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Swimming performance of epigeal and hypogeal species of Characidae, with an emphasis on the troglotrophic *Stygichthys typhlops* Brittan & Böhlke, 1965

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Abstract:

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Swimming performance of fish constitutes a good ecophysiological tool to evaluate the ability of species to use different types of habitats. In order to understand how the swimming performance is related to the hydraulic environment, we compared the critical velocity of five fish (Characidae): *Stygichthys typhlops* (groundwater troglotrophic); *Piabina argentea* and *Bryconamericus stramineus* (riverine); *Hemigrammus marginatus* (generalist, found in rivers and floodplains) and *Psellogrammus kennedyi* (lacustrine). Swimming speed tests were performed in a respirometer-type apparatus. Total body length was the variable that best explained the maximum speed attained by all species under study. The critical swimming speed values (in body lengths per second) for each species were as follows: *P. argentea* (13.75); *B. stramineus* (9.32); *H. marginatus* (6.32); *P. kennedyi* (4.00); and lower in hypogeal species, *S. typhlops* (3.31). All data of this study suggest a strong correlation between swimming performance and the hydraulic environment in which the species are found. The riverine, generalist and lacustrine species (the troglotrophic being included in the last group) showed a trend toward a decrease in speed.

Keywords: characins; troglotrophic; critical swimming speed; fish performance; São Francisco basin; Brazil

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INTRODUCTION

Swimming performance studies are relevant in evaluating the influence that different environmental conditions have on fish, as well as the survival of fish in a given ecological system (Plaut, 2001). Such studies can also increase the understanding of ecological factors related to the establishment of a certain species in an environment with specific hydraulic characteristics.

The subterranean fish (troglomorphic and non-troglomorphic) present a wide distribution throughout the world, occurring in several types of environments such as the phreatic and karstic aquifers (including the epicarst), hyporheic habitats and base level courses (Bichuette & Trajano, 2010), and most of the

knowledge of those species arises from caves (Weber et al, 1996). About 150 described hypogeal species are distributed in those environments (Proudlove, 2010), and in Brazil that ichthyofauna represents an expressive diversity, with about 25 species (Trajano & Bichuette, 2010).

Although some studies conducted with species hypogeal have not specifically focused on the swimming performance, some studies in that line have been contributing to the understanding of that important activity in fish, for example the natatory behavior of amblyopsids (Poulson & White, 1969) and the swimming of *Astyanax fasciatus* as an orientation element in its surroundings (Holbrook et al., 2007; Windsor et al., 2008, 2010a,b). In comparative studies of hypogeal and epigeal species, in general, many cave fish studied presented natatory behaviors completely different from their epigeal relatives, where they are oriented mainly by vision (Parzefall, 1996).

The swimming performance of fish can fall into one of three general categories: sustained swimming, prolonged swimming, or burst swimming. Sustained swimming occurs at relatively slow speeds and utilizes

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primarily red muscle fibers that are fueled by energy derived from the aerobic metabolism (Beamish, 1978). This allows fish to maintain sustained swimming velocities for long periods (at least 200 min) without fatiguing (Beamish, 1978). Burst swimming involves white muscle fibers that utilize energy derived from anaerobic processes to attain relatively high speeds for less than 15–20 s (Beamish, 1978). Prolonged swimming covers a spectrum of velocities between sustained and burst swimming, using red (aerobic) and white (anaerobic) muscle fibers in concert.

Prolonged swimming speed is the type of swimming speed that is most commonly measured in laboratory. The main subcategory of prolonged swimming speed is critical swimming speed, which was first defined and employed by Brett (1964). Critical swimming speed corresponds to the maximum speed (V_{max}) a fish is able to maintain in a flow whose speed is increased (ΔV) at predetermined time intervals (Δt). Since it was first proposed, critical swimming speed has been the subject of numerous studies (Hammer, 1995), which have allowed detailed comparisons to be drawn among many species in terms of their swimming performance.

The freshwater ichthyofauna of the Neotropical region is the most diverse in the world (Lowe-McConnell, 1999). However, studies of swimming performance are available for few migratory species, with the objective of creating a basis for the use of fish passage systems (Santos, 2007; Santos et al., 2007; 2008) and to understand the perception of objects in the flow fields using the lateral line system (Holbrook et al., 2007; Windsor et al., 2008, 2010a,b).

