ORIGINAL ARTICLE

The effect of temperature on the dynamics of common bream *Abramis brama* migrations between the reservoir and its tributary

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Abstract

An active preference for higher temperatures within a physiological optimum is beneficial for animal movement. For example, ascending temperatures induce an increase in cyprinid fish metabolism and swimming ability. Spring upstream migrations driven by the search for resources may be related to these increases. Conversely, downstream migrations in autumn follow a decrease in temperature. When fish migrations are driven by a search for resources, for example, food availability and reproduction, or to avoid predators, then the temperature effect can be reduced to approximately the threshold temperatures that induce up- and/or downstream movement. To test this assumption, we tracked the seasonal migrations of the common bream *Abramis brama* between a reservoir and its tributary using radio tags with temperature sensors during a 5-year period. Upstream migrations of the species into the tributary were not motivated by seeking temperatures different from those in the reservoir, that is, fish body temperatures in both environments were comparable across seasons. However, for long-distance migrations, increasing temperature did support upstream migrations. Temperature did not determine the direction or intensity of short-distance migration of the species between the reservoir and the tributary. No significant influence of temperature was recorded for the downstream migrations according to the results of the generalised additive mixed model (GAMM1), which related movement distance as the explanatory variable to the signed fish body temperature as the response. The second model (GAMM2) relating fish body temperature as the explanatory variable to the signed movement distance as the response obtained a threshold value of 19.1°C for the upstream migrations and 1.5°C for the downstream migrations of the common bream.

KEYWORDS
body temperature, cyprinids, migrations, radio telemetry, resource use

1 | INTRODUCTION

Migrations of freshwater fish and their intensity are influenced by environmental factors such as water flow, photoperiod, turbidity and/or temperature (Cunjak & Power, 1986; Lucas & Baras, 2001; Parkinson et al., 1999; Pfauserová et al., 2021, 2022; Tracey et al., 2020) An active preference for higher temperatures within the physiological optimum is beneficial for ectothermic animals, including fish, allowing them to achieve higher fitness, faster growth and better movement (Angilletta, 2009; Angilletta et al., 2002; Benjamin et al., 2020). As migrations are energetically consuming (Lennox et al., 2018) and reflect the correlation between increasing metabolism and temperature (Beamish, 1978; Magnuson et al., 1979), the temperature ascent within an optimal range corresponds with an increase in fish migration (Bizzotto et al., 2009; LovellFord et al., 2020; Tracey et al., 2020). In temperate rivers, the effect of temperature ascent can be observed in spring, when a small but rapid increase in temperatures may induce a massive response in the form of upstream spawning migrations in Cyprinid fish (Rakowitz et al., 2008); hence, the temperature can be characterised as a threshold value initiating migrations (Baras & Philippart, 1999; Northcote, 1984; Ovidio et al., 2004).

Apart from their physiological nature, fish migration can be considered behavioural responses to specific habitat conditions; for example, in Cyprinids, seasonal migrations are undertaken to reduce predation risk and/or to increase the growth rate (Brönmark et al., 2014). For example, in autumn, Cyprinids migrate from warmer lakes to colder tributaries that have lower predation risk and food availability; they return in spring (Brodersen et al., 2008). This trade-off between predation avoidance and foraging is further influenced by individual characteristics, such as body size—smaller individuals migrate more frequently as they are more threatened by predators in lakes than larger individuals (Skov et al., 2011).

Likewise, habitats with high food availability provide beneficial conditions enabling faster growth and potentially resulting in higher fitness and reproductive potential. For example, numerous Cyprinid species, such as the roach *Rutilus* (Linnaeus, 1758) with higher fitness levels, exhibited a greater propensity to migrate from a lake into its tributaries (Brodersen et al., 2008). In contrast, the lower fitness level of the common bream *Abramis brama* (Linnaeus, 1758) appeared to be the reason for its migrations from the mainstream to the flood plain area (Grift et al., 2001). Similarly, nomad bream with a lower somatic condition displayed a greater propensity to move between lakes (Brodersen et al., 2019). Furthermore, migrations between a mainstream and flood plain area reflect the ontogenetic development of an individual. For example, immature common bream emigrated from flood plain areas into the mainstreams, while the oldest fish maintained residence in the flood plain areas. The adults migrated between both habitats (Borcherding et al., 2002; Molls, 1999).

