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Short communication

BIPARTITY OF THE YOLK SAC IN CYPRINID EMBRYOS

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ABSTRACT. Studies on fish embryogenesis have demonstrated that, although the yolk sac in most fish is spherical or subspherical and is definitely uniform in its architecture throughout, its shape in some cyprinid species (bream, sun bass, bleak and others) changes considerably during late organogenesis. The changes involve a rapid and conspicuous division of the yolk into two parts; the proximal one occupies about three quarters of the yolk volume and is spherical, while the caudal part, a quarter of the yolk volume, becomes elongated or even cylindrical. The yolk sac walls in the caudal part were observed to pulsate rhythmically, thus preceding the pulsation of the budding heart. It may be contended that the yolk sac wall pulsation causes mixing of the internal fluids in the developing embryo, an activity and role preceding that played by the central part of the emerging circulatory system, i.e., the heart.

Key words: CYPRINIDS, EMBRYOGENESIS, YOLK SAC BIPARTITY, ROLE

In teleost fish, the yolk occupies more than 90% of the egg cell. Initially, during embryogenesis, the yolk is covered by a thin ectoplasm layer which, shortly after the egg has been activated and hydrated and as a result of complex changes, develops into a reception mound which will later evolve into the embryonic disc and the embryo itself.

The yolk is a storage site for substances supplying the developing embryo, and later the larva - freshly out of the egg membranes - with nourishment and energy. Consequently, as the organism develops, the yolk is resorbed at an ever increasing rate. In most fish species, the yolk sac retains a more or less spherical shape until the yolk is entirely resorbed. However, occasionally, and particularly during the later stages of embryonic development and immediately after hatch, the yolk sac becomes oval, pear-shaped, or cylindrical.

Our earlier studies on morphomechanical peculiarities of fish embryonic development provided evidence of a specific yolk sac bipartity in some teleost fish species (Winnicki and Korzelecka 1997, Korzelecka and Winnicki 1998, Bonisławska et al. 1999). Similar observations were reported earlier by other scientists investigating fish embryogenesis (Dziekońska 1956, Gosteeva 1956, Smirnova 1961, Prokeš and Peňáz 1980).

Thus, the present paper attempts to investigate and describe this phenomenon in more detail and strives to look into the mechanisms of formation and the biological sense of the structural feature in question.

The study was based on observations of eggs of bleak (*Alburnus alburnus* (L.)), rudd (*Scardinius erythrophthalmus* (L.)), sun bass (*Leucaspius delineatus* (Heck.)), and bream (*Abramis brama* (L.)). The eggs of the first three species were studied at a field laboratory situated in the vicinity of Krzemień Lake by Sieraków (central Poland), while the bream eggs were examined in the constant temperature room of the Department of Fish Anatomy and Embryology.

The fish eggs and sperm were recovered from ready-to-spawn spawners. The *in vitro* fertilized eggs of bleak and sun bass were incubated after placing them on special nets hung in aquaria filled with lake water maintained at the optimal temperature (Table 1). This ensured that the conditions for egg development were identical to those in the lake.

TABLE 1

Incubation water temperature

Species	Incubation temperature (°C)
Alburnus alburnus (L.)	21 ± 1
Abramis brama (L.)	15 ± 1
Scardinius erythrophthalmus (L.)	21 ± 1
Leucaspius delineatus (Heck.)	20 ± 1

The bream eggs were incubated in tap water which had been filtered and aerated to ensure the appropriate quality. Changes in the yolk sac shape during embryogenesis were followed using methods which had been employed earlier (Winnicki and Korzelecka 1997), so that the developing eggs were continuously observed and embryogenesis monitored and examined in horizontal and vertical light beams. The images were recorded on video and stored in a computer memory. This permitted detailed, frame-by-frame analysis of the images and allowed for the dynamics of the structural and spatial changes in the egg to be followed.

The yolk sac bipartity involves the appearance at a certain moment in embryonic development of a clear constriction which divides the sac into two unequal parts (Fig. 1). The anterior (proximal) part contains about three-quarters of the yolk mass, and the caudal part contains the remaining quarter.

