Initial Development of Carnival Fish of Sweet Water: Systematic Review of Literature

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ABSTRACT

The initial development of carnivorous fish in farms requires intensive care regarding nutrition and management, in order to avoid the stress that can lead to cannibalistic behavior, a major cause of mortality in larvae and juveniles of cultivated carnivorous species. The objective of this article was to evaluate the initial development of carnivorous freshwater fish in South American territory, focusing on the development of the digestive tract and feeding, through a systematic literature review, resulting from research in scientific databases, with the strategy of searching for the key-words: fish and larvae and development and digestive and Brazil and "name of the different species found", besides manual searches made in the bibliographical references of the articles selected. At the end of the selection, 17 articles, published between 2007 and 2017, were included in the review. It was verified that the ontological evaluation of the digestive system of the larvae's is of major importance to adapt the nutritional management to the needs of the young animals, reaching higher productivity of carnivorous fish.

Keywords: Larva; Carnivore; South America.

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In recent years, a large number of freshwater fish species in South America have been receiving increased attention for their potential in aquaculture (Portella et al. 2014). The fish originated in this region have an excellent performance in semi-intensive and intensive systems, not only because of their high conversion rate and above-standard carcass weight, but they also meet the growing demand of the consumer market, which could otherwise be affected by the decrease on the fishery resources.

One of the most critical stages in fish production, especially in carnivorous or piscivorous species, is the initial developmental period that involves larviculture and juvenile production (Hayashi 2014). In this period, changes in the ontogenic state occur, resulting in morphological and physiological alterations, along with behavioral and dietary changes that characterize transitions from embryos to larvae and juveniles, and to the complete development of adult fish (Gomes et al. 2010; Marques et al. 2017).

Functional morphologists believe that the morphology and physiology of an organism, as well as the functions and requirements of each organ, have been shaped by natural selection as an adaptation to environmental variations throughout history (Maciel et al. 2009). Therefore, the investigation of the initial ontogeny of fish larvae is extremely important, in order to meet the optimal path in which the behavioral, reproductive, microhabitat and food needs of each species can be verified, as well as to bring up information on the morphology and physiology that can contribute to the conservation of the species considered endangered (Gomes et al. 2007).

The study of the morphological and physiological aspects and changes in these features that occur during initial development in larvae and juveniles, besides contributing to the early identification of the species, provide answers for the better understanding of factors that involve the apprehension of food and its digestion, fundamental for the determination of the best diet for ingestion and absorption, in order to reach the nutritional needs of the animals in their early life stages (Maciel et al. 2009; Rønnestad et al. 2013; Faccioli et al. 2016).

In the intensive cultivation of carnivorous fish larvae, attention with the quantity and quality of food and stress management should be taken into account, especially when the live food is replaced by dry food, a period where there is a higher incidence of cannibalism. The inadequate nutritional management at this stage may lead to a decrease in productivity as well as an increase in mortality, which may compromise the performance of future adult fish and commercial production (Hayashi 2014; Darias et al. 2015; Luz and Portella 2015).

Among the species of freshwater carnivorous fish that inhabit the South American region we can list: *Salminus brasiliensis, Hoplias malabaricus, Hoplias lacerdae, Zungaro zungaro, Brachyplathystoma filamentosum, Batrachoides surinamensis, Salminus hilarii, Cichla ocellaris, Pseudoplatystoma fasciatum* and *Pseudoplatystoma corruscans*. Each of these species is considered of great economic importance, since its production is spread throughout South America to supply domestic and foreign markets.

Therefore, the present study systematically reviewed the literature to identify studies that analyzed the ontogeny of South American carnivorous fish. So far, no systematic review has been conducted with this purpose, and in order to fill this knowledge gap, the present study aims to conduct a research on the initial development of freshwater carnivorous fish, focusing on the development of the digestive tract and onset exogenous feeding of these animals.

MATERIAL AND METHODS

The systematic review study was conducted according to the methodology of Preferred Reporting Items for Systematic Reviews and Meta-Analyzes (PRISMA) (Moher et al. 2009). To identify the articles that would be used, the main species of freshwater carnivorous fish that inhabited Brazilian regions of tropical and neotropical climates were identified, and 10 species were identified (*Salminus brasiliensis, Hoplias malabaricus, Hoplias lacerdae, Zungaro zungaro, Brachyplathystoma filamentosum, Batrachoides surinamensis, Salminus hilarii, Cichla ocellaris, Pseudoplatystoma fasciatum, Pseudoplatystoma corruscans*). Then a search was performed in the Web of Science, Science Direct and Google Scholar databases, from April to June 2017, with the search strategy that added the words: fish and larvae and digestive and Brazil and "name of the different species found" (one species at a time). Only English terms were used. Manual searches were made in the bibliographic references of the articles found. Used keyword: fish and larvae and digestive and Brazil and "name of the different species found.

