Environmental Biology of Fishes **40**: 241–253, 1994.

Early ontogeny of three *Gymnocephalus* species (Pisces: Percidae): reflections on the evolution of the genus

Vladimír Kováč
Comenius University, Faculty of Natural Sciences, Institute of Zoology, Mlynská dolina B 2, 842 15 Bratislava, Slovakia

Received 1.3.1993 Accepted 1.12.1993

Key words: Early development, Ruff, Balon's ruff, Yellow pope, Evolutionary trajectories, Phylogenetic model

Synopsis

A brief description of the early development of ruff, *Gymnocephalus cernuus*, Balon's ruff, *G. baloni*, and yellow pope, *G. schraetser*, is presented. Developmental steps and thresholds, as well as patterns in the development of the three *Gymnocephalus* species, are discussed with regard to saltatory ontogeny and alprehost theory. Most of the patterns in all three *Gymnocephalus* species were found to be very similar to each other, and a new model of speciation for the genus *Gymnocephalus* is proposed. The hypothesis that the subgenus *Gymnocephalus* (*G. schraetser* and *G. acerinus*) has been evolving precocially and the subgenus *Acerina* (*G. cernuus* and *G. baloni*) altricially is based on the following patterns: (1) embryos and larvae of yellow pope grow and develop faster than those of ruff and Balon's ruff, (2) yellow pope females become mature when older and larger, (3) relative fecundity in yellow pope is considerably lower, (4) eggs of yellow pope are larger, containing a greater amount of yolk, and (5) typical elongation of the snout (preorbital distance) in yellow pope seems to be a deviation from the ancestral state. Several patterns of development in the precocial form (body depth, head depth and shape of mouth) indicate that juvenilisation (paedomorphosis) may have played an important role in the divergence of these subgenera.

Introduction

Three of the four species from the genus *Gymnocephalus* live in the River Danube: ruff *G. cernuus*, Balon's ruff *G. baloni*, and yellow pope *G. schraetser*. Despite certain differences in their ecological requirements, their habitats often overlap. Recent studies of early development (Kováč 1992, 1993a, b) confirmed very close relationships between all three species. Moreover, the Paleodanube River is suspected to have been the center of origin of the genus *Gymnocephalus* (Holčík & Hensel 1974). Therefore, this genus provides a very convenient example for studies of sympatric speciation. A model of phylogeny for the genus *Gymnocephalus* has already been proposed by Holčík & Hensel (1974). These authors also proposed and defined two subgenera of the genus *Gymnocephalus:* subgenus *Gymnocephalus* sensu stricto, comprising *G. schraetser* and *G. acerinus;* and subgenus *Acerina*, consisting of *G. cernuus* and *G. baloni*. They stated that 'speciation within the subgenus *Gymnocephalus* has followed geographical isolation, while speciation in the subgenus *Acerina* probably resulted from ecological specialization'. It should be noted that because of a complete lack of fossil material prior to the Pleistocene, Holčík & Hensel (1974) consider their discussion on the evolution of the species of *Gymnocephalus* to be highly speculative. I concur with them, and the present paper aims at providing an alternative interpretation of evolution of the genus *Gymnocephalus* and to outline some of its possible evolutionary trajectories in light of alprehost theory (Balon 1981, 1988, 1989, 1990). According to this theory, two forms are recognized. Smaller and less morphologically advanced forms at particular thresholds of early development are altricial (i.e. generalists), compared to precocial (i.e. specialists). A central theme is that changes in ontogenetic parameters during the less stable intervals of early development (thresholds) can lead to a bifurcation of alternate evolutionary pathways.

Materials and methods

All of the brood stock used in this study (Table 1) originated from side arms of the River Danube in Slovakia. The ruff *Gymnocephalus cernuus* (Linnaeus, 1758) were captured on 11 June 1989 in a branch near the village of Vojka, Balon's Ruff *Gymnocephalus baloni* Holčík & Hensel, 1974 on 23 May 1990 in a branch near the village of Bodíky and yellow pope *Gymnocephalus schraetser* (Linnaeus, 1758) on 7 May 1990 (female) and 29 April 1991 (male) in the Karlova Ves branch.

Ova were stripped from the fish and then inseminated in Petri dishes using the dry method (see e.g. McElman & Balon 1979). Development was studied in vivo on embryos and larvae anaesthesized with MS 222 (tricaine methane sulfonate). Observations on living and preserved specimens were made with a Meopta binocular stereomicroscope. Photomicrographs were taken through the microscope using ocular attachments and a Practica PLC-3 camera. Drawings were made from living specimens using a Carl Zeiss drawing apparatus, and from photomicrographs. Measurements were made with a Meopta ocular micrometer as described by Lange et al. (1974). The single exception was the postanal distance, which was measured from the anus to the caudal end of the finfold (embryos and larvae) or to the end of the longest caudal ray (juveniles). The description of early ontogeny is based on the terminology proposed by Balon (1975). The letters E (embryonic), L (larval) and J (juvenile) denote the periods of ontogeny; where step E6 would be the sixth embryonic step. Age is given as days:hours:minutes after activation, and represents the start of the sampling interval. The larvae were fed on strained mixed pond plankton. Some of the studied specimens have been preserved in 4% formaldehyde solution for future reference.

Results and discussion

Since most of the developmental patterns in all three *Gymnocephalus* species were found to be very similar to each other (Figs 5, 6, 7, 8), the description of early development presented below represents a generalised model common for the genus *Gymnocephalus*. Only the main events of the developmental steps are described; more detailed de-

Table 1. Standard length of the brood stock used (upper), and diameter of eggs after activation observed in the three *Gymnocephalus* species (lower). The yolk diameters and that of eggs with envelope of each species differed significantly (ANOVA: 57.643 and 112.934 respectively, $p < 0.0001$, df = 34) from all other species (Scheffe F-test comparison of means at 95%).

	mean	(min-max)	n	mean	(min-max)	n
SL (mm)	males			females		
G. cernuus	65.5	–	1	99.2	–	1
G. baloni	86.1	69.4–98.9	8	97.7	91.3–104.0	2
G. schraetser	120.3	–	1	110.8	–	1
diameter (mm)	yolk			eggs with envelope		
G. cernuus	0.87	0.78–0.92	10	1.00	0.97–1.07	10
G. baloni	0.93	0.89–0.98	15	1.12	1.07–1.17	15
G. schraetser	1.06	1.00–1.12	10	1.22	1.18–1.26	10

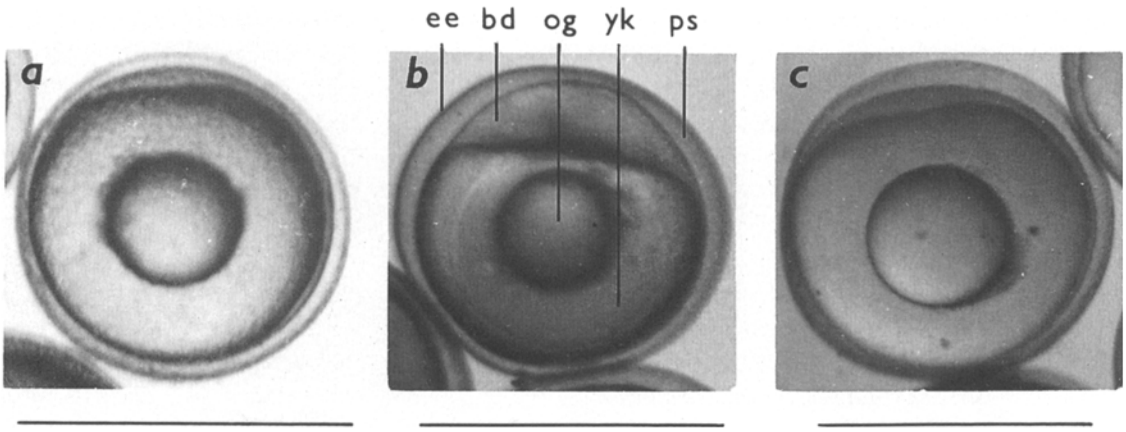

Fig. 1. Perivitelline space and blastodisc formation; step E1, vertical views from above: a – ruff, 00:00:12; b – Balon's ruff, 00:00:52; c – yellow pope, 00:00:06 (ee = egg envelope, bd = blastodisc, og = oil globule, yk = yolk, ps = perivitelline space). Scales = 1 mm.

scriptions have been provided elsewhere (Kováč 1992, 1993a, b).

