# From cold-water refuge to thermal stress: projected warming of Czech rivers and implications for brown trout

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**Abstract.** Water temperature is a fundamental driver of freshwater ecosystem functioning, governing physical, chemical, and biological processes across riverine environments. Despite growing evidence of climate-driven thermal change in Central Europe, region-specific projections linking continuous thermal shifts to ecologically meaningful thresholds for cold-water species remain scarce. Here, we developed a linear air–water temperature regression model (calibrated and validated using observed daily water temperatures from 35 river profiles across the Czech Republic (2002–2022) and forced with an ensemble of seven global circulation models (GCMs) and one regional climate model (RCM) under four SSP scenarios) to analyse observed thermal regimes through 2025 and project future conditions through 2085. Rather than focusing solely on mean temperature trends, we quantified changes in biologically relevant threshold exceedance days for brown trout (*Salmo trutta*), including cold-water persistence (<17 °C), sub-lethal stress (17–19 °C, 19–21 °C, and 21–23 °C), and extreme heat (>23 °C). Results show that thermally suitable habitat – defined as river reaches maintaining water temperatures below 17 °C for at least 350 days per year – declined from nearly 100% of the Czech river network in 1975 to approximately 77% by 2010, and is projected to fall below 5% by 2085 under median projections. This contraction is driven primarily by chronic sub-lethal warming rather than by rare extreme events, and is accompanied by a pronounced redistribution of thermal exposure toward the 19–21 °C and 21–23 °C stress bands in warm and intermediately warm rivers. Cold-season and early spring warming further threatens spawning success and early development. High-altitude headwater systems emerge as the last persistent thermal refugia, underscoring the urgency of protecting longitudinal connectivity and riparian shading as climate adaptation priorities.

## Introduction

The thermal regime of rivers acts as a master variable governing physical, chemical, and biological processes in riverine ecosystems (Caissie, 2006; Hannah and Garner, 2015). It is indeed a principal factor, as freshwater thermal regimes determine dissolved oxygen levels, species distribution and phenology, shaping overall ecosystem health and water quality. In the context of the Czech Republic, a region often referred to as the "roof of Europe" due to its role as a headwater source for major watersheds like the Elbe, Oder, and Danube, the stability of these thermal regimes is therefore particularly critical (Graf and Wrzesiński, 2020). River water temperature dictates the solubility of dissolved gases, specifically oxygen, and governs the kinetics of metabolic pathways in ectothermic organisms (Jonsson, 2023; Sadayappan and Li, 2025). As global atmospheric warming accelerates, the manifestation of this warming in lotic systems presents a multifaceted threat to biodiversity, particularly to cold-water specialist fish species such as the brown trout (*Salmo trutta*) (Gallagher et al., 2022; Borgwardt et al., 2020;

Tissot et al., 2024). Historical observations across Central Europe already underscore a significant upward trajectory in river temperatures, with annual means increasing by approximately 0.3 to 0.4 °C per decade over the last half-century (Dorthe et al., 2025; Ptak et al., 2024). The average increases in mean water temperature (basin average) for 2071–2100 relative to 1971–2000 are in Europe especially high, e.g. 2.1 °C for the Danube, 1.9 °C for the Rhine, and 2.1 °C for the Rhone (Van Vliet et al., 2013). Crucially, the ecological risk is not merely defined by a shift in mean values. The most profound impacts arise from the intensification of thermal extremes, the lengthening of warm-water periods, and the emergence of riverine heatwaves. Yet, equally important and often overlooked are changes in cold-season thermal conditions during autumn and early spring, which govern the most temperature-sensitive life stages of salmonids: spawning, egg incubation, and fry emergence (Sadayappan and Li, 2025; Van Vliet et al., 2023).

The brown trout occupies a narrow thermal niche that is increasingly under pressure from anthropogenically driven climate change (Borgwardt et al., 2020; Gallagher et al., 2022). As a poikilotherm, its body temperature and subsequent metabolic rate are directly determined by the surrounding water (Jonsson, 2023; Borgwardt et al., 2020). The relationship between temperature and metabolic demand typically follows an exponential scaling, often described by the van 't Hoff rule or the $Q_{10}$ temperature coefficient, where $Q_{10} \approx 2.1$ for heart rate in many salmonids (Gilbert et al., 2020; Vornanen et al., 2014). At the lower end of the thermal stress spectrum, the 17 °C threshold serves as a critical marker for the loss of optimal growth conditions. While brown trout can tolerate temperatures up to this point without significant impairment, the efficiency of energy conversion from prey to biomass begins to diminish as metabolic costs rise (Borgwardt et al., 2020; Elliott, 2000; Jonsson, 2023). The transition toward a more volatile thermal environment necessitates a rigorous quantification of risks associated with specific physiological thresholds (Wehrly et al., 2007; Elliott and Elliott, 2010; Brungs and Jones, 1977; Becker and Genoway, 1979). These thresholds, particularly the thresholds of 17 °C, 19 °C, 21 °C, and 23 °C, represent critical transition points from optimal growth to metabolic stress, sublethal impairment, and eventually, acute mortality (Jonsson and Jonsson, 2009; Brungs and Jones, 1977; Borgwardt et al., 2020). Once water temperatures consistently exceed 19 °C, the aerobic scope of the organism (the difference between maximum and basal metabolic rates) starts to contract (Gallagher et al., 2022; Gilbert et al., 2020). This contraction limits the energy available for growth, reproduction, and recovery from exercise or environmental stressors.

The progression from the 21 °C to the 23 °C threshold marks a transition into the lethal range for most populations (Borgwardt et al., 2020; Vornanen et al., 2014). Experimental data show that cardiac function in brown trout becomes critical above 20.9 °C, leading to disturbed rhythmicity, and can culminate in heart arrest as temperatures approach 23.5 °C (Vornanen et al., 2014). These physiological limits are further complicated by the simultaneous decline in dissolved oxygen solubility as water warms. This "thermal-hypoxic squeeze" forces the fish to work harder to obtain oxygen precisely when its metabolic demand is highest, creating a feedback loop that accelerates physiological collapse during heatwaves (Doudoroff and Shumway, 1970; Borgwardt et al., 2020; Jonsson, 2023; Elliott and Elliott, 2010).

Although there is some evidence for thermal adaptation to very low temperatures in cold rivers, there is no corresponding adaptation to increasing temperature (Elliott and Elliott, 2010). Even marginal increases in water temperature can exert disproportionate pressure on aquatic biota due to the nonlinear relationship between temperature and critical physiological processes, such as the "metabolic scissors" effect where oxygen demand rises as solubility declines. Yet despite this well-established physiological knowledge, spatially explicit projections that translate continuous thermal change into threshold-based ecological risk metrics remain absent for Czech rivers specifically, and are rare across Central Europe more broadly. First, most existing projections for Central European rivers focus on changes in mean annual water temperature rather than on the frequency and duration of exceedances of ecologically relevant thresholds. Second, studies that do address threshold-based metrics rarely combine warm-season stress with cold-season thermal changes affecting spawning and early development (two processes that are physiologically distinct yet climatically coupled). Third, spatially explicit analyses at the national scale, using high-resolution gridded meteorological data validated against long-term in situ observations, are lacking for the Czech Republic – a hydrologically important headwater region draining into three major European basins. Addressing these gaps is essential for translating climate projections into actionable information for fisheries management and river conservation.

To address these gaps, we developed a modelling framework to reconstruct historical and project future water temperature regimes across upper reaches of Czech rivers using multi-model climate projections. We tested the hypothesis that climate warming will manifest not only through increasing summer thermal stress but also through a progressive erosion of cold-water conditions and a systematic warming of the extended cold season.

To evaluate these processes, we quantified changes in biologically relevant temperature thresholds (<17 °C, 17–19 °C, 19–21 °C, 21–23 °C, >23 °C), the contraction of thermally suitable habitat defined as ≥350 days per year below 17 °C (Fig. 1), and seasonal indicators capturing autumn–winter (>10 °C; October–January) and late winter–spring (>12 °C; February–May) warming. By linking continuous thermal change to ecologically meaningful thresholds across both summer and cold-season periods, the study aims to identify spatial patterns of thermal vulnerability and river systems most at risk of long-term habitat degradation and to assess the future persistence of brown trout as a sentinel species of Central European cold-water ecosystems.

