

The daily rhythms of temperature preference are conserved in nocturnal and blind fish

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ARTICLE INFO

Keywords:

Daily rhythms
Circadian clock
Nocturnal species
Cavefish
Thermal preference

ABSTRACT

Light and temperature are key environmental cues that synchronize circadian clocks, and in nature, these cycles are tightly linked. As ectotherms, fish cope with these daily cycles by adjusting their body temperature through behavioural strategies, as moving to warmer/colder areas depending on their internal state. While this pattern has been described in diurnal fish, it remains poorly explored whether nocturnal fish species show similar or opposite daily patterns, or whether blind cave-dwelling fish exhibit daily variations in thermal preference. To this end, we investigated potential circadian rhythms of thermal preference in two nocturnal species of commercial interest (*Tinca tinca* and *Ameiurus melas*) and two blind cavefish (blind *Astyanax mexicanus* and *Phreatichthys andruzzii*), both models for studying adaptive and regressive evolutionary traits. Using multi-chambered tanks with a horizontal thermal gradient, fish were allowed to choose preferred temperature over 27 days under different Light/Dark conditions (LD, DL), and constant darkness (DD). All species showed significant daily rhythms of thermal preference, moving to warmer temperatures during the day and cooler ones at night. After shifting from LD to DL, fish quickly resumed diurnal rhythms. Under DD, nocturnal species maintained significant behavioural rhythms of temperature selection, while both cavefish species became arrhythmic. These results reveal a conserved daily rhythm of thermal selection, regardless of the fish's daily activity pattern, pointing to a primarily circadian control. Our results may be applied to improve welfare of fish reared in captivity by providing different time-temperature niches that mimic natural daily light/temperature cycles.

1. Introduction

In the natural environment light and temperature are not constant but fluctuate according to geophysical cycles such as the Earth's rotation on its axis, which defines day/night changes. These rhythmical environmental cycles (so called *Zeitgeber*) entrain the circadian clock of most organisms (Menaker et al., 1997; Ouyang et al., 1998; Harmer et al., 2001; Panda et al., 2002; Bell-Pedersen et al., 2005; Jabbur and Johnson, 2022). This endogenous time-keeping system provides an adaptive advantage, allowing organisms to predict dependable daily changes in order to implement behavioural and physiological processes at the right time of the day. From a molecular point of view, core clock mechanisms in animals typically consist of transcription/translation feedback loops, which complete an oscillation at ~24 h period (Takahashi, 2017;

Stanton et al., 2022). Circadian rhythms persist under constant conditions (e.g., constant darkness) and free run with a period (τ) close to 24 h (Aschoff, 1981; Herrero et al., 2003). Circadian clocks can be entrained by several cyclic environmental factors, such as light-dark alternation, temperature cycles, food availability and intra- and inter-species competitions (social interaction or prey-predator activities; Sharma and Chandrashekar, 2005). The light-dark (LD) cycle is considered the primary environmental factor synchronising (entraining) circadian rhythms via the light-entrainable oscillator (Reppert and Weaver, 2002; Kasai and Kiyohara, 2010), affecting many biological processes that contribute to the organisms' survival performance (Hammer, 1960; Walton et al., 2011; Villamizar et al., 2013; Frøland Steindal and Whitmore, 2019). In the wild, daily cycles of light and temperature are closely linked, with an alternation of thermophase

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<https://doi.org/10.1016/j.jtherbio.2025.104339>

Received 4 June 2025; Received in revised form 14 November 2025; Accepted 18 November 2025

Available online 20 November 2025

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(warmer temperatures) and cryophase (lower temperatures) between day and night during 24 h (Beck, 1983; Sánchez-Vázquez and López-Olmeda, 2018). Thus, daily thermocycles influence biological rhythms affecting behavioural and physiological patterns of most living beings (López-Olmeda and Sánchez-Vázquez, 2009; Villamizar et al., 2012). However, ambient temperature variations alone could be also, in the absence of photoperiod, a powerful *Zeitgeber* in entraining primarily the circadian clocks of ectotherms (Firth et al., 1999; Foà and Bertolucci, 2001; Rensing and Ruoff, 2002; Lahiri et al., 2005; Glaser and Stanewsky, 2007; Cai et al., 2024). Indeed, because endothermic organisms maintain their body temperature independently of ambient thermal fluctuations, external temperature could act as either a well-established or weak *Zeitgeber* in these animals, depending on the species (Sharma and Chandrashekar, 2005; Preußner and Heyd, 2018). Still, they display circadian oscillation in body temperature (Refinetti, 2020).

In the aquatic environment, water temperature variations have important effects on several biological processes, such as growth, metabolic and survival rates, spawning activity, spatial distribution of the species, cognition and memory, locomotor and feeding behaviour (Toni et al., 2019; Volkoff and Rønnestad, 2020; Gomez-Maldonado and Camacho-Cervantes, 2022). Aquatic poikilotherms, like fish, evolved behavioural strategies to thermoregulate (Angilletta Jr et al., 2002) by actively choosing an optimal thermal environment that enhances their biological performances (Brett, 1971; Reynolds and Casterlin, 1979; Golovanov, 2006; Christensen et al., 2021).

In a challenging ecosystem as the aquatic one (Geist and Hawkins, 2016), temperature synchronization and preference choice during daily and seasonal changes are important adaptations in order to cope with stress and disease and to increase the fitness and consequent survival (Schaefer and Ryan, 2006; Boltana et al., 2013; Rey et al., 2015). In an ever-changing world, where anthropic influence has led to a major modification of ecosystems, climate change and its consequences have been importantly affecting fish ecophysiology and fitness (Rountrey et al., 2014; Alfonso et al., 2021). Indeed, global warming has already been shown to alter the distribution of fish populations, depending on the thermal affinities of the species (Payne, 2013; Burrows et al., 2019; Free et al., 2019), by modifying their behaviour (Alfonso et al., 2021), prey-predator interactions or by reducing oxygen availability (Breitburg et al., 2018). In addition, global warming directly impacts on fish stress physiology increasing exponentially their basal metabolic rates (Gillooly et al., 2001; Dillon et al., 2010), affecting their reproduction, maintenance of homeostasis, immune system and susceptibility to diseases (Kandalski et al., 2018; Martínez et al., 2018; Kim et al., 2019; Li et al., 2019; Graziano et al., 2023).

