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SHORT COMMUNICATION

Thermal biology and plasticity of the thermal metabolic scope of angelfish *Pterophyllum scalare* acclimated to different temperatures

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Abstract The angelfish *Pterophyllum scalare* ornamental species from continental waters has economic importance due to its diversity and color patterns. Because this fish is sensitive to environmental changes and handling conditions, knowing its thermal biology is vital to provide optimal conditions for its management and use in aquaculture. This study determines the thermal tolerance, window width, and thermal metabolic scope (TMS) in angelfish juveniles acclimated at 20, 24, 28, and 32 °C temperatures. The thermal window width calculated for *P. scalare* was 269 ºC^2. The thermal metabolic scope obtained in animals acclimated at the interval 20-32 °C ($P > 0.05$) had the maximum efficiency value of 1026.0 (mg O_2 h^{-1} kg^{-1}w.w) at 28 °C, which coincides with the preferred temperature. The results showed that the metabolic rate decreased at the lowest and highest fish acclimation temperatures. To conclude, integrating all the data, this fish species is eurythermal tropical, based on its thermal window and compared to other cichlids. Therefore, the present research study contributes to the knowledge of thermal biology of organisms that can be applied to management plans of aquaculture farms for their maintenance and care.

Keywords Thermotolerance . Metabolic scope . Metabolic rate . Angel fish . Ornamental fish . Aquaculture

Introduction

Temperature is one of the critical factors for fish distribution that expands or restricts the use of a given area. The species thermal tolerance behavior is an essential physiological feature that influences the possibility of adapting or not to a new environment or surviving in it when the conditions have changed (Cussac et al. 2009). The analysis of fish tolerance to higher and lower temperatures has been performed with different techniques since the beginning of the 20th century, in which the acclimation temperature is an important variable (Fry 1971). Nonetheless, studies on thermal tolerance of ornamental freshwater fish species are scarce (Prodocimo and Freire 2001; Perez et al. 2003; Bierbach et al. 2010; Martinez et al. 2016; Yanar et al. 2019; Mukherjee et al. 2022).

Fish from tropical and subtropical environments have different capacities to acclimate to changes in environmental conditions, for example, the increase in temperature due to climate change; many species of tiny fish have body temperatures that fluctuate exactly with the enviroment (Haesemeyer 2020). Temperature affects all aspects of these species' biology, including metabolic responses and thermal tolerance (Perez et al. 2003). Thermal tolerance is a crucial trait that allows organisms to deal with thermal stress and respond to environmental conditions, which can be used to understand how species distributions are impacted by climate change (Pinsky et al. 2019). Therefore, measuring the upper and lower thermal limits

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is critical to obtain valuable information for forecasting changes in community composition and species distributions in response to rising temperatures (Hoffmann et al. 2013). Thermal limits can be predictors of the biogeographical distribution of ectotherms, which are calculated using the Critical Thermal Maximum (CTMax) and Critical Thermal Minimum (CTMin) by exposing the individuals to a constant rate of increasing or decreasing temperature, until a sublethal or non-lethal point is reached. The level at which individuals start to display muscular spasms and unorganized locomotion has been described (Ørseted et al. 2022; Leong et al. 2022). Bennett and Beitinger (1997); Noyola-Regil et al. (2015); Larios-Soriano et al. (2020; 2021), for example, show how the thermal tolerance window (TTW) could be calculated with CTMin and CTMax responses. This tool is helpful to describe the extension of the temperature range that fish can tolerate, providing essential insights into the ecology and distribution of aquatic animals and used to identify temperature-related survival tactics.

Halsey et al. (2015, 2018) mentioned that a strong and predictable relationship exists between activity and temperature in ectotherms since a certain level of activity may be induced by thermal exposure. Paschke et al. (2018) proposed using the temperature-induced metabolic rate (TIMR) method, which can estimate the aerobic power budget of aquatic organisms to induce high metabolic rates. This purpose can also be obtained by stimulating the organisms' activity using high and non-lethal temperatures that produce a high metabolic rate (HMR). A minimum metabolic rate can be achieved when the activity is depressed by exposure to a temperature low enough to provoke a forced low metabolic rate (LMR).

