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Locomotor Activity of the Intact and Visually Deprived Senegal Bichir *Polypterus senegalus* (Cladistia) at Different Water Temperatures

A. O. Kasumyan[a], V. V. Zdanovich[a, *], and V. V. Sataeva[a]

[a] *Lomonosov Moscow State University, Moscow, Russia*

**e-mail: zdanovich@mail.ru*

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Abstract—For the first time, the locomotor activity of the intact and visually deprived Senegal bichir *Polypterus senegalus* was assessed at different water temperatures (20, 25, 30 and 34°C). Using the open field test, it was shown that in intact fish, with increasing temperature, locomotor activity increases (most rapidly in the range of 20–25°C) and reaches a maximum at a temperature of 30°C, which can be close to the temperature optimum (or correspond to it) for the Senegal bichir. In visually deprived fish, locomotor activity is maximum at 20°C and decreases monotonically with increasing temperature; all indicators of locomotor activity (frequency of crossing test lines; time spent crossing the test line; distance covered by the fish; swimming speed) vary in visually deprived fish weaker than in intact ones. The differences in the behavior of intact and visually deprived fish indicate the presence of a functional relationship between vision and locomotor activity in evolutionarily ancient Cladistia.

Keywords: Senegal bichir *Polypterus senegalus*, Cladistia, water temperature, locomotor activity, visual deprivation

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INTRODUCTION

Changes in locomotor activity in responses to changing external conditions are the most important adaptation ensuring the successful existence of fish and other ectothermic aquatic organisms in the natural environment (Holyoak et al., 2008; Cooke et al., 2022). The abiotic factors that have the strongest impact on spatial movements and many other characteristics of fish behavior include water temperature. Temperature changes affect the behavior of fish in the water current and their swimming speed, initiate or interrupt migrations, modulate intra-school contacts, change the distribution of fish in water bodies and locomotor responses to various stimuli (Reynolds, 1977; Beamish, 1978; Pavlov, 1979; Goniea et al., 2006; Childs et al., 2008; Edeline et al., 2009; Welsch and Liller, 2013; Kasumyan and Pavlov, 2018; Andrzejaczek et al., 2019; Heuer et al., 2021).

In a natural environment, the influence of changing water temperature on fish is usually combined with the influence of many factors and signals—illumination, salinity, pH and turbidity of water, currents, odors, sounds, the presence of danger or food, and others. Along with the movements and distribution of fish, various functions directly related to swimming and orientation are affected by water temperature (Linløkken et al., 2010; Forsythe et al., 2012; Schlaff et al., 2014; Nakayama et al., 2018; Cooke et al., 2022; García-Vega et al., 2023). It has been shown, in particular, that fish exposed in water with different temperatures differ not only in swimming ability, but also in the ability for visual orientation—in the parameters of the optomotor reaction, as well as in such characteristics of visual reception as the critical frequency of flickering of visual landmarks and threshold illumination sufficient for the manifestation of an optomotor reaction (Pavlov, 1979). Vision is the leading sensory system for spatial orientation of fish in natural water bodies (Smith, 1985; Reese, 1989; Braithwaite, 1998; Mazeroll and Montgomery, 1998; New et al., 2001; Odling-Smee and Braithwaite, 2003; Standen et al., 2004).

A large number of papers are devoted to studying the influence of water temperature on the locomotor activity of fish. However, the information obtained concerns mainly fish inhabiting water bodies of the boreal zone, where natural changes in water temperature, for example seasonal ones, can be significant. Less data is known on fishes of the tropical zone, especially freshwater ones. Among the studied species, representatives of teleosts (Teleostei), the evolutionarily most advanced group in the class of ray-finned fishes (Actinopterygii), dominate. Less studied are the more ancient cartilaginous ganoids (Chondrostei). Polypterids (Cladistia), representing the basal group in the class Actinopterygii, have not been studied at all. Despite the fact that polypterids, which have retained many primitive characteristics, attract the

attention of many biologists in connection with the problems of the origin and phylogeny of ancient groups of vertebrates, the behavior and other aspects of the life of these tropical freshwater fish remain poorly studied.

The objective of this paper is to study the effect of water temperature and visual deprivation on the locomotor activity of the Senegal bichir *Polypterus senegalus*.

