The effect of beaver dams on the physico-chemical 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 large areas of Europe. The ability of this species to build dams of varying durability and extent has a significant impact on ecological processes, making beaver reintroduction an important environmental factor in 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 across the seasons of the flooding extent and age of beaver pond sequences on the physico-chemical properties of the water in and below beaver ponds compared to upstream channel sections.

The study was conducted on nine beaver-inhabited streams distributed across the Western Carpathians (Poland and Slovakia). The beaver ponds were divided into two categories based on flooding extent: overflowing the river banks, or confined to the river channel. The age of the ponds ranged from ≤ 3 years to ≥ 10 years. Water samples were collected above, within, and below the beaver pond sequences under baseflow conditions during four seasons in 2022–2023.

The results showed that beaver dams have a strong impact on stream water chemistry during warm periods, when high temperatures accelerate biogeochemical activity. The age of the beaver ponds was a more statistically significant factor in altering stream water chemistry than the flooding extent of the ponds. There was a greater decrease in dissolved oxygen, pH and SO_4^{2-} concentrations in older ponds compared to younger ones. These changes might be regulated by the decomposition and aerobic/anaerobic oxidation of organic matter, which is more abundant in older ponds. Moreover, greater decreases in NO_3^- concentrations were observed in overflowing ponds than within in-channel ponds, which suggests a more intense denitrification process in the former. The denitrification process requires anoxic conditions, which were favoured in overflowing ponds due to their higher temperatures and longer water residence time compared to in-channel ponds. The decrease in NO_3^- concentrations may also be due to the increased uptake of mineral nitrogen by vegetation and the accumulation of nitrogen-rich organic sediment at the bottom of overflowing ponds. Most of the effects observed within the ponds were attenuated in downstream river sections. However, further research based on a larger dataset and a more frequent

sampling strategy is needed to identify the biogeochemical processes that occur in beaver ponds under specific hydro-meteorological conditions.

1 Introduction

Beavers, the two semi-aquatic species of the genus Castor, significantly alter riverine ecosystems through their foraging activity and construction of dams, canals, burrows and 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 a 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 ponds they create and their influence on biogeochemical cycles affect habitat availability for other organisms and lead to increased biodiversity (Wright et al., 2002; Larsen et al., 2021). In addition, beavers are recognised as providers of important ecosystem services, for example, in the way their activities support 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. By the beginning of the 20th century, only eight remnant populations were left (Nolet and Rosell, 1998). 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 to be 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 programme aimed at re-establishing Carpathian populations was successfully carried out between 1980 and 1985 (Żurowski and Kasperczyk, 1990). The beavers now present 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 their recovering beaver populations (Čanády et al., 2016; Wróbel and Krzysztofiak-Kaniewska, 2020).

In recent decades, there has been a growing interest in studying the impact of beavers on river water chemistry. Understanding the implications of beaver activity 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 is commonly assumed that both species exert a similar influence on the environment, even though the Eurasian beaver expresses less advanced building activity in terms of the number and size of the structures it creates

(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 focused on lowland areas (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 mountain regions (Giriat et al., 2016; Gorczyca et al., 2018). The species has recently become a prominent environmental factor across the Carpathian mountains after centuries of absence, making an understanding of its impact in this area particularly important.

Beaver dams reduce water flow velocity, thereby promoting the sedimentation of suspended solids and increased nutrient retention (Maret et al., 1987; Puttock et al., 2018). Consequently, 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 filtering effect of beaver dams results in the attenuation of heavy metal concentrations downstream of beaver ponds compared to upstream river sections (Čiuldienė et al., 2020; Murray et al., 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, as these depend on flow rate and ecosystem productivity (Maret et al., 1987; Wegener et al., 2017; Murray et al., 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 impact of a single pond compared to a sequence of multiple ponds. Such issues may get in the way of deriving general conclusions about 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 that reflect the diversity of beaver ponds and their impact on water chemistry would improve our understanding of the effects of beaver presence in river systems. The age of beaver ponds has often been proposed as such a feature in previous studies on the 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 sediment organic matter content inside beaver ponds also rise with pond age, according to the study by Murray et al. (2021). Hydrological and thermal differences have been observed between various geomorphic units within beaver ponds, for example, the main channel, its margins and backwater areas (Majerova et al., 2020). The effect of these different units in relation to floodplain inundation especially has been 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 and increases in water residence time, the extent of the hyporheic zone, overbank sedimentation, and the growth of aquatic vegetation, compared to ponds confined to the river channel. Both the age of a beaver pond and its flooding extent may correspond with prolonged sediment-water interactions, resulting in enhanced biogeochemical processes.

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), taking into account seasonality and pond characteristics. The paper focuses on answering the following three questions:

1) 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) How do these differences vary seasonally?
3) How are these differences affected by the flooding extent and age of beaver ponds?

2 Methods

2.1 Study area

The study was conducted on nine beaver-inhabited gravel-bed streams in the Outer Western Carpathians (Fig. 1a). This region consists mainly of alternating layers of sandstones, conglomerates, mudstones and shales, which make up the sedimentary deposits of the Carpathian flysch (Ślączka et al., 2006; Łajczak et al., 2014). The relief morphology of the study area corresponds to the general underlying geological units. The lower-lying foothills in the north are composed largely of the shale-rich thin-bedded flysch of the Silesian Nappe, while the mountains in the south are composed of the Magura Nappe, dominated by thick-bedded sandstones (Margielewski, 2012; Golonka et al., 2019; Święchowicz et al., 2021). In just over half of the studied catchments (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; Kováčik et al., 2011). 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 that drain areas underlain by shales and mudstones are typically characterised by higher concentrations of bicarbonate, 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 a lower level of total dissolved solids (e.g. Siwek, 2021; Solár and Tomaškovič, 2023).

The geomorphologically diverse terrain in the study area ranges from 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 (with a gradient that often exceeds 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. These 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 from 40 to 300 m above the flat valley floors (Starkel, 1990). The mean annual temperature in all the selected catchments ranges from 5.1 to 9.1°C, and the average precipitation is 770–1140 mm (based on the 2000–2010 period; CARPATCLIM, 2013; Szalai et al., 2013). Rivers in this area are mainly characterised by a nival–pluvial hydrological regime (Wrzesiński, 2017).

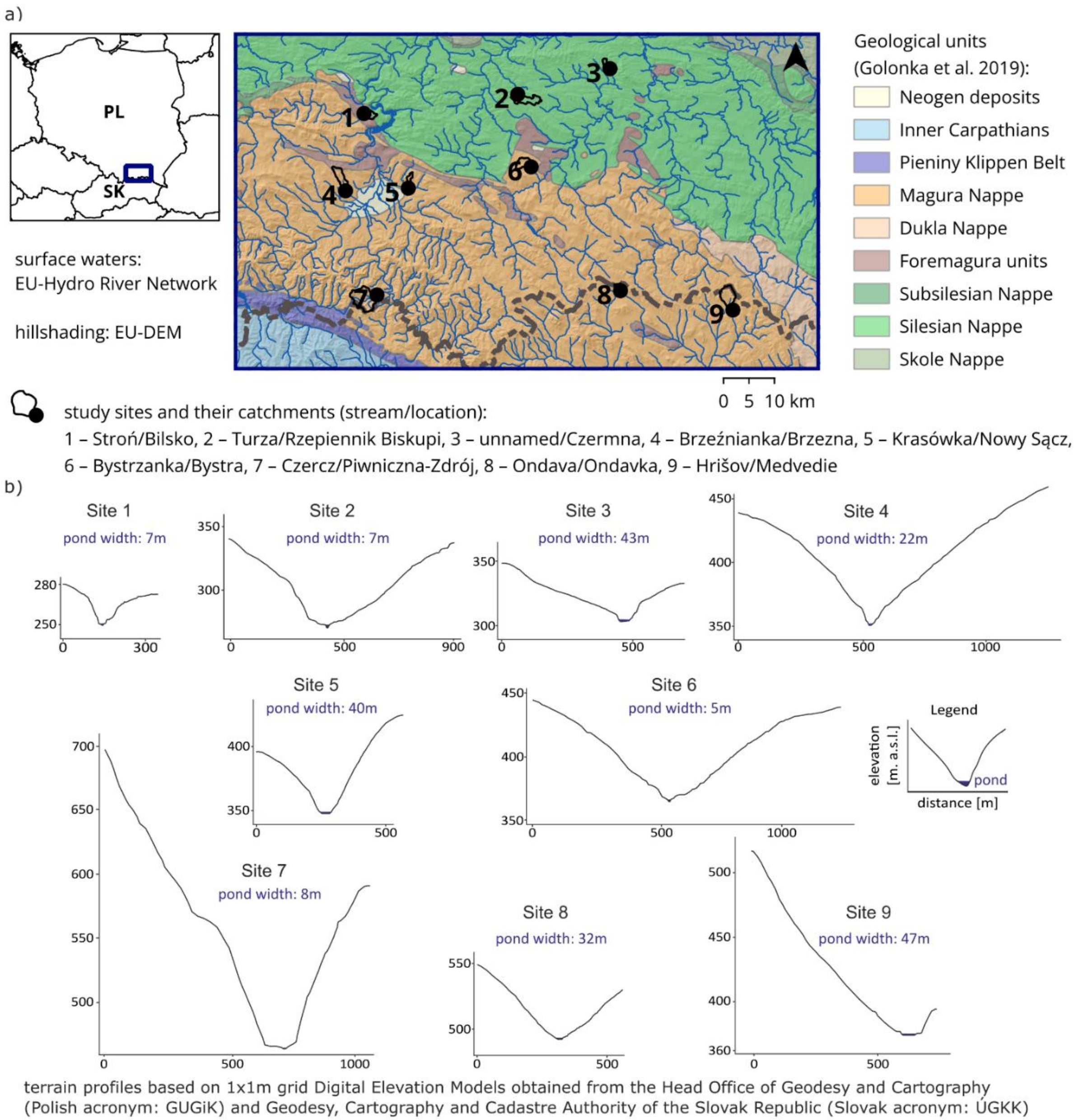

Figure 1: Study area – location (a) and valley cross-sections (b).