Lakes and reservoirs modify the temperature gradient of rivers, and riverine fish communities are replaced with pelagic species in lakes and by nonnative generalists in reservoirs (L'Abée-Lund & Vøllestad, 1987; Liew et al., 2016; Šmejkal et al., 2023). Generalist species are not fully adapted to lentic environments; hence, their migrations into tributaries to exploit resources, for example, reproduction opportunities, spatial requirements and/or food availability, are regularly observed (Fernando & Holčík, 1991; Šmejkal et al., 2023). For example, the common bream is frequently found in lakes and reservoirs, from which it occasionally migrates into tributaries (Brodersen et al., 2019; Hladík & Kubečka, 2003). Migrations of the common bream from a reservoir into tributaries are expected in spring, followed by a return to the reservoir in autumn (Pfauserová et al., 2021). Reservoirs serve as autumn and winter refuges for the common bream, while tributaries appear to provide opportunities to utilise resources during spring and summer.

According to our 5-year field observations, a prolonged photoperiod seems to be the key factor influencing common bream migrations from the reservoir to the tributary, supported by flow conditions in the tributary (Pfauserová et al., 2021, 2022). The common bream migrated from the reservoir into the tributary during the period when the temperature in the reservoir was higher than in its tributary (Pfauserová et al., 2022); hence, its effect appears to be overshadowed by the search for seasonal resources. Considering reported threshold temperatures for the interval between minimal and maximal intensity of the common bream migrations (7–17°C), we observed the effect of temperature on up- and downstream migrations of the species around these threshold values (Borcherding et al., 2002; Heermann & Borcherding, 2006; Prignon et al., 1998). We used radiotelemetry with temperature sensors and the findings allowed us to assess the relation between individual body temperature and the ability to utilise distant resources.

2 | MATERIALS AND METHODS

Our study site covered 45 km in total and was composed of a 30-km section of the free-flowing Vltava River and the upper 15 km of the Lipno Reservoir (Czech Republic, Central Europe), of which the Vltava is the main tributary. Fish tagging was conducted during the period from May 2014 to September 2015 in the lotic segment of the Vltava River in the area approximately 15–20 km upstream of the Lipno Reservoir (Pfauserová et al., 2021). Under anaesthesia (using 2-phenoxy-ethanol; $0.2\,mL \times L^{-1}$), fish were equipped with radio transmitters (Lotek Engineering, Inc., Newmarket, ON, Canada) that never exceeded 2% of the body mass of the fish (J. D. Winter, 1983). In total, we tagged 50 adult common bream individuals (body mass range: 260–965 g). Four individuals died during the study period (tags were found and identified), and four others were found only once during the tracking period; hence, these individuals were not included in the data analyses. Transmitters with a uniform frequency of 138.300 MHz (MCFT2-3FM, mean operational lifespan of 1432 days) and a uniform burst rate (5 s) were implanted into fish body cavities through a mid-ventral incision and secured by three separate stitches (using sterile braided absorbable sutures; Ethicon-coated Vicryl, Coated