Embryo period

During the cleavage phase, the developmental patterns of species in the genus *Gymnocephalus* basically do not differ from those of other percids, e.g. perch (Řepa 1969), pike-perch (Bastl 1978), walleye (McElman & Balon 1979), northern logperch (Paine & Balon 1984a) or rainbow darter (Paine & Balon 1984b); see also Kryzhanovsky et al. (1953).

The first embryonic step (E1) begins with activation of the eggs (Fig. 1). Within the first minute, the perivitelline space begins to form and the cytoplasm concentrates at the animal pole. The diameter of yolk is smallest in ruff, followed by Balon's ruff, and yellow pope, with the diameter being significantly different in all three species (Table 1). The same pattern is observed in the eggs measured with envelope. Similar results have been presented by Bastl (1988) who dealt with the reproductive biology of the three Danubian *Gymnocephalus* species in more detail. He found that before spawning, the diameter of ripe eggs attained 0.60 mm to 0.98 mm in ruff, 0.92 mm in Balon's ruff and 1.00 mm in yellow pope.

The second embryonic step (E2) commences with the onset of cleavage and appearance of 2 blastomeres. During this step, cleavage occurs rapidly, forming the blastula (Fig. 2).

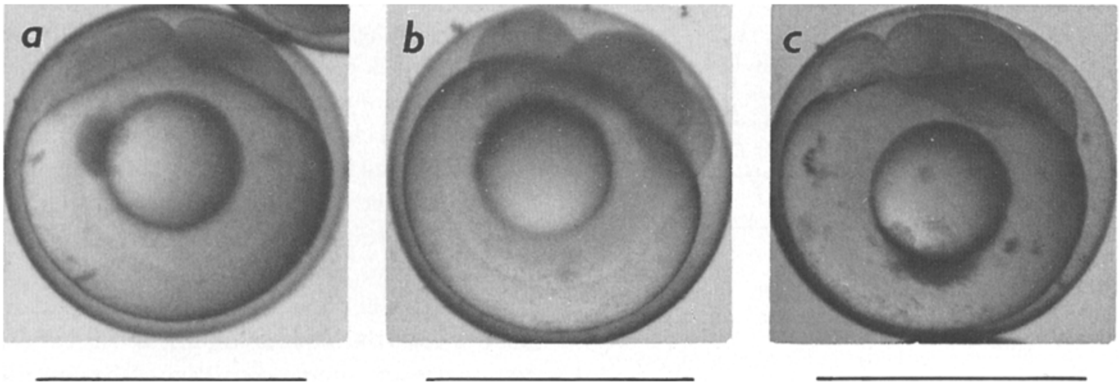

Fig. 2. Cleavage; step E2, vertical views from above, yellow pope; a – first cleavage, 00:02:09; b – second cleavage, 00:03:37; c – third cleavage, 00:04:50. Scales = 1 mm.

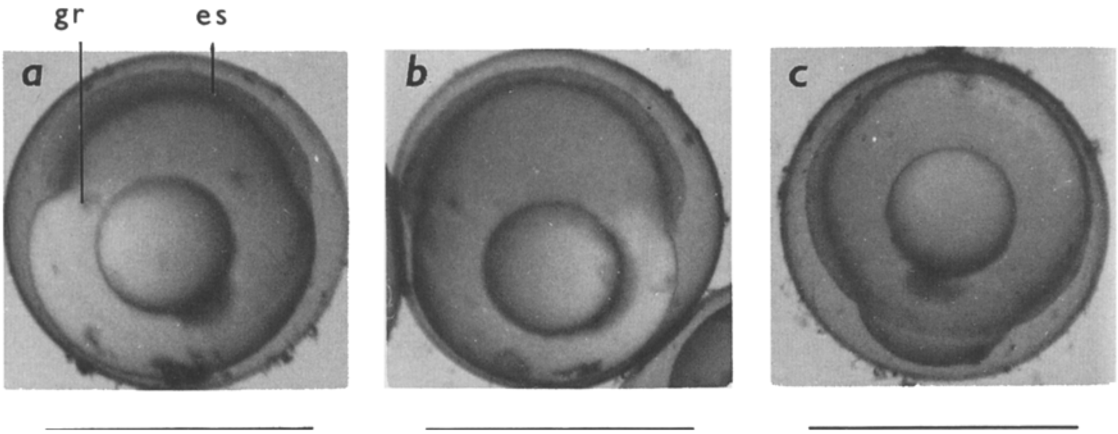

Fig. 3. Epiboly (the oil globule is not the last part covered by the advancing cell layer); step E3, vertical views from above, yellow pope: a – 00:19:27 (es = embryonic shield, gr = germ ring); b – 00:22:20; c – 01:02:58. Scales = 1 mm.

The third embryonic step (E3) begins with the onset of epiboly. Rapidly dividing cells form an advancing layer that covers the yolksac surface. Unlike walleye (McElman & Balon 1979) and northern logperch (Paine & Balon 1984b), the oil globule is not the last part being covered by the advancing cell layer in *Gymnocephalus* spp. (Fig. 3).

During the embryonic phase, I recorded two decisive thresholds: the onset of muscular contractions and the onset of blood circulation. The fourth embryonic step (E4) starts with the onset of germ ring closure. An embryonic axis appears and the head becomes distinguishable. The brain anlage, eyes, olfactory and auditory vesicles, notochord, and Kupffer's vesicle appear. Segmentation of the body also occurs (Fig. 4). In northern logperch, 'segmentation of the body and formation of the brain regions in step E4 and E5 are necessary for the initiation and control of muscular contractions in succeeding steps' (Paine & Balon 1984a). The development of *Gymnocephalus* spp. is similar in this respect; therefore I consider the segmentation of the body and differentiation of the nervous system to be the main events of E4. Since displacement of the oil globule in *Gymnocephalus* did not seem to be as apparent as in the northern logperch, I consider this interval of development as a single step only.

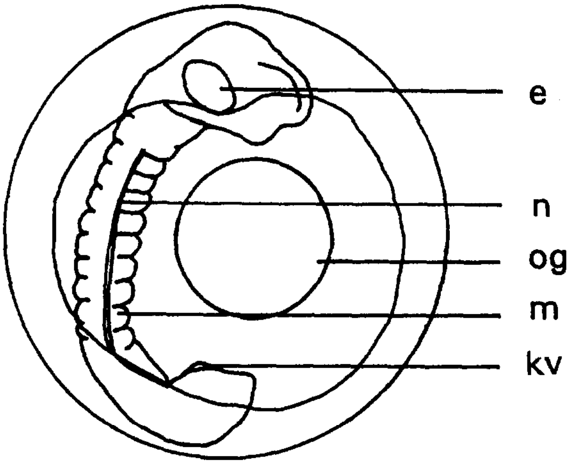

Fig. 4. Embryo with segmented body (the brain anlage and sense organs are not yet visible); step E4, vertical view from above, Balon's ruff, 01:02:27 (e = eye, n = notochord, og = oil globule, m = myotomes, kv = Kupfer's vesicle). Scale = 1 mm.

