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Allometric Growth Pattern During Early Developmental Stages of Featherback, *Chitala chitala* (Hamilton 1822) (Osteoglossiformes: Notopteridae)

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Abstract

In the present study the relationships between morphometric variables of *Chitala chitala* (Hamilton 1822) (Osteoglossiformes: Notopteridae) larvae reared at a constant temperature (30±2°C) from hatching to 30 days after hatching (DAH) were characterised through analysis of their allometric growth. The yolk sac and preflexion stage (TL = 13.24 to 16.90 mm) was distinguished by a precedence of sensorial, feeding, respiratory and swimming systems, and the accelerated growth of head ($b = 1.36$, $r^2 = 0.94$) and tail length ($b=1.12$, $r^2 = 0.97$). The flexion stage (TL = 17.89 to 25.35 mm) was characterised by a change in growth priorities. The body depth ($b= 1.28$, $r^2 =0.86$), snout length ($b= 1.51$, $r^2 =0.95$) and pectoral fin length (($b= 1.83$, $r^2 =0.87$) showed positive allometry in this phase. At the end of the postflexion stage (TL = 25.97 to 30.45 mm) there is a tendency to isometry for all the growth coefficients including the head length ($b= 1.07$, $r^2 =0.90$) and the tail length ($b= 1.0$, $r^2 =0.98$), corresponding to transition towards metamorphosing stage for the acquisition of the juvenile form.

Introduction

The featherback, *Chitala chitala* (Hamilton 1822) represents an important fishery resource in different parts of South-East Asia and particularly in India. Due to overexploitations of natural populations and subsequent decline in number, this species has been categorised as endangered (EN) in the Conservation Assessment and Management Plan, 1998 (Ayyappan et al. 2001). Therefore, large-scale farming would ensure effective resource utilisation, biodiversity conservation and widening consumer's choice for this new candidate species for the diversification of freshwater Indian aquaculture (Mitra et al. 2014).

The information on larval morphology and relative growth patterns during early development of the new candidate species for aquaculture upholds the optimal rearing protocols

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and greatly improve effective production of high quality juveniles and adults (Çoban et al. 2009). In this aspect morphometric ratios could be used as a combine criteria for the qualitative evaluation of control and cultured larvae and juveniles to determine intraspecific variations (Koumoundouros et al. 1999).The allometric growth model is widely used for relative growth analysis during early larval development (Celik and Cirik 2011) especially in the last decade with many taxa of teleost, such as sparids (Çoban et al. 2009), sturgeon (Gisbert and Doroshov 2006), catfish (Huysentruyt et al. 2009), sea horse (Roos et al. 2010) and serpae tetra (Celik and Cirik 2011). Allometric growth model, also evaluates the developmental plasticity of a particular species (Koumoundouros et al. 1999; Celik and Cirik 2011). However, there has been no detailed report on differential growth during larval development in the featherback *C. chitala* using allometric growth model.

Thus the aim of the present study was to describe the allometric growth patterns in combination with an analysis of inflexion points in growth curves *C.chitala* larvae reared under controlled culture conditions.

Materials and Methods

The larvae used in the present study were obtained from the local fish farm, in West Bengal, India by induced spawning of domesticated broodstocks of featherback, *C. chitala*. The induction and spawning conditions were previously described by Sarkar et al. (2006). Fourteen to eighteen hours after injection, courtship and spawning occurred. The spawned adhesive eggs were removed from the pond and placed in a 100 L recirculatory tank until hatching (168-192 h) at 27-28°C, pH 7.81±0.12 and water flow 0.3 liter sec^{-1}. After hatching, larvae were reared in three tanks at the density of 45,000 larvae m^{-3}. The photoperiod was maintained on a 12 L: 12 D cycle. Temperature and pH ranged from 30±2°C and 7.4±0.6, respectively throughout the experiment. Dissolved oxygen was maintained above 8.0±2.50 mg. L^{-1} by constant aeration. The larvae were fed *ad libitum* with *Artemia* nauplii three times daily. Throughout the study, daily water exchanges (10-15% of total tank volume) and bottom siphoning prevented accumulation of dead *Artemia* and other organic matter. A random sample of 60 larvae was collected from hatching to 30 days after hatching (DAH) every day prior to feeding during the morning. Sampled larvae were subjected to overexposure in an anaesthetic solution (MS-222 at a dose of 150 mg. L^{-1}) and the morphometric characteristics were recorded using an ocular micrometer and digital calipers with precision of 0.01 mm. The morphometric characters and their descriptions measured during the experiment are described in Table: 1. All measurements were taken along lines parallel or perpendicular to the horizontal axis of the body (Gisbert 1999). Dead and abnormal specimens (presence of malformations) were excluded from the analysis. In yolk sac larvae, the diameter (maximum and minimum) of the ellipsoidal yolk sac was also measured and the volume (mm^3) calculated using the following formula: $V = 0.1667\ \pi\ LH^2$; where H is the minimum diameter and L is the maximum diameter of the yolk sphere (Heming and Buddington 1988). After this, the larvae were fixed in a 4% phosphate-buffered formaldehyde (pH 7.2) solution for further detailed examinations of the form of sensory, feeding and swimming structures. Developmental stages were identified according to Kendall et al. (1984) as yolk-sac larvae (after hatching and until mouth opening), preflexion larvae (from mouth opening to the start of the flexion of the caudal tip of the notochord), flexion larvae (notochord tip reached its final position at approximately 45 degrees from the notochord axis and the principal caudal-fin rays and supporting skeletal elements are in the adult longitudinal position), and postflexion larvae (completion of notochord flexion to start of metamorphosis). The measured morphometric characters during the developmental stages of *C. chitala* are presented in Fig.1.