Vicryl®, Ethicon Inc.). Tags were equipped with temperature sensors measuring fish body temperature and movement activity. For five consecutive years (May 2014–December 2018), the primary study area was surveyed by boat every 14 days, on average. Data on fish positions in the longitudinal profile of the reservoir and its tributary, differences between individual fish positions within a time interval, status of movement activity of fish (yes/no) and fish body temperature were available for the statistical analyses. Detailed information on the site and methodology has been provided in previous publications (Pfauserová et al., 2021, 2022). Data were collected in accordance with the Guide for the Care and Use of Animals from the Czech University of Life Sciences Prague, and all experimental protocols were approved by the Faculty of Agrobiology, Food and Natural Resources Licensing Committee (Expert Commission Ensuring Welfare of Experimental Animals). All of the experimental procedures complied with valid legislative regulations (Law no. 246/1992, §19, art. 1, letter c), which were derived from Directive 2010/63/EU; additionally, the permit from the Ministry of Environment of the Czech Republic (no. 53139/ENV/14–3074/630/14) was submitted to O. Slavík, who is qualified according to Law no. 246/1992, §17, art. 1; permit no. CZ00167. All sampling procedures were carried out with the relevant permissions from the Departmental Expert Committee for Authorization of Experimental Projects of the Ministry of Agriculture of the Czech Republic (permit no. 88042/2014-MZE-17214) in compliance with EU legislation. The study complied with ARRIVE guidelines. The internal licensing committee gave ethical approval for the same project documentation as the Ministry of Environment of the Czech Republic, that is, approved project no. 53139/ENV/14–3074/630/14.

2.1 | Statistical analyses

In total, we collected 670 positions, including fish body temperature records, of 42 common bream individuals who were included in the analyses.

We used the following generalised additive mixed model (GAMM1) for fish body temperatures:

$$
\begin{aligned}
Y_{it} = \mu + &\beta_M . I(\text{motion sensor } i, t \text{ shows activity}) \\
&+ \beta_L . I(i, t \text{ is in Lipno Reservoir}) + b_i + s_{\text{length}}(\text{length of } i) \\
&+ s_{\text{movement}}(\text{movement}_{it}) + s_{\text{seas,river}}(yday_t) . \\
&[1 - I(i, t \text{ is in Lipno Reservoir})] + s_{\text{seas,reservoir}}(yday_t) . \\
&I(i, t \text{ is in Lipno Reservoir}) + \varepsilon_{it}
\end{aligned}
$$

where

Y_{it} is the body temperature of fish I observed at time t

$I(.)$ is an indicator function. It assumes a value of 1 when its argument is true and a value of 0 otherwise.

μ is an overall mean parameter

β_M is the effect of current fish movement activity (comparing current motion sensor status 1 to status 0)

β_L is the effect of presence in the Lipno Reservoir (comparing the Lipno Reservoir to the Vltava River)

b_i is the random individual fish effect (assuming $b_i \sim N(0, \sigma^2)$)

s_{length} is the smoothing effect of fish length (shows changes in body temperature with fish length measured at the time of tagging)

$s_{\text{seas,river}}$ is the seasonal smooth effect for the Vltava River sites (shows how mean fish body temperature changes with the day of the year for detection sites in the Vltava River, either consistently or systematically over the years, after the adjustment for all other explanatory variables present in the GAMM1)

$s_{\text{seas,reservoir}}$ is the seasonal smoothing effect for the Lipno Reservoir sites (shows how the mean fish body temperature changes with the day of the year for detection sites in the Lipno Reservoir)

s_{movement} is the smooth effect of movement (signed) distance since the last detection (a positive value means upstream and negative downstream movement distance)

We used the following generalised additive mixed model (GAMM2) relating temperature as the explanatory variable for the signed movement distance (Z) as the response:

$$
Z_{it} = \mu + b_i + s_{\text{temperature}}(\text{temperature}_{it}) + \varepsilon_{it}
$$

where

Z_{it} is the current fish movement (signed) activity i observed at time t (a positive value means upstream and negative downstream movement distance)

μ is an overall mean parameter

b_i is the random individual fish effect (assuming $b_i \sim N(0, \sigma^2)$)

$s_{\text{temperature}}$ is the smoothing effect of the fish body temperature

The unknown smooth (a priori unknown and potentially nonlinear) functions were implemented as penalised splines. For seasonal components ($s_{\text{seas,river}}, s_{\text{seas,reservoir}}$), we acknowledged the annual periodicity (enforcing it by cyclic cubic spline).

We estimated unknown model parameters (μ, β_M, β_L) and unknown smooth functional parameters ($s_{\text{length}}, s_{\text{seas,river}}, s_{\text{seas,reservoir}}, s_{\text{movement}}$) simultaneously via penalised likelihood optimisation (where penalty coefficients and σ^2 were estimated by generalised cross-validation). To this end, we utilised the mgcv library in R.

