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Larval Developmental Intervals in *Tribolodon hakonensis* (Cyprinidae)

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Abstract The larval development of *Tribolodon hakonensis* is described, and its sequence is characterized by six intervals of morphological, functional and behavioral development. The larval development of this species is a roughly double-folded process consisting of feeding and swimming functions, developments of which begin independently. A comparison with other related species of different reproductive and larval life styles reveals that the development of only one function, such as feeding-related development, may be shifted in adapting and regulating their sequence of intervals to the natural environments. Then the path through the development, i.e. the sequence of intervals, can vary according to different reproductive and larval life styles. For example, *Abramis*, a phyto-lithophils open substratum spawner, and *Carassius*, a phytophils open substratum spawner, develop feeding-related functions, absorb yolk and start to feed before notochord flexion. In the case of an ostracophils brood hider, *Rhodeus* reserves rich yolk and does not feed until it metamorphoses to a juvenile, although it develops feeding-related characters just after notochord flexion as in the case of *T. hakonensis*. On the other hand, *T. hakonensis* is a lithophils open substratum spawner and the larval adaptation of this species is characterized by its rich supply of yolk persisting beyond the start of notochord flexion. It starts to feed after notochord flexion with a short mixed endo-and exogeneous feeding period. This is probably closely related not only to the reproductive style but also to the scarcity of food for the larvae of this species.

Although the larval characters and metamorphic changes in fishes are usually subtler than in amphibians, many fishes do undergo a very abrupt ecological and morphological transformation, for example, from a pelagic larva to a bottom inhabiting juvenile (Orton, 1953). Therefore, numerous studies have been focused on the larval development and systematics of fishes (see American Society of Ichthyologists and Herpetologists, 1984). However, the classification and terminology of developmental intervals are different among authors (reviewed by Snyder, 1976; Okiyama, 1979; Kendall et al., 1984; see also Richards, 1976; Balon, 1976) and the objective groups researched (Balon, 1975 b).

Recently, Balon (1979, 1985) and Balon and Goto (1989) advanced the theory of saltatory ontogeny. In that theory the ontogeny is grasped as a sequence of longer homeorhetic or steady states (developmental intervals or steps) interrupted by rapid changes in form and function (thresholds); prolonged accumulation and canalization of complex structures developing at various rates render the next rapid change possible (Balon, 1985; Balon and Goto, 1989). However, the recognition of thresholds is often difficult (McElman and Balon, 1979; Balon, 1979, 1985), and it does not always seem clear how we can recognize a threshold between two developmental intervals. The aim of this study is to clarify the process of larval development, to present its useful subdivisions and to show how the early life history proceeds.

The Far Eastern cyprinid *Tribolodon hakonensis* (Günther) is a lithophilous open substratum spawner (Balon, 1975 a), spawning en masse in stream rapids on gravel bottoms. Its sex ratio is skewed to males (Okada, 1935; Kawajiri, 1956; Tabeta and Tsukahara, 1964; Nakamura, 1969; Ito, 1975; Sakai, 1987). Eggs, attached to the under surface of the gravel, and hatched larvae, hidden in the interstices of gravels, are both rather large compared to other cyprinid relatives (Nakamura, 1969).

The morphological and behavioral development of the larvae of this species was investigated in detail, and then a practical scheme of subdivisions of larval development was developed based on the observed developmental events. Discussions of the developmental structure of these intervals are given as well. More detailed descriptions are presented in this study than the fragmentary descriptions available heretofore (e.g. Nakamura, 1969).

The saltatory model of ontogeny has been advocated in the form of a hierarchical system of inter-

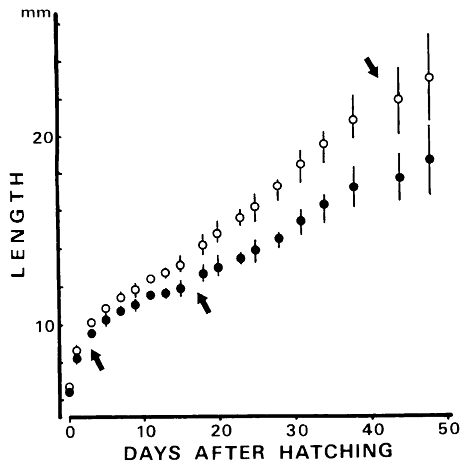

Fig. 1. Growth in TL and SL of reared larvae of *Tribolodon hakonensis*. Open circle, closed circle, vertical line and arrow indicate TL, SL, range and inflexion point of growth, respectively.

vals—periods, phases and steps (Balon, 1975 b, 1985). However, it is not the aim of this study to discuss the hierarchy and terminology of developmental intervals. Therefore, no particular terminology is employed in this study other than the name "larva" which traditionally denotes the period from after hatching to before juvenile stage (Okiyama, 1979).

Materials and methods

Parental fish, one ripe female, 309.0 mm total length (TL) and 252.5 mm standard length (SL), and two males, 280.2 mm TL, 233.4 mm SL and 281.0 mm TL, 231.1 mm SL, of *T. hakonensis* were caught from fish aggregated on a spawning ground in the Kotoh River, Shuho-cho, Mine-gun, Yamaguchi Pref., Japan, on 8 April, 1987.

