R E V I E W   A R T I C L E

Characters of larvae – what are they?

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A b s t r a c t . The larval period in fishes has several definitions, each one deviating slightly from the other. Small discrepancies in the definitions, especially concerning the end of the larval period, can create misunderstandings when applied in practice. I examine the different definitions of a larva, the larval period, including metamorphosis, and the juvenile period. Various criteria used to identify the transition from the larval to juvenile periods are contradictory and refer mostly to the length of the larval period. Ignorance of definitions used to identify the juvenile period has caused many larvae to be regarded as juveniles. I discuss the feasibility of various definitions and the nomenclature on the basis of character evaluation. The occurrence of larval morphological characters, i.e. larval fin fold, differentiation of fins, temporary organs, absence of scale cover, non-adult like body proportions and pigmentation, is examined and some features are compared in eleven species. Irrespective of the different definitions of a larva, there are considerable differences in the schedule and duration of development in certain characters between species and, in terms of duration, also within species owing to environmental conditions. Ontogenetic processes seem to be sufficiently flexible to allow larvae to adapt to their environment, which on the other hand may also shape the phenotype. Determination of the environment in which a larva develops depends not only on the location of the spawning grounds but also on the dispersion of larvae. Dispersal strategies are examined in light of larval morphology and behaviour. After fin differentiation, the transition from larva to juvenile would seem to be best described by the dominant morphological changes in body proportions and coloration, combined with behavioural aspects and habitat changes. I suggest the differences and functional aspects of larvae be examined. The main character of larvae is that they are adapted to make use of resources not normally used by adults.

Key words: early ontogeny, development, ecology, metamorphosis, juvenile, habitat changes

Introduction

Most authors accept the division of fish ontogeny into five periods: embryo, larva, juvenile, adult and senescence, but that a 'decisive' threshold separates each one is open to debate (K o v á č & C o p p 1999). The meaning of the term larva, however, has been used rather vaguely. Definitions of a larva and the larval period involve subtle differences (e.g. R a s s 1946, B a l o n 1971, L a n g e et al. 1972, S n y d e r 1976, K e n d a l l et al. 1984, B a l o n 1990, P e ň á z 2001). The reasons for the differences are not so obvious and the grounds given are sometimes rather superficial. The issue was a subject of some discussion in the 1970s and 1980s, resulting in recommendations for both the nomenclature and definitions. Nevertheless, problems still frequently occur with the current use of terminology, not only because there is no commonly accepted standard, but also because the words larva and metamorphosis, for instance, seem to mean different things to different people. In the worst case, by omitting reference to previous definitions and/or the relation to fish length,

authors provide readers with useless information. The variation in the concept of the larval period and the messy nomenclature are due not only to the different perceptions we have, but also to the different perspectives with which we view the development of larvae. First of all, difficulties emerge with the purposes for which we apply the terms and our use of the terms for one particular branch or group of fish, e.g. 'alevin', 'fry', 'parr', 'fingerling' and 'smolt' for some salmonids. Despite attempts (B a l o n 1975, 1990, S n y d e r 1976) to discourage the use of confusing terms such as 'fry' or indeterminate descriptive terms such as 'fingerling' (A l l a n & R i t t e r 1977), these are unfortunately still commonly seen in the literature (Table 1). Later, P e ň á z (2001) suggested avoiding usage of the term 'alevin', which is as poorly and confusingly defined as 'fry'. Secondly, the huge variety of species and developmental schedules makes it difficult to find standard terms. The drive for consensus has probably left us with too few categories.

Table 1. Usage of early life history terminology in the literature based on search in ASFA 1978–96.

Term	No. of articles	Term	No. of articles
Larva	1 995	Larvae	22 793
Fry	4 568	Fries	95
Alevin	147	Alevins	370
Parr	819	Parrs	44
Fingerling	835	Fingerlings	2 100
Underyearling	142	Underyearlings	147
Juvenile	10 762	Juveniles	10 915
Smolt	949	Smolts	1 385
Free embryo	7	Free embryos	28
Eleuthero embryo	7	Eleutero embryos	19
Metamorphosis	2 520	Smoltification	434

B r u t o n (1989) concluded that several names have been given to the 'phenotype pairs' arising from the theory of r- and K-selection formulated by M a c A r t h u r & W i l s o n (1967), such as generalist and specialist, maintenance and dispersal phenotypes. But little attention has been paid to the mechanism behind the dichotomies. Correspondingly, B a l o n (1979a, 1981a, 1985) introduced the terms 'altricial' and 'precocial, 'direct' and 'indirect' ontogeny to promote understanding of the life histories of fish in general. But in doing so, the dichotomous point of view was emphasized (see B a l o n 1979a, B a l o n 1981a, B a l o n 1985, B r u t o n 1989, F l e g l e r - B a l o n 1989). By inserting an intermediate category (transitory ontogenies) between the 'indirect' and 'direct' ones, C r a w f o r d & B a l o n (1996) elaborated the dichotomous perspective, but unnecessarily complicated the 'life-history model'. The addition of an alevin period to replace the larval period challenged even the existence of the accepted divisions into five periods. We clearly need to reconsider the life of larvae by comparing the differences in larval and juvenile development and behaviour in a range of fish species; indeed, some progress has already been made in this respect. We also need to accentuate the importance of environment in ontogenetic differences with reference to mutual interactions.

One landmark for defining the larval period could be metamorphosis, which, according to most definitions, is the transition phase at the end of the larval period when a fish becomes a juvenile and starts to resemble an adult fish. According to B a l o n (1975, 1985, 1990), many fish species do not undergo metamorphosis and have no larvae. Salmonids, for instance, are said to change directly from 'free embryos' into juveniles (B a l o n 1975),

though this idea has been subsequently modified (B a l o n 1980a), and instead of metamorphosis they undergo smoltification. Note that some authors simply include smoltification as part of metamorphosis (B a r r i n g t o n 1961, 1968) or as a secondary or second metamorphosis (see e.g. Y o u s o n 1988). P e ň á z (2001) regards this latter definition as incorrect.

When one is used to certain terms or definitions fitted to a certain purpose, it is not easy to start using different ones, even though they may often turn out to be more appropriate and acceptable. Nomenclature is less important than the clear definition and understanding of what the terms represent and the events they describe. Thus, ill-defined and conflicting terms or definitions should be revised. Understanding the significance of the similarities and differences in development between fish species within their environment context may provide a more comprehensive view, not only of an appropriate terminology but also of the function of natural selection and evolution.

My intention is, first, to examine the different definitions of a larva, the larval period, including metamorphosis, and the juvenile period, and to identify weak points in them, pointing in particular to the use of characters or period boundaries that I consider ill-advised, conflicting or unjustified. Second, by comparing larval development in eleven different fish species with some reference to their ecology, I shall try to illustrate the similarities and sequential disparities in the developmental schedule in order to encourage a new way of thinking with regard to the early development of fishes life cycle and the usage of the term 'larva'. Third, by looking at changes in larval development from a functional and ecological perspective, I shall also seek to emphasise the significance of morphological and behavioural variability in fish larvae when population dynamics and adaptation to variable environmental conditions are considered. I agree with K o v á č & C o p p (1999) that in the workshop "When do fishes become juveniles" my statement "larva life only from the ontogenetic point of view" was perhaps not ideally formulated. Misunderstandings can occur because we use different terms even though we deal with a same topic: organisms-to-environment interactions. Nevertheless, I still want to emphasize that we, indeed, need to break away from the conventional way of considering larval life exclusively from the ontogenetic point of view in order to provide fresh insight into how nature functions. Ontogeny is here considered in its common meaning, see e.g. H e n d e r s o n (1979). A holistic approach to the study of ontogeny was considered necessary by many workshop participants (K o v á č & C o p p 1999). Integration of physiological, morphological, behavioural and ecological aspects (suggested by C o p p) is the central to this endeavour including a functional approach to achieve a more concrete evolutionary vision than the "theory of saltatory ontogeny" and "life-history model" (B a l o n 1986a), which despite their updated versions (B a l o n 1990, 1999) remain confused and contain a number of inconsistencies.