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 locally significant, 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 widespread, but 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 the 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. A 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 streams is minimal, although local enrichment may occur near farms or areas of intensive grazing. In contrast, domestic wastewater has been 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.

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 the slopes, and land reform has led to a progressive fragmentation of agricultural land (arable land and grassland) due to the constant division of land between successive owners (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 spanned the entire riverbed. The study sites were distributed randomly across the North-South transect of the Outer Western Carpathians in Poland and Slovakia. In addition to their varying topography, the sites differed in terms of human activity, such as catchment land use and the presence of river control structures (Table 1). 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 analysis, the study sites were classified based on the beaver pond characteristics. Two types were distinguished, based on the extent of the beaver dam: in-channel (dams within river banks) and overflowing (dams that extended beyond the river bank, with flooding that affected adjacent parts of the river valley). The types of ponds were partly determined by the morphology of the river valleys (Fig. 1b). 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 the beaver ponds was assessed based on the archival orthophotos, and they were divided into three categories: young (≤ 3 years old), moderate (4–9 years old), and old (≥ 10 years old) (Table 1).

Table 1: Characteristics of the study sites.

Subject	Parameter	Study sites								
		1	2	3	4	5	6	7	8	9
Catchment	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] [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] [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 closure points for all characterised catchments were located at the sampling sites downstream of the beaver ponds.

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

2.2 Water sampling and chemical analysis

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

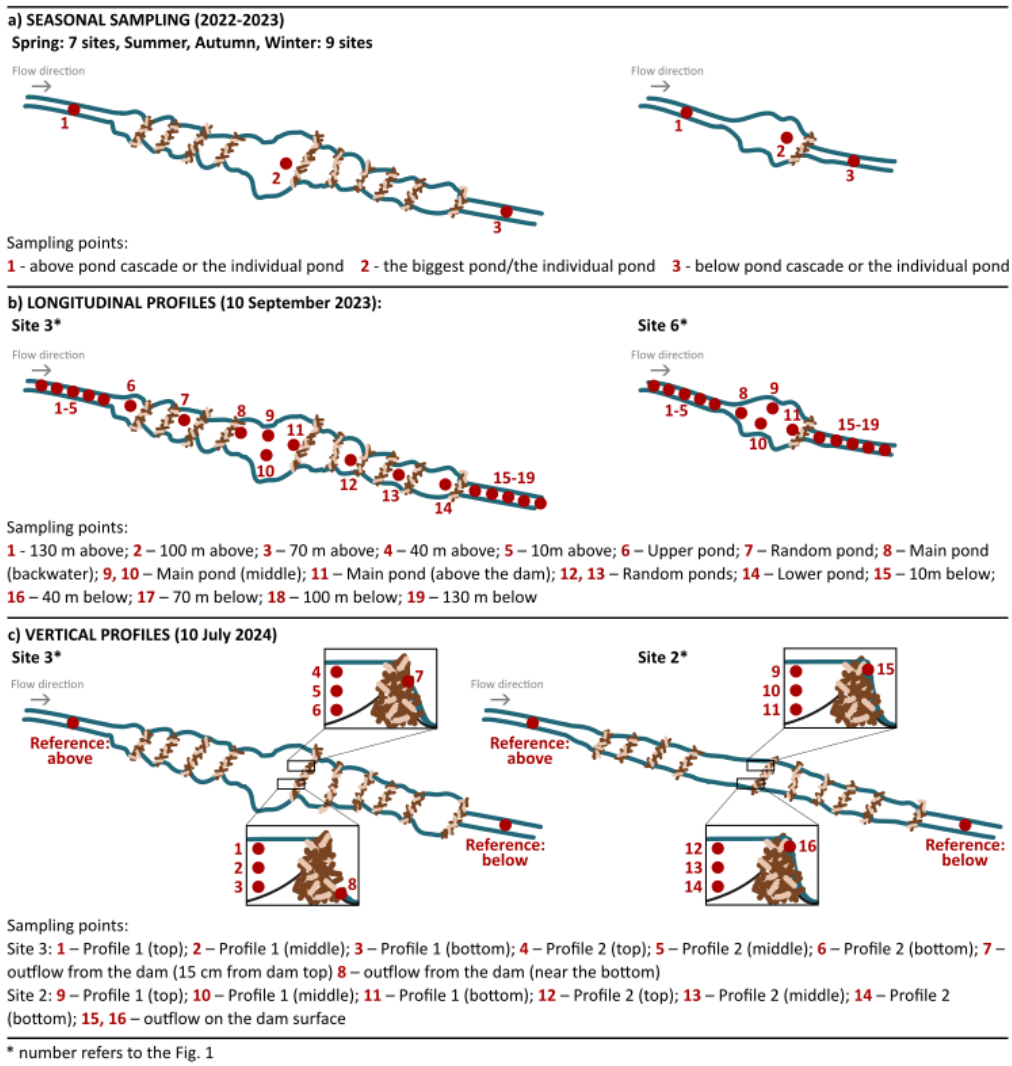

Figure 2: Study sampling schemes.

Although both geological variability and human pressure affect the chemical composition of stream water, a sampling design based on comparisons along the longitudinal gradients helped to minimise the impact of differences between the catchments. Three samples were collected at each site in late spring (June), summer (July–September), autumn (October–November) and winter (February) in 2022–2023, during baseflow conditions (i.e. excluding periods of 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 the 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 the sampling at each site being completed within about an hour. A total of 102 samples were collected from nine sites during the seasonal sampling.

Two sites were selected for additional measurements to create the longitudinal stream profiles (Fig. 2b). This sampling was conducted on 10 September 2023 at site 6 (a single in-channel beaver pond created ≤ 3 years ago) and at site 3 (an old overflowing beaver pond sequence created ≥ 10 years ago). Measurements and water samples 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 2024 at two beaver pond sequences, sites 2 and 3, which represented the two different pond types (Fig. 2c). Only in-channel ponds were observed at site 2. By contrast, overflowing stream banks were common at site 3. Measurements and water samples were taken from near the bottom of the water column, from its surface, and from dam outlets. Additionally, on-site measurements alone were taken from the middle of the water column. At site 3, outlet samples were taken from leaks in the upper part of the dam and near its bottom, while at site 2 they were taken from water overflowing the dam. In addition to the previously mentioned parameters, this scheme also involved determining the total organic carbon (TOC) concentration ($mg \cdot L^{-1}$).

Sampling and in situ measurements were conducted without disturbing turbidity. The basic physico-chemical parameters – T (°C), DO ($mg \cdot L^{-1}$), SEC ($\mu S \cdot cm^{-1}$) 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 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 1,41$mS \cdot cm^{-1}$ standard solution, selected according to anticipated conductivity of the sampled waters; DO probe: air-saturation calibration (100%) followed by zero-oxygen verification using a sodium sulphite solution. In addition, 250 ml water samples were collected at each site for laboratory analysis.

The HCO_3^- concentration ($mg \cdot L^{-1}$) was determined by titrating the water with a standard solution of hydrochloric acid. The ionic composition ($mg \cdot L^{-1}$) was analysed in a Dionex ICS-3000 ion chromatograph with the analytical columns IonPac CS16

3×250 mm and IonPac AS18 2×250 mm. Each sample was first filtered through a Whatman GF/D glass microfiber filter. The calibration curve was based on the Dionex certified reference materials (CRM) Combined Six Cation Standard II and Seven Anion Standard II. All solutions were prepared with 1% nitric acid (Suprapur). The following concentrations were prepared for calibration: 0 (blank), 1, 10, 50, 100 and 1000 $\mu g \cdot dm^{-3}$. The Vario TOC Cube Analyzer (Elementar) was used to determine the total organic carbon (TOC) concentration ($mg \cdot L^{-1}$) of the unfiltered water samples. The percent relative error, as determined by a data quality assessment based on CRM (KEIJM-02, GAW/WMO), was less than 5.0% for all parameters except K^+ and NH_4^+. The values in the last two cases were 5.8% for K^+ and 7.0% for NH_4^+. The detection limits were 0.4 $mg \cdot L^{-1}$ for Ca and 0.1 $mg \cdot L^{-1}$ for the other ions. For any ion concentrations below the detection limit, the values 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. Across all the analysed water samples (n = 102), the NO_3^- and NH_4^+ concentrations were below the detection limit in 17 and 20 samples of the samples, respectively. According to Hites (2019), the inclusion of values below the detection limit in analyses is justified if they do not exceed 20%. This applies in the case of both these ions.

