Circadian rhythm of preferred temperature in fish: Behavioural thermoregulation linked to daily photocycles in zebrafish and Nile tilapia

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ABSTRACT

Ectothermic vertebrates, *e.g.* fish, maintain their body temperature within a specific physiological range mainly through behavioural thermoregulation. Here, we characterise the presence of daily rhythms of thermal preference in two phylogenetically distant and well-studied fish species: the zebrafish (*Danio rerio*), an experimental model, and the Nile tilapia (*Oreochromis niloticus*), an aquaculture species. We created a non-continuous temperature gradient using multichambered tanks according to the natural environmental range for each species. Each species was allowed to freely choose their preferred temperature during the 24h cycle over a long-term period. Both species displayed strikingly consistent temporal daily rhythms of thermal preference with higher temperatures being selected during the second half of the light phase and lower temperatures at the end of the dark phase, with mean acrophases at Zeitgeber Time (ZT) 5.37 h (zebrafish) and ZT 12.5 h (tilapia). Interestingly, when moved to the experimental tank, only tilapia displayed consistent preference for higher temperatures and took longer time to establish the thermal rhythms. Our findings highlight the importance of integrating both light-driven daily rhythm and thermal choice to refine our understanding of fish biology and improve the management and welfare of the diversity of fish species used in research and food production.

1. Introduction

Both light and temperature are considered the main abiotic factors influencing ectotherms' behaviour, physiology, and habitat distribution (Brett, 1971). Thermoregulation through behaviour is the most important mechanism to keep body temperature within a physiological range in ectotherms (Crawshaw, 1979; Hutchison and Maness, 1979; Angilletta et al., 2002; Gordon, 2005; Haesemeyer 2020), that determines their preferred temperature in a thermal gradient. When initially placed in a wide thermal gradient, the acute thermal preference is strongly influenced by previous thermal acclimation but after some time they move to a preferred temperature known as the final thermal preferendum (Reynolds and Casterlin, 1979; Johnson and Kelsch, 1998; Fangue et al., 2006). This final preferendum is species-specific and displays little variation even in fish species with a broad geographic distribution (Beitinger and Fitzpatrick, 1979). In addition to the acclimation temperature, the preferred temperature is also influenced by various factors

such as the season of the year (Sauter et al., 2001; Mortensen et al., 2007), feeding and nutritional state (Wallman and Bennett, 2006), developmental state (McCauley and Huggins, 1979; Morita et al., 2010; Nivelle et al., 2019), health status (Golovanov, 2006; Boltana et al., 2013; Rakus et al., 2017), and stress levels (Rey et al., 2015a).

The circadian system has evolved as an internal timekeeper mechanism that synchronizes biological processes with environmental cycles, allowing the organisms to predict and anticipate events, thereby adjusting their behaviour and physiology according to the time of the day (Wilkins, 1960; Ding et al., 1994; Villamizar et al., 2013). In all vertebrates the molecular mechanism controlling circadian rhythmicity involves interlocked transcriptional-translational feedback loops of circadian clock genes and proteins (Vatine et al., 2011) which is ultimately entrained by external cues that show daily cycles, also called zeitgebers (ZT; Zeitgeber Time), such as photoperiod (Panda et al., 2002), thermal cycles (Rensing and Ruoff, 2002) or food availability (Mistlberger, 2009). Among these, the light-dark (LD) cycle is

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considered the main zeitgeber, synchronizing many functions in living organisms (DeCoursey, 2014; Metcalfe et al., 1999). However, in nature, there is a direct relationship between the light-dark cycles and the daily variations in temperature: temperature peaks during the day, whereas the lowest temperatures are registered at night. In this way, organisms can synchronize their biological rhythms with the time of day with the best thermal conditions that guarantee the optimal performance of their physiological processes (Angilletta et al., 2002).

Increasing temperatures due to climate change are impacting the aquatic ecosystems, affecting the organisms' ecophysiology. Recently, predictive models have revealed that fish inhabiting tropical regions might be particularly affected by global warming, potentially limiting the performance of these species (Hasting et al., 2020; Lavender et al., 2021). Zebrafish (*Danio rerio*) and Nile tilapia (*Oreochromis niloticus*) are both tropical fish species that can tolerate a wide range of water temperatures, ranging from 24 to 32 °C (Cortemeglia and Beitinger, 2005; Spence et al., 2008) and 22–34 °C (Trewavas, 1983), respectively. However, in their natural habitat they might experience and survive under more extreme temperatures caused by sudden and drastic increases/decreases in temperature: between 6 and 38 °C in the case of zebrafish (Spence et al., 2008) and between 17 and 40 °C in tilapia (Bezault et al., 2007). In addition, in the wild, both species are subjected to strong daily and seasonal thermal variations caused by the geophysical cycles (Payne et al., 1996; Patterson and Wilson, 1995).

The main objective of the present research was to characterise in detail the daily rhythm of thermal preference for zebrafish and Nile tilapia. To this end, we used a thermal gradient tank model similar to that used in previous thermal preference experiments (Boltana et al. 2013, 2013b). For this, fish were kept under a 12 h L: 12 h D photoperiod and allowed to freely choose between a wide range of water temperatures, in line with those found in their natural environments. Although daily and seasonal variations in preferred temperature have been studied in other ectothermic taxa (Reynolds et al., 1978a,b,c, 1979; Rismiller and Heldmaier, 1982; Hutchison and Spriestersbach, 1986), understanding how temperature preference of fish species varies during the day will provide new data about the thermal biology of ectotherms and shed light upon the evolution of thermal adaptation and its coupling to light-driven circadian rhythm in vertebrates, a theme of increasing urgency in view of biodiversity and global climate change. Additionally, our study directly impacts upon core ideas of animal welfare and improved husbandry by using two extensively exploited fish species that are critical for research (zebrafish) and global food security (tilapia). Likewise, we consider it necessary to highlight the importance of developing biological models to promote optimal animal welfare that provides increased resolution in downstream biological analyses and therefore value in research outcomes.

