THERMOPREFERENTIAL BEHAVIOR OF THE SENEGAL BICHIR *POLYPTERUS SENEGALUS* (POLYPTERIDAE) UNDER CHRONIC VISUAL DEPRIVATION

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The effect of chronic visual deprivation (eye lens removal, 3 months) on the thermopreferential behavior and preferred temperature in fish was studied for the first time on the example of the Senegal bichir *Polypterus senegalus*. In intact Senegal bichir, the thermopreferential range and mean preferred temperature are 32.0–35.0 and 33.8°C, whereas in visually deprived fish they are 26.0–35.0 and 30.2°C, respectively. Compared to intact individuals, the visually deprived fish are more mobile and make 10.3 times more travels from compartment to compartment in the thermogradient tray, their total travel distance is 16.9 times longer, and the distance swum without change of direction is 1.6 times longer and takes 8.7 times less time. The rate of temperature change during movements in visually deprived fish is 14.9 times higher than in intact individuals. Changes in thermal preference and movement activity found in fish experiencing chronic visual deprivation indicate the presence of complex relations between thermoreception and the visual system.

Keywords: Senegal bichir *Polypterus senegalus*, thermopreferential behavior, selective temperature, visual deprivation, interaction of sensory systems.

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INTRODUCTION

Temperature is a constant, strong external factor that determines the rate of metabolic reactions and physiological functions in fish and all other ectothermic animals (Fry, 1971). In a heterogeneous environment, fish prefer to occupy areas where the water temperature optimizes vital processes to the greatest extent (Jobling 1981). The choice of such sites occurs due to thermoreference behavior, implemented on the basis of a thermosensory system that includes thermosensitive free nerve endings of the trigeminal and spinal nerves and brain centers (Haesemeyer, 2020). Thermoreference behavior is considered the fastest and most energetically beneficial way for animals to care for or avoid adverse temperature effects and transition to conditions optimal for the current physiological status of the individual (Hochachka and Somero, 2002).

The preferred temperatures differ among fish living in water bodies of different climatic zones; they do not remain constant and can vary due to the condition of the fish and the influence of various biotic and abiotic factors (Coutant, 1977; Golovanov, 2013a, 2013b; Haesemeyer, 2020). It has been shown that the temperatures preferred by fish depend on the preliminary acclimation temperature (Díaz, Bückle, 1999; Schram et al., 2013), and the oxygen content in the water (Schurmann et al., 1991; Schurmann, Steffensen, 1992). Temperature preferences of fish undergo age-related and seasonal changes (Lafrance et al., 2005; Kapshay, Golovanov, 2013; Christensen et al., 2020; Schakmann et al., 2023), depend on the size of the daily ration and food quality (Boltz et al., 1987; Despatie et al., 2001; Pulgar et al., 2003; Zdanovich, 2006), and can shift in case of fish diseases (Golovanov, 2013b).

The modulating influence of external factors and the state of fish on temperature preferences indirectly indicates the involvement in the regulation of thermal selection not only of information coming from numerous skin thermoreceptors, but also from signals received from other sensory systems. The assumption about the participation of various sensory systems in thermopreferendum behavior is quite acceptable, since animal behavior, including fish, in many cases has a polysensory basis (Manteifel, 1987; Pavlov, Kasumyan, 1990; Gonçalves-de-Freitas et al., 2019). Regulation of behavior by several sensory systems simultaneously – leading and auxiliary – increases the reliability and plasticity of behavioral reactions (Kasumyan, Marusov, 2007). It is known, in particular, that the thermopreferendum behavior of fish is subject to an endogenous rhythm associated with daily fluctuations in illumination. Fish (Nile tilapia *Oreochromis niloticus* , zebrafish *Danio rerio*) consistently prefer the highest water temperatures with the onset of evening twilight and the lowest with the increase in morning illumination (Vera et al., 2023; de Alba et al., 2024). However, information demonstrating the participation of the visual system of fish in thermopreferendum behavior is scarce in the available literature (Zdanovich, 2017).

To date, thermopreferendum behavior has been studied mainly in teleost fish (Teleostei) and cartilaginous ganoids (Chondrostei) (Coutant, 1977; Golovanov, 2013a). Recent studies (Zdanovich et al., 2024) show that thermal selection is also characteristic of bichirs (Polipteridae), evolutionarily the most ancient among the existing ray-finned fish (Actinopterygii).

The purpose of this work is to study the effect of chronic visual deprivation on thermopreferendum behavior and the selected temperature of the Senegal bichir *Polypterus senegalus* .

