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Morphological development of *Hypophthalmus fimbriatus* and *H. marginatus* post-yolk-sac larvae (Siluriformes: Pimelodidae)

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Abstract

Descriptions of stages in the larval development of two sympatric and congeneric freshwater fishes from the rio Negro (Amazon basin), *Hypophthalmus fimbriatus* and *H. marginatus*, are presented. Larval development is described in terms of ontogenetic changes in morphology, pigmentation and fin development. Developmental changes during the larval period of the two species are similar, but they can be separated mainly by the following variables: eye diameter, head width, body depth and pre-pectoral distance. Aspects of their reproduction strategies are also discussed.

Key words: mapará, morphological description, larval development, rio Negro, Amazon

Resumo

São apresentadas descrições dos estágios de desenvolvimento larval de duas espécies de peixes de água doce simpátricas e congêneres do rio Negro (Bacia Amazônica), *Hypophthalmus fimbriatus* e *H. marginatus*. O desenvolvimento larval é descrito em termos de mudanças ontogênicas na morfologia, pigmentação dos olhos e desenvolvimento das nadadeiras. As mudanças durante o desenvolvimento larval das duas espécies são similares, mas podem ser separadas principalmente pelas seguintes variáveis: diâmetro do olho, largura da cabeça, altura do corpo e distância pré-peitoral. Aspectos relativos às suas estratégias reprodutivas são também discutidos.

Introduction

The South American catfishes known as the "maparás" (*Hypophthalmus* spp.) are commercially important freshwater species. Of the four species known from Brazil, three are found in the Amazon basin: *H. edentatus* Spix & Agassiz, 1829, *H. fimbriatus* Kner, 1858 and *H. marginatus* Valenciennes, 1840. They are characterized by their deep and large body, and their pelagic and zooplanktivorous feeding habits (Lundberg & Littmann, 2003).

Morphological similarities, along with the lack of recent taxonomic revisions, represent the major difficulties found in the study and identification of early life stages of many fish species. The use of morphometric characters has been shown to be an important tool in the study of the different developmental phases and identification of siluriform species. In Brazil these studies are rare, examples include Sanches *et al*. (1999), Naka-

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tani *et al*. (1998) and Nakatani *et al*. (2001) who describe morphometric characters of the catfishes of the Paraná basin, and Leite *et al*. (2007) who studied ten species of migratory catfishes of the Amazon basin.

Due to lack of taxonomic information on the larval forms in the rio Negro (Oliveira 2003), most larvae are identified only to family or genus. This is especially true of congeners and sympatric species. Our objective is to: (i) describe ontogenetic development; (ii) analyze morphometric and meristic data; and (iii) compare the larvae of two species of *Hypophthalmus* using morphological characters. Some aspects of the spawning behavior of these species are also discussed.

