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RESEARCH ARTICLE



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Water quality shapes the community structure of zoobenthos in rivers but only has a minor effect on the fatty acid composition of zoobenthos and salmonids

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Abstract

Many river ecosystems in the boreal zone have faced remarkable changes due to intensive human activities, including land-use changes in the catchments and channelization. Recently, restoration efforts have increased, hoping to restore a more natural hydromorphology. We studied the community structure of benthic macroinvertebrates (zoobenthos) in seven rivers in Eastern Finland, using samples that covered pre- and post-restoration periods, to examine how environmental metrics relate to the zoobenthos community structure, and the fatty acid (FA) composition and content of Ephemeroptera, Plecoptera, and Trichoptera nymphs and larvae. We also analyzed the FA composition and content of land-locked salmon (Salmo salar m. sebago) in three of the rivers and brown trout (Salmo trutta) in two of the rivers. Zoobenthos communities differed significantly among most of the rivers: 24% of the differences between the zoobenthos communities were driven by water quality parameters related to the loading of terrestrial organic matter (water color, pH, and iron concentration). Temporal changes in zoobenthos communities could not be fully attributed to restorations. The FA composition of zoobenthos was mostly explained by phylogenetic origin (47%). However, especially mayfly Heptagenia sulphurea (Ephemeroptera: Heptageniidae) had variable FA composition and content among the rivers suggesting an environmental quality indicator role for this species. FA composition and content of salmonids were mostly size-dependent (24%), but river identity also influenced their FA composition (22%). Our results indicate that water quality affects the availability of essential FAs for consumers by altering the zoobenthos community structure and their FA composition and content.

KEYWORDS

benthic macroinvertebrates, community ecology, polyunsaturated fatty acids, salmonids

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1 | INTRODUCTION

Benthic macroinvertebrates (zoobenthos) are important food for many riverine fishes including salmonids. Many taxa, especially species from Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies) (EPT-taxa), are sensitive to environmental quality, and are routinely used to evaluate the ecological state of European rivers according to EU water framework directive (WFD, 2000/60/EY). Zoobenthos groups vary systematically in their fatty acid (FA) composition (Makhutova et al., 2016), and feeding guilds exploit different resources (Cummins, 1973) with specific FA composition (Makhutova et al., 2011). In aquatic ecosystems, phytoplankton and benthic algae are the primary synthesizers of important omega-3 (ω 3) polyunsaturated FA (PUFAs), of which especially the long-chain eicosapentaenoic acid (EPA, 20:503) and docosahexaenoic acid (DHA, 22:603) are physiologically important for aquatic consumers. Consumers mainly depend on algal production of these ω 3 PUFAs because they cannot synthesize physiologically essential FAs (EFAs) arachidonic acid (ARA, 20:406). EPA, and DHA de novo (Cook & McMaster, 2002). Since the content of EPA and DHA vary among the algal taxa and water quality changes can influence algal community composition, water quality changes can also affect the availability of these essential compounds higher up in the food web (Peltomaa et al., 2017; Taipale et al., 2016). Correspondingly, Guo et al. (2018) found that the FA composition of epilithic algae affects the FA composition of zoobenthos in riverine systems. Since fish need ω 3 PUFAs to maintain normal physiological functions (Ahlgren et al., 2009; Glencross, 2009; Tocher, 2010), it is important to examine how environmental gualities affect the availability of these EFAs in zoobenthos and in higher trophic level consumers, such as fish. Furthermore, fish, especially salmonids, are important sources of $\omega 3$ PUFAs for humans (Hixson et al., 2015) with significant health benefits (e.g., Kris-Etherton et al., 2002).

Most rivers and streams in Finland have been heavily modified by human activities: channelization and dredging for timber floating (Jutila, 1992) and drainage of peatlands. These modifications have led to the loss of habitats for salmonids and many aquatic invertebrates. Furthermore, the majority of Finnish forests are utilized for industrial forestry with significant impacts on the water quality, especially the concentration of dissolved organic carbon (DOC) and amount of suspended particulate organic material in the aquatic ecosystems have increased in recent decades (Aaltonen et al., 2021; Albrecht et al., 2023; Laudon et al., 2009; Lepistö et al., 2021; Nieminen et al., 2015; Rääpysjärvi et al., 2016). The so-called "browning" phenomenon, indicative of an increase in DOC and iron concentrations due to multiple mechanisms affects many waterbodies in the northern hemisphere (de Wit et al., 2016; Lepistö et al., 2021; Monteith et al., 2007). Most of the rivers and streams in North Karelia have a high humic (DOC) content (Rouvinen, 2010), which may have a major influence on the community structure of zoobenthos (Kesti et al., 2021; Robbins et al., 2020) and thus sets the main criteria for river types in the EU WFD classification system.

To overcome the biodiversity declines caused by the hydromorphological modifications of rivers, significant

hydromorphological restoration efforts have been made during the past decades. While the restorations aim to improve overall biodiversity, they have often been driven by the need to increase recruitment habitats for salmonids, mostly brown trout (Salmo trutta) (Marttila et al., 2019). Overall, the results of restoration efforts have been monitored poorly and the documented results have been variable. While most of the studies have found positive responses of zoobenthos communities to restoration (Albertson et al., 2011; Kil & Bae, 2012; Louhi et al., 2016; Muotka et al., 2002; Pilotto et al., 2018; Suurkuukka et al., 2014; Verdonschot et al., 2016), some have reported little or no changes in the community composition (Smith et al., 2020; Tetu et al., 2016). It is also commonly reported that zoobenthos communities are heavily obscured by river restoration procedures and show lower biomass and diversity acutely after restorations (dos Reis Oliveira et al., 2019; Louhi et al., 2011; Molina-Moctezuma et al., 2021).

In this study, we focus on small to medium-sized boreal rivers in Eastern Finland and their native zoobenthos and fish fauna. Some of the rivers support resident populations of endangered brown trout and some are stocked with hatchery-reared juveniles of critically endangered landlocked Atlantic salmon (Salmo salar m. sebago). Virtually, all the waterways in this area have been modified by humans. and substantial restoration efforts have been conducted on several occasions during the past 50 years. In the years 2011-2015, several rivers were modified to create new breeding habitats for the endangered salmonids (Rouvinen, 2010). Zoobenthos reported as favorable food sources for salmonids include larvae of Diptera and caddisflies, and nymphs of stoneflies, mayflies, and dragonflies (Khrennikov et al., 2007; Regerand et al., 2002; Shustov et al., 2012). Hydromorphological conditions in the river, eutrophication, and high humic content can affect the quality of zoobenthos assemblages via changes in the community structure, as well as via changes in the FA composition and content within taxa (Kesti et al., 2021; Strandberg et al., 2023; Taipale et al., 2016). Changes in the communities of these prey species or their FA composition and content could thus influence the overall availability of EFAs to salmonids (Strandberg et al., 2023). Specifically, we aimed to examine (1) which river characteristics drive zoobenthos community structure, (2) how past river restorations might affect zoobenthos community structure, and (3) if the FA composition and content, especially physiologically essential FAs ARA, EPA, and DHA of zoobenthos and salmonids differ among the rivers.

2 | MATERIALS AND METHODS

2.1 | Study rivers

We sampled zoobenthos from seven rivers with past restoration activities (Figure 1, Table 1, Table S1). We focused on rivers in North Karelia in Eastern Finland to limit the impact of regional differences. The selected rivers were restored at different periods: Kalliojoki, Koitajoki, Kuusoja, and Venejoki at the end of the 1990s,



FIGURE 1 Zoobenthos community data and sampling sites and salmonid sampling sites. Detailed coordinates and sampling sites are presented in Table S1. Background orthophotos are an open aerial photo dataset (2023) provided by the National Land Survey of Finland. [Color figure can be viewed at wileyonlinelibrary.com]

Ala-Koitajoki and Naarajoki during the year 2010, and Hanhijoki and Ulkkajoki in 2015 (Rouvinen, 2010). These rivers were restored mainly by increasing channel complexity by adding varying-sized stones and gravel suitable for spawning large salmonids, but two sites in River Ala-Koitajoki (Hiiskoski and Räväkkäkoski) were also restored by translocation of small stones with attached aquatic mosses (Hynninen & Vehanen, 2022; Rouvinen, 2010). We retrieved physical and chemical data of six of the sampled rivers from the Finnish Environment Institute (SYKE) Hertta-database (www.syke. fi/avoindata): Ala-Koitajoki, Hanhijoki, Kalliojoki, Kuusoja, Ulkkajoki, and Venejoki. The data had been collected as a part of monitoring for EU WFD. There was no physical-chemical data for Naarajoki. The selected rivers have a relatively high water color (ranging 110–190 mg L⁻¹ Pt, Table 1), which is typical for rivers in the study region (Rouvinen, 2010).

2.2 | Zoobenthos community analyses

Supplementary zoobenthos community data, as collected according to EU WFD standards (i.e., four pooled kick-net samples collected from shallow rapids per river), were retrieved from the Hertta-database in December 2020 for four of the rivers: Ala-Koitajoki, Hanhijoki, Kallio-joki, and Kuusoja. For the rest of the rivers (Naarajoki, Ulkkajoki, and Venejoki), we relied on the self-collected primary data (Figure 1,

Table S1). The zoobenthos community data were sorted according to the years from restoration for each river (before [-] or after [+] restoration), with five-year intervals. The total time scale for the zoobenthos community data related to the time (years) from restoration was: In River Ala-Koitajoki -0 to 4 to +5 to 9, in River Hanhijoki -0to 4 to +5 to 9, in River Kalliojoki +10 to 14 to +20 to 24, in River Koitajoki +10 to 14 to +20 to 24, in River Kuusoja +5 to 9 to +20 to 24, in River Ulkkajoki +0 to 4, and in River Venejoki +20 to 24, respectively. We calculated the relative abundance (percentage, %) of each taxon from the total number of individuals of all taxa present in the samples from the community.

