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Does the karst spring improve fish abiotic habitat in mountain streams?

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Highlights
- Fish habitat conditions in stream improving below the karst spring recharge.
- Karst spring influences the thermal regime and chemistry of stream water.
- Karst springs act as significant recharge sources during low-flow periods.

Abstract: Mountain streams constitute challenging habitat for many fish species due to rapid and variable flow, cool temperature, and limited food resources. Groundwaters recharge by karst spring may however mitigate harsh habit conditions of mountain streams providing niches for different fish species. This study aims to assess the suitability of mountain streams, replenished by karst springs, for various fish species like alpine bullhead, European grayling, brown and brook trout. The study was conducted in the Chochołowski Stream in the Western Tatra Mountains, Poland. The assessment of abiotic habitat is based on different characteristics of hydrological and thermal regimes as well as water chemical composition investigated between 01.09.2012 and 31.09.2014. The findings reveal that: 1) downstream variability of habitat abiotic conditions (such as water temperature, flow, water chemical composition) may affect the distribution of fish species, 2) karst springs contribute up to 100% of the stream's recharge during periods of winter low flow, 3) karstic groundwater reduces the variability and amplitudes of stream water temperature and weaken the periodicity in water temperature associated with daily course of air temperature and solar radiation, 4) groundwaters prevent stream freezing in winter and moderate summer temperatures, 5) increasing mineralisation of water below the spring recharge may positively affect fish distribution. The findings underscore the importance of karst springs in modifying the abiotic conditions of fish habitat in mountain streams.

Keywords: abiotic environment, fish species, groundwater recharge, streamflow, Tatra Mts., water chemistry, water temperature

INTRODUCTION

Karst springs and spring-fed streams contribute to diverse habitat conditions that support a wide range of aquatic species and promote biodiversity (Cantonati *et al.*, 2022; Cíbik *et al.*, 2022). They can serve as potential refuges of rare and threatened species, maintaining their ecological integrity over geological time scales (Beracko and Revajová, 2019; Lai *et al.*, 2019). Physical and chemical characteristics of karst springs significantly affect the habitat conditions of the streams fed by karst waters. This habitat encompasses various physical, chemical, and biological factors. Key among these are abiotic factors like water temperature, discharge, chemical composition, and substrate composition, which profoundly influence the abundance and distribution of aquatic species within these habitats. Water temperature is particularly significant, as it can restrict a species' ability to colonise areas with temperatures outside its optimal thermal niche, affecting its physiological processes such as reproduction, growth, and metabolism (Volkoff and Rønnestad, 2020). Cold groundwater-fed mountain streams not only stabilise the streamflow and maintain favourable conditions during low-flow periods but also create thermal refugia that support unique assemblages of cold-water species like salmonids (Kurylyk *et al.*, 2015; Sullivan *et al.*, 2021).

Discharge influences the availability of food, shelter, and migration to spawning habitats. Low flows can isolate populations and reduce the abundance of certain species, particularly those requiring swift currents for feeding and reproduction. For example, they can limit the ability of brown trout to access upstream spawning habitats in mountain streams. High flows, in turn, may displace some species temporarily, disrupt habitats and wash away eggs, larvae, and juvenile fish (Wang, Wang and Kuo, 2022). Fish species, however, tend to seek refuge within pools in response to increases in discharge and velocity (Bozek and Rahel, 1991; Rosenfeld and Boss, 2001). High flows can as well create new habitats and facilitate nutrient transport. Discharge influences both the depth and velocities of water. Various fish species exhibit distinct preferences for water velocity, seeking optimal ranges within streams for feeding, resting, or spawning. Ultimately, the abundance and distribution of fish species may be influenced by water chemical composition, with higher levels of mineralisation favouring the occurrence of mineral-tolerant fish and invertebrate species (Benstead, Valett and Webster, 2009).

The waters of the Tatra Mountains and the Podhale region present an exceptionally challenging habitat for most fish species with persistently low water temperatures, prolonged periods of ice and snow cover, occasionally swift currents coupled with frequent floods that sweep away a significant portion of their inhabitants downstream each year. These formidable obstacles make it a harsh environment for fish species adapted to the more typical conditions found in lowland rivers. Nevertheless, certain species that have evolved to thrive in the unique and demandant environment of mountain streams demonstrate remarkable adaptability and resilience to these challenging conditions. Among the documented fish species inhabiting the Tatra streams, are those belonging to (1) Cyprinidae like European minnow (*Phoxinus phoxinus*), (2) Salmonidae such as the brown trout (*Salmo trutta m. fario*), brook trout (*Salvelinus fontinalis*), and European grayling (*Thymallus thymallus*), and (3) Cottidae like European bullhead (*Cottus gobio*) and alpine bullhead (*Cottus poecilopus*) (Dyk, 2014; Dynowski *et al.*, 2015; Kozłowski *et al.*, 2017; Kuciński *et al.*, 2021). In terms of abundance *Cottus poecilopus* predominates in the Tatra streams representing about 80% of the total fish caught, followed by *Salmo trutta* m. *fario* (~19%) and *Salvelinus fontinalis* (<1%) (Kozłowski *et al.*, 2017). The latter *Salvelinus fontinalis* is however an alien species in the Tatras.