Defining the larval period

What is a larva?

The Collins English dictionary (third edition, 1994) defines a larva as 'an immature free-living form of many animals that develops into a different adult form by metamorphosis'. A larva is a stage between hatching and metamorphosis (W e b b 1999). The larval period is characterised by the persistence of some embryonic organs (K r y z h a n o v s k y 1934,

cited after B a l o n 1975) and by the development of special larval organs (e.g. a finfold with respiratory vessels, external gills, spines, flaps and filamentous appendices) that are later replaced by different definitive organs with the same function or that disappear with the loss of their functional need (B a l o n 1971, 1975). They still, however, lack many of the organs that characterise adult fish, e.g. ventral fins, scales, pyloric caeca (B a l o n 1971). A larva is a transitory vegetative form often inhabiting an entirely different niche from the definitive form, and is equipped with numerous temporary organs and a different body shape (B a l o n 1984b). Larvae represent temporary intervals inserted in the developmental sequence primarily in order to complete the nutrient provision needed for formation of the definitive phenotype (B a l o n 1986b, 1989a, 1989b). A larva is a young animal that is quite different in appearance from the adult (F l e g l e r - B a l o n 1989). She also reminds us that, 'what one author considers a larva is a juvenile in someone else's opinion'. In general, two types of definitions of larvae emerge: one is characterized by morphological attributes, the other by ecological features; some definitions combine both (W a k e & H a l l 1999).

Onset of larval period

There are two schools of thought concerning the beginning of the larval period: according to one, it begins at hatching (K a z a n s k i i 1915, 1925, H u b b s 1943, Y e v r o p e y t s e v a 1946, R a s s 1946, B a l i n s k y 1948, V a s n e t s o v 1953, W i n n & M i l l e r 1954, K o b l i t s k a j a 1981, S n y d e r 1976, B l a x t e r 1988), whereas to an other it begins at the onset of exogenous feeding (K r y z h a n o v s k y 1956, L a n g e et al. 1972, B a l o n 1975, 1990, P e ň á z 1983). Both points of view have been both criticised and justified depending on the author's perspective. Unfortunately, some authors (B a l o n 1990) seem not to understand or acknowledge other points of view, which in the worst case has resulted in unscientific criticism and name calling (B a l o n 1999). Fortunately some other scientists (K a m l e r 1992, P e ň á z 2001) can acknowledge both notions, but prefer one or the other.

Hatching

P e ň á z (1983), for instance, considered hatching insignificant to the definition of periods of early development, since it is dependent on external influences and no qualitatively important morphological or physiological change is associated with it. However, metabolism does change at hatching. For example, a 2.5 to 10-fold increase in the oxygen consumption rate having been reported in many studies (see review in K a m l e r 1992, pp. 147–151). Moreover, a dramatic increase in the vulnerability of newly-hatched larvae to toxic agents, as compared with the embryos inside the egg capsules, is well documented (D a y e & G a r s i d e 1977, R a s k 1984, v o n W e s t e r n h a g e n 1988). In his latest publication, P e ň á z (2001) nicely brings up the justification both for and against hatching as a boundary between the embryonic and larval period. The developmental stage at hatching is influenced by environmental factors such as temperature and oxygen conditions (M u n t j a n 1967, H a m o r & G a r s i d e 1979, H e m i n g 1982, P e ň á z et al. 1983, E c k m a n n 1987). Although the above examples are from laboratory experiments, some variation also exists in natural waters, and 'prematurely' hatched individuals are indeed much more vulnerable to invertebrate predators than are those hatching at a more advanced stage. Thus, from ecological point of view, hatching is an important boundary. Although the swimming ability of most species is poorly developed at hatching, the newly-hatched individuals can already

demonstrate some active avoidance of predators (O s s e & v a n d e n B o o g a a r t 1995), not only by escaping, but also by other behavioural responses, for instance, by hiding. P e ň á z (2001) gives some other examples of the considerably important behavioural changes after hatching.

The influence of environmental factors increases tremendously after hatching, except when it takes place inside the adult fish. Hatching is also easy to determine in non-viviparous fishes. Although hatching is possible only at certain stages, morphologically it seems to be a rather immaterial process, whereas ecologically it may be decisive. The phenotype is formed through interactions with the ambient environment (B a l o n 1984b), and after hatching these interactions are more direct and numerous than before. For the fish themselves, hatching is a tremendously important event.

Onset of exogenous feeding

Although B a l o n (1975) accepts hatching as a boundary between phases, he certainly does not see it as a boundary between periods. The larval period begins at the moment of transition to exogenous nutrition (B a l o n 1971), that is, the commencement of oral ingestion and intestinal digestion (B a l o n 1986b). Yolk absorption tends to be very gradual and to depend on temperature (S n y d e r 1976, K a m l e r 1992). Like hatching, the onset of exogenous feeding occurs over a wide range of developmental features (B a l o n 1979b) and has enormous physiological, ecological and behavioural significance (K o v á č & C o p p 1999, P e ň á z 2001). Sometimes it begins when the embryonic finfold is entirely undifferentiated and at other times not until all fins are fully developed. *Cyphotilapia frontosa* represents the most advanced style, with exogenous feeding starting in early embryos during mouthbrooding (B a l o n 1990). The timing of the first exogenous feeding appears to depend on the quality and quantity of yolk available to the young during endogenous feeding and this, in turn, depends on the condition and size of the parents (B r u t o n 1989, H e y e r et al. 2001). Like hatching or parturition, the transition from endogenous to exogenous feeding, largely a physiological change, does not correlate well with the more obvious morphological features of larval development such as fin morphogenesis (B a l o n 1980a, S n y d e r 1981). However, it seems that there is less variation in the developmental stage of individuals at the onset of external feeding than at hatching, although no exact measurements have been presented to support this opinion. On the other hand, feeding is obligatory and furthermore impossible if food is not available. Thus, many 'embryos' never reach the larval period as defined by Balon. Accordingly, one-third of a group of fish larvae seen swimming around in nearshore waters may turn out on later microscopic examination in the laboratory to be 'free embryos' (after Balon's definition), although they all look alike. The difficulty of determining the onset of feeding has become a critical issue in practice, not only because some larvae may starve but also because the small size and rapid digestion of some prey organisms tends to make determination almost impossible (S n y d e r 1976). P a v l o v (1999) and P e ň á z (2001) have tried to overcome this problem by defining the transition to exogenous feeding "with the acquisition of the ability to ingest orally and digest intestinally", that is, the potential ability to feed; they also refer to cases where the ability to feed orally may exist already in the pre-hatching stages inside of egg envelopes or before "parturition". One of the most intriguing examples is the feeding of leptocephalus larvae with a possibility to uptake of dissolved organic matter (see e.g. S a n d e r s o n & K u p f e r b e r g 1999). The thresholds that separate periods should be more distinct and easier to distinguish than those that separate

developmental steps (B a l o n 1984b). In response to the precise statement of B a l o n (1999), P e ň á z (2001) provides a list of several features to detect the onset of feeding stage. However, I still doubt that, in practice, the use of transition to exogenous feeding would be more precise to detect and use than is hatching. It is self-evident that the transition to exogenous feeding describes well the ontogenetic status, because it is also based on morphological organ development. On the other hand, I do not know if anybody has ever tried to determine the exact ontogenetic stage with hatching. On the contrary, ontogenetic stage is often described with corresponding ontogenetic features at hatching. Similarly, calling hatching as a process and ignoring that feeding is also a process is not a plausible justification. For fish, the potential ability to feed is quite different to actual feeding, that is, if a larva is not really feeding it will definitely die. On the whole, I cannot see very many reasons why the onset of exogenous feeding should be used as a useful sign of the beginning of the larval period. Although there are different interpretations of the term embryo (from the Greek *embruon*, to swell), the most common one is probably that embryos are always inside something (seed cover, egg envelope, maternal body). The onset of feeding may well be an important step in the life of fish larvae, but it is neither as functional nor as practical a boundary as hatching in studies of fish survival and ecology, that is, when one considers also other than only ontogenetic point of view. I therefore consider the larval period to begin at hatching. For humans, the question of the larval period boundaries is how we define the word we use to best serve our purposes, one of which is the understanding between us and another is practicality. For fish, however, hatching and onset of feeding are boundaries, where probabilities to survive may change. Thus, I believe it is important to understand how the life of fish changes in these milestones. I wonder how the beginning of the larval period is defined in the other animal groups having larvae; at least, S a n d e r s o n & K u p f e r b e r g (1999) in their large review of aquatic larval feeding mechanisms among amphibians and fishes acknowledged the disagreement, but considered the larval period begin at hatching.