2. Material and methods

2.1. The use of zebrafish and Nile Tilapia as a model species

Zebrafish (*Danio rerio* Hamilton, 1822) and Nile tilapia (*Oreochormis niloticus* Linnaeus, 1758) are both tropical freshwater fish species. Zebrafish can be found in the Ganges and Brahmaputra rivers in India and in the south-eastern Himalayan region (Engeszer et al., 2007; Spence et al., 2008), Nile tilapia is native to the northern half of Africa (Patterson and Wilson, 1995). Both inhabit shallow and slow-moving waters rich in aquatic vegetation (Patterson and Wilson, 1995; McClure et al., 2006; Spence et al., 2006; Engeszer et al., 2007). Zebrafish and Nile tilapia can easily be raised and maintained in captivity, showing several features that make them interesting research model species (Choi et al., 2021). Thus, they are used in various fields of research such as: neurosciences, developmental biology, genetics, biomedicine, ecotoxicology, physiology (Vascotto et al., 1997; Fishman, 2001; Grunwald and Eisen, 2002) but also for behavioural (Engeszer et al., 2007; Moretz et al., 2007; Oliveira et al., 2011; Rey et al., 2013,

2015b; Cerqueira et al., 2016) and chronobiology studies (Dekens and Whitmore, 2008; Vatine et al., 2011). Zebrafish is the most used ectothermic vertebrate for biomedical research (Choi et al., 2021; Paredes et al., 2019). Tilapia is the second most farmed species in the world after carps and crucial for global food security across the globe (Zhang et al., 2022; FAO, 2022).

2.2. Fish breeding and holding conditions

All zebrafish (*Danio rerio*, AB wild-type strain, 0.9 ± 0.2 g mean body weight; 43.2 ± 2.2 mm total length) were bred at the Institute of Aquaculture of the University of Stirling (Scotland, UK) and raised in a ZS660 stand-alone system (Aquaneering, Inc. USA). Nile tilapia (n = 72) (*Oreochromis niloticus;* 2.3 ± 0.2g mean body weight; 48.1 ± 1.5 mm total length) juveniles (older than 40 dpf) were bred at the facilities of the University of Murcia (Spain) and kept in 300-liter separated tanks connected to a recirculation system, equipped with an aeration system and biological and mechanical filters. 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 our experiment fish density was kept below this threshold (12 fish in 18 L), to avoid overcrowding and negative effects on fish behaviour. Water rearing temperature was controlled using a water heater and a refrigerator (AB Aqua Medic, Gewerbepark, Germany) and it was established at 26 ± 0.5 °C and 30 ± 0.5 °C for zebrafish and Nile tilapia, respectively, in line with the mean temperatures that these species experience in the wild and culture conditions (Payne et al., 1996; Patterson and Wilson, 1995). Fish were fed twice daily to satiation during the holding period with a commercial diet specific for each fish species (Skretting® Gemma Micro and Skretting® Gemma Wean for zebrafish and Nile tilapia, respectively). Zebrafish diet was supplemented with Artemia (Zebrafish Management Ltd, UK). The water quality parameters (pH, ammonia, nitrate, nitrite, and dissolved oxygen) were measured daily. For both fish species, the lighting conditions were set to a 12:12 h Light: Dark (LD) cycle, with lights on at 08:00 h (Zeitgeber Time 0 h, ZT0 h) and lights off at 20:00 h (ZT12 h).

2.3. Experimental setup and procedures

2.3.1. Gradient tank

Thermal preference was assessed using a custom-built multichambered tank (Rey et al., 2015) (Fig. 1a). The 126 L tank (140 × 30 × 30 cm) was divided into seven interconnected chambers divided by six opaque PVC screens, with the two extreme lateral chambers used only for cooling and heating the water, for which a cooler, a water bath and two pumps were installed (AB Aqua Medic, Gewerbepark, Germany). Connection between chambers, allowing movement of fish and water, was enabled by a circular hole on each glass screen (10 cm diameter; 20 cm from the bottom), creating a continuous thermal gradient of 24 °C to 31 °C and 26 °C to 34 °C for zebrafish and Nile tilapia, respectively (Table A1). Water temperature was carefully monitored in different areas of the experimental tank to have an accurate register of the thermal gradient and preferred temperature of fish. For both species, the thermal gradient was designed according to the temperature ranges that fish experience in their natural habitat (Payne et al., 1996; Jindal and Thakur, 2013; Patterson and Wilson, 1995; Ndiwa et al., 2016). Access to the cooler and heater chambers was sealed using a mesh screen to prevent any intrusion of fish in them during the experiments. Mechanical filters were placed in the five central chambers and a picture of gravel substrate, used as environmental enrichment, was fitted under each chamber.

2.3.2. Environmental parameters

Water quality was monitored daily during the experiments. Oxygen (Handy Polaris l OxyGuard International, Farum, Denmark), pH (Mettler Toledo FiveEasy™ FE20, Columbus, USA), TAN and NO_2 (Palin test,
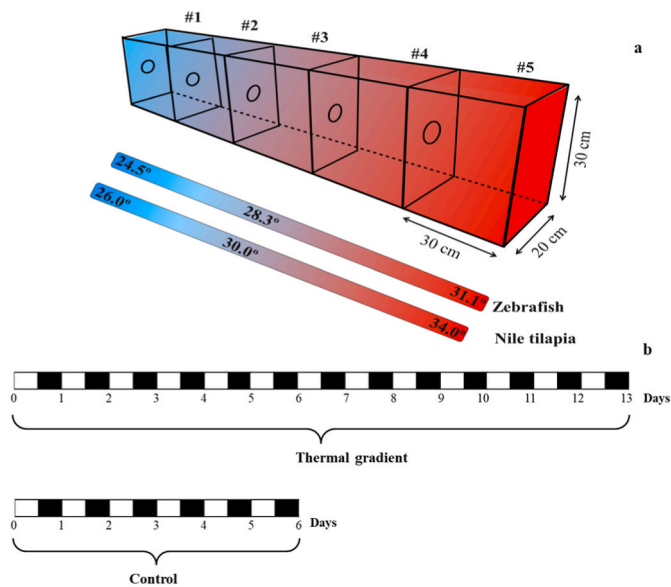
Fig. 1. Schematic representation of the multichambered temperature gradient tank (a) and experimental design (b). Fish were exposed to a temperature gradient during a 13-day period f or maintained to a constant temperature during a 6-day period (control group). .