For the inclusion of the studies in this review, the following criteria were used: descriptive or analytical studies, with a clearly described methodology, a target population of larvae or post-larvae, whose outcome was to describe the life stages, or digestive tract analysis or influence of natural feeding on fishes, carried out in South America, whose target species was tropical or neotropical carnivorous fish and native to the South American region, published or in the process of being published in magazines in the English or Portuguese language, from 2007 to 2017, with texts fully available texts. Articles, whose target species were different from those identified in the search keywords but were classified as freshwater carnivorous fish, or used not only larvae and post-larvae as the target population but also analyzed fish in juvenile stage, were also included.

After the search in the databases and the application of the search strategies, we identified studies that were not classified as articles or had duplication between the bases or between groups of keywords. Articles that deviated from the research topic, such as articles whose species studied were not carnivorous or freshwater, were excluded. All abstracts resulting after the application of the exclusion criteria, were read. In the cases that only the abstract was not sufficient to establish if the article fitted into the review, the analysis of the full article was performed to determine its eligibility. Articles selected after reading only the abstract had their full version obtained for confirmation of their eligibility and inclusion.

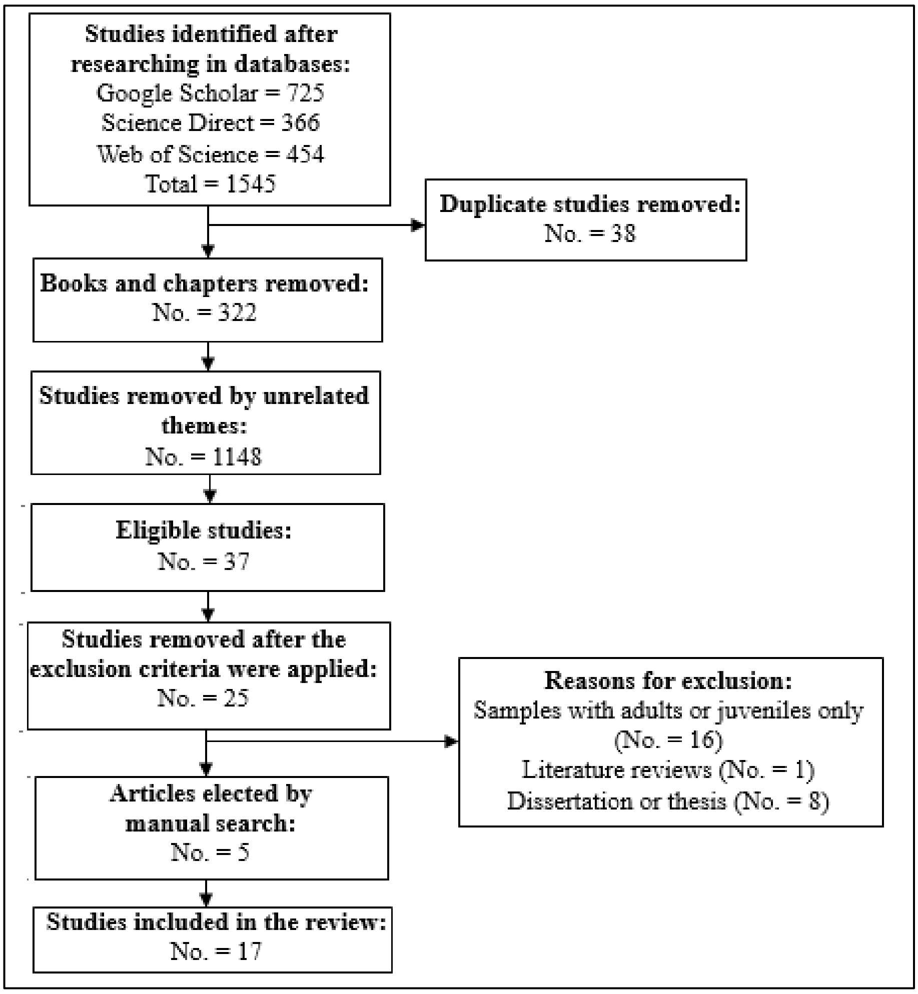
In order to be able to create a review on the development of the digestive tract from hatching or birth and the relationship of feeding with optimal fish development, the current review was structured in such a way as to separate the two topics.

RESULTS

The databases returned 1545 articles. After the removal of 38 duplicate articles and 322 studies that were not classified as articles (chapters and books), 1185 articles were selected. Among these, 1148 were excluded after analysis of the titles and abstracts. Of the 37 eligible studies, 28 were removed after applying the exclusion criteria, which were: 08 were dissertations or theses, one was a literature review and 16 did not make any reference to larvae or post-larvae. Manual searches picked 05 more articles that were included in the present review. At the end of the selection, 17 articles were included in the review, of which five researched juveniles. These were included because they present a study with both phases, larvae and juveniles, and cover the themes studied by the present review. Figure 01 presents the synthesis of the process of inclusion of the articles in this review.