MATERIALS AND METHODS

Senegal bichirs were purchased at the Akvarif pet store (Moscow). After delivery to the laboratory, the fish were kept in 100-liter aquariums (5 ind. per aquarium) for several months; the water temperature was maintained with temperature-controlled heaters AquaEL EH-25W (AquaEL, Poland) within 23–25°C. There was no gravel or other material in the aquariums; changes in illumination corresponded to the natural daily rhythm. Microcompressors were used for aeration. The fish were fed daily until satiation with live or fresh frozen chironomid larvae (Chironomidae). Partial replacement of water in the aquariums was carried out weekly.

For the experiments, we used 10 fish with a total body length (*TL*) of 7.5–9.0 cm, weighing 5.2–6.9 g. The eye lenses of five of them were previously removed, which led to the loss of objective vision in the fish (partial visual deprivation). Before enucleation, to immobilize and reduce stress, the fish were subjected to cold anesthesia—transferred to chilled water (0°C) until they lost balance. The eye lenses were removed through a narrow cross-shaped incision in the cornea. There was no mortality in the postoperative period; food searching activity was completely restored after 4–6 weeks. Experiments on visually deprived fish were carried out 3 months after enucleation.

Locomotor activity was assessed in diffuse daylight in single fish using the open field test in an experimental aquarium (bottom dimensions 48 × 36 cm, water level 15 cm). The bottom of the aquarium was lined with test lines into squares with a side of 12 cm (12 squares in total). The side walls of the aquarium were covered with a gray screen to exclude external influence on the behavior of the fish. One day before the experiment, the fish were stopped being fed. A randomly selected individual was transferred to an experimental aquarium with a water temperature of 24°C, which was then changed using temperature-controlled heaters and maintained at the required level—20, 25, 30 or 34°C. Recording of locomotor activity began after 24 h of acclimation of the fish. Each experiment (registration) lasted 30 min, during which the number of fish crossing the test lines was visually counted. During the day, five to six experiments were carried out at intervals of 1 h. After their completion, the fish were acclimated to a temperature of 24°C and returned to the previous aquarium. The fish were used again for experiments no less than 2–3 weeks later.

A total of 85 and 60 experiments were performed, respectively, with intact and visually deprived fish. To quantitatively assess locomotor activity, it was assumed that each fish crossing the test line corresponds to 0.12 m of the distance traveled. We calculated the distance traveled in 1 h; average time spent crossing one test line; swimming speed of fish, as well as the temperature coefficient (Q_{10}) as a measure of temperature sensitivity of locomotor activity parameters according to the formula: $Q_{10} = (K_2/K_1)^{10/(t_2-t_1)}$, where K_2 and K_1—values of locomotor activity at temperature t_2 and t_1 (Peck et al., 2006). Statistical analysis was performed using the nonparametric Mann–Whitney *U* test.

RESULTS

In intact fish, locomotor activity increases with increasing temperature in the range of 20–30°C. The most dramatic increase in locomotor activity occurs when the temperature rises from 20 to 25°C—the number of test line intersections increases by 4.1 times (Fig. 1). All calculated indicators of locomotor activity change just as strongly–the time spent crossing one test line, swimming speed and distance covered by the fish. Statistical differences for all four indicators are highly significant ($p < 0.001$). Q_{10} of locomotor activity for this interval has a maximum value of 16.7. The differences in locomotor activity at temperatures of 25 and 30°C are similar, but less pronounced–approximately 1.2 times ($p < 0.05$ for all indicators) (Table 1). Q_{10} of locomotor activity for this range is 1.4, for 20–30°C—4.8. At a water temperature of 34°C, locomotor activity becomes 1.4 times lower relative to 30°C, Q_{10} decreases to 0.4.

In visually deprived fish, the dependence of locomotor activity on temperature is different. The frequency of test line crossings made by visually deprived fish at the water temperature values used differs slightly—no more than 1.4 times. The highest frequency of crossing test lines is observed at a temperature of 20°C, which exceeds the corresponding figure for intact fish by almost 4 times ($p < 0.001$). As the water temperature increases, the locomotor activity of deprived fish slowly and evenly decreases, and at temperatures of 25, 30 and 34°C, the frequency of test line crossings is lower than that of intact individuals by 1.2, 1.6 and 1.3 times, respectively ($p < 0.01$) (Fig. 1). With an increase in water temperature, the values of all calculated indicators of locomotor activity also consistently and uniformly change in deprived individuals—the swimming speed and distance covered by the fish decrease, the time spent crossing the test line increases ($p < 0.01$). The variation in all parameters is also weaker than in intact fish (Table 2). Q_{10} of locomotor activity for the ranges 20–25, 25–30, 30–34 and 20–34°C is the same and equal to 0.8.