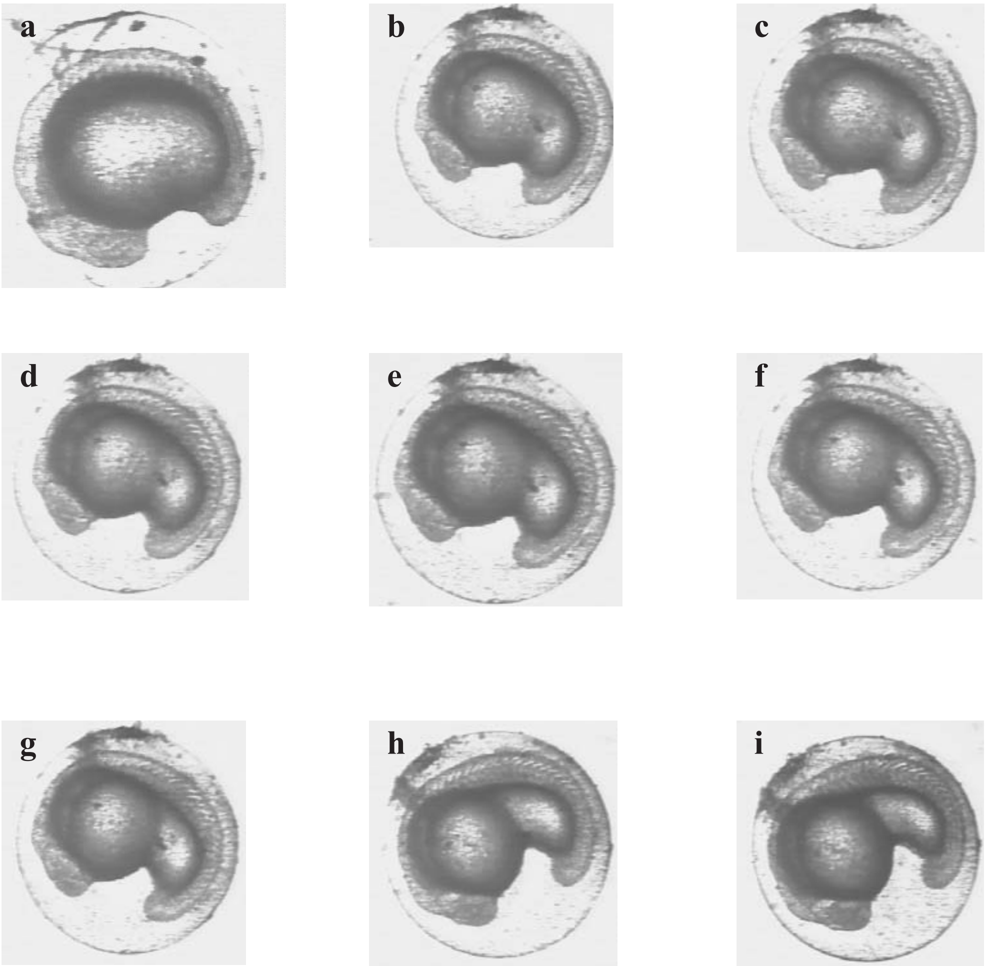

Fig. 1. Bleak (*Alburnus alburnus* (L.)): formation of caudal part of the yolk sac; a 10 min-interval frame--by-frame sequence; viewed from above.

It was characteristic that the yolk sac division occurred at almost the same point during embryogenesis. As shown by Fig. 2, the division took place after the embryogenesis process had been underway for about 30% of its total duration (following activation). Moreover, it can be seen that in all the species whose eggs were examined the constriction in and the division of the yolk sac preceded the appearance of the budding heart. The *in vivo* observations demonstrated that once the yolk sac had become bipartite its caudal part began to pulsate at a slow but fairly regularly rate, and that

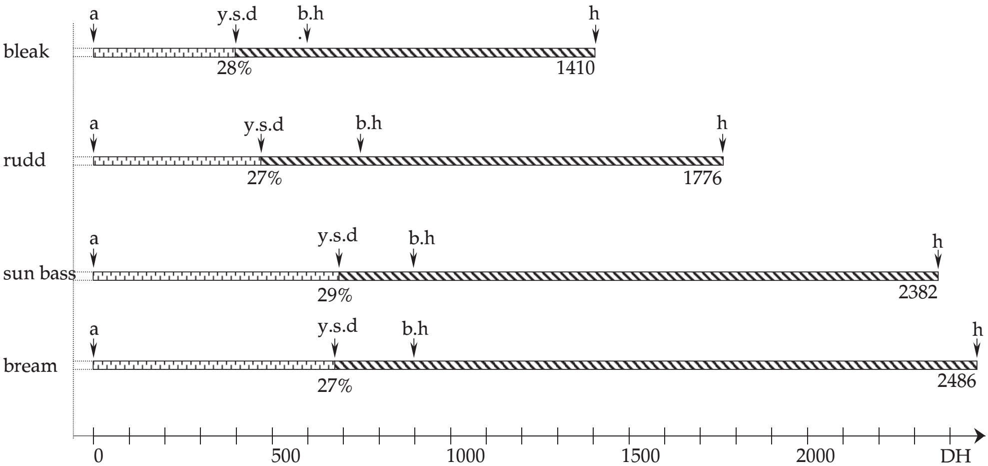

Fig. 2. Duration of embryonic development as expressed in thermal units (degree-hours; DH) and the moment of yolk sac constriction: percentage of the length of time elapsed from activation to constriction; a – activation; y.s.d. – yolk sac division; b.h. – budding heart; h – hatch.