The fifth embryonic step (E5) starts with the onset of first contractions in the embryos. Segmentation continues, lenses appear in the eyes, and otoliths appear in the auditory vesicles. The heart also appears, beating irregularly. The embryos are transparent and lack pigment.

The sixth embryonic step (E6) begins with the onset of blood circulation. During this step the embryos hatch and the free embryo phase begins. After hatching, the embryos lie side down on the bottom and dart vertically from time to time. Pectoral fin buds appear, and the head is bent toward the yolksac. The heart beats regularly (Kováč 1992, 1993a, b), and the blood is colourless. The circulatory system is very simple, consisting of the dorsal aorta, caudal vein, posterior and anterior cardinal veins, Cuvier's duct and cerebral veins (Fig. 5a).

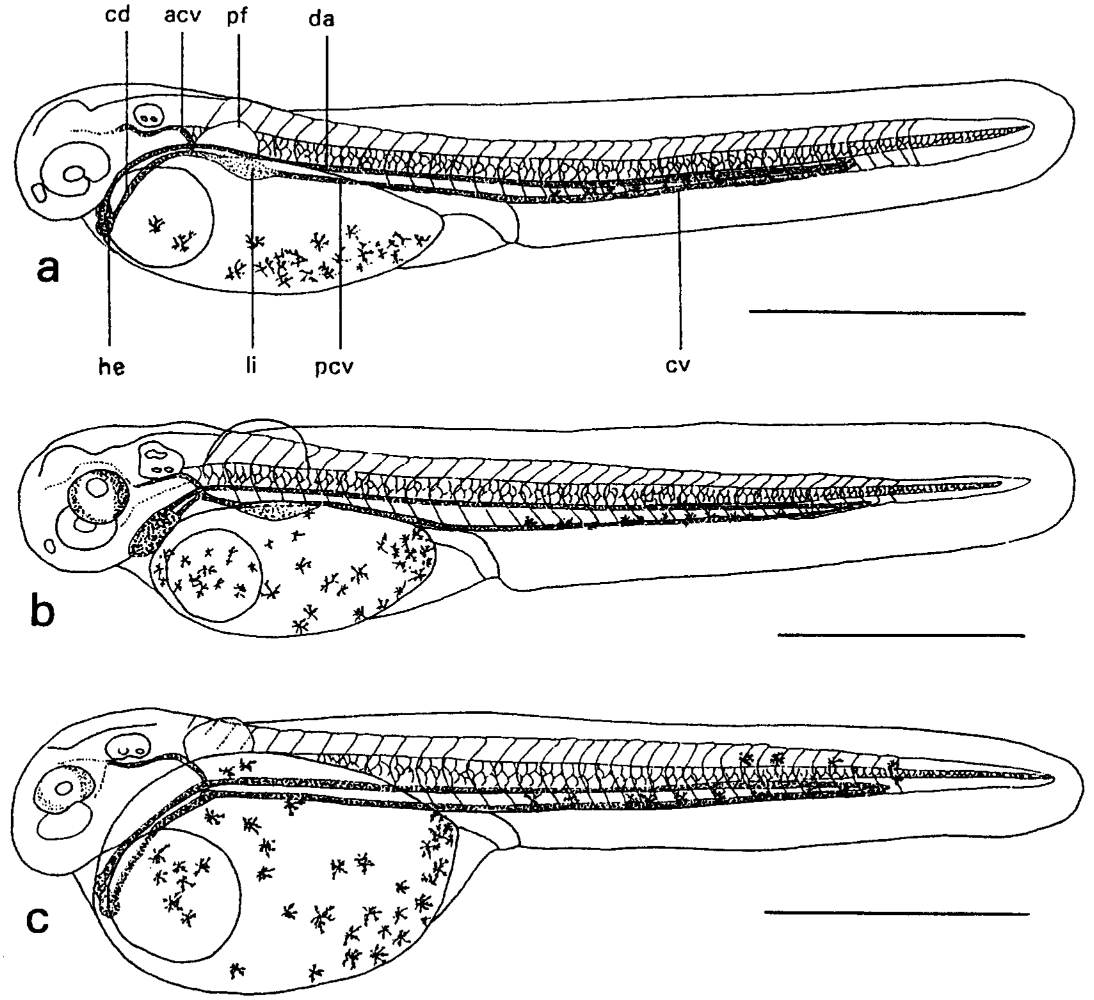

Fig. 5. Free embryos (note the simple circulatory system); step E6, left lateral view: a – ruff, 04:07:00; b – Balon's ruff, 02:20:49; c – yellow pope, 04:05:34 (acv = anterior cardinal vein, ca = caudal artery, cv = caudal vein, da = dorsal aorta, cd = Cuvier's duct, he = heart, li = liver anlage, pcv = posterior cardinal vein). Scales = 1 mm.

Despite the possibility that simple diffusion might be sufficient to cover oxygen requirements, the absence of both the vitelline and segmental vessels, which are very common in other percids (e.g. Řepa 1969, Paine & Balon 1984b), suggests that *Gymnocephalus* embryos require very favourable oxygen conditions to survive. My field studies in the Karlova Ves branch of the Danube support this presumption; ripe adult specimens of all three species were most frequently caught in slowly flowing or stagnant waters adjacent to lotic sections. These well oxygenated parts of the Karlova Ves branch may be the spawning sites and nursery areas for all three *Gymnocephalus* species.

The characters developed during E6 may reflect preparations for controlled movements. Freshly-hatched embryos already possess a well-developed, unpaired finfold and small horizontal immobile pectoral fins. Nevertheless, to be able to swim, the embryos also need well-developed sense organs and a more efficient respiratory system. Intensive development of the eyes is evident, and the lateral line also seems to be undergoing rapid development. At the start of E6, the embryos respond exclusively to direct touch, whereas at the start of E7 they begin to respond to a gentle tap on the aquarium glass. Disler & Smirnov (1977) also reported intensive development of the lateral line in ruff dur-