Gateshead, UK) levels were recorded once a day in the morning before feeding. Water temperature of each chamber was recorded continuously throughout the experiment by a Thermochron iButton (Maxim integrated, Rio Robles, San Jose, CA, USA).

2.3.3. Experimental design

For each fish species, three independent groups of fish (n = 12/group) were placed in the central chamber of the gradient tank and allowed to freely distribute throughout the chambers for 13 days and their behaviour was video recorded to assess temperature preference during the whole period. In addition, to rule out that chamber preference was affected by other factors other than temperature, three additional independent fish groups (n = 12/group) were placed in the same multichambered tank but exposed to a constant water temperature during a 6-day period (control) (Fig. 1b). The water temperature of all tank compartments during control trial coincided with the rearing temperature of fish (26.3 ± 0.1 °C and 30.1 ± 0.1 °C for zebrafish and Nile tilapia, respectively). Prior to the start of each trial, fish were placed in the central chamber of the gradient tank, and recordings immediately started. All animals were fed *ad libitum* a commercial diet delivered evenly in all chambers (Skretting® Gemma Micro and Gemma Wean for zebrafish and Nile tilapia, respectively) to avoid feed chamber preference, twice a day during the duration of the experiments and the behaviour and welfare of the animals was carefully monitored, with no deaths or negative welfare indicators observed (external appearance and normal behaviour monitored). At the end of each trial, fish were returned to their stock tank and the water was completely replaced.

2.3.3.1. Video recording and data acquisition.
For each experiment, video recording started on the first day at zeitgeber time (ZT) = 0 and was restarted daily at that time throughout the 13-day experimental period. During daytime, light was provided by LED strips (SOL-BRIGHT®, LED Flex Strip 1043-W, Rayte, S.L., Murcia, Spain), with a light intensity on the water surface of 0.84 W·m-2 (~200 lx). At night, five infrared LED lamps (BW® 48 LED Infrared Illuminator) were installed behind the experimental tank to allow camera nocturnal vision. A translucent acrylic white sheet (Falken Design WT2447-1-8/2436 Acrylic White Sheet, Translucent 55%, 100 × 30 × 0.3 cm) was fitted on the back wall of the tank to diffuse the infrared light and improve the image quality at night. All experimental videos were recorded using a video camera (Logitech Webcam C300-1.3 MP, Switzerland) and the Multiviewer software (Computer System Department, University of Murcia, Spain), which stored 60 images (1 frame/s) every minute. The Multiviewer software had already been validated in zebrafish (Di Rosa et al., 2015). All video recordings were analyzed using Fish Counter software (Dr. Ginés García Mateos, University of Murcia, Spain, Version 3.0). The software creates a fixed background model (static number of frames) and compares the analysing frames with the background model to detect the fish giving a value that corresponds to the number of fish per chamber in the gradient tank every minute (block of 60 frames) and recorded into a Microsoft Excel spreadsheet.

2.4. Data analysis

To determine how temperature preference changed during the day in the thermal gradient experiment, the mean temperature selected (preferred temperature) during each hour i in each experimental replicate was calculated as:

$$\tau_i = \frac{\sum_{c=1}^{5} n_{ic} T_{ic}}{\sum_{c=1}^{5} n_{ic}}$$

where n_i is the number of fish in chamber $c = 1$–5, and T_{ic} is the temperature of the corresponding chamber.

We constructed hierarchical cosinor generalized additive models to analyse the daily rhythms of preferred temperature and the distribution of fish across chambers (Refinetti et al., 2007; Bürkner 2017; Pedersen et al., 2019). A cosinor model assumes the response follows a cosine curve each cycle, with the MESOR (midline-estimating statistic of the rhythm) serving effectively as an average, the amplitude defining the strength of the cycle, and the acrophase denoting the location of the peak in the cycle. The amplitude is thus constrained to be positive, and acrophase is measured in radians and bound between -π and π. Each response variable for each species was modelled as a smoothed multi-level function of the elapsed hours, H, since the start of the trial. The control and the experiment were each replicated across three tanks.

The preferred temperature, τ_{ij}, at hour i in tank j was modelled as:

$$\tau_{ij} \sim Norm\left(M_{ij} + A_{ij}\cos\left(\theta_i + \varphi_{ij}\right), \sigma\right)$$

$$M_{ij} = \mu + f^M(H_i) + f_j^M(H_i)$$

$$\log\left(A_{ij}\right) = \alpha + f^A(H_i) + f_j^A(H_i)$$

$$\varphi_{ij} = \Phi + f^\varphi(H_i) + f_j^\varphi(H_i)$$

where M_{ij} is the MESOR, A_{ij} is the amplitude, θ_i is the hour in radians (2π * ZT/24), φ_{ij} is the acrophase, and σ is the standard deviation of the residual error. Each cosinor parameter was modelled as a smoothed function of time with functions $f(H_i)$ as global thin plate regression splines and $f_j(H_i)$ as tank-specific splines using a factor-smoother interaction which allow for tank-level variation about the global spline, along with global intercepts μ, α, and Φ, respectively (Pedersen et al., 2019). Global preferred temperature in each hour was calculated from the joint posterior distribution by omitting the tank-level splines. As temperature was held constant within each tank for the control, only observations from the thermal gradient experiment were used in this model.