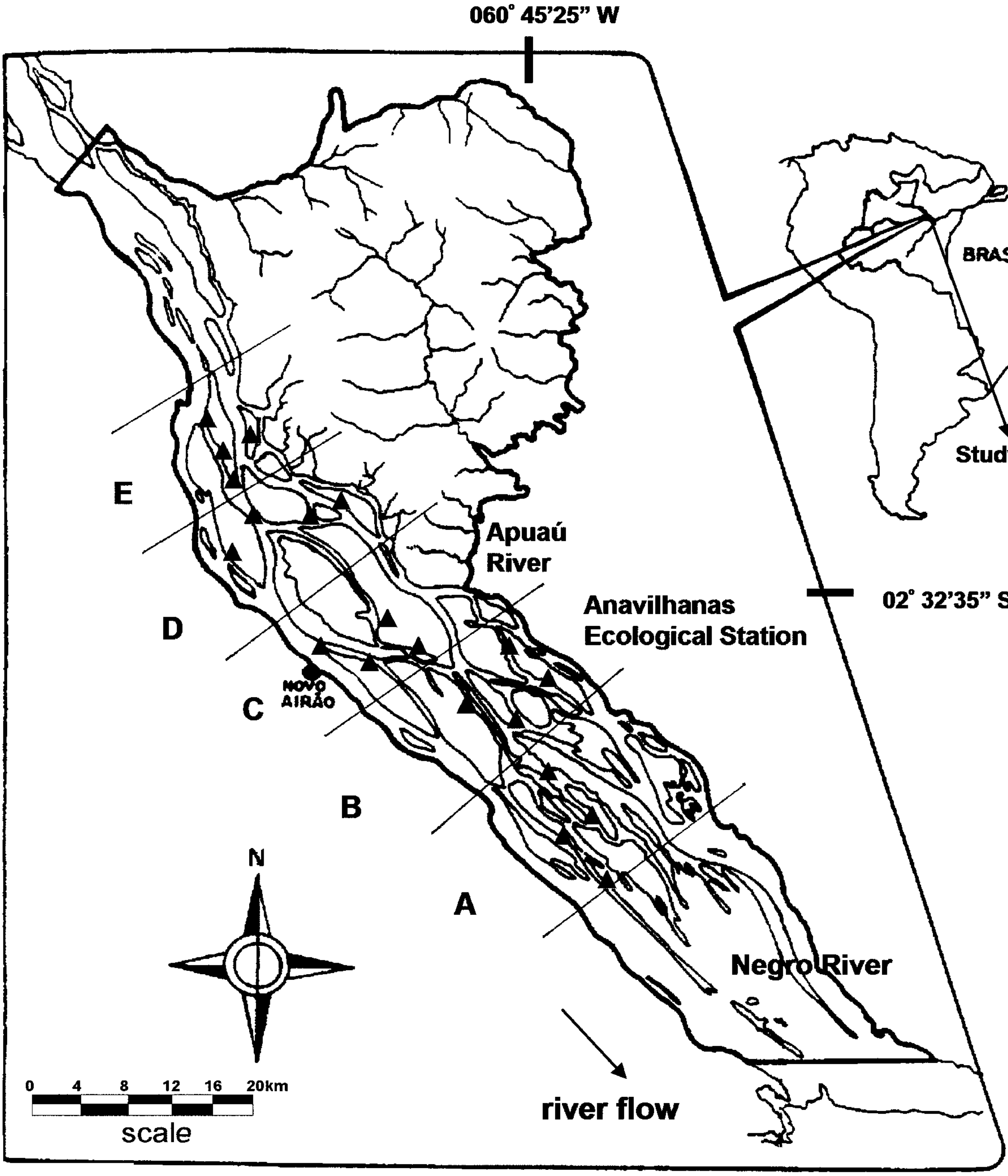

FIGURE 1. Sampling sites in the Anavilhanas Ecological Station – ESEC, rio Negro, with the substations (A, B, C, D and E) where *Hypophthalmus* spp. larvae were collected.

Material and methods

The specimens analyzed came from samples collected in 20 sites located on the lower rio Negro in Anavilhanas Ecological Station, circa 100 km above Manaus, at five stations of 20 km each (Fig. 1). At each one of these stations four sites were sampled from the surface (0.20 m) and at the bottom (2.0 to 9.0 m) during the day and at night totaling 80 samples in two periods: November 2001 (falling waters) and January 2002 (rising waters). These sites were sampled at different depths near the margin, in various flow characteristics, and in different patterns of sedimentation and erosion (Fig. 1).

In each sample, a conical-cylindrical plankton net with a quadrangular mouth measuring 22.5 X 20.5 cm in area and 3.25 m in length (mesh 0.465 mm), and equipped with a General Oceanics™ flowmeter was used. The net was stabilized by a 20 kg metal deflator and pulled vertically by a cable attached by a pulley fixed to a boat. Ten-minute trawls were taken on the surface and river bottom were taken with the boat maintaining constant velocity and moving directly against the current. The samples were later taken to the laboratory, where the larvae and juveniles were separated from the rest of the plankton and identified according to the development sequence technique proposed by Ahlstrom & Moser (1976). After identification, the specimens were separated according to the degree of the notochord flexion into preflexion, flexion and postflexion stages (Ahlstrom *et al*. 1976, modified by Nakatani *et al*. 2001). The material collected is deposited at the Fish Larvae Collection of the Laboratory of Ecology III (NUPIC) at the Federal University of Amazonas.

In order to characterize larval development, the following body measurements were taken (in mm) using a stereomicroscope equipped with a micrometric eyepiece (Ahlstrom & Moser 1976): standard length (SL), snout length (SnL), eye diameter (ED), head depth (HD), head width (HW), interorbital distance (ID), head length (HL), body depth (BD) and pre-pectoral-fin length (PPL), pre-pelvic-fin length (PVL), pre-dorsal-fin length (PDL) and pre-anal-fin length (PAL). When possible, counts were made of the preanal, postanal and total myomeres, as well as the rays of the pectoral (P), pelvic (V), dorsal (D) and anal (A) fins.

Proportions of head hearth, snout length, interorbital distance, eye diameter and head width were expressed as a proportion of HL, and the head length, body depth and pre-pectoral, pre-pelvic and pre-anal distances were expressed as a proportion of SL.

Proportions of eye diameter (expressed as a proportion of HL), and head length and body depth (expressed as a proportion of SL), were determined according to the categories proposed by Leis & Trnski (1989). To evaluate whether the ratios between morphometrical variables and head and standard lengths (covariables) varied between species, an analysis of covariance (ANCOVA) was applied (Dowdy & Wearden 1991).

Illustrations of successive stages in larval development for each species, focusing on ontogenetic changes, were produced with the aid of a camera lucida mounted on a stereomicroscope.

Results

Hypophthalmus fimbriatus (Fig. 2 a–f)

Description of the larvae. Sixty-one larvae (18 preflexion, 22 flexion and 21 postflexion), with standard lengths between 12.7 and 13.1 mm, were analyzed. The larvae of this species exhibit a long body (12.4 to 19.8% SL) while head lengths vary from small to moderate (16.1 to 25% SL) (Table 1). There is no trace of yolk. In preflexion, the mouth is open and terminal during its entire development. The nostrils are single and become double at approximately 10.2 mm SL (postflexion). Barbles were formed: 2 mental pairs and 1 maxillary pair. They are shorter and thicker compared to those of *H. marginatus*. The embryonic membrane (median fin fold) is hyaline and surrounds the body from the middle region of the dorsum to the abdominal portion, become totally absorbed by the end of the postflexion stage (13 mm SL). The eyes are rounded and

