Saltatory Processes and Altricial to Precocial Forms in the Ontogeny of Fishes[1]

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SYNOPSIS. Development is not a gradual but a saltatory process. A combination of qualitative changes in form and function—thresholds—creates boundaries between a succession of quantitative intervals—steps. Thresholds can be modified by an altered time of appearance of structures and functions (heterochrony), especially during early ontogeny, to form an operational basis for the prolongation of juvenile characters and adaptability into later ontogeny. Whereas such prolongation enables juvenilization in phylogeny, analogous principles may operate on a much shorter time scale to produce the *r*-selection-like *altricial* and the *K*-selection-like *precocial* trends in ontogeny. The inherited capacity to adjust constantly to the environment (heterochrony) selects for structural, biochemical and behavioral improvements. The tendency is toward the precocial but the way back to altricial forms is left open. The heterochronous adaptations in early ontogeny can "reverse" the vulnerable specialization, should the environment become less stable and/or the community less competitive. Juvenilization, capable of turning gerontomorphosis into paedomorphosis in evolution, and heterochronous shifts of character anlagen, capable of turning a precocial trend into an altricial trend in ontogeny are both part of the same biological process which operates during early ontogeny.

INTRODUCTION

All of us accept the date of birth as an important point in our social and cultural life but rarely do we realize that this date is meaningless as a life history value (see also Noakes, 1978, 1980*b*). Individuals born prematurely are older on paper than are those born in the normal span of time; they are born in an earlier state of development which renders them retarded by comparison with those born in the usual time. This paradox applies to parturition and hatching (see Glossary on p. 589 for definition of this and other terms used in this paper), both of which are impossible to define in terms of "normality" because both are largely influenced by the environment and do not occur at a particular state of development. One wonders why hatching and parturition continue to be perceived as exact events of ontogeny (*e.g.,* de Beer, 1958).

Much thought has been devoted to the exact timing of ontogeny. With regard to fishes, several proposals come to mind: 1) the thermal sum method expressed as temperature units (or thermal units or degree-

days = the number of degrees over 0°C in each 24 hr), 2) the zero of development theory (Marckmann, 1954), 3) the mitotic or cleavage cycle (Detlaf and Detlaf, 1960; Ignatyeva, 1970; Balon, 1980), and 4) the log-inverse Bělehrádek model (Alderdice and Velsen, 1978). In no case were these attempts at increased precision matched by equally precise events in ontogeny (*e.g.,* Garside, 1959).[2]

Although bureaucrats and fishermen use the date of birth or hatching to calculate age, the biologist finds it hardly satisfactory. Yet, is it possible to correlate more exactly the developmental state with time? Is it clear, for example, when ontogeny begins? In salmonids, for example, gametes can be mixed in coelomic fluid after stripping; the coelomic fluid of a female activates the sperm which penetrates, but becomes arrested half way down the micropyle (Ginsburg, 1963). With the exception of an invasion of sperm into the micropyle, the egg remains unchanged, and under these circumstances *insemination* cannot be considered to be the beginning

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[2] We know almost nothing about variability amongst individuals (Sytina and Timofeyev, 1973) or about hard selection in early ontogeny (Wallace, 1970; Cohen, 1977); both obviously influence the precise determination of any particular developmental state.

of ontogeny. If however, as in the course of natural mating, the gametes are released into the water, insemination coincides with the activation of the ovum by the water (Brummett and Dumont, 1979). The cortical granule content of the egg is discharged (Iwamatsu and Ohta, 1976) which is followed by rapid changes of external tension and density, formation of perivitelline fluid and a simultaneous continuation of meiosis (Ginsburg, 1963, 1968; Epel, 1979). Along with changes in ion concentration there is a subsequent formation of pronuclei. However, the changes in the ova as induced by contact with the water and which initiate normal development also occur in parthenogenetic organisms. Therefore, *activation* should be considered the beginning of ontogeny. Only later, during the course of bipolar differentiation, does the conjugation of the pronuclei of sperm and egg occur, thus forming the zygote (Ginsburg, 1968); this process can be termed *fertilization* but it cannot be considered exclusively to mark the beginning of ontogeny, because it is absent in gynogenetic or parthenogenetic organisms (see Løvtrup, 1974, for other combinations of activation = maturation and fertilization).

It is my hope that these examples suffice to justify my earlier Humpty Dumpty quotations (Balon, 1975a, 1976) or the repetition of one thereof: ". . . if we wish to communicate accurately we are under a kind of moral obligation to avoid Humpty's practice of giving private meaning to commonly used words. (. . .) Do we have an obligation to past usage? In one sense words are our masters, or communication would be impossible. In another we are the masters; otherwise there could be no poetry." After all, the clergy will use its own language and give its own meaning to birth, as will a veterinarian or fisherman. What one calls a baby or child, another will call foetus, puppy, chick, fry or fingerling. However, as all organisms reflect the same general principles of evolution and genetics, biologists should not fall prey to jargon or some lay views of ontogeny to describe otherwise precise observations. The terminology must be consistent for all or-

ganisms (Noakes, 1980b); life history boundaries must be standardized and comparable in all animals, if not plants (Goethe, 1977). In the past many useful generalizations and comparisons were precluded because of interpretation limited to and comprehensible exclusively in one taxon.

Partially for this reason I have tried to continue the work of S. G. Kryzhanovsky, especially as his untimely death prevented us bringing it to fruition together, as planned (Balon, 1962). The main intervals of ontogeny were defined and, for example, the transition from endogenous (or intraparental) to exogenous (or extraparental) feeding identified as the end of the embryonic period (Balon, 1958, 1960, 1971, 1975a). The start of exogenous feeding clearly separates one physiological state from another and is abrupt in contrast to the long span of hatching. In one case I decided to abandon ill defined or confusing lay terms (fry, wriggler, yolksac larva) and introduced eleutheroembryo (free embryo) for the interval of the embryonic period after hatching. This has enraged some (Richards, 1976) to such an extent that the more important issues of standardization, saltation and comparative ontogeny were overlooked (Balon, 1976). Nevertheless, the well defined terms and hierarchy of life history intervals later enabled me to formulate the putative developmental classification of fishes (Balon, 1975b, c; Balon et al., 1977) which has now achieved some acceptance (e.g., Noakes, 1978, 1980b; Bond, 1979; Welcomme, 1979), and has further facilitated the exploration into the significance of the elimination of the larval period (and larvae) in some fishes (Balon, 1977, 1978).

Most of the practical application of studies of fish development centers around "egg and larval" taxonomy (Moser and Ahlstrom, 1964; Ahlstrom and Moser, 1976; Ahlstrom et al., 1976; Snyder, 1976; Snyder et al., 1977). This field has been dominated by marine biologists familiar primarily with species that have extended larval periods (Johannes, 1978). Therefore, the lack of understanding of the proposed model and its integration persists in

studies aimed at identification (*e.g.*, Russell, 1976; Doyle, 1977; Fuiman and Loss, 1977; Allan and Ritter, 1977; Jones *et al.*, 1978; Hardy, 1978; Johnson, 1978; Fritzsche, 1978; Martin and Drewry, 1978; Buynak and Mohr, 1979). Many "larval" taxonomists, in contrast to developmental biologists (*e.g.*, Proctor *et al.* 1980) were unable to appreciate the absence of larvae in some fishes or entirely missed this important aspect of life history (*e.g.*, Morris, 1951), proving Arthur Koestler (1979, p. 240) once more right when stating: "Habit is the denial of creativity and the negation of freedom; a self-imposed straitjacket of which the wearer is unaware."

I hope, in this paper, to shed light on my intentions and unite at least some "larval" taxonomists. More important, the standardization of life history intervals and the classification of various modes of ontogeny should now permit us to pursue more complicated topics in the ontogeny of fishes, such as the theory of saltation and heterochrony.

THE THEORY OF SALTATION

The view that development proceeds gradually is so engraved in our minds that any other possibility is not only treated with disbelief but viewed with distaste. Gould (1977, p. 409) put it admirably: "The reconciliation of our gradualistic bias with the appearance of discontinuity is a classical problem of intellectual history. We have sought to reduce the external phenomena of saltation to an underlying continuity of process—to reduce the qualitative to the quantitative. Philosophies of change and progress have wrestled with this dilemma and have tried to resolve it by formulating such laws as the 'transformation of quantity into quality' of the Hegelian dialectic: the addition of quantitative steps will lead eventually to a qualitative leap . . . ." The more comforting belief is that ontogeny and phylogeny are gradual. Gradual ontogeny can be "proved" by arbitrarily and leisurely sampling a sequence of stages, gradual phylogeny by expectations of finding every "missing link."

First, to alleviate the bad taste, I propose to talk of saltation instead of discontinuity.

Saltation (*e.g.*, Liem, 1974; Waddington, 1975; Ruse, 1977) seems to be a better term for this phenomenon because it means "an advance by a leap or leaps rather than by continuous gradation." Development is not interrupted, but merely "advancing in spurts" (Webster's New International Dictionary of the English Language, 1960).

The theory was first applied to the ontogeny of fishes by Vasnetsov (1953) and Kryzhanovsky *et al.* (1953). They invented a sequence of steps[3] of quantitative morphogenesis and growth, separated by thresholds, a combination of brief but distinct qualitative changes in a developmental process.

Thom's catastrophe theory is probably closest to a mathematical model of steps and thresholds (Thom, 1973; Stewart, 1975), but its application remains doubtful for lack of detailed knowledge of ontogeny in most organisms, and possibly, because of faults in the theory itself (Bari Kobata, 1977). After all, it partly seems nothing more than a geometrical model of Hegelian dialectic. At present "discontinuities" in ontogeny of behavior excite considerable interest (*e.g.*, Flavell, 1971; Isaac and O'Connor, 1976; Bateson, 1978; Kagan, 1978); however, limited only to behavioral aspects, such arguments are incomplete.

Reviewing the step theory Yeremeyeva (1967) added little to the original formulations of Vasnetsov (1953) and Kryzhanovsky *et al.* (1953). She tried, however, to correct some earlier distortions (Matveyev, 1955) forced on the Hegelian dialectic in biology (Engels) by quacks such as Lysenko (see Medvedev, 1969) but failed to provide new evidence in support of or clarify the

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[3] Translations of Russian terms are invariably wrong etymologically; usage of lay jargon words is also unfortunate (*e.g.*, in the AFS version of "Voprosy Ichtiologii," the Journal of Ichthyology). In my translation the Russian "stadia" should be stage, "etap" = step (preferably not stanza), "faza" = phase and "period" = period. Incidentally, the Russian authors usually cite two of Vasnetsov's (1946, 1948) earlier articles in which the concept of 'etapes' was first developed. However, only in 1953 did Vasnetsov clearly formulate the concept, as also recognized by Soin (1964, p. 499).

theory of saltation. Her basic interpretation of thresholds was still that "the anlagen of new organs and their new functions appear at the boundaries of developmental steps during the transition from one step into another. This transition occurs as a leap, as a transition of quantity into quality." More specifically, "during each step, consecutively accumulated quantitative and qualitative changes of structure and in function of the organism gradually result in small changes of the relationship with the environment; accumulation of these changes continues until a certain limit is reached. When this happens a transition into a new step of development occurs . . ." (Yeremeyeva, 1967, pp. 4–5, my translation).

Obviously this interpretation is limited and cannot explain all thresholds in ontogeny. In my later redefinition, "abrupt functional changes" are meant in terms of internal changes in the organism as well as external environmental changes; only a certain combination of leaps from quantity into new quality will form a valid threshold (Sytina and Timofeyev, 1973). Many other isolated changes in quantity and quality will occur within a step but will have no functional significance until they associate in a meaningful combination. At the moment, recognition of such combinations constitutes a major difficulty in the application of the theory of saltation, which I consider an integral part of the hierarchic system of Koestler's (1975) "holons." Koestler (in Koestler and Smythies, 1969) postulated that (his italics) "in *ontogeny*, the apex of the hierarchy is the zygote, and the holons at successive levels represent successive stages in the development of tissues. Each step in differentiation and specialization imposes further constraints on the genetic potential of the tissue, but at each step it retains sufficient developmental flexibility to follow this or that evolutionary pathway" (which he qualifies in the Appendix I of his latest book [Koestler, 1979]) "within the range of its competence, guided by the contingencies of the environment." While the ontogenic events (as said earlier) do not correspond exactly to Koestler's description, in a more

general sense he is obviously correct. Probably, during each step one or more holons are assembled and at thresholds these commence function.

Two examples of such combinations of leaps in structures forming thresholds may elucidate the theory of saltation: In the Danubian zope, *Abramis ballerus* (Cyprinidae), the jaws, finfolds, cement glands and the swimbladder structure take a long time to form. During that time the eleutheroembryo remains at the bottom, displaying a photophobic reaction. Photophobia changes abruptly into phototaxis and while the finfold facilitates swimming motions towards the surface, the moving jaws gulp air which fills the swimbladder. At the same time the cement glands on the head enable the fish to hang on plants thus preventing further contact with the bottom.[4] Several structures developed quantitatively suddenly start functioning or change their function, thus combining into a new qualitative threshold. As a result, there is an environmental change from the bottom to the more oxygenated midwater. This in turn enables a switch from embryonic yolk respiration to branchial respiration (Balon, 1959). A threshold is attained and a new step begins.

