

# Early development and allometric growth in the armoured catfish *Corydoras aeneus* (Gill, 1858)

Frank Huyseentruyt · Beatrijs Moerkerke ·  
Stijn Devaere · Dominique Adriaens

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**Abstract** An ontogenetic series of in-captivity bred *Corydoras aeneus* was used, in order to study the developmental changes in the external morphology. Allometric growth of several body parts was studied, attempting to reveal important steps in the species' early life history. Based on the external morphology, the different stages during early development of *C. aeneus* were identified, according to Balon (Journal of the Fisheries Research Board of Canada 32:1663–1670, 1975). After hatching, at a SL of 3.5 mm, the developmental state corresponded to an eleutherembryonic phase, followed by the protopterygiolarval phase (4.4–5.7 mm SL), the pterygiolarval phase (5.7–14.0 mm SL) and the juvenile period. In addition, an overall growth curve and inflexion points were determined. As such, ontogenetic changes in growth coefficients  $k$  (in  $SL = b \cdot age^k$ ) were determined. Log transformed data were used for a piecewise linear regression method, as per regression spline smoothing procedures. This way, the growth curve could be

divided into six different intervals of growth rate. Initially, the slope was 0.05 until 0.7 dph, then increasing to 0.18 until 4 dph, and 0.36 until 10 dph. After this, growth rate reached a maximum of 0.76 until 24 dph, slowed down to 0.47 until 37 dph and then finally again slowed down to 0.36. A similar growth analysis was also done on the different body parts and these results were compared to both morphological and data from literature. This led to the conclusion that the inflection points found during the early development of *C. aeneus* matched the different key-events known in teleost early life history and development. The transition from endo- to exogenous feeding, at the moment a functional branchial respiratory system becomes increasingly important, was the first point at which allometries changed together with functional demands. A second, similar congruence occurred at the transition to the pterygiolarval phase, when priorities shift towards locomotory needs. Finally, our results also indicated a transition to a carangiform swimming mode at approximately 8 mm SL.

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F. Huyseentruyt (✉) · S. Devaere · D. Adriaens  
Department of Vertebrate Morphology, Ghent University,  
K. L. Ledeganckstraat 35, 9000 Ghent, Belgium  
e-mail: frank.huyseentruyt@ugent.be

B. Moerkerke  
Department of Applied Mathematics and Computer  
Science, Ghent University, Krijgslaan 281 – S9,  
9000 Ghent, Belgium

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## Introduction

The armoured catfish *Corydoras aeneus* (Gill, 1858) is one out of approximately 142 species that belong to

the genus *Corydoras* (de Pinna, 1998). It is widespread in South America, occurring in Trinidad, Venezuela, Suriname, Colombia, Ecuador, Peru, Bolivia and Brazil (Gosline, 1940; Nijssen, 1970; Kramer & Braun, 1983; Fuller, 2001). It is a very popular species in the trade of freshwater ornamental fish and is annually bred and shipped in large quantities all over the world (Tamaru et al., 1997). In addition, *C. aeneus* belongs to the family Callichthyidae, a family which itself belongs to the larger superfamily of the Loricarioidea. In this superfamily, an evolutionary trend has been observed which has led to the development of a sucker-mouth in the families Astroblepidae and Loricariidae, associated with a highly specialised feeding mechanism (i.e., algae-scraping) in the latter family. Placed within this evolutionary lineage, the Callichthyidae take a basal position with a ventrally placed mouth already present but with neither the presence of a sucker-mouth nor algae scraping feeding apparatus. In this context, the study of the morphology and development of *C. aeneus* can contribute to a better knowledge of the differences in cranial morphology and their impact on feeding ecology within the superfamily of the Loricarioidea (Van Wassenbergh et al., 2009). The adult *C. aeneus* has already been studied both from a morphological and physiological point of view (e.g. Kramer & McClure, 1980, 1981; Shiba et al., 1982; Kramer & Braun, 1983; Oliveira et al., 1992, 1993; Sire & Huysseune, 1996; Huysseune & Sire, 1997) as is also the case for its reproductive biology (Kohda et al., 1995, 2002; Pruzsinszky & Ladich, 1998). However, little to nothing is known about its ontogeny and growth. Morphogenesis and differentiation are nevertheless very intense during early life stages (van Snik et al., 1997), and teleost larvae growth is considered as optimised to increase fitness (Fukuhara, 1992). Both of these processes lead to a discontinuous larval growth (in terms of rate) (Gisbert, 1999), of which a thorough knowledge would help to understand functional trends in relation to the ecology of the species at different developmental stages (Fukuhara, 1992).

