

PATTERNS OF ONTOGENETIC CHANGES IN RELATIVE  
GROWTH IN THE PRECOICIAL CYPRINID, BITTERLING  
(*RHODEUS SERICEUS*)

by

MARTIN REICHARD\* and PAVEL JURAJDA

(*Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Květná 8,  
603 65 Brno, Czech Republic*)

ABSTRACT

In order to describe patterns of relative growth during the early life-history of the bitterling *Rhodeus sericeus* (Pallas, 1776), we examined 21 morphometric characters. These were expressed in 24 indices as a percentage of standard length (SL) and head length (HL) respectively, and divided into groups according to their pattern of relative growth. Nine characters exhibited isometric growth (relative proportion did not change with increasing SL). Eleven characters exhibited positive allometric growth (relative proportion increased with increasing SL) and four negative allometric growth. Stabilisation of characters may occur when bitterling reach sexual maturity, however some may continue to grow allometrically during the adult period. Caudal peduncle depth factor and body shape factor were employed to describe changes in morphological indicators of locomotor activity. Both factors exhibit steep allometric growth in specimens with remnants of finfold, gradually stabilizing in immature specimens without finfold, and isometric growth during adult period. Following our results and examination of data from the literature we conclude that bitterling, although a species with a precocial form of development, still retains a larval period. However, its duration is short compared to other cyprinids. Allometric growth is a typical feature of the entire life-history of bitterling and cannot be used as an indicator of the transition from larval to juvenile period.

KEY WORDS: allometric growth, morphometric characters, precocial form, life-history, larval and juvenile periods, body shape.

INTRODUCTION

According to the theory of saltatory ontogeny (BALON, 1975b, 1986, 1990), the life-history of fishes consists of four to five periods; embryonic, larval (often missing), juvenile, adult and senescent. Only some fishes have larvae that undergo metamorphosis, whereas many others do not undergo metamorphosis and do not have larvae. At most, intermediate

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\* Author to whom correspondence should be directed: M. Reichard, Department of Zoology and Ecology, Faculty of Sciences, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic.

states exist, for example, with some persisting temporary organs, representing a vestige of larvae (BALON, 1990). Transition from larva to juvenile in freshwater fishes with indirect development that lack true metamorphosis is characterised by long intermediate stages (BALON, 1984) and is ill defined (see COPP & KOVÁČ, 1996). With regard to this, COPP & KOVÁČ (1996) and KOVÁČ & COPP (1996) have suggested a revision of the threshold between the larval and juvenile periods in fishes. BALON'S (1990) definition of the boundary between larval and juvenile periods is based on the disappearance of larval characteristics (such as a finfold), presence of all fin rays, bifurcation and articulation of soft rays, presence of nasal septa and presence of some scales. KOVÁČ & COPP (1996) direct attention to morphological stabilization of mensural characteristics that can have important functional consequences for locomotion, visual acuity, prey handling and microhabitat use. They propose that larval metamorphosis in roach, *Rutilus rutilus*, is not completed until relative growth has stabilized (becomes isometric) at levels comparable to adults (KOVÁČ & COPP, 1996), *e.g.*, adult phenotype and a new homeorhetic state in growth variability have been attained (COPP & KOVÁČ, 1996). Conversely, inflection of the weight-length relationship (which also may be used to define thresholds) does not follow the break point of the relative growth and occurs earlier than stabilization of relative growth (GARNER & COPP, 1997).

As few studies have examined changes in body shape during the early life stages of European freshwater fishes (KOVÁČ & COPP, 1996), the present study describes growth patterns in early stages of bitterling as an example of a fish with an evolutionary advanced (towards precocial form) ontogeny. Though several morphological studies of bitterling have been undertaken (OLIVA, 1954; HOLČÍK, 1959; PAPADOPOL, 1960; HOLČÍK & DUYVENÉ DE WIT, 1964; ZHUL'KOV & NIKIFOROV, 1988; HOLČÍK & JEDLIČKA, 1994; REICHARD, 1998), they have described adult specimens only.

