The effect of beaver ~~ponds~~ dams on ~~water~~ physico-chemical ~~composition~~ properties of stream water 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 has a significant impact on ecological processes making~~es its~~ beaver reintroduction an important environmental factor in ~~the~~ recolonised areas. Although the effects of beaver dams on stream water chemistry have been studied extensively, general conclusions are often limited by site specific conditions. Therefore, the aim of this study was to assess the impact of a geomorphic type and an age of beaver pond sequences on physico-chemical water properties in and below beaver ponds compared to upstream channel sections throughout the seasons.

This study ~~investigated~~ was conducted on nine beaver-inhabited streams distributed across the Western Carpathians (Poland and Slovakia). ~~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.~~The beaver ponds were classified into two geomorphic categories: overflowing river banks or confined to the river channel. The age of the ponds ranged from <2 years to >10 years. Water samples were collected above, within, and below beaver pond sequences under baseflow conditions during four seasons in 2022-2023.

In general, a greater ~~reductions~~ decrease in NO_3^- and SO_4^{2-} concentrations within and below the ponds was observed ~~were observed with increasing temperatures~~ during the warm ~~period (spring–summer)~~seasons than during the cold seasons. ~~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.~~ The age of ~~B~~beaver pond sequences ~~age~~ was found to be a more significant factor than the pond type. It was positively related to decrease in dissolved oxygen, SO_4^{2-} and pH in the ponds and decrease in SO_4^{2-} in downstream channel sections. A comparison between two geomorphic types of beaver ponds revealed that there was a greater decrease in NO_3^- and Ca^{2+} concentrations within overflowing ponds and a greater decrease in pH downstream of these ponds compared to in-channel ponds. Biogeochemical processes involving organic matter accumulated in beaver ponds, that include its decomposition and~~,~~ aerobic/anaerobic

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oxidation, as well as ~~and~~ $CaCO_3$ precipitation~~,~~ might be~~are~~ responsible for the observed differences~~changes of these physico-chemical parameters in stream water~~.~~.~~ The long residence time of water in overflowing beaver ponds fuels the dynamics of these processes.

The role of the age of beaver ponds suggest that ~~natural development of extensive beaver ponds and~~ their long-term persistence may be important~~crucial~~ for sustaining water purification processes. However, ~~F~~further research based on a larger dataset and a more frequent sampling strategy is needed ~~should aim~~ to identify the biogeochemical processes ~~that~~ occurring in beaver ponds under specific hydro-meteorological conditions: during low flow periods, snowmelt and rainfall events.

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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 and~~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 lead to ~~result in an~~ increased ~~in~~ 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 re-establishing Carpathian populations was successfully carried out between~~from~~ 1980 and ~~–~~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).

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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. Moreover, to our knowledge, most of the studies on the impact of the 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 mountains (Giriat et al., 2016; Gorczyca et al., 2018). The species recently became a prominent environmental factor across the Carpathian mountains after centuries of absence, therefore understanding its impact on this area is particularly important.

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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 downstream of beaver ponds compared to upstream river sections (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. Consequently,~~;~~ they have the potential to be considered as 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 the physico-chemical stream water parameters may not reflect generally recognised trends due to the influence of local site-specific characteristics (Kalvīte et al., 2021). Brazier et al. (2021) also pointed out the potential differences in the impacts of a single pond compared to a sequence of multiple ponds. These may hinder deriving general conclusions regarding the impact of complex beaver-mediated modifications to river channels, especially when contradictory patterns are observed (Majerova et al., 2015; Weber et al., 2017). The identification of factors reflecting the diversity of beaver ponds and their effects on water chemistry, would improve the understanding of the effects of beaver presence in river systems. The age of beaver ponds was commonly proposed as a such feature in previous studies on upstream-downstream gradients of physico-chemical parameters in beaver-occupied streams. For example, Bason et al. (2017) found a greater reduction of suspended solids in older dam sequences compared to younger ones. Metal sequestration rates and a sediment organic matter content inside beaver ponds also rise with the pond age according to the study of Murray et al. (2021).

Hydrological and thermal differences were observed between various geomorphic units within beaver ponds, representing e.g. main channel, its margins and backwater areas (Majerova et al., 2020). The share of such units, especially related to the floodplain inundation, was then suggested as a potential geomorphic factor that could explain differences between study sites (Murray et al., 2021). Spatially expansive beaver ponds are expected to facilitate a higher proportion of low velocity areas, increase in water residence time, extent of a hyporheic zone, overbank sedimentation and growth of aquatic vegetation, compared to the ponds constrained to the river channel. Both beaver pond age and its geomorphic type may correspond with the prolonged sediment-water interactions resulting in the enhanced biogeochemical processes.

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), with regard to seasonality and pond characteristics. The paper focuses on answering the following three questions:

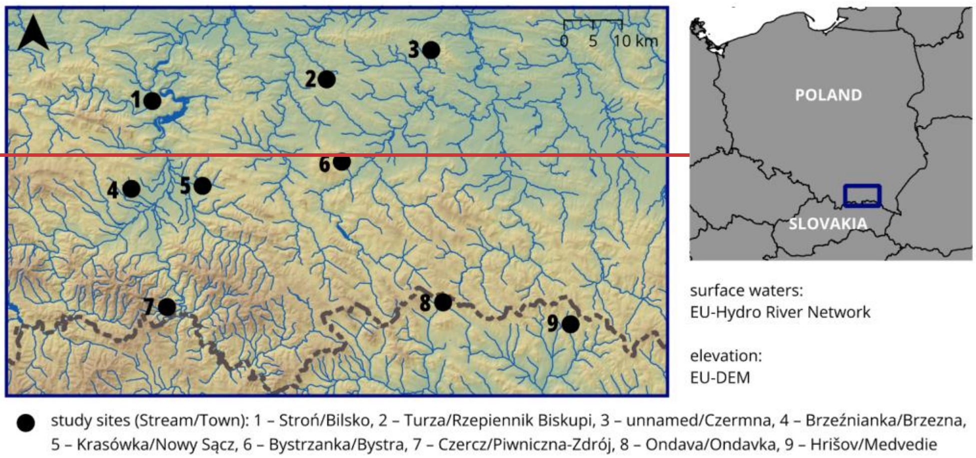
1) Which beaver-driven biogeochemical processes control changes in the physico-chemical parameters of stream water?How do physico-chemical water parameters change between river sections located upstream of, within, and downstream of beaver ponds, and what biogeochemical processes might be responsible for these differences?
2) Does seasonality alter the effects of beaver dams on stream water chemistry?How do these differences vary seasonally?
3) How does beaver dam age and beaver pond geomorphic type affect stream water chemistry?How are these differences affected by the geomorphic type and age of beaver ponds?

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). Streams draining areas underlain by shales and mudstones are typically characterised by higher concentrations of bicarbonates, calcium and magnesium ions due to increased weathering of carbonates and clay minerals, while streams in areas composed mainly of sandstone are usually more diluted and characterised by lower specific conductivity (e.g. Siwek, 2021; Solár and Tomaškovič, 2023).

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). 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).



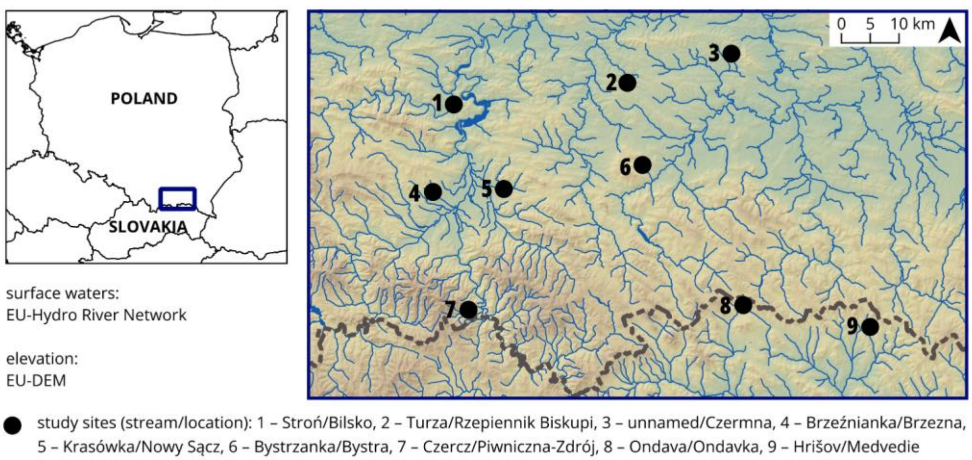


Figure 1: Study area.

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).

All of the catchments consisted of a mixture of forest and agricultural areas, i.e. arable lands and meadows. Despite the widespread abandonment of agricultural land and the generally low-to-moderate intensity of agricultural practices in the mountainous catchments (Pazúr et al., 2014; Kolecka et al., 2017), the impact of these activities may be significant locally, as evidenced by the increase in nitrate concentrations observed in the Ondava catchment due to the use of fertilisers (Pekarova et al., 2006; Balejčíková et al., 2020). Overall, agricultural practices in the Polish and Slovakian Carpathians are mostly extensive, characterised by low–input management and mowing and grazing on a small-scale (Pazúr et al., 2014; Kolecka et al., 2017; Affek et al., 2023). According to national agricultural statistics (Central Statistical Office of Poland, 2025), the average consumption of mineral fertilisers (NPK) in the Małopolskie and Podkarpackie Voivodeships remains one of the lowest in the country (80–95 kg NPK ha^{-1} year^{-1} compared to the national average of ~125 kg ha^{-1}) and has shown little change over the last two decades. Similar situation is observed in the northern part of Slovakia where the average use of industrial fertilisers is less than 60 kg NPK ha^{-1} year^{-1} (Siman and Velísková, 2018). Consequently, the direct inflow of nutrients from fertilisers into watercourses is minimal, although local enrichment may occur near farms or areas of intensive grazing. In contrast, domestic wastewater was identified as the main source of stream water pollution in the rural areas of the Polish Carpathians (Siwek, 2021). The intensity of housing development across the study area ranged from negligible levels to artificial surfaces covering up to 4% of the area and containing a few hundred buildings.

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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 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 height of the beaver dams studied did not exceed 1.5 m. In most dam sequences, the ponds were directly connected. The only exception was site 7, where short sections of free-flowing reaches were observed between the ponds. For further analyses, the study sites were classified based on the beaver pond characteristics. Two geomorphic types were distinguished considering the extent of a beaver dam: in-channel (dams within river banks) or overflowing (dams extending over river banks and leading to inundation of adjacent parts of river valley). The area covered by the overflowing ponds was two to seven times larger than their respective river channels which indicates a substantial proportion of flooded riparian areas. The age of beaver ponds was assessed based on the archival orthophotos and classified into three categories: young (≤3 years old), moderate (4-9 years old), and old (≥10 years old) ~~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
	Approximate number of buildings [c]	250	300	90	530	150	590	650	20	30
	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] [~~e~~d]	0.14	0.24	1.70	0.22	0.42	0.01	0.18	0.57	0.68
	The biggest pond area [ha] [d]	0.04	0.03	0.38	0.07	0.05	0.01	0.02	0.12	0.36
	Approximate age of the beaver pond sequence [years] [~~e~~d]	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
	Ratio of the pond sequence area to the area of the river channel	1:1	1:1	7:1	2:1	4:1	1:1	1:1	5:1	4:1
	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	+	-	-	+	-	+	-	-	+

The catchment characteristics refer to the catchments closed at the sampling sites below the beaver pond sequences.