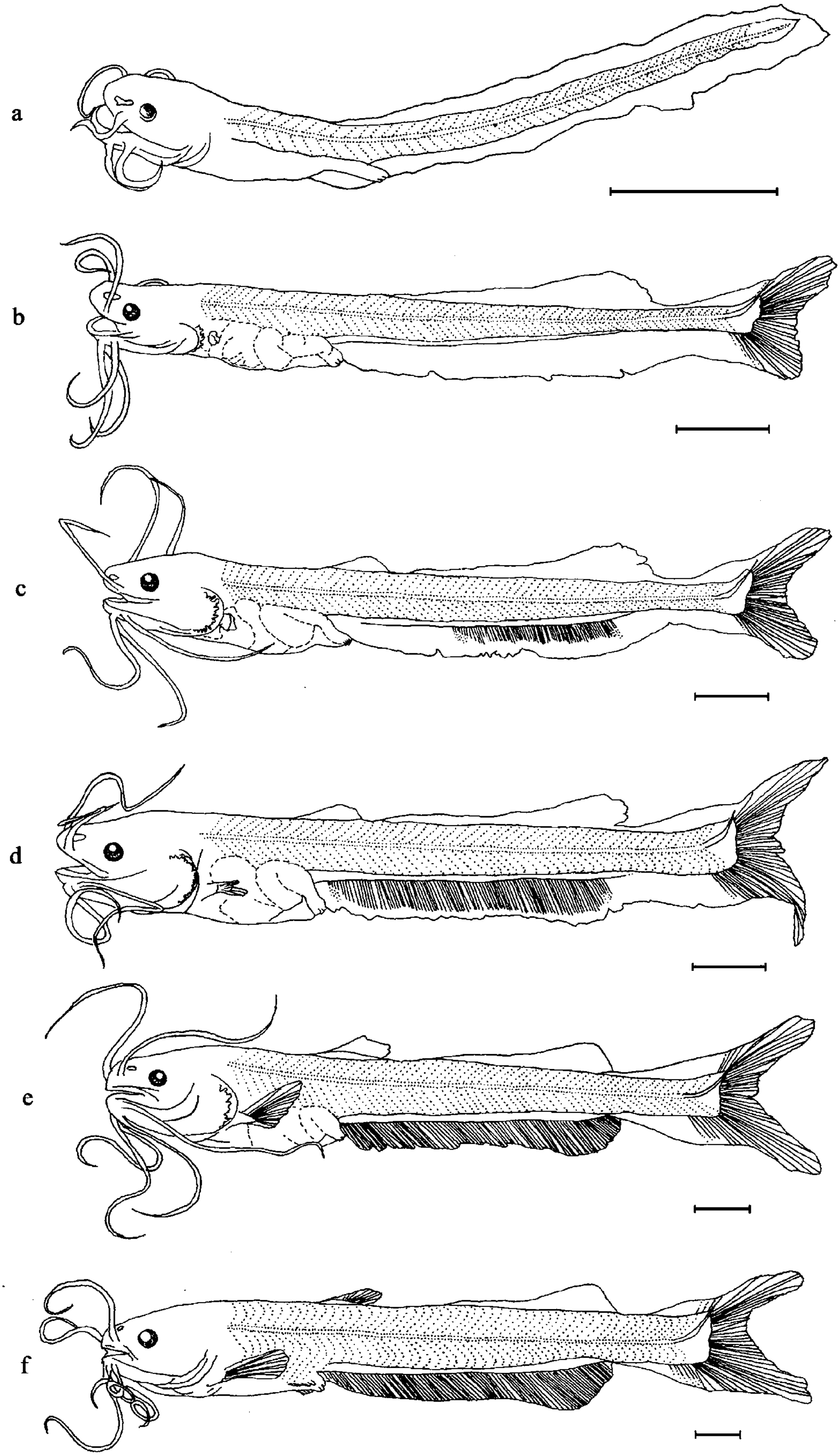

FIGURE 2. Larval development of *Hypophthalmus fimbriatus*. Developmental stages are: a) preflexion (4.20 mm SL); b) early-flexion (7.25 mm SL); c) mid-flexion (9.30 mm SL); d) late-flexion (9.40 mm SL); e) early-postflexion (10.87 mm SL); and f) mid-postflexion (13.28 mm SL). Scale = 1mm.

pigmented, with a diameter varying from 7.8 to 15.7% HL, classifying it as small throughout development (Table 1). The operculum is formed at about 10.1 mm SL. The intestine is short, and the position of the anal opening does not reach the middle portion of the body. The myomeres are evident until the postflexion stage, and the total number varies from 54 to 58 (13 to 16 pre- and 40 to 44 postanal). Proportions of head depth (65.3 to 100% HL), head width (53.3 to 92% HL), and pre-ventral-fin length (34.8 to 36.6% SL) decreased during development, while snout length (25 to 50% HL), interorbital distance (26.3 to 50.3% HL), pre-pectoral-fin length (17.2 to 23.3% SL), pre-dorsal-fin length (36.6 to 41.9% SL) and pre-anal-fin length (37.7 to 43% SL) increased (Table 1).

Pigmentation. The larvae of *H. fimbriatus* are poorly pigmented. The pigments are evident starting at 10.9 mm SL (postflexion) and are restricted to the upper region of the head.

Fin development. The notochord, visible due to transparency, is flexed at 5.1 mm SL, giving support to the rays of the caudal fin that start to appear at 6.4 mm SL (flexion) and are formed at 7.6 mm SL (flexion). At the beginning of the flexion stage, it is possible to see the pectoral fin bud, in addition to the outline of the anal and dorsal fins that until the this stage (about 9.6 mm SL) showed the rays entirely formed. Between the flexion and postflexion stages (11 mm SL), the pelvic fin bud also appears; the first rays appear at approximately 11.9 mm SL. The formation of the unpaired fins is completed during the postflexion stage, including the segmentation of the rays. The numbers of fin rays in *H. fimbriatus* are pectoral: i, 8–10, dorsal: i, 8–9, and anal: 58–60.