Among South American fish, those of the order Characiformes are noteworthy and the order includes herbivorous, detritivorous, and carnivorous species, and some of these are highly specialized (Britski et al., 1999; Lowe-McConnell, 1999).

In Characidae there is considerable diversification among the group in relation to the different environments with which they are associated, including the riverine species, lacustrine species and subterranean species (which inhabit phreatic zones).

Stygichthys typhlops is one of only two troglolobiotic species in the Characidae (Figure 1E). This species

has strong regressive characteristics such as the loss of circumorbital bones, which suggests a much more advanced stage of specialization for the subterranean environment than that observed in the other species, such as the Mexican blind cavefish, *Astyanax fasciatus*, which displays only partial fragmentation of these bones (Romero & Paulson, 2001). This characteristic is strongly associated with the loss of eyes among cave-dwelling fish (Romero & McLeran, 2000). Due to its high degree of specialization, limited geographic distribution, and habitat modification, as well as to being only the second troglolobiotic characid, it is notable among subterranean ichthyofauna (Moreira et al., 2010). Most of the information regarding the species, including population aspects, habitat characteristics, reproduction and feeding remain unknown. Although information regarding *S. typhlops* habitat is scarce (Romero & McLeran, 2000), Moreira et al. (2010) have suggested that the occurrence of the species is associated with a single subterranean drainage basin (small river), and the species is critically endangered due to its high endemism.

The aim of the present study was to provide information on the swimming performance of *Stygichthys typhlops* and to compare with different species of Neotropical fish (Characidae) in terms of their speed and determine whether the hydraulic environment was able to influence the swimming performance of the species tested. Because morphological variations can affect swimming performance (Breda et al., 2005) and habitat use (Fulton et al., 2005), we chose to study five species that presented the same ecomorphological pattern.

METHODS

Species studied

We tested the swimming performance of four epigeal species (*Piabina argentea* (Figure 1A), *Bryconamericus stramineus* (Figure 1B), *Hemigrammus marginatus* (Figure 1C) and *Psellogrammus kennedyi* (Figure 1D)) and one hypogeal species (*Stygichthys typhlops*) (Figure 1E), all of which belong to the order Characiformes. These species occur in riverine, lacustrine and phreatic zones and are included in the *incertae sedis* group of the Characidae.

Averaging approximately 7 cm in length, *P. argentea*, and *B. stramineus*, are widely distributed in the São Francisco River and Paraná River basins (Lima et al., 2003). Both are lotic species that preferably inhabit rivers and streams (Casatti & Castro, 1998; Alves & Pompeu, 2001).

H. marginatus, which grows to maximum length of 4.5 cm, is widely distributed in South America, occurring in the São Francisco River, Paraná River, Paraguay River, Orinoco River, Guaporé River, and Amazon River basins (Lima et al., 2003). It is a generalist, lentic species that inhabits small rivers and floodplains (Alves & Pompeu, 2001; Langeani et al., 2007).

Distributed throughout the São Francisco River and Paraguay River basins, the lentic species *P. kennedyi* can grow to 5.9 cm in length (Lima et al., 2003) and is found in floodplains (Alves & Pompeu, 2001).

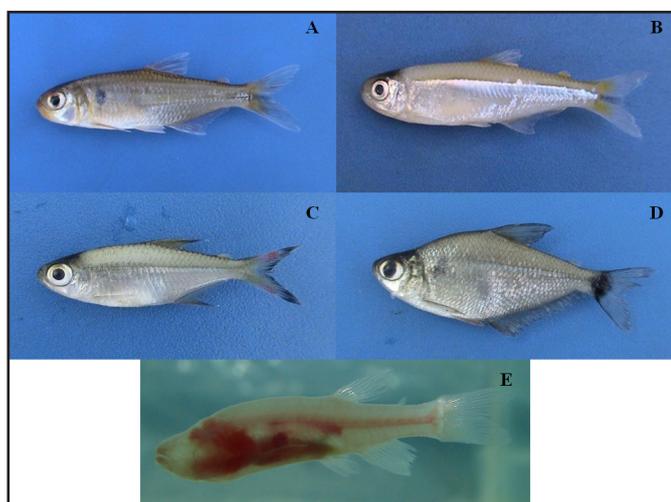


Fig. 1. Fish species tested in this study.