Therefore, our study aims to: 1) characterise abiotic habitat of mountain streams recharged by karst springs, 2) assess the suitability of this physical habitat for selected fish species, 3) identify which characteristics of abiotic fish habitat are improved by the karst spring recharge.

MATERIALS AND METHODS

STUDY SITE

The studies were conducted in the Chochołowski Stream located in the Western Tatra Mountains (Fig. 1). The Tatras represents the highest mountain range in the Carpathians situated on Polish-Slovak border. According to the Köppen classification (Köppen, 1931), the area belongs to the continental climate zone. Mean annual rainfall is 1,378 mm, while mean annual air temperature ranges between 0 and 6°C. The Tatras are characterised by the altitudinal zonation of climatic conditions, water abundance, flora, and fauna (Hess, 1965). The lowest parts of the catchment are located in the lower montane zone (up to 1,200 m a.s.l.), while the highest parts of the catchments are located in the alpine zone (over 1,800 m a.s.l.). The highest, northern parts of the catchments are built of crystalline and metamorphic rocks, while the lowest, southern parts are built of carbonate rocks that form several nappes. The southern part of the catchment possesses a typical karst relief, and the stream in lower section is recharged by karst spring – the Chochołowskie Spring. The spring is recharged beyond the topographic boundaries of the catchment by karst flows (Żelazny *et al.*, 2018). The Chochołowski Stream is a perennial stream with a length of about 9 km. The area of the catchment is about 34.5 km^2 with an altitude ranging between 920 and 2,158.5 m a.s.l., and average slope around 26.8°. The stream is shaded more than in 80%, while the streambed consists mostly of cobbles and boulders, gravels.

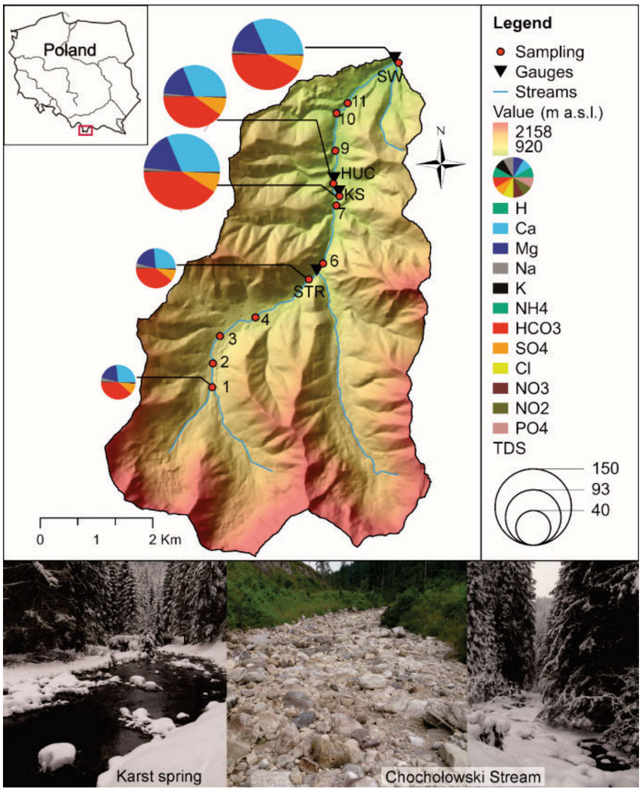

Fig. 1. Study site location; water gauges: STR = above the spring, KS = at the spring, HUC = below the spring, SW = below the spring; 1–11 = sampling sites; source: own study (phot.: *A. Bojarczuk*)

STUDY METHODS

The research was carried out from 2012 to 2014 and it included the seasonal water sampling, discharge measurements, and continuous monitoring of water level and water temperature (Fig. 1). Water samples were collected at 13 points along the stream course of which 7 were located above the spring, 5 were situated below the spring and one located at the spring. Water temperature and water level were recorded at 4 water gauges at a 10-minute interval: one site above the spring (STR), at the spring (KS), and at two sites below the spring (HUC and SW). Measured discharges and water levels were then used to construct the rating curve and compute continuous discharges. Water chemical composition (including: Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, NH_4^{+}, HCO_3^{-}, SO_4^{2-}, Cl^{-}, NO_3^{-}) was determined by means of ion chromatography, using a DIONEX ICS-2000 chromatograph. Different characteristics of streamflow and water temperature time series were calculated such as min., max., average, and coefficient of variability (Cv). Streamflow was characterised using Froude (Fr) and Reynolds (Re) numbers as well as Richard–Baker flashiness index (*RBI*). The *RBI* is a metric used to quantify rapid fluctuations in streamflow over time (Baker *et al.*, 2004). The seasonality of streamflow was characterised using flow-duration curves and monthly flow coefficient (*MF*). The latter represents a ratio of average monthly discharge to the mean annual discharge. The frequency of water temperature for different thermal ranges was calculated. The periodicity in water temperature was analysed using the continuous wavelet transform (CWT) with the complex Morlet wavelet as a base function (Torrence and Compo, 1998). The significance of periods in the CWT was tested against the red noise power spectrum at the 5% significance level using the Monte Carlo method. The wavelet analysis was performed in MATLAB software (Grinsted, Moore and Jevrejeva, 2004). Statistically significant differences between the average values of selected physical and chemical characteristics of stream water above and below the karst spring were tested at $p = 0.05$ significance level using ANOVA and Scheffe's post hoc test, correspondingly. The preference ranges of water temperature, velocity, and depth for spawning of selected stenotherm fish species like brown trout (*Salmo trutta fario*), brook trout (*Salvelinus fontinalis*), European grayling (*Thymallus thymallus*) and alpine bullhead (*Cottus poecilopus*), were established using the Storefish database (Teletchea and Teletchea, 2020) – Table 1.

