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**PROOF**

# Early Development and Allometric Growth in Laboratory-Reared European Chub *Leuciscus cephalus* (Linnaeus, 1758)

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**Abstract**

The morphological development and allometric growth patterns in European chub *Leuciscus cephalus* (L.) (cyprinid fish) were studied under intensive rearing conditions from hatch to day 30. Based on the external morphology, twelve different stages during the early development of chub were identified ($ES8_b$-$JS1_a$; 6.68 ± 0.20 - 20.84 ± 2.15 mm TL).The obtained results revealed that the majority of all allometric changes from the inflection point occurred across a wide range of body lengths. The replacement of temporary organs (e.g. disappearance of finfold) at approximately 21 mm TL did not coincide with a full reduction of relative growth. This growth pattern probably reflects he absence of abrupt changes in the behaviour and habitat of young chubs.

*Keywords*: *Leuciscus cephalus*; early ontogeny; morphologic development; allometry.

## Introduction

*Leuciscus cephalus* (L.) is a rheophilic cyprinid widely distributed throughout Europe (Banarescu, 1992). However, the abundance of this species, as well as other from genus *Leuciscus*, has decreased in some natural populations because of human impact and partly by interspecific hybridization (Durand *et al.*, 2000; Freyhof *et al.*, 2005; Bolland *et al.*, 2008; Kirtiklis *et al.*, 2013, Nowosad *et al.*, 2014). European chub is a fractional, late-spring spawner. Spawning grounds are characterized by 20-50cm $s^{-1}$ current velocity, shallow depth (0.1-0.8m) and a stony bottom, where most eggs adhered (Mann, 1996; Friedrich *et al.*, 2003; Telechtea *et al.*, 2009). The free embryos developed early photophobia and tended to congregate between pebbles. Young chubs shows schooling behavior and prefer those parts of streams and rivers where water currents are minimal (Economou *et al.*, 1991).This species is considered a natural and essential component of many freshwater ecosystems, and they also have some practical meaning, e. g. considerable value in sport fishing, bio-indicator of pollution (Hajkova *et al.*, 2007) as well as a model species used for toxicity tests (Gomułka *et al.*, 2011).

Thus far, studies on larval chub development have been conducted by Kryzhanovskij (1949); Koblickaya (1981); Economou *et al.* (1990); Çalta (2000) and Kupren *et al.* (2008). None of these studies have described the morphological changes during the earliest stages of development in great detail. The transition from larval to juvenile development (metamorphosis) is associated with a shift in allometric growth or shape coupled with an abrupt or gradual changes in morphological characters (e.g. disappearance of finfold, acquisition of the adult complement of fin rays or squamation (Urho, 2002; Nikolioudakis *et al.*, 2010). From an ecological point of view its most significant aspect is the occurrence of a niche and habitat shift of larvae (Urho, 2002; Kuprenet *al.*, 2014a). The objective of the present study was to provide biological knowledge on the morphological and functional development of European chub free embryos, larvae and early juvenile reared under intensive conditions, with a focus on the age and size at transformation. An understanding of the morphological development and allometric growth patterns provides insight into possible functional trends and environmental preferences of different developmental stages and thus is crucial for optimization of production in aquaculture (Koumoundouros *et al.*, 1999; Gisbert *et al.*, 2002; Choo and Liew, 2013). Moreover they may

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be used for determining the quality of chub juveniles in restocking programs.

## Materials and Methods

European chub free embryos were obtained by the controlled reproduction of wild spawners caught in Lake Mosąg (northeast Poland) at the beginning of the reproductive season The reproduction was performed according to the method described by Krejszeff *et al.* (2008) with the application of the double hormonal treatment with Ovopel as was described by Targonska and Kucharczyk (2011) for goldfish. Eggs obtained from four females were fertilized with semen obtained from four males and were subsequently incubated at 18-19° C. After hatching, the free embryos were transferred to experimental rearing units and acclimated to the temperature of 25 °C (for 1 day). Such a thermal regime has been recommended as optimal for both chub eggs and larvae (Kujawa, 2004; Kupren *et al.*, 2011a; b). Larvae were reared in three 15 L aquariums in a closed water system as described by Krejszeff *et al.* (2010). The initial stocking density of larvae was 85 ind. $L^{-1}$. Fish were exposed to a 12L:12D photoperiod and fed three times a day *ad libitum* with freshly-hatched *Artemia* sp. nauplii (San Francisco origin) (Demény*et al.* 2012). During the larval period, oxygen and pH were maintained at >85%, and 7.7, respectively. Ammonia and nitrite (monitored with a photometer, HI 83200, Hanna Instruments, Italy) were always kept below 0.01 mg $L^{-1}$ (Nowosad *et al.* 2013).

