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Review

Larval development of indigenous South American freshwater fish species, with particular reference to pacu (*Piaractus mesopotamicus*): A review

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ABSTRACT

In recent years, a number of South American freshwater fish have gained increasing attention for their potential in aquaculture, not only because of their excellent performance in farming systems but also to meet the high consumer demand for these species due to declining fishery resources. Many South American freshwater species are migratory and produce altricial larvae, with a small amount of yolk reserves. Unlike precocial freshwater species and altricial coldwater marine fish, these freshwater fish investigated have rapid yolk depletion and metamorphosis. Specific studies on the initial development of South American fish are scarce and fragmented. One of the most widely studied species is the pacu (*Piaractus mesopotamicus*), farmed in warm continental waters. In the present review we compile new and published data on the initial development of pacu, including morphogenesis of the skeletal, muscle, digestive and sensory systems; compare it to other Neotropical species; and discuss the importance of this information to develop larviculture protocols. When pacu larvae exhaust yolk reserves, they initiate a new form of interaction with the environment, becoming exclusively exotrophic. This type of interaction is made possible by the rapid development of sensory, skeletal, locomotor and digestive structures. In addition to understanding fish ontogeny, studies on larval development are necessary to improve farming systems and larviculture techniques aimed at producing high-quality juveniles in aquaculture.

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1. Introduction

The Neotropical area exhibits the richest fauna of freshwater fish species in the world, with 4475 species described and at least 1550 yet to be described (Reis et al., 2003). Most of this diversity is represented by three fish orders, the Characiformes, Siluriformes and Gymnotiformes (Pinna, 2006). Owing to Brazilian territorial extent and rich water resources, many of South American Neotropical fish species are found in this country, which is also the largest aquaculture producer of native species, with nearly 20 farmed species (MPA, 2013). Aquaculture in Brazil is based primarily on freshwater fish, whose production was approximately 545 tons in 2011 (MPA, 2013). In addition

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to exotic species such as Nile tilapia (46.6%), carp and trout, South American species, mainly rheophilic Characids, accounted for nearly 250 tons (46%).

Migratory (lotic) fish (Godinho et al., 2010) form schools in the flood (reproductive) season and swim long upstream distances from feeding to spawning grounds, laying a large number of free moving eggs in the water column, presenting high fecundity and no parental care. Many of these species produce demersal eggs (near neutral buoyancy) (Godinho et al., 2010), which undergo rapid embryonic development during downstream drift. The larvae go to marginal areas such as floodplains, where they find abundant food (i.e. plankton) and protection against predators (Godinho et al., 2010; Godóy, 1975). In floodplain areas, marginal lagoons are commonly formed as the river returns to the main channel, producing natural nursery sites for the development of the main fish species that are commercially important and have their biology known.

In aquaculture, the reproduction of migratory fish is induced by synthetic hormones or carp pituitary extract (Zaniboni Filho and Weingartner, 2007). After spawning, eggs are placed in funnel-type incubators supplied with continuous water flow adequate for embryonic development, which generally lasts less than 24 h. After hatching, larvae display erratic swimming movements towards the water surface and then sink. They are kept in the incubators until their mouths open and their swim bladder inflates, 2 to 5 days post-hatching (dph) according to species and water temperature (Godinho et al., 2003); at this stage they improve their swimming skills.

Larviculture of native South American fish is mainly carried out in semi-intensive systems (Chabalin et al., 1989; Jomori et al., 2003; Mai and Zaniboni Filho, 2005), where open-mouthed larvae are directly stocked in plankton-rich fertilized ponds and start exogenous feeding. They are held in these ponds until larval development is complete and small juveniles are formed (30–50 dph). However, survival rates in semi-intensive larviculture are low (Jomori et al., 2003; Mai and Zaniboni Filho, 2005; Senhorini et al., 1991) and highly affected by food availability and the presence of predators such as odonata (dragonfly) nymphs, which account for significant losses (Jomori et al., 2003; Kojima, 2012; Lacerda et al., 2010). As a result, large-scale semi-intensive fish production is unpredictable and strongly dependent on environmental conditions.

Intensive larviculture is an alternative to improve initial survival rates. In this system, the larvae are reared in laboratory conditions for a number of days or weeks, fed adequate amounts of high-quality live feed, and when the larvae reach an advanced development stage they are transferred outdoors to fertilized ponds (Jomori et al., 2003). In earlier studies we showed the feasibility and economic advantages of rearing pacu (*Piaractus mesopotamicus*) larvae under an intensive system (Jomori et al., 2005). As aquaculture develops and becomes increasingly important in Brazil, the demand for high-quality larvae and juveniles also increase. In this scenario, efficient technologies that improve fishery quality must be developed and implemented.