RESULTS AND DISCUSSION

HYDROLOGICAL REGIME

The largest runoff occurred during the warm-half (May–Oct) of the hydrological year (Fig. 2), with peak runoff observed in May during snowmelt, and low flows in February when much of the

Table 1. Preference ranges of water temperature, velocity and depth for spawning of selected fish species

Fish species	Data	Preference range	Reference
Brown trout (*Salmo trutta* m. *fario*)	*T*	6.0–9.0	Mittelbach and Persson (1998), Kerr and Grant (2000)
	v	0.2–0.8	Louhi *et al.* (2008), Crisp (1996)
	H	0.15–0.45	Bruslé and Quignard (2001), Louhi, Mäki-Petäys and Erkinaro (2008)
	M	gravel	Ombredane *et al.* (1996), Bruslé and Quignard (2001)
	S	Oct–Feb	Billard *et al.* (1997), Bruslé and Quignard (2001)
Brook trout (*Salvelinus fontinalis*)	*T*	4.5–10.0	Groot (1996), Kerr and Grant (2000)
	v	0.17–0.29	Bernier-Bourgault and Magnan (2002)
	H	0.20–0.75	Snucins, Curry and Gunn (1992), Fraser (1985)
	M	gravel	Billard *et al.* (1997), Snucins, Curry and Gunn (1992)
	S	Oct–Nov	Billard *et al.* (1997), Snucins, Curry and Gunn (1992)
Grayling (*Thymallus thymallus*)	*T*	7.0–12.0	Ovidio *et al.* (2004), Bruslé and Quignard (2001)
	v	0.4–0.7	Bruslé and Quignard (2001), Persat (2011)
	H	0.2–0.5	Persat (2011), Nykänen and Huusko (2002)
	M	gravel, pebbles	Meyer (2001), Sempeski & Gaudin (1995)
	S	Mar–Apr	Witkowski and Kowalewski (1988), Meyer (2001)
Bullhead (*Cottus poecilopus*)	T	2.0–15.0	Vøllestad *et al.* (2003)
	v	0.1–0.8	Legalle *et al.* (2005)
	H	0.1–0.5	Vøllestad, Olsen and Forseth (2002), Janiga *et al.* (2023)
	M	cobbles, boulders	Kotusz *et al.* (2004)
	S	Feb–Apr	Kottelat and Freyhof (2007)

Explanations: T = water temperature, v = velocity, H = water depth, M = streambed material, S = spawning season.
Source: own study.

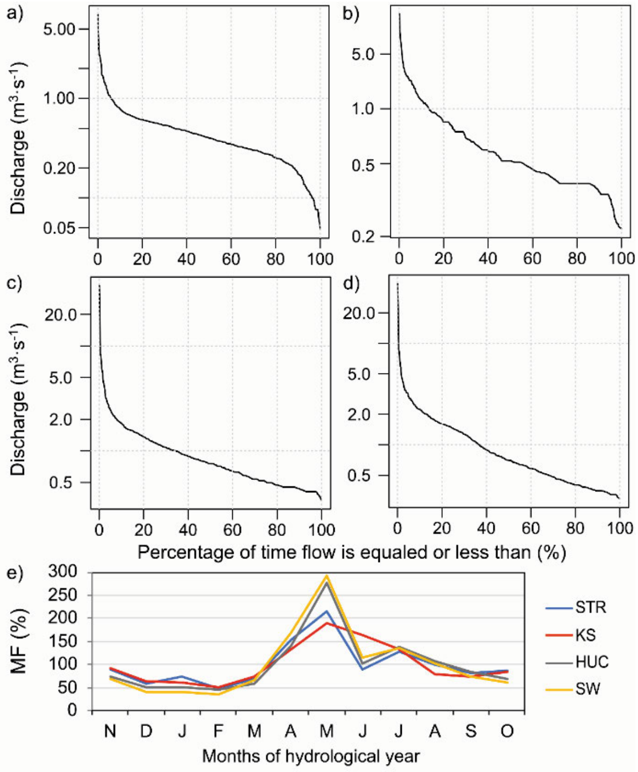

Fig. 2. Flow-duration curves: a) above the spring (STR), b) at the spring (KS), c) below the spring (HUC), d) below the spring (SW), e) monthly flow coefficient; source: own study

precipitation is stored in snow cover. Monthly flow coefficients revealed two distinct hydrological regimes: nival-pluvial for the stream and nival for the karst spring. Although the regime of the karst spring does not impact the stream below it, it significantly affects the volume of runoff.