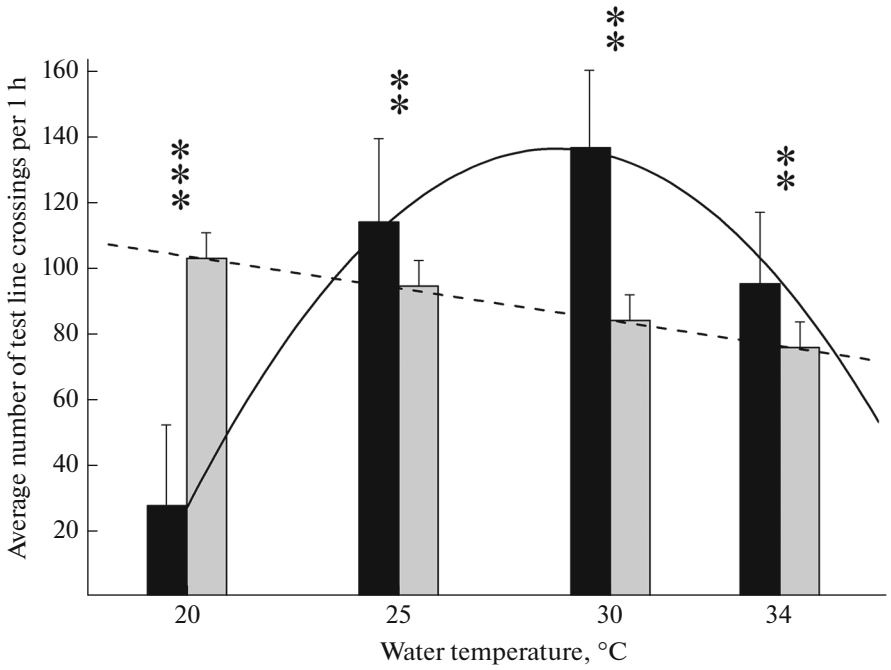

Fig. 1. Dependence of locomotor activity of the intact (■) and visually deprived (▩) Senegal bichir *Polypterus senegalus* in the open field test at different water temperatures: (⊤)—error of the mean; (—), (- - -)—polynomial trend lines. Differences in the number of crossings of test lines by intact and visually deprived fish according to the Mann–Whitney *U* test are significant at *p*: ** < 0.01, *** < 0.001.

Intact and visually deprived fish move in the aquarium mainly along the bottom and only occasionally rise into the water column or to its surface. Such rises are observed more often at high water temperatures. The swimming of fish can be interrupted by stops at the bottom of varying durations.

DISCUSSION

Intact fish. The Senegal bichir is distributed throughout almost all of equatorial Africa from Gambia and Senegal in the west to the Nile River basin in the east (Moritz and Britz, 2019). In rivers and standing water bodies in the habitat areas of the species

Table 1. Indicators ($M \pm m$) of locomotor activity of the intact and visually deprived Senegal bichir *Polypterus senegalus* in the open field test at different water temperatures

Water temperature, °C	Distance covered by fish in 1 h, m	Time spent crossing the test line, s	Swimming speed, m/min	Number of experiments
		Intact fish		
20	3.4 ± 0.7	129.0 ± 37.1	0.06 ± 0.01	17
25	13.7 ± 2.4	31.5 ± 11.2	0.23 ± 0.04	18
30	16.4 ± 1.1	26.3 ± 2.1	0.27 ± 0.02	25
34	11.4 ± 0.5	37.7 ± 1.4	0.19 ± 0.01	25
		Visually deprived fish		
20	12.4 ± 0.7***	34.9 ± 2.1***	0.21 ± 0.01***	15
25	11.4 ± 0.6*	38.0 ± 2.0**	0.19 ± 0.01**	15
30	10.1 ± 0.2**	42.7 ± 1.0**	0.17 ± 0.00**	15
34	9.1 ± 0.2**	47.4 ± 0.9**	0.15 ± 0.00**	15

$M \pm m$—mean value and its error. Differences from the corresponding indicator in intact fish according to the Mann–Whitney *U* test are significant at *p*: * < 0.05, ** < 0.01, *** < 0.001.