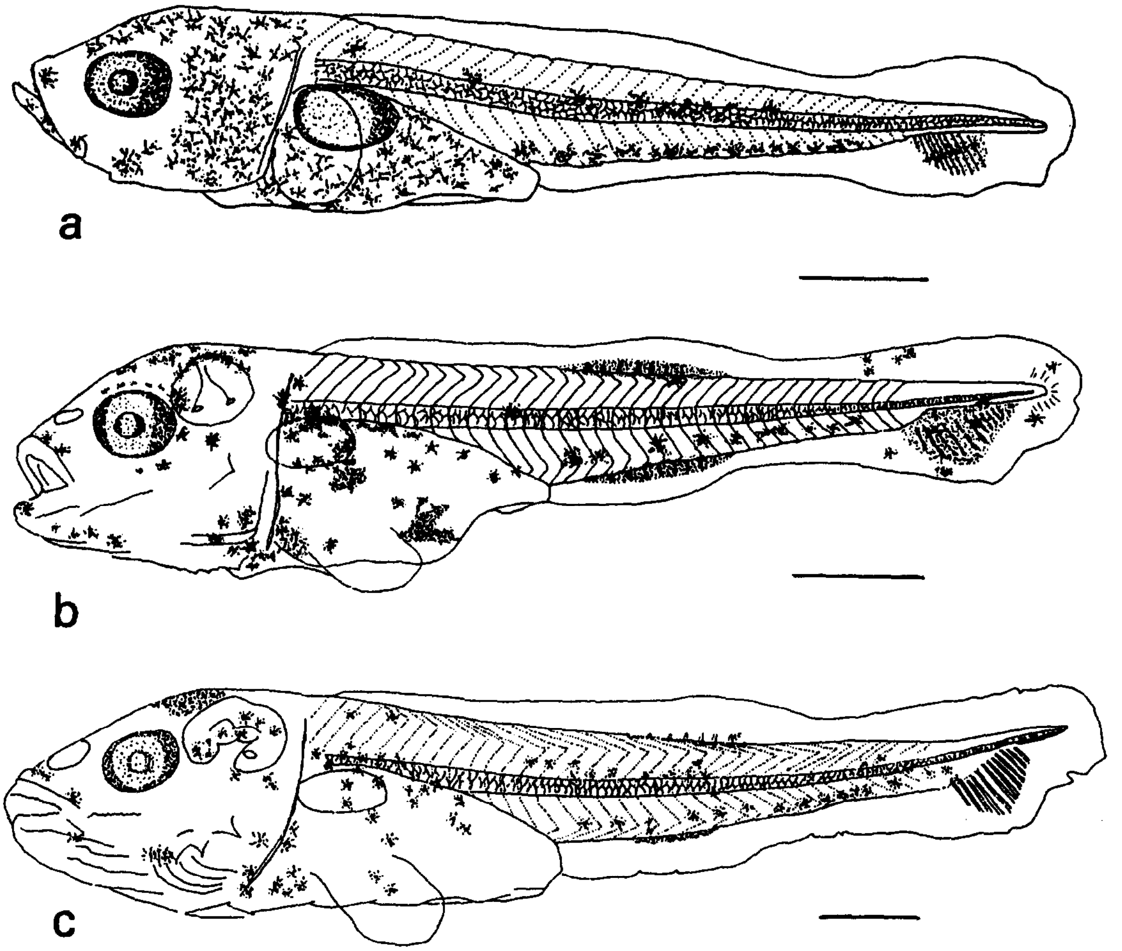

Fig. 6. Larvae; step L3, left lateral view. In ruff (a, 21:01:25) and Balon's ruff (b, 22:21:22) the cranial end of the lower jaw exceeds that of the upper jaw, whereas in yellow pope (c, 20:17:35) the latter is exceeding; otherwise, the larvae are still very similar to each other. Scales = 1 mm.

ing corresponding intervals of ontogeny. With the appearance of colour in blood elements and an increase in the heart beat rate at the start of E7, one may assume that respiration has become more efficient.

During E6, the horizontal, and as yet immobile, pectoral fins increase in size and turn their base vertically. Upon reaching the vertical position, they become mobile. This event strongly affects the behaviour of the embryos, which until then lay passively side down on the bottom; they shift to abdomen down and then begin swimming actively. The embryos are also then able to swim horizontally and to change direction when necessary. Therefore, I consider the onset of pectoral fin movements to be a threshold between E6 and E7. Such a dramatic change in embryo behaviour was not observed either in *Stizostedion* (McElman & Balon 1979, Bastl 1978) or in *Perca* (Řepa 1969, Kryzhanovsky et al. 1953). Therefore, it is obvious that the role of this developmental event is much more important in species of *Gymnocephalus* than in *Stizostedion* or *Perca.*The seventh embryonic step (E7) is characterized by the preparation for exogenous feeding and branchial respiration. The head separates from the yolksac, pigment appears in the eyes and the lower jaw begins to quiver. The mouth is terminal but the cranial end of the upper jaw exceeds that of the lower jaw. As the step advances, the mouth begins to perform regular, respiratory-like movements. The embryos lay abdomen down on the bottom but also try to swim horizontally.

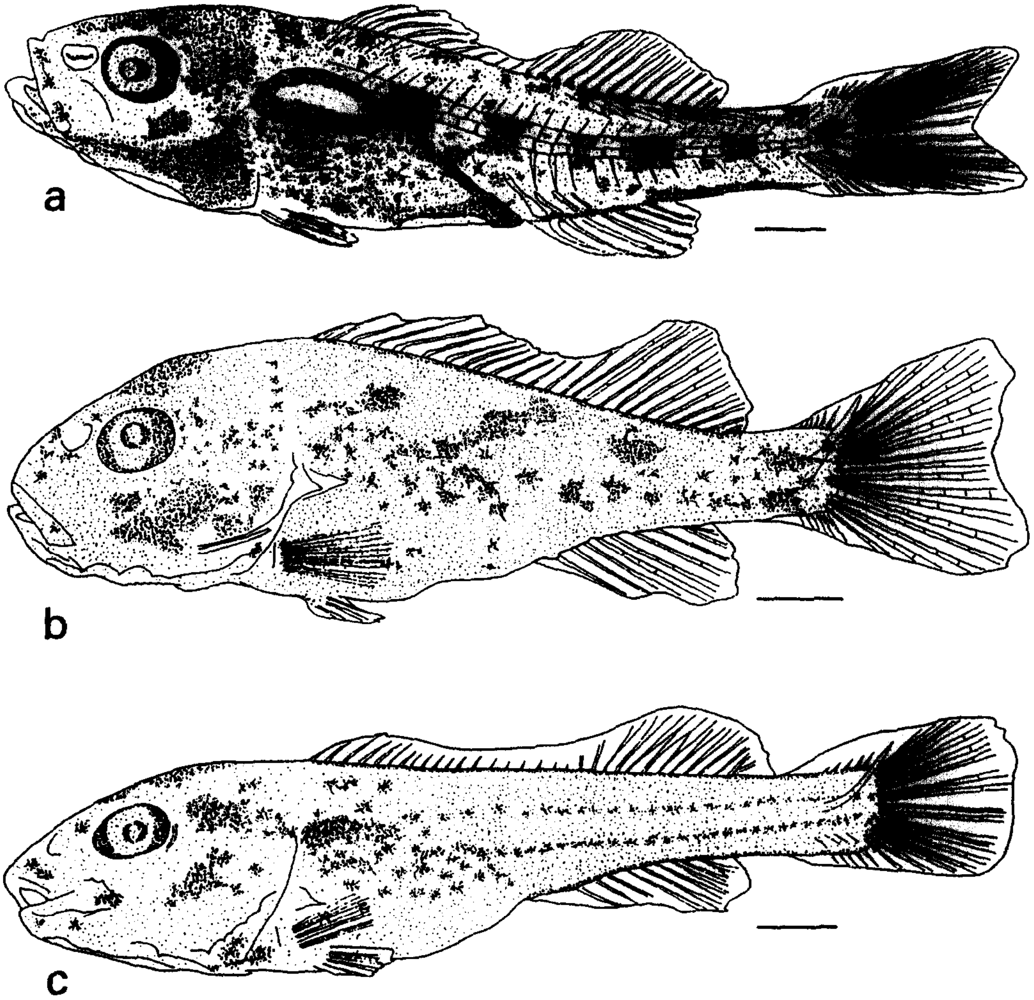

Fig. 7. Juveniles; step J1, left lateral view: a – ruff; b – Balon's ruff; c – yellow pope. Scales = 1 mm.

Larva period

In the finfold phase (Fig. 6), the first larval step (L1) begins with the onset of active feeding. The mouth is large. Melanophores increase in number. The yolksac and oil globule reduce in size, whilst an swimbladder anlage appears. Swimming throughout the water column (in aquarium), the larvae begin to hunt small plankton. According to my observations, they use their sight for orientation. Both the manner of feeding and the construction of the jaw apparatus of larvae differ from those of adults. From the start of exogenous feeding, the larvae have a large terminal mouth. In ruff and Balon's ruff, the cranial end of the lower jaw exceeds that of the upper jaw; whereas, in yellow pope the position of jaws is reversed. A common pattern in all three species is that, owing to very good mobility of the lower jaw, the fully opened mouth exceeds both the depth and the width of the head. This is very important because the larvae seize their prey by rapid darting movements. Such feeding behaviour requires the mouth to be as large as possible to compensate for inaccuracies in movement (Aleyev 1963). On the contrary, adults eat mostly benthos (Nagy 1985) and catch their prey by suction (Elshoud-Oldenhave & Osse 1976). Similarly, adults have a relatively smaller mouth than do larvae, with the cranial end of the upper jaw exceeding that of the lower jaw.

