Egg transport and larval behavior of curimba, *Prochilodus lineatus* (Valenciennes, 1836; Characiformes, Prochilodontidae) in a drift simulator channel

Thays Cristine Bellenzier de Queiroz, Dirceu Baumgartner, Pitágoras Augusto Piana, and Paulo Vanderlei Sanches

ABSTRACT. Landscape changes and hydrologic alterations associated with dam construction have greatly hindered reproductive success and the recruitment of migratory species. However, little is known about the flow conditions that are necessary for the reproductive success of migrators. We aimed to analyze one of the important migrants of the Paraná River, the curimba, *Prochilodus lineatus* (Valenciennes, 1836), to determine the minimum velocities necessary for egg drift and analyze the behavior of larvae at different flow velocities. Thus, we experimentally evaluated the behavior of eggs and larvae released in a drift simulator channel (DSC) under four flow velocities. Additionally, we investigated the swimming ability of larvae in relation to certain morphometric measures of their bodies. We also performed morphometry and calculations of larval body and fin proportions to determine which structures influence swimming ability. The results indicated that environments with flow velocities greater than 0.081 m s\(^{-1}\) were favorable for egg drift and increased the chances of successful transport of eggs to downstream areas. We also observed that soon after hatching, the larvae positioned themselves against the flow, indicating that they had a perception of position and orientation. The larvae were able to maintain and disperse against the flow within the channel 32h after hatching at all velocities, which was mainly due to the development of pectoral and caudal fins that were actively involved in the swimming process, as well as the reduction in the dimensions of the yolk sac, which reduced drag.

Keywords: drifting; fish eggs and larvae; flow velocity; ichthyoplankton.

Introduction

Studies on the drift of eggs and larvae generate important information, such as the minimum flow required for transport from spawning to development areas, and the effects of hydrological characteristics (speed and direction of flow) on the dynamics of ichthyoplankton assemblages (Pavlov & Mikheev, 2017). Thus, it is important to not only understand how the transport of eggs and larvae is influenced by biological characteristics, such as growth rate, egg diameter and density, and larval swimming potential, but also by hydrodynamics and environmental characteristics of the water body (Garcia, Murphy, Valocchi, & Garcia, 2013). Knowledge of the behavior and associated movement patterns that determine the trajectory, drift velocity, and destination of fish larvae drift in rivers and their relationship with larval morphology is critical (Pavlov, Mikheev, Lupandin, & Skorobogatov, 2008; Lechner, Keckeis, & Humphries, 2016). The patterns of transport of fish larvae in rivers and other types of moving water must be understood, modeled, or predicted (Lechner et al., 2016), since this knowledge along with a greater understanding of population dynamics are key factors for species conservation, fisheries management, and restoration ecology.

Researchers have been interested in the relationship between fish and water flow for centuries (Lacey, Neary, Liao, Enders, & Tritico, 2012), because movement is a fundamental process in the lives of the majority of organisms (Nathan et al., 2008). The drift of eggs and larvae from spawning sites to initial development
habitats, such as floodplains and lowland areas (Barros & Rosman, 2018), affects the survival and fitness of an individual, and the probability of completing its life cycle (Daewel, Peck, & Schrum, 2011; Hinrichsen, Hüsey, & Huwer, 2012).

The predominance of hydroelectric power in the energy matrix of Brazil and the recent increase in its demand have resulted in the damming of most major hydrographic basins in the country (Sanches et al., 2020). As changes in freshwater ecosystems caused by dams are related to river hydrodynamics, studies on drift can be useful to determine the minimum speeds and distances necessary for eggs and larvae to be transported in the river stretches of reservoirs. Owing to the reduction in flow velocity with the formation of reservoirs (Agostinho, Gomes, & Pelicice, 2007; Pavlov & Mikheev, 2017), eggs of species not adapted to lentic environments, such as migratory species, will likely descend to the deep regions of the reservoir, where there is a minimal chance of survival (Agostinho et al., 2007).