In a recently hatched walleye, *Stizostedion vitreum* (Percidae), a threshold manifests itself in the following features (McElman and Balon, 1979): The head-trunk axis straightens, causing approximately a 20% elongation of the yolk (Fig. 1). The head tissues become translucent due to the demise of the hatching gland cells. An abrupt reduction in blood volume, passing from the caudal vein to the posterior cardinal veins, causes an increase in the blood volume from the caudal vein to the subintestinal-vitelline vein, the main embryonic respiratory organ at that time of ontogeny. Eventually the blood ceases to flow into the

[4] Hamlett and Wourms (1978) found that in angel fish, *Pterophyllum scalare*, cement glands function two days prior to hatching. In this case the real hatching again proved to be a flexible event under environmental control and the first function of the cement gland signifies the potential hatching time, *i.e.*, saltatory threshold (Balon, 1980).
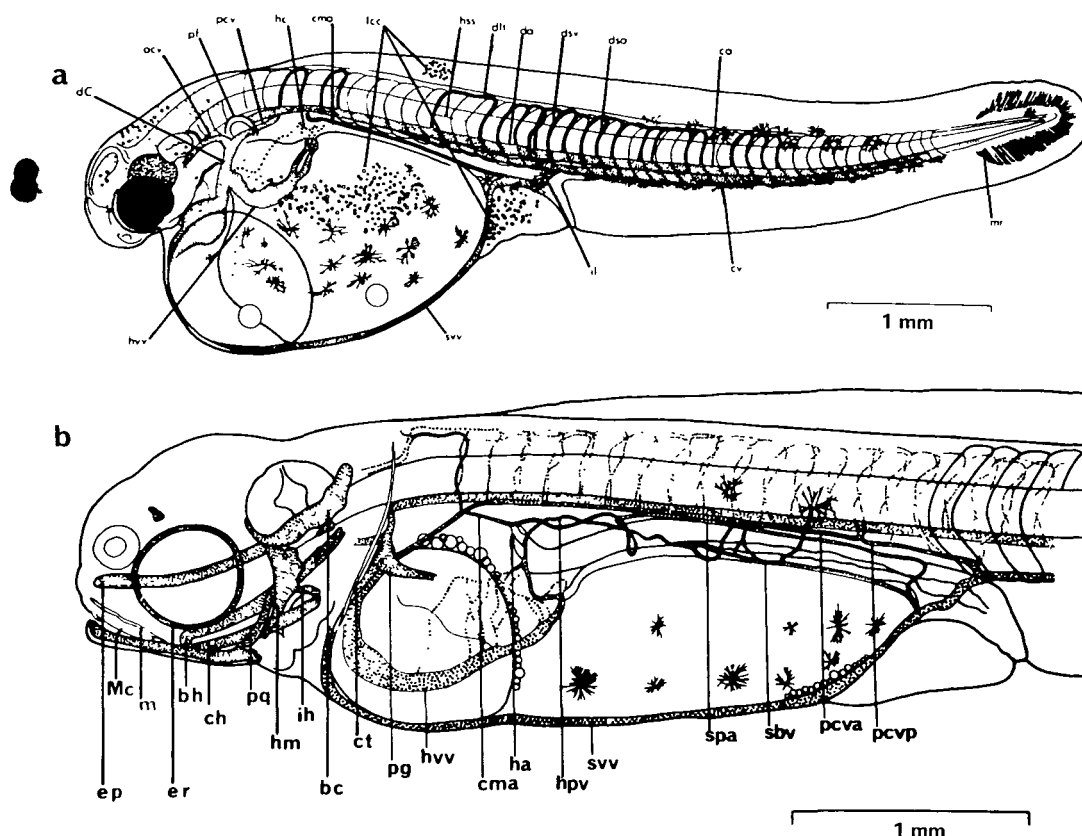
Fig. 1. Main structures of walleye, *Stizostedion vitreum*, at two critical stages of ontogeny: a—embryo at age 6 days 18 hr 10 min (15°C), left side view after excision from egg membranes (acv = anterior cardinal vein; ca = caudal artery; cma = coeliac-mesenteric artery; cv = caudal vein; da = dorsal aorta; dC = duct of Cuvier; dlt = dorsal longitudinal trunk of the segmental vessels; dsa = dorsal segmental artery; dsv = dorsal segmental vein; hc = hepatic capillaries; hss = horizontal skeletogenous septum; hvv = hepatic-vitelline vein; il = intestinal loop of the caudal vein; lcc = large clear cells; mr = mesenchyme rays; pcv = posterior cardinal vein; pf = pectoral fin bud; svv = subintestinal-vitelline vein). b—eleutheroembryo at age 10 days 23 hr (15°C), preanal part (bc = basicapsular commissure; bh = basihyal; ch = ceratohyal; ct = cleithrum; ep = ethmoidian plate; er = eye ring; ha = hepatic artery; hm = hyomandibular; hpv = hepatic portal vein; ih = interhyal; m = maxillary; Mc = Meckel's cartilage; pcva = posterior cardinal vein with anterior directed blood flow; pcvp = posterior cardinal vein with posterior directed blood flow; pg = pectoral girdle (cartilage component); pq = palatoquadrate; sbv = subintestinal vein; spa = supraintestinal artery). After McElman and Balon, 1979.

posterior cardinal veins and the entire caudal vein flow is diverted through the subintestinal-vitelline vein. This diversion is accompanied by a reduction in the rate of heartbeat and the change in the circulatory system signifies maximization of the superficial exposure of blood elements—the largest proportion of the total blood volume becomes exposed in the subintestinal-vitelline vein, the remainder flowing to the head and the anterior myomeres become exposed in the duct of Cuvier. At the same time the embryos swim to the surface and become deposited by the water currents in calmer waters of the river. Unable to maintain position at or near the surface, the eleutheroembryos fall to the bottom where siltation, organic debris, low flow and possibly aquatic vegetation form an environment of low oxygen concentration. The maximum development of the embryonic respiratory systems at that time compensates for the lost oxygen during the switch of environments.
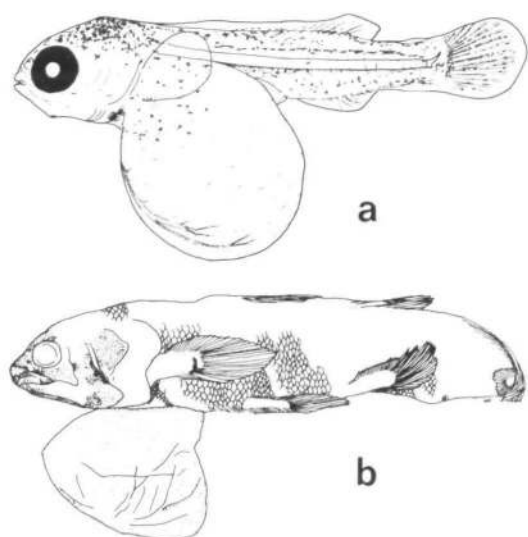
FIG. 2 Eleutheroembryos of the mouthbrooding cichlid *Labeotropheus* (a) and the ovoviviparous coelacanth *Latimeria* (b), with approximately similar residue of yolk supply and development of various degrees of juvenile structures. After Balon, 1977.

Yeremeyeva (1967) aptly concluded that the theory of steps in ontogeny is often misunderstood and undervalued. Recently Koshelev (1978) again addressed the Russian version of the saltation theory in fish ontogeny but added little to the latest recapitulation of Yeremeyeva (1967). Nevertheless Koshelev's (1978, p. 6) insistence on studying intraspecific differences in sequence of "individual—population—species" has already been largely realized in my most recent studies (Balon, 1980).

INTERVALS OF ONTOGENY—STEPS AND THRESHOLDS

For the sake of clarity let me repeat here again (Balon, 1975a) the often confused intervals of ontogeny—periods, phases and steps—whose relationship should be compared to the relationship existing between measurable units of time—days, hours and minutes. Stage refers to an instantaneous state of ontogeny and should not be confused with any interval; *e.g.*, the use of larval stage, yolksac stage, adult stage, etc. is entirely nonsensical. Steps and periods are the units of saltatory development (Kryzhanovsky, 1956, p. 5) and phases artificial intervals inserted for the con-

venience of identification (Balon, 1960). Therefore, only phases are based on visible but vague events (*e.g.*, hatching) of no saltatory significance.[4]

A sequence of steps forms periods, the main intervals of ontogeny (Table 1). However, the larval period, for example, exists in salmonids only as a vestige (Disler, 1957; Smirnov, 1975; Peňaz, 1975; Balon, 1980), is truncated in cyprinodontids (Peters, 1963; Wourms, 1972c; Avni and Soin, 1974) and is entirely eliminated (Fig. 2) in some mouth brooding cichlids, and *Latimeria* (Balon, 1977). In these cases when hatching (or for that matter parturition or release) coincides with the onset of exogenous feeding, the end of the embryonic period will also coincide with these events. As a rule in such cases the larval period is eliminated. This fact was recognized already by de Beer (1958, p. 34) but was confused for lack of useful definitions of periods and stages.

The onset of exogenous feeding occurs over a wide range of developmental features in any given species (Yeremeyeva, 1960) and even more so in various fishes. Sometimes oral feeding begins when the embryonic finfold is entirely undifferentiated and at other times not until all fins are fully developed. Fish with fully developed fins, however, look very much like small adults or at least like their juvenile siblings, and it is illogical to consider them as larvae simply because most other fishes have larvae. Larvae require metamorphosis before they take on the appearance of juveniles or "small adults" (Cohen, 1977).

I demonstrated (Balon, 1977) that oviparous fishes, with reproductive hiding strategies, eliminate the larval period to varying degrees. This enables emergence (in salmonids, acheilognathids) or release (in cichlids) of large juveniles at the start of exogenous feeding (Fig. 3). In an evolutionary context, salmonids evolved hiding of their earliest stages of ontogeny last of most 'brood hiding' fishes. Therefore, they may at times display a vestigial larval period (alevin) incorporating characters typical of both the larval and juvenile periods in other fishes.

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TABLE 1. *The hierarchy of intervals and of stages in ontogeny from the longest (top of the table) to the shortest (bottom).*
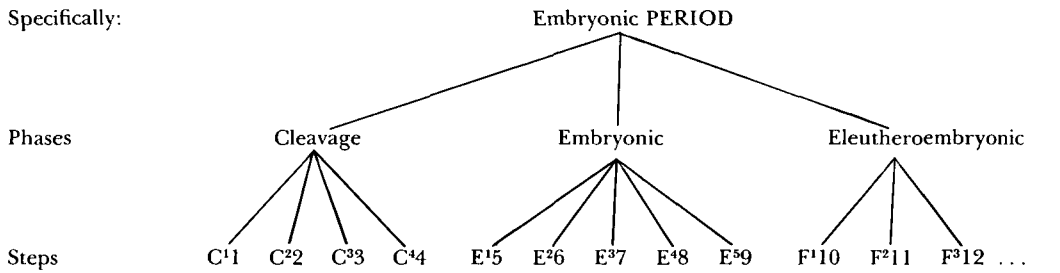
Period = the largest interval of saltatory ontogeny, one of five (or four) constituting the entire life—embryonic, larval (or alevin or missing), juvenile, adult and senescent.

Phase = the second largest interval of ontogeny devised for morphophysiological identification of developmental levels—*e.g.*, the phases of embryonic period are: cleavage, embryonic and eleutheroembryonic; of larval period: protopterygiolarval and pterygiolarval.

Step = the shortest interval of saltatory ontogeny separated by thresholds, a combination of functional (qualitative) leaps—*e.g.*, steps of cleavage phase can be designated $C^1 1$, $C^2 2$, $C^3 3$, $C^4 4$, $C^5 5$; steps of the embryonic phase $E^1 6$, $E^2 7$, $E^3 8$, etc.

Stage = an instantaneous state of ontogeny; should not be used for any interval, *e.g.*, larval stage, adult stage, etc.