Freshwater angelfish (*Pterophyllum scalare*) is one of the most attractive species of ornamental fish from continental waters for the aquarium market, mainly because of its morphological diversity and color patterns (Chapman et al. 1997). In its natural environment (Amazon Basin*), P. scalare* can reach a length of up to 15 cm and inhabits slightly acidic waters with low hardness. The species is sensitive to handling and transportation procedures (Chellappa et al. 1999; Oliveira et al. 2019), but the main limitations for its optimal commercial production are related to the lack of physiological knowledge (Perez et al. 2003).

Therefore, the present study aims to determine the thermal tolerance, window width, and metabolic scope (TMS) in juveniles of *Pterophyllum scalare* acclimated at different temperatures. This information may be useful to evaluate and optimize the culture condition of tropical species for their importance in the trade of ornamental fish.

Materials and methods

Organisms and maintenance

The angelfish specimens (N = 300) of the marbling variety *Pterophyllum scalare* were used for this research study. The organisms came from the fish and aquatic plant farm Emmanuel located in Merida Yucatan, Mexico. The organisms were shipped to the Wet Laboratory at CICESE (Centro de Investigacion Cientifica y de Educacion Superior de Ensenada). Upon arrival, the fish size was 1 cm; they were kept for three months in a reservoir in a 2000 L at 28 °C with aeration and constant fresh water replacement in an open flow system, fed three times a day with tropical TetraMin® (Tetra, VA, USA) flakes with 47% raw protein. The remaining food and feces were siphoned daily. After reaching the desired size, the organisms (N = 160) were randomly selected and acclimated in eight 500-L tanks with constant aeration and water exchange in an open system at 20, 24, 28, and 32 °C for 30 days. The rate of increase and decrease in temperature was one °C / day. The tanks were maintained at a constant temperature by a 1000-W immersion heater connected to a controller.

Thermal tolerance

The Critical Thermal Maximum (CTmax) of 80 juvenile angelfish was determined and were gradually acclimated to experimental temperatures of 20, 24, 28, and 32 °C. Each fish was introduced into a 40-L aquarium with a 1000-W immersion heater and constant aeration to maintain a constant temperature increase. The water was kept at the experimental temperature for 30 min to reduce the stress produced by management with a heating rate of 1 °C min according to the criteria (Cereja 2020; Leong et al. 2022). The recorded stress event was the loss of righting response (LRR), as mentioned by Lutterschmidt and Hutchison (1997), that is, when the fish reached this point, they returned to their acclimation temperature (Perez et al. 2003). The Critical Thermal Minimum (CTmin) was determined individually through a descending temperature gradient of the angelfish acclimated for 30 days to the experimental temperatures. The initial temperature was acclimation, and the stress response criteria (LRR), mentioned by Lutterschmidt and Hutchison (1997) were used. When the fish were introduced into individual chambers, they were kept for 15 min to reduce the stress produced by handling. Subsequently, the temperature decreased by 1 °C/min until the loss of equilibrium was observed (Bennett and Beitinger 1997). The exact temperature at the time of balance loss was measured with a digital thermometer (Hanna Instrument Rhode Island, NY, USA). At the end of the experiment, the recovered fish were returned to the corresponding acclimation temperature. In all the experiments, the organisms were used only once, and the data of the animals that were not recovered by determining critical temperatures after returning them to their acclimation temperature were discarded. Once the critical temperatures of the angelfish were obtained, the thermal window was calculated.

Thermal metabolic scope

To determine the thermal metabolic rate (TMS) of each experimental group (N = 10), TIMRmax was first determined by adjusting CTmax to 90% and TIMRmin was determined by adjusting CTmin to 110% for each group of fish acclimated (20, 24, 28, 32 °C).TIMRmax is the temperature that induces fish metabolism at the high end, called High Metabolic Rate (HMR). TIMRmin is the temperature that causes fish metabolism at the low end, called Low Metabolic Rate (LMR), according to Paschke et al. (2018). These metabolic states were measured through the intermittent system of respirometry. The system consisted of a fiber-optic sensor inside a respirometric chamber connected to an OXY-10 mini-amplifier (PreSens Precision Sensing GmbH, Regensburg, DE) inside an aquarium with temperatures TIMRmax and TIMRmin corresponding to each experimental fish group. In this system, the respirometric chamber has a valve that allows it to close or open the water flow within it. Each experiment had a respirometric chamber without an organism under the same conditions as a control, indicating microbial oxygen consumption in the filtered water to make the necessary corrections. The fish were individually introduced into each chamber and kept with open water flow until reaching an oxygenation value that would close to saturation. This value corresponded to the first reading of dissolved oxygen, and subsequently, the chambers were closed for 5 min taking data every 30 seconds. The respiration rate was calculated as follows:

$$MO_2 = (O_2(_A) - O_2(_B)) \times (V/t) / M$$

MO_2 represents the respiration rate (mg O_2 h^{-1} kg^{-1} w.w.) and is equivalent to the substraction of the initial $O_2(_A)$ (mg O_2 L^{-1}) and the final $O_2(_B)$ (mg O_2 L^{-1}) oxygen concentration in the chamber. The result is multiplied by the water volume in the chamber minus the water volume displaced by the animal (V) and divided by the time (t) elapsed during the measurement (h). M is the body mass of the experimental animal (kg w.w.). HMR and LMR were expressed in mg O_2 h^{-1} kg^{-1} ww. TMS was calculated with the formula proposed by Paschke et al. (2018).

Data analyses

The data analyses and figure plotting were done with the SigmaPlot v.15 program. The analysis algorithm for the data group is described below: Shapiro-Wilks normality test, Brown-Forsythe variance equality test, one-way variance analysis (ANOVA) with a 95% confidence level, and Tukey's posthoc test for multiple comparisons.

Results

Thermal biology

The thermal window was constructed with the CTmax and CTmin values. In this study, the CTMax increased from 34.0 ± 0.5 °C to 36.8 ± 0.7 °C in angelfish acclimated from 20 to 32 °C, whereas CTMin values increased from 13.3 ± 0.5 to 15.4 ± 0.5 °C as acclimation temperatures increased (Fig. 1). With these values, a thermal window width for angelfish was obtained as 269.0 °C^2 (Fig. 1).

Thermal metabolic scope, TIMR method

The CTmax and CTmin were used to obtain the HMR and LMR by making an adjustment which considers CTMax and CTmin with an adjustment of 90% and 110%, respectively. The highest value of HMR was obtained at the temperature of 28 °C at 1560.36 mg O_2 h^{-1} kg^{-1} w.w. ($P < 0.05$). The lowest values were observed at 20 and 32 °C at 1117.36 and 1374.00 mg O_2 h^{-1} kg^{-1} w.w., respectively (Fig. 2). The low metabolic rate (LMR) was not significantly affected ($P < 0.05$) by acclimation temperature in the range between 20 and 28 °C with a minimun value of 480.68 mg O_2 h^{-1} kg^{-1} w.w., but the level significantly increased ($P < 0.05$) at 32 °C, reaching a value of 670.0 mg O_2 h^{-1} kg^{-1} w.w. (Fig. 2). The graphical representation of the thermal metabolic scope shows that the highest value of 1026.0 mg O_2 h^{-1} kg^{-1} w.w. was obtained at 28 °C (Fig. 3).