Although studies using drift simulators for flow peak analysis (Bradford, 1997; Halleraker et al., 2003) and flood pulses (Chun et al., 2011; Cocherell et al., 2012) are common in the Northern Hemisphere, no such studies have been conducted in the Neotropical region (particularly Brazil). Therefore, assuming that the life cycle of migratory fish species depends on the characteristics and flow velocities of the rivers, this study aimed to evaluate the transport of eggs and behavior of *P. lineatus* larvae at different flow speeds in a drift simulator channel. In this study, we aimed to answer the following questions: i) what is the minimum flow speed necessary for eggs to be transported, ii) how will *P. lineatus* larvae behave in relation to the different flow velocities, iii) how long after hatching do the larvae actively swim (positive rheotaxis), and iv) which morphological structures most influence larvae swimming?

### Materials and methods

#### Species characteristics, structure, functioning of the drift simulator channel, and experiment

*Prochilodus lineatus*, commonly known as curimba, is a long migratory species (Baumgartner, Oliveira, Agostinho, & Gomes, 2018; Ota, Deprá, Graça, & Pavanelli, 2018) that needs to annually migrate more than 100 km upstream to complete its gonadal development and spawning processes (Baumgartner et al., 2018). Native to the Paraná River (Ota et al., 2018), this species reaches 78 cm in length and is of great importance to professional fishing (Agostinho, Gomes, Suzuki, & Júlio, 2003). *Prochilodus lineatus* depends on floods for the success of their reproduction and recruitment, and their abundance has been significantly affected by the damming processes (Piana et al., 2017).

*Prochilodus lineatus* undergoes external fertilization with no parental care for its offspring. Its eggs are translucent and pelagic, with ample perivitelline space (Nakatani et al., 2001), and an accumulation of yolk in their vegetal pole (telolecitic egg) (Botta et al., 2010). The larvae hatch approximately 16 hours after fertilization at 26°C (Nakatani et al., 2001).

The experiment was conducted in a drift simulator channel (DSC) installed at the Environmental Aquaculture Research Institute (InPAA) linked to the *Universidade Estadual do Oeste do Paraná*, Toledo Campus, Paraná, Brazil. The dimensions and structure of the DSC system are shown in Figure 1. The DSC consists of a closed circulation system, whereby the water stored in a reservoir is released through a centrifugal pump into the channel via piping and, after entering the system, it is launched through a ‘flow disperser’ that reduces the turbulence generated by the water flow. Water then flows through the system and returns to the reservoir, restarting the cycle. The DSC is constructed of steel, with an 8 mm-thick transparent tempered glass front panel for viewing the organisms, and a metric scale to determine the transport distance of the organisms on its rear panel.

The DSC piping consists of a set of polyvinyl chloride (PVC) pipes that connect the reservoir to the pump, pump to the reservoir, and pump to the flow disperser inside the channel. The pump is a 5 HP centrifugal pump that pushes water into the channel. The return pipe and pipe connecting the pump to the channel are equipped with registers that allow changes to determine and control the flow velocities by adjusting the degrees of opening and closing between them.

The flow velocities were determined by filling a container positioned at the water outlet of the DSC with a known volume and measuring the time taken for filling, and using the following equation: \( Q = \frac{V}{t} \), where \( Q \) is the volumetric flow, \( V \) is the volume (L), and \( t \) is time (s). This procedure was conducted with ten repetitions for each speed, and the average values were calculated. The units of \( \text{L s}^{-1} \) were transformed into \( \text{m}^3 \text{s}^{-1} \). We then used the equation: \( Q = \frac{V}{A} \), where \( Q \) is the flow obtained in \( \text{m}^3 \text{s}^{-1} \), and \( A \) is the cross-sectional...
area of the DSC in m². The final four speeds obtained were 0.032, 0.044, 0.068, and 0.081 m s⁻¹. These velocities were selected based on the approximate values, which are lower than those observed for the tributaries that forming the arms of the Itaipu Reservoir (Ouchi-Melo et al., 2021).

**Figure 1.** Diagram of the frontal view, dimensions (cm), and structural components of the drift simulator channel (DSC). A) Reservoir; B) connection pipe between the reservoir and centrifugal pump; C) return pipe from the centrifugal pump to the reservoir; D) record of the flow control of the return pipe; E) centrifugal pump; F) water inlet pipe in the DSC; G) flow control record of the inlet pipe; H) flow disperser; I) DSC water outlet.

