Pangasius larnaudii（ナマズ目：パンガシウス科）仔稚魚の外部形態の発育

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Abstract: We describe the morphological development of hatchery-reared *Pangasius larnaudii* using 150 larvae and juveniles 3.42 to 46.7 mm in body length (BL), sampled from day 0 to day 35. BLs of larvae and juveniles on day 0 were 3.53 ± 0.1 mm (mean ± SD), reaching 15.9 ± 1.45 mm on day 15 and 39.4 ± 4.03 mm on day 35. Notochord tip flexion began in the smallest larva of 3.42 mm BL, and a completely flexed notochord tip was evident in specimens of about 9 mm BL. Melanophores started appearing in larvae on such body regions as the eyes, ventral contour of the tail, dorsal surface of the gut, anal fin-fold, pectoral symphysis, lower jaw, maxillary barbel, anterolateral part of the body, dorsal contour of the body and tail, caudal fin base, etc. There were individual variations among larvae as to the appearance of these melanophores, but all juveniles exhibited all of these melanophores. The juvenile stage started at 14.4 mm BL, at which point most of the body proportions relative to BL reached peak or constant values.

Key words: *Pangasius larnaudii*; Larvae; Juveniles; Morphology

*Pangasius larnaudii* is a freshwater fish belonging to the family Pangasiidae, which includes 5 genera: *Cetopangasius* (as fossil genus), *Helicophagus* (3 species), *Pangasianodon* (2 species), *Pangasius* (22 species), and *Pseudolais* (*Pteropangasius* is presently treated as a junior synonym of *Pseudolais*) (2 species) (Roberts and Vidthayanon 1991; Vidthayanon 1993; Rainboth 1996; Pouyaud et al. 2000; Gustiano 2003; Ferraris 2007). *Pangasius larnaudii* is presently treated as a junior synonym of *Pseudolais* (2 species) (Roberts and Vidthayanon 1991; Vidthayanon 1993; Rainboth 1996; Pouyaud et al. 2000; Gustiano 2003; Ferraris 2007). *Pangasius larnaudii* is found in large rivers and floodplains of the Chao Phraya and Mekong basins and is one of the most esteemed food fishes (Rainboth 1996; Vidthayanon et al. 1997; Kottelat 1998). This species is distinguishable from all other *Pangasius* species in having unique color features, such as a large black roundish blotch behind the gill openings (above the base of the pectoral fins) and a black longitudinal stripe along each caudal fin lobe (Taki 1974; Kottelat 1985; Roberts and Vidthayanon 1991; Kottelat 1998). *Pangasius larnaudii* is an omnivorous fish and feeds on fruits and other plant parts, mollusks, crustaceans, and small fishes (Roberts 1993; Rainboth 1996). It can reach a maximum of 150 cm body length (BL), but it more commonly grows to 90 to 100 cm (Poulsen et al. 2004). Poulsen et al. (2004) report that this species migrates upstream to spawning grounds and spawns at the beginning of the monsoon season between May and July in the Mekong River; the larvae then drift to the floodplains, where they grow during the flood season.
Together with other pangasiids, *P. larnaudii* is recognized as an important target fish of commercial fisheries, as well as for its potential use in aquaculture in the Mekong region (Roberts and Vidthayanon 1991; Rainboth 1996; Trong et al. 2002); such activities have put pressure on river environments and led to a reduction in their natural resources (Allan et al. 2005).

There have been many studies of the pangasiids to date, but they have focused primarily on their ecology and aquaculture (Cacot et al. 2002; Hung et al. 2002; Poulsen et al. 2004; Bui et al. 2010; Jiwyam 2010). The guidelines for identifying adult pangasiids are well established and based mainly on morphology (Roberts and Vidthayanon 1991). However, there is little information available on the morphological development of pangasiid larvae and juveniles other than the descriptions of *Pangasianodon hypophthalmus* by Islam (2005) and Morioka et al. (2009), some figures of *Pangasianodon gigas* and *P. larnaudii* drawn by A. Termvichakon and included without any additional comments in the work of Roberts and Vidthayanon (1991), and a study of the development of sensory organs and changes in behavior of larvae of the sutchi catfish, *P. hypophthalmus* (Mukai et al. 2010). Acquisition of more information about the morphological development of pangasiid larvae and juveniles, therefore, would not only lead to further consideration of pangasiid ecology and phylogeny, but also contribute to the identification of larvae and juveniles for stock assessment and to the improvement of seed production. We therefore examined the growth and morphological development of larvae and juveniles of hatchery-reared *P. larnaudii*.

**Materials and Methods**

The *P. larnaudii* larvae and juveniles used in this study originated at the spawning and rearing facilities of the fish breeding center, Ubon Ratchathani, Thailand. The larvae and juveniles were reared at ambient water temperature. Four to ten fish larvae and juveniles were sampled every day from hatching (day 0) to day 15 and on days 21, 28, and 35; these specimens were preserved in 5% formalin immediately after collection. The 150 specimens (3.42 to 46.7 mm BL) used in this study were deposited in the Museum of the Tokyo University of Marine Science and Technology under catalog numbers MTUF-P(L)-26316 and -26317.