2.3 | Zoobenthos sampling and preparation for FA analysis

Zoobenthos field sampling and preparation procedures were conducted following Kesti et al. (2021). Zoobenthos were collected with a standardized kick-net sampling method (SFS-EN 27828). Samples from River Ala-Koitajoki were collected in August 2018, and the rest of the samples were collected in August–October 2019, respectively (Figure 1, Table S1). Zoobenthos samples were filtered through a 0.5 mm mesh-sized sieve, transported to the laboratory, and first sorted according to class/family and stored in Eppendorf tubes at -80° C until further identification. For further identification, samples

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		Ala-Koit	ajoki	Hanhijo	G.	Kalliojoki		Kuusoja		Ulkkajoki		Venejoki	
Indicator	Factor	Mean	ß	Mean	ß	Mean	SD	Mean	ß	Mean	ទ	Mean	ß
Morphometry	Length (km)	24.2		20.2		8.5		16.9		13.4		10.0	
Morphometry	Catchment area (km²)	67.4		80.7		29.8		102.2		101.7		129.2	
Oxygen	Oxygen saturation (%)	86.0	7.3	87.8	5.3	88.8	1.9	97.0	6.6	82.0	12.7	N/A	N/A
Oxygen	Oxygen, soluble (mg L $^{-1}$)	10.5	2.4	10.8	2.2	11.0	1.4	11.6	1.1	10.9	2.9	N/A	N/A
Suspended matter	Suspended matter (mg L $^{-1}$)	1.2	0.6	1.8	0.9	2.5	0.5	1.7	0.0	3.9	3.2	N/A	N/A
Nutrients	Phosphorous ($\mu g \ L^{-1}$)	13.1	4.8	18.8	2.8	14.5	0.5	8.1	0.0	16.3	3.1	10.5	1.5
Nutrients	Nitrogen ($\mu g \ L^{-1}$)	535.0	326.5	412.5	34.9	605.0	5.0	480.0	0.0	373.3	40.3	565.0	55.0
Terrestrial organic matter loading	Hd	6.4	0.2	6.4	0.2	5.8	0.4	6.7	0.0	5.8	0.7	6.0	0.3
Terrestrial organic matter loading	Iron ($\mu g L^{-1}$)	810.0	220.1	967.5	87.9	1062.9	256.9	327.3	211.6	820.0	157.5	1090.0	210.0
Terrestrial organic matter loading	Color (mg L $^{-1}$ Pt)	160.0	69.6	170.0	17.3	185.0	25.0	110.0	0.0	153.3	20.6	190.0	30.0
Conductivity	Conductivity (mS m^{-1})	2.4	1.2	2.2	0.2	3.2	0.0	3.5	0.0	2.3	0.6	2.7	0.1
Bottom material	Fine detritus (0.45 µm to 1 mm) (%)	0-5		5-25		0-5		0-5		N/A		N/A	
Bottom material	Coarse detritus (>1 mm) (%)	0-5		0-5		5-25		5-25		N/A		N/A	
Bottom material	Boulders (256–4000 mm) (%)	5-25		0-5		0-5		0-5		N/A		N/A	
Bottom material	Small rocks (16–64 mm) (%)	5-25		5-25		25-75		0-5		N/A		N/A	
Bottom material	Tree branches and trunks (%)	0-5		5-25		5-25		0-5		N/A		N/A	
Bottom material	Gravel (2–16 mm) (%)	0-5		5-25		5-25		0-5		N/A		N/A	
Bottom material	Fontinalis sp. water mosses (%)	5-25		0-5		0-5		5-25		N/A		N/A	
<i>Note:</i> When possible, the standard dev factor in the riverbed. Data were retric Abbreviation: N/A, no data available.	viation (SD) of the factor has been noted. eved from the Finnish Environment Instit	. Values for cute (SYKE)	the botton Hertta-dat	n material f abase (ww	actors hav w.syke.fi/a	e been pres avoindata) ir	sented as ca April 2022	ategorial va 2.	lues, and th	iey describe	e the cover	age of a part	ticular

TABLE 1 Physical and chemical factors of the study rivers.

were briefly thawed and rinsed with MilliQ water. We identified EPTtaxa to species level, when possible. After identification, the samples were stored at -80° C until further analyses.

We selected members of the EPT-taxa for the FA analyses (Table S2). Prior to the analysis of FAs, the samples were freeze-dried using Christ ALPHA 1-4 Ldplus (Martin Christ Gefriertrocknungsanlagen GmbH, Osterode, Germany) and further pulverized with mortar and pestle.

2.4 | Salmonid sampling and preparation for FA analysis

Salmonids (*S. salar* and *S. trutta*) were electrofished from four rivers as a part of fish monitoring in collaboration with Natural Resources Institute Finland (LUKE) except the River Kuusoja salmonids that were self-collected (Figure 1, Table S1). Endangered and protected salmonids were caught using the electrofishing method (SFS-EN 14011) under the licenses from the Regional Centre for Economic Development, Transport, and the Environment (ELY-centre) (POSELY/1015/5716-2016, POSELY/1738/5716-2017). Salmonid body mass (to 0.1 g) and length (to 1.0 mm) were measured in the field (Table S3). All captured salmonids were assumedly juveniles, but the fish were not dissected for maturity analysis. In the laboratory, we dissected part of the dorsal muscle tissue from the fish. The samples were stored at -80° C until further analyses. The muscle tissue was freeze-dried and pulverized with mortar and pestle.

2.5 | FA analysis

We analyzed the FA composition and content from the members of the EPT-taxa (Table S2). FA extraction was done with 2:1 chloroform:methanol (by volume) extraction following Folch et al. (1957). We used gas chromatography (GC) and mass spectrometry (MS) to quantify and identify our FAs. FA extraction, GC, and MS for zoobenthos were done following Kesti et al. (2021). We used an Agilent 6890N GC (Agilent Technologies, Wilmington, DE, USA) equipped with a mass selective spectrometer (Agilent 5973N). The column was an Agilent DB-23 (0.25 mm × 60 m × 0.25 µm). The gas chromatography temperature program was as follows: The starting temperature was 50°C for 1 min, after which raised from 50 to 150°C at 15°C min⁻¹, then to 170°C at 0.5°C min⁻¹, then to 230°C at 2°C min⁻¹. The total running time for samples was 77.67 min.

FA extraction from the salmonid samples was done in the same way, using 5–10 mg of pulverized tissue. For salmonid GC and MS, we used the same instrument as mentioned before, but we used split injection (20:1) with an oven program: The starting temperature was 150°C, after which raised from 150 to 180° C at 1° C min⁻¹, then to 210° C at 2° C min⁻¹, then to 230° C. The final temperature was held for 2 min. The total running time for samples was 49.00 min.

We used saturated FA 23:0 (Nu-Check prep., Elysian, MN, USA) as an internal standard. GLC-538 (Nu-Chek prep) was used for the

calibration. Mass spectra and GLC-538 were used for the identification of FAs.

2.6 | Statistical methods

We used permutational multivariate analysis of variance (PERMANOVA) to investigate the effects of the river, sampling site within the river, and time from restoration on the zoobenthos community structure. We utilized a nested design in the PERMANOVA analyses, where sites were nested in rivers. PERMANOVA was also used to analyze the taxon-, river-, and site-specific differences in the FA composition of zoobenthos. Finally, PERMANOVA was used to analyze the taxon-, river-, and site-specific differences in the FA composition of salmonids. For zoobenthos, we ran an unrestricted permutation of raw data using type III sum of squares. For salmonids, total body length was used as a covariate in the PERMANOVA analyses, so we ran a permutation of residuals under a reduced model using type I sum of squares.

We used similarity percentage (SIMPER) analysis to examine, which taxa were driving the differences in the zoobenthos community structure among the rivers. Additionally, SIMPER was used to identify which FAs were driving the differences in the zoobenthos and salmonid FA composition among the rivers, sampling sites, and taxa.

We used a non-metric multidimensional scaling (NMDS) ordination to visualize the differences in the FA composition of zoobenthos among the taxa and rivers. NMDS ordinations and PERMANOVA were based on Euclidean distance. We used stress values to describe how well the ordinations described the data: Stress values <0.2 were considered acceptable, whereas stress values >0.2 were considered random ordinations (Clarke, 1993). The proportion of zoobenthos taxa in a river community and the proportion of individual FAs from the total FAs of zoobenthos and salmonids were arcsine square root transformed before the analyses.

Additionally, we used distance-based linear modeling (DistLM) to evaluate how much of the variation in the zoobenthos community structure could be explained by different river characteristics. We used a stepwise selection of environmental factors with adjusted *R*² as model selection criteria. Several of the environmental predictors were strongly correlated, thus these predictors were assigned to specific indicators, based on their collinearity and environmental attributes. The indicators were morphometry (river length and size of the catchment area), oxygen (summertime concentration and saturation percentage), nutrients (concentration of phosphorous and nitrogen), terrestrial organic matter (tOM) loading (pH, water color, and iron concentration), and bottom material (e.g., percentage of detritus, rocks, and water mosses) as listed in Table 1.

We used Kruskall–Wallis *H*, one-way analysis of variance (ANOVA), and Bonferroni post hoc tests to examine differences in the EFA composition and content, total FA content, and $\omega 3/\omega 6$ ratio of zoobenthos and salmonid taxa among the rivers.

PERMANOVA, SIMPER, NMDS, and DistLM analyses were conducted in Primer 6 and Permanova+ program package (PRIMER-E Ltd, Plymouth, UK). Kruskall-Wallis H, ANOVA, and Bonferroni post hoc analyses were conducted using IBM SPSS Statistics 27 (IBM Corp., Armonk, New York, USA).

RESULTS 3

Zoobenthos community structure 3.1

A total of 339 zoobenthos taxa were found in the database and our self-collected samples (for a complete list, see Table S4). Zoobenthos community structures differed statistically significantly among most of the study rivers, with river identity explaining 28% of the variation in structure (PERMANOVA, zoobenthos community Pseudo- $F_{7.55} = 4.11$, p < 0.001). Zoobenthos community structures did not differ statistically significantly between Rivers Hanhijoki and Ulkkajoki (t = 1.02, p > 0.10) and Rivers Hanhijoki and Venejoki (t = 1.49, p > 0.10)p > 0.10) (PERMANOVA, pair-wise tests).