To fill this gap, it is our objective to study the ontogeny of *C. aeneus* and, as a first step in this study, we gathered information on growth of the species in order to obtain insights into the temporal patterns of ontogenetic allometries. Further, knowledge on the

ontogeny can also serve aquacultural applications (Fukuhara, 1992).

## Materials and methods

### Breeding preparations

Specimens were commercially obtained from a pet shop (Poisson d'Or—Belgium). Since origin of the adult specimens was unknown and since long-term breeding under artificial conditions could affect early development, a projection of the results of this study onto the whole species should be considered with caution. Still, since our main interest is to describe the general patterns of allometric growth that characterise early development of the species (in relation to size and age) the use of this brood stock seems justifiable, apart from the practical reasons (ability to obtain and breed them). A total of 35 specimens (25 were males), were put together in a  $1.0 \times 0.5 \times 0.6$  m tank. The tank had a 3-cm sand layer, a box filter, a heating apparatus and was heavily furnished with plant material (*Microsorum*, *Echinodorus* and *Anubias*-species). A temperature of 24–26°C, pH-level of 8–8.5 and global hardness of 9–12° was maintained. The specimens were fed on a diet of flakes (TetraMin). In the tank, dry-season conditions were imitated by lowering the water level to 10 cm and lowering light intensity for a period of 20–30 days. This was followed by an imitation of rain season conditions (daily adding of fresh, colder water and sufficient aeration) (Fuller, 2001). About a week after the start of this artificial rain season, several egg clutches (maximum 10) were found on the glass walls of the tank for several consecutive days.

### Hatching

After hatching, which took place at about 3 days after fertilisation, the hatchlings were moved to a smaller tank with similar water conditions (24–26°C and pH 8–8.5) and a photoperiod of 12 h of darkness/light. From 3 days up to 3 weeks after hatching, the larvae were fed on a diet of *Artemia*-nauplii. After that, the diet was changed to crushed flakes, and 2 weeks later to the adult diet of whole flakes (TetraMin).

## Collection and study of specimens

Specimens from various nests were removed post hatching at 1 h, 2 h, 3 h, 6 h, 12 h, 24 h, 2 days, 3 days up to 14 days, every 2 days up to 22 days, 25 days, then every 4 days up to 45 days, followed by one specimen every 5 days until 60 days, one specimen every ten days until 90 days and the last two specimens at 120 days (in total 37 specimens were used). The specimens were sedated and killed with an overdose of MS-222 (3-aminobenzoic acid ethyl ester, Sigma), measured and preserved in a paraformaldehyde/glutaraldehyde-fixative (15%/25%).

Based on standard length (SL) (body length with the exclusion of the caudal fin), in function of age (in days), an overall growth curve was established and inflection points were determined. Hence, it was of interest to determine the growth coefficient  $k$  in  $SL = b \text{ age}^k$  (Fuiman, 1983), with the possibility to allow for changing  $k$  over different time points. To this end, both variables were transformed on the log-scale ( $\log(SL) = \log(b) + k \log(\text{age})$ ), and a piecewise linear regression method was applied where we followed the ideas of regression spline smoothing procedures (see e.g. Friedman & Silverman, 1989).

Suppose we have  $n$  data points  $(x_i, y_i)$  ( $i = 1, \dots, n$ ). In this case,  $x_i$  and  $y_i$ , respectively, represent the age and SL of observation  $i$  on the log-scale. Assume further that the data points satisfy:

$$y_i = f(x_i) + \varepsilon_i \quad \varepsilon_i \sim N(0, \sigma^2); \quad i = 1, \dots, n \quad (*)$$

with

$$f(x_i) = \beta_0 + \beta_1 x_i + \sum_{j=1}^m \beta_{j+1} (x_i - t_j) I_{(x_i > t_j)}.$$

$m$  is the number of ‘knots’ or inflection points and  $\{t_j; j = 1, \dots, m\}$ , which is the set of these knots ( $\{10^j; j = 1, \dots, m\}$  is then the set on the original scale). Note that  $\min(x_i) < t_1 < \dots < t_m < \max(x_i)$  and that we restrict  $\{t_j; j = 1, \dots, m\}$  to be a subset of  $\{x_i; i = 1, \dots, n\}$ .  $I_{(x_i > t_j)} = 1$  as soon as  $x_i > t_j$  and 0 otherwise. Model (\*) implies that the slope or growth rate before the first knot equals  $\beta_1$ . After the first  $\ell$

knots ( $\ell \leq m$ ), the slope becomes  $\beta_1 + \sum_{j=1}^{\ell} \beta_{j+1}$ . The

goal is to estimate  $f(x_i)$  based on the observed data points. This means that a set of knots needs to be

chosen and that the parameters  $\beta = (\beta_0, \beta_1, \beta_2, \beta_{m+1})$  need to be estimated.

