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RESEARCH ARTICLE

Allochthonous versus autochthonous carbon subsidies in small river food webs depend on seasonality and riparian tree species

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Abstract

The river continuum concept (RCC), which proposes that terrestrial allochthonous inputs, namely, leaf litter, is the main source of organic carbon in trophic webs of forested headwater streams, was based on gut content analyses of benthic invertebrates. Modern methods, such as stable isotope analysis (SIA), fatty acid (FA) biomarker analysis, and elemental analysis (C:N stoichiometry), indicate autochthonous sources (periphytic microalgae) to be the main basal source of carbon in streams. However, these modern methods were applied in a comparatively limited number of cases. We hypothesize that: (1) proportions of incorporation of organic carbon of leaf litter by benthic consumers can be higher in spring than in autumn due to conditioning of the leaves during winter, and (2) carbon of leaf litter of certain tree species can be incorporated in river food webs to a higher degree than carbon of other tree species. Using SIA, FA, and C:N, allochthonous and autochthonous sources of organic matter and their quality in food webs of a small forest river in the Russian Far East were studied. It was found that some benthic animals obtained organic carbon mainly or exclusively from the allochthonous basal source, leaf litter. The other animals relied heavily or exclusively on the autochthonous basal source of organic carbon, periphytic microalgae, but some of them shifted to the conditioned leaf litter as the principal basal source in spring. Leaves of one of the tree species, Manchurian alder, appeared to be significantly more valuable food for primary consumers than leaves of the other studied species. Thus, the RCC should not be rejected but rather specified in terms of the seasonality and species composition of riparian vegetation.

Keywords Zoobenthos · Leaf litter · Periphyton · Stable isotopes · Fatty acids

Introduction

One of the main fundamental tasks of ecology is studying the sources of matter and energy in ecosystems and the pathways of their transfer through food webs (Cloern et al. 2002). In aquatic ecology, sources of organic matter (carbon) for lotic food webs have been debated for nearly the last 50 years (Thorp and Bowes 2017). The river continuum concept (RCC), which receives the most attention, proposes that terrestrial allochthonous inputs, namely, leaf litter, is the main source of organic carbon in trophic webs of forested headwater streams (Vannote et al. 1980). The RCC is based on facts that are visible to the naked eye: the vast quantity of leaf litter on the bottom of the streams and some kind of activity of bottom macroinvertebrates on these leaves. The fact that bottom macroinvertebrates feed mainly on leaf litter has been shown by visual (microscopic) studies of their gut contents. However, visual gut content analysis has often been found to give erroneous results because some visualized ingested materials pass through the intestines intact and are not digested and assimilated, while many other materials (shapeless organic matter) cannot be identified under a microscope (Porter 1976; Knisley and Geller 1986; Gladyshev et al. 2000; Lancaster et al. 2005).

Since visual studies of feeding can be problematic, in recent decades, new methods have been applied to reveal food sources and unravel lotic food webs based on stable isotope analysis (SIA), fatty acid (FA), and amino acid

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biomarker (tracer) analyses, elemental analysis (e.g., C:N stoichiometry) and their combinations (Cloern et al. 2002; Füreder et al. 2003; Imberger et al. 2014; Lu et al. 2014; Thorp and Bowes 2017; Twining et al. 2017; Kühmayer et al. 2020; Ebm et al. 2023). Many data obtained by using the new methods contradicted the RCC predictions with respect to small, shaded forest streams depending mostly on allochthonous organic carbon (Lau et al. 2009; Descroix et al. 2010; Thorp and Bowes 2017; Moyo and Richoux 2018; Kühmayer et al. 2020; Torres-Ruiz and Wehr 2020; Bogatov et al. 2021; Ebm et al. 2021; Labed-Veydert et al. 2021, 2023). A number of authors reported that material of both types, autochthonous (periphytic microalgae) and allochthonous (leaf litter), represented important basal sources of carbon for communities of benthic macroinvertebrates (Doucett et al. 2007; Bergfur 2013). Conversely, there are some data based on the new methods that support the RCC (Finlay 2001).

The above discrepancies deserve subsequent evaluation since the RCC, as one of the core concepts of aquatic ecology, should be specified if needed. The main problem of the RCC is ignoring the quality of the allochthonous terrestrial carbon, which is largely recalcitrant (Thorp and Bowes 2017). Meanwhile, in recent decades, food quality has been recognized as a factor that can be more important for determining the functioning of trophic webs of stream ecosystems than the quantity of bulk carbon (organic matter) (Leberfinger and Bohman 2010; Guo et al. 2016a, b, c). Conventionally, indicators of food quality are stoichiometric ratios of organic carbon to inorganic nutrients (e.g., nitrogen, C:N) and contents of essential polyunsaturated fatty acids of family omega-3 (n-3 PUFA) (Leberfinger and Bohman 2010; Volk and Kiffney 2012; Guo et al. 2016a,b,c, 2018; McInerney et al. 2020). Although it is well known that the organic carbon of leaf litter falling into forest streams far exceeds that produced by algae, high-quality algal food boosts the growth of invertebrate shredders and regulates their ability to incorporate organic carbon from low-quality leaf litter (Torres-Ruiz and Wehr 2010, 2020; Guo et al. 2016c). In addition, algal n-3 PUFA is likely to provide a priming effect, which allows bacteria to degrade refractory organic matter of leaf litter and, thereby, to condition them for benthic invertebrate consumption (Guo et al. 2016c). Therefore, leaf litter, per se, is believed to be a poor food source, although it can serve as a substrate for nutritive algal production (Kühmayer et al. 2020).

Nevertheless, the poor nutritive quality of leaf litter, supported by modern methods and, thereby, challenging the RCC, may not be completely true. First, as mentioned above, the conditioning of leaf litter during their stay in rivers may increase their nutritive value. Second, leaves of different tree species may differ in their nutritive quality (e.g., Hladyz et al. 2009; Volk and Kiffney 2012). Thus, we hypothesize that: (1) proportions of incorporation of organic carbon of leaf litter by benthic consumers can be higher in spring than in autumn due to conditioning of the leaves during winter, and (2) carbon of leaf litter of certain tree species can be incorporated in river food webs to a higher degree than that of other ones.

The aim of our study is to test the above two hypotheses using both SIA and biomarkers in food webs of a small forest river situated in the ecoregion of Ussuri temperate broadleaf and mixed forests in the Russian Far East.

Materials and methods

Study area

The Komarovka River (source, 43°38′52″ N, 132°23′36″ E, southern slopes of the Przewalski Ridge) is situated in Primorsky Krai (Russia) (Fig. 1). Its ecological features are given elsewhere (Bogatov et al. 2010, 2013). Briefly, the length of the river is 67 km, and the size of the catchment area is 1490 km^2. Conifer and broadleaf forests cover the catchment area. The width of the river increases from 6–8 m in the upper reaches to 25–28 m, and its depth varies from 0.2 to 1.2 m. The flow velocity is from 0.8 to 2.0 m s^{-1} on rapids to 0.3–0.7 m s^{-1} in pools. The river bottom is pebbly. The summer water temperature increases to 24 °C. The river water is weakly mineralized, of hydrocarbonate class, with pH 7.0–7.2. In the ecoregion, cyclonic activity takes place, and concomitant floods usually occur from late summer to early autumn. The river freezes up in late November. The spring flood begins in late March to early April and continues until the end of April.

The broadleaf mixed forest along the river consisted of several tree species, including Japanese pink pussy willow (*Salix gracilistyla*), narrow-leaf willow (*Salix schwerinii*), Manchurian alder (*Alnus hirsuta*), and Japanese elm (*Ulmus japonica*).

Sampling

Samples were collected in November 2021 and in April and October 2022, at the same site from depths of 0.2–1.0 m. Leaf litter, both whole leaves and their unidentified fragments, was collected directly from the river bottom. Leaves and fragments were rinsed with ambient water and wiped with filter paper. Perithyton (epilithic and epiphytic biofilms) was brushed off from the pebbles and the whole leaves and washed into plastic containers through a 500-µm mesh to separate large debris. For each sample, 12–56 pebbles with approximately 100–150 cm^2 surface area per one pebble were brushed with hard-bristles toothbrush, and 80–120 leaves with approximately 50–100 cm^2 surface area per one

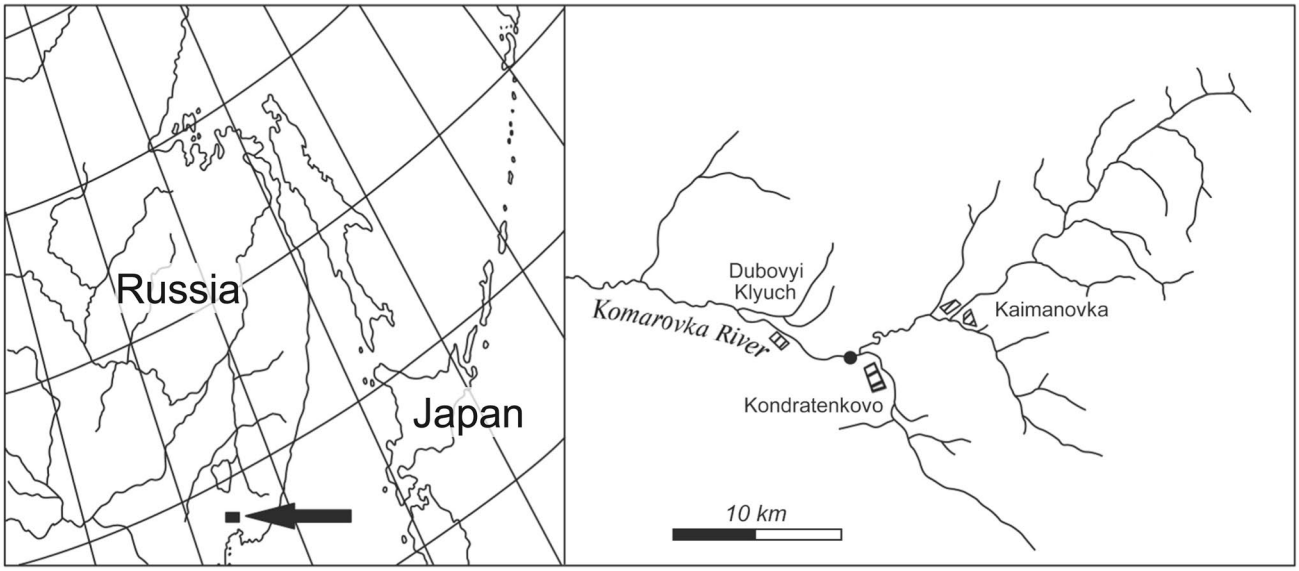

Fig. 1 Map of the studied area

leaf were gently brushed with a soft-bristle toothbrush. Zoobenthos were collected by a kick-bottom sampler (quadrate 30 cm × 30 cm, mesh size 1000 µm). Fish were not sampled purposely but caught occasionally by the kick-bottom sampler.

In the laboratory, the live invertebrate animals were placed in beakers with filtered (pore size 80 µm) ambient water for 24 h to empty their guts. The animals' body surfaces were then gently wiped with filter paper to remove water, and the individuals were separated into samples of two types for isotope and fatty acid analyses. Each subsample consisted of three to five individuals. The animals for fatty acid analysis were weighed and placed in a chloroform:methanol mixture (2:1, v/v) and kept at −20 °C until further analysis. The subsamples for isotope and elemental measurements were dried until constant weight and kept in dry conditions until analysis.

The portions of water in which benthic animals were kept in the laboratory for 24 h were settled, and feces were collected on glass-fiber filters and dried.

Stable isotope and elemental analyses

For stable isotope and elemental analyses, samples of periphyton, leaf litter, benthic animals, and their feces were dried at 65 °C and then mechanically homogenized. The measurement of stable carbon and nitrogen isotopes is described in detail elsewhere (Gladyshev et al. 2015). Briefly, ~1 mg of each sample was taken and analyzed with a continuous flow isotope ratio mass spectrometer (model Delta V Plus, Thermo Scientific Corporation, USA) interfaced with an elemental analyzer (Flash EA 1112 Series, Thermo Scientific Corporation, USA). All the samples were analyzed in duplicate. The accuracy and precision of the measurements were verified twice or three times per day by the secondary reference material USGS40 (L-glutamic acid) from the International Atomic Energy Agency. Analytical reproducibility was ± 0.2‰ for C and ± 0.3‰ for N. Stable isotope data were expressed conventionally in the per mil delta notations, $\delta^{13}C$ for carbon relative to Vienna Pee Dee Belemnite and $\delta^{15}N$ for nitrogen relative to atmospheric N_2 (Fry 1988).

The trophic position (TP) was calculated conventionally:

$$TP_x = \left(\delta^{15}N_x - \delta^{15}N_{\text{base}}\right)/\Delta\delta^{15}N + TP_{base}, \quad (1)$$

, where $\delta^{15}N_x$ is the isotope ratio of the taxon in question, $\delta^{15}N_{\text{base}}$ is the average trophic position of the baseline, $\Delta\delta^{15}N$ is the trophic enrichment (fractionation) constant, and TP_{base} is the trophic position of the baseline (Vander Zanden and Rasmussen 2001). The generalized isotopic fractionation factor for aquatic animals is $\Delta\delta^{15}N = 2.5‰$ (Caut et al. 2009). A zoobenthic species with the lowest $\delta^{15}N$ value is taken as the baseline, and $TP_{base} = 2$ (Lancaster and Waldron 2001; Vander Zanden and Rasmussen 2001; Nilsen et al. 2008; Lau et al. 2009).