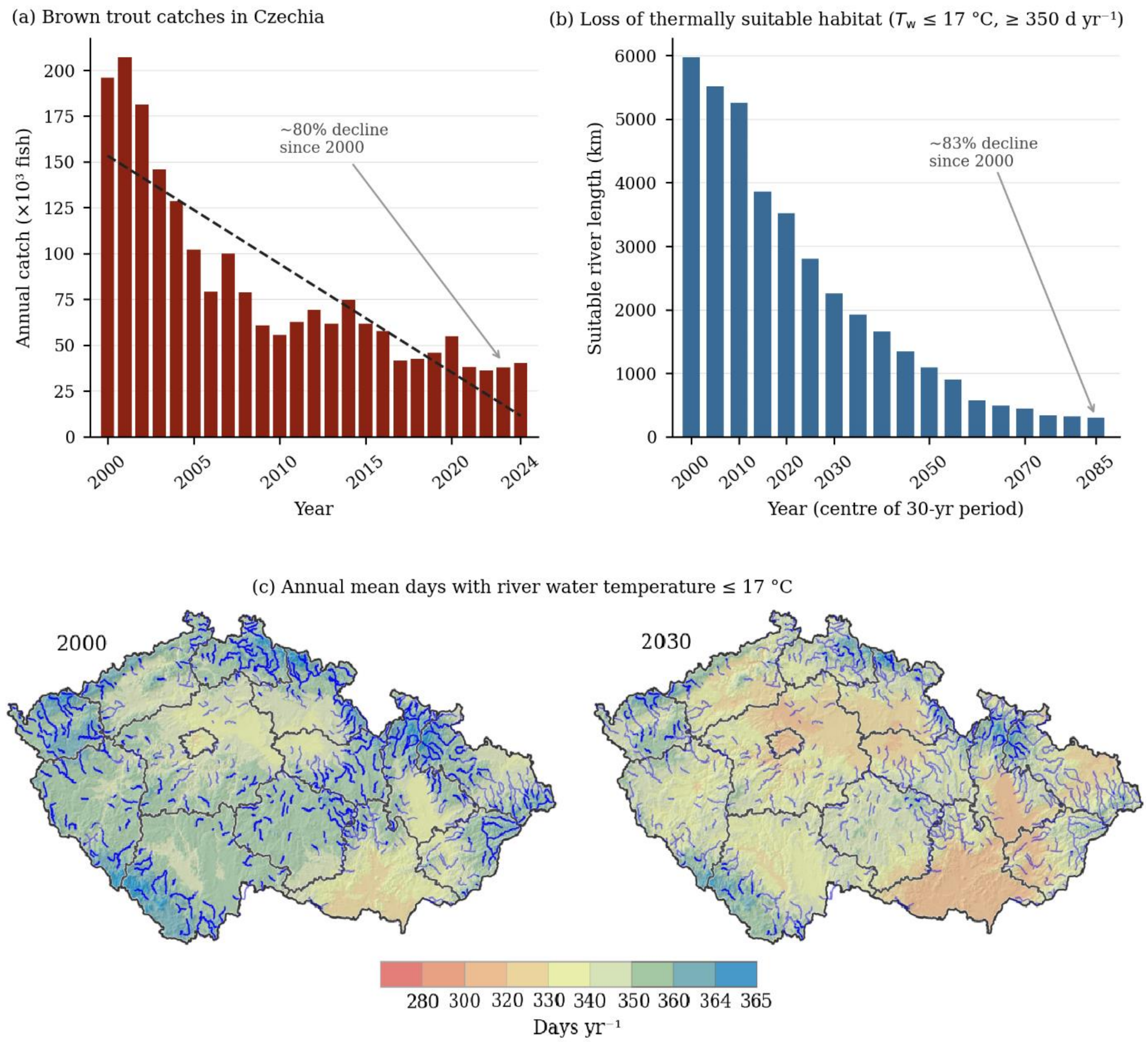


Figure 1. Observed and projected decline of thermally suitable habitat for brown trout (Salmo trutta) in Czech rivers. (a) Annual brown trout catches in the Czech Republic declined by approximately 80 % between 2000 and 2024 (dashed line: linear trend). (b) (b) Contraction of river reaches maintaining water temperatures below 17 °C for at least 350 days per year from 2000 to 2085 under median multi-model projections; dotted line marks the transition from observed to projected values. (c) Spatial distribution of the annual mean number of days with river water temperature below 17 °C for the periods centred on 2000 and 2030, illustrating the progressive loss of cold-water conditions across the river network.

## 2 Material and methods

The study focuses on brown trout-bearing river systems across the Czech Republic, covering a wide range of climatic and geomorphological conditions from lowland rivers to higher-altitude headwater streams. The analysis is based on long-term in situ observations of river water temperature collected at 35 river profiles. As primary meteorological input, daily mean air temperature data were used.

### 2.1 River water temperature data

Daily water temperature observations were obtained from the monitoring network of the Czech Hydrometeorological Institute (ČHMI), which operates continuous temperature sensors across the Czech river network. Data were available for 35 river profiles distributed across a wide range of altitudinal and climatic conditions, from lowland rivers below 197 m a. s. l. to mountain headwater streams above 917 m a. s. l. The observational period spans primarily 2002–2022, with individual profiles differing in record length depending on sensor installation date (Table 1).

Table 1. Summary statistics of observed daily water temperature at 35 river profiles and availability of daily water temperature data. The table reports mean, median and upper percentiles P75, P95, P99. The rivers are sorted according to annual median water temperature. Upper percentiles characterize the frequency and magnitude of high summer temperatures.

| Profile ID | River | Alt. (m) | Median | P75 | P95 | P99 | Available data | Coordinates |
|---|---|---|---|---|---|---|---|---|
| Radotín | Radotínský potok | 197 | 10.8 | 15.1 | 18.0 | 19.1 | 2009-2022 | 49.9836N, 14.3607E |
| Železný Brod | Jizera | 282 | 10.3 | 17.0 | 21.1 | 23.0 | 2010-2022 | 50.6399N, 15.2744E |
| Valašské Meziříčí | Rožnovská Bečva | 295 | 10.2 | 16.6 | 21.2 | 23.2 | 2004-2022 | 49.4730N, 17.9775E |
| Jarcová | Vsetínská Bečva | 302 | 9.9 | 16.5 | 21.5 | 23.5 | 2004-2022 | 49.4444N, 17.9701E |
| Bílovice nad Svitavou | Svitava | 223 | 9.7 | 15.0 | 18.7 | 20.7 | 2008-2022 | 49.2455N, 16.6750E |
| Dolní Loučky | Loučka | 277 | 9.6 | 15.6 | 19.5 | 21.1 | 2010-2022 | 49.3569N, 16.3596E |
| Slověnice | Chotýšanka | 340 | 9.5 | 14.9 | 18.4 | 20.0 | 2007-2022 | 49.7515N, 14.8886E |
| Sázava u Žďáru | Sázava | 496 | 9.4 | 15.1 | 18.5 | 19.8 | 2011-2022 | 49.5552N, 15.8493E |
| Štěchovice | Kocába | 210 | 9.4 | 15.3 | 19.3 | 21.2 | 2009-2022 | 49.8481N, 14.4029E |
| Vestřev (Hostinné) | Labe | 338 | 9.1 | 13.5 | 16.2 | 17.7 | 2007-2022 | 50.5144N, 15.7416E |
| Sušice | Otava | 483 | 9.0 | 14.2 | 18.0 | 20.0 | 2006-2022 | 49.2366N, 13.5249E |
| Svahy-Třebel | Kosový potok | 435 | 8.8 | 14.5 | 18.4 | 20.2 | 2008-2022 | 49.8267N, 12.8389E |
| Čichořice | Střela | 450 | 8.7 | 13.5 | 16.7 | 18.3 | 2011-2022 | 50.0964N, 13.2700E |
| Branka | Moravice | 263 | 8.6 | 14.5 | 20.2 | 22.5 | 2004-2022 | 49.8936N, 17.8899E |
| Krnov | Opava | 317 | 8.6 | 14.3 | 18.9 | 21.2 | 2004-2022 | 50.0886N, 17.7084E |
| Rejštejn | Otava | 585 | 8.6 | 13.5 | 16.7 | 18.7 | 2004-2022 | 49.1394N, 13.5083E |
| Dolní Libchavy | Tichá Orlice | 331 | 8.5 | 13.5 | 17.0 | 18.4 | 2004-2022 | 49.9886N, 16.3959E |
| Mikulovice | Bělá | 345 | 8.5 | 13.7 | 17.9 | 20.2 | 2004-2022 | 50.2905N, 17.2939E |
| Němětice | Volyňka | 428 | 8.5 | 13.7 | 17.8 | 19.8 | 2007-2022 | 49.1974N, 13.8854E |
| Stříbrné Hory | Borovský potok | 445 | 8.4 | 13.6 | 17.0 | 18.4 | 2011-2022 | 49.5996N, 15.7019E |
| Hracholusky | Zlatý potok | 487 | 8.3 | 12.2 | 14.9 | 16.3 | 2007-2022 | 49.0562N, 14.0788E |
| Jablunkov | Olše | 383 | 8.3 | 14.3 | 19.3 | 21.8 | 2004-2022 | 49.5767N, 18.7685E |
| Chocnějovice | Mohelka | 236 | 8.2 | 13.2 | 16.9 | 18.4 | 2011-2022 | 50.5753N, 14.9638E |
| Stará Role | Rolava | 393 | 7.9 | 13.4 | 17.1 | 18.9 | 2009-2022 | 50.2486N, 12.8199E |
| Slaná | Oleška | 332 | 7.8 | 13.6 | 17.7 | 19.5 | 2009-2022 | 50.5887N, 15.3345E |
| Horní Stropnice | Stropnice | 547 | 7.7 | 13.8 | 18.4 | 20.2 | 2007-2022 | 48.7622N, 14.7397E |
| Raškov | Morava | 370 | 7.7 | 12.2 | 15.5 | 16.9 | 2004-2022 | 50.0410N, 16.9114E |
| Velká Šťáhle | Moravice | 549 | 7.1 | 11.7 | 15.2 | 17.1 | 2004-2022 | 49.9325N, 17.3518E |
| Stodůlky | Křemelná | 771 | 6.8 | 12.5 | 16.3 | 18.2 | 2004-2022 | 49.1176N, 13.4276E |
| Hronov | Metuje | 367 | 6.4 | 12.1 | 16.1 | 18.1 | 2004-2022 | 50.4832N, 16.1809E |
| Jezdecká | Černá Desná | 785 | 6.4 | 11.4 | 15.1 | 17.0 | 2012-2022 | 50.8076N, 15.2931E |
| Jizerka | Jizera | 855 | 5.9 | 11.3 | 14.5 | 16.6 | 2011-2022 | 50.8195N, 15.3478E |
| Lenora | Teplá Vltava | 766 | 5.8 | 9.7 | 13.1 | 14.7 | 2004-2022 | 48.9278N, 13.7949E |
| Jablonec nad Jizerou | Jizera | 448 | 5.4 | 9.5 | 12.2 | 13.6 | 2006-2022 | 50.6950N, 15.4384E |
| Obří Důl | Úpa | 917 | 5.4 | 9.9 | 12.9 | 14.5 | 2012-2022 | 50.7115N, 15.7247E |

All records consist of directly measured daily mean water temperatures. Prior to analysis, data underwent quality control based on visual inspection of interannual temperature dynamics at each profile. Observations deviating anomalously from the expected seasonal signal, including physically implausible values and apparent sensor errors, were removed. No gap filling was applied; removed values were treated as missing data and excluded from subsequent analyses. The final dataset provided 10–18 years of continuous daily observations per profile, forming the observational basis for model calibration and validation.

## 2.2 Modelling of river water temperature

River water temperature was modelled using a linear regression framework linking daily water temperature to a moving average of air temperature with a temporal lag. The approach assumes that river water temperature follows short-term air temperature variability with a delay reflecting heat storage and transport processes in the river system. Daily air temperature data were obtained from 268 climatological stations operated by ČHMI and interpolated to a 500 × 500 m grid using regression kriging, accounting for elevation and terrain characteristics. For each river profile, air temperature was extracted from the grid cell corresponding to its location (Trnka et al., 2021).

All analyses were conducted in the statistical software R 4.2.1 (R Core Team, 2025) at a daily temporal resolution. Time series handling relied on the R package zoo (Zeileis and Grothendieck, 2005). Model parameters were optimized using the Differential Evolution algorithm implemented in the R package DEoptim (Ardia et al., 2011), minimizing the root mean square error (RMSE) between observed and simulated water temperature. Model performance was evaluated using goodness-of-fit metrics computed with the R package hydroGOF (Zambrano-Bigiarini, 2024), including RMSE, mean bias error (MBE) and the coefficient of determination ($R^2$).