Hypophthalmus marginatus (Fig. 3 a–f)

Description of the larvae. A total of 66 larvae (14 preflexion, 49 flexion and 3 postflexion) with standard lengths between 3.0 and 13.1 mm were analyzed. The larvae of this species exhibit a relatively long body (12.4 to 16.7% SL) and a head length varying from small to moderate (14.6 to 25% SL) (Table 1). There is no trace of yolk. During the preflexion stage the mouth is open and terminal. The nostrils are single and become double at approximately 12.2 mm SL (postflexion). The barbles are formed: 2 mental pairs and 1 maxillary pair. They are longer and thinner compared to those of *H. fimbriatus*. The embryonic membrane (median fin fold) is hyaline and surrounds the body from the middle region of the dorsum to the abdominal portion and is totally absorbed at the end of the postflexion stage (13.1 mm SL). The eyes are rounded and pigmented with a diameter varying from 5.6 to 9.4% HL, classifying it as small during it's entire development (Table 1). The operculum is formed at about 12.2 mm SL. The intestine is short, and the position of the anal opening does not reach the middle portion of the body. Myomeres are evident until the flexion stage with a total number varying from 54 to 57 (13 to 15 pre- and 40 to 42 post-anal). Proportions of head depth (62.5 to 100% HL), head width (54.8 to 100%) and interorbital distance (33.5 to 54% HL) decrease during development while snout length (25 to 54% HL), pre-pectoral-fin length (17.9 to 26.% SL), pre-dorsal-fin length (39.9 to 44.7% SL), and pre-anal-fin length (39.8 to 43.2% SL) increase (Table 1).

Pigmentation. As with the larvae of *H. fimbriatus* those of *H. marginatus* are also poorly pigmented. Some pigments can be observed dispersed along the body starting at 9 mm SL (postflexion). At about 10.8 mm SL they can also be barely visible on the upper region of the head.

Fin development. The transparent notochord is visible and flexed at 4.3 mm SL giving support to the caudal-fin rays that appear at 4.5 mm SL (flexion) and are fully formed at 7.1 mm SL (flexion). At the beginning of the flexion stage, it is possible to see the pectoral fin bud in addition to the outline of the anal and dorsal fins. By the end of this stage (about 10.8 mm SL), all of the aforementioned rays are formed except the pectoral. Between the flexion and postflexion stages (about 12.5 mm SL), the pelvic fin bud appears, and the first rays are formed at about 13.1 mm SL. In the postflexion stage, the formation of the unpaired fins is completed including the segmentation of the rays. The numbers of fin rays in *H. marginatus* are pectoral: i+9, dorsal: i, 6–8, and anal: 61–62.

