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Ontogeny and Growth of Early Life Stages of Barred Spiny Eel *Macrognathus pancalus* (Hamilton, 1822)

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ABSTRACT

Background: The objective of the study was to examine the growth and development of *M. pancalus* larvae in captive conditions, including pigmentation patterns, yolk and oil globule utilization, growth rates and metamorphosis, as well as to identify suitable live food for larviculture.

Methods: The larvae, produced through induced breeding, were kept unfed until the yolk-sac absorption and then fed with freshwater rotifer, mixed zooplankton and *Tubifex* worms at different stages of development. The larvae were reared in indoor glass tanks and outdoor reinforced plastic tanks to document their morphological and chronological development.

Result: The findings showed that the larvae exhibited typical characteristics of eel. Notably, dentition was observed before yolk resorption, indicating the highly predatory nature of the larvae. The bands of melanophores, which were prominent at the beginning, disappeared between 5-7 days post-hatch. Additionally, the study identified distinct features of spiny eels, such as a trunk-like rostral projection at 14 days post-hatch and erectile dorsal spines at 21 days post-hatch. The growth pattern, morphological changes and adaptation to benthic burrowing habits indicated that the larvae metamorphosed into the fry stage between 28-45 days post-hatch. These results provide valuable insights into the ontogenetic development and rearing of *M. pancalus* and can be used to support future aquaculture and conservation programs.

Key words: Larval rearing, *M. pancalus*, Ontogeny, Spiny eel, Yolk utilization.

INTRODUCTION

The barred spiny eel *Macrognathus pancalus* (Hamilton, 1822) is a very popular food and an ornamental fish (Borah *et al.*, 2022) in South Asia known for its unique taste, brilliant colour pattern and behavior. This small, benthopelagic fish belongs to the Mastacembelidae family and is indigenous to India, Pakistan, Bangladesh, Sri Lanka, Nepal and Myanmar (Froese and Pauly, 2023). It tolerates wider ecological conditions and inhabits a variety of freshwater and low-saline brackish water habitats, making it a potential climate-resilient species for aquaculture. Recently, the catch of spiny eels has declined due to overfishing for food and ornamental fish markets and various ecological changes. In the Ganga River basin, *M. pancalus* was found to be over-exploited, indicating growth overfishing (Suresh *et al.*, 2022). In recent years, several captive breeding programs have been initiated to address this issue (Borah *et al.*, 2020; Chattopadhyay *et al.*, 2024). However, there have been significant variations in the larval development stages of the species across different studies (Afroz *et al.*, 2014; Islam and Rani, 2017; Borah *et al.*, 2020). The knowledge of larval fish ontogeny is essential for better understanding the larval dynamics and mechanisms of adapting to its environment and improving larval survival, welfare and growth of a species. Factors such as larval size, yolk and oil reserves, onset of feeding and feeding behavior can all influence their survival during larviculture (Sulaeman and Fotedar, 2017). The ability to capture prey relies on factors such as locomotory ability, mouth size and eye development. Therefore, this study on the morphological and chronological development stages in the ontogeny of *M. pancalus*, along with subsequent larval rearing, can help establish hatchery practices.

MATERIALS AND METHODS

Matured fish were raised with *Tubifex* worms in 3 m^3 reinforced plastic tanks and maintained with the provision of refuges (P.V.C. pipes), aeration and regular water exchange at the Rahara Regional Centre of ICAR-Central Institute of Freshwater Aquaculture, Kolkata, India (Lat. 22°43′50.2″ -22°44′2.9″ N, Long. 88°23′11.4″ -88°23′26.6″E). The embryo and larvae were produced through volitional spawning and artificial fertilization using a commercial

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sGnRH analog and domperidone @0.5 µl and 1.5 µl g^{-1} body weight of males and females, respectively. The developing eggs were incubated at @12 eggs L^{-1} water in six glass tanks (90-L capacity) under continuous aeration. The newly hatched larvae were not fed until 72 hours post-hatch (hph). Due to their fast swimming and agile nature, the larvae at 28 days post-hatch (dph) were shifted and reared at 400 larvae m^{-3} water in reinforced plastic tanks (1000-L capacity) prepared with a sand base in three replicates. The freshwater rotifer (*Brachionus calyciflorus*), measuring 185-240 µm in length and 90-150 µm in width, was offered three times per day to maintain a density of 5 rotifers ml^{-1} until 14 dph. Micro-zooplankton was given *ad libitum* daily for two weeks from 11 dph. Live *tubifex* worm was introduced from 14 dph and continued until 91 dph. Visual observations were made on the larval behaviour during daylight conditions.