We used a similar structure to model the proportion of fish, ρ_{ijc}, at hour i in tank j in each chamber c, such that:

$$\boldsymbol{\rho}_{ij} \sim Dirichlet\left(\boldsymbol{\nu}_{ij}, \psi\right)$$

$$\nu_{ijc} = e^{\eta_{ijc}} \bigg/ \sum_{c=1}^{5} e^{\eta_{ijc}}$$

$$\eta_{ijc} = M_{ijc} + A_{ijc} \cos\left(\theta_i + \varphi_{ijc}\right)$$

$$M_{ijc} = \mu_c + f^{M_c}(H_i) + f_j^{M_c}(H_i)$$

$$\log\left(A_{ijc}\right) = \alpha_c + f^{A_c}(H_i) + f_j^{A_c}(H_i)$$

$$\varphi_{ijc} = \Phi_c + f^{\varphi_c}(H_i) + f_j^{\varphi_c}(H_i)$$

where ρ_{ij} is a compositional vector of length 5 of the proportion of fish in each chamber 1–5, ν_{ij} is a vector of length 5 of the expectations, ψ is the precision, η_{ijc} is the expectation on an unconstrained scale, and the remaining are as above, but with chamber-specific regressions. For identifiability, the central chamber (3) was used as a reference category such that $\eta_{ij3} = 0$. In the absence of strong priors, this is necessary due to the compositional constraints, i.e., the response variable is a vector of probabilities that must sum to one (Sennhenn-Reulen 2018; Douma and Weedon 2019). Consequently, η_{ijc}, M_{ijc}, A_{ijc}, φ_{ijc}, and all corresponding smoothers were fitted only for $c = 1, 2, 4,$ and 5. As above, global proportions were calculated from the joint posterior distribution by omitting all tank-level splines. Separate models were fit for the control and the temperature gradient experiment.

Models were fit in R 4.1.3 using the package *brms* 2.17.0 (Bürkner 2017), which fits hierarchical Bayesian models using Markov Chain Monte Carlo with the statistical platform Stan (Stan Development Team, 2022). For each model, we used four chains of 4000 iterations, with the first 2000 iterations as warmup, and the final 2000 iterations as samples from the posterior distribution. Diffuse prior distributions were used for each parameter to constrain sampling to plausible ranges (Table A2). To assess model fit, we performed posterior predictive checks and confirmed that all R-hat <1.01, effective sample size was >2000 for all parameters, and that no divergences occurred during sampling. Credible intervals were calculated as the highest posterior density intervals, which identify the smallest range containing the specified proportion of probability mass. All code is available in the associated repository (https://doi.org/10.5281/zenodo.7756617).

3. Results

3.1. Acclimation and daily rhythm of thermal preference

During the thermal gradient experiment, both zebrafish and Nile tilapia showed variation in their preferred temperatures throughout the day (Fig. 2). For zebrafish, the highest preferred temperature occurred during the middle of the light phase, showing a modest shift earlier over the first several days (Fig. 3a, light blue; acrophase on day 0: ZT 7.54 h [5.74–9.29], and day 7: ZT 5.42 h [4.81–6.03], mean days 7–13: ZT 5.37 h [4.43–6.28], mean [95% credible interval]; average daily maximum days 7–13: 28.7 °C [28.3–29.2]). The minimum preferred temperatures occurred accordingly during the middle of the dark phase (average daily minimum on days 7–13: 27.2 °C [26.8–27.7]). In Nile tilapia, the highest preferred temperatures were instead found at the transition from the light phase to the dark phase, with higher variability among tanks (Fig. 3a, dark green; acrophase on day 0: ZT 13.0 h [9.85–15.9], and day 7: ZT 11.4 h [9.85–13.0], mean days 7–13: ZT 12.5 h [10.5–14.4]; average daily maximum days 7–13: 30.6 °C [30.1–31.2]). The minimum preferred temperatures occurred at the transition from the dark phase to the light phase (average daily minimum on days 7–13: 29.4 °C [28.8–29.9]).

Zebrafish showed stable mean temperature preferences (i.e., MESOR) throughout the thermal gradient experiment (Fig. 3b, light blue; day 0: 28.2 °C [27.7–28.7], mean of days 7–13: 28.0 °C [27.6–28.3]), as well as similar amplitudes (Fig. 3c, light blue). In contrast, Nile tilapia showed a clear preference toward warmer temperatures at the start of the experiment, appearing to show a stress induced hyperthermia (SIH) response and acclimating after
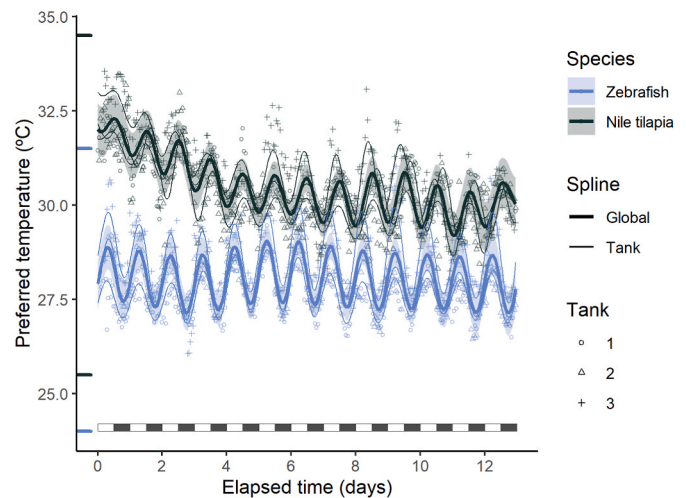
Fig. 2. Hourly mean preferred temperatures. Lines show posterior means (thick solid: global trend; thin dashed: tank-specific trends) with 95% credible interval for the global trend for Nile tilapia (dark green) and zebrafish (light blue). Points indicate observed values in each tank. The rug along the y-axis marks the maximum and minimum temperatures available to each species, with the light and dark phases (white and black bars, respectively) shown along the x-axis.

approximately 4 days (Fig. 3b, dark green; day 0: 32.3 °C [31.6–32.9], mean of days 7–13: 30.0 °C [29.6–30.5]). During the first seven days, mean preferred temperatures declined 2.20 °C [1.35–2.95]. Amplitude showed a possible increase during this time as well, though uncertainty in amplitude remained relatively high across the experiment corresponding with high variability among tanks (Fig. 3c, dark green).

