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The effect of beaver ponds on water physico-chemical composition in the Carpathians (Poland and Slovakia)

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Abstract. In recent decades, the population of the Eurasian beaver (*Castor fiber*) has undergone a rapid recovery from near extinction to abundance across vast areas of Europe. The ability of this species to build dams makes its reintroduction an important environmental factor in the recolonised areas. This study investigated nine beaver-inhabited streams distributed across the Western Carpathians to assess the effects of geomorphic type, age of beaver pond sequence and seasonality on the physico-chemical changes to water in and below beaver ponds.

In general, greater reductions in NO_3^- and SO_4^{2-} were observed with increasing temperatures during the warm period (spring–summer). A comparison of two distinct types of beaver ponds revealed that there was a greater decrease in NO_3^- and Ca^{2+} in overflowing ponds and a greater decrease in pH downstream to these ponds compared to in-channel reservoirs. Beaver pond sequence age was positively related to decrease in dissolved oxygen, SO_4^{2-} and pH. Biogeochemical processes involving organic matter accumulated in beaver ponds, that include decomposition, aerobic/anaerobic oxidation and $CaCO_3$ precipitation, are responsible for changes of these physico-chemical parameters in stream water. The natural development of extensive beaver ponds and their persistence may be crucial for sustaining water purification processes. Further research based on a more frequent sampling strategy should aim to identify the biogeochemical processes that occur in beaver ponds under specific hydro-meteorological conditions: during low flow periods, snowmelt and rainfall events.

1 Introduction

Beavers, the two semi-aquatic species of the genus Castor, significantly alter riverine ecosystems through foraging activity and the construction of dams, canals and burrows or lodges (Rosell et al., 2005; Brazier et al., 2021). Their influence on hydrological, geomorphological and ecological processes makes them perfect examples of environmental engineers and keystone species (Jones, 1994; Holtmeier, 2015). Their ability to build dams is particularly important because of the strong impact their structures have on the hydrogeomorphological system (Gurnell, 1998). The physical features of the created ponds and their influence on biogeochemical cycles affect habitat availability for other organisms and result in an increase in

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biodiversity (Wright et al., 2002; Larsen et al., 2021). In addition, beavers are recognised as providers of important ecosystem services, (e.g., through their support of water retention and purification) (Puttock et al., 2017, Thompson et al., 2021).

The Eurasian beaver (Castor fiber) was once widespread across both continents until excessive hunting resulted in the disappearance of the species from most of its former range. Only eight remnant populations were left at the beginning of the 20th century (Nolet and Rosell, 1998). Their subsequent reintroductions, hunting restrictions and natural dispersal led to a substantial population increase and the near re-establishment of the species distribution (Halley et al., 2020). According to the data collected by Wróbel (2020), the highest beaver population density among the six Carpathian countries is currently found in Poland, followed by Slovakia. A few centuries before the species disappeared from the lowest parts of the Polish Carpathians in the 19th century, it was extirpated from more elevated catchments (Żurowski, 1986). Beaver releases in Poland, conducted since the 1940s, have mainly focused on the lowlands (Dzięciołowski and Gozdziewski, 1999). The first reintroduction program aimed at reestablishing Carpathian populations was successfully carried out from 1980–1985 (Żurowski and Kasperczyk, 1990). Beavers in the northern part of Slovakia originated solely from the Polish reintroduction (Pachinger and Hulik, 1999) and were first documented along the Ondava river in 1981 (Valachovič, 2012). Since then, both countries have observed substantial increases in the range and abundance of recovering beaver populations (Čanády et al., 2016; Wróbel and Krzysztofiak-Kaniewska, 2020).

In recent decades, there has been increasing interest in studying the impact of beavers on river water chemistry. Understanding the implications for water resource management and nature conservation (Bason et al., 2017; Čiuldienė et al., 2020; Stevenson et al., 2022; Bylak et al., 2024) is particularly important in the face of contemporary environmental crises. Most beaver-related studies have focused on the areas inhabited by the Canadian beaver (Castor canadensis) (Halley et al., 2020; Larsen et al., 2021). It's commonly assumed that both species exert similar influences on the environment even though the Eurasian beaver expresses less advanced building activity in terms of the number and size of created structures (Gurnell, 1998; Rosell et al., 2005) and inhabits different ecosystems. Thus, the impacts of the Eurasian beaver are still relatively understudied even as its significance for shaping fluvial processes is growing due to the increasing population.

Beaver dams decrease water flow velocity, which promotes the sedimentation of suspended solids and increases nutrient retention (Maret et al., 1987; Puttock et al., 2018). Therefore, beaver ponds may act as substantial catchment-scale sinks for nitrogen (Lazar et al., 2015). The accumulation of organic carbon and phosphorus is also commonly observed (Lizarralde et al., 1996; Wohl et al., 2012; Čiuldienė et al., 2020). Moreover, the filtration capacity of beaver dams results in the attenuation of downstream heavy metal concentrations (Čiuldienė et al., 2020; Murray, 2021). The influence of beavers on river water quality is often recognised as positive because they enhance self-purification processes; they have the potential to be a restoration tool for degraded streams (Bason et al., 2017; Puttock et al., 2017; Bylak et al., 2024). However, most studies highlight the role of seasonal changes in source and sink transitions, depending on flow rate and ecosystem productivity (Maret et al., 1987; Wegener et al., 2017; Murray, 2021). The impact of a particular beaver dam on chemical composition may not reflect generally recognised trends because of the strong influence of local site-specific characteristics (Kalvīte et al., 2021). For example, Bason et al. (2017) found a greater reduction of nitrogen concentrations in lower-order streams and a greater reduction of suspended solids concentrations in older ponds than in younger ones. Contradictory patterns of water temperature changes have also been observed (Majerova et al., 2015; Weber et al., 2017).

Previous research has indicated a need to identify geomorphic factors that explain variations in the physico-chemical effects of beaver activity (Murray et al., 2021). In addition, Brazier et al. (2021) pointed out the potential differences in the impacts of a single pond compared to a sequence of multiple ponds. Therefore, a framework that takes into account varying geographical settings and beaver pond characteristics may help to explain the varying environmental responses to beaver dams. Moreover, to our knowledge, most of the studies on the impact of Eurasian beaver on water properties have been focused on the lowlands (Puttock et al., 2018; Čiuldienė et al., 2020; Kalvīte et al., 2021; Bylak et al., 2024) despite the high activity rates of the species and its influence on hydrogeomorphological processes in the mountainous region (Giriat et al., 2016; Gorczyca et al., 2018). Understanding the influence of beavers on Carpathian ecosystems is particularly important because the species recently became a prominent environmental factor across this mountain range after centuries of absence.

Therefore, the objective of this study was to determine the effects of beaver dams on physico-chemical water properties in mountain streams of the Western Carpathians (Poland and Slovakia). The paper focuses on answering the following three questions:

1) Which beaver-driven biogeochemical processes control changes in the physico-chemical parameters of stream water?
2) Does seasonality alter the effects of beaver dams on stream water chemistry?
3) How does beaver dam age and beaver pond geomorphic type affect stream water chemistry?

2 Methods

2.1 Study area

The study was conducted on nine beaver-inhabited streams in the Outer Western Carpathians (Fig. 1). The region consists mainly of alternating series of sandstones, conglomerates, mudstones and shales that make up the sedimentary deposits of Carpathian flysch (Ślączka et al., 2006; Łajczak et al, 2014). Generally, in the northern, lower-lying foothills of the study area (sites 1, 2, 4-6), easily weathered, soluble shales comprise a large portion of the geological structure (Burtan et al., 1994, Kopciowski et al., 1997; Jankowski, 2014). In the southern part of the study area (sites 7–9), less weathered sandstones predominate (Kopciowski, 2000). The stream at site 3, despite its location in the northern foothills of the mountains, drains one of the highest foothill ranges, the Brzanka Range, which is largely composed of sandstone (Marciniec and Zimnal, 2009).

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The geomorphologically diverse terrain in the study area ranges from low foothills to medium mountains (Gilewska et al., 1982; Borzuchowski and Olędzki, 2011). The highest parts of the Outer Western Carpathians are classified as medium mountains. These areas are characterised by steep slopes that often exceed 30% and significant relative relief ranging from 400 to 800 m. Low mountains can be found at the margins of these ranges and in isolated ridges. They feature steep slopes and smaller relative relief ranging from 200 to 400 m. The foothill zone is primarily located in the northern part of the study area. It reaches elevations of approximately 500 m above sea level. This zone is mainly characterised by wide, gently sloping ridges that rise 40 to 300 m above the flat valley floors (Starkel, 1990).

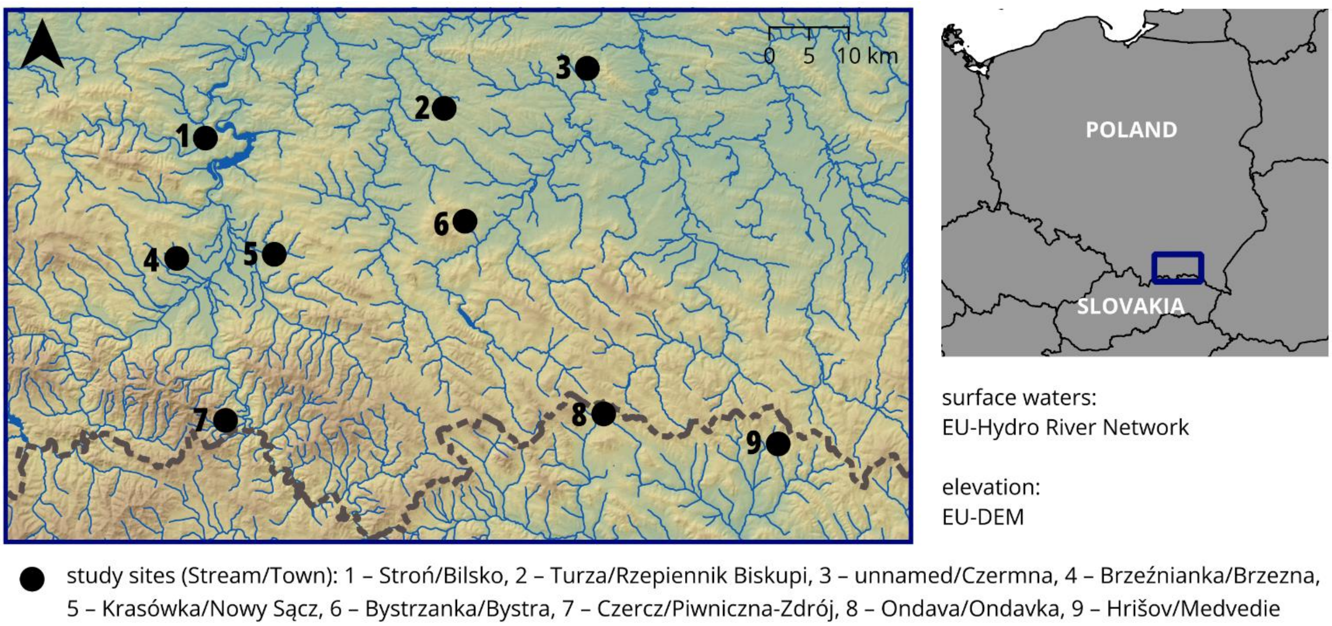

Figure 1: Study area.

The mean annual temperature in all selected catchments ranges from 5.1 to 9.1°C and the average precipitation is 770–1140 mm (based on the 2000–2010 period; Szalai et al., 2013; CARPATCLIM, 2013). Rivers in this area are mainly characterised by a nival–pluvial hydrological regime (Wrzesiński, 2017).

The Slovak part of the Carpathians is characterised by large plots of agricultural land and small, dispersed settlements that are mainly concentrated in the valleys. This pattern is due to the impact of the post-1990 land reforms on land use and farm structure, both of which are characterised by large corporate farms and agricultural cooperatives (Lazikova et al., 2017). Despite the privatisation of land in Slovakia, land continues to be managed by large holdings and production companies (Bański, 2017) and the average size of an arable land parcel is 21.0 ha (Lieskovský et al., 2015). In the Polish Western Carpathians, settlements are more dispersed throughout slopes, and the land reform led to a progressive fragmentation of agricultural land (arable land and grassland) due to the constant division of land between successive owners, usually

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descendants (Kroczak et al., 2018). In the Polish Carpathians, the average agricultural parcel size is 0.5 ha (Kolecka and Kozak, 2019).

The primary criterion for the selection of streams for the study was the presence of beaver dams that span the entire riverbed. The study sites were distributed randomly through the transect of the relatively low-elevation areas in the north to the southern slopes of the ridgeline close to the Poland–Slovakia border. In addition to varying in topography, the sites differed in terms of human activity, such as catchment land use and presence of river control structures. The extent of beaver activity, as indicated by the pond to channel ratio, the size and persistence of dam sequences, also varied across the study area (Table 1).

Table 1: Characteristics of the study sites.