The bitterling, *Rhodeus sericeus* (Pallas, 1776) is a species with an unusual mode of reproduction and early development as it spawns into the gills of freshwater mussels (ostracophilous species according to BALON, 1975a). As bitterling spawn over a long reproductive season (from beginning of May to late August in central Europe; HOLČÍK, 1993), the gills of mussels can contain from 1 to 100 specimens of bitterling at different stages of development (BALON, 1962). The embryos hatch from large eggs soon after spawning and their development exhibit a number of modifications as a results of this reproductive strategy. An extensive description of the development of bitterling has been conducted by KRYZHANOVSKII (1949) and recently by ALDRIDGE (1999).

Fish leave the body cavity of the mussel when their total length (TL) is 9-10.5 mm (KRYZHANOVSKII, 1949; ALDRIDGE, 1999), one or two days after resorption of the yolk sac (REYNOLDS *et al.*, 1997). Although they have well developed (lepidotrichia present) unpaired fins and a differentiated gas bladder (KRYZHANOVSKII, 1949; KOBlickAYA, 1981), the preanal finfold enlarges at this time (KRYZHANOVSKII, 1949) and the ventral fins are only starting to differentiate (KOBlickAYA, 1981). When leaving the mussel, bitterling are similar to larvae of other cyprinid fishes of comparable length (KRYZHANOVSKII, 1949). When reaching a standard length (SL) of approximately 13 mm (16 mm TL), the first scales appear. Complete scale cover occurs at 17.7 mm SL (21.8 mm TL) (BALON, 1959). Bitterling reach sexual maturity during their first year of life at 25-30 mm SL (PAPADOPOL, 1960; HOLČÍK, 1993, REICHARD, 1998) and grow to a maximum size of 75 mm SL but usually less (about 50 mm SL). The bitterling is a short lived species (maximum 5 years, usually 2-3 years) (HOLČÍK, 1959; BARUŠ & OLIVA, 1995).

The aim of the present study was to describe patterns of relative growth of morphometric characters during the life history of bitterling. As bitterling is sometimes described as a species with direct development, *i.e.*, without a larval period (*e.g.*, HOLČÍK, 1993), whereas other authors use the term larva (*e.g.*, KRYZHANOVSKII, 1949; PAPADOPOL, 1960; BALON, 1962; PEŇÁZ *et al.*, 1978; KOBlickAYA, 1981; ALDRIDGE, 1999), we will discuss whether during the ontogeny of bitterling a larval period occurs and if the patterns in relative growth of morphometric characters can serve as an indicator of the transition between periods.

## MATERIAL AND METHODS

168 individuals of bitterling ranging from 10.1 to 30.4 mm SL were caught in August 1996 in a small (2.0 ha) oxbow lake, isolated from the River Morava (Danube basin, Czech Republic) in the 1970's following channelisation of the main channel. Fish were captured by electrofishing (DC 220-240 V, 1.5-2.5 A, 20-50 Hz) and immediately preserved in 4% formaldehyde.

In the laboratory, computer analysis of video scans was used for measuring (software Image Pro Plus for Windows) 21 plastic characters according to Holčík (1989). All were expressed as a percentage of SL (henceforth % SL). From the allometric growth of the head length with respect to SL, 4 characters (describing proportions of the head) were also expressed as a percentage of head length (henceforth % HL). Pectoral, ventral, dorsal, anal and caudal fins are denoted in the text by their

respective capital initials. The terminology of early development used throughout this article follows that of BALON (1975b, 1986, 1990).

Characters were divided into two groups according to their relative growth. Characters with an isometric pattern of growth were determined as those for which the proportion expressed in % SL (or HL, respectively) did not change with increasing SL (HL), whereas allometric growth was determined as those characters which changed significantly with increasing SL (HL). Correlation coefficient ( $r$ ) and F-test value ( $p < 0.05$ ) were used to divide the characters into groups with isometric and allometric growth rate and to evaluate the regression models (SOKAL & ROHLF, 1995). In the group of characters with allometric growth, Student's t-tests for coefficient  $c$  ( $p < 0.05$ ) were employed to assess whether linear or second order polynomial regression fitted the data best.