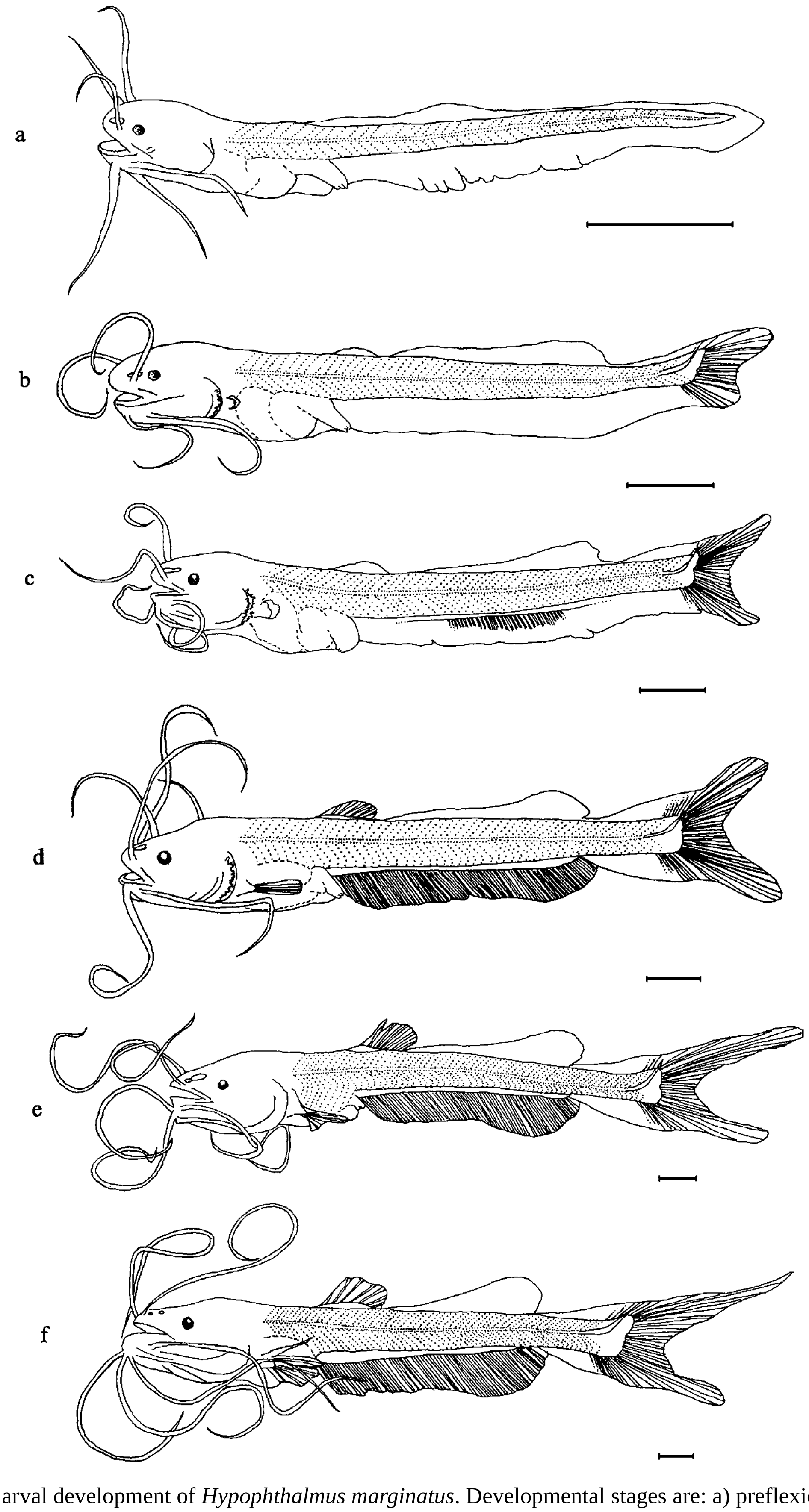

FIGURE 3. Larval development of *Hypophthalmus marginatus*. Developmental stages are: a) preflexion (3.95 mm SL); b) early-flexion (6.58 mm SL); c) mid-flexion (8.60 mm SL); d) late-flexion (10.29 mm SL); e) early-postflexion (14.62 mm SL); and f) mid-postflexion (12.98 mm SL). Scale = 1mm.

TABLE 1. Minimum (Min) and maximum (Max) values (mm and %) of the morphometric and meristic variables measured in larvae of *Hypophthalmus fimbriatus* and *H. marginatus* (PF=Preflexion; FL=flexion; FP=Postflexion).

Body measures (mm)	*H. fimbriatus*			*H. marginatus*		
	PF (n=20)	FL (n=20)	FP (n=20)	PF	FL	FP (n=20)
	Min/Max	Min/Max	Min/Max	Min/Max	Min/Max	Min/Max
SL	3.1–4.4	5.1–9.6	10.1–12.7	3.0–4.3	4.6–13.5	12.2–13.1
HD	0.5–0.7	0.7–1.6	1.6–2.2	0.4–0.7	0.6–1.8	2.1–2.3
HL	0.5–0.8	0.9–2.0	2.2–3.1	0.5–0.8	0.8–2.5	2.8–3.3
SnL	0.1–0.3	0.3–1.0	0.8–1.2	0.2–0.3	0.3–1.0	1.0–1.5
ED	0.1–0.1	0.1–0.3	0.3–0.3	0.03–0.1	0.1–0.2	0.3–0.3
ID	0.2–0.3	0.3–0.9	0.8–2.1	0.2–0.3	0.3–0.9	1.0–1.1
HW	0.3–0.6	0.6–1.5	1.6–1.9	0.4–0.6	0.5–1.8	1.9–2.3
BD	0.5–0.6	0.7–1.6	1.6–2.3	0.5–0.7	0.7–1.6	2.9–3.4
PPL	0.8–0.8	1.2–2.1	2.3–3.3	0.5–0.7	0.9–2.5	2.9–3.4
PVL	-	-	3.8–4.6	-	-	-
PDL	-	3.7	3.7–5.3	-	-	4.9–5.8
PAL	-	3.8	3.8–5.5	-	-	5.0–5.7
Proportions (%)						
HD/HL	73.3–100	66.5–83.9	65.3–81.2	62.5–100.0	64.1–100.0	70.9–79.1
SnL/HL	24.5–40.0	31.3–50.0	33.3–50.0	25.0–46.7	26.4–54.0	36.7–45.9
ED/HL	7.8–14.3	8.6–15.7	8.6–12.4	5.6–8.3	6.0–10.7	8.6–9.0
IDI/HL	26.3–46.7	31.0–50.3	35.0–43.6	22.5–50.0	26.4–54.0	33.6–34.5
HW/HL	53.3–83.0	62.4–92.0	59.0–75.2	56.3–100.0	54.8–100.0	68.7–75.5
BD/SL	12.9–17.1	12.4–16,8	14.7–19.8	12.5–16.5	12.4–16.7	13.8–16.6
HL/SL	16.1–21.1	16.7–21.9	20.8–25.0	14.6–21.9	16.2–22.9	21.8–25.0
PPL/SL	17.2–17.6	18.0–23.3	21.3–25.8	15.9–16.5	16.9–22.9	24.1–26.0
PVL/SL	-	-	34.8–36.6	-	-	-
PDL/SL	-	39.8	36.6–41.9	-	-	39.9–43.2
PAL/SL	-	41.3	37.7–43.0	-	-	39.8–43.2
Myomeres						
Total	54–58	55–57	55–55	54–57	54–58	-
Preanal	13–15	13–16	41–41	13–15	12–17	-
Postanal	40–43	41–44	14–15	40–42	40–47	-
Rays						
Pectoral	-	-	i, 7–10	-	-	i, 9
Dorsal	-	-	i, 8–9	-	-	i, 6–8
Anal	-	-	58–60	-	-	61–62

Proportions of body. ANCOVA showed a significant relationship between head depth, snout length, interorbital distance, eye diameter and head width (all as a proportion of HL) (Fig. 4 a–e), and between head length, body depth and pre-pectoral-fin length. Pre-dorsal-fin length and pre-anal-fin length (all as a proportion of SL) (Fig. 5 a–e) also showed significant relationships. The variable pre-ventral-fin length was not analyzed due to the lack of data on *H. marginatus*.