3 | RESULTS

3.1 | Comparison of the fish body temperatures in the reservoir and the tributary

During our study, 28 (67%) individuals of the common bream migrated between the reservoir and its tributary; 13 (31%) migrated within the tributary; and one (2%) individual was found in the reservoir only. GAMM1 indicated significant body temperature changes across seasons with differences between the Vltava River and Lipno Reservoir. A significant relationship was also found for the movement distance but not for the current fish movement activity or fish length. The final values of GAMM1 are presented in

Table 1. The individuals present in the reservoir showed the highest body temperatures in June before the subsequent decrease to the minimum temperature in winter, while for the individuals in the tributary, the highest body temperature occurred in August, followed by a decrease to the minimum in winter (Figure 1). Individuals occupying the reservoir over the winter period had slightly lower body temperatures compared to those in the tributary. Both curves showed constituent maxima in different months,

and their courses were similar (maximum in summer, minimum in winter), indicating that across the environments, fish body temperature was comparable.

3.2 | The relationship between fish body temperature and fish migrations

The maximal length of the common bream migrations was approximately 30 km (Figure 2). At low temperatures, the species displayed stationary behaviour (Figure 2). Surprisingly, low temperatures also occurred during the short-distance upstream migrations. Only long-distance upstream migrations (distances longer than approx. 20 km) occurred when temperatures significantly increased. No significant influence of increasing temperature was found for downstream migrations. Short-distance up- and downstream migrations of the species occurred within the comparable range of temperatures in relation to the stationary behaviour, while long-distance migrations were realised during higher temperatures only. The results of GAMM2 showed a threshold temperature value of 1.5°C for downstream migrations and 19.1°C for upstream migrations (Figure 3). GAMM2 revealed a significant relationship between movement distance and fish body temperature; the final value of GAMM2 is presented in Table 1. No relationship was found between fish body temperature and current movement activity or fish body length.

TABLE 1 p Values and degrees of freedom for individual components of the models (GAMM1 and GAMM2).

Effect	(Equivalent) degrees of freedom	p value
GAMM1		
Motion status	1	.4441
Lipno reservoir presence	1	.0055
$s_{seas,river}$	7.2	<.0001
$s_{seas,reservoir}$	6.3	<.0001
s_{length}	1.0	.6850
$s_{movement}$	6.3	<.0001
GAMM2		
$s_{temperature}$	5.2	.0018

4 | DISCUSSION

We conducted a long-term field study to assess the influence of temperature on the seasonal migrations of the common bream between a reservoir and its tributary. The length of observed common bream migrations between the reservoir and its tributary corresponded with its behaviour in riverine systems where the species migrates for comparably long distances and displays homing behaviours (Caffrey et al., 1996; Le Pichon et al., 2017; Lyons & Lucas, 2002; Molls, 1999; Whelan, 1983; E. R. Winter et al., 2021a). Similarly, the bream exhibited movements within the reservoirs and/or downstream migrations from the reservoirs (Jurajda et al., 2018; Knott et al., 2020). In our study, most individuals migrated between the reservoir and the tributary, some stayed in the tributary inflow to the reservoir and one individual was found in the reservoir. Similarly, local groups of the common bream occurred separately, except during the reproductive period (E. R. Winter et al., 2021a, 2021b).