To calculate the proportions of the contribution of potential sources to carbon obtained by benthic animals, the standard linear mixing mass balance model and relevant software packages IsoError 1.04 and IsoSource 1.3 (https://www.epa.gov/eco-research/stable-isotope-mixing-models-estimating-source-proportions) for two and greater than two sources, respectively, were used (Phillips and Gregg 2003; Phillips et al. 2005; Zeug and Winemiller

2008; Boecklen et al. 2011; Prokopkin et al. 2021; Liu et al. 2023). The isotopic signatures of each food source were corrected to account for fractionation during digestion and assimilation (Phillips and Gregg 2003; Phillips et al. 2005). Fractionation factors were $\Delta^{13}C \approx 0.25‰$ for invertebrates, $\Delta^{13}C \approx 1.75‰$ for fish and $\Delta\delta^{15}N = 2.5‰$ for both invertebrates and fish (Caut et al. 2009).

The organic carbon and nitrogen contents of the samples were measured with a Flash 2000 NC-Soil elemental analyzer (Thermo Fisher Scientific, USA). Calibration curves were generated using aspartic acid and standard soil reference material (Thermo Fisher Scientific, USA).

Fatty acid analysis

Fatty acid analysis is described elsewhere (Gladyshev et al. 2020). Briefly, lipids were extracted from sample material simultaneously with mechanical homogenization with a chloroform/methanol mixture (2:1, v/v) three times. The dried lipids were hydrolyzed under reflux at 90 °C for 10 min in 8 mg/mL methanolic sodium hydroxide solution. Then, the mixture was added to an excess methanolic solution of 3% sulfuric acid and refluxed at 90 °C for 10 min to produce fatty acid methyl esters (FAMEs). The mixture was washed twice with portions of NaCl saturated solution, and FAMEs were extracted with a portion of hexane. FAMEs were analyzed with a gas chromatograph–mass spectrometer (model 6890/5975C, Agilent Technologies, USA) equipped with a 30-m long, 0.25-mm internal diameter capillary HP-FFAP column. Data were collected and analyzed using ChemStation Software (Agilent Technologies, USA). The peaks of FAMEs were identified by their mass spectra, comparing them to those in the integrated database NIST 2005 and to those in the standard 37-FAME mixture (U-47885, Supelco, USA). FAMEs were quantified according to a peak area of the internal standard, 19:0-FAME (Sigma-Aldrich, USA), which was added to samples prior to lipid extraction after adding the first portion of the chloroform/methanol mixture.

Statistical analyses

One-way analysis of variance (ANOVA) with Tukey honest significance test (HSD) post hoc test and multivariate canonical correspondence analysis (CCA) (Legendre and Legendre, 1998) were calculated conventionally using STATISTICA software, version 9.0 (StatSoft, Inc., Tulsa, OK). Only datasets with normally distributed variables (Kolmogorov−Smirnov one-sample test for normality) were used for ANOVA; otherwise, $\log(x+1)$ transformation was used to achieve normality.

Results

In Table 1, the number of all kinds of samples of each component at each period are given. Leaf litter of Japanese pink pussy willow (*S. gracilistyla*), narrow-leaf willow (*S. schwerinii*), and Manchurian alder (*A. hirsuta*) were collected in November 2021 and October 2022, while leaves of Japanese elm (*U. japonica*) were taken in October 2022 only. In the spring, April 2022, species of the collected leaf litter could not be identified. Larvae of caddisflies (*Stenopsyche marmorata* and *Hydatohpylax nigrovittatus*), larvae of stoneflies (*Pteronarcys reticulata* and *Oyamia nigribasis*), larvae of dragonfly (*Davidius lunatus*), and larvae of mayfly (*Ephemera strigata*) were collected in the spring and in autumn, while larvae of mayfly (*Drunella aculea*) and snail (*Parajuga amurensis*) were taken in the spring only, and water bug (*Appasus major*) and the fish Siberian stone loach (*Barbatula toni*) were caught only in the autumn (Table 1).

Stable isotopes

In November 2021, the mean $\delta^{13}C$ values of the leaf litter of *S. gracilistyla*, *S. schwerinii* and the unidentified leaf litter were significantly (Tukey post hoc test) lower than those of periphyton (epilithic biofilms) and animals, except *E. strigata* and *S. marmorata* (Fig. 2). However, *E. strigata* and *S. marmorata* had significantly higher $\delta^{13}C$ values than the leaves of *S. gracilistyla* and *S. schwerinii* (Fig. 2). In addition, the mean carbon isotope signature of *A. hirsuta*, as well as that of the leaf periphyton, was significantly higher than those of all the other leaf litters but lower than that of the pebble periphyton (Fig. 2). The mean $\delta^{13}C$ value of *O. nigribasis* was similar to those of *S. marmorata*, *P. reticulata* and *D. lunatus* but significantly higher than that of *E. strigata* (Fig. 2). The mean carbon isotope signature of *D. lunatus* was close to that of *P. reticulata* (Fig. 2). The mean $\delta^{13}C$ value of the pebble periphyton differed significantly from all other groups of organisms, except *D. lunatus* and *O. nigribasis* (Fig. 2). The mean carbon isotope signature of the feces of *S. marmorata* did not differ significantly from that of their bodies, while the mean $\delta^{13}C$ values of the feces of *P. reticulata* tended to be lower than those of their bodies, although this difference was statistically insignificant (Fig. 2).

In November 2021, *P. reticulata* had significantly lower mean $\delta^{15}N$ values than the other animals (Fig. 2) and was therefore taken as the baseline (Eq. 1), i.e., as the primary consumer of trophic level II with $TP_{base} = 2$. In turn, *O. nigribasis* had significantly higher $\delta^{15}N$ values than *D. lunatus*, *E. strigata* and *S. marmorata* after one-way

Table 1 Number of samples for analyses of stable isotopes (SI), organic carbon and nitrogen (C&N), and fatty acids (FA) in components of ecosystem of the Komarovka River (Primorsky Krai, Russia): leaf litter [*Sg*, Japanese pink pussy willow (*Salix gracilistyla*); *Ss*, narrow-leaf willow (*Salix schwerinii*); *Ah*, Manchurian alder (*Alnus hirsuta*); *Uj*, Japanese elm (*Ulmus japonica*); LL, unidentified leaf fragments], periphyton (PL—from leaf litter, PP—from pebbles), benthic invertebrates [*Sm*, larvae of caddisfly (*Stenopsyche marmorata*); *Pr*, larvae of stonefly (*Pteronarcys reticulata*); *On*, larvae of stonefly (*Oyamia nigribasis*); *Dl*, larvae of dragonfly (*Davidius lunatus*); *Es*, larvae of mayfly (*Ephemera strigata*); *Da*, larvae of mayfly (*Drunella aculea*); *Hn*, larvae of caddisfly (*Hydatohpylax nigrovittatus*); *Pa*, snail (*Parajuga amurensis*)]; *Am*, water bug (*Appasus major*); fish *Bt*, Siberian stone loach (*Barbatula toni*), and their feces (f). Gray shaded cells indicate no data

Component	Nov 2021		Apr 2022			Oct 2022		
	SI	C&N	SI	C&N	FA	SI	C&N	FA
Sg	7	14				4	4	3
Ss	6	6				4	5	3
Ah	7	10				5	5	3
Uj						5	5	3
LL	5	5	5	5	4			
PL	10	12						
PP	9	11	5	4	5	9	4	4
Sm	9	18	5	6	6			
Pr	7	17			1	4	4	5
On	9	10	4	4		5	5	5
Dl	7	14	5	5	5			
Es	3		4	4	3	4	4	
Da			6	6	4			
Hn			3	3		8	7	5
Pa			5	5	5			
Am						5	3	4
Bt						6	6	4
f*Sm*	2		2	2				
f*Pr*	3	3				3	3	
f*On*						3		
f*Dl*								
f*Es*			3			2		
f*Da*			3					
f*Hn*			3			7	7	
f*Pa*			2					
f*Am*						2		
f*Bt*						3		

ANOVA with post hoc Tukey's test (Fig. 2). According to Eq. (1), the trophic positions of *D. lunatus*, *E. strigata*, *S. marmorata*, and *O. nigribasis*, *TP*, were 2.89, 2.91, 3.10, and 3.48, respectively, i.e., approximately one trophic level higher, than that of *P. reticulata*. Thus, *D. lunatus*, *E. strigata* and *S. marmorata* were secondary consumers of trophic level III in the ecosystem under study, as well as *O. nigribasis* (Fig. 2). However, the $\delta^{15}N$ value of *O. nigribasis* (i.e., *TP*) was significantly higher than those of *D. lunatus*, *E. strigata* and *S. marmorata*; therefore, *O. nigribasis* had a higher degree of predation than the other secondary consumers (Fig. 2). The mean values of $\delta^{15}N$ in the feces of *S. marmorata* and *P. reticulata* were significantly lower than those in their bodies (Fig. 2).

According to the IsoSource model, in November 2021, *O. nigribasis* obtained the principal part of its carbon (~0.93 on average) from the autochthonous basal source, periphyton (Fig. 3). *D. lunatus* also had the main part of carbon from the autochthonous basal source, primarily from the pebble periphyton (epilython, ~0.56) but also had a considerable part of allochthonous carbon, primarily from leaf litter of *A. hirsuta* (~0.34) (Fig. 3). *P. reticulata* obtained the main part of its carbon (~0.55 on average) from the autochthonous source, periphyton, but allochthonous food sources, especially leaf litter of *A. hirsuta* and unidentified leaf fragments, contributed a considerable part of carbon to this species as well (Fig. 3). *S. marmorata* had nearly similar proportions of autochthonous (~0.49) and allochthonous carbon, but in contrast to the above two species, obtained more carbon from leaf litter of *S. gracilistyla* and *S. schwerinii* rather than from that of *A. hirsuta* (Fig. 3). The largest average contribution of allochthonous carbon as the basal source (~0.79) was characteristic of *E. strigata*, which obtained carbon

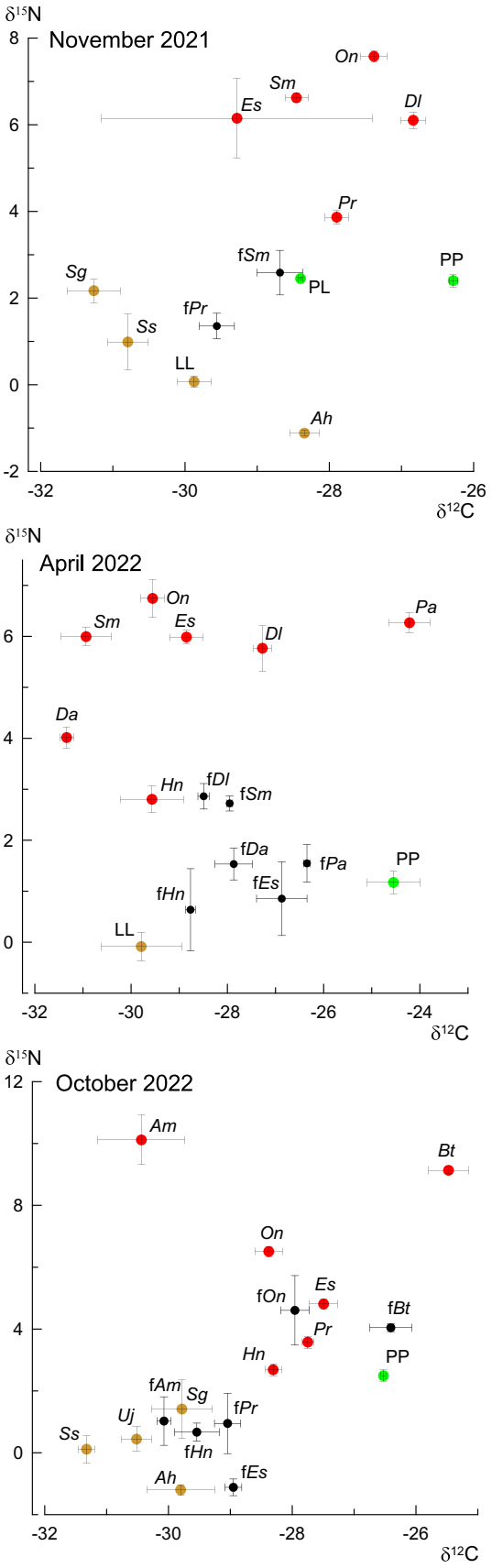

Fig. 2 Mean values of the isotope ratios (‰) in leaf litter (*Sg*, *Salix gracilistyla*; *Ss*, *Salix schwerinii*; *Ah*, *Alnus hirsuta*; *Uj*, *Ulmus japonica*; LL, unidentified leaf fragments; all in yellow); periphyton [PL—from leaf litter, PP—from pebbles (epilithon); all in green], benthic invertebrates (*Sm*, larvae of *Stenopsyche marmorata*; *Pr*, larvae of *Pteronarcys reticulata*; *On*, larvae of *Oyamia nigribasis*; *Dl*, larvae of *Davidius lunatus*; *Es*, larvae of *Ephemera strigata*; *Da*, larvae of *Drunella aculea*; *Hn*, larvae of *Hydatohpylax nigrovittatus*; *Pa*, *Parajuga amurensis*); water bug (*Am*, *Appasus major*) and fish (*Bt*, *Barbatula toni*), all are in red and their feces (f) are all in black. The Komarovka River (Primorsky Krai, Russia). Bars represent standard

primarily from the leaf litter of *S. gracilistyla* and *S. schwerinii* (Fig. 3).