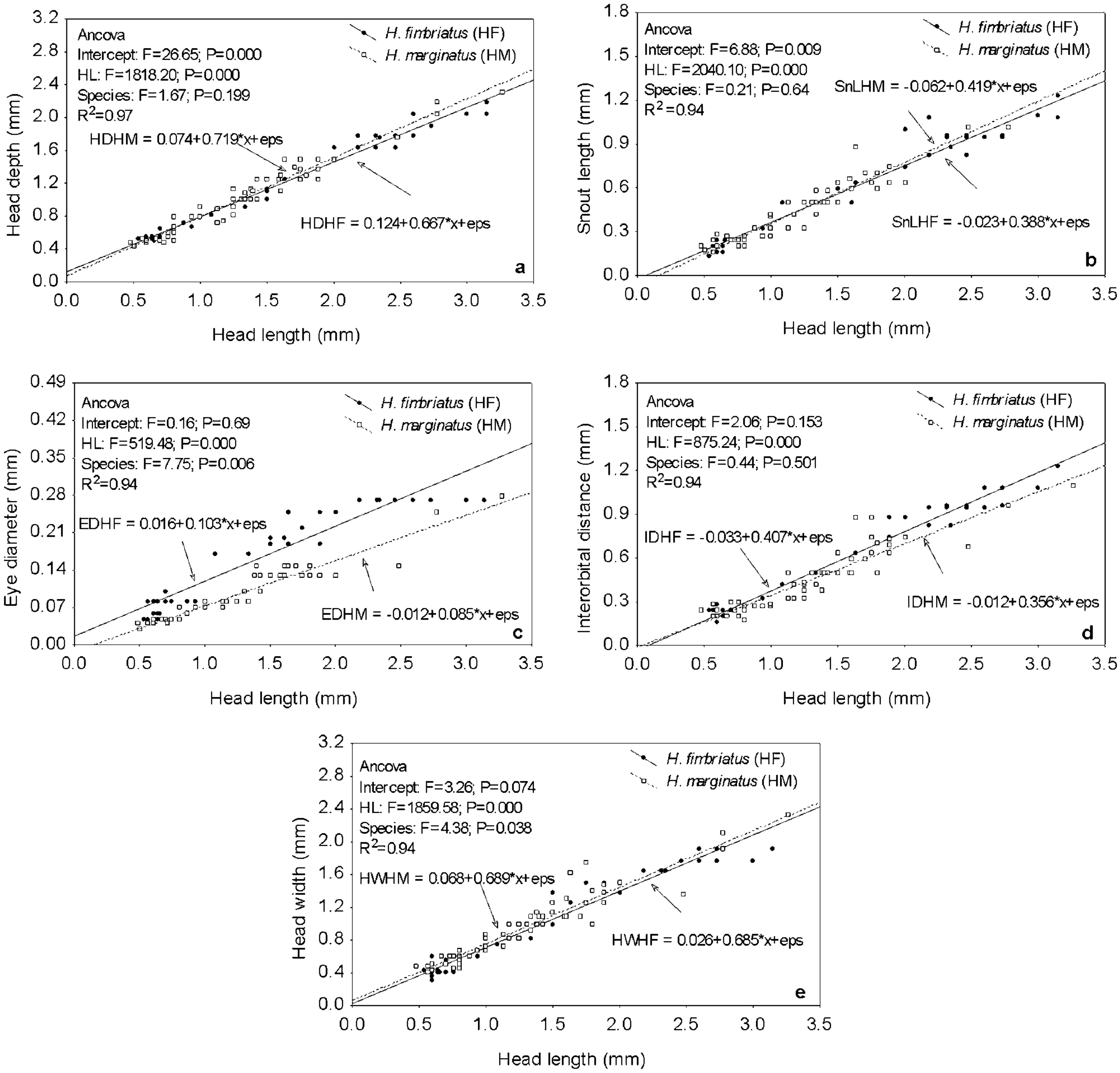

FIGURE 4. Body proportions for larvae of *Hypophthalmus fimbriatus* and *H. marginatus* in relation to head length: a) head depth; b) snout length; c) eye diameter; d) interorbital distance and e) head width.

Only a few of the analyzed variables showed differences between the two species. Eye diameter is initially similar between the two species. It increases gradually but more so in *H. fimbriatus* (Fig. 4d). Head width also differed between the two species, being slightly greater in *H. marginatus* (Fig. 4e).

The analysis showed significant differences between the two species for both body depth and pre-pectoral-fin length. Both were initially greater in *H. marginatus*, but became greater in *H. fimbriatus* at about 5.5 mm SL for body depth and 9.5 mm SL for pre-pectoral-fin length (Fig. 5 b–c).

Discussion

The larvae of *H. marginatus* and *H. fimbriatus* showed typical characteristics of catfishes: medium-sized to small head and a long body in relation to standard length, little pigmentation, mandibular barbels, eyes in a ventro-lateral position and small in relation to the head (Nakatani *et al*. 2001; Leite *et al*. 2007). These species showed myomeres varying from 54 to 58. This same pattern is also observed in *H. edentatus* larvae from the Itaipu Reservoir (Paraná River, Brazil) with myomeres varying from 53 to 56 (Nakatani *et al*. 1998). The absence of pigments during the entire larval period reflects the pelagic habitat of both species. The pattern of development of the fins for these species was similar to those of other reported patterns of development for catfishes (Nakatani *et al*. 2001).