Statistical analysis

Allometric growth patterns during the developmental stages of *C. chitala* were modelled by a power function of TL. The patterns in allometry were described by the growth coefficient (i.e. power function exponent) in the equation $Y = aX^b$, where Y is the dependent variable (measured character) and X, the independent variable (TL), a is the intercept and b, the growth coefficient (Fuiman 1983). Isometric growth occurred when $b = 1$. A positive allometric growth occurred when $b > 1$ and a negative allometric growth when $b < 1$ (Osse and Boogaart 2004). Linear regressions were performed on log-transformed data (TL as independent variable) and the inflection points were calculated for HL, HD, SNL, ED, MG, BD, TRL, TAL, TAD, PecL, PelL (Gisbert 1999; Gisbert et al. 2002). Inflection points are the X values where the slope changes. The inflection points were calculated according to van Snik et al. (1997), in which linear regressions were calculated for X*min* to X*intermediate* and for X *intermediate* to X*max* and then compared by t-tests to evaluate if the two slopes (*b*) for X *min*- X*intermediate* and X*intermediate*- X*max* differed significantly. The X*intermediate* value that iteratively showed the largest t from the comparison was defined as the inflection point. X*intermediate* was defined as a value that ranged iteratively from X*min* + 2 to X*max* – 2. Growth coefficients were compared statistically using a t-test. The accepted significance level was $P < 0.05$. SPSS version- 21 was used for the analyses.

Table1. Abbreviations and description of the measured morphometric characters

Characters	Abbreviations	Descriptions
Total Length	TL	From tip of snout to tip of the caudal fin
Head Length	HL	From tip of snout to posterior margin of opercle
Head Depth	HD	Measured at the level of the opercula
Body Depth	BD	Posterior to the anus
Eye Diameter	ED	Measured through the centre of the eye parallel to the main axis of the body
Snout length	SNL	From the tip of the snout to the anterior margin of the eye
Tail length (Post anal)	TAL	Measured between the anus and the tip of the notochord
Tail depth	TAD	Measured at the peduncle level
Pectoral fin length	PecL	Measured from the origin of the pectoral fin to its distal end
Pelvic fin length	PelL	Measured from the origin of the pelvic fin to its distal end
Trunk length	TRL	Measured from the posterior end of the opercle to the anus
Mouth Gape width	MG	Maximum opening of the mouth

