed by the analysis of FA composition (see below), likely due to light constraints on photosynthesis and increasing cell decay.

Fatty acid composition of the river periphytic communities Analysis of samples taken from separate colonies gave evidence that a main portion of the following FA 18:4ω3, 16:4ω3, 22:5ω3, and 18:3ω3 in periphyton originated from filamentous green algae (*Ulothrix*). Acids 18:3ω3, 18:2ω6, 16:3ω3, and 16:1ω9 are usually regarded as FA markers for green algae (Thompson 1996; Leveille et al. 1997; Napolitano 1999). We also found high percentages of these acids in *Ulothrix* colonies; however, these natural populations of green algae contained a greater part of ω3 tetraenoic than trienoic and dienoic acids. High content of C16–18 acids with four double bonds also has been previously reported for another green alga, *Chlamydomonas* (Grenier et al. 1991). Thus, acids 18:4ω3 and 16:4ω3 seem to be more appropriate markers for tracing periphytic populations of green algae in oligotrophic lotic systems than the conventional FA markers for green algae. Comparatively high percentage of 22:5ω3 in *Ulothrix* colonies (Table 3) might be due to specific microfauna of ciliates and flagellates associated with the filamentous green bands because these algae are known not to synthesize the long-chain PUFA (Thompson 1996).

The fatty acid composition of *Didymosphenia* colonies was similar with those reported for most diatoms and contained high levels of 20:5ω3 and ω4 and ω1 C16 PUFA and had the ratio 16:1ω7/16:0 close to 1, also regarded as the characteristic of diatoms (Brown et al. 1997; Shin et al. 2000). Nevertheless, it has been shown that some freshwater diatom populations can have low PUFA content (Sushchik et al. 2004). Biomass of diatoms in two freshwater reservoirs correlated with 16:1ω7 and 14:0 rather than with 20:5ω3 (Sushchik et al. 2003a). Hence, the fatty composition of diatoms and their FA markers are species-specific. Since the taxa composition of diatoms in the Yenisei littoral was very diverse, FA percentages in periphyton of various months may significantly differ from that of the isolated colony of *Didymosphenia*.

Data on FA in lotic periphyton are very scarce. A stream periphyton community which contained diatoms and filamentous green and blue-green algae was very rich in 18:3ω3, 16:0, 16:1ω7, and 16:3ω4, while 20:5ω3 was at a moderate level (Napolitano 1994). Fatty acids of isolated *Cladophora* culture were also dominated by 18:3ω3. This acid and 16:3ω3 in our study were relatively high in *Ulothrix*; however, these were not correlated with its typical tetraenoic acids, 18:4ω3 and 16:4ω3 (Figs. 3, 4, and 5). Their percentages generally had two peaks: in spring, coupled with increase in ω3 tetraenoic acids and in late autumn and winter. We suppose that 18:3ω3 and 16:3ω3 in the periphyton may originate from two sources: in spring and early summer—from filamentous greens, while in autumn—from cyanobacteria, because the filamentous green algae disappeared in the latter period. This agrees with our previous data from a eutrophic reservoir showing high content of 18:3ω3 in some species of cyanobacteria (Sushchik et al. 2004).

Among FA of biofilms grown in situ in a fluvial lake, 18:3ω3, 16:0, 16:1ω7, 20:5ω3, and 18:2ω6 have been found to dominate (Huggins et al. 2004). The community studied in the cited work was distinctly dominated by chlorophytes, mostly *Cladophora* sp.; however, the percentages of 20:5ω3 were high and comparable with those in our study. The highest percentages of this PUFA occurred in samples in which diatoms were dominated by *Melosira* sp. and *Amphora* sp. (Huggins et al. 2004). We also found the peak of group 2 containing 20:5ω3, in June and December 2003 (Fig. 6), when *A. islandica* was a dominant species (Table 1).

Fatty acid groups at the correlation graphs Evidently, part of the fatty acids may potentially originate from different organisms, for instance, saturated FAs are synthesized by all periphytic algae. However, several FAs or their groups in complex have been proved to be markers for particular groups of hydrobionts (Reuss and Poulsen 2002). Moreover, the ratio between some FA or specific indexes has been used to estimate the physiological state of algal populations (Shin et al. 2000).

We considered iso and anteiso acids with odd-numbered chains as markers of bacteria (Reemtsma et al. 1990; Desvilettes et al. 1997) and saturated C16–C20 acids as a signature of detritus derived from algae (Hama 1999). Most of these acids formed the joint group in all correlation graphs (Fig. 6, group *1*) and their total percentages increased in late autumn and winter. This likely resulted from the seasonal decaying algal biomass and accompanying increase in detritus and bacterial components of the periphytic biofilms. Thus, the correlation graph analysis of FA composition allowed estimating the seasonal dynamics of the tangled detritus and bacterial components in the periphytic biofilms.