In April 2022, the mean $\delta^{13}C$ value of the unidentified leaf litter was significantly lower than that of pebble periphyton and two animal species, *D. lunatus* and *P. amurensis* (Fig. 2). In turn, the periphyton had a significantly higher mean $\delta^{13}C$ value than all animals, except *P. amurensis* (Fig. 2). The mean carbon isotope signature of *P. amurensis* was significantly higher than those of all the other animals, while the mean $\delta^{13}C$ value of *D. lunatus* was significantly higher than those of *D. aculea* and *S. marmorata* (Fig. 2). The mean carbon isotope signatures of the feces of *D. aculea* and *S. marmorata* were significantly higher than those of their bodies, while the mean $\delta^{13}C$ values of the feces of *E. strigata*, *D. lunatus*, *H. nigrovittatus* and *P. subtegulata* did not differ significantly from those of their bodies (Fig. 2).

In April 2022, *H. nigrovittatus* and *D. aculea* had significantly lower mean $\delta^{15}N$ values than the other animals (Fig. 2). As the species with the minimum $\delta^{15}N$ value, *H. nigrovittatus* was taken as the baseline (Eq. 1), i.e., as the primary consumer of trophic level II with $TP_{base}=2$. According to Eq. (1), the trophic position of *D. aculea* $TP=2.48$, i.e., it occupied trophic level II and was the primary consumer (Fig. 2). In turn, the trophic positions of *D. lunatus*, *E. strigata*, *S. marmorata*, and *O. nigribasis*, *TP*, were 3.19, 3.27, 3.28, and 3.58, respectively, i.e., approximately one trophic level higher, than those of *H. nigrovittatus* and *D. aculea* (Fig. 2). Since *P. amurensis* had a significantly higher mean $\delta^{13}C$ value (Fig. 2) than all the other animals, it evidently belonged to another trophic chain and was not included in the *TP* calculations with *H. nigrovittatus* as the baseline. The mean values of $\delta^{15}N$ in the feces of *P. amurensis*, *E. strigata*, *S. marmorata*, *D. lunatus* and *D. aculea* were significantly lower than those in their bodies (Fig. 2).

According to the IsoError model, in April 2022, *D. aculea*, *S. marmorata*, *O. nigribasis*, and *H. nigrovittatus* obtained the principal part of their carbon (~1 on average) from the allochthonous basal source, leaf litter (Fig. 4). *E. strigata* and *D. lunatus* obtained the majority of their carbon (~0.92 and ~0.61, respectively) from the allochthonous source, leaf litter (Fig. 4). In contrast, *P. amurensis* obtained

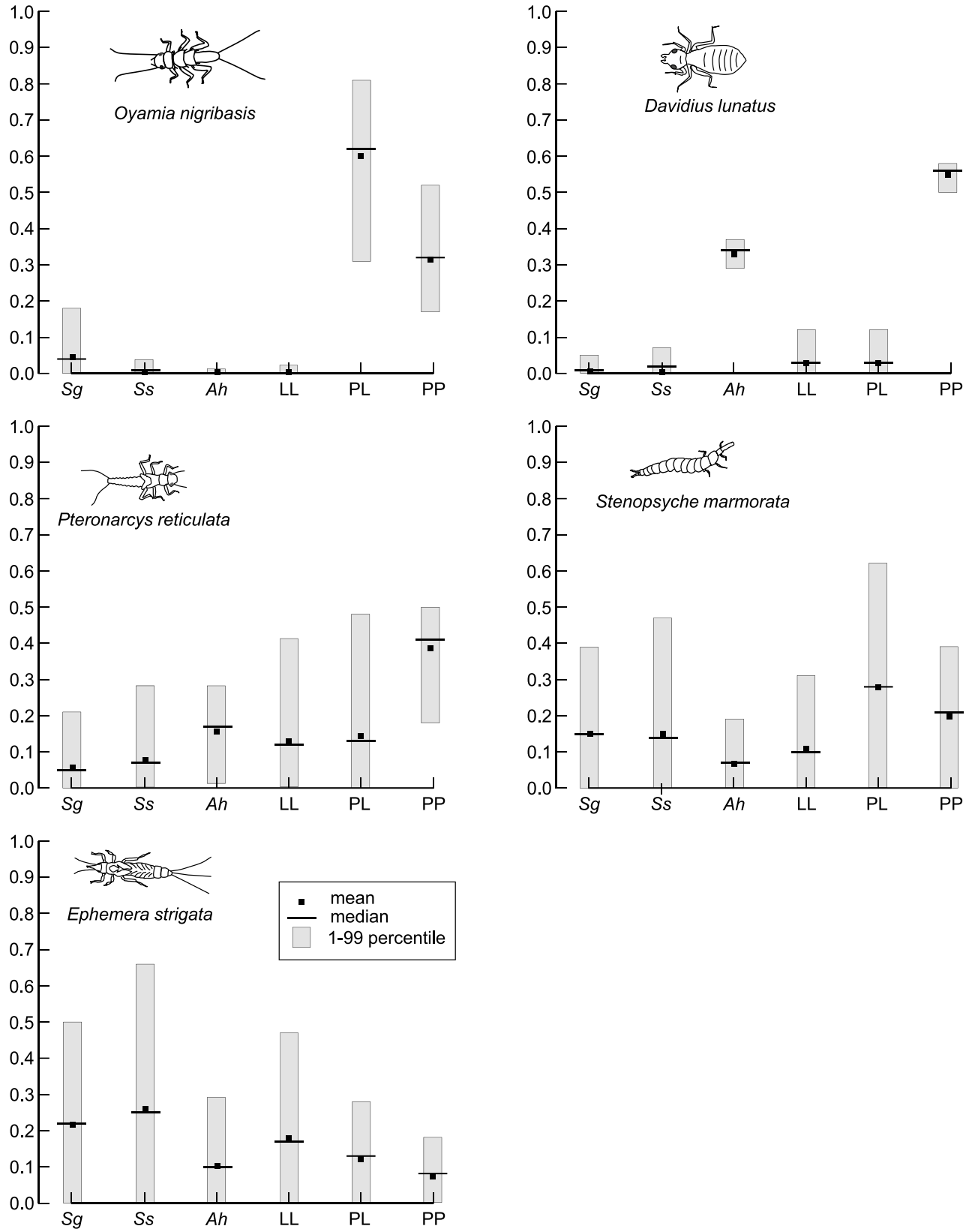

Fig. 3 Model IsoSource estimates of use of different basal resources for benthic consumers in November 2021. *Sg*, *Salix gracilistyla*; *Ss*, *Salix schwerinii*; *Ah*, *Alnus hirsuta*; LL, unidentified leaf fragments; PL, periphyton from leaf litter; PP, periphyton from pebbles (epilython). The Komarovka River (Primorsky Krai, Russia)

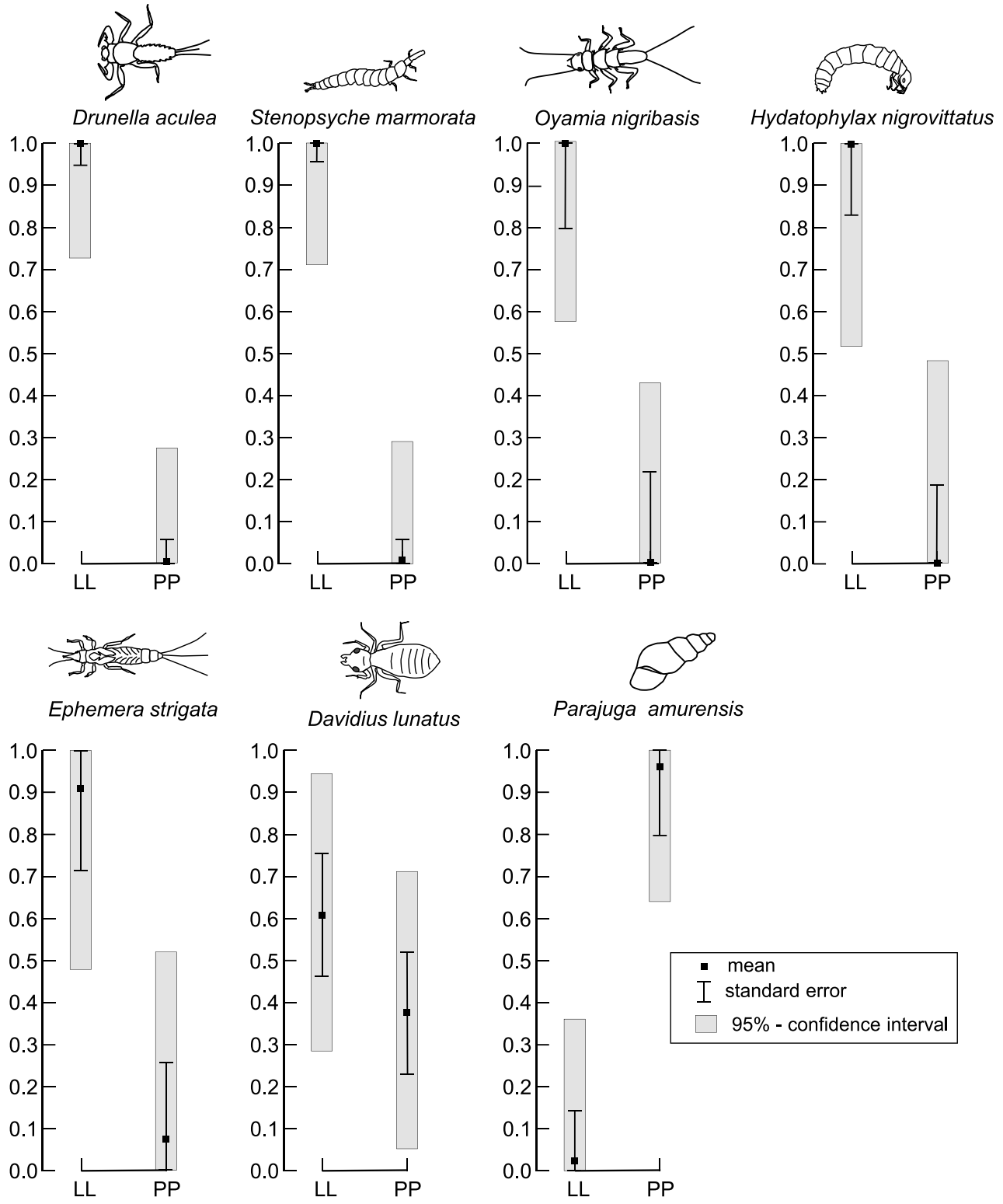

Fig. 4 Model IsoError estimates of use of different basal resources for benthic consumers in April 2022. LL, unidentified leaf fragments; PP, periphyton from pebbles (epilython). The Komarovka River (Primorsky Krai, Russia)

its carbon primarily (~0.97) from the autochthonous source, periphyton (Fig. 4).

In October 2022, the mean $\delta^{13}C$ value of all species of leaf litter was significantly lower than those of the pebble periphyton and three animal species, *P. reticulata*, *E. strigata*, and *B. toni* (Fig. 2). In turn, the periphyton had a significantly higher mean $\delta^{13}C$ value than that of three other animals, *H. nigrovittatus*, *O. nigribasis*, and *A. major* (Fig. 2). The mean carbon isotope signature of *A. major* was significantly lower than that of all the other animals, while the mean $\delta^{13}C$ value of *B. toni* was significantly higher than that of the other animals (Fig. 2). The mean carbon isotope signature of the feces of *H. nigrovittatus* was significantly lower than that of their bodies, while the mean $\delta^{13}C$ values of the feces of *O. nigribasis*, *E. strigata*, *A. major*, *P. reticulata*, and *B. toni* did not differ significantly from those of their bodies, although the latter species had a tendency toward lower fecal isotope signatures (Fig. 2).