Characteristics		Study sites (number refers to the Fig. 1)								
Subject	Parameter	1	2	3	4	5	6	7	8	9
Catchment to the sampling point below the pond sequence	Area [km^2]	2.6	7.7	2.2	7.1	2.0	5.2	16.9	1.1	9.8
	Outlet altitude [m a.s.l.] [a]	245	271	294	348	343	364	457	487	368
	Dominating land cover category: [b] B - broadleaved forest; C - coniferous forest; H - permanent herbaceous	B	H	B	H	C	H	C	H	B
	Share of sealed artificial surfaces [%] [b]	2.1	1.8	1.1	3.1	2.3	4.1	1.0	0.2	0.1
	Share of forests [%] [b]	51.2	46.9	59.0	40.4	55.3	37.9	85.4	38.8	86.8
Stream section	Channel gradient [%] [a]	1.9	0.8	1.1	2.1	1.8	1.8	3.1	2.6	2.0
	Length [km]	0.4	0.6	1.3	0.2	0.5	0.1	0.3	0.6	0.3
	Pond sequence area [ha] [c]	0.14	0.24	1.70	0.22	0.42	0.01	0.18	0.57	0.68
	Approximate age of the beaver pond sequence [years] [c]	4-9	4-9	≥10	≤3	≥10	≤3	≤3	≥10	≥10
	Beaver pond type: I - in-channel; O - overflowing	I	I	O	O	O	I	I	O	O
	Number of ponds in the sequence	6-10	6-10	>10	3-5	6-10	1-2	3-5	>10	3-5
	River regulation structures: + presence, - absence	+	-	-	+	-	+	-	-	+

Data sources:

a - digital elevation models (1x1m) obtained from Polish Office of Geodesy and Cartography, and Geodesy Cartography and Cadastre Authority of the Slovak Republic

b – dataset CLCplus Backbone 2018 (10x10m) obtained from Copernicus Land Monitoring Service

c - orthophotos obtained from Polish Office of Geodesy and Cartography (PZGiK) and available in Google Earth Pro

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2.2 Water sampling and chemical analysis

The research followed a three-dimensional sampling scheme (Fig. 2) that involved three-point measurements repeated seasonally at all study sites in 2022–2023. For three streams, more extensive sampling was conducted to elucidate spatial variation.

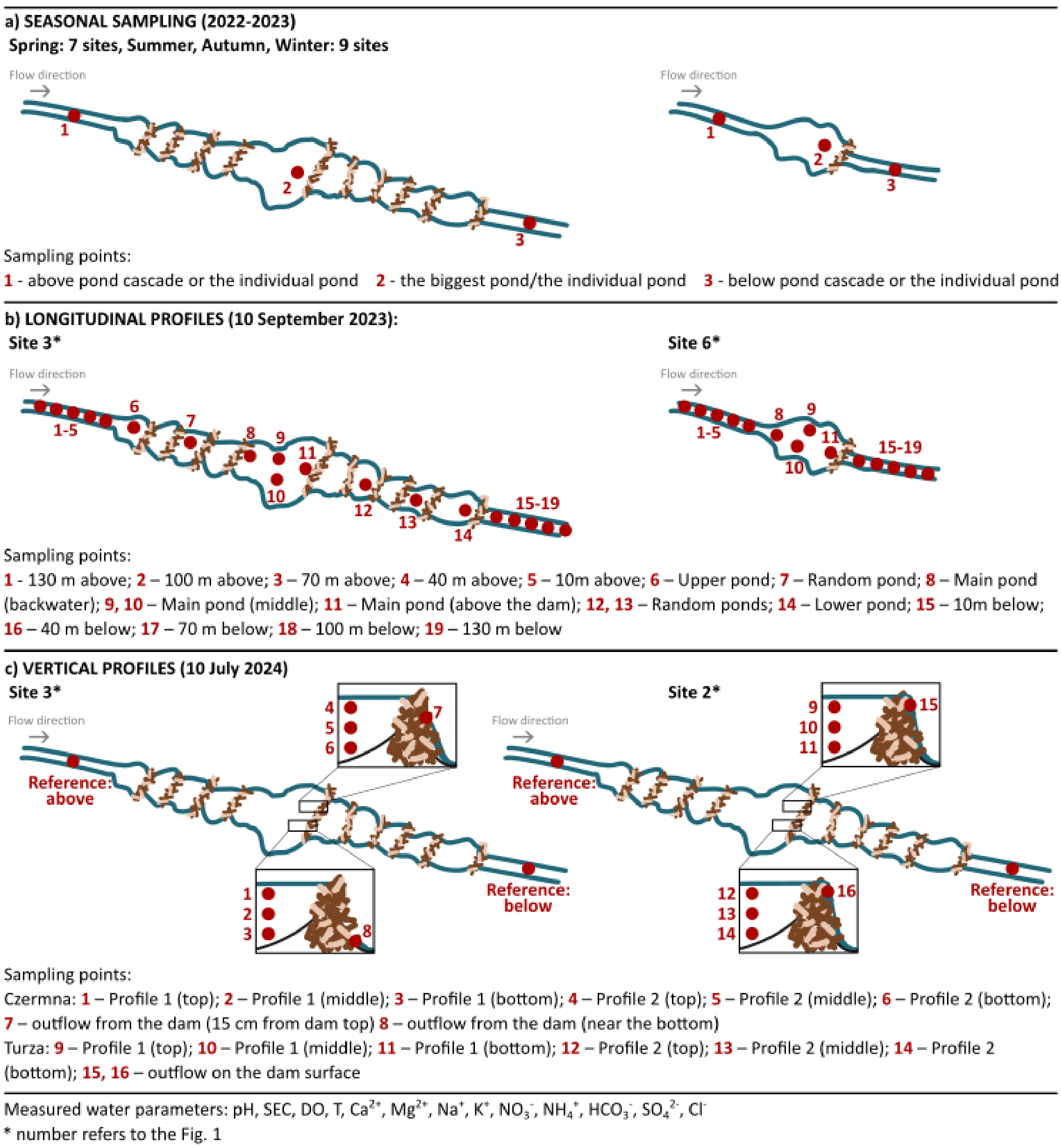

Figure 2: Study schemes.

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Three samples were collected at each site in spring, summer, autumn and winter during normal water levels (i.e., excluding periods of precipitation or snowmelt) (Fig. 2a). The section 'above' the beaver pond or pond sequence was defined as 50–100 m upstream from a backwater, and the section 'below' was 50–100 m downstream from the last dam. For sequences of multiple ponds, the representative 'pond' sample was collected from the biggest reservoir in the system. A total of 7 sites were sampled in the first spring, and then 2 sites were added for subsequent seasons. A total of 102 samples were collected from the 9 sites.

Two sites were chosen for additional measurements to create longitudinal stream profiles (Fig. 2b). The sampling was conducted during the summer of 2023 at the Bystrzanka stream (a single beaver pond created < 2 years ago) and an unnamed stream in Czermna (an old beaver pond sequence created > 10 years ago). Measurements in the 'above' and 'below' sections were taken every 30 m, starting at a distance of 130 m from the ponds. Moreover, 4 locations within the 'ponds' were sampled to represent the front, middle and periphery of the water body.

To analyse the variation of physico-chemical characteristics in a pond's vertical profile, water samples were collected in the summer of 2024 at two beaver pond sequences, Czermna and Turza, which have different pond types (Fig. 2c). In Turza, solely in-channel ponds were observed. By contrast, overflowing stream banks were common in Czermna. Measurements were taken from various depths (near the bottom, in the middle of the water column and from the surface) and from dam outlets. In Czermna, outlet measurements were collected from leaks in the upper part of the dam and near its bottom, and in Turza, they were taken from water overflowing the dam.

Sampling and in situ measurements were conducted without disturbing turbidity. Basic physico-chemical parameters – temperature (T), dissolved oxygen (DO), specific electrolytic conductivity (SEC) and pH – were determined on-site using an ELMETRON CX-401 multifunction meter with the GXZ-3tk multiparameter immersion head. Additionally, 250 ml water samples were collected at each site for laboratory analyses.

HCO3- concentration was determined by titrating the water with a standard solution of hydrochloric acid. Each sample was filtered through a glass Whatman GF-D microfiber filter. The ionic composition (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, NO_3^{-}, NH_4^{+}, SO_4^{2-}, Cl^{-}) was analysed in the Dionex ICS3000 ion chromatography. Each sample was previously filtered through a glass microfiber filter Whatman GF-D. The calibration curve was based on the certificate reference standard (CLMS 2AN). All solutions were prepared with 1% nitric acid (Suprapur). The following concentrations were prepared for calibration: 0 (blank), 1, 10, 50, 100 and 1000 $\mu g \cdot dm^{-3}$.

2.3 Statistical analysis

Principal component analysis (PCA) was performed on raw (standardised) data and on the percentage change (Dc [%]) in the values of individual physico-chemical parameters of water in ponds and streams below the beaver dams relative to their values above the ponds, which was calculated using the following formula:

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$$Dc[\%] = \frac{(Bx-Ax)}{Ax \cdot 100}, \tag{1}$$

where:

Bx is the value of the physico-chemical parameter x in the pond or stream below the dam, while Ax is the value of the physico-chemical parameter x in the stream above the dam during particular sampling session and N is the total number of sampling sessions (n = 34).

Physico-chemical water parameters were included in the PCA if their mean absolute difference in Dc [%] (for all sampling sites combined) exceeded 5%. This calculation used the following formula:

$$|Dc|[\%] = \sum \frac{\left|\frac{Bx-Ax}{Ax}\right| \cdot 100}{N}, \tag{2}$$

The PCA method reduces the complexity of a large data set to a smaller set of easily interpretable factors that can be associated with specific processes (Drever, 1997). A matrix of factor scores, one of the most important parts of the PCA output, was also analysed. Factor scores provide a measure of the relation between each observation (i.e., each sample) and the identified factors (Shaw, Wheeler, 1997). The Kolmogorov–Smirnov and Lilliefors tests were used to determine the normality of the distributions of the variables. Variables that were not normally distributed were logarithmically transformed to achieve a normal distribution. The Kaiser criterion was used to separate factors (the eigenvalues >1), and a significance level of $p<0.05$ was used for all calculations.

Seasonal and site-to-site variations in Dc [%] were also assessed. To compare the study sites, they were first classified according to the age and type of each beaver pond sequence. The ‘overflowing’ pond type has more extensive ponds that cover areas outside of the river channel. They are characterised by more abundant aquatic vegetation, and the water retention time is presumed to be longer than in the ‘in-channel’ pond type, which is restricted to the area between river banks. All the characteristics were estimated in the field or through the use of orthophotos (Table 1). After applying the Shapiro–Wilk test for normality, either a one-way ANOVA or its non-parametric equivalent (the Mann–Whitney U test for two-group comparisons or the Kruskall–Wallis test for multiple-group comparisons) was conducted for each parameter. In addition to the analysis of the entire data set, a separate analysis was performed on the parameters obtained during the spring–summer period because of an observed difference between this period and the other seasons. In addition, correlations between physico-chemical parameters and land use cover, catchment area, channel slope and channel width were analysed. Results characterised by $r>0.6$ and $p<0.05$ were considered significant. All analyses were performed in STATISTICA 12.0. The statistical distribution of the data obtained in this study was described by medians and quartile deviation.

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3 Results

3.1 Physico-chemical background of the studied streams

There were clear differences in the physico-chemical properties of the stream water among the studied catchments (Table 2). Significantly higher SEC and concentrations of major ions were found in streams located in the northern, lower-lying foothills of the Outer Carpathians, where there is a high proportion of shale in the bedrock (sites 1, 2, 4, and 6). Lower SEC and concentrations of major ions were found in streams draining catchments in the southern, higher part of the Outer Carpathians that have a high proportion of sandstone (sites 7–9). The stream at site 5 has physico-chemical characteristics that are intermediate between those of the first and second groups of streams. The stream at site 3, despite its location in the northern foothills of the mountains, was characterised by very low SEC values and concentrations of major ions because it drains a range mainly composed of sandstone.

Table 2: Input water parameters, measured above beaver ponds (annual median values).