Locally known as piaba-branca or piaba-cega (“white cavefish” or “blind cavefish”), *S. typhlops* is a troglolithic species that occurs in phreatic zones in the Jaíba region of northern Minas Gerais, a state in southeastern Brazil. The distribution of *S. typhlops* is limited to that area, at the drainage basin of Escuro Creek, a tributary of the Verde Grande River, in the upper São Francisco River region. The species was accidentally discovered in 1962, during groundwater pumping, being subsequently rediscovered by Moreira et al. (2010).

Sampling

The fish were collected from the São Francisco River and Grande River basins, in the state of Minas Gerais between september and october 2008, except for *S. typhlops* (june 2008). *P. argentea* individuals were collected from the Curimataí River (17°59'33.3"S, 44°10'48.2"W), in São Francisco basin and sampling was carried out with the aid of hand trawl nets and seines. *B. stramineus* individuals were captured in the Grande River (21°08'39.0"S, 45°02'14.2"W), by means of hand trawl nets and seines. *H. marginatus* and *P. kennedyi* individuals were collected from the Olaria lake in the floodplains of the das Velhas River (17°36'53.6"S, 44°40'35.6"W), using seines. *S. typhlops* individuals were collected from a well on the Lajeado Farm (15°24'41.7"S; 43°45'19.7"W), located in north of the state of Minas Gerais, in São Francisco basin. The well is located at the bottom of a sinkhole, approximately 3 m below ground level, where groundwater emerges from among the rocks. For many years, the local residents used the well for irrigation. The well is currently deactivated. *S. typhlops* individuals were captured using hand nets.

The fish were transported in aerated plastic containers at controlled temperatures. In the laboratory, the fish were acclimatized and transferred to fish tanks, and the temperatures were similar to those at the collection sites (19-20°C).

To avoid any loss of swimming performance, the fish were maintained in the laboratory for no more than 7 days before testing.

Experimental procedure

An experimental apparatus, based on the Brett respirometer, was constructed in order to test the swimming performance of the fish (Figure 2). The apparatus consisted of a flume, in which the fish were swim against the current generated by a centrifugal pump (Figure 2A).

The main tube was composed of three sections. Two of the sections were made of PVC and one of the sections (the central part of the tube), where the fish were confined, was made of acrylic (Figure 2B), which allowed the swimming visualization. The fish were introduced via a T-junction with an upward positioned intake (Figure 2C) and removed via a T-junction with a downward positioned outtake. The fish were confined in the central part of the tube by two screens (Figure 2D). The polyvinyl chloride tubes were connected to the two ends of the acrylic tube in order to reduce the interference of the pumps and the drain.



Fig. 2. General view of the apparatus and its components.

To determine water discharge, the apparatus was equipped with an electromagnetic flowmeter (Figure 2E) and the flow was changed by frequency converter (Figure 2F), which allow to increase the mean velocity in small steps of values (1 cm/s).

The critical swimming speed tests, or increasing velocity tests, were performed based on the experimental procedure described by Brett (1964). We tested 20-27 individuals of the epigeal species and 12 individuals of the hypogeal species in order to ensure that a wide range of sizes were being tested (Figure 3). Fewer *S. typhlops* individuals were tested due to the smaller size of this population.

After the fish had adapted to the temperature of the water in the apparatus and had been introduced into the test section, the test began, with the pumps at low rotation speed (5 cm/s). After the first 5 min, the mean velocity was increased, in 5 cm/s increments (ΔV), at 5-min intervals (Δt). These incremental values were based on the speed control options offered by the apparatus and the total time of the test. We measured how long the fish were able to swim at that speed (V_{max}) before suffering fatigue. This was considered the moment when the fish were no longer able to stay in the test section, after several bursts of swimming activity.

The values of critical swimming speed were calculated with the following formula (equation 1):

$$V_{crit} = V_{max} + \frac{t_{max}}{\Delta t} \times \Delta V$$

where V_{max} is the maximum speed (m/s), ΔV is the increase in speed (m/s), Δt is the time interval (s), and t_{max} is the swimming time during the last time interval (s).

Data analysis

During each test, water quality parameters such as dissolved oxygen, pH and temperature were monitored. After the tests, the fish were weighed and measured: total length – TL (distance from snout to end of caudal peduncle); standard length – SL (distance from snout to end of caudal fin); maximum height and maximum width. Weights and lengths are expressed in grams and centimeters, respectively.