To date, temporal variations in preferred temperature have been studied in a range of ectothermic species; but in fish mainly in diurnal ones (Reynolds and Casterlin, 1978a, 1978b; Reynolds et al., 1978a; Hutchison and Spriestersbach, 1986; Mortensen et al., 2007; Vera et al., 2023; de Alba et al., 2024). Here we investigate four fish species: two nocturnal as tench (*Tinca tinca*) and black bullhead catfish (*Ameiurus melas*), and two blind cavefish, the Mexican tetra (*Astyanax mexicanus*) and Somalian cavefish (*Phreatichthys andruzzii*). Temperature is a key parameter for these nocturnal species affecting spawning activity and maturation, feed conversion and growth rate, immunity and consequent stress response and survival (tench: Kennedy and Fitzmaurice, 1970; Horoszewicz, 1983; Kamiński et al., 2017; Wolnicki et al., 2017; black bullhead catfish: Novomeská and Kováč, 2009; Rypel, 2011; Novomeská et al., 2013; Roncarati et al., 2014; Copp et al., 2016). Blind Mexican and Somalian cavefish are two important model organisms for the investigation of adaptive evolutionary changes to life underground (Beale et al., 2013; Pavlova and Krylov, 2023), where key environmental parameters do not fluctuate on a daily basis (i.e., constant darkness, stable temperature and limited food sources; Borowsky, 2008; Foulkes et al., 2016). Previous reports showed that different populations of blind Mexican tetra may display differences in temperature preference, also in response to infection with parasites (Tabin et al., 2018) probably due to

a behavioural fever or stress response (Boltana et al., 2013; Rey et al., 2015), and Somalian cavefish may show a reduced clock temperature compensation (Cavallari et al., 2011). Therefore, it is likely that the daily rhythms of temperature selection, though not yet fully explored in this species, can be crucial to understanding their life history.

The main objective of this research is to investigate the potential daily rhythmic patterns of thermal preference in commercially important nocturnal fish and blind cavefish, in order to deepen our understanding of coupled light and temperature-entrainable oscillators in fish (López-Olmeda and Sánchez-Vázquez, 2009). Furthermore, we investigate whether daily thermal preferences are driven by the circadian system, pointing out temperature changes as a feasible *Zeitgeber* for the investigated species. We could hypothesise that nocturnal species exhibit daily variations in thermal preference, either similar or opposite to those of diurnal species, driven by the endogenous circadian clock, while cave-dwelling species may be arrhythmic. In addition, as no long-term records on the nocturnal behaviour of the black bullhead catfish have been performed, we also aim to verify and characterize daily pattern of activity of this commercially interest species (Savini et al., 2010). The outcomes could provide new interesting data about the thermal biology and thermal adaptation of fish that have been demonstrated to exhibit different daily activity patterns (Herrero et al., 2003; Cavallari et al., 2011; Preiszner et al., 2020; Simon et al., 2019; Jačimović et al., 2021; Di Rosa et al., 2024; Conti et al., 2025a), also in the context of aquaculture. Indeed, under artificial rearing conditions (e.g., fish farms, fish used for scientific purposes or as pets), natural environmental fluctuations are rarely considered, despite previous studies pointing out several behavioural and physiological advantages of thermoregulation in captive breeding (Boltana et al., 2013; Rey et al., 2015, 2017; Sanhueza et al., 2018, 2023; Huntingford et al., 2020). Therefore, the resulting data obtained from this study could be leveraged for improving husbandry protocols to refine fish farming conditions and improve the overall welfare of the species.

2. Materials and methods

2.1. Ethic statement

Experiments on tench and Mexican blind cavefish were conducted in the Department of Physiology of the University of Murcia (Spain), while the other part of the investigation (experiments on black bullhead catfish and Somalian cavefish) was conducted in the Department of Life Sciences and Biotechnology of the University of Ferrara (Italy). Husbandry and experimental procedures were performed in accordance with European Legislation for the Protection of Animals used for Scientific Purposes (Directive 2010/63/EU), Spanish (RD 53/2013 and Law 32/2007) and Italian (D.L. 26/2014) animal protection standards. Research was also approved by the Committee of the University of Murcia on Ethics and Animal Welfare (A13220605), by the University of Ferrara Institutional Animal Care and Use Committee (auth. num. CB/01-2019). No physical invasive manipulations were performed on the fish during the experiments and no fish showed sign of distress. At the end of the experiments, all subjects were returned to stock tanks.

2.2. Animals housing

Tench and Mexican blind cavefish juveniles were obtained from a Spanish fish farm (Tencas Atanasio, Badajoz, Spain) and from a commercial supplier (Alimar Pets, S.L., Murcia, Spain), respectively. Because the supplier did not provide any information on the origin of the Mexican cave fish strain, the cave ancestry of the specimens used in this study remains unknown. All fish were housed in a 54 L glass tank divided into six compartments (9 L each; 10–11 animals/tank) placed inside the animal facility of the University of Murcia for two months prior to the experiment. The tank contained dechlorinated fresh water in recirculation, which was constantly filtered by biological and