MATERIAL AND METHODS

The Senegalese bichir was purchased at the "Aquarif" store (Moscow). After delivery to the laboratory, the fish were kept for several months in a 150-liter aquarium with daily feeding to satiation with live chironomid larvae (Chironomidae). Water temperature was maintained by an AquaEL thermoregulator (Poland) at 24.0 ± 0.5°C. Changes in illumination corresponded to the natural daily rhythm. Forced aeration ensured complete oxygen saturation of the water.

For the experiments, 10 fish were used (weight 5.2–6.9 g), of which 5 specimens remained intact, while the other 5 specimens had their eye lenses removed, depriving the fish of focused vision (partial visual deprivation). The lens was removed through a small incision in the cornea; the operation was performed under cold anesthesia (Kasumyan, Marusov, 2002; Kasumyan et al., 2024). The experimental and intact fish were kept under standard conditions but in different aquariums. There was no mortality in the post-operative period, and feeding activity was fully restored after 4–6 weeks. Experiments with visually deprived fish were conducted 3 months after lens removal.

Observations of the thermal preferendum behavior of the bichir were carried out visually in a thermal gradient apparatus, which created a horizontal temperature gradient from 20 to 35°C. The apparatus consisted of a plexiglass trough (1.50 × 0.12 × 0.15 m), divided into 12 compartments by partial partitions that did not impede the free movement of fish along the trough. The temperature gradient in the trough was created by controlled heating and cooling of water at opposite ends of the trough using a Juwel heater (Germany) and a Hailea chiller (China) for aquariums, respectively. The gradient value was 0.1°C/cm. To monitor the water temperature in each compartment, a thermometer with a measurement accuracy of 0.1°C was installed. To prevent vertical temperature stratification, ceramic air diffusers connected to operating micro-compressors were placed in the compartments (Zdanovich, 1999).

For the experiment, one polypterid was placed in a compartment with a temperature of 24°C in the thermal gradient setup. According to preliminary observations, as well as in previous studies (Zdanovich et al., 2024), the movement zone of intact and sensory-deprived fish stabilizes after the first 3-4 hours of being in the thermal gradient setup and does not change in subsequent hours. Therefore, experiments were conducted from 4 to 24 hours after placing the polypterid in the thermal gradient setup. Each experiment lasted 30 minutes, during which the fish's location was recorded second by second. The compartment in which the fish was located was determined by the position of the fish's head. This resulted in a digital ethogram of the experimental individual's movements. After completing the experiment, the fish were placed in a separate aquarium with a temperature of 24 ± 0.5°C. Two experiments were conducted with each intact and sensory-deprived polypterid with an interval of at least 2-3 weeks. In total, 10 experiments were performed with intact fish and 10 with visually deprived fish.

Based on digital ethograms, several parameters of fish behavior in the thermal gradient space were calculated: the boundaries and width of the thermal preferendum range (the difference between the compartments with extreme water temperatures visited by the fish), the number of visits by fish to compartments, the duration of continuous stay of fish in compartments, the number and parameters of vectors of individual movement from one compartment to another. It was assumed that these vectors are parallel to the longitudinal axis of the setup and can have only two directions - towards the zone of high or low temperatures. The vector length was considered as the distance from the middle of the initial sector to the middle of the final sector. In both initial and final sectors, fish change the direction of movement to the opposite. The path of an individual during its single movement was taken equal to the vector length (L) and calculated using the formula: $L = Ls/2 + \sum Lm + Lf/2$, where Ls, Lm, and Lf are the lengths of the initial, intermediate, and final sectors, respectively, through which the fish movement vector passed. The length of one sector is 12.5 cm, the number of intermediate sectors can be from 0 to 10. The duration of one movement (T) was calculated using the formula: $T = Ts/2 + \sum Tm + Tf/2$, where Ts, Tm, and Tf are the duration of fish stay in the initial, intermediate, and final sectors, respectively, through which the individual's movement vector passed. The temperature shift during one movement equals the absolute value of the difference in water temperatures between the initial and final sectors. The rate of temperature change during a single movement was determined as the quotient of the temperature shift magnitude divided by the duration of movement. The length of the path swum by the fish per hour was calculated based on the sum of lengths and durations of movements during the experiment. Additionally, the mean preferred temperature weighted by the time fish spent in each compartment was determined : $t_{\text{pref}} = \sum(k_i t_i)/\sum k_i$, where i is the compartment number; k_i is the total time spent by all studied individuals in the *i* -th compartment, s; t_i is the temperature in the *i* -th compartment, °C (Konstantinov, Zdanovich, 1993).