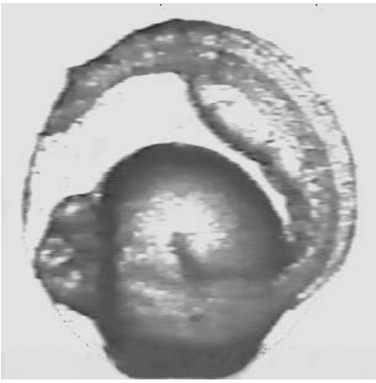

Fig. 3. Sun bass (*Leucaspius delineatus* (Heck.)): the spherical (proximal) and cylindrical (caudal) parts of the yolk sac.

the pulsation preceded that performed by both the budding and fully-formed heart (Korzelecka 1999).

The proximal part of the yolk sac retained its spherical shape throughout embryonic development (until hatch), its size and volume gradually diminishing. At the same time, the initially elongated caudal part gradually turned cylindrical (Fig. 3), as the embryo resting on it grew in length.

Towards the end of embryonic development, the embryo bent its body by 90°, in a bilateral symmetry plane, at the place where the yolk sac constricted (Fig. 4).

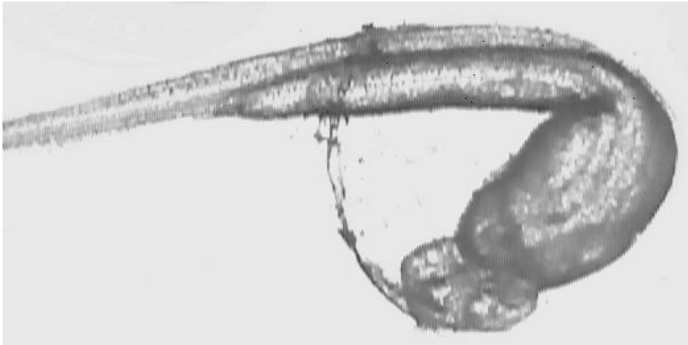

Fig. 4. Bleak (*Alburnus alburnus* (L.)): embryonic body at the site of yolk sac constriction.

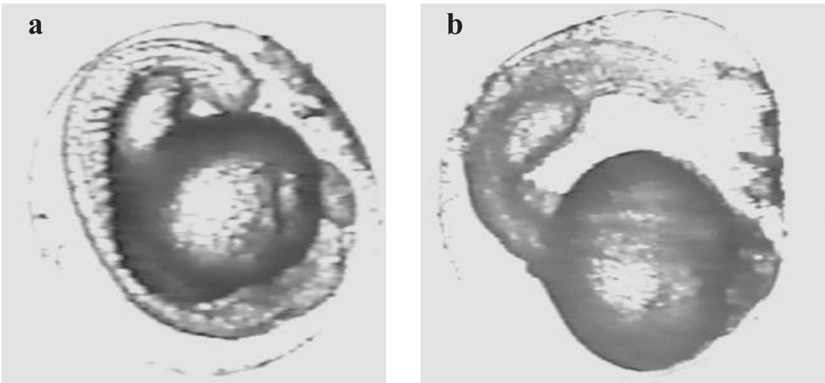

Fig. 5. Positioning of a relatively long bream (*Abramis brama* (L.)) embryo in the egg at the terminal stage of embryogenesis.

It is worth mentioning that the process of yolk sac constriction and division is rapid, taking as little as 30 degree-hours (DH).

Before any biological interpretation of the morphomechanical phenomena in the cyprinid egg, described above, is attempted, it is necessary to cite several well-known facts pertaining to cyprinid embryogenesis and to relate them to environmental conditions under which embryonic development usually proceeds.

The first fact concerns the size of the eggs examined; as a rule, they are small, which seems obvious, since embryonic development takes place at fairly high temperatures. The direct relationship between the S/V (surface/volume) ratio and the rate and amount of oxygen supply to the tissues of a developing embryo has already been established (Bonisławska and Winnicki 2000). On the other hand, as temperature increases, metabolic processes speed up as well. Hence, an increased S/V ratio is one of the means for an individual to survive and develop. This is indeed the case as the eggs of fish species, including those examined in the current study, which develop in high water temperatures are usually small. This strategy is insufficient, so cyprinids evolved an additional way to improve their chances by maximally reducing the size of their egg cells which occupy as little as one-third of the volume of the already minute eggs, thus rendering their S/V ratio still more advantageous. However, their survival strategies are not limited to just this. It turns out that the tiny egg (containing a minute egg cell) develops a relatively large perivitelline space that houses the embryo until it is fully formed and capable of independent life in the water once released from the egg membranes.