In the absence of knots,  $f(x_i) = \beta_0 + \beta_1 x_i$  and the model to be fitted is a simple linear regression model. We opted to select a number of knots using a forward search procedure and to estimate  $\beta$  using ordinary least squares. More in particular, we followed the forward addition strategy as described in Lee (2002) who gives an overview of algorithms for ordinary least squares regression spline fitting.

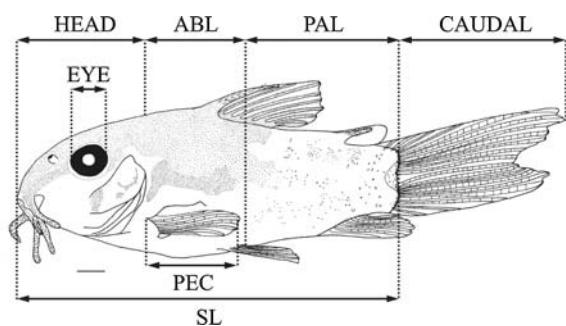
The generalised cross-validation (GCV, see Friedman & Silverman, 1989) was used as the criterion to select the ‘best’ model. The best model is then the model which minimises

$$\text{GCV} = \frac{1/n \sum_{i=1}^n (y_i - \hat{f}(x_i))^2}{(1 - (3m + 1)/n)^2}$$

with  $\hat{f}(x_i)$  the estimate for  $f(x_i)$ .

The sequential search procedure is performed as follows. The initial model is the model without knots and its GCV-value is calculated. In each step of the search procedure, a knot is added such that the largest decrease or smallest increase in GCV is seen. This process is repeated until a user-defined maximum number of knots is obtained. In all our analyses, this maximum was set equal to 10. After this procedure, the model with the smallest GCV among all candidate models is chosen as the final model.

In order to investigate allometric growth, a similar analysis was done on growth of the different body parts, this time using SL as the independent



**Fig. 1** Different measurements taken on *Corydoras aeneus* as exemplified in a juvenile specimen of 14 mm SL. *ABL* Abdominal length, *EYE* horizontal eye diameter, *HEAD* head length, *PAL* post-anal length, *PEC* pectoral fin length, *SL* standard length, *CAUDAL* caudal fin length (scale bar = 1 mm)

variable. For this purpose, head length, abdominal length, post-anal length, caudal fin length, pectoral fin length and eye diameter (measured in a horizontal plane) were measured (Fig. 1) and used as dependent variables. Not all the measurements could be made on all the specimens (e.g. a damaged caudal fin, anal opening not yet present, etc.), and in such cases, specimens were omitted from the analysis. This resulted in slightly different sample numbers for these measurements.

Afterwards, the specimens were drawn and external morphology was described. Based on morphological criteria, different phases of early development were demarcated and terminology was used according to Balon (1975, 1999). However, testing whether ontogeny in *C. aeneus* occurred saltatorily, was beyond the scope of this study, since this would require a more extensive study of disruptive morphogenetic events throughout the species' ontogeny.