Specifically: Embryonic PERIOD

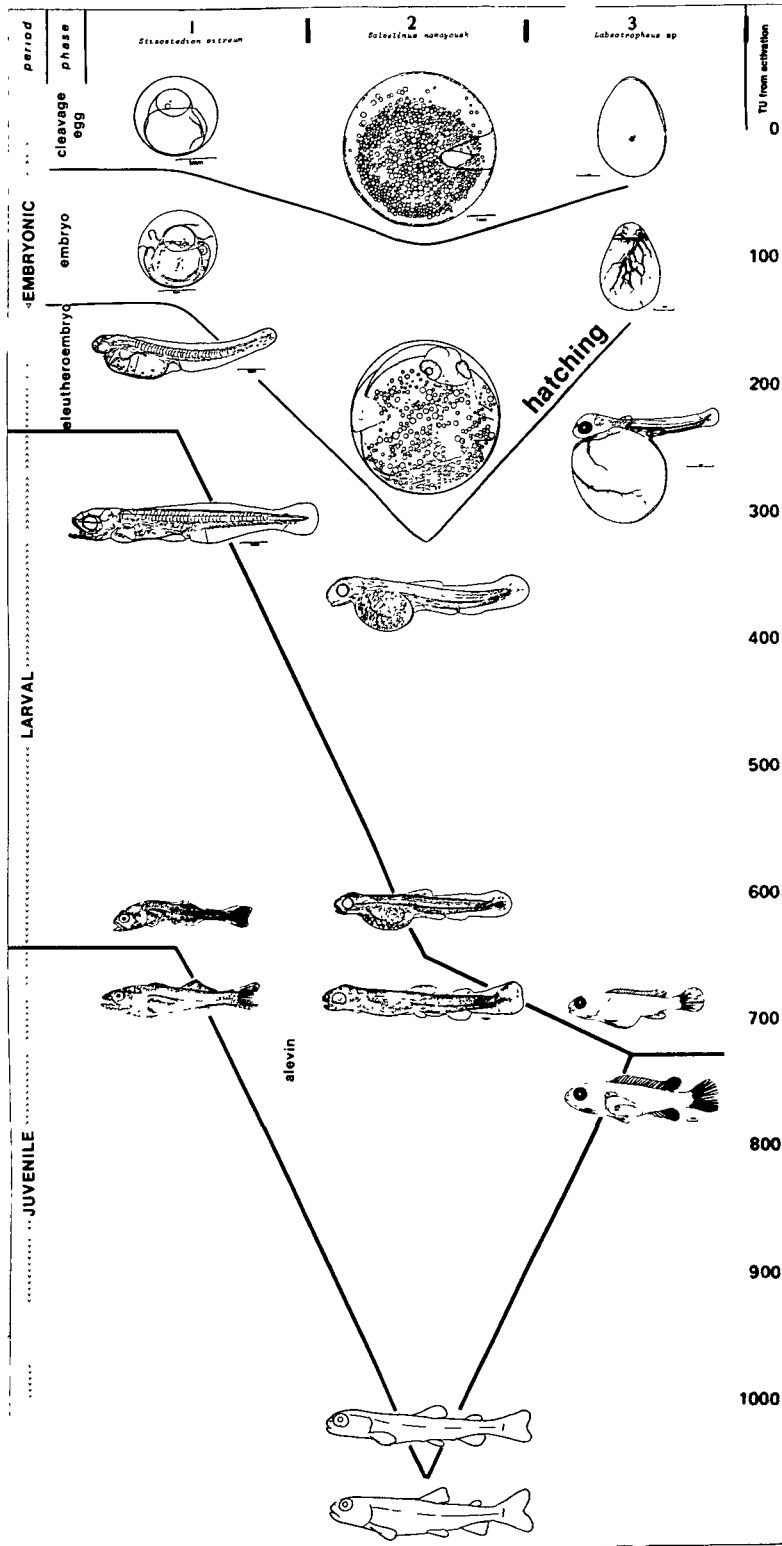| Phases	Cleavage				Embryonic					Eleutheroembryonic		
Steps	$C^1 1$	$C^2 2$	$C^3 3$	$C^4 4$	$E^1 5$	$E^2 6$	$E^3 7$	$E^4 8$	$E^5 9$	$F^1 10$	$F^2 11$	$F^3 12$ ...

hiding the earliest stages of ontogeny is associated with an increase in egg size and yolk density, the graylings and landlocked salmons, with relatively small eggs, should exhibit the larval vestige to a greater extent than other salmonids. The evidence presented by Soin (1963) and Peňaz (1975) for grayling, and by Smirnov (1975) for landlocked Pacific salmon supports this contention. This means that species with the least developed hiding strategies retain more of the vestigial larval period during and immediately after the transitory interval of mixed feeding which separates the embryonic period of endogenous nutrition and the juvenile period in which all final adult structures have appeared. In fishes with more advanced hiding strategies this transitory vestige of the larval period does not exist. In these, all juvenile characters (Balon, 1975a) develop initially while feeding is still endogenous (Fig. 4), either from the yolk (Balon, 1977) or ultimately, as in viviparous fishes, from the female via special absorptive organs. With the advancement of hiding strategies, the transition from endogenous to exogenous feeding is more sudden, and the interval of mixed feeding is very brief or nonexistent.

It is obvious from the foregoing that truncations or prolongations in ontogeny will not only eliminate or expand the periods but also the steps. Consequently, steps are specific to every guild, every species and perhaps every intraspecific form (Balon, 1980). The various life history traits are only possible thanks to early ontogeny's flexibility for adaptation to new requirements. Some of these adaptations occur through heterochronous shifts of anlagen.

Thresholds occur at the end of steps as distinct functional changes (Vasnetsov, 1953; Balon, 1958, 1959, 1960). In this sense a threshold should be defined as *a combination of abrupt functional changes* during ontogeny and be presented as a median time from the first to the last appearance of such changes in individuals. I disagree that "the earliest morphological stage at which commencement of the functioning of an organ becomes possible and at which the change of function occurs in the individual most advanced with respect to this indicator should be recognized as a transitional" (Sytina and Timofeyev, 1973, p. 241) threshold from step to step. Such an approach would certainly require the redefinition of steps as "a period of development in the course of which a new func-

tion is established in a group of individuals of the same age." It is unnecessary. As thresholds occur in different individuals not at exactly the same time and/or state of development they must be presented as a median threshold if reference is made to a group of individuals (in order to parallel, for example, the way morphological variability is expressed).

At present it is impossible to decide if changes in the mitotic cycle or cleavage, including the multiplication, differentiation and eventually, the locomotory ability of cells (*e.g.*, Betchaku and Trinkaus, 1978) can be considered a threshold. The saltatory development may be expressed, during the cytoplasmically programmed initial interval of ontogeny, at a molecular level better than in external cytomorphology. For example, "the switchover from egg cytoplasmic to embryo nuclear direction," *i.e.*, the assumption of complete genomic control (Davidson, 1976) may be a well defined threshold reflected little in external morphology. Furthermore, the distinction between a change of structure and a change of function is not always clear. The theory of steps or, more correctly, the theory of saltation will require detailed elaboration of all aspects—biochemical, physiological, morphological, ethological (and not necessarily in that order)—before the exact placement of all thresholds in ontogeny will be possible. Some advances in this direction are already available (Vernidub and Guzeva, 1950; Neyfakh, 1971; Shaklee *et al.*, 1974; Whitt *et al.*, 1977; Philipp and Whitt, 1977; Shaklee and Whitt, 1977; Fisher and Whitt, 1978; and see Davidson, 1976, for more), some preceded the formulation of the theory itself (*e.g.*, Trifonova, 1937; Strelkovsky, 1940).

At the biochemical level, however, the thresholds may not coincide exactly with the thresholds of morphogenesis due, for

FIG. 4. Probably a freshly released specimen of *Latimeria chalumnae*, the smallest free swimming individual caught near Comoro Island (labeled C79 in the collection of the Laboratoire d'Anatomie Comparée in Paris). Photo. E. K. Balon.

example, to an earlier occurrence of the biosynthetic activity (Neyfakh, 1964; Giudice *et al.*, 1968).

The terminology of all intervals of ontogeny—periods, phases and steps—should be consistent and should reflect the hierarchic theory of saltation, as opposed to the "normal stages." It is immaterial whose terms are used as long as they are meaningful, consistent, etymologically correct and logical (see petit on p. 590 and Table 1). In my hierarchic model of ontogeny (Balon, 1975a) the terms were selected in accordance with the saltation theory, and to facilitate comparisons. I see no logic in such terms as prolarva, postlarva (Hubbs, 1943), protolarva, mesolarva, metalarva (Snyder, 1976) or aptero- and pterolarva (Rass, 1968), especially when no larvae exist. Such terms, used or copied automatically (Maekawa, 1977; Allan and Ritter, 1977; Bagenal and Braum, 1978), would not be employed if there were a complete understanding of the contemporary data on comparative ontogeny. Even the Russian school, which benefited greatly from nomenclatorial reviews and criticism repeatedly made by Kryzhanovsky (*et al.*,

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FIG. 3. A comparison of main intervals in early ontogeny of the egg scattering walleye, *Stizostedion vitreum* (1), egg hiding lake charr, *Salvelinus namaycush* (2) and mouthbrooding cichlid, *Labeotropheus* sp. (3). Developmental time is expressed in thermal units (TU) against which the boundaries of periods (bold lines) and phases (thin lines), and illustrations of selected stages are placed. One from McElman and Balon, 1979; 2 from Balon, 1980; 3 from Balon, 1977.

1953 and alone 1956), occasionally falls into dubious nomenclature (*e.g.*, Smirnova, 1978, p. 56).

As an explanation of the meaning of comparative ontogeny, I should like to consider the relationship of a fish embryo to the avian and mammalian embryos. If endogenous nutrition characterizes the embryonic period in all vertebrates, certain modifications of ontogeny will become more obvious and will form a more uniform pattern than if hatching and parturition were considered the boundaries of the embryonic period (Noakes, 1980*b*). Delayed exogenous feeding of early-hatched birds and glandular feeding of early-born mammals, *e.g.*, marsupials (Cohen, 1977), clearly parallels the practices of nonhiding generalists in fishes (Balon, 1977). This unifying definition of the embryonic period eliminates many contradictory conclusions (Gould, 1977) and clearly determines the altricial character of such reproductive strategies (Balon, 1977) irrespective of the form parental investment takes, *i.e.*, higher yolk density, glandular feeding, protective guarding (Stearns, 1976, 1977). However, the theory of saltation has yet to be applied to higher vertebrates (*e.g.*, Shilov, 1965).

The "normal stages" are, therefore, considered a combination of saltatory although mostly arbitrary moments of development, constructed as a vehicle for embryological experimentation (*e.g.*, Balinsky, 1948; Witschi, 1962; Vernier, 1969; Ballard, 1973; Yamamoto, 1975) and may now be replaced by steps. Steps characterize natural intervals of quantitative morphogenesis and growth (Fry in Martin, 1949), separated by a combination of brief but distinct leaps forming a threshold. Structural and functional adaptations to the environment switch their mode of action at this threshold. Thresholds may well be the most important intervals of ontogeny, during which adaptations to the environment express themselves and the future course of ontogeny is determined by heterochronous shifts in character anlagen (Balon, 1959, 1971). Unfortunately, limited observations rarely permit exact recognition and placement of all the existing

thresholds (McElman and Balon, 1980), forcing investigators to make decisions from uncertain leaps, or to adopt a sequence of steps distinguished by others for the same or a closely related taxon. Such treatment should be strongly discouraged because thresholds are not only species specific but, due to heterochrony, are expected to vary even between intraspecific forms.

HETEROCHRONY—THE SHIFTING OF CHARACTER ANLAGEN

> ... *ontogenesis is not the realization of a blueprint encoded in the genome, but a creative process, resulting from a succession of causally related epigenetic events, each of which is the outcome of interaction between agents which may be called the 'ontogenetic substrate' and the 'ontogenetic mechanisms.'*
>
> Løvtrup (1977)

Some may feel that Gould's (1977) compilation and lengthy exploration of heterochrony has exhausted the topic. Unfortunately, I must agree with Løvtrup (1978) that the concept of heterochrony (or "changing of the gears"—Berrill, 1945) deserves a better and less confusing treatment, in spite of Gould's (1979*c*) defence.

Irrespective of the mistaken emphasis given to hatching, de Beer (1958, p. 34) correctly showed "that the strength of the internal factors of development can vary and exert their effect at different rates, with the result that the time of appearance of a structure can be altered. To this shifting along the time-scale the term *heterochrony* is applied." The ability to adapt to a fluctuating environment through the heterochronous appearance of structures and functions varies not only among species but among forms of the same taxon, depending on the genetic variability (White, 1978) accumulated and selected for in former ontogenies. Incidentally, scientists only guess at the more general principles of these modifying processes: the saltation theory on transformation of quantity into quality comes nearest to explaining accumulation, the laws of chance or the game theory (*e.g.*, Ruse, 1979), to explaining selection processes guided by

something akin to Kauffman's (1969) homeostasis, or even better, by SOHO ("self-regulating Open Hierarchic Order" of Koestler and Smythies, 1969) and the "phylogenetic selfrepair" of Koestler (1979, p. 221), which causes that "the sum total of (. . .) ontogenies reflects the active striving of living matter towards the optimal realization of the planet's evolutionary potential" (p. 213).

Let me use the example of charrs (*Salvelinus*), the object of my latest and most detailed comparative study of early ontogeny (Balon, 1980), to elucidate some aspects of heterochronous shifts in character anlagen, although some events in the ontogeny of annual fishes (Wourms, 1972*a*, *b*) would be more convincing.