To describe and analyze various stages of larval development, twenty larvae (*n* = 20) were sampled randomly and observed, photographed and measured under a microscope (Leitz Wetzlar GmbH, Germany). The morphological and chronological development of the larvae, as well as their morphometric measurements, were recorded every 12 hours until the yolk-sac absorption. Following this, weekly measurements were taken until the larvae reached 91 dph. The reduction in volume of the yolk sac and oil globule over time was used to quantify yolk utilization. The yolk sac volume was calculated using the mathematical formula for a prolate spheroid:

$$V_{ys} = 1/6 \times \pi\, l\, h^2$$

Where,
l= Yolk sac length.
h= Yolk sac height.

The volume of the oil globule was estimated from the equation:

$$V_{og} = 1/6 \times \pi\, d^3$$

Where,
d= Oil globule diameter.

Weekly measurements of the total length (TL) and body weight (BW) were performed in a pooled sample of at least 20 larvae (*n*=3) until 14 dph and in individual specimens at 21 dph or later stages. The specific growth rate (SGR) of the TL at different periods was estimated using the formula (Árnason *et al.*, 2009):

$$\text{SGR of TL} = (e^g - 1) \times 100\%$$

Where,

$$g = \frac{[\ln (L_2) - \ln (L_1)]}{t_2 - t_1}$$

L_2 and L_1 represent the mean TL on day t_2 and t_1, respectively.

The length-weight relationship (LWR) of larvae was established using the equation of the log-transformed data (Froese, 2006):

$$\log BW = \log a + b \log TL$$

Where,
TL and BW= Length and weight of larvae.
a, b= Regression constants.

The allometric (K_A) condition factor, which is the best condition factor to study the well-being of *M. pancalus* (Rahman *et al.*, 2020), was calculated using the equation:

$$K_A = (BW \times 100)/TL^b$$

The data were analyzed using SPSS version 23.0 for Windows and one-way ANOVA was performed. Duncan's multiple range test was employed to determine significant differences between the observations ($p<0.05$). This study was conducted between February-2022 to November-2022.

RESULTS AND DISCUSSION

Larval development stages

The developmental stages of the larvae were classified as pro-larvae (hatching to complete yolk absorption) and post-larvae (yolk absorption to miniature adult shape) (Table 1), as recommended by *Hubbs* (*1943*). Upon hatching, the fertilized eggs emerged into a relatively undeveloped pro-larval stage, measuring 3.434±0.16 mm in length, with a protuberant yolk sac measuring 0.797±0.075 mm^3. Although smaller in length compared to *Macrognathus aculeatus* (4-5 mm) (Sahoo *et al.*, 2007), the newly hatched larvae had well-differentiated brains, otic capsules, U-shaped jaws, elongated pectoral fin buds and intense melanophores without any pattern on the body (Fig 1a, b). From 6-48 hph, the larvae underwent significant morphological changes, including the appearance of melanophore stripes on the body (Fig 1c-1g). Complete eye pigmentation was observed at 60 hph, coinciding with the typical time for exogenous feeding (Pepe-Victoriano *et al.*, 2021). At 54 hph, a pair of olfactory pits, a few sharp teeth, and widening of the intestine with an anal pore were noticed (Fig 1h-1j). By 60 hph, the larvae had distinct lenses in their eyes, functional opercula, rayed pectoral fins, prominent swim bladder and melanophore stripes (Fig 2a) and a depleted yolk-sac (90.8% or above) (Fig 3), with the yolk sac being fully absorbed between 60-72 hph. A study by Pongjanyakul *et al.* (2020) on *Macrognathus siamensis* larvae also reported complete yolk absorption at 72 hph. The open mouth, dentition for grasping and holding live prey, opening of anal aperture, wide rectum and formation of a pouch-like intestine (Fig 1l) in the present study suggested that the exogenous feed should be available on the third day of hatching. The timing of exogenous feeding varies depending on the fish species, yolk-sac utilization and larval development rates. In several fish species, the onset of exogenous feeding occurred between 2 and 4 dph (Pradhan *et al.*, 2012; Saxena *et al.*, 2019; Kumar *et al.*, 2021; Reyes-Mero *et al.*, 2022).