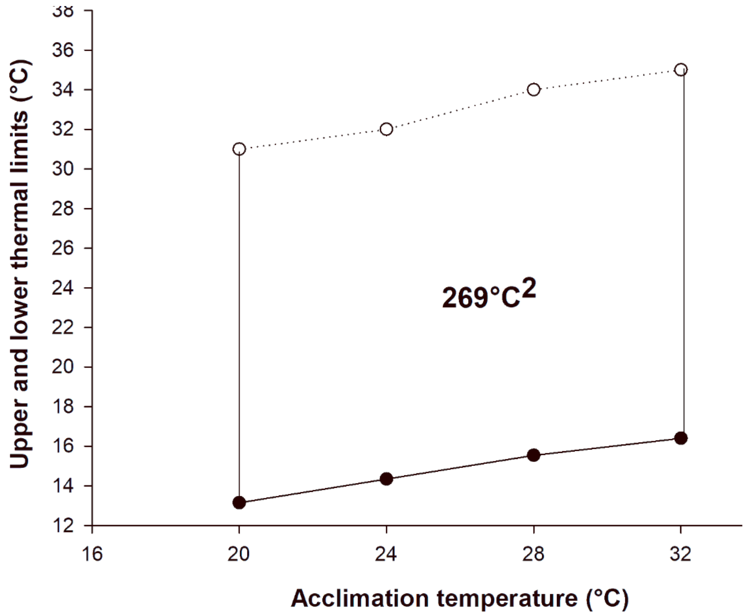

Fig. 1 Thermal window of *Pterophyllum scalare*

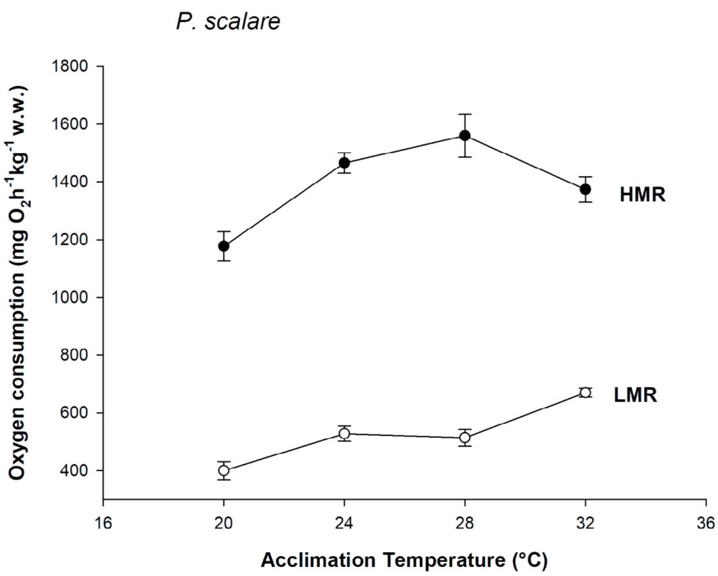

Fig. 2 Oxygen consumption when fish metabolism is induced by the TIMR method. (●) High metabolic rate (HMR); (○) Low metabolic rate (LMR)

Discussion

The angelfish is native to the Amazons with a wide distribution of its varieties in South American countries, they usually live at a depth from 1-2 m among dense submerged vegetation. Thus, temperature and oxygen remain stratified with concentrations fluctuating during the day and declining at night associated to flood or dry season (Axelrod and Walker 2000, Perez et al. 2003; Braz-Mota and Almeida-Val 2021). Few reports of the thermal biology of freshwater ornamental fish have been available. The Cauca molly (*Poecilia caucana*), a neotropical poecilid species from the Magdalena River basin in Colombia, was reported by Martinez et al. (2016) in an area comprised by the thermal window at 214.65 °C^2. One of the most complete reports published to date is from Yanar et al. (2019) who evaluated the critical limits of 13 ornamental fish species, using three acclimation temperature ranges to calculate the thermal windows. The species with the greatest thermal window was *Carassius auratus* with 281.0 °C^2 and the lowest one was *Puntius tetrazuna* with an area of 188.0 °C^2. Among the fish evaluated in Yanar et al. (2019), the angelfish was included by the authors, reporting a thermal window of 210.6 °C^2. Thus, our results disagree with that reported by Yanar et al. (2019). The thermal window area obtained for us was 58.4 °C^2 greater due to the addition of a temperature of 32 °C, and also because a heating and cooling rate different from 1 °C min was used, as recommended by Cereja (2020) and Leong et al. (2022). These results suggest that the thermal windows reported by Yanar et al. (2019) for angelfish could be underestimated, since the thermal window area obtained for angelfish in the present study was 269 °C^2, which allowed us to characterize it as eurythermal tropical fish. These properties allow these species to be preferred in ornamental fish farming, especially in tropical and subtropical areas because the organisms may be exposed outside their optimal range.

The acclimation temperature of the organisms is directly related to the thermal tolerance range, since the critical thermal maximum and critical thermal minimum of the organism increase as the acclimation temperature increases. In the present research study, acclimation temperatures differed from 4<°C to 20 to 32<°C, where extreme temperatures decrease aerobic capacity (Fig. 2). This physiological response can be associated with the compensatory metabolic mechanisms described in Amazonian fish by Almeida-Val and Hochachka (1995), Braz-Mota and Almeida-Val (2021). These mechanisms reflect the capacity to change the oxygen level in blood circulation through oxygen intake volume by reversibly remodeling the gills, ventilatory frequency, heart rate, increasing red blood cells in circulation, which lead to an increase in concentration of heme groups or changes in affinity to oxygen, a stronger ability of metabolic depletion, and high-energy storage to maintain the anaerobic metabolism for a compensation with lower ATP demands.