The progress of epiboly, as evidenced by the arrival of the germ ring at the equator and its subsequent closure, is slower in lake (*Salvelinus namaycush*) and brook (*S. fontinalis*) charrs than in dolly varden (*S. malma*), arctic (*S. alpinus alpinus*) and sunapee (*S. a. oquassa*) charrs (Fig. 5). Similarly, the median hatching time in dolly varden charr is earliest and brook charr latest. The onset of the cardiac pulse, however, is similar in all charrs, though slightly earlier in the brook charr. Exogenous feeding begins earliest in dolly varden and arctic charr, later in sunapee and lake charr, and later still in brook charr. The appearance of flank blotches (parr marks) follows a similar pattern, appearing extremely early in dolly varden, much later in arctic charr, and latest in sunapee and lake charrs. Parr marks appear slightly earlier in brook charr than in sunapee and lake charrs. They are the first character which can be explained directly in terms of environmental adaptation.

By disruptive coloration, flank blotches probably facilitate concealment (Noakes, 1980*a*). Fluvial charrs in shallow water will require such concealment earlier than lacustrine forms. The blotches are most important after emergence, when active life begins (=exogenous feeding). As would be expected, flank blotches form just before the onset of exogenous feeding. Although exogenous feeding begins latest in the brook charr, flank blotches form earlier

than in sunapee and lake charrs. This reflects an adaptation to the fluvial environment. In the charrs that are mostly fluvial—dolly varden and brook charr—flank blotches form well in advance of feeding.

Buoyancy adaptations, as expressed by the filling of the swimbladder and perhaps the timing of calcification, coincide only in the arctic charr. In sunapee the onset of calcification occurs much earlier than in arctic charr, but the swimbladder fills much later. Would the retention of oil globules for buoyancy and the longer ice cover explain this discrepancy in more precocial (specialized) charrs, or would the need for denser bodies in the open fluvial habitats of brook charr explain the earlier calcification and relatively late filling of swimbladders?

THE JUVENILIZATION PROCESS IN EVOLUTION

Can evolution be put into reverse so that the race retreats backwards away from specialization down the pathway up which it came? Not exactly, but something very like it.

A. C. Hardy (1958)
in Evolution as a Process

If environmental constancy is instrumental in creating populations of closest replicas with low genetic variability (*e.g.*, Siebenaller, 1978, but some, *e.g.*, Valentine and Ayala, 1974, have earlier argued that it may not be so), the consequence must be an inability to tolerate fluctuations in the environment. If this process were irreversible, no living form would survive the alternating periods of stability and catastrophic changes in topography and climate (Bretsky and Lorenz, 1970*a*, *b*). Evolution would be impossible, extinction inevitable. As this is not always the case, some mechanism must preserve life by counteracting the disastrous consequences of stability (Snyder and Bretsky, 1971).

Juvenilization, the process of paedomorphosis, may recover the adaptive flexibility of organisms by protracting early ontogeny (embryo, larva or juvenile) so that it becomes the principal adaptive interval, thus avoiding hypermorphic infertility and subsequent extinction (Hardy, 1958). This
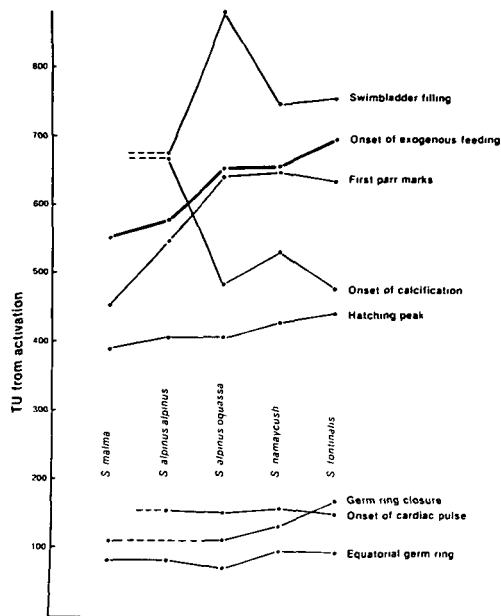
Fig. 5. Comparison of some events of the ontogeny of the five studied charrs (*Salvelinus*) in relation to temperature units at 4.4°C. From Balon, 1980.

time I am, however, in agreement with Gould (1977, p. 293) that "paedomorphosis has little meaning as a category of immediate adaptation. It is an artificial amalgam of two processes conferring the common result of juvenilized morphology." I tend to view and refer to the results of these two processes differently.

Paedomorphosis, being exposed to a sequence of geohistorical forces similar to those which shaped evolution prior to it, may repeat the processes of gerontomorphosis by starting with altricial forms (generalists) which are more adaptable, and ending with precocial forms (specialists) which are less adaptable (see also Noakes, 1978, 1980*b*). The altricial forms— very vaguely related to *r*-selected (MacArthur and Wilson, 1967), progenetic, paedogenetic (Gould, 1977), or hypomorphic[5] forms (Løvtrup, 1978)—either occupy habitats with persistent unpredictable fluctuations or invade new habitats

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[5] It is hard to escape the plague of terminology (Gould, 1979*c*).

before these stabilize. Precocial forms— similarly analogous to *K*-selected (MacArthur and Wilson, 1967), or neotenic forms (Gould, 1977)—are products of stability and the resultant competition, or specialization or both. If stability persists, the level of the ancestral form may again be reached through hypermorphosis (terminal addition), sometimes called "normalizing selection." If the new environmental changes are drastic enough to induce heterochronic adaptations prior to or at the point of advanced gerontomorphosis, juvenilization resets the "clock" to the beginning of another paedomorphosis, akin (perhaps) to "directional selection." In other words, evolution may proceed on two levels at different times, the primary hypermorphic level being ancestral to the secondary paedomorphic level. From hypomorphosis to hypermorphosis—ancestral phylogeny is repeated after juvenilization by paedomorphosis, along the altricial (generalist) to the precocial (specialist) sequence (Fig. 6), akin to the undoing-redoing pattern of Koestler (1979). This sequence, earlier linked to *r*- and *K*-selection, actually fits the stochastic concept of Murphy (1968) better: "In a stationary population where resources are limiting and competition is fierce, variation in juvenile survival may be greater than variation in adult survival [Hirshfield and Tinkle, 1975]. Similarly, in a population moving through a series of colonizing episodes, adult survival must vary considerably, perhaps much more than juvenile survival" (Stearns, 1977, p. 153).

Obviously many more alternatives are available than offered by the *r*- and *K*-selection concept (Constantz, 1979). Of the four "alternative evolutionary pathways" proposed by Gill (1978), dispersibility and tolerance to crowded conditions would be solved by altricial traits, whereas diapause (Wourms, 1972*c*) and competitive ability would represent precocial patterns. Juvenilization may actually be a saltatory threshold of phylogeny (Takhtajan, 1954) akin to "large steps" in evolution (*e.g.,* Schindewolf, 1950). Juvenilization may also be accompanied by DNA duplication and hypermorphosis by DNA loss (Hinegardner
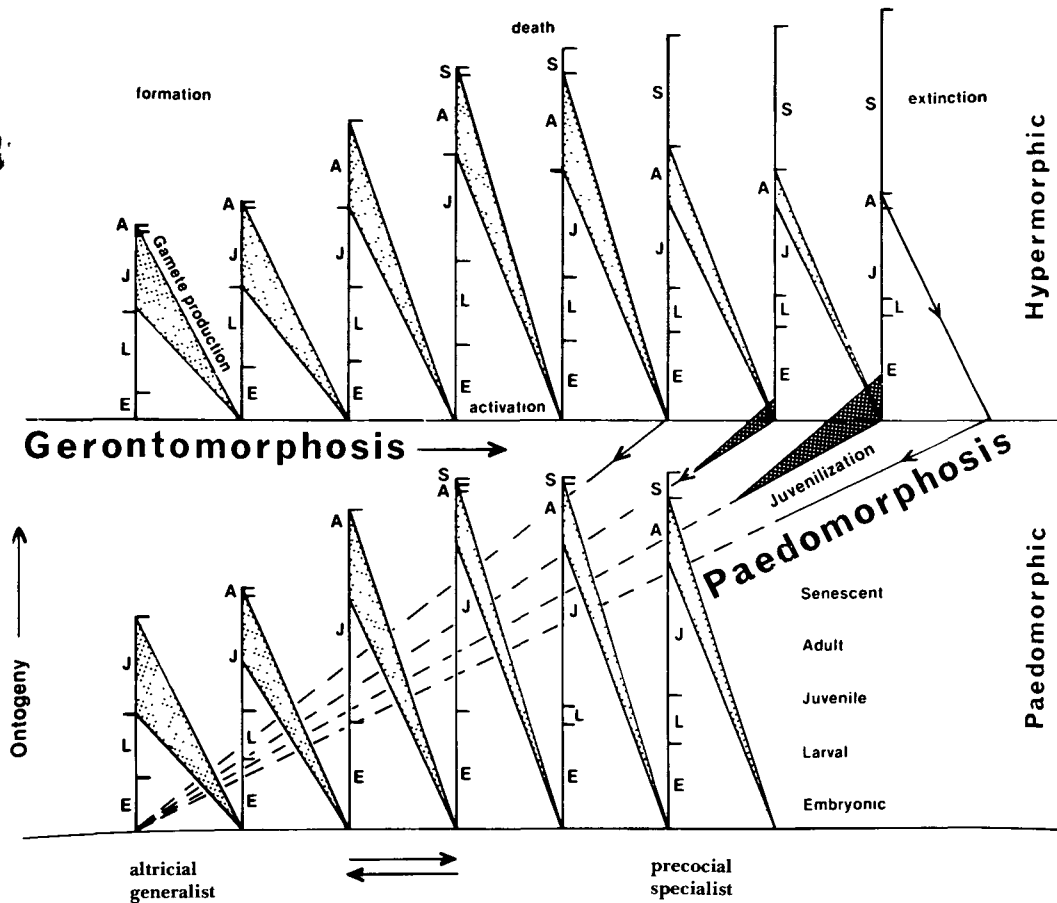
FIG. 6. Abbreviated scheme of fish ontogenies in evolutionary sequence: the ancestral sequence of gerontomorphosis (upper part with abscissa of geological time) may lead to extinction without the juvenilization process which is capable of forming the paedomorphic sequence (lower part with abscissa of generation time). The relationship of periods (E = embryonic, L = larval or alevin, J = juvenile, A = adult, S = senescent) and the relative quantity of gamete production (diagonal) are hypothetical. From Balon, 1979b.

and Rosen, 1972, pp. 634–635). Juvenilization as presented in Figure 6, in my opinion, gives a new dimension to the hypothesis of "dispersal capability" (Sheltema, 1978).

During juvenilization metamorphosis of many structures is accelerated or prolonged. In that sense my view of paedomorphic heterochrony and its consequences is not unidirectional (Kryzhanovsky, 1939). Paedomorphosis is achieved by truncation, by distributing metamorphic changes, usually accumulated at the end of the larval period, throughout the embryonic period (as in most it-

eroparous salmonids) and also, in the case of some less vital structures, by prolongation, by postponing their transformation to the time of transition into adults (as in semelparous Pacific salmon). The resultant pattern is the same as for most hiding strategists: better formed young fish emerge or are released from hiding (Balon, 1977).

ALTRICIAL AND PRECOCIAL FORMS IN ONTOGENY

I submit that Mickey Mouse's evolutionary road down the course of his own growth in reverse reflects the unconscious discovery of

this biological principle by Disney and his artists.

S. J. Gould (1979*a*)
in Mickey Mouse Meets Konrad Lorenz

In early ontogeny, heterochrony serves as a regulatory repatterning capable of creating altricial (generalists) or precocial (specialists) forms within the same taxon and the same guild. Since "the phyletic succession of adults is the product of successive ontogenies" (Garstang, 1922), the initially insignificant repatterning may be cumulative. It may play an important role in speciation or in facilitating a switch to another guild (Balon, 1975*b*), whichever comes first. Such cumulative repatterning may express itself in a variety of ways in a succession of adults. This may explain how "mutations" or evolutionary innovations are established (Løvtrup, 1974, 1977).[6]

As a first example let us use the guild of livebearing fishes. Contribution of yolk and of "placental" analogues (Wourms and Lombardi, 1979) can vary substantially among (*e.g.*, Soin, 1968) and also within species. The exclusive metabolic (or gaseous) "placental" contribution led Thibault and Schultz (1978) to separate ovoviviparity from viviparity. Moreover, in viviparity morphogenetic substances and nutrients are supplied via "placental" adaptations. This conflicts with my earlier definition of

the viviparous guild (Balon, 1975*b*), where "partial or entire nutrition [and/or gaseous exchange—new addition] is supplied by the female via special absorptive organs." The various proportions of yolk and "placental" contribution may be an expression of altricial to precocial styles (Noakes, 1980*b*).[7] Consequently, the life history patterns found by Constantz (1979) in gila topminnow (*Poeciliopsis occidentalis*) again reflect the paired appearance of altricial and precocial traits within the same species. Such paired traits are present in most fishes, for example *Coregonus clupeaformis* (Fenderson, 1964) or *Osmerus mordax* (Rupp and Redmond, 1966; Copeman and McAllister, 1978), but are often overlooked.