Flow rates varied significantly, ranging from 0.04 to 38.75 $m^3 \cdot s^{-1}$, with the lowest at STR and the highest at SW (Tab. 2). However, medium flows predominated in the analysed section of the stream (Fig. 2). Low flows, which may impede fish migration, constituted about 5% and mostly occurred in the upper section of the stream (STR). During exceptionally low flows, water above KS may completely disappear (between sampling sites 6 and 7 – Fig. 1), and the flow in the downstream section is entirely sustained by the karst spring. Similar observations were made in other regions (Dufresne *et al.*, 2020). The intermittency of stream can offer both benefits and challenges for fish populations. On one hand, intermittent streams can provide breeding grounds and refuge from predators and harsh environmental conditions for fish from larger watercourses. On the other hand, when exacerbated by low water levels, stream fragmentation can disrupt the longitudinal continuity of rivers. This disruption hinders species migration and isolates fish populations, potentially leading to increased mortality rates (Kukuła and Bylak, 2022). Among studied fish species, alpine bullhead, is considered as a bio-indicator of the integrity of running waters (Tomlinson and Perrow, 2003). This species has adapted to thrive in a narrow range of conditions including good water quality, low temperature, and high dissolved oxygen saturation, and it tends to display sedentary behaviour, often settling in permanent shelters under stones (Reyjol *et al.*, 2009). Interestingly, alpine bullhead, was found at the highest position in the Chochołowski stream (Kozłowski *et al.*, 2017), suggesting its resilience to extremely low winter flows.

This aligns with previous studies of Mignien and Stoll (2023), who noted that cold stenotherm species exhibit higher susceptibility to frequent and prolonged low-flow events, yet they displayed tolerance to the magnitude of such events. Anticipated climate changes and the expected increase in the frequency of extreme events like hydrological droughts are likely to hinder fish migration towards upper stream courses. Recent studies in the Tatras revealed however increasing trends in annual low flows as well as winter average flows in the Tatras (Rajwa-Kuligiewicz and Bojarczuk, 2024a), potentially enhancing environmental flow and stream habitat conditions. Moreover, land cover changes associated with windthrows may decrease the frequency of hydrological droughts, especially in winter (Rajwa-Kuligiewicz and Bojarczuk, 2024b). Windfalls, however, may as well act as physicochemical stressors, causing not only hydrological changes, but also increased sediment transport, altered thermal and light regimes, and deterioration of water quality (Kuglerová *et al.*, 2021).

Flood events occur regularly either during spring freshet or in summer during torrential rainfalls of short duration causing so-called flash floods (Pociask-Karteczka *et al.*, 2018). These flood events reflect high flashiness; however, they are relatively short in duration and constitute less than 2% of the time. They typically occur beyond the spawning period and mostly affect lower sections of streams characterised by a gentler bed slope (SW).

Streamflow variability, represented by the coefficient of variability (*Cv*), ranged from 58% to 163%, with the highest variability observed at HUC and the lowest at KS. Streamflow variability at the upstream (STR) and downstream ends (SW) of the stream section was 94 and 161%, respectively. Flashiness

Table 2. Selected characteristics of the streamflow in the Chochołowski Stream and karst spring

Site	*Q* ($m^3 \cdot s^{-1}$)				*RBI* (–)	Low flow				High flow			
	min.	avg	max.	*Cv* (%)		*H* (m)	*v* ($m \cdot s^{-1}$)	Fr (–)	Re (–)	*H* (m)	*v* ($m \cdot s^{-1}$)	Fr (–)	Re (–)
STR	0.05	0.5	7.0	94	0.14	0.29	0.17	0.10	28,932	0.43	1.16	0.27	330,901
KS	0.22	0.7	3.3	58	0.06	–	–	–	–	–	–	–	–
HUC	0.34	1.1	37.8	163	0.16	0.27	0.37	0.23	61,583	0.53	2.16	0.42	749,951
SW	0.29	1.2	38.8	161	0.18	0.19	0.57	0.42	64,614	0.94	2.76	0.30	1,786,408

Explanations: *Q* = discharge, *RBI* = flaschiness index, *H* = depth, *v* = velocity, Fr = Froude number, Re = Reynolds number; water gauges as in Fig. 2. Source: own study.

index (*RBI*) ranged between 0.06 and 0.17. The lowest was observed at KS, while the highest at SW. Streamflow flashiness below the karst spring (HUC and SW) were higher than above it (STR).

Recent research indicates that various fish species may exhibit distinct responses to the magnitude, frequency, and duration of high-flow events (Mignien and Stoll, 2023). For instance, grayling and brown trout tend to be positively affected by both the frequency and duration of high flows, although the duration has both positive and negative effects on these species. Meanwhile, bullhead and minnow positively respond to longer durations of high flow events. According to this study, species with an equilibrium life history strategy like alpine bullhead, brown trout, and grayling, are positively affected by longer durations of high-flow, while periodic and opportunistic species exhibit positive response to the timing, frequency, and magnitude of high-flow events.