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 - dataset based on Open Street Map obtained through QuickOSM plugin (QGIS)

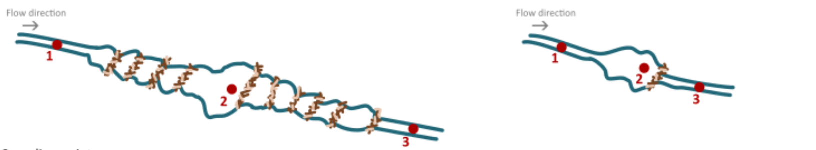
d~~e~~ - orthophotos obtained from Polish Office of Geodesy and Cartography (PZGiK) and available in Google Earth Pro

Tabela sformatowana

2.2 Water sampling and chemical analysis

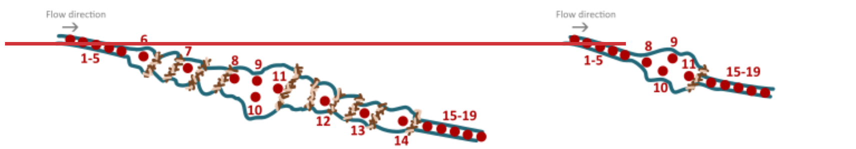
The research followed a three-dimensional sampling scheme: seasonal sampling, longitudinal and vertical profile sampling (Fig. 2). The following water parameters were measured: temperature (T), dissolved oxygen (DO), specific conductivity (SEC), pH and the ionic composition (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, NO_3^{-}, NH_4^{+}, HCO_3^{-}, SO_4^{2-}, Cl^{-}). 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.

a) SEASONAL SAMPLING (2022-2023)
Spring: 7 sites, Summer, Autumn, Winter: 9 sites



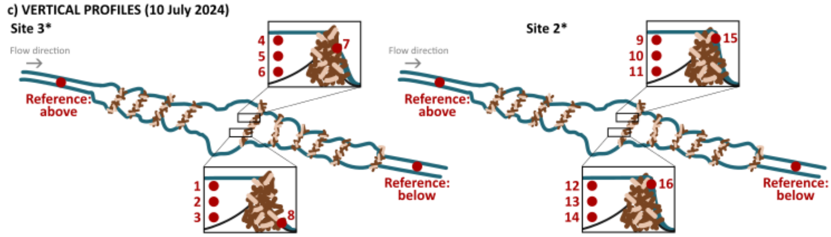
Sampling points:
1 - above pond cascade or the individual pond **2** - the biggest pond/the individual pond **3** - below pond cascade or the individual pond

b) LONGITUDINAL PROFILES (10 September 2023):
Site 3* **Site 6***



Sampling points:
1 - 130 m above; **2** – 100 m above; **3** – 70 m above; **4** – 40 m above; **5** – 10m above; **6** – Upper pond; **7** – Random pond; **8** – Main pond (backwater); **9, 10** – Main pond (middle); **11** – Main pond (above the dam); **12, 13** – Random ponds; **14** – Lower pond; **15** – 10m below; **16** – 40 m below; **17** – 70 m below; **18** – 100 m below; **19** – 130 m below

c) VERTICAL PROFILES (10 July 2024)
Site 3* **Site 2***



Sampling points:
Czermna: **1** – Profile 1 (top); **2** – Profile 1 (middle); **3** – Profile 1 (bottom); **4** – Profile 2 (top); **5** – Profile 2 (middle); **6** – Profile 2 (bottom); **7** – outflow from the dam (15 cm from dam top) **8** – outflow from the dam (near the bottom)
Turza: **9** – Profile 1 (top); **10** – Profile 1 (middle); **11** – Profile 1 (bottom); **12** – Profile 2 (top); **13** – Profile 2 (middle); **14** – Profile 2 (bottom); **15, 16** – outflow on the dam surface

Measured water parameters: pH, SEC, DO, T, Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, NO_3^{-}, NH_4^{+}, HCO_3^{-}, SO_4^{2-}, Cl^{-}
* number refers to the Fig. 1

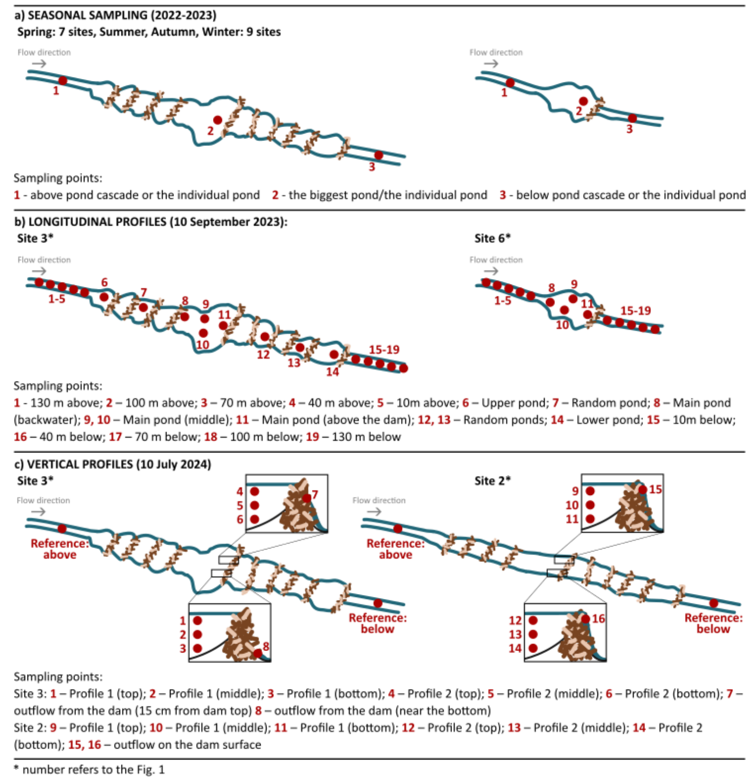


Figure 2: Study schemes.

Although both geological variability and human pressure affect the chemical composition of stream water, the sampling design based on comparisons along the longitudinal gradients, helps to minimise the impact of differences between catchments. Three samples were collected at each site in late spring (June), summer (July-September), autumn (October-November) and winter (February) during baseflow conditions~~normal water levels~~ (i.e., excluding periods of ~~precipitation~~ rainfall events or snowmelts) in 2022–2023 (Fig. 2a). The section 'above' the beaver pond or pond sequence that reflected baseline conditions was defined as 50–100 m upstream from a backwater, and the section 'below' was 50–100 m downstream from the last dam. The 'pond' sample was taken from the main channel section of the pond, i.e. excluding channel margins and backwaters. It was collected approximately 1m above the dam, from the middle of a water column. For sequences of multiple ponds, the representative ‘pond’ sample was collected from the biggest reservoir in the system. Samples were collected between late morning and afternoon, with sampling at each site completed within about an hour. 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 9nine sites during the seasonal sampling.

Two sites were chosen selected for additional measurements to create longitudinal stream profiles (Fig. 2b). The sampling was conducted on 10 September 2023 during the summer of 2023 at the Bystrzanka streamsite 6 (a single beaver pond created < 2 years ago) and an unnamed stream in Czermnaat site 3 (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 on 10 July 2024in the summer of 2024 at two beaver pond sequences, Czermna and Turzasite 2 and 3, which have represented different pond types (Fig. 2c). In Turza, sSolely in-channel ponds were observed at site 2. By contrast, overflowing stream banks were common at site 3in Czermna. Measurements were taken from various depths (near the bottom, in the middle of the water column and from the surface of the water column) and from dam outlets. At site 3In Czermna, outlet measurements were takencollected from leaks in the upper part of the dam and near its bottom, while at site 2and 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 (°C)), dissolved oxygen (DO (mg·L^{-1})), specific electrolytic conductivity (SEC (µS·cm^{-1})) and pH – were determined on-site using an ELMETRON CX-401 multifunction meter with the GXZ-3tk multiparameter immersion head. All pH, SEC and DO probes were calibrated using certified standards before each field study at the laboratory of the Institute of Geography and Spatial Organization Polish Academy of Sciences. Calibration was performed according to the manufacturer’s guidelines using certified analytical standards: pH probe: three-point calibration (pH 4.0, 7.0, and 9.0 buffers); SEC probe: calibration with a 1,41mS·cm^{-1} standard solution, selected according to anticipated conductivity of the sampled waters; DO probe: air-saturation calibration (100%) followed by zero-oxygen verification using sodium sulfite solution. Additionally, 250 ml water samples were collected at each site for laboratory analyses.

The HCO_3^- (mg·L^{-1}) 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 (mg·L^{-1}) (Ca^{2+}, Mg^{2+}, Na^+, K^+, NO_3^-, NH_4^+, SO_4^{2-}, Cl^-) was analysed in the Dionex ICS3000 ion chromatographyy with analytical columns: IonPac CS16 3×250 mm and IonPac AS18 2×250 mm. Each sample was previously filtered through a glass microfiber filter Whatman GF-D. The calibration curve was based on the certificate reference standard (CRM) (CLMS 2AN) Dionex Combined Six Cation Standard II and Seven Anion Standard II. All solutions were prepared with 1% nitric acid (Suprapur). The following concentrations

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were prepared for calibration: 0 (blank), 1, 10, 50, 100 and 1000 µg·dm^{-3}. The percent relative error, as determined by the data quality assessment based on CRM (KEIJM-02, GAW/WMO) was less than 5.0% for all parameters except K^+ and NH_4^+. The respective values were 5.8% for K^+ and 7.0% for NH_4^+. The detection limits were 0.4 mg·L^{-1} for Ca and 0.1 mg·L^{-1} for the other ions. Any ion concentrations below the detection limit were replaced with 75% of the detection limit, which is a common procedure in chemistry (Palarea-Albaladejo and Martín-Fernández, 2013). Concentrations below the detection limit were found only for the NO_3^- and NH_4^+ ions. Of all the analysed water samples (n=102), the NO_3^- and NH_4^+ concentrations were below the detection limit in 17 and 20 samples, respectively.

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:

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

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 a particular sampling session and N is the total number of sampling sessions (n = 34).