We may now return to the example of charrs, all of which belong to the guild of nonguarding, brood hiding lithophils. The initial ecological classification into reproductive guilds (Balon, 1975*b, c*, 1978; Balon *et al.*, 1977) established a basic but tentative ecomorphological framework (*e.g.*, armpit brooder, *Dactyloscopus tridigitatus*, Böhlke and Chaplin, 1968, p. 490, aerophils of Kramer, 1978 were overlooked, and some fishes placed in a wrong guild as, for example, revealed by McElman, 1981). The charrs demonstrate again that even within a single guild there exists a variety of character anlagen shifts from one part of ontogeny to another.

The start of exogenous feeding separates the embryonic (E) and alevin (A) periods (Balon, 1975*a*). In charrs the alevin period is actually a vestige of the larval period, common in hypermorphic ancestors (Fig. 3). The relative length of each of these two initial periods in life history should roughly quantify the shifts of characters. The relative durations of the embryonic and alevin periods (E:A) at 4.4°C are as follows:

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[6] Koestler's (1975, 1979) "holons," among other stimulating concepts, have revealed a number of previously unexplored angles that are closely related to the theories of saltation and of altricial to precocial trends. For example, along with the transformation of an old structure into a new one, a new structure can be superimposed on top of an old one. Hence, paedomorphosis may lead to a crude violation of the "rules of homology." A recent example is the discovery (Legler, 1979) of highly efficient cloacal gills in Australian turtles (*Rheodytes*) in addition to lungs. These cloacal gills allow the turtle to avoid exposure during their ascent for air in crocodile infested waters. The "evolutionary holon"—a respiratory organ—retained its "basic arrangement" as an "evolutionary canon" but its location is modified as a part of the "evolutionary strategy" and a new structure is superimposed opposite (in this case) an old one. All this gives a new credability to the statement I read somewhere, that it was rather an evolutionary accident that human speech evolved at the present end of the digestive tract; it could have developed at the opposite end equally well.

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[7] The role of carotenoid pigments, deposited in the yolk and body tissues of fishes belonging in the ovoviviparous guild (as defined by me in 1975*b*), in oxidative metabolism (Karnaukhov, 1973, 1979; Karnaukhov *et al.*, 1977) is also worthy of consideration (*e.g.*, Soin, 1962, 1967; Avni and Soin, 1974; Mikulin and Soin, 1975; Balon, 1977, 1979*c*; Rohmer *et al.*, 1979; Czeczuga, 1979).

arctic charr, *Salvelinus alpinus*   1:1.2,
sunapee charr, *S. alpinus oquassa* 1:0.7,
lake charr, *S. namaycush*   1:0.7, and
brook charr, *S. fontinalis*   1:0.6.

These values were expected to indicate a trend from altricial to precocial. The arctic charr, which has a longer alevin than embryonic period, fits well the most altricial taxon. It is the northernmost pioneer invader or relict in severe environments. The shortest alevin period observed in brook charr does not fit the hypothesis. The brook charr is not expected to be the most precocial species, as it inhabits the most unstable systems. Therefore the relative lengths of the embryonic and alevin periods express a sum of heterochronic shifts that may differ in each taxon depending on the actual form the taxon belongs to at that time. If so, the value of this sum as an interspecific difference would be limited. However, E:A expresses well the invading ability of each taxon in accordance with the extent of its geographic range as given by Scott and Crossman (1973).

There are probably as many different combinations of character anlagen shifts resulting from heterochronous adaptations as there are charr populations. My sample, although inadequate, suggests a pattern the validity of which can now be tested by a more inclusive study. At least it can provide a theoretical position from which to view the problem (see also Noakes, 1978).

The sympatric occurrence of two forms—altricial and precocial—of the same taxon of charr is more widespread than has been previously documented. Explanations for the existence of such paired forms (*e.g.*, forma *autumnalis* and forma *vernalis* in Windermere [Frost, 1965]), as resulting from a mysterious ice (caused) barrier similar to the one which separated the herring races (Blaxter, 1958), conform to the dominant theories or authorities of that time, but really explain very little.

Every time sympatric forms are found, an attempt is made to explain them according to the presently accepted theory (Brooks, 1950, 1957; Svärdson, 1958, 1961, 1979; McPhail, 1961; Fryer and Iles,

1969, 1972; Henricson and Nyman, 1976; Klemetsen and Grotnes, 1980), weak as such a theory may be by admission of its most forceful advocate (Mayr, 1976, p. 144). The conformistic explanations in the case of charrs, for example, has been repeatedly challenged by Reisinger (1953), Savvaitova (1966, 1973, 1976), Vasiliev and Savvaitova (1972), Skreslet (1973) and Savvaitova and Vasiliev (1976). If genetic resources in adults are truly finite, juvenilization will simply exploit a set of somatic and genetic variations retained in early ontogeny. "The shifting of characters from one part of ontogeny to another may represent regulatory repatterning" and cause the "evolution of regulatory genome" (Valentine, 1977, p. 260). If any additions to the genetic resources are possible, for example, by genetic assimilation (Waddington, 1957; Wilson, 1975), the adaptations caused by heterochrony and reflected in paedomorphosis may, *ceteris paribus*, increase the organism's chances of success. In either case, paedomorphosis and heterochrony encompass all the known data and can account for ecological polymorphism (Savvaitova, 1973, 1980). The associated speciation process, if any, may be similar to quantum (Carson, 1973; Powell, 1978) or allochronic speciation (White, 1978), a defined type of sympatric speciation (Maynard-Smith, 1966). But it is quite possible that in some cases the trend from altricial to precocial (or from generalist to specialist for that matter) may not involve speciation and that it only acts as an adaptive modifier of life histories (Stearns, 1977). A good example is the case of the ferox trout (Schäferna, 1928; Campbell, 1979; Went, 1979). It is a precocial form of the altricial brown trout (*Salmo trutta* forma *fario*).

Hennig's (1966) assumptions may possibly be explained by the principle of constant formation of altricial and precocial twin forms (remember, akin to the undoing-redoing pattern of Koestler); Løvtrup's (1977, p. 232) conclusion that "the outcome of taxonomic divergence is the dichotomous splitting of a taxon T_j into two twin taxa T_{j+1} "may also be justified by this principle."

THE SIGNIFICANCE OF JUVENILIZATION: A CONCLUSION

. . . our children will be difficult to raise, but their capacity for new learning will greatly enhance the chances of survival . . .

Carl Sagan (1977)
in The Dragons of Eden

The ideas of many previous authors form the basis for the theories, hypotheses and speculations expressed in this paper. I cannot recall many but some come immediately to mind. Garstang (1922, 1928, 1962) seems to have promoted the role of paedomorphosis, which was then further elaborated by Kryzhanovsky (1939), de Beer (1958), Hardy (1958), and revived by Gould (1977). Takhtajan (1954), Løvtrup (1974), Popper (1974), and especially Koestler (1975, 1979) and White (1978) presented some ideas which, in conjunction with data compiled by Dobzhansky *et al.* (1977), Grant (1977), Gould (1977) and Pianka (1978) gave birth to the concept of the omnipresence of the altricial and precocial trends. It became obvious that one ought to link the ideas of saltatory ontogeny and evolution,[8] the principles of ecological selection, reproductive guilds, life history styles and speciation, hierarchic holons and phylogenetic selfrepair, ontogeny of behavior (Noakes, 1978, 1980*b*), and that all this should be based on early ontogeny rather than, as is the current practice, only on the adult interval of life.

"It seems that there is no grade of organism to which the principle of paedomorphosis could not apply provided only that the conditions of genetical make up and selective advantage are appropriate," wrote Hardy (1958) in one of his tributes to Walter Garstang. Earlier in the same essay he stated: "However specialized the adults of a stock may have become in relation to life in some particular environment, it is still open to their young stages to become modified in some quite other

way and then by neoteny to produce a new paedomorphic line leading perhaps to a quite new type of animal . . . ." The principles of heterochronous shifts in character anlagen, *i.e.*, particular thresholds of saltatory ontogeny, explain how paedomorphosis operates; the process of juvenilization explains how the evolutionary potential of specialized structures is retained (Holmes, 1977).

However, whereas the principles of paedomorphosis enable juvenilization in evolution, similar principles operate on a much shorter time scale in altricial and precocial life history trends. The hereditary adjustment to the environment is expressed as heterochronous shifts of character anlagen during the formative part of early ontogeny. It constantly selects for structural, physiological and behavioral patterns that equip individuals to survive and/or reproduce in a given environment better than other members of the same species or form. It constantly tends to create precocial forms but in most cases a way back to altricial forms is left open. By something like a "change of gear" the heterochronous adaptations in early ontogeny can reverse the vulnerable specialization, if the environment again becomes less stable and/or the community less competitive.

Consequently, juvenilization, capable of turning gerontomorphosis into paedomorphosis in evolution, and heterochronous shifts of character anlagen, capable of turning a precocial into an altricial trend, are part of the same biological process which operates during early ontogeny. Both turning points probably occur at important saltatory thresholds. If so, the scarcity of intermediate states *sensu stricto* in both ontogeny and evolution may be more readily explained. After all, the existence of distinct species as evolutionary units (*e.g.*, Gould, 1979*b*) would be all but impossible in a continuous world.

If the see-sawing of specialization and despecialization does indeed occur all the time, then the presence of hypermorphic and paedomorphic, or altricial and precocial pairs, at the same time or in succession in any form or species is possible and should not be a reason for taxonomic dis-

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[8] Retention of the term saltatory for evolution, instead of rectangular (Stanley, 1975) or punctuated equilibria (Eldredge and Gould, 1972) evolution, is part of my desire to keep the excessive proliferation of names in check as well as to identify, comparatively, the same general principle by the same name.

tinction, neither in the sense of species nor in the sense of guilds. I suspect, however, that juvenilization, as a force creating hypermorphic $\rightleftharpoons$ paedomorphic organisms, may have a greater taxonomic significance than the shifts in character anlagen creating altricial $\rightleftharpoons$ precocial forms, and I suggest that the former is capable of creating a new species or another recognizable taxon, if the genetic and environmental conditions are right; a conclusion that Garstang (1928) and Hadži (1923, 1952, 1963) arrived at a long time ago.

The earlier concept of saltation, *i.e.*, the large-scale mutations (Mivart, 1871; Schindewolf, 1950), aimed against Darwin's *natura non facit saltum* and rejected by neodarwinists, was revived very convincingly by Løvtrup (1977). The "large-step mutations," however, may be analogous to or act along with the accumulation of heterochronous changes in early ontogeny which "entail far-reaching changes in the ontogenetic end-product, the adult body" (Løvtrup, 1977, p. 280).

Not all thresholds need be alike; their intensity, *i.e.*, the size of their qualitative changes, may vary. Thresholds at the boundaries of periods, for example, could combine into more intense changes than between steps, and the thresholds between gerontomorphosis and paedomorphosis into more marked changes than those between altricial and precocial forms. The evidence for the omnipresence of twin forms is everywhere around us if we know what to look for. Not coincidentally (at least to me) had Laurens van der Post (1975) hinted at it in his latest tribute to the altricial Bushman, concluding that "union of diversity and of opposites was the only real unity and source of strength" (p. 103). His reasoning, unconsciously, parallels some of Arthur Koestler's (1979) ideas, who should, therefore, have the last word in this review: "Biological evolution is to a large extent a history of escapes from the blind alleys of over-specialization, the evolution of ideas a series of escapes from the tyranny of mental habits and stagnant routines. In biological evolution the escape is brought about by a retreat from the adult to a juvenile (. . .) as the

starting-point for the new line; in mental evolution by a temporary regression to more primitive and uninhibited modes of ideation, followed by the creative forward leap" (p. 219).

ACKNOWLEDGMENTS

GLOSSARY

Gene Helfman complained that "much of the controversy surrounding the general acceptance of [my] developmental hypotheses stems from difficulties with terminology." His request for a glossary was repeated by Gregory Whitt and others. While most of the terms are explained in the text and are well defined in my earlier papers, I feel that compliance with this request is justified, if somewhat at variance with my Popperian attitudes. Having made a valiant effort, I nevertheless feel that most of the brief definitions are far from adequate due to the complexity of the concept or because the content can only be fully comprehensible in a historical context. I am not interested in contributing to the debate about terminology. I am, as I was in the past, forced to address that subject in order to clarify what I mean in a conceptual context. Adaptations of old terms proved impossible due to their past association and wrong usage.

ACTIVATION: the actual beginning of ontogeny as characterized by discharge of cortical granuli and usually by the formation of the perivitelline space

(fluid) in eggs, normally upon contact with water (*e.g.*, =maturation of Løvtrup, 1974); this natural activation differs from activation in the old sense, meaning an artificially induced phenomenon.