Common bream prespawning migrations within the mainstream and between the mainstream and its tributaries were reported in relation to temperature increases in spring (Borcherding et al., 2002; Gardner et al., 2013; Heermann & Borcherding, 2006; Prignon et al., 1998). In our study, however, in the longitudinal gradient (reservoir–river), an increase in temperature did not appear to be a necessary condition for the initiation of migrations. The stimulation effect of temperature was observed for long-distance upstream migrations with a threshold value of 19.1°C. These findings correspond
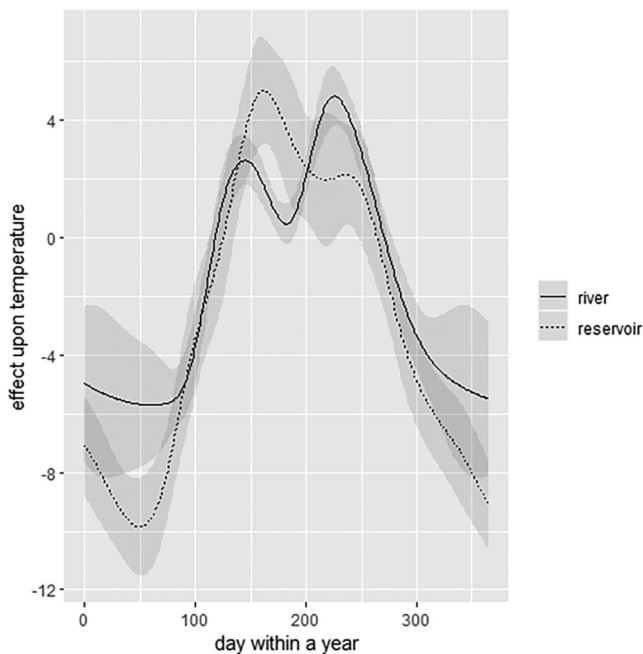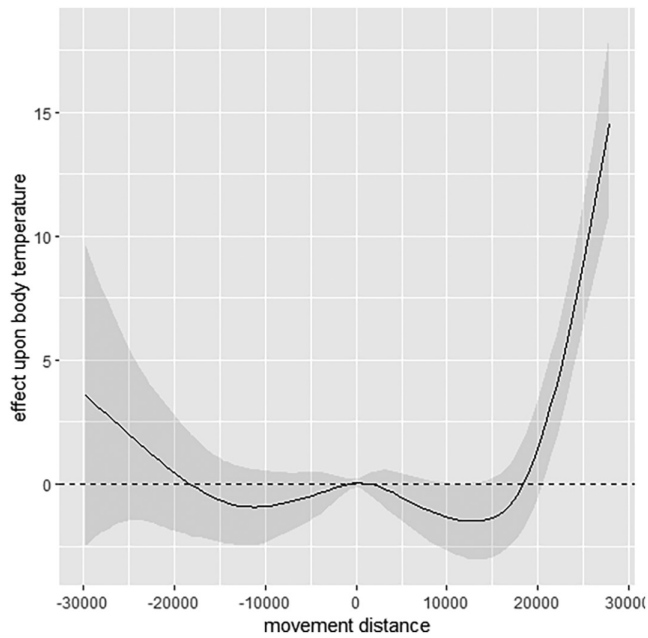

FIGURE 1 Body temperature of the common bream in the Lipno Reservoir and its tributary Vltava River throughout the year. Estimates of the smooth seasonal effect on fish body temperature for the tributary (solid line, estimate of the GAMM1 component $s_{seas,river}$) and the reservoir (dotted line, estimate of the GAMM1 component $s_{seas,reservoir}$), together with their confidence regions constructed via pointwise 95% confidence intervals (depicted in grey). X-axis units (day of year) express time positions of observed individuals within a year (Julian day, ranging from 1 to 365); Y-axis units (°C) express values of fish body temperature (adjusted to GAMM1 model terms other than seasonality).

FIGURE 2 The relationship between movement distance and fish body temperature (GAMM1). Estimates of the movement distance effect on the fish body temperature (solid line, estimate of the GAMM1 component s_{movement}), together with the confidence region constructed via pointwise 95% confidence intervals (depicted in grey). X-axis units (m) express the distances between the locations of tracked individuals in subsequent controls; Y-axis units (°C) express values of fish body temperature.

