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To be a juvenile and not to be a larva: an attempt to synthesize

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The question – when does a fish becomes a juvenile – might seem strange to some, and even totally worthless, mainly to those fish and fishery biologists who designate all the small ontogenetic stages of fishes by the banal term 'fry' (for a commentary on this unfortunate term, see Balon 1990). Despite this, a group of predominantly younger scientists met at a workshop in Bratislava to exchange views on this topic. Ontogeny is a process during which one event is related to another and everything is related to everything else. Therefore, besides the title subject, the participants of the workshop discussed also such topics as fish metamorphosis, whether the larva period begins with hatching or with the onset of exogenous feeding, and eventually, whether fish ontogeny is saltatory or otherwise.

A variety of views emerged on ontogeny being either a gradual process (insisting on this view were some scientists engaged in the domain of fishery biology, or behavioral ecology), or a saltatory one. It also became obvious that certain specialists looked at ontogeny from the narrow angle of that group of fishes with which they were familiar, failing to consider other fish groups (not to mention other animals). Some rooted opinions and strongly held views were defended by 'practicality'.

Ontogeny is a formative process taking place in every species at a specific rate and rhythm, in which the so-called heterochrony, i.e. change in rates and timing of developmental events, becomes manifest. Hence, ontogeny cannot be understood as a gradual process during which small and inconspicuous changes in form and function accumulates continuously, but neither as a discontinuous process (as some erroneously understood 'the theory of saltatory ontogeny'). Ontogeny is a continuous sequence of longer stabilized states (steps) alternating with shorter less stable intervals (thresholds, Figure 1), in short, some sort of 'a stepwise progression' (Balon 1986). At the same time, changes in anatomy, physiology, behavior and ecology may take place at different rhythms and at varying rates. Consequently, it is at times quite difficult to pinpoint the onset, but especially the completion, of the various steps and therefore to compare individual ontogenies of different species of fishes. This also causes the existing confusions, leaving several questions open.

One of these questions is whether insemination, activation, or fusion of male and female pronuclei may be considered as the beginning of ontogeny, or only the first division of a zygote. Balon (1985, 1990), because of the existence of gynogenesis and parthenogenesis, considers activation the only precise beginning of ontogeny for bisexual organisms.

A further question was whether the embryo period of fishes ends with hatching, or with the onset of exogenous feeding. Balon (1985, 1999 this volume) has presented arguments showing that the start of external feeding is characteristic of larvae or juveniles. Therefore, the term 'yolksack larva' is inappropriate[1] and we should speak of a free embryo or eleutheroembryo. Hatching is thus a process in which the embryo leaves the egg envelope and this occurs at different steps during the embryo period; in certain animals this already takes place at the blastula stages (hatched blastula of sea urchins, or hatching blastocyst of mammals). According to Balon (1999 this volume), the popular lay usage of 'egg hatched' or of 'freshly hatched larva', when the

[1] This similarly applies to the term 'prelarva'. Its illogical use was pointed out by Kryzhanovsky (1956). Nonetheless, Makeyeva (1988) gave priority to this term and objected to that of 'free embryo' as not corresponding to the state of organism freed from an egg envelope, because, allegedly, the Greek word embryo designates 'in envelope'. That, however, is not true. The term embryo has its root in the Greek expression 'em bryein' – to swell inside.