It is interesting to remark that in 2 years (Figs. 3 and 4) acids 18:3ω3 and 16:3ω3 also tightly joined group *1* due to the simultaneous increase in autumn and winter. Although these acids can be potential biomarkers for both green algae and cyanobacteria (Sushchik et al. 2003a), we suppose that they mostly reflected the dynamics of cyanobacteria.

According to the number of data, diatoms can synthesize and accumulate the following FAs: 14:0, 16:1ω7, ω7, ω4 and ω1 C16 PUFA, and ω3 C 20 PUFA, while PUFAs with C22 chain length are not prominent in diatoms (Volkman et al. 1989; Cobelas and Lechado 1989; Brown et al. 1997). In all correlation graphs, the typical diatom acids of the Yenisei periphyton were divided into two groups with different seasonal dynamics. One of them was the united group of C16 PUFA and C20 PUFA which peaked in early summer (Fig. 6, *2*). Saturated 14:0 and monoenoic 16:1ω7 either had a separate position or aggregated in the additional group, like in the 2005–2006 graph. Their percentages usually peaked in mid-summer (Fig. 6, *4*) when water temperature substantially increases. Hence, the difference in seasonal dynamics between diatom PUFAs and diatom monoenic and saturated acids might be considered a result of adaptation to water temperature. At higher summer temperatures, either PUFA content in the cells could decrease at the expense of 14:0, 16:0, and 16:1ω7 acids, or diatom taxa with less unsaturated FA biosynthesis might take advantage and become dominant in the community. Indeed, diatom taxonomic composition in late summer markedly differed from that in spring and early summer (Table 1). We have previously found for freshwater phytoplankton that spring diatom populations were rich in PUFA, while the summer populations of the same taxa had lower PUFA content and higher content of monoenoic and saturated acids (Sushchik et al. 2004). Thus, temperature-dependent changes in fatty acids of the periphytic diatoms in general agree with those in the freshwater planktonic populations. Diatoms are often considered as a valuable source of essential PUFA, particularly eicosapentaenoic acid, for aquatic primary consumers (Gulati and DeMott 1997). In contrast to this notion, our study together with the previous data for plankton proves that freshwater diatoms can differ strongly in the content of the essential PUFA and some of them could not be considered as a valuable quality food.

Group 3, which included tetraenes of C16–18 carbon atoms and 22:5ω3, were formed during those years when green algae strongly dominated (Fig. 2). These acids likely originated from filamentous green algae. Note that their seasonal peaks and the peak of 16:4ω3 in 2003 occurred in spring, while the increase in summer was comparatively weak. Moreover, the FA peaks often preceded the spring peaks of green alga biomass (Figs. 2 and 6). Hence, these highly unsaturated acids were likely mostly synthesized by the intensively grown spring populations of the algae adapted to low temperatures, 0–4°C (Fig. 1). Indeed, summer populations of *Ulothrix* showed markedly lower 16:4ω3 and 18:4ω3 percentages (Table 3). It is well known for laboratory cultures of both green algae and diatoms that the degree of FA unsaturation increases when algae grow at lower temperatures (Sushchik et al. 2003c; Jiang and Gao 2004). Our finding of temperature effect on PUFA percentages in the natural populations of green algae is in good agreement with these laboratory data. Nevertheless, the present work is the first report on the likely influence of temperature on PUFA composition of natural populations of periphytic green algae.

As known, the nutritional value of organisms with regard to their essential PUFAs for consumers of a higher trophic level primarily depends on their contents of long-chain PUFA, such as eicosapentaenoic (EPA, 20:5ω3) and docosahexaenoic (DHA, 22:6ω3; Olsen 1999). The percentages of these two PUFAs in periphyton of the Yenisei significantly correlated in each year (Figs. 3, 4, and 5). Based on their annual dynamics, one could conclude that the studied periphytons were of the highest nutritional value with regard to their PUFA content for benthic primary consumers in May–June when spring "psychrophilic" diatom populations dominated.

In conclusion, FA composition of the periphyton showed regular changes during annual cycles and reflected following phases of species composition: (1) the actively grown spring population of "psychrophilic" filamentous green algae; (2) the spring "psychrophilic" and summer communities of diatoms; (3) the autumn populations of cyanobacteria; and (4) detritus derived from decaying eukaryotic algae along with bacteria in late autumn and winter. The FA biomarkers for green microalgae living in oligotrophic lotic systems were specified.

Besides this, there were evidences that seasonal variation in temperature resulted in different PUFA contents and FA compositions of spring and summer populations of both green and diatom periphytic algae. We managed to distinguish the spring and summer diatom populations with the specific FA composition on the basis of the correlation graph analysis. Thus, seasonal dynamics of FA composition

of the river periphyton was driven both by changes in taxa composition and by temperature adaptations of algal populations. The spring "psychrophilic" populations of diatoms had the highest content of essential PUFAs, EPA, and DHA, and thereby the spring periphyton had the highest nutritive value for zoobenthic primary consumers.

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