About 300 eggs fertilized by the dry method were scattered on gravel in a closed circulating aquarium (63 *l*) for incubation and rearing. Hatching occurred five days after fertilization at about 15℃. The larvae were reared for 48 days until they were juveniles at 14.8–20.5℃(average 17.4℃) in the same aquarium, fed mainly on commercially prepared Tetramin (TM, Tetra Research) and occasionally on water fleas (*Daphnia*).

Five to 20 larval and juvenile specimens were sampled at two- to three-day intervals beginning at hatching and ending after 48 days. They were fixed (5% formalin) and measured (TL and SL). The outward appearance and gut development were sketched from one specimen of every sample (except for the day 38 sample) under 10×–50× magnification.

Three specimens of each sample were stained by the methods of Dingerkus and Uhler (1977) (two specimens) and Tylor (1967) (one specimens) for the observation of bone development. Observations were carried out about one month after staining when the over-stained specimens had been washed out in 100% glycerol.

Results

Growth. Range and mean in TL and SL of the samples are shown in Fig. 1. In the course of development, three inflexions in rate of growth in length were observed (arrows in Fig. 1). First, the growth rate declined three to five days after hatching. On 15 to 18 days, the rate again slightly increased, marking the completion of the upward flexion of the notochord. Growth also slowed down 44 days after hatching, just before the larvae entered the juvenile stage.

Development of larvae. Alphabetical namings, nominal stages A to R, are given to each sample (Fig. 2). Gut development is shown in Fig. 3, and developments of fin support and bony feeding organs are presented in Tables 1 and 2, respectively. Developments of form and behavior concerned in swimming and feeding as well as some other characters are schematically represented in Fig. 4.

Stage A (Fig. 2A): Immediately after hatching, 6.5–6.8 (mean 6.7) mm TL, 6.2–6.5 (6.4) mm SL (5 individuals). No pigmentation. Yolk pear-shaped. Intestine straight and filamentous, liver seen on left side of the intestine (Fig. 3). The fish only lie on the bottom.

Stage B (Fig. 2B): One day after hatching, 8.3–8.9 (8.6) mm TL, 7.9–8.5 (8.2) mm SL (5 individuals). Head detached from the yolk. Eyes slightly pigmented. Small pectoral fin rudiments (finfolds) appear. Yolk elongated. Pancreas appears on right side of the intestine (Fig. 3B). Cuvier's duct and circulating blood visible. Negative phototaxis, the fish hide in the bottom gravel.

Stage C (Fig. 2C): Three days after hatching, 9.9–10.2 (10.1) mm TL, 9.4–9.6 (9.5) mm SL (5 individuals). Mouth opened. Eyes pigmented black. Small melanophores on dorsal and ventral sides of the anterior trunk. Vertical finfolds developed to the

