Arch. Pol. Fish.	Archives of Polish Fisheries	Vol. 16	Fasc. 4	421-436	2008

CHANGES IN MORPHOMETRIC PARAMETERS IN SELECTED EARLY ONTOGENIC STAGES OF THREE FISH SPECIES FROM THE GENUS *LEUCISCUS* (TELEOSTEI, CYPRYNIDAE)

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ABSTRACT. Observations were conducted of the changes in the measurements of selected morphometric characters in embryos and larvae of three closely-related fish species (dace, *Leuciscus leuciscus* (L.), ide, *Leuciscus idus* (L.), European chub, *Leuciscus cephalus* (L.)). It was confirmed that individual development immediately following hatching is fast with rapid changes in body proportions that stem from the development of particular systems. It was also observed that in dace and ide the values of the biometric characters observed were very similar, as were the trends of these changes. Although chub differed insignificantly from the other two species, statistically significant relative values and the character of growth were noted especially with regard to the lowest height of the tail fold, head depth, body depth, and yolk sac length. Differences in body proportions can be explained by the different maintenance strategies of these species during the earliest stages of ontogenesis.

Key words: EMBRYONIC DEVELOPMENT, LARVAL DEVELOPMENT, METAMORPHOSIS, GROWTH, *LEUCISCUS*

INTRODUCTION

Fish from the rheophilic cyprinid group, including dace, *Leuciscus leuciscus* (L.); ide, *Leuciscus idus* (L.); and chub, *Leuciscus cephalus* (L.), have in recent years come under increasing scrutiny from scientists, who, through artificial reproduction and the rearing of stocking material (Kucharczyk 2002, Shiri Harzevili et al. 2003, 2004, Krejszeff et al. 2008), are searching for ways to rebuild often decimated local populations of these species. Many of the environmental adaptations of dace, ide, and chub differ distinctly despite the fish being closely related. These differences are apparent even in the earliest development stages, and are noted, for example, in temperature ranges tolerated by developing embryos or the rates of embryogenesis (Kupren 2005,

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DOI 10.2478/s10086-008-0029-x

Kupren et al. 2008). Since these species are highly sensitive to disadvantageous environmental conditions during metamorphosis, any and all new information regarding embryonic and larval development is crucially important as it influences the results of rearing and provides guidelines for attempts to preserve these species in the natural environment.

Most of the papers regarding embryonic and larval development of the species examined in the current work have been published for ide (Kryzhanovsky 1949, Cala 1970, Florez 1972, Koblickaya 1981, Rechulicz et al. 2002, Ostaszewska et al. 2003) and chub (Kryzhanovsky 1949, Penaz 1968, Penaz and Sterba 1969, Prokes et al. 1978, Koblickaya 1981, Economou et al. 1991, Calta 2000), while fewer have referred to dace (Kennedy 1969, Koblickaya 1981, Mann 1996). Although these publications contain information regarding the earliest life stages, most of them do not analyze changes in quantifiable characters during the earliest stages of ontogenesis, or, if they do, the range is very limited. Because of this, the aim of the current study was to supplement the current cursory knowledge of selected quantifiable characters of the species investigated and to try to relate these characters to the specific living conditions preferred by these very young organisms.

MATERIALS AND METHODS

METHOD FOR OBTAINING HATCHLINGS AND CONDITIONS FOR HOLDING LARVAE

The studies were conducted at the Department of Lake and River Fisheries, University of Warmia and Mazury in Olsztyn. The subject of the observations was hatched embryos and developing larval ide, dace, and chub. The individuals for the studies were obtained by incubating eggs that had been stripped artificially from spawners from the Pasłęka and Wałsza rivers (northern Poland). The hormonal preparation Ovopel (Unic-trade, Hungary) was applied to the male and female spawners of all species to synchronize spawning. The eggs were incubated and the larvae held in 40 l aquaria at a constant water temperature of 15.7°C (Kupren et al. 2008). The studied individuals (approximately 2000 indiv. of each species) were the progeny of 23 dace spawners (13 females and 10 males weighing from 80 to 295 g), 26 ide (12 females and 14 males weighing from 300 to 1150 g), and 15 chub (3 females and 12 males weigh-

ing from 160 to 390 g). The experiment focused on larval development from the moment 5% of individuals had hatched to the moment of full yolk sac resorption in 50% of individuals.

SAMPLING AND ANALYTICAL METHODS

Samples of 30 individuals of each species were collected every morning throughout the experiment, and also at moments when the fish achieved a typical developmental stage. These included hatching (50% of individuals hatched) and the beginning of exogenous feeding (50% of individuals began exogenous feeding). Collected fish were preserved in a 4% formaldehyde solution (Takizawa et al.1994). The larvae were examined under a stereo microscope coupled with a digital camera at magnifications ranging from 10 to 40 times. The characters were measured according to a modification of systems developed for larval carp (Hoda and Tsukahara 1971) and chub (Penaz 1968, Penaz and Sterba 1969) (Fig. 1). The microscope images were analyzed and archived with the DP-Soft program (Olympus, Japan). The absolute values (in mm) obtained of