During the prevailing streamflow (within the limits of low and medium flows), the width of the stream bed increased in the downstream direction, while the average depth of the stream decreased. The width of the stream significantly increased during floods. According to previous studies the extended high-flow events enhance lateral connectivity with the floodplain, which promotes the transfer of organic matter and nutrients (Liu and Wang, 2018). The flow was turbulent with approximately Re is within the range 28,932–64,614 for low and for high flows in the range 33,090–17,864. During low flow conditions maximum Fr number increased in the downstream direction from 0.10 to 0.42. During high flow Fr ranged between 0.27 and 0.42, whereby the highest was observed directly below the karst spring (HUC). The Fr number was predominantly below 1, indicating sub-critical flow with greater depths and lower velocities. Turbulent flow conditions, and moderate Froude numbers at all sites and for different flows, provide favourable habitat conditions for analysed fish species. Streambed composed of boulders, pebbles and gravels create a suitable habitat for fish. Poor fish communities are usually associated with narrow riparian buffers, a high percentage of fine sediments, substantial embedding of coarse substrates, and uniform run habitat (Mundahl and Mundahl, 2022). The turbulent flow conditions and high *RBI* at HUC are not conducive to the presence of fish. Fish generally avoid high levels of turbulence as it impairs swimming performance, but stronger swimmers may prefer more turbulent flows. For instance, brown trout tend to inhabit the lower 5 cm of the stream where shear forces create high turbulence (Cotel, Webb and Tritico, 2006). Peaking flows unlikely displace brown trout downstream due to the presence of coarse substrate that creates low-water-velocity micro-niches, providing habitat stability for the fish (Heggenes, 1988). Brown trout potentially can find small patches of suitable spawning habitat also at KS and SW. The last site (SW) provides stable flow conditions with depths and velocities that closely align with the preferences of brook trout. As shown in previous studies the reductions in flow have little impact on brook trout density or survival from spring to fall, however, it may significantly imped spring-to-fall growth when flow is reduced by 75% (Nuhfer, Zorn and Wills, 2017). While brook trout may potentially occur at KS and STR, SW remains the most suitable habitat for this species. Water gauge STR offers moderate variability in flow and flashiness along with relatively low depths and velocities that meet the preferences of bullhead. Alpine bullhead tend to avoid areas with a high density of brown trout (Baran *et al.*, 2015; Vøllestad, 2024), which likely to occur at downstream sites due to higher water depths.

THERMAL REGIME

Minimum water temperature ranged between 0.0 and 2.2°C, the highest was observed at HUC while the lowest at STR. Maximum water temperature varied between 7.2°C and 12.4°C, the highest was observed at SW while the lowest at KS. Average water temperature for STR and KS were similar (~4.6°C), however STR exhibited much higher variability of water temperature (Cv = 60.7%) than KS (Cv = 30.8%). Both average water temperature and its variability below the spring increased in the downstream direction, with averages rising from 5.1 to 5.5°C and variability increasing from 34.9% to 53.9%, respectively. In winter, water temperature below the spring (HUC) was significantly higher than above it (STR) – Figure 3b. Conversely, in summer, the opposite situation was observed (Fig. 3b). Water temperature was below freezing at STR for 2% of time (Fig. 3a). Maximum water temperatures occurred about 4% of time at STR and about 8% of time at SW. Minimum water temperature occurred most frequently (37%) at STR. At KS water temperature frequently (63%) ranged between 3.0 and 6.0°C, in the remaining 37% of time water temperature at this site varied between 0.0 and 3.0°C. At HUC, water temperature frequently (44%) varied between 3.0–6.0°C. Water temperatures in ranges of 0.0–3.0°C and 6.0–9.0°C occurred with a slightly lower frequency (~32%).

Water temperature at KS is almost completely devoid of periodicity, except for an annual periodicity (Fig. 4b). Unlike the KS, stream water exhibits several periodical patterns. Water temperature at STR displays a semidiurnal, diurnal, and annual periodicity (Fig. 4b). Diurnal and semidiurnal periodicities occur only in the warm period of the year and diminish in winter. Diurnal and annual periodicities in water temperature correspond to the daily and annual course of air temperature in the temperate climate zone while semidiurnal periodicity is associated with solar radiation (Rajwa-Kuligiewicz, Bialik and Rowiński, 2016; Żelazny *et al.*, 2018). At HUC water temperature exhibits annual and daily periodicity (Fig. 4c). Interestingly, the semidiurnal periodicity disappears at this site due to the inflow of spring water that has almost constant temperature during the day. Similarly weaker semidiurnal cycles in water temperature are observed in large lowland rivers, which is associated with greater inertia of large water volumes (Rajwa-Kuligiewicz, Bialik and Rowiński, 2016).