In October 2022, *H. nigrovittatus* had significantly lower mean $\delta^{15}N$ values than the other animals, except *P. reticulata* (Fig. 2). As the species with the minimum $\delta^{15}N$ value, *H. nigrovittatus* was taken as the baseline (Eq. 1), i.e., as the primary consumer of trophic level II with $TP_{base} = 2$. According to Eq. (1), the trophic position of *P. reticulata* $TP = 2.36$, i.e., it occupied trophic level II and was the primary consumer. In turn, the trophic positions of *E. strigata* and *O. nigribasis*, *TP*, were 2.85, and 3.53, respectively, i.e., approximately one trophic level higher than those of *H. nigrovittatus* and *P. reticulata* (Fig. 2). *A. major* had $TP = 4.97$; i.e., it probably occupied trophic levels IV–V, although it was characterized by a significantly lower $\delta^{13}C$ value (Fig. 2) than all the other animals and, therefore, most likely belonged to a peculiar trophic chain. *B. toni,* with its TP = 4.58, also probably occupied trophic level IV, although its mean $\delta^{13}C$ value was significantly higher (Fig. 2) than those of all the other animals, which most likely made it part of another trophic chain compared with all other animals.

The mean values of $\delta^{15}N$ of the feces of *O. nigribasis* did not differ significantly from those of their bodies, while the $\delta^{15}N$ values of the feces of *P. reticulata*, *E. strigata*, *H. nigrovittatus*, *A. major*, and *B. toni* were significantly lower than those of their bodies (Fig. 2).

According to the IsoSource model, in October 2022, *B. toni* and *P. reticulata* obtained the majority of their carbon (~0.67 and ~0.57 on average, respectively) from the autochthonous basal source, periphyton (Fig. 5). In turn, *O. nigribasis* received only ~0.34 of basal carbon from periphyton, while receiving the main part of the carbon from the allochthonous sources, primarily from leaf litter of *S. gracilistyla* (~0.45) (Fig. 5). *H. nigrovittatus* and *E. strigata* also obtained the main part of their carbon from allochthonous sources, primarily from the leaf litter of *A. hirsuta* (~0.61 and ~0.59, respectively) (Fig. 5). *A. major* had the principal part of its carbon (~1) from allochthonous sources, primarily from the leaf litter of *S. gracilistyla* (~0.92) (Fig. 5).

All the data on food sources and trophic positions of studied animals in autumn and spring are generalized in Fig. 6. In the autumn of November 2021, the primary consumer, larvae of stonefly (*P. reticulata*), and the secondary consumers, larvae of stonefly (*O. nigribasis*) and larvae of dragonfly (*D. lunatus*) obtained their organic carbon from periphyton, while the secondary consumers, larvae of mayfly (*E. strigata*) and larvae of caddisfly (*S. marmorata*) mainly obtained their food from leaf litter as the basal source. Since some benthic invertebrates, namely, small chironomid larvae, were omitted in this study, intermediate links for some secondary and higher consumers also seemed to be omitted.

In spring in April 2022, the primary consumers, larvae of the caddisfly (*H. nigrovittatus*), larvae of the mayfly (*D. aculea*), and the secondary consumers, *O. nigribasis*, *S. marmorata*, and partly *D. lunatus*, mainly obtained their carbon from leaf litter as the basal source (Fig. 6). Only the snail *P. amurensis* appeared to scrape pebble periphyton and, thereby, represented the peculiar food chain, which made it stand apart from the insect larvae (Fig. 6). Thus, unlike in autumn, leaf litter rather than periphyton appeared to be the main basal carbon source for most benthic invertebrates.

In the next autumn, in October 2022, the primary consumer *P. reticulata* obtained its carbon mainly from periphyton, as in November 2021, while the primary consumer *H. nigrovittatus* and the secondary consumer *O. nigribasis* partly or exclusively obtained their carbon from leaf litter as the basal source (Fig. 6). The secondary consumer *E. strigata*, unlike November 2021 and April 2022, had a shift to periphyton as its basal source (Fig. 6). Water bug (*A. major*) and Siberian stone loach (*B. toni*), which were provisionally regarded as the quaternary consumers taking *H. nigrovittatus* as the baseline, likely had lower trophic levels, representing peculiar food chains, where intermediate links were omitted. In the assumed peculiar trophic chain of *A. major*, leaf litter was the principal basal carbon source (Fig. 6).

Carbon to nitrogen ratios

In November 2021, the C:N ratios of all kinds of leaf litter were significantly higher than those of periphyton and macroinvertebrates (Fig. 7). However, leaves of *A. hirsuta* had significantly lower C:N values than leaves of *S. gracilistyla* and *S. schwerinii* (Fig. 7). The periphyton brushed from the leaf litter had a significantly higher C:N value than the periphyton scraped from the pebbles (Fig. 7). The C:N values of the macroinvertebrates did not differ significantly from each other or from those of the pebble periphyton (Fig. 7). The C:N value of the feces of *P. reticulata* was significantly higher than that of their bodies but nearly similar to that of

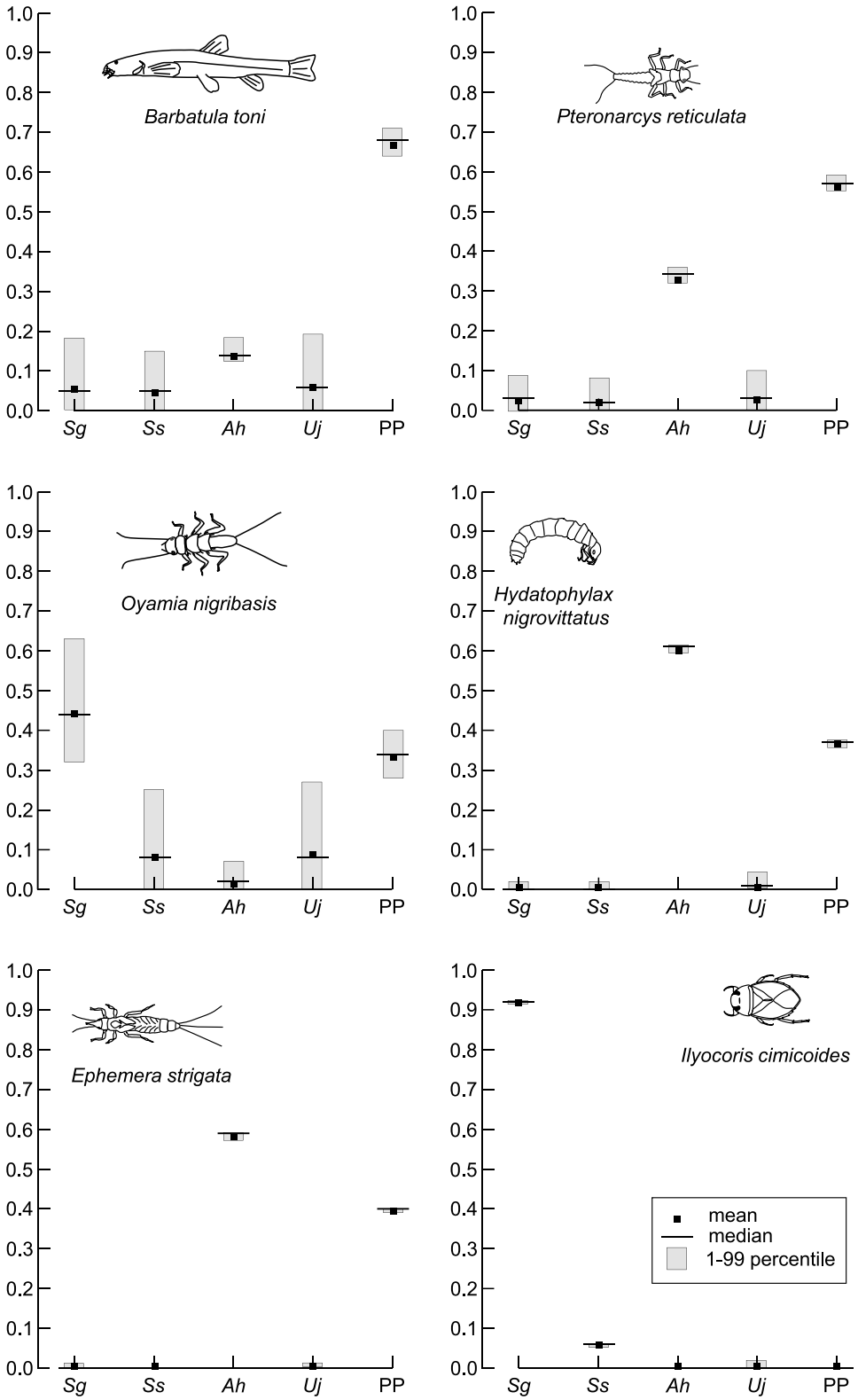

Fig. 5 Model IsoSource estimates of use of different basal resources for benthic consumers in October 2022. Sg, *Salix gracilistyla*; Ss, *Salix schwerinii*; Ah, *Alnus hirsuta*; Uj, *Ulmus japonica*; PP, periphyton from pebbles (epilython). The Komarovka River (Primorsky Krai, Russia)

the unidentified leaf litter and leaves of *A. hirsuta* and *S. schwerinii* (Fig. 7).

In April 2022, the C:N ratio of the leaf litter was significantly higher than those of the periphyton and macroinvertebrates (Fig. 7). The values of the C:N ratio of periphyton did not differ significantly from those of many animals, but *D. lunatus*, *D. aculea*, and *P. amurensis* had significantly lower values than periphyton (Fig. 7). Feces of

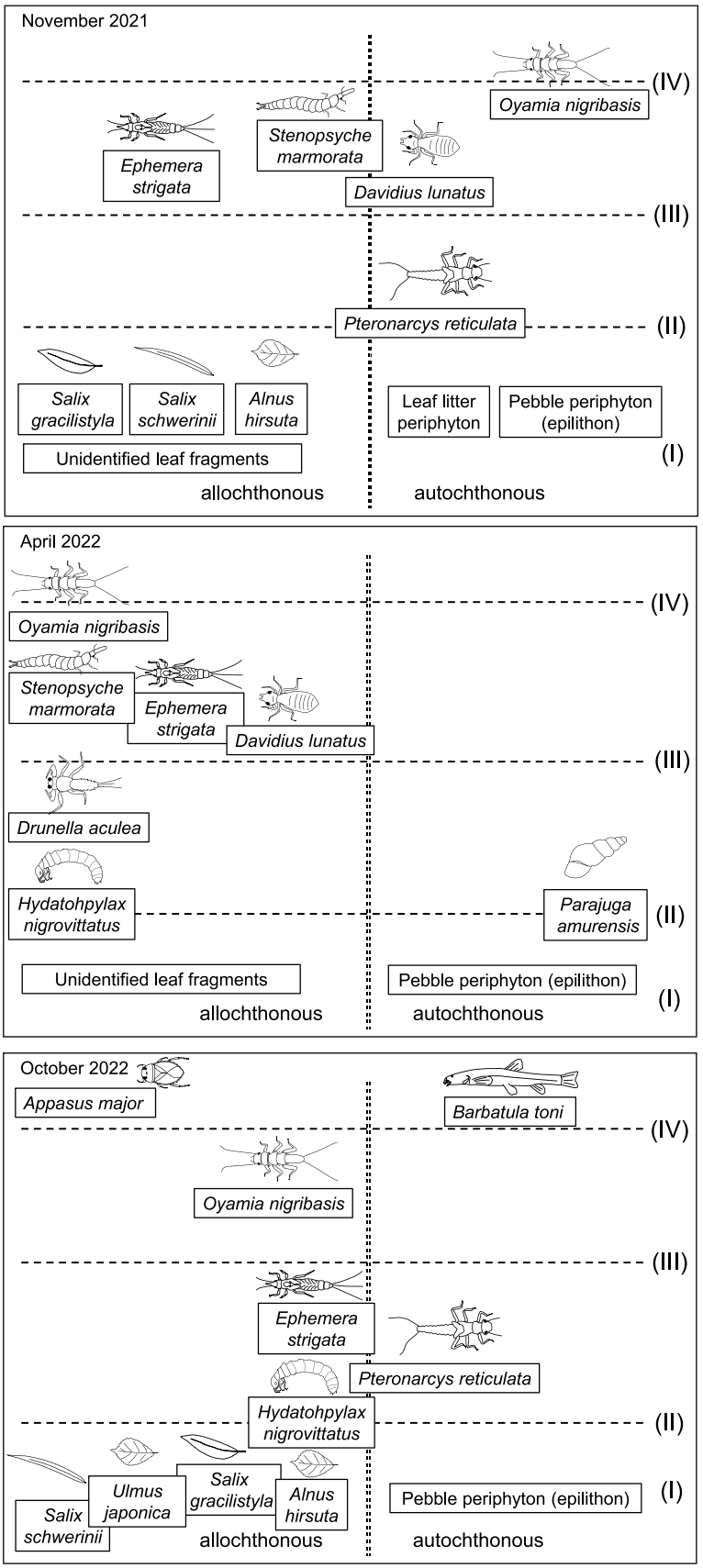

Fig. 6 Draft of trophic pathways in the Komarovka River. I–IV designate trophic levels (horizontal dashed lines). Vertical dashed double-line separates allochthonous and autochthonous basal carbon sources

