The use of morphometric analysis to predict the swimming efficiency of two Neotropical long-distance migratory species in fish passage

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This study investigated the external body morphology (based on morphometric data) and the swimming efficiency in fish passages (based on the ascent time in a fish ladder) of two Neotropical long-distance migratory species. The fish were collected in the fish ladder of the Porto Primavera Hydroelectric Power Plant (known as Engenheiro Sergio Motta), upper Paraná River, Brazil. The species differ in several morphometric ratios related to swimming performance. *Prochilodus lineatus* exhibited a higher muscle ratio and caudal fin length ratio. However, *Leporinus elongatus* showed higher values for the fineness ratio, a higher length from snout to pectoral fin base ratio, and a higher caudal peduncle depth factor. Although both species show good swimming performance, the characteristics listed above may enable *L. elongatus* to apply greater power and propulsion, allowing it to reach a high swimming speed and to exhibit greater efficiency than *P. lineatus*. *Leporinus elongatus* moves faster than *P. lineatus* and has a lower mean ascent time (1.39 hours) than *P. lineatus* (3.76 hours). *Prochilodus lineatus* would require a somewhat longer time to pass through the fish ladder.

Este estudo investigou a relação entre a morfologia externa do corpo (baseado em dados morfométricos) e eficiência de natação em passagem para peixes (baseado no tempo de ascensão em uma escada para peixes) de duas espécies neotropicais migradoras de longas distâncias. Os peixes foram coletados na escada para peixes da Usina Hidrelétrica de Porto Primavera (conhecida como Engenheiro Sérgio Motta), alto Rio Paraná, Brasil. As espécies diferem em algumas razões morfométricas referentes ao desempenho de natação: *Prochilodus lineatus* apresentou valores mais elevados para razão muscular e razão do comprimento da nadadeira caudal. No entanto, *Leporinus elongatus* apresentou valores mais elevados para razão fineza, para razão do comprimento do focinho à base da nadadeira peitoral e para fator de largura do pedúnculo caudal. Embora ambas as espécies tenham um bom desempenho natatório, essas características podem permitir a *L. elongatus* aplicar uma maior potência e propulsão, permitindo atingir velocidades de natação elevadas e apresentar uma melhor eficiência em relação a *P. Lineatus*. *Leporinus elongatus* movimenta-se mais rápido, com um tempo médio de ascensão (1,39 horas) inferior ao de *P. lineatus* (3,76 horas), que requer um tempo um pouco maior para passar através da escada para peixes.

Key words: Fineness ratio, Fish swimming, Fishway, Morphology, Swimming performance.

Introduction

Most of the major rivers in South America have been severely segmented by dams, and this is particularly the case for the Paraná River Basin. The management actions taken to minimize the impacts of dams on migratory species in South American river systems include the construction of fish passages, fishery control and stocking (Agostinho *et al.*, 2008; Pompeu *et al.*, 2011). Fish passage systems, especially fish ladders, have been deployed in hydropower projects, and the challenge that they must meet is to mitigate the effects of the blockage of the river by the dam in a way that provides passage routes that are both safe and effective (Castro-Santos & Haro, 2010) for Neotropical migratory species.

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The fish of the Paraná River Basin show diverse migratory patterns (Makrakis *et al.*, 2012), and fish species could react differently to obstacles that hinder migration. Despite the importance of the characteristics of Neotropical migratory species, including their behavior, morphology, physiology, and capacities, these characteristics have been ignored in formulating design criteria for fish passages in Brazil. The factor of greatest concern in fish passage design is the swimming performance of migratory species (Beach, 1984; Santos *et al.*, 2008). This factor is considered one of the primary determinants of survival because it defines the ability of the fish to conduct activities in which swimming is involved (Beamish, 1978; Plaut, 2001). Swimming performance can be influenced by the locomotion pattern, body size, shape, physiology, temperature and behavior (Beamish, 1978; Videler & Wardle, 1991; Hammer, 1995) and can limit the use of the habitat by a species (Sambilay, 1990; Bandyopadhyay *et al.*, 1997; Gerstner, 1999).