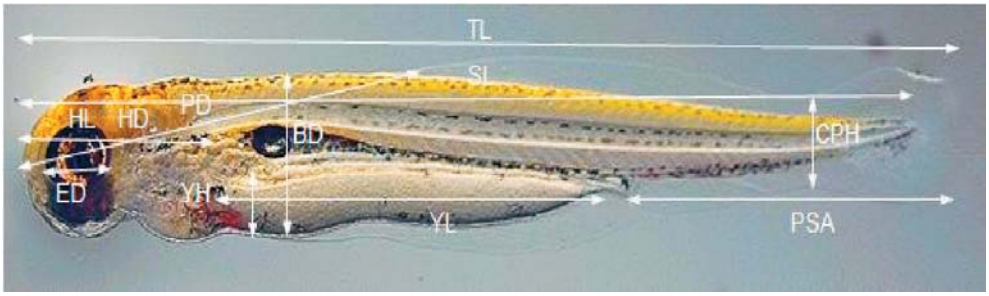

Fig. 1. Analyzed morphometric characters of larval dace, *Leuciscus leuciscus*, ide, *L. idus* and chub, *L. cephalus*. TL – total length, SL – standard length, PD – pre-dorsal distance, PSA – post-anal distance, HL – head length, HD – head depth, BD – body depth, YL – yolk sac length, YH – yolk sac height, ED – eye diameter, CPH – caudal peduncle height.

the various morphometric parameters were used to determine their relative values (% of total length (TL) or head length (HL)) on given days of rearing. These were then compared among the species at selected stages of early ontogenesis. The absolute values of quantifiable characters were compared at the moment of hatching (HAT), on day 11 after fertilization (FER), and the moment when exogenous feeding began (FED).

The patterns of relative growth of were expressed by a power function that considers TL as the standard measurement using non-transformed data:

$$y = a\,x^{b}$$

where: y is the independent variable, x is the dependent variable, a is the intercept, and b is the growth coefficient. Isometric growth occurs when the growth of the dependent variable is proportional to that of standard length (SL) throughout ontogeny (b = 1). Allometric growth is positive when b > 1, and negative when b < 1 (Van Snik et al. 1997).

The analyzed study period during which changes in the parameters of individual characters were observed differed among the three species. The longest was noted for chub (13 days), followed by dace (8.5 days), and was the shortest for ide (7 days). During this period the fish achieved different mean total lengths, the largest of which at the end of the study were noted for dace (9.07 mm), followed by ide (8.65 mm), and the smallest were noted for chub (8.09 mm) (Fig. 2).

ANOVA was used to compare the selected morphometric parameters of the three species, and Duncan's post hoc test was applied when significant values were obtained. However, dependencies among absolute values of selected biometric characters of the developing embryos and larvae and their age (days) were expressed with the linear regression function y = ax + b. The analysis was conducted with STATISTICA 6 and Excel 2003 for Windows.

RESULTS

DACE

Most of the morphometric characters analyzed in dace grew distinctly on subsequent days of the observations (Table 1). More or less pronounced negative allometric growth was noted in SL (Fig. 3), pre-dorsal distance (PD) (Fig. 4), eye diameter (ED) (Fig. 5), and the lowest caudal peduncle height (CPH) (Fig. 6). In the first days following hatching, SL and PD grew distinctly more slowly than TL, but by the end of the observations growth was nearly proportional to TL. Although head depth (HD) growth on subsequent days of the observations did not change as pronouncedly with regard to total length, it still should be placed with the group of negative allometric growth (Fig. 7). Post-anal distance (PSA) (Fig. 8) and head length (HL) (Fig. 9) were allometrically posi-

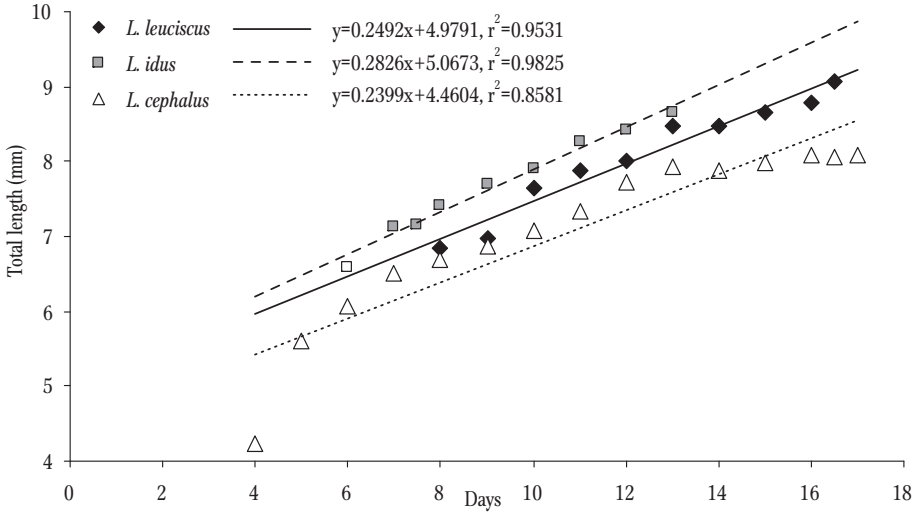

Fig. 2. Increases in total length of dace, *Leuciscus leuciscus*, ide, *L. idus* and chub, *L. cephalus* during early ontogenesis at a temperature of 15.7°C.