For the purpose of percentage change calculation, temperature values were converted from °C to K, to account for potential disruptive impacts of values close to 0°C on the percentage change in winter. Physico-chemical water parameters were included in the PCA if their mean absolute difference |*Dc*| in Dc [%] (for all sampling sites combined) exceeded 5%. This procedure was used to account for the accuracy of analytical measurements defined as percent relative errors. The differences in parameters, which relative percent errors slightly exceeded 5% (i.e. NH_4^+ and K^+), were many times greater than their respective errors, which allowed for their inclusion in the analysis. TheThis calculation of |*Dc*| used the following formula (N is the total number of sampling sessions):

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

The variables that fulfilled the aforementioned assumption were: DO, H^+, Ca^{2+}, K^+, HCO_3^-, SO_4^{2-}, Cl^-, NO_3^-, and NH_4^+ (Table A1). The H^+ concentration was used instead of the pH value to avoid the analysis involving logarithmic variables. The aim of using *Dc* in the PCA analysis was to identify the factors that determine changes in the physico-chemical parameters of water

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caused by the presence of beaver dams. 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 and~~,~~ 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 for T and parameters that met the same criteria as those used for PCA. To compare the study sites, they were first classified according to the age and type of each beaver pond sequence (Table 1). ~~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 (hereafter: warm season)~~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 as demonstrating a strong correlation~~significant~~. All analyses were performed in STATISTICA 12.0. The significance level of p<0.05 was used for all the calculations. Additionally, to reduce the risk of family-wise error for multiple comparisons based on the same dataset, we applied a Bonferroni correction to the significance threshold (p<0.017) (Armstrong, 2014). 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

The physico-chemical properties of stream water at baseline conditions varied between the catchments studied ~~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 that drained areas with ~~located in the northern, lower-lying foothills of the Outer Carpathians, where there is~~ a high proportion of shales in the bedrock (sites 1, 2, 4, and 6). Lower SEC and concentrations of major ions were found in streams draining catchments dominated by ~~in the southern, higher part of the Outer Carpathians that have a high proportion of~~ sandstones (sites 3, 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.Concentrations of Cl^-, Na^+ and K^+ showed high correlations with the share of artificial surfaces in the studied catchments (r=0.85, 0.78 and 0.61 respectively). Additionally, concentration of Cl^- correlated with the number of buildings in the catchments (r=0.61).

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

Study site*	pH	SEC [µS·cm⁻¹]	DO	Ca^{2+}	Mg^{2+}	Na^+	K^+ [mg·L⁻¹]	NO_3^-	NH_4^+	HCO_3^-	SO_4^{2-}	Cl^-
1	8.20	537.3	9.767	77.50	18.64	18.50	2.71	2.658	0.109	249.22	64.12	14.765
2	8.12	562.7	8.71	76.218	23.02.97	18.658	1.24	1.32	0.109	266.42	35.219	13.54
3	7.44	272.6	7.94	40.876	7.92	7.63	1.326	1.439	0.215	155.329	28.50	4.03.97
4	8.325	486.0	9.04	70.62	15.71	28.545	2.92	2.54	0.10	269.109	31.549	34.658
5	8.547	376.2	11.02	61.00.95	11.53	12.10	0.82	2.82	0.216	205.04.96	27.84	8.988
6	8.03	410.7	8.41	58.90	7.875	28.545	5.548	4.439	0.10	239.80	27.06.98	14.768
7	8.436	285.7	10.219	51.20	10.548	5.30	0.985	3.44	0.218	183.766	17.94	4.326
8	7.986	350.0	8.329	67.23	6.30	9.64	0.84	0.34	0.13	251.328	10.327	0.82
9	8.11	303.9	10.23	59.436	6.107	9.52	1.22	0.658	0.216	207.546	24.24	3.547

* number refers to the Fig. 1

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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 (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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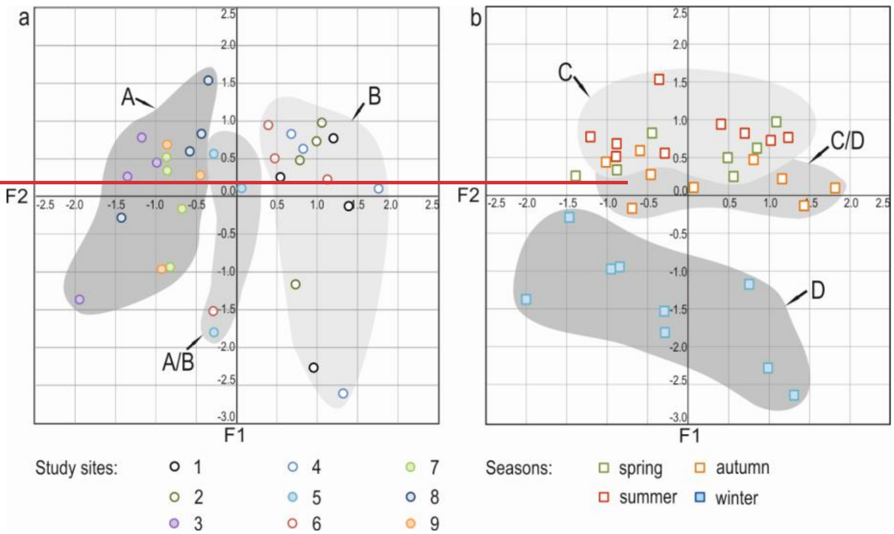

Figure 3: Results of the principal component analysis (PCA), shown as factor scores. Water samples were classified according to study site (a) and season (b).

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. 34, A1 and A2). Those differences were greater in the pond water than in the stream water below the dams (Fig. 34, Table A13). There were no strong correlations between the percentage change in the physico-chemical parameters and the catchment and stream characteristics (e.g. land use, catchment area, stream width) or the water parameters above beaver ponds. Larger differences were observed in streams with older beaver dams than in streams with younger ones (Fig. 34, 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, Tthe largest changes in the values of the physico-chemical water parameters obtained within beaver ponds (|*Dc*|>20%) were seenfound in H^+ (pH), NO_3^-, NH_4^+, and DO (in consecutive order). Intermediate changes (|*Dc*|=5–20%) were seenoccurred in K^+, SO_4^{2-}, Cl^-, HCO_3^-, and Ca^{2+}., while tThe smallest changes (|*Dc*|<5%) were seen observed in SEC, Mg^{2+} and Na^+ (Table A1).

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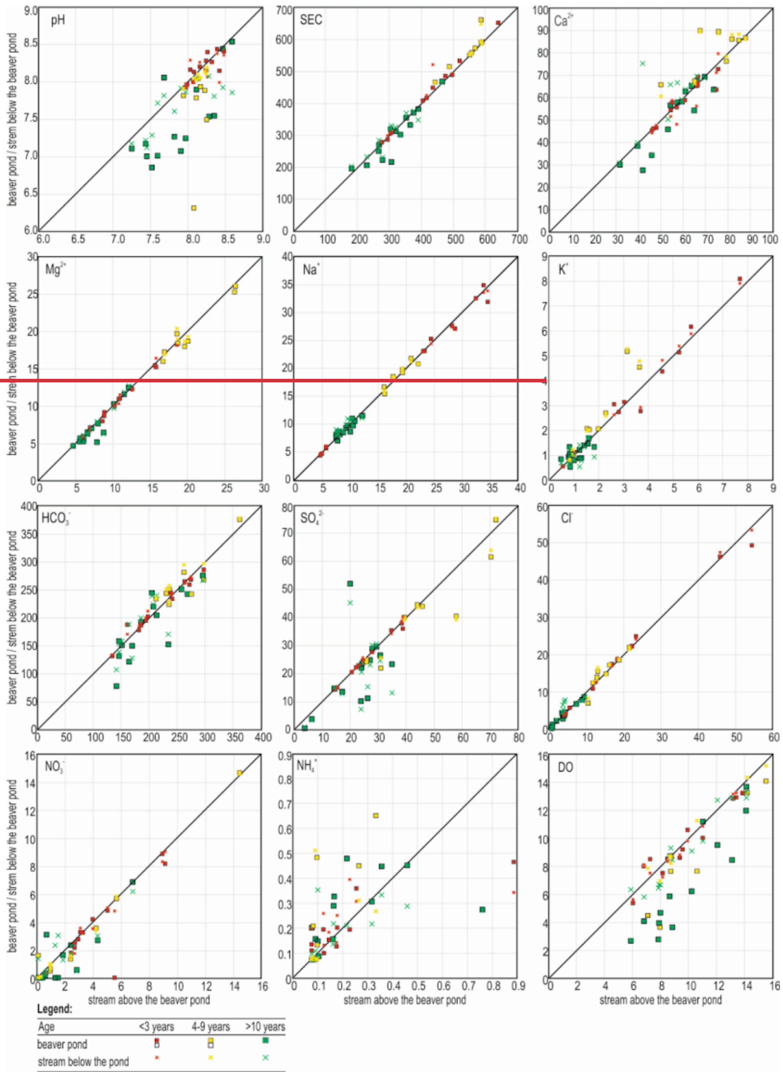
pH
SEC
Ca2+
Mg2+
Na+
K+
HCO3-
SO42-
Cl-
NO3-
NH4+
DO
beaver pond / strem below the beaver pond
stream above the beaver pond
Legend:
Age
<3 years
4-9 years
>10 years
beaver pond
stream below the pond

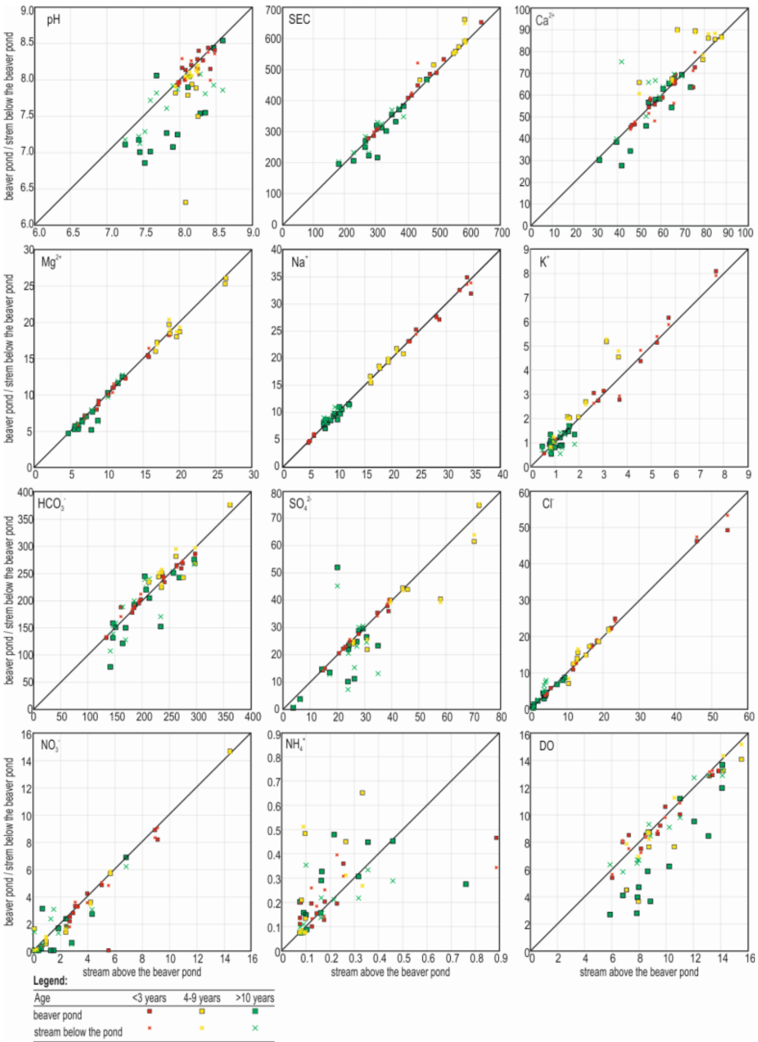

Figure 34: The physico-chemical water parameters, such as pH, SEC [μS·cm^{-1}], major ions, NH_4^+, NO_3^-, and DO concentrations [mg·L^{-1} mg·l^{-1}] within and below beaver ponds of different ages in relation to the inlet values.