The developmental study was conducted on samples of 20 specimens randomly taken every day from hatching to 30 DPH (Days Post Hatch).The sampled specimens were subjected to overexposure in an anesthetic solution (MS-222 at a dose of 150 mg $L^{-1}$) and digital photographs of each specimen were taken using DP-Soft digital image analysis software (Olympus, Japan). After this, the larvae were fixed in a 4% phosphate-buffered formaldehyde solution for further detailed examinations. For monitoring of the early development of chub during the free embryo and larval phase from hatching loss of larval finfold and acquisition of the full finray complement and beginning of squamation (Kendall *et al.*, 1984), the system of developmental stages proposed for carp *Cyprinus carpio* L. By Peňaz *et al.* (1983) was used. The system was based on the instantaneous stages of ontogeny, i.e. on the characteristic moments of development. During identification of the developmental stages of chub, special attention was also paid to the flexion of the notochord – one of the key events in the development of many fish, which is important from the point of view of other terminologies of early development (Kendall *et al.*, 1984). Moreover, the onset of metamorphosis was additionally defined using the inflection points of allometric as indicators (Kendall *et al.*, 1984; Mihelakakis *et al.*, 2005). Thresholds during early development, such as the filling of the swim bladder and exogenous feeding commencement, were considered to be achieved when at least 50% of the specimens represented this particular stage. In each digital photograph, several body proportions associated with feeding and locomotion were measured (±0.01mm) (Table 1). The body characteristics were measured along or perpendicular to the body axis. Dead or abnormal specimens (with malformations) were excluded from the analysis.

The allometric growth of each character was expressed as a power function of TL, with the intercept and exponent obtained from linear regressions on log-transformed data. When isometric growth occurred, $b=1$, allometric growth was positive when $b>1$ and negative when $b<1$. The inflexion points of growth curves were calculated according to van Snik *et al.* (1997) and Kupren *et al.* (2014).

## Results

Between the day of hatching and 30 DPH, the TL of the European chub body (TL) grew continuously and increased by 21.31 mm (mean length was 6.68 and 27.99 mm in 0 DPH and 30 DPH, respectively) (Figure 1). During this period, twelve developmental stages were observed ($ES8_b$-$JS1_a$) (Table 2). The hatching occurred at the stage described as $ES8_b$. The yolk sac was completely consumed at 4 DPH ($LS2/LS3_a$), when TL was 8.25 ± 0.27 mm. The notochord flexion occurred between

**Table 1.** Abbreviations and description of morphometric characters measured in the present study

| Character | Abbrev. | Description |
|---|---|---|
| Body depth | BD | Posterior to the gill cover |
| Body depth at anus level | BDA | Posterior to the anus |
| Eye diameter | ED | Parallel to the longitudinal axis of the body |
| Head depth | HD | From the bottom of the mouth cavity to the top of the head |
| Head length | HL | From tip of snout to the margin of gill cover |
| Snout length | SNL | From the tip of the snout to the eye |
| Tail depth | TD | Minimum depth of the caudal peduncle |
| Tail length | TAL | Post anal length |
| Total length | TL | From the tip of the snout to the end of the caudal fin |
| Trunk length | TRL | From the end of the operculum to the anus |

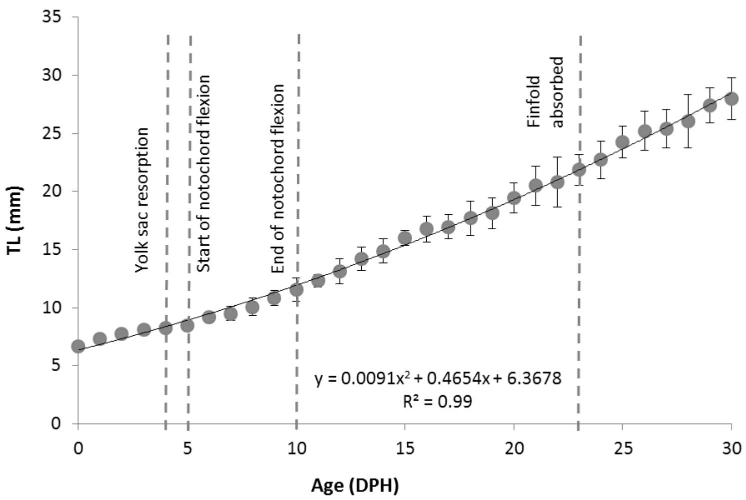


**Fig ure 1.** Changes in total length (TL) *L. cephalus* (L.) during early stages of development (from hatching to 30 DPH, days post hath) at 25°C. Bars indicated SD (standard deviation).