Study site*	pH	SEC [$\mu S \cdot cm^{-1}$]	Chemical composition [$mg \cdot dm^{-3}$]									
			DO	Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	NO_3^-	NH_4^+	HCO_3^-	SO_4^{2-}	Cl^-
1	8.20	537.3	9.67	77.50	18.64	18.50	2.71	2.58	0.09	249.22	64.12	14.65
2	8.12	562.7	8.71	76.18	22.97	18.58	1.24	1.32	0.09	266.42	35.19	13.54
3	7.44	272.6	7.94	40.76	7.92	7.63	1.26	1.39	0.15	155.29	28.50	3.97
4	8.25	486.0	9.04	70.62	15.71	28.45	2.92	2.54	0.10	269.09	31.49	34.58
5	8.47	376.2	11.02	60.95	11.53	12.10	0.82	2.82	0.16	204.96	27.84	8.88
6	8.03	410.7	8.41	58.90	7.75	28.45	5.48	4.39	0.10	239.80	26.98	14.68
7	8.36	285.7	10.19	51.20	10.48	5.30	0.85	3.44	0.18	183.66	17.94	4.26
8	7.86	350.0	8.29	67.23	6.30	9.64	0.84	0.34	0.13	251.28	10.27	0.82
9	8.11	303.9	10.23	59.36	6.07	9.52	1.22	0.58	0.16	207.46	24.24	3.47

* number refers to the Fig. 1

The relationship between the physico-chemical properties of stream water and the bedrock properties of the catchment was confirmed by the PCA. The first main factor (F1), which explained 38% of the variability in the stream water chemistry, controls the values of the geogenic parameters, which include SEC and major ions (Table 3). This geological factor (F1) clearly grouped water samples by catchments that are more and less resistant to weathering: water samples taken in catchments dominated by sandstone were characterised by negative factor scores (cluster A), while water samples taken in catchments dominated by shale were characterised by positive factor scores (cluster B) (Fig. 3a). In the intermediate group (cluster A/B) was stream 5, which is characterised by intermediate physical and chemical stream water properties (Fig. 3a, Table 2). The second factor (F2), which accounted for 26% of the chemical composition variability in the studied streams, was the factor associated with changes in water temperature during the year. F2 was negatively related to DO and NO_3^- and NH_4^+ concentrations (Table 3). This seasonal factor (F2) grouped the factor scores of water samples collected in the warm seasons

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(i.e., spring and summer; cluster C) and the winter (cluster D) (Fig. 3b). Samples taken in the autumn comprised an intermediate C/D cluster. The third factor, which explained just 12% of the variability in the stream water chemistry, controls the variability in Na^+ and K^+ ion concentrations. Concentrations of Na^+ and K^+ showed high correlations with the percentage of artificial surfaces in the studied catchments, (0.83 and 0.77, respectively, $p<0.05$), suggesting that the third factor is related to human activity (the anthropogenic factor). Almost no correlations were found between the physico-chemical water parameters above beaver ponds and the catchment area, or the width and slope of the stream, although a moderate relation between pH and stream width was noted ($r=0.48$, $p<0.05$).

Table 3: Results of the PCA analyses of the water characteristics above beaver ponds. Absolute values of loadings that exceeded 0.5 are marked in bold.

Parameters	PCA factors		
	1	2	3
DO	-0.06	**-0.93**	-0.22
SEC	**0.95**	0.15	-0.15
T	0.17	**0.88**	0.14
HCO_3^-	**0.73**	0.43	-0.26
Cl^-	**0.74**	-0.34	0.29
SO_4^{2-}	**0.59**	-0.40	-0.09
Ca^{2+} (log)	**0.77**	0.10	-0.24
Mg^{2+}	**0.76**	-0.11	-0.47
Na^+	**0.83**	-0.12	**0.51**
K^+	**0.52**	-0.00	**0.79**
NO_3^-	0.18	**-0.79**	0.14
NH_4^+	-0.09	**-0.76**	-0.01
H^+	**-0.61**	-0.01	0.29
Eigenvalue	4.89	3.36	1.52
% of expl. variance	0.38	0.26	0.12

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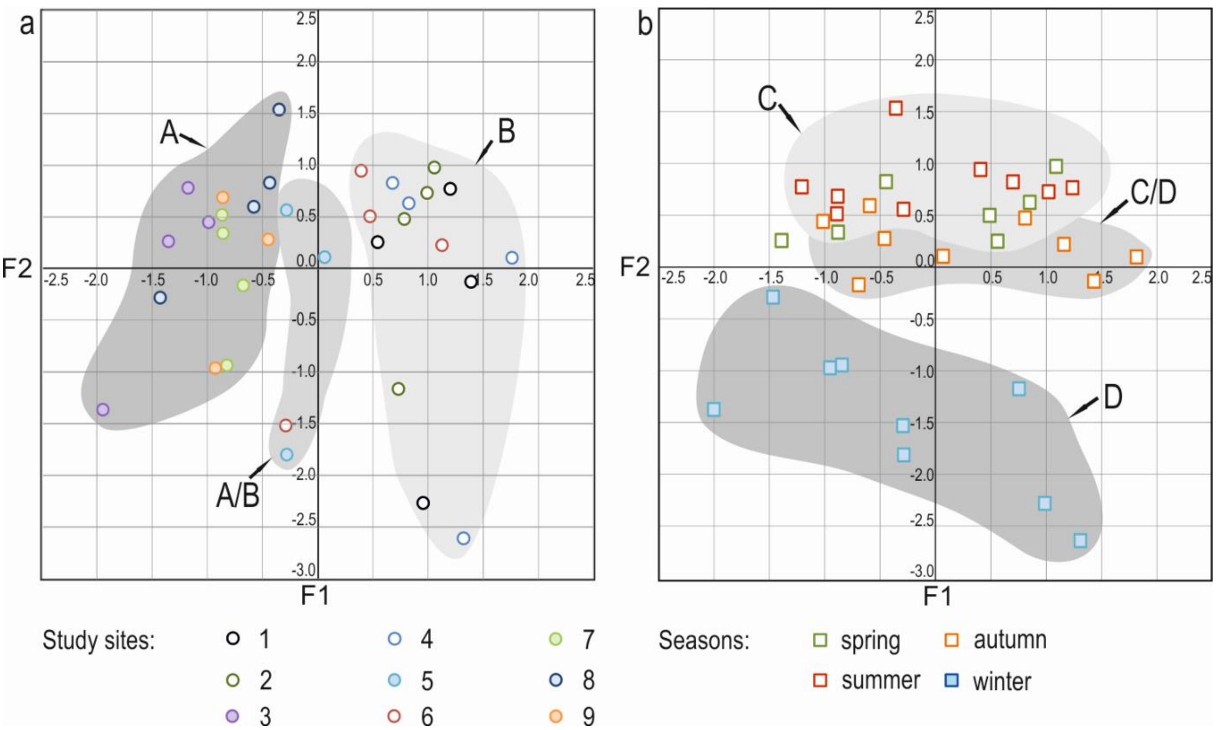

Figure 3: Results of the principal component analysis (PCA), shown as factor scores. Water samples were classified according to study site (a) and season (b).

3.2 The effect of seasonal and site-specific variability of beaver dams on physico-chemical water parameters

There were clear differences in the values of most physico-chemical parameters in and below the beaver ponds compared to the streams above (Figs. 4, A1 and A2). Those differences were greater in the pond water than in the stream water below the dams (Fig. 4, Table A3). Larger differences were observed in streams with older beaver dams than in streams with younger ones (Fig. 4, A1 and A2). Notably larger differences in most physico-chemical parameters were observed in the warm seasons (i.e., spring, summer and autumn) than in the cold season (i.e., winter) (Fig. 5, A1 and A2). For the comparison of water inside beaver ponds relative to the water above the ponds, the largest changes in the values of the physico-chemical parameters (|Dc|>20%) were seen in H^+ (pH), NO_3^-, NH_4^+, and DO (in consecutive order). Intermediate changes (|Dc|=5–20%) were seen in K^+, SO_4^{2-}, Cl^-, HCO_3^-, and Ca^{2+}. The smallest changes (|Dc|<5%) were seen in SEC, Mg^{2+} and Na^+ (Table A1).

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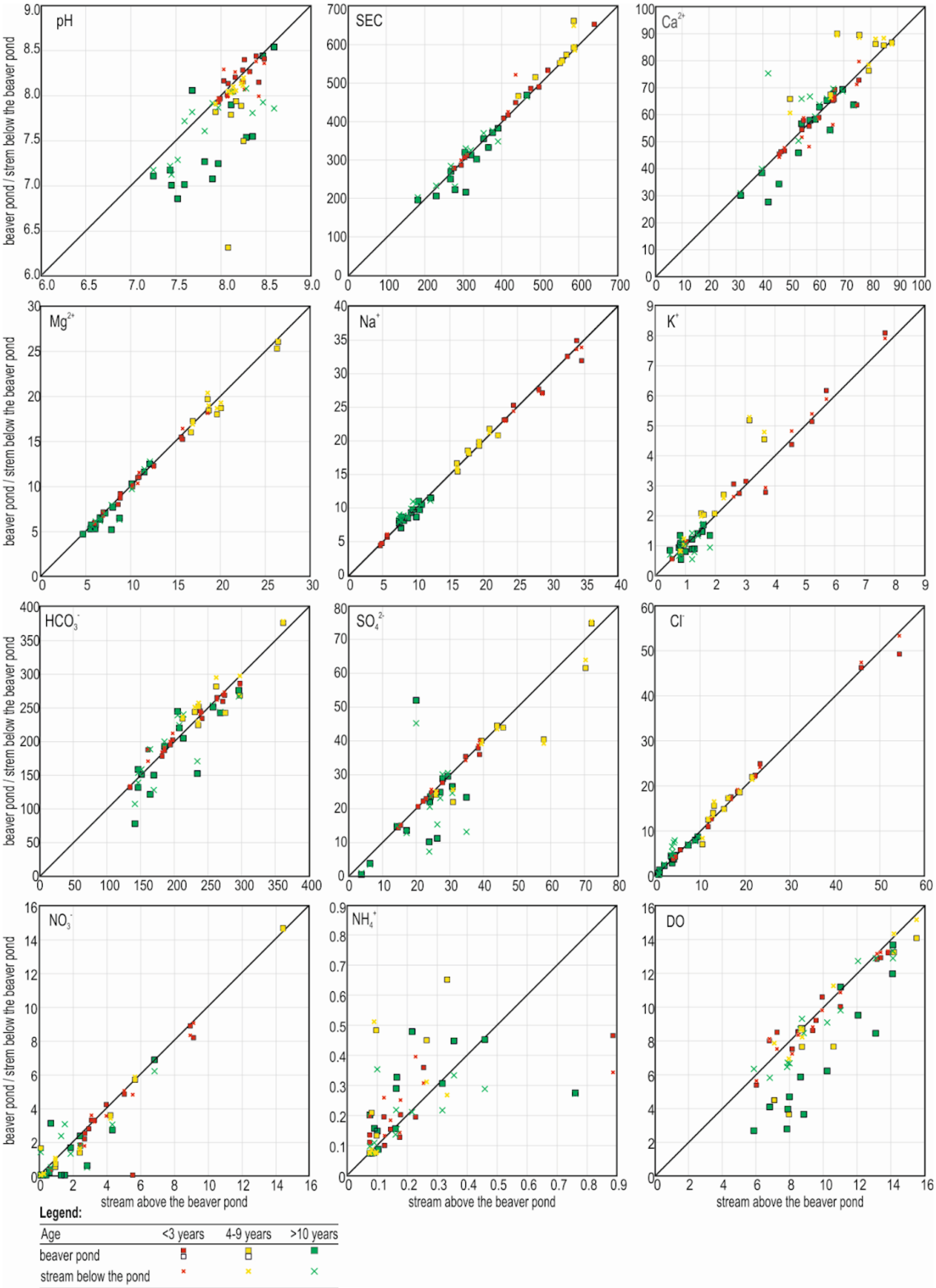

230 **Figure 4: The physico-chemical water parameters, such as pH, SEC [µS·cm-1], major ions, NH_4^+, NO_3^-, and DO concentrations [mg·l-1] within and below beaver ponds in relation to the inlet values.**

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For streams below the dams, the largest changes in physico-chemical parameters relative to streams above the ponds (|Dc|>20%) were seen in NO_3^-, H^+ (pH), and NH_4^+. Intermediate changes (|Dc|=5–20%) were seen in Cl^-, SO_4^{2-}, K^+, Ca^{2+}, HCO_3^-, and DO. The smallest changes (|Dc|<5%) were seen in SEC, Mg^{2+} and Na^+ (Table A1). Despite large absolute differences in the values of some parameters (|Dc|), the direction of the changes were not strongly consistent across seasons or study sites (Figs. 5, A1, and A2). However, distinctly lower pH values and DO concentrations within and below the beaver ponds, compared to the upstream channels, were observed at most study sites during all seasons. Moreover, several patterns in physico-chemical parameter changes were consistently observed for the majority of the study sites during particular seasons. For example, significant decreases in NO_3^- and SO_4^{2-} concentrations within and below the beaver ponds in comparison to the upstream channels occurred during the spring and summer at most study sites (Figs. 5, A1 and A2).