ALEVIN: the vestige of larva of an organism, from the start of exogenous feeding, that has developed most of the definitive adult structures in the embryonic period without metamorphosis, but has retained remnants of some temporary embryonic structures (*e.g.*, finfold, vitelline vein).

ALTRICIAL: describes a mode of ontogeny characterized by a demand for ova with low energy content, by less developed larvae or alevins and by relatively large clutches in early maturing and slow growing fishes; common in unpredictable, harsh and uncolonized environments; a generalist *sensu lato*.

ANLAGE: earliest discernible indication of an organ or structure during early ontogeny, primordium.

CLEAVAGE EGG: a zygote or developing ovum prior to the formation of the neural plate, *i.e.*, before the assumption of complete genomic control.

ELEUTHEROEMBRYO: an organism in the last phase of the embryonic period, from hatching to the beginning of exogenous feeding; a free embryo, outside the egg envelope(s).

GERONTOMORPHOSIS: modification of highly specialized adult structures leading to senescence.

HATCH: a process by which an embryo leaves the egg envelope(s) (an egg cannot hatch, an embryo hatches).

HETEROCHRONY: altered time of appearance of structures and functions caused by varied strength of internal factors of development exerting their effect at different rates, *i.e.*, shifting or "changing of gears" along a time scale.

HYPERMORPHOSIS: primary evolution produced by terminal addition and leading to extinction (=gerontomorphosis).

HYPOMORPHOSIS: a form of paedomorphosis, produced by early sexual maturation in a morphologically juvenile organism; secondary phyletic evolution after juvenilization produced by terminal subtraction.

JUVENILIZATION: a process known otherwise as paedomorphosis.

LARVA: an organism from the beginning of exogenous feeding to metamorphosis into juvenile, *i.e.*, to the demise of all temporary embryonic structures and appearance of all permanent structures of a small adult.

METAMORPHIC CHANGE: the transformation into permanent organ(s) of a temporary isolated structure, in form and function, or of a few structures which do not combine into abrupt metamorphosis but occur at any given time of early ontogeny.

METAMORPHOSIS: a combination of abrupt changes in form and function of many temporary (embryonic) structures into permanent (adult) organs.

NEOTENY: a form of paedomorphosis, produced by prolonging or arresting somatic development.

PAEDOMORPHOSIS: the prolongation of juvenile characters and adaptability into later ontogeny.

PRECOCIAL: describes a mode of ontogeny leading to a form characterized by a demand for ova with high energy content, well developed alevins or

juveniles directly from embryos in relatively small clutches from late maturing and fast growing parents; common in predictable and competitive environment; a specialist *sensu lato*.

PROGENESIS: a synonym for hypomorphosis.

REFERENCES

Ahlstrom, E. H., J. L. Butler, and B. Y. Sumida. 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the Eastern Pacific: Kinds, distributions, and early life histories and observations on five of these from the Northwest Atlantic. Bull. Mar. Sci. 26:285–401.

Ahlstrom, E. H. and H. G. Moser. 1976. Eggs and larvae of fishes and their role in systematic investigations and in fisheries. Rev. Trav. Inst. Pêches Marit. 40:379–398.

Alderdice, D. F. and F. P. J. Velsen. 1978. Relation between temperature and incubation time for eggs of chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Board Can. 35:69–75.

Allan, I. R. H. and J. A. Ritter. 1977. Salmonid terminology. J. Cons. Int. Explor. Mer. 37:293–299.

Avni, A. A. and S. G. Soin. 1974. Adaptive characteristics of the embryogeny of *Nothobranchius guentheri* in connection with existence in temporary tropical habitat. J. Ichthyol. 14:735–746.

Bagenal, T. B. and E. Braum. 1978. Eggs and early life history. *In* T. Bagenal (ed.), *Methods for assessment of fish production in fresh waters*, pp. 165–201. IBP Handbook 3, Blackwell, Oxford.

Balinsky, B. I. 1948. On the development of specific characters in cyprinid fishes. Proc. Zool. Soc. London 118:335–344.

Ballard, W. W. 1973. Normal embryonic stages for salmonid fishes, based on *Salmo gairdneri* Richardson and *Salvelinus fontinalis* (Mitchill). J. Exp. Zool. 184:7–25.

Balon, E. K. 1958. About developmental intervals of the life of fishes. Biuletyn Zakładu Biologii Stawów PAN 7:5–75. (In Polish)

Balon, E. K. 1959. Die embryonale und larvale Entwicklung der Donauzope (*Abramis ballerus* subsp.). Biologicke práce 5:1–87.

Balon, E. K. 1960. Über die Entwicklungsstufen des Lebens der Fische und ihre Terminologie. Z. wissenschaft. Zool. 164:294–314.

Balon, E. K. 1962. In memory of Professor S. G. Kryzhanovsky (1891–1961). Zoologicke listy (Brno) 11:383–384. (In Slovak)

Balon, E. K. 1971. The intervals of early fish development and their terminology (A review and proposals). Věst. Čs. Spol. Zool. 35:1–8.

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

Balon, E. K. 1975*b*. Reproductive guilds of fishes: A proposal and definition. J. Fish. Res. Board Can. 32:821–864.

Balon, E. K. 1975*c*. Ecological guilds of fishes: A short summary of the concept and its application. Verh. Internat. Verein. Limnol. 19:2430–2439.

Balon, E. K. 1976. A note concerning Dr. Richard's comments. J. Fish. Res. Board Can. 33:1254–1256.

Balon, E. K. 1977. Early ontogeny of *Labeotropheus Ahl*, 1927 (Mbuna, Cichlidae, Lake Malawi), with a discussion on advanced protective styles in fish reproduction and development. Env. Biol. Fish. 2:147–176.

Balon, E. K. 1978. Reproductive guilds and the ultimate structure of fish taxocenes: Amended contribution to the discussion presented at the mini-symposium. Env. Biol. Fish. 3:149–152.

Balon, E. K. 1979a. The theory of saltation and its application in the ontogeny of fishes: Steps and thresholds. Env. Biol. Fish. 4:97–101.

Balon, E. K. 1979b. The juvenilization process in phylogeny and the altricial to precocial forms in the ontogeny of fishes. Env. Biol. Fish. 4:193–198.

Balon, E. K. 1979c. The role of carotenoids in endogenous respiration of fish embryos. Abstracts of 59th Annual Meeting of American Society of Ichthyologists and Herpetologists, Orono, Maine.

Balon, E. K. (ed.) 1980. Charrs: Salmonid fishes of the genus *Salvelinus*. In *Perspectives in vertebrate science* 1. Dr. W. Junk Publishers, The Hague.

Balon, E. K., W. T. Momot, and H. A. Regier. 1977. Reproductive guilds of percids: Results of the paleogeographical history and ecological succession. J. Fish. Res. Board Can. 34:1910–1921.

Bari Kobata, G. 1977. Catastrophe theory: The emperor has no clothes. Science 196:287, 350–351.

Bateson, P. P. G. 1978. How does behavior develop? In P. P. G. Bateson and P. K. Klopfer (eds.), *Perspectives in ethology 3*, pp. 55–66. Plenum Press, New York.

Berrill, N. J. 1945. Size and organization in the development of ascidians. In W. E. Le Gros Clark and P. B. Medawar (eds.), *Essay on growth and form presented to D'Arcy Thomson*, pp. 231–239. Oxford Univ. Press, Oxford.

Betchaku, T. and J. P. Trinkaus. 1978. Contact relations, surface activity, and cortical microphilaments of marginal cells of the enveloping layer and of the yolk syncytial and yolk cytoplasmic layers of *Fundulus* before and during epiboly. J. Exp. Zool. 206:381–426.

Blaxter, J. H. S. 1958. Racial problem in herring from the viewpoint of recent physiological evolutionary and genetical theory. Rapp. Cons. Explor. Mer. 143:10–19.

Böhlke, J. E. and C. C. G. Chaplin. 1968. *Fishes of the Bahamas and adjacent tropical waters*. Livingston Publishing Comp., Wynnewood.

Bond, C. E. 1979. *Biology of fishes*. Saunders, Philadelphia.

Bretsky, P. W. and D. M. Lorenz. 1970a. Adaptive response to environmental stability: A unifying concept in paleoecology. In Proc. North American Paleont. Convention, pp. 522–550. Sept. 1969, part E.

Bretsky, P. W. and D. M. Lorenz. 1970b. An essay on genetic-adaptive strategies and mass extinction. Bull. Geol. Soc. Amer. 81:2449–2456.

Brooks, J. L. 1950. Speciation in ancient lakes. Quart. Rev. Biol. 25:30–60 and 131–176.

Brooks, J. L. 1957. The species problem in freshwater animals. In E. Mayr (ed.), *The species problem*, pp. 81–123. AAAS Publ. 50.

Brummett, A. R. and J. N. Dumont. 1979. Initial stages of sperm penetration into the egg of *Fundulus heteroclitus*. J. Exp. Zool. 210:417–434.

Buynak, G. L. and W. H. Mohr, Jr. 1979. Larval development of the shorthead redhorse (*Moxostoma macrolepidotum*) from the Susquehanna River. Trans. Amer. Fish. Soc. 108:161–165.

Campbell, R. N. 1979. Ferox trout, *Salmo trutta* L., and charr, *Salvelinus alpinus* (L.), in Scottish lochs. J. Fish Biol. 14:1–29.

Carson, H. L. 1973. Reorganization of the gene pool during speciation. In N. E. Morton (ed.), *Genetic structure of populations*, pp. 274–280. Univ. Press, Hawaii.

Cohen, J. 1977. *Reproduction*. Butterworths, London.

Constantz, G. D. 1979. Life history patterns of a life-bearing fish in contrasting environments. Oecologia (Berl.) 40:189–201.

Copeman, D. G. and D. E. McAllister. 1978. Analysis of the effect of transplantation on morphometric and meristic characters in lake populations of the rainbow smelt, *Osmerus mordax* (Mitchill). Env. Biol. Fish. 3:253–259.

Czeczuga, B. 1979. Carotenoids in fish. XIX. Carotenoids in the eggs of *Oncorhynchus keta* (Walbaum). Hydrobiologia 63:45–47.

Davidson, E. H. 1976. *Gene activity in early development*. Academic Press, New York.

de Beer, G. 1958. *Embryos and ancestors*. Clarendon Press, Oxford.

Detlaf, T. A. and A. A. Detlaf. 1960. On dimensionless characteristics of developmental time in embryology. Dokl. Akad. Nauk SSSR 134:199–202. (In Russian)

Disler, N. N. 1957. Development of the chum salmon of the Amur River *Oncorhynchus keta* (Walb.). Tr. Inst. Morph. Zhivotn. Severtsova 20:3–70. (In Russian)

Dobzhansky, T., F. J. Ayala, G. L. Stebbins, and J. W. Valentine. 1977. *Evolution*. Freeman, San Francisco.

Doyle, M. Y. 1977. A morphological staging system for the larval development of the herring, *Clupea harengus*, L. J. Mar. Biol. Ass. U.K. 57:859–867.

Eldredge, N. and S. J. Gould. 1972. Punctuated equilibria: An alternative to phyletic gradualism. In T. J. M. Schopf (ed.), *Models in Paleobiology*, pp. 82–115. Freeman, San Francisco.

Epel, D. 1979. The triggering of development at fertilization. In J. Ebert and T. Okado (eds.), *Mechanisms of cell change*, pp. 17–31. John Wiley and Sons, London.

Fenderson, O. C. 1964. Evidence of subpopulations of lake whitefish, *Coregonus clupeaformis*, involving a dwarfed form. Trans. Amer. Fish. Soc. 93:77–94.

Fisher, S. E. and G. S. Whitt. 1978. Evolution of isozyme loci and their differential tissue expression. Creatine kinase as a model system. J. Mol. Evol. 12:25–55.

Flavell, J. H. 1971. Stage-related properties of cognitive development. Cognitive Psychology 2:421–453.

Fritzsche, R. A. 1978. *Development of fishes in the Mid-Atlantic Bight. An atlas of egg, larval and juvenile stages,* Vol. 5, *Chaetodontidae through Ophidiidae.* U.S. Gov. Print. Off., Washington, D.C.

Frost, W. E. 1965. Breeding habits of Windermere charr, *Salvelinus willughbii* (Gunther)*, and their bearing on speciation of these fish. Proc. Royal Soc. B 163:232–284.

Fryer, G. and T. D. Iles. 1969. Alternative routes to evolutionary success as exhibited by African cichlid fishes of the genus *Tilapia* and the species flocks of the Great Lakes. Evolution 23:359–369.

Fryer, G. and T. D. Iles. 1972. *The cichlid fishes of the Great Lakes of Africa.* T. F. H. Publications, Neptune City.

Fuiman, L. A. and J. J. Loos. 1977. Identifying characters of the early development of the daces *Rhinichthys atratulus* and *R. cataractae* (Osteichthyes:Cyprinidae). Proc. Acad. Nat. Sci. Philadelphia 129·23–32.