The second larval step (L2) begins when the yolk is fully depleted and feeding becomes exclusively

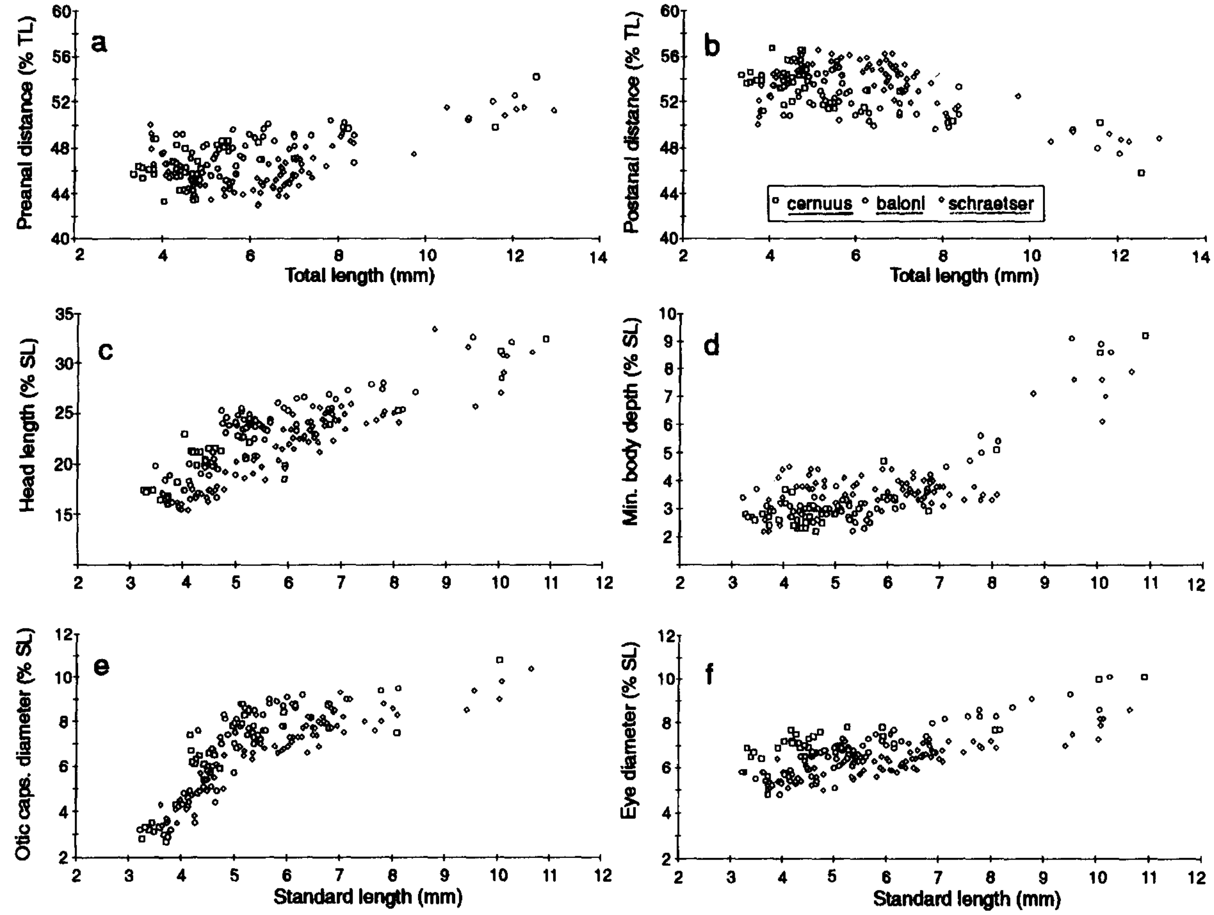

Fig. 8. Changes in relative mensural characters during early development of three *Gymnocephalus* species: ruff (*cernuus*), Balon's ruff (*baloni*) and yellow pope (*schraetser*): a – preanal distance (% TL); b – postanal distance (% TL); c – head length (% SL); d – minimum body depth (% SL); e – horizontal otic capsula diameter (% SL); f – horizontal eye diameter (% SL).

exogenous. Air appears in the swimbladder, taking over the hydrostatic function of the now absorbed oil gobule (Kryzhanovsky et al. 1953).

In the finformed phase, the third larval step (L3) begins with the onset of finfold differentiation. Fin rays appear in the prospective caudal fin, then in the dorsal and anal fins, the pectoral fins and finally in the ventral fins. Changes in the relative values expressed in % of SL occur in minimum body depth, head length and eye diameter; the preanal-to-postanal distance ratio tends towards an increase in the preanal distance (Kováč 1992, 1993a, b).

Juvenile period

The first juvenile step (J1, Fig. 7) begins with the onset of elimination of the axial lobe of the caudal fin. Several mensural characters (minimum body depth, head length, eye diameter, preanal-to-postanal distance ratio) attain relative values similar to adults. In other words, the slender larval body with a finfold and a long tail transform to a more corpulent, deeper body, with a shorter and deeper tail. The juveniles also possess a complete set of fins. This provides a dramatic improvement in locomotion and manoeverability of the fish (e.g. Aleyev 1963). The pigmentation of juveniles also resembles that of adults.

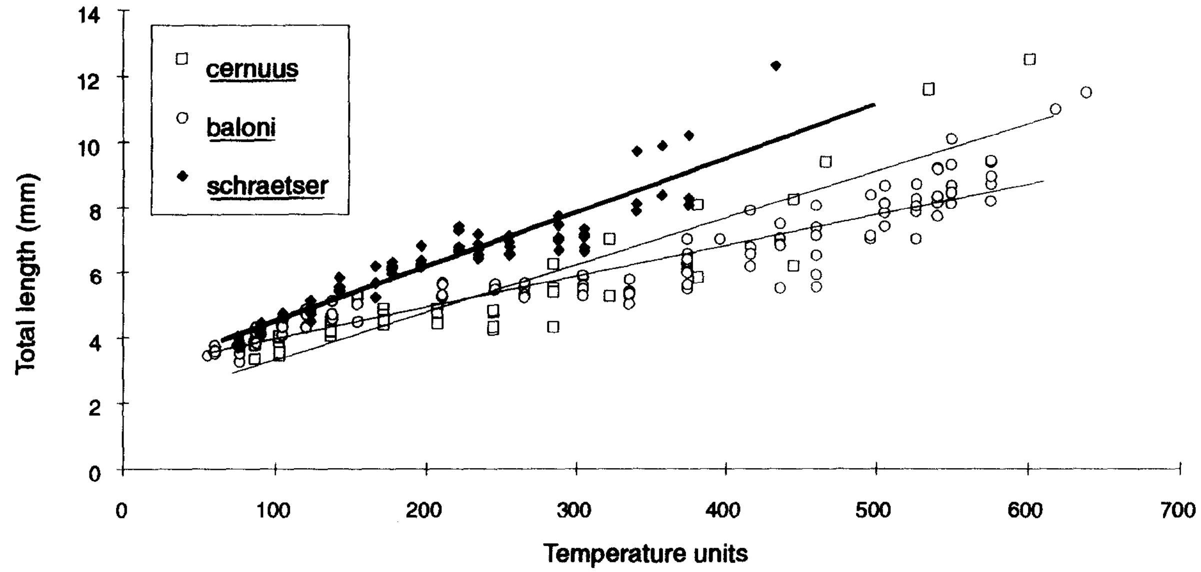

Fig. 9. Growth during early development of three *Gymnocephalus* species (legend as in Fig. 8), plotted against temperature units. The growth was most rapid in yellow pope throughout early development, the regression equations being $TL = 1.888 + 0.014\,TU$ ($r = 0.832$, $n = 39$, $p < 0.001$) for ruff; $TL = 3.091 + 0.009\,TU$ ($r = 0.863$, $n = 118$, $p < 0.001$) for Balon's ruff; and $TL = 2.854 + 0.017\,TU$ ($r = 0.874$, $n = 73$, $p < 0.001$) for yellow pope.