**Development of the experiment**

The eggs and larvae used in the experiment were obtained from induced spawning at the InPAA and placed in a 200 L conical-cylindrical fiberglass incubator with constant water circulation and an average temperature of 21.6 ± 0.3ºC until the end of the experiment. For the observations, the organisms (both eggs and larvae) were released into the channel 1 m from the outlet of the flow disperser to avoid turbulence of the water entering the system from influencing the organisms.

For the experiment, ten organisms at each developmental stage (replicates) were used to test each of the four flow velocities. Each egg or larva was individually released into the channel, the horizontal displacement distance and time were recorded, and larval swimming behavior was observed. The eggs were stained with methylene blue to allow visualization inside the channel, and were subjected to tests every 4 hours from fertilization to the phase before hatching. After hatching, the larvae were evaluated every 8 hours until they reached 48 hours of development, followed by 12 hours intervals until the end of the experiment. The sampling times were determined based on previous information on the development of the species (Nakatani et al., 2001; Botta et al., 2010), considering the occurrence of ontogenetic events of embryonic development (initial cleavage stages, early embryo, free tail, and late embryo) and early larval development (hatching, endogenous feeding, and early exogenous feeding). As our objective was to evaluate the swimming behavior of the initial stages of larval development, we only used larvae in the larval vitelline and pre-flexion larval stages, with the classification of these stages according to Nakatani et al. (2001).

For the larvae, only the time spent in the water column was considered, and their behavior was observed until they touched the bottom or side of the channel. For analysis, the time of egg development was grouped into hours post-fertilization, with 0 being freshly fertilized and 24 as pre-hatch. The larvae were grouped based on the number of hours after hatching, with 0 representing newly hatched larvae. The drift velocity of organisms was calculated using the following equation: \( V = \frac{d}{t} \), where \( V \) is the volume (L), \( d \) is the horizontal displacement distance (m), and \( t \) is displacement time (s).

Before each experiment in the DSC, a sample containing around 20 organisms (both eggs and larvae) from each developmental time were fixed in 4% formaldehyde, and morphometric measurements (expressed in millimeters) were obtained from images captured with a digital camera (OLYMPUS, model DP-25) coupled to a stereoscopic microscope (OLYMPUS, model SZX7) using the DP2-BSW software. Based on the morphometric measurements, the morphometric indices of Gatz Jr.(1979), Watson and Balon (1984), Ferreira (2007), and Andrade et al. (2014) were adapted. These included the relative pectoral fin length (RPFL), pectoral fin length divided by standard length; pectoral fin proportion (PFP), pectoral fin length divided by pectoral fin height; relative caudal fin length (RCFL), caudal fin length divided by standard length; caudal fin proportion (CFP),
caudal fin height divided by square root of caudal fin area; relative body height (RBH), body height divided by standard length; and yolk sac proportion (YSP), yolk sac area divided by body height.

Data analysis

The experiment followed a factorial-type design with two factors (water flow and developmental hours). The results were analyzed using repeated-measures ANOVA tests. To check the assumptions of the analysis, Mauchly's test of sphericity was applied, and if violations were found in the assumed sphericity, Greenhouse-Geisser correction was performed to obtain the valid critical F-value. When a significant difference was observed, the data were subjected to Tukey's test to identify the factor level that differed. When the assumptions of normality (Shapiro-Wilk test) and homoscedasticity (Levene test) were not met, the corresponding nonparametric test (Kruskal-Wallis) was conducted, followed by a median test. A significance level of 5% (p < 0.05) was set for all analyses. The effects of the interactions between the development times (h) and flow velocities (m s⁻¹) for eggs and larvae within the DSC were also analyzed. The morphometric indices were analyzed using principal component analysis (PCA) to assess the possible relationships between the speed of larval displacement in the DSC and the development of these structures at the highest flow speed. The analysis was conducted using Statistica® 7.0 (Statsoft, 2004).

Results

During the experiment, a significant difference between the flow velocities was only observed under the highest flow velocity analyzed, 0.081 m s⁻¹ (Figure 2).

![Image](Figure 2. Transport distance of Prochilodus lineatus eggs within the drift channel at the four tested flow rates (different letters represent significant differences between the means at 5% according to the Tukey test).)