End of larval period

Several of the definitions for the end of the larval period or beginning of the juvenile period are, albeit loose, rather similar. The differences between the extreme views are, however, immense due to the different ways in which the definitions are interpreted and the rather slow development of certain features, as will be discussed later on. The larval period is said to last until the axial skeleton has formed or is ossified and until the undifferentiated (embryonic) median finfold is differentiated or no longer apparent (B a l o n 1971, 1975); until the disappearance of all larval characters and the onset of the development of the scaly integument (L a n g e et al. 1972); until the occurrence of the first scales and the complete disappearance of the embryonic finfold (P e ň á z 1975); until the full count of fin rays has been attained and squamation has begun (K e n d a l l et al. 1984); until metamorphosis (B a l o n 1984b) or until growth in most morphological characters has stabilised with coinciding completed squamation and development of sensory features (e.g. nasal septa) as well as habitat shifts (K o v á č & C o p p 1999). S n y d e r (1986) lists three points in fin development to signal the end of the last larval phase:(1) acquisition of the adult complement of spines and rays in all fins, including secondary rays; (2) the appearance of segmentation in at least a few rays in each fin characterised by segmented rays; and (3) the loss beyond recognition of all finfolds and atrophying fins, if any.

On the other hand, fish are recognised as being juveniles when metamorphosis has come to an end, a stage usually corresponding to the appearance of scales on the sides of the body or the assuming of an outline (habitus) resembling that of the adults of the species (R a s s 1946), that is, when they have acquired an adult-like appearance (B a l o n 1990). The juvenile period begins when the fins are fully differentiated and most of the temporary organs have been replaced by definitive organs (B a l o n 1975). In the juvenile period, all final adult structures have appeared (B a l o n 1981a). The juvenile period is characterised by specimens with the appearance of small adults – all fin rays and scales are formed, the skeleton is almost completely ossified, the larval pigment pattern is overgrown or has been lost and replaced by dermal pigment similar to that of the adults, and the body shape approximates that of adults (K e n d a l l et al. 1984). Studying the onset of the juvenile period, C o p p & K o v á č (1996) and K o v á č & C o p p (1999) noted that the start of the juvenile period is still ill-defined; the criteria used in some studies do not appear to support the view that juveniles are little adults, as proposed by other authors.

K e n d a l l et al. (1984) were not the first to suggest a 'transformation stage' between larva and juvenile (see also B a r a s & N i n d a b a 1999 and G o z l a n et al. 1999). For instance, A h l s t r ö m et al. (1976) suggested two criteria, the complete formation of rays in all fins and/or the initial development of scales, to distinguish a larva from a juvenile. According to the latter authors, the secondary caudal rays are the last fin rays to complete their formation. The changes in the transformation stage listed by K e n d a l l et al. (1984) are pigmentation pattern, body shape, fin migration, photophore formation, loss of elongate fin rays and head spines, eye migration and scale formation, that is to say, a change from larval body form and characters to juvenile-adult body form and characters, i.e. metamorphosis. The transformation stage may be abrupt or prolonged and is accompanied by a habitat change (K e n d a l l et al. 1984). B a l o n (1984b) introduced an intermediate group to cover species between 'direct' and 'indirect' ontogeny, and replaced the larval period therein with the alevin period. I assume that he meant that individuals in this intermediate group, like those in 'direct ontogeny', do not undergo metamorphosis, since, according to B a l o n (1990), metamorphosis takes place only in larvae with 'indirect ontogeny'. Recently, P e ň á z (2001) has shown that Balon's categorisation into 'direct' and 'indirect' ontogeny remains invalidated.

Metamorphosis

Entire books have addressed the subject of metamorphosis (E t k i n & G i l b e r t 1968, G i l b e r t & F r i e d e n 1981), and yet some conflicting views still remain concerning different fish species. Metamorphosis is designated as an event of larval life (Y o u s o n 1988), being the threshold separating the larval and juvenile periods (B a l o n 1985). In Balon's life-history model, however, metamorphosis and allometric growth are placed in the juvenile period and confined to exist only in some species (see B a l o n 1986b, Fig. 7 & B a l o n 1989a, Fig. 5). According to him, a larva requires major remodelling – metamorphosis – to permit definitive structures to replace the temporary organs, but a larger endogenous food supply enables the embryo to produce permanent organs directly, without the need for extensive remodelling of larval structures (B a l o n 1984a, 1990). He therefore considers that only some fishes have larvae that undergo metamorphosis (B a l o n 1984b, 1990). Accordingly, many others do not, nor do they have larvae; their embryos develop directly into juveniles in possession of most of the definitive adult structures, e.g. round goby

Neogobius melanostomus (B a l o n 1990). This narrow definition of metamorphosis and larva leads to problems with nomenclature and wider applicability of the model. Balon faces some of them in the intermediate states he calls alevins. Initially, he ignored the problem by declaring that salmonids have no larval period or larvae at all (B a l o n 1975). Later (B a l o n 1979b, 1980a), he admitted that salmonids may at times display a vestige larval period, incorporating characters typical of both the larval and juvenile periods in other fishes. Graylings and landlocked salmon, which have relatively small eggs, should exhibit the larval vestige to a greater extent than other salmonids (B a l o n 1979b). What about other salmonids, e.g. whitefish, ciscoes and osmerids? They seem to fit even less into this vestigial system, and I cannot see why they would not have a larval period. Balon's proposal of a special alevin phase for some species instead of a larval period, with some persisting temporary organs, has not received the full support of other authors (see e.g. P e ň á z 1981, 1983). I agree with P e ň á z (2001) that the name alevin only confuses matters and should not be used. S n y d e r (1976) noticed that an illustration (Fig. 3 in B a l o n 1975) labelled an alevin by Balon should properly be designated a larva, even according to Balon's definition. This inconsistency in terminology continues in the ontogeny of charrs (see e.g. Fig. 14 in B a l o n 1980b). G o z l a n et al. (1999) suggested a term 'metamorphic larvae' for the stage when most adult structures are present, but individuals being morphologically closer to larva morphotype and the relative growth is not stabilized. When a young animal looks quite different from an adult, it is a larva and has to undergo a major structural transformation, i.e. metamorphosis (F l e g l e r - B a l o n 1989). The question as to how different from the adult the larva must be still remains.

