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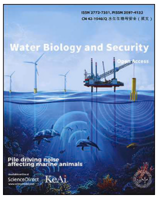

Research Article

Differences in temperature-dependent performance curves of the Endangered *Brachymystax tsinlingensis* and its prey *Phoxinus lagowskii* in a vulnerable stream ecosystem

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ABSTRACT

Understanding the ecophysiological effects of temperature on interacting species is essential for assessing their vulnerability to climate warming and evaluating the potential impacts on interspecific dynamics. However, empirical studies focused on these effects in freshwater fishes remain rare. *Brachymystax tsinlingensis* and *Phoxinus lagowskii* serve as ideal teleost models for exploring climate change impacts due to their established predator–prey relationships within sentinel systems in the Qinling Mountain region of China. We predicted that warming would differentially affect the ecophysiological performance of these two species, where *B. tsinlingensis* is the predator and *P. lagowskii* is the prey, thereby exacerbating the vulnerability of the Endangered, endemic *B. tsinlingensis*. To test this, we assessed multiple physiological metrics including standard metabolic rate (SMR), maximum metabolic rate (MMR), aerobic metabolic scope (AS), critical swimming speed (U_{crit}), and energetic cost of transport (COT) across a range of temperatures (6, 10, 14, 18, and 22 °C) for both species. We found that elevated temperatures increased mortality rates and substantially reduced swimming performance and physiological capacity in *B. tsinlingensis* compared to *P. lagowskii*. Notably, we observed a remarkable difference in the temperature-dependent performance curves between these ecologically linked species. The findings offer valuable insights into the species-specific physiological adaptations of *B. tsinlingensis* and underscore the conservation needs for this Endangered species, as well as into the implications for interspecific dynamics in vulnerable stream ecosystems facing climate warming.

1. Introduction

Global climate change is expected to impact ecosystems at all levels of function and structure (Scheffers et al., 2016; Zhang et al., 2022). This is increasingly recognized as a critical conservation issue, with far-reaching consequences for biodiversity and ecosystem services (McCarty, 2001; Comte and Olden, 2017). Freshwater ecosystems are highly vulnerable to climate change dynamics, with their vulnerability further exacerbated by the limited dispersal capabilities of species confined to fragmented habitats (Woodward et al., 2010; Comte and Olden, 2017). Freshwater fishes, as ectotherms, are particularly vulnerable to warming because water temperature directly governs their body temperature, intrinsically determining their energy budgets, metabolic demands, physiological processes, and macromolecule stability (Ficke et al., 2007; Ormerod, 2009; Martins et al., 2011). Understanding and predicting the consequences of potential future climate

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trends on freshwater fishes of interest are a critical goal for researchers (Ormerod, 2009; McKenzie et al., 2021).

The capability of species to adapt to climate change is determined by their existing thermal tolerance, acclimation capacity, and genetics (Crozier and Hutchings, 2014; Norin and Metcalfe, 2019; Morgan et al., 2020). From an ecophysiological perspective, aerobic metabolic scope (AS) quantifies the range of aerobic capacity available beyond baseline metabolic maintenance, thereby serving as a critical indicator of fish performance (Pörtner and Farrell, 2008; McKenzie et al., 2021; Hinchcliffe et al., 2025). Theory predicts a unimodal thermal performance curve for AS, wherein AS values rise until the fish warms up to an optimal temperature (T_{opt}) and decline beyond T_{opt} (McKenzie et al., 2021; Jutfelt et al., 2024; Andreassen et al., 2025). Similarly, Sandblom et al. (2016) proposed that warming imposes physiological constraints on fishes following a “plastic floors and concrete ceilings” principle: resting cardiorespiratory functions (floors) are thermally plastic, whereas maximum capacities (ceilings) demonstrate limited flexibility. This asymmetry inevitably reduces the thermal suitability of warming environments. For instance, European perch (*Perca fluviatilis*) in artificially warmed enclosures displayed thermally compensated basal physiological rates but maintained non-plastic maximum physiological performance, compared to conspecifics under natural thermal regimes (Sandblom et al., 2016). Thermal performance curves constitute a fundamental framework for understanding fish thermal tolerance and predicting climate warming impacts.

An additional important but insufficiently addressed aspect is that the effects of climate change on individual species are interrelated, shaped by their interactions with others across similar or different trophic levels (Marras et al., 2015; Pintanel et al., 2021; Ding et al., 2024). As species exhibit different rates and magnitudes of response, essential interspecific interactions are likely to be disrupted (Pecl et al., 2017; Chung et al., 2021). These interactions play a crucial role in shaping the effects of climate change on species at multiple scales, influencing their fitness, geographic distributions, and the overall structure and dynamics of the communities to which they belong (Blois et al., 2013). Therefore, beyond identifying the specific vulnerabilities of individual species, it is critical to explore how climate change may affect the ecophysiological performance of interacting species, such as predators and prey, ecological niche competitors, particularly through changes in their temperature-dependent performance curves (Bozinovic and Pörtner, 2015; Pintanel et al., 2021). However, few studies to date have comprehensively examined climate change's potential impacts on the physiological and ecological performance of freshwater fishes at distinct trophic levels.