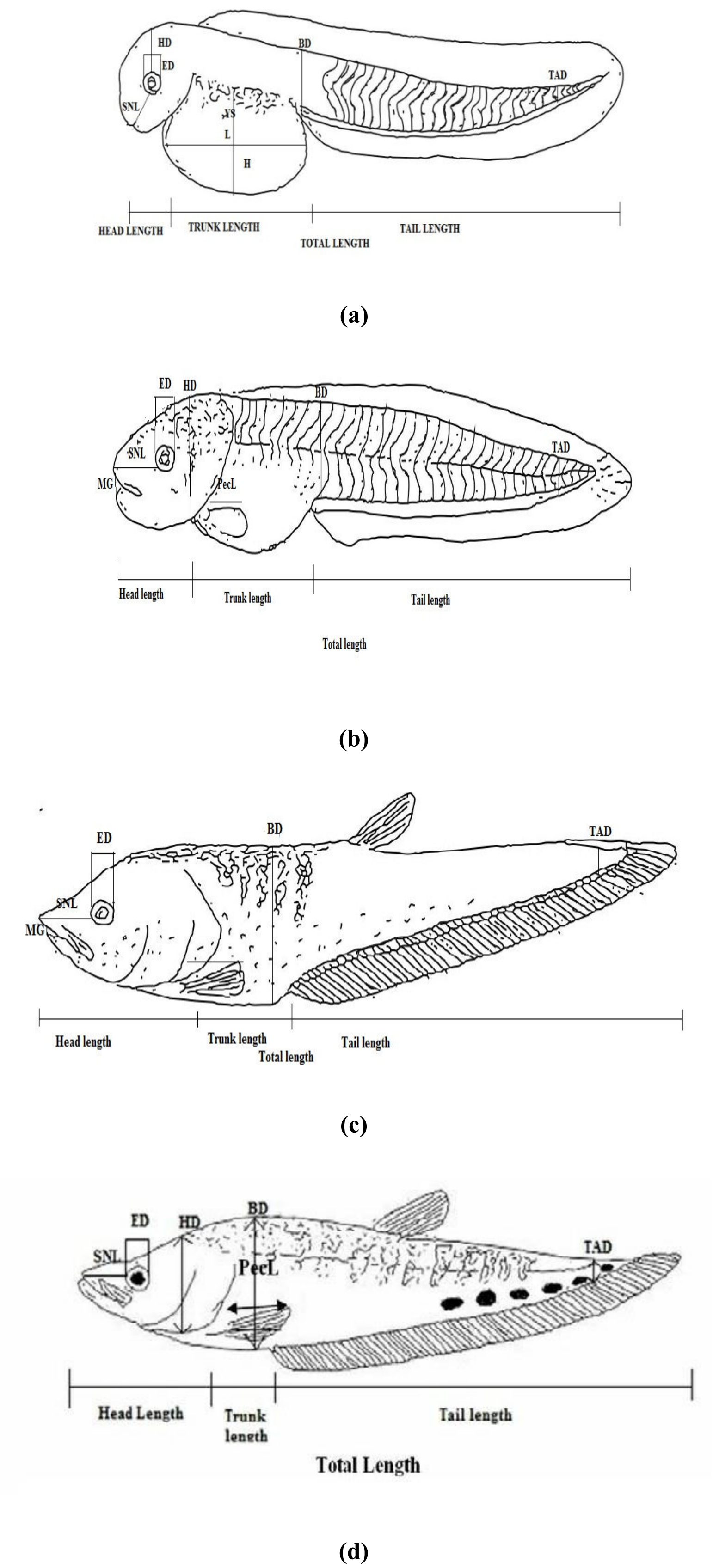

Fig 1. Morphometric characters measured in the *C.chitala* during various developmental stages. (a) Yolk sac stage (b) Preflexion stage (c) Flexion stage (d) Post flexion stage. Abbreviations: H, minimum diameter of the yolk sphere; L, maximum diameter of the yolk sphere; YS, yolksac; SNL, snout length; ED, eye diameter; HD, head depth; BD, body depth; PecL, pectoral fin length; TAD, tail depth; TL, total length; TRL, trunk length; HL, head length; MG, mouth gape.

Results

At hatching, the *C. chitala* larvae measured 10.21±0.04 mm TL (n = 35) and grew to attain a final TL of 30.45±1.36 mm (n = 25). Four larval development stages were observed after hatching: yolk sac larvae, preflexion larvae, flexion larvae and postflexion-larvae. The relation between total length and age (DAH) in *C. chitala* from hatching to metamorphosis followed a linear function (Fig. 2).

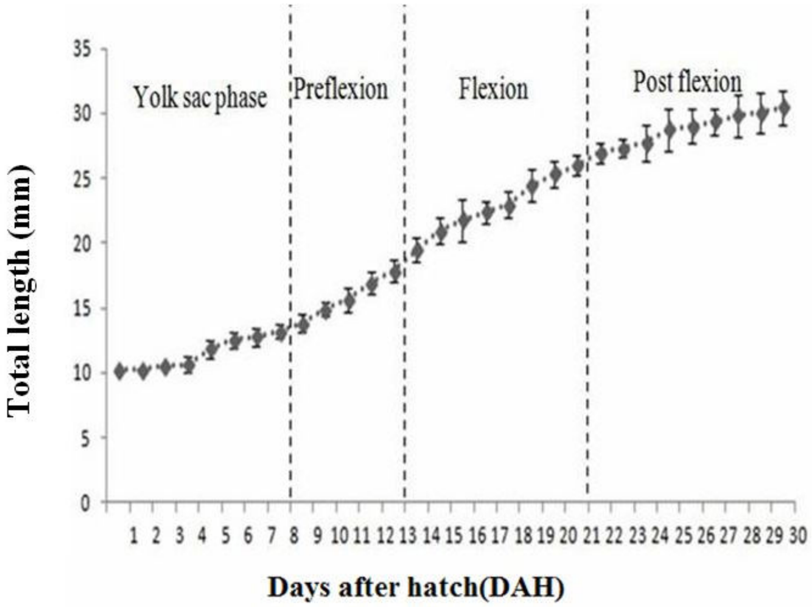

Fig. 2. Growth in total length (TL) of *C.chitala* during early stages of development (from 0-30 DAH). During the period studied, growth could be defined by 8.8505+0.7793*DAH (days after hatch). Each point represents the mean ± SE. (r^2=0·987; P<0·05; n=350).

The newly hatched larvae had the head bent ventrally with a large yolk sac (volume 3.97±0.08 mm^3) (n =35) containing several oil droplets in the posterior region that migrated towards the anterior region with further development. A finfold covered the body from the dorsal area of the trunk to the ventral area of the yolk sac and was higher in the dorsal part of the trunk and narrower in the caudal region. Auditory capsules and otoliths were visible in the posterior region of the head. Scattered melanophores were observed in the dorsal part of the head and in the posterior part of the yolk sac. The eyes were darkly pigmented. The undifferentiated primordial digestive tract was observed lying dorsally to the yolk sac.