2.3 Statistical analysis

The percentage change (*Dc*) in the values of the individual physico-chemical parameters of the water in ponds and streams below the beaver dams relative to their values above the ponds was calculated using the following formula:

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

where *Bx* is the value of the physico-chemical parameter x in the pond or stream below the dam during a particular sampling session, and *Ax* is the value of the physico-chemical parameter *x* in the stream above the dam during the same session.

For the purpose of calculating the percentage change, 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 subsequent statistical analysis if their mean absolute difference $|Dc|$ (for all sampling sites combined) exceeded 15% (Table A1). The calculation of $|Dc|$ used the following formula (where N is the total number of sampling sessions):

$$|Dc| = \frac{\sum\left|\frac{Bx - Ax}{Ax}\right|}{N} \cdot 100\%. \quad (2)$$

This procedure was used to account for the impact of any analytical errors (percent relative errors) on the *Dc* calculations. Thus, for each sample, the lowest (Dc_{min}) and highest (Dc_{max}) possible Dc values of a given physico-chemical parameter were calculated, with maximum percent relative errors (+/-) assumed for each (Fig. A3a). For most of the selected chemical parameters, such as DO, Cl^-, K^+, SO_4^{2-}, and NO_3^-, the majority of the maximum possible differences in *Dc* (Dc_{min}-Dc_{max}) were less than 10–15% (Fig. A3b). However, these differences were higher for H^+ and NH_4^+, though still many times smaller than the mean absolute difference |*Dc*| values (Fig. A3b, Table A1). This allowed for their inclusion in the subsequent analysis. Thus, only the chemical parameters for which the maximum possible differences due to analytical errors were smaller than the measured changes were considered for further analysis.

Seasonal and site-to-site variations in *Dc* were assessed for T and parameters that met the aforementioned criteria (DO, H^+, K^+, SO_4^{2-}, Cl^-, NO_3^-, and NH_4^+; Table A1). To compare the study sites, they were first classified according to the age and type of each beaver pond sequence (Table 1). The Mann–Whitney U tests (for two-group comparisons) and the Kruskal–Wallis tests (for multiple-group comparisons) were 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). In addition, correlations between the physico-chemical parameters and land use cover, catchment area, channel slope and channel width were analysed. Results characterised by $r > 0.6$ were considered as demonstrating a strong correlation. All analyses were performed using STATISTICA 12.0. The significance level used for all calculations was $p < 0.05$. Despite statistical significance being obtained, the results of site-to-site comparisons were further verified to exclude those deemed unreliable due to the potential influences of noise and the relationship between the grouping variables. When comparing the differences between groups based on pond age, the only parameters retained were those for which there was a clear upward or downward trend in the median difference between groups as age increased. Additionally, to mitigate 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). If the same parameter was found to be dependent on both pond characteristics (age and type), the result that failed to meet this stricter threshold was excluded, to account for any potential correlation between the characteristics.

3 Results

3.1 Physico-chemical background of the studied streams

The physico-chemical properties of the stream water at baseline conditions varied between the catchments studied (Table 2). Significantly higher SEC and concentrations of major ions were found in streams that drained areas with 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 sandstones (sites 3, 7–9). Concentrations of Cl^-, Na^+ and K^+ showed high correlations with the proportion 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 (median values).

Study site*	pH	SEC	DO	Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	NO_3^-	NH_4^+	HCO_3^-	SO_4^{2-}	Cl^-
		[$\mu S \cdot cm^{-1}$]					[$mg \cdot L^{-1}$]					
1	8.2	537.3	9.7	77.5	18.6	18.5	2.7	2.6	0.1	249.2	64.1	14.7
2	8.1	562.7	8.7	76.2	23.0	18.6	1.2	1.3	0.1	266.4	35.2	13.5
3	7.4	272.6	7.9	40.8	7.9	7.6	1.3	1.4	0.2	155.3	28.5	4.0
4	8.3	486.0	9.0	70.6	15.7	28.5	2.9	2.5	0.1	269.1	31.5	34.6
5	8.5	376.2	11.0	61.0	11.5	12.1	0.8	2.8	0.2	205.0	27.8	8.9
6	8.0	410.7	8.4	58.9	7.8	28.5	5.5	4.4	0.1	239.8	27.0	14.7
7	8.4	285.7	10.2	51.2	10.5	5.3	0.9	3.4	0.2	183.7	17.9	4.3
8	7.9	350.0	8.3	67.2	6.3	9.6	0.8	0.3	0.1	251.3	10.3	0.8
9	8.1	303.9	10.2	59.4	6.1	9.5	1.2	0.6	0.2	207.5	24.2	3.5

* number refers to the Fig. 1

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

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. The largest changes in the physico-chemical water parameters obtained within beaver ponds ($|Dc|>15\%$) were found in H^+ (pH), NO_3^-, NH_4^+, DO, K^+ and SO_4^{2-} (in descending order). For streams below the dams, the largest changes in the physico-chemical parameters relative to streams above the ponds ($|Dc|>15\%$) were found in NO_3^-, H^+ (pH), and NH_4^+, Cl^-, SO_4^{2-}, and K^+ (Fig. 3, Table A1).

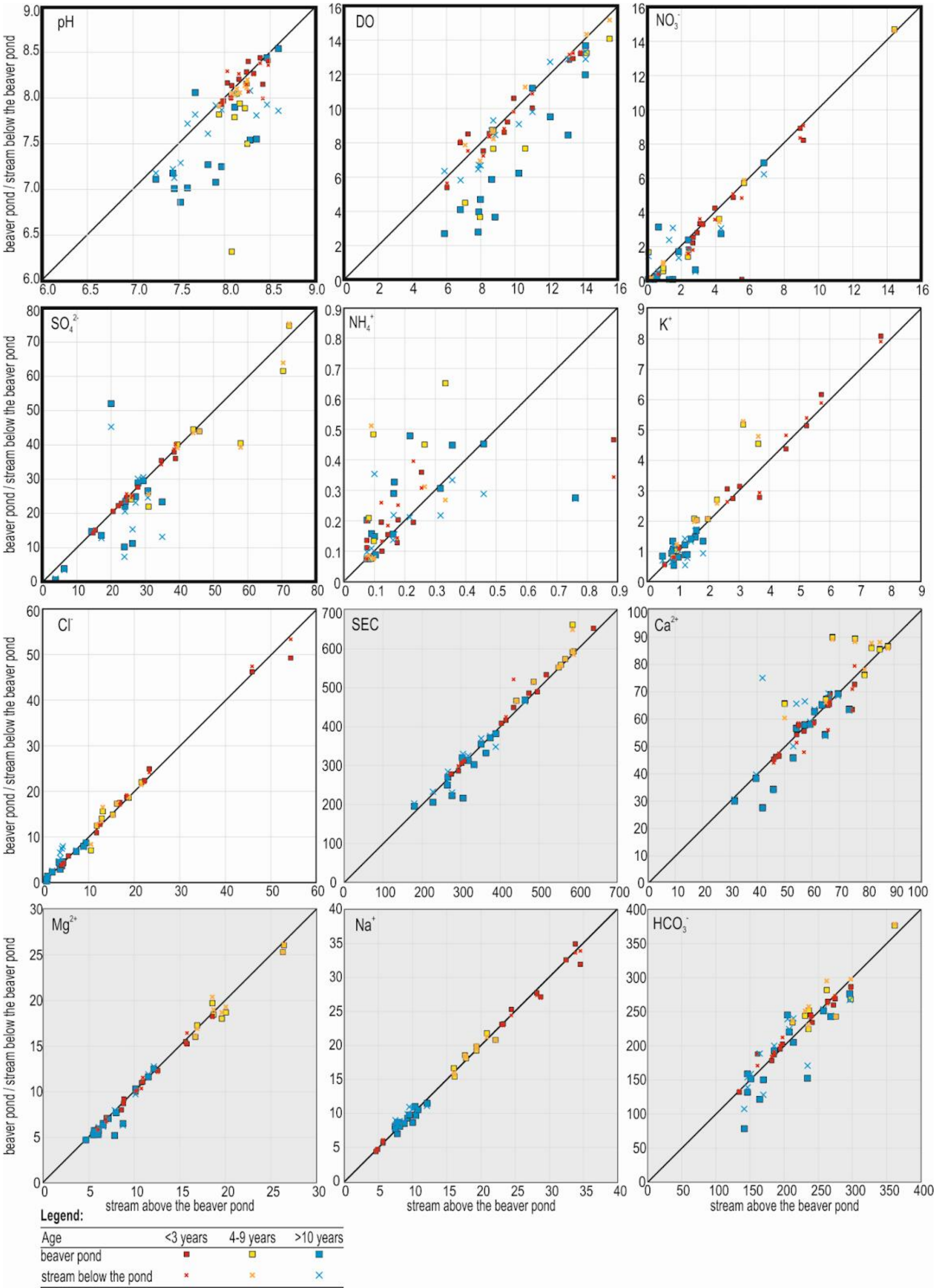
pH
DO
NO_3^-
SO_4^{2-}
NH_4^+
K^+
Cl^-
SEC
Ca^{2+}
Mg^{2+}
Na^+
HCO_3^-
beaver pond / stream below the beaver pond
stream above the beaver pond
Legend:
Age
<3 years
4-9 years
>10 years
beaver pond
stream below the pond