As for the general characteristics of the articles, during the decade studied, only in 2013 no studies on the larviculture of carnivorous fish were found. The peak of the publications on the subject were found in 2007 and 2014, with three and four articles selected, respectively. Regarding the location of each study, seven articles were conducted in the state of São Paulo, seven were administered in Minas Gerais, one article was made in the state of Santa Catarina and two studies were conducted outside Brazilian territory, in the city of Iquitos, studying *Pseudoplatystoma punctifer* in the Peruvian Amazon. External analysis, such as length and weight measurements, were predominant, while internal analysis, like histological cuts were only made by 29.4% of the studies, and the sample size ranged from 90 to 3,600 fish.

Figure 01. Flowchart of the study selection process.



Source: Authors.

Table 01 presents the general information about the eight articles that discuss the initial development of carnivorous fish. The use of different terminologies to separate the different stages of larval development was observed. Five articles investigated development during the larval and post-larva phases and only one study characterized the juvenile phase.

The species sampled in the articles that studied the early development were very heterogeneous, three articles evaluated *Hoplias lacerdae* (Gomes et al. 2007; Maciel et al. 2009; Gomes et al. 2010), two evaluated *Hemisorubim platyrhynchos* (Andrade et al. 2014; Faccioli et al. 2016), while the other species were evaluated by only one article each.

Lophiosilurus alexandri was the most studied specimen in the articles that dealt with the feeding relationship with the development and survival of carnivorous fish (Table 02), appearing in four of nine articles. The analysis used to evaluate the relationship between development and feeding were varied:

Table 01. Studies that describe the external morphology and the development of carnivorous fish in South America.

Authors, year	Location	Fish Species	Total Sample Size	Phase of Development	Division of Ontogeny Used	External or Internal Analysis	Analysis Used
Gomes et al., 2007	Minas Gerais	*Hoplias lacerdae, Hoplias malabaricus* and *Hoplias unitaeniatus*	90	Larvae	Larvae	External and Internal	External descriptions and histological sections
Andrade et al., 2014	Castilho, SP	*Hemisorubim platyrhynchos*	210	Larvae, post larvae and juvenile	Yolk-sac stage, pre-flexion, flexion and post-flexion phase	External	External description, total length, standard length, snout length, eye diameter, head length, tail length, pre-anal length, head height, body height and number of arches
Maciel et al., 2009	Viçosa, MG	*Hoplias lacerdae*	510	Larvae and post larvae	Yolk-sac stage, larvae and juvenile	External	External description, total length and standard length
Honji et al., 2012	Paraibuna, SP	*Steindachneridion parahybae*	Unclear	Larvae and post larvae	Yolk-sac stage, larvae and juvenile	External and Internal	Total length and histological sections
Gisbert et al., 2014	Iquitos, Peru	*Pseudoplatystoma punctifer*	Unclear	Larvae and post larvae	Larvae and juvenile	External and Internal	Total length and histological sections
Gomes et al., 2010	Vicosa, MG	*Hoplias lacerdae*	140	Larvae	Larvae	External	External description, total length, standard length, total weight, yolk sac length and histological sections
Faciole et al., 2016	Jupia, SP	*Hemisorubim platyrhynchos*	690	Larvae and post larvae	Stages I, II, III and IV of development	External and Internal	Standard length and histological sections
Marques et al., 2017	Jaboticabal, SP	*Zungaro jahu*	160	Larvae	Larvae	External and Internal	Total length and histological sections

Source: Authors.

Table 02. Flowchart of the study selection process.

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Author, year	Location	Fish species	Total sample size	Study design	Phase of development studied	External or Internal analysis	Food type	Food amount	Outcome
Hayashi, 2014	São Paulo, SP	*Salminus brasiliensis*	3600	6 treatments and 4 repetitions	Post larvae	External	Plankton, artemia nauplii and ration (micro grinded and wet)	T1: plankton (100ml); T2: artemia (20ml); T3: plankton (50ml)+artemia (20ml); T4: plankton (100ml)+ration; T5: artemia (20ml)+ration; T6: plankton (50ml)+artemia	Fish fed with artemia associated with plankton had increased survival and weight gain