Accordingly, the distribution of fish among chambers showed strong circadian patterns in both species during the thermal gradient experiment (Fig. 4, Fig. A1-3). Zebrafish showed strongest daily variation in chambers 2 and 5, exhibiting alternating preferences focused between the warmest chamber during the light phase (mean daily peak in chamber 5 of days 7–13: 0.348 [0.209–0.499]) and the second coolest during the dark phase (mean daily peak in chamber 2 for days 7–13: 0.434 [0.286–0.585]) (Fig. 4, Fig. A1;Fig. A3). Nile tilapia showed a strong preference for the two warmest chambers during the first several days (Fig. 4, Fig. A2-3, day 0 peak in proportion: chamber 4 = 0.418 [0.175–0.674], chamber 5 = 0.452 [0.125–0.793]).

3.2. Control

In the absence of a thermal gradient, neither zebrafish nor Nile tilapia presented clear daily rhythms nor change over time in preferred chamber (Fig. 4, Fig, A1-4). Zebrafish likewise did not show any overall preferences among chambers. However, Nile tilapia showed a likely preference (>85% confidence) for edge chambers over interior chambers (null expectation: 0.4; posterior mean: 0.470, 85% HDPI: 0.403–0.538; Fig. 4, Fig. A1-3), in clear contrast to the temperature-driven chamber preferences during the thermal gradient experiment (Fig. A4).

4. Discussion

Our study reveals the existence of a robust daily rhythm of temperature preference in both the zebrafish and the Nile tilapia. When fish were exposed to a temperature gradient, both fish species selected higher temperatures during the second half of the light phase and colder temperatures at the end of the dark phase. Furthermore, Nile tilapia exhibited a stress-induced hyperthermia response by selecting higher average temperatures during the first several days.

Light-dark cycles have been described as the environmental variable
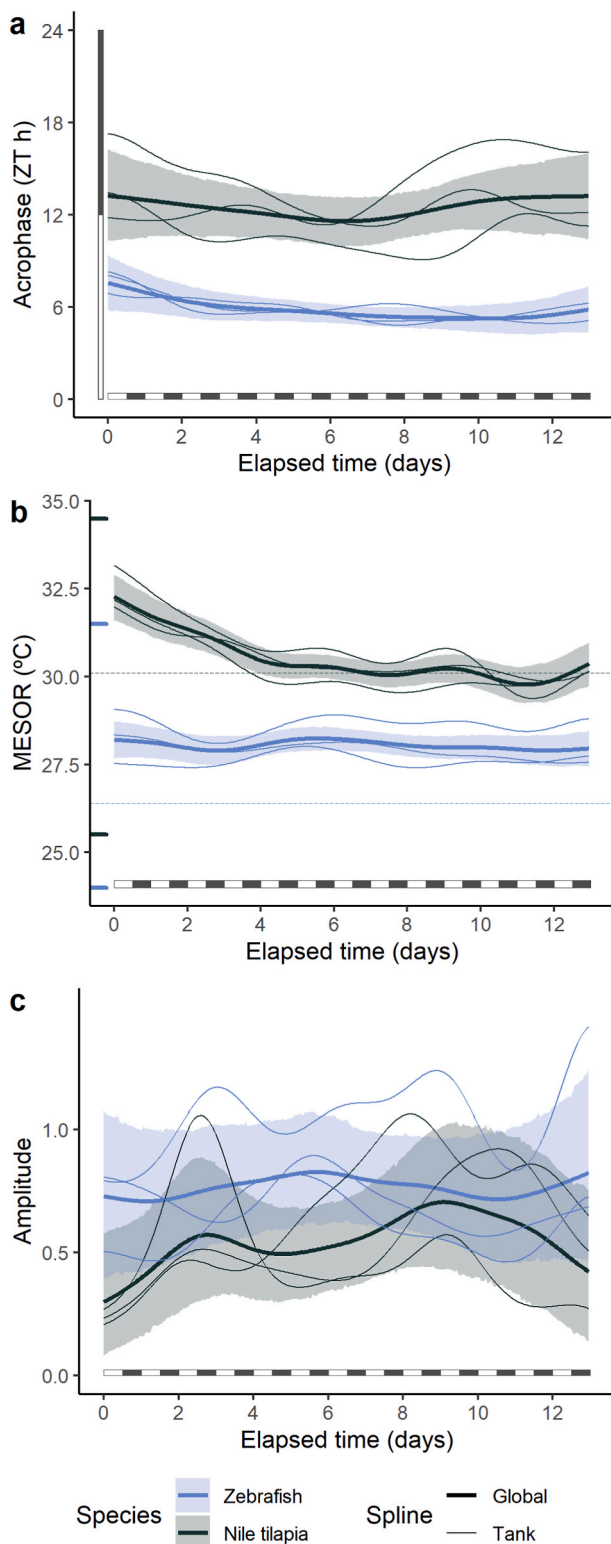
Fig. 3. Cosinor parameters as smoothed functions of time. Lines show posterior means (thick: global trend; thin: tank-specific trends) with 95% credible interval for the global trend for Nile tilapia (dark green) and zebrafish (light blue). Light and dark bars show the daily light cycle. a) acrophase denotes the time at which the maximum preferred temperature occurs. b) MESOR represents an average preferred temperature and c) amplitude is the intensity of the daily rhythms. Horizontal lines in b) show Control CTE temperature, with y-axis rug indicating the range available in the thermal gradient experiment.