The Qinling Mountain region in China is recognized as a global biodiversity hotspot and serves as the ecological boundary between North and South China. The thermal conditions in Qinling area are experiencing a progressive intensification under the influence of anthropogenic warming (Liu and Yu, 2025; Su et al., 2025). The freshwater ecosystems within the Qinling region can be viewed as sentinel systems, as they exhibit pronounced ecological sensitivity and vulnerability that can be used for the early detection of environmental changes at broader scales (Woodward et al., 2010). The salmonid species known as the Qinling lenok (*Brachymystax tsinlingensis*) has emerged as a potential biological indicator for assessing the effects of warming on stream fish populations (Xia et al., 2021) and is classified as Endangered in China (Yue and Chen, 1998; Zhao and Zhang, 2009). As a remnant of Quaternary glacial species, it is land-locked and cold-water adapted, residing exclusively in the streams of the Qinling Mountain region and representing one of the southernmost distributions of salmonids in the Northern hemisphere (Zhao and Zhang, 2009; Xing et al., 2015; Xia et al., 2017, 2025). Notably, the lowest elevation at which *B. tsinlingensis* occurs has recently risen from 900 m to 1200 m above sea level (Zhao and Zhang, 2009), likely indicating a shift thermal range due to climate change (Gao et al., 2012; Li et al., 2021; Liu and Yu, 2025) and suggesting this species faces thermal stress at lower altitudes due to increasing mean water temperatures. As the apex predator in Qinling stream ecosystems, *B. tsinlingensis* preys primarily on *Phoxinus lagowskii,* which is often the only other fish species present, as well as benthic organisms and various insects fluttering on the water surface. Contrasting with the narrow distribution of *B. tsinlingensis*, *P. lagowskii* has a wider range (Deng et al., 2024). This predator–prey relationship provides an ideal model for exploring climate change-driven ecophysiological traits and inferring interspecific dynamics (Deng et al., 2024). We predicted that warming will affect the temperature-dependent performance curves in these two species differently, thereby potentially disrupting established predator–prey dynamics and exacerbating the vulnerability of the southernmost-distributed salmonid *B. tsinlingensis* within the “sentinel system” of the Qinling Mountain region. Our findings are expected to advance the understanding of divergent ecophysiological traits in stream fish communities under climate change, and to underscore the urgency of conservation efforts for the Endangered *B. tsinlingensis*.

2. Materials and methods

2.1. Fish collection and housing

Wild, free-swimming *B. tsinlingensis* and *P. lagowskii* were collected using pot traps from ecological pools along the Baiyun tributary of the Shitou River in the Qinling Mountain region, Shaanxi Province, China, in early May 2021. The average daily temperature at the sampling sites (34°03′N, 107°65′E) was 11.7 ± 0.4 °C. These sites were situated close to the Experimental Base for Artificial Breeding of Qinling Lenok, Shaanxi Fisheries Institute, Taibai County, China. After collection, fishes were promptly transported to the research station in 120-L aerated tanks, with transit completed within 10 min post-capture. To prevent long-distance translocation stress in the vulnerable *B. tsinlingensis*, all experimental procedures were conducted at the field station.

B. tsinlingensis and *P. lagowskii* were kept in separate 1800 L circulating tanks under natural light conditions for one week prior to grouping. Water for the experiment was sourced from the stream and subjected to settling and filtration. Water temperature was controlled at 11.5 ± 0.5 °C, and the dissolved oxygen concentration was maintained above 8 mg L^{-1}. Fish were fed daily to satiation at 0800 with an equal proportion of chopped *Tenebrio molitor* larvae and a commercial diet (crude protein ≥52 %, crude fat ≥8.0 %, fiber ≤4 %, ash ≤16 %, and lysine ≥3.0 %) (Hanye Ltd., Shandong, China). This diet was used throughout the study. Uneaten food and feces were removed using a siphon 20 min post-feeding.

2.2. Experimental protocol

For each species, similarly sized fish were employed (*B. tsinlingensis*: 10.2 ± 0.32 g, 9.23 ± 0.12 cm, $n = 40$; *P. lagowskii*: 9.85 ± 0.26 g, 8.85 ± 0.10 cm, $n = 40$). Field surveys indicated co-occurrence in microhabitats at the specific size range studied, whereas other sizes were extremely rare. Fishes were randomly allocated into five groups ($n = 8$ per group) and transferred to separate 1800 L flow-through holding tanks, with each species held separately. The temperature treatments were 6, 10, 14, 18, and 22 °C. All tanks received settled, filtered stream water, and other environmental conditions were kept consistent across tanks. The target temperatures were achieved by adjusting from the initial 11.5 °C at a rate of 1 °C every 12 h, controlled automatically using heaters and chillers (model C-1000A, Risheng Group, Guangdong, China). Following temperature stabilization and a 1-week post-grouping time, fish were maintained at treatment temperatures for 2 weeks.

After the 2 weeks, fish were fasted for 48 h. Individual fish were then placed in a swim tunnel respirometer (Li et al., 2010; Yan et al., 2013; Fu et al., 2018; Killen et al., 2021) to assess swimming performance and measure oxygen uptake rate ($\dot{M}O_2$) during swimming using the standard

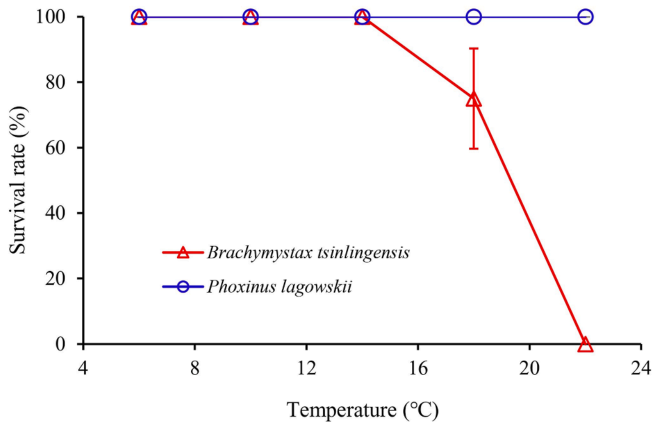

Fig. 1. Effects of five temperature treatments on the survival of *Brachymystax tsinlingensis* and *Phoxinus lagowskii* after 2 weeks. Data are mean ± SE.

critical swimming speed (U_{crit}) method (Brett, 1964). Following this, standard metabolic rate (SMR), maximum metabolic rate (MMR), AS, and energetic cost of transport (COT) were derived or calculated based on the characteristics of the oxygen uptake rate curves. Fish in each temperature treatment underwent respirometry trials concurrently on the same day.