During statistical data processing for comparing the parameters of thermopreferendum behavior of intact and visually deprived fish, we used the *U* -Mann-Whitney test.

RESULTS

Thermal selection . Placed in a compartment with water temperature of 24°C, intact and visually deprived fish begin to move quite quickly along the thermal gradient tray. But after 4 h and subsequently, visits to different compartments and the duration of fish stay in them is limited to a certain temperature zone, the boundaries of which differ between intact and visually deprived individuals (figure). In intact fish, movements in the thermal gradient are limited to the range of 32.0-35.0°C, with an average preferred temperature of 33.8°C, while in visually deprived bichirs these indicators are 26.0-35.0 and 30.2°C, respectively (table). Thus, the movement zone of deprived fish in the thermal gradient is 6°C wider and shifted toward lower temperatures. The variation series of occurrence frequency and residence time of fish in the installation compartments are similar for both intact and visually deprived bichirs, i.e., the frequency of visits to a particular compartment of the thermal gradient tray corresponds to the total duration of fish stay in them.

Characteristics ($M \pm m$) of thermopreferendum behavior of intact and visually deprived Senegalese bichir *Polypterus senegalus*

Parameter	Intact	Visually deprived
Number of movements from compartment to compartment per 1 h	6.5 ± 1.1	67.2 ± 11.4***
Distance of movement (vector length), m	0.155 ± 0.005	0.246 ± 0.013***
Duration of movement, s	578.0 ± 55.0	66.4 ± 7.7**
Path traveled by fish per 1 h, m	1.01 ± 0.17	17.08 ± 3.41***
Thermopreferendum range boundary, °C:		
– lower	32.4 ± 0.2	27.5 ± 0.5***

– upper	34.1 ± 0.1	33.1 ± 0.2**
Width of thermopreferendum range, °C	2.3 ± 0.2	5.6 ± 0.7**
Temperature shift during movement, °C	1.4 ± 0.03	2.2 ± 0.13***
Rate of temperature change during movement, °C/s	0.0028 ± 0.0003	0.0417 ± 0.0085**
Preferred temperature, °C	33.8 ± 0.10	30.2 ± 0.31***

Note. $M \pm m$ – mean value and its error. Parameter values differ between deprived and intact fish according to the U -Mann-Whitney test at p : ** < 0.01, *** < 0.001.

Behavior . Thermopreferendum behavior exhibited by intact and visually deprived fish significantly differs in all recorded and calculated parameters (table). Compared to intact individuals, visually deprived fish are more mobile and make 10.3 times more movements between compartments, swim 1.6 times longer distance without changing direction, spending 8.7 times less time doing so. As a result, the distance traveled per 1 h by visually deprived fish is 16.9 times greater than that of intact fish. At the same time, the width of the preferred range and the rate of temperature change during movements in visually deprived fish are 2.4 and 14.9 times higher, respectively, than in intact individuals. The mean preferred temperature also differs highly significantly – in visually deprived fish it is 3.6°C lower than in intact fish, constituting 30.2 and 33.8°C respectively (table).

DISCUSSION

The obtained data confirm the results of a previously conducted study (Zdanovich et al., 2024), which showed that bichirs inhabiting tropical African water bodies are capable, like fish from boreal and other climatic zones, of exhibiting thermoselection (Konstantinov, Zdanovich, 1993; Fangue et al., 2009; Golovanov, Smirnov, 2011; Christensen et al., 2020). Under experimentally created thermogradient conditions, bichirs limit their movements to a temperature zone within hours, the boundaries of which are maintained thereafter, with different bichir species exhibiting species-specific preferred temperature ranges (Zdanovich et al., 2024).

In the present work, it was established for the first time that the ability for thermoselection is preserved in fish deprived of object vision, however, the boundaries of the thermopreferendum range and the behavior accompanying thermoselection change significantly. Compared to intact individuals, a visually deprived Senegalese bichir placed in a heterothermal field exhibits much higher swimming activity, longer single movement distances, and, consequently, experiences a much higher rate of change in surrounding temperature. Visually deprived fish also have a wider thermopreferendum range due to a shift in the lower boundary toward lower temperature values and, accordingly, a lower mean preferred temperature - by 3.6 °C (figure, table). Similar changes in thermopreferendum were found in the tetragonopterus *Psalidodon anisitsi* (= *Hemigrammus caudovittatus*) (Characidae) after visual deprivation (lens removal) combined with anosmia (Zdanovich, 2017). Deprived tetragonopterus individuals exhibit a wider coverage of temperature zones when moving in a thermogradient field compared to intact individuals, and their thermopreferendum range is noticeably shifted, ranging from 25-31°C in deprived individuals versus 22-26°C in intact ones. Unlike intact individuals, sensorially deprived tetragonopterus can linger for extended periods in any zone of the thermogradient field.