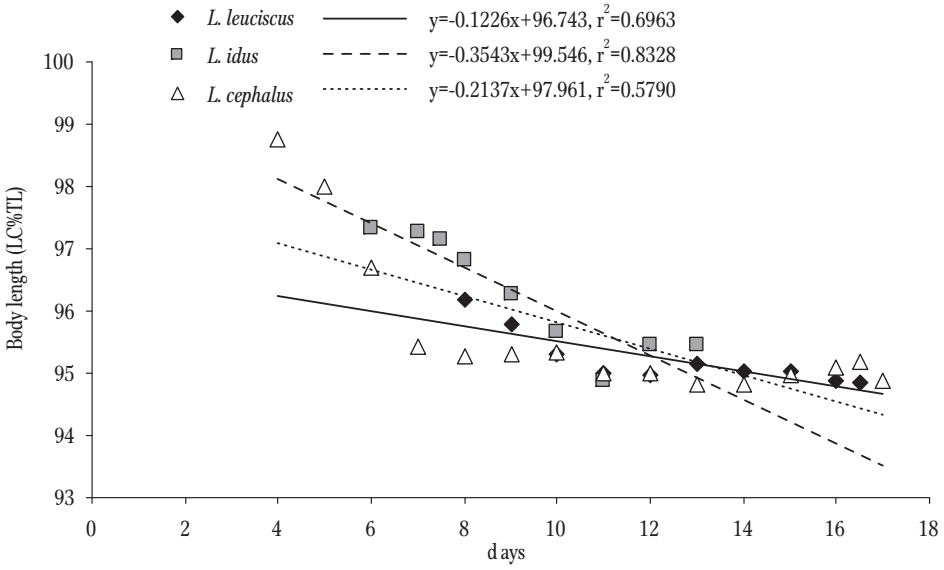

Fig. 3. Changes in the mean body length expressed in % TL during early ontogenesis of dace, *Leuciscus leuciscus*, ide, *L. idus,* and chub, *L. cephalus*.

tive. In turn, body depth (BD) (Fig. 10), yolk sac length (YL) (Fig. 11), and yolk sac height (YH) (Fig. 12) decreased very rapidly on the subsequent days of observation.

TABLE 1

Values of growth coefficient (b) obtained by fitting the power function among chosen body parameters and total length or head length (only ED) of dace, *Leuciscus leuciscus*, ide, *L. idus*, and chub, *L. cephalus*

	Dace		Ide		Chub	
Biometric character	b	r^2	b	r^2	b	r^2
Standard length (SL)	0.97	0.99	0.92	0.99	0.94	0.99
Pre-dorsal distance (PD)	0.81	0.77	0.72	0.74	0.69	0.93
Post-anal distance (PSA)	1.20	0.90	1.28	0.94	1.65	0.98
Head length (HL)	1.02	0.77	1.33	0.60	1.10	0.63
Head depth (HD)	0.77	0.72	0.86	0.78	1.65	0.98
Body depth (BD)	-0.51	0.18	-0.57	0.36	-0.68	0.76
Eye diameter (ED)	0.59	0.51	0.57	0.75	0.81	0.71
Lowest caudal peduncle height (CPH)	0.39	0.2	0.19	0.049	0.37	0.16

IDE

Most of the morphometric characters analyzed in ide grew distinctly on subsequent days of the observations (Table 1). Five of these characters exhibited more or less pronounced negative allometric growth. Among these were SL (Fig. 3), PD (Fig. 4), ED (Fig. 5), CPH (Fig. 6), and HD (Fig. 7). In the first days after hatch, SL and PD grew dis-

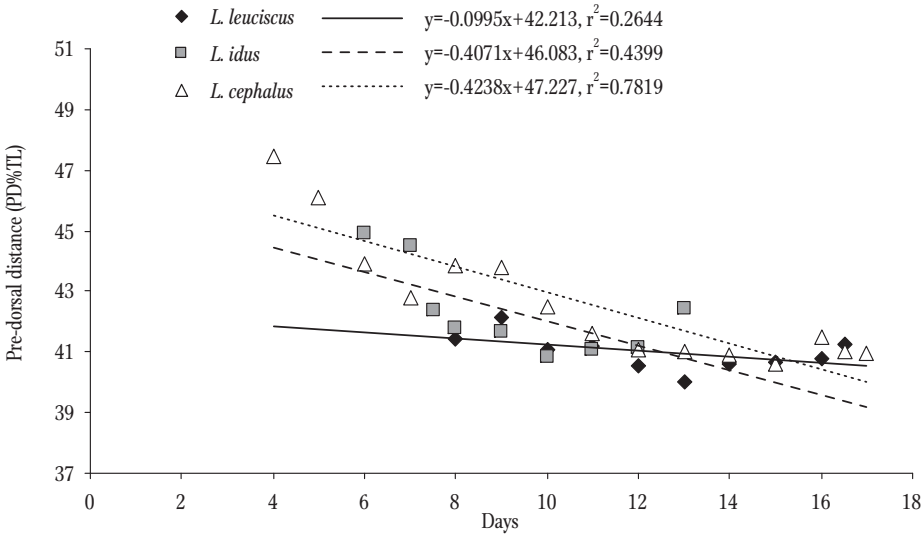

Fig. 4. Changes in the mean pre-dorsal distance expressed in % TL during early ontogenesis of dace, *Leuciscus leuciscus*, ide, *L. idus*, and chub, *L. cephalus*.

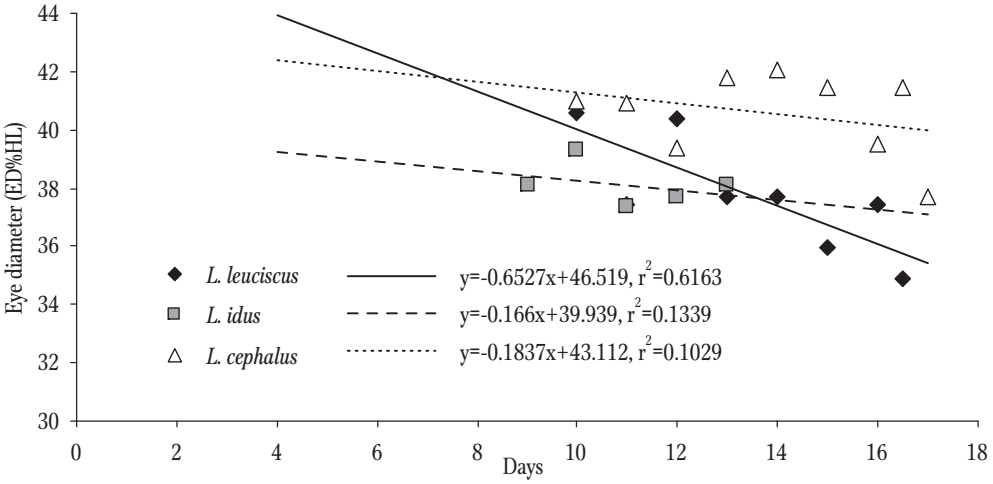

Fig. 5. Changes in mean eye diameter expressed in % TL during early ontogenesis of dace, *Leuciscus leuciscus*, ide, *L. idus*, and chub, *L. cephalus*.