After the experiment, the temperature for each group was returned to 11.5 °C at a rate of 1 °C every 12 h. Fish were then kept for an additional 48 h, receiving equal amounts of chopped *T. molitor* larvae and the commercial diet to aid recovery before being released at the collection sites.

2.3. Measurement of metabolism and swimming performance

The U_{crit} for each individual fish was assessed using a Brett-type swimming tunnel respirometer with a swim chamber that had a cross-sectional area of 20 cm^2 and a total volume of 3.5 L (Li et al., 2010). The respirometer was submerged in a mountain spring-fed flow-through tank (3 × 1.5 × 0.8 m, water depth 0.6 m) maintained at constant temperature and water quality with continuous flow replacement (180 L/h). Fish were carefully placed into the swimming tunnel and allowed to habituate to the continuous flow of aerated water for 12 h (overnight) before U_{crit} measurement. Water temperature in the respirometer matched the acclimation temperature and was maintained within ±0.2 °C using a water bath connected to a stainless steel heat exchanger. During the habituation, the water velocity was set as 6 cm s^{-1} (approximately 2/3 body length s^{-1}; close to the inductive velocity of experimental fish) and was subsequently increased by increments of 6 cm s^{-1} every 20 min until the fish displayed signs of fatigue. Fatigue was defined as failure to move from the rear honeycomb screen for 20 s (Lee et al., 2003). U_{crit} for each fish was calculated using Brett's equation (Brett, 1964):

$$U_{crit} = U + (t / T)\Delta U \tag{1}$$

where U (cm s^{-1}) represents the maximum speed at which the fish swam for the entire period (20 min); $\triangle U$ denotes the velocity increment (6 cm s^{-1}); T indicates the designated swimming period at each speed (20 min); and t refers to the duration for which the fish swam at the final speed (min). U_{crit} was divided by the body length (BL), yielding relative U_{crit} (rU_{crit}) to reduce body size effects.

Oxygen concentration was measured every 2 min using an oxygen probe (HQ40d, Hach Company, Loveland, CO, USA). To minimize stress on the fish, the oxygen level in the respirometer was maintained above 80 % saturation by alternating between the open and closed mode of the respirometer. During $\dot{M}O_2$ measurements at each test velocity, the respirometer was kept sealed, and the rear covers were opened only between velocity transitions and resealed within 20 s. The $\dot{M}O_2$ (mg O_2 kg^{-1} h^{-1}) for each fish during swimming was calculated based on the reduction of oxygen level using the following equation:

$$\dot{M}O_2 = 60(S - S_0)V / m^{0.75} \tag{2}$$

where S and S_0 (mg L^{-1} min^{-1}) represent the slopes of dissolved oxygen decline per minute in the water with and without the fish (i.e., background/bacterial oxygen uptake rate, $\dot{M}O_{2\ bacertial}$), respectively; V refers to the total volume of the respirometer (3.5 L) minus the volume of the fish; and m (kg) is the body mass of the fish. Microbial respiration background ($\dot{M}O_{2\ bacertial}$) remained statistically the same before and after U_{crit} determination based on initial experiments, warranting exclusive use of pre-swim measurements for baseline correction. Slopes were determined by linear regression of time (min) versus dissolved oxygen concentration (mg L^{-1}). Slope values with an r^2 greater than 0.95 were included in the analysis. The $\dot{M}O_2$ was normalized to a body mass of 1 kg using a mass coefficient of 0.75 (Reidy et al., 2000; Woodward et al., 2010; Yan et al., 2013).

In individual swimming trials, the relationship between $\dot{M}O_2$ (y) and swimming speed (x) was generally described by the equation (Webb, 1975; Roche et al., 2013):

$$y = ae^{bx} \tag{3}$$

where a represents $\dot{M}O_2$ at zero swimming speed calculated from equation (2), which corresponds to the SMR; b is a constant; and e is the natural constant (i.e., Euler's number). The maximum $\dot{M}O_2$ recorded during the U_{crit} test was defined as the MMR (Yan et al., 2013; Killen et al., 2021). AS was determined by subtracting SMR from MMR.

COT (J m^{-1}), the metabolic energy required to move a unit mass over a specific distance, is commonly used to assess overall swimming efficiency, with lower COT values representing more efficient locomotion (Tucker, 1970). At each swimming speed, $\dot{M}O_2$ values were converted to J kg^{-1} m^{-1} using an oxycalorific equivalent of 13.56 J mg O_2 (Elliott and Davison, 1975). These values were then divided by the respective swimming speed to calculate the COT. The COT for each individual swimming fish was computed using the following equation:

$$COT = 13.56\dot{M}O_2/(36U) \tag{4}$$

Table 1
Effects of temperature (6, 10, 14, 18, and 22 °C) and species (*Brachymystax tsinlingensis* and *Phoxinus lagowskii)* on their survival and aerobic swimming performance.

	Temperature	Species	Body mass	Body length	Temperature × Species
Survival (%)	$F = 12.010, p < 0.001$	$F = 21.740, p < 0.001$	$F = 2.654, p = 0.107$	–	$F = 37.625, p < 0.001$
U_{crit} (cm s^{-1})	$F = 5.144, p = 0.001$	$F = 10.748, p = 0.002$	–	$F = 0.012, p = 0.913$	$F = 2.492, p = 0.069$
rU_{crit} (BL s^{-1})	$F = 4.497$ $p = 0.003$	$F = 7.217$ $p = 0.009$	–	–	$F = 4.602$ $p = 0.006$
SMR (mg O_2 kg^{-1} h^{-1})	$F = 11.000, p < 0.001$	$F = 7.259, p = 0.010$	–	–	$F = 0.300, p = 0.825$
MMR (mg O_2 kg^{-1} h^{-1})	$F = 14.470, p < 0.001$	$F = 13.757, p < 0.001$	–	–	$F = 5.261, p = 0.003$
AS (mg O_2 kg^{-1} h^{-1})	$F = 5.360, p < 0.001$	$F = 4.813, p = 0.032$	–	–	$F = 5.443, p = 0.002$
COT (J m^{-1})	$F = 14.890, p < 0.001$	$F = 44.470, p < 0.001$	–	–	$F = 14.950, p < 0.001$

SMR: standard metabolic rate; MMR: maximum metabolic rate; AS: metabolic scope; U_{crit}: critical swimming speed; COT: energetic cost of transport; BL: Body length.