The relationship between swimming performance and body morphology is an appropriate topic to consider in evaluating fish functional anatomy because performance depends on the drag force and on propulsion (Videler, 1993). This relationship influences the capacity of the fish to maintain its position in flowing water. In addition, this topic is relevant to the acquisition of food and the avoidance of predators (Videler, 1993), as well as to migration success (Fisher & Bellwood, 2003). Many morphological traits of the body of a fish are considered important for defining the swimming capacity, including the aspect and muscle ratios (Sambilay, 1990; Fisher *et al.*, 2000), caudal peduncle depth factor (Webb & Weihs, 1986), propulsive ratio (Fisher *et al.*, 2000), caudal fin length ratio (Nanami, 2007), and fineness ratio (Bainbridge, 1960; Webb, 1975; Blake, 1983; Scarnecchia, 1988). The body shape and the fin size can accurately indicate the behavior, swimming mode and habitat preferences of fish (Keast & Webb, 1966; Webb, 1984), providing a more accurate understanding of the fish's body shape and its structure and functions (Winemiller, 1991).

Several studies have explored the relationship among habitat selection, morphology and swimming capacity (*e.g.*, Ohlberger *et al.*, 2006; Fisher & Hogan, 2007; Nanami, 2007; Aedo, 2008), and some have correlated habitat use with morphological characters for Neotropical fish species. However, studies of the swimming performance of these species have been conducted only recently, and this information is available for two migratory species: *Leporinus reinhardti* (Characidae) and *Pimelodus maculatus* (Pimelodidae) (Santos *et al.*, 2007; 2008). Furthermore, information on the functional relationships associated with morphology and with behavior in fish passages remains scarce.

Given that morphological characteristics can be reliably used to predict fish swimming performance, this study aims to investigate the external body morphology (based on morphometric data) and swimming efficiency in fish passages (based on the ascent time in a fish ladder) of two Neotropical long-distance migratory species, *Leporinus elongatus* Valenciennes, 1850, known as piapara, and *Prochilodus lineatus* (Valenciennes, 1837), known as curimbata. These species are

long-distance migrants in the Paraná River Basin (Agostinho *et al.*, 2007; Makrakis *et al.*, 2012), moving upstream in the Paraná River to reproduce (Agostinho *et al.*, 2003). Both species are highly important for fisheries. They have been observed in the fish passage systems along the Paraná River, including the fish ladder at the Porto Primavera Hydroelectric Power Plant (Makrakis *et al.*, 2007a) and Piracema Canal, a lateral channel at Itaipu Dam (Makrakis *et al.*, 2007b). Progress in the knowledge of Neotropical migratory species may facilitate research on swimming performance and on the planning of future fish passage systems.

Material and Methods

Study area

This study was conducted at the fish ladder (Fig. 1) of the Porto Primavera Hydroelectric Power Plant, also known as Engenheiro Sérgio Motta, belonging to Companhia Energética de São Paulo (CESP). The site is located on the upper Paraná River on the border between São Paulo and Mato Grosso do Sul States, Brazil. The fish ladder (weir and orifice type) is located on the left side of the dam and is 520 m long. It consists of fifty concrete weirs forming pools 5 m wide x 2 m high. These structures aid the fish to reach the reservoir (for details see Makrakis *et al.*, 2007a).

Morphological characterization

The specimens (40 fish of each species) of *Leporinus elongatus* and *Prochilodus lineatus* (Fig. 2) were caught between November 2007 and October 2009 in the fish ladder with seine and casting nets. The total length of the specimens ranged from 40.1 to 54.5 cm for *L. elongatus* and from 42.7 to 53.7 cm for *P. lineatus*.

The fish caught were anesthetized (benzocaine-75 mg/l). Each fish was photographed in a lateral position with a Sony Cybershot DSC-H50 camera with 9.1 megapixels. Data for morphometric measurements were obtained from the digital images of the fish according to Fisher & Hogan (2007). These measurements were taken to the nearest 0.1 mm with UTHSCSA Image Tool 3.0 software. The morphometric variables used are shown and defined in Fig. 3.

The total (TL) and standard length (SL) and body maximum width (BMW, measured at the widest region) were also measured to the nearest 0.1 mm with a digital caliper. This procedure was performed for TL and SL to obtain the true values for use in calibrating the unit of measurement (mm) for the images obtained from the software. The BMW was measured to calculate the fineness ratio because this width measurement could not be obtained from the images with the software.