								(20ml)+ration	
Pedreira et al., 2008	Três Marias, MG	*Lophiosilurus alexandri*	1500	4 treatments and 5 repetitions	Post larvae	External	Plankton (650 and 1300μm) and commercial ration	Plankton and ration at will	Greater survival, biomass, length and weight gain for fish fed 1300μm plankton
Darias et al., 2015	Iquitos, Peru	*Pseudoplatystoma punctifer*	3600	5 treatments and 3 repetitions	Post larvae	External	Artemia and 4 formulated diets	Artemia (0.6-9 nauplii/ml) until day 17; diets of 30:15, 30:10, 45:15 and 45:10 (protein:lipid)	Great survival, weight and length gain for fish fed diets of 45:15
Schutz and Nuner, 2007	São Carlos, SC	*Salminus brasiliensis*	360	6 treatments and 4 repetitions	Post larvae	External	Artemia and fish prey	Artemia (40 nauplii/fish) and fish prey (6 preys/fish)	Higher survival, weight, length and size gain for larvae fed fish prey
Luz, 2007	Jaboticabal, SP	*Pseudoplatystoma corruscans*	Unclear	4 treatments and 4 repetitions	Post larvae	External	Artemia, fish prey and commercial ration	Artemia (500-1000 nauplii/fish) and fish prey (10 preys/fish) and additional ration	Increased stress resistance for post larvae fed fish prey
Luz et al., 2011	Três Marias, MG	*Lophiosilurus alexandri*	720	4 treatments and 3 repetitions	Post larvae	External	Artemia, extruded commercial ration and Scott emulsion	T1: artemia (1300 nauplii/fish); T2: artemia (2600 nauplii/fish); T3: ration+10g of artemia; T4: ration+10ml of Scott emulsion	Higher weight, biomass and length gain and lower mortality for post larvae fed artemia associated with ration
Cordeiro et al., 2016	Belo Horizonte, MG	*Lophiosilurus alexandri*	640	2 treatments and 4 repetitions	Post larvae and juvenile	External	Formulated diets (1.2 or 2.6mm pellet)	50% of total biomass of each tank	Higher weight, biomass and length gain and lower mortality for post larvae fed 1.2mm pellet
Filho et al., 2014	Belo Horizonte, MG	*Lophiosilurus alexandri*	1440	4 treatments and 5 repetitions	Post larvae and juvenile	External	Beef formulated diet, artemia and extruded dry ration	Artemia (1300-3250 nauplii/fish) +100% of biomass in formulated diet in the concentrations of 2, 4, 6 and 8% of the fish weight/day	Higher biomass gains and feed conversion rate in fish fed at a concentration of 8% of weight/day
Luz and Portella, 2015	Unclear	*Hoplias lacerdae*	3000	5 treatments and 4 repetitions	Post larvae and juvenile	External	Artemia	Artemia in the concentrations of T1:300; T2: 500; T3: 700; T4: 900 and T5: 1100 nauplii/day	High concentration influence weight gain and growth, but doesn't influence survival rate

Source: Authors.

the use of weight gain and length evaluation, as well as the survival rate and cannibalism, predominated. Other criteria employed were biomass gain (Pedreira et al. 2008; Luz et al. 2011; Cordeiro et al. 2016; Melillo Filho et al. 2014), resistance to stress (Luz 2007) and feed conversion rate (Melillo Filho et al. 2014). The diets used also differed: nauplii of artemia were the most used, showing in 77.7% of the studies (Hayashi 2014; Darias et al. 2015; Schütz and Nuñer 2007; Luz 2007; Luz et al. 2011; Melillo Filho et al. 2014; Luz and Portella 2015), followed by dry commercial feed in 44.4% of the articles (Pedreira et al. 2008; Luz 2007; Melillo Filho et al. 2014).

DISCUSSION

ONTOGENY DIVISION

The ontogeny division of the fish is extremely convenient because, having well-established divisions at given intervals, it facilitates independent research, comparison of results by researchers from different locations, and the dissemination of new technologies and discoveries to psychologists.

Despite the apparent easiness of using ontogenic division, this is hampered by the variety of terminologies used to describe different stages of larval development. 50% of the studies evaluated by this review presented the division of the phases into larva, post-larva and juvenile, while 37.5% used the term larval-vitelinico together with other denominations such as the one proposed by Ahlstrom (1976), which divides the larval development in pre-flexion, flexion and post-flexion, according to the notochord flexion. Faccioli et al. (2016), studying larvae of *H. platyrhynchos*, divided development in stages I to IV: stage I begins with hatching and concludes with mouth opening; stage II ranges from the beginning of exogenous feeding to complete depletion of the yolk sac; in stage III the larvae feed exclusively on exogenous food, but they do not yet have functional stomach; and Stage IV is marked by the development of the gastric glands.

CHARACTERISTICS OF LARVAL DEVELOPMENT

The development of fish larvae is an important stage in the life cycle of the animal and provides clarification on the biology of the species and its evolution, especially aspects related to ontogeny, feeding and reproduction (Gomes et al. 2007). Egg hatching time varies from 13 hours for *Zungaro jahu* to 54 hours for *Hoplias lacerdae* after fertilization, with eggs being incubated at 25-30 ° C (Marques et al. 2017; Honji et al. 2012). The morphological and physiological changes suffered by the fish in this period is critical for the survival and reproductive success of the animal, so its detailed study is required for species of great commercial appeal.