The preflexion stage began at first feeding (8 DAH) (13.24±0.73 mm TL) (n =30) and ended at 12 DAH (16.9±0.92 mm TL) (n = 25). At the onset of this stage, the yolk sac and oil globule were almost consumed. At 8 DAH lens appeared in the eye; mouth and anus opened, and rudimentary maxilla and lower jaw bone were detected. Branchial arches were also observed from 8 DAH. The number of melanophores increased on the dorsal and lateral parts of the body. At 10 DAH (14.94±0.50 mm TL) (n = 27), a few small teeth were visible in the mouth. At 10 DAH with the coincidence of exogenous feeding the larvae initiated swim bladder inflation by swallowing air directly from the water surface. A convoluted digestive tract was evident from 8-

10 DAH. At 12 DAH (16.9±0.84 mm TL) (n = 25), the dorsal, pectoral, anal and caudal finfold began to differentiate but rays were not clearly visible.

The flexion stage started from 13 DAH (17.89±0.84 mm TL) (n = 25) and continued until 20 DAH (25.35±1.02 mm TL) (n = 25). From the onset of this stage most of the larvae showed a 45° upward flexion of the notochord tip. At 15 DAH, the notochord was shortened and caudal rays filled its end. Pigmentation occurred on the bases of pelvic, anal and dorsal fins. After these stages, less drastic changes were observed.

The post flexion stage was observed from 21 DAH (25.97±1.02 mm TL) (n = 25) to 30 DAH (30.45±1.36 mm TL) (n = 25). The pectoral, anal and dorsal fins were elongated with melanophores covering most of the fins. Body pigmentation increased in the middle of the body. The first typical juvenile pigmentation pattern was observed from 25 DAH (28.78±1.6 mm TL) (n = 25) and continued throughout the study period. Several light and dark transverse bars were observed along the dorsal ridges. The body shape of larvae and the pigmentation pattern on the lateral side of the body resembled the ‘miniature adults’, but the scales were yet to form. The major morphological landmarks during larval development of *C. chitala* are summarised in Fig. 3.

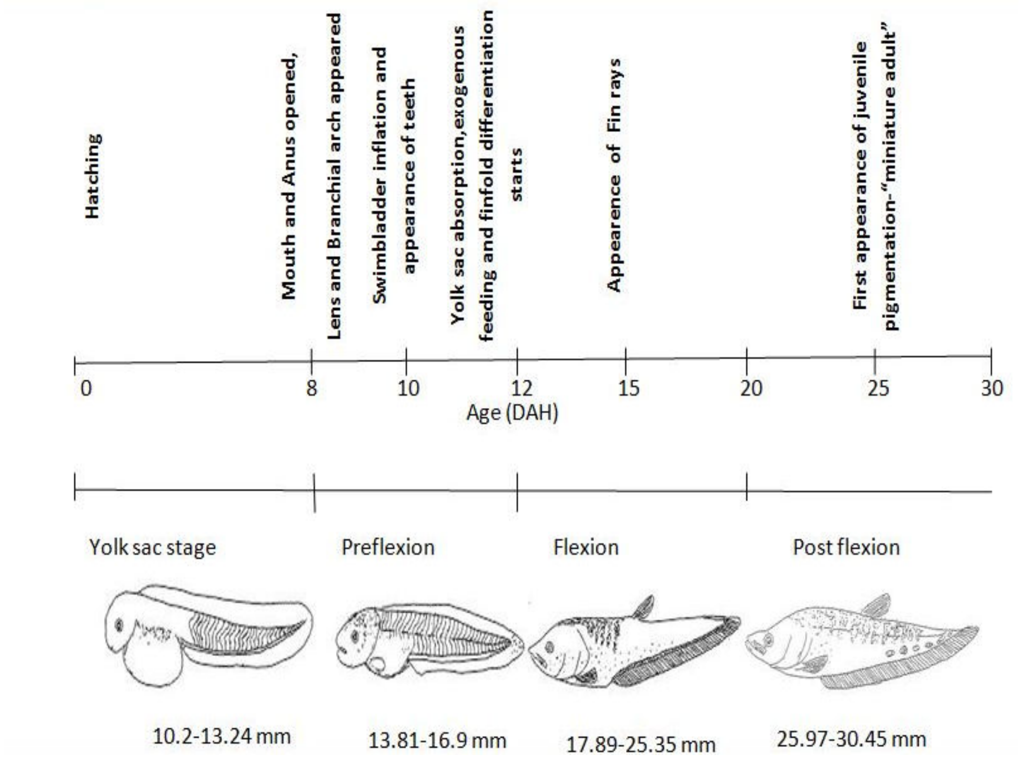

Fig. 3. Major morphological landmarks in *C. chitala* early development.