The fish were released in the fish ladder after the completion of the procedures.

A total of 13 morphometric measurements (expressed in mm) were analyzed (Fig. 3; Table 1). These measurements included lengths (total length, standard length, snout length to the base of pectoral fin, and caudal fin length), widths (maximum body width), heights (maximum body height, caudal
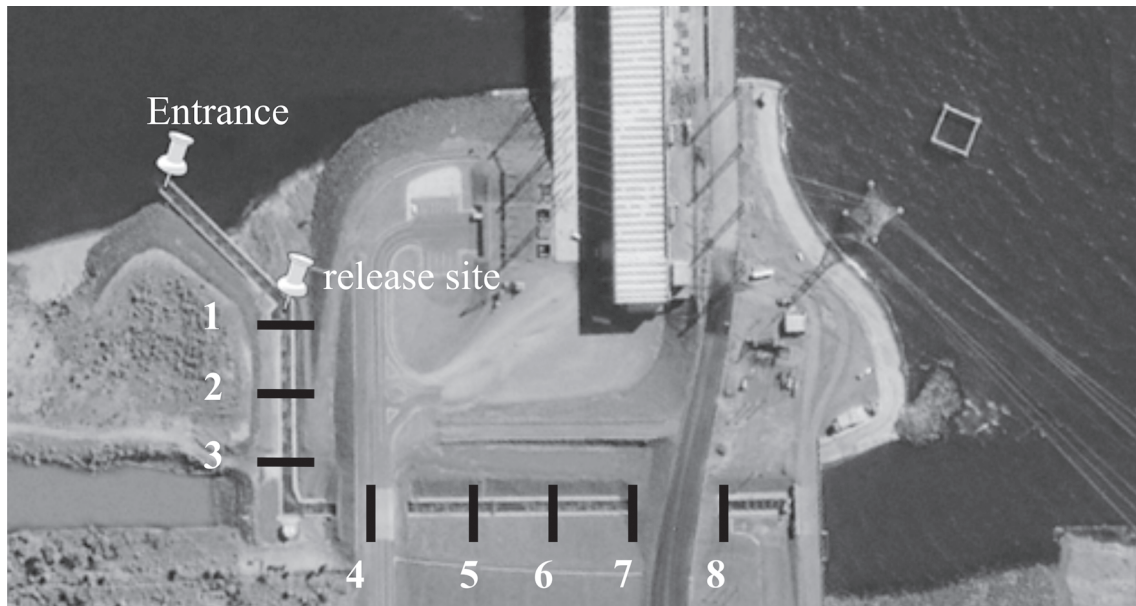
Fig. 1. Distribution of the antennas (1 to 8) along the fish ladder of the Porto Primavera Hydroelectric Power Plant, upper Paraná River, Brazil. Source: "Fish ladder". 22º29'02.82"S and 52º57'28.94"W. Google Earth. June 28, 2002. February 6, 2012.

peduncle height and caudal fin height) and areas (body area, propulsion area, muscle area, caudal fin area, and pectoral fin area). These measurements were used to obtain the morphometric ratios (Table 2) that are considered potentially important for describing the swimming performance of fish (Fisher & Hogan, 2007; Nanami, 2007).

Fig. 2. Photographs of *Leporinus elongatus* (**a**) and *Prochilodus lineatus* (**b**) collected in the fish ladder.

Ascent time

To analyze the time spent ascending the fish ladder by the two species studied, eight antennas with dimensions of 1.5 x 3.0 m were installed. The antennas were constructed with electric wires of 4 mm² in size, inserted into polyvinyl chloride tubes, and attached to the wall of the fish ladder with a wooden frame. The first antenna (antenna 1) was installed 100 m upstream from the entrance to the ladder, just upstream from the first resting pool. The last (eighth) antenna was positioned 50 m downstream from the exit from the ladder. The other antennas were distributed equidistantly along the fish ladder (Fig. 1). The Radio Frequency Identification (RFID) system was used in the fish ladder.