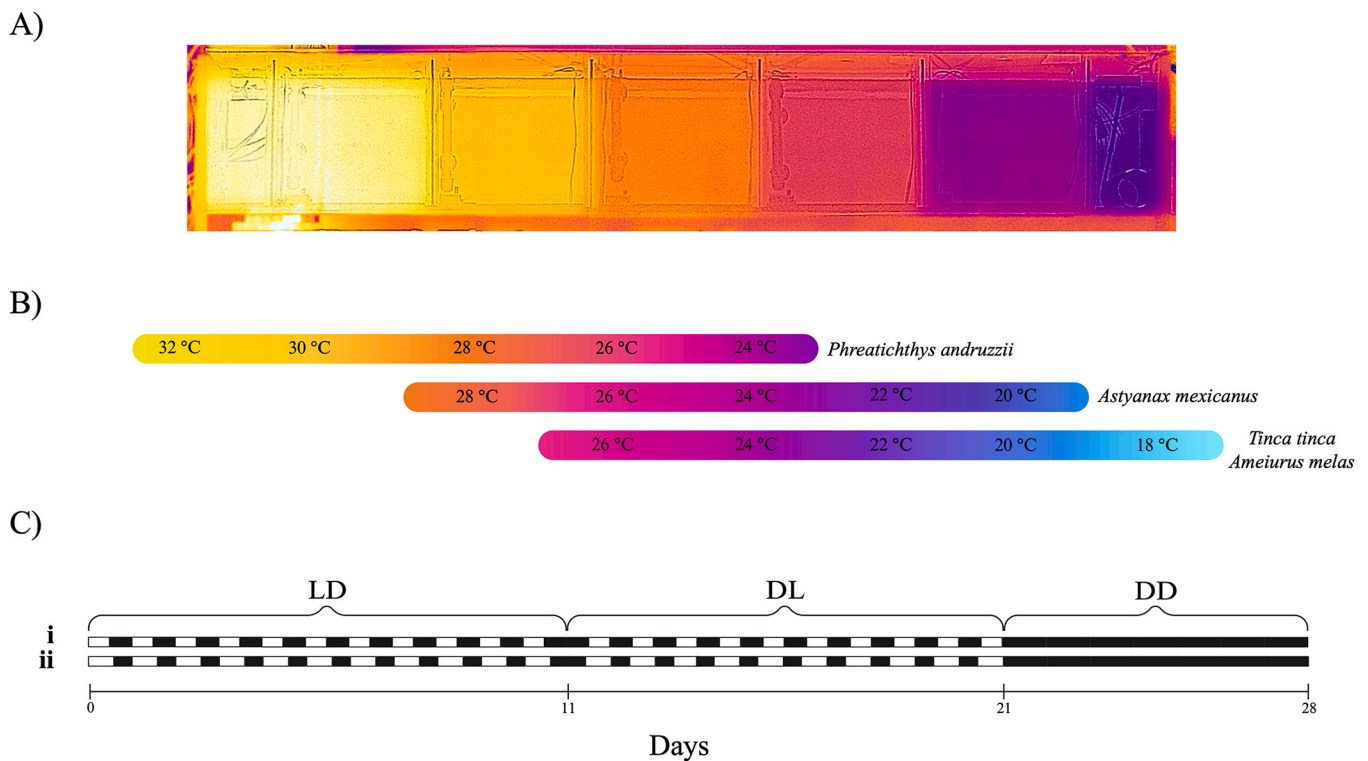


Fig. 1. A) Picture of the experimental multichambered tank taken with the thermal imaging camera to highlight the horizontal thermal gradient created and maintained. B) Different thermal gradients created depending on the biology of the species: tench *Tinca tinca*, black bullhead catfish *Ameiurus melas*, blind Mexican cavefish *Astyanax mexicanus* and Somalian cavefish *Phreatichthys andruzzii*. C) Fish were kept 11 days in light-dark (LD) cycle, 10 days in reversed LD cycle (DL) and finally 7 days in constant darkness (DD). Tench, blind Mexican and Somalian cavefish had 12h light: 12h dark photoperiod (i) and black bullhead catfish had 14h light: 10h dark photoperiod (ii).

mechanical filters. Both fish species were maintained under controlled lighting and constant temperature conditions (22.0 ± 0.5 °C for tench, Wedekind et al., 2003; and 24.0 ± 0.5 °C for Mexican cavefish, Borowsky, 2008). LED strips (SOLBRIGHT®, LED Flex Strip 1043-W, Rayte, S.L., Murcia, Spain) provided light, with a photoperiod set at 12h light:12h dark (LD 12:12) cycle. In chronobiology, the time of light onset is defined as Zeitgeber Time 0 (ZT0), to standardize time points regardless local time (Guerra-Santos et al., 2017; Santo et al., 2020). Therefore, light onset at 09:00 h corresponds to ZT0 and light offset at 21:00 h corresponds to ZT12. To avoid synchronization to feeding time, tench were randomly fed once a day during the night phase with commercial feed (Interval function = $12 + \text{Random} * 12$; Gemma Wean, Skretting, Stavanger, Norway) and blind Mexican tetra were fed randomly once per day during either light or dark phase (Interval function = $12 + \text{Random} * 24$) with freeze-dried *Artemia salina* (Prodac International, Padova, Italy) by means of automatic feeders (model 3581, Eheim GmbH & Co. KG, Deizisau, Germany).

Juveniles of black bullhead catfish were supplied by a fish farm pond (Soc. Agr. I Persici Srl., Finale Emilia, Italy) and kept in 50 L tanks (13–14 fish/tank) at the University of Ferrara facility for two months preceding the experiment. The dechlorinated fresh water was constantly filtrated and oxygenated using mechanical filters and air pumps. Animals were kept under controlled lighting and temperature conditions, resembling those found in the original farm pond (22.0 ± 0.5 °C; Quigley, 2021). The natural photoperiod of 14h light:10h dark (LD 14:10; ZT0 = 06:00 h; ZT14 = 20:00 h) was provided by means of LED strips (TMR, Elcart, Milano, Italy) placed above each tank. To avoid synchronization to feeding time, catfish were randomly fed once per day during the night phase with a commercial feed (Interval function = $14 + \text{Random} * 10$; Caviar, BernAqua NV, Olen, Belgium) by means of automatic feeders (Eheim GmbH & Co. KG, model 3581, Deizisau, Germany).

Somalian cavefish were originally collected around the locality of

Bud-Bud ($04^{\circ}11'19''\text{N}$ – $46^{\circ}28'27''\text{E}$, central Somalia) during several expeditions (1972–1982) and then breed and kept in the laboratory using standard methods (Cavallari et al., 2011). This colony was established from more than 300 original specimens and currently consists of mainly F0, F1 and F2 generation fish which are expected to represent the original population in terms of genetic variation. *P. andruzzii* adults (F2) born in 2012 from the colony maintained at the University of Ferrara facility, were used for the present study. Cavefish of both sexes were kept in 160 L tanks dechlorinated fresh water constantly filtered and oxygenated by means of mechanical, biological filter, aerators and at constant temperature of 28.0 ± 1.0 °C (Di Rosa et al., 2024). They were maintained in total darkness and fed twice per week with frozen *Chironomidae* larvae (Amtra Pro Nature, Germany).

2.3. Experimental set up and protocol

Daily thermal preference of the species of interest was assessed by means of a 108 L custom-multichambered glass tank ($180 \times 30 \times 20$ cm) built in triplicate, in which fish can move freely through a hole placed in the centre of black PVC panels separating the chambers and where a stable horizontal thermal gradient can be created and maintained (Fig. 1A). The aforementioned system has already been described and validated in previous studies (Boltana et al., 2013; Rey et al., 2015; Vera et al., 2023; de Alba et al., 2024; Conti et al., 2025b). The sample size was chosen according to the UE recommendations to guarantee animal welfare (2010/63/UE), establishing a maximum density of 1 fish/L. In the present study fish density in each chamber was kept below this threshold (a maximum of 12 fish in 18 L), to avoid overcrowding and negative effects on fish behaviour. Specifically, we used three independent groups of each species: tench ($n = 12/\text{group}$; 6.29 ± 0.69 g), black bullhead catfish ($n = 8/\text{group}$; 6.57 ± 0.36 g), Mexican blind cavefish ($n = 10/\text{group}$; 0.71 ± 0.16 g) and Somalian cavefish ($n =$

8/group; 2.67 ± 0.64 g; sex ratio 50:50). A continuous thermal gradient was designed and created using heaters and coolers, controlled by temperature probes, according to the physiology and ecology of these species (from 18 °C to 26 °C for tench and black bullhead catfish, from 20 °C to 28 °C for blind Mexican cavefish and from 24 °C to 32 °C for Somalian cavefish; Fig. 1B; Ercolini et al., 1982; Smale and Rabeni, 1995; Tabin et al., 2018; Avlijaš et al., 2022). Precisely, the temperature of the central chamber of the tank corresponds to the housing temperature. In addition, water quality parameters (percentage (%) and concentration (mg/L) of dissolved oxygen (DO) and conductivity ($\mu\text{S}/\text{cm}$): ProSolo Optical DO Meter, YSI Xylem Inc, Ohio, USA; NO_2^- and NO_3^- concentrations (mg/L): HI98192, Hanna Instruments, Villafranca Padovana, Italy) were monitored during the experiments to maintain the same water quality as during housing and ensure the health of the fish.