The general morphology and fin development of all of the specimens were observed, and the following 37 body dimensions were measured and expressed as a percentage of BL: head length, head depth, snout length, upper jaw length, lower jaw length, maxillary barbel length, mandibular barbel length, prepectoral fin length, pre-dorsal fin length, caudal fin length, maximum body depth, body width, pelvic fin base length, dorsal fin base length, head width, mouth width, eye diameter, interorbital distance, internarial distance, pelvic fin height, pre-pelvic fin length, pre-adipose fin length, pectoral fin base length, pectoral spine length, pectoral fin length, caudal peduncle depth, dorsal fin height, pre-dorsal fin fold length, dorsal spine length, anal fin length, anal fin base length, adipose fin height, caudal peduncle length, anal fin fold height, dorsal fin fold height, adipose fin width, and pre-anal length. The specimens sampled from day 0 to day 13 (3.42 to 10.87 mm BL) were measured under a binocular microscope with an ocular micrometer, and those from day 14 and older (11.14 to 46.7 mm BL) were measured by using a dial caliper; both types of measurement were recorded to the nearest 0.01 mm.

The myomeres were counted on the specimens from days 1 to 11 (*n* = 89). The distribution of melanophores was observed on all specimens from day 0 to day 15 (3.42 to 18.0 mm BL). Drawings were made of specimens collected on days 0 (3.65 mm BL), 1 (4.59 mm BL), 2 (5.89 mm BL), 4 (6.20 mm BL), 6 (7.38 mm BL), 9 (9.10 mm BL), 12 (9.65 mm BL), and 14 (10.2 mm BL), and photos were taken of specimens collected on days 21 (24.6 mm BL), 28 (28.9 mm BL), and 35 (37.3 mm BL) (MTUF-P(L)-26316) to show the development of gross morphology. The volume of the yolk and oil globule was computed by applying the equation of Blaxter and Hempel...
Morphological Development of *Pangasius larnaudii* (1963):

\[ V = \frac{\pi}{6} \cdot l h^2 \]

where \( l \) is length and \( h \) is height. “Yolk volume” in this study refers to the combined volume of the yolk and oil globule. Measurement and counting methods mainly followed those of Leis and Trnski (1989), Vidthayanon (1993), Pouyaud et al. (1999), and Carl and Karl (2004).

**Results**

**Growth**

The mean BL (± SD) of newly hatched larvae on day 0 was 3.53 ± 0.10 mm (\( n = 10 \)) (Fig. 1), and the larvae grew to 6.09 ± 0.21 mm BL (\( n = 10 \)) by day 3, when the yolk was almost completely absorbed. Thereafter, the larvae grew to 7.43 ± 0.72 mm BL (\( n = 10 \)) at day 7, 15.9 ± 1.45 mm BL (\( n = 6 \)) at day 15, 29.0 ± 3.13 mm BL (\( n = 4 \)) at day 28, and 39.4 ± 4.03 mm BL (\( n = 6 \)) at day 35.

**Notochord flexion**

The smallest specimen (3.42 mm BL, day 0) had a slightly upward-bent notochord tip (19.2°, Fig. 2). Subsequently, notochord flexion progressed slowly with larval growth, to 15° to 30° at about 6 mm BL on day 3 and 30° to 40° at about 9 mm BL on days 10 to 11. Thereafter, notochord flexion was complete, although the angle could not be measured in specimens larger than about 11 mm BL (day 14) because of heavy pigmentation on the caudal fin base.

**General morphology**

The head and body of newly hatched larvae (3.42 to 3.74 mm BL) were transparent and compressed laterally, and a large oval yolk sac was located at the anterior part of the body (Fig. 3a); the yolk sac length and height ranged from 1.26 to 1.40 mm (mean ± SD, 1.34 ± 0.05 mm) and from 0.84 to 1.00 mm (0.92 ± 0.06 mm), respectively. The yolk volume in the newly hatched larvae (0.60 ± 0.07 mm³) decreased to 0.38 ± 0.06 mm³ at day 1 (4.57 to 5.13 mm BL, Fig. 3b) and to 0.06 ± 0.02 mm³ at day 2 (5.69 to 6.03 mm BL, Fig. 3c). The yolk was completely absorbed by day 3, at a BL of 5.76 to 6.38 mm (Fig. 3d).

The mouth angle and anus were open and the eyes were well developed in the day 1 specimens (Fig. 3b). The mouth reached beyond the vertical line of the eyes in the day 2 specimens (Fig. 3c). The nostril buds appeared at day 0 and were well developed at day 1 (Fig. 3b), their shape having changed from round to slender gourd-shaped with larval growth, and they were divided into two portions by 7.54 mm BL (day 9; Figs. 3f-3h, 4a-4c).

Maxillary buds appeared on day 0, whereas mandibular buds appeared at day 1 (Figs. 3a, 3b). The maxillary buds began to develop through elongation at day 1 (Fig. 3b), whereas the mandibular buds became more prominent through elongated growth at day 2 (Fig. 3c). The lengths of both maxillary and mandibular barbels increased with increasing size of the larvae (Figs. 3b-3h, 4a-4c).