Thermopreferential behavior is carried out due to numerous thermosensitive free nerve endings localized in the skin of fish, information from which enters the brain centers and is realized in the form of motor and other actions of fish (Haesemeyer, 2020). Changes in thermopreferential behavior can be a consequence of shifts or disturbances occurring at different levels of the thermoreceptor system - from peripheral (receptor) to central (brain). Thus, intact individuals of the green sunfish *Lepomis cyanellus* and goldfish *Carassius auratus* in a thermal gradient spend about 70% of their time in the zone with water temperature close to the temperature to which the fish were acclimated before the start of the experiments (5, 15, or 25°C). But after bilateral damage to the medial and lateral preoptic areas of the brain (hypothalamus), which in mammals are associated with thermoregulation, fish do not exhibit any thermal preference and move throughout the entire thermal gradient (Hardy, 1961; Nelson, Prosser, 1979).

It is known that sensory systems in animals, including fish, are in close functional interaction (Moller, 2002; Maaswinkel, Li, 2003; Devitsina, Marusov, 2007; Kasumyan, Marusov, 2007). This is manifested in the polysensory support of most forms of fish behavior, such as social, reproductive, feeding, orientational, and others (Moller et al., 1982; Pavlov et al., 1997; Pavlov et al., 2000; New et al., 2001; Braun et al., 2002; Candolin, 2003; Coleman, Rosenthal, 2006; Ernst, Di Luca, 2011; Schumacher et al., 2017; von der Emde, Zeymer, 2020). Interaction is also expressed in the compensatory morphological and functional development of intact sensory systems when animals damage/completely lose other systems or when there is a deficit of sensory input due to natural or artificially induced causes (Lessard et al., 1998; Wagner, 2001; Chapman et al., 2010). For example, in the cave form of Astyanax *Astyanax mexicanus* , which lacks vision, the lateral line and external taste system receive compensatory development. Due to large and numerous neuromasts and their higher cupula than in the terrestrial sighted form, the cave (blind) Astyanax can navigate in complete darkness, react to obstacles, determine the size and shape of underwater objects (von Campenhausen et al., 1981; Weissert, von Campenhausen, 1981; Teyke, 1990; Montgomery et al., 2001).

In cartilaginous ganoids and teleost fish, experimentally induced chronic anosmia initiates proliferation of external taste buds, leading to the restoration of the fish's ability to respond to food odors and locate their source 1.5 months after deprivation (Devitsina, Marusov, 2007; Kasumyan, Marusov, 2007). In fish used in our work, visual deprivation lasted for 3 months and could quite possibly have caused compensatory processes in the thermosensory system and led to changes in temperature preferences and related behavior. To test the hypothesis about compensatory transformations in the thermosensory system of chronically deprived fish and to find out which structural or functional mechanisms of thermoreception were affected by these processes, special studies are required. However, it is already possible to say with confidence that the differences in thermopreference behavior between intact and visually deprived individuals are a consequence of the functional relationship between the thermosensory and visual sensory systems in the subclass Cladistia. It is believed that bichirs have weak visual capabilities, which corresponds to their lifestyle (Pfeiffer, 1968; Znotinas, Standen, 2019). It can be assumed that fish with more developed visual reception will experience stronger changes in thermoregulatory behavior under the influence of visual deprivation.

One of the consequences of visual deprivation is a significant increase in the swimming activity of the Senegal bichir. Similar changes in the behavior of individuals of this species were identified when simultaneously blocking vision and the seismosensory system (lateral line) (Hainer et al., 2023). Blocking the function of neuromasts in the cave astyanax, which experiences chronic complete visual deprivation, also leads to increased swimming activity (Hassan et al., 1992). Hainer and colleagues (Hainer et al., 2023) attribute the identified disorders to the loss or deficit of sensory control over swimming speed in fish. When only one of these two sensory systems is blocked, particularly the visual one, the effect is absent, which does not contradict our data, since in Hainer and colleagues' experiments, visual deprivation was achieved by placing fish in darkness (short-term deprivation), whereas in our experiments, fish with long-term (chronic) visual deprivation were used. Increased swimming speed is exhibited by eyeless cave fish *Sinocyclocheilus tianlinensis* and *S. furcodorsalis* (= *S. tianeensis*) (Cyprinidae) compared to other representatives of this genus that possess vision (Chen et al., 2024).