Two modelling strategies were evaluated. First, a single global model was calibrated using data from multiple river profiles to obtain a universal parameter set suitable for spatially consistent applications. The global model was calibrated on 25 river profiles and validated on the remaining 10. River water temperature on day $t$ was estimated as

$$T_{water}(t) = \alpha + \beta \cdot \overline{T}_{air}(t-\delta, w)\ , \tag{1}$$

where $\overline{T}_{air}(t-\delta, w)$ is the trailing moving average of air temperature over a window of $w$ days ending at day $t$, shifted by a lag of $\delta$ days.

$$\overline{T}_{air}(t-\delta, w) = \frac{1}{w} \sum_{i=t-\delta-w+1}^{t-\delta} T_{air}\ (i) \tag{2}$$

Four parameters were optimized by DEoptim: the moving average window $w$ (1–10 days), the temporal lag $\delta$ (0–10 days), the intercept $\alpha$ (−20 to 10), and the slope $\beta$ (0.1–10). Although DEoptim optimizes over a continuous parameter space, $w$ and $\delta$ were rounded to the nearest integer prior to model evaluation. The optimised parameter set was: moving average window $w$ = 5 days, temporal lag $\delta$ = 1 day, intercept $\alpha$ = 2.91 °C, and slope $\beta$ = 0.69, yielding the equation

$$T_{water}(t) = 2.91 + 0.69 \cdot \overline{T}_{air}(t - 1,5). \quad (3)$$

Calibration performance was good ($R^2 = 0.94$, RMSE = 1.73 °C, MBE = −0.54 °C, Pearson r = 0.97), and validation confirmed model transferability to independent profiles ($R^2 = 0.93$, RMSE = 1.95 °C, MBE = −0.48 °C, Pearson r = 0.96). Second, applying an identical methodology, site-specific models were developed independently for each river profile to better represent local thermal regimes and extreme temperature behaviour. In this case, all available observations were used for calibration to preserve the full range of observed water temperature variability. These site-specific models were subsequently applied to assess future changes in water temperature and the occurrence of ecologically relevant thermal thresholds.

### 2.3 Climate projections and future scenarios

Future river water temperature projections were generated by forcing the calibrated site-specific models with daily air temperature data derived from an ensemble of global and regional climate models. The ensemble comprises seven Coupled Model Intercomparison Project Phase 6 (CMIP6) GCMs (CMCC-ESM2, CNRM-CM6-1-HR, EC-EARTH3, GFDL-ESM4, MPI-ESM1-2-HR, MRI-ESM2-0, and TAIESM1) and one RCM (ALADIN). Four Shared Socioeconomic Pathways (SSP) scenarios were considered: SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5. The majority of GCMs covered all scenarios, except CNRM-CM6-1-HR, where only SSP1-2.6 and SSP5-8.5 were available. Two scenarios (SSP2-4.5 and SSP5-8.5) were available for RCM ALADIN. All models were evaluated for their performance over the Czech Republic prior to selection, using validation metrics including distance from the GCM ensemble mean (calculated from a larger CMIP6 ensemble of more than 20 GCMs), annual cycle correlation, and spatial correlation across key meteorological variables (Trnka et al., 2021).

Raw climate model outputs were downscaled to the 500 × 500 m national meteorological grid using the Advanced Delta Change (ADC) method, which adjusts not only mean temperature but also its variability, allowing extremes to change independently of the mean. This approach is well established for Czech climate impact studies and is more robust than direct bias correction for long-term projections (Trnka et al., 2021). Since temperature is transformed linearly in the ADC framework, systematic model biases do not affect the resulting temperature transformation (Bernsteinová et al., 2026).

Analyses were conducted for successive 30-year periods centred on representative target years: 2030 (2015–2044), 2035 (2020–2049), continuing at 5-year intervals through 2085 (2070–2099). The historical baseline corresponds to the period 1961–2024, derived from observed station data interpolated to the same grid. This longer baseline period was retained to maximise the representativeness of observed climatological conditions used for model calibration; comparisons with future projections are based on the most recent 30-year climatological period (1995–2024) unless otherwise stated.

For each river profile, climate scenario, and time period, daily water temperature time series were simulated for all available model realisations. Ensemble uncertainty was summarised using multi-model percentiles (P05, P25, median, P75, P95). In addition to threshold exceedance days, the following indicators were calculated for each profile and period: degree-days above 23 °C, total number of heat-wave days, number of heat-wave events, and maximum heat-wave duration, where a heat wave was defined as a period of at least three consecutive days with water temperature exceeding 23 °C.

### 2.4 Temperature-based indicators of thermal stress

Rather than focusing solely on changes in mean water temperature, the analysis emphasizes biologically relevant temperature-based indicators that better capture thermal stress conditions for cold-water fish species.

#### 2.4.1 Threshold exceedance days

For each river profile, year, and analyzed period, the annual number of days exceeding selected water temperature thresholds was calculated. Thresholds were chosen based on commonly reported thermal preferences and stress levels for salmonids, particularly brown trout (*Salmo trutta*).

For the warm season, the evaluated thresholds included days with water temperature below 17 °C (representing thermally favorable conditions) as well as exceedance classes of 17–19 °C, 19–21 °C, 21–23 °C, and above 23 °C. River heat waves were defined as periods of at least three consecutive days with water temperature exceeding 23 °C. For each profile and period, the annual number of such events was calculated to characterize the frequency and persistence of extreme thermal conditions.

To capture changes in the extended cold season, additional indicators were computed:

the annual number of days with water temperature exceeding 10 °C during October–January (ONDJ), and the annual number of days exceeding 12 °C during February–May (FMAM). These thresholds were selected to reflect biologically relevant departures from typical cold-season thermal conditions associated with spawning, egg incubation, and early development stages of brown trout. All threshold-based indicators were calculated consistently for the historical baseline and for future projections, with future statistics summarised across climate models using multi-model percentiles.

### 2.5 Spatial visualisation and large-scale context

In addition to the site-based analyses, a gridded river water temperature dataset derived from the global modelling framework was used to visualize large-scale spatial patterns across the Czech Republic. This dataset was employed to illustrate the spatial distribution and projected changes in the number of days with water temperature below 17 °C (Fig. 2), and the contraction of thermally suitable brown trout habitat defined by a ≥350 days per year threshold with water temperature below 17 °C. For each grid cell representing a river segment, the annual number of days with water temperature below 17 °C was calculated. River segments were classified as thermally suitable if this threshold was met. The proportion of the total river network fulfilling this criterion was then quantified for selected time slices using multi-model median projections. The gridded outputs were used exclusively for spatial visualisation and network-scale quantification of habitat extent. Quantitative analyses of thermal stress indicators and group comparisons were conducted using the profile-based dataset. To facilitate interpretation of future changes in threshold exceedance days, river profiles were grouped according to their mean annual water temperature during the observed period. The long-term mean annual water temperature was calculated for each profile based on in situ observations and used as an integrative descriptor of the prevailing thermal regime. Based on this metric, river profiles were classified into three thermal groups: cold (< 7.5 °C), intermediate (7.5–9.0 °C), and warm (> 9.0 °C). This classification reflects fundamental differences in baseline thermal conditions and sensitivity to warming. The thermal grouping was used exclusively for result aggregation and visualisation and did not influence model calibration or projection procedures.

## 3 Results

### 3.1 Model performance

The calibrated water temperature model performed consistently across river profiles. During calibration (n = 25 profiles), the global model achieved $R^2 = 0.94$, RMSE = 1.73 °C, MBE = -0.54 °C, and Pearson r = 0.97. Independent validation on the remaining 10 profiles confirmed model robustness ($R^2 = 0.93$, RMSE = 1.95 °C, MBE = -0.48 °C, Pearson r = 0.96). The consistency of MBE between calibration and validation periods indicates a systematic rather than random bias, reflecting a marginal tendency to underestimate water temperature. At the site level, explained variance ranged from 84 to 96 % during calibration and 88 to 94 % during validation, with RMSE between 1.3 and 2.8 °C and 1.5 and 3.1 °C, respectively. Full site-level statistics are provided in Supplementary Table S1.

### 3.2 Observed thermal conditions and thermal grouping

Observed water temperature statistics revealed a strong and consistent altitudinal control on the thermal regime of Czech river profiles. Thresholds of 7.5 °C and 9.0 °C for thermal grouping were selected to achieve an approximately equal distribution of profiles across the three thermal classes, while remaining consistent with the observed altitudinal stratification of thermal regimes. Lowland sites located below approximately 300 m a.s.l. exhibited the highest median annual water temperatures (≈9.7–10.8 °C), frequent warm episodes, and upper percentiles commonly exceeding 21 °C, with observed maxima reaching 23–24 °C. Mid-altitude profiles (≈300–550 m a. s. l.) showed intermediate thermal characteristics, with median temperatures around 8–9 °C and episodic exposure to temperatures above 19 °C. In contrast, high-altitude headwater and mountain profiles above ~700 m a. s. l. were characterized by persistently cold conditions, with median water temperatures below 6 °C and upper percentiles rarely exceeding 15 °C. This pronounced and consistent thermal stratification provided a robust observational basis for grouping river profiles into warm, intermediate, and cold thermal classes. These groups exhibited fundamentally different projected responses to future warming and therefore serve as a useful framework for interpreting changes in thermal exposure and stress.

### 3.3 Projected loss of cold-water conditions (<17 °C)

Projected changes reveal a progressive and spatially heterogeneous erosion of cold-water conditions (<17 °C) across Czech rivers throughout the 21st century (Fig. 2).

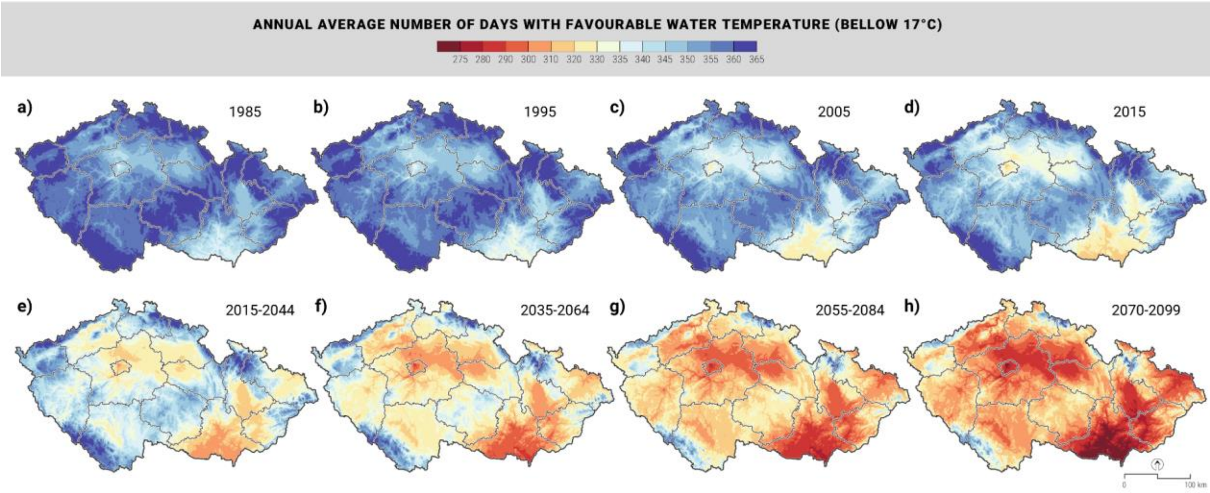


Figure 2. Spatial patterns of the annual average number of days with favourable river water temperature below 17 °C across the Czech Republic (continuous scale). Panels show historical snapshots centred on 1985, 1995, 2005, and 2015, and future projections for 30-year periods centred on 2030, 2040, 2060, and 2085, based on the median of an ensemble of eight climate models (seven CMIP6 GCMs and one RCM) under four SSP emission scenarios. Warmer colours indicate fewer days with favourable thermal conditions. The maps illustrate a progressive and spatially coherent decline in thermally suitable conditions, with remaining cold-water refugia becoming increasingly restricted to higher-altitude regions towards the end of the century. Note that this figure shows the continuous thermal signal across the full network; Fig. 3 translates this into a binary habitat suitability criterion (≥350 days per year below 17 °C). The bottom row is then based on the median value from the considered ensemble of eight climate models and four emission scenarios.