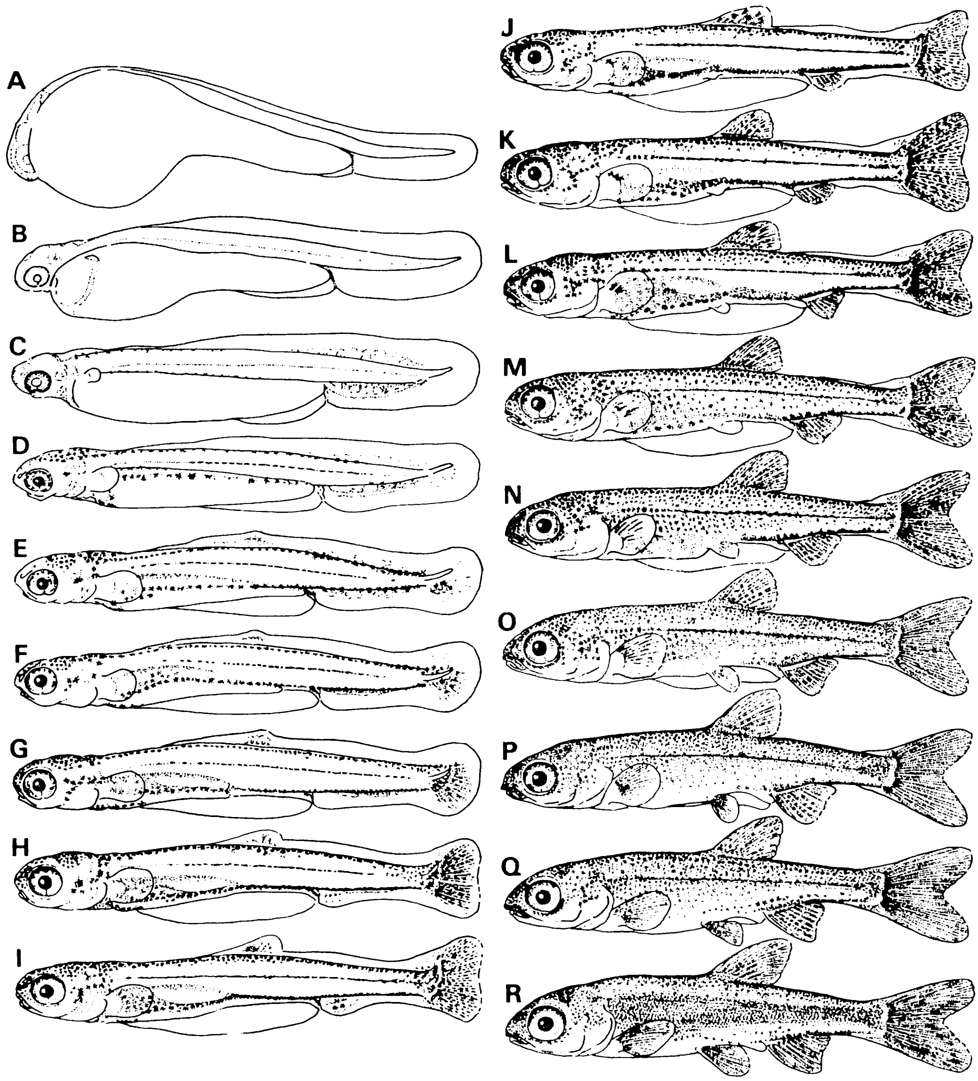

Fig. 2. Development of larvae of *Tribolodon hakonensis*. A, immediately after hatching, 6.7 mm TL (6.4 mm SL); B, 1 day (after hatching), 8.9 mm (8.5 mm); C, 3 days, 10.1 mm (9.6 mm); D, 5 days, 11.0 mm (10.4 mm); E, 7 days, 11.4 mm (10.7 mm); F, 9 days, 11.8 mm (11.1 mm); G, 11 days, 12.3 mm(11.5 mm); H, 13 days, 12.6 mm (11.5 mm); I, 15 days, 13.4 mm (12.2 mm); J, 18 days, 14.0 mm (12.6 mm); K, 20 days, 14.6 mm (12.9 mm); L, 22 days, 15.6 mm (13.7 mm); M, 25 days, 16.6 mm (14.4 mm); N, 28 days, 17.3 mm (14.6 mm); O, 31 days, 18.7 mm (15.8 mm); P, 34 days, 20.1 mm (16.7 mm); Q, 44 days, 22.9 mm (18.6 mm); R, 48 days, 25.1 mm (20.5 mm).

highest degree. Blood circulatory system developed, branchial circulation visible. Temporary respiratory organs (Balon, 1975 a), lower caudal vein in anal finfold and segmental respiratory vessels in dorsal finfold, developed to the highest degree. Rudimental gas bladder appears on the dorso-dextral side of the intestine (Fig. 3C). Meckel's cartilage appears in lower jaw. Branchial arches start to develop from cartilaginous ceratobranchials. Intense negative phototaxis.

Stage D (Fig. 2D): Five days after hatching, 10.6–11.0 (10.8) mm TL, 9.9–10.4 (10.2) mm SL (9 individuals). Silver pigmented eyes. Melanophores appear on head, thorax and lateral midlines. Noto-

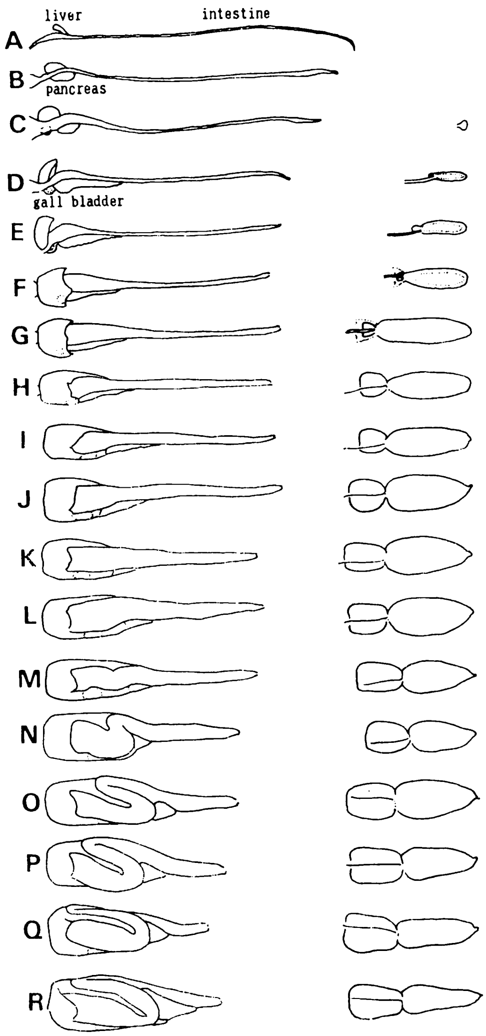

Fig. 3. Gut development of *Tribolodon hakonensis* in ventral view. Left, digestive gut; right, gas bladder (removed from behind the intestine). Alphabetical nomenclature A to R corresponds to that of the nominal stages shown in Fig. 2.

chord flexion begins. Caudal and pectoral fin supports begin to develop. Gall bladder and small anterior chamber of gas bladder appear (Fig. 3D). Mouth gasping and gill respiration begin. Negative phototaxis.