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For streams below the dams, the largest changes in the physico-chemical parameters relative to streams above the ponds (|*Dc*|>20%) were found~~seen~~ in NO_3^-, H^+ (pH), and NH_4^+. Intermediate changes (|*Dc*|=5–20%) ~~were seen~~occured in Cl^-, SO_4^{2-}, K^+, Ca^{2+}, HCO_3^-, and DO, while t~~. T~~he smallest changes (|*Dc*|<5%) were ~~seen~~ observed 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 (Fig~~s~~. 4~~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 (Fig~~s~~. 4~~5~~, A1 and A2).

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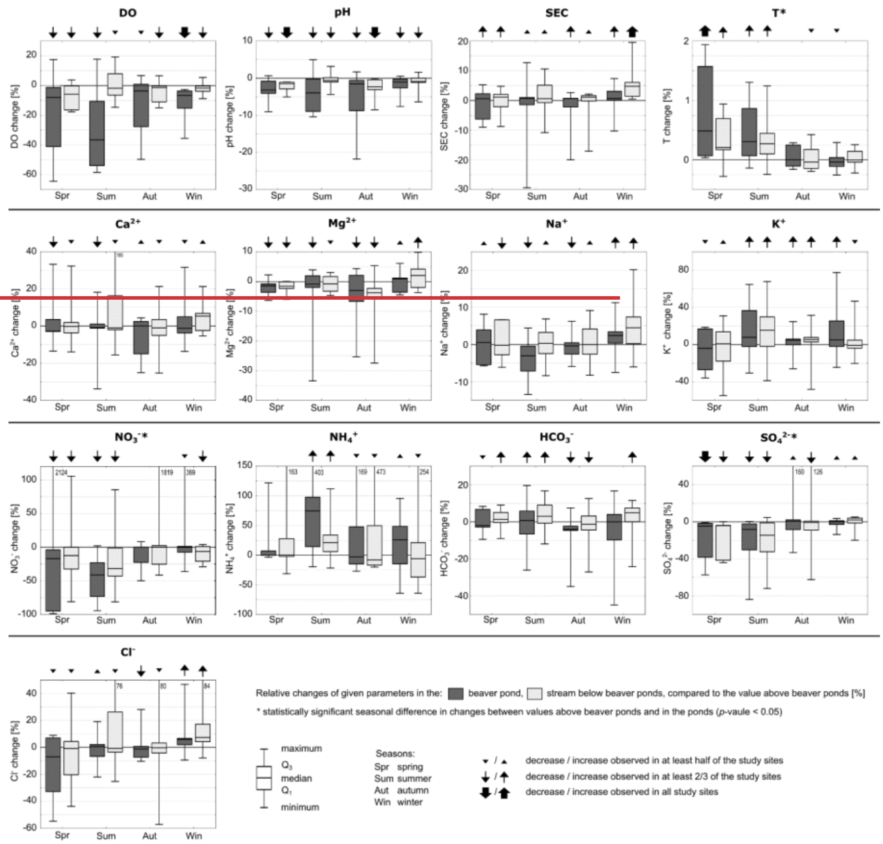
DO
pH
SEC
T*
Ca2+
Mg2+
Na+
K+
NO3-*
NH4+
HCO3-
SO42-*
Cl-
Spr
Sum
Aut
Win
Relative changes of given parameters in the: beaver pond, stream below beaver ponds, compared to the value above beaver ponds [%]
* statistically significant seasonal difference in changes between values above beaver ponds and in the ponds (p-vaule < 0.05)
maximum
Q3
median
Q1
minimum
Seasons:
Spr spring
Sum summer
Aut autumn
Win winter
decrease / increase observed in at least half of the study sites
decrease / increase observed in at least 2/3 of the study sites
decrease / increase observed in all study sites

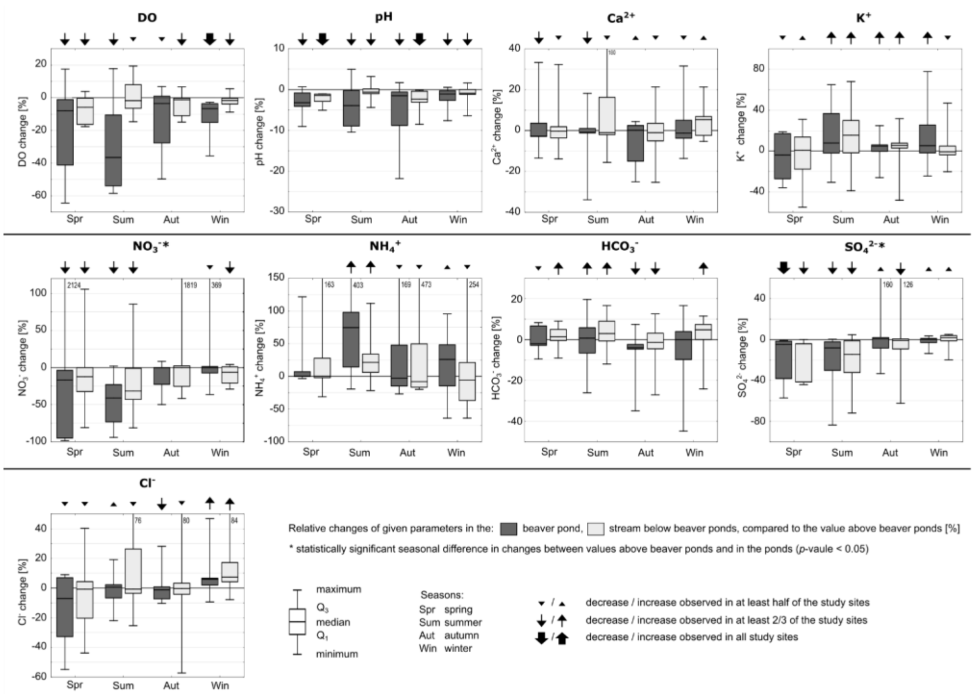

Figure 45: Percentage change *(Dc)*, DC [%], in the physico-chemical water parameters within and below beaver ponds in relation to the upstream channelsstream water above beaver ponds. Only the parameters for which |*Dc*| >5% are shown.

The observed variability in responses to beaver damming was attributed to both the season and the pond type (Table 34, 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 (T: 1.0±0.5%; NO_3^-: -75.3±22.4%; Ca^{2+}: -2.4±7.4%) 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.

Table 34: Results of group comparisons (ANOVA/Mann–Whitney U/Kruskall–Wallis tests) of the differences *(Dc)* 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.

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			Parameter									
			DO	pH	T	Ca^{2+}	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			**						**	

*** $p < 0.001$; ** $p < 0.017$ (Bonferroni correction); * $p < 0.05$; ‡ $p < 0.1$

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 34). 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 (≤3, 4-9, and ≥10 years old) 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 decreasereduction was noted in ≥10 years old sites (-47.7±18.3% within ponds and -42.8±21.9% below).

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 A25). Factor 1 (F1) controls determines the concentration differences in most major ions: K^+, Ca^{2+}, HCO_3^-, and Cl^-, and demonstrates their positive relationships. Factor 2 (F2) controls is responsible for the negative relationship between the differences in DO and SO_4^{2-} concentration and NH_4^+, while factor 3 controls is responsible for 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. 56). 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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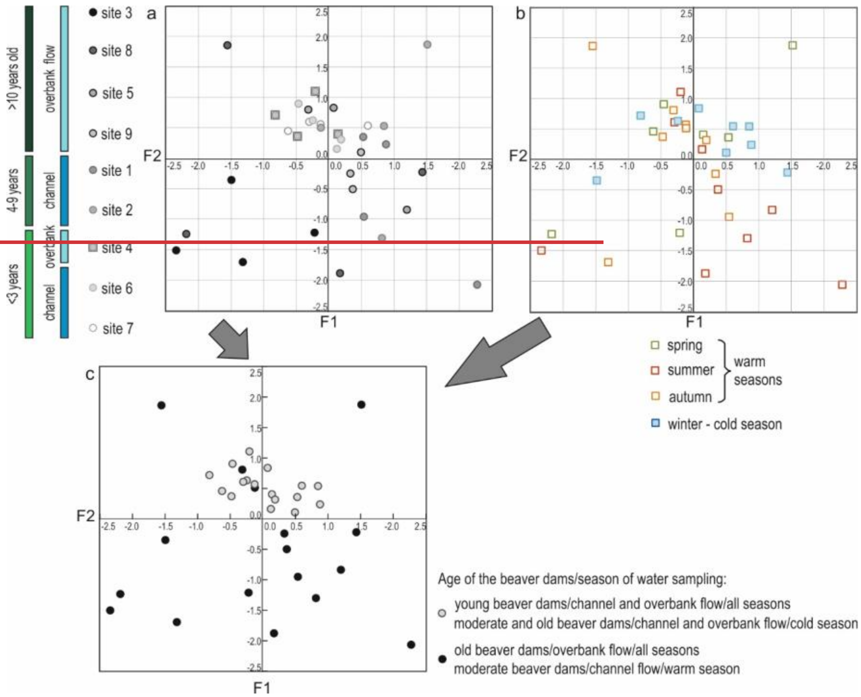
a
b
c
site 3
site 8
site 5
site 9
site 1
site 2
site 4
site 6
site 7
>10 years old
4-9 years
<3 years
overbank flow
channel
overbank
channel
F1
F2
spring
summer
autumn
warm seasons
winter - cold season
Age of the beaver dams/season of water sampling:
young beaver dams/channel and overbank flow/all seasons
moderate and old beaver dams/channel and overbank flow/cold season
old beaver dams/overbank flow/all seasons
moderate beaver dams/channel flow/warm season