Leporinus elongatus and *Prochilodus lineatus* were caught along the fish ladder between September 2009 to January 2010 with seine and cast nets, anesthetized using benzocaine, and marked with PIT (Passive Integrated Transponder) tags of 32 mm. The tag was implanted through a small opening in the peritoneal cavity. After marking, the fish were placed in a cage located near the release site for recovery (20 minutes). The fish were released 85 m upstream from the entrance to the fish ladder (Fig. 1).

A total of 139 adult fish were tagged (30 specimens of *L. elongatus* and 109 specimens of *Prochilodus lineatus*). The total length of the specimens ranged from 40.2 to 52.4 cm for *L. elongatus* and from 33.5 to 58.0 cm for *P. lineatus*. Of the 139 tagged fish, 41 were recorded (RFID system) by all antennas during upward movements during the monitoring period (September 2009 to April 2010). These fish included nine (30%) *L. elongatus* and 32 (29%) *P. lineatus*. It is probable that most of the tagged fish migrated downstream after tagging or were not detected by the RFID system.
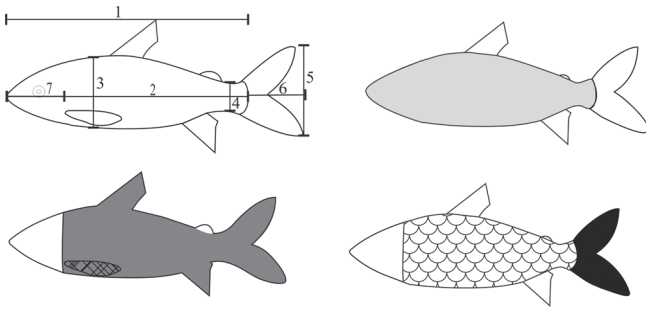
Fig 3. Morphological measurements (1-7) and areas related to swimming performance for *Leporinus elongatus* and *Prochilodus lineatus*: 1) standard length (SL), 2) total length (TL), 3) body maximum height (BMH), 4) caudal peduncle height (CPdH), 5) caudal fin height (CFH), 6) caudal fin length (CFL), and 7) length from snout to pectoral fin base (LNPtFB). Body area - BA (gray), propulsive area - PA (dark gray), muscle area - MA (fish scale), caudal fin area - CFA (black), and pectoral fin area - PtFA (crosshatching).

Data analysis

The data on the total and standard lengths were investigated to determine whether the body size in the group used for the morphometric measurements differed from the body size in the group marked with the PIT tags (including the fish showing upward movement). This comparison was used to increase the robustness of the subsequent analysis. These variables were tested with a one-way ANOVA.

A Principal Component Analysis (PCA) of the morphometric ratio values (log-transformed) was conducted with PC-ORD v.4.01 software (McCune & Mefford, 1999). The PCA was applied to investigate the morphological patterns shown by the species. The selection of axes for interpretation was performed with the Broken-Stick method (Jackson, 1993). An ANOVA was applied to the scores on the retained axis from the PCA to evaluate significant differences between species in the morphometric ratios.

The efficiency of swimming during the ascent of the fish ladder was evaluated based on the time spent in each section (antennas) and in the fish ladder (total time) for each species. A Kruskal-Wallis one-way analysis (for non-normal data) was used to examine the differences in the time taken by each species to ascend different sections of the fish ladder. A Mann-Whitney rank sum test (for non-normal data) was used to examine the mean time taken by each species to ascend the fish ladder.

Statistica 7.0 software was used for the ANOVA, Kruskal-Wallis one-way and Mann-Whitney tests. The level of significance was $p < 0.05$.

Results

Morphological characterization

The Principal Component Analysis (PCA) applied to evaluate the morphometric ratios between *Leporinus elongatus* and *Prochilodus lineatus* yielded two axes. These axes explained 66.66% of the variability of the data set. According to the *Broken-Stick* method (Table 3), only the first axis (PC1) was significant, explaining 47.77% of the total variability. The morphometric variables that contributed positively to the formation of the spatial gradient of the PC1 scores were the fineness ratio (FR) (0.884), the caudal peduncle depth factor (CPdF) (0.777), and the length from snout to pectoral fin base ratio (LNPtFBR) (0.889). The variables with negative coefficient values were the muscle ratio (MR) (-0.773) and the caudal fin length ratio (CFLR) (-0.771) (Table 3).