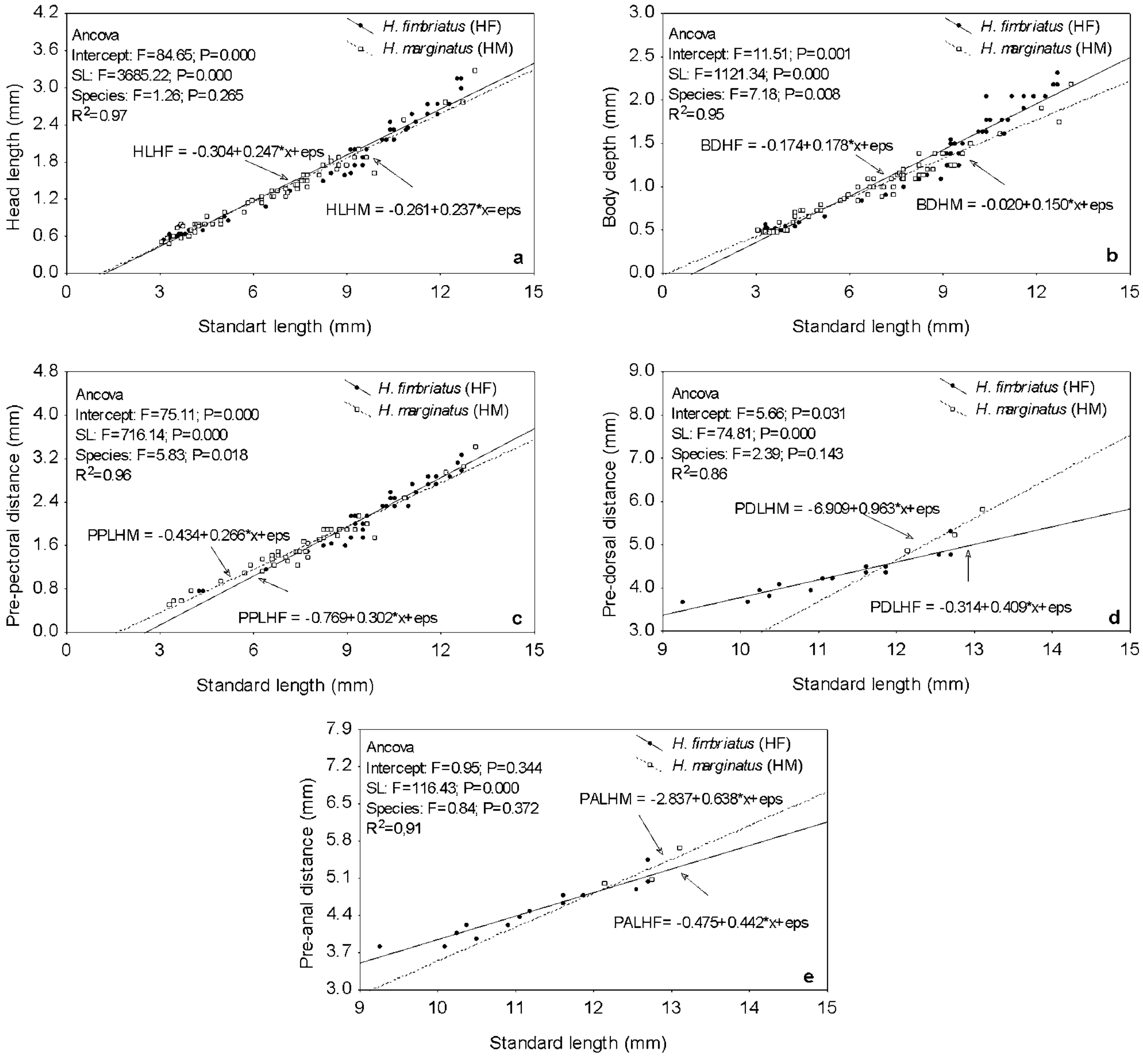

FIGURE 5. Body proportions for larvae of *Hypophthtalmus fimbriatus* and *H. marginatus* in relation to head width: a) head length; b) body depth; c) pre-pectoral distance; d) pre-dorsal distance; and e) pre-anal distance.

Although exhibiting very similar larvae development, the two species can be separated by the eye diameter, head width, body depth and pre-pectoral-fin length. But the eye diameter (smaller in *H. marginatus*) and the shape and size of the barbles (shorter and thicker in *H. fimbriatus*) are the characters that best differentiate these two species (Fig. 6). Another species occurring in the region, *H. edentatus*, exhibits an eye diameter that is comparatively larger, and has shorter, thinner barbles.

Nakatani *et al*. (1998), in a morphological description of *H. edentatus* of the Paraná basin, affirmed that the increase in standard length was linear in relation to various measurements, and high values were obtained with correlation coefficients showing a proportional growth between the all parts of the individual. In this study, *H. marginatus* and *H. fimbriatus* also showed a linear and proportional increase in body measurements relative to standard length (Figs. 4 and 5). Different from *H. edentatus, H. marginatus* and *H. fimbriatus* showed a disproportional growth during ontogenetic development in eye diameter and interorbital distance in relation to head length (Fig. 4).