Caudal peduncle factor (minimum caudal peduncle depth divided by maximum body depth) and body shape factor (standard length divided by maximum body depth) were employed to describe morphological indicators for swimming ability (generate lift, reduce drag and energy inefficient recoil) of bitterling of different sizes (WEBB & WEIHS, 1986). The original measurements for adult specimens used for this analysis were presented in REICHARD (1998). Statistical analysis was conducted in the same way as for the other characters, except they are plotted against the ratio between SL and length at hatching ( $L_c$ ) (WEBB & WEIHS, 1986). Mean length at hatching was assessed from KRZYZHANOVSKII (1949) and was calculated as 5.4 mm. In the study by WEBB & WEIHS (1986) TL value was used to describe body length. As TL is an example of an isometric character (the proportion between SL and TL is stable with increasing SL with the ratio of 1:1.2), values of SL were employed in the present study because of the increased accuracy of measuring (little damage to the caudal fin during preservation).

## RESULTS

According to their pattern of relative growth we were able to divide the characters of bitterling into two major groups, isometric and allometric. Nine characters exhibited isometric growth (regression models: F-tests,  $p > 0.05$ ), eight of them in % SL and one in % HL (Table 1). Fifteen characters showed allometric growth (linear or polynomial regression model: F-tests,  $p < 0.05$ ). Within this group, eleven exhibited positive allometric growth (see Fig. 1 for examples) and four negative (see Fig. 2 for examples) with increasing SL and HL (Table 2). Head length, eye

TABLE 1

Morphometric characters with isometric growth pattern in young bitterling from the Moravská Nová Ves oxbow lake. Mean, standard error (SE), minimum value (min), maximal value (max), coefficient of variance (CV) and number of fish examined (n).

Variables	mean	SE	min	max	CV	n
standard length	18.210	0.395	10.114	30.384	28.122	168
head length	4.895	0.084	2.836	7.841	22.323	168
in % of standard length						
preorbital distance	5.771	0.042	4.022	7.586	9.592	168
head depth	21.490	0.084	17.868	23.681	5.090	168
predorsal distance	52.035	0.095	49.221	55.573	2.373	168
preventral distance	48.318	0.117	44.096	51.666	3.120	164
preanal distance	58.291	0.098	55.526	63.393	2.196	168
caudal peduncle length	24.170	0.150	19.906	29.679	8.096	168
V-A distance	11.395	0.101	8.087	15.479	11.314	164
C-fin length	24.571	0.156	19.593	29.778	8.095	162
in % of head length						
eye diameter	32.899	0.153	23.557	37.514	6.033	168

diameter, P-V distance, D-fin length, A-fin length and D-fin depth (in % SL) were fitted better by linear regression model (Student's t-tests for coefficient  $c$ ,  $p > 0.05$ , Table 2). For body depth, postorbital distance, caudal peduncle depth, minimum body depth, V-fin length and A-fin depth (in % SL) and preorbital distance, postorbital distance and head depth (in % HL), the second order polynomial regression model fitted the data better (Student's t-tests for coefficient  $c$ ,  $p < 0.05$ , Table 2). Complete finfold reabsorption, one of the main characteristics at the end of the larval period (BALON, 1975b) appeared at around 12.8 mm SL in our sample.

Factors describing swimming ability were fitted by a polynomial regression model (Fig. 3). To analyse patterns in consecutive intervals of development, we assessed these growth factors in three groups (divided according to important events in life-history) separately. In fish with remnants of finfold (up to 12.8 mm SL,  $L_c = 2.35$ ) body shape factor showed positive allometric growth and a linear regression model fitted the data best (linear regression:  $r = 0.709$ ,  $F = 13.1$ ,  $p = 0.003$ ,  $n = 15$ ). Caudal peduncle depth factor showed a steep but non-significant decrease (see Fig. 3) in fish with remnants of finfold ( $r = 0.396$ ,  $F = 2.42$ ,  $p = 0.14$ ,  $n = 15$ ) during the same interval. This is probably due to the small number of fish examined.