Myomeres numbered 16-17 + 26-28 = 43-45 in the day 1 to 11 specimens. Photos showing the gross morphology of larger specimens are presented in Fig. 4.
Fin development

The day 0 specimens (3.42 to 3.74 mm BL) had a fin-fold originating from the anterior part of the dorsal contour, continuing around the caudal region and ending at the yolk sac; the height of the fin-fold was almost constant, except for a tapering at the anterior starting point on the dorsal side (Fig. 3a). The fin-fold was constricted around the caudal peduncle in specimens of 4.57 mm BL and larger (Fig. 3b), and it became separated dorsally into the adipose and caudal-anal fin-folds at 6.80 mm BL (day 7, Fig. 3e). The central part of the adipose fin was higher in the specimens with BL between 4.57 and 6.80 mm (Figs. 3c, 3d), and thereafter the posterior part became overhung and roundish. The caudal and anal fins became separated at a BL of 10.5 mm on day 14.

The dorsal fin bud first appeared at 6.80 mm BL in a position anterior to the adipose fin-fold (Fig. 3e). The first dorsal fin-ray formation was apparent at 8.33 mm BL, when 5 soft fin rays were observed (Fig. 5a); a full complement of fin rays (I, 5-7) was attained at 10.2 mm BL.
The anterior part of the anal fin-fold was higher in specimens of BL 5.89 mm and larger, although the anal fin-fold was connected to the caudal fin-fold (Figs. 3c-3h). The smallest specimen with anal fin rays was 6.55 mm BL, in which 4 soft fin rays were observed (Fig. 5b), and the full complement of 26 to 29 soft fin rays was attained at 11.14 mm BL on day 14.

The caudal fin was rounded fan-shape in the day 0 specimens of 3.42 to 3.74 mm BL (Fig. 3a). The dorsal part extended posteriorly, becoming pointed with the progress of notochord flexion at 4.57 mm BL (day 1, Figs. 3b-3d), and subsequently the lower part extended posteriorly to form an asymmetrical forked caudal fin at 6.03 mm BL (Fig. 3e). The lower lobe extended to almost the same length as the upper one in specimens of 8.99 mm BL and larger (Figs. 3f-3h, 4a-4c). The principal caudal fin rays first appeared at 6.03 mm BL, with 4+5 rays being observed. The full complement of 8+9 principal caudal fin rays was attained at 7.54 mm BL (day 9; Figs. 3f-3h, 4a-4c, 5c).

The pectoral fin buds first appeared at 6.72 mm BL. The first pectoral fin rays to appear were 4 soft fin rays at 10.2 mm BL, and a full complement of fin rays (I, 8-11) was attained at 14.4 mm BL (day 15, Fig. 5d).

The smallest specimen having pelvic fin buds
was 7.54 mm BL (Fig. 3f), and the first pelvic fin rays to appear were 4 soft fin rays at 10.2 mm BL. The full complement of 5 or 6 soft fin rays was attained at 11.1 mm BL (day 14, Fig. 5e).

Relative growth
Thirty-seven body dimensions were measured and expressed as a proportion of BL. On the basis of their developmental patterns, these measurements were classified into Group I, with 10 measurements (Fig. 6), Group I' with 3 (Figs. 7a-7c), Group I'' with 1 (Fig. 7d), Group II with 12 (Figs. 8a-8l), Group II' with 1 (Fig. 8m), and Group III with 6 (Figs. 9a-9f). The four remaining measurements did not fit into any of the groups (Figs. 9g-9j).

The 10 Group I measurements, namely head length, head depth, snout length, upper jaw length, lower jaw length, maxillary barbel length, mandibular barbel length, pre-pectoral fin length, pre-dorsal fin length, and caudal fin length, showed the same developmental pattern, first increasing in proportion to BL and reaching a peak before a gentle decline, and thereafter remaining constant (Fig. 6). The ratios of head length (Fig. 6a) and depth (Fig. 6b) to BL increased rapidly from 14.4% and 10.1% at 5.90 and 6.03 mm BL, respectively, to peaks of 32.0% and 18.7% at about 25 and 18 mm BL, and maintained constant proportions of about 30% and 17%, respectively, in specimens of about 30 and 25 mm BL and larger. The snout length (Fig. 6c) was initially 5.1% of BL at BL of 3.52 mm, increased to a peak of 14.1% at 14.2 mm BL, declined thereafter, and attained a constant level of 12% to 13% in specimens of about 20 mm BL and larger. The upper (Fig. 6d) and lower jaw (Fig. 6e) lengths increased

![Fig. 6](http://example.com/fig6.png)

**Fig. 6.** Measurements of hatchery-reared larval and juvenile *Pangasius loraudii* dimensions relative to body length (BL). Head length (a), head depth (b), snout length (c), upper jaw length (d), lower jaw length (e), maxillary barbel length (f), mandibular barbel length (g), pre-pectoral fin length (h), pre-dorsal fin length (i) and caudal fin length (j).
Morphological Development of *Pangasius larnaudii*