Stage E (Fig. 2E): Seven days after hatching, 11.2–11.7 (11.4) mm TL, 10.5–11.0 (10.7) mm SL (9 individuals). Five principal rays appear in caudal fin. Concentration of mesenchyme in dorsal fin. Five gill rakers develop on the first branchial arch. Negative phototaxis.

Stage F (Fig. 2F): Nine days after hatching, 11.6–12.2 (11.8) mm TL, 10.7–11.3 (11.0) mm SL (9 individuals). Principal caudal rays 11. Gill rakers 6. Liver, pancreas and gall bladder developed, intestine thick (Fig. 3F). The temporary respiratory organs gradually reduced. Negative phototaxis.

Stage G (Fig. 2G): 11 days after hatching, 12.3–12.6 (12.4) mm TL, 11.3–11.7 (11.5) mm SL (9 individuals). The peritonium and breast tinted silver. Principal caudal rays 18. One pectoral actinost appears. Dorsal pterygiophores begin to develop. All of jaw structure elements appear. The first three pharyngeal teeth ankylosed to pharyngeal bone, and continue to develop by the ankylosing pattern reported by Nakajima (1984) from this stage. Branchial arches nearly complete. Posterior chamber of gas bladder inflated. Emerging out of the gravel, the fish start to feed on small suspended particles, but yolk still remains.

Stage H (Fig. 2H): 13 days after hatching, 12.6–12.9 (12.7) mm TL, 11.4–11.8 (11.6) mm SL (9 individuals). Opercle tinted silver. Anal pterygiophores begin to develop. Gill rakers 8. Yolk completely absorbed. The anterior chamber of gas bladder enlarged but not yet inflated (Fig. 3H).

Stage I (Fig. 2I): 15 days after hatching, 12.7–13.6 (13.1) mm TL, 11.4–12.3 (11.8) mm SL (12 individuals). Principal caudal rays 19, caudal fin supports nearly completed. Seven rays in dorsal and 4 rays in anal fins appear. The lower caudal vein completely disappears from the anal fin fold. The fish begin to pick up food lying on the bottom.

Stage J (Fig. 2J): 18 days after hatching, 13.6–14.7 (14.1) mm TL, 12.2–13.1 (12.6) mm SL (20 individuals). Dorsal fin rays fixed at 8. Caudal fin rays segmented. Preanus finfold develops to its highest degree as a vertical stabilizer. Small pelvic fin rudiments (finfolds)appear. Gill rakers 12. The anterior chamber of gas bladder inflated (Fig. 3J). The pancreas impossible to observe under the dissecting microscope, and heavy accumulation of fat in or around the former pancreas. (The same phenomenon is commonly seen in fish development; Iwai, 1962; Tanaka, 1971). Fluently swimming, able to pick up food in a headstanding style, and also able to eat surface floating foods and some attached algae.

Stage K (Fig. 2K): 20 days after hatching, 14.1–15.4 (14.7) mm TL, 12.5–13.6 (12.9) mm SL (14 individulas). Pectoral actinosts separated into 2. Membranous posttemporal and supracleithrum appear.