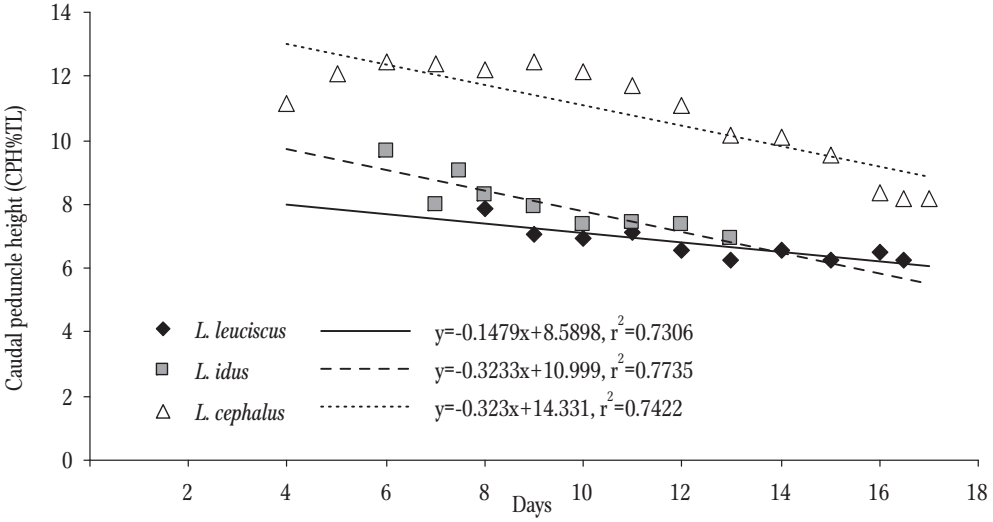

Fig. 6. Changes in mean caudal peduncle height expressed in % TL during early ontogenesis of dace, *Leuciscus leuciscus*, ide, *L. idus*, and chub, *L. cephalus*.

tinctly more slowly than total length, but by the end of the observation period their growth was nearly proportional to that of TL. Both post-anal distance (PSA) (Fig. 8) and head length (HL) (Fig. 9) were clearly allometrically positive. On subsequent days of

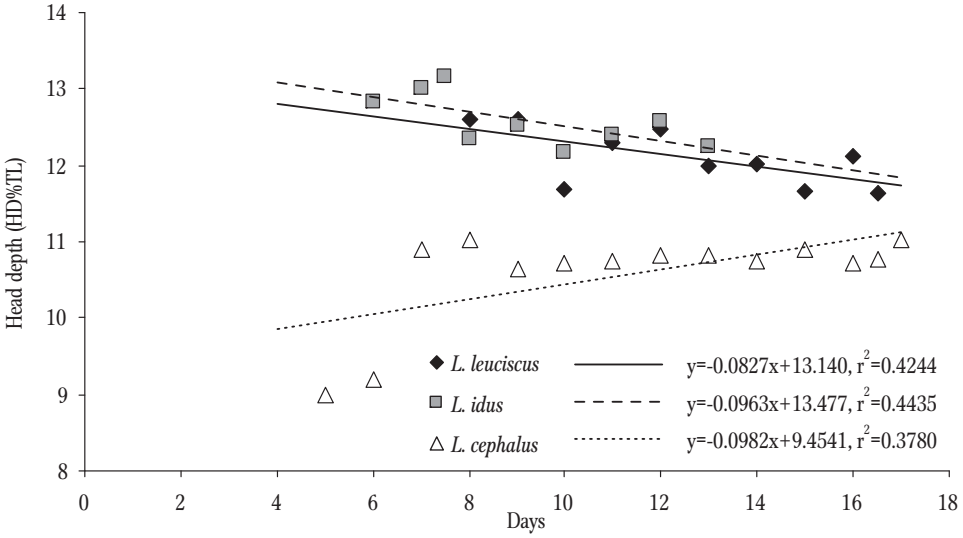

Fig. 7. Changes in mean head depth expressed in % TL during early ontogenesis of dace, *Leuciscus leuciscus*, ide, *L. idus*, and chub, *L. cephalus*.

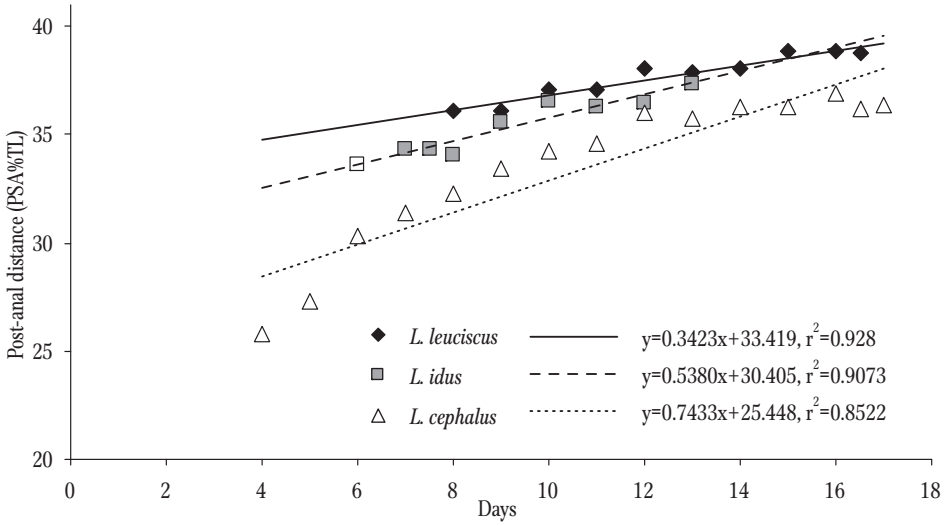

Fig. 8. Changes in mean post-anal distance expressed in % TL during early ontogenesis of dace, *Leuciscus leuciscus*, ide, *L. idus*, and chub, *L. cephalus*.