Rather than an abrupt late-century shift, reductions emerge early and intensify gradually, indicating a steady upward displacement of the annual thermal regime. In warm lowland rivers, the median number of days below 17 °C declines from approximately 330–335 days per year during the baseline period to ~300 days by 2050 and further to ~280 days by 2085 (P25 ≈ 260 days). This corresponds to an increase from roughly 30 to more than 80 days per year exceeding the 17 °C threshold. The most thermally exposed profiles – Železný Brod (Jizera), Valašské Meziříčí (Rožnovská Bečva), and Jarcová (Vsetínská Bečva) – are projected to exceed 120 days per year above 17 °C by 2085. Intermediate rivers show a comparable relative trend, with median values decreasing from ~350 days below 17 °C to ~330 by mid-century and ~310 days by 2085, reflecting a systematic lengthening of the warm-season exposure. In contrast, cold high-altitude and headwater systems retain predominantly cold regimes throughout the analysed period. Even by 2085, median values generally remain above ~350 days per year below 17 °C. The decline in cold-water days was the most robust signal across the entire analysis: all 36 monitored profiles showed a robust reduction in days below 17 °C (P25 > 0) at every analysed time horizon from 2030 through 2085. The rate of change in the 17–19 °C band was the strongest among all thermal classes, averaging 1.8 days per decade across profiles (range: −1.4 to 4.0 days per decade), indicating that the shift from cold-water to moderately warm conditions is already well underway and spatially pervasive. Taken together, these results indicate that climate-driven thermal degradation is already accelerating in lowland and mid-altitude systems, while upland rivers continue to function as climatic refugia. Importantly, this continuous decline in cold-water days forms the basis for threshold-based habitat contraction described below.

### 3.4 Contraction of thermally suitable trout habitat (≥350 days <17 °C)

To translate the continuous thermal shift into an ecologically interpretable metric, we defined thermally suitable trout habitat as river reaches maintaining water temperatures below 17 °C for at least 350 days per year (Fig. 3).

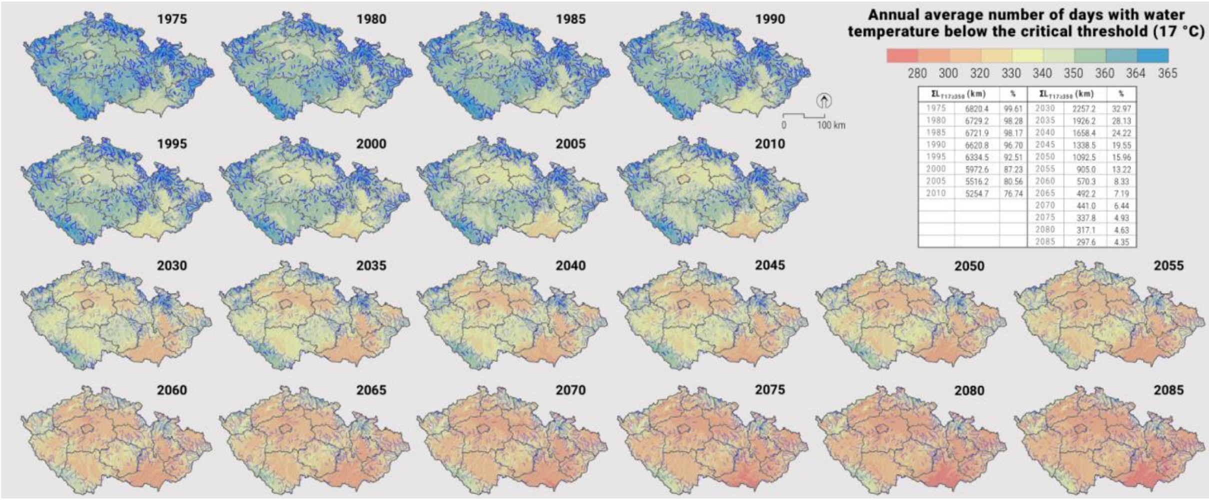


Figure 3. Spatial contraction of thermally suitable trout habitats in Czech rivers (binary threshold). While Fig. 2 shows the continuous annual count of days below 17 °C, this figure applies an ecological threshold: river reaches are classified as thermally suitable only if water temperature remains below 17 °C for at least 350 days per year (near-continuous cold-water conditions). Maps show 30-year running averages centred on selected years. Historical panels (1975–2010) illustrate baseline conditions, while future panels (2030–2085) represent the multi-model median across climate projections. The accompanying table quantifies the total river length (km and %) meeting the ≥350-day criterion. Maps show the annual mean number of days with water temperature below 17 °C, based on 30-year running averages centred on selected years. The threshold of ≥350 days per year was used to define thermally suitable reaches for cold-water salmonids. Historical panels (1975–2010) illustrate baseline conditions, while future panels (2030–2085) represent the multi-model median across climate projections. The accompanying table quantifies the total river length (km and %) meeting the ≥350-day criterion.

This threshold represents near-year-round cold-water conditions and approximates the persistence of a stable salmonid thermal niche. Under historical conditions, almost the entire river network satisfied this criterion (≈99% of total river length in 1975). By 2010, suitable reaches had already declined to approximately 77%, reflecting the early phase of thermal erosion identified in Section 3.3. Future projections indicate a marked acceleration of this contraction. Under the multi-model median, suitable habitat declines to roughly one-third of the network by 2030 and falls below 5% by 2085. By the end of the century, thermally suitable reaches are largely confined to high-altitude headwaters and mountain systems, whereas lowland and most mid-altitude rivers experience a near-complete loss of year-round cold-water regimes. Thus, the gradual reduction in cold-water days documented in Fig. 2 translates, when evaluated against an ecologically meaningful threshold, into a pronounced and spatially concentrated contraction of suitable trout habitat.

### 3.5 Redistribution of moderate and sub-lethal thermal conditions (17–23 °C)

The decline in cold-water conditions was accompanied by a pronounced redistribution of thermal exposure toward warmer temperature classes, rather than a uniform increase across all ranges (Fig. 4, upper panel).

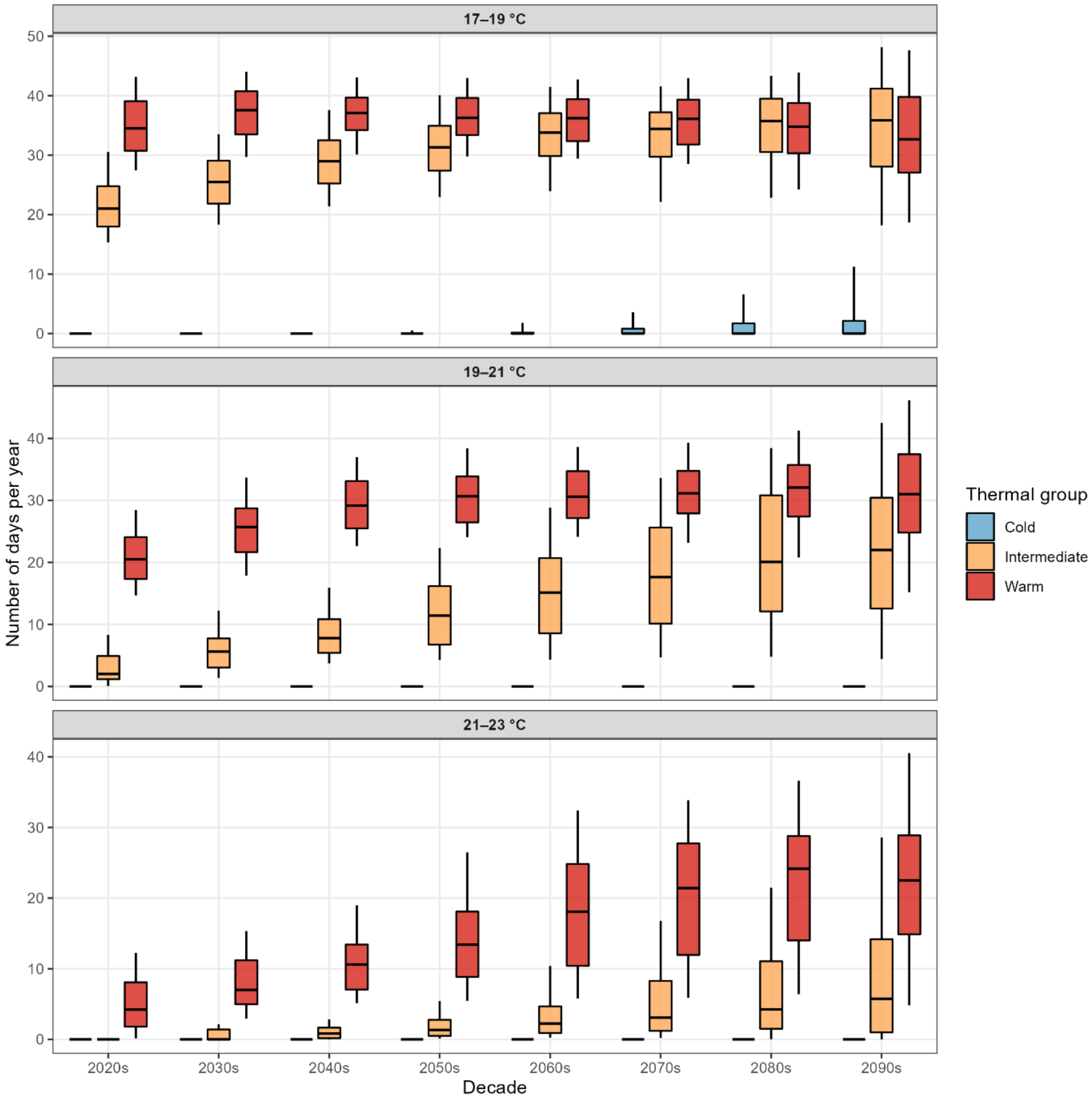


Figure 4. Decadal boxplots of projected thermal exposure across Czech river profiles for three temperature ranges (17–19 °C, 19–21 °C, and 21–23 °C) during the period 2020–2090. River profiles were grouped into cold, intermediate, and warm thermal categories based on observed long-term median water temperature. Boxplots summarize ensemble-based projections aggregated across sites within each thermal group, with boxes representing the interquartile range (P25–P75), central lines indicating the median, and whiskers denoting the 5th and 95th percentiles. Values represent the annual number of days falling within each temperature range, aggregated by decade to emphasize distributional changes and reduce the influence of interannual variability. The figure illustrates systematic shifts in the thermal regime, including a redistribution of days from moderately warm (17–19 °C) toward warmer (21–23 °C) conditions, particularly in thermally warm river profiles.