Stage L (Fig. 2L): 22 days after hatching, 15.1–

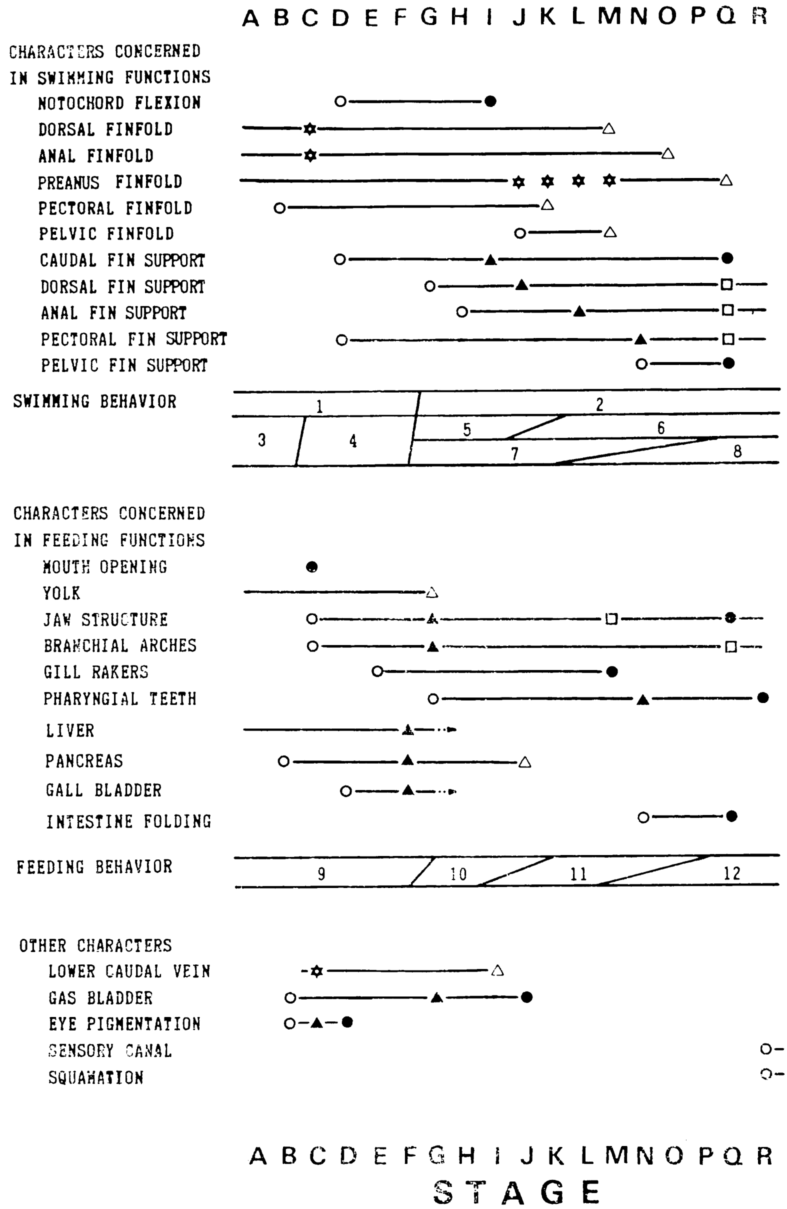

Fig. 4. Schematic representation of the development of characters involved mainly in swimming and feeding in *Tribolodon hakonensis*. Alphabetical nomenclature of stage corresponds to that in Fig. 2. Event: open circle, start of development; solid triangle, near completion; solid circle, completion of event or completion of calcification; open square, start of calcification; open triangle, extinction of character; asterisk, the greatest degree of development. Behavior: 1, hiding in the interstices of gravels; 2, swimming up, 3, recumbent; 4, negative phototaxis; 5, jerky swimming; 6, fluent swimming; 7, gathering; 8 schooling; 9, absorbing yolk; 10, swallowing; 11, begin to peck bottom food; 12, biting off attached algae and actively attacking drifting food.

16.0 (15.5) mm TL, 13.0–13.7 (13.4) mm SL (12 individuals). Anal fin rays fixed at 9. Four pectoral fin rays appear.

Stage M (Fig. 2M): 25 days after hatching, 15.3–16.8 (16.1) mm TL, 13.2–14.4 (13.8) mm SL (10 individuals). Pectoral rays 6. Cleithrum calcified. Jaw structure nearly complete and begins to calcify. Gill rakers fixed to adult complement 13. Schooling

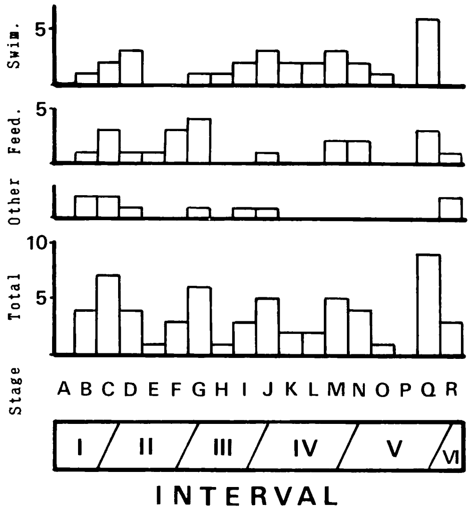

Fig. 5. Histograms of numbers of developmental events related to swimming (swim.), feeding (feed.) and other functions occurring during each nominal developmental stage in *Tribolodon hakonensis.* Numbers of events in these functions for each stage are summed in a total histogram. The nominal stages A to R are collected into intervals I to VI by the peaks conspicuous in the total histogram.

tendency gradually expressed. The fish begins actively attacking surface floating food and biting off attached algae.

Stage N (Fig. 2N): 28 days after hatching, 16.4–17.6 (17.2) mm TL, 13.9–14.8 (14.4) mm SL (7 individuals). Dorsal and anal rays segmented. Pectoral fin supports nearly complete, actinosts separated into 4, postcleithrum appears. Six pelvic fin rays and basipterygium appear. Preanal finfold starts to degenerate. Dorsal finfold completely disappeared. Major row of pharyngeal teeth completed. Intestine folding starts (Fig. 3N).

Stage O (Fig. 2O): 31 days after hatching, 17.4–19.2 (18.4) mm TL, 14.6–16.0 (15.8) mm SL (18 individuals). Pectoral fin rays 13, pelvic fin rays 8.

Stage P (Fig. 2P): 34 days after hatching, 18.4–20.2 (19.5) mm TL, 15.1–16.8 (16.2) mm SL (8 individuals). Pectoral fin rays 15, segmented. Pelvic fin rays segmented. Anal finfold disappears.

Stage Q (Fig. 2Q): 44 days after hatching, 20.0–23.6 (22.9) mm TL, 16.4–19.0 (18.6) mm SL (17 individuals). Pectoral and anal fin rays fixed to adult complement 17 and 10, respectively. Dorsal, anal, and caudal fin rays branched. Only a small preanal finfold remains. Almost all bony elements calcified except dorsal and anal pterygiophores, pectoral actinosts and some branchial elements. Intestine deeply folded (Fig. 3Q).