observation body depth (BD) (Fig. 10), yolk sac length (YL) (Fig. 11), and yolk sac height (YH) (Fig. 12) all decreased rapidly accompanied by a very clear downward trend in relative values.

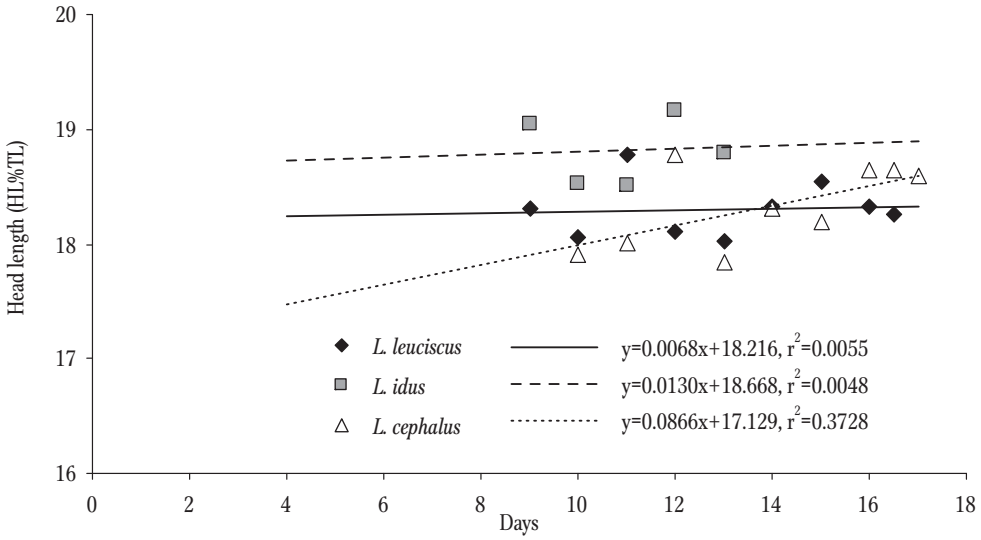

Fig. 9. Changes in mean head length expressed in % TL during early ontogenesis of dace, *Leuciscus leuciscus*, ide, *L. idus*, and chub, *L. cephalus*.

CHUB

Among the ten biometric characters analyzed, four exhibited negative allometric growth (Table 1). Among these were SL (Fig. 3), PD (Fig. 4), and ED (Fig. 5). Decreases in the absolute values of the first two were distinct in the first days after emerging from the egg membrane, but by the end of the observations these exhibited nearly proportional growth to total length. The changes in the lowest caudal peduncle height (CPH) were different (Fig. 6). Despite the slightly slower growth of this character with regard to TL throughout the observation period (coefficient b = 0.32), the absolute values of this distance in the beginning period increased so distinctly that a rapid decrease began after day 6 following hatch. The highest relative value of this character was about 12%, which decreased to about 8% at the end of the study. Positive allometric growth was noted for head height (Fig. 7), post-anal distance (Fig. 8), and head length (Fig. 9). These increases were particularly dynamic, as was indicated by the growth parameters (the values of b for these characters were, accordingly, 1.65, 1.10, and 1.65) (Table 1). Body depth (BD) (Fig. 10), yolk sac length (YL) (Fig. 11), and yolk sac height (YH) (Fig. 12) decreased drastically on subsequent days of the observation as the development of the young organisms progressed. These often reached absolute values of zero (YL, YH), which disallowed determining the precise character of their growth.

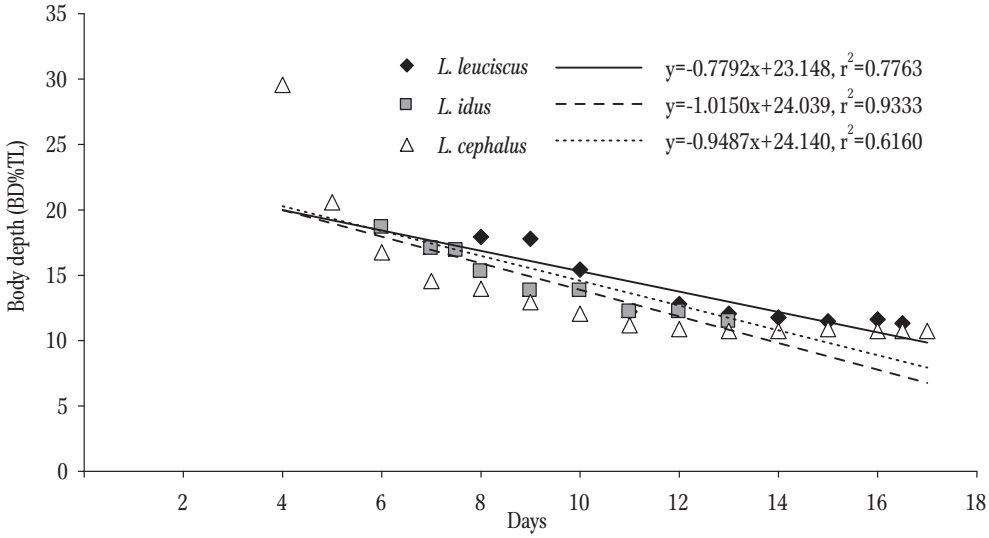

Fig. 10. Changes in mean values and body depth expressed in % TL during early ontogenesis of dace, *Leuciscus leuciscus*, ide, *L. idus*, and chub, *L. cephalus*.