Reflections on the evolution of the genus *Gymnocephalus*

The fact that most developmental patterns of the three *Gymnocephalus* species were found to be very similar to each other (Figs 5, 6, 7, 8; also Kováč 1992, 1993a, b) confirms that ruff, Balon's ruff and yellow pope are very close relatives. Nonetheless, there are some different features that suggest prevailing trends in the evolution of the genus *Gymnocephalus*. A model of phylogeny for the genus *Gymnocephalus* proposed by Holčík & Hensel (1974) considers the subgenus *Acerina* (comprising *G. cernuus* and *G. baloni*) to be more specialized than the subgenus *Gymnocephalus* (*G. schraetser* and *G. acerinus*). They suggest this based on the fact that the subgenus *Gymnocephalus* exhibits more primitive characters, such as more elements in the dorsal and anal fins, more scales in the lateral line, a primitive type of coloration and exclusively rheophilous habits. However, in light of the results presented here, and considering alprehost theory (Balon 1981, 1988, 1989, 1990), I propose an alternative interpretation of the evolution of the genus *Gymnocephalus*. Central to the following discussion is the relationship between the subgenera *Acerina* and *Gymnocephalus*.

Percids are thought to have originated from some of the anadromous percoid families (Collette et al. 1977), the *Perca* ancestor having arisen from some of the European anadromous serranid stocks. Subsequently, the genus *Gymnocephalus* apparently derived from *Perca* (Collette & Banarescu 1977, Ráb et al. 1987). According to Balon (1988) 'the ability to create a generalist or a specialist at the same time is the only solution that can be prepared

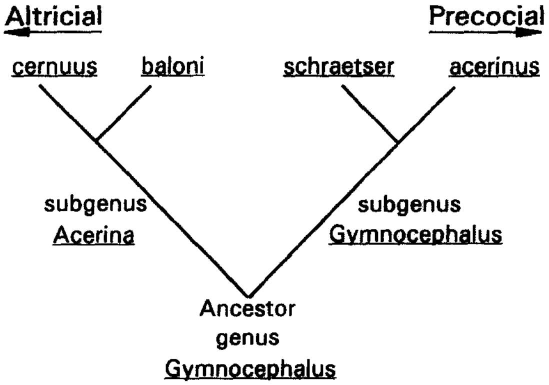

Fig. 10. A new model of phylogeny proposed for the genus *Gymnocephalus*.

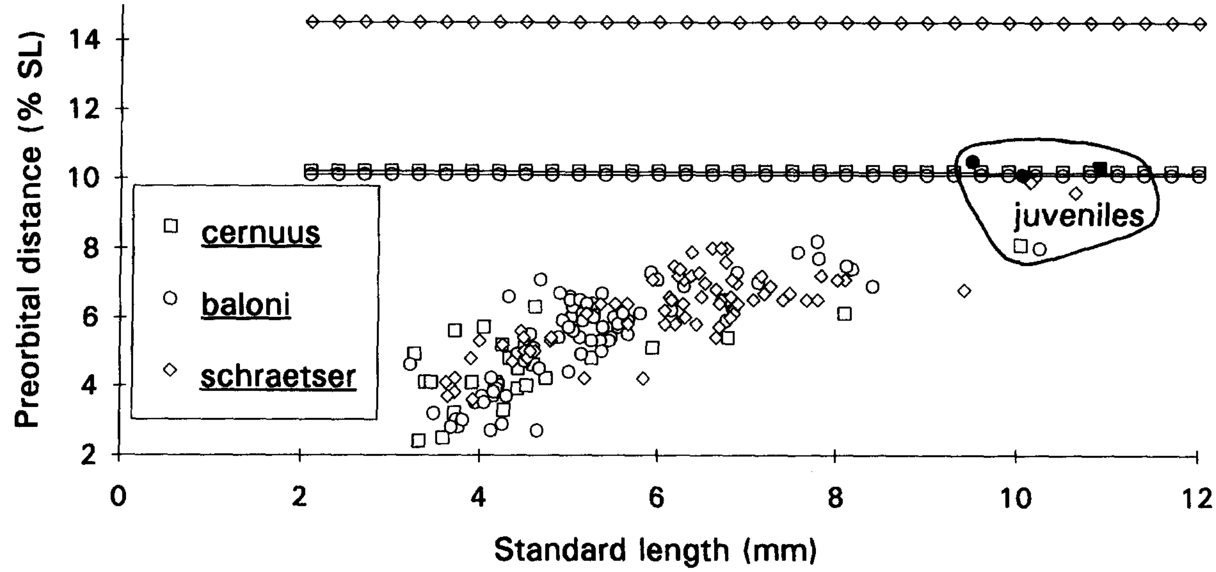

Fig. 11. Changes in relative preorbital distance during early development of three *Gymnocephalus* species (legend as in Fig. 8). Ruff and Balon's ruff already achieve definite (as adults) relative preorbital distance at the start of juvenile period (closed circles and squares). Signs connected with line represent mean relative preorbital distance of adults (data for ruff from Kubina unpublished, for Balon's ruff from Holčík & Hensel 1974, and for yellow pope from Kováč 1992); values for juvenile specimens are inside the area encircled.

for questions in a co-evolving system... Beyond the time scale of generations identical mechanisms are probably responsible for taxonomic divergence and paedomorphosis, i.e. the processes [that] cause change in ontogeny and reproduction may be canalized into the creation of a new taxon. Every successive reproductive cycle, as a consequence of changing genetic and epigenetic variations, will produce both forms with more specialized characters in comparison with previous generations. For example, the larval period will become shorter and shorter, egg number per reproductive cycle lower and lower, but the yolk volume and density will be increasingly higher'.

In the case of the genus *Gymnocephalus*, all of the characteristics cited above are apparent in yellow pope: (1) embryos and larvae grow and develop faster than those of ruff and Balon's ruff (Fig. 9, also Kováč 1992, 1993a, b); (2) females become mature when older and larger (Bastl 1988); (3) absolute and relative fecundity is considerably lower (Bastl 1988); (4) eggs are larger, containing higher amounts of yolk than those of ruff and Balon's ruff (Table 1, also Bastl 1988). Similarly, the eggs of *G. acerinus* are larger and its relative fecundity is lower (Kryzhanovsky et al. 1953).

As already emphasized, most patterns of early development in the three species are very similar. In the evolution of the original genus *Gymnocephalus*, the epigenetic mechanisms, I suggest, appeared very early and caused its split into two evolutionary trajectories (Fig. 10). The altricial trajectory led to the recent subgenus *Acerina,* and the precocial trajectory to the recent subgenus *Gymnocephalus* (both subgenera sensu Holčík & Hensel 1974).