Figure 3: The physico-chemical water parameters, such as pH, SEC [µS·cm⁻¹], major ions, NH_4^+, NO_3^-, and DO [mg·L⁻¹], within and below beaver ponds of different ages compared to the inlet values. The graphs with a white background indicate parameters where the |*Dc*| between the beaver pond and/or the stream below the ponds and the stream above the beaver ponds were higher than 15%, while the graphs with a grey background highlight parameters where the |Dc| < 15%. The graphs with bold borders illustrate parameters that differ significantly based on the beaver dam properties, which will be discussed later in this paper.

Despite large absolute differences in the values of some parameters (|*Dc*|), the direction of the changes was not strongly consistent across seasons or study sites (Fig. 4, 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 the physico-chemical parameter changes were consistently observed for the majority of the study sites during particular seasons. For example, clear 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. 4, A1 and A2). The concentration of NH_4^+ increased distinctly in the ponds during the summer.

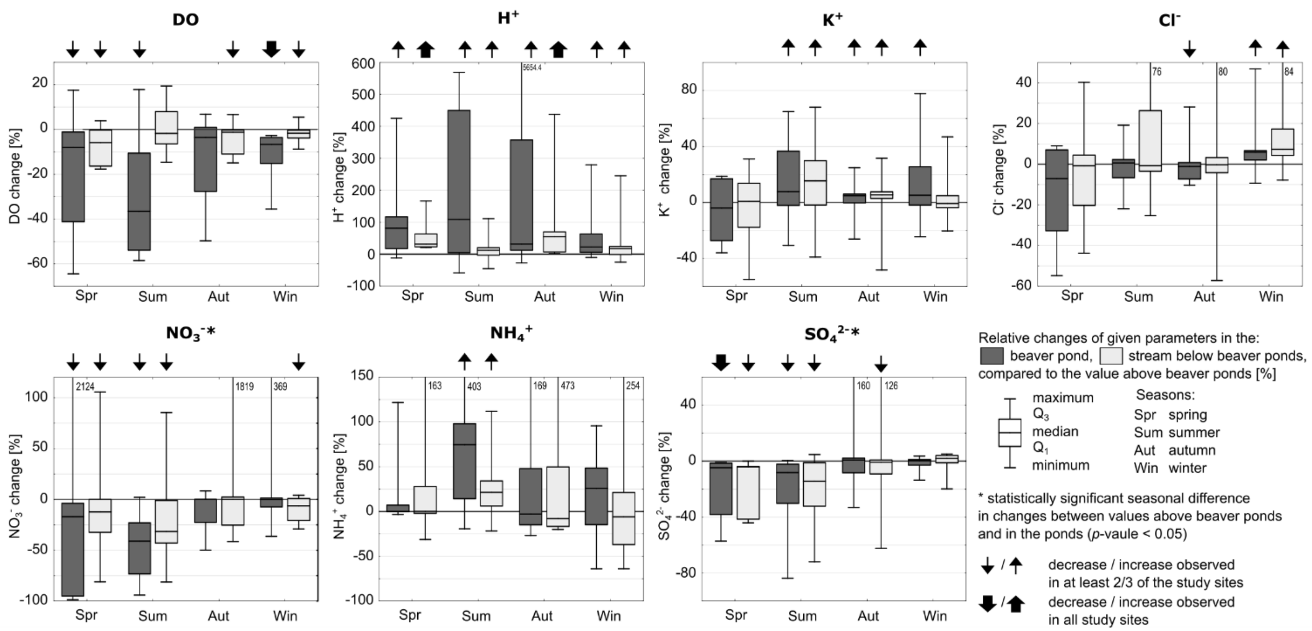

Figure 4: Percentage change (*Dc*) in the physico-chemical water parameters within and below beaver ponds in relation to stream water above beaver ponds. Only the parameters for which |*Dc*| > 15% are shown.

Table 3: Results of the group comparisons (Mann–Whitney U/Kruskal–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 the ponds (i.e. less than 3 years, 4–9 years, or more than 10 years) and seasons (i.e. spring–summer or autumn–winter). Statistical significance thresholds are explained in the footnote.

			Parameters							
			DO	pH(H^+)	T	K^+	NO_3^-	NH_4^+	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); * $p < 0.05$

() - differences deemed unreliable based on the verification process.

Among the significant differences in *Dc* between the ponds grouped by age, only changes in DO, pH and SO_4^{2-} showed a clear upward or downward trend (Table 3, Fig. 5). There were more significant differences in *Dc* compared to the upstream sections within the ponds themselves than in the streams below the ponds. While pH was barely modified in the youngest ponds (≤ 3 years old), decreases were observed in the older ponds, with the greatest *Dc* values obtained in ponds older than 10 years. A similar trend was observed in DO. The downward trend in the relative amount of DO with increasing pond age (≤ 3, 4–9, and ≥ 10 years old) was more prominent during the spring–summer period.

During the spring–summer period, a decrease in SO_4^{2-} compared to the upstream sections was observed both within the beaver ponds and in the downstream channel sections (Table 3, Fig. 5). Young beaver ponds and the streams below them showed the lowest percentage changes (*Dc*) in SO_4^{2-} concentrations. A moderate decrease of SO_4^{2-} was observed in the moderately old sites, and the highest decrease was noted in sites ≥ 10 years old.

Greater increases in T and greater decreases in NO_3^- were noted in overflowing ponds compared to in-channel ponds during the spring–summer period (Table 3, Fig. 5). The identification of a difference in pH changes between the pond types was likely a result of the partial overlap between the two categorisations (type and age). This assumption is based on the p-value, which did not exceed the Bonferroni threshold for reducing the risk of a family-wise error.