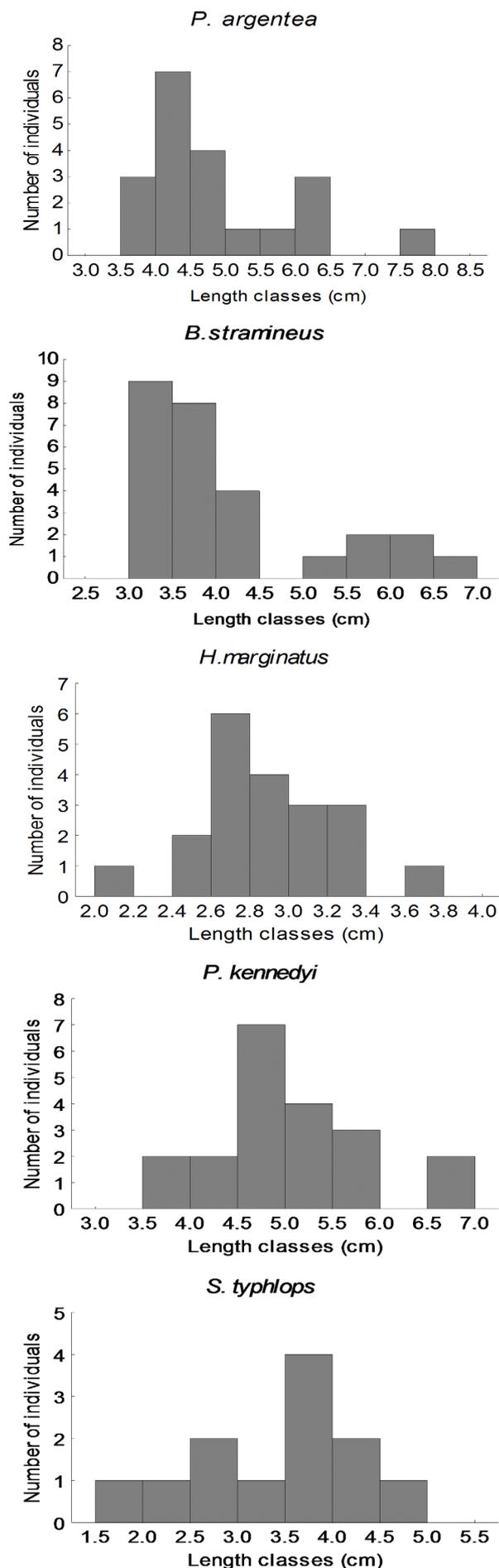


Fig. 3. Number of fish tested to determine critical swimming speed, by length class.

The solid blocking effect occurs due to the obstruction of the flow by the body. In this case the fish block the water flow in the test section and, according Webb (1975) equations (2) can be applied for swimming studies inside hydrodynamics apparatus:

$$V_{corrected} = \frac{V_{measured} K_3 \tau_1 (\text{fish volume})}{C^{3/2}}$$

Where $V_{measured}$ is the critical measured speed (m/s), K_3 is a dimensionless factor of the body shape (Pope & Hae, 1966), τ_1 is dimensionless factor of the test section layout (for circular sections $\tau_1 = 0.8$ cm (Pope & Hae, 1966)), C is the cross-sectional area of the tunnel (cm²) and Vol is the fish volume (cm³). According to Pope & Hae (1966), a good approximation for volume of a circular revolution solid (cm³) is equation (3):

$$Volume = 0,45e^2L$$

In this study, e (cm) is the maximum width of the fish (the mean between the maximum width and weight) and L (cm) is the total length of the fish.

The relationship between critical swimming speed and fish length (total and standard length) and the relationship between critical swimming speed and fish weight were tested by linear regression. Relative velocities in length per second were compared among species using ANOVA. Variables with non-normal distribution were transformed into their natural logarithms. All analyses were performed using the Statistica software (Statsoft, 2009).

RESULTS

In all tests performed, the quality of the water in the experimental apparatus was satisfactorily maintained, with dissolved oxygen concentrations higher than 5 mg/L and pH ranging from 6 to 7. The temperatures (°C) during the tests were: *P. argentea* (20.3±1.07); *B. stramineus* (20.6±1.14); *H. marginatus* (20.9±0.91); *P. kennedyi* (20.0±1.06) and *S. typhlops* (19.8±0.30).