The taxa that contributed to the differences in the zoobenthos community structure among the rivers mainly belonged to the EPTtaxa, along with some other taxa (Table S5). In river-specific analysis, the taxa that contributed the most to the aforementioned differences were: In River Ala-Koitajoki: caddisfly Hydropsyche pellucidula (Trichoptera: Hydropsychidae) (11.4%), in River Hanhijoki: mayfly Baetis niger (Ephemeroptera: Baetidae) (7.1%), in River Kalliojoki: stonefly Leuctra sp. (Plecoptera) (4.4%), in River Koitajoki: caddisfly Neureclipsis bimaculata (Trichoptera: Polycentropodidae) (8.0%), in River Kuusoja: mayfly Habrophlebia lauta (Ephemeroptera: Leptophlebiidae) (3.4%), in River Naarajoki: bivalve Sphaeriidae (Bivalvia) (9.8%), in River Ulkkajoki: stonefly Protonemura meveri (Plecoptera: Nemouridae) (11.7%), and in River Venejoki: chironomids (Chironomidae) (4.4%) (SIMPER). Within rivers, we found no statistically significant differences in zoobenthos community structure among the sampling sites.

Variables explaining zoobenthos community 3.2 structure

The factors explaining most of the variation in the zoobenthos community structure among the rivers were factors related to tOM loading (24% of the variation, Pseudo- $F_{7.55} = 3.42$, p < 0.001) and bottom material (22% of the variation, Pseudo- $F_{7.55} = 3.9197$, p < 0.001) (DistLM).

We found significant temporal changes in the zoobenthos community structure within two rivers in relation to the time from restoration (PERMANOVA, Pseudo- $F_{6,56} = 2.84$, p < 0.001). PERMANOVA pair-wise tests revealed that the differences were statistically significant in Rivers Koitajoki and Kuusoja. In River Koitajoki, there was a statistically significant difference between the communities +10 to 14 and +15 to 19 years after restoration (t = 3.16, p < 0.05). The differences were mostly related to the proportions of chironomids (Chironomidae) and caddisfly Hydropsyche in the communities: Chironomidae were more common in the +10 to 14 years than in the +15to 19 years after restoration communities, whereas Hydropsyche were less common in the +10 to 14 years than in the +15 to 19 years after restoration communities (SIMPER, Contribution: Chironomidae 14.43%, Hydropsyche 6.0%) (Table 2).

In River Kuusoja, there was a statistically significant difference between the communities +5 to 9 years and +20 to 24 years after restoration, (t = 1.53, p < 0.05), and the communities +10 to 14 and +20 to 24 years after restoration (t = 1.36, p < 0.05) (PERMANOVA, pair-wise tests). The differences were mostly related to the proportion of Ephemeroptera and Plecoptera: mayfly H. lauta was more common

TABLE 2 Proportions of different zoobenthos taxa and their contributions to the dissimilarities of zoobenthos community structure between communities differing according to time from restoration (SIMPER).

Note: The plus (+) in front of years indicates the time after restoration. PERMANOVA pair-wise test results for the statistical significance are also presented.

9	9					
Таха	Mean (%)	Mean (%)	Contribution (%)	Cumulative contribution (%)	t	р
	Koitajoki (+10 to 14)	Koitajoki (+15 to 19)			3.16	<0.05
Chironomidae	72.6	8.5	14.3	14.3		
Hydropsyche	2.0	2.7	6.0	20.3		
Neureclipsis bimaculata	1.4	2.0	5.4	25.7		
	Kuusoja (+5 to 9)	Kuusoja (+20 to 24)			1.37	<0.05
Habrophlebia lauta	19.2	4.4	4.4	4.4		
Baetis rhodani	3.5	8.0	3.1	7.5		
Leptophlebia	0.0	2.5	3.0	10.5		
	Kuusoja (+10 to 14)	Kuusoja (+20 to 24)			1.36	<0.05
Leuctra hippopus	4.1	0.6	4.6	4.6		
Gyraulus	9.7	0.0	3.8	8.4		
Ephemerella	0.5	8.9	3.0	11.4		

3.3

communities, and stonefly Leuctra hippopus (Plecoptera: Leuctridae) was more common in the +10 to 14 years than in the +20 to 24 years after restoration communities (SIMPER, Contribution: H. lauta 4.4%, L. hippopus 4.6%) (Table 2). In other rivers, no statistically significant differences in zoobenthos community structure were observed in relation to the time from restoration. FA composition and content of zoobenthos Taxon and river identity had a statistically significant effect on the FA composition of zoobenthos. Taxon alone explained 47% of the variation in the zoobenthos FA composition (PERMANOVA, Pseudo- $F_{12.89} = 8.54$, p < 0.001), river identity 5% (PERMANOVA, Pseudo- $F_{6.96} = 2.01$, p < 0.005), and taxon and river in combination 16% of the variation in zoobenthos FA composition among the rivers (PERMANOVA, Pseudo-F_{28,74} = 2.21, p < 0.001). We found FAs that correlated strongly (Pearson's r > 0.6) with

one of the axes in the ordination (Figure 2) of the EPT-taxa FA composition. In Ephemeroptera, there were biomarker FAs (Taipale et al., 2015) indicative of diatoms (Bacillariophyceae) (16:207, 16:304), bacteria (15:0, i15:0), and tOM (22:0). In Plecoptera, we also found biomarker FAs for bacteria (15:0, i15:0), and in Trichoptera, we found biomarker FAs for diatoms (Bacillariophyceae) (16:20), bacteria (16:1ω5), and tOM (20:0, 22:0), respectively.

in the +5 to 9 years than in the +20 to 24 years after restoration

Within Ephemeroptera, we found statistically significant differences in Heptagenia sulphurea FA composition and content among the

rivers. Significant differences were found between Rivers Ala-Koitajoki and Venejoki, Rivers Ala-Koitajoki and Naarajoki, and Rivers Ala-Koitajoki and Kalliojoki (Table S6). Most of the differences in EFA percentage and content were related to the percentage and content of ARA. There was also a statistically significant difference in the percentage of EPA between Rivers Ala-Koitajoki and Naarajoki and ω3/ ω6 ratio between Rivers Ala-Koitajoki and Kalliojoki (Tables 3 and 5).

In Trichoptera, we found statistically significant differences in the FA composition of Polycentropus flavomaculatus between Rivers Kalliojoki and Venejoki. We also found a significant difference in the FA composition between the two sites in River Ala-Koitajoki (Hiiskoski and Räväkkäkoski) for Hydropsyche angustipennis (PERMANOVA pairwise test, t = 1.69, p < 0.05) (Table S6). The percentage and content of EFAs in Trichoptera species also differed among the rivers. In P. flavomaculatus, there was a significant difference in ARA content between Rivers Kalliojoki and Venejoki. In Lepidostoma hirtum, we found a significant difference in the $\omega 3/\omega 6$ ratio between Rivers Ala-Koitaioki and Naaraioki (Tables 3 and 5).

No statistically significant differences were detected in Plecoptera species with respect to FA composition and content among the rivers.

3.4 FA composition and content of salmonids

Body size had a great influence on the FA composition of salmonids, with total body length explaining 24% of the differences in the FA composition (PERMANOVA, Pseudo- $F_{1.86} = 44.73$, p < 0.001).



NMDS1

FIGURE 2 Non-metric multidimensional scale (NMDS) ordination of the fatty acid (FA) composition of zoobenthos. Species are presented with different markers. Each river is represented by its own color. The ordination was based on Euclidean distance. FAs that correlate strongly (Pearson r > 0.6) with either of the axes are visualized with vectors. The 2D stress value for the ordination was 0.15. [Color figure can be viewed at wileyonlinelibrary.com]

ABLE 3	Mean percentage (%) and content (c, µg mg DW-1) of essential fatty acids (EFA), total fatty acid (FA) content (c, µg mg DW-1), and
o3/ω6 ratio v	vith standard deviations (±) of zoobenthos in rivers.