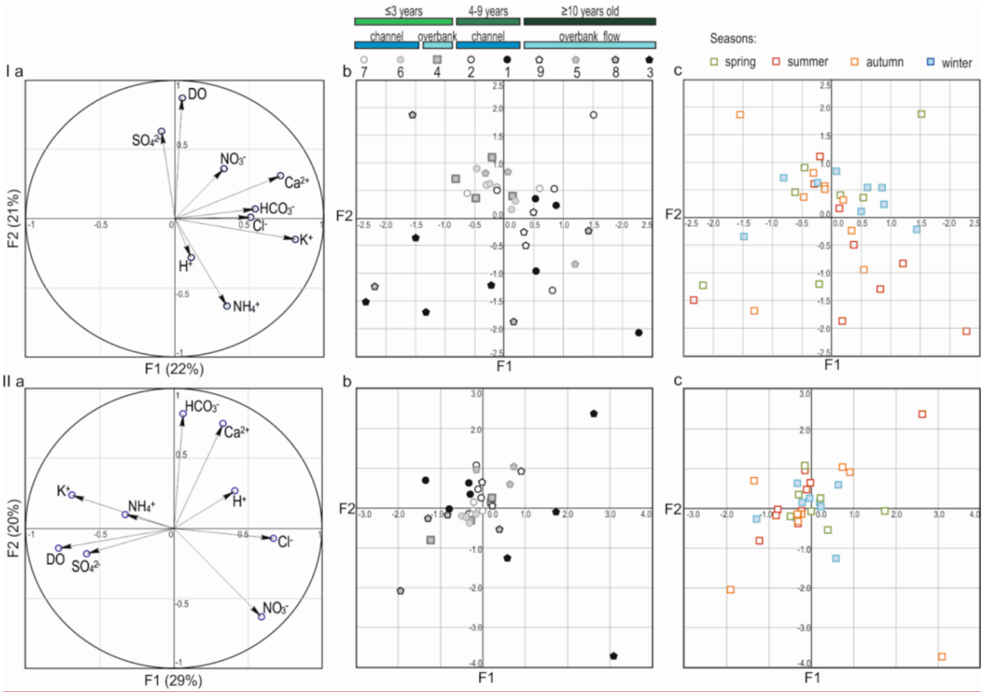

Figure 56: Results of factor analysis (factor scores) for the differences (Dc) between inlet values and beaver ponds (I) or streams below beaver ponds (II), Dc [%]:, factor loadings (a), The factor scores for the water samples were classified according to study site (numbers 1-9) (ba) and season (b). 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 A26). F1 controls determines the concentration differences of DO, SO_4^{2-} and K^+, which are negatively related to NO_3^- and Cl^-. F2 controls determines the differences in HCO_3^- and Ca^{2+} concentrations, which are negatively related to NO_3^-. F3 controls is responsible for 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. 57). 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, while. T the second cluster includes samples from streams below the overbank flowing ponds (mainly old ponds), that have an inconsistent pattern of with primarily positive factor scores for F1. The samples in the first cluster have a stronger correlation with F1 and

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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.

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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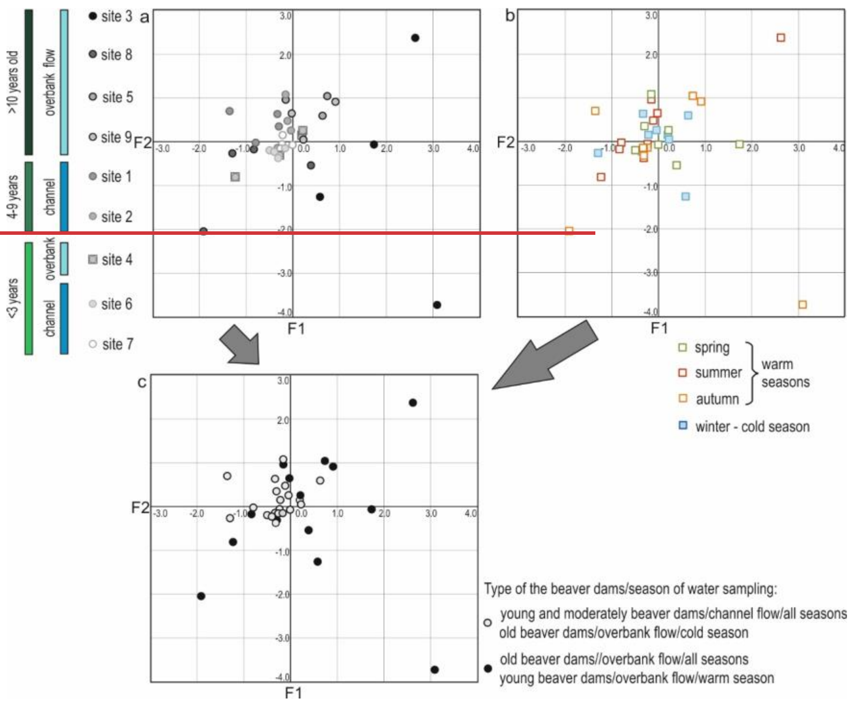


~~**Figure 7: Results of factor analysis (factor scores) for the differences between inlet values and streams below beaver ponds, Dc [%]. The water samples were classified according to study site (a) and season (b). The combined results are also shown (c).**~~

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

As demonstrated by the longitudinal profiles (Fig~~s~~. 6~~8~~ and B1~~9~~), the older~~,~~ over~~bank~~ flowing 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.

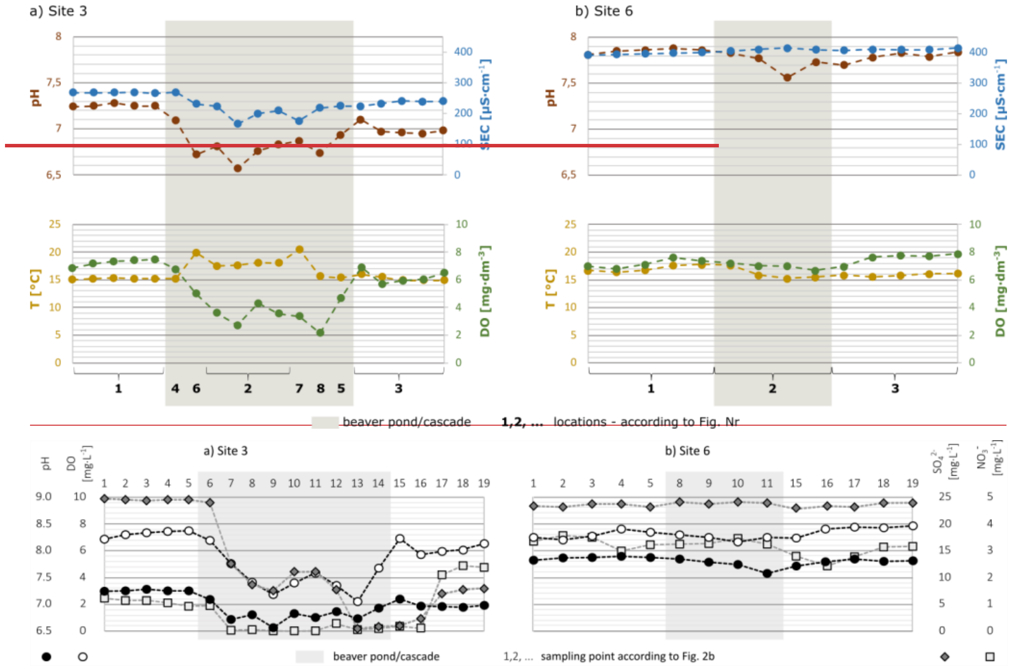
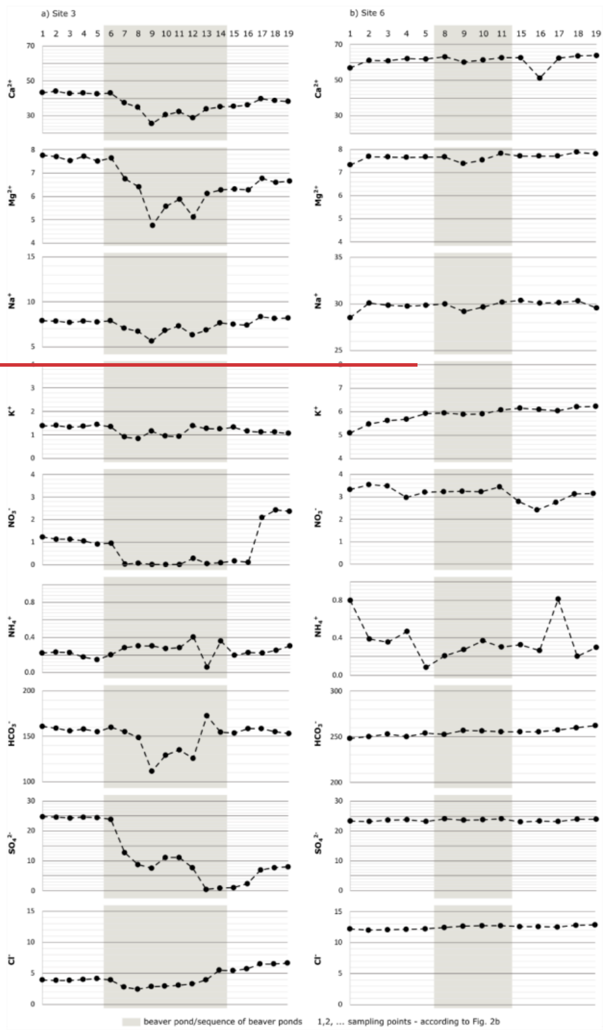


Figure 68: A longitudinal profile of the selected physico-chemical parameters at study sites 3 (a) and 6 (b) (on 10 September 2023).



~~**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.**~~

There were significantly greater vertical variations in physico-chemical parameters in the old, overbank flowing 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. 710 and B2). TAt site 3, the outflow water parameters (observed and measured near the base of the dam) were notably different from the top of the dam at site 3. 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).