The post-larval stage of development varies among species in terms of size, shape, fin size, pigmentation, shape and time of organ formation. In the present study, the post-larvae undertook significant changes in the head, eyes, jaws, mouth, fins and body pigmentation. The upper jaw extension was noticed at 14 dph and the formation of erectile dorsal spines at 21 dph (Fig 2b), two striking features of Mastacembelids. At four weeks of age, the larvae displayed a V-shaped rostrum, an inferior mouth and prominent black stripes on the anal and dorsal fins (Fig 2c). The jaw length continued to increase until the rostrum formation- a trunk-like appendage at 45 dph (Fig 2d). At this stage, the larvae underwent metamorphosis into the fry stage (81%), resembling miniature adults with the beginning of benthic and burrowing habits. In several species, metamorphosis from larvae to juveniles occurred between 32-50 dph (Anil *et al*., 2018; Anzeer *et al*., 2019). In fish, the metamorphosis is reported to be accompanied by changes in habitat, body proportions, fin differentiation, pigmentation patterns and scale formation (Kendall *et al*., 1984; Urho, 2002). In the present study, a denser juvenile-adult body with patterns of white dots along the body girth forming a series of rings was noticed during 45-91 dph (Fig 2d). The environmental temperature plays a crucial role in larval development and growth. Larvae at higher temperatures tend to deplete their yolk reserves more quickly than those at lower temperatures (McMahon *et al*., 2023). The temperature during the study (29.3±1.4°C) was found to be optimal for the larval development of most tropical fish species.

Yolk reserves and utilization

Fish larvae contain two kinds of energy reserves: yolk and oil globule (Bjelland and Skiftesvik, 2006). In the case of *M. pancalus*, the newly hatched larvae had a large elliptical-shaped yolk sac with a mean length of 1.329±0.044 mm and a volume of 0.797±0.075 mm^3. Additionally, there was an oil globule located at the anterior tip of the yolk sac, with an average diameter of 0.440±0.018 mm and a volume of 0.045±0.005 mm^3. The yolk-sac was utilized at a faster rate compared to the oil-globule exhaustion rate (Fig 3), with 41.8% of the initial yolk sac being significantly utilized within 12 hours. On the other hand, there was no significant decrease (8.9%) in oil globule reserves during this period (Fig 3). Over time, the yolk-sac reserves were reduced by 79% at 36 hph and were completely exhausted within 72 hph. In silver perch larvae, similar observations of faster

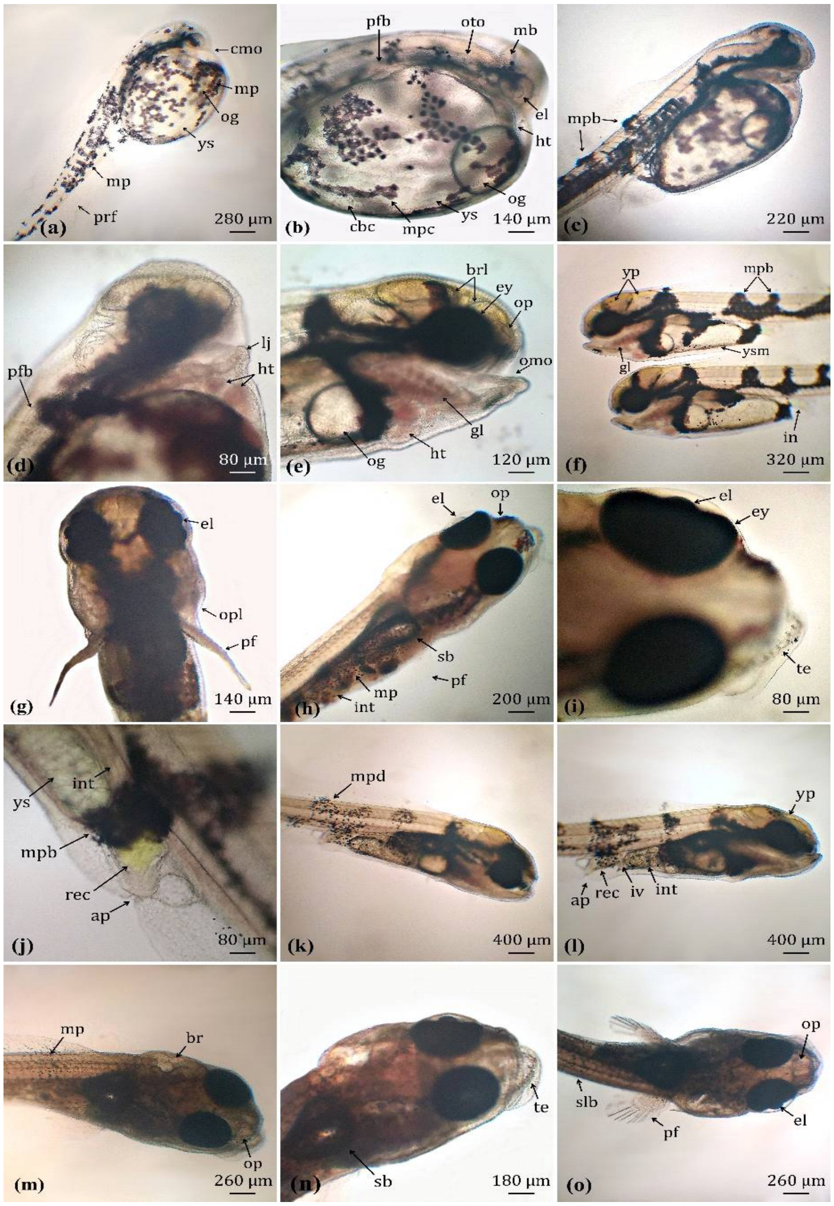
Table 1: Larval development stages of *M. pancalus* at 29.3±1.4°C.