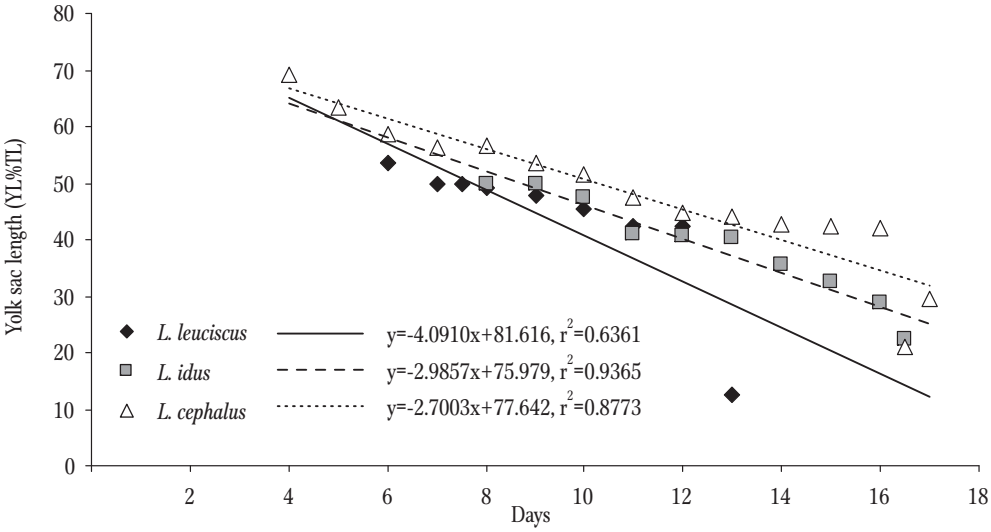

Fig. 11. Changes in mean yolk sac length expressed in % TL during early ontogenesis of dace, *Leuciscus leuciscus*, ide, *L. idus*, and chub, *L. cephalus*.

In addition to the differences in the tendencies and dynamics of change of the individual biometric characters, the absolute values of the species studied also differed at selected moments of development (Table 2). Differences in the individual parameters

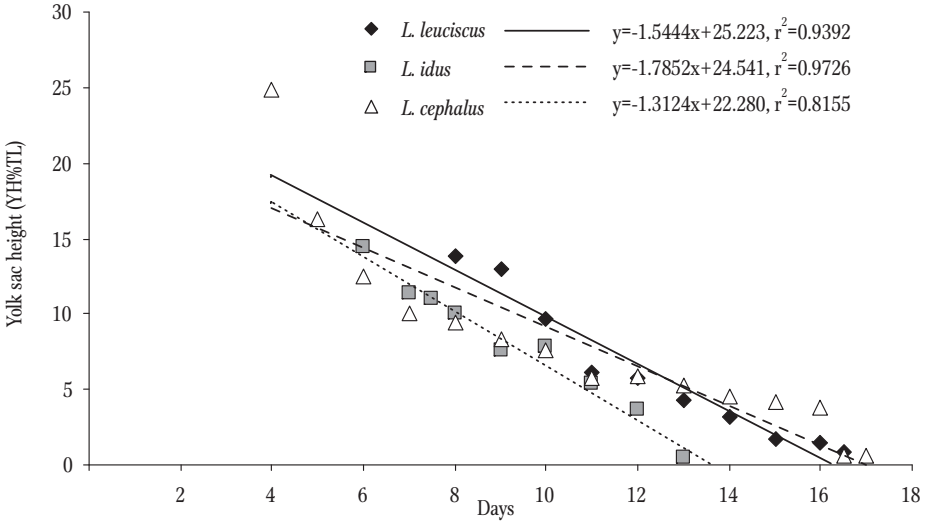

Fig. 12. Changes in mean yolk sac height expressed in % TL during early ontogenesis of dace, *Leuciscus leuciscus*, ide, *L. idus*, and chub, *L. cephalus*.

expressed in relation to total length were usually very distinct immediately following hatching, but by the time exogenous feeding began they occurred much less frequently. Dace and ide had similar body proportions, and statistically significant differences were noted when exogenous feeding began only with regard to characters such as PSA, HL, and CPH ($P < 0.05$). The values of parameters SL, HL, PD, ED in larval chub were similar to those of the other two species (Table 2).

DISCUSSION

Based on the results obtained, it is clear that the most dynamic changes in the analyzed morphometric parameters of dace, ide, and chub occurred in the first days following hatching (approximately 10-11 days after fertilization), which can be explained by the necessity of adapting to new environmental conditions. The survival of the organism that has just emerged from the egg membrane and encounters wholly new living conditions is dependent on rapid changes in breathing and feeding strategies and improving motility (El-Fiky and Wieser 1988, Van Snik et al. 1997, Nunc et al. 2002). The rapid changes in the biometric characters of the species in the current study that were observed in the first days following hatching are also typical of the development of many other fish species (Hoda and Tsukahara 1971, Osse and Van den Boogaart 1995, Van Snik et al. 1997, Gisbert 1999).