8.45 ± 0.32 mm TL at 5 DPH ($LS3_b$) and 11.57 ± 1.01 mm TL on 10 DPH ($LS5_a$). The finfold was completely absorbed at 22 DPH (JS1; 20.84 ± 2.15 mm TL). During the first two days after emergence, the free embryos lay on the bottom of the tank, showed photophobia and tended to congregate in the corners of the tanks. During this time, respiration was accomplished mainly through the body surface and the network of vessels present on the yolk sac and ventral fin fold. Two days after hatching, most of the embryos started to swim up to the surface in order to fill their swim bladders. At 3 DPH, the second chamber of the swim bladder was filled by air and most larvae actively swam and maintained their position in the water column. From that time until the end of the experiment, the larvae were visual feeders, actively searching for food in all parts of the tank.

Table 2 gives details of the stages of free embryo and larval which are illustrated in Figure 2.

The allometric growth patterns of 10 body parts (including TL) were measured in 563 *L. cephalus* larvae (Figure 3 a-i). Two growth stanzas (biphasic growth) were observed for all measured parameters except for the TRL, which showed negatively isometric growth throughout the studied period (simple linear regression), with a constant growth rate of 0.74 (negatively allometrically) (Figure 3i). In every case, there was a reduction in the growth coefficients after the inflection point. The *b* value of these body parts differed significantly between their sequential stages ($P<0.001$).Three parameters: SNL, TAL and BDA showed still positive allometric growth after the inflexion point. For HL, HD and BD isometric growth after the inflexion point were observed. ED changed to negative allometric growth Figure 3 a-h). During the flexion of the notochord (corresponding to the TL interval of 8.45 to 11.57 mm) there was a decline in the growth rate of the tail and head lengths (b = 1.47 to 1.19 and 1.59 to 0.99,respectively). A few days later at the 15.02 mm TL growth of ED and HD slows down toa rate of 0.83 and 1.06 respectively ($P<0.001$). During the next stages of development, growth concerned all body segments, but was particularly fast for the SNL, BDA and TD. The inflexion points of these parameters were situated at a TL of 24.30, 22.11 and 25.69, respectively (Figure 3).

## Discussion

The morphological changes and the size distribution during each developmental stage reported in this study are in accordance with that previously described by Economou *et al.* (1990) and Çalta (2000) in reared larvae of the same species. In our study, the morphological findings on early development were reported more details and the morphologic findings were supported by allometric growth patterns. At hatching, most functional systems of European chub embryos are incompletely differentiated. Consequently, significant morphogenesis occurs during free embryo and larval development. The newly-hatched individuals have an elongated yolk sac containing the vitelline reserves. The head is bent downwards, the primordial marginal finfold is not differentiated, the eyes lack guanidine pigmentation and the mouth is not formed. During this time, respiration is accomplished mainly through the body surface and the network of vessels present on the yolk sac and ventral finfold. A similar level of development at hatching is characteristic for other lithophilic cyprinids, such as barbus *Barbus barbus*or nase *Chondrostoma nasus* (L.), which are not able to swim freely soon after emergence and stay close to the bottom before inflation of the swim bladders (Peňaz, 1974; Krupka, 1988). The level of ontogenic