Rapidly from 5.8% and 4.5% at 4.85 and 4.87 mm BL, respectively, to peaks of 17.6% and 15.2% at 9.65 and 10.5 mm BL, and subsequently declined gradually to constant levels of 11% to 12% and 10%, respectively, at about 33 and 30 mm BL and larger. The lengths of the maxillary and mandibular barbels (Figs. 6f, 6g) increased rapidly from 8.19% and 5.42% at 4.76 and 5.90 mm BL, respectively, to peaks of 56.7% and 39.0% at 9.65 and 14.4 mm BL, and thereafter declined, reaching respective constant levels of about 30% and 23% at about 30 and 35 mm BL and larger. The pre-pectoral fin length (Fig. 6h) increased from 20.2% at 6.80 mm BL to a peak of 29.3% at 27.9 mm BL, and thereafter showed a gentle decline, maintaining a constant level of about 27% in specimens larger than about 28 mm BL. The pre-dorsal fin length (Fig. 6i) showed a slow increase from 27.3% at 8.10 mm BL to a peak of 41.6% at 27.9 mm BL, thereafter declining quickly and maintaining a constant level of about 35% in specimens of about 40 mm BL and larger. The caudal fin length (Fig. 6j) increased rapidly from 29.76% at 6.72 mm BL to a peak of 42.6% at 8.68 mm BL, and then declined quickly and attained a constant level of 35% to 40% at about 15 mm BL and larger.

In the Group I’ measurements of maximum body depth (Fig. 7a), body width (Fig. 7b), and pelvic fin base length (Fig. 7c), the ratios to BL first increased and reached peak levels before gradually declining, as in the Group I measurements. However, thereafter they did not remain constant but rather increased again over the size range of specimens examined in this study, up to 46.7 mm BL. All three of these body dimensions showed a parabolic development from about 15% of BL at 6 mm BL (maximum body depth), 5% at 4 mm BL (body width), and 0.6% at 8 mm BL (pelvic fin base length) to peaks of about 30% at 25 mm BL, 23% at 26 mm BL, and 5% at 25 mm BL, respectively, then declining quickly to 25% at 33 mm BL, 20% at 35 mm BL, and 4.5% at 29 mm BL, and thereafter increasing again.

The dorsal fin base length (Fig. 7d) was classified alone into Group I”, because its proportional length did not remain constant as in the Group I measurements, nor did it increase as in Group I’. Instead, the ratio increased rapidly from 4.6% at 7.54 mm BL to 12.4% at 15.4 mm BL and then decreased to 6.4% at 46.7 mm BL.

Twelve characteristics were included in Group II: head width, mouth width, eye diameter, interorbital distance, internarial distance, pelvic fin height, pre-pelvic fin length, pre-adipose fin length, pectoral fin base length, pectoral spine length, pectoral fin length, and caudal peduncle depth. Their ratios relative to BL first increased and then remained constant without declining (Figs. 8a-8l). The head width (initially 8.4% of BL at 4.76 mm BL) increased to a constant 18% to 20% of BL in specimens of about 15 mm BL and larger (Fig. 8a). The mouth width increased from 6.3% of BL at 4.93 mm BL to a constant level of 16% to 17% at about 10 mm BL and larger (Fig. 8b). The eye diameter (initially 0.3% of BL at 3.74 mm BL) increased and

![Fig. 7. Measurements of hatchery-reared larval and juvenile *Pangasius larnaudii* dimensions relative to body length (BL). Maximum body depth (a), body width (b), pelvic fin base length (c) and dorsal fin base length (d).]
attained a constant level of about 5% at 17 mm BL and larger (Fig. 8c). The ratios of interorbital and internosril distances to BL, initially 7.4% at 4.87 mm BL and 4.9% at 6.38 mm BL, respectively, increased and attained respective constant values of 17% at 14 mm BL and 12% to 16% at about 22 mm BL and larger (Figs. 8d, 8e). The ratios of interorbital and internosril distances to BL, initially 7.4% at 4.87 mm BL and 4.9% at 6.38 mm BL, respectively, increased and attained respective constant values of 17% at 14 mm BL and 12% to 16% at about 22 mm BL and larger (Figs. 8d, 8e). The pelvic fin height increased rapidly from 1.6% of BL at 7.10 mm BL to a constant value of about 11% at 17 mm BL and larger (Fig. 8f).

Although the initial increase in pre-pelvic fin length was slight and difficult to see, the initial ratio of 37.7% at 7.10 mm BL increased to a constant level of 45% to 50% in specimens of about 15 mm BL and larger (Fig. 8g). The pre-adipose fin length showed a rapid increase from 40% of BL at 7.10 mm BL to 61.9% at 9.43 mm BL and reached a constant value of 60% to 70% at about 15 mm BL, although there was a slight jump at about 30 mm BL and larger, where the ratio was 70% to 75% (Fig. 8h). The pectoral fin base length increased from 1.2% of BL at 9.65 mm BL to a peak of 6.8% at 16.2 mm BL and remained constant at about 6% at 25 mm BL and larger (Fig. 8i). The pectoral spine initially was 8.36% of BL at 14.4 mm BL and increased to a constant 13% to 14% in specimens larger than 33 mm BL (Fig. 8j). The pectoral fin length increased from 2.0% of BL at 8.07 mm BL to a constant level of 16% to 20% in specimens of 23.7 mm BL and larger (Fig. 8k). The increase in caudal peduncle depth was slight and difficult to see; the initial ratio was 7.4% of BL at 10.9 mm BL, and the ratio remained at 8% to 9% in specimens larger than 14 mm BL (Fig. 8l).