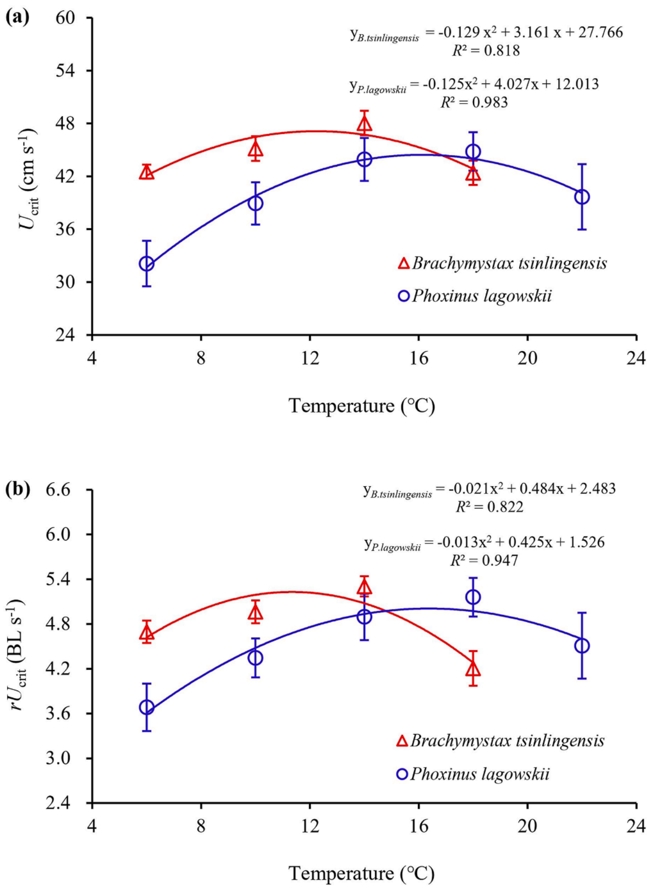

Fig. 2. Effects of five temperature treatments on the critical swimming speed (U_{crit}) and relative U_{crit} (rU_{crit}) of *Brachymystax tsinlingensis* and *Phoxinus lagowskii*. Note that no *B. tsinlingensis* survived to be tested at 22 °C.
(**a**) critical swimming speed (U_{crit}); (**b**) relative critical swimming speed (rU_{crit}).

where $\dot{M}O_2$ (mg O_2 kg^{-1} h^{-1}) refers to the rate of oxygen uptake by the swimming fish, while U (cm s^{-1}) denotes the swimming speed.

2.4. Data handling and analysis

The optimal temperature (T_{opt}) for each species was determined by calculating the peak of the polynomial regression for AS (Eliason et al., 2011). The lower and upper pejus temperatures (T_{pejus}) corresponded to the temperature at 90 % AS, and the T_{opt} window was calculated as the difference between the upper T_{pejus} and lower T_{pejus} (Farrell, 2016). The predicted critical thermal minima (CT_{min}) and critical thermal maxima (CT_{max}) were estimated by extrapolating the polynomial regression for AS to the points where AS dropped to zero (Eliason et al., 2011; Farrell, 2016). $T_{U\text{-cross}}$ was defined as the temperature where the polynomial regression curves for U_{crit} of the two fish species intersected.

Statistical analyses were conducted using R v3.4 (R Core Team, 2020) with the packages *mgcv* (Wood, 2004). Generalized Additive Models (GAMs) were employed to assess the effects of temperature, species, and their interaction on survival and U_{crit}, with temperature and species as fixed variables, and body mass or body length as covariates, respectively. GAMs were also used to evaluate the influence of temperature, species, and their interaction on metabolic traits (SMR, MMR, and AS), rU_{crit} and COT. Results are presented as mean ± standard error (SE), with significance set at $\alpha < 0.05$.