Table 2. Coefficient of variation in the number of test line crossings by the intact and visually deprived Senegal bichir *Polypterus senegalus* in the open field test at different water temperatures, %

Water temperature, °C	Fishes	
	intact	visually deprived
20	77.0	21.3
25	72.9	19.9
30	34.7	9.6
34	20.7	7.9

(Upper Volta), the water temperature varies throughout the year from 22 to 30°C, and the temperature also changes during the day (Pekkola, 1919; Arnoult, 1964). The Senegal bichir stays near the bottom in coastal areas overgrown with aquatic vegetation and abundant in other shelters; in the middle of the day, it prefers to rise up into a well-warmed layer of water and linger here at the edge of the aquatic thickets (Froese and Pauly, 2023). This feature indicates the important role of the temperature factor in the behavior of the Senegal bichir. The results of our research confirm that water temperature is an important external stimulus for this fish species. It was shown for the first time that an increase in water temperature leads to a significant increase in the locomotor activity of the Senegal bichir. The mobility of intact fish increases especially quickly in the temperature range of 20–25°C, when the highest value of the temperature coefficient is observed (Q_{10} = 16.7). With a further increase in temperature, locomotor activity continues to increase, but more slowly (Q_{10} = 1.4), this process ends at a water temperature of 30°C, when locomotor activity indicators reach maximum values—the fish demonstrate the fastest swimming. At higher temperatures (34°C), locomotor activity decreases (Q_{10} = 0.4). The obtained values of the locomotor activity of the Senegal bichir at different water temperatures are well approximated by a parabolic dependence (Fig. 1).

A similar nature of the dependence of locomotor activity on water temperature was also revealed for other fish species. In the juvenile roach *Rutilus rutilus*, with an increase in water temperature from 7°C, the swimming speed and length of the distance traveled increase by 2.2 times, reaching maximum values at 25°C, but at higher temperatures (28 and 31°C), these indicators are lower (Smirnov and Smirnova, 2020). In other experiments with roach, the swimming speed of fish in the temperature range from 4 to 20°C also naturally increased (Linløkken et al., 2010). In juvenile guppy *Poecilia reticulata*, the swimming speed increases 1.5 times with an increase in temperature from 17 to 29°C, but decreases with a further increase in temperature to 32°C (Kent and Ojanguren, 2015). The swimming speed of the juvenile sterlet *Acipenser ruthenus* with an increase in water temperature from 5 to 15°C becomes 1.7 times higher and decreases slightly with a further increase to 25°C (Mandal et al., 2016). A positive relationship between swimming ability and water temperature has also been found in other fish (Alsop et al., 1999; Jain and Farrell, 2003; Lee et al., 2003; Claireaux et al., 2006; Pang et al., 2011). It is believed that the increase in the swimming abilities of fish with increasing temperature may be due to a decrease in water viscosity (Lutek and Standen, 2021).

According to available data, the water temperature at which the locomotor activity of fish reaches its maximum corresponds to the temperature optimum for the life activity of the species—the temperature optimum for growth in the juvenile sterlet or the maximum swimming ability of the juvenile roach (Mandal et al., 2016; Smirnov and Smirnova, 2020). Since the Senegal bichir is most mobile and exhibits maximum swimming speed at a temperature of 30°C, it can be assumed that this temperature value is close to or corresponds to the temperature optimum of this fish species. Indirectly, the validity of the assumption is confirmed by the information that successful incubation of the Senegal bichir eggs takes place at a water temperature of 28°C (Arnoult, 1964; Bartsch et al., 1997). However, additional research is needed to strictly substantiate the value of the temperature optimum.

The open field test does not allow obtaining exact values of swimming speed, but it does provide an opportunity for comparative assessments of this parameter in fish of different species. Since the absolute values of swimming speed depend on the size of the fish, for this analysis we used the *TL*/s indicator, which for the intact Senegal bichir at a temperature of 30°C is equal to 0.055. This is significantly lower than that of other fish, the swimming speed of which was also determined by the open field test–1.3–1.9 *TL*/s in the roach at 16–25°C, 2.1–2.2 in the juvenile guppy at 23–26°C, 1.3– 1.6 in the juvenile sterlet at 24°C and different daily diets, 0.5–2.0 in several species of Black Sea fish at a temperature of 20°C (Belokopytin, 1993; Zdanovich and Pushkar, 2004; Kent and Ojanguren, 2015; Smirnov and Smirnova, 2020). However, according to the results of another study, the swimming speed of the Senegal bichir *TL* 12.8 cm at 25–26°C turned out to be significantly higher than in our study—0.837 *TL*/s; this may be due to the use of a different method of recording swimming (Hainer et al., 2023).