According to the reviewed studies, the larvae of South American carnivorous fish can be considered "altricial", since at the hatch, these larvae present low development level for all organs: nonfunctional mouth and anus, little or none pigmentation and large yolk sac. Despite this similarity, the species presented significant differences in the ontogeny period and in the morphometric analyzes.

PIGMENTATION

Newly hatched larvae of all species analyzed by the present review are translucent and show little or no pigmentation. The pigmentation in fish larvae is an important characteristic, since it favors the survival of the animals by camouflage since, in the larval phase, they present great susceptibility to predators. For the species *Hemisorubim platyrhynchos, Zungaro jahu, H. lacerdae, H. malabaricus and H. unitaeniatus*, a small amount of chromatophores were located in the ventral region, in the anterior and posterior regions of the yolk sac, as well as pigments in a round shape in the cephalic region (Gomes et al. 2007; Andrade et al. 2014; Marques et al. 2017). *H. malabricus* also exhibits dendritic pigmentation. After complete absorption of the yolk sac and the progression to the post-larvae stage, there is an increase in the concentration of chromatophors in the posterior region of the head and the appearance of a large number of dendritic chromatophores in the chest region of the animals, still that does not resemble the pigmentation found in adults. However, juvenile animals present a larger number of chromatophores distributed throughout the body, including barbels and pigmented fins (Honji et al. 2012). This chronological evolution of pigment distribution in animals suggests that evolutionary habits and strategies for survival undergo changes throughout fish development.

FINS

When hatching, none of the fins that are present in adult individuals is developed in the larvae. The larvae hatch with the finfold, which begins in the posterior portion of the yolk sac, round the caudal peduncle and follow dorsally towards the head until reaching the level of the posterior part of the yolk sac (Andrade et al. 2014). Also during the larval stage, the pectoral fins begin to develop between the second and seventh days (Maciel et al. 2009; Gomes et al. 2010), although the primordial fin is still visible. Among the species studied by the included articles, the growth of caudal and anal fins occurred at different stages of development. It was observed that *H. lacerdae* presented the dorsal, caudal and anal fins with completely formed rays and first pigmentation on the tenth day, while the yolk sac was still present (Maciel et al. 2009), which implies the development of fins still in the larval stage. Andrade et al. (2014)reported that for *H. platyrhynchos* the yolk sac absorption occurs before the anal and caudal fin are fully formed, and prior to the appearance of the pelvic fin bud. During the post-larval stage, the caudal, anal and dorsal fin rays are fully formed and the pelvic fin slowly begins to take form, but the primordial fin is still in the process of being reduced and will only disappear in the juvenile phase, when all of the fins, including the pelvic fins, are formed and pigmented.

YOLK SAC

Yolk sac depletion is one of the most striking events in larval development: after complete absorption of the yelk, the larva begins to show rapid development of the digestive tract, which will allow a better use of the exogenous food. It is also the most critical period for larvae, since the passage from endogenous to exclusively exogenous feeding may result in high mortality rates and cannibalism, if larval feed is not properly administered (Honji et al. 2012).

There is, however, a large discrepancy in relation concerning the time for complete absorption of the yolk sac. The larvae of *Steindachneridion parahybae* present complete depletion of the yolk two days after hatching, whereas the *H. lacerdae*, needs twelve days to complete the same process. However, the time taken to completely absorb the yolk sac appears to have an inverse association with the development of the digestive tract. For *H. platyrhynchos* larvae, which presented yolk sac depletion 04 days post hatching (4 dph), the complete formation of the J-shaped stomach was observed only after 20 dph (Andrade et al. 2014). While Gisbert et al. (2014) observed the total absorption of the yolk sac at the 5th and 6th dph, and the complete morphoanatomical formation of the stomach at 14th dph. The histochemical properties of the mucosal cells aligned to the regions of the gastric fundus visualized at the 7th dph can be considered as an indirect signal of the functionality of the stomach.

MOUTH OPENING

The main factor responsible for the high mortality rate in carnivorous fish larviculture in South American territory is linked to incorrect food management at a time when trophic needs are no longer supplied by endogenous supplies and depend on exogenous foods. In this case, the observation of the buccal cavity opening becomes of extreme necessity, since it will be only after this event that the larva will be able to capture external food (Cordeiro et al. 2016). The time for complete mouth opening and its size allow us to infer when must be initiated food management and the size of food that the fish larva will be able to ingest.

According to the reviewed studies, the mouth opening process tends to occur at any time between the first and the sixth day after the larvae hatch. It is important to note, however, that the development level of the animals at the opening time varied among species. (Gomes et al. 2007) observed the opening of the mouth occurring between the fifth and sixth day after hatching for the Erythrinidae studied, when they already had a complete and functional stomach. In the study by

Facciole et al. (2016)specimens of *H. platyrhynchos* presented the buccal opening in the 2nd dph and went through a period of nine days with exogenous feeding before their stomach became functional in the 14th dph.