Allometric growth equations between 12 measured body parts and TL during the larval developmental stage (0-30 DAH) are presented in Fig. 4. The growth of HL was triphasic, showing positively allometric trend until 20 DAH with first inflexion point ($b = 1.36$, $r^2 = 0.94$) situated at 16.9 mm TL (at 12 DAH) and second inflexion point ($b = 1.17$, $r^2 = 0.97$) at 25.35 mm TL (at 20 DAH) and isometric growth trend from 21 to 30 DAH ($b = 1.07$, $r^2 = 0.90$) ($P<0.05$) (Fig. 4a). Growth in tail length could be divided into three different stages during larval development (Fig. 4b). From hatching to 12 DAH, growth showed positive allometry ($b=1.12$, r^2

= 0.97) and from the inflexion point at 16.9 mm TL until 24.47 mm TL at 19 DAH, it increased sharply (b=1.51 r^2 =0.95). Tail length growth showed isometry (*b*=1.0 r^2=0.98) between 19 and 30 DAH. Growth of HD showed a significant reduction in growth coefficient at 16 DAH ($P<0.05$) at the inflexion point 21.77 mm TL showing biphasic growth of positive allometry (b = 1.46, r^2 = 0.97) and isometry (b = 1.02, r^2 = 0.86) ($P<0.05$) (Fig. 4c). A triphasic growth was observed in the case of TAD during larval development (Fig. 4d). From hatching to 16.9 mm TL at 12 DAH, the growth of tail depth showed positive allometry (b=1.15, r^2 =0.96), while from 17.89 to 25.35 mm TL (20 DAH), tail depth growth rapidly increased (b=3.0 r^2=0.92). Thereafter, the allometric coefficient decreased (b=1.03, r^2=0.91) ($P<0.05$). Eye diameter showed positive allometric growth pattern until 14 DAH (19.49 mm TL; b = 1.62, r^2 = 0.94) but from 15 DAH onwards it showed isometric pattern of development (b = 1.04, r^2 = 0.9) ($P<0.05$) (Fig. 4e). The allometric growth of SNL showed a single flection point situated at a 25.97 mm TL, exhibiting the initial positive allometric growth (b=1.51, r^2 =0.95) between hatching to 20 DAH and followed by a decrease in growth rate to attain isometric growth pattern (b=1, r^2 =0.95) from 21 DAH to 30 DAH ($P<0.05$) (Fig.4f). Biphasic growth model for body depth and pectoral fin length was observed. An increase in growth coefficient were observed at 24.47 mm TL (b =2.12, r^2 = 0.94) in case of BD whereas a decrease in growth coefficient was observed at 25.97 mm TL (b = 1.83, r^2 = 0.87) in the case of PecL ($P<0.05$) (Fig. 4g and 4h, respectively). Two flection points were observed in the case of TRL indicating its triphasic growth (Fig. 4i). The first flection point was situated at 17.89 mm TL (b =0.87, r^2 = 0.90) showing a negative allometric growth from hatching to 13 DAH, followed by an increase in growth coefficient (b=1.28, r^2 =0.86) ($P<0.05$). After 19 DAH (24.47 mm TL) a sharp decrease in growth coefficient occurred approaching isometry (b =0.98, r^2 = 0.95) ($P<0.05$). While MG showed a negative allometric growth until 12 DAH (b=0.81, r^2 = 0.95) followed by an isometric growth pattern until the completion of the experiment (b=1.08, r^2 = 0.87) (Fig. 4j) ($P<0.05$). The flection points for the measured body segments mainly occurred during the notochroda flexion stage between 12 and 20 DAH, corresponding to the 16.9 to 25.35 mm TL. The development of pelvic fin was rudimentary in *C. chitala* during the entire studied period.

Discussion

In the present study *C. chitala* followed a typical course of teleost ontogeny and the entire developmental period was differentiated into different phases according to the following morphological growth trajectories: the yolk sac phase (from 0 to 8 DAH), between hatching and yolk sac resorption and first feeding at 8 DAH; the preflexion larval phase (from 9 to 12 DAH); the flexion period (from 13 to 20 DAH); and the postflexion-juvenile phase, from notochord flexion to the completion of metamorphosis (from 21 to 30 DAH). During the yolk sac phase, the larvae of *C. chitala* showed an insignificant growth rate in body mass as well as length. Endogenous reserves were depleted moderately fast until mouth opening (65% of yolk and 32 % of oil globule in 8 days).

Thus, the larvae showed a period of short mixed nutrition (lecithoexotrophic period) based on endogenous (lecithotrophic period) and exogenous (exotrophic period) nutrients that extended from mouth opening at 13.24 mm TL (at 8 DAH) to around 16.9 mm TL (at 12 DAH).

The complete depletion of the yolk sac and oil globule indicated the onset of the preflexion stage (Kendall et al. 1984), during which there was a change in the growth coefficients of the head, trunk and tail segments. The head length, head depth, snout length and eye diameter growth of *C. chitala* larvae was positively allometric from hatching to 12 DAH (16.9 mm TL) and indicated continuous cerebral development, possibly allowing the improvement of the motor and sensorial ability to contribute to increase the probability of prey detection (Fuiman 1983; Gisbert and Doroshov 2006).