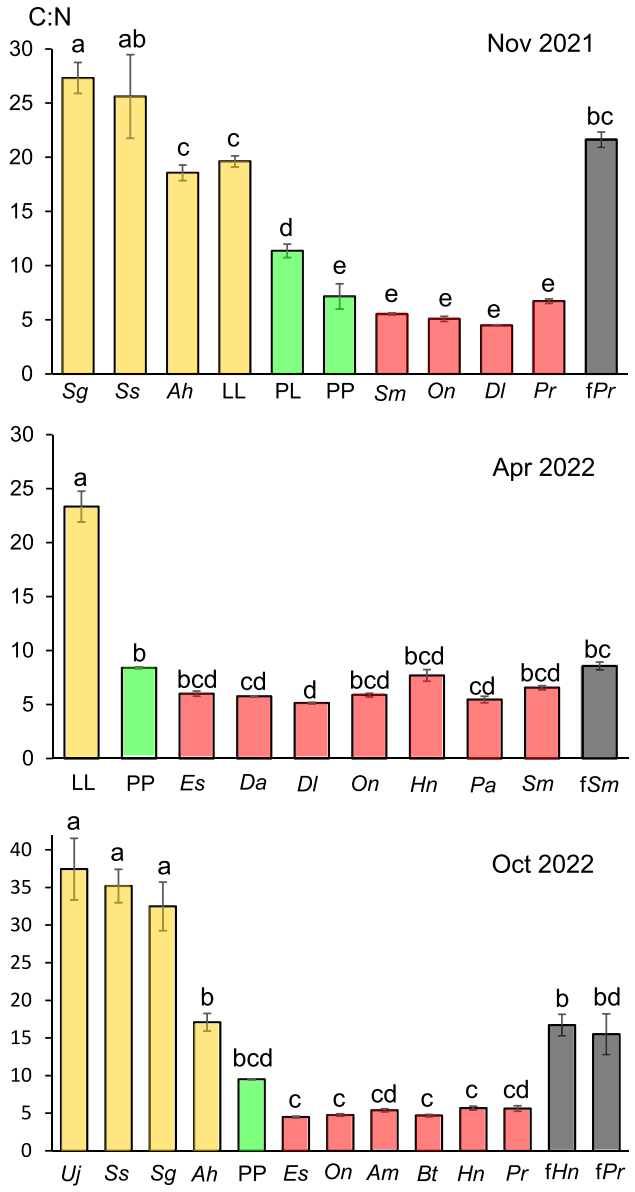

Fig. 7 Mean values of C:N ratios (mol:mol) in leaf litter (*Sg*, *Salix gracilistyla*; *Ss*, *Salix schwerinii*; *Ah*, *Alnus hirsuta*; *Uj*, *Ulmus japonica*; LL, unidentified leaf fragments; all in yellow), periphyton (PL—from leaf litter, PP—from pebbles (epilithon); all in green), benthic invertebrates (*Sm*, larvae of *Stenopsyche marmorata*; *Pr*, larvae of *Pteronarcys reticulata*; *On*, larvae of *Oyamia nigribasis*; *Dl*, larvae of *Davidius lunatus*; *Es*, larvae of *Ephemera strigata*; *Da*, larvae of *Drunella aculea*; *Hn*, larvae of *Hydatohpylax nigrovittatus*; *Pa*, *Parajuga amurensis*); water bug *Am*, *Appasus major*; fish *Bt*, *Barbatula toni*; all animals are in red and their feces (f) are all in black. The Komarovka River (Primorsky Krai, Russia). Bars represent standard errors. Means labeled with the same letters are not significantly different at $P < 0.05$ according to Tukey HSD post hoc test in the one-way analysis of variance (ANOVA)

S. marmorata did not differ significantly in C:N values from those of their bodies (Fig. 7).

In October 2022, the C:N ratios of the leaf litter of all species were significantly higher than those of animals (Fig. 7). However, the C:N value of leaves of *A. hirsuta* was significantly lower than that of leaves of the other species and was nearly similar to that of periphyton (Fig. 7). In turn, the C:N value of the periphyton did not differ significantly from that of animals (Fig. 7). Feces of *H. nigrovittatus* had a significantly higher C:N ratio than their bodies, and a similar tendency was characteristic of feces and bodies of *P. reticulata*, although this difference was insignificant (Fig. 7).

Fatty acids

The canonical correspondence analysis (CCA) of fatty acid (FA) percentages in the biomass of the studied components of the river ecosystem revealed their considerable partitioning (Fig. 8). In April 2022, along dimension 1, which represented the largest proportion of inertia, most overall differences in FA composition were found between *P. amurensis* and the other components (Fig. 8). The differences along dimension 1 were primarily due to the contrast between levels of ∑22:4n-6, ∑20:2, ∑20-22MUFA, 22:5n-3, and 20:4n-6, on the one hand, and ∑24-30SFA and ∑20-22SFA, on the other hand (Fig. 8). Along dimension 2 with the lower part of inertia, most differences were between the leaf litter and the periphyton (epilitic biofilms), and all the animals were considerably closer to the perithyton than to the leaf litter (Fig. 8). These differences along dimension 2 were primarily due to the contrast between the levels of ∑24-30SFA and ∑20-22SFA, on the one hand, and ∑14:1, ∑16PUFA and ∑14PUFA, on the other hand (Fig. 8).

In October 2022, along dimension 1, which represented the largest proportion of inertia, most overall differences in FA composition were found between the periphyton and leaf litter of all species, while *B. toni* was very close to the periphyton, and other animals had intermediate positions between the basal resources (Fig. 8). The differences along dimension 1 were primarily due to the contrast between levels of 22:5n-3, 22:6n-3, 20:4n-3 and ∑16PUFA, on the one hand, ∑24-30SFA and ∑20-22SFA, on the other hand (Fig. 8). Along dimension 2, with the lower part of inertia, most differences were between the litters of *U. japonica*, *S. gracilistyla*, and *P. reticulata* (Fig. 8). These differences along dimension 2 were primarily due to the contrast between levels of ∑24-30SFA and ∑20-22SFA, on the one hand, and ∑12:2, ∑12:1 and ∑14PUFA, on the other hand (Fig. 8).

The overall differences in FA composition of the ecosystem components, revealed by CCA, were specified by ANOVA. Notably, in April 2022, *E. strigata* and *D. aculea* had significantly higher levels of 16:1n-7 in their biomass compared with the other animals (Table 2). *E. strigata* had significantly higher levels of 15:0, 16:1n-5 and

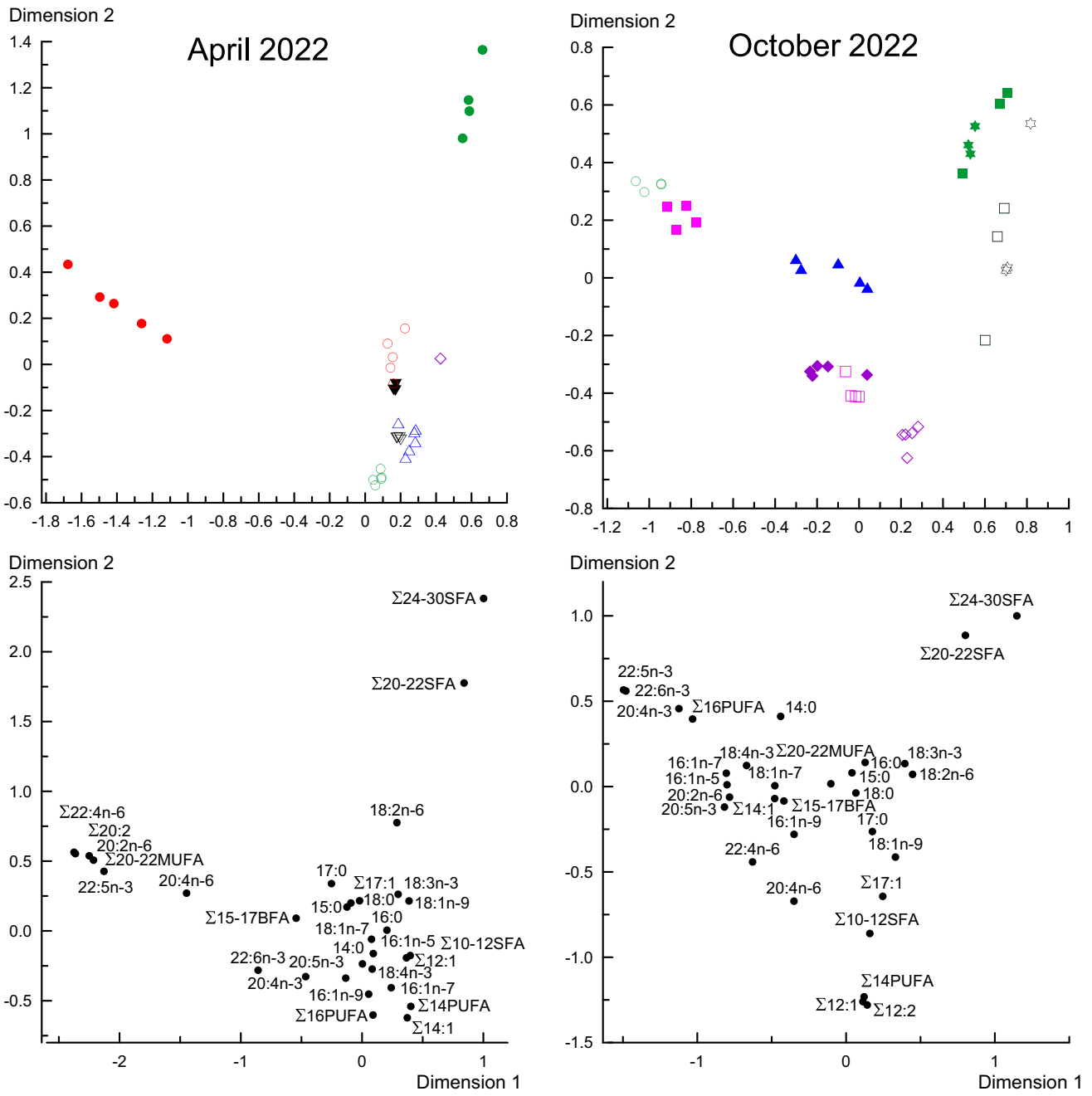

Fig. 8 Multivariate canonical correspondence analysis of proportions of fatty acids (% of total) in the biomass of components of the Komarovka River (Primorsky Krai, Russia) ecosystem: open green circles are periphyton (epilithon), closed green circles are leaf litter, open green squares are *Alnus hirsuta*, closed green squares are *Ulmus japonica*, open green stars are *Salix schwerinii*, closed green stars are *Salix gracilistyla*, open blue triangles are larvae of *Stenopsyche marmorata*, closed blue triangles are larvae of *Hydatohpylax nigrovittatus*, open violet diamonds are larvae of *Pteronarcys reticulata*, closed violet diamonds are larvae of *Oyamia nigribasis*, open black inverted triangles are larvae of *Drunella aculea*, closed black inverted triangles are *Ephemera strigata*, open red circles are *Davidius lunatus*, closed red circles are *Parajuga amurensis*, open pink squares are *Appasus major*, and closed pink squares are *Barbatula toni*. Proportions of explained variance (inertia): April 2022, along axis 1, 40.0%; along axis 2, 26.9%; $\chi^2 = 2938$, df = 992; October 2022, along axis 1, 44.9%; along axis 2, 19.2%; $\chi^2 = 2707$, df = 1140

Σ17:1 than the other components, and together with *P. amurensis*, it had a higher level of Σ15-17BFA (Table 2). *P. amurensis* had significantly significantly higher level of 22:6n-3 than all the other animals (Table 2). In the leaf litter, significantly higher levels compared to the other components of 18:2n-6, 18:3n-3, Σ20-22SFA, and

Table 2 Mean levels of fatty acids (% of total ± standard error) and their mean total contents (∑FA, mg g^{-1} wet weight ± standard error) in components of ecosystem of the Komarovka River (Primorsky Krai, Russia), April 2022