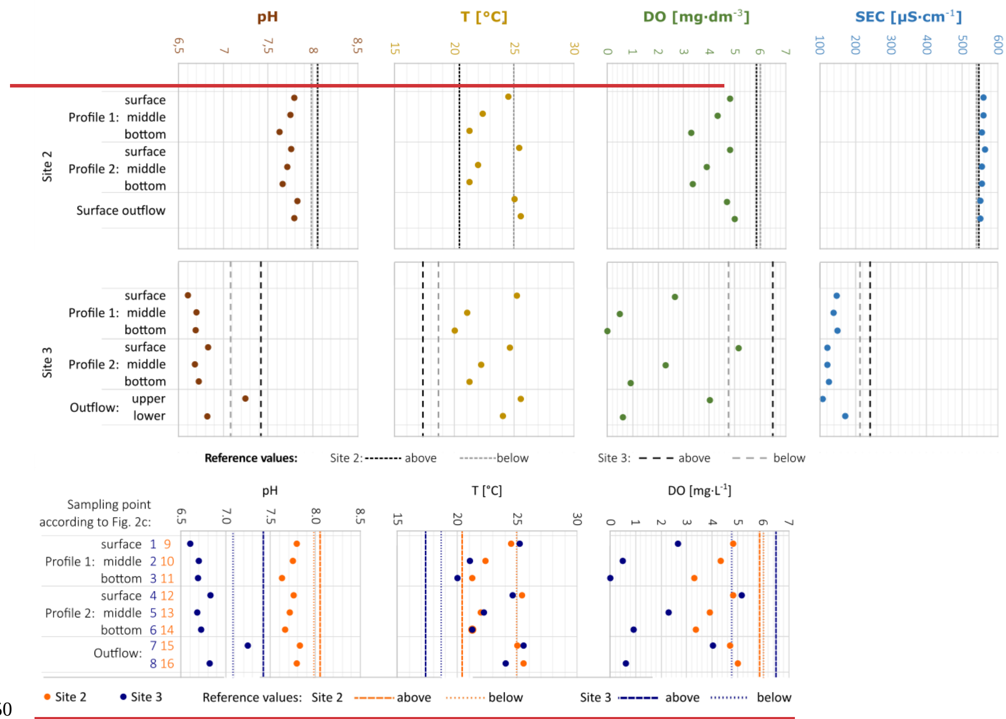


Figure 710: Differentiation of the selected physico-chemical parameters in the vertical profiles of study sites 2 and 3 on (10 July 2024).

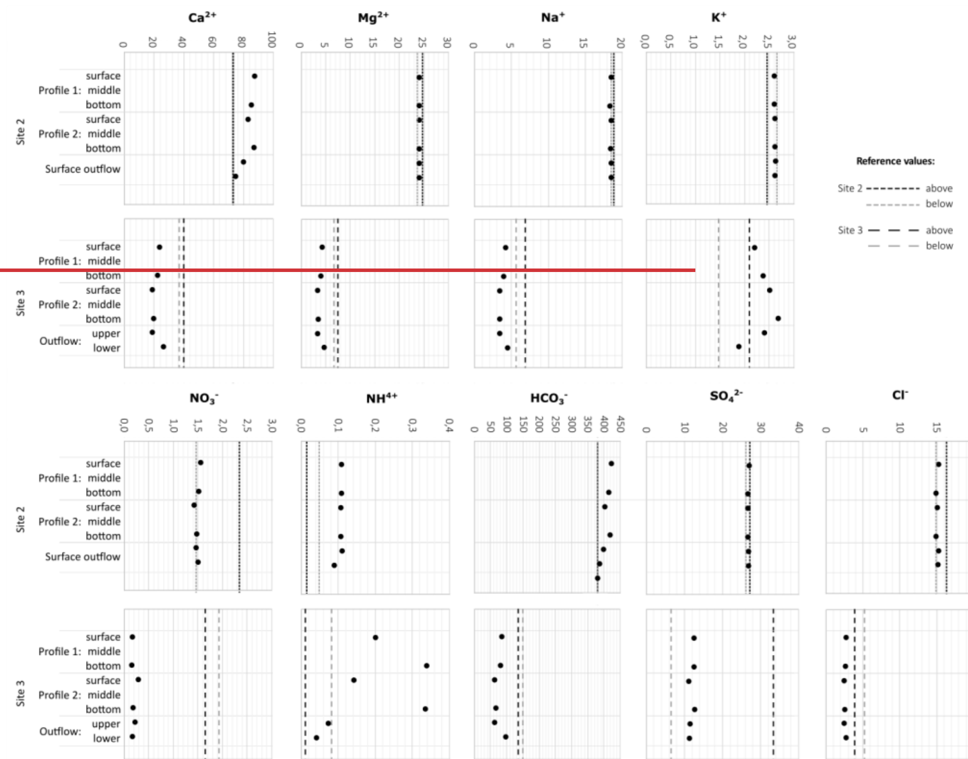


Figure 11: Concentration of the chemical components of water [mg·dm^{-3}] in the vertical profiles of study sites 2 and 3 (10 July 2024).

3.4 Study limitations

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 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 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 physico-chemical water parametersstream water chemistry triggered by the presence of beaver dams

The extensive distribution of the study sites resulted in a diverseified representation of initial physico-chemical water properties, which that corresponded mainly to the various geological structurefeatures. 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 and it is likely associated with a different resistance to weathering (Siwek et al., 2011; Siwek, 2021; Solár and Tomaškovič, 2023). The relation between Cl^-, Na^+, K^+ and anthropogenic modification of the catchment suggests human activity as an important factor for concentration of these ions in the study area. Despite the diversity of the selected Carpathian streams, since we based further analysis mainly on concentration differences of physico-chemical parameters rather than raw concentrations, our results indicated that there are several patterns in physico-chemical water parametersthe 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 under aerobic conditions in the ponds. 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) compared to the stream water upstream. For example, At site 3,the TOC concentration in the beaver pond at site 3 was found to be more than exceeded 13 mg·dmL^{-13}, which was . Moreover, TOC concentrations were almost three times higher within the ponds than in the streams that flowing 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). Briggs et al. (2012, 2013) found that the accumulation of organic matter in beaver ponds generates specific streambed morphologies, which enhance the exchange of stream water and groundwater within the hyporheic zone behind beaver dams. Furthermore, the high water pressure at the bottom of the ponds causes a downwelling flow over the dam structures. This promotes the transport of organic carbon and DO from the water column to the hyporheic zone, fuelling biogeochemical processes.

The oxidation of organic matter in ponds may also have caused the decrease in ~~resulted in decreased oxygen and~~ SO_4^{2-} concentrations at most of the study sites. Under the anoxic~~aerobic~~ conditions that prevail at the bottom of ponds (as measured at site 3 in July 2024; see Fig. 7~~10~~), as well as in the hyporheic zone, SO_4^{2-} ions are likely to~~can~~ 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 under relatively low redox potential (Sutton-Grier et al., 2011). The ~~reduction of~~decrease in SO_4^{2-} concentrations in streams with beaver dams has previously been identified and attributed to the expansion of anoxic~~aerobic~~ 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.

The decomposition and mineralization of organic matter in the process of ammonification, under both aerobic and anaerobic conditions, leads to the production of NH_4^+ ions in water (Stefanakis et al., 2014). ~~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 anoxic~~aerobic~~ conditions in water (Drever 1997). ~~Reduced~~ Decreased 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~~decrease in NO_3^- and SO_4^{2-} concentrations 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 ponds and streams~~ 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 difference~~ing~~ in baseline 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 studied 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.~~

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 downstream effect of beaver impoundment depends on the structural properties of the dam and, thus, the type of outflow. Due to the vertical complexity of the water column in the ponds, the water flowing out of the ponds through the bottom of the dams has different physico-chemical properties than the water flowing out through the top of the dams. For instance, the oxygen concentrations in the water flowing out from the bottom of the dams are lower than in the water flowing out through the top. Decreasing DO with beaver pond depth is consistent with the results reported by Stevenson et al. (2020). Nevertheless~~However~~, the changes in the physico-chemical parameters in the water below the ponds, regardless of the type of outflows, are smaller than the changes in the ponds compared to the upstream sections. 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 oxic~~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 streams above the ponds and within the ponds. The increased DO concentrations in streams below ponds favour the aerobic oxidation of organic matter, including the oxidation of organic acids. This increases the pH of stream water compared to pond water. 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 generally 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 under anaerobic conditions in other studies (Cirmo and Driscoll, 1993; Larsen et al., 2021).

4.2 Role of seasonality in the beaver dams impact on the physico-chemical water parameterswater chemistry

For most physico-chemical parameters, tThe greatest changes in most of the physico-chemical parameters within and below the beaver ponds compared to the streams above the ponds were observed during the warm season (spring and summer). (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 temperature at which water has the highest density (Vega and Abascal, 2005). 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. Biogeochemical processes in beaver pond water and sediments of the hyporheic zone, such as organic matter decomposition, denitrification and microbial sulphate reduction, are very slow at low temperatures compared to the warm conditions (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 (NH_4^+ production) and denitrification processes (NO$_3^-$ depletion). This is consistent with the findings of Margolis et al. (2001) and Law et al. (2016): the greatest NO$_3^-$ decrease downstream ~~to~~ of beaver ponds occurs in the summer. NO$_3^-$ ion is one of the most effective electron acceptors (oxidants) in the process of anaerobic oxidation of organic matter; therefore, NO$_3$ is the preferred oxidising agent for anaerobic microbes. The process of NO$_3^-$ reduction (denitrification) under anaerobic oxidation of organic matter occurs at a relatively high redox potential level (Anderson and Fidel, 2025). 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 also likely due to the high rate of anaerobic oxidation of organic matter during that time~~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)~~. According to Smith et al. (1991), Cirmo and Driscoll (1993), and Margolis et al. (2001), the intensive anaerobic oxidation of organic matter can occur despite the relatively low redox potential of the water during the low-flow conditions of summer. During that time anaerobic microbes used even relatively inefficient oxidants, such as SO$_4^{2-}$, in the anaerobic oxidation of organic matter due to the low concentration of NO$_3^-$ (a more effective oxidant) in the studied waters. The average concentration of NO$_3^-$ in ponds and streams below them was very low during the summer, the average was up to 1.5 mg·L^{-1}.