At the lowest speeds evaluated, the percentage of eggs transported along the entire length of the drift channel was below 40%; however, at the highest speed, this percentage exceeded 60%, and at the 4, 16, and 20 hours development times, all released eggs were transported along the entire canal (Figure 3a). Generally, the transport pattern at the lowest speeds (0.032 and 0.044 m s⁻¹) was similar to the reduction in drift speeds throughout development, particularly from the eighth hour after fertilization. At these speeds, a higher oscillation was observed between egg transport speeds throughout the development period (Figure 3b). There was a significant difference between the highest speed of flow and the other velocities, although a reduction in the transport speed under the 0.081 m s⁻¹ flow rate was also observed when the eggs were in the final stages of development.
In the first stages after hatching (up to 40 hours), the larvae were either completely transported at the highest flow speeds, while there was a significant difference at the highest speed (0.081 m s⁻¹), or they swam in favor of the direction of flow (negative rheotaxis). From 48 to 110 hours after hatching, a drift pattern was observed between the different flow rates and development times. An irregular pattern in the transport speed was then recorded between the flow speeds (Figure 4).

Regarding the behavior of the larvae during the experiment, the newly hatched larvae (larval vitelline stage) were oriented against the flow at all evaluated speeds; however, they searched for the areas of lower flow velocity within the channel (bottom and side), where it was possible to reduce their swimming speed against the direction of flow. Forty-eight hours after development (early pre-flexion stage), active swimming began to occur along with pectoral fin movement, and the larvae remained close to the surface, the canal walls, or even swam against the flow (positive rheotaxis), which became more evident throughout the development time. In the final developmental stages, at 134 and 146 hours (late pre-flexion stage), all larvae exercised active swimming movements against and in favor of the flow direction, traveling up and down in the water column and beyond the observation area of the DS channel.
Figure 4. Interactions between the flow velocities (m s\(^{-1}\)) and development times of *Prochilodus lineatus* larvae for the four flow rates tested in the drift simulator channel.

The morphometric indices were analyzed using PCA, which summarized 69.43% of the data variability, 41.15% of which was contained in the first axis (PCA 1) and 28.28% in the second axis (PCA 2). The results of PCA applied to the morphological data and larval displacement velocity indicated the formation of two groups (Figure 5a). The first group consisted of organisms with 0, 16, and 24 hours of development time, which were positively associated with the PCA 1 axis. The second group included animals belonging to other development times (32, 48, 86, 98, 134, and 146 hours), which were negatively associated with the PCA 1 axis. By analyzing the first axis of PCA, it was observed that the yolk sac proportion (YSP) and larval drift velocity (LDV) were more strongly positively associated with PCA 1, while the pectoral fin proportion (PFP) and caudal fin portion (CFP) were more strongly negatively associated with PCA 1 (Figure 5b).

Figure 5. Spatial projection of the larvae sample scores for each development time (a) and vectors of the morphometric indexes and displacement speed (b) in the two axes of the PCA under a flow speed 0.081 m s\(^{-1}\) in the DSC. RPFL - relative pectoral fin length; PFP - pectoral fin proportion; RCFL - relative caudal fin length; CFP - caudal fin proportion; RBH - relative body height; YSP - yolk sac proportion and LDV - larval drift velocity.

Therefore, from the analysis, we observed that PFP and CFP were inversely associated with LDV, indicating that after 32 hours of development, these fins began to influence the larvae by providing greater autonomy and swimming capacity. The yolk sac showed a positive association with larval drift, indicating that larvae with larger yolk sacs presented greater buoyancy and consequently higher drift velocities.
Discussion