The distribution of PCA scores (Fig. 4) showed that the two species differ in several morphometric ratios associated with swimming performance. *Prochilodus lineatus* exhibited higher values of the muscle ratio (MR) and the caudal fin length ratio (CFLR). However, the scores for *Leporinus elongatus* were positive and showed higher values for the fineness ratio (FR), an indication of the thinner body of this species; a higher length from snout to pectoral fin base ratio (LNPtFBR); and a higher caudal peduncle depth factor (CPdF), an indication that the height of the caudal peduncle

Table 1. Description of the morphological measurements.

Morphological measurements (mm)	Acronym	Description
Total length	TL	Distance between the tip of the snout and the end of the caudal fin.
Standard length	SL	Distance between the tip of the snout and the end of the caudal peduncle.
Length from snout to pectoral fin base	LNPtFB	Distance from the snout to the pectoral fin base.
Caudal fin length	CFL	Distance from the end of the caudal peduncle to its posterior extremity.
Body maximum width	BMW	Greatest horizontal distance perpendicular to the longitudinal axis of the body.
Body maximum height	BMH	Greatest ventral-dorsal distance on the longitudinal axis of the body.
Caudal peduncle height	CPdH	Smaller caudal peduncle depth.
Caudal fin height	CFH	Greatest vertical distance perpendicular to the length axis.
Body area	BA	Area in lateral view, excluding the fins.
Propulsive area	PA	Area including the fins (naturally fully extended) but excluding the head and gut region where they are inflexible or lack overlying muscle and cannot be used for propulsion.
Muscle area	MA	Area excluding the fins, head and gut region.
Caudal fin area	CFA	Area with the caudal fin naturally fully extended.
Pectoral fin area	PtFA	Area with the pectoral fin naturally fully extended.

Table 2. Morphometric ratios calculated for *Leporinus elongatus* and *Prochilodus lineatus*.

Morphometric ratios	Acronym	Calculation	Description	Reference
Muscle ratio	(MR)	MA/BA	The ratio of the muscle area of the fish to the total body area	Fisher *et al.* (2000)
Propulsion ratio	(PR)	PA/BA	The ratio of the propulsion area to the total body area	Fisher *et al.* (2000)
Fineness ratio	(FR)	SL/[(BMW+ BMH)/2]	Length divided by the average of the body width and the body depth	Bainbridge (1960)
Aspect ratio	(AR)	CFH /CFA ½	Caudal fin height divided by the square root of the caudal fin area	Sambilay (1990)
Caudal fin length ratio	(CFLR)	CFL/TL	Caudal fin length divided by total length	Nanami (2007)
Caudal peduncle depth factor	(CPdDF)	CPdH/BMH	Caudal peduncle depth divided by body depth	Webb & Weihs (1986)
Pectoral fin length ratio	(PtFLR)	PtFA/BA	Pectoral fin area divided by body area	Gatz (1979)
Length from snout to pectoral fin base ratio	(LNPtFBR)	LNPtFB/TL	Length from snout to pectoral fin base divided by total length	Nanami (2007)

of this species is lower. The scores on the axis (PC1) retained in the Principal Component Analysis also showed that the morphometric ratios of *P. lineatus* differed significantly from those of *L. elongatus* (ANOVA, n = 80, $F_{(1, 78)}$ = 415.08, p < 0.001).

Ascent time

The data on total length (TL) and standard length (SL) from individuals marked with the Pit tags (nine specimens of *Leporinus elongatus* and 32 of *Prochilodus lineatus*) and from the individuals measured morphometrically (40 specimens of each species) showed no significant differences between groups (one-way ANOVA) (TL: $F_{(1,39)}$ = 1.3496, p = 0.25; SL: $F_{(1,39)}$ = 2.7883, p = 0.10). These results indicated that the two groups (the tagged and morphometrically measured fish) did not differ in size.

A Kruskal-Wallis test showed significant differences between the species in the times taken to ascend different sections of the fish ladder: antennas 1-2 (KW-$H_{(1,41)}$ = 6.1915, p < 0.01), 2-3 (KW-$H_{(1,41)}$ = 5.4325, p < 0.02), and 7-8 (KW-$H_{(1,41)}$ = 7.8581, p < 0.01) (Fig. 5). However, no significant differences between the species were detected in the time taken in the remaining sections: antennas 3-4 (KW-$H_{(1,41)}$ = 0.0089, p = 0.92), 4-5 (KW-$H_{(1,41)}$ = 3.8135, p = 0.05), 5-6 (KW-$H_{(1,41)}$ = 0.8929, p = 0.34), and 6-7 (KW-

$H_{(1,41)}$ = 2.5804, p = 0.11) (Fig. 5). For both species, a longer time was spent in the section corresponding to antennas 3-4.