**Table 2.** Developmental stages of European chub *Leuciscus cephalus*(L.)reared at 25°C (ES – embryonic stage; LS – larval stage; JS – juvenile stage; DPH – days post hatch)

| Developmental stages | DPH | Total length range, mean (mm) | Characteristic feature | Behaviour |
|---|---|---|---|---|
| ES8$_b$ | 0 | 6.34–7.13 (6.68) | The body is straightened The head bent forward over the yolk sac, but separated, yolk sac pear-shaped. The urostyle is straight. No pigmentation is present on the body, except for the eyes. Ducti Cuvieri visible. Blood circulate from the dorsal aorta to the caudal artery, which supply the caudal vein. The caudal vein consists of a very thin network of twisted vessels (Figure 2a). | Hatching. The embryos show photophobia, lay on the bottom and tend to congregate in the corners of tank. |
| ES9$_a$ | 1 | 6.99–7.56 (7.56) | Reflective guanin in the eyes. Head slightly bent down, body straight. Blood circulation in the branchial arteries. The lower jaw is not formed (mouth is closed). The first stellar melanophores appear on the surface of the body (Figure 2b). | The embryos still show photophobia and lay on the bottom. The embryos cannot swim actively, but short periods of horizontal darting movements are observed. |
| ES9$_b$ | 2 | 7.21–8.17 (7.75) | The whole body is straight. The yolk sac at an advanced stage of resorption. Lower jaw is mobile and reaches the front edge of the eye. The second chamber of the swim bladder is filled by water. The Cuvier ducts have disappeared. The gill covers are developing. The number and size of melanophores on the surface of the body is increasing (Figure 2c). | Embryos start to swim up to the surface in order to fill their swim bladder. |
| ES9c/ LS1 | 3 | 7.59–8.39 (8.14) | The filaments form on the branchial arches. The second chamber of the swim bladder is filled by air. The mouth is in terminal position. Beginning of exogenous (mixed) feeding, the remains of the yolk sac are present (Figure 2d). | Larvae swim actively in the water column. |
| LS2/ LS3$_a$ | 4 | 7.73–8.89 (8.25) | The yolk sac is completely resorbed. Lepidotrichia in the caudal and pectoral fin. | Larvae swim actively in the whole water column. |
| LS3$_b$ | 5 | 7.87–8.95 (8.45) | Start of notochord flexion, heterocercal shape of caudal fin (Figure 2e). | Larvae swim actively in the whole water column. |
| LS4$_a$ | 7 | 7.99–10.61 (9.49) | Ossified rays in the caudal fin. Lepidotrichia in the dorsal fin (Fig. 2f). | Larvae swim actively in the whole water column. |
| LS4$_b$ | 9 | 9.42–12.07 (10.84) | The first chamber of swimbladder is filled with gas. Lepidotrichia in the anal fin. The caudal fin is bifurcate and has a definite homocercal shape (Figure 2g). | Larvae swim actively in the whole water column. |
| LS5$_a$ | 10 | 9.04 – 13.13 (11.57) | Notochord flexion finished, pelvic fin buds present, the dorsal fin is almost fully detached from the finfold (Figure 2h). | Larvae swim actively in the whole water column. |
| LS5$_b$ | 16 | 14.44–18.37 (16.77) | Pelvic fins reach the edge of the finfold (Figure 2i). | Larvae swim actively in the whole water column. |
| LS6 | 17 | 15.61–19.23 (16.84) | The pelvic fins extend beyond the edge of the finfold. Finfold present only between the pelvic and anal fin. | Larvae swim actively in the whole water column. |
| JS1$_a$ | 22 | 18.12–22.09 (20.84) | Finfold completely reduced. Scale primordia present (Figure 2j). | Juveniles swim actively in the whole water column. |

development at hatching is species-specific and highly dependent on environmental conditions, especially of water temperature (Kamler, 1992; Teletchea *et al.*, 2009; Kupren *et al.*,2011b, Kucharczyk *et al*,. 2014, Palińska *et al.*, 2014). For example, many marine species from warm and temperate regions which produce numerous small eggs are extremely poorly developed at hatching (Gisbert, 2002; Peña and Dumas, 2009; Çoban*et al.*, 2012).

The ontogenetic shifts in morphology and phenotypic plasticity in specific environments and rearing conditions are reflected in allometry (Simonovic *et al.*, 1999; Khemis *et al.*, 2013). Teleostean embryonic and larval stages are usually characterized by a high degree of allometric growth patterns (Fuiman, 1983; Osse *et al.*, 1997; van Snik *et al.*, 1997). In juvenile and adult stages, all growth