Fig. 8. Measurements of hatchery-reared larval and juvenile *Pangasius larnaudii* dimensions relative to body length (BL). Head width (a), mouth width (b), eye diameter (c), interorbital distance (d), internosril distance (e), pelvic fin height (f), pre-pelvic fin length (g), pre-adipose fin length (h), pectoral fin base length (i), pectoral spine length (j), pectoral fin length (k), caudal peduncle depth (l) and dorsal fin height (m).
The dorsal fin height was classified alone into Group II'. This measurement increased from 1.2% of BL at 8.68 mm BL to a constant level of 18% to 20% at about 15 mm BL; however, the ratio again increased in specimens larger than about 38 mm BL (Fig. 8m).

Group III (Figs. 9a-9f) consists of six body measurements for which there were no clear inflection points: pre-dorsal fin-fold length, dorsal spine length, anal fin length, anal fin base length, adipose fin height, and caudal peduncle length. However, some general trends of increase or decrease were recognized: dorsal spine length showed an increasing tendency (Fig. 9a), whereas the other body dimensions tended to decrease in proportion to BL with growth (Figs. 9b-9f).

The remaining four body dimensions showed individual developmental patterns (Figs. 9g-9j).

The anal fin-fold height increased slowly at first, from 2.3% of BL at 3.55 mm BL to about 6% at 7.50 mm BL, and rapidly increased thereafter (Fig. 9g), whereas the proportional dorsal fin-fold height increased almost linearly from 0.9% of BL at 3.52 mm BL to 7.2% at 8.77 mm BL (Fig. 9h). Adipose fin width varied from 3.5% to 8.6% in specimens of 7.54 to 11.1 mm BL, decreased thereafter, and remained constant at 2.4% to 5.2% in specimens of about 20 mm BL and larger (Fig. 9i). Pre-anal length first decreased from 61.8% of BL at 3.48 mm BL to 48.7% at 6.80 mm BL, and increased thereafter to a constant level of about 60% in specimens of about 18 mm BL and larger (Fig. 9j).

Pigmentation
Yolk sac and intestine
Yolk sac: Many small melanophores were
scattered on the lateral-ventral surface of the yolk sac of day 0 to 2 larvae (3.42 to 6.03 mm BL, Figs. 3a-3c), although the number of yolk sac melanophores decreased as the yolk was absorbed during days 1 and 2. After the absorption of the yolk on day 2, the melanophores remained on the lateral-ventral surface of the abdominal cavity of day 3 and 4 larvae (5.76 to 6.44 mm BL, Fig. 3d) and increased in size in those of day 5 (5.90 to 6.60 mm BL) and older or larger larvae. Abdominal cavity melanophores were observed on the lateral or ventral, or both, surfaces in all specimens examined for pigmentation, the largest being 18.0 mm BL.

Dorsal surface of gut: Several small melanophores started appearing on the dorsal surface of the gut at 5.76 mm BL, but in only 36% of larvae up to 6.20 mm BL. All specimens of 6.20 mm BL and larger had melanophores on the dorsal surface of the gut (Figs. 3e-3h, 4a-4c), and the number of melanophores increased to form the pigmented cap of the gut in specimens of 8.07 mm BL and larger (Figs. 3f-3h, 4a-4c).

Rectum: One to five melanophores appeared along the ventral side of the rectum in the smallest specimen of 3.42 mm BL on day 0, and 81% of specimens between 3.42 and 14.4 mm BL possessed rectum melanophores (Figs. 3b-3h).

Head region

Eyes: Melanophores were detected on the eyes of the smallest specimen, of 3.42 mm BL (day 0, Fig. 3a). All larvae had fully pigmented eyes at day 1 (4.57 to 5.13 mm BL) and later (Fig. 3b).

Snout, opercle, cheek: One small melanophore appeared on the snout, opercle, and cheek, at 5.76, 5.90, and 5.95 mm BL, respectively. Although the number of melanophores increased and the pigmented areas expanded with growth, the proportions of specimens with these respective melanophores were 50%, 63%, and 52% in specimens up to 7.70, 9.65, and 9.10 mm BL (Figs. 3d-3f). These body areas were more or less heavily pigmented in all specimens larger than 7.77, 9.76, and 9.10 mm BL, respectively (Figs. 3g-3h, 4a-4c).

Head: Some melanophores appeared on the top of the head at 5.89 mm BL (Figs. 3d, 3e), and the number increased, covering the entire head at 7.21 mm BL and larger (Figs. 3f-3h, 4a-4c). Eighty percent of specimens between 5.89 and 6.80 mm BL and 100% of larger ones possessed these melanophores.

Jaws and barbels

Lower jaw: A melanophore appeared on the posterior edge of the lower jaw at 7.10 mm BL. The proportion of specimens possessing lower jaw melanophores was 39% at BL between 7.10 and 10.8 mm, reaching 100% thereafter (Figs. 4a-4c).