The ascent times of the two species differed significantly, as shown by a Mann-Whitney rank sum test (Z = 2.87, p = 0.004). *Leporinus elongatus* had a shorter ascent time (mean of 1.39 hours) than *Prochilodus lineatus* (mean of 3.76 hours) (rank sum test = 30 and 75, respectively).

Discussion

This study identified several aspects of external body morphology that are important for swimming efficiency in two long-distance migratory fish species. Although both species studied, *Leporinus elongatus* and *Prochilodus lineatus*, show a hydrodynamic body shape and a good swimming performance, they differ in several morphometric traits related to swimming performance. *Leporinus elongatus*, with a greater caudal peduncle depth factor, a greater length from snout to the pectoral fin base ratio and a greater fineness ratio, has greater swimming efficiency and moved more rapidly through the fish ladder than *P. lineatus*, in which the muscle ratio and caudal fin length ratio are greater.

The thinner caudal peduncle in *L. elongatus* can produce a decrease in the waves of turbulence caused by the movement

Table 3. Eigenvalues of the Principal Components Analysis (PCA) for morphometric ratios values (PC1 = Axis 1, PC2 = Axis 2), and mean values of morphometric ratios for *Leporinus elongatus* (LE) and *Prochilodus lineatus* (PL). The variables with high eigenvalues are indicated in bold.

| Eigenvalues/morphometric ratios	Mean morphometric ratios		PC1	PC2
	LE	PL		
Eigenvalue			**3.822**	1.511
Eigenvalue - *Broken-Stick*			2.718	1.718
% of variability explained			**47.77**	18.89
Muscle ratio (MR)	0.860	0.887	**-0.3952**	-0.3103
Caudal fin length ratio (CFLR)	0.174	0.202	**-0.3943**	-0.2154
Propulsion ratio (PR)	1.091	1.109	-0.255	-0.5888
Aspect ratio (AR)	2.062	2.151	-0.1222	0.2569
Pectoral fin length ratio (PtFLR)	0.031	0.027	0.1979	-0.6002
Caudal peduncle depth factor (CPdDF)	0.397	0.367	**0.3974**	-0.2245
Fineness ratio (FR)	4.679	4.018	**0.452**	-0.1289
Length from snout to pectoral fin base ratio (LNPtFBR)	0.193	0.153	**0.455**	-0.132
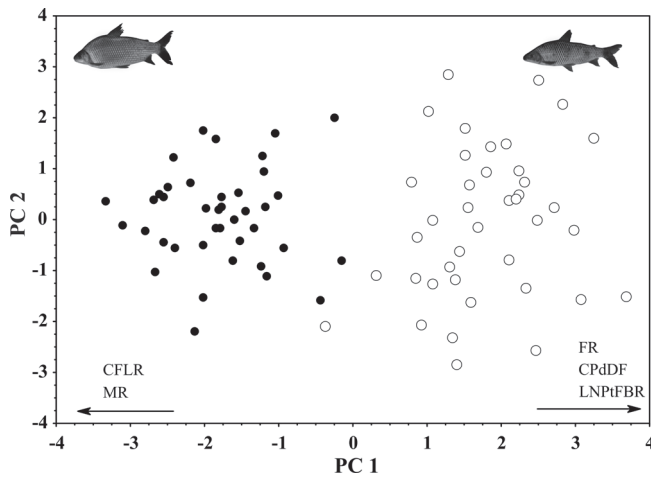
Fig. 4. Individual scores from Principal Component Analysis (PCA) showing the sources of interspecific variability for *Leporinus elongatus* (white circle) and *Prochilodus lineatus* (black circle). CFLR= caudal fin length ratio; MR= muscle ratio; FR= fineness ratio; CPdDF= caudal peduncle depth factor, and LNPtFBR= length from snout to pectoral fin base ratio.