Stage R (Fig. 2R): 48 days after hatching, 20.7–25.4 (23.0) mm TL, 16.7–20.6 (18.6) mm SL (16 individuals). Canalization of cephalic lateral-line system and squamation of body begin. Minor row of pharyngeal teeth completed.

Division of developmental intervals. The developmental events represented in Fig. 4 are summarized in histograms (Fig. 5). In the histogram of swimming-related characters, four peaks are observed at nominal stages D, J, M and Q. Four different peaks are conspicuous at stages C, G, M, N and Q in the histogram of feeding-related characters. It is remarkable that the peak at stage J in the swimming-related characters is not found in the feeding-related characters. Conversely, the peak at stage G in the feeding-related characters is not seen in the swimming-related characters (Fig. 5). There is a minor difference in the stage where the first peak appears, namely at stage D in the swimming-related characters and at stage C in the feeding-related characters (Fig. 5).

Summing all events, five clear peaks are recognized at stages C, G, J, M and Q (Fig. 5). These peaks represent the major events where many developmental processes end or begin. These events correspond to the threshold of Balon's (1979). The nominal stages A to R can be collected into six developmental intervals I to VI by these five peaks of events or thresholds (Fig. 5). The characters and behaviors diagnostic of the intervals are as follows.

Interval I (stages A–B): Tadpole-shaped but swiftly elongating. No pigmentation. Recumbent on the bottom or in the gravel. The threshold marking the next interval includes the starting of many events (Fig. 4) and the changing of the growth rate (Fig. 1).

Interval II (stages C–F): Mouth opens. Eyes silver. Notochord end slightly flexed. Melanophores appear. The temporary respiratory organs develop in caudal and anal finfolds but gradually reduce. Negative phototaxis, actively hiding in the gravel. The threshold marking the next interval is characterized by the development of larval feeding characters and of positive phototaxis (Figs. 4, 5). Such a threshold is also recognized in many other groups (Tanaka, 1969a, b).

Interval III (stages G–I): Notochord flexion and

Table 1. Fin support development in *Tribolodon hakonensis*. Alphabetical nomenclature of stage coincides with that in Fig. 2. Rays are intermembranous and pterygiophores and actinosts are cartilaginous before calcification. c, cartilaginous; m, intermembranous; o, calcified bone; numeral, No. of element.

	Stage																	
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
Dorsal fin																		
principal rays									7	8	8	8	8	8	8	8	o, 8	o, 8
proximal pterygiophores							3	5	7	7	8	8	8	8	8	8	8	8
Anal fin																		
principal rays									4	7	8	9	9	9	9	9	o, 9	o, 9
proximal pterygiophores								3	5	5	8	9	9	9	9	9	9	9
Caudal fin																		
principal rays					5	11	18	18	19	19	19	19	19	19	19	19	o,19	o,19
epural									c	c	c	c	c	c	c	c	o	o
hypural 6								c	c	c	c	c	c	c	c	c	o	o
5							c	c	c	c	c	c	c	c	c	c	o	o
4					c	c	c	c	c	c	c	c	c	c	c	c	o	o
3				c	c	c	c	c	c	c	c	c	c	c	c	c	o	o
2				c	c	c	c	c	c	c	c	c	c	c	c	c	o	o
1				c	c	c	c	c	c	c	c	c	c	c	c	c	o	o
parhypural				c	c	c	c	c	c	c	c	c	c	c	c	c	o	o
Pectoral fin																		
rays												4	6	11	13	15	o; 17	o, 17
actinosts							1	1	1	1	2	2	2	4	4	4	4	4
posttemporal											m	m	m	m	m	m	o	o
supracleithrum											m	m	m	m	m	m	o	o
cleithrum				m	m	m	m	m	m	m	m	m	o	o	o	o	o	o
postcleithrum														m	m	m	o	o
coraco-scapular				c	c	c	c	c	c	c	c	c	c	c	c	c	o	o
Pelvic fin																		
rays														6	8	8	o, 10	o, 10
basipterygium														c	c	c	o	o

caudal fin support develop nearly to completion. Posterior chamber of gas bladder inflated. Preanal finfold develops but no pelvic fin. Emerging out of the gravel, jerky swimming and gathering. Feeding starts, swallowing small suspended particles. After a time of mixed endo- and exogenous feeding, the fish absorbs the yolk and depends only on exogenous feeding. The threshold marking the next interval is mainly characterized by fin developmental events, and gradual change in swimming and feeding behavior (Figs. 4, 5) It also includes the changing of the growth rate (Fig. 1).

Interval IV (stages J–M): Preanus finfold develops to its greatest extent during this interval. Pelvic finfolds appear. Dorsal and anal fins completed. Anterior chamber of gas bladder inflated, which enables head standing posture. Fluent swimming. Able to peck bottom food and surface floating food. The threshold marking the next interval is related to the onset of what is called metamorphosis.