Species		River	ARA (%)	ARA (c)	EPA (%)	EPA (c)	Total FA (c)	w3/w6
Baetis rhodani		Ala-Koitajoki	2.8 ± 0.6	3.6 ± 0.3	12.3 ± 1.3	16.3 ± 3.6	131.4 ± 15.3	3.5 ± 0.0
		Hanhijoki	6.5	5.3	11.4	9.3	82.1	2.3
		Naarajoki	0.0	0.0	10.5	9.9	95.0	4.1
Cheumatopsyche lepid	a .	Ala-Koitajoki	3.5 ± 0.7	3.2 ± 1.0	14.3 ± 1.4	12.8 ± 2.3	90.2 ± 20.9	4.1 ± 0.5
		Naarajoki	5.4 ± 0.6	5.9 ± 0.6	12.6 ± 0.7	16.3 ± 0.4	129.1 ± 3.6	3.3 ± 0.1
Diura bicaudata		Kuusoja	8.7 ± 0.4	6.3 ± 0.6	11.6 ± 0.5	8.4 ± 1.1	72.0 ± 8.5	1.3 ± 0.0
		Naarajoki	5.6 ± 1.0	6.4 ± 1.0	9.5 ± 8.3	11.2 ± 9.7	115.0 ± 3.5	2.2 ± 0.5
	,	Venejoki	5.9 ± 0.2	6.1 ± 0.4	10.6 ± 0.1	11.0 ± 1.3	104.1 ± 11.4	1.2 ± 0.0
Habrophlebia lauta		Kalliojoki	6.4 ± 1.2	7.6 ± 4.3	4.8 ± 0.7	5.7 ± 3.1	114.2 ± 46.1	0.5 ± 0.0
		Kuusoja	5.1	8.4	5.4	8.9	165.7	0.8
	,	Venejoki	3.9	5.9	3.1	4.7	152.7	0.6
Heptagenia sulphurea		Ala-Koitajoki	6.82 ± 1.4^{b}	5.2 ± 2.0^{a}	8.7 ± 1.4	7.4 ± 2.2	89.7 ± 21.4	1.7 ± 0.3
		Hanhijoki	6.1	4.6	4.3	3.2	74.7	1.0
		Kalliojoki	10.7 ± 4.8 ^b	15.8 ± 3.2 ^b	2.7 ± 1.3	3.9 ± 1.0	165.2 ± 61.2	0.3 ± 0.0
		Kuusoja	4.7	7.9	4.8	8.0	166.6	1.2
		Naarajoki	2.9 ± 0.8 ^a	3.9 ± 0.9 ^a	3.3 ± 1.8	4.5 ± 2.3	136.6 ± 6.7	1.3 ± 0.1
		Venejoki	5.9 ± 0.2 ^b	6.8 ± 0.5 ^a	5.3 ± 0.8	6.0 ± 0.6	115.2 ± 11.5	0.9 ± 0.2
Hydropsyche newae		Ala-Koitajoki	3.6 ± 0.5	9.5 ± 2.1	9.2 ± 0.5	23.7 ± 3.2	256.2 ± 19.2	3.1 ± 0.2
		Naarajoki	2.9 ± 0.6	4.0 ± 0.3	10.4 ± 0.3	14.6 ± 1.6	140.8 ± 20.0	3.7 ± 0.1
Lepidostoma hirtum		Ala-Koitajoki	0.6 ± 0.5	0.7 ± 0.6	1.1 ± 1.0	1.5 ± 1.3	132.2 ± 3.4	9.1 ± 5.6
		Naarajoki	4.4 ± 0.3	5.0 ± 2.2	4.2 ± 1.7	4.4 ± 0.4	115.7 ± 57.4	1.2 ± 0.2
Leuctra hippopus		Ala-Koitajoki	8.9 ± 2.4	7.8 ± 0.5	9.1 ± 1.1	8.1 ± 0.7	89.7 ± 17.8	0.9 ± 0.1
	,	Venejoki	12.6	9.7	7.1	5.5	77.1	0.6
Nemoura flexuosa		Kuusoja	10.5 ± 2.3	17.5 ± 1.3	4.2 ± 0.2	7.2 ± 0.8	170.1 ± 26.0	0.9 ± 0.1
	,	Venejoki	7.8 ± 1.3	9.3 ± 1.3	3.3 ± 0.8	3.8 ± 0.3	121.3 ± 36.3	1.4 ± 0.0
Polycentropus flavoma	culatus	Ala-Koitajoki	6.1	6.7	14.2	15.7	110.0	2.2
		Kalliojoki	12.3 ± 1.2	18.5 ± 3.4	9.0 ± 0.7	13.7 ± 2.3	152.6 ± 32.5	0.7 ± 0.1
		Venejoki	5.7 ± 0.5	7.2 ± 0.5	10.8 ± 0.2	13.7 ± 0.1	126.8 ± 1.9	0.9 ± 0.1
Protonemura intricata		Hanhijoki	2.1 ± 2.9	2.0 ± 2.9	3.0 ± 0.3	2.6 ± 0.2	87.4 ± 15.3	1.2 ± 0.1
		Ulkkajoki	4.0 ± 0.7	4.2 ± 0.4	2.9 ± 0.6	3.1 ± 0.3	106.4 ± 9.7	1.1 ± 0.0

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Note: Values with statistically significant differences (p < 0.05) between each EFA, total FA content, and $\omega 3/\omega 6$ ratio between rivers have been highlighted and noted with letters.

Nevertheless, we found a statistically significant difference in the salmonid FA composition among the rivers (Pseudo- $F_{3.84} = 7.09$, p < 0.001) (Figure 3), with river identity explaining 22% of the variation. Taxon alone explained only 4% of the variation between the two salmonid species (Pseudo- $F_{1,86} = 2.88, p < 0.05$).

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There was a significant difference in the salmon FA composition among three of the study sites (Ala-Koitajoki, Naarajoki site in Lieksanjoki and Ruunaa site in Lieksanjoki) (PERMANOVA, Pseudo- $F_{3.84} = 16.683$, p < 0.001) (Figure 3). The essential FA DHA contributed to the differences in the salmon FA composition among these rivers (Table S7). Additionally, we found statistically significant differences in the FA composition between the two sites from River Ala-Koitajoki (Räväkkäkoski and Hiiskoski) (PERMANOVA, pair-wise test, t = 1.6204, p < 0.05). The FAs mostly responsible for the differences were DHA (16.1%), 12:0 (9.7%) and alpha-linolenic acid (ALA) (9.7%) (SIMPER, Table S7).

Salmon FA content differed statistically significantly among the rivers. There was a significant difference in the total FA content between Rivers Ala-Koitajoki and Naarajoki (Figure 3). In essential FA content, most of the differences were found between Rivers Ala-Koitajoki and Naarajoki, but we also found a significant difference in the ARA content and $\omega 3/\omega 6$ ratio between Rivers Ala-Koitajoki and Ruunaa (Tables 4 and 5).

In brown trout, statistically significant differences in FA composition were detected between Rivers Ala-Koitajoki and Kuusoja (PERMANOVA, pair-wise test, t = 5.43, p < 0.001). The FAs mostly responsible for the differences were DHA (22.5%), 16:0 (12.2%) and ALA (10.4%) (SIMPER, Table S7). Brown trout EFA composition

I ABLE 4 Mean percen salmonids in rivers.	tage (%) and content	(c, hg mg UW) of essential fatty	acids (EFAS), tot	al ratty acid (FA) co	ntent (c, µg mg UV	/v ⁻), and 0.3/00 rati	io with standard deviatio	ons (±) of
Species	River	ARA (%)	ARA (c)	EPA (%)	EPA (c)	DHA (%)	DHA (c)	Total FA (c)	თ 3/თ 6
Salmo salar m. sebago	Ala-Koitajoki	1.7 ± 0.4	1.80 ± 0.9^{a}	6.0 ± 1.5	6.50 ± 2.8^{a}	9.1 ± 5.0	8.50 ± 2.2^{a}	119.8 ± 64.9^{a}	6.5 ± 4.5^{a}
	Naarajoki	2.0 ± 0.3	$3.00 \pm 1.3^{\rm b}$	5.6 ± 0.7	8.50 ± 3.3 ^b	8.1 ± 2.4	11.50 ± 3.4^{b}	157.8 ± 66.8 ^b	$4.2 \pm 0.5^{a,b}$
	Ruunaa	1.6 ± 0.3	2.1 ± 1.3^{a}	5.4 ± 1.4	7.20 ± 4.3 ^{a,b}	9.4 ± 4.1	$10.90 \pm 5.0^{a,b}$	$150.2 \pm 108.7^{a,b}$	$3.7 \pm 1.0^{\rm b}$
Salmo trutta	Ala-Koitajoki	1.8 ± 0.4	2.90 ± 2.1	5.5 ± 0.9	9.00 ± 6.6	8.2 ± 2.5	11.90 ± 6.9	182.0 ± 173.3	4.8 ± 0.7
	Kuusoja	1.6 ± 0.7	0.80 ± 0.4	6.5 ± 1.8	3.40 ± 1.8	22.0 ± 8.6	9.70 ± 1.8	53.1 ± 28.4	10.7 ± 11.0
Mote: Walnes with statistically	cianificant difference	s (n < 0.05) hotw	aan aach EEA total	EA content and	3/a6 mile between	rivers have been h	whichted and noted w	with lattars	

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and content also differed statistically significantly between these rivers. There was also a significant difference in the total FA and EPA content, as well as the w3/w6 ratio and DHA percentage between these rivers (Tables 4 and 5). The total FA content, EFA composition and content, and $\omega 3/\omega 6$ ratio of salmonids in the study rivers are presented (Table 4).

Despite the small contribution of phylogeny to the FA composition of salmonids, we found a statistically significant difference between salmon and brown trout FA composition (PERMANOVA, Pseudo- $F_{1.86} = 5.95$, p < 0.005) in River Ala-Koitaioki (PERMANOVA, pair-wise test, t = 1.85, p < 0.01). The FAs were mostly responsible for the differences were DHA (14.8%), 12:0 (10.4%), and 16:0 (9.0%) (SIMPER).

DISCUSSION 4

Expectedly, zoobenthos communities differed among the study rivers with variation being explained mainly by water quality parameters related to water color and DOC concentration. There was intraspecific variation in the FA composition and content of certain EPT-taxa, irrespective of the measured environmental characteristics of their home river. Our results indicate that the availability of physiologically EFAs to salmonids is primarily regulated by the zoobenthos community structure, but also by the intraspecific variability of EFAs in zoobenthos. Importantly, we found differences in the FA composition and content of salmon and brown trout irrespective of the body size of the fish, indicating potential dietary differences between these species.

4.1 Zoobenthos community structure

Zoobenthos community structure is affected by local (river-specific), regional (species pool), and large-scale (e.g., climate, longitude, and latitude) factors (Sandin, 2009). Properties of the catchment area also play a role in determining zoobenthos community structure (Hämäläinen et al., 2007). The studied rivers were situated relatively close to each other, so the factors affecting the zoobenthos community structure were likely local rather than climatic. The zoobenthos communities were generally unique in each river, and the differences were mostly driven by differences in EPT-taxa abundances. Species of these taxa have different tolerances for multiple environmental conditions (Ficsor & Csabai, 2021; Smith et al., 2007), and they are, therefore, used as the key indicators in EU WFD-based ecological status classification.

Water quality parameters related to tOM loading mainly explained the zoobenthos community structure among the studied rivers. These rivers are dark in water color (ranging 110-190 mg L^{-1} Pt), which is typical for rivers in the study region (Rouvinen, 2010). Increased concentration of DOC can reduce the abundance and biodiversity of zoobenthos communities (Arzel et al., 2020; Brüsecke et al., 2022) but some taxa, such as mayfly

TABLE 5 Statistically significant (p < 0.05) test results for different FAs (individual EFAs, $\omega 3/\omega 6$ ratio, total FA) for individual zoobenthos and salmonid species.

