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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, 20:5 ω 3) and docosahexaenoic acid (DHA, 22:6 ω 3) 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, 20:4 ω 6), 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 qualities 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 ω 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: Kaliojoki, Koitajoki, Kuusoja, and Venejoki at the end of the 1990s,

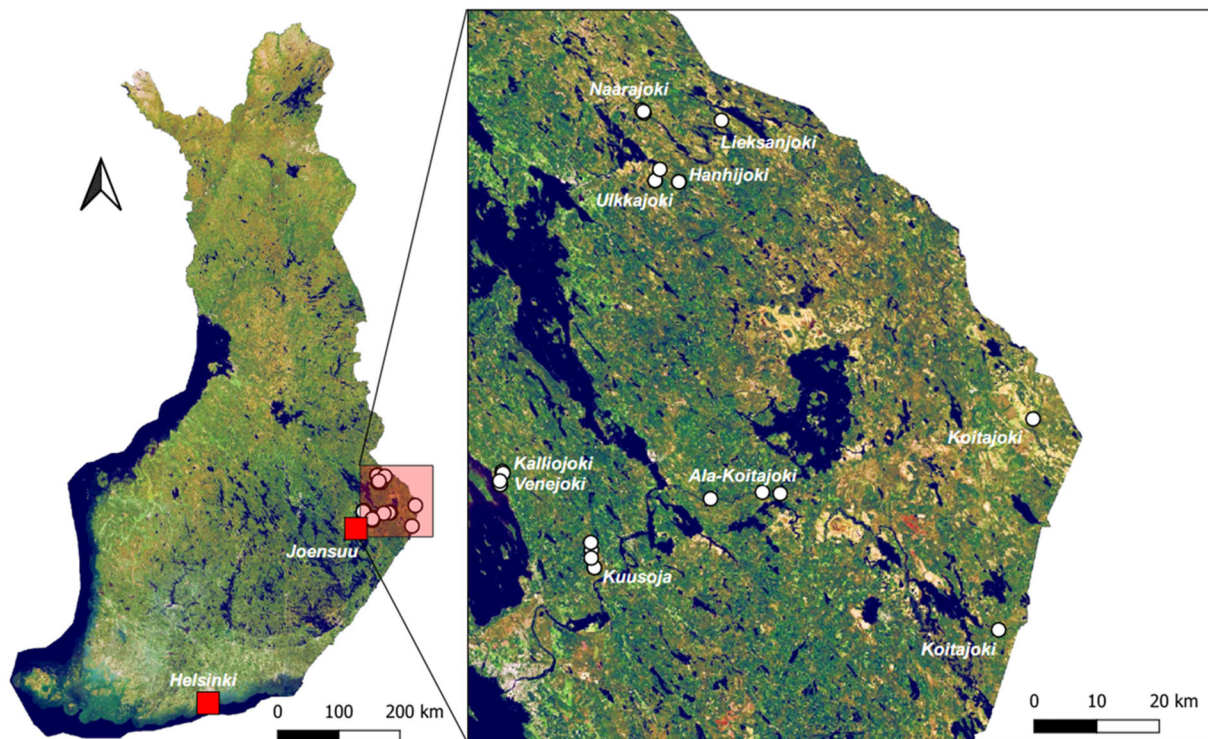


FIGURE 1 Zoobenthos community data and sampling sites and salmonid sampling sites. Detailed coordinates and sampling sites are presented in Table S1. Background orthophotos are an open aerial photo dataset (2023) provided by the National Land Survey of Finland. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/j.1365-3113.2024.100027.x)]

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, Kuusaja, 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, Kalliojoki, and Kuusaja. 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 –0 to 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 Kuusaja +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

TABLE 1 Physical and chemical factors of the study rivers.

Indicator	Factor	Ala-Koitajoki		Hanhijoki		Kalliojoki		Kuusoja		Ulkkajoki		Venejoki	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Morphometry	Length (km)	24.2		20.2		8.5		16.9		13.4		10.0	
Morphometry	Catchment area (km ²)	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 (µg 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 (µg 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	pH	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 (µg 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	<i>Fontinalis</i> sp. water mosses (%)	5-25		0-5		0-5		5-25		N/A		N/A	

Note: When possible, the standard deviation (SD) of the factor has been noted. Values for the bottom material factors have been presented as categorical values, and they describe the coverage of a particular factor in the riverbed. Data were retrieved from the Finnish Environment Institute (SYKE) Herta-database (www.syke.fi/avoindata) in April 2022. Abbreviation: N/A, no data available.