The definitive phenotype is formed during metamorphosis (B a l o n 1989b) and most ontogenetic effects essentially cease at metamorphosis (F u i m a n & H i g g s 1997). In the broadest sense, metamorphosis is any abrupt change in the form or structure of an organism during its post-embryonic development (Y o u s o n 1988). It is not always clear which of the post-embryonic changes in fishes are true metamorphic events. A h l s t r ö m (1968), among others, regards metamorphosis as an interval during which marked changes occur in body proportions and structures without any marked increase in length. He located the metamorphosis in clupeid larvae using fin positions. B a r r i n g t o n (1961, 1968) considers even this definition too narrow, for it excludes consideration of changes in function and in mode of life. The term metamorphosis is, in fact, a misnomer, for much more is going on than changes in form (W a l d 1981, F l e g l e r - B a l o n 1989); physiology and behaviour, both of which consume energy, are also changing (T h o r i s s o n 1994). Moreover, the larval and adult forms live in different niches or entirely different environments (F l e g l e r - B a l o n 1989). Metamorphosis is a series of changes aimed at adapting the young to a new ecology in the course of their ontogeny (L i n d s t r ö m 1989).

Many salmonids undergo a distinct transformation before their seaward migration. Typically, the cryptically coloured, stream-dwelling 'juvenile' (usually called a parr) changes into the more streamlined, silvery and active pelagic individual, referred to as a smolt, which is physiologically adapted for life in sea/ocean waters (H o a r 1988). In Atlantic salmon *Salmo salar*, the grey markings of the stream-dwelling parr are concealed by a silvery layer of purines, and the body form becomes more slender with a decline in weight per unit length. In addition, the fins – particularly the pectorals and caudal – develop distinctly black margins (see references in H o a r 1988). Smoltification meets the requirements of most of the definitions of metamorphosis: nevertheless, some authors would

like to exclude it and call it a second or secondary metamorphosis (J u s t et al. 1981, Y o u s o n 1988). Let us remember that, in fish, metamorphosis is never as thorough as it is in many amphibians or insects, which change their habitat from water to land or from land to air. There are, however, different levels of less complete metamorphosis in fishes.

To see the validity and rationality of the different opinions about metamorphosis and larva, despite their dependence on different classifications and nomenclatures, it is important to compare the development of different fish species (e.g. salmonids), excluding these categories (e.g. 'indirect'-'direct' development) but including habitat changes. First, though, we must look into the subject of larval characters.

Larval characters?

It is difficult to define which of the characters present at some time during the larval period are really larval characters, but once we agree what the characters are, we must keep to them when defining the larval period. Some characters may appear earlier, and as the development of different features in various larvae is not uniform (see later), none of the characters will be observed throughout the larval period. K o v á č et al. (1999) pointed out with several variables that the use of different mensural characters is not unequivocal, since the development of features is not in equal phase (U r h o 1992), which also makes the use of thresholds more artificial. If some species have no larval period, then should they have no larval characters either? The characters deviating from those of adults are frequently used to identify larvae (e.g. see K o b l i t s k a y a 1981). I think that more important than the existence of a character is its purpose or usefulness for the larva. Hence, I ask: What are the characters for?

Yolk sac

The yolk sac is said to be an embryonic organ, but it also plays an important role after the larva has hatched; it is definitely not an organ of adults or juveniles. Depending on the definition of a larva, the yolk sac is either typical of the larval period (at the beginning of it) or not so typical (when only the remains of the yolk are present in mixed feeding). With his definition of the beginning of the larval period, B a l o n (1979a, 1999) recommended that use of the term yolksac larva be abandoned for the sake of consistency, but gives no other explanation. On the other hand, if larval life is considered to begin at hatching, the yolksac larva represents the first part of the larval period. B a l o n (1989b), however, states that it is of little consequence what we call the young after hatching, but before transition to exogenous feeding, a free embryo, an eleutheroembryo or a yolksac larva; what is imperative is the recognition of a difference between 'direct ontogeny' without a larva and 'indirect ontogeny' with a larva. I agree that the use of precocial and less precocial may sometimes be useful when species are compared, but I would not recommend use of 'direct and indirect ontogeny' to classify species, since 'direct' and 'indirect' there are not the only two alternatives but rather an entire continuum between them. P e ň á z (2001) came to a similar conclusion stating that truely direct ontogeny (sensu B a l o n) is rare in fishes. I also agree that the nomenclature is not the point, but a useful tool, and we must keep in mind the tools we are applying. First, to be specific, a 'free embryo' is not a synonym for a yolksac larva. The yolk cannot be considered as a source for embryonic development alone (even if the embryonic period is considered to end at the first feeding) since some development takes place after the first feeding with the assistance of the remainder of the yolk. Neither the

development nor its rate is dependent on the source of the nutrient, but on the quantity and quality of it. Second, I shall show later that it is the rate and sequence of ontogenetic events that causes the differences between species.

The primary function of a yolk sac is probably as a food reserve providing nourishment both before and after hatching and even for a short time after the onset of feeding. Other functions, connected with respiration, hydrostatics and protection against bright light, have also been attributed to the yolk sac (K r y z h a n o v s k y 1960). A larva with a large amount of yolk often not only looks quite different from one with little or no yolk (S n y d e r 1986), but also the swimming ability of a larva changes once some yolk is exhausted. Although a large yolk sac may be a hydrodynamic disadvantage, poor swimming performance during the yolk sac phase is due to other changes as well, e.g. late development of pectoral fins in some species. Many species with a large yolk sac seem to have solved the poor swimming ability problem by hiding themselves after hatching (see the section: Distribution and habitat changes of larvae). For some other species, the purpose of the yolk is also to assist in the dispersion or transport of the larvae from spawning sites to larval feeding grounds and not to postpone the onset of feeding (K i ø r b o e et al. 1985, U r h o 1992).

Larval fin (fin fold)

The fin fold seems to be present in all fish larvae. It is typical of late embryos and early larvae. The fin fold has a function in respiration and locomotion, although the respiratory function seems to be the less important of the two (O s s e & v a n d e n B o o g a a r t 1995). In species that undertake much develop inside the egg shell, the fin fold is not usually very wide and starts to differentiate before hatching (e.g. bullhead *Cottus gobio*, and trout *Salmo trutta*). It often seems to be greatest at or shortly after hatching. A large finfold enhances larval buoyancy and locomotion (M o s e r 1984), aiding the dispersal of smelt *Osmerus eperlanus* and herring *Clupea harengus* larvae (U r h o 1992). In salmonids, the finfold is relatively smaller in the genus *Salmo* than in the genera *Coregonus* and *Thymallus*, only the latter two having a dispersal phase after hatching (see later). Therefore, the fin fold is a larval rather than an embryonic organ, even though it originates in the embryonic period. It is often difficult to determine when the rest of the larval fin finally disappears from around the caudal peduncle and therefore, in practice, it is slightly easier with the preanal remnants thereof. Although the fin fold decreases rapidly in size, it does not totally disappear until at 30–40 mm TL in herring and smelt (U r h o 1992), even in species such as trout and salmon, which, originally according to B a l o n (1975, 1980a), lack larvae. Trout larvae may still have some preanal finfold at least until 31–32 mm TL (e.g. G o r o d i l o v 1996). In the blue bream *Abramis ballerus,* fin differentiation begins at 9 mm TL, but the rest of the preanal fin fold is still visible up to 40 mm TL. Some vestiges of the finfold may still be evident when the length-weight relationship changes (C o p p & P e ň á z 1988).

Fin differentiation (incomplete fin rays)

Fin differentiation is apparently often equated with acquisition of the adult fin-ray complements in all fins. M a n s u e t i & H a r d y (1967, after S n y d e r 1976) specifically noted that 'these counts are frequently attained before the rays are fully ossified'. Actually, the number of fin rays can be counted long before the rays are completely formed and correspond to those of adults. As an example, in the red sea bream *Pagrus major,* segmentation begins after the

complement of fin rays is attained, at 7.6–8.6 mm SL, and the rays are completely segmented by 18 mm SL: moreover the branching of rays is finished when the fish are 34 mm SL (F u k u h a r a 1985). The pectoral and ventral fins gradually become pointed and elongate between stages 1C and J, 7.6–30.8 mm SL (F u k u h a r a 1985). Thus, there is a huge difference between the complement of fin rays and fin ray completion (completely differentiated fins including articulation and bifurcation of rays). Compare this to the different definitions in the section 'End of larval period'. The appearance of segmentation and early bifurcation of larval fin rays is not always enough to justify classification as juveniles (C o p p & P e ň á z 1988).