FORMATION OF THE DIGESTIVE TRACT

When hatching, the larvae present a digestive system as a straight tubule, closed in its cranial and caudal portion, and histologically undifferentiated (Honji et al. 2012). The tract undergoes small changes in the first days of life, such as the appearance of goblet cells in the esophagus and buccopharyngeal region, dilatation of the region connecting the esophagus to the intestine, indicating the stomach location. But, it will remain practically unchanged until the mouth opening and the yolk sac depletion, events that mark the rapid metamorphosis of the studied larvae.

After yolk sac depletion, the tract will gradually differentiate into buccopharynx, stomach, anterior, middle and posterior intestine and rectum. Goblet cells, which are described before mouth opening and remain scarce during the days following this event, increase after the third day (Faccioli et al. 2016), after the opening of the buccal cavity.

At the time of hatching, the intestine presents a single layer of epithelium, and as the digestive tract differentiates, the intestine begins to develop several folds. The middle intestine presents several folds, while the posterior intestine presents a straight line with several internal longitudinal villi that optimize the absorption of nutrients (Marques et al. 2017). The rectum shows no fold or villi. Goblet cells are described before differentiation of the intestine into four sections, but these will multiply as the fish develops and at the end of the differentiation of the digestive system they are present in great quantity in the posterior intestine (Gisbert et al. 2014).

The accessory glands of the digestive tract are histologically undifferentiated at the time of hatching, but the liver and pancreas are visualized between 16 hours and 24 hours after birth (Marques et al. 2017; Faccioli et al. 2016). From the liver, which occupies the anterior region of the yolk sac, it was possible to observe hepatocytes and hepatic glycogen, right after the observation of beginning of the differentiation, and increased in number as the larva developed. The pancreas, located between the liver and the yolk sac, has few and spaced zymogen granules that are enzyme precursors, which considerably increases in number until the depletion of the yolk.

The stomach is the last organ to be differentiated. The incipient form of this organ is still verified in the first days of life, between the esophagus and the anterior intestine, but the first gastric glands appear between the second and third week of life (Gisbert et al. 2014). And the formed stomach, with gastric glands and functional pyloric cecum, is observed between three and four weeks after hatching (Marques et al. 2017; Gisbert et al. 2014; Faccioli et al. 2016). Until the stomach formation occurs, the digestion of the exogenous food will occur in the larvae intestine, at alkaline pH and with the aid of the enzymes obtained via live foods. When the stomach differentiates, it is possible to observe three distinct regions: cardiac, fundic and pyloric stomach. The cardiac and pyloric regions have valves that will limit the passage of food into and out of the stomach, and the pyloric region has no gastric glands.

FEEDING

LIVE FOODS

The establishment of an adequate feeding protocol, adapted to the digestive capacity and nutritional needs during the initial development of carnivorous fish, besides addressing options for the reduction of cannibalism, is of extreme importance for the survival and growth of the larvae (Darias et al. 2015).

The determination of a single feeding protocol for all larvae and juveniles of carnivorous fish has not been established, because there are variations among the species, which may have different nutritional needs. Thus, some authors have studied different foods provided for larvae and juveniles of specific species (Luz 2007; Schütz and Nuñer 2007; Pedreira et al. 2008; Luz et al. 2011; Darias et al. 2015; Cordeiro et al. 2016), in an attempt to improve their growth and survival, seeking to increase their productivity.

Because they don't have the digestive system developed enough to assimilate the dry diet, having fewer digestive enzymes and unable to take advantage of the nutrients provided, the larvae need to be fed with live foods at the beginning of their exogenous feeding. The superiority of live food as the first food offered to the larvae may be related to the presence of some enzymes in the prey itself, which, when ingested, collaborates with the digestive process of the larva. During this period, a more intensive management is required in the maintenance and supply of live food to larvae, which makes larviculture costs higher (Pedreira et al. 2008).

According to Luz (2007), food plays an important role in the growth and resistance to stress in larvae of *P. coruscans*, and the supply of live food provides better conditions for the larvae to withstand the initial stress of intensive cultivation. The authors evaluated the resistance to stress after feeding different diets (forage larvae: Colosoma macropomum, artemia sp. and extruded dry diet) for *P.*

coruscans larvae, and found that the larvae that received dry diet had inferior results ($p < 0.05$) regarding stress resistance, as well as lower growth.

The size of live food offered to carnivorous fish larvae also influences their survival and growth (Luz 2007; Schütz and Nuñer 2007; Pedreira et al. 2008). According to Schütz and Nuñer (2007), the supply of forage larvae *Prochilodus lineatus*, due to their larger size than the *Artemia* sp., are more visible and consequently more consumed by *Salminus brasiliensis* larvae, resulting in a higher survival rate, lower cannibalism rate, and superiority in relation to growth ($p < 0.05$). Pedreira et al. (2008) also observed the influence of larger food on the growth of L. alexandri larvae after supplying selected zooplankton in sieves with meshes of different diameters. Where larvae fed with selected plankton in a 1300 μm sieve, which contained more and larger adult copepods, presented higher yield (weight, length, biomass and condition factor) than those fed with selected plankton in 650 μm, which had a larger proportion of smaller nauplii.