Fatty acid	Periphyton	Leaf litter	*Ephemera strigata*	*Drunella aculea*	*Stenopsyche marmorata*	*Davidius lunatus*	*Parajuga amurensis*
Σ10-12SFA	0.18 ± 0.01^{A}	0.32 ± 0.04^{A}	0.04 ± 0.04^{A}	0.32 ± 0.02^{A}	1.07 ± 0.22^{B}	0.48 ± 0.03^{AB}	0.08 ± 0.01^{A}
Σ12:1	0.00 ± 0.00^{A}	0.01 ± 0.01^{A}	0.00 ± 0.00^{A}	0.28 ± 0.01^{B}	0.18 ± 0.04^{B}	0.02 ± 0.01^{A}	0.07 ± 0.01^{A}
14:0	5.65 ± 0.26^{A}	2.10 ± 0.04^{BD}	2.64 ± 0.38^{BC}	3.58 ± 0.31^{C}	1.74 ± 0.11^{BD}	1.60 ± 0.17^{D}	2.21 ± 0.25^{BD}
Σ14:1	0.09 ± 0.02^{A}	0.05 ± 0.01^{A}	0.00 ± 0.00^{A}	0.32 ± 0.03^{A}	6.86 ± 1.39^{B}	0.24 ± 0.02^{A}	0.19 ± 0.01^{A}
Σ14PUFA	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	2.11 ± 0.18^{B}	2.04 ± 0.41^{B}	0.02 ± 0.01^{A}	0.06 ± 0.02^{A}
15:0	0.31 ± 0.01^{AC}	0.44 ± 0.02^{AE}	1.17 ± 0.17^{B}	0.20 ± 0.01^{CD}	0.16 ± 0.02^{D}	0.39 ± 0.06^{AE}	0.49 ± 0.04^{E}
16:0	14.54 ± 0.15^{A}	20.66 ± 0.41^{BC}	24.95 ± 0.44^{C}	19.77 ± 0.50^{B}	20.16 ± 0.67^{B}	16.30 ± 0.82^{A}	8.99 ± 0.54^{D}
16:1n-9	0.64 ± 0.22^{A}	0.00 ± 0.00^{B}	0.52 ± 0.06^{AB}	0.15 ± 0.02^{AB}	0.40 ± 0.11^{AB}	0.35 ± 0.04^{AB}	0.16 ± 0.07^{B}
16:1n-7	17.20 ± 1.36^{A}	3.26 ± 0.14^{B}	15.62 ± 0.66^{A}	14.34 ± 1.05^{A}	8.67 ± 1.29^{C}	8.57 ± 0.94^{C}	1.72 ± 0.43^{D}
16:1n-5	0.39 ± 0.01^{A}	0.18 ± 0.01^{B}	2.08 ± 0.09^{C}	0.41 ± 0.04^{AD}	0.29 ± 0.03^{AB}	0.64 ± 0.11^{D}	0.27 ± 0.03^{A}
Σ15-17BFA	0.98 ± 0.06^{A}	0.60 ± 0.03^{AC}	2.67 ± 0.10^{B}	0.30 ± 0.02^{C}	0.50 ± 0.07^{C}	1.06 ± 0.19^{A}	2.42 ± 0.18^{B}
Σ16PUFA	19.36 ± 0.64^{A}	1.25 ± 0.19^{B}	1.72 ± 0.09^{BD}	7.88 ± 0.39^{C}	11.12 ± 1.31^{C}	2.34 ± 0.35^{BD}	3.61 ± 0.64^{D}
17:0	0.17 ± 0.02^{A}	0.65 ± 0.01^{B}	0.78 ± 0.14^{B}	0.17 ± 0.02^{A}	0.32 ± 0.03^{A}	0.84 ± 0.09^{B}	0.84 ± 0.05^{B}
Σ17:1	0.00 ± 0.00^{A}	0.23 ± 0.04^{ACD}	0.92 ± 0.11^{B}	0.08 ± 0.02^{AD}	0.11 ± 0.04^{AD}	0.44 ± 0.12^{C}	0.25 ± 0.06^{CD}
18:0	1.29 ± 0.17^{A}	4.50 ± 0.09^{BE}	3.75 ± 0.26^{BCE}	3.11 ± 0.14^{C}	3.71 ± 0.23^{BC}	6.35 ± 0.44^{D}	4.86 ± 0.20^{ED}
18:1n-9	2.30 ± 0.12^{A}	16.78 ± 1.12^{B}	$10.44 \pm 0.39C^{CD}$	7.53 ± 0.18^{D}	14.70 ± 1.37^{BC}	15.66 ± 1.90^{BC}	2.82 ± 0.22^{A}
18:1n-7	1.42 ± 0.06^{A}	1.78 ± 0.06^{A}	9.14 ± 0.29^{B}	5.74 ± 0.25^{B}	1.66 ± 1.04^{A}	9.37 ± 0.82^{B}	2.49 ± 0.13^{A}
18:2n-6	2.25 ± 0.09^{AE}	13.73 ± 0.87^{B}	4.07 ± 0.25^{CE}	1.59 ± 0.03^{A}	1.66 ± 0.13^{A}	6.69 ± 0.93^{D}	2.95 ± 0.22^{E}
18:3n-3	3.88 ± 0.14^{AC}	9.29 ± 0.37^{B}	2.82 ± 0.23^{C}	5.55 ± 0.26^{DE}	4.33 ± 0.46^{AE}	6.59 ± 0.50^{D}	2.00 ± 0.15^{C}
18:4n-3	1.77 ± 0.03^{AB}	0.79 ± 0.10^{A}	1.24 ± 0.20^{A}	3.16 ± 0.36^{B}	1.54 ± 0.49^{A}	1.34 ± 0.22^{A}	1.00 ± 0.19^{A}
Σ20-22SFA	0.45 ± 0.10^{A}	6.00 ± 0.38^{B}	0.04 ± 0.04^{C}	0.12 ± 0.02^{C}	0.11 ± 0.05^{C}	0.50 ± 0.04^{A}	0.00 ± 0.00^{C}
Σ20-22MUFA	0.02 ± 0.02^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.27 ± 0.06^{B}	6.59 ± 0.48^{C}
20:2n-6	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.08 ± 0.04^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.10 ± 0.05^{A}	3.12 ± 0.36^{B}
20:4n-6	1.10 ± 0.30^{A}	0.13 ± 0.13^{BC}	1.46 ± 0.10^{AD}	0.34 ± 0.02^{C}	0.32 ± 0.06^{C}	2.06 ± 0.16^{D}	9.15 ± 0.87^{E}
20:4n-3	0.37 ± 0.01^{A}	0.00 ± 0.00^{B}	0.10 ± 0.05^{BC}	0.16 ± 0.02^{C}	0.08 ± 0.02^{BC}	0.14 ± 0.02^{C}	0.32 ± 0.04^{A}
20:5n-3	21.92 ± 0.86^{A}	2.11 ± 0.37^{B}	11.54 ± 0.59^{C}	19.67 ± 0.32^{AD}	16.58 ± 1.08^{AC}	15.69 ± 1.15^{CD}	16.72 ± 1.48^{AC}
Σ22:2	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	9.80 ± 0.84^{B}
22:4n-6	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	2.45 ± 0.27^{B}
22:5n-3	0.32 ± 0.01^{A}	0.00 ± 0.00^{B}	0.00 ± 0.00^{BC}	0.14 ± 0.05^{CD}	0.12 ± 0.02^{CD}	0.04 ± 0.01^{BD}	7.19 ± 0.28^{E}
22:6n-3	2.05 ± 0.08^{A}	0.00 ± 0.00^{B}	0.19 ± 0.04^{BC}	0.22 ± 0.03^{C}	0.28 ± 0.06^{C}	0.11 ± 0.01^{BC}	2.07 ± 0.12^{A}
Σ24-30SFA	0.00 ± 0.00^{A}	12.75 ± 1.68^{B}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}
∑FA	0.88 ± 0.12^{A}	8.42 ± 2.46^{B}	51.74 ± 9.63^{C}	44.17 ± 1.25^{C}	37.45 ± 7.75^{CD}	21.22 ± 2.50^{D}	5.53 ± 0.60^{B}

Means labeled with the same letter are not significantly different at $P < 0.05$ after Tukey HSD post hoc test for ANOVA of $\log(x+1)$ transformed data

Σ24-30SFA occurred (Table 2). In contrast, the leaf litter had a significantly lower level of 20:5n-3 than the other components (Table 2). In October 2022, *O. nigribasis* had a significantly higher level of 20:5n-3 compared with the other animals (Table 3). *B. toni* had the significantly higher levels of 16:1n-7, 18:4n-3 (except that of periphyton) and 22:6n-3 (Table 3). In leaf litter, significantly higher levels of Σ20-22SFA and Σ24-30SFA occurred compared with the other components (Table 3). In contrast, leaf litter had a significantly lower level of 20:5n-3 than the other components (Table 3). *A. major* had significantly higher levels compared with the other components and 20:4n-6 (Table 3).

Discussion

Differences between autumn and spring trophic chains revealed by SIA seem to be the most conspicuous finding of this study. This finding supports our first hypothesis

Table 3 Mean levels of fatty acids (% of total ± standard error) and their mean total contents (∑FA, mg g^{-1} wet weight ± standard error) in components of ecosystem of the Komarovka River (Primorsky Krai, Russia), October, 2022