Non-adult-like appearance

One could also say that the "non-adult-like appearance" is a complex of characters, but it is frequently used to characterise larvae without individualising different features of which it is made. Furthermore, being adult-like is often regarded as a phase in which only certain characters resemble those of adults; one can somehow imagine the final phenotype, based only on the habitus of a fish or its fin positions, being that the fish resembles an adult to some extent. If, for instance, we look at the developmental stages of the red sea bream by F u k u h a r a (1985), then we see that the larvae in his Figs 1C (7.6 mm SL) and 1D (8.3 mm SL) bear some resemblance to the young fish in Fig. 1K (46.1 mm SL). However, the shape of the fins is still developing, as are pigmentation, body form, the position and relative size of the eyes, etc. Fukuhara's own choice for the transformation from larvae to juvenile ranges from 6.3 to 10.3 mm SL, and seems to be based on the appearance of two lobes on the caudal fin (F u k u h a r a 1985, page 733) rather than on those features that change later on and apparently do not attain their definitive form until the change from a pelagic to a bottom-dwelling life style occurs, at 30–32 mm SL. When different larval characters disappear gradually, at an unequal rate and not simultaneously, the borderline between non-adult-like and adult-like appearance is not easy to discern. Even fish such as *Neogobius melanostomus,* with their 'direct' development (F l e g l e r - B a l o n 1989, B a l o n 1990), are not exactly adult-like until long after the onset of exogenous feeding (see e.g. K o b l i t s k a y a 1981 and P e ň á z 2001), the most striking difference being in colour. Adult-likeness can be difficult to assess, and therefore we need some rules to help us do so. I suggest that if we define juveniles as adult-like, they should be identifiable by species-specific features known in adults.

I think that we have probably all thought of salmonid 'parr' as juveniles. But why? The 'parr' may well seem to look much like adults in the sea (Fig. 1), but there are in fact several differences, not only in body shape but also in the relative size of head, eyes and fins. And then there are the parr marks. If we use adult-like or definitive phenotype for juveniles, then a salmon should also be called a juvenile only after smoltification. In fact, the definitive phenotype could mean that there is no larval fin or larval organs but that a body shape and pigmentation pattern equal to those of non-spawning adults, although not necessarily a full scale cover, already exist.

Temporary organs

The most undeniable characters of larval life are the special, temporary organs, e.g. armature on the head bones, precocious, elongate or serrate fin spines, that certain fish larvae have in addition to specific pigmentation pattern (see M o s e r 1984, K e n d a l l et al. 1984). The
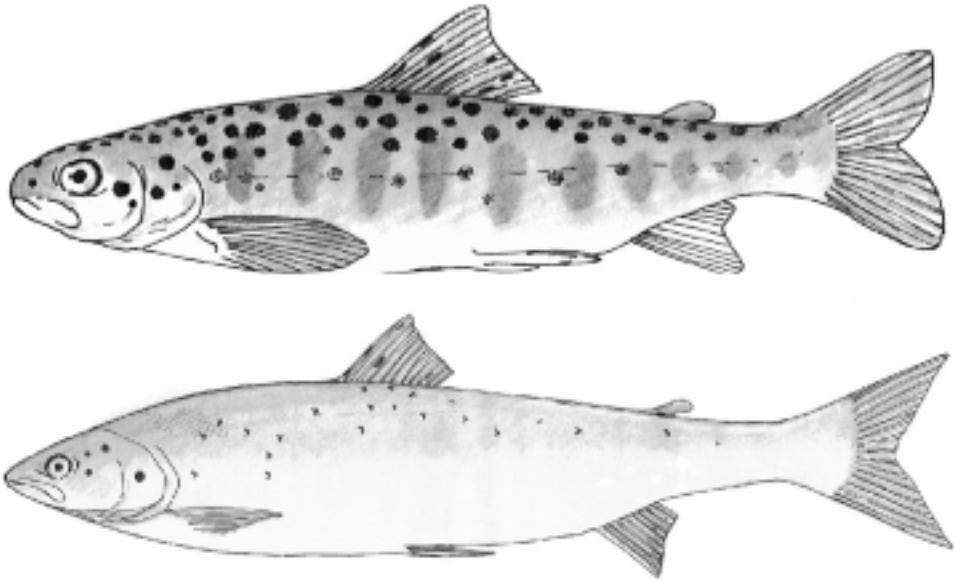
Fig. 1. Atlantic salmon (*Salmo salar*) at the size of 15 cm TL (above) and 45 cm TL (below). Drawn after O t t e r s t r ø m (1935). Note the difference in colour and proportions of different body parts (eyes, fins etc.) to the total length.

appearance at 5.5–7.5 mm SL, and its disappearance at 10–12 mm SL, of a special fin structure in larvae of the Japanese flounder *Paralichthys olivaceus* (F u k u h a r a 1986) is a good example of the temporary nature of larval organs. At this time, the larvae had the definitive number of fin rays, although some segmentation and branching of the fin rays continued. Eye migration was completed at 17 mm SL, when squamation began (14–18 mm SL), and the preanal length decline steeply (F u k u h a r a 1986). Full squamation was not observed until at 39–48 mm SL.

Temporary larval teeth are known to occur in eels, for instance, but probably smaller larval teeth are common in other fish groups as well. But can we confine larval life to the interval during which the special, temporary organs exist? Premaxillary and mandible teeth appear in whitefish *Coregonus lavaretus* some days after hatching and are used during the larval period, but in adults only the sharp tips of the teeth protrude from the thick mucous membrane on the mandible and premaxillary bones (N a g i ę ć & N a g i ę ć 1995). Most likely, the special larval structures are functional only during the larval period, although some rudiments may still be present later on.

Lack of squamation (scale cover)

Larvae are said to lack scales (squamation). But does this mean there are no scales at all or that not all scales are present? There is, of course, a big difference between the point at which the first and the last scales appear: in the red sea bream, for instance, the first appear at 7.5–9.0 mm SL and the last at 14 mm SL (F u k u h a r a 1985), and in the blue bream at 25.1 mm and 40 mm TL, respectively (B a l o n 1959). The onset of scale cover is probably less valuable as an attribute than completion of scale cover in defining a threshold (C o p p

& K o v á č 1996). All in all, at least under field conditions, use of scale cover may be difficult. Recently, however, the reflectance of the silvering skin (guanine crystals) has been used to determine smoltification (D u s t o n 1995, H a n e r et al. 1995). The reflecting layers in and under the scales are important for camouflage (B l a x t e r & H u n t e r 1982), and changes thereof, before the individuals leave the larval areas may be crucial for survival. The appearance of silvering entails changes in the pigmentation pattern.

Pigmentation pattern

Most species have a distinct pigment pattern as larvae (K e n d a l l et al. 1984). This pattern is not stable but develops during larval ontogeny and disappears shortly after squamation. In Eurasian perch *Perca fluviatilis,* the initial typical line-shaped melanophores between the myomeres become fainter until, at a larval length of 15–20 mm TL, the stellate melanophores start to take over and form denser aggregates. At 20 to 30 mm TL, these gradually appear as the darker banding characteristic of juvenile and adult perch (U r h o 1996a). Similarly, the larval spots of grayling *Thymallus thymallus* appear at 27–30 mm TL, after the melanophores in dorsal and ventral longitudinal lines (originated in yolk-sac larvae) have spread more diffusely over the flanks; at the same time, the larval finfold gradually disappears and the first scales appear. The spots become more marked before the size of 40 mm is reached, but later on the spots are covered by scales and become visible only if the scales are lost (or the specimens are fixed in certain conservation liquids). It is not only the scales but often the silvering layers (reflecting guanine crystals) that overlie larval pigmentation. The intensity of larval pigmentation depends on the type of water body in which the larvae live (U r h o 1994, 1996a), as probably does the exact appearance of the adult-like pigmentation pattern in larvae. There are some indications that the acquisition of an adult-like pigmentation pattern is connected with habitat changes.