TABLE 2

Morphometric characters with allometric growth pattern in young bitterling from the Moravská Nová Ves oxbow lake. Intercept (a), parameter of slope (b) and parameter of second order polynomial regression model (c), probability of parameters ( $P_b$ ,  $P_c$ ), F-test value of fitted regression model, correlation coefficient (r) and number of fish examined (n).

	a	b	$P_b$	c	$P_c$	F-test	r	n
in % of standard length								
body depth	7.51	1.54	<0.001	-0.03	<0.001	430.70	0.92	168
head length	32.83	-0.30	<0.001		0.679	299.42	0.80	167
eye diameter	10.61	-0.09	<0.001		0.574	206.65	0.75	168
postorbital distance	19.32	-0.58	<0.001	0.01	0.011	93.92	0.73	167
caudal peduncle depth	6.39	0.37	<0.001	-0.01	0.017	143.80	0.80	168
minimum body depth	6.66	0.23	<0.001	-0.01	0.019	58.83	0.65	168
P-V distance	17.09	0.20	<0.001		0.183	38.98	0.44	164
D-fin length	13.74	0.28	<0.001		0.596	84.96	0.58	164
A-fin length	15.76	0.20	<0.001		0.175	59.49	0.51	167
V-fin length	5.08	0.68	<0.001	-0.01	0.005	26.13	0.50	162
D-fin depth	17.91	0.15	<0.001		0.697	39.91	0.45	168
A-fin depth	7.04	1.14	<0.001	-0.03	<0.001	37.07	0.56	168
in % of head length								
preorbital distance	8.41	3.94	<0.001	-0.26	0.022	51.40	0.62	168
postorbital distance	61.35	-5.72	0.005	0.42	0.033	19.81	0.44	168
head depth	37.75	13.36	<0.001	-0.96	0.001	59.90	0.65	168

The second interval consisted of fish ranging from  $L_c = 2.35$  (12.8 mm SL) to  $L_c = 5.5$  (29.9 mm SL). The upper limit represents the size when both factors attain adult values in thunniform species (WEBB & WEIHS, 1986). Body shape factor was fitted by a polynomial regression model ( $r = 0.879$ ,  $F = 255.94$ ,  $p = 0.001$ ,  $n = 153$ ) significantly better (Student's t-test for c coefficient:  $t = 4.25$ ,  $p = 0.001$ ) than a linear regression. The same was true for caudal peduncle factor (polynomial regression:  $r = 0.632$ ,  $F = 49.82$ ,  $p = 0.001$ , Student's t-test for c:  $t = 2.23$ ,  $p = 0.027$ ,  $n = 153$ ). It shows that in this interval both factors change with increasing  $L_c$  (and SL), but stabilize at the end of interval (see Fig. 3).

In the third interval individuals with adult-like body form are found ( $L_c > 5.5$ ;  $SL > 29.9$  mm) (WEBB & WEIHS, 1986; COPP & KOVÁČ, 1996). 96.5 % of fish were in their adult period of development with mature gonads as determined by examination of the gonad tissue after dissection. Both body form factors were stable during this interval (regression model:  $r = 0.138$ ,  $F = 0.97$ ,  $p = 0.33$  for caudal peduncle factor and  $r = 0.228$ ,  $F = 2.77$ ,  $p = 0.10$  for body shape factor;  $n = 57$ ).