Thermal selection involves spatial search and selection of places with preferred water temperature by fish and is one of the forms of orientation behavior, in which vision plays an important role for most fish (Reese, 1989; Warburton, 1990; Hughes, Blight, 2000; Braithwaite, de

Perera, 2006; Rodr í guez et al., 2021). Differences in thermal preference and motor activity found in fish experiencing chronic visual deprivation indicate the presence of complex connections between thermoreception and vision, and most likely with other sensory systems as well. Therefore, intersystem interactions, including those between visual and thermosensory systems, should be considered as an important functional adaptation that increases the efficiency and reliability of thermal preference in fish. Further development of this research direction will provide a more accurate understanding of the sensory mechanisms underlying thermoregulatory behavior in fish.

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COMPLIANCE WITH ETHICAL STANDARDS

The experiments were conducted in accordance with international principles and rules for the treatment of laboratory animals (http://oacu.od.nih.gov/regs/index.htm). The conditions of fish maintenance did not contradict the requirements of the MSU Bioethics Commission (Protocol No. 108-o dated January 16, 2020).

CONFLICT OF INTEREST

The authors of this work declare that they have no conflict of interest.

REFERENCES

Golovanov V.K. 2013a. Temperature criteria for the vital activity of freshwater fish. Moscow: Polygraph-Plus, 300 p.

Golovanov V.K. 2013b. Ecological and physiological patterns of distribution and behavior of freshwater fish in thermal gradient conditions // Journal of Ichthyology. Vol. 53. No. 3. P. 286-314. https://doi.org/10.7868/S0042875213030016

Golovanov V.K., Smirnov A.K. 2011. Features of thermoregulatory behavior of early roach juveniles *Rutilus rutilus* under thermogradient conditions // Ibid. Vol. 51. № 4. P. 551 – 558.

Devitsina G.V., Marusov E.A. 2007. Interaction of sensory systems and feeding behavior of fish // Advances in Modern Biology. Vol. 127. № 4. P. 387–395.

Zdanovich V.V. 1999. Some growth characteristics of juvenile Mozambique tilapia *Oreochromis mossambicus* at constant and variable temperatures // Journal of Ichthyology. Vol. 39. № 1. P. 105–110.

Zdanovich V.V. 2017. Behavior and motor activity of intact and sensory deprived tetragonopterus *Hemigrammus caudovittatus* in a thermogradient field // Abstracts of the VI All-Russian Conference on Animal Behavior. Moscow: KMK Scientific Press. P. 57.

Zdanovich V.V., Sataeva V.V., Kasumyan A.O. 2024. Thermal selection in sympatric bichirs: Senegal bichir *Polypterus senegalus* and Endlicher's bichir *P. endlicherii* (Polypteridae) // Journal of Ichthyology. Vol. 64. № 6.

Kapshay D.S., Golovanov V.K. 2013. Behavior and distribution of juvenile thermophilic fish in thermogradient conditions during summer and winter seasons // Bulletin of Mordovia University. № 3–4. P. 78–82.

Kasumyan A.O., Marusov E.A. 2002. Behavioral responses of minnow *Phoxinus phoxinus* (Cyprinidae) to chemical signals in normal conditions and after acute and chronic anosmia // Journal of Ichthyology. Vol. 42. № 5. P. 684–696.

Kasumyan A.O., Marusov E.A. 2007. Chemoreception in chronically anosmiated fish: the phenomenon of compensatory development of the gustatory system // Ibid. Vol. 47. № 5. P. 684–693.

Kasumyan A.O., Zdanovich V.V., Sataeva V.V. 2024. Motor activity of intact and visually deprived Senegal bichir *Polypterus senegalus* (Cladistia) at different water temperatures // Ibid. Vol. 64. № 3. P. 354–362. https://doi.org/10.31857/S0042875224030097

Konstantinov A.S., Zdanovich V.V. 1993. Some characteristics of juvenile fish behavior in a thermogradient field // Moscow University Bulletin. Series 16. Biology. № 1. P. 32–37.

Manteifel B.P. 1987. Ecological and evolutionary aspects of animal behavior. Moscow: Nauka, 270 p.

Pavlov D.S., Kasumyan A.O. 1990. Sensory foundations of fish feeding behavior // J. Ichthyol. V. 30. № 5. P. 720–732.

Pavlov D.S., Sadkovsky R.V., Kostin V.V., Lupandin A.I. 1997. The influence of photo-, thermo- and barogradients on the behavior and vertical distribution of juvenile cyprinid fish // Ibid. V. 37. № 1. P. 72–77.