Deprived fish. The influence of water temperature on the locomotor activity of the Senegal bichir changes significantly after the fish lose their objective vision as a result of enucleation. In contrast to intact individuals, visually deprived individuals are most mobile at 20°C, i.e., at the lowest water temperature used. With increasing temperature, locomotor activity does not increase, but monotonically decreases (Q_{10} =

0.8) and reaches its lowest values at 34°C. Compared to intact fish, the swimming speed of deprived fish is characterized by low variability (Table 2); this may be due to the absence or limited amount of incoming visual information. The visual reception capabilities of intact polypterids are weak and correspond to the predominantly twilight-nocturnal lifestyle of these fish and the low transparency of water in their habitats, as well as the characteristics of their feeding behavior (Pfeiffer, 1968; Znotinas and Standen, 2019; Sataeva and Kasumyan, 2022). Nevertheless, the differences we identified in the locomotor activity of intact and visually deprived fish indicate that vision is apparently very important in the behavior of polypterids. This may also be indicated, for example, by the complex spawning ritual characteristic of the Senegal bichir (Bartsch et al., 1997; Britz and Bartsch, 1998). Vision may be important for polypterids when orienting themselves in space, in particular, when these fish ascend during the daytime to the upper, well-warmed and more illuminated layers of water (Pekkola, 1919; Arnoult, 1964).

We used visually deprived fish for experiments 3 months after enucleation. According to existing data, this time is sufficient for partial replacement of lost functions due to the compensatory development of sensory systems that remain intact. It has been shown that chronic bilateral anosmia causes hypertrophied development of taste perception in fish with external taste buds. 1.5–2.0 months after a complete loss of olfaction, the ability to react to food odors and successfully find their source is partially restored in anosmic fish (Devitsina and Marusov, 2007; Kasumyan and Marusov, 2007). Whether enucleation in polypterids causes the development of similar vicariation processes in other sensory systems remains unknown. The differences in locomotor activity that we discovered in the intact and visually deprived Senegal bichir convincingly indicate the presence in fish of this species, and most likely in other Cladistia, of complex relationships and connections between vision and other sensory systems and brain functions related to the control and regulation of locomotor reactions and movements of fish in space. The results of a recent study performed on intact and sensory-deprived individuals of the Senegal bichir (Hainer et al., 2023) show that separate or joint blocking of vision and the lateral line disrupts the parameters of locomotion in these fish. The authors suggest that the feedback provided by these, and possibly other sensory systems, is necessary for fish to maintain optimal swimming patterns in changing external conditions. The conclusion about the importance of obtaining a variety of sensory information about swimming for efficient locomotion of fish was previously obtained using mathematical models (Lutek and Standen, 2021).

Similar results were previously obtained for Teleostei. The Buenos Aires tetra *Psalidodon anisitsi* (= *Hemigrammus caudovittatus*) (Characidae), after visual deprivation combined with anosmia, moved in a thermogradient field in a wider temperature range than intact fish—23–31 and 22–26°C, respectively (Zdanovich, 2017). At the same time, sensory deprived individuals, unlike intact ones, could linger for a long time in any zone of the thermogradient field. Sensorily deprived and intact fish differed significantly in average preferred temperature—25.7 and 22.9°C, respectively. The mobility of these fish also differed: the distance covered by intact Buenos Aires tetra individuals under conditions of a thermogradient field was 2.6 times greater than that of sensory deprived ones. This correlates well with the results of the present study—the distance covered in 1 h at water temperatures presumably close to the chosen ones (25 and 30°C) for the intact Senegal bichir is 1.2–1.6 greater than for the sensory deprived one (Table 1).

CONCLUSIONS

It has been revealed that water temperature is an important abiotic factor influencing the locomotor activity of the Senegal bichir and, most likely, all other modern Cladistia (14 species), despite the fact that these fish inhabit tropical freshwater bodies, in which temperature changes are expressed to a much lesser extent than in water bodies of the temperate zone. The dependence of locomotor activity on water temperature in the Senegal bichir and the studied Teleostei is similar and has a dome-shaped character with an extremum at a point that apparently corresponds to the temperature optimum for the studied fish species. Chronic visual deprivation (deprivation of objective vision in fish) changes the effect of water temperature on the locomotor activity of the Senegal bichir. This indicates that the functional relationship between visual reception and locomotor activity is a property shared not only by the evolutionarily advanced Teleostei, but also by the more ancient Cladistia.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

The authors confirm that all the experiments were performed in accordance with relevant guidelines and regulations for the treatment of animals and did not cause harm to fish involved in research. The method used in this study was approved by the Lomonosov Moscow State University Bioethic Committee (Protocol No. 108-0).

CONFLICT OF INTEREST

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

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