## Results

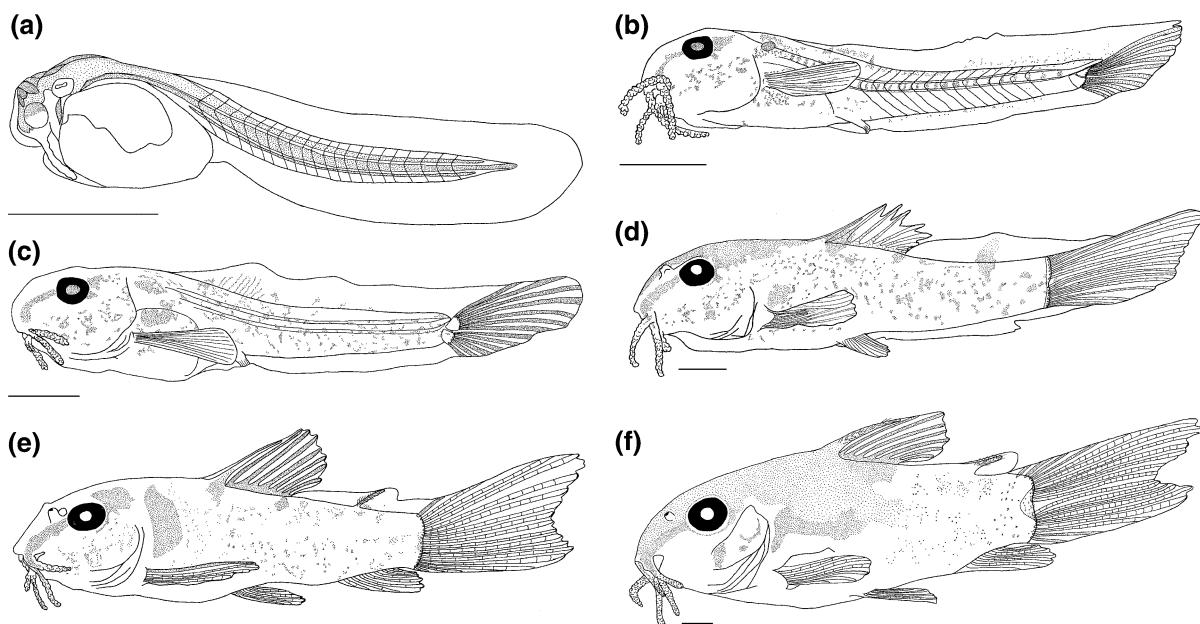
Hatching occurs after an incubation period of 3–4 days. Early development after hatching was

divided into four different phases: the eleutherembryonic phase (between hatching and exogenous feeding), protopterygiolarval phase (until start of finfold differentiation), pterygiolarval phase (until completion of finfold differentiation) and juvenile period (until sexual maturation).

### Morphological development

At hatching, larvae have a SL of  $3.5 \pm 0.2$  mm ( $\pm SD$ ). From this size up to 4.4 mm SL, a yolk sac is present. During this eleutherembryonic phase (Fig. 2a), specimens are unpigmented and the mouth and anal opening are still closed. Distinctly large, oval-shaped, pectoral fins are present, lacking any fin rays and mainly consisting of a large skin fold. Two pairs of oral barbels, the maxillary and external mandibular barbels, are present and the median finfold is undifferentiated. The eye diameter in these free swimming embryos is small ( $0.16 \pm 0.02$  mm) and the eyes are still almost devoid of pigmentation.

From 3 to 5 dph, at a SL of 4.4–5.7 mm, a yolk sac is no longer present and an extra pair of oral barbels, i.e. the internal mandibular barbels, begin to develop

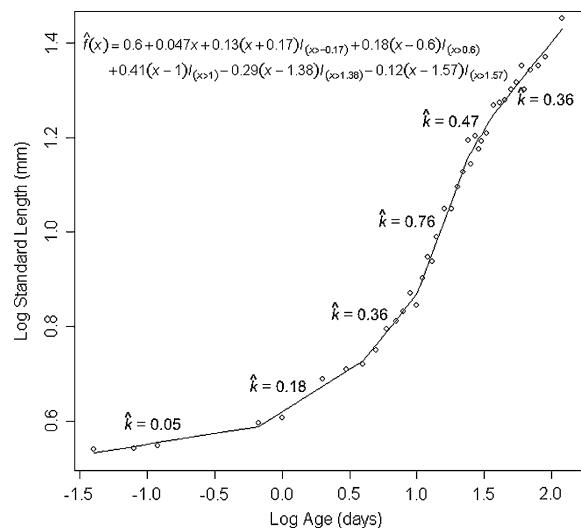


**Fig. 2** Different stages in the development of *Corydoras aeneus*: (a) eleutherembryonic phase (3.6 mm SL), (b) protopterygiolarval phase (5.3 mm SL), (c) pterygiolarval phase (6.4 mm SL), (d) pterygiolarval phase (8.6 mm SL), (e) pterygiolarval phase (10.7 mm SL), (f) juvenile period (14.0 mm SL) (scale bar = 1 mm)

phase (6.4 mm SL), (d) pterygiolarval phase (8.6 mm SL), (e) pterygiolarval phase (10.7 mm SL), (f) juvenile period (14.0 mm SL) (scale bar = 1 mm)