Boltz J.M., Siemien M.J., Stauffer J.R. Jr. 1987. Influence of starvation on the preferred temperature of *Oreochromis mossambicus* (Peters) // Arch. Hydrobiol. V. 110. № 1. P. 143–146. https://doi.org/10.1127/archiv-hydrobiol/110/1987/143

Braithwaite V.A., De Perera T.B. 2006. Short-range orientation in fish: how fish map space // Mar. Freshw. Behav. Physiol. V. 39. № 1. P. 37–47. https://doi.org/10.1080/10236240600562844

Braun C.B., Coombs S., Fay R.R. 2002. What is the nature of multisensory interaction between octavolateralis sub-systems? // Brain Behav. Evol. V. 59. № 4. P. 162–176. https://doi.org/10.1159/000064904

Candolin U. 2003. The use of multiple cues in mate choice // Biol. Rev. V. 78. № 4. P. 575–595. https://doi.org/10.1017/S1464793103006158

Chapman B.B., Morrell L.J., Tosh C.R., Krause J. 2010. Behavioural consequences of sensory plasticity in guppies // Proc. R. Soc. B. V. 277. № 1686. P. 1395–1401. https://doi.org/10.1098/rspb.2009.2055

Chen B., Dai W.-Z., Li X.-L. et al. 2024. Wall-following – phylogenetic context of an enhanced behaviour in stygomorphic *Sinocyclocheilus* (Cypriniformes: Cyprinidae) cavefishes // Ecol. Evol. V. 14. № 6. Article e11575. https://doi.org/10.1002/ece3.11575

Christensen E.A.F., Svendsen M.B.S., Steffensen J.F. 2020. The combined effect of body size and temperature on oxygen consumption rates and the size-dependency of preferred temperature in European perch *Perca fluviatilis* // J. Fish Biol. V. 97. № 3. P. 794 – 803. https://doi.org/10.1111/jfb.14435

Coleman S.W., Rosenthal G.G. 2006. Swordtail fry attend to chemical and visual cues in detecting predators and conspecifics // PLoS ONE. V. 1. № 1. Article e118. https://doi.org/10.1371/journal.pone.0000118

Coutant C.C. 1977. Compilation of temperature preference data // J. Fish. Res. Board Can. V. 34. № 5. P. 739–745. https://doi.org/10.1139/f77-115

De Alba G., Conti F., Sánchez J. et al. 2024. Effect of light and feeding regimes on the daily rhythm of thermal preference in Nile tilapia (*Oreochromis niloticus*) // Aquaculture. V. 578. Article 740122. https://doi.org/10.1016/j.aquaculture. 2023.740122

Despatie S.-P., Castonguay M., Chabot D., Audet C. 2001. Final thermal preferendum of Atlantic cod: effect of food ration // Trans. Am. Fish. Soc. V. 130. № 2. P. 263–275. https://doi.org/10.1577/1548-8659(2001)130<0263:FTPOAC>2.0.CO;2

Díaz F., Bückle L.F. 1999. Effect of the critical thermal maximum on the preferred temperatures of *Ictalurus punctatus* exposed to constant and fluctuating temperatures // J. Therm. Biol. V. 24. № 3. P. 155 – 160. https://doi.org/10.1016/S0306-4565(99)00005-4

Ernst M.O., Di Luca M. 2011. Multisensory perception: from integration to remapping // Sensory cue integration. N.Y.: Oxford Univ. Press. P. 224–250. https://doi.org/ 10.1093/acprof:oso/9780195387247.003.0012

Fangue N.A., Podrabsky J.E., Crawshaw L.I., Schulte P.M. 2009. Countergradient variation in temperature preference in populations of killifish *Fundulus heteroclitus* // Physiol. Biochem. Zool. V. 82. № 6. P. 776 – 786. https://doi.org/10.1086/606030

Fry F.E.J. 1971. The effect of environmental factors on the physiology of fish // Fish physiology. V. 6. N.Y.: Acad. Press. P. 1–98. https://doi.org/10.1016/S1546-5098(08)60146-6

Gonçalves-de-Freitas E., Bolognesi M.C., Gauy A.C.D.S. et al. 2019. Social behavior and welfare in Nile tilapia // Fishes. V. 4. № 2. Article 23. https://doi.org/10.3390/fishes4020023

Haesemeyer M. 2020. Thermoregulation in fish // Mol. Cell. Endocrinol. V. 518. Article 110986. https://doi.org/10.1016/j.mce.2020.110986