In warm rivers, days with water temperature between 17–19 °C increased until mid-century but stabilized or slightly declined thereafter. Median exposure in this range remained around 32–35 days per year by the end of the century, reflecting a progressive shift of moderately warm days into higher, more stressful temperature bands. This signal was robust (P25 > 0) at 29 of 36 profiles by 2030 and 33 profiles by 2050, confirming a near-universal shift across the monitored network.

Days with water temperature between 19–21 °C increased substantially in both warm and intermediate rivers (Fig. 4 middle panel). In warm rivers, median exposure rose from approximately 9 days per year during the baseline period to more than 31 days by 2085. Intermediate rivers showed an even stronger relative response, with median exposure increasing from approximately 2 days per year during the baseline period to over 22 days by 2085. The 19–21 °C signal was robust (P25 > 0) at 20 of 36 profiles by 2030, rising to 27 profiles by 2050, confirming that moderate thermal stress is already an emerging reality across much of the monitored network. These results indicate that intermediate rivers are projected to undergo a marked transition toward warmer summer regimes. Exposure to sub-lethal thermal stress, represented by days with water temperature between 21–23 °C, emerged primarily in warm rivers (Fig. 4, lower panel). Median values increased from approximately 1 day per year during the baseline period to nearly 10 days by 2085, while upper quartile values exceeded 20 days per year. Intermediate rivers exhibited a delayed but detectable emergence after mid-century, with median exposure remaining low but P75 values reaching up to 5 days per year by 2085. In contrast, cold rivers maintained near-zero exposure across all projections, underscoring their continued role as thermal refugia.

### 3.6 Emergence of thermal stress and loss of refugia

Loss of thermal refugia, defined as conditions under which even the lower quartile (P25) of days with water temperature between 21–23 °C exceeded zero, was confined to a limited number of warm lowland rivers. The earliest loss was projected for Železný Brod profile on the Jizera River around 2030, followed by Jarcová on the Vsetínská Bečva around 2050 and Valašské Meziříčí on the Rožnovská Bečva in 2055. In contrast, most mid-altitude and upland profiles retained thermal refugia throughout the 21st century, with P25 values remaining close to zero even by 2085, indicating that exposure to temperatures of 21–23 °C remains episodic rather than persistent. By the 2070s, P25 values in warm rivers reached several days per year, indicating that sub-lethal thermal stress becomes persistent rather than episodic. In intermediate and cold rivers, P25 values generally remained close to zero throughout the analysed period, suggesting that stressful conditions remain sporadic and interannually variable. Importantly, the emergence of sub-lethal thermal stress consistently preceded the emergence of extreme temperatures above 23 °C. Across all profiles, 13 of 36 showed no detectable emergence of the 21–23 °C band within the analysed period, predominantly cold high-altitude sites. Among profiles where emergence was detected, the median emergence year was 2037 (range: 2020–2074), with the earliest signals appearing in the warmest lowland systems. This indicates that biologically relevant thermal pressure intensifies well before rare extreme events become frequent, potentially reducing physiological resilience prior to the onset of acute thermal extremes.

### 3.7 Extreme temperatures and heat waves (>23 °C)

Projected changes in the annual number of days with river water temperature exceeding 23 °C show strong spatial heterogeneity across Czech river profiles (Fig. 5).

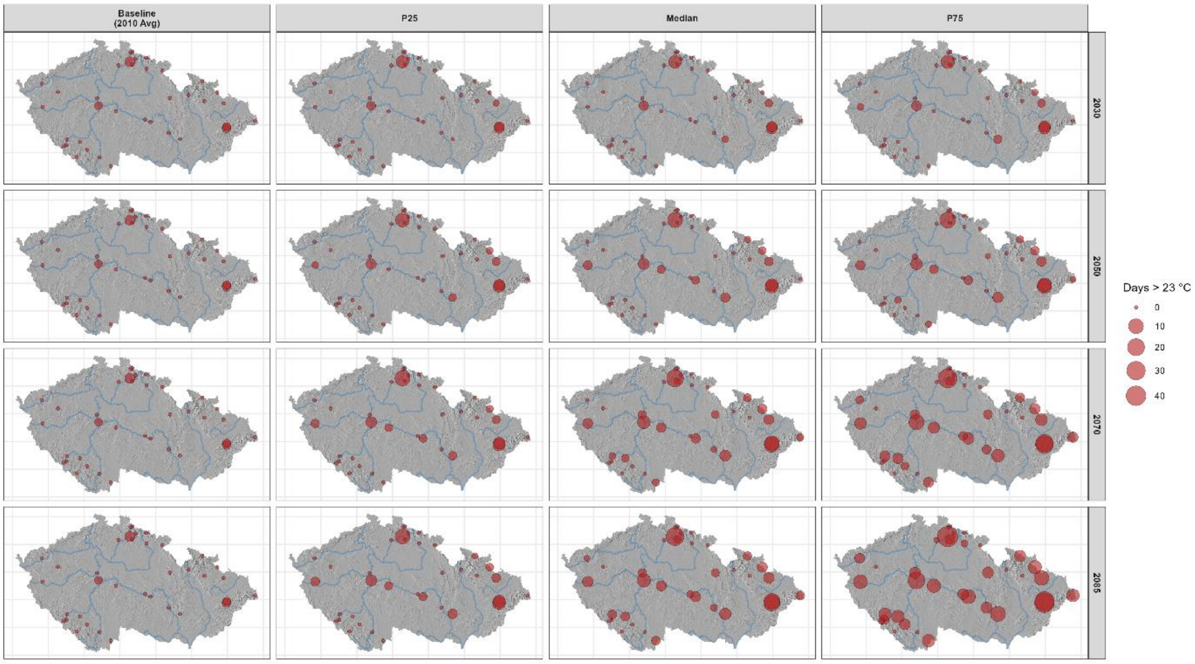


Figure 5. Spatial distribution of the annual number of days with river water temperature exceeding 23 °C across Czech river profiles. Rows show future 30-year periods centered on 2030, 2050, 2070, and 2085, while columns represent statistical summaries: the baseline multi-model average for 2010 (Avg) and future projections expressed as the 25th percentile (P25), median, and 75th percentile (P75) across individual model realizations. Point size indicates the number of days per year exceeding the 23 °C threshold. Baseline values are identical across rows to facilitate visual comparison with future periods. Transparency and square-root scaling of point size were applied to improve readability in areas with overlapping profiles.

For most cold and high-altitude rivers, the median number of days above this threshold remains zero throughout the 21st century, with only sporadic exceedances emerging in the upper quartile toward the end of the analyzed period. Many intermediate rivers exhibit a delayed response, with median values remaining close to zero until mid-century and increasing to approximately 0.5–2 days per year by 2085, while upper-quartile values locally reach several days per year.

In contrast, a limited set of warm lowland rivers displays a pronounced increase in extreme thermal exposure. At sites such as Železný Brod (Jizera), Valašské Meziříčí (Rožnovská Bečva), Jarcová (Vsetínská Bečva), and Štěchovice (Kocába), median values rise from roughly 1–4 days per year in the 2030s to about 10–25 days per year by 2070–2085. Upper-quartile projections indicate substantially higher exposure, with 30–40 days per year above 23 °C by the late 21st century and local maxima exceeding 45 days per year.

Associated heat-wave metrics showed a generally later and less consistent emergence compared to sub-lethal thermal stress. In warm rivers, the median number of heat-wave events increased from zero during the baseline period to less than 0.5 events per year by 2070–2085, with upper quartile values reaching around 0.6 events per year (Fig. 6).

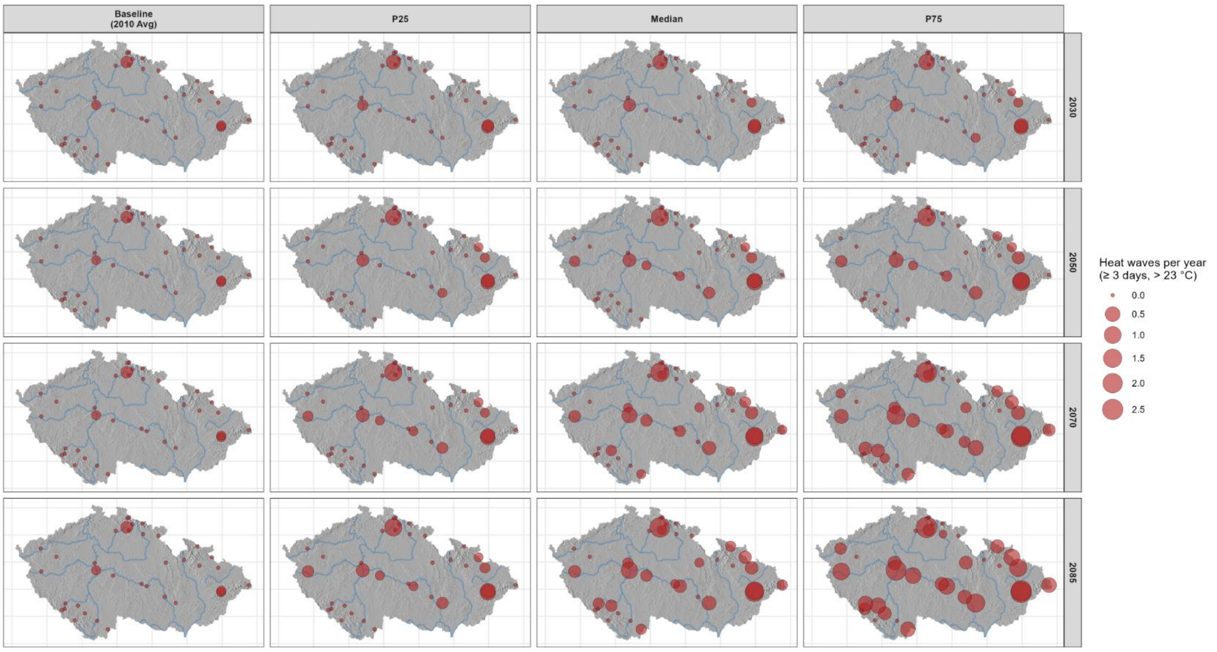


Figure 6. Spatial distribution of the annual number of river water heat waves (≥ 3 consecutive days with water temperature > 23 °C) for Czech river profiles. Rows correspond to future 30-year periods centred on 2030–2085, and columns present the baseline average (2010) and future P25, median, and P75 projections. Point size represents the number of heat-wave events per year.