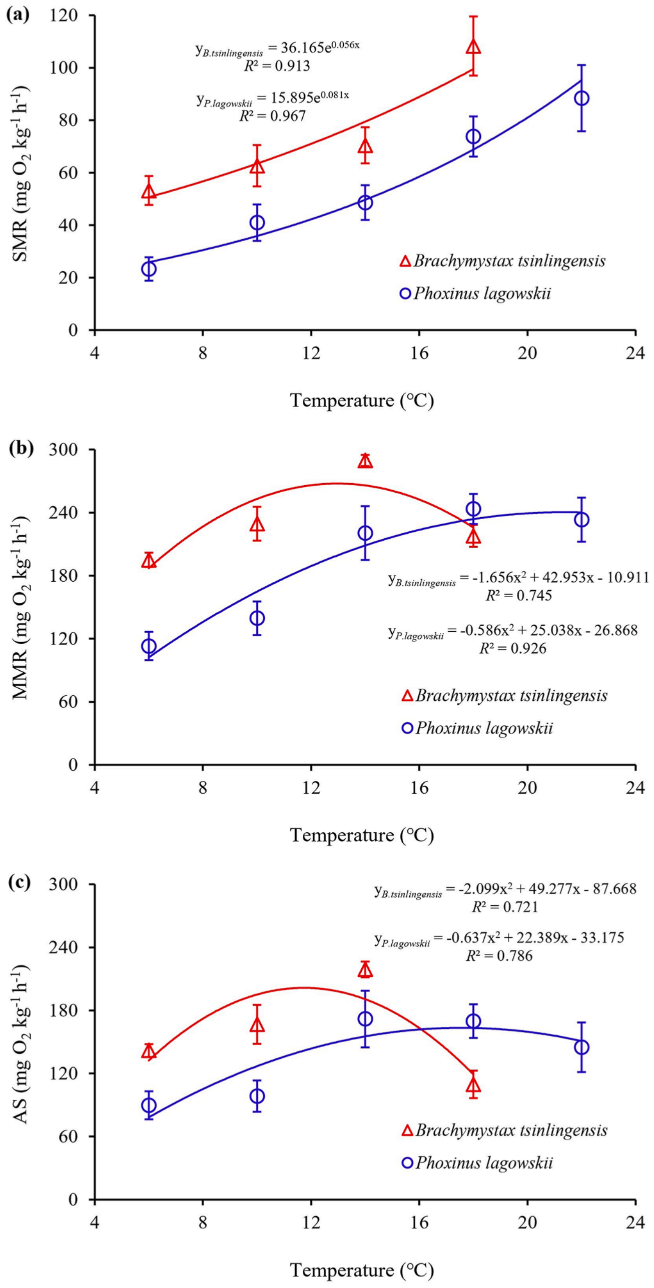

Fig. 3. Effects of five temperature treatments on the metabolic characteristics of *Brachymystax tsinlingensis* and *Phoxinus lagowskii*. Note that no *B. tsinlingensis* survived to be tested at 22 °C.
(**a**): standard metabolic rate (SMR); (**b**): maximum metabolic rate (MMR); (**c**): metabolic scope (AS).

3. Results

Temperature influenced the survival of *B. tsinlingensis*, with temperatures of 18 °C and 22 °C leading to 25 % and 100 % mortality, respectively (Fig. 1; Table 1). The 18 °C treatment had two mortalities on Day 13, while the 22 °C treatment had 2, 1, 2, and 3 individuals die on Days 9, 11, 12, and 13, respectively. In contrast, the survival of *P. lagowskii* was unaffected by temperature, with no mortality observed (Fig. 1; Table 1).

Both temperature and species had significant effects on U_{crit}, while their interaction had no effect (Fig. 2a; Table 1). For *B. tsinlingensis*, the relationship between U_{crit} (y) and temperature (x) was expressed by the equation $y = -0.129x^2 + 3.161x + 27.766$, yielding an optimal U_{crit} temperature of 12.25 °C and a maximum U_{crit} of 47.13 cm s^{-1} (Fig. 2a). In contrast, for *P. lagowskii*, the equation $y = -0.125x^2 + 4.027x + 12.013$ described the relationship, indicating an optimal U_{crit}

Table 2

Comparison of thermal–physiological characteristics of *Brachymystax tsinlingensis* and *Phoxinus lagowskii*.

Species	T_{opt} (°C)	Lower T_{pejus} (°C)	Upper T_{pejus} (°C)	T_{opt} window (°C)	Predicted CT_{min} (°C)	Predicted CT_{max} (°C)	Predicted T_{crit} range (°C)	$T_{\text{AS-cross}}$ (°C)	$T_{U\text{-max}}$ (°C)	$T_{U\text{-cross}}$ (°C)
Brachymystax tsinlingensis	11.74	8.64	14.84	6.20	1.94	21.54	19.60	16.07	12.25	16.88
Phoxinus lagowskii	17.57	12.51	22.64	10.13	1.55	33.60	32.05		16.11	

T_{opt}: optimal AS temperature; T_{pejus}: pejus temperature (temperature at 90 % AS); T_{opt} window: upper T_{pejus}-lower T_{pejus}; Predicted CT_{min} and CT_{max}: extrapolated minimum and maximum temperature when AS reached zero, respectively; Predicted T_{crit} range: predicted (CT_{max}-CT_{min}); $T_{U\text{-max}}$: optimal U_{crit} temperature; $T_{\text{AS-cross}}$ and $T_{U\text{-cross}}$: temperature at the intersection point of the polynomial regression curves for AS and U_{crit}, respectively.

temperature of 16.11 °C and a maximum U_{crit} of 44.45 cm s^{-1} (Fig. 2a). Similar temperature response patterns were observed for rU_{crit} (Fig. 2b) with temperature and species having a significant interaction (Table 1).

The interaction of temperature and species affected MMR and AS, but not SMR; SMR was affected by temperature and species separately (Fig. 3; Table 1). For both species, SMR increased with temperature, and *B. tsinlingensis* had a higher SMR than *P. lagowskii* (Fig. 3a). MMR and AS both initially showed an upward trend across a range of temperatures, followed by a decline after reaching a certain temperature; however, a notable difference was that the peak of *B. tsinlingensis* occurred at a lower temperature (Fig. 3b and c). The relationship between AS (y) and temperature (x) for *B. tsinlingensis* was represented by the equation $y = -2.099x^2 + 49.277x - 87.668$, indicating an optimal AS temperature of 11.74 °C, with a maximum AS of 201.5 mg O_2 kg^{-1} h^{-1} at this temperature (Fig. 3c; Table 2). In contrast, for *P. lagowskii,* the relationship was described by the equation $y = -0.637x^2 + 22.389x - 33.175$, with an optimal AS temperature of 17.57 °C, and a maximum AS of 163.6 mg O_2 kg^{-1} h^{-1} (Fig. 3c; Table 2). Moreover, the extrapolated upper T_{pejus} (14.84 °C) and CT_{max} (21.54 °C) for *B. tsinlingensis* were lower than those for *P. lagowskii* (22.64 °C and 33.60 °C, respectively) (Table 2).

Additionally, both temperature and species affected $\dot{M}O_2$. The $\dot{M}O_2$ increased with swimming speed, but the rate of increase tended to diminish at higher temperature (Fig. 4). The interaction of temperature and species affected COT (Table 1). COT exhibited a pattern of initially decreasing and then slightly increasing with swimming speed, with *B. tsinlingensis* generally showing higher COT than *P. lagowskii* except when swimming at high speeds in low temperature (e.g., 6 °C) (Fig. 4).