•						
Species	FA	River	Mean	Df	р	Test
Heptagenia sulphurea	ARA (c)	Ala-Koitajoki	5.2 ± 2.0	1.9	<0.001	Bonferroni
		Kalliojoki	15.8 ± 3.2			
	ARA (c)	Kalliojoki	15.8 ± 3.2	1.3	<0.001	Bonferroni
		Naarajoki	3.9 ± 0.9			
	ARA (c)	Kalliojoki	15.8 ± 3.2	1.5	<0.001	Bonferroni
		Venejoki	6.8 ± 0.5			
	EPA (%)	Ala-Koitajoki	8.7 ± 1.4	1.8	<0.05	Bonferroni
		Naarajoki	3.3 ± 1.8			
	ARA (%)	Naarajoki	2.9 ± 0.8	1.4	<0.05	Kruskal-Wallis H
		Venejoki	5.9 ± 0.2			
	ARA (%)	Kalliojoki	10.7 ± 4.8	1.3	<0.01	Kruskal-Wallis H
		Naarajoki	2.9 ± 0.8			
	ARA (%)	Ala-Koitajoki	6.82 ± 1.4	1.8	<0.05	Kruskal-Wallis H
		Naarajoki	2.9 ± 0.8			
	ω3/ω6	Ala-Koitajoki	1.7 ± 0.3	1.9	<0.05	Kruskal-Wallis H
		Kalliojoki	0.3 ± 0.0			
Lepidostoma hirtum	ω3/ω6	Ala-Koitajoki	9.1 ± 5.6	1.3	<0.05	Kruskal-Wallis H
		Naarajoki	1.2 ± 0.2			
Polycentropus flavomaculatus	ARA (c)	Kalliojoki	18.5 ± 3.4	1.5	<0.001	Bonferroni
		Venejoki	7.2 ± 0.5			
Salmo salar m. sebago	ARA (c)	Ala-Koitajoki	1.80 ± 0.9	1.47	<0.001	Bonferroni
		Naarajoki	3.00 ± 1.3			
	ARA (c)	Naarajoki	3.00 ± 1.3	1.17	<0.05	Bonferroni
		Ruunaa	2.1 ± 1.3			
	EPA (c)	Ala-Koitajoki	6.50 ± 2.8	1.47	<0.001	Bonferroni
		Naarajoki	8.50 ± 3.3			
	DHA (c)	Ala-Koitajoki	8.50 ± 2.2	1.47	<0.001	Bonferroni
		Naarajoki	11.50 ± 3.4			
	ω3/ω6	Ala-Koitajoki	6.5 ± 4.5	1.46	<0.001	Kruskal-Wallis H
		Ruunaa	3.7 ± 1.0			
	Total FA	Ala-Koitajoki	119.8 ± 64.9	1.47	<0.001	Bonferroni
		Naarajoki	157.8 ± 66.8			
Salmo trutta	EPA (c)	Ala-Koitajoki	9.00 ± 6.6	1.28	<0.05	Bonferroni
		Kuusoja	3.40 ± 1.8			
	DHA (%)	Ala-Koitajoki	8.2 ± 2.5	1.28	<0.001	Kruskal-Wallis H
		Kuusoja	22.0 ± 8.6			
	ω3/ω6	Ala-Koitajoki	4.8 ± 0.7	1.28	< 0.005	Kruskal-Wallis H
		Kuusoja	10.7 ± 11.0			
	Total FA	Ala-Koitajoki	182.0 ± 173.3	1.28	<0.05	Bonferroni
		Kuusoja	53.1 ± 28.4			

Note: Mean values and standard deviations (±) for FAs have been given (% = percentage of total FAs, c = FA content [µg/mg DW⁻¹]). Statistical tests with degrees of freedom (df) and statistical significance (*p*) are also shown.

Baetis and Chironomidae might even benefit from it (Bellamy et al., 2019; Robbins et al., 2020). The concentration of DOC (especially humic matter) also decreases the pH (Oliver et al., 1983), which

has been found to drive the taxonomical diversity of zoobenthos communities, together with nutrient availability (Baker et al., 2022; Heino et al., 2003). Similarly to our observation on river benthos, terrestrial

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FIGURE 3 Non-metric multidimensional scale (NMDS) ordination of the fatty acid (FA) composition of salmonids. Species are presented with different markers. Each river is represented by its own color. The ordination was based on Euclidean distance. FAs that correlate strongly (Pearson *r* > 0.7) with either of the axes are visualized with vectors. The 2D stress value for the ordination was 0.09. [Color figure can be viewed at wileyonlinelibrary.com]

DOC also contributes to the differences in the zoobenthos community structure among boreal lakes (Kesti et al., 2021; Strandberg et al., 2023).

In addition to tOM loading, characteristics of riverbed substratum (bottom material) explained zoobenthos community structure among the studied rivers. Diverse riverbed substrata support zoobenthos diversity (Huttunen et al., 2022); particularly many hydropsychids prefer specific substrata (Ficsor & Csabai, 2021). Aquatic macrophytes offer suitable microhabitats for several zoobenthos taxa, and macrophyte coverage can greatly influence the zoobenthos community structure (Huttunen et al., 2017). They also provide attachment sites for net-spinning zoobenthos taxa (Richardson & Clifford, 1986). Particularly water mosses are important hiding places for many key invertebrates and are thus central in river restoration (Korsu, 2004; Muotka & Laasonen, 2002). In the site Hiiskoski in River Ala-Koitajoki, water mosses were transplanted in 2018 as a part of the restoration. However, it can take several years for the moss-planting to influence the zoobenthos community structure (Hynninen & Vehanen, 2022). Therefore, the moss-transplantations were likely too recent to produce a clear impact on zoobenthos community structure in site Hiiskoski.

Only two rivers (Koitajoki and Kuusoja) showed changes in the zoobenthos community structure related to the time from restoration. In Koitajoki, the changes in the community structure were mostly related to the increased proportion of the caddisfly *Hydropsyche* and the decreased proportion of Chironomidae. In River Kuusoja, the changes included several other taxa, but the changes were not clearly indicative of improving diversity. Due to the lack of proper reference sites for the past restorations, these results should be treated with caution as they could reflect overall land use and climatic changes or

other temporal changes in these rivers. The interpretation is further hampered by the lack of pre-restoration data for the rivers.

In general, river restoration includes the addition of gravel and boulders to the riverbed (Louhi et al., 2011; Luhta et al., 2012), which creates new bottom substrata and alters the flow regime of the river. These procedures usually decrease water velocity (Marttila et al., 2016), which could affect the zoobenthos community structure. The addition of gravel and boulders could benefit different EPT-taxa by providing them with new microhabitats. Improvement of water quality, especially the rising pH, has also been reported as beneficial for hydropsychids (Ficsor & Csabai, 2021). Sasaki et al. (2005) found that an increased concentration of nutrients and organic matter might also be beneficial for hydropsychids. Elevated levels of phosphorous and nitrogen, however, are harmful to less tolerant zoobenthos (Smith et al., 2007).

Large proportions of Chironomidae and mollusk Lymnaeidae (Gastropoda) are usually indicative of degraded environmental conditions (Nascimento et al., 2018; Scholl et al., 2016). Thus, their decreased proportion in River Koitajoki (Chironomidae) and River Kuusoja (Lymnaeidae) following restoration could indicate improved ecological status of the river ecosystems. Supporting our findings, some studies have shown that river restoration might decrease the relative abundance of Chironomidae in the zoobenthos community (Al-Zankana et al., 2021; Pilotto et al., 2018).

4.2 | FA composition and content of zoobenthos

Taxon and river in combination explained less of the differences in zoobenthos FA composition than taxon alone. This supports the

previously observed, strong contribution of phylogeny to the zoobenthos FA composition (Lau et al., 2012, 2013; Makhutova et al., 2011, 2016; Sushchik et al., 2003; Vesterinen et al., 2021). Despite the strong control of phylogeny, we found significant riverand even site-specific differences in the FA composition and content of certain EPT-taxa.

We found biomarker FAs indicative of diatoms, bacteria, and tOM within the Ephemeroptera taxa. Especially mayfly H. sulphurea FA composition and content differed significantly among the study rivers. Heptagenia are grazers, feeding on periphyton (Merritt & Cummins, 1984). The differences in their FA composition among the rivers indicate that the periphyton composition and/or quality could differ among the study sites. Yet, it should be noted that many zoobenthos taxa, despite their associated feeding guilds, can be considered opportunists (Tierno de Figueroa et al., 2019). The FA profiles of scrapers may strongly correlate with the physical variables of the watershed. Specifically, PUFAs are positively associated with canopy cover, whereas saturated FAs (SAFAs) are negatively correlated with increased canopy cover (Wang et al., 2022). Also, we found in a previous study (Kesti et al., 2021) that shore type affected the FA composition of Heptagenia. These findings indicate that Heptagenia are generalists.

We found biomarker FAs indicative of diatoms, bacteria, and tOM also in Trichoptera taxa. Cashman et al. (2016) found high autochthonous signatures from the FA composition of Trichoptera, but some evidence suggests that site characteristics might also affect the FA composition of *Hydropsyche* (Cashman et al., 2016). Even though many hydropsychids are classified as filter-feeders (Cummins, 1973), there is evidence that they also practice selective feeding and omnivory (Basaguren et al., 2002; Ficsor & Csabai, 2021; Hellmann et al., 2013; Torres-Ruiz & Wehr, 2020). Previous study has documented high levels of 12:0 and 18:1 ω 9 and low levels of 16:1 ω 7 and EPA in Hydropsychidae, which may indicate a high contribution of allochthonous detritus in their diet (Descroix et al., 2010). Our results indicate both autochthonous and allochthonous resource utilization in the documented Trichoptera taxa.

There was one significant exception among the hydropsychids in their FA composition. The FA composition of Hydropsyche newae did not differ between Rivers Ala-Koitajoki and Naarajoki, despite the difference in the latitude between the two rivers. Unfortunately, we could not acquire physico-chemical data from River Naarajoki, so we cannot say if the physico-chemical characteristics were similar between these two rivers. This is worth discussing since it has been reported that the members of Hydropsychidae have very limited abilities to synthesize and modify their dietary FAs (Torres-Ruiz et al., 2010). This would indicate that the food sources were similar between these two rivers. Thus, it was even more interesting to find differences in the FA composition of H. angustipennis between the two sites in River Ala-Koitajoki (Hiiskoski and Räväkkäkoski). These differences in the FA composition could indicate differences in their diet between the two sites. Hiiskoski, right below the upstream Lake Koitere, has been restored and aquatic mosses have been transplanted onto the site (Hynninen & Vehanen, 2022). In Hydropsyche,

ARA has been reported to originate from aquatic mosses (Torres-Ruiz & Wehr, 2020). Recent studies have also indicated that aquatic mosses can be an important food source for certain invertebrates (Kalachova et al., 2011; Labed-Veydert et al., 2021) and might influence the FA composition of their consumers. In the case of Hiiskoski, the differences may also be explained by the proximity of the lake and outlet effect, affecting the hydropsychids in Hiiskoski more than the hydropsychids in the downstream Räväkkäkoski.