(Fig. 2b). The anus and mouth open, as does the opercular cavity. At this protopterygiolarval phase, faint body pigmentation appears on the lateral side and head of these specimens. The pigmentation on the head is concentrated in a double line, which runs from the buccal area over the eye, to the back of the head. Further, pigmentation is concentrated in spots on the lateral side of the body and in the median finfold and pectoral fins. In these fins, pigmentation is concentrated where future fin rays will develop. The eye in these specimens is larger ( $0.28 \pm 0.08$  mm) and more pigmented. Near the end of this phase the median finfold begins to differentiate, which starts with an indentation behind the future dorsal fin and a slight narrowing of the finfold near the caudal peduncle.

In specimens aged 7–23 dph, with a SL between 5.7 and 14.0 mm (the pterygiolarval phase), the finfold further differentiates (Fig. 2c). At 11 dph (SL 7–8 mm), the dorsal fin is almost fully detached from the finfold, the pelvic fins start to develop and pigmentation is present at the base of the future anal and adipose fin, where in both cases the finfold also starts to indentate. At 16 dph (SL 11–12 mm), all the fins are fully detached, except for the adipose fin. This fin is still surrounded anteriorly by a small part of the median finfold, which totally disappears at a SL of 14 mm. The fin rays in the different fins develop in a partially different order. Fin rays begin to develop in the caudal fin, pectoral and dorsal fins, and at a SL of 8 mm both dorsal and caudal fin would have reached their definite number of fin rays. At this time, the pelvic and anal fin rays start to develop, both of which become fully developed at a SL of 9–10 mm. An adipose fin spine is present from a SL of 11–12 mm on and in the pectoral fins, while the definite number of fin rays is reached at 22–25 mm SL. At 11 mm SL, the first bony scutes, typical for callichthyid fishes, start to develop as well. The first scute that develops is the one anterior to the adipose fin, which partially covers the adipose fin spine. From thereon, three more, small, dorsal scutes develop in an postero-anterior sequence. At a SL of 15 mm, several small scutes develop dorsally and ventrally on the caudal peduncle. Finally, at approximately 16 mm SL, the first lateral scutes start to develop postero-anteriorly along the midline of the body with a further centrifugal development of all scutes.