Garside, E. T. 1959. Some effects of oxygen in relation to temperature on the development of lake trout embryos. Can. J. Zool. 37:689–698.

Garstang, W. 1922. The theory of recapitulation: A critical re-statement of the biogenetic law. Linn. Soc. J. Zool. 35:81–101.

Garstang, W. 1928. The morphology of the Tunicata, and its bearing on the phylogeny of the Chordata. Quart. J. Microscop. Sci. 72:51–187.

Garstang, W. 1962. *Larval forms with other zoological verses.* Blackwell, Oxford.

Gill, D. E. 1978. On selection at high population density. Ecology 59:1289–1291.

Ginsburg, A. S. 1963. Sperm-egg association and its relationship to the activation of the egg in salmonid fishes. J. Embryol. Exp. Morphol. 11.13–33.

Ginsburg, A. S. 1968. *Fertilization in fishes and the problem of polyspermy.* Nauka, Moskva. (In Russian; 1972, English translation by Z. Blake, Israel Program for Scientific Translations, Jerusalem)

Giudice, G., V. Mutolo, and G. Donatuti. 1968. Gene expression in sea urchin development. Wilhelm Roux' Arch. Entwicklungsmech. Org. 161:118–128.

Goethe, J. W. 1977. *Die Metamorphose der Pflanzen mit Anmerkungen und Einleitung von Rudolf Steiner.* Verlag Freies Geistesleben, Stuttgart.

Gould, S. J. 1977. *Ontogeny and phylogeny.* The Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts.

Gould, S. J. 1979a. Mickey Mouse meets Konrad Lorenz. Nat. Hist. 88:30–36.

Gould, S. J. 1979b. A quahog is a quahog. Nat. Hist. 88:18–26.

Gould, S. J. 1979c. On the importance of heterochrony for evolutionary biology. Syst. Zool. 28:224–226.

Grant, V. 1977. *Organismic evolution.* Freeman, San Francisco.

Hadži, J. 1923. Über den Ursprung, die Verwandschaftsverhältnisse und die systematische Position der Ktenophoren. Razpr. Slovensk. Akad. Mat. Prirod. (Ljubljana) 17:53–62.

Hadži, J. 1952. Application of the principles of phylembryogenesis to the Protista. Nature (London) 169:1019.

Hadži, J. 1963. *The evolution of the Metazoa.* Macmillan, New York.

Hamlett, W. C. and J. P. Wourms. 1978. Differentiation of a transient larval adaptation: Cement secreting glands of angelfish. Amer. Zool. 18·608. (Abstr.)

Hardy, A. C. 1958. Escape from specialization. *In* J. Huxley, A. C. Hardy, and E. B. Ford (eds.), *Evolution as a process,* pp. 122–142. Allen & Unwin, London.

Hardy, J. D., Jr. 1978. *Development of fishes in the Mid-Atlantic Bight. An atlas of egg, larval and juvenile stages,* Vol. 2, *Anguillidae through Syngnathidae.* U.S. Gov. Print. Off., Washington, D.C.

Hardy, J. D., Jr. 1978. *Development of fishes in the Mid-Atlantic Bight. An atlas of egg, larval and juvenile stages,* Vol. 3, *Aphredoderidae through Rachycentridae.* U.S. Gov. Print. Off., Washington, D.C.

Hennig, W. 1966 *Phylogenetic systematics.* University of Illinois Press, Urbana.

Henricson, J. and L. Nyman. 1976. The ecological and genetical segregation of two sympatric species of dwarfed char (*Salvelinus alpinus* (L.) species complex). Inst. Freshw. Res. Drottningholm Rep. 55:15–37.

Hinegardner, R. and D. E. Rosen. 1972. Cellular DNA content and the evolution of teleostean fishes. Amer. Nat. 106:621–644.

Hirshfield, M. F. and D. W. Tinkle. 1975. Natural selection and the evolution of reproductive effort. Proc. Natl. Acad. Sci. U.S.A. 72:2227–2231.

Holmes, E. B. 1977. Is specialization a dead end? Amer. Nat. 111:1021–1026.

Hubbs, C. L. 1943. Terminology of early stages of fishes. Copeia 1943:260.

Ignatyeva, G. M. 1970. Regularities of early embryogenesis in salmonid fishes as revealed by the method of dimensionless characterization of development time. Ontogenez 1:28–41. (In Russian, English Transl. SJDBA9 1:20–32)

Isaac, D. J. and B. M. O'Connor. 1976. A discontinuity theory of psychological development. Human Relations 29:41–61.

Iwamatsu, T. and T. Ohta. 1976. Breakdown of the cortical alveoli of medaka eggs at the time of fertilization, with a particular reference to the possible role of spherical bodies in the alveoli. Wilhelm Roux's Archives 180:297–309.

Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fish. 3:65–84.

Johnson, G. D. 1978. *Development of fishes in the Mid-Atlantic Bight. An atlas of egg, larval and juvenile stages,* Vol. 4, *Carangidae through Ephippidae.* U.S. Gov. Print. Off., Washington, D.C.

Jones, P. W., F. D. Martin, and J. D. Hardy, Jr. 1978. *Development of fishes in the Mid-Atlantic Bight. An atlas of egg, larval and juvenile stages,* Vol. 1, *Acipenseridae through Ictaluridae.* U.S. Gov. Print. Off., Washington, D.C.

Kagan, J. 1978. Continuity and stage in human development. *In* P. P. G. Bateson and P. K. Klopfer (eds.), *Perspectives in ethology 3*, pp. 67–84. Plenum Press, New York.

Karnaukhov, V. N. 1973. Functions of carotenoids in animal cells. Nauka Press, Moscow. (In Russian)

Karnaukhov, V. N. 1979. The role of filtrator molluscs rich in carotenoid in the self-cleaning of fresh waters. Symp. Biol. Hung. 19:151–167.

Karnaukhov, V. N., N. Y. Milovidova, and I. N. Kargopolova. 1977. On a role of carotenoids in tolerance of sea molluscs to environment pollution. Comp. Biochem. Physiol. 56A:189–193.

Kauffman, S. A. 1969. Metabolic stability and epigenesis in randomly constructed genetic nets. J. Theoret. Biol. 22:437–467.

Klemetsen, A. and P. E. Grotnes. 1980. Coexistence and immigration of two sympatric arctic charr. *In* E. K. Balon (ed.), *Charrs: Salmonid fishes of the genus Salvelinus*, pp. 757–763. Perspectives in Vertebrate Science 1. Dr. W. Junk Publishers, The Hague.

Koestler, A. 1975. *The ghost in the machine.* Pan Books, London.

Koestler, A. 1979. *Janus: A summing up.* Pan Books, London.

Koestler, A. and J. R. Smythies (eds.) 1969. *Beyond reductionism.* The Alpbach Symposium, London.

Koshelev, B. V. 1978. Studies of the ecomorphological principles of fish development in relation to environmental change. *In* B. V. Koshelev (ed.), *Ecomorphological and ecophysiological studies of fish development,* pp. 3–9. Nauka, Moscow. (In Russian)

Kramer, D. L. 1978. Terrestrial group spawning of *Brycon petrosus* (Pisces: Characidae) in Panama. Copeia 1978:536–537.

Kryzhanovsky, S. G. 1939. Das Rekapitulationsprinzip und die Bedingungen der historischen Auffassung der Ontogenese. Acta Zool. 20:1–87.

Kryzhanovsky, S. G. 1956. Development of clupeid fishes. Tr. Inst. Morph. Zhiv. Severtsova 17:1–255. (In Russian)

Kryzhanovsky, S. G., N. N. Disler, and E. N. Smirnova. 1953. Ecomorphological principles of development of percids. Tr. Inst. Morph. Zhiv. Severtsova 10:3–138. (In Russian)

Legler, J. M. 1979. Cloacal gills in Australian chelid turtles. Videotape and in Abstracts of 59th Annual Meeting of American Society of Ichthyologists and Herpetologists, Orono, Maine.

Liem, K. F. 1974. Evolutionary strategies and morphological innovations: Cichlid pharyngeal jaws. Syst. Zool. 22:425–441.

Løvtrup, S. 1974. *Epigenetics—a treatise on theoretical biology.* John Wiley and Sons, London.

Løvtrup, S. 1977. *The phylogeny of Vertebrata.* John Wiley and Sons, London.

Løvtrup, S. 1978. Review of S. J. Gould's Ontogeny and Phylogeny. Syst. Zool. 27:125–130.

MacArthur, R. H. and E. O. Wilson. 1967. *The theory of island biogeography.* Princeton Univ. Press, Princeton.

Maekawa, K. 1977. Studies on the variability of the land-locked mijabe charr, *Salvelinus malma mijabei* Oshima. 1. Development and early life history. Jap. J. Ecol. 27:91–102. (In Japanese)

Marckmann, H. 1954. Is there any correlation between metabolism and number of vertebrae (and other meristic characters) in sea trout (*Salmo trutia trutta* L.)? Medd. Damm. Fish. Havundersg. 1:3–9.

Martin, F. D. and G. E. Drewry. 1978. *Development of fishes in the Mid-Atlantic Bight. An atlas of egg, larval and juvenile stages,* Vol. 6, Stromateidae through Ogcocephalidae. U.S. Gov. Print. Off., Washington, D.C.

Martin, W. R. 1949. The mechanics of environmental control of body form in fishes. Univ. Toronto Studies 58, Publ. Ont. Fish. Res. Lab. 70:1–73.

Matveyev, B. S. 1955. Teaching on the "stepwise (stagewise)" ontogeny in animals. In *Problems of present embryology,* pp. 111–122. Proc. Embryol. Conf., Leningrad. (In Russian)

Maynard-Smith, J. 1966. Sympatric speciation. Amer. Nat. 100:637–650.

Mayr, E. 1976. *Evolution and the diversity of life.* Selected essays. The Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts.

McElman, J. F. 1981. Comparative early ontogeny of walleye (*Stizostedion vitreum*) and white sucker (*Catostomus commersoni*). Copeia. (In press)

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

McElman, J. F. and E. K. Balon. 1980. Early ontogeny of white sucker, *Catostomus commersoni,* with steps of saltatory development. Env. Biol. Fish. 5:191–224.

McPhail, J. D. 1961. A systematic study of the *Salvelinus alpinus* complex in North America. J. Fish. Res. Board Can. 18:793–816.

Medvedev, Z. A. 1969. *The rise and fall of T. D. Lysenko.* Columbia University Press, New York.

Mikulin, A. Y. and S. G. Soin. 1975. The functional significance of carotenoids in the embryonic development of teleosts. J. of Ichthyol. 15:749–759.

Mivart, S. G. 1871. *On the genesis of species,* 2nd ed. Macmillan, London.

Morriss, R. W. 1951. Early development of the cottid fish, *Clinocottus recalvus* (Greeley). Calif. Fish and Game 37:281–300.

Moser, H. G. and E. H. Ahlstrom. 1964. Role of larval stages in systematic investigations of marine teleosts: The Myctophidae, a case study. U.S. Fish. Bull. 72:391–413.

Murphy, G. J. 1968. Pattern in life history and the environment. Amer. Nat. 102:391–403.

Neyfakh, A. A. 1964. Radiation investigation of nucleo-cytoplasmic interrelations in morphogenesis and biochemical differentiation. Nature (London) 201:880–884.

Neyfakh, A. A. 1971. Steps of realisation of genetic information in early development. Curr. Topics in Devel. Biol. 6:45–78.

Noakes, D. L. G. 1978. Ontogeny of behavior in fishes: A survey and suggestions. *In* G. M. Burghardt and M. Bekoff (eds.), *The development of*

behavior: Comparative and evolutionary aspects, pp. 103–125. Garland STPM Press, New York.

Noakes, D. L. G. 1980a. Social behavior in young charrs. In E. K. Balon (ed.), Charrs· Salmonid fishes of the genus Salvelinus, pp. 683–701. Perspectives in Vertebrate Science 1, Dr. W. Junk Publishers, The Hague.

Noakes, D. L. G. 1980b. Comparative aspects of behavioral ontogeny: A philosophy from fishes. In G. W. Barlow, K. Immelmann, L. Petrinovitch, and M. Man (eds.), The interdisciplinary study of early development. Cambridge University Press, Cambridge. (In press)

Peňaz, M. 1975. Early development of the grayling Thymallus thymallus (Linnaeus, 1758). Acta Sc. Nat. Brno 9:1–35 + 8 pl.

Peters, N., Jr. 1963. Embryonale Anpassungen oviparer Zahnkarpfen aus periodisch austrocknenden Gewässern. Int. Rev. ges. Hydrobiol. 48:257–313.

Philipp, D. P. and G. S. Whitt. 1977. Patterns of gene expression during teleost embryogenesis: Lactate dehydrogenase isozyme ontogeny in the medaka (Oryzias latipes). Develop. Biol. 59:183–197.

Pianka, E. R. 1978. Evolutionary ecology. Harper & Row, New York.