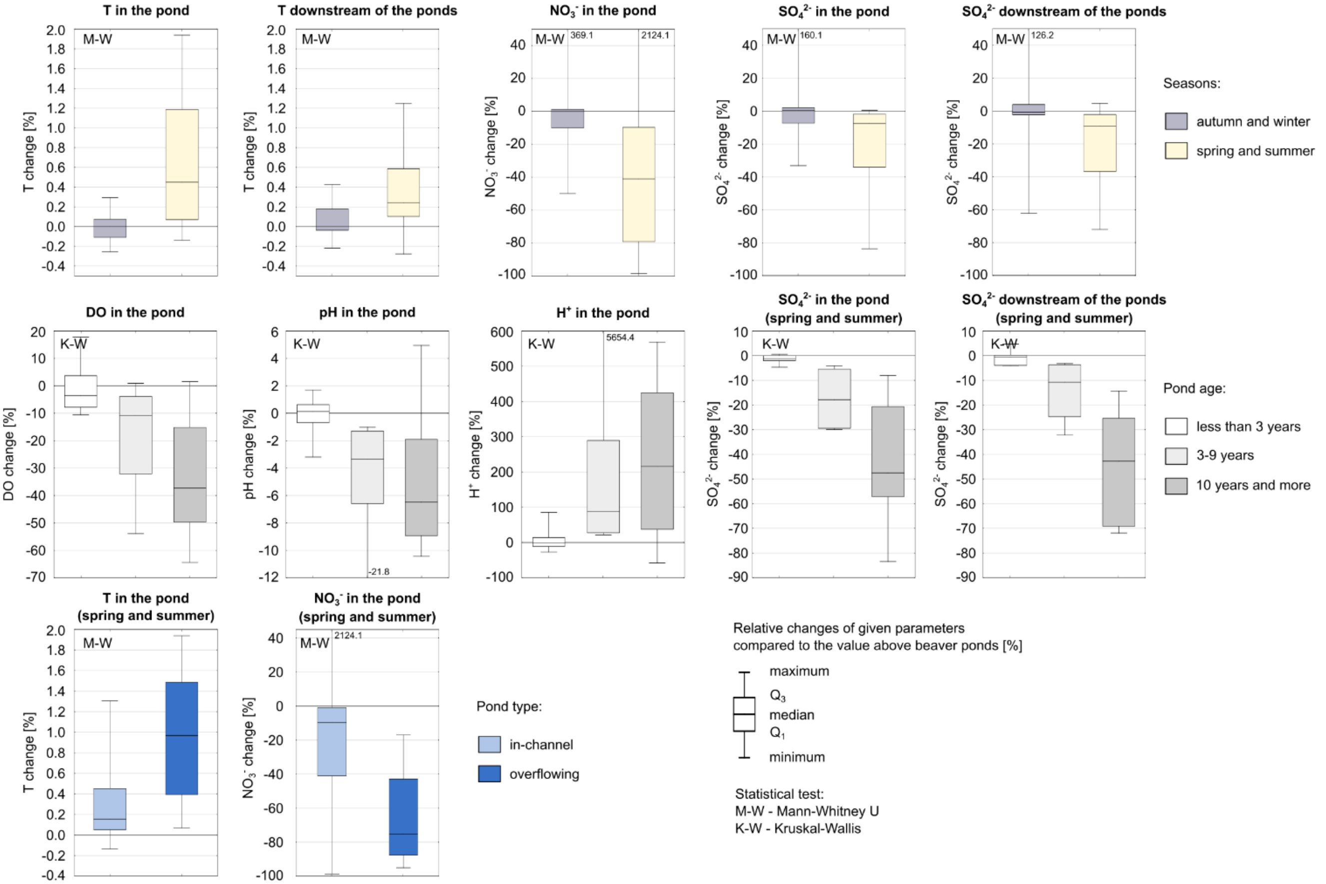

Figure 5: Comparison of *Dc* [%] for parameters significantly different across the categories of season, age, and type of pond in the Mann–Whitney U/Kruskal–Wallis tests (Table 3). Corresponding values in the measurement units are presented in Fig. A4..

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

As demonstrated by the longitudinal profiles (Fig. 6 and B1), the older overflowing beaver pond sequence (site 3) had 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.

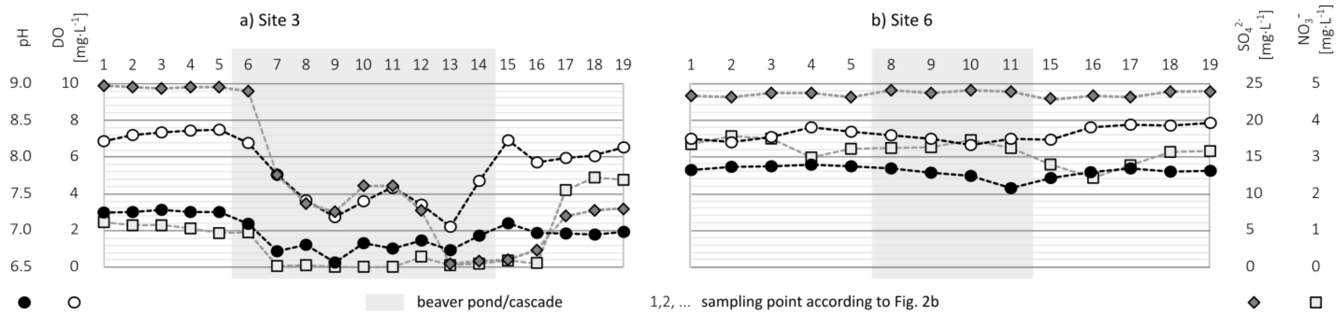

Figure 6: A longitudinal profile of the selected physico-chemical parameters at an overflowing and old site (Site 3 – a), and an in-channel and young site (Site 6 – b) on 10 September 2023.

There were greater vertical variations in physico-chemical parameters in the old overflowing beaver pond (site 3) than in the younger in-channel beaver pond (site 2). DO, pH and T were found to decrease with pond depth in both types of beaver pond; however, the range of variation was greater at site 3 than at site 2 (Fig. 7 and B2). The pH and DO concentrations were lower and the TOC concentrations were higher at the overflowing, old pond (site 3) than at the in-channel, younger pond (site 6). The pH and the concentrations of DO and TOC of the outflow measured near the base of the dam were notably lower than those measured at the top of the dam at site 3. The TOC concentration in the beaver pond at site 3 was found to be more than 13 mg·L^{-1}, which was almost three times higher than in the stream flowing into the pond.

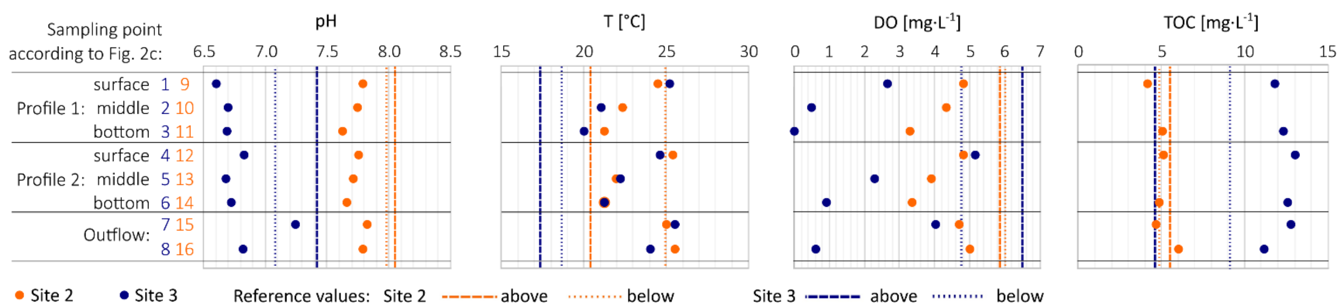

Figure 7: Differentiation of the selected physico-chemical parameters in the vertical profiles of study sites 2 (in-channel, moderately old) and 3 (overflowing, old) on 10 July 2024.

4. Discussion

4.1 Biogeochemical processes controlling physico-chemical water parameters that are triggered by the presence of beaver dams

The creation of beaver dams on streams alters the hydrological conditions of the catchment by flooding part of the valley and forming ponds. Specific biogeochemical processes take place in the newly formed aquatic environment that alter the chemical composition of the stream water (Larsen et al., 2021). Our study shows at most study sites a decrease in DO concentrations within the beaver ponds compared to the DO concentrations above the ponds. This suggests that DO is consumed during the oxidation of organic matter under the 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). High TOC concentrations in beaver ponds, compared to the stream water above the ponds, indicates the deposition of organic matter that has come 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 the 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 SO_4^{2-} concentrations at most of the study sites during warm seasons. Under the anoxic conditions that prevail at the bottom of ponds (as measured at site 3 in July 2024; see Fig. 7), as well as in the hyporheic zone, SO_4^{2-} ions are likely to 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 a relatively low redox potential (Sutton-Grier et al., 2011). The decrease in SO_4^{2-} concentrations in streams with beaver dams has been previously identified, and attributed to the expansion of anoxic 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 mineralisation 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). 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 conditions in water (Drever 1997). 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^- loading at the catchment scale.

The decomposition of organic matter results in the formation of organic acids, and this 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 reduce water pH (Driscoll et al., 1989). A decrease in stream pH due to 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 the stream water below beaver dams increased due to reduced concentrations of acidic ions such as NO_3^- and SO_4^{2-}. According to Margolis et al. (2001), the 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 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 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, and the latter 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 facilitated 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).

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 to the water flowing out through the top of the dams. For instance, the DO concentrations in the water flowing out from the bottom of the dams were 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, 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, which cause the physico-chemical properties of the pond water to revert to the original properties of the stream water. For example, the deoxygenated water flowing out of the ponds is slowly reoxygenated, aided by the turbulent water flow in the mountainous stream channels. DO concentrations in the streams below the beaver ponds were still lower than in the streams above the ponds, but 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 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 the ponds themselves. The increased DO concentrations in the 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 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).

4.2 Role of seasonality in the beaver dams' impact on the physico-chemical water parameters

The 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). This result can be explained by the greater 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 at the surface of the studied ponds was low, and 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 the sediments in the hyporheic zone, such as organic matter decomposition, denitrification and microbial sulphate reduction, are very slow at low temperatures, compared to in warm conditions (Qu et al., 2022). As a result, there are intensive physico-chemical transformations in the stream water flowing into the ponds in the warm season. 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 (summer) due to 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 of beaver ponds occurs in the summer. The NO_3^- ion is one of the most effective electron acceptors (oxidants) in the anaerobic oxidation of organic matter; therefore, NO_3^- is the preferred oxidising agent for anaerobic microbes. The process of NO_3^- reduction (denitrification) under the 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 can be partly related to the nitrogen fixation process, which is associated with increased microbial activity in sediments mediated by anaerobic conditions, as well as to 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. 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 this period anaerobic microbes would have 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 1.5 $mg \cdot L^{-1}$.