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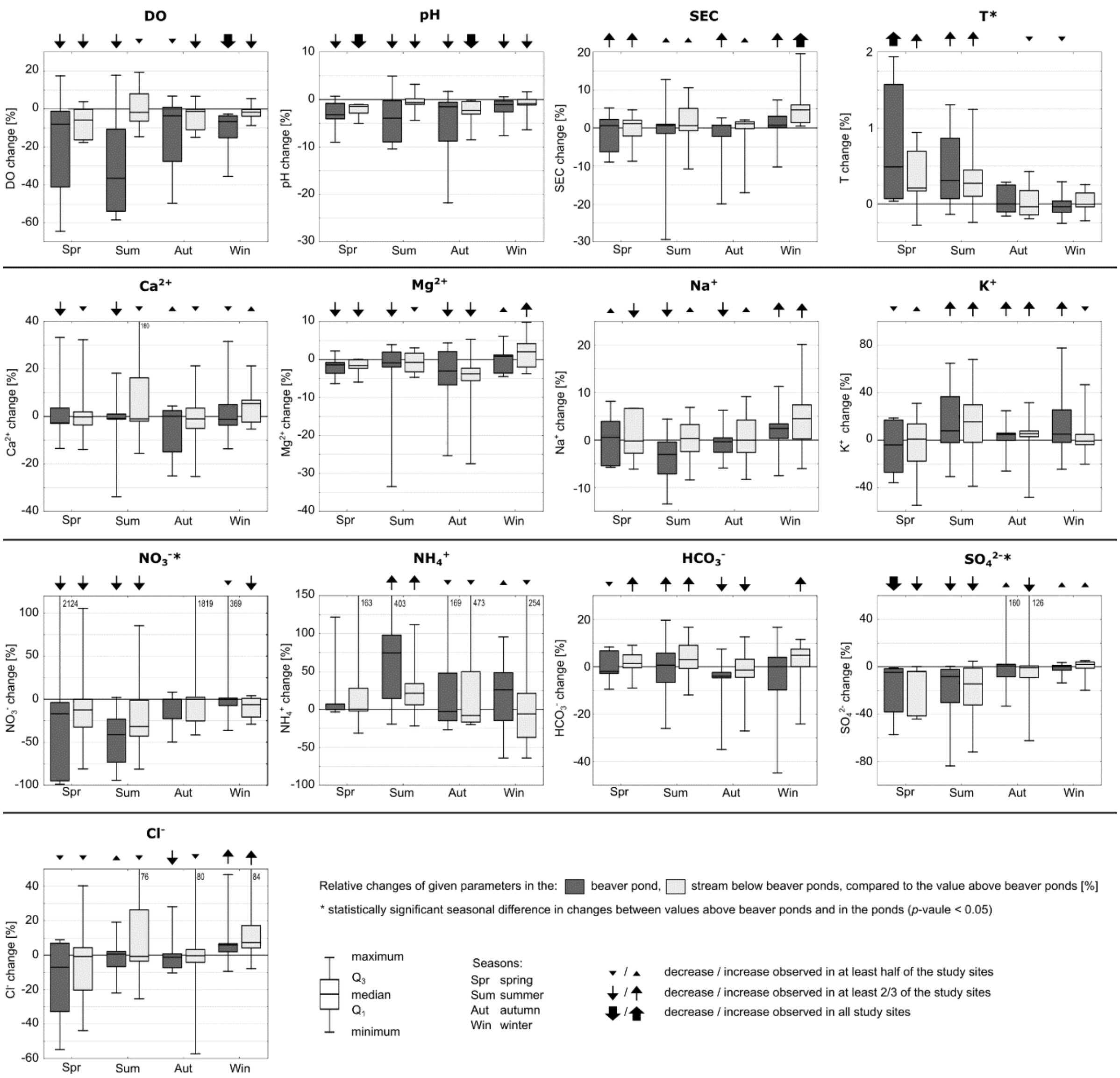

Figure 5: Percentage change, DC [%], in the physico-chemical water parameters within and below beaver ponds in relation to the upstream channels above beaver ponds.

245 The observed variability in responses to beaver damming was attributed to both the season and the pond type (Table 4, Figs. A1 and A2). In general, a greater decrease in pH value was observed downstream of overflowing ponds than in-channel ponds, which had a median value of change of -2.4% (±1.7%) vs. -0.7% (±0.3%), respectively. In addition, greater increases in T (1.0±0.5%) and greater decreases in NO_3^- (-75.3±22.4%) and Ca^{2+} (-2.4±7.4%) were noted in overflowing ponds compared to in-channel ponds (T: 0.2±0.2%; NO_3^-: -9.6±20.1%; Ca^{2+}: 0.6±3.5%) during the spring–summer period.

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Table 4: Results of group comparisons (ANOVA/Mann–Whitney U/Kruskall–Wallis tests) of the differences between inlet values and beaver pond/below the pond in relation to the pond type (i.e., in-channel or overflowing), the age of ponds (i.e., less than 3 years, 4–9 years and 10 years or more) and aggregated seasons (i.e., spring–summer and autumn–winter). Statistical significance thresholds are explained in the footnote.

			Parameter												
			DO	pH	SEC	T	Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	NO_3^-	NH_4^+	HCO_3^-	SO_4^{2-}	Cl^-
Pond type	all seasons	pond			†		*						†		
		below		*						†	†				
	spring and summer	pond			†	*					*				
		below												†	
Age of the pond cascade	all seasons	pond	*	**	*		*								
		below		†			†			*		†		†	
	spring and summer	pond	**		†		*				*			*	
		below					†		†	†		†		*	
Spring-summer/ autumn-winter		pond				**					*			*	
		below				*								*	

** $p < 0.001$; * $p < 0.05$; † $p < 0.1$

Grouping the study sites by the age of the dams yielded a greater number of statistically significant differences, although only changes in DO, pH and SO_4^{2-} showed a clear upward or downward trend (Table 4). There were more significant differences within the ponds than in the streams below the ponds compared to the upstream sections. While pH was barely modified in the youngest (<3 years old) ponds (0.1±0.7%), decreases were observed in moderately old ponds (3–9 years old; -3.4±2.6%) and in ponds older than 10 years (-6.5±3.5%). A similar trend was observed in DO, with changes of -3.6±5.7% in the youngest ponds, -10.8±14.1% in moderately old ponds and -6.5±3.5% in the oldest ponds. The downward trend of the relative amount of DO with increasing pond age was more prominent during the spring–summer period, where changes of -3.5±12.8%, -24.4±19.3% and -47.6±9.3% were observed, respectively.

A decrease in SO_4^{2-} during the spring–summer period was observed both within beaver ponds and in downstream channel sections compared to the upstream sections. Young beaver ponds and the streams below them were characterised by the lowest changes in SO_4^{2-} concentrations, -1.3% (±1.0%) and -0.6% (±2.1%), respectively. A moderate decrease of SO_4^{2-} was observed in the moderately old sites (-17.9±12.0% within the ponds and -10.7±10.5% below), and the highest reduction was noted in ≥10 years old sites (-47.7±18.3% within ponds and -42.8±21.9% below).

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The importance of beaver dam age in modifying physico-chemical parameters in beaver ponds was also indicated by the PCA, which identified three factors that explain 61% of the variation in physico-chemical parameters between beaver ponds and the upstream channels (Table 5). Factor 1 (F1) controls the concentration differences in most major ions: K^+, Ca^{2+}, HCO_3^-, and Cl^-, and demonstrates their positive relationships. Factor 2 (F2) controls the negative relationship between the differences in DO and SO_4^{2-} concentration and NH_4^+, while factor 3 controls the negative relationship between the concentration differences in Cl^- and SO_4^{2-} to NO_3^-. Two clusters of samples were clearly separated by the factor scores of F2 (Fig. 6). The first cluster includes samples from the young beaver ponds in all seasons and moderate beaver ponds in the winter (positive factor scores), and the second cluster includes samples from old beaver ponds in all seasons and moderate beaver ponds in warm seasons: spring, summer and autumn (most have negative factor scores). The samples in the first cluster are more strongly correlated with F1 and F2, as indicated by their concentration near the value of 0 on both the X and Y axes. In contrast, the samples in the second cluster are more dispersed and farther from 0 on both axes.

Table 5: Results of the PCA analyses of the differences between inlet values and beaver ponds Dc [%]. Factor loadings that exceed 0.5 are marked in bold.

Parameters	PCA factors		
	1	2	3
DO	0.05	**0.87**	-0.12
HCO_3^-	**0.54**	0.07	0.36
Cl^-	**0.51**	0.01	**-0.73**
SO_4^{2-}	-0.09	**0.63**	**-0.58**
Ca^{2+}	**0.71**	0.31	0.36
K^+	**0.81**	-0.15	-0.31
NO_3^-	0.33	0.36	**0.58**
NH_4^+	0.35	**-0.63**	-0.14
H^+	0.11	-0.28	0.01
Eigenvalue	1.97	1.88	1.60
% of expl. variance	0.22	0.21	0.18

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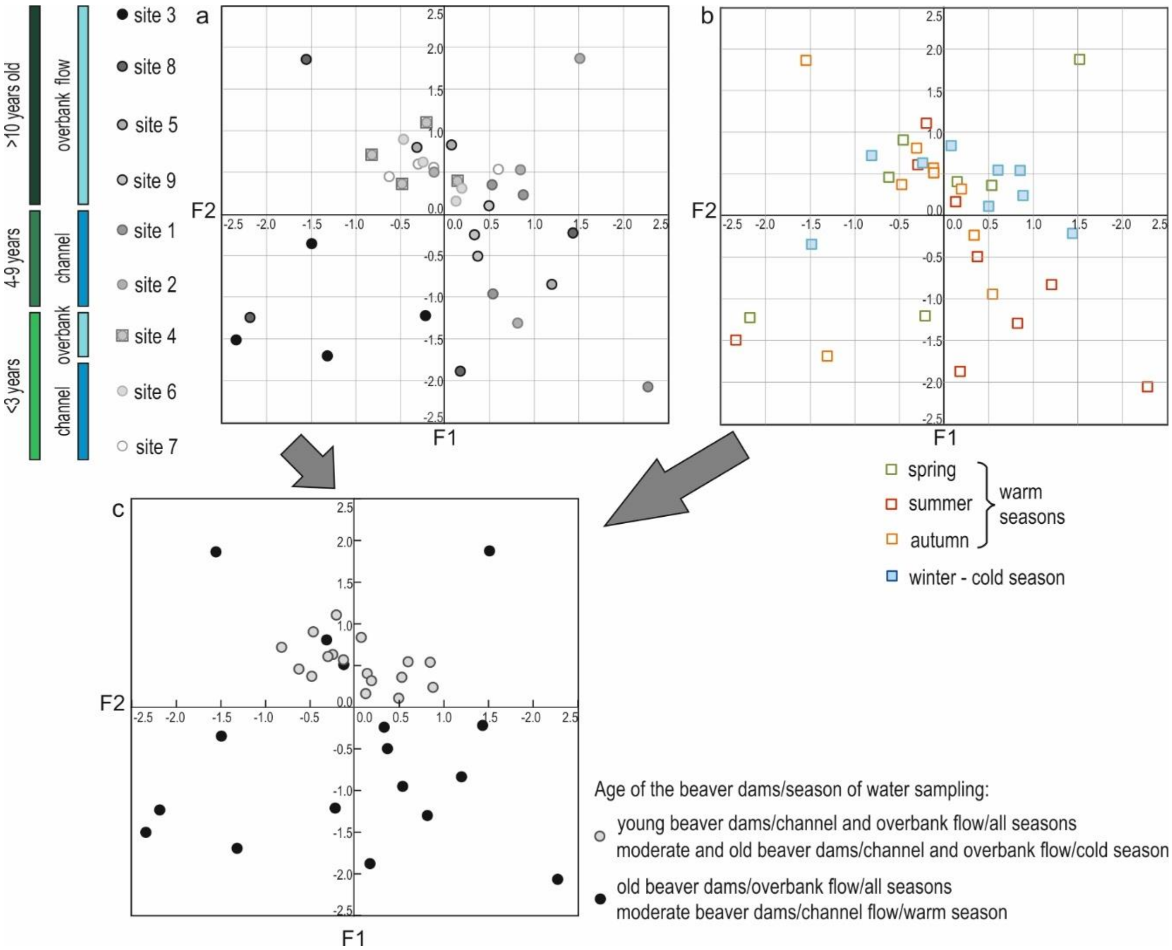

Figure 6: Results of factor analysis (factor scores) for the differences between inlet values and beaver ponds, Dc [%]. The water samples were classified according to study site (a) and season (b). The combined results are also shown (c).

In the case of streams below the beaver dams, PCA analysis identified three factors that together explained 65% of the variation in the differences in physico-chemical parameters (Table 6). F1 controls the concentration differences of DO, SO_4^{2-} and K^+, which are negatively related to NO_3^- and Cl^-. F2 controls the differences in HCO_3^- and Ca^{2+} concentrations, which are negatively related to NO_3^-. F3 controls the differences in SO_4^{2-} and H^+ concentrations, which are negatively related to Cl^-. The factor scores of individual water samples from streams below the beaver dams form less distinct clusters than the samples from beaver ponds (Fig. 7). However, two clusters of factor scores for the stream water samples can be distinguished for F1. Generally, the first cluster includes samples from streams below the in-channel ponds (mainly young and moderately old ponds), that primarily have negative factor scores for F1. The second cluster includes samples from streams below the overbank flowing ponds (mainly old ponds), with primarily positive factor scores for F1. The samples in the first cluster have a stronger correlation with F1 and F2, as indicated by their concentration near the value of 0 on both the X and Y axes. By contrast, the samples in the second cluster are more dispersed and farther from 0 on both axes.

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Table 6: Results of the PCA analyses of the differences between inlet values and the streams below beaver ponds, Dc [%]. Absolute values of loadings that exceed 0.5 are marked in bold.