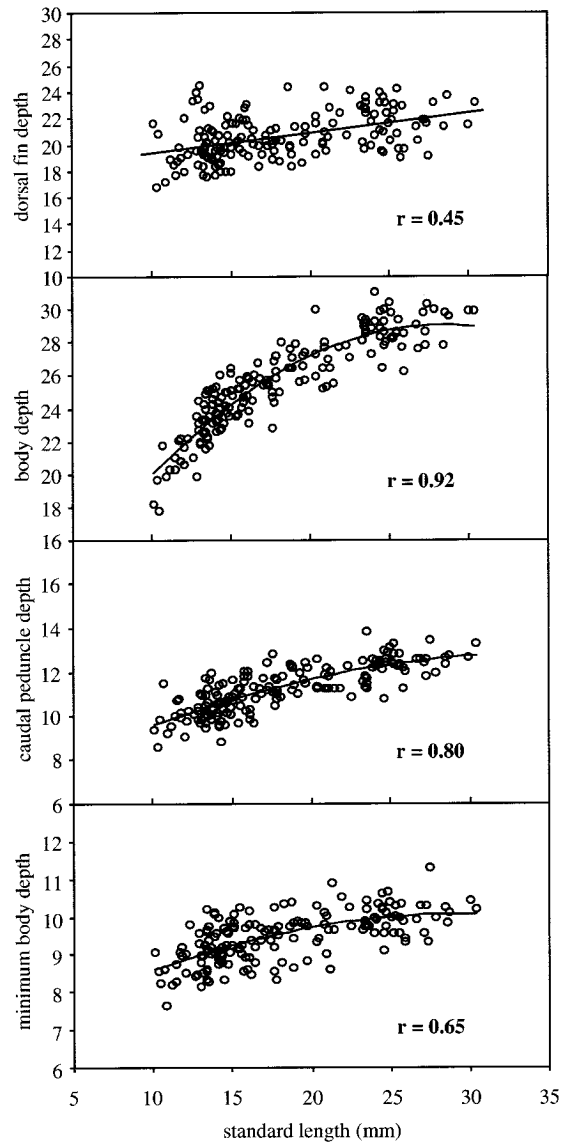


Fig. 1. Dorsal fin depth, body depth, caudal peduncle depth and minimum body depth as examples of characters with positive allometric growth (in % SL against increasing SL) for young bitterling from the oxbow with correlation index ( $r$ ) indicated.

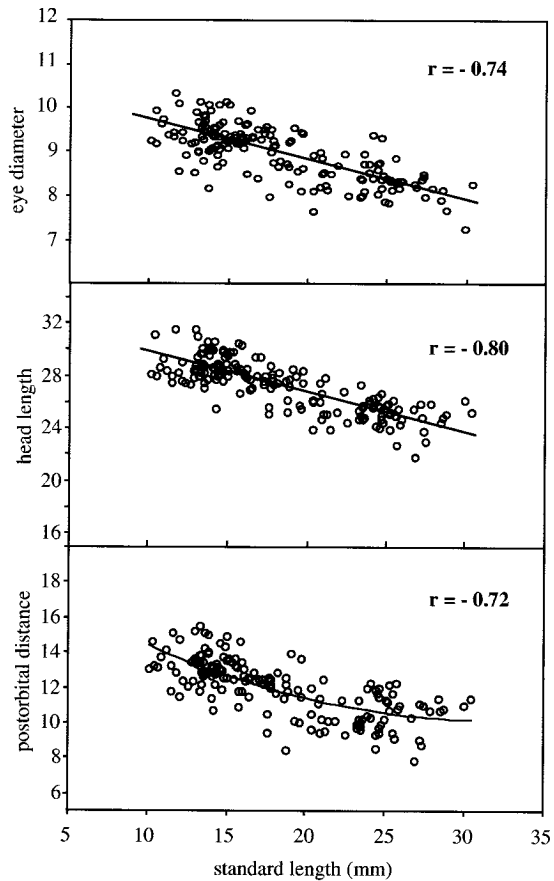


Fig. 2. Eye diameter, head length and postorbital distance as examples of characters with negative allometric growth (in % SL against increasing SL) for young bitterling from the oxbow with correlation index ( $r$ ) indicated.

## DISCUSSION

Examination of the relative growth of 24 morphometric characters revealed that 63% exhibited allometric growth in the interval of SL 10.1-30.4 mm. Within this group, 60% were fitted best by a polynomial regression model. Characters appeared to stabilize their relative growth between 25-30 mm SL (Figs 1 and 2).

Comparison of these data from the present study with those for adult fish taken from OLIVA (1954) and REICHARD (1998) reveals that some characters are stable in their pattern of relative growth, while others can