4. Discussion

Biotic interactions are fundamental to ecological and evolutionary dynamics and play a crucial role in shaping ecosystem responses to climate change (Blois et al., 2013; Sohlström et al., 2021; Sasaki et al., 2024). By analyzing thermal performance curves, we can assess the thermal sensitivities of predators and their prey, which may have functional significance. *B. tsinlingensis* and *P. lagowskii* exhibit a typical predator–prey dynamic within the “sentinel system” of the Qinling Mountain region (Xia et al., 2021; Deng et al., 2024). We identified interspecific differences in the temperature-dependent performance curves of these two interacting fish species within a Qinling stream. To our knowledge, this represents the first study to systematically assess differences in physiological vulnerability under climate warming in an endangered predator and their prey. Our results demonstrated that high temperatures led to increased mortality and more drastic declines in swimming performance and physiological functions (e.g., decreased AS) in the Endangered *B. tsinlingensis* compared to its prey, *P. lagowskii.* These findings align with the prediction that warming will differentially impact the ecophysiological performance of predator–prey system and suggest that warming could exacerbate the vulnerability of *B. tsinlingensis*.

Survival serves as a crucial and intuitive indicator of fitness (Biro et al., 2007). In this study, temperature impacted the survival of *B. tsinlingensis*, with 25 % mortality at 18 °C and 100 % mortality at 22 °C. In contrast, temperature did not influence the survival of *P. lagowskii*, as no mortalities occurred at any temperature. Notably, thermal refuges for these species in the wild are minimal and consist of just a few deep pools. However, the natural habitat of both species often experiences temperatures exceeding 24 °C for short periods, with average daily temperatures sometimes surpassing 18 °C for over 2 weeks (Li et al., 2021). These peak and sustained average temperatures greatly exceeded the predicted CT_{max} and upper T_{pejus} for *B. tsinlingensis*, while remaining below those predicted for *P. lagowskii.* Consequently, current summer high temperatures are likely to adversely affect the survival of *B. tsinlingensis*, but not *P. lagowskii*. Furthermore, ongoing warming trends are expected to increase the extinction risk of the Endangered *B. tsinlingensis* (Table 2).

U_{crit} is commonly regarded as a predictor for evaluating how environmental factors influence the Darwinian fitness of fishes (Lee et al., 2003; Yan et al., 2013). The relationship between U_{crit} and temperature is typically characterized by a bell-shaped curve (Zeng et al., 2009; Pang et al., 2013). Generally, when the surrounding temperature surpasses the optimum temperature, the swimming performance of fishes declines (Pang et al., 2013; Eliason et al., 2011). This reduction in swimming performance may increase an individual's susceptibility to predation and negatively impact foraging efficiency and other daily activities (Blake, 2004; Xia et al., 2017). Our findings revealed a difference in the optimal U_{crit} and rU_{crit} temperature of *B. tsinlingensis* (12.25 °C and 11.52 °C, respectively) compared to *P. lagowskii* (16.11 °C and 16.35 °C, respectively), underscoring the interspecific differences in optimal swimming temperatures. Importantly, the intersection point ($T_{U\text{-cross}}$) of the U_{crit}-temperature curves for the two species occurred at 16.88 °C, marking it a watershed for their relative swimming performance. At higher temperatures, the predatory *B. tsinlingensis* exhibited inferior swimming ability compared to its prey, *P. lagowskii* (Fig. 2). Given the use of relatively uniform sizes of fishes in this experiment, it would be valuable for future research to investigate how variation in predator–prey size ratios, guided by optimal foraging theory, affect physiological functions and ecological processes. Nonetheless, our results indicate that rising temperature in the future could disrupt established predator–prey dynamics, decreasing the swimming ability of *B. tsinlingensis* and potentially leading to energy deficits if they struggle to capture prey.

Energy serves as a fundamental currency in ecology, influencing how climate change affects fitness and population dynamics in ectotherms (Dillon et al., 2010; Woodward et al., 2010; Huang et al., 2020; Brownscombe et al., 2022; Gvoždík, 2024). At the molecular level, prolonged thermal stress induces various metabolic changes in *Brachymystax lenok*, including repression of energy metabolism, shifts in lipid metabolism, and alterations in amino acid, choline, and nucleotide metabolism (Liu et al., 2019). From a physiological perspective, it has been suggested that a decline in aerobic performance under rising temperature is one of the initial processes leading to extinction or migration to cooler waters (Pörtner and Knust, 2007; Clark et al., 2013; Fu et al., 2022). Specifically, AS has been proposed as a measure of fish resilience to climate warming and it could serve as an indicator of ecosystem thermal suitability across various climate scenarios (Marras et al., 2015; Pörtner et al., 2017; Lefevre et al., 2021). In our study, as expected, SMR increased with temperature for both species. However,