To evaluate daily and circadian thermal preference, fish behaviour was long-term videorecorded for approximately one full month (28 days). During this experimental time, the animals were kept in LD cycle for 11 days (light intensity on the water surface of 0.84 W·m⁻²; LD 12:12 for tench, blind Mexican cavefish and Somalian cavefish, Fig. 1Ci; and LD 14:10 for black bullhead catfish, Fig. 1Cii) to determine the daily rhythms of thermal preference. This cycle was subsequently reversed (DL cycle; Fig. 1C) for another 10 days to assess the resynchronizing effect of light on the rhythm of thermal selection. Finally, to evaluate the endogenous nature of this behavioural rhythm, fish were kept in constant darkness (DD; Fig. 1C) for the last 7 days. The photoperiod was provided and controlled by LED strips placed 15 cm above each tank and connected to electronic timers. In the case of Somalian cavefish, only one LED above each chamber was used, to lower light intensity as this species previously have showed a photophobic response (light intensity on the water surface of 0.01 W·m⁻²; Ercolini and Berti, 1975; Tartelin et al., 2012). During the LD and DL cycle phases (21 days) food was randomly administrated (using interval functions for every species already described in Animals housing 2.1 section) to avoid feeding entrainment (Boujard and Leatherland, 1992) and was provided using automatic feeders, placed above each chamber, at a daily feeding rate of 2 % of the total biomass using the different rearing diets. In addition, during the DD phase, fish were fasted to remove any possible synchronising stimulus of the clock (Menaker et al., 1997; Herrero et al., 2003).

At the start of the trials, three independent replicated groups for each investigated species were placed in the central chamber of each gradient tank and immediately videorecorded.

2.4. Video recording and video analysis

Video recordings were carried out using a webcam (Logitech Webcam C300–1.3 MP, Switzerland) at the University of Murcia and three different camera modules connected each to a Raspberry Pi (Raspberry Pi 4 model B, Raspberry Pi, UK) at the University of Ferrara. Video recording was performed by Multiviewer software (Computer System Department, University of Murcia, Spain; Vera et al., 2023; de Alba et al., 2024) at the University of Murcia and a custom written Python script (Conti et al., 2025b) at the University of Ferrara. All the videos were recorded at one frame per second. To allow video recording in the dark, infrared LED lamps ($\lambda = 938\text{--}942$ nm) were placed on the back of each multi-chamber tank (de Alba et al., 2024; Conti et al., 2025b). To disperse infrared light and to achieve a good image quality at night, a translucent acrylic white sheet (Falken Design WT2447-1-8/2436 Acrylic White Sheet, Translucent 55 %; de Alba et al., 2024; Conti et al., 2025b) was installed on the back wall of the tanks.

All the behavioural video recordings performed at the University of Murcia were automatically analysed with the Fish Counter software (Dr. Ginés García Mateos, University of Murcia, Spain, Version 3.0; Vera et al., 2023; de Alba et al., 2024) that counts the number of fish per chamber in the experimental tank every minute. All the videos collected at the University of Ferrara were automatically analysed by using the EthoVision XT tracking software (Noldus, The Netherlands) obtaining

the cumulative time spent by fish in each chamber of the experimental tanks (Conti et al., 2025b). All video tracking analyses were performed by a single user and the inter-rater reliability of the score was assessed by manually counting the number of fish per chamber, from a subsample of randomly chosen video (14 days overall calculated from 3551 frame), by a second blind experimenter. The reliability test showed a strong correlation between the manual count and the output from the tracking software (96.73 % concordance, Pearson's product-moment correlation $t_{93} = 36.794$, $p < 0.001$).

For black bullhead catfish, the average distance moved was also calculated.

2.5. Statistical analysis

The mean temperature chosen at each time of the day (ZT) for experimental replicates was calculated using a formula described below and previously published for data collected using Fish Counter software (de Alba et al., 2024).

$$\text{Preferred temperature} = \frac{(n_1T_1 + n_2T_2 + n_3T_3 + n_4T_4 + n_5T_5)}{N}$$

Where N is the total number of fish, n_x is the number of fish per chamber and T_x is the temperature of the corresponding chamber.

$$\text{Preferred temperature} = \frac{(ts_1T_1 + ts_2T_2 + ts_3T_3 + ts_4T_4 + ts_5T_5)}{TS}$$

For data collected using Ethovision XT, we applied the same formula using the cumulative time spent by fish in each chamber (ts_x) and total cumulative time spent by fish (TS).

We excluded the first day in the experimental tanks (day 0) from the analysis due to fish acclimation to the new tank.

The rhythm parameters (mesor, amplitude, acrophase and significance) for thermal preference were determined by Cosinor analysis, a least squares regression-based model fitted with cosine function to ascertain the presence of daily changes in thermal preference: $Y = M + A * [\text{Cos}(\Omega t + \Phi)]$, where M is mesor, A is amplitude, Ω is angular frequency ($360^\circ/24$ h for the circadian rhythms) and Φ is acrophase (Marler et al., 2006; Cornelissen, 2014). The chronobiology software "El Temps" (v.1.313, Prof. Díez Noguera, University of Barcelona, Spain) was used to determine the period length (τ , tau) of the circadian rhythm in the absence of environmental synchronizers (DD and fasting) by a Lomb-Scargle (LS) periodogram analysis and to plot thermograms with data obtained from all three experimental replicates pooled together and showing mean for preferred temperature for each species. To study the effect of ZT on thermal preference, we used a linear mixed-effects model (LMER, 'lmer' function of the 'lmer4' R package; Bates et al., 2015) fitted with ZT as numerical covariate, and Day and group identifier as random factor to account for repeated measure structure of data. This analysis was performed using RStudio software (version 2022.02.3 Build 492; Team RStudio, 2019). The linear mixed-effects models provided a robust tool for estimating model parameters of interests to violations of assumptions (Schielzeth et al., 2020). After visual inspection, the inclusion of random factors (i.e., day and group identifier) improved the Gaussian-shape distribution of model's residuals. Differences in the average temperature preferences expressed by species between the LD and DL cycles were assessed using a similar LMER approached by fitting a model with the "photoregime" as fixed factors, and "group identifier" as random factor. We performed this analysis separated for light phase and night phase. The inclusion of "day" as random factor did not improve the quality of residuals, thus we did not include this term in the model. All statistical tests had significant threshold at $p < 0.05$. Data are shown as mean \pm SEM and graphically represented using ggplot2 R library (Wickham, 2016).