The precocial tendency of the subgenus *Gymnocephalus* also seems to be evident from comparison of development of the preorbital distance. This distance was not very different in all three species throughout early development (Fig. 11), and judging from illustrations of Kryzhanovsky et al. (1953), *G. acerinus* appears to present a similar pattern. I believe, that therefore, the preorbital distance in the ancestor of the original genus *Gymnocephalus* was approximately the same. Furthermore, even at the beginning of the juvenile period, the preorbital distance in yellow pope was very similar to that in both ruff and Balon's ruff (Figs 7, 11). However, in the latter two, the proportion of the preorbital distance averaged 90.2 and 94.1% of the values observed in adults, respectively; whereas in yellow pope the proportion was only 67.6% (Kováč 1992, 1993a,

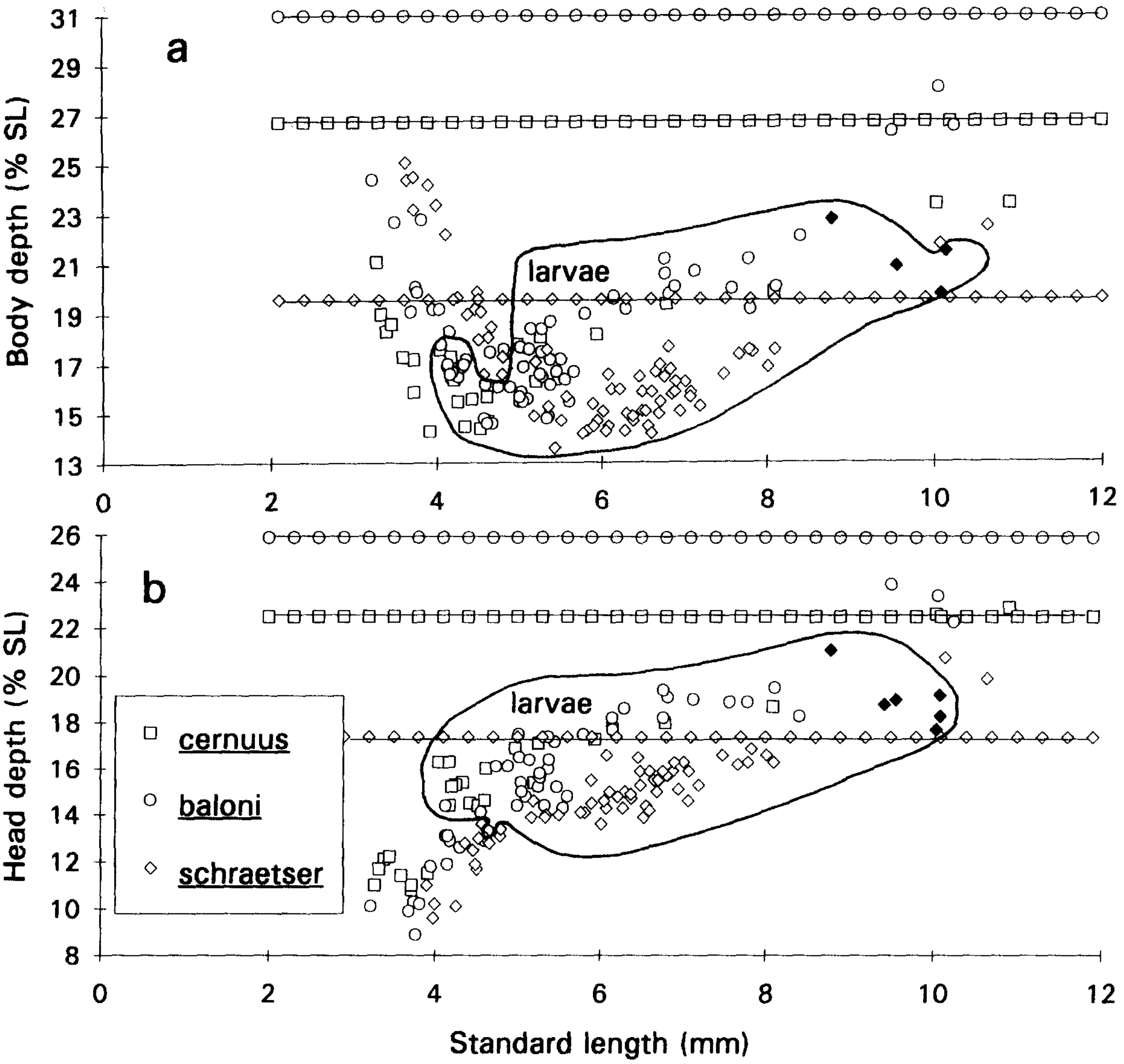

Fig. 12. Changes in relative body depth (a) and head depth (b) during early development of three *Gymnocephalus* species (legend as in Fig. 8). Yellow pope already achieve definite (as adults) relative body depth and head depth at the end of larva period (closed rhombi). Data for adults as in Figure 11; values for larval specimens are inside the area encircled.

b; Fig. 11). Thus, the typical prolongation of the preorbital distance in the subgenus *Gymnocephalus* does not occur earlier than the juvenile period. In other words, the subgenus *Gymnocephalus* presents a deviation from its ancestral state.

Moreover, in comparing the development of morphological characters during early ontogeny with those of adults, I found characters that might suggest the occurrence of juvenilisation (paedomorphosis) in the precocial evolution of the subgenus *Gymnocephalus*. These characters had already attained definite (i.e. adult) proportions during the larva period in yellow pope (unlike ruff and Balon's ruff): (1) protruding upper jaw (Fig. 6c), typical for adults in all four *Gymnocephalus* species; (2) relative body depth (Fig. 12a); and (3) relative head depth (Fig. 12b). The mouth appears during E7. It is terminal and the cranial end of the upper jaw exceeds that of the lower jaw in all three species. Then, during the larva period, a difference between the *Acerina* species and yellow pope appears. In the subgenus *Acerina*, the cranial end of the lower jaw begins to exceed that of the upper jaw, whereas in yellow pope the cranial end of the upper jaw protrudes. If we accept the hypothesis that the genus *Gymnocephalus* apparently derived from *Perca* (Collette & Banarescu 1977, Ráb et al. 1987), then it is obvious that the shape of mouth in *Acerina* larvae represents one of the patterns that reflects phylogenetic relations between these two genera (the same shape of mouth is known both in *Perca* larvae and adults; Kryzhanovsky et al. 1953, Řepa 1969). Thus, it is also obvious that yellow pope larvae show a derived pattern in this respect. Consequently, as the shape of mouth in yellow pope is the same in larvae and adults, I consider this to be an effect of juvenilisation (paedomorphosis). Juvenilisation may transform a precocial specialist back into an altricial generalist; otherwise, excessive specialisation might lead to extinction (Balon 1985). Therefore, I propose that precocially evolving ancestor of the subgenus *Gymnocephalus*, under certain conditions, shifted via juvenilisation towards a less specialized form. This also indicates that juvenilisation may have played an important role in the divergence of the subgenera discussed.

With regard to the subsequent evolution of subgenus *Gymnocephalus*, I agree with Holčík & Hensel (1974), who proposed that after the connections between the rivers Dnepr and Danube had disappeared, the ancestral *Gymnocephalus* form evolved into *G. acerinus* in the former and into *G. schraetser* in the latter. Further evidence of this was reported by Oliva (1959). Comparing mensural and meristic characters, he found that eastern populations of *G. schraetser* had a very obvious relationship to western populations of *G. acerinus*.