We analyzed the behavior of the fish as they attempted to avoid contact with the confining screen downstream. This behavior consisted of short, rapid bursts of swimming, with strong forward propulsion, similar to the behavior observed during burst swimming, which is commonly evaluated under laboratory conditions (Beamish, 1978). This movement was observed in all species, in individuals belonging to different length classes. This type of swimming occurred at a speed that was close to the maximum speed limit that each species was able to attain: *P. argentea* (mean 0.66 m/s); *B. stramineus* (0.37 m/s); *P. kennedyi* (0.20 m/s); *H. marginatus* (0.18 m/s) and *S. typhlops* (0.11 m/s).

Significant correlations were observed between critical swimming speed and the size of the fish tested, as well as between critical swimming speed and the weight. Total length was the variable that best explained critical swimming speed, and this correlation was significant for all species evaluated (Figure 4, Table 1). Standard length and weight were also significantly related to critical swimming speed in all but two species (*H. marginatus* and *P. argentea*), in which only standard length was significantly related to critical swimming speed.

Table 1. Relationship between the critical swimming speed (CSS) of the species tested and the variables "total length" (TL), "standard length" (SL) and "weight" (W), as well as the equations between TL.

Species	TL			SL		Weight	
	r ²	p	Equations	r ²	p	r ²	p
<i>Piabina argentea</i>	0.37	< 0.01	CSS = 3.02 + 0.73 Log TL	0.38	< 0.01	0.22	0.03
<i>Bryconamericus stramineus</i>	0.60	< 0.01	CSS = 1.16 + 1.7 Log TL	0.60	< 0.01	0.59	< 0.01
<i>Hemigrammus marginatus</i>	0.22	< 0.05	CSS = 1.54 + 1.2 Log TL	0.12	0.12	0.22	0.03
<i>Psellogrammus kennedyi</i>	0.68	< 0.01	CSS = 0.4 + 1.59 Log TL	0.68	< 0.01	0.67	< 0.01
<i>Stygichthys typhlops</i>	0.72	< 0.01	CSS = 1.15 + 1.03 Log TL	0.73	< 0.01	0.46	< 0.01