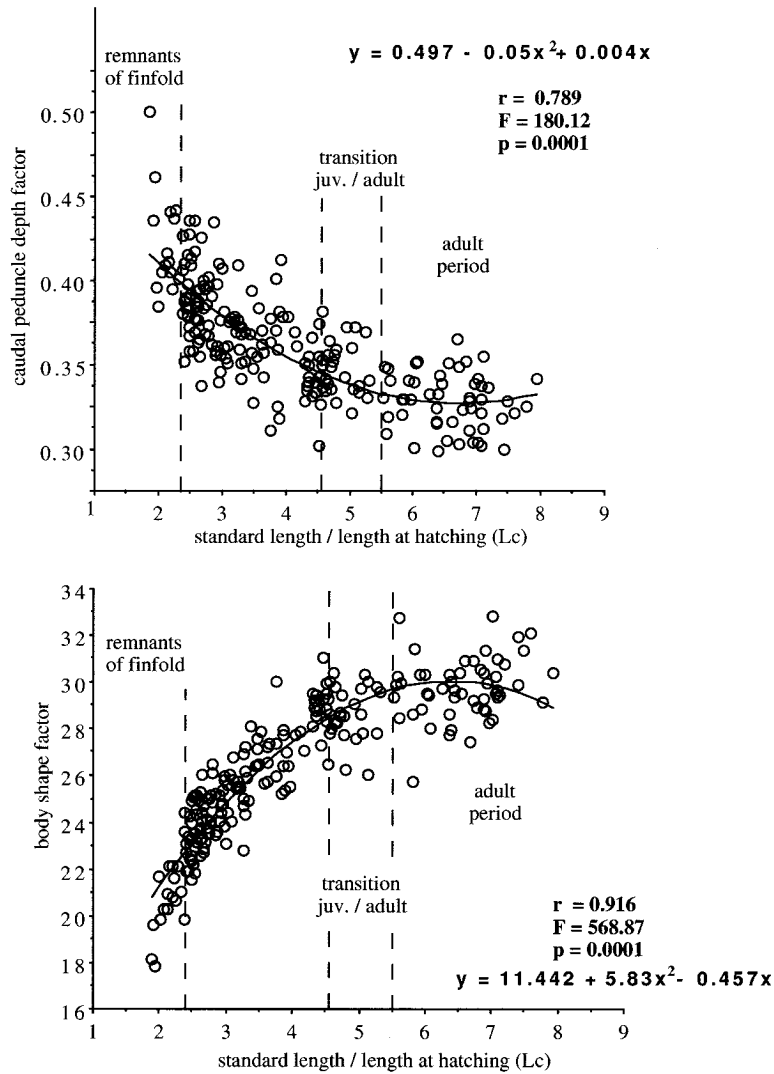


Fig. 3. Caudal peduncle depth factor and body shape factor (plotted against the ratio between standard length and length at hatching) for young and adult (taken from REICHARD, 1998) bitterling from the oxbow with polynomial regression equation, correlation coefficient (r), F-test value (F) and probability of regression model (p) indicated.

TABLE 3

Isometric (-), positive (P) and negative (N) allometric growth of characters in the four bitterling populations studied. Young specimens from Moravská Nová Ves oxbow lake population (SL = 10.1-30.4 mm, HL = 2.8-7.8 mm; present study), adults from Moravská Nová Ves oxbow lake population (SL = 24.4-42.9 mm, HL = 6.2-10.5 mm; from REICHARD, 1998), adults from the main channel of the River Morava (SL = 31.4-65.8 mm, HL = 7.7-16.7 mm; from REICHARD, 1998) and adult fish originating from an unspecified locality in the River Labe basin (SL = 35-54 mm; from OLIVA, 1954).

	young oxbow	adults oxbow	adults river	adults Labe basin
in % of standard length				
body depth	P	P	P	P
head length	N	-	N	N
preorbital distance	-	P	N	-
eye diameter	N	N	N	-
postorbital distance	N	-	-	-
head depth	-	-	-	-
predorsal distance	-	-	-	-
preventral distance	-	-	-	-
preanal distance	-	P	-	-
caudal peduncle length	-	-	P	N
caudal peduncle depth	N	-	P	-
minimum body depth	P	-	P	-
P-V distance	P	-	P	-
V-A distance	-	P	-	-
D-fin length	P	P	P	-
A-fin length	P	-	P	-
V-fin length	P	-	-	-
C-fin length	-	-	-	-
D-fin depth	P	-	-	N
A-fin depth	P	-	N	N
in % of head length				
preorbital distance	P	-	-	P
eye diameter	-	N	-	N
postorbital distance	N	-	-	P
head depth	P	-	P	P