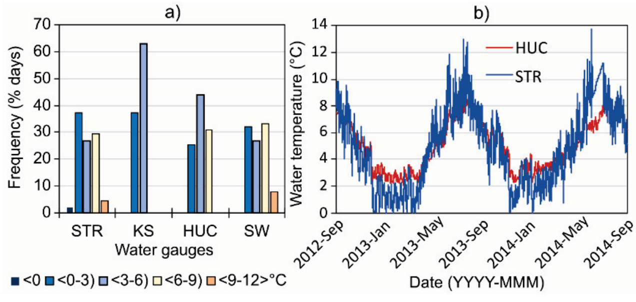

Fig. 3. Frequency of water temperature (in % of days in hydrological year) for selected thermal ranges (a), time series of water temperature recorded above and below the sampling site at the spring (b); water gauges (STR, KS, HUC, SW) as in Fig. 1; source: own study

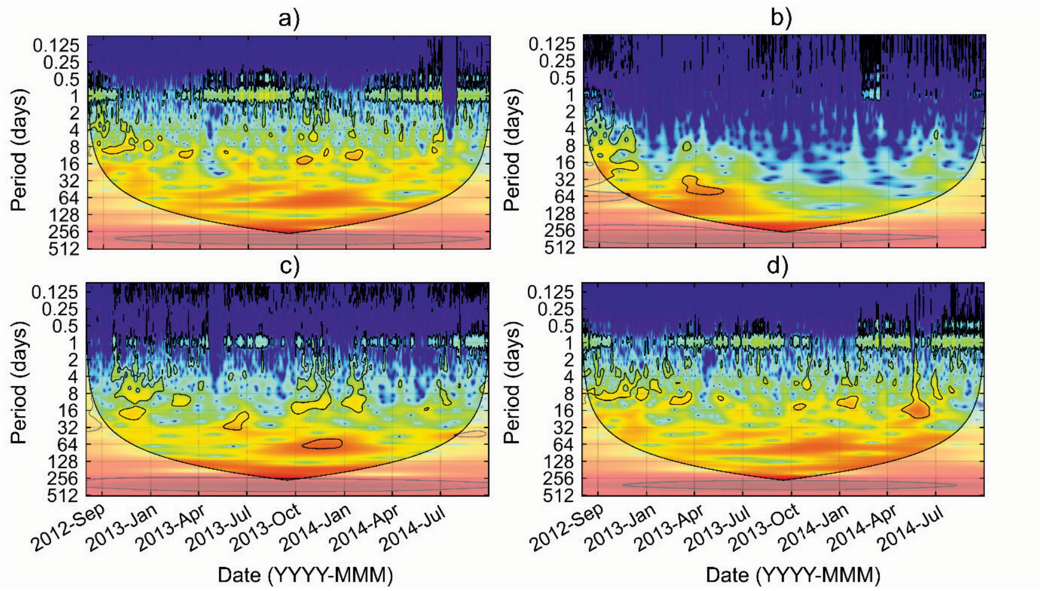

Fig. 4. Wavelet power spectra of water temperature: a) above the spring (STR), b) at the spring (KS), c) below the spring (HUC), d) below the spring (SW); the contour lines identify peaks of greater than 95% confidence for a red noise process with a lag-1 autocorrelation; source: own study

Further downstream (SW), semidiurnal periodicity in water temperature is strengthened (Fig. 4d).

Water gauge HUC characterised by higher average water temperatures and stable flow conditions, particularly during winter, emerges as an ideal habitat for brown trout. Conversely, SW, with its higher water temperatures and stable flow conditions, appears to be well-suited for grayling and brook trout. Karst spring (KS) with its relatively stable thermal conditions, seems favourable for bullhead. The karst springs has been found to have a significant impact on the stability of stream fish habitats over time (Mundahl and Mundahl, 2022; Hitt *et al.*, 2023) regulating stream water temperature (Chen *et al.*, 2021). Meanwhile, STR, characterised by high variability and occasional extreme temperatures may pose challenges for successful reproduction. Progressing climate change, especially the increase in air temperature, will have a negative impact on habitats for cold-water fish (Isaak *et al.*, 2012; Isaak *et al.*, 2013; Oomen and Hutchings, 2015). However, the habitat ranges of cyprinids (e.g. brook minnow) may move to Tatra sections of streams, which is currently very rarely observed (Wyżga *et al.*, 2009).

WATER CHEMICAL COMPOSITION

Changes in the physico-chemical parameters of water along the Chochołowski Stream are influenced by the geological structure of the catchment. In the crystalline part, the stream water exhibits a weakly alkaline pH and low conductivity, along with low ion concentrations. However, upon entering the carbonate part, there is a notable increase in pH, electrical conductivity (*EC*), and ion concentration, particularly evident below the groundwater recharge from the karst spring (Figs. 1, 2, Tab. 4). The ANOVA (analysis of variance) revealed significant differences in the values of most physicochemical water parameters (except K^+ and Cl^- ions) between measurement points above and below the KS inflow (Fig. 5). The chemistry of the Chochołowski Stream downstream from the recharge point is primarily influenced by the chemistry of the karst spring (Tab. 3), extending up to the section closing the catchment, despite the input of highly mineralised waters from tributaries. Within the carbonate segment, the Chochołowski stream displays alkaline pH, elevated conductivity, and increased concentrations of most ions.