4.3 The effects of beaver dam age and beaver pond flooding extent on the physico-chemical water parameters

Our research suggests that the age of beaver dams and the type of the beaver ponds (i.e. overflowing vs. in-channel) play important roles in altering the chemical composition of stream water (Fig. 8). Previously, the impact of beaver dams on various physico-chemical water parameters has typically been 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, the magnitudes of the decrease in pH, 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 are influenced mainly by the decomposition and aerobic/anaerobic oxidation of organic matter. 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. 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 the 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.

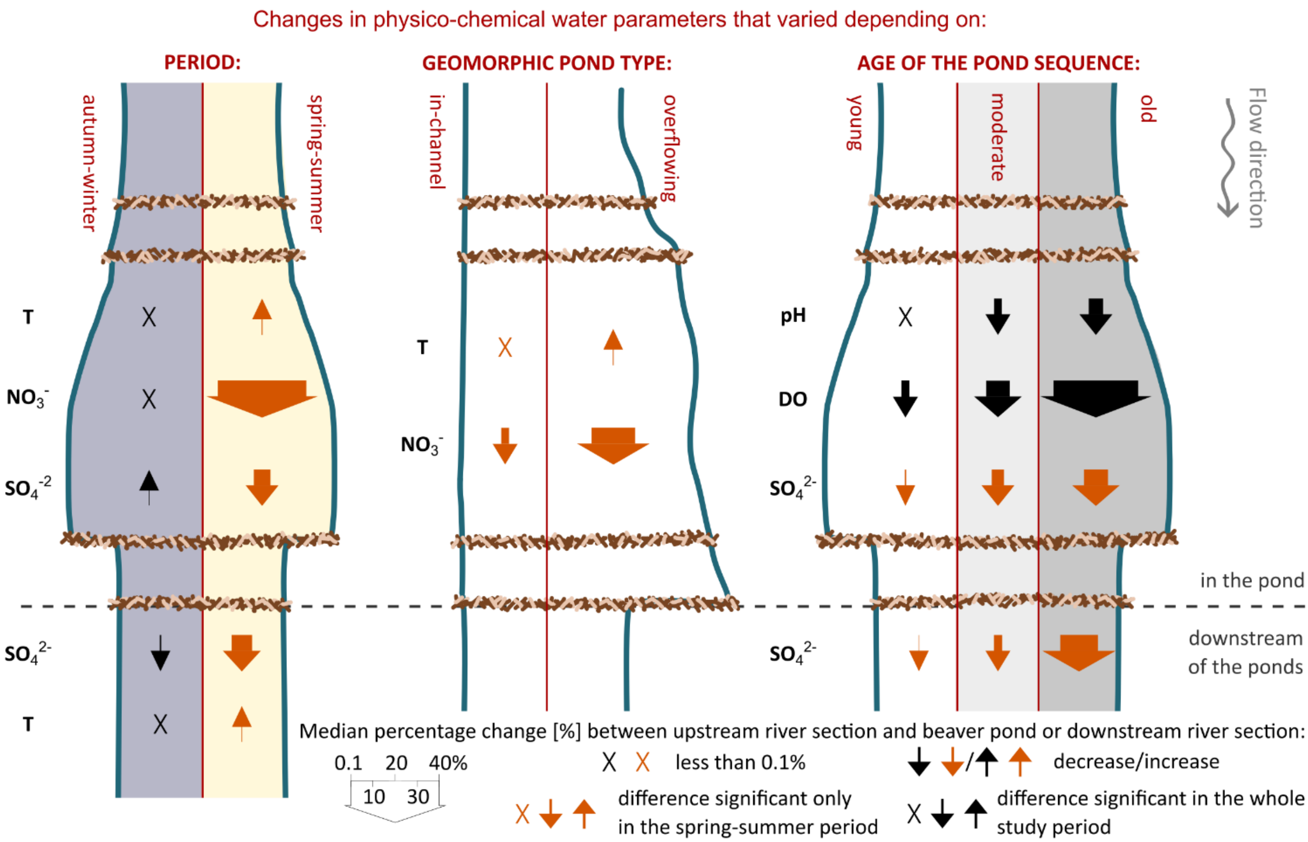

Figure 8: The scheme of the role of seasons and the characteristics of a beaver pond sequence in changes to physico-chemical water properties within and downstream of the beaver ponds. See Figure A4 for the presentation of the differences in measurement units.

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 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). The observed thermal difference is most likely due to the larger area of open water created by overflowing ponds, as opposed 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). 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 this is what determines the length of contact between solutes and microbial communities (Briggs et al., 2012). Extended hyporheic zones, which are associated with the formation of overflowing ponds, are probably areas of NO_3^- removal due to denitrification. Furthermore, as demonstrated by Puttock et al. (2018), total nitrogen storage per unit area in beaver pond sediments increases with pond size. This may indicate that the relationship between the overflowing pond type and the decrease in water NO_3^- concentrations is connected to the enhanced mineral nitrogen uptake by vegetation and the accumulation of nitrogen-rich organic sediment at the bottom of territorially expansive ponds. 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 attributed the greater extent of NO_3^- decrease in pond water to higher sediment loads and seasonal expansion of the beaver pond area.

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 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. This probably 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 the area concerned, 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 of the 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 the beaver ponds. Such measurements would have enabled the direct identification of redox conditions in the studied waters, and thus avoided the need to rely on speculation based on the concentration of key redox reaction ions. Direct measurements of redox potential, microbial activity and vegetation cover in 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 of the variables. Beaver ponds tend to be more persistent in smaller streams, and the length of 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.

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 reductions in pH, DO, NO_3^- and 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 also affected the downstream sections of the streams, in general, they were partially attenuated within a short distance of the dam.

The processes involving NO_3^- and SO_4^{2-} decrease were found to be more effective during the warm period of the year than during the cold period. Moreover, a larger reduction in NO_3^- concentrations occurred in overflowing ponds compared to in-channel ponds. The denitrification process, which is responsible for reducing NO_3^- concentration, requires anoxic conditions in the pond water. These are favoured in overflowing ponds during warm seasons due to the greater temperature increases and longer water residence time than in in-channel 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 SO_4^{2-} 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 removal, 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 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 extent and temporal persistence of the influence of beaver dams, and to elucidate the thresholds that determine their impact on the ecological properties of streams.

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 (https://doi.org/10.5281/zenodo.17937225).

Competing interests

The authors declare that they have no conflict of interest.