The transport of eggs during the experiment was proportional to the increase in flow, with only small vertical oscillations possibly caused by turbulence within the channel. At the highest speed, the eggs mainly floated close to the surface, whereas at the lowest speed, although the eggs that immediately entered the flow showed fluctuations, the flow was insufficient to transport them along the entire course of the channel. This relates to the pelagic characteristics of the eggs of this species, which in addition apart to influencing buoyancy and shape, cause them to drift passively (Videler, Fluder, Kehmeier, Medley, & Valdez, 2012). Eggs of migratory species do not have adaptations that guarantee their buoyancy, such as oil drops in species that spawn in lentic environments (sedentary species), and therefore need adequate flow speeds for transportation (Nakatani et al., 2001; Agostinho et al., 2007; Sanches et al., 2020). Thus, if the eggs of migratory species drift to areas where there is no minimum speed to guarantee their buoyancy and transport, they generally drift to the bottom, where no adequate conditions would exist for hatching (Agostinho et al., 2007). The reduction in egg transport during the most advanced development times can be attributed to the increase in the density of eggs in the final stages of development, which decreases their buoyancy (Petersen, Hinrichsen, Franke, & Köster, 2014) and transport by the flow. These characteristics were confirmed mainly in the lower flow rates, when lower percentages of eggs were transported along the total DSC (total path), indicating that egg transport would be minimal at these speeds. Therefore, if an environment had a slow flow rate, the eggs would not drift to the development areas (Worthington, Brewer, Farless, Grabowski, & Gregory, 2014). At the highest flow speed, the longest drift distances and percentage of eggs transported across the entire channel length were observed, demonstrating that speeds above 0.081 m s\(^{-1}\) were efficient in transporting \( P. \ lineatus \) eggs at all stages of embryonic development to downstream areas. These results corroborate the study by Murphy and Jackson (2013), who determined that eggs of grass carp would settle at mean current velocities of flow lower than 0.081 m s\(^{-1}\). Thus, at flow velocities below 0.081 m s\(^{-1}\), such as those recorded in the arms of the Itaipu HPP reservoir, which served as the basis for determining the flow velocities used in this study (0.0 to 0.050 m s\(^{-1}\)), eggs would not be transported to the lower reaches and would tend to settle to the bottom where the conditions for their development are not favorable (Agostinho et al., 2007).

Soon after hatching (approximately 4 hours after hatching or the larval vitelline stage), the larvae had attempted to position themselves against the flow within the channel, indicating that they could perceive their position and orientation, despite their low level of development. This orientation occurs because the larvae create a flow field when swimming that generates an impulse that reaches the lateral line receptors on the body surface (Feitl, Ngo, & McHenry, 2010). Even fish larvae without completely developed fins can generate powerful edge vortices during undulatory swimming that enhance thrust only with oscillating appendages (paired fins and tail fins), fin folds, and body undulations (Lí, Müller, Leeuwen, & Liu, 2016).

It is clear that the swimming performance and morphology of larvae are related, as the performance depends on the drag and propulsion force that the organism will develop (Videler, 1995); however, there are other factors related to the development and swimming ability of the larva, such as eye development, (and other sensory organs) because both swimming ability and visual acuity increase with size and are more limited in the early stages (Flore, Reckendorfer, & Keckeis, 2000). For the \( P. \ lineatus \) larvae used in this study, eye pigmentation started soon after hatching and was completed at the beginning of the pre-elongation stage.

The ability of newly hatched larvae to orient themselves is a major factor for their survival, as they need to develop the ability to swim almost immediately after hatching to find food before they have completely exhausted their vitelline reserves (Voesenek, Muijres, & Leeuwen, 2018). Newly hatched larvae have limited yolk supplies and need to feed before the reserve runs out (Hunter, 1981). Starvation is the result of the inability of the larvae to find sufficient food and was originally suggested to be the main cause of mortality during this ‘critical period’ of mass mortality (China, Levy, Liberzon, Elmaliach, & Holzman, 2017). In addition, the relationship between swimming ability and vision development is important for fleeing predators. Compared to sound or touch, visual responses result in more escape trajectories directed away from the stimulus (Voesenek et al., 2018). Swimming also supports breathing, renews the diffusive limit layer of gases and ions (Green, Ho, & Hale, 2011), and aids in maintaining and controlling the body’s orientation (Ehrlich & Schoppik, 2017).

In the early stages of development, \( P. \ lineatus \) larvae were transported throughout the channel or followed the flow direction (negative rheotaxis). In the first few hours after hatching (approximately 4 hours), the caudal beats were accelerated, but were insufficient to achieve active swimming. Many characteristics are important for defining the swimming capacity of the larvae, such as the proportion and aspect of the fins.
Typically, even fins (pectoral and pelvic) are more sensitive to buoyancy and flow velocity variability in larval behavior and movement patterns, and correlations between drift densities and discharge increase in buoyancy of the larvae, despite the reduction in swimming power. Thus, with a larger yolk sac, the likelihood of passive drift increases, and these individuals are redistributed according to their body shape and buoyancy (Copp, Faulkner, Doherty, Watkins, & Majecki, 2002).