Positive allometric growth of the head is a common feature in the early ontogeny of fish like the carps (Osse et al. 1997) sturgeons (van Snik et al. 1997; Gisbert 1999; Osse and Boogaart 2004) and catfishes (Huysentruyt et al. 2009). The positive allometric growth of eye diameter during this period concurs with the findings of Packard and Wainwright (1974), where the linear eye dimension is a direct indicator of brain growth during early life history of fish to enhance the vision. The positive allometric growth of eyes is considered an indicator of development and differentiation of neural and sensorial structures; which would allow the larvae to react to light stimuli, detect zooplankton prey and potential predators in the water column (Gisbert et al. 2002; Gisbert and Doroshov 2006). An increment in the growth coefficient of the head segment during preflexion stage can also be correlated with the development of the respiratory (branchial filaments) system in *C. chitala* at 8 DAH. During most of the fish larval stage, cutaneous respiration is known to be more important than gill respiration (de Silva 1974).

The development of gill arches and filaments allow switching from temporary (cutaneous) to branchial respiration, resulting in a better oxygen supply and an increase in swimming activity (Gisbert et al. 2002). The swim bladder inflation also occured around 10 DAH in *C. chitala* larvae, which seems to have a crucial function for controlling buoyancy and swimming activity and also for capturing prey more efficiently and avoid predators during larval development (Russo et al. 2007). The first growth period ended at the beginning of differentiation of primordial finfold shortly before the notochordal flexion stage, which indicated that the larvae began to modify their swimming mode (Bone et al. 1995). This similar developmental pattern during early fish ontogeny has also been reported in larvae of different teleosts (Fuiman 1983; Osse et al. 1997; van Snik et al. 1997; Koumoundouros et al. 1999; Gisbert 1999; Gisbert et al. 2002; Osse and Boogaart 2004) and seems to be genetically programmed (Gisbert et al. 2002).

During the notochorda flexion stage, a main shift in the growth allometry was observed in *C. chitala* like most teleosts (Peña and Dumas 2009). A significant increase in tail depth occurred concomitantly with the development of unpaired fins and fin rays in *C. chitala* during this stage. This increment in tail depth may correspond to the development and differentiation of the hypural plate (Ortíz-Galindo et al.2000) and the caudal peduncle (Johnston and Hall 2004).