TABLE 2

Mean relative values (in % TL or HL) of selected biometric characters of dace, *Leuciscus leuciscus*, ide, *L. idus*, and chub, *L. cephalus* at the moment of hatching (HAT), on day 11 after fertilization (FER) and the moment when exogenous feeding began (FED). The lack of values for HL%TL and ED%HL resulted from difficulties with taking precise measurements of head length

Biometric parameters	Dace	Ide	Chub
	HAT		
SL%TL	$95.3^{a} \pm 0.5$	$97.3^{b} \pm 0.7$	$98.0^{c} \pm 0.3$
PD%TL	$41.1^{a} \pm 1.5$	$44.5^{b} \pm 1.8$	$46.1^{b} \pm 1.0$
PSA%TL	$37.1^{a} \pm 1.0$	$34.3^{b} \pm 0.9$	$27.3^{c} \pm 0.6$
HL%TL	-	-	-
HD%TL	$11.7^{a} \pm 0.3$	$13.0^{b} \pm 0.9$	$9.0^{c} \pm 0.7$
BD%TL	$15.4^{a} \pm 1.0$	$17.0^{b} \pm 1.5$	$20.6^{c} \pm 1.3$
YL%TL	$47.3^{a} \pm 1.4$	$49.8^{b} \pm 1.2$	$63.3^{c} \pm 1.0$
YH%TL	$9.6^{a} \pm 1.1$	$11.4^{b} \pm 1.6$	$12.5^{c} \pm 1.2$
ED%HL	-	-	-
CPH%TL	$6.9^{a} \pm 0.4$	$8.0^{b} \pm 0.7$	$12.1^{c} \pm 0.6$
	FER		
SL%TL	$95.0^{a} \pm 0.4$	$94.9^{a} \pm 1.0$	$95.0^{a} \pm 0.3$
PD%TL	$41.2^{a} \pm 1.5$	$41.1^{a} \pm 1.7$	$41.6^{a} \pm 1.3$
PSA%TL	$37.1^{a} \pm 0.9$	$36.3^{b} \pm 0.7$	$34.6^{c} \pm 0.4$
HL%TL	$18.8^{a} \pm 0.3$	$18.5^{a} \pm 0.7$	$18.0^{a} \pm 0.7$
HD%TL	$12.3^{a} \pm .0.4$	$12.4^{a} \pm 0.5$	$10.7^{b} \pm 0.4$
BD%TL	$12.3^{a} \pm 1.0$	$12.2^{a} \pm 0.4$	$11.2^{b} \pm 0.4$
YL%TL	$41.1^{a} \pm 1.1$	$42.8^{a} \pm 0.8$	$47.6^{b} \pm 0.8$
YH%TL	$6.2^{a} \pm 2.1$	$5.4^{a} \pm 0.8$	$5.8^{a} \pm 0.1$
ED%HL	$37.4^{a} \pm 1.1$	$37.4^{a} \pm 1.5$	$40.9^{b} \pm 0.3$
CPH%TL	$7.1^{a} \pm 0.4$	$7.5^{a} \pm 0.4$	$11.7^{b} \pm 0.3$
	FED		
SL%TL	$95.2^{a} \pm 0.8$	$95.5^{a} \pm 0.4$	$94.9^{a} \pm 0.5$
PD%TL	$40.0^{a} \pm 0.9$	$41.1^{a} \pm 1.1$	$41.0^{a} \pm 1.0$
PSA%TL	$37.9^{a} \pm 0.7$	$36.4^{b} \pm 0.6$	$36.4^{b} \pm 1.0$
HL%TL	$18.0^{a} \pm 0.2$	$19.2^{b} \pm 1.0$	$18.6^{ab} \pm 0.4$
HD%TL	$12.0^{a} \pm 0.5$	$12.6^{a} \pm 0.2$	$11.0^{b} \pm 0.4$
BD%TL	$12.0^{a} \pm 1.0$	$12.2^{a} \pm 0.2$	$10.7^{b} \pm 0.7$
YL%TL	$40.4^{a} \pm 2.0$	$42.2^{a} \pm 2.0$	$29.4^{b} \pm 18.5$
YH%TL	$4.3^{a} \pm 1.3$	$3.6^{a} \pm 0.6$	$0.6^{b} \pm 0.2$
ED%HL	$37.7^{a} \pm 1.1$	$37.7^{a} \pm 1.6$	$37.7^{a} \pm 3.5$
CPH%TL	$6.3^{a} \pm 0.4$	$7.4^{b} \pm 0.2$	$8.2^{c} \pm 0.3$

The most dynamic growth in all three species during the period between hatching and yolk resorption was noted in the post-anal distance (PSA). This tendency is characteristic of all species whose anterior body section (snout to anus) following hatch is longer than the posterior one (e.g., *Esox lucius* (L.), *Coregonus albula* (L.), *Cyprinidae*). The

opposite occurs in species like *Percidae*, and *Lota lota* (L.), in which the posterior part of the body is longer following hatch (Urho 2002). Rapid development of the posterior section of the body, which is used for motility, is one of the developmental priorities of newly hatched fish. Being capable of active swimming permits the organisms to obtain food and avoid predators (Van Snik et al.1997, Gisbert 1999).

The other quantifiable characteristics analyzed in the species studied that grew faster than TL were those that characterized head development, including length (dace, ide, chub) and depth (chub). In the present study, the allometric growth observed was certainly linked to the dynamic development of the respiratory and alimentary systems. The relatively small, undeveloped heads of newly hatched fish must, in a short span of time, grow enough to provide space for the intensely developing gills and to ensure that it is possible to ingest increasingly large food particles (Van Snik et al.1997, Gisbert 1999).