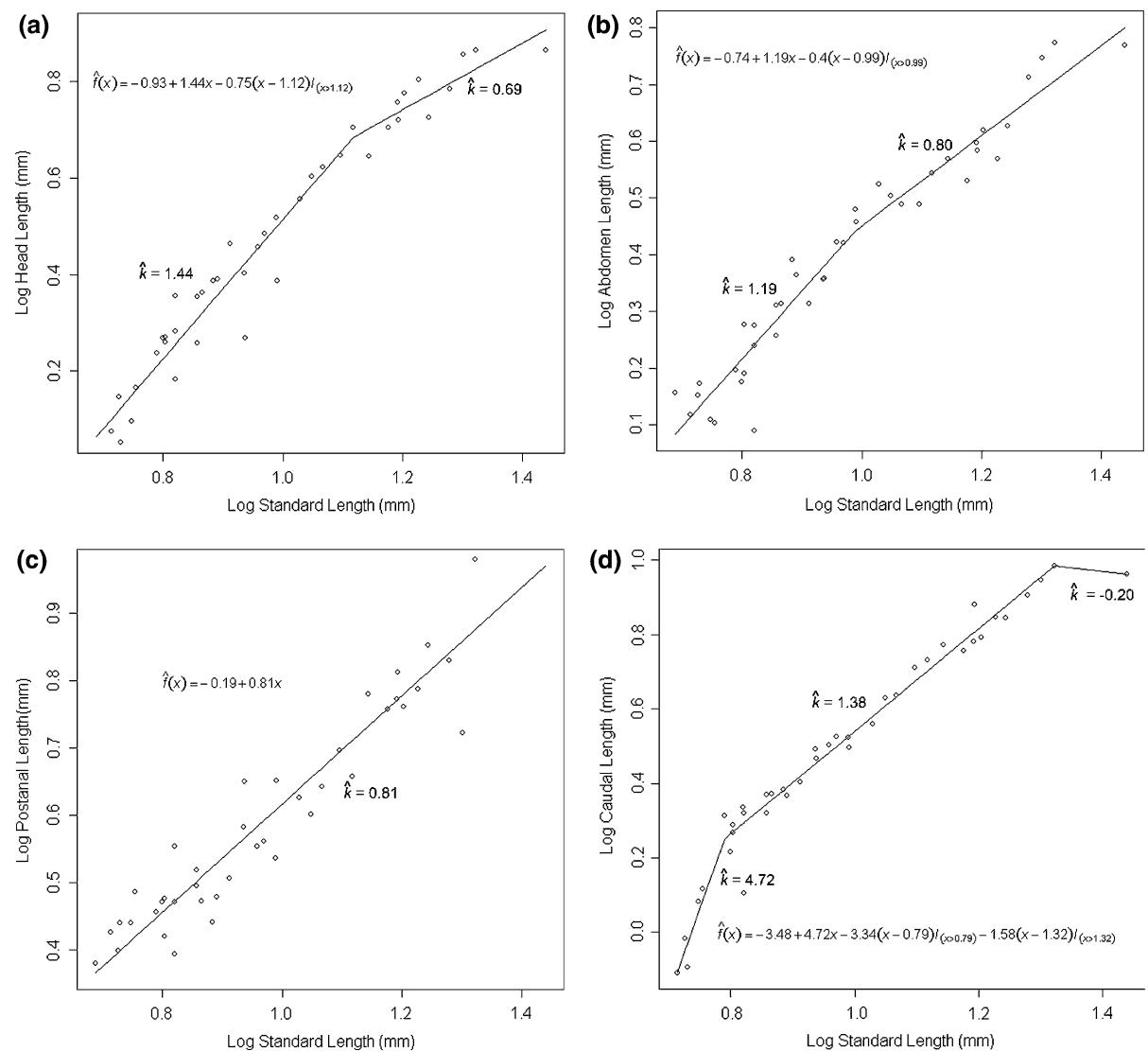


**Fig. 3** Inflexion points in the overall growth curve of *C. aeneus* ( $\hat{k}$  = estimated slope)

#### Allometric growth

In the growth curve of *Corydoras aeneus*, which ranges from 0 to 120 dph, five different inflection points were calculated, reflecting significant changes in growth rate (slope) (Fig. 3). The first inflection in the growth curve occurs at 0.7 dph (which corresponds to a fitted value of 3.9 mm SL), at which the estimated growth rate increases from 0.05 to 0.18 ( $P < 0.01$ ). Further, the growth curve in specimens over 0.7 dph shows a second inflection at 4 dph (5.4 mm SL), where the slope further increases to 0.36 ( $P < 0.01$ ). A subsequent third inflection is present at 10 dph (7.4 mm SL), where growth rate increases even further up to 0.76 ( $P < 0.001$ ). After this, at 24 dph (14.5 mm SL), growth slows down to a rate of 0.47 ( $P < 0.01$ ). Finally, the last inflection in this growth curve is located at 37 dph (17.9 mm SL), where growth rate again decreases to 0.36 (though not significantly different,  $P = 0.20$ ). Note that we used the GCV-criterion to select the best model but not statistical significance.

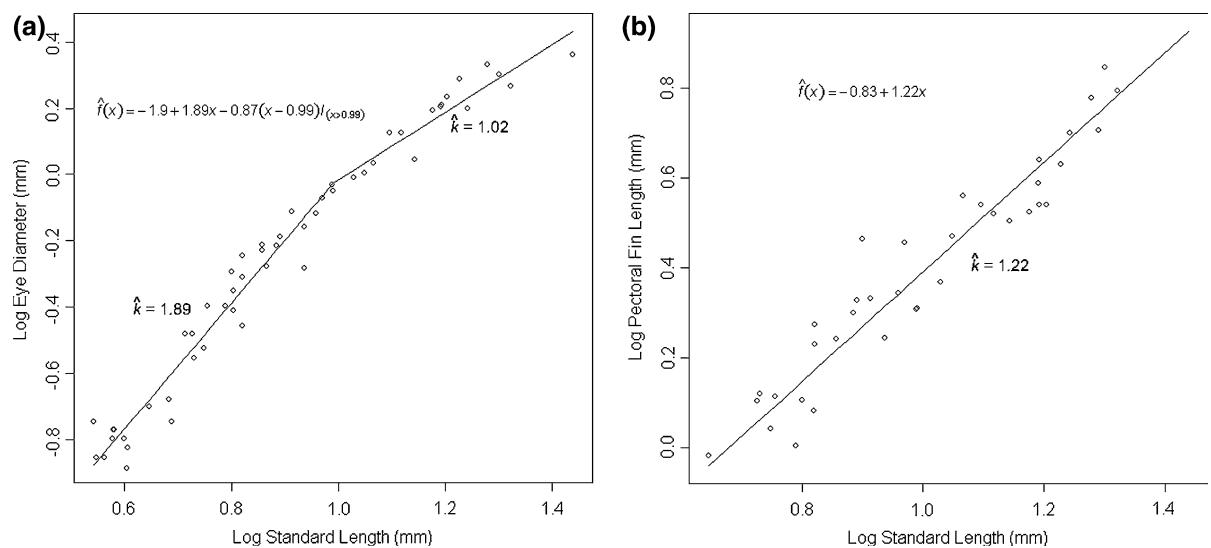
In the context of body part allometries, the model with one inflection point ( $R^2 = 0.958$ ) has the smallest GCV. This model shows that growth of the head is positively allometric (slope = 1.44) up to a SL of 13.1 mm, after which the rate drastically decreases to 0.69 ( $P < 0.001$ ) (Fig. 4a). Growth of the abdomen is also best modelled by a single inflection point model