Fatty acid	*U. japonica*	*S. schwerinii*	*S. gracilistyla*	*A. hirsuta*	Periphyton	*P. reticulata*	*O. nigribasis*	*H. nigrovittatus*	*A. major*	*B. toni*
Σ10-12SFA	0.31 ± 0.05^{A}	0.19 ± 0.04^{A}	0.48 ± 0.28^{A}	0.26 ± 0.02^{A}	0.22 ± 0.02^{A}	2.74 ± 0.34^{B}	1.67 ± 0.36^{C}	0.10 ± 0.01^{A}	0.22 ± 0.02^{A}	0.23 ± 0.06^{A}
Σ12:1	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	1.25 ± 0.20^{B}	0.89 ± 0.10^{B}	0.00 ± 0.00^{A}	0.01 ± 0.01^{A}	0.00 ± 0.00^{A}
Σ12:2	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.30 ± 0.30^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.67 ± 0.09^{B}	0.41 ± 0.05^{B}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}
14:0	2.08 ± 0.19^{A}	1.05 ± 0.09^{BE}	1.27 ± 0.27^{AD}	1.32 ± 0.07^{BD}	4.01 ± 0.16^{C}	0.67 ± 0.04^{E}	0.98 ± 0.06^{BE}	0.99 ± 0.11^{BE}	1.07 ± 0.12^{BE}	3.22 ± 0.30^{C}
Σ14:1	0.04 ± 0.02^{A}	0.00 ± 0.00^{A}	0.30 ± 0.30^{A}	0.00 ± 0.00^{A}	0.26 ± 0.04^{AB}	0.19 ± 0.02^{AB}	0.43 ± 0.12^{B}	2.27 ± 0.10^{C}	0.51 ± 0.14^{B}	0.91 ± 0.02^{D}
Σ14PUFA	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.30 ± 0.30^{A}	0.00 ± 0.00^{A}	0.01 ± 0.01^{A}	1.39 ± 0.35^{A}	0.52 ± 0.11^{A}	0.10 ± 0.05^{A}	0.00 ± 0.00^{A}	0.08 ± 0.02^{A}
15:0	0.41 ± 0.02^{ACDE}	0.51 ± 0.07^{AE}	0.69 ± 0.026^{A}	0.51 ± 0.04^{ACE}	0.46 ± 0.03^{ACE}	0.36 ± 0.02^{CDE}	0.22 ± 0.01^{B}	0.36 ± 0.05^{ED}	0.39 ± 0.02^{AED}	0.27 ± 0.05^{BD}
16:0	21.37 ± 2.40^{AC}	11.66 ± 1.50^{BE}	13.46 ± 3.25^{C}	15.27 ± 1.67^{ABD}	18.54 ± 0.42^{AD}	16.62 ± 0.46^{ADF}	14.86 ± 0.70^{DEF}	19.58 ± 1.40^{AD}	20.01 ± 1.05^{AC}	12.87 ± 0.40^{BF}
16:1n-9	0.00 ± 0.00^{A}	0.13 ± 0.02^{AB}	0.39 ± 0.29^{AB}	0.14 ± 0.07^{AB}	0.29 ± 0.02^{BC}	0.30 ± 0.03^{BC}	0.43 ± 0.02^{CD}	0.48 ± 0.05^{CD}	0.62 ± 0.07^{D}	0.56 ± 0.05^{D}
16:1n-7	1.62 ± 0.33^{A}	1.02 ± 0.23^{A}	1.50 ± 0.33^{A}	0.93 ± 0.36^{A}	24.87 ± 0.38^{B}	6.22 ± 0.36^{C}	6.62 ± 0.71^{C}	8.69 ± 1.94^{C}	11.14 ± 1.01^{C}	16.79 ± 0.49^{B}
16:1n-5	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.33 ± 0.30^{AC}	0.00 ± 0.00^{A}	0.51 ± 0.04^{B}	0.12 ± 0.01^{C}	0.22 ± 0.02^{CD}	0.17 ± 0.02^{C}	0.31 ± 0.03^{DE}	0.46 ± 0.06^{BE}
Σ15-17BFA	0.43 ± 0.08^{AB}	0.18 ± 0.04^{A}	0.60 ± 0.28^{BCDE}	0.32 ± 0.06^{ABE}	1.38 ± 0.25^{CDF}	0.35 ± 0.02^{AE}	0.78 ± 0.08^{BCD}	0.30 ± 0.01^{AE}	2.19 ± 0.02^{F}	1.28 ± 0.30^{D}
Σ16PUFA	0.00 ± 0.00^{A}	0.07 ± 0.03^{A}	0.48 ± 0.29^{AC}	0.00 ± 0.00^{A}	18.01 ± 0.80^{B}	1.03 ± 0.11^{CD}	1.49 ± 0.27^{D}	12.61 ± 0.55^{B}	0.26 ± 0.06^{A}	7.14 ± 1.14^{E}
17:0	0.81 ± 0.15^{ACD}	0.41 ± 0.08^{AB}	0.64 ± 0.27^{ABD}	0.57 ± 0.02^{AD}	0.20 ± 0.07^{B}	1.06 ± 0.10^{C}	0.91 ± 0.03^{CD}	0.53 ± 0.08^{A}	0.64 ± 0.08^{AD}	0.41 ± 0.05^{AB}
Σ17:1	0.28 ± 0.05^{AC}	0.22 ± 0.03^{ACE}	0.51 ± 0.28^{AD}	0.35 ± 0.07^{AD}	0.08 ± 0.03^{CE}	1.00 ± 0.05^{B}	0.62 ± 0.07^{DF}	0.02 ± 0.02^{E}	0.88 ± 0.07^{BF}	0.10 ± 0.08^{CE}
18:0	4.87 ± 0.54^{AE}	1.79 ± 0.12^{CD}	2.62 ± 0.64^{AE}	2.44 ± 0.17^{BC}	1.26 ± 0.13^{D}	2.58 ± 0.18^{BC}	5.67 ± 0.29^{E}	2.88 ± 0.33^{B}	4.61 ± 0.36^{AE}	3.69 ± 0.13^{AB}
18:1n-9	10.37 ± 0.88^{AC}	33.29 ± 6.25^{B}	19.48 ± 4.25^{C}	35.44 ± 4.92^{B}	1.91 ± 0.11^{D}	40.17 ± 1.22^{B}	22.02 ± 1.18^{E}	21.42 ± 1.27^{E}	31.12 ± 0.46^{B}	8.99 ± 0.43^{A}
18:1n-7	1.38 ± 0.35^{AB}	0.64 ± 0.06^{AC}	1.18 ± 0.32^{B}	0.75 ± 0.05^{AC}	1.91 ± 0.15^{B}	0.64 ± 0.05^{C}	3.84 ± 0.52^{D}	0.78 ± 0.05^{AC}	3.34 ± 0.38^{D}	6.18 ± 0.32^{E}
18:2n-6	11.09 ± 0.72^{AE}	12.94 ± 0.61^{A}	8.69 ± 1.62^{ACE}	12.72 ± 0.90^{A}	1.60 ± 0.07^{B}	6.97 ± 0.35^{CF}	4.50 ± 0.13^{D}	7.72 ± 1.35^{CF}	8.06 ± 0.71^{EF}	3.55 ± 0.11^{D}
18:3n-3	21.93 ± 2.81^{A}	16.91 ± 1.39^{AC}	11.13 ± 2.07^{AC}	12.26 ± 1.88^{AC}	2.50 ± 0.09^{B}	10.95 ± 0.23^{C}	12.11 ± 1.35^{C}	16.25 ± 1.36^{AC}	2.37 ± 0.42^{B}	4.19 ± 0.89^{B}
18:4n-3	0.23 ± 0.23^{AC}	0.11 ± 0.06^{A}	0.44 ± 0.29^{AD}	0.25 ± 0.09^{AD}	1.69 ± 0.13^{B}	0.34 ± 0.02^{AD}	0.68 ± 0.08^{CD}	0.64 ± 0.17^{CD}	0.53 ± 0.04^{AD}	0.81 ± 0.11^{D}
Σ20-22SFA	4.97 ± 0.45^{A}	2.31 ± 0.39^{B}	3.49 ± 0.85^{C}	2.74 ± 0.36^{B}	0.65 ± 0.15^{D}	0.22 ± 0.02^{E}	0.40 ± 0.05^{DE}	0.25 ± 0.03^{E}	0.29 ± 0.02^{DE}	0.30 ± 0.02^{DE}
Σ20-22MUFA	0.68 ± 0.09^{AD}	0.10 ± 0.02^{BC}	0.45 ± 0.29^{AB}	0.19 ± 0.10^{BCE}	0.00 ± 0.00^{C}	0.22 ± 0.02^{BCE}	0.53 ± 0.11^{AD}	0.17 ± 0.04^{BC}	0.51 ± 0.05^{ADE}	0.88 ± 0.14^{D}
20:2n-6	0.03 ± 0.03^{A}	0.00 ± 0.00^{A}	0.30 ± 0.30^{A}	0.00 ± 0.00^{A}	0.09 ± 0.03^{AB}	0.04 ± 0.00^{A}	0.04 ± 0.02^{A}	0.04 ± 0.02^{A}	0.22 ± 0.02^{BC}	0.32 ± 0.08^{C}
20:4n-6	0.21 ± 0.04^{AB}	0.00 ± 0.00^{A}	0.30 ± 0.30^{A}	0.00 ± 0.00^{A}	0.58 ± 0.03^{BC}	0.69 ± 0.10^{C}	1.80 ± 0.16^{D}	0.22 ± 0.04^{AB}	5.62 ± 0.55^{E}	1.66 ± 0.39^{D}
20:4n-3	0.09 ± 0.09^{A}	0.00 ± 0.00^{A}	0.30 ± 0.30^{A}	0.00 ± 0.00^{A}	0.27 ± 0.01^{B}	0.00 ± 0.00^{A}	0.06 ± 0.02^{A}	0.06 ± 0.01^{A}	0.07 ± 0.02^{A}	0.52 ± 0.05^{C}
20:5n-3	0.53 ± 0.19^{A}	0.07 ± 0.07^{A}	0.51 ± 0.29^{A}	0.00 ± 0.00^{A}	14.59 ± 0.59^{B}	2.56 ± 0.21^{C}	16.20 ± 1.57^{B}	2.64 ± 0.51^{C}	2.91 ± 0.53^{C}	8.73 ± 0.35^{D}
22:4n-6	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.30 ± 0.30^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.21 ± 0.21^{B}	0.14 ± 0.06^{B}
22:5n-3	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.30 ± 0.30^{A}	0.00 ± 0.00^{A}	0.52 ± 0.06^{B}	0.00 ± 0.00^{A}	0.05 ± 0.03^{A}	0.01 ± 0.01^{A}	0.08 ± 0.03^{A}	3.71 ± 0.08^{C}
22:6n-3	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.30 ± 0.30^{A}	0.00 ± 0.00^{A}	1.53 ± 0.07^{B}	0.02 ± 0.01^{A}	0.13 ± 0.03^{A}	0.18 ± 0.07^{A}	0.09 ± 0.04^{A}	7.73 ± 0.66^{C}
Σ24-30SFA	13.59 ± 4.13^{A}	14.64 ± 2.92^{A}	10.44 ± 1.73^{A}	10.52 ± 2.26^{A}	0.32 ± 0.18^{B}	0.00 ± 0.00^{B}	0.00 ± 0.00^{B}	0.00 ± 0.00^{B}	0.07 ± 0.03^{B}	0.00 ± 0.00^{B}
ΣFA	2.35 ± 0.25^{AB}	5.52 ± 1.05^{AD}	3.47 ± 0.64^{AB}	5.82 ± 1.13^{AD}	1.48 ± 0.30^{B}	46.61 ± 3.67^{C}	18.77 ± 2.56^{E}	29.06 ± 4.57^{CE}	39.90 ± 6.41^{C}	6.79 ± 0.87^{D}

Means labeled with the same letter are not significantly different at $P < 0.05$ after Tukey HSD post hoc test for ANOVA of $\log(x+1)$ transformed data

that the incorporation of organic carbon in leaf litter in spring, at least by certain species of benthic consumers, larvae of *O. nigribasis*, *D. lunatus*, *S. marmorata*, and *H. nigrovittatus* is higher than that in autumn. Thus, unlike in autumn, leaf litter rather than periphyton appeared to be the main basal carbon source for most benthic invertebrates in spring. It is worth noting that the $\delta^{13}C$ values of leaf litter in our study remained the same from autumn to spring despite their breakdown (conditioning), similar to the data of other authors (Yang et al. 2014).

In the assumed peculiar trophic chain of the water bug *A. major*, leaf litter was the principal basal carbon source. In another study, the water bug *Anisops* was also found to be an apex predator, using leaf litter as a principal basal carbon source (McInerney et al. 2020). In contrast, the assumed peculiar trophic chain of the fish *B. toni* was based on periphyton as the basal source. In other similar studies of subalpine rivers, fish were also found to have periphyton as the basal resource (Guo et al. 2022; Ebm et al. 2023).

Thus, according to our first hypothesis, some benthic consumers, which mainly or exclusively relied on periphyton as the basal carbon source in autumn, appeared to switch to leaf litter in spring. Most likely, in autumn, periphyton was comparatively more abundant than in spring. Indeed, for instance, in another Russian Far East river, the content of chlorophyll per m^2 in periphyton in autumn was ~4-fold higher than that in spring (Yavorskaya 2017). Similarly, in small temperate forest streams, epilithic biofilms (mainly diatoms) in autumn had from ~2.5-fold to ~5-fold higher biomass than in spring (Twining et al. 2017; Labed-Veydert et al. 2023). However, in another study, autochthonous sources were the main carbon supply for zoobenthos in spring, while leaf litter composed of beech *Fagus sylvatica* had limited decomposition rates and a low palatability (Labed-Veydert et al. 2023).

Regarding the C:N stoichiometric ratio as the indicator of nutritive value, leaf litter represented food of low quality, with the average C:N varying from 17.1 to 37.4 mol:mol compared with the average values of the periphyton in the range of 7.1–11.4 mol:mol. For the studied animals, average C:N ratios varied from 4.5 to 7.7 mol:mol. The above values of C:N ratios of the allochthonous and autochthonous components of the ecosystem under study, plants and animals showed good fit with the data available in literature (Cloern et al. 2002; Fink et al. 2006; Clarke 2008; Hladyz et al. 2009; Leberfinger and Bohman 2010; Imberger et al. 2014; Lu et al. 2014; Yang et al. 2014; Torres-Ruiz and Wehr 2020). Interestingly, among the plants, the lowest average C:N = 17.1 mol:mol was characteristic of leaves of the Manchurian alder *A. hirsuta*. It is worth noting that in another study, leaves of alder *Alnus glutinosa* also had the lowest C:N ratio among leaves of other species (Hladyz et al. 2009). Another species of this genus, nitrogen-fixing red alder *Alnus rubra*, also had comparatively low C:N = 23.1 mol:mol (Volk and Kiffney 2012). In our study, the $\delta^{13}C$ signatures of leaves of *A. hirsuta* were the closest to those of benthic animals, and the IsoSource model gave their comparatively high contribution to the carbon of *P. reticulata* and *D. lunatus*, as well as *E. strigata* in October 2022, which could be probably explained by the higher nutritive value. However, in October 2022, the leaves of *S. gracilistyla* contributed comparatively more to the carbon of *O. nigribasis*, although the leaves of this species had too high of an average C:N = 32.5 mol:mol. The above findings support our second hypothesis that the incorporation of organic carbon into the leaf litter of certain tree species by benthic consumers can be higher than that of other tree species.

Evidently, leaf litter is a low-quality food for benthic animals compared with periphyton because of the higher imbalance between resource and consumer C:N stoichiometry, as was found in some other studies (Fink et al. 2006; Leberfinger and Bohman 2010; Hessen et al. 2013; Kühmayer et al. 2020). To overcome the C:N imbalance, animals need to assimilate more nitrogen from ingested food and excrete more carbon (Urabe and Watanabe 1992; Hessen et al. 2013). Indeed, the average C:N of the feces of primary consumers of *P. reticulata* was approximately three times higher than that of their bodies in November 2021 and in October 2022. The same was true of the primary consumer *H. nigrovittatus* in October 2022. Moreover, the $\delta^{13}C$ signatures of the feces of *P. reticulata* and *H. nigrovittatus* were lighter than those of their bodies and closer to those of the leaves. Evidently, in autumn, these larvae mainly excreted the ingested leaf litter rather than assimilated it. Excreting ingested leaf litter instead of assimilating it based on stable isotope signatures was found for yet another benthic primary consumer, *Gammarus coreanus* (Bogatov et al. 2021). In contrast, the secondary consumer *S. marmorata* in April 2022 had C:N ratios of feces approximately the same as in their bodies, and $\delta^{13}C$ values of their feces were not significantly different or heavier than those of their bodies, which could be likely explained by their carnivory. Indeed, in another study, heavier $\delta^{13}C$ signatures were found in the feces of carnivorous benthic larvae of *Pedicia* sp. (Bogatov et al. 2021). Remarkably, in spring, in contrast to autumn, the $\delta^{13}C$ values of the feces of the primary consumers *H. nigrovittatus* and *D. aculea* were similar or heavier than those of their bodies, which was probably indicative of a higher degree of assimilation of the overwintering leaf litter compared with autumn leaves. This finding seems to be in good agreement with our first hypothesis that incorporation of organic carbon of leaf litter in spring, at least by certain species of benthic consumers, can be higher than that in autumn.

In general, the above data are believed to evidence low, if any, consumption and/or assimilation of leaf litter, except

that of *A. hirsuta*, by the benthic animals in autumn but not in spring. The overwintering leaf litter in spring seemed to be more suitable for consumption than the fresh litter in autumn due to conditioning (breakdown), i.e., physicochemical and microbial degradation, which likely made the leaves more palatable (Hladyz et al. 2009). This finding supports our first hypothesis, which implies that the higher incorporation of organic carbon of leaf litter benthic consumers in spring could be a result of conditioning of the leaves during winter. Nevertheless, it is worth noting that in spring, the average C:N ratio of the leaf litter was nearly as high as that in autumn, i.e., it did not decrease as a result of the putative microbial degradation. Indeed, bacteria also need nitrogen (i.e., a low C:N ratio) for effective growth (Taylor and Townsend 2010), and fungal biomass does not correlate with litter C:N during breakdown (Hladyz et al. 2009). Hence, it is not at least surprising that in our study, the C:N ratio in leaf litter did not change during conditioning from autumn to spring. However, some authors reported a relative increase in nitrogen (decrease in C:N) in leaf litter during its decomposition in streams (Torres-Ruiz and Wehr 2010; Eckert et al. 2020).