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

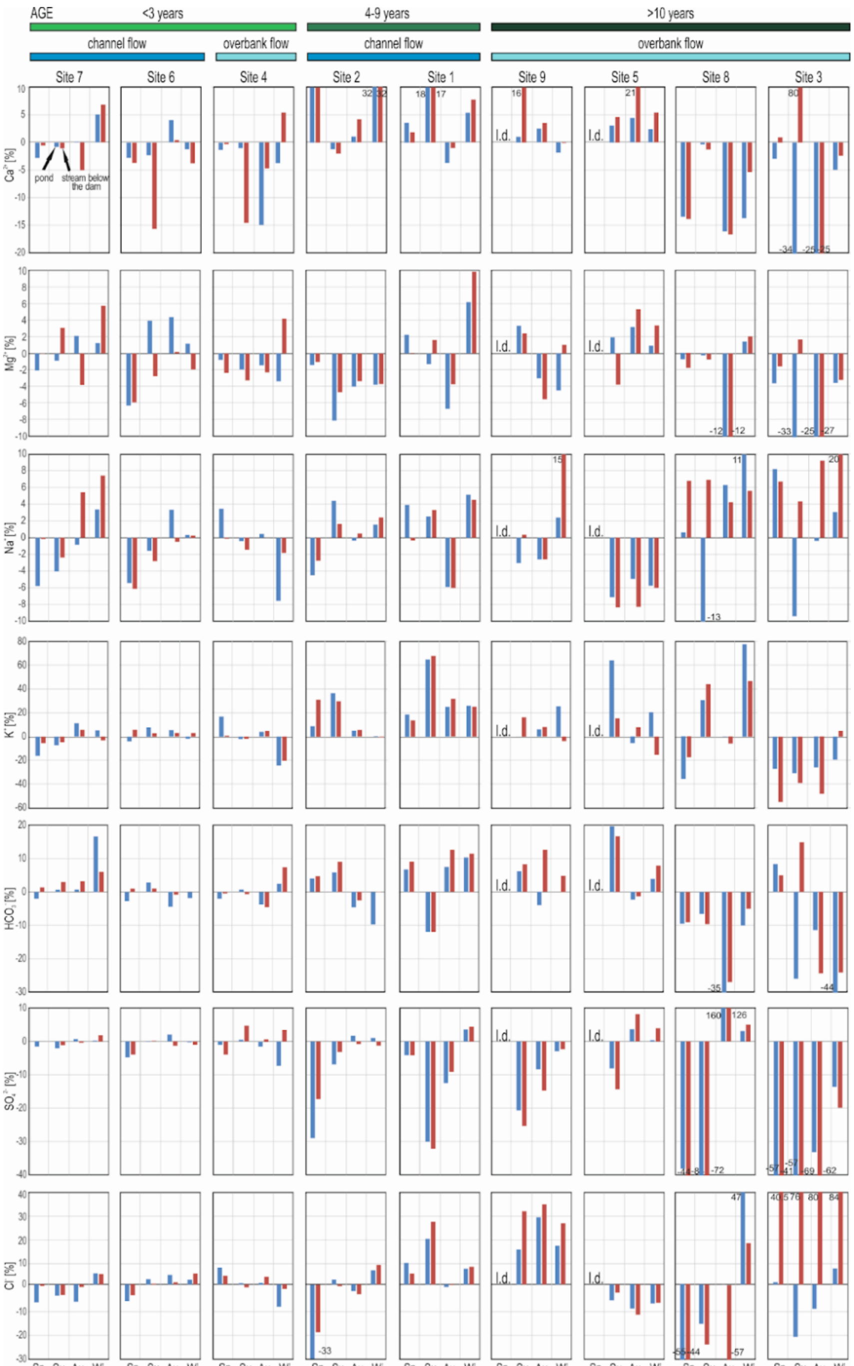


Figure A1: Percentage changes (*Dc*) in main ion concentrations in and below beaver ponds compared to their upstream values (Sp – spring; Su – summer; Au – autumn; Wi – winter; l.d. – lack of data).

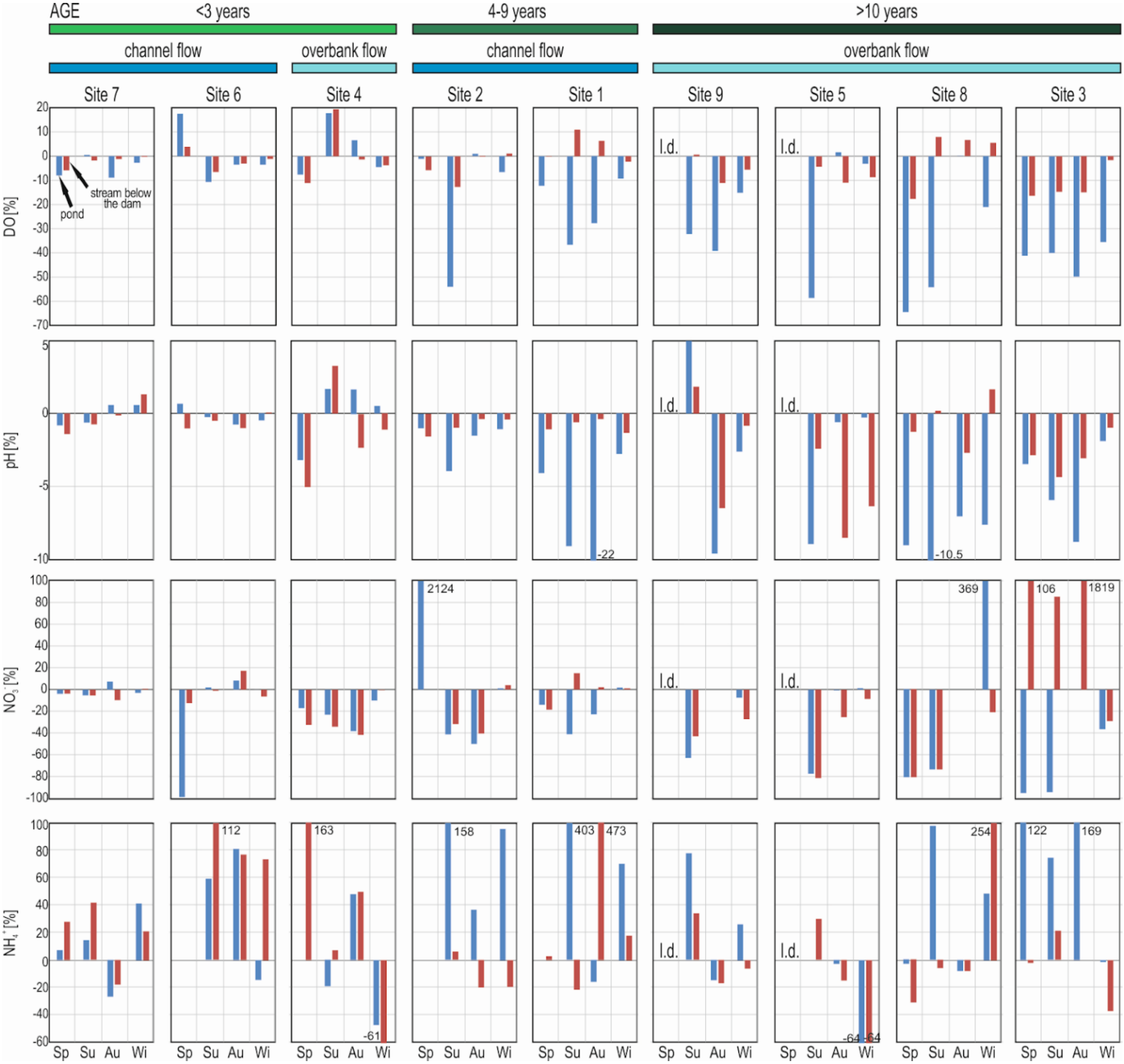
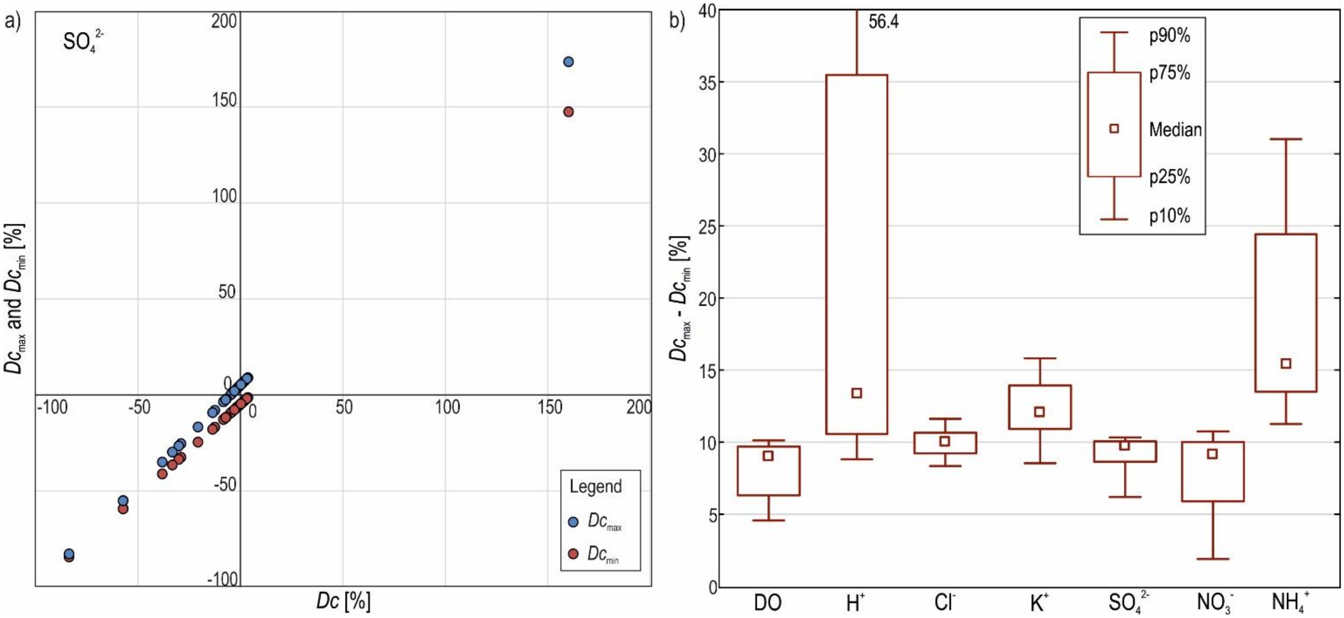


Figure A2: Percentage changes (*Dc*) in pH, and DO, NH_4^+ and NO_3^- concentrations in and below beaver ponds compared to their upstream values (Sp – spring; Su – summer; Au – autumn; Wi – winter; l.d. – lack of data).