In addition, to confirm and characterize from a chronobiological point of view the nocturnal activity pattern in the black bullhead catfish

Table 1

Cosinor parameters of daily thermal preference rhythms of all the species assessed under different photoregimes. Table shows thermal preference numeric values of mesor, amplitude, acrophase, with respective confidence intervals, and significance of the rhythms (p-value) calculated via the cosinor analysis. Acrophase is given as Zeigeber time (ZT). Asterisks indicate statistically significant rhythms: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and non-significant rhythms are indicated as n.s.

Species	Photoregimes	Mesor	Amplitude	Achrophase (ZT)	Significance (p-value)
<i>Tinca tinca</i>	LD 12:12	23.78 ± 0.06	0.80 ± 0.12	5.47 ± 0.55	***
	DL 12:12	23.47 ± 0.06	0.43 ± 0.10	4.45 ± 0.85	***
	DD	23.27 ± 0.05	0.18 ± 0.10	5.22 ± 2.16	***
<i>Ameiurus melas</i>	LD 14:10	24.65 ± 0.09	0.55 ± 0.16	7.20 ± 1.13	***
	DL 10:14	24.98 ± 0.22	0.88 ± 0.39	6.25 ± 1.85	***
	DD	24.27 ± 0.07	0.32 ± 0.12	4.39 ± 1.64	***
<i>Astyanax mexicanus</i>	LD 12:12	23.96 ± 0.03	0.18 ± 0.05	5.12 ± 1.17	***
	DL 12:12	24.22 ± 0.04	0.36 ± 0.08	5.33 ± 0.90	***
	DD	–	–	–	n.s.
<i>Phreatichthys andruzzii</i>	LD 12:12	30.38 ± 0.05	0.38 ± 0.10	4.55 ± 1.18	***
	DL 12:12	30.16 ± 0.05	0.15 ± 0.08	4.19 ± 2.31	***
	DD	–	–	–	n.s.

throughout the experiment, double-plot actogram, mean waveforms and LS periodogram analysis were performed (El Temps software).

3. Results

Activity records (average distanced covered per fish) of black bullhead catfish revealed a rhythmic nocturnal activity pattern during LD (65.36 ± 21.54 % of the daily activity displayed during the dark phase) as well as DL (71.58 ± 19.35 % of activity during nighttime) cycles, as it is shown in the relative actogram and mean waveform graphs (Fig. 1S A–C). Furthermore, under DD condition, they exhibited a free-running activity with a period close to 24 h ($\tau = 23.8 \pm 0.2$ h), as evidenced in the LS periodogram analysis (Fig. 1S D). Activity records of the other three species have been previously reported elsewhere (tench: Herrero et al., 2003; Somalian cavefish: Cavallari et al., 2011; blind Mexican cavefish: Simon et al., 2019).

During the first 10 days under LD conditions, all species display significant daily rhythms of thermal preference (Tables 1 and 1S). Specifically, the nocturnal tench and black bullhead catfish significantly and rhythmically select higher temperatures during the day and lower temperatures at night with diurnal acrophases for both tench (ZT5.47, LMER: $F_{1,707} = 306.240$ $p < 0.001$, Cosinor $p < 0.001$, Fig. 2A and 3A, Fig. 2S A and 3S A, Table 1) and black bullhead catfish (ZT7.20, LMER: $F_{1,610} = 79.731$ $p < 0.001$, Cosinor $p < 0.001$, Fig. 2B and 3D, Fig. 2S B and 3S D, Table 1). Both blind cavefish species investigated, display a significant preference for warmer temperatures during the day and cooler temperatures at night with diurnal acrophases (Table 1; blind Mexican cavefish: ZT5.12, LMER: $F_{1,707} = 93.687$ $p < 0.001$, Cosinor $p < 0.001$, Fig. 2C and 3G, Fig. 2S C and 3S G; Somalian cavefish: ZT4.55, LMER: $F_{1,635} = 70.430$ $p < 0.001$, Cosinor $p < 0.001$, Fig. 2D and 3J, Fig. 2S D and 3S J).

When the LD cycle was reversed (DL condition), all fish species keep displaying significant daily thermal preferences exhibiting the previously described patterns (Tables 1 and 1S; tench: diurnal acrophase at ZT4.45, LMER: $F_{1,707} = 121.200$ $p < 0.001$, Cosinor $p < 0.001$, Fig. 2A and 3B, Fig. 2S A and 3S B; black bullhead catfish: diurnal acrophase at ZT6.25, LMER: $F_{1,650} = 378.21$ $p < 0.001$, Cosinor $p < 0.001$, Fig. 2B and 3E, Fig. 2S B and 3S E; blind Mexican tetra: diurnal acrophase at ZT5.33, LMER: $F_{1,707} = 168.090$ $p < 0.001$, Cosinor $p < 0.001$, Fig. 2C and 3H, Fig. 2S C and 3S H; Somalian cavefish: diurnal acrophase at ZT4.19, LMER: $F_{1,557} = 14.228$ $p < 0.001$, Cosinor $p < 0.001$, Fig. 2D and 3K, Fig. 2S D and 3S K) confirming the behavioural entrainment to the new DL cycle. When comparing the observed behaviour between the LD and DL cycles within species, we observed a general significative alteration of the average preferred temperature during light phase (tench: $F_{1,56} = 15.480$ $p < 0.001$; black bullhead catfish: $F_{1,56} = 17.231$ $p < 0.001$; blind Mexican tetra: $F_{1,46} = 10.050$ $p = 0.002$ and Somalian cavefish: $F_{1,51} = 14.328$ $p < 0.001$) but no significative differences emerged during the dark phase (tench: $F_{1,56} = 0.254$ $p = 0.616$; black

bullhead catfish: $F_{1,53} = 1.179$ $p = 0.282$; blind Mexican tetra: $F_{1,56} = 2.927$ $p = 0.093$; Somalian cavefish: $F_{1,52} = 0.303$ $p = 0.366$).

During the last 7 days in constant conditions (DD and fasting), both tench and black bullhead catfish kept displaying significant daily rhythms of thermal preference (Table 1; tench: diurnal acrophase at ZT5.22, LMER: $F_{1,494} = 19.387$ $p < 0.001$, Cosinor $p < 0.001$, Fig. 2A and 3C, Fig. 2S A and 3S C; black bullhead catfish: diurnal acrophase at ZT4.39, LMER: $F_{1,458} = 49.353$ $p < 0.001$, Cosinor $p < 0.001$, Fig. 2B and 3F, Fig. 2S B and 3S F). Moreover, the circadian nature of these behavioural rhythms was confirmed by the LS periodogram analysis (tench: $\tau = 22.8 \pm 0.9$ h in Fig. 2E; black bullhead catfish: $\tau = 24.0 \pm 0.1$ h in Fig. 2F). On the contrary, both cavefish species became arrhythmic under these constant conditions (Table 1; Fig. 2G–H and 3I, L; Fig. 3S I, L), pointing out that both species lost their light entrainment observed in the previous LD and DL phases.