Interval V (stages N–Q): The fish gradually metamorphose to juvenile during this interval. Pectoral fins develop, become triangular. Anal fins also completed. Preanal finfold degenerates. Dorsal and anal finfolds distinct. Caudal fin notching deeper. Gill rakers with adult complement. At least the major row of pharyngeal teeth completed. Intestine folding. Schooling tendency gradually expressed. Actively attacks floating food and bites off attached algae. At the last stage of this interval, most of the bony elements are calcified (Tables 1, 2) and growth retards (Fig. 1). The threshold marking the next interval represents the completion of metamorphosis, the completion of nearly all structures and functions. The same threshold is recognized in many fishes as reported in many papers.

Interval VI (stage R, juvenile): No finfold. Adult-like in profile. Squamation of body and canalization of cephalic lateral-line system begin, and are completed at 30–40 mm TL. Pharyngeal teeth complete, the teeth replacement pattern of adult is attained (Nakajima et al., 1983).

Discussion

Notes on the division of larval development. The larval development of *T. hakonensis* was divided into six (five larval and one juvenile) intervals. The thresholds between these intervals were recognized as evident peaks of frequencies of developmental events (Fig. 5). These peaks represent the stages where many developmental processes end and begin. The succession of the above intervals and thresholds involves not only morphological development but also behavioral and functional changes. Therefore the intervals and thresholds in this study may correspond to those of Balon's (1979, 1985).

Of course the development of a larva is a continuous phenomenon (Snyder, 1976) and a mosaic of variously overlapped patterns of formation of individual characters (Kohno et al., 1983, 1984). It may often be difficult to recognize the thresholds (McElman and Balon, 1979). In this study, however, such thresholds were clearly displayed in the histogram of developmental events as some peaks (Fig. 5). The method employed in this study is considered to be very practical and simple to make the thresholds remarkable.

Larval life history of *T. hakonensis*. Spawning of *T. hakonensis* occurs en masse on rapids with gravel bottoms, with a preponderance of males (Okada, 1935; Kawajiri, 1956; Tabeta and Tsukahara, 1964; Nakamura, 1969; Ito, 1975; Sakai, 1987). The eggs are attached to the under surfaces of the gravel. Hatched larvae migrate down into the interstices of gravels (Interval I in this study), and then actively hide themselves deep in the gravel (Interval II) (Okada, 1935; Nakamura, 1969). The larvae emerge out of the gravel at Interval III when they have grown to about 12 mm TL and are able to eat large food such as water fleas (*Daphnia*). As the developmental intervals proceed, the larvae acquire new food habits enabled by advancing swimming ability. Finally they metamorphose to juveniles in Interval VI, extending their habitat from the slow-flowing shallows to the riffles as well as to ponds where many sessile organisms and/or drifting prey are available.

Structure of larval interval sequence. It is important to point out here again that the characters related to swimming and feeding display separate peak frequencies of developmental events at some thresholds of *T. hakonensis* development (Fig. 5). In the course of fish larval development, it is well known that changes occur in nearly all systems, such as feeding, swimming and other organs and functions, when the late larva metamorphoses to a juvenile (seen in many textbooks, e.g. Tanaka, 1975). This is generally true of *T. hakonensis* (Fig. 5). Advanced feeding functions are necessarily based on more developed swimming functions, and these two must necessarily be related to each other in the advanced intervals. On the other hand, the first

Table 2. Development of bony elements involved in feeding in *Tribolodon hakonensis.* Alphabetical nomenclature of stage corresponds with that in Fig. 2. c, cartilaginous; m, intermembranous; o, calcified; +, on developing; Mr, major row completed; Mmr, minor row also completed; numeral, No. of element.

	Stage																	
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
Jaw structure																		
premaxillary							m	m	m	m	m	m	o	o	o	o	o	o
maxillary						m	m	m	m	m	m	m	o	o	o	o	o	o
Meckel's cartilage			c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
dentary							m	m	m	m	m	m	o	o	o	o	o	o
Branchial arches																		
ceratobranchial 1			c	c	c	c	c	c	c	c	m	m	m	m	m	m	o	o
2			c	c	c	c	c	c	c	c	c	c	c	c	c	c	o	o
3				c	c	c	c	c	c	c	c	c	c	c	c	c	o	o
4				c	c	c	c	c	c	c	c	c	c	c	c	c	o	o
hypobranchial 1					c	c	c	c	c	c	c	c	c	c	c	c	c	c
2					c	c	c	c	c	c	c	c	c	c	c	c	c	c
3					c	c	c	c	c	c	c	c	c	c	c	c	c	c
4						c	c	c	c	c								
epibranchial 1							c	c	c	c	c	c	c	c	c	c	o	o
2							c	c	c	c	c	c	c	c	c	c	o	o
3							c	c	c	c	c	c	c	c	c	c	o	o
4							c	c	c	c	c	c	c	c	c	c	o	o
pharyngobranchial 1												c	c	c	c	c	c	o
2											c	c	c	c	c	c	c	o
3											c	c	c	c	c	c	c	o
4												c	c	c	c	c	c	o
Pharyngeal bone				c	c	c	c	c	c	c	c	o	o	o	o	o	o	o
teeth							+	+	+	+	+	+	+	Mr	Mr	Mr	Mr	Mmr
Gill rakers					5	6	6	8	8	12	12	11	13	13	13	13	14	13

feeding may not necessarily require the development of adult-like fins, and vice versa.