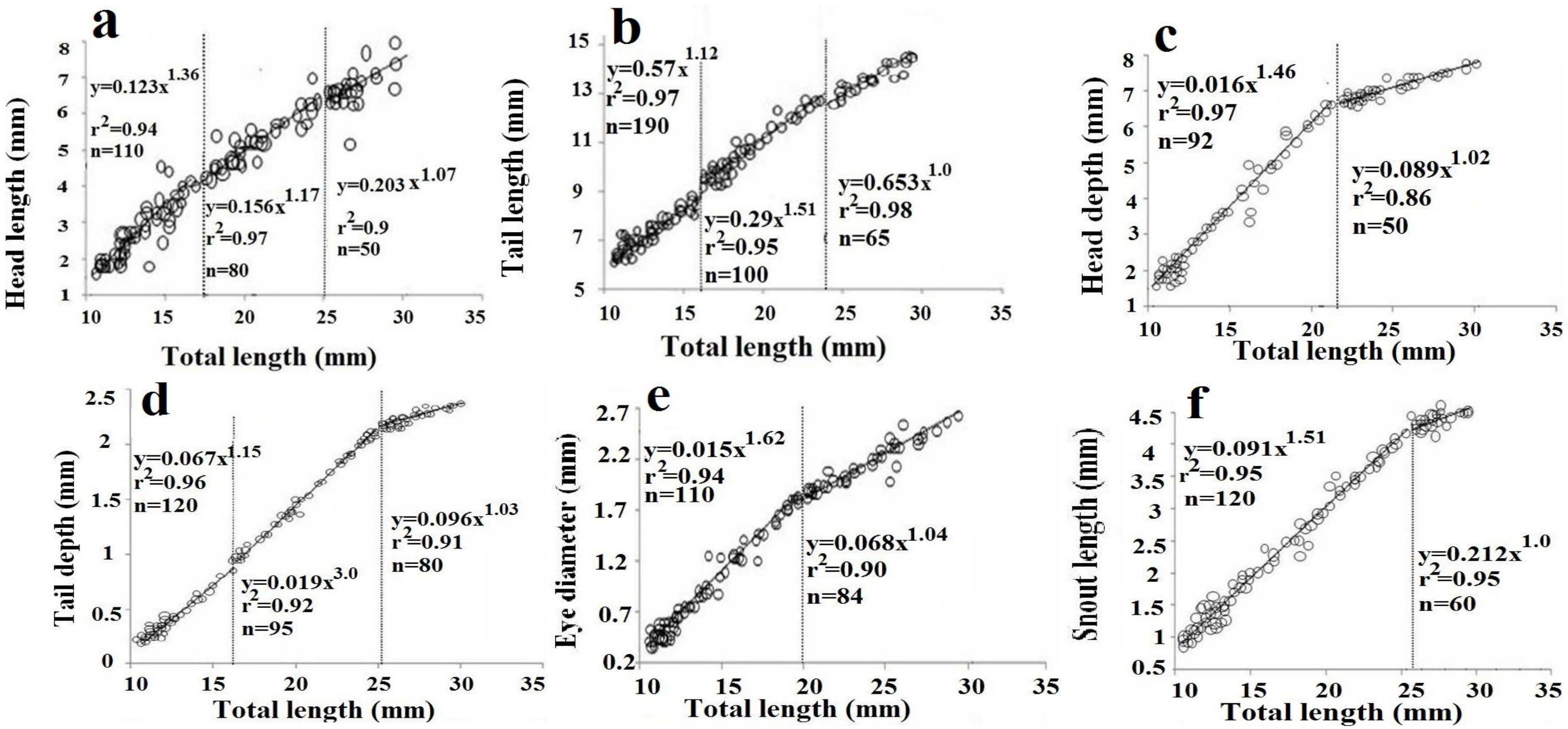

Fig. 4. Allometric growth equations and relationships between different measured body proportions and total length (TL) during early stages of *C. chitala* development. The dashed line represents the inflexion point of growth. (a) Head length (first inflexion point at 16.9 mm TL, at 12 DAH; second inflexion point at 25.35 mm TL, at 20 DAH); (b)Tail length (inflexion point at 16.9 mm TL, at 12 DAH); (c) Head depth (inflexion point at 21.77 mm TL, at 16 DAH); (d) Tail depth (first inflexion point at 16.9 mm TL, at 12 DAH; second inflexion point at 25.35 mm TL, at 20 DAH) ; (e) Eye diameter (inflexion point at 19.49 mm TL, at 14 DAH); (f) Snout length (inflexion point at 25.97 mm TL, at 21 DAH)

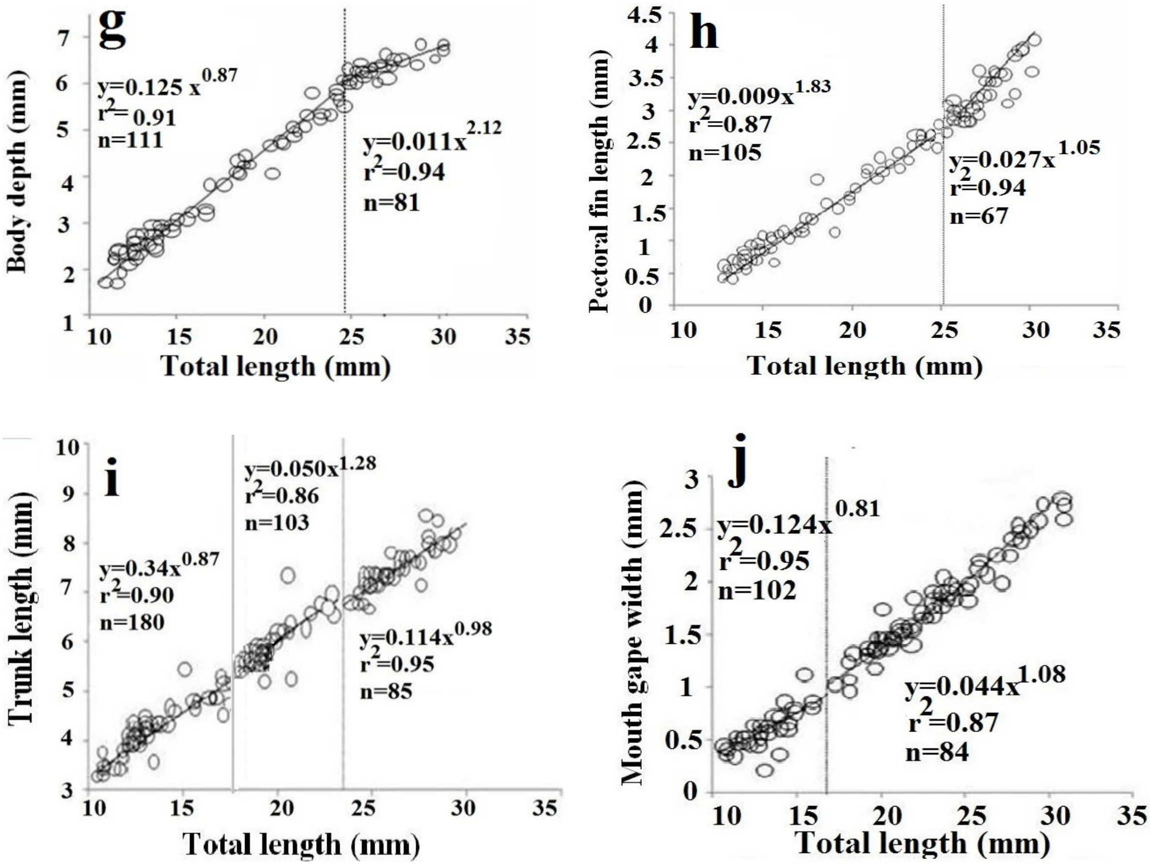

Fig. 4 (continued). Allometric growth equations and relationships between different measured body proportions and total length (TL) during early stages of *C. chitala* development. The dashed line represents the inflexion point of growth. (g) Body depth (inflexion point at 24.47 mm TL, at 19 DAH); (h) Pectoral fin length (inflexion point at 25.35 mm TL, at 20 DAH); (i) Trunk length (first inflexion point at 17.89 mm TL at 13 DAH and 24.47 mm TL; second inflexion point at 19 DAH); (j) Mouth gape width (inflexion point at 16.9 mm TL, at 12 DAH)