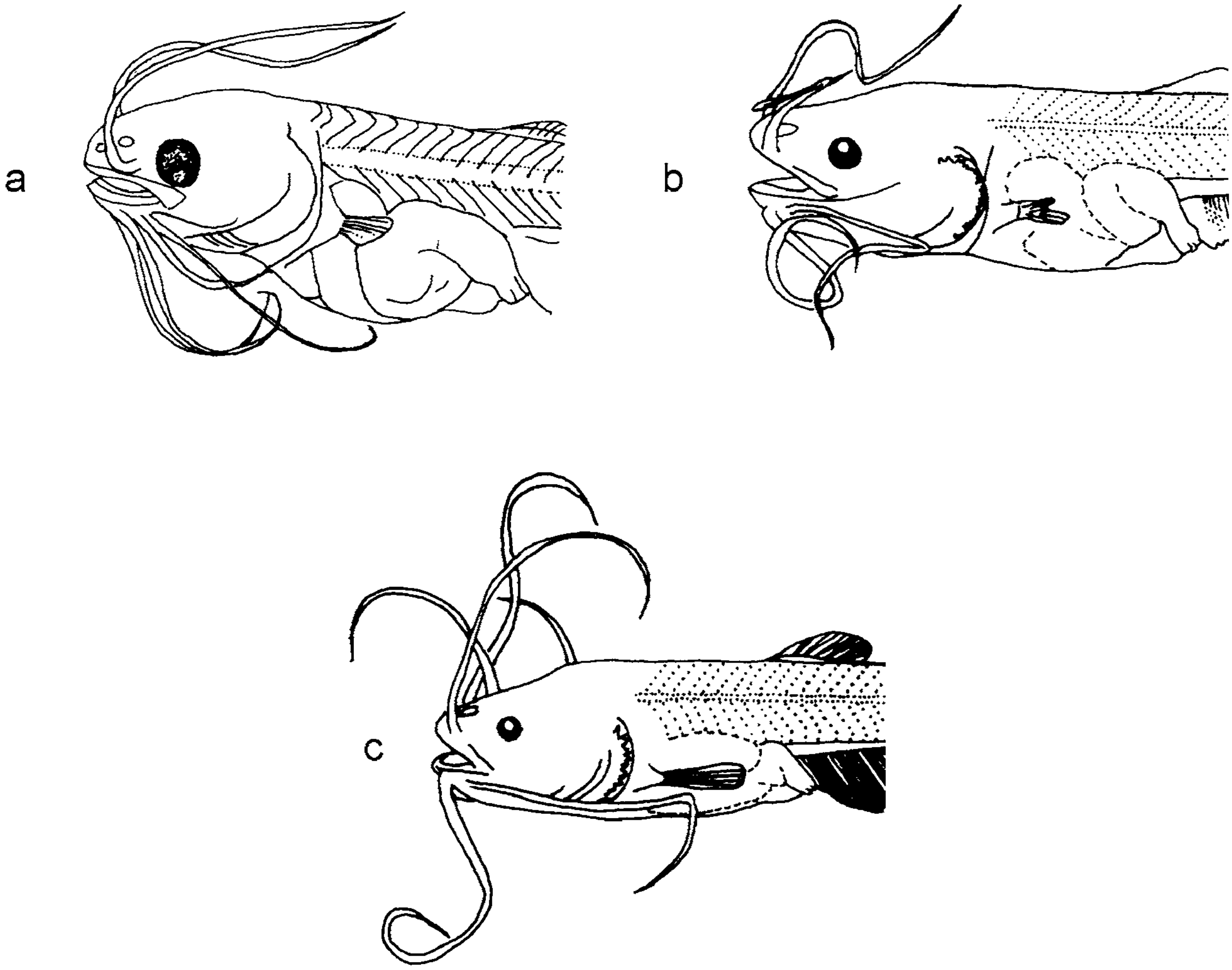

FIGURE 6. Morphological comparison of larvae of a) *Hypophthalmus edentatus* – 9.25 mm SL (adapted from Nakatani *et al.*, 1998); b) *H. fimbriatus* – 9.40 mm SL; and c) *H. marginatus* – 10.29 mm SL.

Morphological changes during ontogenetic development relate to the interaction of an organism with its environment (Balon 1981; 1984). For example, marine pelagic larvae generally hatch with the jaw less developed and eyes less pigmented (Blaxter 1988) in contrast with benthic catfishes that hatch with the jaw more developed and eyes more pigmented (Araujo-Lima 1994). Authors have hypothesized that the variation in early development is an adaptation to the larval habitat or spawning strategy. In this study, the smallest larvae of the two species of *Hypophthalmus* had a standard length of 3.0 to 4.4 mm, possessed a full viteline sac, and had the jaw developed and eyes pigmented. This suggests that this length is very close to the size of the eggs at spawning and to the size of larvae at hatching, indicating that these species have a strategy of spawning in the main river channel, which is typical of migratory species (Rizzo *et al*. 2002).

Araújo-Lima (1994), studying the development of 14 fish species from the Amazon region, compared larvae that hatch in the river channels (migratory species) with those that hatch in margins of the lake channels (sedentary species) regionally known as "paranás". He found a relationship between the pattern of larval development, egg weight and environmental conditions of the spawning sites. The migratory species showed relatively quicker growth compared to the larvae of the sedentary species. Another example of a species that exhibits a sedentary behavior is *Parauchenipterus galeatus*. It has isometric growth (Sanches *et al*. 1999).

We conclude that the disproportional ontogenetic development of body parts described for *H. fimbriatus* and *H. marginatus*, with precocious formation of the jaw and pigmentation of the eyes in relation to the small quantity of yolk in the yolk-sac larval phase, suggests that these species migrate to spawn in the main channel of the river. This hypothesis is reinforced by the fact that *H. fimbriatus* is known in the Amazon region as a migratory species (Santos *et al*. 1984; Carvalho & Merona 1986; Oliveira 2003).

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