were briefly thawed and rinsed with MilliQ water. We identified EPT-taxa 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 Gefrier Trocknungsanlagen 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 Kuusaja 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 \times 60 m \times 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 $15^{\circ}\text{C min}^{-1}$, then to 170°C at $0.5^{\circ}\text{C min}^{-1}$, then to 230°C at $2^{\circ}\text{C min}^{-1}$. 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 $1^{\circ}\text{C min}^{-1}$, then to 210°C at $2^{\circ}\text{C min}^{-1}$, 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-Check 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 Kruskal–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). Kruskal–Wallis H , ANOVA, and Bonferroni post hoc analyses were conducted using IBM SPSS Statistics 27 (IBM Corp., Armonk, New York, USA).

3 | RESULTS

3.1 | Zoobenthos community structure

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 zoobenthos community structure (PERMANOVA, 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 ($t = 1.49$, $p > 0.10$) (PERMANOVA, pair-wise tests).

The taxa that contributed to the differences in the zoobenthos community structure among the rivers mainly belonged to the EPT-taxa, 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 Kuusojoki: mayfly *Habrophlebia lauta* (Ephemeroptera: Leptophlebiidae) (3.4%), in River Naarajoki: bivalve Sphaeriidae (Bivalvia) (9.8%), in River Ulkkajoki: stonefly *Protonemura meyeri* (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.

3.2 | Variables explaining zoobenthos community 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 Kuusojoki. 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 +15 to 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 Kuusojoki, 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).

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

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

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

3.3 | 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) (16:2 ω 7, 16:3 ω 4), 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) (16:2 ω 7), bacteria (16:1 ω 5), and tOM (20:0, 22:0), respectively.

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 ω 3/ ω 6 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 Rävääkköskoski) 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 ω 3/ ω 6 ratio between Rivers Ala-Koitajoki and Naarajoki (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- $F_{1,86} = 44.73$, $p < 0.001$).

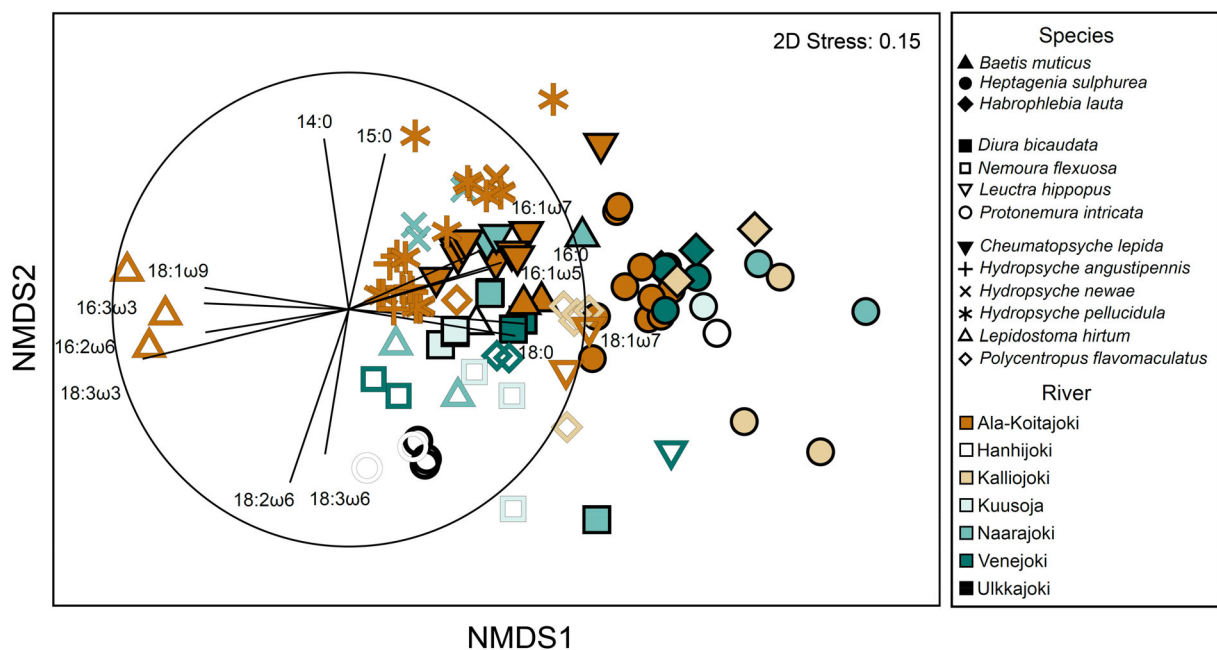


FIGURE 2 Non-metric multidimensional scale (NMDS) ordination of the fatty acid (FA) composition of zoobenthos. Species are presented with different markers. Each river is represented by its own color. The ordination was based on Euclidean distance. FAs that correlate strongly (Pearson $r > 0.6$) with 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]