4. Discussion

Our findings showed that all fish species tested exhibited daily rhythms of thermal preference when kept in LD cycle, selecting warmer temperatures during the day and cooler at night regardless their pattern of behaviour. This diurnal thermal preference was resumed when the light cycle was reversed (DL). In the nocturnal species assessed, the behavioural rhythm persisted under constant lighting conditions (DD) as well, indicating its endogenous circadian control. This finding may be surprising because fish being ectotherms, their body temperature strongly depends on water temperature, and it affects their performances. Indeed, many behavioural and physiological processes rely on ectotherm's body temperature, directly impacting their fitness and consequent survival (Angilletta Jr et al., 2002; Payne et al., 2016). In fact, many ectotherms have a narrow thermal window where reproduction and reproductive traits perform at their optimum, defined in recent times as thermal fertility limits (Iossa, 2019; Massey et al., 2022; Chatten et al., 2025). Nevertheless, these nocturnal fish preferred higher temperatures during the day, not at night when they are active and feed. This could point to an evolutionary adaptation of fish to the natural thermocycle of the environment that allows biological rhythms to be synchronised enabling metabolic processes, hormone release and enzyme production to occur at the appropriate time of day, in order to anticipate and adjust to the phase of activity or rest, regardless of whether the species is diurnal or nocturnal. Thus, considering also previous studies on diurnal fish (Vera et al., 2023; De Alba et al., 2024), our results suggest a primary circadian influence on temperature selection, which evolved in synchrony to the highly dependable environmental cycle of light/temperature (warming up after sunrise and cooling down after sunset).

Light-dark cycles are the most powerful environmental signal able to entrain circadian clocks, playing a key role synchronising most biological rhythms such as locomotor and feeding activity (Zhdanova and

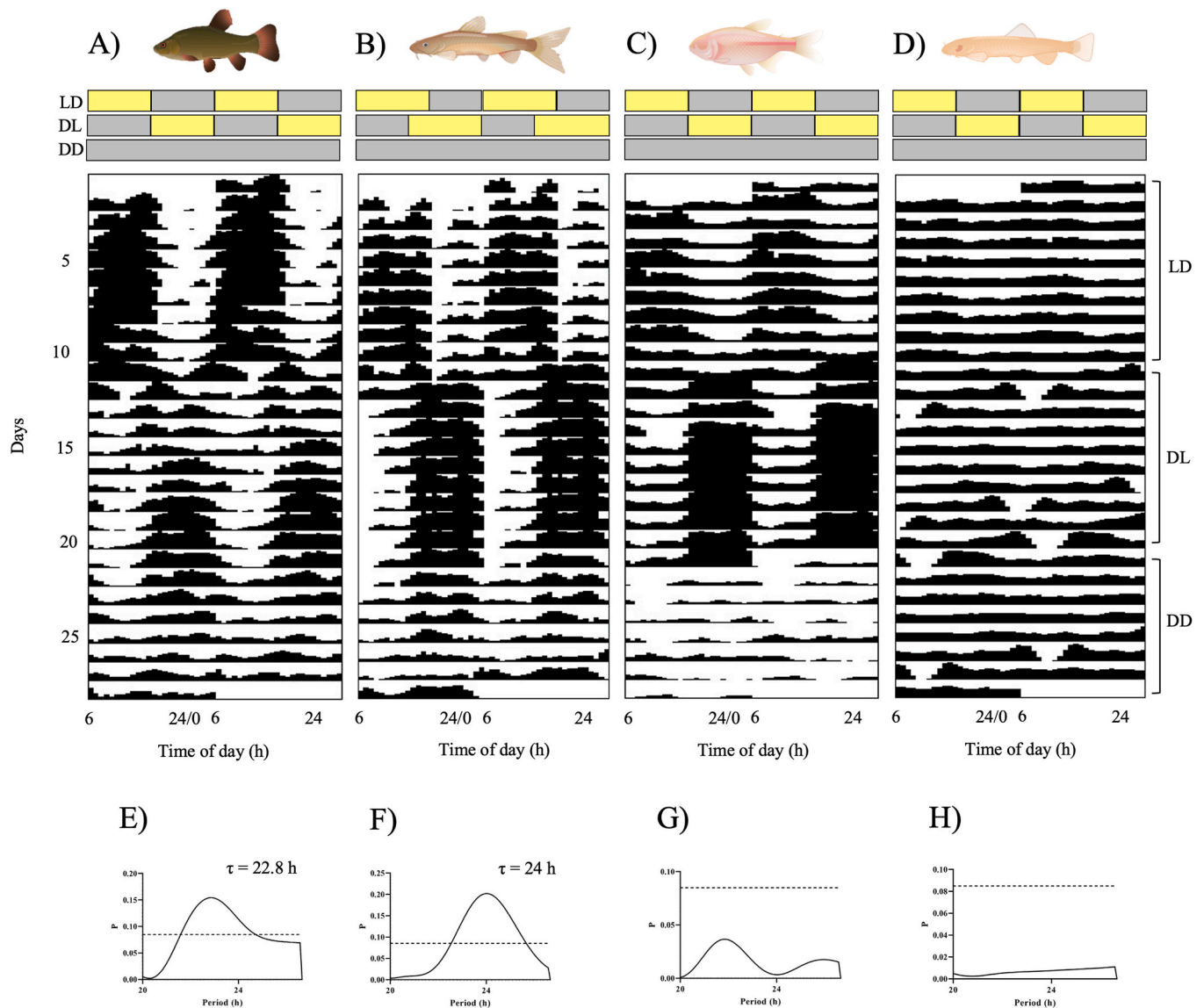
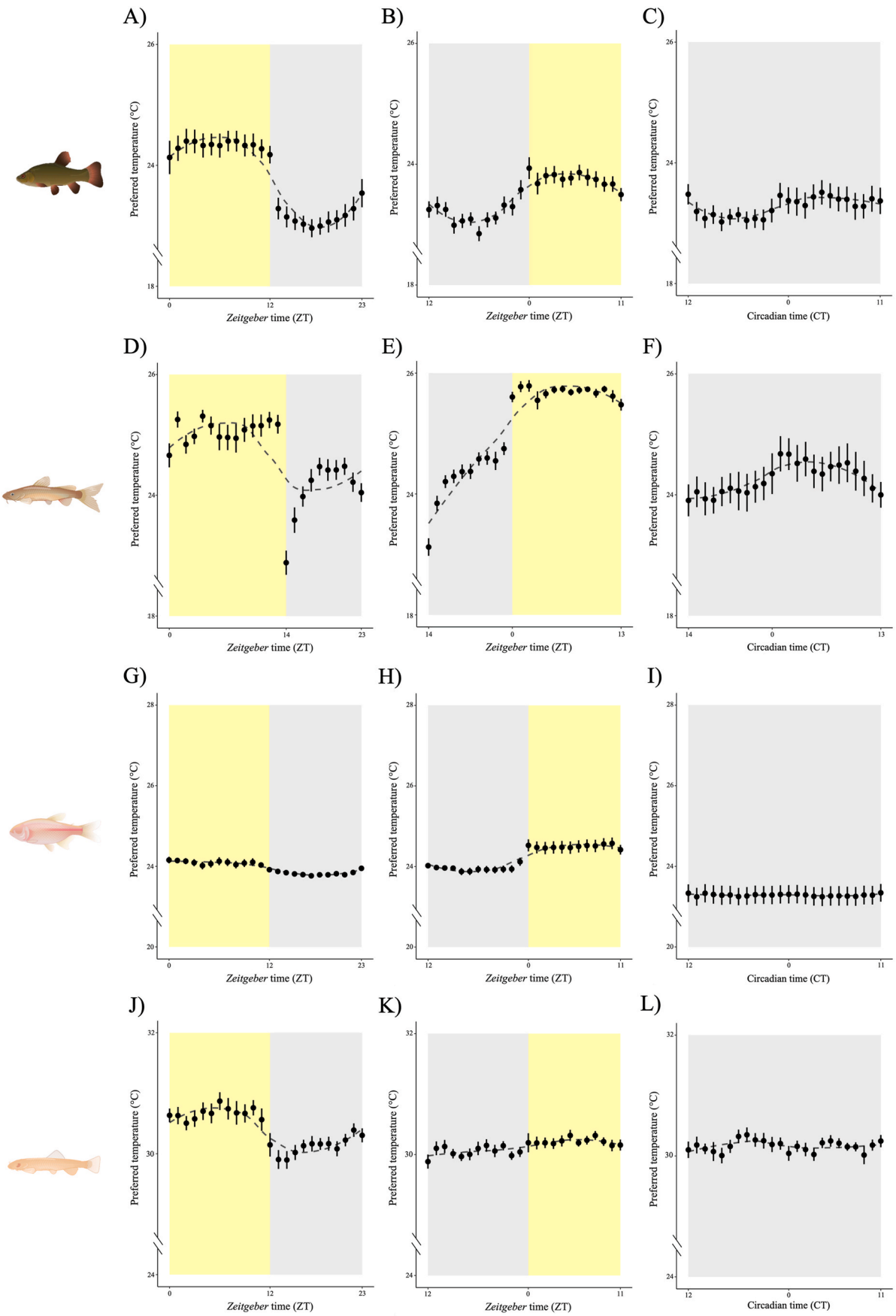