FIGURE 3 The relationship between fish body temperature and movement distance (GAMM2). Estimates of the fish body temperature effect on the movement distance (solid line, estimate of the GAMM2 component $s_{\text{temperature}}$), together with confidence region constructed via pointwise 95% confidence intervals (depicted in grey). X-axis units (°C) express values of fish body temperature; Y-axis units (m) express the distances between locations of tracked individuals in subsequent controls.

with the maximal intensity of the common bream migrations between the mainstream and floodplain area with the threshold value of 17°C reported by Heermann and Borcherding (2006). While the impact of temperature on short upstream migrations was not demonstrated, GAMM2 showed a threshold of 1.5°C for downstream migrations, which is considerably lower than the value reported for the winter emigration of the common bream from the flood plain area to the mainstream (Borcherding et al., 2002). In addition to the geographical differences of the studied areas, the selected methodological approach may affect the determined threshold values. In our study, the individual temperature of migrating individuals was measured using radio tag sensors.

The thermal heterogeneity between different types of environments is a driver of fish spatial distribution (Magnuson et al., 1979; McCullough et al., 2009) and is considered a behavioural response to temperature gradients (Beitinger & Magnuson, 1975; Benjamin et al., 2020; Fullerton et al., 2018). In our study, however, the body temperature of all observed fish individuals across seasons was comparable, indicating that fish in the reservoir occupied environments with similar temperature conditions as those in the tributary. The findings support the view that natively riverine species perform similar behavioural schema in reservoirs, for example, occupation of temperature niche, as in the riverine environment (Fernando & Holčík, 1991; Šmejkal et al., 2023). However, our data do not permit us to determine the reason for the modest difference between the winter body temperatures of individuals from the reservoir and those
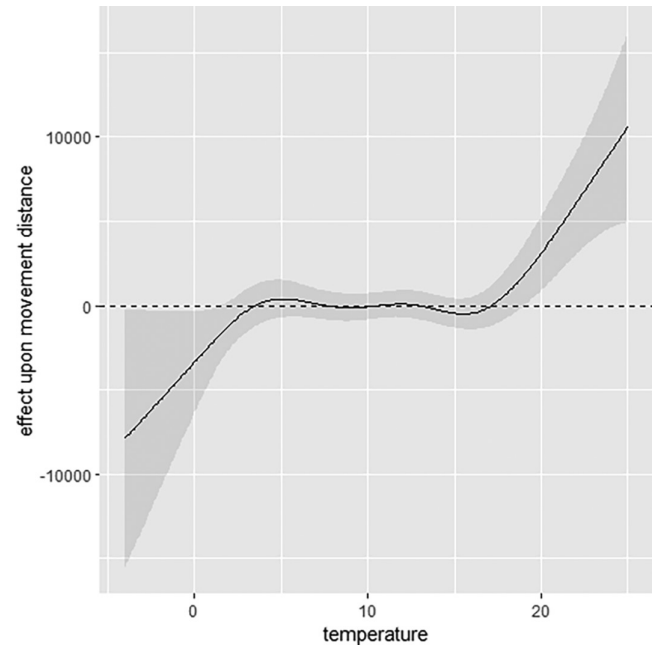
from the tributary. Based on our knowledge of local climate and natural conditions, we can only speculate that an upstream stretch of the Vltava River (the observed tributary of the Lipno Reservoir) freezes sporadically, as it is warmed by many local headwater streams and springs, while the surface of the Lipno Reservoir freezes regularly during the period from December to February. The ice cover of the reservoir can affect the spatial distribution of the common bream and limit migrations (Heermann & Borcherding, 2006).

The results suggested that temperature was not the primary reason for the common bream occurrence in the tributary of the reservoir, as was indicated by observations showing the initiation of species migration into the tributary when the temperature in the reservoir was higher than that in the tributary (Pfauserová et al., 2022). Other behavioural patterns considered in response to specific environmental conditions, for example, the avoidance of predators, did not seem to be the reason for initiating movement during our study. The maximal migration distances were observed during high temperatures, while migrations of Cyprinids from lakes into the tributaries occurred in winter (Brodersen et al., 2008; Brönmark et al., 2014; Skov et al., 2011), when high predator activity can be assumed. Similarly, common bream spawn when the water temperature is above 15°C (Maitland & Campbell, 1992); hence, reproduction did not drive intensive upstream migrations from the reservoir. The search for feeding resources has often been reported as the reason for common bream migrations (Borcherding et al., 2002; Le Pichon et al., 2017; Molls, 1999; E. R. Winter et al., 2021b); in

our study, this appears to be a reason for migrations from the reservoir to the tributary. The drive to find suitable feeding habitats corresponds with the findings that, compared to stationary individuals, migratory individuals had lower somatic conditions (Brodersen et al., 2019; Grift et al., 2001). Moreover, reservoirs may represent a more competitive environment with lower food availability (Šmejkal et al., 2023) than the inflow area of tributaries and/or structured habitats within tributaries (Benda et al., 2004; Bouska et al., 2023; Pander & Geist, 2010).