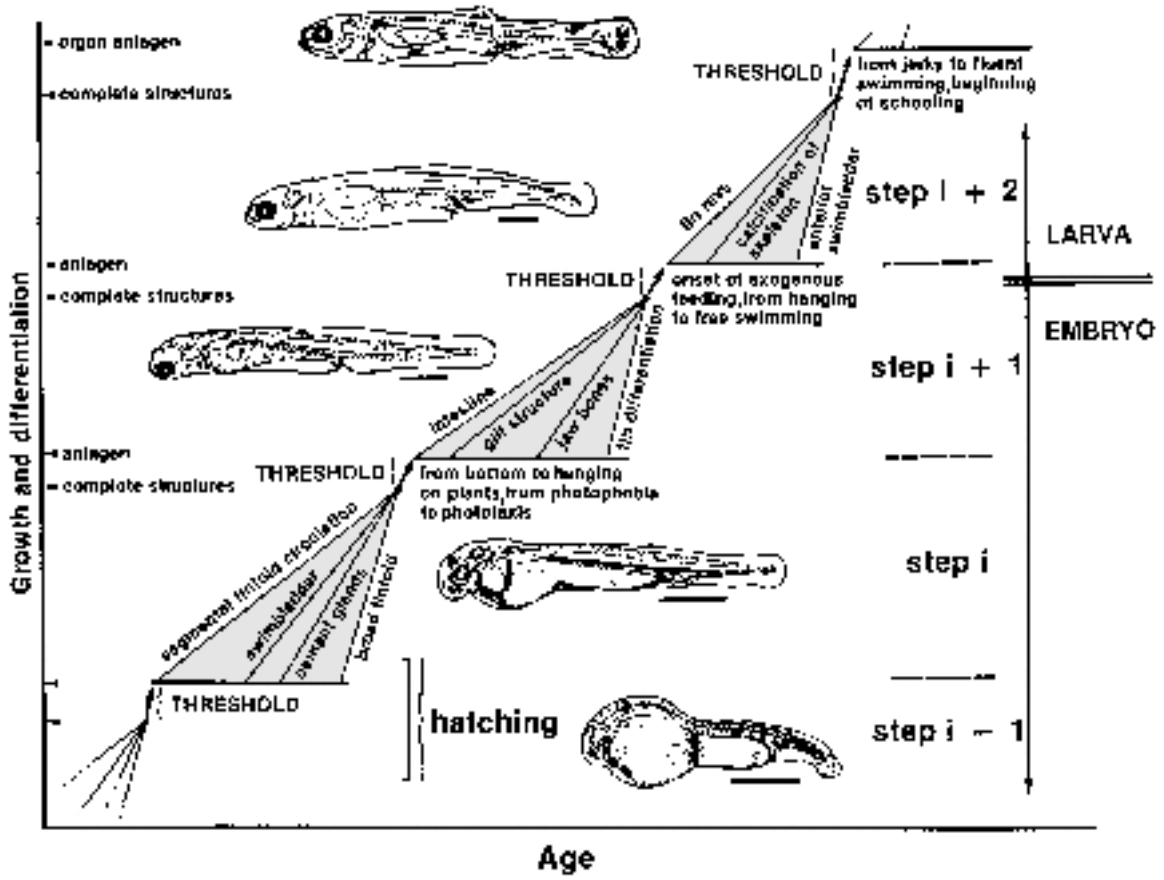

Figure 1. Diagrammatic representation of a few steps in the development of *Abramis ballerus* (from Balon 1959) constructed by Balon (1986) to illustrate his 'theory of saltatory ontogeny'. While not an entirely satisfactory illustration of this theory, it was later used by Greenwood (1989, figure 1) and Bruton (1994, figure 2, reproduced here from the cover of this journal).

embryo leaves the egg during the process of hatching, 'is not a matter of terminology but a matter of understanding what we are talking about'. How true!

Yet, hatching may not be considered a synonym of birth. It may seem strange, but I have met with this problem even in the manual on developmental biology published lately which, right after the first image illustrating the development of a frog, have the terms 'hatching (birth)' printed explicitly. Obviously, neither release, nor egg deposition in oviparous fishes is parturition, as Balon (1999, p. 20) writes in this volume adding: 'Birth, however, is in a broad sense a synonym of parturition . . . '. In this, I would beg to differ from him, because the Latin noun 'parturitio' is derived from the verb 'parturire' meaning 'to prepare for labour', 'to work towards giving birth', 'to feel the throes of childbirth', etc. Therefore, while 'parturitio' is the process of being born (leading to birth), 'birth' is a state resulting from being born. I only fear that some might understand my remark in terms of the Latin adage: 'parturiunt montes, nascetur ridiculus mus'.