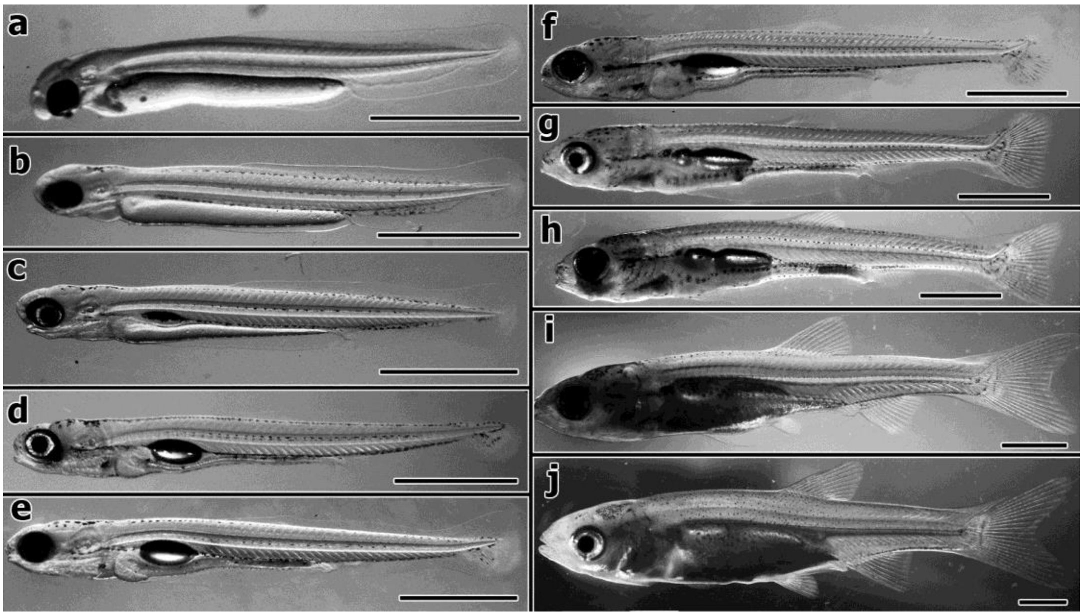


**Figure. 2**. Morphological development of the European chub, *L. cephalus*(L.)(a – stage $ES8_b$, 0 DAH; b –stage $ES9_a$, 1 DPH; c – stage $ES9_b$, 2 DPH; d – stage $ES9_c$/LS1, 3 DPH; e– stage $LS3_b$, 5 DPH ; f – stage $LS4_a$, 7 DPH; g – stage $LS4_b$, 9 DPH; h – stage $LS5_a$, 10 DPH; i – $LS5_b$, 16 DPH; j – stage $LSJ1_a$, 22 DPH). Scale bars = 2 mm.