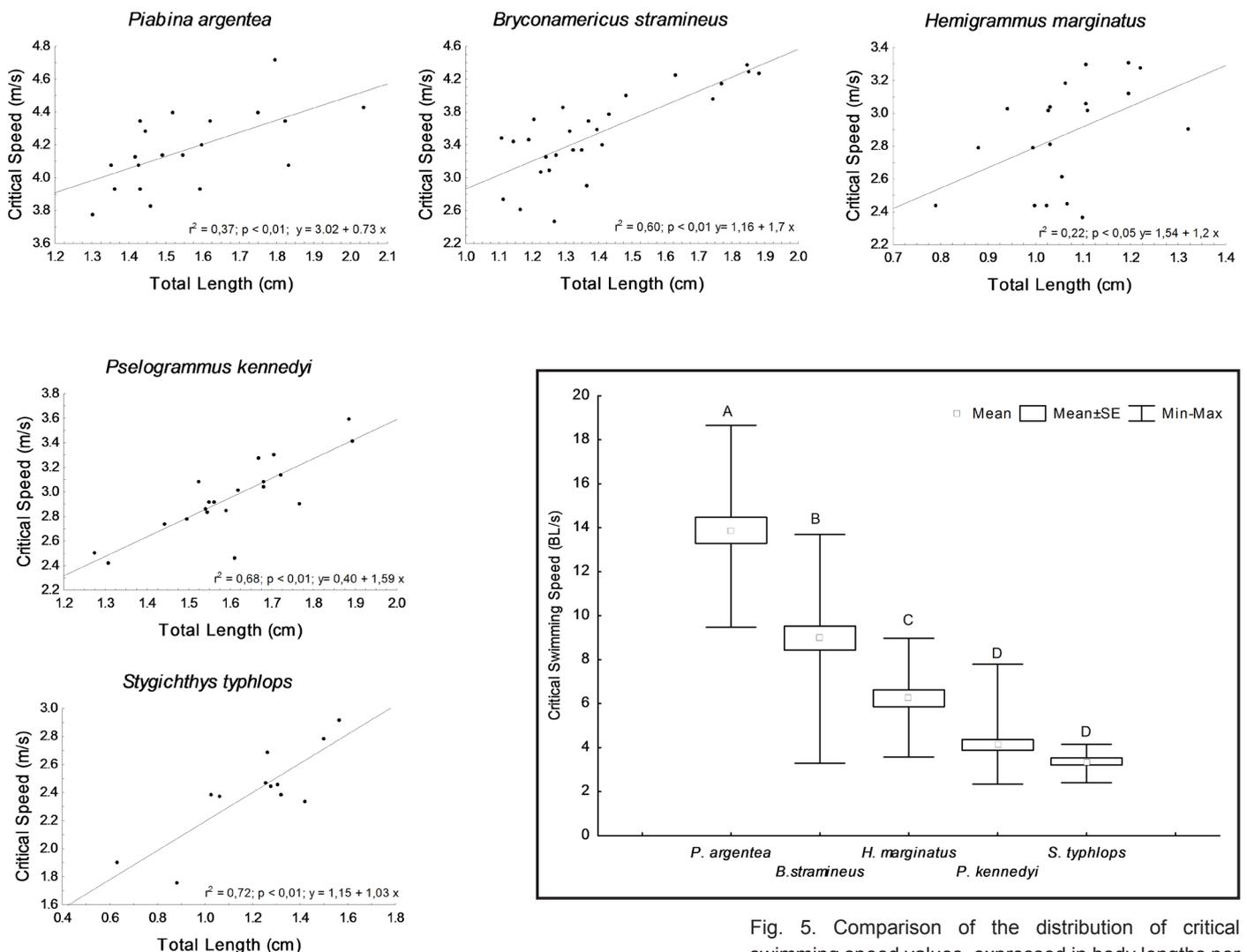


Fig. 4. Relationship between the critical swimming speed (cm/s) (log) and total length (cm) (log) of the species analyzed.

Fig. 5. Comparison of the distribution of critical swimming speed values, expressed in body lengths per second (BL/s), for each of the species tested. Different letters indicate significant differences in speed.

When the relative velocity, expressed in body lengths per second (BL/s), were compared, *P. argentea* showed the highest value (13.75 BL/s), followed by *B. stramineus* (9.32 BL/s), *H. marginatus* (6.32 BL/s), *P. kennedyi* (4.00 BL/s), and *S. typhlops* (3.31 BL/s). Significant differences were observed for all species except the last two. *S. typhlops* also showed the least variation in swimming performance among the species tested (Figure 5).

DISCUSSION

Historically, studies of the swimming performance of fish have principally focused on species from temperate climates (Jones et al., 1974; Beamish, 1978, 1981; Kolok, 1992; Hammer, 1995; Plaut, 2001; Mateus et al., 2008), and in the Neotropical region have focused mostly on migratory fish species (Santos et al., 2007; 2008). Studies on the swimming behavior of subterranean species were performed only for *Astyanax fasciatus*, and have focused on hydrodynamic imaging (Holbrook et al., 2007; Windsor et al., 2008, 2010a,b). Comparative studies on swimming performance of epigeal and hypogeal fish species had never been conducted.

Recent studies about fish swimming show differences between the fish speeds measured in flumes and the fish speeds observed in field (Peake, 2004). The reasons may be due to the fact that confined fish will not swim to complete physiological exhaustion or to differences in the energetic costs, associated with confined and unconfined swimming (Peake, 2004) and related to the use of different gaits during the tests that marks the switch from aerobic to anaerobic power output (Svendsen et al., 2010). Critical swimming speed has little biological significance, because the gradual increases in water velocity applied in laboratory tests are not encountered in nature. However, this experimental methodology has been considered a powerful tool to compare species in terms of their swimming performance (Hammer, 1995), because the experiment is easy to standardize and perform in a laboratory.

The strong propulsion type of swimming behavior (without the use of different gait) - which was observed for all size ranges - generally occurred during the second half of the test period. According to Beamish (1978), fish can swim at this speed only for short periods of time (< 20 s). This burst of speed is essential for the survival of many species, being used as a facilitator for the capture of prey, escape from predators, or negotiation of rapid-flow sections of rivers (Beamish, 1978).

The strong correlation between critical swimming speed and total length reflects the importance of the caudal fin, one of the propulsion elements in fish that present locomotion patterns of the subcarangiform type (Webb, 1975), which is the case of the species evaluated in the present study. The great influence of this variable on the swimming performance of fish had previously been observed in two other Neotropical species already studied - *Pimelodus maculatus* and *Leporinus reinhardti* (Santos et al., 2007; 2008) - both of which present the same locomotion pattern. Body length is one of the most important characteristics

that influence the swimming performance of fish (Beamish, 1978; Hammer, 1995; Plaut, 2001) and has been positively correlated with water velocity (Watson & Balon, 1984; Wikramanayake, 1990).