Wald (1981, p. 1) wrote: 'With metamorphosis it is easy to know where to start, but hard to know where to stop'. During metamorphosis there is, on the one hand, regression of larval structures and functions, on the other, the formation of some new structures and functions that are essential to adults. 'The larva frequently possesses rudiments of adult structures, the adult vestiges of larval structures (. . .) the larva and adult developing not so much in succession as side by side', reminds us Wald (op. cit., p. 5). The consequences of metamorphosis are changes of anatomy,

physiology, behavior and ecology (Balon 1985, 1999 this volume). The outcome of metamorphosis is that the fish turns into a juvenile.

Evidence to the fact that it is possible to learn 'when fish become juvenile' has been provided by several participants of the workshop. They determined the onset of the juvenile period precisely by comparing morphological and ecological changes. Thus, for instance, Kováč et al. (1999 this volume) found that the coincidence in shifts in morphometric (mensural) values with those in microhabitat use suggests that thresholds do occur during this interval of stone loach, *Barbatula barbatula*, life history, and that the larva period ends with the completion of this shift in relative growth. Similarly, Simonović et al. (1999 this volume) found significant shifts in relative growth of six mensural characters of the European minnow, *Phoxinus phoxinus*, in concurrence with significant changes in microhabitat use, which they consider as the threshold between larva and juvenile development. Gozlan et al. (1999a this volume) have shown that the onset of the juvenile period in sofie, *Chondrostoma toxostoma*, takes place at 50 mm SL, coinciding with a change in mouth position to inferior. Gozlan et al. (1999b this volume) interpret the shift of relative growth in sofie (at 23 mm SL) to be rather a threshold that initiates the last interval of the remodeling process and designate it as 'pre-juvenile' interval that is principally metamorphic and completes the 'end-of-larva-period' metabiosis. That is why, in their view, we should consider the last metamorphic (transitional) step of sofie (at 23–50 mm SL) as either the last step of their larva period (metamorphic larvae) or as a separate period (metamorphosis period). However, it seems appropriate here to mention Balon's statement (1999, p. 23 this volume) that 'some decisive events like . . . metamorphosis . . . may not be a part of a saltatory threshold, but an interval undergoing heterochronous shifts according to environmental stimuli'. Metamorphosis may therefore not be a part of a saltatory threshold nor of a specific step.

Is it then possible to determine when a fish becomes juvenile? The results of the above authors have shown that it is possible, though other authors think it is not always possible to do so with precision. Arguing that in certain cases there exists a transitional state (neither larva, nor juvenile), Pavlov (1999 this volume) has attempted to use the term 'state' which has no saltatory significance. To determine the transition from the larva to the juvenile and to determine the onset of the 'juvenile state', Pavlov (op. cit.) made use of exclusively morphological criteria. He advocates the formation of main definitive organs and skeletal elements and the disappearance of larval characters. The terms 'state' then differs from that of 'step' (sensu Balon) which designates the main natural (homeorhetic) intervals of ontogeny within the saltatory process. According to Pavlov (op. cit.), even despite different types of early ontogeny (indirect, transitory and direct), the beginning of the juvenile state that he studied in sea fishes (herring, wolffish and eelpout) occurred at similar total lengths (approx. 35 mm). On the other hand, the results of a composite study of morphology, physiology, behavior and ecology of fishes during ontogenetic development, presented by Sakakura & Tsukamoto (1999 this volume) and Masuda & Tsukamoto (1999 this volume) solve the problem well. Vagelli (1999 this volume) then proved beyond any reasonable doubt that the direct development without a larva exists also in purely marine fish.

The participants in the Bratislava workshop agreed that the question of early ontogeny and particularly metamorphosis of fishes requires more attention. They parted with the conviction that the presentation of their results and mutual exchange of views was of great value and should be continued in the future. Who knows, maybe the organizers of some future workshop will focus attention not solely on 'early', but also 'late' ontogeny and on the interval 'when fish become adults'. Perhaps then P.J. O'Rourke's sentence will prove appropriate: 'You realize that your children have come of age when they stop asking you where they came from and refuse to tell you where they are going.'

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