Our study showed low seasonality in terms of the changes in major ion concentrations (with the exception of SO$_4^{2-}$) in the upstream-pond-downstream gradient~~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. However, ~~B~~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 the physico-chemical water parameters~~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. 8~~12~~). Previously, the impact of beaver dams

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on various physico-chemical water parameters was commonly found to be inconsistent across different study sites. For example, different directions of change in pH were documented by Lizarralde et al. (1996), Harthun (2000) and Čiuldienė et al. (2020). The beaver pond characteristic proposed in our study may to some extent explain those site-to-site differences. For instance~~example~~, the magnitudes of the decrease in pH, ~~was strongly related to the age of the beaver impoundments and was moderately dependent on their type: the decrease 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-} concentrations in the studied beaver ponds were found to be positively related to the age of the beaver pond sequences. These water parameters ~~decreases in pH, DO and SO_4^{2-} concentrations in beaver ponds are regulated~~ are influenced mainly 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. Although the pond age does not cause the difference directly, it can be used as a proxy for the accumulation of organic-rich sediments over time and the enhancement of respective biogeochemical processes. For example, it facilitates the natural removal of pollutants in beaver-occupied streams through metal sequestration (Murray et al., 2021). Our study shows that the long-term durability of beaver ponds increases the extent to which SO_4^{2-} is reduced. The difference may be linked to anaerobic oxidation of organic matter, as indicated by the corresponding differences in DO. The effect of the pond age on SO_4^{2-} persists downstream of the beaver dam, suggesting that it may be an important factor in the stream water purification process.~~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).~~

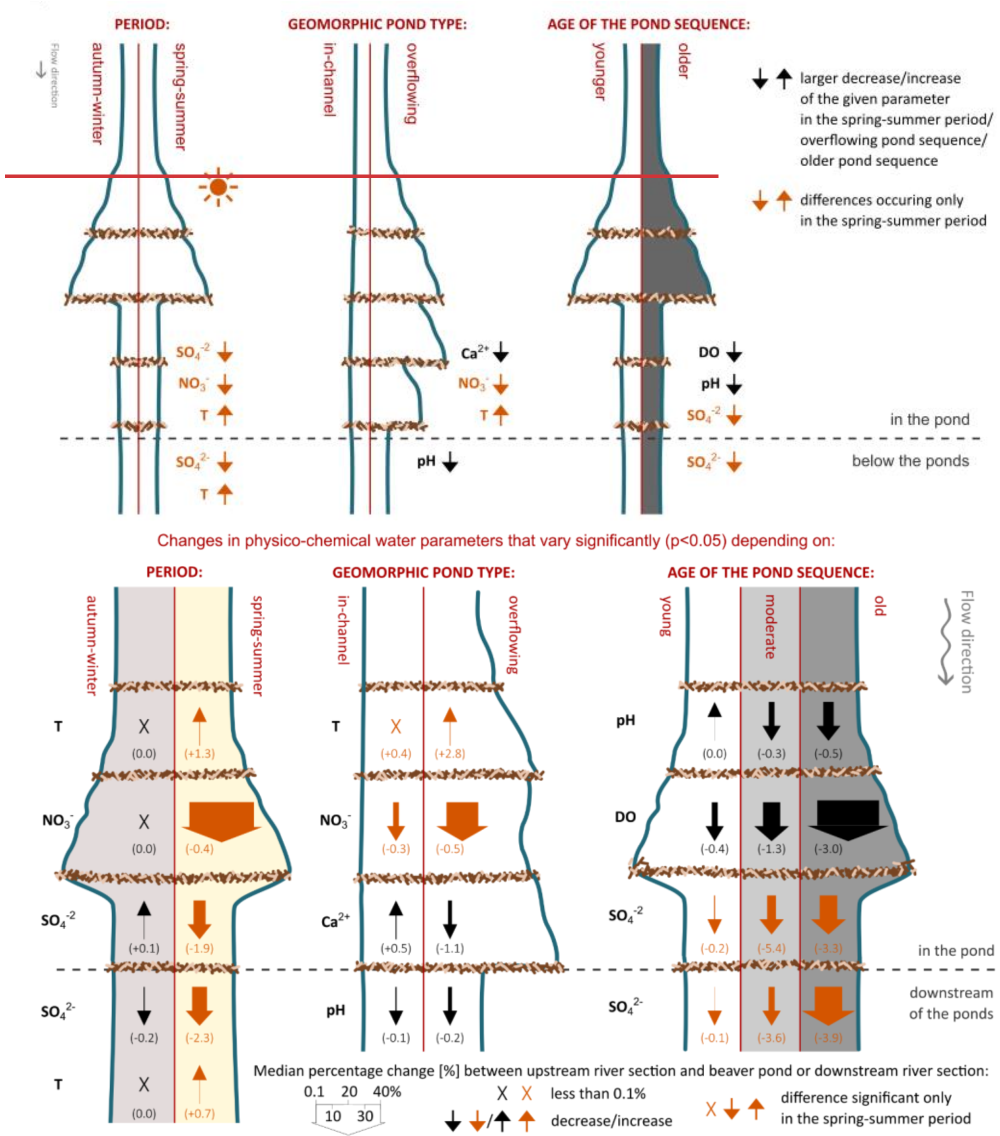
PERIOD:
GEOMORPHIC POND TYPE:
AGE OF THE POND SEQUENCE:
Flow direction
autumn-winter
spring-summer
in-channel
overflowing
younger
older
larger decrease/increase of the given parameter in the spring-summer period/ overflowing pond sequence/ older pond sequence
differences occuring only in the spring-summer period
SO_4^{-2}
NO_3^-
T
Ca^{2+}
DO
pH
SO_4^{2-}
in the pond
below the ponds
Changes in physico-chemical water parameters that vary significantly (p<0.05) depending on:
PERIOD:
GEOMORPHIC POND TYPE:
AGE OF THE POND SEQUENCE:
young
moderate
old
Flow direction
T
X (0.0)
(+1.3)
NO_3^-
X (0.0)
(-0.4)
SO_4^{-2}
(+0.1)
(-1.9)
SO_4^{2-}
(-0.2)
(-2.3)
T
X (0.0)
(+0.7)
T
X (+0.4)
(+2.8)
NO_3^-
(-0.3)
(-0.5)
Ca^{2+}
(+0.5)
(-1.1)
pH
(-0.1)
(-0.2)
pH
(0.0)
(-0.3)
(-0.5)
DO
(-0.4)
(-1.3)
(-3.0)
SO_4^{-2}
(-0.2)
(-5.4)
(-3.3)
SO_4^{2-}
(-0.1)
(-3.6)
(-3.9)
in the pond
downstream of the ponds
Median percentage change [%] between upstream river section and beaver pond or downstream river section:
0.1 20 40%
10 30
X X less than 0.1%
decrease/increase
difference significant only in the spring-summer period

Figure 812: The role of seasons and characteristics of a beaver pond sequence characteristics in changes to physico-chemical water properties within and downstream of the beaver ponds. Median changes in measurement units (T in °C, DO and ion concentrations in mg·L-1) are given in brackets.

Although the significance of pond type was generally lower than that of pond age, the geomorphological context appears to be important in terms of changes in NO_3^- concentration. The decrease in NO_3^- concentration was greater The attenuation of NO_3^- concentrations in beaver ponds was significantly greater in overflowing ponds than in the ponds restricted to river channels. This difference is in line with the higher temperature increase observed in such ponds, since denitrification rates in aquatic ecosystems generally increase with temperature and DO depletion (de Klein et al., 2017). 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. The observed thermal difference This is most likely due to the larger area of open water area created by overflowing ponds, as opposed compared to the more shaded in-channel impoundments. It may also be attributed to the higher proportion of shallow, slow-flowing water at the pond margins, which enhances warming (Majerova et al., 2020)Furthermore, denitrification takes place in the flooded riparian zones of the overbank ponds. The longer residence time of water in the overflowing ponds may also explain the higher denitrification rates in the water of both the pond and the hyporheic zone where the bottom pond water and groundwater mix (Merrill and Tonjes, 2014). The rate of biogeochemical processes is controlled by residence time, as it determines the duration of contact between solutes and microbial communities (Briggs et al., 2012). Extended hyporheic zones, which are associated with the formation of overflowing ponds, are likely areas of NO_3^- removal due to denitrification. Furthermore, aAs demonstrated by Puttock et al. (2018), total nitrogen storage per unit area in beaver pond sediments increases with pond size. It may suggestcan therefore be concluded that the relationship between an overflowing pond type and the decrease in water NO_3^- concentrations is indicative of the enhanced mineral nitrogen uptake by vegetation and the accumulation of nitrogen-rich organic sedimentfixation 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 The inundation of the area surrounding the river channel (the riparian zone) reduces flow velocity and increases water residence time (Larsen et al., 2021). This in turn supports the development of aquatic vegetation which facilitates the attenuation of nitrogen (Murray et al., 2021). Maret et al. (1987) also, was attributed the greater extent of NO_3^- decrease in pond water to higher sediment loads and seasonal expansion of the beaver 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, 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.

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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^{+}.~~:~~ The decrease in~~higher~~ Ca^{+} concentrations was ~~decrease rates were~~ observed in the overflowing ~~beaver~~ ponds, as opposed to the ~~than in~~ in-channel ~~beaver~~ ponds. The decrease in Ca^{2+} concentration in ~~overflowing~~ those 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 (Korchef and Touaibi, 2020, Escoffier et al., 2023). 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 (decrease in 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 that we studied.

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4.4 Study limitations

The wide spatial scope of the study and the high diversity of beaver-influenced streams introduced certain limitations. The spread of the study sites across a vast area restricted the number of samples collected to one sample per site each season, due to the time and cost constraints. In addition, dam failures resulting from floods and their targeted elimination during the research period decreased the planned sample size by half. The remaining study 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 spring high flows have been omitted, which likely explains the similarities between the results from the late spring and the summer.

Although a Before–After–Control–Impact (BACI) model would be the most appropriate approach for studying the impact of beavers on the chemical composition of water, it was not possible to use this method in this area due to the lack of investigations prior to dam construction. Instead, the study focused on spatial and temporal contrasts throughout the year and used a comparative ‘upper-lower river’ method, where upstream sections were used as reference sections. This research approach is commonly used in field studies to assess hydrochemical gradients generated by beaver dams when it is logistically or environmentally impossible to obtain ‘before’ data on dam construction (Green and Westbrook, 2009; Klotz, 2010; Fuller and Peckarsky, 2011; Puttock et al., 2017; Stevenson et al., 2022). It enables the identification of local hydrological and chemical effects caused by beaver damming while minimising the confounding influence of catchment heterogeneity. Although this approach lacks independent control sections, as in a full BACI model, it provides robust comparative evidence for evaluating the magnitude and spatial extent of changes induced by beaver activity under natural field conditions. Future research should be more detailed and extensive to enable the application of the BACI model.

As there was no identified relationship between the initial values and the percentage change in the physico-chemical parameters, it was assumed that the observed changes would not differ significantly based on upstream conditions. This allowed various catchments with different land uses and levels of anthropogenic influence to be included in the study. However, it should be noted that the inclusion of the streams characterised by particularly high concentrations of certain components, e.g. highly anthropogenically modified, may have resulted in different observations.

Although the sample locations were standardised to a certain extent, they may not reflect typical stream or pond conditions. Stream samples are more likely to be well-mixed and representative due to turbulent flow conditions. This is also evidenced by the homogeneity of most longitudinal profiles upstream and downstream of beaver ponds. However, the spatial distribution of the pond samples may be more biased as it did not cover the full spectrum of hydrological units observed within the ponds (Majerova et al., 2020). Additionally, as the samples were taken from the middle of the water column, they do not represent the surface and bottom water layers, which according to the vertical sampling scheme could substantially affect observed physico-chemical parameters. One of the greatest limitations of the study was the absence of field measurements of redox potential in streams and vertical profiles of beaver ponds. Such measurements would have enabled the direct identification of redox conditions in the studied waters rather than relying on speculation based on the concentration of key redox reaction ions. Direct measurements of redox potential, microbial activity and vegetation cover in the future studies would enable empirical assessment of the role of the discussed processes.

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.