Parameters	PCA factors		
	1	2	3
DO	**-0.78**	-0.14	0.33
HCO_3^-	0.06	**0.82**	0.07
Cl^-	**0.67**	-0.07	**0.54**
SO_4^{2-}	**-0.59**	-0.18	**-0.58**
Ca^{2+}	0.33	**0.75**	0.13
K^+	**-0.69**	0.24	0.32
NO_3^-	**0.59**	**-0.63**	0.21
NH_4^+	-0.33	0.10	0.46
H^+	0.41	0.27	**-0.60**
Eigenvalue	2.60	1.84	1.47
% of expl. variance	0.29	0.20	0.16

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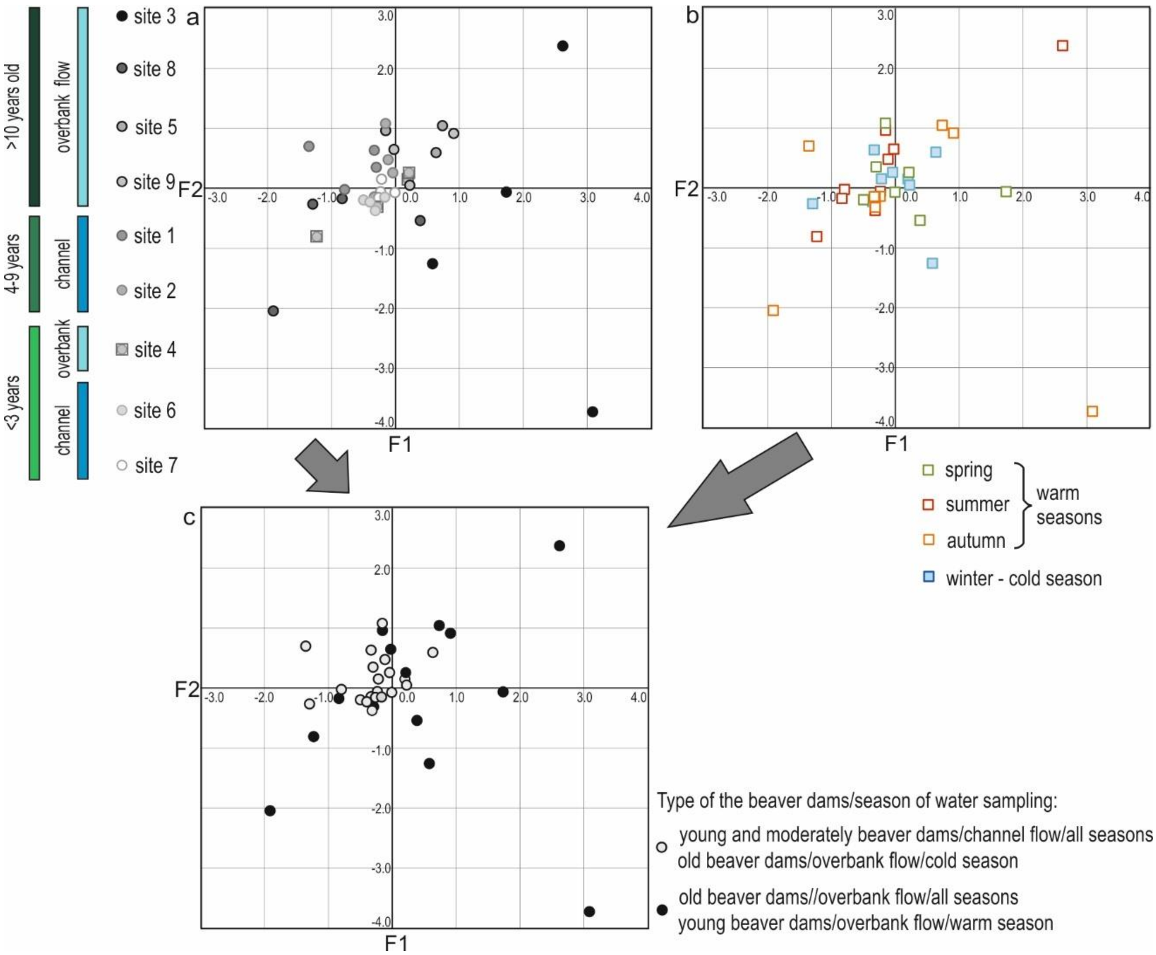

300 **Figure 7: Results of factor analysis (factor scores) for the differences between inlet values and streams below beaver ponds, Dc [%]. The water samples were classified according to study site (a) and season (b). The combined results are also shown (c).**

3.3 Variation of physico-chemical parameters in the longitudinal and vertical stream profiles

As demonstrated by the longitudinal profiles (Figs. 8 and 9), the older, overbank flow beaver pond sequence (site 3) has a greater influence on the physico-chemical parameters of water than the young, in-channel single pond (site 6). The greatest differences in the physico-chemical parameters at site 3 were seen between the free-flowing upper sections and the inside of the ponds; these changes tended to be partially neutralised in the stream below the beaver dam. The largest differences observed at site 3 were a decrease in NO_3^- within the ponds (-95.4%) and a decrease in SO_4^{2-} both within (-64.5%) and downstream (-71.5%) of the ponds.

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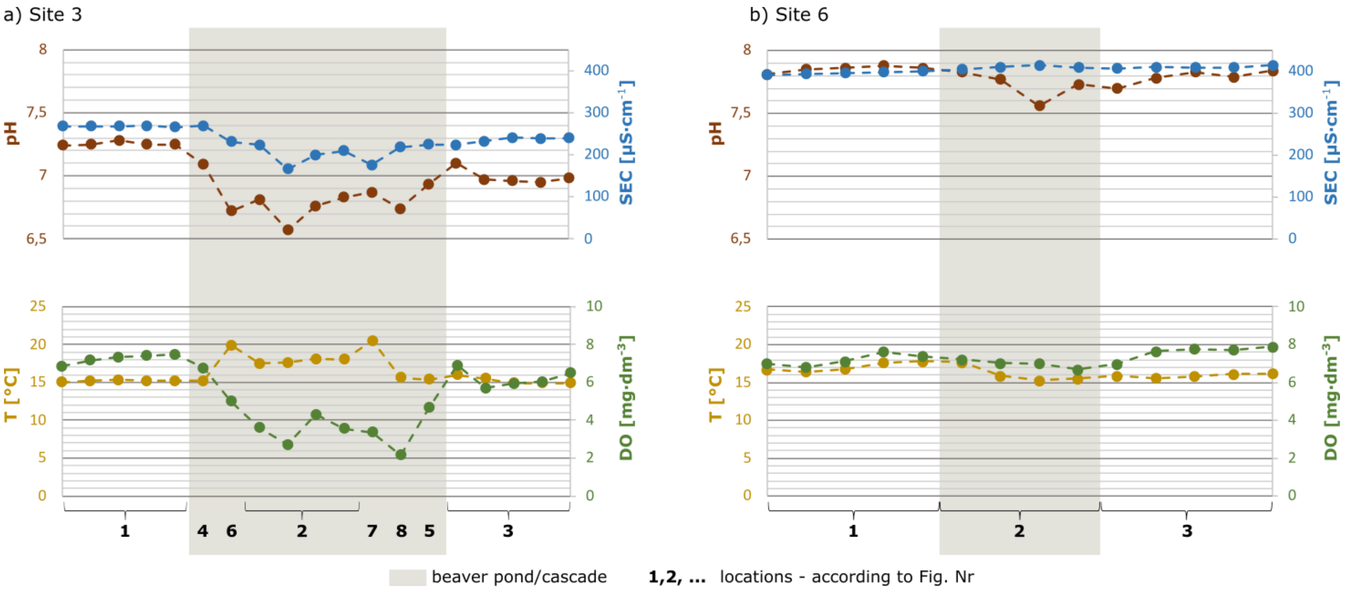

310 **Figure 8: A longitudinal profile of the physico-chemical parameters at study sites 3 (a) and 6 (b) (10 September 2023).**

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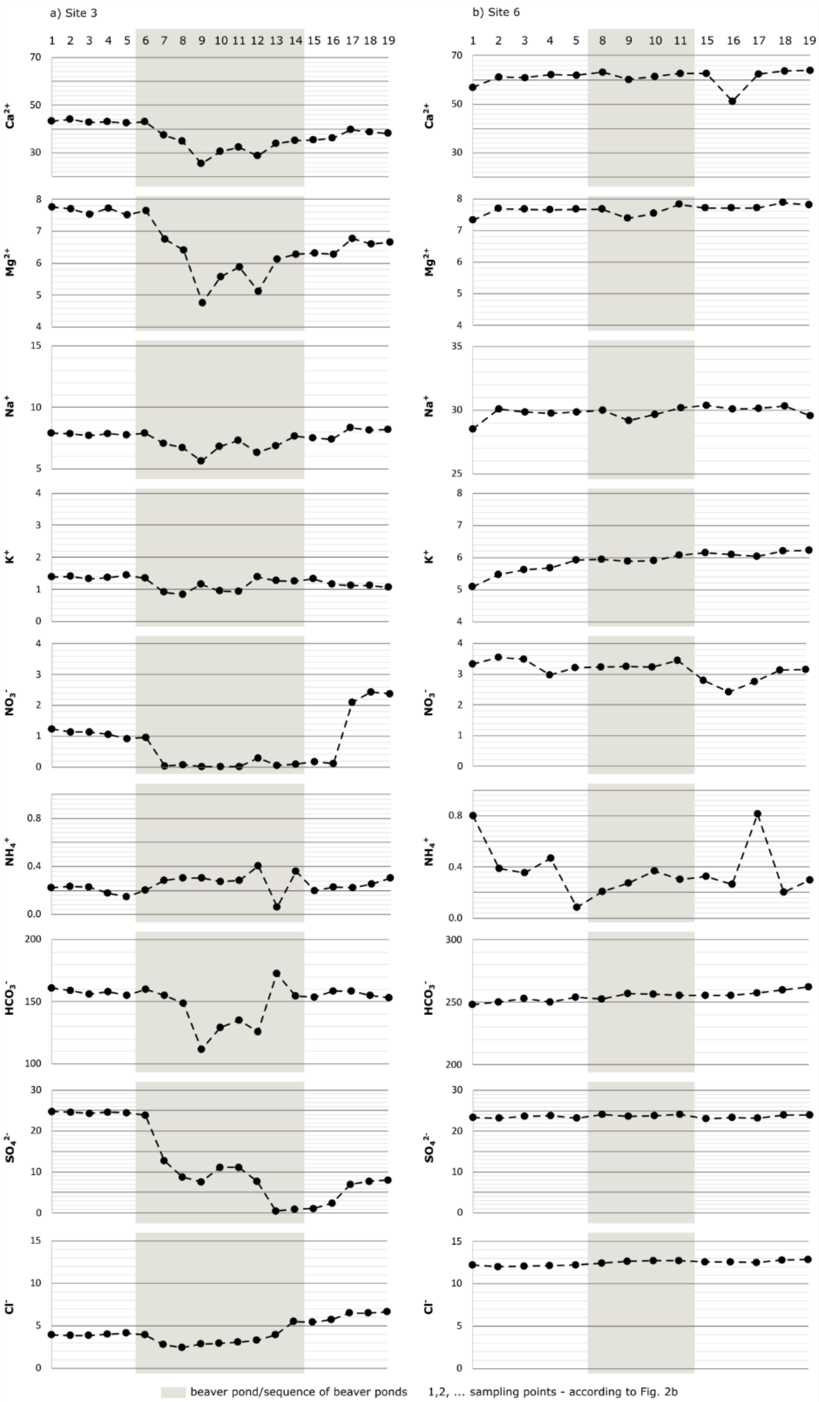

Figure 9: Concentrations of the chemical components of water [mg·dm-3] in the longitudinal stream profiles at study sites 3 (a) and 6 (b) on 10 September 2023.

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There were significantly greater vertical variations in physico-chemical parameters in the old, overbank flow beaver pond (site 3) than in the young, in-channel beaver pond (site 2). DO, pH and T were found to decrease with pond depth in both studied beaver ponds; however, the range of variation was greater at site 3 than at site 2 (Fig. 10). At site 3, the outflow water parameters (observed and measured near the base of the dam) were notably different from the top of the dam. The differences in concentrations of chemical components between the surface and the bottom of the outflows in this study site were generally greater than the changes observed between the surface and bottom of the middle of both ponds (Fig. 11).