TABLE 3 Mean percentage (%) and content (c, $\mu\text{g mg DW}^{-1}$) of essential fatty acids (EFA), total fatty acid (FA) content (c, $\mu\text{g mg DW}^{-1}$), and $\omega 3/\omega 6$ ratio with standard deviations (\pm) of zoobenthos in rivers.

Species	River	ARA (%)	ARA (c)	EPA (%)	EPA (c)	Total FA (c)	$\omega 3/\omega 6$
<i>Baetis rhodani</i>	Ala-Koitajoki	2.8 \pm 0.6	3.6 \pm 0.3	12.3 \pm 1.3	16.3 \pm 3.6	131.4 \pm 15.3	3.5 \pm 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
<i>Cheumatopsyche lepida</i>	Ala-Koitajoki	3.5 \pm 0.7	3.2 \pm 1.0	14.3 \pm 1.4	12.8 \pm 2.3	90.2 \pm 20.9	4.1 \pm 0.5
	Naarajoki	5.4 \pm 0.6	5.9 \pm 0.6	12.6 \pm 0.7	16.3 \pm 0.4	129.1 \pm 3.6	3.3 \pm 0.1
<i>Diura bicaudata</i>	Kuusoja	8.7 \pm 0.4	6.3 \pm 0.6	11.6 \pm 0.5	8.4 \pm 1.1	72.0 \pm 8.5	1.3 \pm 0.0
	Naarajoki	5.6 \pm 1.0	6.4 \pm 1.0	9.5 \pm 8.3	11.2 \pm 9.7	115.0 \pm 3.5	2.2 \pm 0.5
	Venejoki	5.9 \pm 0.2	6.1 \pm 0.4	10.6 \pm 0.1	11.0 \pm 1.3	104.1 \pm 11.4	1.2 \pm 0.0
<i>Habrophlebia lauta</i>	Kalliojoki	6.4 \pm 1.2	7.6 \pm 4.3	4.8 \pm 0.7	5.7 \pm 3.1	114.2 \pm 46.1	0.5 \pm 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
<i>Heptagenia sulphurea</i>	Ala-Koitajoki	6.82 \pm 1.4 ^b	5.2 \pm 2.0 ^a	8.7 \pm 1.4	7.4 \pm 2.2	89.7 \pm 21.4	1.7 \pm 0.3
	Hanhijoki	6.1	4.6	4.3	3.2	74.7	1.0
	Kalliojoki	10.7 \pm 4.8 ^b	15.8 \pm 3.2 ^b	2.7 \pm 1.3	3.9 \pm 1.0	165.2 \pm 61.2	0.3 \pm 0.0
	Kuusoja	4.7	7.9	4.8	8.0	166.6	1.2
	Naarajoki	2.9 \pm 0.8 ^a	3.9 \pm 0.9 ^a	3.3 \pm 1.8	4.5 \pm 2.3	136.6 \pm 6.7	1.3 \pm 0.1
	Venejoki	5.9 \pm 0.2 ^b	6.8 \pm 0.5 ^a	5.3 \pm 0.8	6.0 \pm 0.6	115.2 \pm 11.5	0.9 \pm 0.2
<i>Hydropsyche newae</i>	Ala-Koitajoki	3.6 \pm 0.5	9.5 \pm 2.1	9.2 \pm 0.5	23.7 \pm 3.2	256.2 \pm 19.2	3.1 \pm 0.2
	Naarajoki	2.9 \pm 0.6	4.0 \pm 0.3	10.4 \pm 0.3	14.6 \pm 1.6	140.8 \pm 20.0	3.7 \pm 0.1
<i>Lepidostoma hirtum</i>	Ala-Koitajoki	0.6 \pm 0.5	0.7 \pm 0.6	1.1 \pm 1.0	1.5 \pm 1.3	132.2 \pm 3.4	9.1 \pm 5.6
	Naarajoki	4.4 \pm 0.3	5.0 \pm 2.2	4.2 \pm 1.7	4.4 \pm 0.4	115.7 \pm 57.4	1.2 \pm 0.2
<i>Leuctra hippopus</i>	Ala-Koitajoki	8.9 \pm 2.4	7.8 \pm 0.5	9.1 \pm 1.1	8.1 \pm 0.7	89.7 \pm 17.8	0.9 \pm 0.1
	Venejoki	12.6	9.7	7.1	5.5	77.1	0.6
<i>Nemoura flexuosa</i>	Kuusoja	10.5 \pm 2.3	17.5 \pm 1.3	4.2 \pm 0.2	7.2 \pm 0.8	170.1 \pm 26.0	0.9 \pm 0.1
	Venejoki	7.8 \pm 1.3	9.3 \pm 1.3	3.3 \pm 0.8	3.8 \pm 0.3	121.3 \pm 36.3	1.4 \pm 0.0
<i>Polycentropus flavomaculatus</i>	Ala-Koitajoki	6.1	6.7	14.2	15.7	110.0	2.2
	Kalliojoki	12.3 \pm 1.2	18.5 \pm 3.4	9.0 \pm 0.7	13.7 \pm 2.3	152.6 \pm 32.5	0.7 \pm 0.1
	Venejoki	5.7 \pm 0.5	7.2 \pm 0.5	10.8 \pm 0.2	13.7 \pm 0.1	126.8 \pm 1.9	0.9 \pm 0.1
<i>Protonemura intricata</i>	Hanhijoki	2.1 \pm 2.9	2.0 \pm 2.9	3.0 \pm 0.3	2.6 \pm 0.2	87.4 \pm 15.3	1.2 \pm 0.1
	Ulkajoki	4.0 \pm 0.7	4.2 \pm 0.4	2.9 \pm 0.6	3.1 \pm 0.3	106.4 \pm 9.7	1.1 \pm 0.0