Developmental stage	Length (mm)	Descriptions
Pro-larval phase		
Newly hatched larvae	3.43±0.16	Voluminous yolk-sac, intense melanophores, pectoral fin bud elongated (Fig 1a, b).
6-hr-old larvae	3.74±0.13	Two/three non-prominent bands of melanophores. Lower jaw noticed (Fig 1c, d).
12-hr-old larvae	3.95±0.12	Yolk sac reduced by 41.8% (Fig 3), incipient intestine visible, eye not pigmented (205±30 µm in dia.).
18-hr-old larvae	4.16±0.11	Four/five non-prominent melanophore bands. Eyes still non-pigmented (230±38 µm).
24-hr-old larvae	4.31±0.13	Swim bladder appeared; mouth cleft formation began (71±3.8 µm); gill poorly visible.
36-hr-old larvae	4.57±0.15	Seven/eight prominent melanophore stripes. Eye densely pigmented (351±17 µm) equals the diameter of an oil globule. Olfactory pits and internal yellow pigment in the head region. Gill visible (Fig 1e, f).
48-hr-old larvae	4.85±0.17	Pectoral fin (581±38 µm) with few soft rays. Opercula fold appeared (Fig 1g). Swim bladder elliptical in shape, oil globule reduced by 75.6% (Fig 3). Mouth cleft extended (155±7.8 µm). Eye (409±21 µm) densely pigmented.
60-hr-old larvae	5.14±0.15	Few or no teeth on jaws and larvae started feeding. Dispersion of melanophores from bands begins (Fig 1k). Eyes, about 1.25-1.5 times the oil globule diameter, heavily pigmented with distinct lenses. Digestive tract, like a straight tube. Opercula functional.
72-hr-old larvae	5.34±0.13	Yolk sac completely disappeared; oil globule not fully exhausted. The brain lobe is fully visible.
Post-larval phase		
5th day-old larvae	5.64±0.21	Slender body with fading melanophore stripes. A series of teeth on jaws. Mouth gap 386±9.5 µm. The tip of the lower jaw formed an obtuse angle (Fig 1m-1o).
7th day-old larvae	6.38±0.32	Vertical bands disappeared completely. Pectoral fin with 8-9 soft rays. Mouth gap 436±14 µm.
14th day-old larvae	8.93±1.36	Well-developed digestive tract, anus and gills. All fins with soft rays. Caudal fin non-confluent.
21st day-old larvae	14.78±3.06	Dorsal fin preceded by a series of sharp erectile spines (Fig 2b).
28-35th day-old larvae	27.77±3.86	The rostrum appeared ‘v’ shaped and not fully developed (Fig 2c).
45th day-old larvae	46.20±7.57	Rostrum length increased and the fry resembled the adult morphologically (Fig 2d).

yolk-sac utilization compared to oil-globule exhaustion were documented by Sulaeman and Fotedar (2017).