The larvae of most native rheophilic fish of aquacultural interest (genera such as *Piaractus*, *Colossoma*, *Brycon*, *Salminus*, *Prochilodus*, *Leporinus*, *Pseudoplatystoma*, *Pimelodus*, among others) are typically altricial and hatch with a very small yolk reserve, which is rapidly exhausted (2–5 days). However, although many South American species are produced by aquaculture, studies on their initial development remain scarce. The available information is fragmented, and many studies focus only on the morphological development of the body, fins, mouth opening and pigmentation pattern (Godinho et al., 2003; Maciel et al., 2010; Nakatani et al., 2001; Nascimento and Araújo-Lima, 1993; Sanches et al., 2001; Souza and Severi, 2002). This occurs because few research groups in South America are involved in the systematic research of the development, ontogeny and larviculture of commercial fish. Our team is one the few research groups that has consistently investigated the initial development stages of freshwater Neotropical fish. With 15 years of research in this field, we have focused mainly on three species with altricial larvae, different behavior and feeding habits. The first, pacu larvae, are planktivorous and feed mainly on cladocera (Fregadolli, 1993; Marques et al., 2007; Sipaúba-Tavares and Braga, 1999). The larvae of the second species, the giant South American catfish sorubim (*Pseudoplatystoma* spp.), are piscivorous and cannibalistic, lying almost motionless on tank walls or bottoms until they detect a prey and suddenly lung forward to grasp it. The larvae of the third species studied, the dourado (*Salminus brasiliensis*), also piscivorous, are very aggressive and swim continuously in the water column, attacking prey immediately after sighting them and frequently only partially eating them (type I cannibalism, as described in Baras, 2000). *S. brasiliensis* larvae commonly encounter other conspecific larvae, which attack each other, forming cannibalism chains (Mai, 2009). Given the overall findings obtained by our research team over the years, we propose the compilation of the main information produced.

The present review focuses on the findings obtained for pacu because it is the most widely studied Neotropical freshwater species in terms of the early life stages and ontological development. However, information on other Neotropical species is also provided, particularly on Characiformes (Serrasalmidae: tambaqui *Colossoma macropomum*; Prochilodontidae: curimatã-pacu *Prochilodus marggravii* (=*P. argenteus*); Characidae: lambari *Bryconamericus aff. iheringii*, dourado *S. brasiliensis*, piracanjuba *Brycon orbignyanus*, matrinxã *Brycon orthotaenia*, piabanha *Brycon gouldingi*, and jatuarana *Brycon amazonicus*; Erythrinidae: *Hoplias lacerdae*); Siluriformes (Pimelodidae: barred sorubim *Pseudoplatystoma fasciatum*, spotted sorubim *Pseudoplatystoma corruscans*, mandi-beiçudo *Iheringichthys labrosus* and mapará *Hypophthalmus edentatus*), and Perciformes (Cichlidae: oscar *Astronotus ocellatus*, discus *Symphysodon discus*, bay snook *Petenia splendida* and mojarra castarrica *Cichlasoma urophthalmus*; Sciaenidae: curvina *Plagioscion squamosissimus*). Broadly speaking, larvae of *C. macropomum*, *P. marggravii* (=*P. argenteus*), and *B. aff. iheringii* are in general zooplanktivorous, with eating habits similar to those of pacu, whereas larvae of the genus *Brycon* behave similarly to dourado *S. brasiliensis* larvae (previously described). Accordingly, the feeding habits and behavior of the Pimelodidae and Erythrinidae larvae studied are similar to those abovementioned for *Pseudoplatystoma*, except for *H. edentatus*, which is planktivorous. The cichlids mentioned have species-specific differences in reproductive strategies and parental care. In general, *A. ocellatus*, *P. splendida* and *C. urophthalmus* are substrate spawners and nest guarders, and their larvae eat small zooplankton preys. Larvae of *S. discus* eat parental mucus (parentophagy), and larvae of *P. squamosissimus* (Sciaenidae) are piscivorous.

In the present review, we compiled data from peer-reviewed articles, theses, dissertations and books, as well as unpublished data on the initial development of pacu larvae. We believe that the compilation and organization of information on the morphological, physiological and behavioral changes of pacu larvae will be an important reference to support studies on other South American species. In addition, it will be useful in guiding feed management protocols and farming techniques that are compatible to the requirements, capacities and limitations of these species during development, increasing the production and efficiency of larviculture, and ultimately improving the possibility of obtaining good-quality larvae.

The embryonic development of pacu is rapid (approximately 18–19 h at 26.5 $\pm$ 0.5 °C), and larvae hatch with a standard length of 3.19 $\pm$ 0.04 mm and yolk sac volume of 0.477 $\pm$ 0.061 mm^3 (Clavijo-Ayala, 2008). The terminology adopted in the present study to define embryo, larvae and juvenile follows Kendall et al. (1984).

2. Skeletogenesis

Bone formation is one of the most important events in fish larval development, especially because of the role of bones in internal organ protection and body structuring (Estêvão et al., 2011). Knowledge of skeletogenesis is important to understand vital processes such as