Correspondingly, the median duration of heat-wave conditions increased to approximately 1–1.5 days per year, with upper quartile values exceeding 3 days in the warmest systems. Cold rivers and most intermediate rivers exhibited no systematic emergence of heat waves within the analysed period.

### 3.8 Cold-season and early spring warming

Projected changes indicate a pronounced warming of river water temperatures during both the cold season and early spring (Figs. 7 and 8). The annual number of days with water temperature exceeding 10 °C during autumn and winter (ONDJ) increases consistently across warm and intermediate rivers throughout the 21st century, while remaining low in cold rivers. During the historical baseline, median ONDJ values averaged approximately 14 days in warm rivers and 7 days in intermediate rivers, with cold rivers showing near-zero exposure. By the 2030s, median values rise to approximately 21 days in warm rivers and 14 days in intermediate rivers, increasing further to around 30 and 23 days, respectively, by 2085 (Fig. 7).

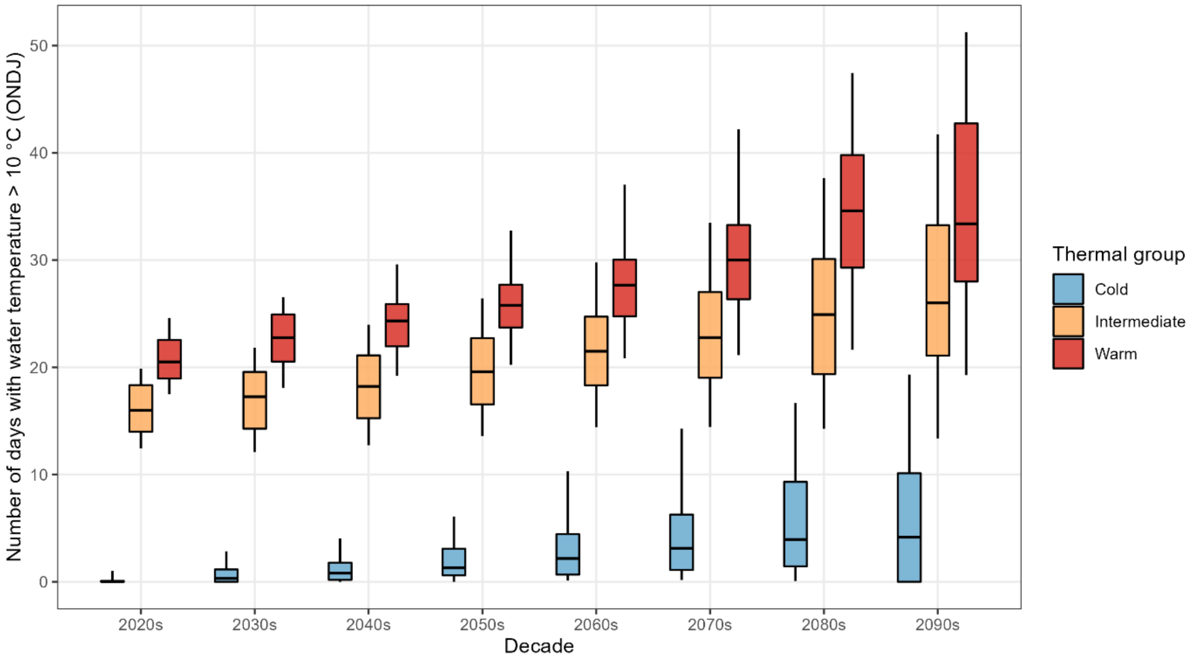


Figure 7. Projected changes in the number of days with water temperature above 10 °C during the autumn–winter period (October–January, ONDJ) across three thermal groups of Czech river profiles (cold, intermediate, warm). Box plots show the interquartile range (P25–P75) and median of the multi-model ensemble for each decade; whiskers extend to P05 and P95. Results illustrate a pronounced and progressive increase in autumn–winter warm-water conditions in warm and intermediate rivers, contrasted with a substantially weaker response in cold headwater streams throughout the 21st century.

A similar but more pronounced pattern is observed for days with water temperature exceeding 12 °C during late winter and early spring (FMAM). During the historical baseline, median FMAM values averaged approximately 20 days in warm rivers, 10 days in intermediate rivers, and fewer than 2 days in cold rivers. Median values in warm rivers increase to approximately 29 days by the 2030s and reach around 36 days by 2085, with upper quartile values approaching 40 days. Intermediate rivers show a comparable upward shift, with median values rising from 10 days during the baseline to approximately 27 days by the end of the century. In contrast, cold rivers retain predominantly low values throughout most of the century, although episodic exceedances emerge in upper percentiles after mid-century (Fig. 8).

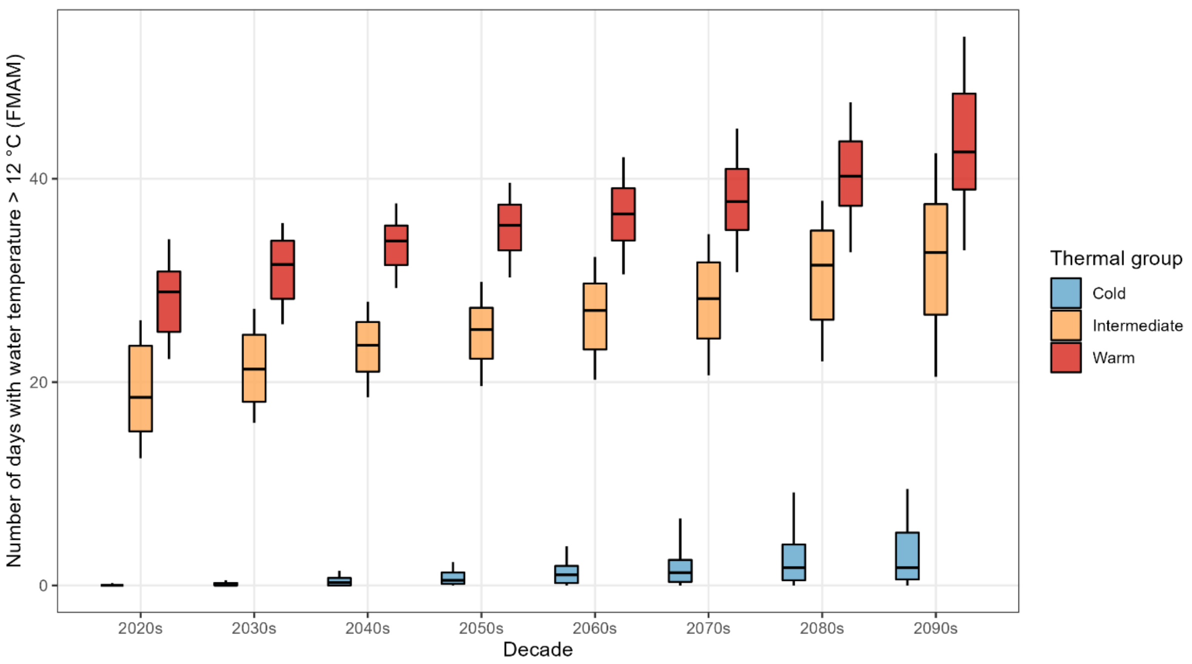


Figure 8. Projected changes in the number of days with water temperature above 12 °C during the late winter–early spring period (February–May, FMAM) across three thermal groups of Czech river profiles (cold, intermediate, warm). Box plots show the interquartile range (P25–P75) and median of the multi-model ensemble for each decade; whiskers extend to P05 and P95. The FMAM period encompasses the main spawning and early development season of brown trout, and the projected warming represents a progressive compression of the thermal window favourable for embryo development and fry emergence.

Taken together, these cold-season and early spring trends indicate a progressive narrowing of the thermal window favourable for brown trout spawning, egg incubation, and fry emergence, compounding the impacts of summer warming across the full annual cycle.

## 4 Discussion

### 4.1 Thermal stress emerges before extreme temperatures

Although extreme water temperatures above 23 °C attract attention because of their acute physiological impacts, our results show that the primary transformation of Czech river thermal regimes is characterised by a progressive structural shift of the entire thermal regime rather than merely an increase in rare extreme events. The spatial analysis of cold-water persistence reveals a marked contraction of thermally suitable habitat (≥350 days <17 °C), declining from near-complete network coverage in the historical period to a small fraction of river length by the late 21st century. This contraction occurs well before extreme heat waves become widespread. At the profile scale, this structural change is expressed as a redistribution of summer temperatures toward the 17–19 °C and 19–21 °C bands. These moderately elevated temperatures expand consistently across warm and intermediate rivers decades before >23 °C events become frequent. While days exceeding 23 °C may become substantial at a limited number of thermally vulnerable lowland rivers, they remain episodic across much of the network. Together, these findings indicate that the primary ecological pressure under climate warming arises from chronic and spatially extensive sub-lethal warming rather than from a sudden proliferation of extreme events. The erosion of cold-water regimes fundamentally reshapes habitat availability, reducing the spatial continuity of thermally suitable conditions long before lethal thresholds are regularly crossed.

### 4.2 Implications for brown trout

Brown trout is a cold-water, stenothermal species whose physiological performance is optimised within a relatively narrow thermal window. While lethal effects are typically associated with temperatures exceeding 23–25 °C, a substantial body of experimental and field-based evidence demonstrates that chronic exposure to lower temperatures (particularly above 17–19 °C) already induces measurable physiological stress. At these temperatures, metabolic demand increases disproportionately relative to oxygen availability, initiating hypoxic–thermal stress (Borgwardt et al., 2020; Gallagher et al., 2022).

As outlined in the Introduction, brown trout physiology defines a cascade of thermal thresholds (17 °C, 19 °C, 21 °C, and 23 °C) representing transitions from optimal growth to metabolic stress, aerobic scope contraction, sub-lethal impairment, and acute cardiac failure, respectively. Our projections indicate that these thresholds will be crossed with increasing frequency and duration across Czech rivers, transforming what were historically episodic stress events into dominant seasonal features. Critically, the most ecologically significant shift is not the emergence of lethal extremes, but the chronic expansion of the 19–21 °C and 21–23 °C bands in warm and intermediate rivers (temperature ranges where growth efficiency declines, disease susceptibility increases, and behavioural thermoregulation becomes energetically costly) (Sadayappan and Li, 2025; Jonsson, 2023; Doudoroff and Shumway, 1970).