Larval feeding and cannibalism

The first feeding marks a critical period for larval survival, growth and development. Larval feeding with live zooplankton and boiled egg yolk was documented in lesser spiny eel (Das and Kalita, 2003; Sahoo *et al.*, 2009). However, boiled egg yolk resulted in 100% mortality of *M. pancalus* larvae on the 17th day (Afroz *et al.*, 2014). Kumar *et al.* (2021) reported successful rearing of stinging catfish larvae until 22 dph with mixed zooplankton without dependence upon *Artemia* nauplii. In *M. aculeatus* larvae, Sahoo *et al.* (2009) reported that the larvae fed mixed



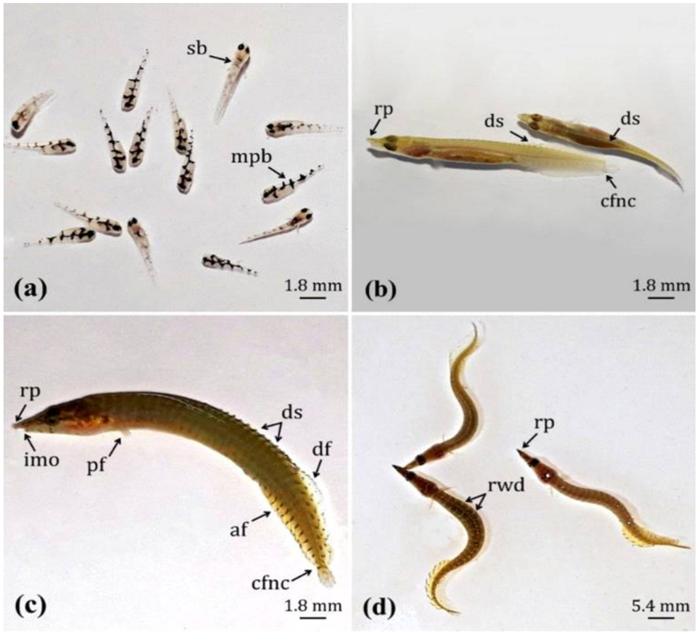
(a, b) Newly hatched larva, (c, d) 6-h-old, (e, f) 36-h-old, (g) 48-h-old, (h, i, j) 54-h-old, (k) 60-h-old, (l) 66-h-old, (m, n, o) 5-day-old larva (ap-anal pore, br-brain, brl-brain lobes, cbc-circulating blood cells, cmo–closed mouth, ey-eye, el-eye lens, gl-gills, ht-heart, in-incipient intestine, int-intestine, lj-lower jaw, mb-mid-brain, mp–melanophores, mpb–melanophore bands, mpc-cluster of melanophores, mpd-dispersion of melanophores, og-oil globule, omo–opened mouth, op-olfactory pit, opl-operculum, oto-otoliths, pf-pectoral fin, pfb-pectoral fin bud, pfr–pectoral fin rayed, prf-primordial fin, rec-rectum, sb-swim bladder, slb-slender body, te-teeth, yp-yellow pigment, ys-yolk sac, ysm-yolk-sac margin).

Fig 1: Photomicrograph showing larval development of barred spiny eel, *M. pancalus*.

zooplankton attained a mean final TL and BW of 21.33 mm and 32.22 mg. In contrast, our study recorded a higher mean TL (28.8 mm) and BW (100 mg) after 30 days of the rearing. The most commonly cultured freshwater rotifer was used for the first feeding, but we observed higher cannibalism between 5-14 dph, as indicated by the disappearance of larvae. Serajuddin and Ali (2005) reported the carnivorous and predatory habits of wild *M. pancalus* specimens, with young individuals feeding on annelids as their basic food. In our study, the development of dorsal spines and the appearance of the inferior mouth at 21 dph with *Tubifex* worm as basic food resulted in a decrease in cannibalism rate.

Larvae behaviour

The newly hatched larvae were inactive and remained attached to the sides and bottom of the tank, taking shelter under the roots of aquatic plants. Due to their large yolks,



(a) 60-h old, (b) 21-day-old, (c) 30-day-old, (d) 45-day-old (af–anal fin, cf-caudal fin, cfnc-caudal fin non-confluent, df-dorsal fin, ds-dorsal spine, imo-inferior mouth, mpb-melanophore bands pf-pectoral fin, rp-rostral projection, rwd-rings of white dots, sb-swim bladder).