Waters are characterised by very good oxygenation in all seasons and display little amplitudes of changes, which is beneficial for all analysed species. This is due to low water temperature, higher velocities and the absence of vascular plants in the streambed. In addition, water is characterised by very high transparency and small amounts of suspended particles, which creates favourable conditions for feeding and spawning. However, event like windfalls and avalanches may intensify erosion and delivery of fine suspended load and organic matter to the stream causing the siltation of the stream bed, clogging fish spawning habitat, affecting feeding behaviour and fish health (Mikołajczyk and Nawrocki, 2019; Kukuła and Bylak, 2020). Previous studies indicate that suspended mineral particles can lead to damage of fish gills, hinder the proper development of fish eggs, and increase egg mortality rates (Sear *et al.*, 2016). Adult fish may become more susceptible to diseases and parasites (Wood and Armitage, 1997). Additionally high amounts of fine sediment may also affect the invertebrate community in streams and hence could reduce prey availability for juvenile salmonids (Sutherland and Meyer, 2007; Sternecker, Wild and Geist, 2013). Low concentrations of sodium and biogenic compounds (for salmonids, a general threshold value of less than 0.03 $mg \cdot dm^{-3}$ for NH_4^+ is recommended), as well as low conductivity of water indicates high quality of water. Clean water supports the growth of algae and aquatic plants, which serve as primary producers at the base of the food chain, providing essential food resources for fish and other organisms (Wojtal, 2013; Smieja, 2014).

The range of pH values (6.5–8.5) at different sites is also suitable for analysed fish species. Fish occur both in silicate and carbonate waters with pH values varying between 7.0 and 8.5. Maximum fish productivity is expected at pH values between 6.5 and 8.5. Extreme pH values below 6 or above 9 are particularly harmful as they can mobilise or activate other toxic

Table 3. Physical and chemical parameters of Chochołowskie karst spring

Statistics	Parameter										
	pH (–)	*EC* (μS·cm^{-1})	Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	NH_4^{+}	HCO_3^{-}	SO_4^{2-}	Cl^{-}	NO_3^{-}
			mg·dm^{-3}								
Min.	7.73	141.4	19.9	6.21	0.32	0.24	0.006	65.07	6.63	0.31	1.43
Mean	7.96	177.2	24.94	8.27	0.77	0.47	0.034	94.42	14.55	0.55	2.02
Max.	8.30	243.0	35.65	13.66	1.16	0.95	0.058	153.89	19.53	1.05	3.26

Source: own study.

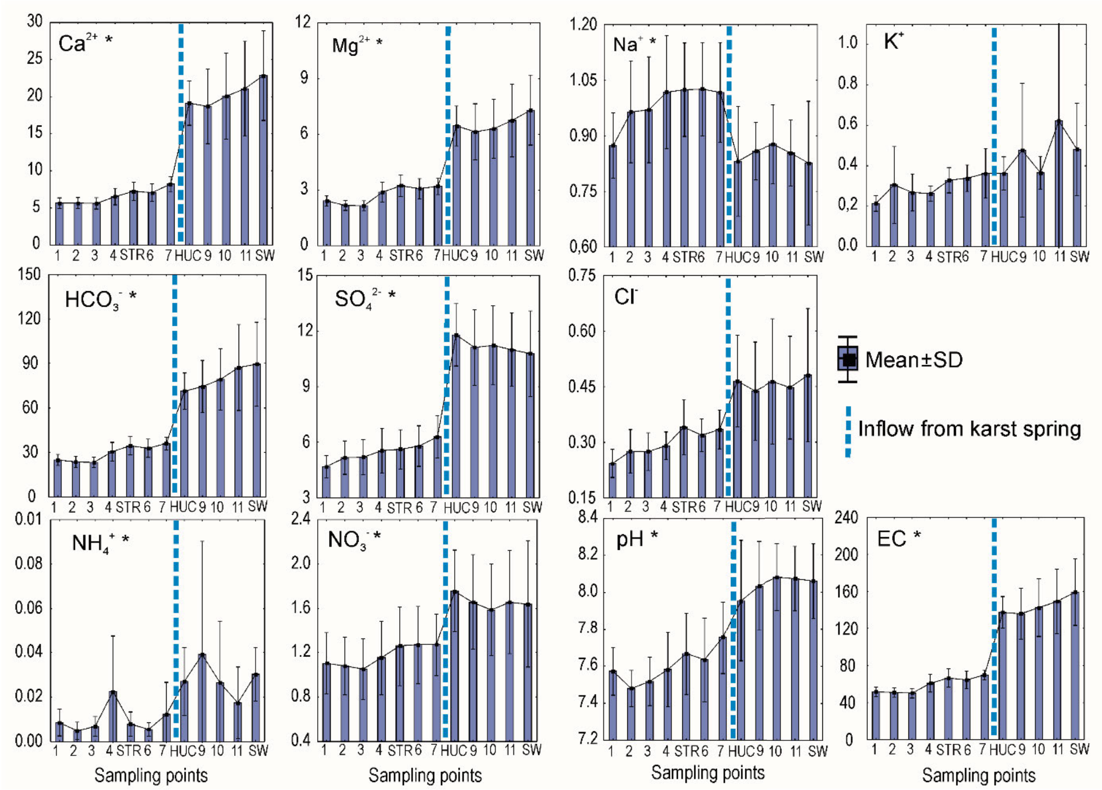

Fig. 5. The variability of selected ion concentrations (mg·dm^{-3}), pH and electrical conductivity (*EC*, μS·cm^{-1}) along the course of the Chochołowski Stream; 1–11 and water gauges (STR, KS, HUC, SW) as in Fig. 1; *SD* = standard deviation; * statistically significant differences between measurement points above and below the KS inflow; source: own study