Body proportions

Fish larvae differ in shape from their adults (e.g. F u i m a n 1983). The changes in body proportions characteristic of early development are measured as changes in preanal/postanal length, body depth, predorsal distance etc. related to standard or total length. With some exceptions, the anterior and posterior parts of the body initially (U r h o 1992) grow more rapidly than the middle section of larvae (F u i m a n 1983). In general, the posterior part grows faster in species with a dominant (longer) anterior part at hatching (smelt, herring, pike *Esox lucius*, eel *Anguilla anguilla,* whitefish, cisco *Coregonus albula,* cyprinids) and the anterior part grows faster in those with a longer posterior part at hatching (percids, burbot *Lota lota*), so that the anus ends up somewhat behind the midbody. There are of course exceptions, such as flounder. In both herring and smelt, relative preanal length increases until 40 mm TL, but the increment in relative head length and body depth ceases earlier in smelt (30 mm TL) than in herring (40–50 mm TL) (U r h o 1992). Owing to different environmental conditions, the timing of the depth increase differs between the spring and autumn spawning herring (Fig. 2). According to K o v á č & C o p p (1996), the stabilisation of relative growth in almost all mensural characters of roach *Rutilus rutilus* does not occur until 40–55 mm SL. There are several other examples of changes in body form after fin differentiation in cyprinids. Body depth in blue bream, for instance, increases and reaches adult proportions by 40 mm TL. A similar observation was made by V o l o d i n &

S t r e l n i k o v a (1985), who reported a greater increase not only in greatest and least body depth but also in the relative length of the caudal peduncle of the blue bream up to about 50 mm SL. The relative body depth of the common bream *Abramis brama*, increases steeply up to about the same size, by when it will have attained 30% of SL (D m i t r i e v a 1957, Y e r e m e y e v a 1960); thereafter the increase is much slower. As mentioned earlier, allometric growth probably continues in some salmonids until smoltification; however, this subject needs further study.

In many species, the position of the differentiating fins changes during the larval period. For example, the dorsal fin in smelt and herring migrates forwards in both species until 45–50 mm TL. In herring, the change is tremendous, being from the last third of the body to just behind the midbody (Fig. 2, also U r h o 1992). Ontogenetic changes in the position of fins affect the mobility of the fish (A l e y e v 1963). Eye position also changes, not only in flounder but also in other species (A l e y e v 1963), e.g. ruffe *Gymnocephalus cernuus* (U r h o 1996a). Relative eye diameter first increases and then starts to decrease (e.g. S h a m a r d i n a 1957). Changes in body proportions are often related to changes in function and habitat. Let us, however, remember that some changes in body proportions may also take place later on during the juvenile and adult periods; both the presence of predators and enhanced food availability may increase the relative body depth of crucian carp *Carassius carassius* (H o l o p a i n e n et al. 1997, S t a b e l l & L w i n 1997).

Fig. 2. The change of body proportions of spring spawning herring (*Clupea harengus*) larvae (about 27, 30, 33, 38 and 39 mm TL, respectively from below) caught in late summer-early autumn (below) and one autumn spawning herring larvae (37 mm TL) caught in spring (above). Note the difference in depth/length ratio and the onset of silvering in the two larvae of spring spawning with highest body depth (all specimens were fixed in formalin and preserved in ethanol).

Agreement of characters?

Several larval characters are known, but they leave much room for different interpretations of what is characteristic of the larval period. Too many changes are involved in the loss of larval characters and attainment of juvenile-adult characters (body form, fin migration, pigmentation and scale formation) for them to take place within a short interval. If we select only one of the characters, then we shall get different end results depending on which one we choose. The above examples of characters and their usefulness demonstrate that interpretations of the end of the larval period are often based on only one character, which conflicts with others, especially the 'adult-like' ones. There might be a point in expanding the idea of larval life to fit better our definitions. Larval features may or may not be functional and may or may not be adaptive during the larval period (W e b b 1999). Before making up our minds, we should perhaps consider comparison of not only morphological but also ecological changes, e.g. migration from larval habitats or nursery grounds into the adult habitats.

Comparison of morphological development in species

Certain steps in the development of eleven fish species, representatives of several ecological groups of fish (K r y z h a n o v s k y 1948, 1949, B a l o n 1981b), are compared in the discussion to follow. The events are related to the total length of the fish (Fig. 3). Time and temperature are important ontogenetic variables, but for practical reasons they are excluded from the diagram. Length at hatching is only roughly related to egg size and incubation time. The developmental stage at hatching or at the onset of exogenous feeding is not directly related to either egg size or incubation day-degrees. The gap between hatching and mixed feeding is largest in salmon, pike and bullhead, all of which have a big yolk and are rather inactive after hatching (see next section). O s s e & v a n d e n B o o g a a r t (1995) concluded that the similarity they found in the timing of the appearance of larval characters in the red sea bream, and in the common carp *Cyprinus carpio* was widespread amongst distantly related groups of teleosts.

It is true that there are strong similarities between certain species, especially when they are closely related, with the exception that in some species, e.g. salmon, development proceeds further inside the egg shell (Fig. 3). Moreover, certain organs or body parts develop at different rates and times in different species. First, the pectoral fin rays tend to develop rather late in the fin differentiation, except among cottids and salmonids, whose pectoral fin rays may already be visible in the yolk sac larvae. Second, inflation of the swim bladder frequently takes place at about the time of mixed feeding, but in smelt and herring much later in the development (Fig. 3, see also U r h o 1992). Last, but not least, the appearance and intensification of melanophore pigmentation occur early in nearshore larvae, such as pike, and late in pelagic larvae, such as herring and smelt.

In general, larvae that are large and advanced at hatching seem to develop faster than less advanced, newly-hatched larvae from smaller eggs. Rapidly-developing, larger larvae (e.g. those of trout, pike and bullhead) do not disperse as extensively and soon as the smaller, slowly developing pelagic larvae (smelt and herring), cisco being an exception (see later). Fast development does not automatically mean a rapid growth rate. This is usually achieved in warm, shallow inshore waters, which may in any case ensure faster development. Note that the larval fin disappears rather late, although the end of fin differentiation is not shown in the diagram (Fig. 3). Nor is the attainment of adult-like coloration and body proportions drawn in the figure, since more exact data are needed to
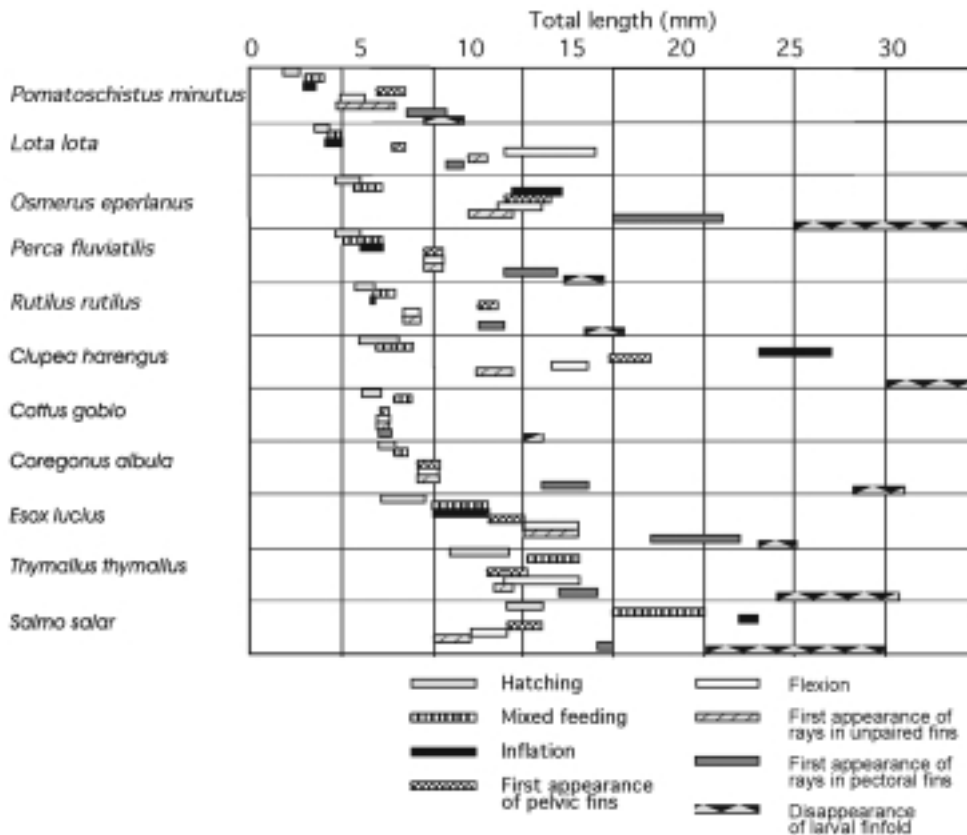
Fig. 3. Comparison of size ranges of eleven fish species with respect to various events during early development.