**Fig. 4** Growth allometries of the different body segments: (a) growth allometry of the head, (b) growth allometry of the abdomen, (c) growth allometry of the postanal region, (d) growth allometry of the caudal fin ( $\hat{k}$  = estimated slope)

( $R^2 = 0.947$ ) and in this case, growth starts nearly isometric (slope = 1.19), and then declines to 0.80 ( $P < 0.05$ ) from 9.8 mm SL on (Fig. 4b). In the regression which describes growth in the postanal region, no improvements over the simple linear regression model were found in GCV by introducing inflection points. This way, growth rate in the postanal region in relation to SL was found to remain constant at 0.81 and significantly different from 0 ( $P < 0.001$ ) throughout the entire ontogenetic series studied here ( $R^2 = 0.909$ ) (Fig. 4c). The analysis of growth in the

caudal region showed a two-inflexion-point model as the best suited ( $R^2 = 0.978$ ). Growth in this region initially is highly positively allometric (slope = 4.71) up to a SL of 6.2 mm, after which it decreases between 6.2 and 21 mm SL to a rate of 1.38 ( $P < 0.001$ ). After this, it finally decreases to a rate of -0.20 ( $P < 0.001$ ) (Fig. 4d). Further, a single inflection point was also found in the growth curve of the eye ( $R^2 = 0.973$ ). This inflection was situated at a SL of 9.8 mm from where the rate drastically decreases (slope = 1.89 to 1.02,  $P < 0.001$ )



**Fig. 5** Growth allometries of several body parts: (a) growth allometry of the eye, (b) growth allometry of the pectoral fin ( $\hat{k}$  = estimated slope)

(Fig. 5a). Finally, the growth of the pectoral fins, showed no inflections (simple linear regression,  $R^2 = 0.924$ ), with a constant growth rate of 1.22 (significantly different from 0 with  $P < 0.001$ ) (Fig. 5b).

## Discussion

Size at hatching is found to be quite constant in *C. aeneus* ( $3.5 \pm 0.2$  mm) at  $25^\circ\text{C}$ , which is presumed to be correlated to the low variance in egg size ( $1.47$  mm  $\pm 0.20$ ) (Osse & van den Boogaart, 1995; Huysentruyt & Adriaens, 2005). The scope of this article, however, was to study growth allometries in *C. aeneus*, and the timing of shifts in growth rates, both for overall growth as for growth of specific body regions (head, abdomen, post-anal region, caudal fin, pectoral fin and eye diameter). We hypothesised that the chronology of these allometric changes would be related to the chronology of important early life history events, and would therefore reflect an evolutionary ontogenetic response to functional demands. It has already been suggested that allometric growth patterns closely match the expected priorities for executing the necessary biological roles (Osse et al., 1997), or as Kováč & Copp (1999) put it: “a certain

level of development is necessary,..., to coincide in functional readiness”. Therefore, in this study, the chronology of relevant shifts in allometric growth rate was statistically assessed by calculating inflection points in growth rates of different body regions during ontogeny. In addition, literature on early life history traits in teleosts in general provided the framework to verify possible correlations with the patterns found in this study.