Importantly, thermal tolerance in brown trout is strongly dependent on exposure duration. Experimental evidence shows that temperatures tolerated for a few days can become physiologically unacceptable when sustained over weeks, with the upper tolerance limit decreasing from approximately 22–23 °C under short exposure to around 21 °C during prolonged warm periods (Becker and Genoway, 1979; Wehrly et al., 2007). This temporal dimension of stress aligns closely with our results, which point to longer-lasting periods within sub-lethal temperature ranges rather than brief extreme peaks. Warming is typically most intense from April to August, a period that coincides with critical life stages for brown trout, including juvenile rearing and adult growth (Dorthe et al., 2025; Gallagher et al., 2022; Graf and Wrzesiński, 2020).

While summer extremes receive most attention, projected changes during autumn, winter, and early spring directly affect spawning, egg incubation, and early development, which constitute the most temperature-sensitive phases of the brown trout life cycle. In warm lowland rivers, the number of days with water temperature exceeding 10 °C during the ONDJ period increases markedly, reaching median values above 30 days per year by the end of the century (Fig. 7). Such conditions exceed the optimal thermal range for brown trout embryonic development and may negatively affect gamete quality and embryo survival (Borgwardt et al., 2020; Cunjak et al., 1998). Concurrently, warming during the FMAM period leads to a strong increase in days above 12 °C, approaching 40 days at upper-quartile projections in warm rivers, with a median of approximately 36 days and becoming increasingly common in intermediate systems (Fig. 8). These conditions are expected to accelerate embryogenesis and fry emergence, increasing the risk of phenological mismatch with food availability and advancing the onset of summer metabolic stress (Elliott and Elliott, 2010; Dorthe et al., 2025). Although cold upland streams largely retain low winter temperatures, upper-percentile projections indicate the emergence of episodic warm winter events later in the century. Even infrequent exceedances may disrupt thermal stability during incubation. The progressive erosion of cold-season thermal conditions suggests narrowing of the reproductive thermal niche of brown trout, compounding the impacts of summer warming.

### 4.3 Loss and fragmentation of suitable thermal habitats

The spatial analysis (Fig. 3) demonstrates not merely a gradual warming, but a structural collapse of the continuous trout zone within the Czech river network. By mid-century, suitable reaches become increasingly fragmented and restricted to isolated headwater systems. Such fragmentation may prevent effective upstream migration and recolonization, thereby increasing the vulnerability of local populations to stochastic events. The projected contraction from nearly the entire river network to approximately 298 km (4.4 % of the monitored network) by 2085 represents a fundamental reorganization of thermal habitat availability rather than a simple shift in temperature averages. This trajectory is broadly consistent with projections for neighbouring Central European countries. In Austria, Borgwardt et al. (2020) projected that thermally suitable habitat for brown trout in small rivers would decline from over 10,000 km under current conditions to approximately 6,500 km under RCP8.5, with the species distribution shifting upstream by around 200 m in altitude. Similarly, long-term observations from Switzerland documented a regionally coherent warming of Alpine rivers and streams since the late 1980s, associated with measurable upstream shifts in brown trout thermal habitat and population declines at lower altitudes (Hari et al., 2006). The contraction documented here for Czech rivers thus represents part of a broader Central European pattern of cold-water habitat loss, with the Czech headwater systems occupying a climatically pivotal position as source areas for three major European river basins. A stricter criterion of 365 days below 17 °C was initially evaluated but proved overly restrictive even under present conditions. The ≥350-day threshold was therefore adopted to represent near-continuous cold-water regimes while allowing for limited seasonal warming. These thermally suitable remnants are increasingly isolated; such a pattern has direct consequences for species persistence. Lowland rivers are projected to lose much of their cold-water character, while intermediate rivers undergo a transitional shift toward warmer regimes. In contrast, high-altitude and headwater rivers retain predominantly cold thermal conditions throughout the 21st century, reinforcing their role as climatic and thermal refugia. These are areas (often small, spring-fed tributaries or shaded deep pools) that maintain temperatures below 17 °C even when the main stem of the river is overheating (Borgwardt et al., 2020; Spanjer et al., 2022; Williams et al., 2015). Recent study (Oexle et al., 2025) documented active chill behaviour (cold seeking), whereby wild brown trout migrate into cold tributaries to mitigate the virulence of proliferative kidney disease. This disease is strongly associated with elevated mortality when water temperatures remain above ~15 °C for several consecutive weeks and is known to spread more rapidly under warm thermal conditions. However, the effectiveness of these refugia depends critically on longitudinal connectivity and the ability of fish populations to access them. Barriers to migration, altered flow regimes, and local habitat degradation may limit the capacity of brown trout to track suitable thermal conditions upstream, thereby amplifying the ecological consequences of warming even where refugia persist (Beechie et al., 2013). In regulated river systems, fragmentation may therefore convert gradual thermal deterioration into abrupt local population losses. As main-stem temperatures rise above 21 °C, they become thermal barriers that prevent migration and genetic exchange between tributaries (Williams et al., 2015; Fullerton et al., 2018). This isolation increases the risk of local extirpation, as small, isolated populations are more vulnerable to other stressors such as drought or pollution. The loss of habitats below 17 °C is thus not just a loss of space, but a loss of the connectivity that ensures the long-term resilience (Williams et al., 2015; Borgwardt et al., 2020; Capon et al., 2013). The identification and protection of these refugia must be a cornerstone of future water management.

### 4.4 Model uncertainty and interpretation of extreme temperatures

The linear air–water temperature regression framework used in this study provides a robust and computationally efficient approach particularly well suited for long-term climate impact assessments, as air temperature serves as an integrated proxy for the net energy budget and is the most reliably simulated variable in global circulation models. Model performance across calibration and validation profiles confirmed that the approach captures the dominant thermal variability in Czech rivers with high fidelity.

One important interpretive consideration concerns projections of extreme temperatures above 23 °C. Statistical regression models reproduce mean conditions and moderate thermal variability more reliably than the upper tail of the thermal distribution, where local processes, such as riparian shading, groundwater inflows, channel morphology, and low-flow conditions can decouple water temperature from air temperature (Arismendi et al., 2014; Dugdale et al., 2017). As a result, projected frequencies of exceedances above 23 °C should be regarded as conservative estimates; actual occurrences during compound heat–drought episodes are likely higher. Importantly, this limitation does not affect the main conclusions of the study, which are grounded in shifts within lower and mid-range temperature bands where model performance is substantially more robust.

### 4.5 Compounding effects of low flow events

Low-flow conditions, already mentioned as a local modulator of the air–water temperature relationship, deserve broader consideration in the context of future projections. Although streamflow was not included among the predictors (most monitoring sites were not directly paired with discharge observations) the projections therefore assume that future flow conditions will remain broadly similar to the recent regime. This assumption is conservative. Czech hydrological studies and recent syntheses indicate that climate change is already altering water balance through rising air temperature, higher evapotranspiration, reduced snow storage, seasonal redistribution of runoff, and expanding deficit areas, even where precipitation trends are not uniformly negative (Brázdil et al., 2021; Vizina et al., 2024; Vizina et al., 2023; Vizina et al., 2017). Additional evidence from Czechia and Central Europe suggests that these processes are likely to intensify in coming decades, with declining snowpack, earlier snowmelt, shifts in runoff seasonality, and more severe warm-season low flows, especially where higher temperature is not offset by increased precipitation (Jenicek et al., 2021; Marx et al., 2018; Vlach et al., 2020; Bernsteinová et al., 2026; Langhammer and Bernsteinová, 2025). In Czech mountain catchments, future snowpack decline has been projected to shift peak runoff earlier in the year, reduce spring runoff volumes, and contribute to more extreme summer low-flow periods (Jenicek et al., 2021). More broadly, warming-driven increases in evapotranspiration and changes in snow and catchment storage are expected to further intensify summer streamflow deficits across Central Europe (Beran et al., 2016; Hanel et al., 2012; Marx et al., 2018; Vlach et al., 2020). In the Thaya river basin, Fischer et al. (2023) further showed that runoff decline is driven primarily by increasing temperature under stagnating precipitation, with the strongest decreases in spring and increasing summer water limitation. These changes are highly relevant for river thermal regimes because lower summer and early-autumn discharges reduce channel depth and thermal inertia, increase residence time, weaken mixing, and may limit the cooling effect of groundwater inflows. Under such conditions, the same atmospheric forcing can generate higher water temperatures than under average discharge.

This interpretation is consistent with broader Central European evidence. River temperature records from Poland show persistent warming and strong seasonal coupling between discharge and thermal conditions, with predominantly negative flow–temperature relationships during the warm season (Graf and Wrzesiński, 2020; Wrzesiński and Graf, 2022). For brown trout, low-flow periods should therefore be understood not as an independent parallel stressor, but as a multiplier of warming impacts that accelerates habitat loss, prolongs sub-lethal exposure, and intensifies oxygen and water-quality stress. Future assessments should explicitly couple discharge and temperature scenarios to quantify compound heat–drought risk more realistically.

### 4.6 Management implications under a warming climate

The dominance of moderate and sub-lethal thermal stress in shaping future river conditions underscores the importance of management strategies targeting chronic warming rather than rare extremes. Measures such as preserving and restoring riparian shading, maintaining sufficient summer baseflows, and enhancing hyporheic exchange can locally reduce water temperature by several degrees, often enough to prevent transitions into critical stress zones (Capon et al., 2013). Riparian shading directly reduces the solar radiation budget of the stream, often cooling the water by several degrees compared to exposed reaches (Roon et al., 2025; Spanjer et al., 2022; Sievers et al., 2017). In small-to-medium streams, increasing canopy cover could mitigate up to 50% of the projected temperature rise, potentially keeping critical reaches below the 19 °C chronic stress threshold even under moderate warming scenarios (Spanjer et al., 2022). Beyond shading, riparian zones provide biological subsidies (Sievers et al., 2017; Spanjer et al., 2022). Deciduous trees contribute terrestrial insects to the stream, which can constitute up to 50% of a trout's diet. This increased prey availability is crucial; bioenergetic models show that trout can maintain positive growth at higher temperatures (up to 22.7 °C) if they have access to abundant, high-energy food sources. Without these subsidies, the threshold for zero growth drops to approximately 18.9 °C (Spanjer et al., 2022).