supplement those given in the previous sections. The developmental differences in morphology become meaningful only when they also reflect functional differences.

Distribution and habitat changes of larvae

Mature fish of the same species gather on spawning grounds to lay eggs at a certain time of the year. That is one of the basic forms of parental care. However, spawning sites are usually so restricted in size that there is insufficient food supply for hundreds to millions of larvae once their yolk is beginning to be exhausted, tiny though most of the larvae may be. The progeny of most species have to disperse after hatching (species with pelagic eggs start earlier), and others after a short inactive phase. The dispersion may be for only a short distance if the larval areas are near the spawning site and the clutch size is not too large. For a tiny fish, the search for food always involves predation risk; so minimising visibility (availability) to predators is therefore an advantage. Most fish larvae change habitat in the course of ontogeny or extend their feeding areas later. There seem to be special areas or habitats where the larvae can feed and attain the size or developmental stage after which individuals are large or developed enough to survive in the feeding areas of the adults.

Morphology and behaviour of larvae seem to affect dispersion and distribution. Although European perch and roach may share the same spawning site, their larval areas do not overlap immediately after hatching, only later in the summer (U r h o 1996b). Burbot and pike larvae, on the other hand may occupy the same areas, but have different spawning sites and a different entrance to their habitat. These examples show that the differences in behaviour of larvae of different species at the time between hatching and onset of feeding greatly influence on the habitat they occupy.

At least two different dispersal tactics exist: 1) immediate dispersion after hatching, and 2) delayed, gradual dispersion after a passive phase (U r h o 1999). After hatching, some species with a direct (or almost immediate) dispersal phase, e.g. smelt, herring, pike-perch, *Stizostedion lucioperca*, burbot and ruffe, spin around their longitudinal axis whilst striving to reach the surface, probably as a result of the longitudinal placement of the tiny pectoral anlage in the shade of the comparatively bigger yolk sac. Without gas in the swim bladder and with undeveloped fins, the ability of larvae to orient themselves in the water column is limited, and the larvae tend to be influenced by currents. With their slow fin development and absence of dorsal melanophores, smelt and herring (Fig. 3) remain in open water areas. They adjust their horizontal distribution by migrating vertically (U r h o 1992, U r h o & H i l d é n 1990) as do many other species of fish larvae in estuary areas (P e a r c y 1962, Q u e l l e t & D o d s o n 1985, S i n c l a i r 1988). In this way, smelt larvae, by remaining in nearshore areas of the Baltic Sea, and spring spawning herring larvae by entering these areas, are able to take advantage of warmer inshore waters during their larval development (U r h o & H i l d é n 1990). Perch larvae, which are often slightly more advanced than ruffe or pike-perch when they hatch, or become so soon after hatching (U r h o 1996a), are able to swim at a 45s angle without spinning around. Soon after the swim bladder has filled, the larvae may therefore approach their inshore nursery areas, although they may have a longer pelagic period in some lakes (W a n g & E c k m a n n 1994, U r h o 1996b). Later in the summer, 0+ perch, after attaining adult-like appearance, may extend their feeding area offshore or out of the estuary (U r h o et al. 1990, J a c h n e r 1991, U r h o 1996b). Other species with immediate dispersion but darker dorsal pigmentation, such as whitefish and burbot, are soon found in very shallow inshore water areas (see later).

Owing to their larger yolk sac and undeveloped pectorals, the larvae of species that do not disperse immediately, such as pike, trout, bullhead and most cyprinids, have even more poorly co-ordinated swimming ability immediately after hatching. They either attach themselves to vegetation or lie among gravel and small stones near the spawning site. After about 1–8 days, when their larval pectorals have grown, their base is turned against the longitudinal axis of the body and the yolk has been further depleted, thus not hampering their movement. Subsequently, pike and cyprinid larvae are better able to direct their swimming to gulp air from the surface and search for food. Note that these changes in swimming behaviour are not directly associated with the onset of feeding, even though they precede it. Cyprinid dispersion has not been studied in great detail, but some larvae are known to descend rivers with the current (e.g. P a v l o v 1994) and in lakes to occur in or near the vegetation area but very seldom in the pelagic zone. The dispersal tactic of roach is different to that of percids (U r h o 1999). Pike larvae remain in the spawning area or at least among shallow vegetation, e.g. in flood areas. At about 20 mm TL, they start to move to deeper waters as the water level falls, in a gradual shift that continues during the rest of the summer (H u n t & C a r b i n e 1951, F r a n k l i n & S m i t h 1963, F o r n e y

1968). The migrations take place on sunny days (F r a n k l i n & S m i t h 1963, J o h n s o n & M ü l l e r 1978). By the time pike reach a length of 40–55 mm SL, their scale cover has started to appear and their eyes have become relatively smaller (S h a m a r d i n a 1957). They are no longer attracted by light and so search for deeper waters (G i r s a 1969). After emergence from the gravel and some days of active feeding, trout larvae gradually begin to disperse from the redds and to station themselves at some distance from each other (M i l l s 1971). It is still under discussion when and how salmon larvae leave the redds (G a r c i a d e L e a n i z et al. 1993, F r a s e r et al. 1994). Anyway, the dispersion is rather slow as with salmon (e.g. W e b b et al. 2001). I have not found any information on the dispersion of bullhead larvae, but when scuba diving I have observed that the larvae remain under a stone in the care of their parent at least until their fins have differentiated. The early development of the pectoral fin rays and rays in unpaired fins (Fig. 3), and negative phototaxis help them to stay in this location whilst the yolk sac is still present.

An interesting group among the Salmoniformes is the whitefish-grayling type (see Soin 1980), whose development stage at hatching (Fig. 3) and dispersion is intermediate between that of the smelt and trout. The whitefish and grayling are known to spawn in lakes and rivers, and even in the Baltic Sea. B a r d o n n e t & G a u d i n (1990) noted that after their emergence from gravel, which mainly occurred at dawn, grayling larvae remained at the point of emergence until nightfall, and then began their initial downstream movement. Both species have only a short, pelagic, dispersal phase. Grayling and whitefish larvae inhabit rivers, which they leave either later in the summer, over a month after hatching (S t r i d s m a n 1987) or, in the case of some whitefish larvae, right away, descend the river to the beaches in the archipelago (L e h t o n e n et al. 1992). All, however, remain as larvae for some time in the shallow water areas (H u d d et al. 1988, L e s k e l ä et al. 1991), where their fins soon become differentiated. L e s k e l ä et al. (1991) found some whitefish up to a length of 40 to 60 mm TL still in shallow nursery areas, though most had probably left at a smaller size. Cisco larvae inhabit shallow water areas that are the same as or similar to those inhabited by whitefish, but they seem to migrate offshore sooner than whitefish. The offshore migration probably takes place gradually, however, and depends on environmental conditions (N a e s j e et al. 1986, L e s k e l ä et al. 1991). On the whole, the larvae of many species occur in secluded, often shallow, inshore areas that tend to be separate from the feeding areas of the adults until the larvae metamorphose into adult-like juveniles and search for deeper waters.