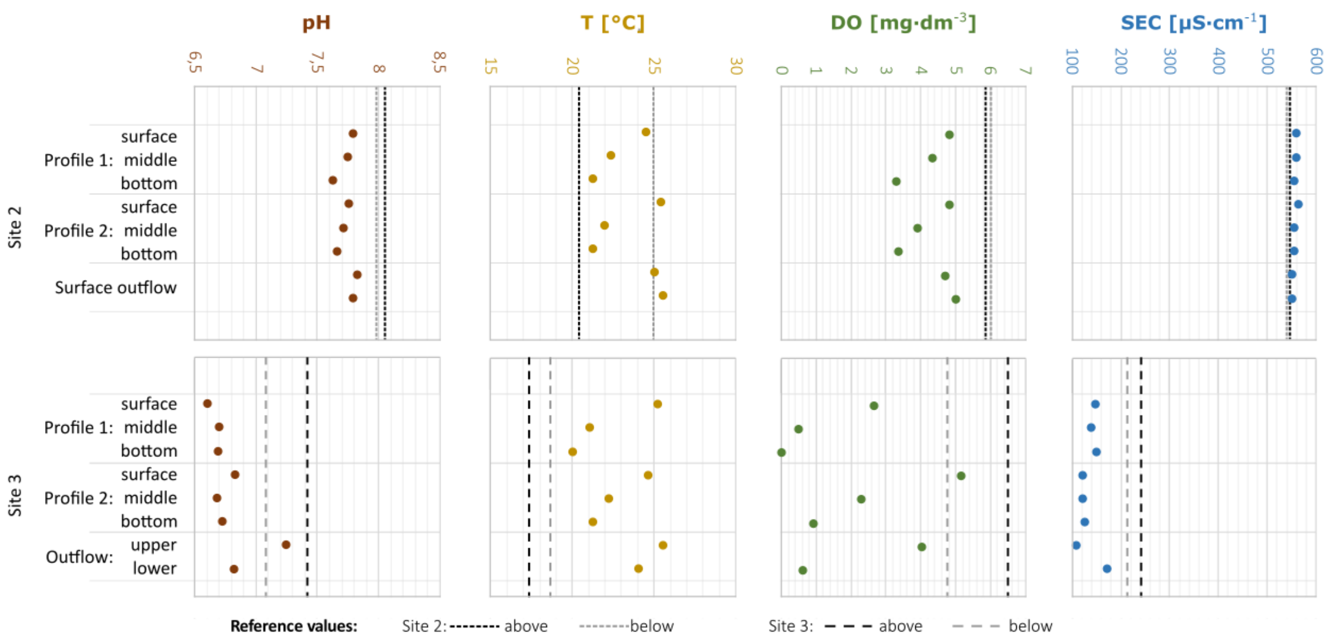

Figure 10: Differentiation of physico-chemical parameters in the vertical profiles of study sites 2 and 3 (10 July 2024).

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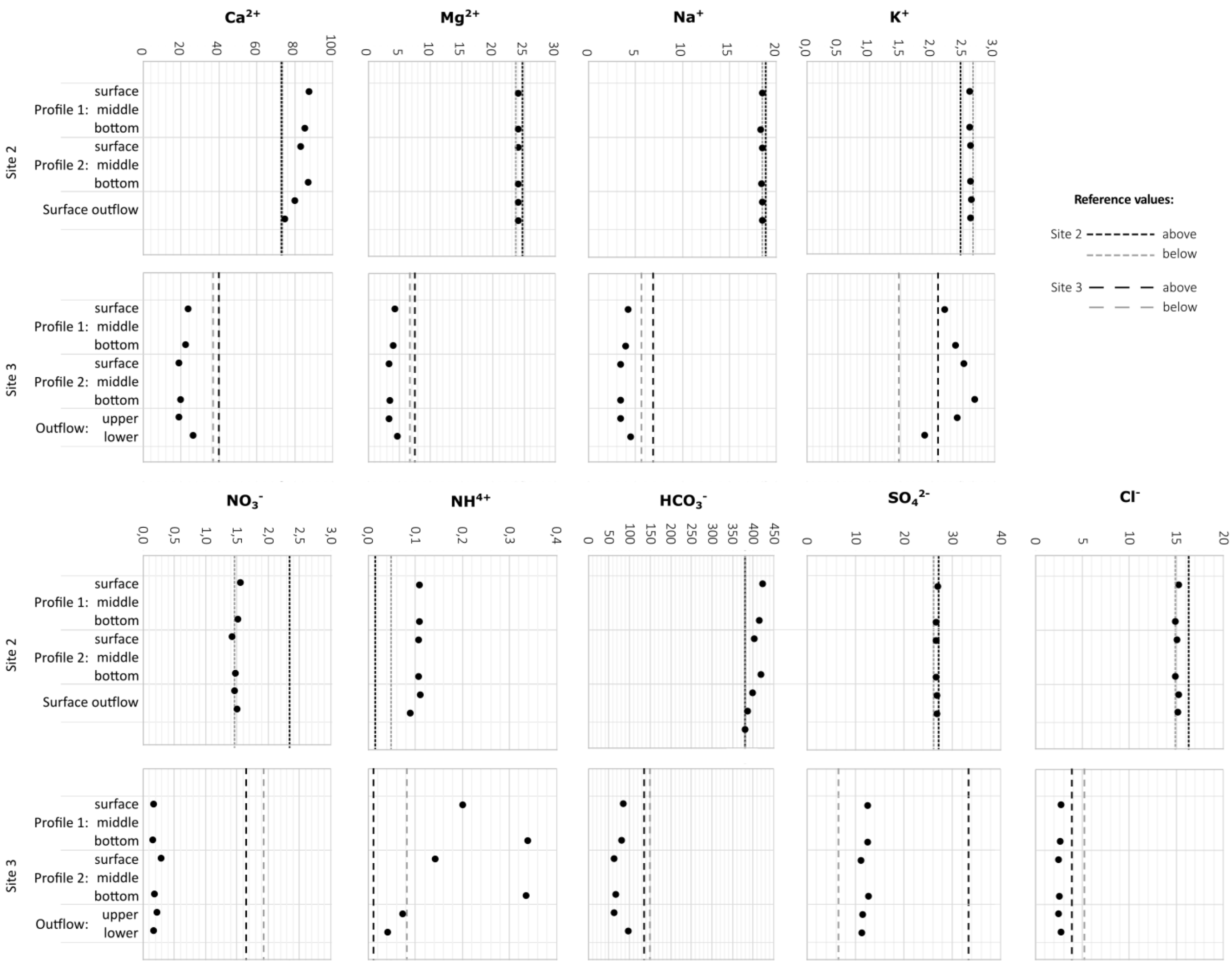

Figure 11: Concentration of the chemical components of water [mg·dm-3] in the vertical profiles of study sites 2 and 3 (10 July 2024).

3.4 Study limitations

325 One of the main objectives of this research was to examine the high diversity of streams occupied by beavers across the Western Carpathians in order to analyse the physico-chemical changes related to various properties of the pond sequences, such as their age, size and type. However, the spread of the study sites across a vast area restricted the number of samples collected to one sample per site each season because of time and cost constraints. In addition, dam failures resulting from floods and their targeted elimination during the research period decreased the overall sample size by half. The remaining study

330 sites may have been affected by continuous dam maintenance by beavers. In the most extreme cases, temporal breaches of the dam may have been overlooked after its reconstruction. Moreover, since the study focused on the base flow conditions, early

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spring high flows have been omitted, which likely explains the similarities between the results from the late spring and the summer.

The assessment of the impact of individual characteristics of beaver dam sequences may be constrained by the interconnections between some variables. Beaver ponds tend to be more persistent in smaller streams, and the length of the beaver occupancy seems to be related, to some extent, to the longitudinal and lateral development of the pond sequences. However, the estimation of mutual correlations was limited by the use of categorical values. Continuous values for the factors representing beaver pond age could not be obtained from the available sources, and the categorisation of the number of ponds was carried out because of the dynamics of this variable during the study period.

4. Discussion

4.1 Biogeochemical processes that control stream water chemistry triggered by the presence of beaver dams

The extensive distribution of the study sites resulted in a diversified representation of initial physico-chemical water properties that correspond to various geological features. Higher SEC and higher concentrations of most of the major ions were found in streams that drain catchments dominated by shales in their bedrock (sites 1, 2, 4-6), and they were lower in streams that drain catchments dominated by sandstones (3, 7, and 8). This pattern is characteristic of the whole of the Outer Carpathians (Siwek, 2021). Despite the diversity of the selected Carpathian streams, since we based further analysis on concentration differences of physico-chemical parameters rather than raw concentrations, our results indicated that there are several patterns in the changes in stream water chemistry triggered by the presence of beaver dams in stream channels. These changes are caused by specific biogeochemical processes that occur in newly formed aquatic environments, such as beaver ponds.

The clear decrease in DO concentrations within the beaver ponds compared to the DO concentrations above the ponds (at all study sites) suggests that DO is consumed in the oxidation processes of organic matter. A beaver-driven decrease in stream DO concentrations was also found by Błędzki et al. (2011) and Stevenson et al. (2022). Detailed investigations carried out in July 2024 at sites 3 and 6 showed that beaver pond water contains high concentrations of total organic carbon (TOC). At site 3, TOC exceeded 13 mg·dm^{-3}. Moreover, TOC concentrations were almost three times higher within the ponds than in the streams that flow into the ponds (data not shown). This indicates the deposition of organic matter supplied from upstream and/or the in situ production of organic matter via the growth of vegetation in the beaver ponds. Increased organic matter deposition in beaver ponds due to reduced stream flow velocity is often reported in the literature (e.g., Pollock et al., 2003; Green and Westbrook, 2009).

The oxidation of organic matter in ponds resulted in decreased oxygen and SO_4^{2-} concentrations at most of the study sites. Under the anaerobic conditions that prevail at the bottom of ponds (as measured at site 3 in July 2024; see Fig. 10), SO_4^{2-} can

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be reduced to H_2S. These reactions are carried out by microorganisms through the microbial sulphate reduction process, where SO_4^{2-} acts as a specific electron acceptor in the anaerobic oxidation of organic matter (Sutton-Grier et al., 2011). The reduction of SO_4^{2-} concentrations in streams with beaver dams has previously been identified and attributed to the expansion of anaerobic conditions (Larsen et al., 2021). According to Naiman et al. (1986; 1994), large accumulations of detritus, in combination with decomposition in expanded wetted areas, result in the development of anaerobic biogeochemical processes.

Aerobic and anaerobic oxidation of organic matter (the process of ammonification) leads to the formation of NH_4^+ ions. In our study, the ammonification process was indicated by the marked increase in NH_4^+ concentrations in most of the beaver ponds studied in summer. The increase in NH_4^+ concentrations in ponds may also partly be explained by the production of this ion during the denitrification process, as indicated by a marked decrease in NO_3^- concentrations in the studied ponds. Denitrification reduces NO_3^- to NH_4^+ or gaseous N_2 under anaerobic conditions in water. Reduced DO concentrations in the studied ponds could positively influence the denitrification processes in beaver impoundments, as suggested in previous studies by Lazar et al. (2015), Wegener et al. (2017) and Dewey et al. (2022). According to Lazar et al. (2015), denitrification in beaver ponds can remove 5–45% of NO_3^- loads at the catchment scale.

The decomposition of organic matter results in the formation of organic acids, which appears to be the cause of the marked decrease in water pH in the studied beaver ponds. According to David and Vance (1991), organic acids constitute most of the dissolved organic carbon in streams and lakes. Strong organic acids with high dissociation capacities significantly decrease water pH (Driscoll et al., 1989). The decrease in stream pH caused by the presence of beaver dams is rarely reported in the literature. In fact, beaver dams most often cause an increase in the stream water pH. For example, in the Appalachian Mountains, USA (Smith et al., 1991; Cirmo and Driscoll, 1993; Cirmo and Driscoll, 1996; Margolis et al., 2001) and the lowlands of Devon, England (Puttock et al., 2017), the pH of stream water increased below beaver dams due to decreased concentrations of acidic ions such as NO_3^- and SO_4^{2-}. According to Margolis et al. (2001), the reduction of NO_3^- and SO_4^{2-} is one of the largest contributors to the acid neutralising capacity of beaver ponds. In the streams we studied, pH decreased despite the decrease in acid ion concentrations (i.e., NO_3^- and SO_4^{2-}) in the stream water below the beaver dams. Furthermore, the streams and beaver ponds studied in the USA and England (Smith et al., 1991; Cirmo and Driscoll, 1993; Cirmo and Driscoll, 1996; Margolis et al., 2001; Puttock et al., 2017) had similar organic carbon concentrations to the streams and ponds in our study. However, the streams that fed the beaver ponds in the USA and England were more acidic (<7 pH) than the streams we studied (>7 pH). The differing water pH is likely a key factor in explaining the difference in results because the intensity of organic matter decomposition increases with increasing pH, which is also associated with better conditions for the growth of the bacteria involved in decomposition (Walse et al., 1998). Higher pH values in the streams that feed the beaver ponds likely facilitate the greater decomposition of organic matter, which explains the increased production of organic acids in the ponds. Organic acids play an important role as a source of acidity in beaver ponds (Cirmo and Driscoll, 1993). As a result, the pH of the water in the beaver ponds we studied is lower than the pH of the water in the streams above the ponds.