Maxillary and mandibular barbels: Several small melanophores appeared on the base of the maxillary barbel at 6.55 mm BL, with 52% of specimens between 6.55 and 9.87 mm BL possessing these melanophores (Figs. 3f, 3g). All specimens of 10.1 mm BL and larger had maxillary barbel melanophores. Although these melanophores did not increase in number or expand distally with growth, the maxillary barbel was fully pigmented in five specimens of 14.4 to 18.0 mm BL. In contrast, no melanophores developed on the mandibular barbel until the larvae reached 14.2 mm BL, but the mandibular barbel was fully pigmented in specimens of 14.4 to 18.0 mm BL.

Body parts

Pre-dorsal fin area and antero-lateral part of the body: Melanophores appeared on the pre-dorsal fin area at 5.90 mm BL, and all specimens of 7.50 mm BL and larger had these melanophores (Figs. 3f-3h). The pre-dorsal fin area became heavily pigmented with growth, and the pigmented area expanded down and posteriorly, especially in specimens larger than about 14 mm BL, to form a horizontal band along the dorsal side of the body (Figs. 4a-4c). Melanophores started appearing on the antero-lateral part of the body, above the dorsal boundary of the gut, at 8.33 mm BL (Fig. 3f). The antero-lateral melanophores did not increase in numbers until 14.2 mm BL, the number of melanophores being small and observed only in 50% of specimens between 8.33 and 14.2 mm BL. In five specimens of 14.4 mm BL and larger, the antero-lateral part of body was heavily pigmented, and the pigmented area was even connected though a lightly pigmented area to the heavily pigmented pre-dorsal fin area (Figs. 4a-4c).
Dorsal contour of body and tail: Although a few melanophores appeared on the dorsal contour of the body and tail of the 5.89 mm BL specimen (Fig. 3e: two melanophores are present but are not visible laterally because they are hidden by the swollen side muscles), only 56.7% of the specimens possessed the melanophores until 11.1 mm BL, and all specimens of 14.2 mm BL and larger had these melanophores (Figs. 4a-4c). In smaller specimens, the dorsal contour melanophores were small and dot-like, but they intruded and formed internal melanophore clusters in the specimens between about 8 and 11 mm BL (Fig. 3f). The inner melanophore clusters were not visible externally in the specimens of 14.2 mm BL and larger.

Ventral contour of tail: One to twenty-two small melanophores appeared on the ventral contour of the tail along the anal fin-fold in all of the larvae smaller than 4.60 mm BL (Figs. 3a, 3b). With growth, the ventral contour melanophores intruded into the tail along the myoseptum and formed inner melanophore clusters (Figs. 3c, 3d), the number of which decreased from more than 10 in the specimens smaller than about 5 mm BL to fewer than 10 in those larger than about 7 mm BL (Figs. 3e, 3f). The melanophore clusters became difficult to see from the outside in specimens of about 11 mm BL and larger.

Caudal peduncle: The sides of the caudal peduncle were externally pigmented at 7.54 mm BL, with 51% of the specimens between 7.54 and 9.43 mm BL possessing melanophores (Fig. 3f), and all specimens larger than 9.43 mm BL had a pigmented caudal peduncle. The caudal peduncle was more heavily pigmented laterally in larger specimens (Figs. 4a-4c).

Anal fin-fold/anal fin: Several melanophores appeared on the posterior part of the anal fin-fold at 5.69 mm BL and increased in number and size to form from 2 to 11 melanophore clusters aligning horizontally as the fish grew (Figs. 3c-3h). These melanophores were observed in 96% of 115 specimens larger than 5.69 mm BL; they were not observed in five specimens of 6.03, 6.20, 6.80, 9.44, and 17.0 mm BL.

Caudal fin: On the anterior and posterior parts of the ventral side of the notochord tip, which eventually develop into the upper and lower hypural parts, melanophores started appearing at 6.80 and 6.03 mm BL, respectively. The melanophores at both locations became larger or formed melanophore clusters with growth, but no melanophores were externally visible in specimens of 14.4 mm BL and larger. The anterior melanophores were observed in 47% of the specimens from 6.80 to 10.8 mm BL, and the posterior ones in 66% of specimens from 6.03 to 9.87 mm BL (Figs. 3f-3h).

The area at the base of the caudal fin rays in both the lower and upper lobes was first pigmented at 6.80 mm BL. The melanophores increased in number and size with growth, although the proportion of specimens with these melanophores was low (31% until 11.1 mm BL for the lower lobe and 53% until 10.8 mm BL for the upper lobe; Figs. 3e-3h). In specimens larger than 14.2 mm BL (for the lower lobe) and 11.1 mm BL (for the upper lobe), the melanophores expanded distally to form black stripes in the caudal fin lobes (Figs. 4a-4c).

Pectoral symphysis: Although a melanophore appeared on the pectoral symphysis at 5.70 mm BL, only 39% of specimens of 5.70 mm BL and larger possessed this melanophore (Figs. 3e-3h).