Larval morphology and behaviour after hatching, together with environmental cues, determine the tactics larvae may use to reach a nursery area where they can find food, avoid predators, develop into the definitive phenotype, and become competitive enough to share the feeding areas of juveniles and adults. Thus, habitat changes during development may help us to identify the boundaries separating ontogenetic periods. Care should be exercised, however, since larval flexibility to environmental cues makes habitat changes both variable and gradual (when populations are examined). Burbot may be a good example of the adaptability and phenotypic plasticity of the larvae. Despite the present systematic status of burbot, there appear to be two distinct larval forms (S n y d e r 1979). One is already well pigmented, with melanophores at the yolk sac phase (see Y e v r o p e y t s e v a 1946, M ü l l e r 1960); it occurs in Europe and North America. The other is without any melanophore pigmentation during the 'protolarval' phase, except for the eyes and dorsal

surface of the air bladder (see F i s h 1930, 1932), and appears to be restricted to the lower Great Lakes and their tributaries (S n y d e r 1979). Published figures suggest that there are other minor differences, too. More important, however, may be that the two forms apparently favour different habitats; after dispersion, the European form moves to near-shore areas but that in the Great Lakes remains longer in the pelagic. Furthermore, it seems to be a question of lake characteristics, since W a n g & A p p e n z e l l e r (1998) also reported late pelagic burbot larvae in Lake Constance in the middle of Europe. Great differences also exist in the timing of the return of Eurasian perch larvae to nearshore waters (U r h o 1996b). Moreover, some intraspecific differences have been observed in the pigmentation of perch larvae (U r h o 1996a). Further studies are, however, needed to establish whether the differences in morphology have any influence on the timing of the shoreward shift, which may also be enforced by environmental cues. Not all ontogenetic structures are adaptations to the environment, which may, nevertheless, affect pigmentation and morphology.

Conclusions

Current definitions of larvae or juveniles and metamorphosis need to be reconsidered as they are conflicting, misleading and do not correspond to reality. The definition of the beginning of the larval period seems to be a minor concern, if you just specify which one of the two options you are using. Bearing in mind that the developmental stage at hatching may vary, definitions stating that the larval period begins at the moment of hatching would still seem to be the most applicable, especially from the ecological point of view, even though only the ontogenetic point of view might favour use of the onset of external feeding as the beginning of the larval period. If the eggs are treated in a certain way, then fish may start feeding within a few hours of emerging from the egg envelopes (L u c z y n s k i & K o l m a n 1987). The fact is, that morphological and physiological development proceeds much further inside the egg shell in some species than in others, and this rate of development can be influenced by external factors also. However, by leaving their egg shells, individuals will expose themselves to different environmental factors, permitting the environment more strongly and diverse not only to shape phenotype but also enabling natural selection to act earlier and more versatile means. Thus, I regard hatching as the onset of the larval period.

The endpoint of the larval period is more open to debate than is the onset. The international workshop "When do fish become juveniles? – Looking beyond metamorphosis to juvenile development", held in Bratislava, September 1997 (C o p p et al. 1999) did not close the debate, on the contrary, stimulated it to broaden the bases and perspectives of organism-to-environment interactions (B a r a s & N i n d a b a 1999, B i s c h o f f & F r e y h o f 1999, G o z l a n et al. 1999, K o v á č et al. 1999, L a g a r d è r e et al. 1999, S i m o n o v i ć et al. 1999, V i l i z z i & W a l k e r 1999, P e ň á z 2001). In fact, it is probably the difficulty of defining the end of larval life that has led some terminology to define a special transitional phase, either at the end of the larval period or at the beginning of the juvenile period, or as a distinct interval between the two (K e n d a l l et al. 1984, S n y d e r & H o l t 1984, M o s e r 1996, G o z l a n et al. 1999, K o v á č & C o p p 1999); this I understand very well. Owing to the great variety of ill-defined characters, we cannot derive an exact, unambiguous definition of larval life. Often only one character is selected, e.g. the full complement of fin rays, and others are ignored. As in the identification

of species, the use of only one character is inadequate. I suggest that several attributes should be used to define the end of the larval period even though we may have to make compromises. It has been demonstrated that allometric growth continues after the loss of larval finfold and acquisition of the full finray complement (see e.g. S h a m a r d i n a 1957, P e ň á z 1975, U r h o 1992, K o v á č & C o p p 1996). I agree with the proposal of C o p p & K o v á č (1996) that the larval period proceeds until the stabilisation of allometric growth and the consequent achievement of adult-like appearance. Given that a larva is a structural state or series of states, which are transitory and lost at metamorphosis but reflect adaptations for larval life, the structural features allow recognition of larvae and their biology, including ecology, development, and evolution (W a k e & H a l l 1999). As in metamorphosis, not only morphological changes are relevant but also the dispersion, survival, distribution and habitat changes of larvae.

The way in which larvae of different species disperse seems to depend on their morphology and developmental stage at hatching. These features in turn have a strong genetic background, although some environmental influence cannot be denied. The environmental effect on larvae becomes stronger after their dispersion into nursery areas, and it may exert a greater influence on the phenotype of species that hatch at an earlier developmental stage. Habitat changes by larvae also have a genetic basis, but the environment (water quality, feeding conditions and predation pressure) has a strong influence, especially on the timing of changes. Fish may change habitat several times during their early development, but after the last change into adult habitat the fish should look like an adult. By applying the concept 'definitive phenotype in definitive niche', we find that the larval period lasts longer than previously assumed. Salmon and trout 'parr', before smoltification, should then also be called larvae.

In the epilogue of the book "The origin and evolution of larval forms" W a k e & H a l l (1999) ask not only "What is a larva", but also "Why larvae evolved at all"? The easy answer usually provided is that larvae contribute to the survivorship of species by diversifying both larval and adult life forms and thereby the habitat and resource availability. They also continue "Why adults evolved?" I gained the impression from certain studies (e.g. B a l o n 1986a,b, 1989b) that it is a disadvantage or a burden to have a larval phase. I beg to differ, however. My conclusion is that larvae provide a means to make more extensive use of the aquatic environment. Spawning grounds do not normally support large quantities of offspring, therefore dispersion and translocation to a nursery area may be vital for survival, especially for small fish larvae to mitigate predation or to use some extreme habitats. For example, wide pelagic zones and extremely shallow, nearshore areas are inhabited by larvae of certain fish species, although sometimes during a short period only. Larval ontogenetic habitat shifts and the partitioning of resources in time and place (U r h o et al. 1990) may be the keys to higher fish production. For many amphibians, larvae reflect the species' ability to exploit aquatic resources, even ephemeral ones. However, since the largest proportion of somatic growth occurs after metamorphosis, W e r n e r (1986) considers that the complex amphibian life history evolved not only to maximize growth but also to minimize the risk of predation. For some aquatic invertebrates, e.g. barnacles and bivalves, larvae function as a way to disperse and invade new areas where they can grow after the larval period. The opposite, growing as larva and dispersing and finding new areas as adults, is true for many insects. The idea that the main purpose of a larva is the acquisition of external nutrients to build a definitive phenotype (B a l o n 1990), however,

includes an important point: larvae are the life stages of fish that are able to utilise even small and very abundant food organisms, and thereby increase fish productivity manyfold. The distinctive character of larvae is that they are adapted to make use of those resources that adults tend not to use.

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