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- $F_{1,86} = 2.88$, $p < 0.05$).

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 (Rävakkäkoski 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

TABLE 4 Mean percentage (%) and content (c, $\mu\text{g mg DW}^{-1}$) of essential fatty acids (EFAs), total fatty acid (FA) content (c, $\mu\text{g mg DW}^{-1}$), and $\omega 3/\omega 6$ ratio with standard deviations (\pm) of salmonids in rivers.

Species	River	ARA (%)	ARA (c)	EPA (%)	EPA (c)	DHA (%)	DHA (c)	Total FA (c)	$\omega 3/\omega 6$
<i>Salmo salar</i> m. <i>sebago</i>	Ala-Koitajoki	1.7 \pm 0.4	1.80 \pm 0.9 ^a	6.0 \pm 1.5	6.50 \pm 2.8 ^a	9.1 \pm 5.0	8.50 \pm 2.2 ^a	119.8 \pm 64.9 ^a	6.5 \pm 4.5 ^a
	Naarajoki	2.0 \pm 0.3	3.00 \pm 1.3 ^b	5.6 \pm 0.7	8.50 \pm 3.3 ^b	8.1 \pm 2.4	11.50 \pm 3.4 ^b	157.8 \pm 66.8 ^b	4.2 \pm 0.5 ^{a,b}
	Ruunaa	1.6 \pm 0.3	2.1 \pm 1.3 ^a	5.4 \pm 1.4	7.20 \pm 4.3 ^{a,b}	9.4 \pm 4.1	10.90 \pm 5.0 ^{a,b}	150.2 \pm 108.7 ^{a,b}	3.7 \pm 1.0 ^b
<i>Salmo trutta</i>	Ala-Koitajoki	1.8 \pm 0.4	2.90 \pm 2.1	5.5 \pm 0.9	9.00 \pm 6.6	8.2 \pm 2.5	11.90 \pm 6.9	182.0 \pm 173.3	4.8 \pm 0.7
	Kuusojä	1.6 \pm 0.7	0.80 \pm 0.4	6.5 \pm 1.8	3.40 \pm 1.8	22.0 \pm 8.6	9.70 \pm 1.8	53.1 \pm 28.4	10.7 \pm 11.0

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.

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 $\omega 3/\omega 6$ 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-Koitajoki (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).