However, as found earlier, the C:N ratio does not exceptionally explain food choice among benthic invertebrates (Leberfinger and Bohman 2010). Indeed, another important indicator of nutritive value for benthic animals is the content of polyunsaturated fatty acids (PUFAs), especially eicosapentaenoic acid (20:5n-3, EPA) and docosahexaenoic acid (22:6n-3, DHA), which are synthesized by some taxa of algae rather than terrestrial vascular plants (Ahlgren et al. 1997; Goedkoop et al. 2000; Sui et al. 2007; Torres-Ruiz et al. 2007; Ruess and Müller-Navarra 2019; Kühmayer et al. 2020; McInerney et al. 2020; Ebm et al. 2021). Since vascular plants cannot synthesize EPA and DHA (Sayanova and Napier 2004; Ward and Singh 2005; Sayanova et al. 2006; Ruiz-Lopez et al. 2012), these PUFAs are naturally absent in the leaf litter, as confirmed in our study. The modest levels of EPA and DHA recorded in leaf litter, 0.0–0.8% in autumn and 2.1% in spring, should be explained by contamination by periphytic algae, as in other studies (Guo et al. 2016c; Kühmayer et al. 2020; Bogatov et al. 2021). In contrast, periphytic algae had very high levels of EPA (~15–20%), which are biomarkers of diatoms (Bacillariophyta), and DHA (~2%), which are markers of *Euglenophyta* and *Chrysophyta* (Makhutova et al. 2022). According to the biomarker fatty acid levels, both EPA and 16:1n-7 (Makhutova et al. 2022), periphyton is made up primarily of diatoms. Indeed, as previous studies have demonstrated, diatoms were the dominant taxa in the periphyton of the Komarovka River, and DHA-rich algae, such as *Euglenophyta* and *Chrysophyta*, also occurred there (Bogatov and Nikulina 2009). Thus, as other studies have shown (Ahlgren et al. 1997; Goedkoop et al. 2000; Sui et al. 2007; Torres-Ruiz et al. 2007; Kühmayer et al. 2020; McInerney et al. 2020; Ebm et al. 2021; Guo et al. 2021), periphyton, due to its high levels of EPA and DHA, has considerably higher nutritive value for benthic animals than leaf litter.

In October 2022, significantly higher levels of EPA were characteristic of larvae of *O. nigribasis* (16.2%) and *B. toni* (8.7%), which could be explained by a higher periphyton contribution to their basal food sources. However, another important marker of diatoms, 16:1n-7, in *O. nigribasis* had nearly the same level as in the other invertebrates. Hence, the higher level of physiologically important EPA in *O. nigribasis* seemed to be due to selective accumulation through the trophic chain, where this species had a higher trophic position, rather than due to a higher consumption of periphyton (Gladyshev et al. 2005, 2011; Guo et al. 2016c). Indeed, the $\delta^{13}C$ signature of *O. nigribasis* indicated identical proportions of carbon from both sources, leaf litter and periphyton. The multidimensional analysis of FA composition, such as the stable isotope analysis, also placed *O. nigribasis* between two sources: leaf litter and periphyton. In contrast, *B. toni*, together with the high level of EPA, had the highest level of 16:1n-7, and the multidimensional analysis of FA composition confirmed the highest closeness between the periphyton and *B. toni*. In addition to the markers of diatom algae, *B. toni* also had the highest level among animals of 18:4n-3 and DHA, markers of the other putative component of the periphyton—*Chrysophyta* (Makhutova et al. 2022). Together with the FA markers, the $\delta^{13}C$ signature of *B. toni* indicated that periphyton was its principal, if not the only, source of carbon. In this case, the trophic position of *B. toni* at trophic level V, calculated by using *H. nigrovittatus* as the baseline, should be revised because *B. toni* likely belonged to another food chain, which was based only on the periphyton, and its putative trophic links were likely omitted in this study. The same seems to be true of the snail *P. amurensis*: according to the $\delta^{13}C$ signature and the highest level of DHA among consumers, this species consumed exclusively periphyton, i.e., belonged to a trophic chain other than the one with *H. nigrovittatus* as the baseline. Indeed, literature describes the snail species as a scraper of periphytic algae (Prozorova and Rasshepkina 2003), i.e., as a primary consumer. In other studies, the possibility of different baselines for benthic macroinvertebrates based on allochthonous and autochthonous sources was also revealed (Lancaster and Waldron 2001). Thus, there was very good agreement between the stable isotope analysis and the fatty acid analysis.

In April 2022, the periphyton, *E. strigata* and *D. aculea* had significantly higher levels of 16:1n-7 than the other components, while *P. amurensis* had the lowest level of this FA. In addition, *P. amurensis* had a middle level of another marker of diatom algae, EPA. Meanwhile, together with the periphyton, *P. amurensis* had the highest level of DHA, which is the marker of *Euglenophyta* and *Chrysophyta*. Most

likely, *P. amurensis*, which grazes periphyton, selectively consumed *Euglenophyta* and *Chrysophyta* rather than diatom algae. In addition, *P. amurensis* together with *E. strigata* had significantly higher levels of the bacterial marker Σ15-17BFA in their biomass. Probably, the periphytic biofilms are not uniform, and the animals might select for grazing spots with preferred food items. However, bacterial biomarkers, FAs with branched and odd-numbered chains (Makhutova et al. 2022), in April 2022 had approximately the same levels in the leaf litter and the periphyton (epilithic biofilms) and, therefore, could not be used for distinguishing basal carbon sources. Similarly, in another small forest stream, biofilms on detritus and rocks also had an overlapping fatty acid composition of microbial communities (Twining et al. 2017).

In the leaf litter, two essential fatty acids, ALA and linoleic acid (18:2n-6, LIN), had the highest levels. Animals can obtain these acids from food only (Bell and Tocher 2009; Lands 2009). Adding LIN to organic matter (cellulose) in laboratory microcosms increased its consumption by benthic invertebrates (Vonk et al. 2016). Algae can also synthesize LIN and ALA, but in our study, the levels of these acids in the leaf litter were approximately 5–10-fold higher than those in the periphyton. Higher proportions of LIN and ALA in leaf litter than in periphyton were found in other studies (Guo et al. 2018; Moyo and Richoux 2018; McInerney et al. 2020; Bogatov et al. 2021). Thus, LIN and ALA should be regarded as markers of leaf litter, as in other studies (Makhutova et al. 2022). Among the animals, in April 2022, larvae of *D. lunatus* had significantly higher levels of LIN and ALA, which could mean a comparatively higher contribution of leaf litter carbon to their ratio. In October 2022, higher levels of LIN and ALA were characteristic of *A. major* and larvae of *H. nigrovittatus*.

It is worth noting that in the spring of (April) 2022, the level of LIN in the leaf litter was ~1.5 times higher than that of ALA. In contrast, in the autumn of (October) 2022, the levels of ALA in the leaves were at least the same, or even twice as high, as those of LIN. Similar changes in the LIN/ALA ratio in leaf litter in spring and autumn were reported by other authors (Torres-Ruiz and Wehr 2010; Labed-Veydert et al. 2023). The comparatively higher proportion of LIN in the leaf litter in spring could be explained by an increase in the biomass of fungi in leaf litter during their conditioning from autumn to spring, since LIN is especially abundant in saprotrophic fungi and is used as a biomarker (Larsen et al. 1998; Torres-Ruiz and Wehr 2010; Nurika et al. 2018). On the other hand, ALA might be degraded faster than LIN in dead plant material (leaf litter) during winter.

In addition to LIN and ALA, the other specific indicators of vascular plants, saturated fatty acids with 24–30 carbons (Σ24-30SFA) (Makhutova et al. 2022) had very high levels in the leaf litter but were practically absent in the animals. Most likely, the primary consumers, who used the leaf litter as the basal food source, did not assimilate these long-chain SFAs but excreted them together with recalcitrant bulk leaf material, in contrast to selectively assimilated unsaturated FAs, as was supposed in other studies (Kirfel and Komnick 1999; Bogatov et al. 2021).

In autumn, primary consumers *P. reticulata* and *H. nigrovittatus* did not digest and assimilate but excreted a considerable portion of the ingested leaf litter, as revealed by CIA and element analyses of their bodies and feces. However, in spring, the comparison of $\delta^{13}C$ signatures of feces and bodies of *H. nigrovittatus*, as mentioned above, probably indicated a higher degree of assimilation. The higher assimilation of leaf litter in spring might be explained by their overwinter microbial conditioning. In addition, the levels of EPA in leaf litter in spring were from 1.4% to 2.9%, while in autumn, values from 0% to 0.53% were detected. This might mean that in spring, the leaf litter had a higher fouling by periphytic diatoms than freshly fallen leaves in autumn. As some other authors had found earlier, the high-quality algae attached to leaf litter could enhance the incorporation of low-quality organic matter of leaf litter to the biomass of invertebrate consumers (Guo et al. 2016c).

The feeding habits of some benthic species were confirmed and/or specified in our study based on SIA and FA analyses. Larvae of stonefly (*P. reticulata*) and caddisfly (*H. nigrovittatus*) were known to be primary consumers (Zwick and Teslenko 2002; Tiunova 2006), and this trophic position of these organisms was supported by our data. Larvae of mayfly (*D. aculea*), stonefly (*O. nigribasis*), dragonfly (*D. lunatus*), and water bug (*A. major*) were known as predators (Kanyukova 2006; Tiunova 2006; Popova 2010; Chung et al. 2012; Petak et al. 2014; Shin et al. 2015), and their trophic positions of secondary and tertiary consumers were confirmed in our study. Larvae of caddisfly (*S. marmorata*) and mayfly (*E. strigata*), previously regarded as omnivorous filtering collectors (Kocharina 1999; Tiunova 2006; Okamoto et al. 2022), in our study were determined to be secondary consumers, i.e., they collected primarily particles of animal origin.

However, trophic positions of two species should be specified in future. Adults of water bug (*A. major*) are strong flyers, which can episodically change their habitats and feed in other water bodies (Csabai et al. 2006). As a result, *A. major* might have isotopic signatures reflecting organic matter from food webs of other ecosystems. Siberian stone loach (*B. toni*) is known to be zoobenthivore, consuming primarily small chironomid larvae (Tokranov 2006; Mercado-Silva et al. 2008), which were omitted in our study. Both SIA and FA markers indicated that a trophic chain of *B. toni* was based primarily or exclusively on periphyton.

Consequently, in contrast to many other studies, which were based on CIA and FA markers and found that autochthonous algal organic carbon was the principal basal source for stream invertebrates (Lau et al. 2009; Descroix et al. 2010; Thorp and Bowes 2017; Moyo and Richoux 2018; Kühmayer et al. 2020; Torres-Ruiz and Wehr 2020; Bogatov et al. 2021; Ebm et al. 2021; Labed-Veydert et al. 2021, 2023, but see Twining et al. 2017), our study revealed considerable assimilation of allochthonous carbon from leaf litter by many species of consumers in small rivers. The proportions of this assimilation depended on the season and the kind of leaf litter.

Conclusions

In the small forest river, some benthic animals, primary consumers [namely, the larvae of caddisfly (*H. nigrovittatus*) and of mayfly (*D. aculea*)] and secondary consumers [namely, the larvae of caddisfly (*S. marmorata*), the larvae of mayfly (*E. strigata*), and the water bug (*A. major*)], obtained organic carbon mainly or exceptionally from the allochthonous basal source, leaf litter. The other benthic animals, primary consumers [namely, the larvae of stonefly (*P. reticulata*) and snail (*P. amurensis*)] and secondary consumers [namely, the Siberian stone loach (*B. toni*)], relied mainly or exceptionally on the autochthonous basal source of organic carbon, such as perithytic microalgae. Certain secondary consumers [namely, larvae of dragonfly (*D. lunatus*) and larvae of stonefly (*O. nigribasis*)] in autumn received carbon mainly from the periphyton, while in spring they shifted to the conditioned leaf litter as their principal basal source.

In general, our study indicated that, in contrast to many other studies, based on SIA and FA biomarker analyses, many primary and secondary consumers in the river bottom community obtained their organic carbon mainly from the allochthonous source, leaf litter, especially in spring. In addition, the leaves of one tree species, Manchurian alder *A. hirsuta*, appeared to be significantly more valuable food for primary consumers than the leaves of the other studied species, even in autumn. Thus, according to our data, the assumption of the RCC that upstream consumers basically depend on allochthonous rather than on autochthonous carbon should not be rejected but rather specified in terms of seasonality and species composition of riparian vegetation.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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