Fig 2: Photograph showing pre- and post-larval features of barred spiny eel, *M. pancalus*.

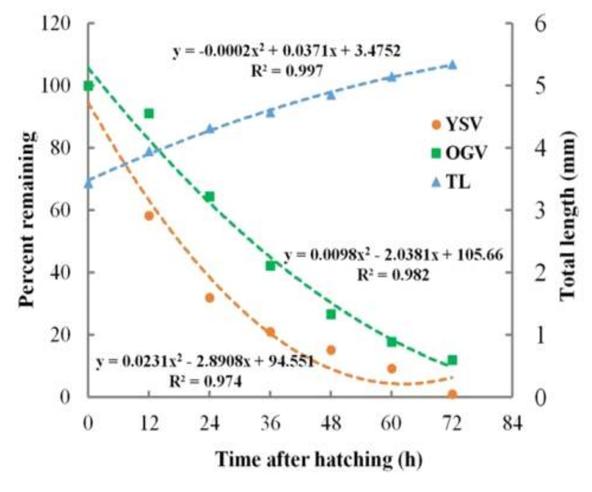
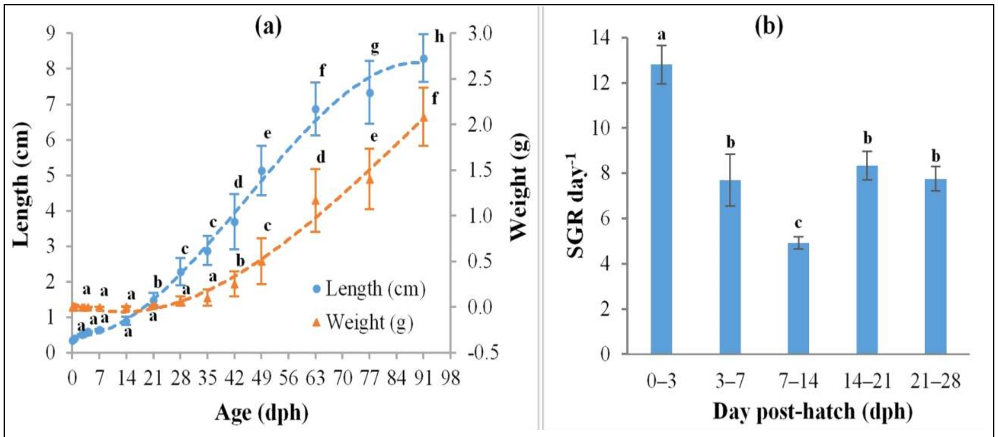


Fig 3: Yolk sac volume (YSV) and oil globule volume (OGV) of *M. pancalus* larvae in relation to the total length (TL) and the time after hatching in hours (h).



Mean values in the same data series with different superscripts differ significantly ($p<0.05$).

Fig 4: Growth of *M. pancalus* during 13 weeks of rearing. (a) polynomial regression of length ($y = -2E\text{-}05x^3 + 0.003x^2 - 0.0026x + 0.4568$, $R^2 = 0.9952$) and weight ($y = -2E\text{-}06x^3 + 0.0006x^2 - 0.0144x + 0.0365$, $R^2 = 0.9883$) and (b) SGR of TL.

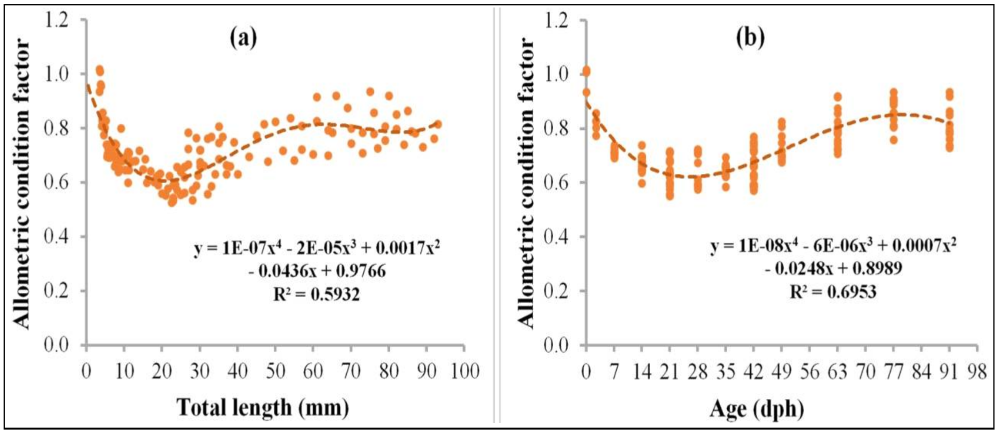


Fig 5: Allometric condition factor (K_A) in relation to the (a) total length and (b) age of *M. pancalus* fed with rotifer (3-14 dph), mixed zooplankton (119-24 dph) and *Tubifex* worms (14-91 dph).