The comparative enhanced development of tail depth in *C. chitala* also implicitly indicates the enlargement of propulsive area and the increase of propulsive power (Fuiman 1983) with the development of two gear red and white muscle system from a single dominant fibre type. This results in a considerable change in body shape from an elongated preflexion larva to a more robust flexion specimen (Blaxter 1988). The morphological differentiation of the caudal fin and development of lepidotrichia in *C. chitala,* particularly in this growth period closely paralleled the progressive change in the larval swimming mode from the anguilliform motion to the subcarangiform swimming (Bone et al. 1995; Osse and Boogaart 1999). These changes and shift in swimming strategy helps the larvae to enhance swimming efficiency (Müller and van Leeuwen 2006) and thus reduces the transport costs (Blaxter 1988; van Snik et al. 1997; Müller and van Leeuwen 2006) for both food capture and predator avoidance (Williams et al. 1996). Similar observation has been reported for other teleost larvae where the development of the fins with fin rays and change in swimming style was correlated (van Snik et al. 1997; Gisbert 1999; Gisbert et al. 2002). Kolmann and Huber (2009) stated that a positive allometry in feeding performance assists predators in overcoming the functional constraints imposed by their prey, and may confer a competitive advantage over isometric ontogenetic trajectories, facilitating access to exclusive trophic resources earlier in life. Thus, the positive allometric growth of the mouth gape in *C. chitala* during this stage helps the larvae to improve their prey capture ability like the other fish larvae (Osse and Boogaart 2004).*Chitala chitala* being a predator fish (Rahman 1989) shows a slow overall movements followed by a rapid strike, like other predatory fishes (Kammerer et al. 2005). According to Walker (2004), these actions are commonly associated with the involvement of both caudal fin movements to generate an impulse and pectoral fins for maneuvering. In the present study, we also observed that pectoral fins showed a positive growth allometry during the flexion period in *C. chitala.* Similar results were found in case of Cuban gar (Comabella et al. 2013), sturgeons (Gisbert and Doroshov 2006), red snappers (Williams et al. 2004) and were attributed to their crucial function in swimming and maneuvering for feeding. According to Betti et al. (2009) the pectoral fins are the first to appear but the last to obtain a full complement of rays, which aid in locomotion and prey capture in larval teleosts (Osse and Boogaart 2004). Being a primitive basal teleost (Mandal et al. 2012) the development of pelvic fin was rudimentary in *C. chitala* during the studied period. Murata et al. (2010), also proposed that primitive teleosteans often have extremely limited pelvic fin function compared with more derived fish, where the pelvic fins have a trimming function that reduces pitching and upward body displacement during braking. The extended low initial growth in *C. chitala* larvae during the first developmental phase can be described by the fact that the available energy was allocated to enhance the vision, improve feeding capabilities and swimming ability. These in turn allow them to attain a better nutritional status (i.e. changes in the prey type selection, shifting from small to larger more nutritious prey) (Morote et al. 2008) to increase the body mass in the latter developmental stages (Parra and Yúfera 2001). Ben Khemis et al. (2013) reported a similar observation during the development of mullets. A significant morphogenesis and occurrence of growth in the trunk region of *C.chitala* larvae may also be due to the differentiation and growth of myotomes and the development of digestive organs (Gisbert and Doroshov 2006).

Like other teleost species (Fuiman 1983; Osse and Boogaart 2004), *C. chitala* showed a decrease in growth rate approaching isometry during the latter stages of growth, which is a typical feature of a juvenile fish growth profile, and defined the end of metamorphosing period (Fuiman 1983). This change to isometry has been considered as a natural transition in growth priorities since primary functions have been fulfilled during the early developmental stages (Osse and Boogaart 2004).

Conclusion

In *C.chitala*, most of the sensorial, feeding, respiratory and swimming systems developed rapidly during the first phase of development, supporting the hypothesis of energy and building materials allocation in priority to functional changes rather than size increase. The subsequent developmental period was mainly categorised by the flexion of notochord, the rapid and intense growth of the trunk and tail segments, the acquisition of adult axial muscle distribution, completion of gill filament development accompanied by the rapid development of fin rays, changes in body shape and a change in locomotive ability and feeding techniques. All these changes in the growth trajectories of *C. chitala,* corroborated the transition from larvae to metamorphosing juvenile phenotype and may act as a potential source of information to describe ontogenetic landmarks, which can be used to facilitate experimental research for developing the intensive culture of this new candidate species. Moreover, the analysis of growth patterns presented in this study provides valuable information on the changes in functional demands throughout ontogeny, which could be useful for aquaculturists to design more suitable rearing conditions for particular life stages. Although, variations in the timing of ontogenetic events and structure formation can occur based on different environmental conditions (e.g. temperature and food availability), further research is needed to identify ossification processes and squamation patterns to define other important landmarks for the onset of the juvenile period more precisely.

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