The concentration of prey (*Artemia* sp.) was evaluated by Luz and Portella (2015), when supplied to larvae of *H. lacerdae,* where their growth was studied, before weaning, in the production of juveniles of this species. It was observed that the concentration of *Artemia* sp. provided has an influence on the larvae growth, especially in the first days of exogenous feeding. Even after the animals were weaned, the concentration of live food initially supplied continues to influence the size of juveniles. However higher concentrations of *Artemia* sp. can generate a greater increase of ammonia in the water, which must be controlled to avoid the death of animals.

WEANING AND ADAPTATION TO DRY FOOD

After a few days or weeks of beginning the exogenous feeding of the larvae, the process known as weaning is performed, where the larvae feed is gradually modified and, in the end, the live food is replaced by a formulated diet. Therefore, food strategies are needed to stimulate the consumption of dry diets for the fish adaptation, without growth being impaired (Luz et al. 2011).

According to Luz and Portella (2015), juveniles of *H. lacerdae* have a good acceptance for formulated diets after training with the replacement of artemia nauplii for a mixed diet of beef and extruded commercial diet. When a gradual transition was made, a greater proportion of meat, provided at the beginning, was modified over time by increasing the amount of dry diet, until the exclusive supply of extruded dry diet. From the results, the authors observed that juveniles from 16mm accepted training with the formulated diet.

Darias et al. (2015) observed that a supply protocol of *Artemia* sp. between days 03 and 14 after larvae hatching, starting a dry diet with high protein content (45%) and high lipid content (15%) on day 12 post-hatching (accompanied by nauplii of artemia) resulted in superior growth and survival of the *P. punctifer* initial stages, in relation to diets with lower levels of protein and lipids, and to a prolonged supply of artemias.

A dry diet, offered directly after the feeding change, with live food, does not present an adequate attraction in relation to the appearance, texture and palatability, leading to inferior rates of juvenile survival and growth when compared to training with a mixture of dry foods and meat (Luz et al. 2011). According to Luz et al. (2011), the inclusion of *Artemia* sp. In the mixture of meat offered to juveniles of *L. alexandri*, did not present significant difference in relation to the survival of the juveniles, but resulted in a biomass increase ($p < 0.05$), to be applied in the training of the animals, as a form of attraction, consequently increasing the acceptance of dry food. In the same study, the inclusion of cod-liver oil enriched with vitamins did not increase the attraction and palatability of the food, not having superior results for survival and growth than the other feed training diets.

The feed rate with dry diet after weaning also influences the survival and biomass gain according to Melillo Filho et al. (2014), who observed an ideal rate of 5.5% wet body weight/day for juveniles of *L. alexandri*.

According to Cordeiro et al. (2016), the size of the pellet offered, after the weaning of juveniles (*L. alexandri*), influences the weight gain, since smaller particles can facilitate the consumption of inert diets. In the study, it was observed that pellets with 1.2 mm diameter produced a higher growth rate of juveniles compared to pellets containing 2.6 mm pellets.

CANNIBALISM

According to Baras and Almeida (2001), cannibalism can be classified into two types, Type I - where the prey is attacked in the tail and is normally bitten and then released; And Type II - where the prey is attacked in the head. Luz et al. (2011)observed both types of cannibalism during the *L. alexandri* feed training phase, even with excess of food in the tanks. But in both types of cannibalism, juveniles did not swallow the prey completely due to the shape of the animal's head.

The first signs of *P. punctifer* cannibalism were observed by Darias et al. (2015), 10 days after larvae hatching, which coincided with the formation of the gastric glands of stomach and oral valves, fully equipped with taste buds to track the quality of food. In this study, it was observed that the incidence of cannibalism clearly increased during weaning.

Cordeiro et al. (2016) also observed an increase in cannibalism behavior in juveniles of *L. alexandri* during weaning period, besides an interaction between the percentage of observed cannibalism and the density of animals in the tank. At higher densities (30-40 juveniles/L) cannibalism presented an average of 56.2%, significantly higher than in tanks containing 05 juveniles per liter, where the average was 30.5%. In the same study, during the initial phase of feeding live foods, the larvae maintained at high density (300 larvae/L) presented an average of 3.1% cannibalism, corroborating with other studies that suggests that the weaning period triggers an increase in cannibalism for this species.

It has been suggested that the inclusion of specific nutrients in the diet, which induce relaxing effects such as phospholipids, can attenuate cannibalism, making the animals less aggressive (Darias et al. 2015).