differ among populations and size interval examined (Table 3). Isometric growth in all examined bitterling populations was observed in head depth, predorsal distance, preventral distance and C-fin length (expressed in % SL). As those characters also exhibited the same pattern of relative growth in roach (KOVÁČ & COPP, 1996), their proportions are probably rather stable during the ontogeny of fish. Body depth, head length, eye diameter and D-fin length (in % SL) grow allometrically throughout the entire life of bitterling (Table 3). Some characters with positive allometric growth

during early development can stabilize their relative growth after fish reach sexual maturity and/or sometimes also begin to exhibit negative allometric growth (and vice versa) (Table 3).

Conversely, there are characters that begin to grow allometrically as late as during the adult period (preanal distance, V-A distance). It is clear that these proportions are linked with sexual maturity (extension of ventral part of body in females with ripe eggs). Individual variation in other characters (and may be those considered isometric) was too high to classify them clearly. As stated by BALON (1990), the description of ontogenetic changes based on samples of different individuals inherently reflects the noise of individual variation rather than the true individual ontogeny. Furthermore, SAGNES (1997) showed that the effect of formalin preservation can differ among length classes of fish.

Both body form factors attain adult values at a SL of approximately 5 times the length at hatching, a typical value for thunniform species (WEBB & WEIHS, 1986). Their proportions changed allometrically, with steep changes in specimens with finfold and a gradual stabilization among the second examined interval and finally stabilizing during the adult period (Fig. 3).

There are three possible descriptions of the early development of bitterling. Firstly, following HOLČÍK (1993), bitterling is a species with direct development, *e.g.*, lacking a larval period. Secondly, following KRYZHANOVSKII (1949), PAPADOPOL (1960), BALON (1962), PEŇÁZ *et al.* (1978), KOBlickAYA (1981) and ALDRIDGE (1999), bitterling is a species with indirect development, however, with regard to a specific reproduction strategy, the larval period is shorter than in other cyprinid species and the evolutionary trajectory is believed to move toward extinction of larval period. Thirdly, considering the newly established threshold between larval and juvenile period (COPP & KOVÁČ, 1996; KOVÁČ & COPP, 1996), bitterling undergoes a relatively long larval period until the majority of allometric characters stabilize and complete scale cover is present.

From our results we conclude that bitterling have a larval period. After the start of exogenous feeding (end of embryonic period; BALON, 1975b, 1986, 1990), characters considered typical for larvae (BALON, 1975b) are still present, *i.e.*, remnants of finfold, no scales present and fin ray bifurcation not completed. When the larva leaves the mussel body, the preanal finfold enlarges (KRYZHANOVSKII, 1949) and the ventral fins have not yet started to differentiate (KOBlickAYA, 1981). This developmental state accords with the pterygiolarva phase (*sensu* BALON, 1975b). The threshold between the larval and juvenile period is observed at about 13 mm SL when reabsorption of the finfold is completed

(KOBLYCKAYA, 1981) and the first scales become apparent (BALON, 1962).

Nevertheless, the evolutionary process which gave rise to direct development and precocial form in bitterling is obvious (*e.g.*, hiding eggs in mussels and further specialisation to mussel species in localities where more than one mussel species occur (REYNOLDS *et al.*, 1997)). As environmental conditions influence development of early life stages (BALON, 1983; SIMONOVIC & JOVANOVIC, 1993; CRAWFORD & BALON, 1996), the duration of the larval period can be different among populations (with respect to both geographic and ecological variation), especially when the wide geographical distribution of bitterling (for details see HOLČÍK & JEDLIČKA, 1994) is taken into account.

If the new proposal for the boundary between larval and juvenile period (COPP & KOVÁČ, 1996, KOVÁČ & COPP, 1996) is accepted, bitterling does not have a juvenile period, as the characters showing allometric growth appear to stabilize as late as the fish reach sexual maturity. We agree with BALON (1990) that allometric growth is a typical feature of the juvenile period. As there is a general increase in morphological variation over the entire course of development (BARLOW, 1961), the stabilization of allometry may be in fact only an increase in individual variability to a degree where differences between individuals mask the allometry of individuals.

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