There was a significant difference in the $\omega 3/\omega 6$ ratio in caddisfly *L. hirtum* between Rivers Ala-Koitajoki and Naarajoki. The $\omega 3/\omega 6$ ratio was exceptionally high in River Ala-Koitajoki which indicates strong utilization of autochthonous resources (Guo et al., 2016; Torres-Ruiz et al., 2007). *L. hirtum* is classified as a shredder (Azevedo-Pereira et al., 2006), but it has been shown to display detritivory, utilizing fine and coarse detritus (Basaguren et al., 2002). Unfortunately, we did not have data on the river characteristics of extensively restored River Naarajoki, but River Ala-Koitajoki had only little (0–5%) fine and coarse detritus, which could contribute to the differences in *L. hirtum* $\omega 3/\omega 6$ ratio between the rivers.

Polycentropus are carnivorous. net-spinning caddisflies (Philipson, 2010). We found statistically significant differences in P. flavomaculatus FA composition between Rivers Kallioioki and Venejoki, which did not differ in their zoobenthos community structure. Therefore, we assume that the food sources utilized by their prev items differ between these two rivers. However, as we have no information on the FA composition of their prey items, the differences in the P. flavomaculatus FA composition between these rivers cannot be attributed to a known source in this study. As mentioned above, Hydropsyche have very little ability to modify their dietary FAs (Torres-Ruiz et al., 2010), but to the best of our knowledge, there are no studies regarding Polycentropus on this matter.

We did not find any statistically significant differences in the FA composition and content of Plecoptera taxa among the rivers. Most of the Plecoptera species in this study were classified as shredders (*L. hippopus*, *N. flexuosa*, and *P. intricata*) (Cummins, 1973), except *D. bicaudata*, which is a predatory stonefly (Huhta et al., 1999). This would indicate that the food sources utilized by different Plecoptera taxa were similar among the study rivers.

4.3 | FA composition and content of salmonids

The FA composition of salmonids was affected more by the river identity than phylogeny. Juvenile salmon and brown trout inhabit slightly different microhabitats with salmon preferring higher water velocity than trout, which could have been predicted to cause diet-related differences in their FA composition. However, total body length had a significant impact on the FA composition suggesting significant ontogenetic niche shifts or alternatively could be caused by selective FA retention/metabolization. In the Great Lakes, length, together with condition factor/muscle lipid content, were found to be significant predictors for muscle FA composition in different fish species, including salmonids (Arnillas et al., 2023). Contrary to our results, Naesje et al. (2006) found no differences in the total lipid content between juvenile salmonid cohorts, when differences in fish body mass were considered. As juvenile salmonids grow, the content of monounsaturated FAs (MUFAs) decreases and the content of EPA and DHA increases (Murzina et al., 2016; Nemova et al., 2015). Consistently, the proportion of DHA in brown trout from River Kuusoja was higher than elsewhere.

Despite the greater influence of length on the FA composition of salmonids, we found small differences in the FA composition and content among the rivers, sites, and species. Based on the results, we can predict that the differences in the FA composition and content of salmonids among the rivers can be attributed to the differences in both the community structure and FA composition and content of zoobenthos among the rivers. Food quality can influence the growth rate of salmonids (Berge et al., 2009) so changes in the quality of zoobenthos could potentially impact salmonid populations in ecologically relevant ways. Also, salmonids with higher total FA content show better winter survival rates and improved swimming performance (Litz et al., 2017). Hence, differences in the community structure and/or the FA composition and content of zoobenthos might influence salmonid recruitment and parr survival.

Unfortunately, the salmonid samples from the Ruunaa site in River Lieksanjoki were collected from locations with no zoobenthos sampling. Thus, we cannot assess how the community composition and/or the FA composition and content of zoobenthos in Ruunaa affect salmonids in this area. Ruunaa is situated upstream from Naarajoki site in the same River Lieksanjoki system so their water quality and zoobenthos community compositions could largely resemble each other. Supporting this, the differences in the EFA percentage and content in salmonids were very small between Naarajoki and Ruunaa.

The amount of DHA was very low in the studied zoobenthos taxa. Most freshwater insect larvae completely lack or have very low levels of DHA (Guo et al., 2016). Salmonids, however, can elongate and desaturate long-chain PUFAs from their shorter-chain analogs (Murzina et al., 2016; Nemova et al., 2015; Tocher, 2003). Despite the low levels of DHA in the zoobenthos taxa in this study, juvenile salmonids could satisfy their nutritional demand by consuming zoobenthos taxa abundant in its shorter chain analogs ALA and EPA (Vesterinen et al., 2021). Changes in the ALA and EPA composition and content could, thus, affect the DHA composition and content of salmonids, which could explain some of the observed differences in the FA composition and content of salmonids between the rivers. Also, environmental changes can affect the food items available for salmonids. High water temperature and low current speed are favorable for the mass reproduction of terrestrial insects, in which shortchain PUFAs are more characteristic (Nemova et al., 2015). Browning of waters may also affect the foraging behavior and negatively impact the growth rate of visually foraging fish (van Dorst et al., 2020), so increased DOC might negatively affect salmonids. Future research questions should be pointed toward examining, how rivers with clear differences in water quality (especially in DOC concentration) affect the FA composition of salmonids.

5 | CONCLUSIONS

Despite the strong control of phylogeny on the FA composition of zoobenthos, differences in the FA composition and content of certain EPT-taxa were identified among the rivers and between the sites. Especially mayfly H. sulphurea appeared to respond to local conditions suggesting that Heptagenia are generalists whose FA characteristics could be used as biomarkers of environmental quality. Using the publicly available environmental data, we observed temporal changes in the zoobenthos communities in Rivers Koitajoki and Kuusoja. The changes, whether resulting from river restorations or other environmental trends, could cascade to changes in the FA content and concentration of salmonids in these rivers. This opens a whole new research field: whether the quality of zoobenthos has an ecological effect on the recruitment of salmonids beyond the quantity of available prey. Due to the lack of diet data for the fish, we cannot link the environmental variables with FAs in salmonids, but future experimental studies could resolve this potentially important question in conservation physiology.

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DATA AVAILABILITY STATEMENT

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

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REFERENCES

- Aaltonen, H., Tuukkanen, T., Palviainen, M., Laurén, A., Tattari, S., Piirainen, S., Mattson, T., Ojala, A., Launiainen, S., & Finér, L. (2021). Controls of organic carbon and nutrient export from unmanaged and managed boreal forested catchments. *Water*, 13, 2363. https://doi. org/10.3390/w13172363
- Ahlgren, G., Vrede, T., & Goedkoop, W. (2009). Fatty acid ratios in freshwater fish, zooplankton and zoobenthos-are there specific optima? In

¹⁴ WILEY-

M. Arts, M. Brett, & M. Kainz (Eds.), *Lipids in aquatic ecosystems* (pp. 147–178). Springer.

- Albertson, L., Cardinale, B., Zeug, S., Harrison, L., Lenihan, H., & Wydzga, M. (2011). Impacts of channel reconstruction on invertebrate assemblages in a restored river. *Restoration Ecology*, 19, 627–638.
- Albrecht, E., Lukkarinen, J., Hakkarainen, M., & Soininen, N. (2023). Hydropowering sustainability transformation: policy frames on river use and restoration in Finland. *Fennia - International Journal of Geography*, 201, 47–64.
- Al-Zankana, A., Matheson, T., & Harper, D. (2021). Secondary production of macroinvertebrates as indicators of success in stream rehabilitation. *River Research and Applications*, 37, 408–422.
- Arnillas, C. A., Abedi, R., Parzanini, C., Strandberg, U., Arts, M. T., Bhavsar, S. P., & Arhonditsis, G. B. (2023). Intra-specific correlations between fatty acids and morphological traits are consistent across fish species. *Journal of Great Lakes Research*, 49, 821–835.
- Arzel, C., Nummi, P., Arvola, L., Pöysä, H., Davranche, A., Rask, M., Olin, M., Holopainen, S., Viitala, R., Einola, E., & Manninen-Johansen, S. (2020). Invertebrates are declining in boreal aquatic habitat: The effect of brownification? *Science of the Total Environment*, 72, 138199. https://doi.org/10.1016/j.scitotenv.2020.138199
- Azevedo-Pereira, H., Graca, M., & Gonzalez, J. (2006). Life history of *Lepi-dostoma hirtum* in an Iberian stream and its role in organic matter processing. *Hydrobiologia*, 559, 183–192.
- Baker, N., Welti, E., Pilotto, F., Jourdan, J., Beudert, B., Huttunen, K., Muotka, T., Paavola, R., Göthe, E., & Haase, P. (2022). Seasonal and spatial variation of stream macroinvertebrate taxonomic and functional diversity across three boreal regions. *Insect Conservation and Diversity.*, 16, 266–284. https://doi.org/10.1111/icad.12623
- Basaguren, A., Riano, P., & Pozo, J. (2002). Life history patterns and dietary changes of several caddisfly (Trichoptera) species in a northern Spain stream. Archiv für Hydrobiologie, 155, 23–41.
- Bellamy, A., Bauer, J., & Grottoli, A. (2019). Contributions of autochthonous, allochthonous, and aged carbon and organic matter to macroinvertebrate nutrition in the Susquehanna River basin. *Freshwater Science*, 38, 616–628. https://doi.org/10.1086/705017
- Berge, G., Witten, P., Baeverfjord, G., Vegusdal, A., Wadsworth, S., & Ruyter, B. (2009). Diets with different n–6/n–3 fatty acid ratio in diets for juvenile Atlantic salmon, effects on growth, body composition, bone development and eicosanoid production. *Aquaculture*, 296, 299–308.
- Brüsecke, J., Muotka, T., Huttunen, K., Litjo, S., Lepo, W., & Jyväsjärvi, J. (2022). Drainage-induced browning causes both loss and change of benthic biodiversity in headwater streams. *Limnology and Oceanography Letters*, 8, 620–627. https://doi.org/10.1002/lol2.10302
- Cashman, M., Pilotto, F., Harvey, G., Wharton, G., & Pusch, M. (2016). Combined stable-isotope and fatty-acid analyses demonstrate that large wood increases the autochthonous trophic base of a macroinvertebrate assemblage. *Freshwater Biology*, *61*, 549–564.
- Clarke, K. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18, 117–143.
- Cook, H., & McMaster, C. R. (2002). Chapter 7 fatty acid desaturation and chain elongation in eukaryotes. New Comprehensive Biochemistry, 36, 181–204.
- Cummins, K. W. (1973). Trophic relations of aquatic insects. Annual Review of Entomology, 18, 183–206.
- de Wit, H., Valinia, S., Weyhenmyer, G., Futter, M., Kortelainen, P., Austens, K., ... Vuorenmaa, J. (2016). Current browning of surface waters will be further promoted by wetter climate. *Environmental Science and Technology Letters*, 3, 430–435.
- Descroix, A., Bec, A., Bourdier, G., Sargos, D., Sauvanet, J., Mission, B., & Desvilettes, C. (2010). Fatty acids as biomarkers to indicate main carbon sources of four major invertebrate families in a large river (the Allier, France). Fundamental and Applied Limnology, 177, 39–55.