Fig. 2. Representative thermograms of daily preferred temperature rhythms of the investigated species kept in temperature gradient for 27 days and subjected to different photoregimes: light-dark (LD) cycle; reversed LD cycle (DL) and constant darkness (DD). Data from all three independent experimental replicates were pooled together and are shown as mean temperature ($^{\circ}\text{C}$) for preferred temperature for each species: **A)** tench *Tinca tinca* ($n = 12$ fish/group); **B)** black bullhead catfish *Ameiurus melas* ($n = 8$ fish/group); **C)** blind Mexican tetra *Astyanax mexicanus* ($n = 10$ fish/group); **D)** Somalian blind cavefish *Phreatichthys andruzzii* ($n = 8$ fish/group). Thermograms were double plotted (48 h). Specifically, the y-axis progresses in single days, indicated on the left, with each day plotted twice. Mean temperature was calculated every hour, and the height of each point correlates with the preferred temperature. The bars above each thermogram represent the different photoregimes assessed; yellow bars correspond to light phases and grey bars to dark phases. The time scale of x-axis is expressed as time of the day (hours). On the right side the different photoregimes and their duration are indicated. Lomb-Scargle (LS) periodogram analysis (95 % confidence level) for each species tested corresponding to DD phase are also shown: **E)** tench; **F)** black bullhead catfish; **G)** blind Mexican cavefish; **H)** Somalian blind cavefish. If present, significant length of the period (τ , tau) is written at the top of graphs.

Reebs, 2005; López-Olmeda and Sánchez-Vázquez, 2010), reproduction (Oliveira and Sánchez-Vázquez, 2010; Cowan et al., 2017), hatching and development (Villamizar et al., 2013). Our results on thermal preferences agree with previous ones (Reynolds et al., 1978a, 1978b; Vera et al., 2023; de Alba et al., 2024), as we found that the daily temperature selection is closely linked to LD cycles. In fact, daily temperature fluctuations occur in nature and all the species analysed displayed rhythms of thermoregulatory behaviours with diurnal acrophases (tench: ZT5.47; black bullhead catfish: ZT7.20; blind Mexican cavefish: ZT5.12 and Somalian cavefish: ZT4.55). Recent studies focused on diurnal fish species (Vera et al., 2023; de Alba et al., 2024), while investigations on nocturnal fish and their thermal preferences are limited (Schram et al., 2013; Wilby et al., 2014; Nay et al., 2015; Avlijaš et al., 2022) due to

several challenges including technological and logistical issues. Literature and the present study show that both tench and black bullhead catfish are active during the night, when they feed, reducing competition and the risk of predation. Our results show that both species, kept in LD cycle, displayed significant daily rhythms of thermal selection preferring lower water temperatures at night-time, reflecting their natural ecology and behaviour. Indeed, both these fish, in the wild, inhabit still and turbid water environments rich in vegetation (Perrow et al., 1996; Preisner et al., 2024), where oxygen levels may be lower during the day. At night, in colder waters, dissolved oxygen increases, improving respiration and physiological performances (Sollid and Nilsson, 2006; Jain et al., 2013; McBryan et al., 2013). Moreover, cooler temperature preferences may reflect their foraging behaviour as their



(caption on next page)

Fig. 3. Preferred temperature of the different species investigated exposed to a horizontal thermal gradient for 27 days and different photoregimes: light-dark (LD) cycle, reversed LD cycle (DL) and constant darkness (DD); respectively in tench *Tinca tinca* (A, B, C), black bullhead catfish *Ameiurus melas* (D, E, F), blind Mexican cavefish *Astyanax mexicanus* (G, H, I) and Somalian cavefish *Phreatichthys andruzzii* (J, K, L). Data from all three independent experimental replicates (tench: n = 12 fish/group; black bullhead catfish: n = 8 fish/group; blind Mexican tetra: n = 10 fish/group; Somalian cavefish: n = 8 fish/group) were pooled together and are shown as mean temperature (°C) ± SEM for preferred temperature. The dashed line represents the adjustment to sinusoidal rhythm (Cosinor, $p < 0.05$) using smoothed conditional means (function argument 'loess' in the 'geom_smooth' function). The yellow and grey areas indicate the light and dark phases, respectively. The time scale (x-axis) is expressed as Zeitgeber Time (ZT), in which ZT0 corresponds to lights on and ZT12/14 corresponds to lights off.

natural prey move to colder waters during the night (Annese and Kingsford, 2005). However, food availability cycles do not seem to be the major drive for temperature selection (e.g., to maximize metabolism), since our results in nocturnal and blind fish did not support this theory. Indeed, when food is delivered to tilapia at different times (mid-light, mid-dark or random), despite some masking effects, fish do not change their basic daily rhythm of temperature selection (de Alba et al., 2024).