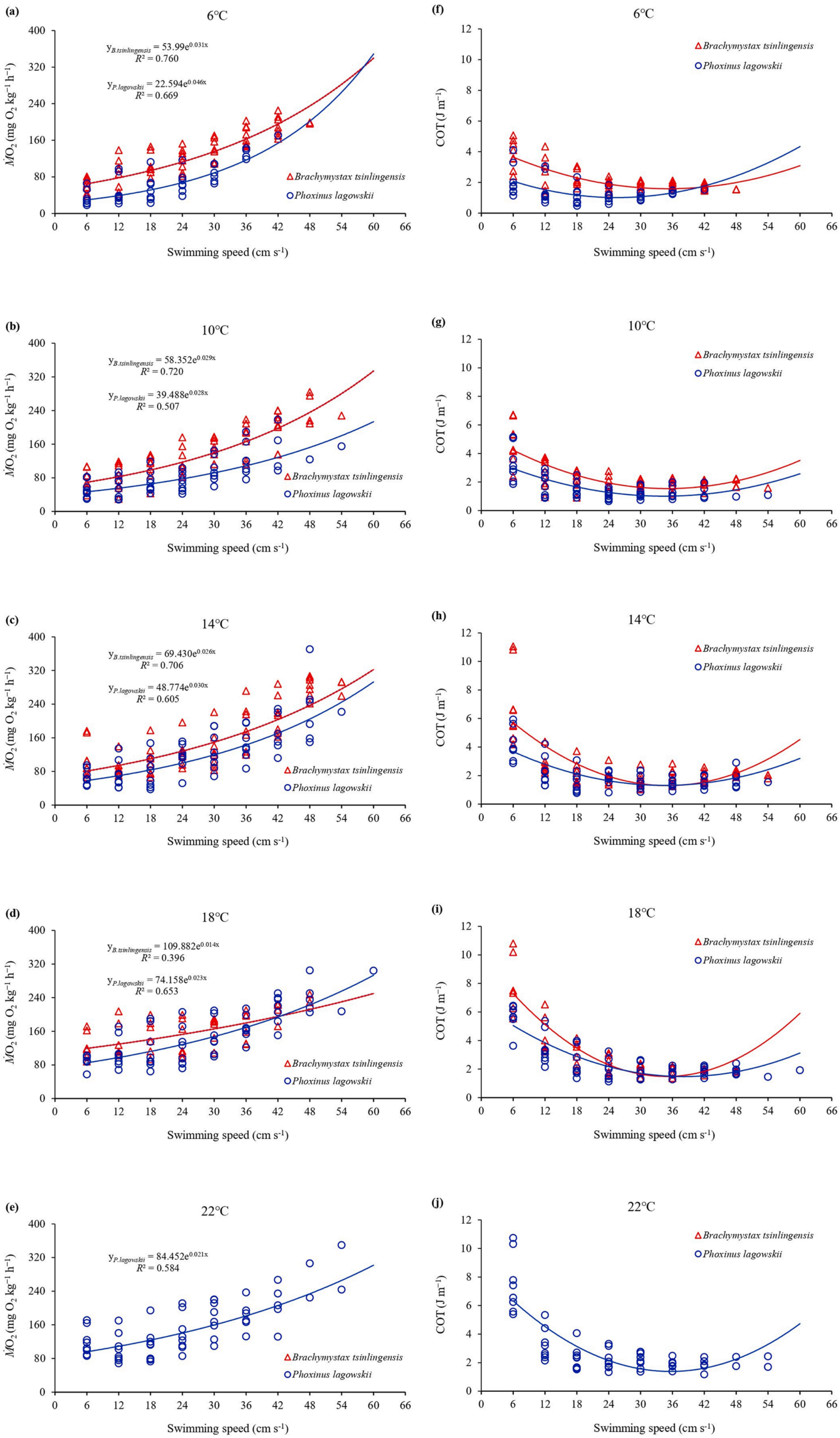

Fig. 4. Effects of five temperature treatments on the oxygen uptake rate ($\dot{M}O_2$) and the energetic cost of transport (COT) of *Brachymystax tsinlingensis* and *Phoxinus lagowskii* at different swimming speeds. Note that no *B. tsinlingensis* survived to be tested at 22 °C.

(**a**), (**b**), (**c**), (**d**), (**e**) represent the oxygen consumption rates ($\dot{M}O_2$) at 6, 10, 14, 18, and 22 °C, respectively. (**f**), (**g**), (**h**), (**i**), (**j**) represent the energetic cost of transport (COT) at 6, 10, 14, 18, and 22 °C, respectively.