The description of thermal biology helps to understand the organisms' life cycles and behavior. Ribeiro et al. (2021) emphasize that in adult fish, temperatures close to 28 °C can influence their behavior for terri-

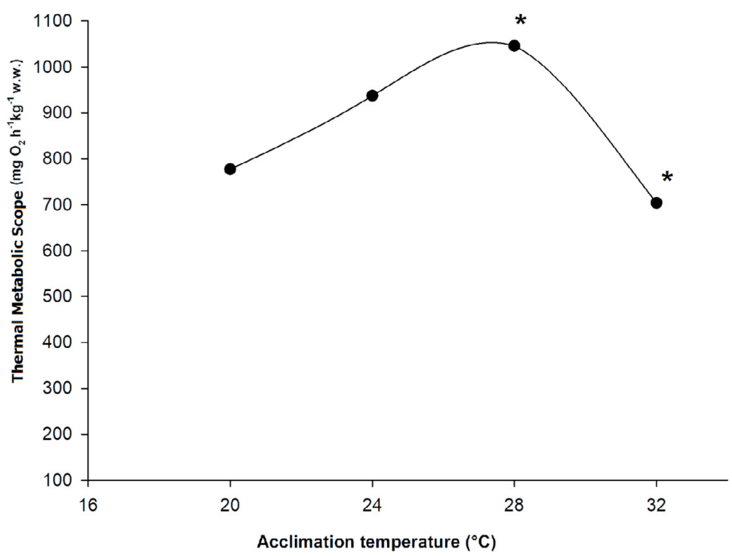

Fig. 3 Thermal metabolic scope of *Pterophyllum scalare* acclimated to different temperatures. (∗) Indicates a significant difference (Tukey's test, P value < 0.05) between oxygen consumption at different acclimation temperatures

torial establishment crucial to the reproductive success of *Pterophyllum scalare*. When angel fish thermal preferences (Perez et al. 2003) were compared with TMS, the preferred temperature corresponded with the maximum TMS in animals acclimated at 28 ºC, indicating that the thermal preference and maximum physiological performance for this species are linked to these temperature ranges. Thereby, a medium temperature of 28 °C should be used in production systems, since it might represent the optimal physiology for the freshwater angel fish given that, in this condition, the animals showed a satisfactory performance.

Although organisms acclimated at 32 °C did not present mortality, the decrease in TMS indicates that their metabolic aerobic range decreased; if the value of 1560 (mg O_2 h^{-1} kg^{-1}) is considered as 100%, their response decreased by 32%, and the value obtained at 20 °C is 25% lower than the optimum. Temperatures above 28 °C have a greater effect on the TMS of juvenile fish than cooler temperatures below the optimal reducing the metabolic field. However, adult breeders have been reported to show a narrower thermal window making them more sensitive to heating because a minimal increase in temperature may exceed the upper critical temperature limit of the individuals needed to reproduce (Brulé et al. 2022). In breeding and selling ornamental fish, knowing where the TMS is optimal would keep the fish at the preferred temperature of 28 °C during cultivation.

Conclusion

To conclude, the angelfish is a eurythermic fish based on thermal window width compared to other cichlids. Therefore, this research contributes to the knowledge of its thermal biology, which can be applied to management plans of aquaculture farms for their maintenance and reproduction.

Conflict of interest The authors declare that they have no conflict of interest.

Compliance with ethical standards The authors followed all applicable international, national, and/or institutional guidelines CICESE for the care and use of animals.

Author contribution L. Alvarez-Lee: wrote the paper, collected the data, investigated, performed the experiment, conceptualized, reviewed and edited the manuscript. A.D. Re: wrote the paper, contributed data and/or analysis tools, collected the data, supervised, conceptualized and provided financial support.F Díaz: wrote the paper, collected the data, performed the experiment, provided financial support, conceived the idea and designed the analysis, investigated, supervised, reviewed and edited the manuscript. J.P. Sanchez-Ovando: collected the data, performed the experiment. L. Perez-Carrasco: performed the experiment and maintained the organisms.

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