Environmental factors

Environmental factors also interfere with larval and juvenile productivity of carnivorous fish. Adequate feeding management (live food and weaning), lighting, and animal density enhances survival and minimizes the occurrence of cannibalism in the early stages of life of carnivorous species according to (Luz and Portella 2015).

According to Luz et al. (2011), *L. alexandri* larviculture can be done with a low water flow (200 ± 50 mL/min), when the larvae are fed with nauplii of artemia, reducing water waste, without increasing cannibalism and having no influence on the growth and survival of the larvae. Probably due to the behavior of the larvae in this species, which remain grouped, having greater movement only at the moment of feeding.

Melillo Filho et al. (2014), concluded that the drainage system on the surface of the tank is more efficient at keeping the food alive for longer, compared to a column drainage system inside the tank, allowing the larvae to have more time to feed, in addition to avoiding accumulation of excess organic material, resulting in greater growth of *L. alexandri* larvae. During the feed training phase, growth and survival rates were also higher in juveniles that remained in the drainage system on the surface of the tank.

The photoperiod did not influence the survival of post-larvae of *S. brasiliensis* according to Schütz and Nuñer (2007). But the behavior of the post-larvae was influenced by the presence or not of light, where the post-larvae that were kept totally in the dark had higher growth, compared to larvae that had a longer period of illumination (14-24h per day), which was related to a lower energy consumption by larvae that moved less in the absence of light.

According to Cordeiro et al. (2016) Larvae of *L. alexandri*, fed with *Artemia* sp. in the first phase of feeding at 2g/L salinity, maintained at high density (300 larvae/L), had a high survival rate (95.7%), demonstrating the potential for intensive larvae in this species. Growth was also not affected by high-density ratios. During the feed training phase, enhanced density (30 and 40 juveniles/L) increased cannibalism (52.6 - 56.2%), resulting in a lower survival of these animals (28.3%), even though, greater quantity of individuals was produced with high density, compared to smaller densities at the end of the experiment. Thus, the higher density resulted in higher values of biomass and number of individuals produced.

FINAL CONSIDERATIONS

The main events during the initial development of South American freshwater carnivorous fish larvae are mouth opening, yolk depletion, exogenous feeding onset, and histological differentiation of the digestive tract in the oropharynx, stomach, anterior, middle and posterior intestine and rectum. Neotropical carnivorous fish larvae can coordinate the development of locomotion, digestive, and sensory structures, and when the complete depletion of the energy reserve occurs, they are able to perceive, pursue and capture exogenous foods. The larvae then grow rapidly, bulking up in a few weeks up to 6 times larger than the initial size, and develop the ability to feed exclusively on dry food. Each of these events, however, will only be possible and optimized by exposing the larvae to a favorable environment and feeding.

The larvae of South American freshwater carnivorous fish are altricial, that is, they hatch at an unfinished stage of development, which makes the establishment of exogenous feeding a competitor against the development of the digestive tract, as well as that of the critical systems for an optimal nutrition, such as vision and sensory organs. For these reasons, the food offered for the larvae must be qualitative and quantitatively adequate, made with foods of great nutritional quality and with size compatible with the mouth opening of the larvae. In order to supply the enormous nutritional demand of the larvae, several foods have already been tested, but no food obtained better results than the supply of live prey, since these present enzymes that assist in the digestion process of the larva.

Besides the biological understanding of larval ontogeny, the information compiled in this review supports the establishment of feeding and management protocols to increase the quality and production of South American freshwater carnivorous fish larvae and to reduce the incidence of production losses due to cannibalism, which would result in a significant increase in the profitability of aquaculture production throughout the South American territory.

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Desenvolvimento Inicial de Peixes Carnívoros de Água Doce: Revisão Sistemática da Literatura

Resumo

O desenvolvimento inicial de peixes carnívoros em fazendas requer cuidados intensivos em relação à nutrição e manejo, a fim de evitar o estresse que pode levar ao comportamento canibalístico, uma das principais causas de mortalidade em larvas e juvenis de espécies carnívoras cultivadas. O objetivo deste artigo foi avaliar o desenvolvimento inicial de peixes de água doce carnívoros em território sul-americano, enfocando o desenvolvimento do trato digestivo e da alimentação, por meio de uma revisão sistemática da literatura, resultante de pesquisas em bases de dados científicas, com a estratégia de busca as palavras-chave: peixes e larvas e desenvolvimento e digestivo e Brasil e "nome das diferentes espécies encontradas", além de buscas manuais feitas nas referências bibliográficas dos artigos selecionados. Ao final da seleção, 17 artigos, publicados entre 2007 e 2017, foram incluídos na revisão. Verificou-se que a avaliação ontológica do sistema digestivo das larvas é de grande importância para adaptar o manejo nutricional às necessidades dos animais jovens, atingindo maior produtividade de peixes carnívoros.

Palavras-Chave: Larva; Carnívoro; Sul América.

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