they exhibited upside-down, irregular movements when disturbed. By 60 hph, they displayed intermittent swimming activity with pauses. Sahoo *et al.* (2009) observed similar hiding behavior in *M. aculeatus,* which lasted for 7-8 days. Fast swimming in *M. pancalus* was initiated between 5-7 dph, which coincided with the disappearance of the vertical black stripes. The low specific gravities in pro-larvae, due to the presence of a protuberant yolk sac and oil globule, probably needed to remain under the roots of floating weeds. However, with the absorption of the yolk sac and oil globule, the specific gravity of the larvae increased and they moved with the water column. This coincided with the formation of the swim bladder, indicating the ontogenetic change in the buoyancy (Table 1). In burbot *Lota lota* larvae, Palińska-Żarska *et al*. (2014) recommended a low water depth (up to 10 cm) until the moment of the swim bladder inflation. The presence of a swim bladder in the early larval stages of barred spiny eel is likely necessary for its benthopelagic life.

Larval growth, allometric analysis and condition factor

The mean TL values at 21 and 28 dph were significantly higher than the values until 14 dph ($p<0.05$) (Fig 4a). During the pro-larval phase, a significantly higher SGR of 12.81±0.8%/day for TL was noticed, compared to 6.91±0.6%/day at 14 dph ($p<0.05$). Thereafter, SGR increased to 7.44±0.6% at 28 dph, followed by a significant decrease, reaching 3.57±0.3% at 91 dph. Weekly observations showed a significantly higher SGR of 8.91±0.9% in the first week than the second week (4.92±0.3%), followed by a significant increase ($p<0.05$) in the third (8.33±0.6%) and fourth (7.75±0.5%) weeks (Fig 4b). Several authors reported the rapid growth phase of fish larvae immediately following hatching, followed by a period of slow growth during yolk depletion. In the Pacific fat sleeper *Dormitator latifrons*, the larvae exhibited the fastest growth during the initial 24 hph, with approximately 52% of yolk absorption (Reyes-Mero *et al*., 2022). In silver perch, the SGR of TL reached approximately 12% per day during the first 4 dph, followed by a slow growth rate of 4.8% only, from 4 to 10 dph (Sulaeman and Fotedar, 2017).

The LWR, log BW = 2.5628 log TL-1.7094 indicated negative allometric growth (b=2.56, R^2=0.997, $p<0.05$). The larvae appeared slender as they grew, becoming faster and more agile, with increasing TL suited to their predatory nature. However, the estimated b value fell within the expected range of 2.5-3.5 (Froese, 2006). The condition factor is a crucial indicator of the well-being and nutritional status of fish (Rao *et al.*, 2024). It is used to monitor feeding intensity, age and growth rates in fish. Generally, when the condition factor is close to or equal to 1, it indicates a satisfactory fitness level for fish species (Jisr *et al.*, 2018). The lower 'K_A' value of less than 1.0 and declining values observed in this study are likely associated with their transition to an anguilliform/ eel-like shape in the early life stages of *M. pancalus*. Furthermore, K_A values decreased sharply, reaching the lowest value at 20-30 mm TL and 21-28 dph (Fig 5a, b), followed by an increase in the K_A values and SGR, indicating the suitability of feeding *Tubifex* worms to *M. pancalus* larvae.

CONCLUSION

In this study, we provide a descriptive and illustrative account of both morphological and chronological development of larvae in the ontogeny of *M. pancalus*. Notably, several of these, typical to eel larvae, were hypothesized to hold adaptive significance. Additionally, we examine the growth performance resulting from a specific feeding protocol and assess the suitability of *Tubifex* worms as live food. However, further studies on the ontogeny of larval fish digestive system and the profile and dietary adaptation of digestive enzymes will be necessary to improve diet optimization and feeding strategies.

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Conflict of interest

There is no conflict of interest between authors.

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