Furthermore, a lower body temperature indicated no preference for migration, that is, no differences between downstream and/or short-distance upstream migrations or even for stationary behaviour of the species. The effect of temperature on the pattern of movement by fish may be masked at comfortable temperatures and become predominant outside this range (Lucas & Baras, 2001), that is, temperature cannot necessarily play an important role and/or cannot be even detectable for fish migrations when environmental conditions are suitable (Hohausová et al., 2003; Koster et al., 2021; McCullough et al., 2009). Similarly, this seems to also be the case during uncomfortable conditions, for example, migrations during cold winter conditions were reported for Cyprinidae species not only within lenitic habitats but also between lentic and lotic habitats (Brönmark et al., 2013; Jurajda et al., 2018; Skov et al., 2011). These observations support cyprinid migrations during low temperatures within and across habitats, although a relation between migration intensity and temperature gradient was not found. Thermal regulation is associated with energy expenditures (Tanaka et al., 2000), and a difference of 1°C may lead to changes in the proportion of physiological processes by a few percentage points (Johnston & Bennett, 1996). Hence, if common bream migrated during the lower temperature range, their thermal regime was probably not associated with significant changes in physiological status and energetic costs. The speed of migration tends to be more important for energy consumption than the temperature itself (Lennox et al., 2018); hence, lower temperatures limit swimming ability in fish (Cunjak & Power, 1986) more than the motivation to migrate does. The reported results showed that energy costs for downstream migrations with flow and short-distance upstream migrations were insignificant, while the effort by fish to utilise resources during cold conditions was reflected as successive short-distance migrations. Furthermore, the comparable body size of the selected fish, which was limited by the necessary relationship between fish body mass and radio tag weight (J. D. Winter, 1983), may explain the lack of association between fish body length and thermal preference detected in our study. The limited resource availability in the reservoir and the subsequent effort of the common bream to utilise resources in the riverine environment were the probable reasons for migrations from the reservoir to the tributary (Šmejkal et al., 2023). Migrations of the species from the tributary to the reservoir reflected an effort to overcome harmful winter conditions in the reservoir, where a higher water column and low velocity reduced predation risk and energy costs (Pfauserová et al., 2021). Similar migrations between a reservoir and tributaries have been observed for salmonids, where migrants between a tributary and a reservoir exhibited higher reproductive success than those fish remaining across seasons in a tributary (Benjamin et al., 2020). As reservoirs apparently disrupt and change the temperature gradient of riverine environments, the impact of a newly created temperature gradient (the reservoir–tributary gradient) on the biology of both native and nonnative fish species spreading from reservoirs is poorly understood and should be investigated in more detail (Šmejkal et al., 2023). In conclusion, the importance of understanding the preferred temperatures and related behavioural aspects and spatial distribution of fish is magnified in the context of the current process of global warming (Amat-Trigo et al., 2023).

AUTHOR CONTRIBUTIONS

OS was involved in conceptualization, investigation, writing—original draft, writing—review and editing; NP was involved in data curation, writing—review and editing; MB was involved in methodology, data curation, data interpretation, formal analysis, visualisation, writing—review and editing; JK was involved in methodology, writing—review and editing; DČ was involved in data curation, writing—review and editing; PH was involved in conceptualization, supervision, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work summarised herein.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data set supporting this article has been deposited in the Mendeley Data repository (Slavík, Pfauserová, & Horký, 2023; data preview https://data.mendeley.com/datasets/6tv6z2pxrp/draft?a=31ddb7b9-8224-4f41-9a79-20c3a2fa861e).

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