This perspective is reinforced by comparing the developments of related species which have various timings of first exogenous feeding. The cyprinid *Abramis brama* develops its digestive system far earlier than it develops any fin rays, and its first exogenous feeding begins at a far younger stage (Vasnetsov, 1953) than that of *T. hakonensis* demonstrated in the present study. *A. brama* is a phyto-lithophils open substratum spawner, depositing eggs on submerged plants or other item (Balon, 1975a). Its larvae do not show very strong photophobia and start to swim after a short hanging life to the substratum by their cement glands. They can feed on small inactive planktons such as rotifers even if their swimming ability is very weak (Vasnetsov, 1946). The situation of the cyprinid *Carassius* spp. is similar to that of *A. brama*. Members of this genus are all phytophils open substratum spawners (Balon, 1975 a), depositing eggs to submerged or floating plants. Their larvae never show any photophobia, start to swim after a short hanging life and start to feed far earlier than fin ray development (Tomoda, 1965).

Conversely, in the cyprinid *Rhodeus ocellatus ocellatus*, which hides its eggs in the mantle cavity of freshwater mussels and the larvae develop inside of the mussels for a long time with endogenous feeding (ostracophils brood hiders), the first exogenous feeding does not occur until the larvae develolp into juveniles, emerging from the mussles (Nakamura, 1969). However, its develolpment of feeding- and swimming-related characters proceeds roughly in the same manner as that of *T. hakonensis* except for some retardation of development in jaw structures and pharyngeal teeth (Suzuki, 1984). Needless to say, this style of larval life is based on their very rich supply of yolk materials.

Consequently, the development of feeding and swimming functions can be independent in early larval development (*T. hakonensis* vs. *A. brama* or *Carassius* spp.) and, in some cases, yolk persistency can also be independent of other processes (e.g. in the case of *R. ocellatus ocellatus*). Such independence might possibly be true of characters involved in other functions such as the nervous system, respiratory structures, etc. Wild larvae of these species must accomplish their life history by adapting and regulating their developmental intervals to the structures of the natural environments in which they live. The difference of the developmental intervals among them would not necessarily be performed by shifts of all functions; only one, such as feeding function, might be shifted in relation to a certain regulated threshold between two adapted intervals. In other words, the path through the development, i.e. the sequence of intervals taken, can vary among species with different reproductive and larval life styles.

In the above manner, *T. hakonensis* has its own developmental intervals of different characters from those of its relatives such as *Abramis*, *Carassius* or *Rhodeus*. The difference in intervals may relate to the difference in reproductive and larval life style among them. The developmental intervals of *T. hakonensis* are characterized by the rich supply of yolk persisting beyond the start of notochord flexion. This is probably closely related to the reproductive style of this species. *T. hakonensis* is a lithophils open substratum spawner and its larvae show strong photophobia which helps them to hide under stones. The rich supply of yolk enables them to grow for a while in the interstices of gravels without food. When they emerge from the gravel, they have already grown large enough to be able to eat large food such as water fleas. This phenomenon may be closely related to the scarcity of food for the larvae in early spring (spawnings occur March to April in the Kotoh River, which is far earlier than in other cyprinid relatives).

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ウグイ仔魚の発育段階区分

酒井治己

ウグイ仔魚（孵化から稚魚に変態するまで）の発育を記載し，形態と機能および行動の発達という観点から，それを6段階に区分した．仔魚の発育は，大まかに摂餌および遊泳に関した二つの機能の発達からなると把握され，しかも各々の発達の始まりは，必ずしも一致していなかった．そうした発育を，繁殖および仔魚の生活様式の異なる近縁種間で比較すると，それらの発育様式の違いは，たとえば，摂餌に関した発育や，場合によっては卵黄量のみを変更することによって達成されているように思われた．それゆえ，発育のあり方，すなわち一連の発育段階区分は，繁殖様式によって異なりうる．すなわち，沈積物付着型産卵魚の *Abramis* や植物付着型産卵魚の *Carassius* などでは，脊索末端の上屈前に摂餌に関する機能を発達させ，卵黄を消費して摂餌を開始する．一方，無脊稚動物隠ぺい魚の *Rhodeus* では，摂餌に関する形態は，ウグイの場合と同様に脊索末端の上屈後に発達するものの，稚魚に変態するまで卵黄を保持し，二枚貝から浮出するまで摂餌を開始しない．それに対して，底生幼生型岩・礫底産卵魚のウグイ仔魚の発育は，脊索末端の上屈後まで卵黄を保持し，そのときまでに摂餌を開始することに特徴づけられる．このことは，本種が卵を砂利中に産み込むという繁殖様式と，早春に孵化する仔魚にとっての餌の得難さに深く関係していると思われる．

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