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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 during warm seasons, including an increase in water temperature and decreases in pH, ~~dissolved oxygen~~DO, ~~and nitrate~~ NO_3^- and ~~sulphate~~SO_4^{2-} 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 NO_3^- ~~nitrate~~ and SO_4^{2-} ~~sulphate~~ decrease were found to be more effective during the warm period of the year than during the cold period. Moreover, ~~the study involved a comparison of the two geomorphic types of beaver pond complexes. A~~a larger decrease in NO_3^- ~~nitrate~~ and Ca^{2+} ~~calcium~~ concentrations occurred in ponds that overflow river banks, and higher pH decrease was identified below overflowing ponds, compared to the ~~than below~~ ponds restricted to the banks. The denitrification process, which is responsible for the decrease in NO_3^- concentration, requires anoxic~~anaerobic~~ conditions in the pond water, which are favoured in overflowing ponds due to greater temperature increases and longer water residence time 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 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 mountain ~~mountainous and lowland~~ streams (including~~,~~ side-channel and main-channel ponds and various levels of geomorphic beaver activity), as well as comparative data from lowland streams, 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 at Zenodo open access data repository (doi: 10.5281/zenodo.17937225)~~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

Sformatowano: Nagłówek 1

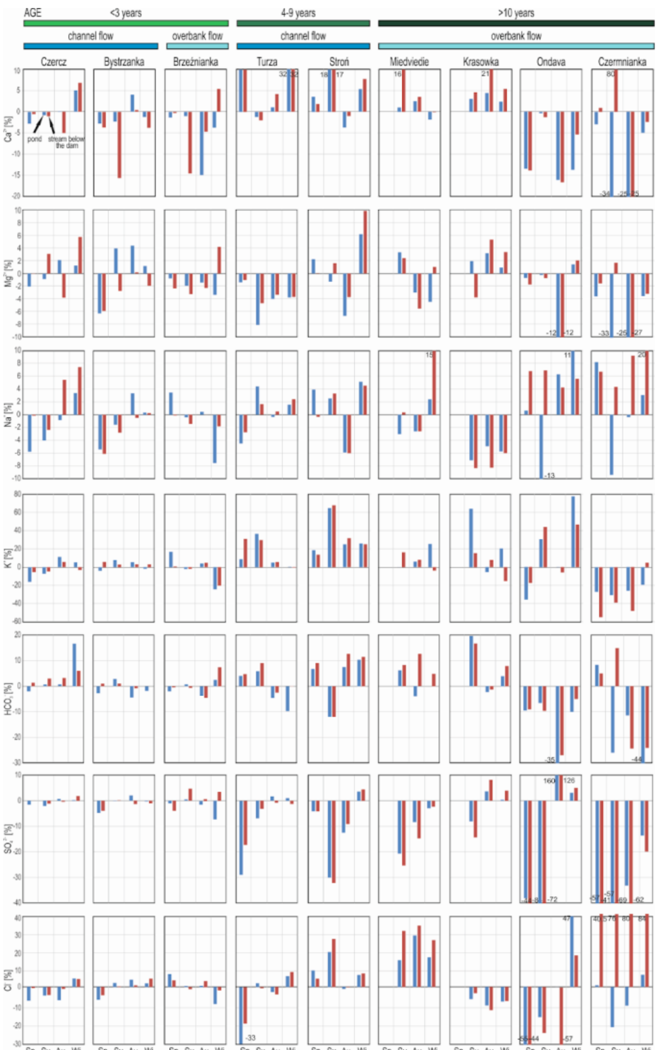

Figure A1: Percentage changes (*Dc*), DC [%], in main ion concentrations in and below beaver ponds compared to their upstream values (Sp – spring, Su – summer, Au – autumn, Wi – winter).

— **sformatowano:** Czcionka: Kursywa

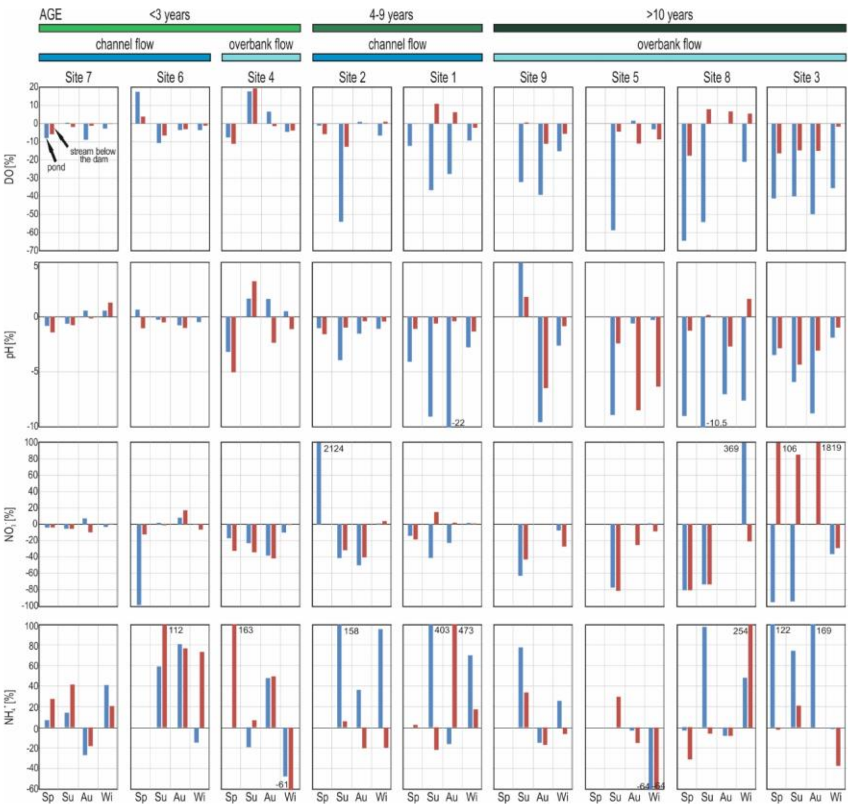

Figure A2: Percentage changes (*Dc*), DC [%], in -pH, and DO, NH_4^+ and NO_3^- concentrations in and below beaver ponds compared to their upstream values (Sp – spring, Su – summer, Au – autumn, Wi – winter).

— **sformatowano:** Czcionka: Kursywa

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

Table A2: Results of the PCA analyses of the differences between inlet values and beaver ponds/streams below beaver ponds (*Dc*). Factor loadings that exceed 0.5 are marked in bold.

Parameters	PCA factor loadings					
	Beaver pond			Stream below beaver ponds		
	1	2	3	1	2	3
DO	0.05	**0.87**	-0.12	**-0.78**	-0.14	0.33
HCO_3^-	**0.54**	0.07	0.36	0.06	**0.82**	0.07
Cl^-	**0.51**	0.01	**-0.73**	**0.67**	-0.07	**0.54**
SO_4^{2-}	-0.09	**0.63**	**-0.58**	**-0.59**	-0.18	**-0.58**
Ca^{2+}	**0.71**	0.31	0.36	0.33	**0.75**	0.13
K^+	**0.81**	-0.15	-0.31	**-0.69**	0.24	0.32
NO_3^-	0.33	0.36	**0.58**	**0.59**	**-0.63**	0.21
NH_4^+	0.35	**-0.63**	-0.14	-0.33	0.10	0.46
H^+	0.11	-0.28	0.01	0.41	0.27	**-0.60**
Eigenvalue	1.97	1.88	1.60	2.60	1.84	1.47
% of expl. variance	0.22	0.21	0.18	0.29	0.20	0.16

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Appendix B – Concentrations of the chemical components in the longitudinal and vertical profiles

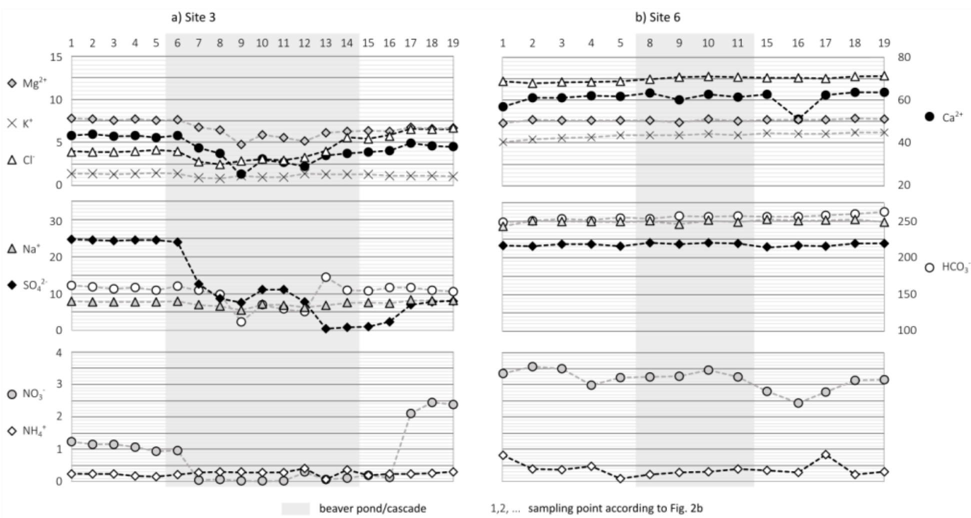

Figure B1: Concentrations of the chemical components of water [mg·L^{-1}] in the longitudinal stream profiles at study sites 3 (a) and 6 (b) on 10 September 2023.

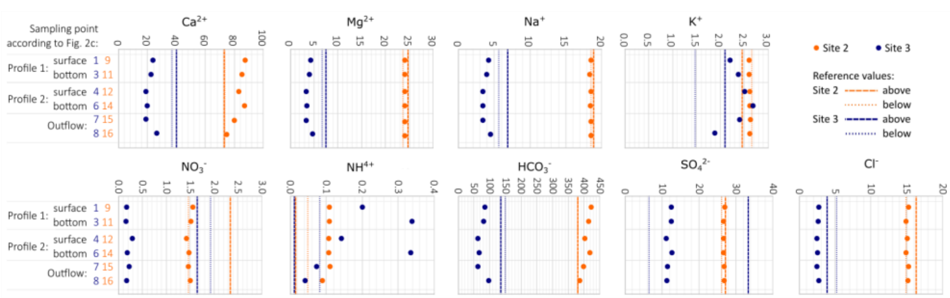

Figure B2: Concentration of the chemical components of water [mg·L^{-1}] in the vertical profiles of study sites 2 and 3 on 10 July 2024.

— **sformatowano:** Czcionka: 10 pkt, Pogrubienie, Angielski (Stany Zjednoczone)

— **sformatowano:** Czcionka: 10 pkt, Pogrubienie, Angielski (Stany Zjednoczone)

— **sformatowano:** Czcionka: 10 pkt, Pogrubienie, Angielski (Stany Zjednoczone)

Sformatowano: Normalny

— **sformatowano:** Czcionka: 10 pkt, Nie Pogrubienie, Kolor czcionki: Automatyczny