Regarding the cavefish species tested, our results show that both exhibited significant daily rhythms of thermal preference, although with smaller amplitudes compared to the nocturnal species (Tables 1 and 1S). Specifically, they displayed a daily rhythm of selection with diurnal acrophases: higher temperatures during the daytime and lower ones during the night. Thus, blind cavefish can still show preference for temperature changes if they are given the opportunity to thermoregulate when kept in LD cycle, despite their evolutionary history. In fact, groundwater is insulated from many cyclical natural events so that water temperature is very stable throughout the year (fluctuations of less than 1 °C in a year), as a previous study carried out in the Subterranean cave (Mexico) showed (Tabin et al., 2018). However, the same study highlighted how blind Mexican cave populations still retain a thermal preference, despite the absence of an obvious need for it (Tabin et al., 2018). Though, in the wild, both cavefish species investigated can be sensitive to even the slightest change in water temperature, due to the alternation between the dry and rainy seasons, which is important for spawning activity and subsequent reproduction (Ercolini et al., 1982; Espinasa et al., 2023). However, we could also speculate that, regarding Somalian cavefish findings, the observed daily rhythm of thermal preference in LD and DL cycles could be explained as a masking phenomenon associated with the photophobic response already described in this species (Tarttelin et al., 2012; Friedrich, 2013).

When the photoperiod is reversed (DL), all species continue to exhibit daily thermal preference patterns, selecting warmer temperatures during the day and cooler ones at night. However, we observed significant differences in preferred temperatures during the light phase between LD and DL conditions in all the species assessed. We could hypothesise that inverting the light-dark cycle may alter fish physiology, as it is something that they never experience in the wild. Moreover, it should be noted that during the first few days a gradual resynchronization of the rhythms, as can be seen in Fig. 2 and 2S, would be expected affecting the average thermal preference results. Thus, it is possible that if the DL condition had lasted longer than 10 days, fish would have shown the same average temperature preference as in the LD light phase. The resynchronization of the thermal preference patterns observed after the inversion of the light-dark cycle (from LD to DL) in all fish species tested could suggest a passive behavioural response to light. However, when all the Zeitgeber were removed and fish were kept in constant conditions (DD and fasting), the rhythmicities were found with free running periodicities within the circadian range ($\tau = 22.8 \pm 0.9$ h and 24.0 ± 0.1 h in tench and black bullhead catfish, respectively). The persistence of the behavioural thermoregulation rhythms for 7 days would indicate and confirm that thermal preference rhythms in both nocturnal species tested, are endogenously driven by the circadian clock. In contrast, in the cavefish species we did not find any significant circadian rhythm of thermal preference as both became arrhythmic in DD. As this species have evolved underground in constant conditions, they may have retained a weak circadian clock or lost circadian regulation (Mack et al., 2021). Previous studies in the Somalian cavefish

revealed a significant food-entrainable rhythm, which could be potentially susceptible to temperature changes (Cavallari et al., 2011; Di Rosa et al., 2024). Our research pointed out the absence of endogenous and clock-driven thermal selection rhythm; meaning that for this species the most important environmental signal could be food availability. Blind Mexican cavefish, in laboratory conditions, is already proved to retain an endogenous clock that is light- and food-entrainable (Beale et al., 2013; Di Rosa et al., 2024; Conti et al., 2025a). Our study verified that the daily significant rhythm of thermal preference in blind Mexican cavefish species, observed here, could be totally driven by the photic stimulus and not endogenously controlled. However, one of the limitations of this study was the unknown origin of the Mexican blind cavefish specimens, because the natural populations evolved independently and might exhibit distinct behavioural and physiological patterns (Beale et al., 2013; Kowalko, 2020).

In summary, these results have deepened our understanding of fish thermal biology with different daily activity patterns and different evolutionary backgrounds by shedding light on the master role of the circadian clock and environmental cycles in temperature selection. Moreover, these results can be used to improve husbandry protocols in fish captivity conditions in order to allow them to exploit their behavioural thermoregulation.

5. Conclusions

In our study we verified the existence of daily rhythms of thermal preference for all the tested species, nocturnal and blind ones. Specifically, when kept in LD cycle all fish showed significant daily rhythms of temperature selection, preferring warmer temperatures during the day and lower ones during the night similarly to previously observed in diurnal fish. When the LD cycle was reversed (DL) all the species resumed their significant daily pattern of temperature selection. Under aperiodic conditions (DD and fasting), nocturnal species kept displaying daily rhythm of thermal preference with circadian-periodicity, pointing out its endogenous and circadian clock-controlled nature. This research highlights the importance of behavioural thermoregulation in fish, and the conservation of a diurnal daily rhythm regardless fish behavioural patterns.

CRedit authorship contribution statement

F. Conti: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **E. Gatto:** Writing – review & editing, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **G. de Alba:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **S. Pintos:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **J.F. López-Olmeda:** Methodology, Funding acquisition, Conceptualization. **L.M. Vera:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **S. Rey Planellas:** Writing – review & editing. **S.A. Mackenzie:** Writing – review & editing. **C. Bertolucci:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **F.J. Sánchez-Vázquez:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization.

Funding statement

This research was supported by the European Union's Horizon 2020 research and innovation programme under Marie Skłodowska-Curie grant No 956129 "EasyTRAIN" to F.C., F.J.SV., and C.B.; by research contract co-financing by European Union—PON Ricerca e Innovazione 2014–2020 ai sensi dell'art. 24, comma 3, lett. a, della Legge 30 dicembre 2010, n. 240 e s.m.i. e del D.M. 10 agosto 2021 n. 1062 to E.G. Research was also funded by projects "BBLUE-AQUA" and "CHRONOLIPOFISH" (RTI2018-100678-A-I00), granted by the Spanish Ministry of Science and Innovation (PID2021-123640OB-C21 and RTI2018-100678-A-I00) and FEDER Funds to F.J.SV., L.M.V. and J.F.LO.

Declaration of competing interest

The authors declare no competing or financial interests

Acknowledgements

We are grateful to Andrea Margutti for building the experimental tanks in Ferrara and to all the students, from both University of Murcia and Ferrara, who worked on the video analysis. Parts of figures 1, 2, 3 and 1S, 2S, 3S were created with [Biorender.com](https://biorender.com).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2025.104339>.

Data availability

Datasets are available as supplementary materials

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