In regulated river systems, the management of dam releases offers a high-precision tool for thermal mitigation (Bradford et al., 2023; Dorthe et al., 2025). Utilizing deep-water (hypolimnetic) releases from stratified reservoirs can provide cold-water pulses to downstream reaches during heatwaves, effectively acting as an emergency cooling system for the river. However, this strategy is only viable as long as the reservoir's cold pool remains intact; long-term warming under SSP5-8.5 may eventually deplete these cold-water reserves, making this mitigation tool less reliable by mid-century (Dorthe et al., 2025). In this context, high-altitude and well-shaded headwater systems represent disproportionately valuable assets for biodiversity conservation. Protecting these systems, restoring longitudinal connectivity, and preventing further degradation of groundwater-fed reaches should be considered priorities for climate adaptation in river management. While global climate trajectories cannot be altered at the catchment scale, local interventions can meaningfully delay or mitigate the ecological consequences of warming. The identification and protection of thermal refugia must therefore be a cornerstone of future water management, alongside restoration of longitudinal connectivity and prevention of further degradation of groundwater-fed reaches.

Although this study focuses on the Czech Republic, its findings carry broader relevance for Central European river management. The Czech territory functions as a headwater source for three major European drainage basins (the Elbe, Oder, and Danube), meaning that thermal degradation of Czech headwater streams propagates downstream into internationally shared river systems. Moreover, the modelling framework developed here, combining high-resolution gridded meteorological data with site-specific air–water temperature regression and threshold-based ecological indicators, is directly transferable to other data-rich regions where long-term river temperature observations are available. The progressive contraction of cold-water habitat documented here is unlikely to be unique to the Czech Republic; similar dynamics can be expected across montane and sub-montane river systems throughout Central and Western Europe, where brown trout and other cold-water species face comparable thermal pressures under accelerating climate warming.

## 5 Conclusions

The thermal regimes of Czech rivers are undergoing a fundamental and progressive transformation driven by anthropogenic climate change. The dominant ecological pressure on cold-water species does not arise from a sudden proliferation of lethal heat extremes, but from the chronic and spatially extensive erosion of thermally suitable conditions. The contraction of river reaches maintaining water temperatures below 17 °C for at least 350 days per year, from near-complete network coverage in the historical period to approximately 4 % of the river network by 2085 under median projections, represents a structural reorganisation of cold-water habitat availability rather than a simple shift in temperature averages.

This habitat loss is driven primarily by the systematic expansion of moderately elevated temperature ranges (17–21 °C) across warm and intermediate rivers, while high-altitude headwater systems retain cold-water conditions throughout the century and emerge as the last persistent thermal refugia. Concurrently, warming during the cold season and early spring progressively narrows the thermal window favourable for brown trout spawning, egg incubation, and fry emergence, compounding the impacts of summer warming across the full annual cycle.

Safeguarding brown trout and cold-water biodiversity more broadly will require targeted management interventions focused on chronic sub-lethal warming rather than rare extremes. Preserving and restoring riparian shading, maintaining sufficient summer baseflows, and protecting longitudinal connectivity to allow access to upstream refugia are among the most tractable near-term adaptation measures. High-altitude headwater systems represent disproportionately valuable conservation assets and should be treated as priorities in river management planning under a warming climate. Future work should extend this framework to assess the combined effects of thermal change and hydrological drought, which are likely to interact nonlinearly in driving thermal extremes during compound events.

## Author contributions.

MO conceived the study, developed the modelling framework, conceptualization, conducted the analyses, and prepared the manuscript. RK contributed to ecological interpretation and brown trout biology. JB processed the baseline and projection datasets and DS contributed to spatial visualisations. MF inspired model development and with AV contributed to hydrological interpretation. PS contributed to the selection and evaluation of the GCM and RCM ensemble. PŠ and PZ prepared the gridded meteorological input data. JM contributed domain expertise in fisheries ecology and brown trout biology. MT conceived the overall research vision, supervised the study, assembled the author team, and contributed to the overall design and interpretation. All authors contributed to the interpretation of results and reviewed and approved the final manuscript.

## Competing interests

The authors declare that they have no conflict of interest.

**Data availability**

Input data used in this study is available from the corresponding author upon request.

**Acknowledgement**

The authors used AI-assisted tools (Claude, Anthropic) for editing R scripts and language editing. All scientific content, analyses, and conclusions were developed and verified by the authors.

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## Supplementary Material

Supplementary Table S1. Overview of the statistical metrics $R^2$, RMSE, MBE and Pearson R, for the set of calibration and validation files. Sorted descending by RMSE.

| Calibration (n=25) | $R^2$ | RMSE | MBE | PearsonR |
|---|---|---|---|---|
| RadotinII_RadotinskyPotok | 0.94 | 1.28 | 0.20 | 0.97 |
| VestrevHostinne_Labe | 0.94 | 1.33 | -0.23 | 0.97 |
| Rejstejn_Otava | 0.94 | 1.35 | -0.26 | 0.97 |
| DolniLibchavy_TichaOrlice | 0.96 | 1.35 | -0.82 | 0.98 |
| StribrneHory_BorovskyPotok | 0.96 | 1.41 | -0.81 | 0.98 |
| Cichorice_Strela | 0.94 | 1.42 | -0.50 | 0.97 |
| Bilovice_Svitava | 0.96 | 1.44 | -0.80 | 0.98 |
| Jizerka_Jizera | 0.91 | 1.47 | 0.04 | 0.96 |
| StaraRole_Rolava | 0.95 | 1.50 | -0.85 | 0.98 |
| Svahy-Trebel_KosovyPotok | 0.96 | 1.53 | -0.16 | 0.98 |
| Raskov_Morava | 0.95 | 1.53 | -1.02 | 0.98 |
| Jezdecka_CernaDesna | 0.92 | 1.55 | -0.40 | 0.96 |
| Susice_Otava | 0.95 | 1.57 | -0.42 | 0.97 |
| Slana_Oleska | 0.94 | 1.59 | -0.73 | 0.97 |
| DolniLoucky_Loucka | 0.96 | 1.61 | -0.21 | 0.98 |
| Hracholusky_ZlatyPotok | 0.94 | 1.64 | -0.98 | 0.97 |
| Krnov_Opava | 0.94 | 1.74 | -0.48 | 0.97 |
| Stechovice_Kocaba | 0.96 | 1.87 | -0.62 | 0.98 |
| ObriDul_Upa | 0.91 | 1.88 | -1.23 | 0.95 |
| Chocnejovice_Mohelka | 0.90 | 2.02 | -1.06 | 0.95 |
| Jablunkov_Olse | 0.91 | 2.18 | -0.57 | 0.95 |
| ValasskeMezirici_RoznovskaBecva | 0.93 | 2.33 | 1.00 | 0.97 |
| Hronov_Metuje | 0.93 | 2.40 | -1.93 | 0.96 |
| Lenora_TeplaVltava | 0.86 | 2.51 | -1.70 | 0.92 |
| ZeleznyBrod_Jizera | 0.94 | 2.65 | 1.09 | 0.97 |

| Validation (n=10) | $R^2$ | RMSE | MBE | PearsonR |
|---|---|---|---|---|
| Mikulovice_Bela | 0.95 | 1.40 | -0.40 | 0.97 |
| SazavaUZdaru_Sazava | 0.95 | 1.53 | 0.45 | 0.98 |
| Slovenice_Chotysanka | 0.94 | 1.60 | -0.17 | 0.97 |
| Stodulky_Kremelna | 0.92 | 1.70 | -0.62 | 0.96 |
| VelkaStahle_Moravice | 0.92 | 1.70 | -0.89 | 0.96 |
| Nemetice_Volynka | 0.95 | 1.80 | -0.93 | 0.97 |
| HorniStropnice_Stropnice | 0.89 | 1.89 | -0.04 | 0.95 |
| Branka_Moravice | 0.91 | 2.12 | -0.11 | 0.95 |
| Jarcova_VsetinskaBecva | 0.94 | 2.38 | 0.79 | 0.97 |
| JablonecNJ_Jizera | 0.90 | 3.34 | -2.90 | 0.95 |

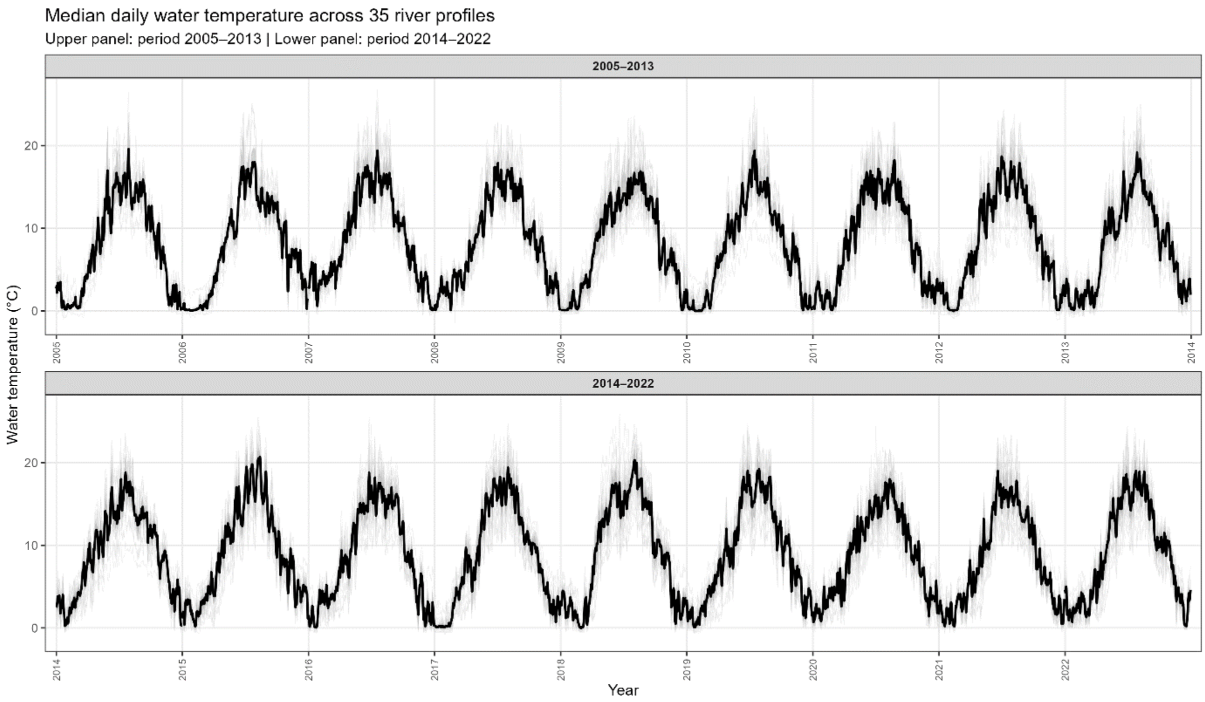


Figure S1. Median daily water temperature (black solid line) and interquartile range (grey shading) across 35 river profiles for two sub-periods: 2005–2013 (upper panel) and 2014–2022 (lower panel).