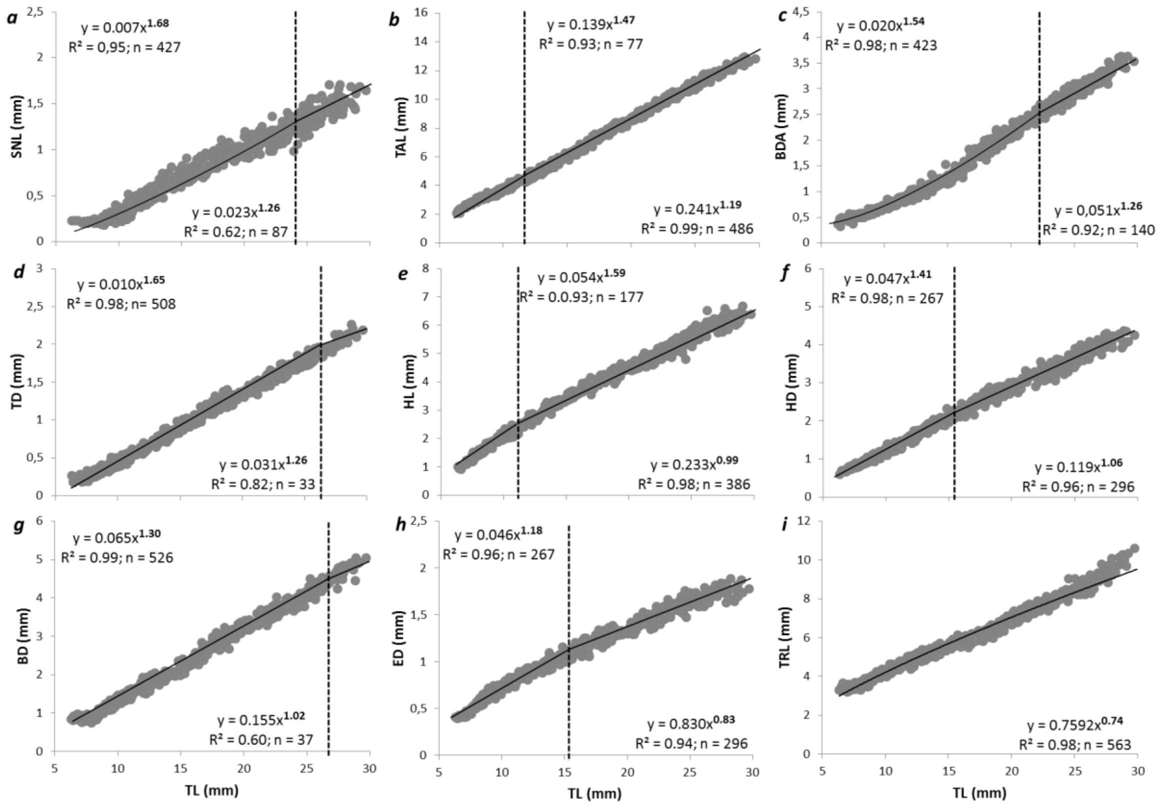


**Figure 3 a-i.** Allometric growth equations and relationship between measured body proportions and total length during European chub *L. cephalus* (L.) development (from hatching up to day 30). Morphometric abbreviations are listed in Table 1.

coefficients approach 1 (near-isometric growth). It has been generally accepted that this faster growth is related to rapid development of essential feeding structures (head region), and the need for improved swimming performance (tail region) (Fuiman, 1983; van Snik *et al.*, 1997; Osse and van der Boogart, 2004). In agreement with the former hypothesis, the present results showed that the anterior and posterior body regions of chub specimens initially showed positive allometric growth. The rapid growth in the head region (especially rapidly before the end of the flexion of the notochord) of chub individuals (allometric growth of HL, HD, ED and SNL), is probably linked to the development of nervous (midbrain and hindbrain), sensory (vision and olfaction), respiratory (gill arches and filaments) and feeding systems, as increasing head size is associated with a more developed nervous system, allowing better oxygen uptake and the uptake of food particles of increasing size (Fuiman, 1983; van Snik*et al.*, 1997; Koumoundouros *et al.*, 1999; Gisbert *et al.*, 2002; Kupren *et al.*, 2014a; b). In the posterior part of the body, rapid tail growth (allometric growth of TAL, BDA and TD) was concomitant with the development of musculature, unpaired fins, caudal peduncle and fin rays. Such changes contribute to improved swimming ability (increasing the probability of zooplankton detection and predator avoidance) (Fuiman, 1983; Gisbert, 1999; Gisbert *et al.*, 2002)

The replacement of temporary organs and the appearance of definitive structures in chub individuals at approximately 21 mm TL did not coincide with a full reduction of relative growth. This particularly relates to BD, BDA, SNL and TD. This pattern of development resulted in the transition from a longitudinally-elongated body shape to more fusiform streamlined body and has been explained as an adaptation to reduce and optimize the energy costs of larval transport (van Snik *et al.*, 1997), reduce drag forces on the body and attain higher locomotion speed. A similar growth tendency is also observed in other fish species with good swimming abilities during their larval period (Koumoundouros *et al.*, 1999; Peña and Dumas, 2009; Kupren *et al.*, 2014b).The positive allometry of body depth (BD)observed during the larval period is also probably linked with the development of the digestive tract and associated glands. In a closely-related species *Leuciscus idus* (L.), the development of mucosa folds and the coiling of the digestive tract and an increase in enzymatic activity enhance the digestive capability taking place during this time (Ostaszewska *et al.*, 2003)

In many fish species a reduction in the growth coefficients of various organs and tissues occurs at very similar body length sand are correlated to typical morphogenetic events (usually taking place close to the end of the notochord flexion). In *Cyprinus carpio* Linnaeus, 1758 (van Snik*et al.*, 1997), for example, it was found around 7 mm TL and is probably related to a change in swimming mode from an anguilliform larval-type to a sub-carangiform juvenile-type. The present study showed that the reduction in the growth coefficients of various body parts in chub occurred across a wide range of body lengths and ages (Figure 3).These gradual changes in body proportions are probably related to the lack of sharp changes in behavior and habitat and may be also considered to be a gradual adaptation to life in flowing water. According to the available literature, such changes strictly depend on both environmental (rearing conditions) and genetic factors.

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