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Our studies indicate that the processes of denitrification, decomposition and oxidation of organic matter, which modify the physico-chemical properties of the beaver pond water, determine the physico-chemical properties of the water below the beaver ponds. The water that flows out of the ponds takes on the physico-chemical properties of the pond water. This is evidenced by the similar directions of changes in physico-chemical parameters within and below the beaver ponds compared to the streams above the ponds. However, the changes in the physico-chemical parameters in the water below the ponds are smaller than the changes in the ponds. This is the result of processes specific to running water that cause the physico-chemical properties of pond water to return to the original properties of the stream water. For example, deoxygenated water flowing out of the ponds is slowly reoxygenated, facilitated by the turbulent water flow in the mountainous stream channels. DO concentrations in the streams below the beaver ponds are still lower than in the streams above the ponds, but it is higher than the DO concentrations in the ponds. Similar decreases in DO within beaver ponds and the subsequent reoxygenation of downstream waters have been observed in previous studies (Smith et al., 1991; Harthun, 2000; Błędzki et al., 2011; Ecke et al., 2017). The return of the stream water to aerobic conditions results in the intensification of the nitrification processes, as evidenced by increased NO_3^- concentrations and decreased NH_4^+ downstream of the beaver ponds in our study. NO_3^- concentrations below the beaver ponds were still lower than upstream of the ponds, and the NH_4^+ concentrations were still higher, but the differences between the streams above and below the beaver ponds were smaller than the differences between the stream above the ponds and within the ponds. The increase in DO concentrations in the streams below the ponds also favours the oxidation of organic matter and the production of organic acids, which in turn increases the pH of the stream water compared to the pond water. The reoxygenation of the water in the streams below the beaver ponds involves a series of biogeochemical processes, such as the aerobic oxidation of organic matter and nitrification, which counterbalance the effects of the ponds. Our longitudinal study showed that the changes in the physico-chemical properties of the water were partially neutralised within a relatively short downstream distance from the ponds (<100 m).

In the studied streams, the effect of beaver dams on changes in the concentrations of major ions (with the exception of SO_4^{2-}), was negligible (i.e., their effect on Na^+ and Mg^{2+}) or moderate (i.e., Ca^{2+}, K^+, HCO_3^- and Cl^-). Observed changes in these ions were not statistically significant. The non-significant effect of beaver dams on Cl^- is similar to the results reported by Margolis et al. (2001). No clear trends were observed for HCO_3^- concentrations, despite their connection to SO_4^{2-} reduction and NH_4^+ production in other studies (Cirmo and Driscoll, 1993; Larsen et al., 2021).

4.2 Role of seasonality in the beaver dams impact on the water chemistry

For most physico-chemical parameters, the greatest changes were observed during the warm season (spring, summer and autumn) within and below the beaver ponds compared to the streams above the ponds. Smaller changes were observed in the winter for all study sites. This result can be explained by the higher intensity of the biogeochemical processes that modify the chemical composition of water at higher temperatures. In the winter, the water temperature in the streams and the surface of the ponds was low; it did not exceed 1.5ºC. Winter water temperatures in ponds are generally not expected to exceed 4ºC, the

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temperature at which water has the highest density (Vega and Abascal, 2005). Biogeochemical processes in beaver pond water and sediments, such as organic matter decomposition, denitrification and microbial sulphate reduction, are very slow at low temperatures (Qu et al., 2022). The situation is different in the warm season, especially in the summer, when water temperatures in the studied streams and the near-surface layer of the ponds generally exceed 15ºC and sometimes rise above 20ºC. In the summer, pond water temperature decreases noticeably with depth, but in shallow ponds (with depths up to 1 m), the difference in water temperature at the surface and the bottom is only a few degrees (see Fig. 10). Therefore, biogeochemical processes in pond water occur more intensively in the warm seasons than in the winter. As a result, there are intensive physico-chemical transformations in the stream water flowing into the ponds in the warm seasons. The increase in NH_4^+ concentrations and the decrease in NO_3^{--} concentrations in the studied beaver ponds were particularly prominent in the warm period of the year due to the intensive ammonification and denitrification processes. This is consistent with the findings of Margolis et al. (2001) and Law et al. (2016): the greatest NO_3^- decrease downstream to beaver ponds occurs in the summer. However, it should be noted that the decrease in NO_3^- concentrations in the beaver ponds and streams below the ponds in the summer is partly related to the nitrogen fixation process, which is associated with increased microbial activity in sediments mediated by anaerobic conditions, as well as uptake by aquatic vegetation (Naiman and Melillo, 1984; Maret et al., 1987; Songster-Alpin and Klotz, 1995). Furthermore, the decrease in SO_4^{2-} concentrations in the studied ponds and downstream of the beaver dams was mainly observed during the warm period. This is likely due to the high rate of anaerobic oxidation of organic matter during the summer, which takes place despite the relatively low redox potential of the water under summer low flow conditions (Smith et al., 1991; Cirmo and Driscoll, 1993; Margolis et al., 2001).

Our study showed low seasonality in terms of the changes in major ion concentrations (with the exception of SO_4^{2-}) within and below beaver ponds compared to the streams above the ponds. However, a slight decrease in the concentrations of Ca^{2+}, Mg^{2+} and Na^+ within and below the beaver ponds was observed during the summer at most of the studied sites. These results may be related to the H+ ion exchange processes in the sediments, which were indicated by a decrease in water pH. Based on the small changes in the concentrations of these ions, this process likely plays a minor role in modifying the chemical composition of beaver ponds. According to Cirmo and Driscoll (1993), beaver pond sediments and vegetation act as temporal sinks for Ca^{2+}, Mg^{2+} and Na^+ in the summer, presumably as a result of H^+ exchange and their enhanced biological uptake during the growing season. The slight increase in K^+ concentrations within and below the studied beaver ponds in the summer and autumn may indicate the decomposition and mineralisation of organic matter as a source of K^+. Lizarralde et al. (1996) found that the net K^+ export in beaver-occupied streams was attributed to the decomposition of leaf litter inputs.

4.3 The effects of beaver dam age and beaver pond geomorphic type on water chemistry

Our research suggests that the age of beaver dams and the geomorphic type of beaver ponds (i.e., overflowing vs. in-channel) play important roles in altering the chemical composition of stream water (Fig. 12). For example, the magnitude of the decrease in pH was strongly related to the age of the beaver impoundments and was moderately dependent on their type: the decrease

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in pH was greater in streams with old beaver dams and overflowing ponds than in streams with young dams and in-channel ponds. Similarly, the magnitude of the decreases in DO and SO_4^{2-} were found to be positively related to the age of the beaver pond sequences. The decreases in pH, DO and SO_4^{2-} concentrations in beaver ponds are regulated by the decomposition and aerobic/anaerobic oxidation of organic matter. Therefore, knowing the availability of organic matter in the ponds is important to determine changes in these parameters. According to Gurnell et al. (1998), Meentemeyer and Butler (1999), Bason et al. (2017) and Puttock et al. (2018), older ponds have greater pools of organic matter deposited on their bottoms. Our study also suggests that the age of the pond, which determines the amount of organic matter in the pond, plays an important role in the degree of change in pH, DO and SO_4^{2-} concentrations. This was confirmed by the longitudinal and vertical approach studies. There was a greater longitudinal and vertical transformation of physico-chemical properties, such as T, DO and pH, in old beaver ponds compared to young beaver ponds. Decreasing DO with beaver pond depth is consistent with the results reported by Stevenson et al. (2020). In our study, the maximum difference between surface and bottom water temperature (5.2°C) was close to that observed by Harthun (2000). Harthun (2000) also points out that physico-chemical properties in beaver ponds, particularly within the surface layer, may be sensitive to significant daily fluctuations in pH and DO due to algae photosynthesis during the day. Given the aforementioned vertical complexity of the water column and the diversity of beaver dams (in terms of type and outflow location) (Woo and Waddington, 1990; Ronnquist and Westbrook, 2021), we can conclude that the downstream effect of beaver impoundment is dependent on structural properties of the dam, which hinders generalisations of overall beaver impacts. This could explain the lack of consistency in terms of the effects of beaver dams on stream water chemical composition. A lack of consistency in the effects of beaver dams on pH changes has also been observed by Lizarralde et al. (1996), Harthun (2000) and Čiuldienė et al. (2020).

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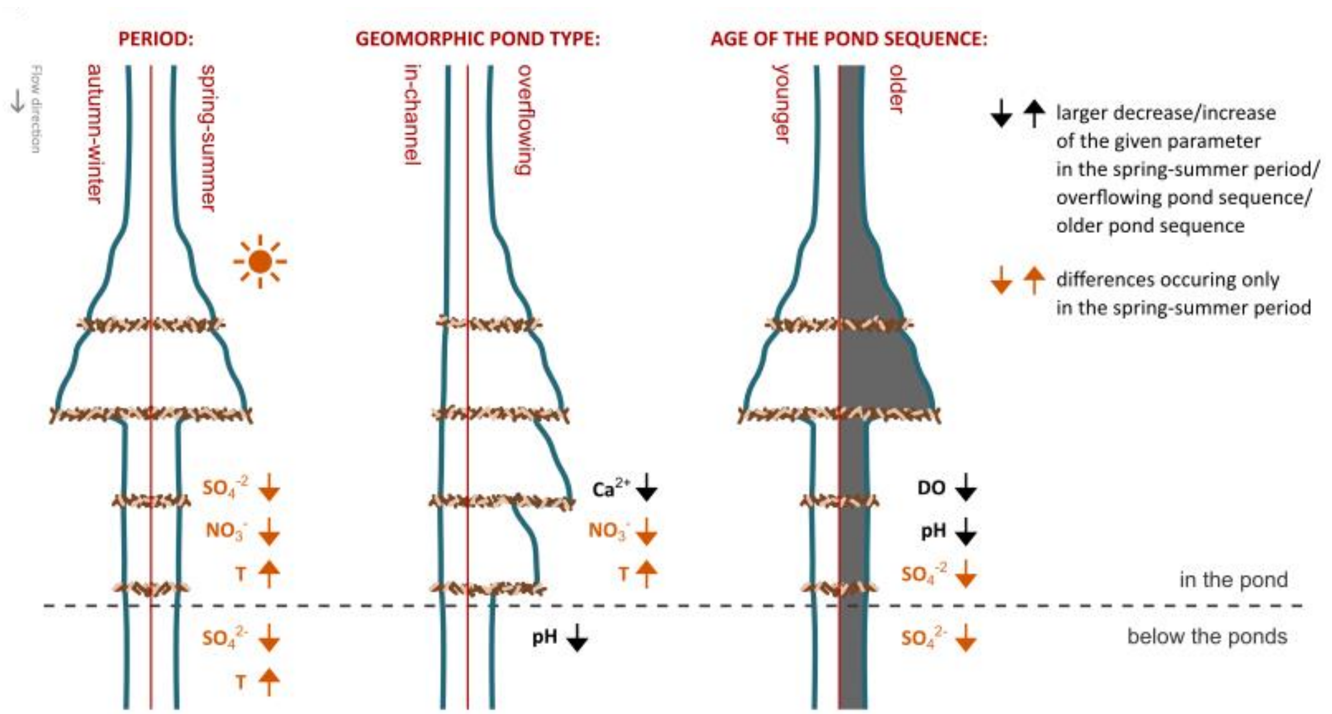

Figure 12: The role of season and beaver pond sequence characteristics in changes to physico-chemical water properties within and downstream of the beaver ponds.

The attenuation of NO_3^- concentrations in beaver ponds was significantly greater in overflowing ponds than in the ponds restricted to river channels. In the case of NO_3^-, the effect of geomorphological context appears to be more significant than the effect of pond age (contrary to their effects on DO). Similar to the present study, Bason et al. (2017) found that nitrogen fixation was not related to beaver pond age. The denitrification process requires anaerobic conditions, which are favoured in overflow ponds. Our study shows that the lower DO concentrations in overflowing ponds during warm seasons is connected to greater temperature rises than in in-channel ponds. This is likely due to the larger open water area compared to the more shaded channel impoundments. Furthermore, denitrification takes place in the flooded riparian zones of the overbank ponds. As demonstrated by Puttock et al. (2018), nitrogen storage per unit area in beaver pond sediments increases with pond size. It can therefore be concluded that the relationship between an overflow pond type and the decrease in NO_3^- concentrations is indicative of the enhanced nitrogen fixation at the bottom of territorially expansive ponds. In addition, the greater extent of NO_3^- reduction during spring runoff compared to the summer low flow, as observed by Maret et al. (1987), was attributed to higher sediment loads and seasonal pond area expansion. In addition, extensive beaver ponds support the development of aquatic vegetation, which may make large contributions to the nitrogen cycle. Our study indicates that the differing effects of old/young beaver ponds or overflowing/in-channel beaver ponds are determined by the physico-chemical parameters, which are subject to strong seasonal changes. This was summarised in the PCA: the seasonal factor that controls changes in DO,

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SO_4^{2-}, NO_3^- and NH_4^+ concentrations for both the ponds (F2) and the streams below the ponds (F1) clearly grouped the water samples by age category and pond geomorphic type.