4 | DISCUSSION

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	p	Test
<i>Heptagenia sulphurea</i>	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
	ARA (%)	Naarajoki	3.3 ± 1.8			
		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				
$\omega 3/\omega 6$	Ala-Koitajoki	1.7 ± 0.3	1.9	<0.05	Kruskal–Wallis H	
	Kalliojoki	0.3 ± 0.0				
<i>Lepidostoma hirtum</i>	$\omega 3/\omega 6$	Ala-Koitajoki	9.1 ± 5.6	1.3	<0.05	Kruskal–Wallis H
		Naarajoki	1.2 ± 0.2			
<i>Polycentropus flavomaculatus</i>	ARA (c)	Kalliojoki	18.5 ± 3.4	1.5	<0.001	Bonferroni
		Venejoki	7.2 ± 0.5			
<i>Salmo salar m. sebago</i>	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			
	$\omega 3/\omega 6$	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			
<i>Salmo trutta</i>	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			
	$\omega 3/\omega 6$	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 (\pm) for FAs have been given (% = percentage of total FAs, c = FA content [$\mu\text{g}/\text{mg DW}^{-1}$]). 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

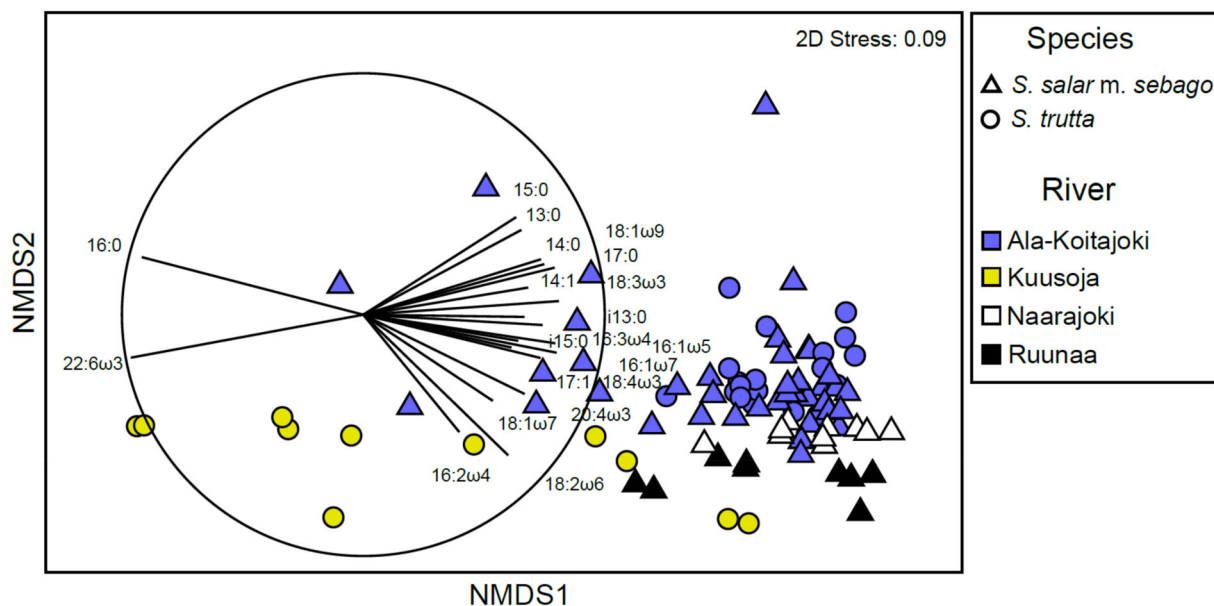


FIGURE 3 Non-metric multidimensional scale (NMDS) ordination of the fatty acid (FA) composition of salmonids. Species are presented with different markers. Each river is represented by its own color. The ordination was based on Euclidean distance. FAs that correlate strongly (Pearson $r > 0.7$) with 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](https://onlinelibrary.wiley.com/doi/10.1111/jlms.12420)]

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-Koitaajoki, 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 (Koitaajoki and Kuusoja) showed changes in the zoobenthos community structure related to the time from restoration. In Koitaajoki, 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 Koitaajoki (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 river- and 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 Rävääkkökoski). 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; Labeled-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 Rävääkkökoski.

There was a significant difference in the ω 3/ ω 6 ratio in caddisfly *L. hirtum* between Rivers Ala-Koitajoki and Naarajoki. The ω 3/ ω 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* ω 3/ ω 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 Kalliojoki and Venäjoki, which did not differ in their zoobenthos community structure. Therefore, we assume that the food sources utilized by their prey 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 Kuusojä 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 short-chain 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 Kuusojä. 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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SUPPORTING INFORMATION

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

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