Discussion

The largest specimen possessing a yolk sac was 6.03 mm BL on day 2, although the smallest one in which the yolk was completely absorbed was 5.76 mm BL on day 3. The notochord tip was bent slightly upward, even in the smallest specimen examined (3.42 mm BL, day 0), and none of the specimens observed had a straight notochord. Therefore, in this study we did
not detect the yolk-sac and preflexion larval stages; the 3.42 to 6.03 mm BL larvae (day 0-2) were classified in the yolk-sac/flexion stage (Table 1). In the pangasiid *P. hypophthalmus*, Morioka et al. (2009) reported the appearance of the yolk-sac/preflexion larval stage in specimens of 2.8 to 3.2 mm BL (day 0) and of the yolk-sac/flexion larval stage at 3.3 to 6.4 mm BL (days 0 to 2). It is possible that the yolk-sac/preflexion stage is present in *P. larnaudii* because, as shown by Morioka et al. (2009) in *P. hypophthalmus*, this stage lasts a surprisingly short time.

We could not clearly determine the size of *P. larnaudii* specimens with a completely flexed notochord tip, but it was about 9 mm BL on day 10 or 11, and thus the flexion larval stage was defined as from 5.76 mm BL (day 3) to about 9 mm BL (day 10 or 11), after which the larvae entered the postflexion stage, which lasted until the completion of fin ray numbers at 14.4 mm BL on day 15 (Table 1).

Fin rays in *P. larnaudii* first appeared in the caudal fin (6.03 mm BL), followed by the anal (6.55 mm), dorsal (8.33 mm), and then pectoral and pelvic fins (10.2 mm); the order for completion in number was caudal (7.54 mm), dorsal (10.2 mm), pelvic (11.1 mm), anal (11.14 mm), and pectoral fin (14.4 mm). The largest specimen with incomplete fin ray numbers was 14.2 mm BL at day 14, and the smallest one with complete fin numbers was 14.4 mm BL at day 15; thus the juvenile stage starts at 14.4 mm BL.

Note that the caudal fin rays considered in this study are the principal ones of 8+9 rays. Morioka et al. (2009) pointed out that the number of procurent caudal fin rays in the pangasiid fishes increases continuously with growth, and that the juvenile stage in *P. hypophthalmus* begins at the time of completion of the pectoral fin rays at 12.8 mm BL, following to Doi et al. (2004) and Takemura et al. (2004). However, the completion of pectoral fin ray number cannot be applied to all fish species to determine the start of the juvenile stage, because the sequence of fin formation varies with the species (Neira et al. 1998). The size of specimens having the complete principal caudal fin ray number was almost the same for *P. larnaudii* (7.54 mm BL, present study) and *P. hypophthalmus* (7.1 mm BL, Morioka et al. 2009).

The developmental stages defined by yolk absorption, notochord tip flexion, and fin ray completion in *P. larnaudii* coincide with the patterns of melanophore distribution and relative growth examined in this study (Table 1, Fig. 10). Yolk sac larvae smaller than about 6 mm BL were characterized by scarcely developed melanophores, the pigmented body parts being limited to the yolk-sac surface, eyes, and ventral contour of the tail. In flexion larvae from about 6 to 9 mm BL, although there were no points of inflection or peaks in the curves showing the relative growth of body dimensions, melanophores started appearing on some body parts such as the dorsal surface of the gut, the head region, and the pre-dorsal fin area. At about 9 mm BL, the division between flexion and postflexion larvae, the ratios of upper jaw and lower jaw lengths, maxillary barbel length, caudal fin length, and mouth width to BL reached maxima. Peak and constant values of relative growth occurred at about 14 mm BL and it was at the same BL when the juvenile stage started. Although almost all of the melanophores had appeared by the start of the juvenile stage, body proportions changed during the juvenile stage and became constant at 35 to 40 mm BL.

Table 1. Body length (BL, mm) and age (days) for each developmental stage of *Pangasius larnaudii*.

<table>
<thead>
<tr>
<th>Stage</th>
<th>BL (mm)</th>
<th>Age (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yolk sac/flexion larva</td>
<td>3.42-6.03</td>
<td>0-2</td>
</tr>
<tr>
<td>Flexion larva</td>
<td>5.76-approx. 9</td>
<td>3-10 or 11</td>
</tr>
<tr>
<td>Postflexion larva</td>
<td>approx. 9-14.2</td>
<td>12-14</td>
</tr>
<tr>
<td>Juvenile</td>
<td>&gt;14.4</td>
<td>&gt;15</td>
</tr>
</tbody>
</table>

BL, following to Doi et al. (2004) and Takemura et al. (2004). However, the completion of pectoral fin ray number cannot be applied to all fish species to determine the start of the juvenile stage, because the sequence of fin formation varies with the species (Neira et al. 1998). The size of specimens having the complete principal caudal fin ray number was almost the same for *P. larnaudii* (7.54 mm BL, present study) and *P. hypophthalmus* (7.1 mm BL, Morioka et al. 2009).

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It is difficult to compare the morphological characteristics of larval and juvenile *P. larnaudii* obtained from this study with those of other pangasiid species, because no such information is available for pangasiid larvae and juveniles, other than descriptions of *P. hypophthalmus* (Islam 2005; Morioka et al. 2009), some figures of *P. gigas* and *P. larnaudii* drawn by A. Termvichakorn without any comments (included in the work of Roberts and
Vidthayanon (1991), and a study of the development of sensory organs and changes in behavior in larvae of the sutchi catfish, P. hypophthalmus, by Mukai et al. (2010). Therefore, we emphasize the need to collect information about the morphological development of pangasiid larvae and juveniles. Islam (2005) made drawings of P. hypophthalmus embryos and larvae reared in hatcheries. The following diagram illustrates the growth (change in dimensions relative to body length) and the development of pigmentation in hatchery-reared P. larnaudii.