that has the most influence on physiological functions in fish, being capable of synchronizing circadian rhythms during development, locomotor activity, reproductive behaviour, feeding and stress response (Kulczykowska et al., 2010; Cowan et al., 2017; Sánchez-Vázquez and López-Olmeda, 2018; 2019). In addition, the effect of temperature on the circadian biology of fish has also been explored, with most studies focusing on variations of activity when both day length and temperature change (Reebs, 2002), on the molecular effects of temperature cycles on circadian rhythms (Lahiri et al., 2005) and the relative importance of light and temperature cycles as synchronisers of behavioural rhythms (López-Olmeda et al., 2006; López-Olmeda and Sánchez-Vázquez, 2009). Daily thermal cycles can set the phase of the clock rhythm (Sweeney and Hastings, 1960) and they are also able to entrain biological rhythms in fish, as reported for zebrafish activity rhythms (López-Olmeda et al., 2006). However, when conflicting LD and temperature cycles are imposed, zebrafish display their activity mostly during the day, irrespective of the temperature, suggesting that light is a stronger zeitgeber than temperature (López-Olmeda et al., 2006; López-Olmeda and Sánchez-Vázquez, 2009). Many investigations have determined the preferred temperature of marine and freshwater fish using theoretical and experimental models (Beitinger and Fitzpatrick 1979; Golovanov 2013; Angilletta et al., 2002), showing that thermal preference varies widely across fish species but the strategies of behavioural regulation of the internal temperature are conserved (Beitinger and Fitzpatrick 1979). However, few studies have considered the effect of the daily photocycle on the rhythm of temperature selection by fish. Early investigations by Reynolds et al. (1978a, 1978b, 1978c, 1979) showed daily variations in the preferred temperature of fish, which were species-specific. For example, *Amia calva* showed a diurnal peak of preferred temperature while *Salmo trutta* and *Carassius auratus* preferred maximum temperatures at night (Reynolds et al., 1978a, 1978b, 1979). In fact, maximum values of preferred temperature were opposite in congeneric species, suggesting that different thermal rhythms might reflect niche segregation (Reynolds and Casterlin 1978).

In our study, fish were allowed to freely choose between a thermal gradient with a wide range of temperatures (24–32 °C and 26-34 °C for zebrafish and Nile tilapia, respectively), allowing us to characterise the daily rhythm in thermal preference, which was species-specific and related to the daily behavioural patterns. Zebrafish is a diurnal species which presents higher activity during the first hours of the light period and lower activity at night (López-Olmeda et al., 2006). In the present investigation, zebrafish preferred the highest temperature (28.7 °C) during the active phase whereas the minimum value (27.2 °C) was selected during the resting phase (at night). Likewise, similar results have been found in terrestrial animals and humans regarding the effect of temperature on the sleep pattern (Murphy and Campbell, 1997; Harding et al., 2019). In the case of Nile tilapia, the daily pattern of activity can differ between individuals, being diurnal or nocturnal (Vera et al., 2009). Although this species may present dualism in its locomotor activity rhythms, other studies suggest that maximum swimming activity levels are displayed towards the end of the light period, when reproductive behaviour and spawning events also occur (Baroiller and Toguyeni 2004). When fish were allowed to choose between a thermal gradient, Nile tilapia selected the highest temperature during the last hours of the light phase whereas coldest temperatures were preferred at the end of the dark phase. Our results in zebrafish and tilapia agree with the behavioural thermoregulation hypothesis known as "hunt-warm-rest-cool", which proposes that fish would select cold waters during periods of inactivity to reduce metabolic rates (Sims et al., 2006; Gleiss et al., 2017). This hypothesis agrees with other results observed in ectothermic animals from other taxa such as the fruit fly (*Drosophila melanogaster*), the salamander (*Necturus maculosus*), and the green lizard (*Lacerta viridis*) which selected the highest temperatures when locomotor activity levels peaked (Rismiller and Heldmaier, 1982; Hutchison and Spriestersbach, 1986; Goda and Hamada, 2019). However, contrary to this hypothesis, the results of Macnaughton et al. (2018) in cutthroat
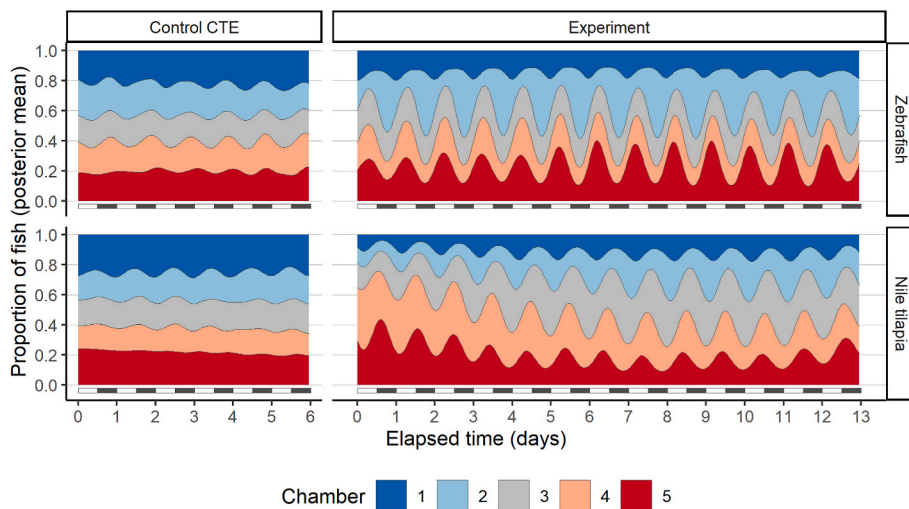
Fig. 4. Fitted distribution of fish among chambers. Values show the posterior mean for the global trend at each hour for the proportion of fish found in each chamber for Nile tilapia (top) and zebrafish (bottom) during the control (left) and thermal gradient experiment (right). During the thermal gradient experiment, chambers increased in temperature from 1 to 5. During the control, all chambers were equal temperature. See Fig. A2 and A3 for uncertainty in the proportions for each chamber.

trout (*Oncorhynchus clarkia lewisi*) showed that the preferred temperature at night increased while swimming activity decreased. Also, other studies observed that when zebrafish were allowed to choose between two temperatures (24 °C *versus* 20 °C), fish mostly chose the higher temperature, although their selection was influenced by their daily behavioural rhythms, displaying a diurnal pattern when choosing the higher temperature and a nocturnal pattern when selecting the compartment with the lower temperature (López-Olmeda and Sánchez-Vázquez, 2009). Altogether, these data suggest a complex relationship between behavioural thermoregulation and circadian activity rhythms in fish.