A first correlation we hypothesised is related to predation, being one of the main agents that result in larval mortality (Bailey & Houde, 1989). As a result, a higher efficiency of those structures involved in predator avoidance can be expected to exist during these early life stages. In contrast to some callichthyid congeners that produce foam nests for their hatchlings (e.g., *Megalechis*), such hiding facilities are not provided for larval *C. aeneus*. Consequently, predator avoidance due to increased swimming efficiency, and thus burst swimming can be expected to be an important escape response in *C. aeneus* hatchlings. Weihs (1980), in his study on *Engraulis mordax* Girard, 1854, found a continuous swimming mode to be more efficient in larvae under 5 mm, while in larvae with a length between 5 and 10 mm burst-and-coast swimming became more effective. Blaxter (1986), on the other hand, mentions that a

change in swimming mode occurs as the caudal fin develops and inertial forces start to play a bigger role during locomotion. Our observations do show a higher growth rate of the caudal region (slope = 4.71) up to 6.2 mm SL, which may provide for a “functional readiness” for burst and coast swimming after this stage. At a SL of about 5 mm, notochord flexion occurs, which precedes both a drastic increase in overall growth rate (0.18–0.36) and the start of the pterygiolarval phase (both at about 5.5 mm SL). These changes in the components of the locomotory apparatus may be related to an onset of a change in swimming mode at 5 mm SL. A shift towards burst and coast swimming is believed to enlarge the dispersal and foraging range and improve predator avoidance (Gisbert, 1999). Therefore, based on these findings, we expect a similar change in swimming mode to occur at that point, but a kinematic analysis of the ontogeny of larval swimming in *C. aeneus* will have to confirm this.

Apart from predation, a second correlation we predict is based on that of starvation becoming a major threat to larval survival once the yolk sac becomes depleted (Bailey & Houde, 1989). The moment at which this depletion occurs, is critical during larval development (Pedersen et al., 1990; Jardine & Litvak, 2003). After this depletion, exogenous feeding becomes obligatory and the presence of a functional feeding apparatus is required (van Snik et al., 1997; Jardine & Litvak, 2003). Given this, we expected that under 4.4 mm SL (=point of yolk sac depletion) development would, next to predator avoidance, also be focussed on the completion of the differentiation of a functional feeding apparatus. Our observations show that, around this transition in *C. aeneus* (4.4 mm SL), growth rate of head length is positively allometric (slope = 1.44). During the early life stages, protrusion of upper jaw bones is not yet functional so that high suction forces must be generated in order to catch prey. Higher suction forces can be related to head volume (Osse, 1990), which implies that a fast head growth (as is the case here) would indeed allow an increase in suction efficiency.

Given the properties of the physical environment, such as the high viscosity of the aqueous medium, and of the biological environment, such as the relatively large size of the available prey organisms, size acts as an important constraint on development of form and function during early ontogeny. This is a

view that gains importance in many recent developmental studies on fish larvae (Strauss, 1984; Buckel et al., 1995; Stern & Elmen, 1999; Adriaens & Verraes, 2002) and can be exemplified here too. Feeding strategies of fish larvae, as well as locomotor habits, show pronounced changes at certain developmental stages and certain size ranges are rather strictly correlated to typical morphogenetic events or differentiation of particular organ systems. In *Cyprinus carpio* Linnaeus, 1758 (van Snik et al., 1997), for example, a second change in swimming mode from anguilliform to subcarangiform was found around 8 mm SL. Gisbert (1999) found a change in swimming style to be correlated to the first appearance of caudal fin rays in the chondrostean fish *Acipenser baeri* Brandt, 1869. Our observations show that at 8 mm SL, caudal fin rays start to develop and anal, adipose and pelvic fins separate from the respective finfolds and that, just prior to this, at 7 mm SL, overall growth rate reaches a maximum (0.76). Therefore, a similar change in swimming mode is expected around 8 mm SL in *C. aeneus*. This altered swimming would also imply a decrease of the head yaw (Osse, 1990), which again results in better aiming skills for prey capture. In this context a decrease of eye and abdomen growth rates (1.19–0.8 and 1.89–1.02, respectively) shortly after this shift indeed may indicate changes in prey preference and/or visual performance in relation to predation.

Conclusively, the analysis of inflection points in growth curves, in combination with observed changes in morphological development, holds valuable information on changes in functional demands throughout ontogeny. Such an analysis can provide a framework of these shifting functional demands placed on a developing larvae, useful for both comparative studies of the ontogeny in other species as well as for aquacultural applications.

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