Hainer J., Lutek K., Maki H., Standen E.M. 2023. Sensorimotor control of swimming *Polypterus senegalus* is preserved during sensory deprivation conditions across altered environments // J. Exp. Biol. V. 226. № 9. Article jeb245192. https://doi.org/10.1242/jeb.245192

Hardy J.D. 1961. Physiology of temperature regulation // Physiol. Rev. V. 41. № 3. P. 521 – 606. https://doi.org/10.1152/physrev.1961.41.3.521

Hassan El.-S., Abdel-Latif H., Biebricher R. 1992. Studies on the effects of Ca $^{++}$and Co $^{++}$on the swimming behavior of the blind Mexican cave fish // J. Comp. Physiol. A. V. 171. № 3. P. 413–419. https://doi.org/ 10.1007/BF00223971

Hochachka P.W., Somero G.N. 2002. Biochemical adaptation: mechanism and process in physiological evolution. N.Y.: Oxford Univ. Press, 466 p. https://doi.org/10.1093/oso/9780195117028.001.0001

Hughes R.N., Blight C.M. 2000. Two intertidal fish species use visual association learning to track the status of food patches in a radial maze // Anim. Behav. V. 59. № 3. P. 613–621. https://doi.org/10.1006/anbe.1999.1351

Jobling M. 1981. Temperature tolerance and the final preferendum – rapid methods for the assessment of optimum growth temperatures // J. Fish Biol. V. 19. № 4. P. 439–455. https://doi.org/10.1111/j.1095-8649.1981.tb05847.x

Lafrance P., Castonguay M., Chabot D., Audet C. 2005 . Ontogenetic changes in temperature preference of Atlantic cod // Ibid. V. 66. № 2. P. 553–567. https://doi.org/10.1111/j.0022-1112.2005.00623.x

Lessard N., Paré M., Lepore F., Lassonde M. 1998. Early-blind human subjects localize sound sources better than sighted subjects // Nature. V. 395. № 6699. P. 278–280. https://doi.org/10.1038/26228

Maaswinkel H., Li L. 2003. Olfactory input increases visual sensitivity in zebrafish: a possible function for the terminal nerve and dopaminergic interplexiform cells // J. Exp. Biol. V. 206. № 13. P. 2201–2209. https://doi.org/10.1242/jeb.00397

Moller P. 2002. Multimodal sensory integration in weakly electric fish: a behavioural account // J. Physiol. Paris. V. 96. № 5–6. P. 547–556. https://doi.org/10.1016/s0928-4257(03)00010-x

Moller P., Serrier J., Squire A., Boudinot M. 1982. Social spacing in the mormyrid fish *Gnathonemus petersii* (Pisces): a multisensory approach // Anim. Behav. V. 30. № 3. P. 641–650. https://doi.org/10.1016/S0003-3472(82)80134-6

Montgomery J.C., Coombs S., Baker C.F. 2001. The mechanosensory lateral line system of the hypogean form of *Astyanax fasciatus* // Environ. Biol. Fish. V. 62. № 1–3. P. 87–96. https://doi.org/10.1023/A:1011873111454

Nelson D.O., Prosser C.L. 1979. Effect of preoptic lesions on behavioral thermoregulation of green sunfish, *Lepomis cyanellus* , and of goldfish, *Carassius auratus* // J. Comp. Physiol. A. V. 129. № 3. P. 193–197. https://doi.org/10.1007/BF00657653

New J.G., Fewkes L.A., Khan A.N. 2001. Strike feeding behavior in the muskellunge, *Esox masquinongy* : contributions of the lateral line and visual sensory systems // J. Exp. Biol. V. 204. № 6. P. 1207–1221. https://doi.org / 10.1242/jeb.204.6.1207

Pavlov D.S., Sadkovskii R.V., Kostin V.V., Lupandin A.I. 2000. Experimental study of young fish distribution and behaviour under combined influence of baro-, photo- and thermo-gradients // J. Fish Biol. V. 57. № 1. P. 69–81. https://doi.org/10.1111/j.1095-8649.2000.tb00776.x

Pfeiffer W. 1968. Retina and retinomotor activity of Dipnoi and Brachiopterygii // Z. Zellforsch. V. 89. № 1. P. 62–72. https://doi.org/10.1007/BF00332652

Pulgar J.M., Aldana M., Bozinovic F., Ojeda F.P. 2003. Does food quality influence thermoregulatory behavior in the intertidal fish *Girella laevifrons* ? // J. Therm. Biol. V. 28. № 8. P. 539–544. https://doi.org/10.1016/j.jtherbio.2003.08.001