In the present study, the relative speed (BL/s) developed by the different species was clearly dependent on the conditions of the flow as observed by Fulton et al. (2005). The speed attained by the species that are typically found in lotic environments - *P. argentea* and *B. stramineus* - constituted the highest critical swimming speed values (in BL/s) ever obtained in laboratory experiments involving freshwater species (Figure 5). These values were higher than those found by Santos et al. (2007, 2008) for the Neotropical migratory species *P. maculatus* and *L. reinhardti*, which attained speeds of approximately 6 and 8 BL/s, respectively. This might be due to the fact that these species often occupy environments in which the speed of the current varies.

Although the *H. marginatus* and *P. kennedyi* individuals analyzed in the present study were captured in the same lake, *H. marginatus* individuals (which can also be found in lotic systems) swam at intermediate speed (Figure 5), which was nevertheless higher than that of *P. kennedyi* individuals (the occurrence of which is limited to floodplains) (Alves & Pompeu, 2001).

Body shape can explain the low speeds attained by *P. kennedyi* individuals, whose bodies are laterally compressed and taller than those of the remaining individuals tested in the present study, which had lower, fusiform bodies (Wikramanayake, 1990). Since *P. kennedyi* individuals occur in lakes with abundant submerged vegetation, this morphology can be related to maneuverability in situations of capture of prey and escape from predators (Breda et al., 2005). Undulatory swimmers use the mid-dorsal and mid-ventral fins more than their other fins. These organisms are specialized for precise maneuvers such as those executed amid tangled aquatic vegetation (Breda et al., 2005; Hildebrand & Goslow, 2006), since tall, laterally compressed, bodies are inversely correlated with high speed (Wikramanayake, 1990). The speed values for this species were close to those observed for *S. typhlops*, suggesting that the lake and the subterranean environment inhabited by the species presented similar hydraulic conditions (Figure 5). During the process of specialization of the species for the conditions of the subterranean environment (as evidenced by aspects such as the lack of eyes and pigmentation), there are indications of a swimming specialization for the velocity of groundwater.

Previous studies have indicated that faster swimming blind cave fish would enhance their ability to detect their surroundings (Teyke, 1989). However, studies on hydrodynamic imaging by blind Mexican cave fish (*Astyanax fasciatus*) have indicated that, in still water with no environmental noise, the relative change in the stimulus to the lateral line is only weakly affected by swimming speed, and at higher swimming speeds the predicted detected distance actually decreases (Windsor et al., 2008a, 2008b).

Of the species studied, *S. typhlops* presented the smallest swimming performance, the smallest intraspecific differences in swimming performance

in BL/s, and the explanatory power of body size (for the speed attained) was therefore high. This might be due to the greater stability of the environment in which the species lives, where groundwater velocity is probably low and relatively constant. The low speed and small variation observed among individuals might correspond to the specialization of the species for the subterranean environment. This reflects a possible advantage of mean swimming speed over extreme swimming speed, because extreme swimming is energetically costly and might be disadvantageous. A reduction in extremely high swimming speeds for an environment with low discharge can represent a major economy of energy for the individuals. Since food resources are generally scarce in the subterranean environment, a reduction in metabolic rates can represent a positively selected condition in these environments (Culver, 1982). A reduction in metabolism can directly reflect on mobility and, consequently, on a reduction in high speeds. The low swimming performance of *S. typhlops* might be evidence of the hydrodynamics in the phreatic zone, a habitat about which there is little information. The occurrence of *S. typhlops* in this environment suggests that measures should be adopted to ensure appropriate management of soil and groundwater use, thereby ensuring the conservation of the species.

The determination of the swimming performance of fish constitutes a good ecophysiological tool to evaluate the ability of species to use different types of habitats according to their speed (Plaut, 2001), indicating a division of the use of space. In addition, studies conducted in this area reinforce the role of hydraulic influence in the appearance of certain species that tolerate high discharge (Langerhans et al., 2003). In the present study, the comparison of different species from the same family, with the same swimming pattern (subcarangiform), and existing in different hydraulic environments showed that swimming performance can vary widely among species, probably in response to different environmental conditions as suggested by Fulton et al. (2005).

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