Fig. 5. Mean ascent time (hours) ± standard error for *Leporinus elongatus* and *Prochilodus lineatus* relative to antennas in the fish ladder. Bars: white (Antennas 1-2), black (2-3), gray (3-4), horizontal line (4-5), dark gray (5-6), dashed line (6-7), vertical line (7-8).

of the anterior region of the body. This feature is associated with a greater caudal fin height, with the upper and lower extremities of the fin outside the zone of turbulence, and it allows the fish to apply more power and propulsion (Breda *et al.*, 2005). However, the greater muscle ratio (MR) demonstrated for *P. lineatus* indicates that it may be more resistant to moving water, remaining in position at high water velocities. A greater muscle ratio also enables this species to sustain itself in rapid and turbulent waters. The associated energy expenditure is lower because the body is larger and higher. As the body size increases, the volume corresponding to the muscle mass also increases, allowing the fish to reach higher speeds during prolonged swimming (Beamish, 1978).

Although the propulsion ratio (PR) is related to the muscle mass of the fish (Fisher & Hogan, 2007), this ratio was similar between species. Ohlberger *et al.* (2006) verified that *Mugil cephalus* Linnaeus, 1758 has better swimming ability due to its morphological characteristics (greater muscle and propulsion areas), suggesting that superior swimming capacity is based primarily on the development of muscles and other traits related to fish locomotion. Studies by Fisher *et al.* (2000) showed similar results for the three reef fish species *Pomacentrus amboinensis* Bleeker, 1868, *Sphaeramia nematoptera* (Bleeker, 1856) and *Amphiprion melanopus* Bleeker, 1852. In these species, the critical swimming speed was positively correlated with the propulsion area.

A streamlined body is an elongated and fusiform shape that minimizes drag while maximizing volume, and the fineness ratio is the most common and straightforward method of measuring this characteristic (Langerhans & Reznick, 2010). Fineness ratios between 2 and 6 result in a decrease of the drag produced by the fish, and species with a fineness ratio of 4.5 have an optimum
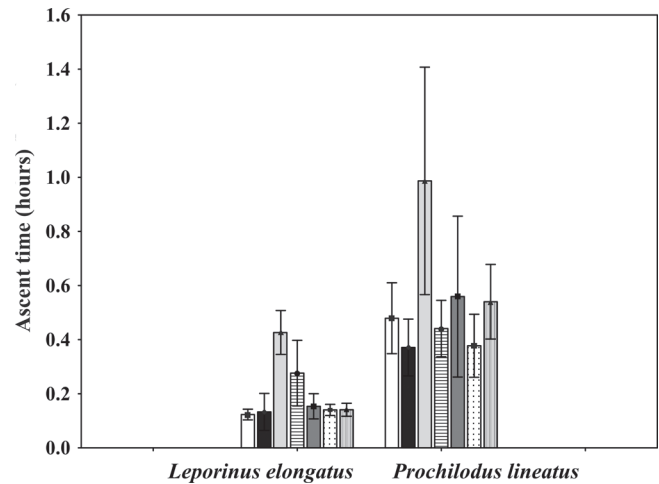
swimming capacity (Webb, 1975; Blake, 1983; Langerhans & Reznick, 2010). The streamlined body and mean fineness ratio of 4.6 observed for *L. elongatus* may indicate a greatly superior swimming performance. Studies conducted with *Cyprinus carpio* Linnaeus, 1758 and *Rutilus rutilus* (Linnaeus, 1758) to evaluate differences in swimming capacity demonstrated a fineness ratio lower than 4.5 for *C. carpio*, whereas *R. rutilus* showed greater values. These results showed that the hydrodynamic body shape of *R. rutilus* was appropriate to facilitate swimming performance (Ohlberger *et al.*, 2006). However, according to Castro-Santos (2005), all fish can optimize their swimming velocity, although certain species are better able to do so.