Reese E.S. 1989. Orientation behaviour of butterflyfishes (family Chaetodontidae) on coral reefs: spatial learning of route specific landmarks and cognitive maps // Environ. Biol. Fish. V. 25. № 1 – 3. P. 79–86. https://doi.org/10.1007/BF00002202

Rodríguez F., Quintero B., Amores L. et al. 2021. Spatial cognition in teleost fish: strategies and mechanisms // Animals. V. 11. № 8. Article 2271. https://doi.org/10.3390/ani11082271

Schakmann M., Christensen E.A.F., Steffensen J.F., Svendsen M.B.S. 2023. The influence of body size on behavioral thermal preference in Atlantic cod (*Gadus morhua*): larger fish favor colder waters // Fishes. V. 8. № 12. Article 596. https://doi.org/10.3390/fishes8120596

Schram E., Bierman S., Teal L.R. et al. 2013. Thermal preference of juvenile dover sole (*Solea solea*) in relation to thermal acclimation and optimal growth temperature // PLoS ONE. V. 8. № 4. Article e61357. https://doi.org/10.1371/journal.pone.0061357

Schumacher S., Burt de Perera T., von der Emde G. 2017. Electrosensory capture during multisensory discrimination of nearby objects in the weakly electric fish *Gnathonemus petersii* // Sci. Rep. V. 7. Article 43665. https://doi.org/10.1038/srep43665

Schurmann H., Steffensen J.F. 1992. Lethal oxygen levels at different temperatures and the preferred temperature during hypoxia of the Atlantic cod, *Gadus morhua* L. // J. Fish Biol. V. 41. № 6. P. 927–934. https://doi.org/10.1111/j.1095-8649.1992.tb02720.x

Schurmann H., Steffensen J.F., Lomholt J.P. 1991. The influence of hypoxia on the preferred temperature of rainbow trout *Oncorhynchus mykiss* // J. Exp. Biol. V. 157. № 1. P. 75–86. https://doi.org/10.1242/jeb.157.1.75

Teyke T. 1990. Morphological differences in neuromasts of the blind cave fish *Astyanax hubbsi* and the sighted river fish *Astyanax mexicanus* // Brain Behav. Evol. V. 35. № 1. P. 23–30. https://doi.org/10.1159/000115853

Vera L.M., de Alba G., Santos S. et al. 2023. Circadian rhythm of preferred temperature in fish: behavioural thermoregulation linked to daily photocycles in zebrafish and Nile tilapia // J. Therm. Biol. V. 113. Article 103544. https://doi.org/10.1016/j.jtherbio.2023.103544

Von Campenhausen C., Riess I., Weissert R. 1981. Detection of stationary objects by the blind cave fish *Anoptichthys jordani* (Characidae) // J. Comp. Physiol. V. 143. № 3. P. 369–374. https://doi.org/10.1007/BF00611175

Von der Emde G., Zeymer M. 2020. Multisensory object detection in weakly electric fish // The senses: a comprehensive reference. V. 7. Amsterdam et al.: Elsevier Inc. P. 281–297. https://doi.org/10.1016/B978-0-12-809324-5.24211-9

Wagner H.-J. 2001. Sensory brain areas in mesopelagic fishes // Brain Behav. Evol. V. 57. № 3. P. 117–133. https://doi.org/10.1159/000047231

Warburton K. 1990. The use of local landmarks by foraging goldfish // Anim. Behav. V. 40. № 3. P. 500–505. https://doi.org/10.1016/S0003-3472(05)80530-5

Weissert R., von Campenhausen C. 1981. Discrimination between stationary objects by the blind cave fish *Anoptichthys jordani* (Characidae) // J. Comp. Physiol. V. 143. № 3. P. 375–381. https://doi.org/10.1007/BF00611176

Zdanovich V.V. 2006. Alteration of thermoregulation behavior in juvenile fish in relation to satiation level // J. Ichthyol. V. 46. Suppl. 2. P. S188 –S 193. https://doi.org/10.1134/S0032945206110087

Znotinas K.R., Standen E.M. 2019. Aerial and aquatic visual acuity of the grey bichir *Polypterus senegalus* , as estimated by optokinetic response // J. Fish Biol. V. 95. № 1. P. 263–273. https://doi.org/10.1111/jfb.13724

FIGURE CAPTION

Frequency of visits by intact (◆) and visually deprived (●) Senegal bichir *Polypterus senegalus* to temperature zones of the thermal gradient field (a) and duration of stay in them (b).