815 **Figure A3. The lowest (Dc_{min}) and highest (Dc_{max}) possible Dc values, taking into account the percent relative errors of the chemical analysis, using the difference in SO_4^{2-} concentration in pond water and stream water above the ponds as an example (a). The differences between the lowest (Dc_{min}) and highest (Dc_{max}) possible Dc values for the selected chemical parameters are shown in (b).**

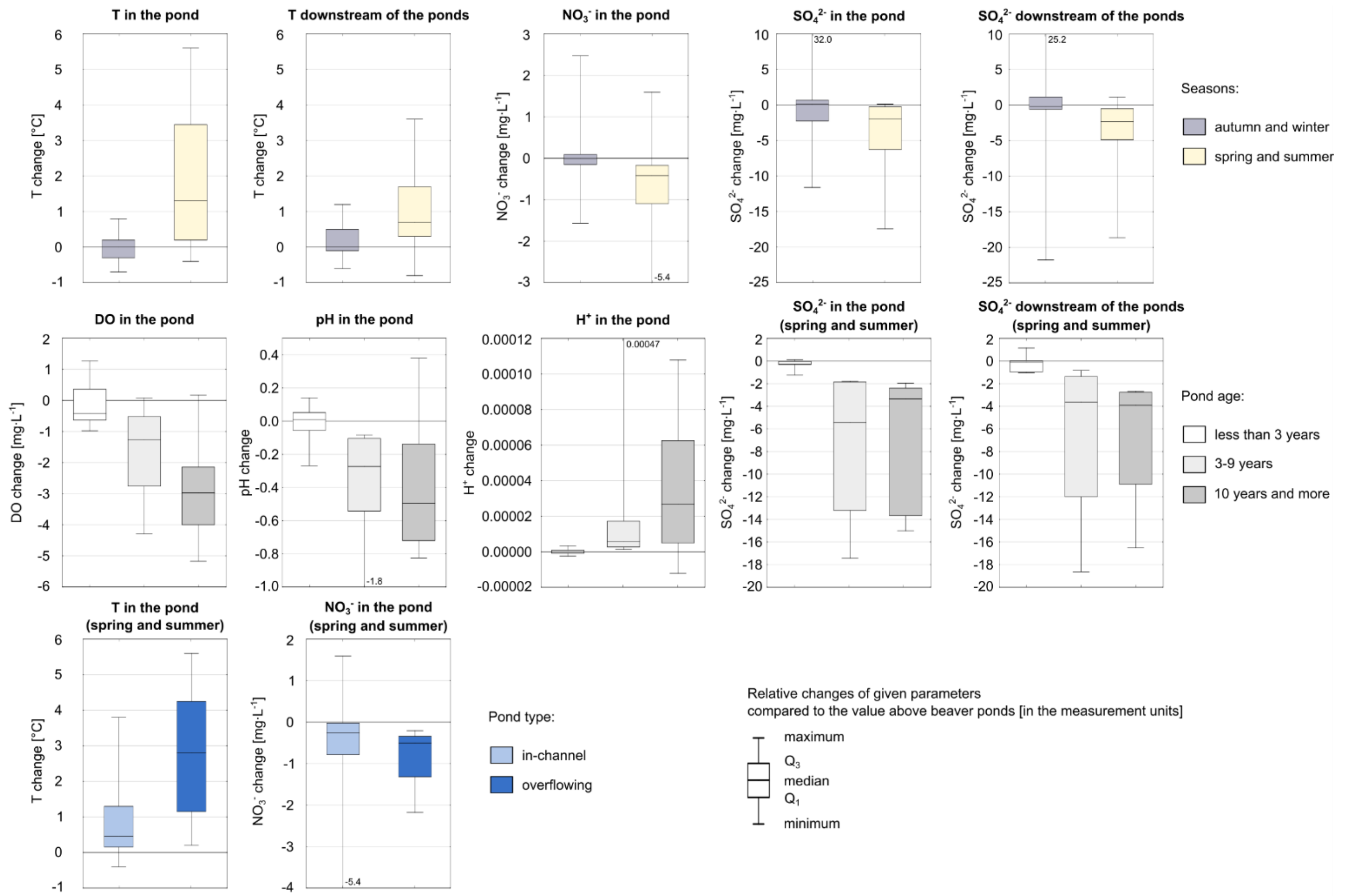


Figure A4: Comparison of the absolute changes of the selected parameters in the ponds/downstream of the beaver ponds (Table 3), across the different seasons, pond age and type of pond.

Table A1: Statistical characteristics of absolute changes (|*Dc*|) of physico-chemical parameters values in ponds and streams below the beaver dams in relation to values in streams above the beaver dams (n = 34). Average absolute changes > 15% 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

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

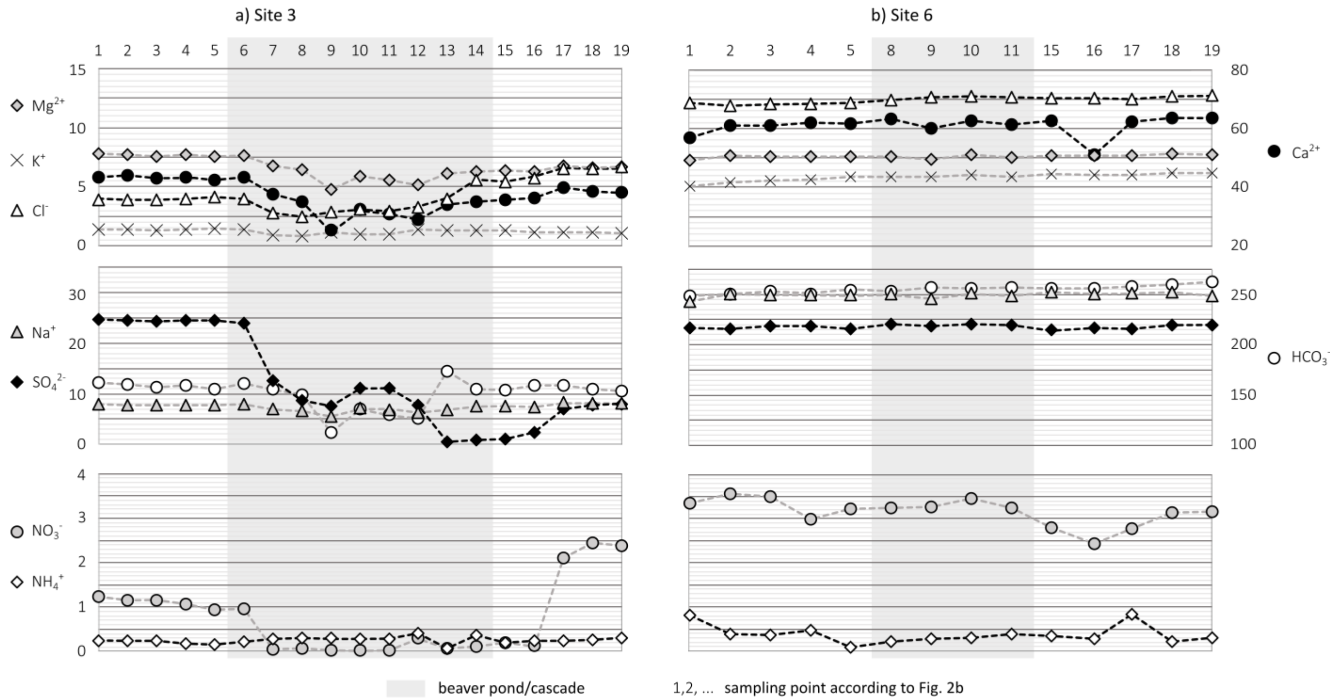


Figure B1: Concentrations of the chemical components of water [mg·L^{-1}] in the longitudinal stream profiles at study sites 3 (a) and 6 (b) on 10 September 2023.

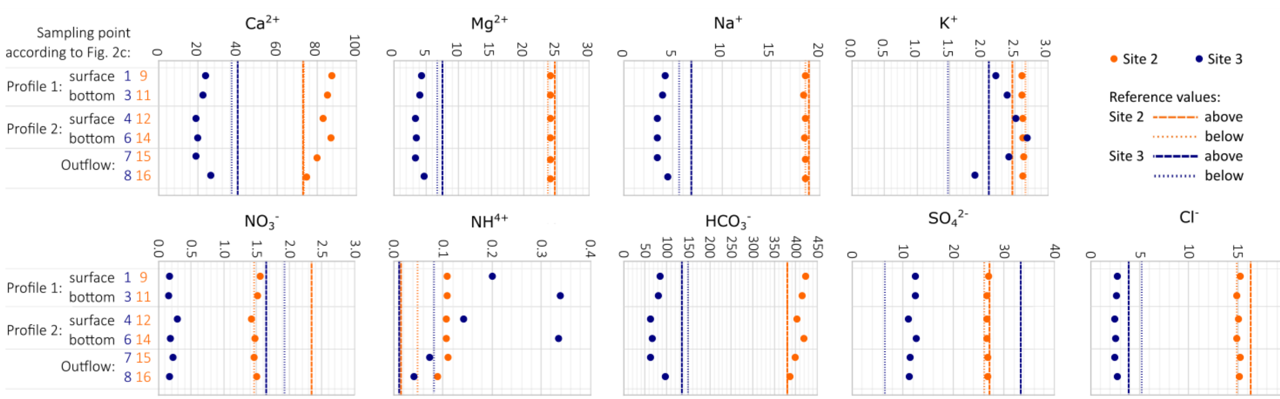


Figure B2: Concentration of the chemical components of water [mg·L^{-1}] in the vertical profiles of study sites 2 and 3 on 10 July 2024.