In the wild, the internal temperature of fish fluctuates throughout the day, which mainly depends on the environmental temperature, thermoregulatory behaviour (thermoregulators or thermoconformers) and on the characteristics of the aquatic habitat (current speed, degree of shade or maximum depth) (Carey, 1978; Meek, 1995; Haesemeyer, 2020). For example, animals that live in deep standing or fast-flowing water would have nearly stable body temperatures. However, the internal temperature of animals that live in surface stagnant waters will be conditioned by natural thermocycles (caused by solar radiation) and thus, they will experience daily fluctuations. Accordingly, we might expect that fish selected higher temperatures during daytime, coinciding with the natural thermophase, and the lowest at night, coinciding with the natural cryophase. This hypothesis coincides with the phenomenon of voluntary hypothermia in reptiles which allows this animals to reduce energy expenditure (Regal, 1967). In addition to the daily thermocycle, a vertical thermal gradient is also present in stagnant or slow-flowing waters, with temperatures being higher at the water surface and decreasing with depth (Rudstam and Magnuson, 1985). Thus, in the habitats of freshwater fish species, Diel Vertical Migrations (DVM) are commonly observed phenomena (Rudstam and Magnuson 1985). The vertical distribution of fish is influenced by several factors, including temperature, light, dissolved oxygen, prey/food availability and predator risk (Tarling et al., 2000, Afonso et al., 2014). In the case of Nile tilapia, DMV rhythms are influenced by photoperiod and feeding behaviour. Thus, tilapias are usually found in the deepest (coldest) layers at dawn and move to the surface (warmest) when it gets dark, coinciding with the peak of active feeding in this species, at the end of the night (Piet and Guruge, 1997). This fact suggests that fish may move towards warmer temperature to enhance digestion and growth rates, indicating a link between feeding state and thermoregulatory behaviour, as described in other fish species (Reynolds and Casterlin, 1979; Wurtsbaugh and Neverman, 1988).

Interestingly, when tilapias were firstly placed into the experimental tank, they selected higher temperatures than during the rest of the

experimental phase. This behavioural response has been previously observed in this species, as well as in zebrafish, subjected to a stressful agent, and it is known as Stress Induced Hyperthermia (SIH) or emotional fever (Rey et al., 2015a, Boltana et al., 2013; Rakus et al., 2017). In terrestrial endothermic animals including humans, exposure to continuous stress conditions causes an increase in body temperature, leading to emotional fever (Stress Induced hyperthermia, SIH) which is endogenously generated by the same neural mechanism as infectious fever (Briese, 1995; Bouwknecht et al., 2007, Bhatnagar et al., 2006; Vinkers et al., 2008; Oka, 2018; Bicego et al., 2007; Oka, 2018). Seemingly, in ectothermic animals such as fish, when exposed to situations that cause immunological (e.g. pyrogens) or social stress (e.g. anxiety), the animals move to higher temperature areas to increase their body temperature and cope with the possible stressor to maintain the homeostasis (stress-induced hyperthermia) (Rey et al., 2015a, Rakus et al., 2017; Key et al., 2017; Rey et al., 2017). On the contrary, when fish are in constant temperatures (without thermal gradient), they cannot perform this behavioural response, limiting the effectiveness of the immune response to the stressor (Rey et al., 2015a, Huntingford et al., 2020). The fact that our study offered the animals a gradient of temperatures allowed us to describe this SIH response related to the daily rhythm of thermal preference. In the case of zebrafish, they did not show a noticeable SIH response possibly due to the quick transfer from the holding tanks to the novel gradient tanks that did not elicit a stress response. Also, both zebrafish and tilapia exhibited a different temporal pattern of stabilization of thermal preference rhythm. From being moved to the novel experimental tank, the daily rhythm of thermal preference appeared from the first day of acclimation in zebrafish, while tilapia needed more than 24 h to establish the daily rhythm, selecting higher temperatures during this phase. This could indicate that tilapia, compared to zebrafish, is a more sensitive species in which, in addition to the stress caused by the movement of animals to the multichamber tank (handling stress), exposure to a new environment might generate environmental and social stress as in the case of the establishment of the hierarchy in a new group and environment (e.g. fights, food hierarchy, aggressiveness) (Rey et al., 2015a; Cunningham et al., 2017). Consequently, in thermal experiments this species specific SIH effect needs to be accounted for by allowing the animals to acclimatize and recover from the stressor event before determining final thermal preferences. Furthermore, under stressful environmental conditions, the presence of congeners can affect the behavioural response of fish. For example, zebrafish exposed individually to a behavioural test presented higher levels of stress in comparison to those exposed in groups (Pagnussat et al., 2013). This difference in the stress response might affect the fish thermoregulatory behaviour. Thus, studies carried out in *Gasterosteus*

aculeatus, have shown that when fish were exposed to stress as a group they seem to deviate their preferred temperature to associate with a shoal of conspecifics (Cooper et al., 2018). This effect has also been observed in *Chromis atripectoralis*, which selected lower temperatures in the presence of conspecifics (Nay et al., 2021). However, for most fish species the effect of conspecific interactions on thermal preference patterns is still unknown. On the other hand, the recent thermal history of the individual (rearing temperature) might affect the preferred temperature pattern during acclimatization (Hutchison and Maness, 1979; Johnson and Kelsch, 1998; Hadamová and Gvoždík, 2011; Haesemeyer, 2020). Actually, rearing temperatures below the thermal optimum may cause a preference for higher temperatures, as observed in the lizard *Sceloporus occidentalis* (Wilhoft and Anderson, 1960). In our study the rearing temperatures were close to the thermal optimum of both zebrafish and tilapia (Beamish, 1970; López-Olmeda and Sánchez-Vázquez, 2011). However, it would be interesting to investigate this effect in future investigations.