This is important because the embryo grows rapidly. As its size increases, the embryo's body has to bend sharply. This could not be achieved if the embryo rested on a uniformly spherical yolk sac all the time. The possibility of bending is provided by yolk sac constriction, whereby the yolk sac divides into two parts. One of them is cylindrical in shape and rapidly reduces its diameter and elongates. The elongation accompanies the rapidly growing caudal part of the embryo. Following yolk resorption, the yolk sac part in question is transformed into the caudal part of the hatching larva's body cavity (Fig. 5). If the division did not occur, it would be impossible for the embryo to bend and to position its body, which is three times the length of the diameter of the egg, equatorially around the yolk sphere (proximal part of the yolk sac) (Fig. 6), which diminishes in size over time. Additionally, this body positioning makes somatic embryonic movements possible as well.

Besides, the yolk sac's caudal section – through its quasi-peristaltic, rhythmical pulsation (Korzelecka 1999) – sets the embryo's internal fluids in motion. In this way it precedes the future function of specialized organs (the budding and the fully-developed heart) which will soon appear.

It seems thus that yolk sac bipartity serves two biological functions: it allows a large embryo to become "packed" within the relatively small space of the egg membrane confines and sets in motion the embryo's internal fluids during a period of intensified gas exchange rate, thereby providing conditions for internal respiration (impossible to achieve by means of regular diffusion).

Consequently, yolk sac bipartity, specific to numerous cyprinids, can be regarded as an expression of temporary morphofunctional adaptations, or idioadaptations in the terminology introduced by Severcov (1967a, b). These adaptations may, at some point in the future, prove to be a permanent evolutionary achievement of some cyprinid taxa.

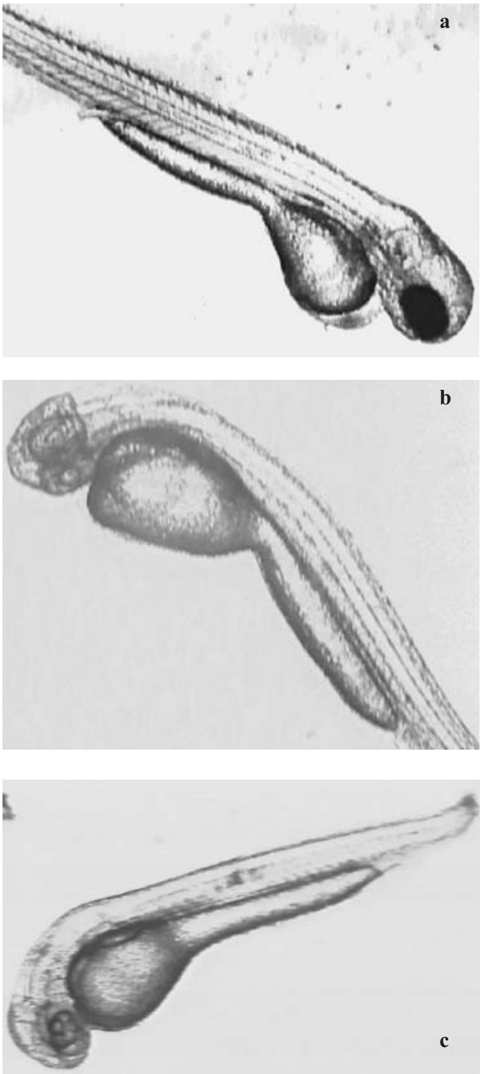

Fig. 6. The almost entirely resorbed yolk sac in freshly hatched larvae of: a – sun bass; b – bleak; c – bream.

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STRESZCZENIE

DWUDZIELNOŚĆ WORECZKA ŻÓŁTKOWEGO U ZARODKÓW RYB KARPIOWATYCH

W trakcie badań nad embriogenezą ryb stwierdzono, że o ile u większości z nich woreczek żółtkowy zachowuje przez cały czas formę kulistą lub zbliżoną do kuli, a na pewno stanowi on twór jednorodny pod względem architektonicznym, to u niektórych ryb karpiowatych (leszcz, słonecznica, wzdręga i in.) woreczek żółtkowy ulega znacznym zmianom w okresie późnej organogenezy.

Zjawisko to polega na bardzo szybkim i wyraźnym podziale żółtka na dwie części (oddziały), z których proksymalny (przedni) stanowi około 3/4 objętości i zachowuje kształt kulisty, natomiast odcinek kaudalny (1/4) przybiera kształt podłużny, aż do walcowatego.

Stwierdzono, że ścianki woreczka w części kaudalnej podejmują rytmiczne skurcze, wyprzedzające w czasie powstanie pulsacji zawiązków serca.

Można by mniemać, że skurcze ścian woreczka żółtkowego powodują mieszanie płynów środowiska wewnętrznego rozwijającego się zarodka, wcześniej niż podejmuje tę rolę odcinek centralny powstającego układu krwionośnego - serce.

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