The caudal peduncle depth factor (CPdDF) is strongly related to the swimming speed (Fisher & Hogan, 2007), and it is an important determinant of the swimming ability of the fish. This factor was also essential for differentiating *L. elongatus* and *P. lineatus*: *L. elongatus* exhibited a higher mean CPdDF (0.39) than *P. lineatus* (0.36). Similar values were found for *Leporinus obtusidens* (Valenciennes, 1847) and *P. lineatus* (0.40 and 0.37, respectively) by Carneiro (2003). Fish that show a superior ability to accelerate have a deep caudal peduncle (Webb, 1994). In contrast, a narrow caudal peduncle is typical of thunniform fish, which use an axially oscillating caudal fin to generate thrust for cruising at high speed (Webb, 1984; Webb & Weihs, 1986).

According to Gosline (1971), propulsive force is related to caudal peduncle width. A thin caudal peduncle with a higher caudal fin overcomes the waves induced by the movement of the anterior region of the body, promoting a higher propulsive force (Aleev, 1969). In addition, the caudal peduncle and the frequency of tail flapping are important for producing a jet of high propulsive efficiency (Triantaffylou & Triantaffylou, 1995). A greater caudal fin

area, as observed in the longer caudal fin of *P. lineatus*, is important for acceleration (Balon *et al.*, 1986), and the caudal fin length ratio is significantly related to swimming performance. This ratio has important consequences for thrust and for drag reduction (Videler, 1993).

The length from snout to pectoral fin base ratio differed between the species studied. In *Leporinus elongatus*, the pectoral fins are located closer to the center of gravity of the fish's body, indicating that the fish can easily turn its body (Nanami, 2007) and has a greater positioning ability. In contrast, a lower value of this ratio indicates that the axis for turning is located farther from the center of gravity, resulting in greater drag during turning (Nanami, 2007). A high pectoral fin length ratio (PtFLR) is associated with high swimming speed (Breda *et al.,* 2005), as shown by the narrow and long fins of large migratory fish (Keast & Webb, 1966). Nevertheless, this morphological ratio associated with fish locomotion was similar for the two species studied.

Several morphometric ratios differ between the species studied. In addition, the species exhibit different swimming efficiency. *Leporinus elongatus* is faster than *Prochilodus lineatus*; it had a lower mean ascent time (1.39 hours) than *P. lineatus* (3.76 hours), which required a longer time to pass through the fish ladder. According to Santos *et al.* (2007), the swimming capacity of the piau (*Leporinus reinhardti*) explained the success of this genus in ascending fishways in Brazil. It is possible that the swimming capacity of this genus is greater than that of other migratory characiformes.

Despite the difference in the time taken to ascend the fish ladder, both species *Leporinus elongatus* and *Prochilodus lineatus* moved relatively more rapidly in the section between antennas 1-2 and 2-3, showing that more rapid swimming is required to pass through this section of the fish ladder. The section between antennas 3-4 is the longest section of the fish ladder. The two species spent a longer time in this section because it is a resting pool. The maximum possible ascent distance through fishways is governed by the swim speed–fatigue time relationship (Bainbridge, 1960). Data on this relationship have been used extensively to determine the location and size of resting pools within fishways (Beamish, 1978). Castro-Santos (2005) stated that any recommendations for fishway designs based on the swim speed–fatigue time relationship should therefore recognize the expected variability around the optimum and the costs of such variability in terms of the ascent distance if predictions of passage success are necessary.

In conclusion, this study identified several morphometric characteristics associated with swimming efficiency. *Leporinus elongatus* and *Prochilodus lineatus* differed in several morphometric traits related to swimming performance, including the muscle ratio, caudal fin length ratio, caudal peduncle depth factor, length from snout to pectoral fin base ratio, and fineness ratio. *Prochilodus lineatus* has a higher body and greater muscle mass (MR). Nevertheless, *L. elongatus* has a thinner caudal peduncle and a greater fineness ratio, and its body is more streamlined than *P. lineatus*. Although both species show good swimming performance in the fish ladder, these characteristics may enable *L. elongatus* to apply greater power and propulsion, allowing it to reach a high swimming speed. The efficiency shown by this species is greater than that shown by *P. lineatus*. Morphometric ratios can be used to predict the swimming performance of *L. elongatus* and *P. lineatus* in conjunction with studies of swimming capacity (tests of prolonged and burst speed) to investigate possible differences in swimming speed/swimming capacity between the species. The predictive character of this type of approach would provide better accuracy. In addition, this approach would represent a significant contribution to help address the absence of basic information on the biology of Neotropical migratory fish species.

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