The mechanisms involved in behavioural thermoregulation in fish are still unknown. However, the temperature detection system must play a fundamental role in the behavioural response, to prevent physiological damage caused by acute increases/decreases in temperature (Morash et al., 2021). Thermal environmental information is perceived through membrane pores or channels that are extremely sensitive to temperature variations, known as thermoTRP channels (transient receptor potential channels) (Saito and Shingai, 2006; Patapoutian, 2005). These thermoreceptor mechanisms are distributed in various fish tissues, but mainly in neurons of the trigeminal and dorsal root ganglia that innervate the skin (Germanà et al., 2018). In zebrafish, numerous subfamilies of thermo TRPs have been described which are activated by different temperature thresholds. In addition, the expression of these thermoreceptors showed daily rhythms that are synchronized by light-dark cycles in zebrafish (Jerônimo et al., 2017; de Alba et al., 2021). Thus, in previous studies the genes involved in warm thermal sensitivity presented the highest expression during daytime, coinciding with the highest preferred temperature in our study. However, the cold-sensing gene displayed higher expression levels during the dark phase, when zebrafish chose the lower temperature (de Alba et al., 2021). The harmonization of the thermoTRPs with the environment is essential to achieve an appropriate temperature perception and trigger a behavioural response that maintains the thermal homeostasis of the fish. However, the link between the daily rhythms of gene expression of thermoTRPs and the temperature selection rhythms should be further explored, as well as the underlying mechanisms of how SIH modifies the thermal preference after a stress challenge.

In the absence of the thermal gradient, tilapia likely showed a tendency to prefer certain chambers over others. This effect was observed in the chambers located at both ends of the tank and it could be attributed to the fact that in new environments the fish respond behaviourally by moving to the corners or edges of the tanks displaying a thigmotaxis behaviour or scototaxis if the corners are darker and less exposed (Blaser and Rosemberg, 2012), a phenomenon that has also been described in insect species (Dillon et al., 2009). However, when fish are exposed to a thermal gradient, they show a completely different chamber preference with a daily occupation rhythm. Further, the preference for elevated temperatures at the start of the thermal gradient experiment was stronger than the potential preference for edges, though the thigmotaxis observed in the control may have led the tilapia to select somewhat higher temperatures than otherwise preferred. This fact demonstrates how temperature is an important environmental factor which impacts on the selection of space and the daily behavioural pattern of fish (Krylov et al., 2021).

The fact that both fish species showed daily rhythms of preferred temperature suggests that behavioural regulation of preferred temperature is an evolutionarily conserved response in fish. According to this recent hypothesis, thermal adaptation would be determined by the evolution of thermosensitivity, thermoregulation and acclimatization

mechanisms to the thermal environment caused by the selective pressure exerted by spatial and temporal variations in environmental temperature (Angilletta, 2009). Other speculations have indicated that the role of the preferred temperature lies in its direct relationship with physiological performance (Beitinger and Fitzpatrick 1979; Angilletta et al., 2002). Thus, fish that choose a preferred temperature that maximizes their physiological processes will be able to enjoy a better physical condition. Consequently, the preferred temperature might present phenotypic plasticity in which a change in the thermal physiology of the animal (thermal sensitivity) will lead to a change in the thermoregulatory response and vice versa (Angilletta et al., 2002; Angilletta, 2009). During the last decades, the increase in temperature of aquatic ecosystems due to climate change has altered the abundance and composition of species, modifying the structure and function of ecosystems (Pörtner and Peck, 2010). However, the effect of the temperature increase on the thermal physiology of fish has been little studied. Recent studies have shown the response of fish populations to the general warming of the oceans during the last century. Marine fish populations decreased in abundance in tropical areas near the equator and were more abundantly distributed in areas closer to the poles (Hastings et al., 2020). This phenomenon could extend to coastal subsistence species in the coming years. Latitudinal changes in the abundance of fish populations will mean that species must face large temperature fluctuations close to their thermal tolerance limits. Therefore, their thermal physiology could be compromised, which could have a considerable impact with profound effects on the biochemical, physiological and life cycle activities of the fish (Alfonso et al., 2021).

5. Conclusion

The present paper revealed the existence of daily rhythms in temperature preference of zebrafish and Nile tilapia, mainly synchronized to the LD cycle. Furthermore, during the acclimation period, tilapia presented a stress induced hyperthermia response by choosing higher temperatures. These findings reveal the need to consider daily rhythms when discussing thermal preferences of fish. Studies related to thermoregulation and thermal ecology need to consider the circadian rhythms to clearly establish a real diurnal pattern of thermal preference and the optimal ranges of temperature. If, due to climate change, ranges are narrower and waters do not cool down at night or thermoclines change, the implications could be dramatic and multiply exponentially due to the changes in natural thermal cycles. This work shows the adaptive nature of the behavioural regulation of the preferred temperature in which fish species with broad geographic ranges present different daily patterns of preferred temperature. Our results may be useful in understanding the ecological and evolutionary aspects of thermoregulatory behaviour and in discussing the effect of climate change on the biochemical, physiological and life cycle activities of fish. In addition, our results have clear implications for the health and welfare of fish under confined environments including research, farming or as pets, and suggest that husbandry procedures should incorporate thermal cycles where possible or at least provide animals with a range of temperatures from which to choose.

Credit author statement

LMV, GA, SM, SS, FJSV and SRP conceived and designed the experiments; LMV, GA, TS, SS, FJSV and SRP analyzed the data; All authors contributed on the writing of the manuscript; LMV, FJSV and SRP provided funding.

Ethical statement

The experimental procedure complied with the Guidelines of the European Union (2010/63/UE) and the Animal (Scientific Procedures) Act 1986 UK under the approval of the Animal Welfare and Ethical

Review Body (AWERB) of the University of Stirling (ref number: AWERB/1819/065/New Non ASPA) and Murcia (RD 1201/2005 and Law 32/2007; ref number A13191003).

Data accessibility

The datasets supporting this article have been uploaded in the Dryad at the DOI https://doi.org/10.5061/dryad.r2280gbh2.

Conflict of interest declaration

The authors declare no competing or financial interests.

Data availability

Dataset link shared in document

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2023.103544.

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