- dos Reis Oliveira, P., Kraak, M., Verdonschot, P., & Verdonschot, R. (2019). Lowland stream restoration by sand addition: Impact, recovery, and beneficial effects on benthic invertebrates. *River Research and Applications*, 35, 1023–1033.
- Ficsor, M., & Csabai, Z. (2021). Longitudinal zonation of larval Hydropsyche (Trichoptera: Hydropsychidae): Abiotic environmental factors and biotic interactions behind the downstream sequence of central European species. *Hydrobiologia*, 848, 3371–3388.
- Folch, J., Lees, M., & Sloane Stanley, G. (1957). A simple method for the isolation and purification of total lipids from animal tissues. *The Journal* of *Biological Chemistry*, 226, 497–509.
- Glencross, B. (2009). Exploring the nutritional demand for essential fatty acids by aquaculture species. *Reviews in Aquaculture*, 1, 71–124.
- Guo, F., Bunn, S., Brett, M., Fry, B., Hager, H., Ouyang, X., & Kainz, M. (2018). Feeding strategies for the acquisition of high-quality food sources in stream macroinvertebrates: Collecting, integrating, and mixed feeding. *Limnology and Oceanography*, *63*, 1964–1978.
- Guo, F., Kainz, M., Sheldon, F., & Bunn, S. (2016). The importance of highquality algal food sources in stream food webs—Current status and future perspectives. *Freshwater Biology*, *61*, 815–831.
- Hämäläinen, H., Aroviita, J., Koskenniemi, E., Bonde, A., & Kotanen, J. (2007). Suomen jokien tyypittelyn kehittäminen ja pohjaeläimiin perustuva ekologinen luokittelu. Länsi-Suomen ympäristökeskuksen Raportteja, 4, 1–66. (In Finnish).
- Heino, J., Muotka, T., & Paavola, R. (2003). Determinants of macroinvertebrate diversity in headwater streams: Regional and local influences. *Journal of Animal Ecology*, 72, 425–434.
- Hellmann, C., Wissel, B., & Winkelmann, C. (2013). Omnivores as seasonally important predators in a stream food web. *Freshwater Science*, 32, 548–562.
- Hixson, S., Sharma, B., Kainz, M., Wacker, A., & Arts, M. (2015). Production, distribution, and abundance of long-chain omega-3 polyunsaturated fatty acids: A fundamental dichotomy between freshwater and terrestrial ecosystems. *Environmental Reviews.*, 23, 414–424. https:// doi.org/10.1139/er-2015-0029
- Huhta, A., Muotka, T., Juntunen, A., & Yrjonen, M. (1999). Behavioural interactions in stream food webs: The case of drift-feeding fish, predatory invertebrates and grazing mayflies. *The Journal of Animal Ecology*, *68*, 917–927.
- Huttunen, K., Mykrä, H., Oksanen, J., Astorga, A., Paavola, R., & Muotka, T. (2017). Habitat connectivity and in-stream vegetation control temporal variability of benthic invertebrate communities. *Scientific Reports*, 7, 1448. https://doi.org/10.1038/s41598-017-00550-9
- Huttunen, K., Väisänen, L., Paavola, R., & Muotka, T. (2022). Partitioning of benthic biodiversity in boreal streams: Contributions of spatial, interannual, and seasonal variability. *Freshwater Biology*, 67, 774–783.
- Hynninen, M., & Vehanen, T. (2022). Stream restorations and their impacts for trout and salmon in FRESHABIT LIFE IP-projects. Natural resources and bioeconomy studies 45/2022 (p. 34). Natural Resources Institute Finland.
- Jutila, E. (1992). Restoration of salmonid rivers in Finland. In P. Boon, P. Calow, & G. Petts (Eds.), *River conservation and management* (pp. 353–362). John Wiley & Sons Ltd.
- Kalachova, G., Gladyshev, M., Sushchik, N., & Makhutova, O. (2011). Water moss as a food item of the zoobenthos in the Yenisei River. Open Life Sciences, 6, 236–245.
- Kesti, P., Hiltunen, M., Strandberg, U., Vesterinen, J., Taipale, S., & Kankaala, P. (2021). Lake browning impacts community structure and essential fatty acid content of littoral invertebrates in boreal lakes. *Hydrobiologia*, 849, 967–984. https://doi.org/10.1007/s10750-021-04760-1
- Khrennikov, V., Baryshev, I., Shustov, Y., Pavlov, V., & Ilmast, N. (2007). Zoobenthos of salmon rivers in the Kola Peninsula and Karelia (north east Fennoscandia). *Ecohydrology and Hydrobiology*, 7, 71–77.

- Kil, H., & Bae, Y. (2012). Effects of low-head dam removal on benthic macroinvertebrate communities in a Korean stream. *Animal Cells and Systems*, 16, 69–76.
- Korsu, K. (2004). Response of benthic invertebrates to disturbance from stream restoration: The importance of bryophytes. *Hydrobiologia*, 523, 37–45.
- Kris-Etherton, P., Harris, W., & Appel, L. (2002). Fish consumption, fish oil, omega-3 fatty acids, and cardiovascular disease. *Circulation*, 106, 2747–2757. https://doi.org/10.1161/01.CIR.0000038493.65177.94
- Labed-Veydert, T., Koussoroplis, A., Bec, A., & Desvilettes, C. (2021). Early spring food resources and the trophic structure of macroinvertebrates in a small headwater stream as revealed by bulk and fatty acid stable isotope analysis. *Hydrobiologia*, 848, 5147–5167.
- Lau, D., Goedkoop, W., & Vrede, T. (2013). Cross-ecosystem differences in lipid composition and growth limitation of a benthic generalist consumer. *Limnology and Oceanography*, 58, 1149–1164.
- Lau, D., Vrede, T., Pickova, J., & Goedkoop, W. (2012). Fatty acid composition of consumers in boreal lakes–Variation across species, space and time. *Freshwater Biology*, 57, 24–38.
- Laudon, H., Hedtjärn, J., Schelker, J., Bishop, K., Sørensen, R., & Ågren, A. (2009). Response of dissolved organic carbon following forest harvesting in a boreal forest. AMBIO: A Journal of the Human Environment, 38, 381–386.
- Lepistö, A., Räike, A., Sallantaus, T., & Finér, L. (2021). Increases in organic carbon and nitrogen concentrations in boreal forested catchments— Changes driven by climate and deposition. *Science of the Total Environment*, 780, 146627. https://doi.org/10.1016/j.scitotenv.2021.146627
- Litz, M., Miller, J., Copeman, L., & Hurst, T. (2017). Effects of dietary fatty acids on juvenile salmon growth, biochemistry, and aerobic performance: A laboratory rearing experiment. *Journal of Experimental Marine Biology and Ecology*, 494, 20–31.
- Louhi, P., Mykrä, H., Paavola, R., Huusko, A., Vehanen, T., Mäki-Petäys, A., & Muotka, T. (2011). Twenty years of stream restoration in Finland: Little response by benthic macroinvertebrate communities. *Ecological Applications*, 21, 1950–1961.
- Louhi, P., Vehanen, T., Huusko, A., Mäki-Petäys, A., & Muotka, T. (2016). Long-term monitoring reveals the success of salmonid habitat restoration. *Canadian Journal of Fisheries and Aquatic Sciences*, 73, 1733– 1741.
- Luhta, P., Huusko, A., & Louhi, P. (2012). Re-building brown trout populations in dredged boreal forest streams: In-stream restoration combined with stocking of young trout. *Freshwater Biology*, 57, 1966–1977.
- Makhutova, O., Shulepina, S., Sharapova, T., Dubovskaya, O., Sushchik, N., Baturina, M., Pryanichnikova, E. G., Kalachova, G. S., & Gladyshev, M. (2016). Content of polyunsaturated fatty acids essential for fish nutrition in zoobenthos species. *Freshwater Science*, 35, 1222–1234.
- Makhutova, O., Sushchik, N., Gladyshev, M., Ageev, A., Pryanichnikova, E., & Kalachova, G. (2011). Is the fatty acid composition of freshwater zoobenthic invertebrates controlled by phylogenetic or trophic factors? *Lipids*, 46, 709–721.
- Marttila, M., Louhi, P., Huusko, A., Mäki-Petäys, A., Yrjänä, T., & Muotka, T. (2016). Long- term performance of in-stream restoration measures in boreal streams. *Ecohydrology*, *9*, 280–289.
- Marttila, M., Louhi, P., Huusko, A., Vehanen, T., Mäki-Petäys, A., Erkinaro, J., ... Muotka, T. (2019). Synthesis of habitat restoration impacts on young-of-the-year salmonids in boreal rivers. *Reviews in Fish Biology and Fisheries*, 29, 513–527.
- Merritt, R., & Cummins, K. (1984). An introduction to the aquatic insects of North America (2nd ed.). Kendall/Hunt.
- Molina-Moctezuma, A., Ellis, E., Kapuscinski, K., Roseman, E., Heatlie, T., & Moerke, A. (2021). Restoration of rapids habitat in a Great Lakes connecting channel, the St. Marys River, Michigan. *Restoration Ecology*, 29, e13310. https://doi.org/10.1111/rec.13310
- Monteith, D., Stoddard, J., Evans, C., de Wit, H., Forsius, M., Hogasen, T., Wilander, A., Skjelkvåle, B., Jeffries, D., Vuorenmaa, J., Keller, B.,

Kopacek, J., & Vesely, J. (2007). Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature* 450, 537-540.