During the evolution of subgenus *Acerina*, recent species have not been isolated from each other, and presumably both altricial and precocial tendencies also occur. However, their relationships are so close that the characters liable to reveal evolutionary trajectories are hardly detectable. Nevertheless, a more advanced (derived) karyotype with more metacentric elements (Ráb et al. 1987) and higher amounts of yolk in *G. baloni*, as well as earlier maturity and higher relatively fecundity in *G. cernuus* (Bastl 1988), suggest that the former species has been evolving rather as a precocial specialist and the latter as an altricial generalist (Fig. 10). This hypothesis is also based on one of the main ideas of the alprehost theory, that unlike specialists, the generalists are able to survive in most unpredictably perturbed environments (Balon 1988). An example of this is the success of *G. cernuus* in man-made river reservoirs (Chaban 1959, Bastl 1969, Polivannaya 1974, Kiyashko 1981, Zadorozhnaya & Spanovskaya 1981, Fernando & Holčík 1991). I suggest that *G. cernuus* followed the evolutionary trend of some percids (e.g. *Perca* and *Stizostedion* spp.), enabling them to colonize stagnant waters and to expand their range to lentic environments. However, this trend did not lead towards specialisation but rather enhanced the ecological adaptability of *Perca* and *Stizostedion*. Indeed, these species (as well as *G. cernuus*) have kept the ability to survive and to reproduce in their original riverine environments. On the other hand, precocial *G. baloni* evolved as a specialised rheophil.

Acknowledgements

This article is based on my C.Sc. thesis, which was prepared under the guidance of K. Hensel. M. Peňáz, O. Oliva and I. Bastl contributed with critical comments. G.H. Copp corrected my English text and provided valuable comments. Many thanks to all of them. I also thank J. Černý for help in catching brood stock and fertilizing the eggs, as well as J. Kodada and M. Vater for assisting me in the field. My special thanks are extended to two anonymous reviewers for improvements to the original manuscript.

References cited

Aleyev, Yu. G. 1963. Functional principles of the external construction of fishes. Izd. AN SSSR, Moscow. 248 pp. (In Russian).

Balon, E.K. 1975. Terminology of intervals in fish development. J. Fish. Res. Board Can. 32: 1663–1670.

Balon, E.K. 1981. Saltatory processes and altricial to precocial forms in the ontogeny of fishes. Amer. Zool. 21: 573–596.

Balon, E.K. 1985. Reflection on epigenetic mechanisms: hypotheses and case histories. pp. 239–270. *In:* E.K. Balon (ed.) Early

Life History of Fishes: New Developmental, Ecological and Evolutionary Perspectives, Dr W. Junk Publishers, Dordrecht.

Balon, E.K. 1988. Tao of life: universality of dichotomy in biology, 2. The epigenetic mechanisms. Rivista di biologia/Biology forum 81: 339–380.

Balon, E.K. 1989. The epigenetic mechanisms of bifurcation and alternative life-history styles. pp. 467–501. *In:* M.N. Bruton (ed.) Alternative Life-History Styles of Animals, Kluwer Academic Publishers, Dordrecht.

Balon, E.K. 1990. Epigenesis of an epigeneticist: the development of some alternative concepts on the early ontogeny and evolution of fishes. Guelph Ichthyol. Rev. 1: 1–48.

Bastl, I. 1969. Spawning of pike-perch (*Stizostedion lucioperca* [Linnaeus, 1758]) in bottom nests conditions of the Orava Reservoir (northern Slovakia). Práce Lab. Rybárstva 2: 159–184.

Bastl, I. 1978. Early development of pike-perch *Stizostedion lucioperca* (Linnaeus, 1758) under conditions of Orava Reservoir. Biologické práce 24: 99–179.

Bastl, I. 1988. On the reproduction biology of three *Gymnocephalus* species (Pisces: Percidae). Práce Úst. Rybár. Hydrobiol 6: 9–31.

Chaban, A.P. 1959. On the biology of some fish species from Ust-Kamenogorsk basin. Sb. rabot po ichtiologii i gidrobiologii. Izd. AN Kazach. SSR, Alma Ata 2: 245–255. (In Russian).

Collette, B.B. & P. Banarescu. 1977. Systematics and zoogeography of the fishes of the family Percidae. J. Fish. Res. Board Can. 34: 1450–1463.

Collette, B.B., M.A. Ali, K.E.F. Hokanson, M. Nagiec, S.A. Smirnov, J.E. Thorpe, A.H. Weatherley & J. Willemsen. 1977. Biology of the percids. J. Fish. Res. Board Can. 34: 1890–1899.

Disler, N.N. & S.A. Smirnov. 1977. Sensory organs of the lateral-line canal system in two percids and their importance in behavior. J. Fish. Res. Board Can. 34: 1492–1503.

Elshoud-Oldenhave, M.J.W. & J.W.M. Osse. 1976. Functional morphology of the feeding system in the ruff – *Gymnocephalus cernua* (L., 1758) – (Teleostei, Percidae). J. Morphol. 150: 399–422.

Fernando, C.H. & J. Holčík. 1991. Fish in reservoirs. Int. Revue ges. Hydrobiol. 76: 149–167.

Holčík, J. & K. Hensel. 1974. A new species of *Gymnocephalus* (Pisces: Percidae) from the Danube, with remarks on the genus. Copeia 1974: 471–486.

Kiyashko, V.I. 1981. Diurnal rhythms of the feeding in *Acerina cernua* (L) in the Rybinsk Reservoir. Trudy Inst. Biol. vnutr. Vod. 47: 64–71. (In Russian).

Kováč, V. 1992. Early development of the yellow pope, *Gymnocephalus schraetser*. Folia Zool. 41: 372–385.

Kováč, V. 1993a. Early development of ruff, *Gymnocephalus cernuus*. Folia Zool. 42: 269–280.

Kováč, V. 1993b. Early development of the Balon's ruff, *Gymnocephalus baloni* Holčík & Hensel 1974. Folia Zool. 42: 351–362.

Kryzhanovsky, S.G., N.N. Disler & E.N. Smirnova. 1953. Ecomorphological principles of development in percoids. Trudy Inst. Morf. Zhiv. A.N. Severtsova. 10: 3–138. (In Russian).

Lange, N.O., E.N. Dmitrieva, E.N. Smirnova & M. Peňáz. 1974. Methods of study the morpho-ecological peculiarities of fish development during embryonic, larval and juvenile periods. pp. 56–71. *In:* Standard Methods of Study the Production of Fish Species in Their Distribution Areas, Vilnyus. (In Russian).

McElman, J.F. & E.K. Balon. 1979. Early development of walleye, *Stizostedion vitreum*, with steps of saltatory development. Env. Biol. Fish. 4: 309–348.

Nagy, Š. 1985. The food of three sympatric species of ruffe (*Gymnocephalus cernuus, G. schraetser* and *G. baloni*) in the side arms of the Danube at Baka. Práce Lab. Rybár. Hydrobiol. 5: 101–138. (In Slovak).

Oliva, O. 1959. A note on *Acerina acerina* (Güldenstadt) (Osteichthyes: Percidae). Acta Univ. Carol. – Biologica 3: 165–168.

Paine, M.D. & E.K. Balon. 1984a. Early development of the northern logperch, *Percina caprodes semifasciata,* according to the theory of saltatory ontogeny. Env. Biol. Fish. 11: 173–190.

Paine, M.D. & E.K. Balon. 1984b. Early development of the rainbow darter, *Etheostoma caeruleum,* according to the theory of saltatory ontogeny. Env. Biol. Fish. 11: 277–299.

Polivannaya, M.F. 1974. Feeding of perch and ruff in the zone of effluent from the Kurakhova Power Plant. Hydrobiol. J. 10: 70–71. (In Russian).

Ráb, P., P. Roth & B. Mayr. 1987. Karyotype study of eight species of European percid fishes (Pisces, Percidae). Caryologia 40: 307–318.

Řepa, P. 1969. On the morphology, proportional growth and organogenesis of early stages of the perch (*Perca fluviatilis* [Linnaeus 1758]). Acta Univ. Carol. – Biologica 1969: 61–92.

Zadorozhnaya, E.A. & V.D. Spanovskaya. 1981. Diurnal feeding rhythms and rations of the ruffe *Acerina cernua* (L.) in water storage reservoirs of the Volga river basin. Vopr. Ikhtyol. 21: 665–674. (In Russian).