Differences in the relative values of the morphometric parameters analyzed in the studied species were usually very distinct at hatching. Over time, these became less apparent and at the moment exogenous feeding began they usually did not occur. The distinct differences at the beginning of the observations were due to the differences in the degree of development of the individual species at the moment they hatched (Kupren et al. 2008).

The fewest differences in body proportions during early ontogenesis were noted between larval dace and ide. During the observation period, all of the analyzed characters of these species were of similar magnitudes and directions of change. While the biometric characters of embryonic dace and ide in the most significant moments of development did not differ significantly statistically, by comparison chub exhibited not only statistically significant differences in the relative values obtained, but also in the direction and magnitude of these changes. The differences in body proportions that are detectable among chub and dace and ide are partially confirmed by the study results of Penaz and Sterba (1969). The relative values of selected biometric character of chub are nearly identical to those noted in the current study.

The build of chub in the early stages of ontogenesis is adapted for inhabiting fast-flowing bottom waters. The streamlined embryonic and larval body shape (lowest head and body depth and longest yolk sac) that is achieved shortly after hatching undoubtedly eases hiding and moving among the small pebbles on the bottom (Kryzhanovsky 1949, Economou 1991, Calta 2000). The slight motor activity manifested at this stage of life is probably due to the influence of the body shape. Among the three species studied, larval chub had the lowest relative post-anal distance and the

highest caudal peduncle with an embryonic fold. Such a wide fold increases the body surface area, thus effectively aiding respiration (Van Snik et al. 1997). The slight activity mentioned above is largely responsible for rapid forward movements that are repeated from time to time. This probably helps prevent silt from accumulating on the fish as they gather in groups (Economou 1991, Calta 2000).

Among the species analyzed from the genus *Leuciscus*, dace is the best adapted for moving in water currents immediately after hatching. This is thanks to its long tail (highest relative post-anal distance) with the most differentiated fin fold (smallest tail fold width) that enables relatively effective swimming similar in character to that of adult specimens (Van Snik et al.1997). The motility demonstrated is good for this stage of development and is probably an adaptation to the conditions experienced by the freshly hatched embryos that are swept away on river currents to calmer areas, where the swim bladder inflates very quickly and the fish begin to feed (Kennedy 1969, Mann 1996, Kupren et al. 2008).

The behavior of embryonic ide after they beginning active swimming (at approximately day 11 at a temperature of 15.7°C) is very similar to that observed in dace (Kryzhanovsky 1949, Mann 1996). This is why the biometric characters of these two species are nearly identical during this period. The differences observed slightly earlier are manifested above all else in the larger yolk sac dimensions and the shorter, less differentiated tail fin fold, as well as the more dynamic tendency in the changes of other quantifiable characters. These are probably linked to ide hatching much earlier than dace, which means that they are developed to a far lesser degree after hatching (Kupren et al. 2008). This indisposition to new living conditions during the first part of metamorphosis forces the embryo to take a longer rest period, which it is able to do thanks to the adhesive glands that allows it to attach to submerged substrate (Kryzhanovsky 1949, Balon 1975, Mann 1996, Kupren et al. 2008).

The study results presented indicate that the slightly different environmental conditions within a single river ecosystem have forced organisms inhabiting them to develop various types of indistinct, and often very subtle, morphological adaptations over the course of hundreds of thousands of years of species specialization that permit them to exploit these differences optimally. The differences occurring among representatives of systematically close species that are apparent in the morphological structure at such early stages of ontogenesis once again confirms that fish are highly capable of adaptation.

ACKNOWLEDGEMENTS

The study was financed as part of the project "Thermal conditions of the embryonic development of fish from the genus Leuciscus" No. 2PO4F07727 by the State Committee for Scientific Research and "Optimizing the production of rheophilic cyprinid fish stocking material under controlled conditions", Sectoral Operational Programme "Fisheries and Fish Processing 2004-2006" (00040-61535-OR1400009/07)

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Received – 11 September 2008

Accepted – 26 October 2008

STRESZCZENIE

ZMIANY PARAMETRÓW MORFOMETRYCZNYCH WYBRANYCH WCZESNYCH STADIÓW ONTOGENEZY TRZECH GATUNKÓW RYB Z RODZAJU *LEUCISCUS* (TELEOSTEI, CYPRYNIDAE)

Przeprowadzono obserwacje poświęcone zmianom wartości wybranych cech morfometrycznych przetrzymywanych w warunkach laboratoryjnych embrionów i larw trzech blisko spokrewnionych gatunków tj. jelca *Leuciscus leuciscus* (L.), jazia *Leuciscus idus* (L.) oraz klenia *Leuciscus cephalus* (L.). Potwierdzono, że rozwój osobniczy ryb zaraz po wykluciu związany jest z szybkimi i bardzo gwałtownymi zmianami proporcji ciała, które wynikają z rozwoju i doskonalenia poszczególnych układów. Dla określenia charakteru wzrostu danej cechy względem długości całkowitej posłużono się funkcją potęgową. Wykazano, że większość spośród analizowanych cech biomerycznych wykazywało wzrost allometryczny ujemny (SL, PD, ED, CPH). Natomiast szybszy wzrost niż długość całkowita ciała charakteryzował takie cechy jak PSA i HL Zaobserwowano, że analizowane cechy biometryczne zarówno jelca jak i jazia wykazywały po wykluciu bardzo duże podobieństwo w osiąganych wartościach oraz tendencji tych zmian. Kleń różnił się nieznacznie, ale istotnie statystycznie, od pozostałych dwóch gatunków wartościami względnymi oraz charakterem wzrostu, szczególnie takich parametrów jak CPH, HD, YH i BD. Zaobserwowane różnice w proporcjach ciała pomagają wytłumaczyć odmienne strategie zachowawcze tych gatunków podczas najwcześniejszych etapów ontogenezy.