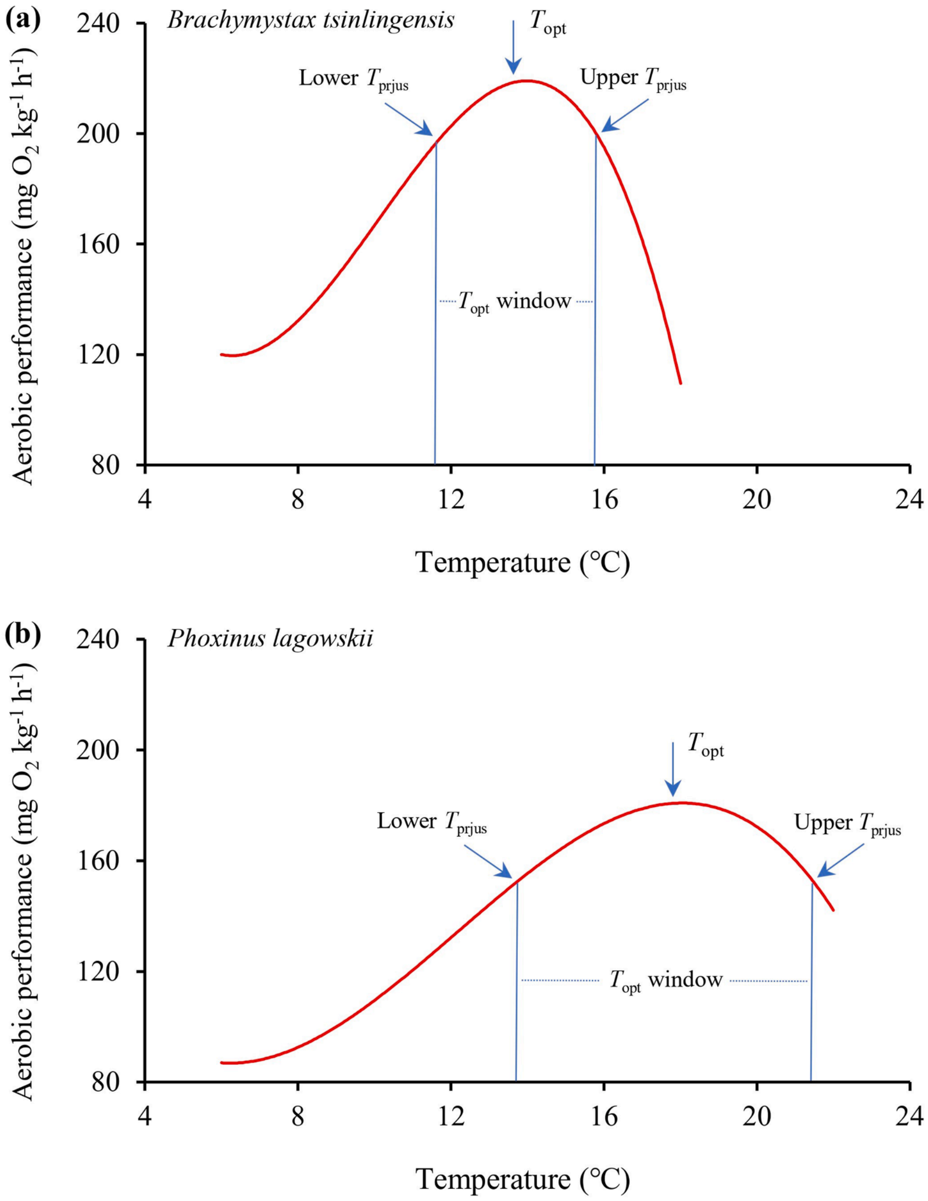

Fig. 5. Hypothetical thermal performance curves showing the species-specific physiological adaptations in *Brachymystax tsinlingensis* and *Phoxinus lagowskii*. T_{opt}: optimal temperature; T_{pejus}: pejus temperature; T_{opt} window: upper T_{pejus}-lower T_{pejus}.
(**a**) thermal performance curves for *Brachymystax tsinlingensis*; (**b**) thermal performance curves for *Phoxinus lagowskii*.

we found a species difference in the optimal temperature for AS (i.e., T_{opt}), which was 11.74 °C for *B. tsinlingensis* and 17.57 °C for *P. lagowskii*. This underscores the importance of temperature in influencing energy availability of the two species. The divergent metabolic rates observed under low temperatures are likely related to the superior mitochondrial function of *B. tsinlingensis* relative to *P. lagowskii* (Hunter-Manseau et al., 2019). However, as a cold-adapted species, *B. tsinlingensis* may experience greater oxidative stress and reach thermal tolerance thresholds earlier than *P. lagowskii* under climate warming. It is worth noting that the intersection point of the AS-temperature curves ($T_{AS\text{-}cross}$) for the two species occurred at 16.07 °C, closely aligning with the $T_{U\text{-}cross}$ (Table 2). The predicted CT_{max} of *B. tsinlingensis* (21.54 °C) was substantially lower than that of *P. lagowskii* (33.60 °C). Additionally, both the T_{opt} window and predicted T_{crit} range were notably narrower for *B. tsinlingensis* compared to *P. lagowskii* (Fig. 5; Table 2), suggesting that *P. lagowskii* possesses a greater capacity to deal with future increase in temperature or abrupt climatic shifts. In contrast, the physiological functions of *B. tsinlingensis* are more susceptible to disruption by high temperatures and thermal fluctuations. This difference in tolerance capacity is likely to intensify vulnerability disparities between the two species and disrupt existing predator–prey relationships in warmer climates due to the asynchronous or even opposing nature of their ecophysiological responses.

5. Conclusion

In conclusion, this study highlighted the differences in temperature-dependent performance curves between two fish species exhibiting a typical predator–prey dynamic in a vulnerable stream ecosystem. Our results indicate that: (1) current elevated temperatures (Liu and Yu, 2025) are already threatening the survival of *B. tsinlingensis*, necessitating urgent habitat protection or restoration measures (Su et al., 2025), and (2) continuous warming will not only intensify the physiological challenges faced by *B. tsinlingensis*, but also exacerbate its vulnerability by disrupting established interspecific dynamics. These results shed light on the physiological traits of *B. tsinlingensis*, underscore its conservation requirements in the context of global warming, and highlight the broader implication for potential interspecific relationships within fragile stream ecosystems.

CRediT authorship contribution statement

Jigang Xia: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Zizhu Wang:** Writing – review & editing, Formal analysis, Data curation. **Minrui Peng:** Methodology, Investigation, Data curation. **Ping Li:** Resources, Investigation. **Xueli Zheng:** Methodology, Investigation, Data curation. **Jingyi Xia:** Methodology, Investigation, Data curation. **Youjin Hao:** Writing – review & editing, Methodology. **Shuangxi Li:** Resources, Investigation. **Shijian Fu:** Writing – review & editing, Methodology. **Steven J. Cooke:** Writing – review & editing, Methodology.

Ethical statement

B. tsinlingensis, a species of conservation concern, is listed as Endangered in the China Red Data Book of Endangered Animals (Yue and Chen, 1998). *P. lagowskii* is the most common prey fish within the habitat of *B. tsinlingensis*. The investigation received approval from Shaanxi Provincial Forestry Bureau (LinHu-2020-33) and Shaanxi Taibaishan National Nature Reserve Administration, supported by the National Natural Science Foundation of China (No. 31770442), and adhered to the ethical standards and guidelines for animal care established by the Chongqing Key Laboratory of Conservation and Utilization of Freshwater Fishes, China (Permit No. FU-20200115-02). Following completion of the experimental procedures, all subjects were released to their capture locations.

Data accessibility

Data are archived and freely available via Open Science Framework (https://osf.io/zcmn3/).

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: The authors declare that Ping Li is affiliated with Power China Northwest Engineering Corporation Limited, the research presented in this paper was conducted impartially and independently, with the companies having no influence over the study's design, data collection, analysis, or writing of the manuscript. All opinions, findings, and conclusions are solely those of the authors and do not necessarily reflect the views of their respective companies. Steven J. Cooke serves as an editorial board member for *Water Biology and Security* and was not involved in the editorial review or the decision to publish this article.

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