The geomorphic type of beaver ponds (i.e., overbank flow vs. in-channel flow), also plays an important role in altering the concentration of Ca^+: higher Ca^+ decrease rates were observed in overflowing beaver ponds than in in-channel beaver ponds. The decrease in Ca^{2+} concentration in overflowing ponds is probably related to calcium carbonate ($CaCO_3$) precipitation from the aqueous solution. The precipitation of $CaCO_3$ is favoured by the removal of CO_2 from the pond water due to an increase in water temperature. Our study shows that the temperature increase in overflowing ponds is higher than in in-channel ponds during warm seasons. Such interactions between water temperature, water CO_2 concentration and $CaCO_3$ precipitation were previously reported in the literature, e.g. Korchef, Touaibi (2020), Escoffier et al. (2023). Furthermore, Escoffier et al. (2023) pointed out that the precipitation of calcium carbonate causes a decrease in the alkalinity (pH) of water, as the bicarbonate concentration in the water is reduced. Such pH decrease, coinciding with Ca^{2+} concentration decrease, occurred in the overflowing beaver ponds.

5 Conclusions

This study addressed the relatively new ecosystem role of beavers in the mountainous environment of the Western Carpathians, where beaver populations have recently recovered after more than a century of absence. We found that beaver dams had a strong impact on the physico-chemical water properties inside the ponds, including an increase in temperature and decreases in pH, dissolved oxygen and nitrate and sulphate concentrations. These changes were the result of specific biogeochemical processes occurring in the newly formed aquatic environments of beaver ponds. Although these processes affect the downstream sections of the streams, in general, they were partially attenuated within a short distance of the dam. The processes involving nitrate and sulphate decrease were found to be more effective during the warm period of the year. Moreover, the study involved a comparison of the two geomorphic types of beaver pond complexes. A larger decrease in nitrate and calcium concentrations occurred in ponds that overflow river banks, and higher pH decrease was identified below overflowing ponds than below ponds restricted to the banks. The denitrification process, which is responsible for the decrease in NO_3^- concentration, requires anaerobic conditions in the pond water, which are favoured in overflowing ponds due to greater temperature increases than in in-channel ponds during warm seasons. Furthermore, the higher temperature in overflowing ponds leads to the removal of CO_2 from the pond water and the precipitation of $CaCO_3$, which is probably responsible for the decrease in Ca^{2+} concentration in the overflowing ponds. The age of the dams was identified as an important factor affecting the decrease in dissolved oxygen and pH in beaver ponds and the decrease in sulphate within and below the ponds. These changes were regulated by the decomposition and aerobic/anaerobic oxidation of organic matter, which was more abundant in older ponds. Although much is known about the contribution of beavers to water purification through nitrogen fixation, their

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less recognised role in sulphate reduction may be equally important from a water management perspective. Finally, the extensiveness and persistence of beaver pond complexes may be critical for the effectiveness of these processes.

Although most of the processes identified in the present study are consistent with previous research, our results are complemented by additional insights. Attention should be drawn to newly emerging issues, such as the widespread decrease in water pH as a result of beaver dams. These results indicate that there is still much to address in future research on the effects of beaver presence. A larger dataset would improve our understanding of the effects of beaver impoundments, especially in streams with varying inlet conditions, outflow types and topographic characteristics. Likewise, more data from representative mountainous and lowland streams, side-channel and main-channel ponds and various levels of geomorphic beaver activity would be useful. Lastly, further research is needed to identify the spatial and temporal durability of the influence of beaver dams and elucidate the thresholds that determine their impact on the ecological stream properties.

Author contributions (CRediT)

JW: Conceptualization, Project administration, Methodology, Investigation, Formal analysis, Visualization, Writing – original draft, Writing – review and editing

JPS: Methodology, Investigation, Formal analysis, Visualization, Writing – original draft, Writing – review and editing

MKS: Conceptualization, Funding acquisition, Project administration, Methodology, Investigation, Writing – review and editing, Supervision

EG: Investigation, Writing – review and editing, Supervision

Data availability

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

Competing interests

The authors declare that they have no conflict of interest.

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Appendix A – Variation in percentage changes of physico-chemical parameters at all study sites

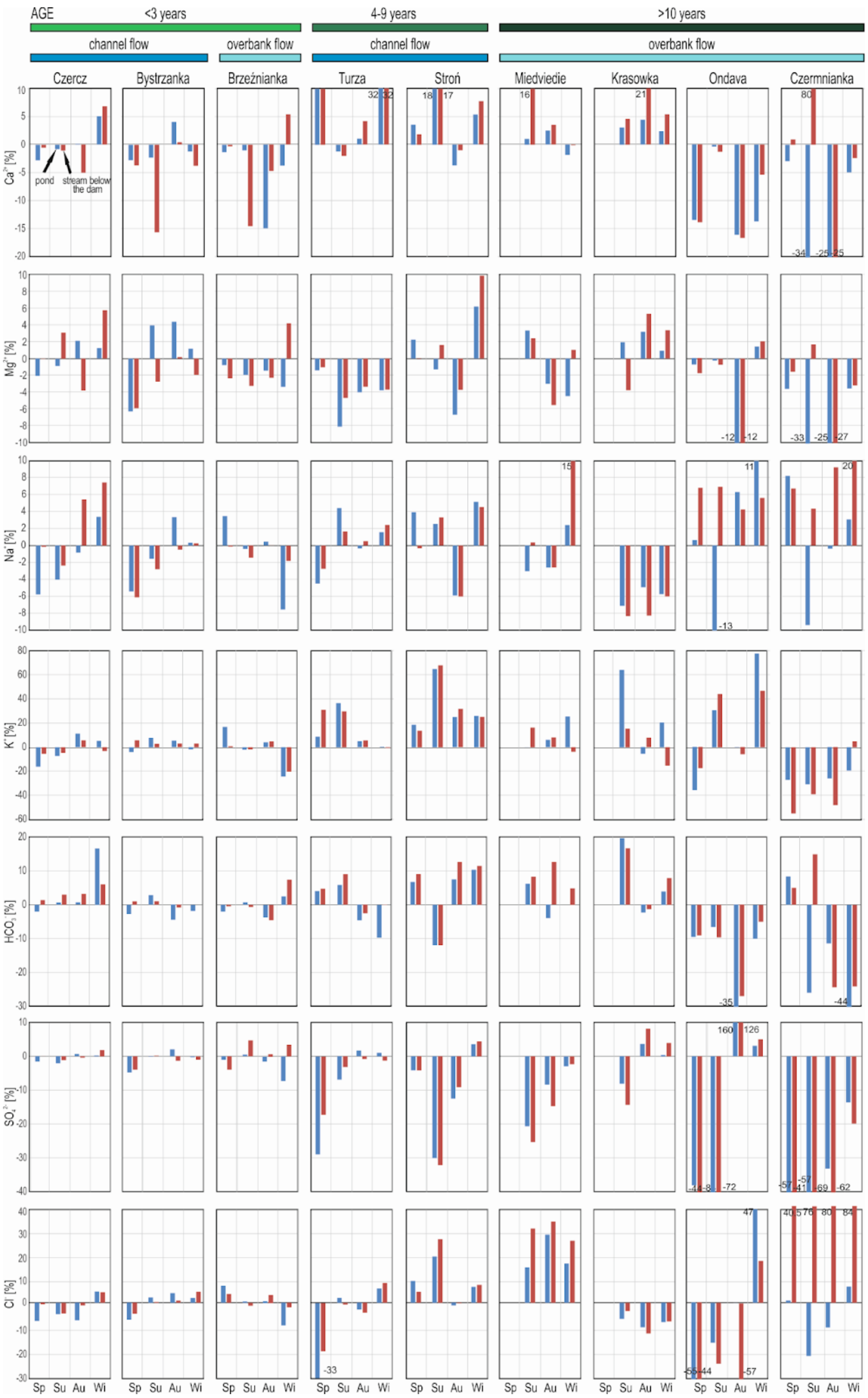

Figure A1: Percentage changes, DC [%], in main ion concentrations in and below beaver ponds compared to their upstream values (Sp – spring, Su – summer, Au – autumn, Wi – winter).

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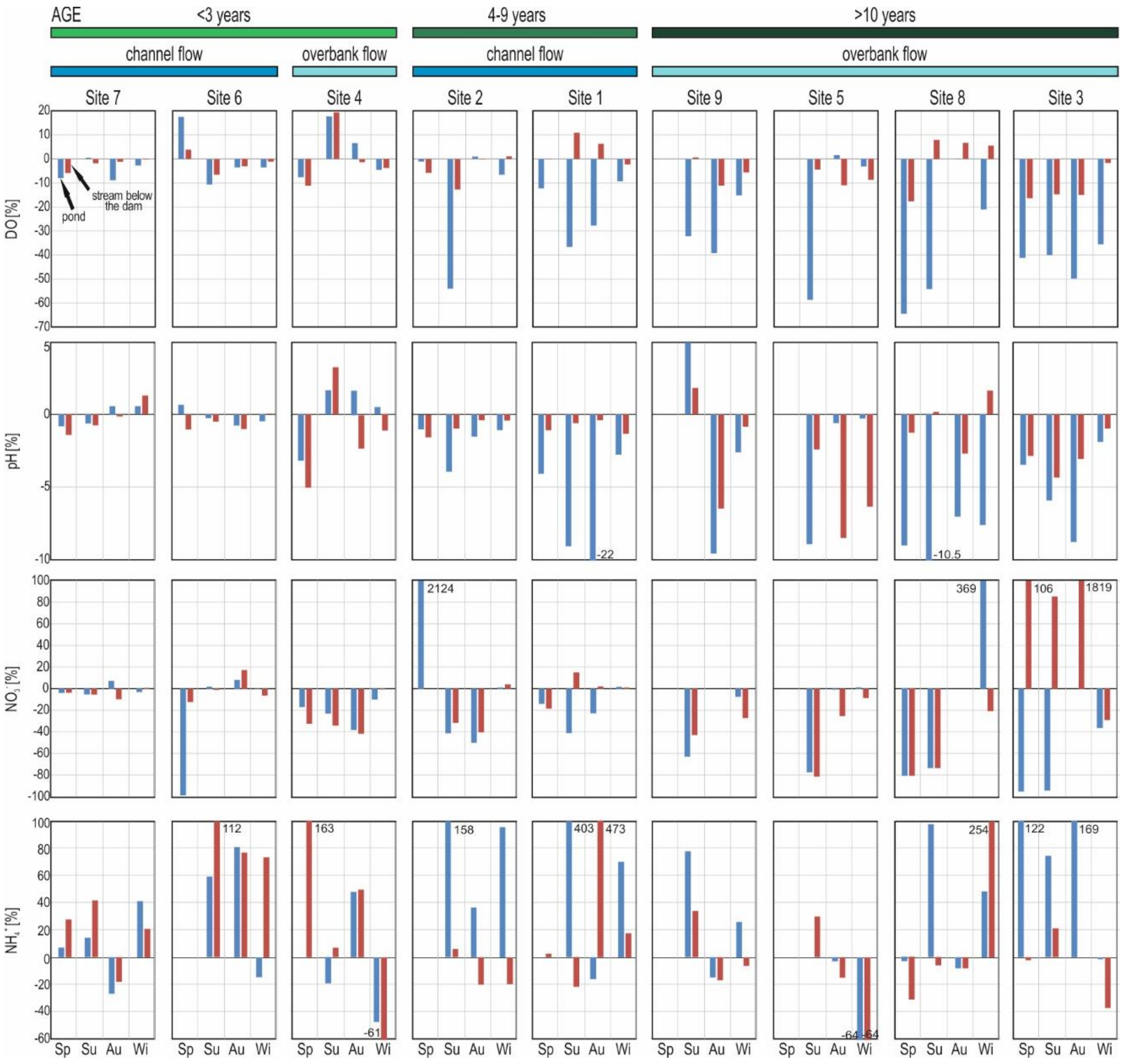

Figure A2: Percentage changes, DC [%], in pH, and DO, NH_4^+ and NO_3^- concentrations in and below beaver ponds compared to their upstream values (Sp – spring, Su – summer, Au – autumn, Wi – winter).

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Table A1: Statistical characteristics of absolute changes, |Dc| [%], of physico-chemical parameters values in ponds and streams below beaver dams in relation to values in streams before beaver dams (n=34). Average absolute changes >5% are marked in bold.

Parameters	Beaver ponds		Streams below the beaver dams	
	Average value	Standard deviation	Average value	Standard deviation
DO	**20.5**	19.7	**6.6**	5.6
SEC	4.4	6.2	4.3	5.0
HCO_3^-	**8.5**	9.9	**7.7**	7.2
Cl^-	**11.1**	12.7	**18.8**	24.1
SO_4^{2-}	**17.7**	32.1	**17.8**	28.0
Ca^{2+}	**7.8**	9.9	**10.2**	14.8
Mg^{2+}	4.7	6.8	4.0	4.8
Na^+	4.2	3.2	4.6	4.4
K^+	**19.4**	19.2	**17.5**	18.1
NO_3^-	**100.3**	363.7	**78.8**	308.9
NH_4^+	**54.4**	76.4	51.1	90.5
H^+	**294.9**	962.6	**57.8**	90.2