Table 4. Physical and chemical parameters of the Chochołowski stream

Sampling site / water gauge	Parameter										
	pH (–)	*EC* (μS·cm^{-1})	Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	NH_4^{+}	HCO_3^{-}	SO_4^{2-}	Cl^{-}	NO_3^{-}
			mg·dm^{-3}								
1	7.57	51.7	5.65	2.41	0.87	0.21	0.009	24.98	4.69	0.24	1.10
2	7.48	50.9	5.66	2.17	0.96	0.31	0.005	23.65	5.17	0.28	1.08
3	7.52	50.2	5.61	2.15	0.97	0.27	0.007	23.33	5.19	0.27	1.05
4	7.58	60.8	6.52	2.89	1.02	0.26	0.022	30.55	5.55	0.29	1.15
STR	7.67	66.5	7.24	3.23	1.02	0.33	0.008	34.52	5.62	0.34	1.26
6	7.63	64.4	7.06	3.07	1.03	0.34	0.005	32.86	5.80	0.32	1.27
7	7.75	69.9	8.22	3.20	1.02	0.36	0.012	36.09	6.30	0.33	1.27
HUC	7.96	137.4	19.12	6.46	0.83	0.36	0.027	71.33	11.79	0.47	1.76

cont. Tab. 4

Sampling site / water gauge	Parameter										
	pH (–)	*EC* ($\mu S \cdot cm^{-1}$)	Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	NH_4^{+}	HCO_3^{-}	SO_4^{2-}	Cl^{-}	NO_3^{-}
			$mg \cdot dm^{-3}$								
9	8.04	135.9	18.69	6.14	0.86	0.48	0.039	74.46	11.12	0.44	1.66
10	8.08	142.5	20.06	6.30	0.88	0.37	0.026	79.34	11.23	0.46	1.59
11	8.07	149.1	21.07	6.75	0.85	0.62	0.017	87.33	10.99	0.45	1.66
SW	8.06	159.2	22.85	7.31	0.83	0.48	0.030	89.47	10.78	0.48	1.64

Explanations: 1–11 and water gauges (STR, HUC, SW) as in Fig. 1.
Source: own study.

substances, for example ammonium and heavy metals. Studies showed that a change in pH, especially in the early-life stages of salmonids, lead to high mortality rates (Smialek, Pander and Geist, 2021). Relatively higher electrolytic conductivity of the stream observed below the karst spring, creates better habitat conditions than the water above the spring. Notably, the increase in conductivity is associated with increasing concentration of calcium and magnesium in the stream water. These are the major ions that significantly improve osmotic regulation preventing leaching of blood salts and provide minerals important for many biological processes of fish populations. Karst springs with intermediate concentrations of calcium and increased acid neutralising capacity (*ANC*) provide improved water quality for salmonids as compared to siliciclastic aquifers (Teears *et al.*, 2020). Results indicated a significant relationship between *ANC* and fish species richness in streams, such that low *ANC* streams in siliciclastic watersheds support less fish species diversity than relatively higher *ANC* streams in granitic and basaltic-carbonate watersheds.

CONCLUSIONS

The study emphasises the pivotal role of karst springs in shaping the hydrological and physicochemical characteristics of mountain stream ecosystems. Karst springs act as significant recharge sources during low-flow periods and profoundly influence downstream habitat conditions, notably in terms of water temperature stability and mineralisation. By mitigating water temperature fluctuations and maintaining favourable conditions year-round, karst springs create an environment conducive to the diverse fish communities inhabiting these streams.

Recent studies suggest that climate changes can affect the distribution of organisms. Increased frequency and intensity of flood and drought events may hinder future recovery of stream habitats and biota. Climate changes are anticipated to have the greatest impact on cold mountain stream habitats, particularly affecting populations that experience colder temperatures during early life, which are more sensitive to temperature changes.

Rising water temperatures may lead to the shrinking of suitable habitats for cold-water species such as salmonids or shifting the extent of cyprinids habitats like European minnow, which presently only sporadically migrates into the lower sections of the Tatra streams. This in turn will affect their reproductive success and spawning periods leading to cooler temperatures during critical developmental stages and a male-skewed population. Therefore, habitats associated with karst spring fed streams will play a pivotal role in preserving and maintaining optimal conditions for cold-water fish species in the light of observed and future climate changes.

Our study demonstrates that high-yield karst springs significantly influence habitat conditions in mountain streams, altering hydrological, thermal, and water quality parameters. Therefore, karst springs warrant special protection, not just for their biodiversity but also for their broader impact on the entire karst spring–stream system, which extends over a larger spatial scale.

Integrating hydrological and ichthyological studies can further enhance our knowledge of habitat requirements for different fish species, facilitating targeted conservation efforts and ensuring the long-term health and resilience of mountain stream ecosystems.

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CONFLICT OF INTERESTS

All authors declare that they have no conflict of interests.

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