**Fig. 10.** Schematic representation of the growth (change in dimensions relative to body length) and the development of pigmentation in hatchery-reared P. larnaudii. ○, peak value of body dimension relative to BL; ●, attainment of constant proportional body dimension relative to BL; ▲, local minimum value of body dimension relative to BL, with increasing values thereafter; ▼, inflection point in proportional body dimension relative to BL; □, appearance of pigment subject to individual variation; ■, pigment present in all specimens examined; gray color, no specimen available.

**Relative growth**
- Head length
- Head depth
- Snout length
- Upper jaw length
- Lower jaw length
- Maxillary barbel length
- Mandibular barbel length
- Pre-pectoral fin length
- Pre-dorsal fin length
- Caudal fin length
- Maximum body depth
- Body width
- Pelvic fin base length
- Dorsal fin base length
- Head width
- Mouth width
- Eye diameter
- Interorbital distance
- Internostril distance
- Prepelvic fin height
- Pre-pelvic fin length
- Pectoral fin base length
- Pectoral fin base length
- Pectoral spine length
- Pectoral fin length
- Caudal peduncle depth
- Dorsal fin height
- Adipose fin width
- Anal finfold height
- Pre-anal length

**Pigmentations**
- Yolk sac
- Dorsal surface of gut
- Rectum
- Eyes
- Snout
- Opercle
- Check
- Head
- Lower jaw
- Maxillary barbel
- Mandibular barbel
- Pre-dorsal fin area
- Antero-lateral part of body
- Dorsal contour of body and tail
- Ventral contour of tail
- Caudal peduncle
- Dorsal fin
- Anal finfold/fin
- Lower lobe of the base caudal fin ray
- Upper lobe of the base caudal fin ray
- Posterior part of ventral side of notochord
- Anterior part of ventral side of notochord
- Pectoral symphysis
up to 14 days after hatching, but, as pointed out by Morioka et al. (2009), the information is incomplete and the juvenile transition phase was overlooked. Morioka et al. (2009) described in detail the morphological development of *P. hypophthalmus* reared up to 25 days after hatching, (from 2.9 to 26.4 mm BL), but they took only seven body measurements in addition to BL. The following is a comparison of those seven body dimensions for *P. larnaudii* (this study) and *P. hypophthalmus* (Morioka et al. 2009).

The proportional lengths of the head and maxillary barbel, once they reach constant levels, are almost the same in both species, about 30% and 60% of BL, respectively. The body of *P. larnaudii* is more slender than that of *P. hypophthalmus* during the larval size intervals of 5 to 10 and 10 to 15 mm BL. The maximum body depth of *P. larnaudii* in the size interval of 5 to 10 mm BL is 10% to 15% of BL, compared with 15% to 20% for *P. hypophthalmus*; in the 10 to 15 mm BL size range it is less than about 20% for *P. larnaudii*, compared with more than about 20% for *P. hypophthalmus*. The pre-anal length is slightly greater in *P. larnaudii* than in *P. hypophthalmus*, about 60% of BL vs. 55% to 57% once constant levels are reached. The snout is distinctly longer in *P. larnaudii* than in *P. hypophthalmus*, about 60% of BL vs. 55% to 57% once constant levels are reached. The eye of *P. larnaudii* is smaller than that of *P. hypophthalmus*; the ratio to BL is 2% to 4%, vs. 3% to 5% in the larval sizes of 5 to 10 mm BL, and about 5% vs. 5% to 6% once the proportional size becomes constant in specimens >10 mm BL. The upper jaw length relative to BL is much greater in *P. larnaudii* than in *P. hypophthalmus*; the maximum and stable proportions are about 18% and 11% to 12% in the former and 14% and 5% to 7% in the latter.

**Acknowledgments**

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**References**


**Pangasius larnaudii** (ナマズ目：パンガシウス科)

仔稚魚の外部形態の発育

Viseth HAV

ナマズ目パンガシウス科 Pangasius larnaudii の稚魚個体（150個体，体長3.42～46.7 mm，孵化後0～35日）にもとづいて外部形態の発育を記載した。孵化当日の体長は3.53 ± 0.1 mm（平均体長 ± 標準偏差）で，孵化後15日には体長15.90 ± 1.45 mm，孵化後35日には体長39.43 ± 4.03 mm に成長した。脊索末端部は，体長3.42 mm の最小個体ですべて上層を開始しており，体長約9 mm になると上層が完成した。黒色色素は，卵黄囊の表面，眼，直腸，尾部腹側正中線上，腹部の背面前，頭部，臀鰭の腹鰭，肩帯梨形部，下顎，口角の鰭，背鰭前方部，体側の前方部，背鰭正中線上，尾鰭基底部，尾柄部などに出現したが，これらの出現には個体差が見られた。鰭条は，尾鰭，臀鰭，背鰭，胸鰭と腹鰭の順に出現し，定数に達したのは尾鰭，背鰭，腹鰭，臀鰭と胸鰭の順で，臀鰭と胸鰭は体长14 mm で完成し稚魚となった。