- Muotka, T., & Laasonen, P. (2002). Ecosystem recovery in restored headwater streams: The role of enhanced leaf retention. *Journal of Applied Ecology*, 39, 145–156.
- Muotka, T., Paavola, R., Haapala, A., Novikmec, M., & Laasonen, P. (2002). Long-term recovery of stream habitat structure and benthic invertebrate communities from in-stream restoration. *Biological Conservation*, 105, 243–253.
- Murzina, S., Nefedova, Z., Pekkoeva, S., Veselov, A., Efremov, D., & Nemova, N. (2016). Age- specific lipid and fatty acid profiles of Atlantic salmon juveniles in the Varzuga river. *International Journal* of Molecular Sciences, 17, 1050. https://doi.org/10.3390/ ijms17071050
- Naesje, T., Thorstad, E., Forseth, T., Aursand, M., Saksgård, R., & Finstad, A. (2006). Lipid class content as an indicator of critical periods for survival in juvenile Atlantic salmon (*Salmo salar*). Ecology of Freshwater Fish, 15, 572–577.
- Nascimento, A., Alves-Martins, F., & Jacobucci, G. (2018). Assessment of ecological water quality along a rural to urban land use gradient using benthic macroinvertebrate-based indexes. *Bioscience Journal*, 34, 194–209.
- Nemova, N., Nefedova, Z., Murzina, S., Veselov, A., Ripatti, P., & Pavlov, D. (2015). The effect of environmental conditions on the dynamics of fatty acids in juveniles of the Atlantic Salmon (*Salmo salar L.*). *Russian Journal of Ecology*, 46, 267–271.
- Nieminen, M., Koskinen, M., Sarkkola, S., Láuren, A., Kaila, A., Kiikkilä, O., Nieminen, T. M., & Ukonmaanaho, L. (2015). Dissolved organic carbon export from harvested peatland forests with differing site characteristics. *Water Air Soil Pollution*, 226, 181. https://doi.org/10.1007/ s11270-015-2444-0
- Oliver, B., Thurman, E., & Malcolm, R. (1983). The contribution of humic substances to the acidity of colored natural waters. *Geochimica et Cosmochimica Acta*, 47, 2031–2035. https://doi.org/10.1016/0016-7037 (83)90218-1
- Peltomaa, E., Aalto, S., Vuorio, K., & Taipale, S. (2017). The importance of phytoplankton biomolecule availability for secondary production. Frontiers in Ecology and Evolution., 5, 128. https://doi.org/10.3389/fevo. 2017.00128
- Philipson, G. (2010). The effect of water flow and oxygen concentration on six species of caddis fly (Trichoptera) larvae. Proceedings of the Zoological Society of London, 124, 547–564.
- Pilotto, F., Nilsson, C., Polvi, L., & McKie, B. (2018). First signs of macroinvertebrate recovery following enhanced restoration of boreal streams used for timber floating. *Ecological Applications*, 28, 587–597.
- Rääpysjärvi, J., Karjalainen, S., Karttunen, K., Kuoppala, M., & Aroviita, J. (2016). Metsätalouden vaikutukset purojen ja jokien biologiseen tilaan-MEBI-hankkeen tulokset. Suomen Ympäristökeskuksen Raportteja, 20, 32. (In Finnish).
- Regerand, T., Nefedova, Z., Toivonen, L., Dubrovina, L., Vuori, K., Markova, L., & Ruokolainen, T. (2002). Lipid metabolism of caddisfly larvae at low pH. *Russian Journal of Developmental Biology*, 33, 236-241.
- Richardson, J., & Clifford, H. (1986). Phenology and ecology of some trichoptera in a low-gradient boreal stream. *Journal of the North American Benthological Society*, 5, 191–199.
- Robbins, C., Yeager, A., Cook, S., Doyle, R., Maurer, J., Walker, C., Back, J. A., Whigham, D. F., & King, R. (2020). Low-level dissolved organic carbon subsidies drive a trophic upsurge in a boreal stream. *Freshwater Biology*, 65, 920–934.
- Rouvinen, J. (2010). Pohjois-Karjalan kalataloudellinen kunnostusohjelma vuosille 2011-2015. ELY-keskus, 133. (In Finnish).
- Sandin, L. (2009). The effects of catchment land-use, near-stream vegetation, and river hydromorphology on benthic macroinvertebrate

¹⁶ ↓ WILEY-

communities in a south-Swedish catchment. Fundamental and Applied Limnology, 174, 75–87.

- Sasaki, A., Ito, A., Aizawa, J., & Umita, T. (2005). Influence of water and sediment quality on benthic biota in an acidified river. Water Research (Oxford), 39, 2517–2526.
- Scholl, E., Rantala, H., Whiles, M., & Wilkerson, G. (2016). Influence of flow on community structure and production of snag-dwelling macroinvertebrates in an impaired low-Gradient river. *River Research and Applications*, 32, 677–688.
- Shustov, Y., Baryshev, I., & Belyakova, E. (2012). Specific features of the feeding of juvenile Atlantic salmon (*Salmo salar* L.) in the subarctic varzuga river and its small tributaries (Kola Peninsula). *Inland Water Biol*ogy, 5, 288–292.
- Smith, A., Bode, R., & Kleppel, G. (2007). A nutrient biotic index (NBI) for use with benthic macroinvertebrate communities. *Ecological Indicators*, 7, 371–386.
- Smith, R., Neideigh, E., Rittle, A., & Wallace, J. (2020). Assessing macroinvertebrate community response to restoration of Big Spring Run: Expanded analysis of before-after- control-impact sampling designs. *River Research and Applications*, 36, 79–90.
- Strandberg, U., Arhonditsis, G., Kesti, P., Vesterinen, J., Vesamäki, J., Taipale, S., & Kankaala, P. (2023). Environmental drivers alter PUFA content in littoral invertebrate assemblages via changes in richness and abundance. *Aquatic Sciences*, 85, 100.
- Suurkuukka, H., Virtanen, R., Suorsa, V., Soininen, J., Paasivirta, L., & Muotka, T. (2014). Woodland key habitats and stream biodiversity: Does small-scale terrestrial conservation enhance the protection of stream biota?. *Biological Conservation* 170, 10–19.
- Sushchik, N., Gladyshev, M., Moskvichova, A., Makhutova, O., & Kalachova, G. (2003). Comparison of fatty acid composition in major lipid classes of the dominant benthic invertebrates of the Yenisei River. Comparative Biochemistry and Physiology, Part B: Biochemistry and Molecular Biology, 134, 111–122.
- Taipale, S., Peltomaa, E., Hiltunen, M., Jones, R., Hahn, M., Biasi, C., & Brett, M. (2015). Inferring phytoplankton, terrestrial plant and bacteria bulk δ¹³C values from compound specific analyses of lipids and fatty acids. *PLoS ONE*, 10(7), e0133974. https://doi.org/10.1371/journal. pone.0133974
- Taipale, S., Vuorio, K., Strandberg, U., Kahilainen, K., Järvinen, M., Hiltunen, M., Peltomaa, E., & Kankaala, P. (2016). Lake eutrophication and brownification downgrade availability and transfer of essential fatty acids for human consumption. *Environment International*, 96, 156–166.
- Tetu, C., Mitchell, S., MacInnis, C., & Taylor, B. (2016). Restoration of a Nova Scotia stream to enhance Atlantic salmon provides few benefits to benthic invertebrates. *Proceedings of the Nova Scotian Institute of Science (NSIS)*, 48, 211–237.
- Tierno de Figueroa, J., Lopez-Rodriguez, M., & Villar-Argaiz, M. (2019). Spatial and seasonal variability in the trophic role of aquatic insects:

An assessment of functional feeding group applicability. *Freshwater Biology*, 64, 954–966.

- Tocher, D. (2003). Metabolism and functions of lipids and fatty acids in teleost fish. *Reviews in Fisheries Science*, 11, 107–184.
- Tocher, D. (2010). Fatty acid requirements in ontogeny of marine and freshwater fish. Aquaculture Research., 41, 717–732. https://doi.org/ 10.1111/j.1365-2109.2008.02150.x
- Torres-Ruiz, M., & Wehr, J. (2020). Complementary information from fatty acid and nutrient stoichiometry data improve stream food web analyses. *Hydrobiologia*, 847, 629–645.
- Torres-Ruiz, M., Wehr, J., & Perrone, A. (2007). Trophic relations in a stream food web: Importance of fatty acids for macroinvertebrate consumers. *Journal of the North American Benthological Society*, 26, 509–522.
- Torres-Ruiz, M., Wehr, J., & Perrone, A. (2010). Are net-spinning caddisflies what they eat? An investigation using controlled diets and fatty acids. *Journal of the North American Benthological Society*, 29, 803–813.
- van Dorst, R., Gårdmark, A., Svanbäck, R., & Huss, M. (2020). Does browning-induced light limitation reduce fish body growth through shifts in prey composition or reduced foraging rates? *Freshwater Biol*ogy, 65, 947–959.
- Verdonschot, R., Kail, J., McKie, B., & Verdonschot, P. (2016). The role of benthic microhabitats in determining the effects of hydromorphological river restoration on macroinvertebrates. *Hydrobiologia*, 769, 55–66.
- Vesterinen, J., Keva, O., Kahilainen, K., Strandberg, U., Hiltunen, M., Kankaala, P., & Taipale, S. (2021). Nutritional quality of littoral macroinvertebrates and pelagic zooplankton in subarctic lakes. *Limnology* and Oceanography, 66, 81–97.
- Wang, X., Li, J., Tan, X., Wang, W., & Zheng, Y. (2022). Fatty acid composition of macroinvertebrate scrapers in relation to environmental conditions in subtropical mountain streams. *Environmental Science and Pollution Research International*, 29, 81037–81047.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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