During the experiment, the larvae searched for the regions with the lowest flow close to the bottom or walls of the simulator channel from the first hours after hatching. This behavior may be related to the need to save energy, since without a properly formed caudal fin, most larvae use high amplitude body undulations to swim, which can be energetically expensive (Downie, Illing, Faria, & Rummer, 2020), and can reach 80% of a larval fish’s energy budget in the Atlantic cod (Gadus morhua) (Ruzicka & Gallager, 2006).

This behavior has also been observed in natural environments, where larvae generally seek to float on the margins and not in the center of the stream (Reichard & Jurajda, 2004; Kynard, Parker, Kynard, & Parker, 2007), allowing them to maintain their position without being swept by the flow. Some species of larvae are able to determine their position in the water column (Schludermann, Tritthart, Humphries, & Keckeis, 2012), even at low levels of light and currents by responding to hydraulic gradients. This was observed in studies with zebrafish larvae that were guided by neuromasts of the lateral line, allowing them to sense water flows and orient themselves in currents (Olszewski, Haehnel, Taguchi, & Liao, 2012; Stewart, Cardenas, & McHenry, 2013). This behavior indicates that the larvae are rheotactic and can manage this perception by locating the lowest speeds at which they can remain at a lower energy cost and avoid stress (Pavlov et al., 2008).

Other studies have also found that larvae exert active movement in flow situations and do not behave as passive particles (Robinson, Clarkson, & Forrest, 1998; Schludermann et al., 2012; Lechner et al., 2017; Zens, Glas, Tritthart, Habersack, & Keckeis, 2017). Owing to the verification of the existence of active movements in the dispersion of the larvae, Lechner et al. (2016) proposed a new concept of drift for larvae, referred to as "active-passive", as there would not be adequate separation between active and passive drift because of the variability in larval behavior and movement patterns, and correlations between drift densities and discharge and flow velocity are common (Lechner et al., 2013), as observed in this study.

Marine species have been more commonly studied than freshwater species in terms of flow. Staaterman, Paris, and Helgers (2012), and Mouritsen, Atema, Kingsford, and Gerlach (2013), stated that fish larvae do not undergo passive transport and can detect signals from the environment and exhibit sophisticated behavior, such as directional swimming, which is important for effective dispersion. Observations of larvae moving in hydraulic gradients (Stoll & Beeck, 2012), regulating swimming speeds and drifting to the predominant flow regime (Hogan & Mora, 2005), and adapting their depth distribution according to the currents (Kunze, Morgan, & Lwiza, 2013) also indicate active responses to the hydrodynamic environment.
The results of this study revealed that *P. lineatus* larvae exhibited active behavior during the first hours of development (approximately 4 hours after hatching in the larval vitelline stage), which was indicated by the decrease in larval drift in the final stages of larval development and swimming behavior. They also searched for areas with low flow within the simulator channel. Therefore, larval movement should be considered when attempting to understand and model patterns of fish larval dispersion in rivers, as the assumption of only passive transport is generally inaccurate.

**Conclusion**

Based on the data obtained in this study, we can conclude that environments with flow velocities greater than 0.081 m s\(^{-1}\) are favorable to the drift of *P. lineatus* eggs, which may extend to other species of migratory fish because these speeds provide greater probabilities of success in transporting the eggs to downstream areas. We can also conclude that the larvae exhibited active behavior during the first few hours of development, similar to that presented in a natural environment. The larvae were able to maintain themselves and disperse against the flow within the channel 48 hours after hatching (early pre-flexion stage), mainly because of the development of pectoral and caudal fins that are actively involved in the swimming process, as well as a reduction in the dimensions of the yolk sac, allowing for the reduction of drag through the flow.

Studies on the influence of flow velocity on the transport and behavior of ichthyoplankton are scarce, and further research should be conducted in this area to gain a greater understanding of the processes involved in the transport and survival of eggs and larvae, which can contribute to future conservation measures.

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