Popper, K. R. 1974. Unended quest. An intellectual autobiography. Fontana/Collins, London.

Post van der, L. 1975. A mantis carol. The Hogarth Press, London.

Powell, J. R. 1978. The founder-flush speciation theory: An experimental approach. Evolution 32:465–474.

Proctor, C., P. R. L. Mosse, and R. L. Hudson. 1980. A histochemical and ultrastructural study of the development of the propulsive musculature of the brown trout, Salmo trutta L., in relation to its swimming behaviour. J. Fish Biol. 16:309–329.

Rass, T. S. 1968. Spawning and development of polar cod. In R. W. Blacker (ed.), Symposium on the ecology of pelagic fish species in Arctic waters and adjacent seas, pp. 135–137. Cons. Per. Int. l'Explor. Mer. Rapp. Proc.-Verb. Reun. 158, Copenhague.

Richards, W. J. 1976. Some comments on Balon's terminology of fish developmental intervals. J. Fish. Res. Board Can. 33:1253–1254.

Reisinger, E. 1953. Zum Saiblingsproblem. Carinthia II, nat.-wiss. Beiträge zur Heimatkunde Karntens 63:74–102.

Rohmer, M., P. Bouvier and G. Ourisson. 1979. Molecular evolution of biomembranes: Structural equivalents and phylogenetic precursors of sterols. Proc. Natl. Acad. Sci. U.S.A. 76:847–851.

Rupp, R. S. and M. A. Redmond. 1966. Transfer studies of ecologic and genetic variation in the American smelt. Ecology 47:253–259.

Ruse, M. 1977. Karl Popper's philosophy of biology. Philosophy of Science 44:638–661.

Ruse, M. 1979. Sociobiology: Sense or nonsense? Reidel, Dordrecht.

Russell, F. S. 1976. The eggs and planktonic stages of British marine fishes. Academic Press, London.

Savvaitova, K. A. 1966. Kundzha—Salvelinus leucomaenis (Pallas) from some lakes of Kunashir Island (Kuril Islands). Vestnik MGU 4:35–42. (In Russian)

Savvaitova, K. A. 1973. Ecology and systematics of freshwater charr of the genus Salvelinus (Nilsson) Richardson from some waters of Kamchatka. Voprosy Ikhtiologii 13:67–78. (In Russian)

Savvaitova, K. A. 1976. Ecologo-systematical analysis of form development in the salmon family (based on the study of Salvelinus). Ichthyologia 8:101–107.

Savvaitova, K. A. 1980. Taxonomy and biogeography of charrs in the Palearctic. In E. K. Balon (ed.), Charrs: Salmonid fishes of the genus Salvelinus, pp. 281–294. Perspectives in Vertebrate Science 1, Dr. W. Junk Publishers, The Hague.

Savvaitova, K. A. and V. P. Vasiliev. 1976. On the sympatric populations of charr genus Salvelinus (Salmoniformes, Salmonidae) from Natchikinskoe Lake (Kamchatka). Nautch. Dokl. Vysh. Shkoly Biol. Nauki 2:80–86. (In Russian)

Schäferna, K. 1928. Gigantic trout and a thought on fish growth. Rybářsky Věstnik 8:1–2 reprint pages. (In Czech)

Scheltema, R. S. 1978. On the relationship between dispersal of pelagic veliger larvae and the evolution of marine prosobranch gastropods. In B. Battaglia and J. A. Beardmore (eds.), Marine organisms: Genetics, ecology and evolution, pp. 303–322. Plenum Press, New York.

Schindewolf, O. H. 1950. Grundlagen der Paläontologie. Schweizerbartsche Ver., Stuttgart.

Scott, W. B. and E. J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184.

Shaklee, J. B., M. J. Champion, and G. S. Whitt. 1974. Developmental genetics of teleosts: A biochemical analysis of lake chubsucker ontogeny. Develop. Biol. 38:356–382.

Shaklee, J. B. and G. S. Whitt. 1977. Patterns of enzyme ontogeny in developing sunfish. Differentiation 9:85–95.

Shilov, J. A. 1965. On steps in ontogeny of birds. Zool. Zh. 44:1825–1834. (In Russian)

Siebenaller, J. F. 1978. Genetic variability in deep-sea fishes of the genus Sebastolobus (Scorpaenidae). In B. Battaglia and J. A. Beardmore (eds.), Marine organisms: Genetics, ecology and evolution, pp. 95–122. Plenum Press, New York.

Skreslet, S. 1973. Group segregation in landlocked arctic charr, Salvelinus alpinus (L.), of Jan Mayen Island, in relation to the charr problem. Astarte 6:55–58.

Smirnov, A. I. 1975. Biology, reproduction and development of Pacific salmons. Izd. Moskovskogo Univ., Moskva. (In Russian)

Smirnova, E. N. 1978. Development of the domesticated carp in the embryonic period. In B. V. Koshelev (ed.), Ecomorphological and ecophysiological studies of fish development, pp. 56–71. Nauka, Moscow. (In Russian)

Snyder, D. E. 1976. Terminologies for intervals of larval fish development. In J. Boreman (ed.), Great Lakes fish egg and larvae identification: Proceedings of a workshop, pp. 41–58. National Power Plant Team, Power Plant Project FWS/OBS 76/23, Ann Arbor, Michigan.

Snyder, D. E., M. B. M. Snyder, and S. C. Douglas. 1977. Identification of golden shiner, Notemigonus crysoleucas, spotfin shiner, Notropis spilopterus,

and fathead minnow, *Pimephales promelas*, larvae. J. Fish. Res. Board Can. 34:1397–1409.

Snyder, J. and P. W. Bretsky. 1971. Life habits of diminutive bivalve mollusks in the Magnoketa Formation (upper Ordovician). Amer. J. Sci. 271:227–251.

Soin, S. G. 1962. Embryonic respiratory adaptations in fishes and their development in the Baikal sculpins (Cottoidei). Voprosy Ichtiologii 2:127–139. (In Russian)

Soin, S. G. 1963. On the reproduction and development of the Baikal grayling (*Thymallus arcticus baicalensis* Dybowski). Zool. Zh. 42:1817–1840. (In Russian)

Soin, S. G. 1964. Reproduction and development of *Limanda limanda* (L.) from the White Sea. Voprosy Ichtiologii 4:495–511. (In Russian)

Soin, S. G. 1967. Ecomorphological data on the relationship of carotenoids with the embryonic respiration in fishes. In *Metabolism and biochemistry of fishes*, pp. 340–350. Nauka Press, Moscow. (In Russian)

Soin, S. G. 1968. Some developmental features of *Zoarces viviparus* (L.) in connection with livebearing. Voprosy Ichtiologii 8:283–293. (In Russian)

Stanley, S. M. 1975. A theory of evolution above the species level. Proc. U.S. Acad. Sci. 72:646–650.

Stearns, S. C. 1976. Life-history tactics: A review of the ideas. Quart. Rev. Biol. 51:3–47.

Stearns, S. C. 1977. The evolution of life history traits: A critique of the theory and a review of the data. Ann. Rev. Ecol. Syst. 8:145–171.

Stewart, I. 1975. The seven elementary catastrophes. New Scientist 68:447–454.

Strelkovskiy, V. I. 1940. *Development of the Russian sturgeon*. C.Sc. Thesis (not seen, cited after Sytina and Timofeyev, 1973).

Svärdson, G. 1958. Specification in freshwater fish as illustrated by *Coregonus*. Proc. IXth Inter. Conf. Zool., Sect. 2:137–141.

Svardson, G. 1961. Young sibling fish in northwestern Europe. In W. F. Blair (ed.), *Vertebrate speciation*, pp. 498–513. Univ. Texas Press, Austin.

Svärdson, G. 1979. Speciation of Scandinavian *Coregonus*. Rep. Inst. Freshw. Res. Drottningholm 57:3–95.

Sytina, L. A. and O. B. Timofeyev. 1973. Periodization in the development of sturgeons (Acipenseridae) and the problem of the variability of organisms. J. of Ichthyol. 13:230–244.

Takhtajan, A. L. 1954. *Essays on the evolutionary morphology of plants*. Leningrad University, Leningrad (English translation by O. H. Gankin, 1959, The American Institute of Biological Sciences, Washington, D.C.)

Thibault, R. E. and R. J. Schultz. 1978. Reproductive adaptations among viviparous fishes (Cyprinodontiformes: Poeciliidae). Evolution 32:320–333.

Thom, R. 1973. A global dynamical scheme for vertebrate embryology. In J. D. Cowan (ed.), *Some mathematical questions in biology IV*, pp. 1–45. The American Mathematical Society, Providence.

Trifonova, A. N. 1937. La physiologie de la différenciation et de la croissance. I. L'équilibre Pasteur-Mayerhoff dans le développement des poissons. Acta Zool. 18:375–445.

Valentine, J. W. 1977. Transspecific evolution. In T. Dobzhansky, F. J. Ayala, G. L. Stebbins, and J. W. Valentine, *Evolution*, pp. 233–261. W. H. Freeman, San Francisco.

Valentine, J. W. and F. J. Ayala. 1974. On scientific hypotheses, killer clams, and extinctions. Geology 1974:69–71.

Vasiliev, V. P. and K. A. Savvaitova. 1972. Immunological analysis of the arctic charr (*Salvelinus alpinus* (L.)) from the Kamchatka River Basin. Nautch. Dokl. Vysh. Shkoly Biol. Nauk. 6:19–22. (In Russian)

Vasnetsov, V. V. 1953. Steps in the development of bony fishes. In *Otcherky po obshtch. vopr. ichtiol.*, pp. 207–212. Akad. Nauk Press, Moskva. (In Russian)

Vernidub, M. F. and M. I. Guzeva. 1950. On the morphophysiological steps in the development of fish larvae. Dokl. Akad. Nauk SSSR 71:585–588. (In Russian)

Vernier, J.-M. 1969. Table chronologique du développement embryonnaire de la truite arc-en-ciel, *Salmo gairdneri* Rich. 1836. Ann. d'Embryol. Morphogen. 2:495–520. (Transl. by J.-G. J. Godin, Fish. & Mar. Serv. Transl. Ser. 3913, Nanaimo, 1977)

Waddington, C. H. 1957. *The strategy of the genes: A discussion of some aspects of theoretical biology*. Allen & Unwin, London.

Waddington, C. H. 1975. *The evolution of an evolutionist*. Cornell Univ. Press, Ithaca, N.Y.

Wallace, B. 1970. *Genetic load, its biological and conceptual aspects*. Prentice-Hall, Englewood Cliffs, New Jersey.

Welcomme, R. L. 1979 *Fisheries ecology of floodplain rivers*. Longman, London.

Went, A. E. J. 1979. 'Ferox' trout, *Salmo trutta* L. of Longhs Mask and Corrib. J. Fish Biol. 15:255–262.

White, M. J. D. 1978. *Modes of speciation*. Freeman, San Francisco.

Whitt, G. S., D. P. Philipp, and W. F. Childers. 1977. Aberrant gene expression during the development of hybrid sunfishes (Perciformes, Teleostei). Differentiation 9:97–109.

Wilson, E. O. 1975. *Sociobiology. The new synthesis*. The Belknap Press of Harvard University Press, Cambridge.

Witschi, E. 1962. Characterization of developmental stages: Salmonid fishes. In P. L. Altman and D. S. Dittmer (eds.), *Growth including reproduction and morphological development*, pp. 329–331. Federation of Amer. Soc. for Exp. Biol., Washington, D.C.

Wourms, J. P. 1972a. Developmental biology of annual fishes. I. Stages in the normal development of *Austrofundulus myersi* Dahl. J. Exp. Zool. 182:143–168.

Wourms, J. P. 1972b. Developmental biology of annual fishes. II. Naturally occurring dispersion and reaggregation of blastomeres during the development of annual fish eggs. J. Exp. Zool. 182:169–200.

Wourms, J. P. 1972c. Developmental biology of annual fishes. III. Preembryonic and embryonic

diapause of variable duration in the eggs of annual fishes. J. Exp. Zool. 182:389–414.

Wourms, J. P. and J. Lombardi. 1979. Convergent evolution of trophotaeniae and other gut-derived embryonic adaptations in viviparous teleosts. Abstracts of 59th Annual Meeting of American Society of Ichthyologists and Herpetologists, Orono, Maine.

Yamamoto, T. 1975. *Medaka (killifish) biology and strains.* Keigaku Publishing Company, Tokyo, Japan.

Yeremeyeva, E. F. 1960. Transition from one developmental step to another as exemplified by the Kuban roach. Trudy Inst. Morfol. Zhiv. Severtsova 25. (In Russian)

Yeremeyeva, E. F. 1967. The step theory of fish development and its relationship to other theorems on developmental discontinuity. *In* A. M. Gibalevitch and M. T. Tshernyakova (eds.), *Morfo-ecologitchesky analiz razvitya ryb,* pp. 3–17. Nauka, Moskva. (In Russian)