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Comparative Morphology and Scale Formation in Four Species of *Oncorhynchus* during Early Life

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Abstract Morphological divergence including scale formation in alevin and juvenile stages of masu (*Oncorhynchus masou*), coho (*O. kisutch*), chum (*O. keta*) and pink (*O. gorbuscha*) salmons reared in freshwater was investigated. Chum and coho salmons developed faster than the other species when raised at constant water tempertaure. Growth decreased suddenly at emergence from the gravel bed in all the four species. Morphology changed significantly from hatch through emergence to squamation. Two distinct morphological types were identified: the rotund type (masu and coho), and the streamlined type (chum and pink salmons). The former had well-developed parr marks, a deeper body and caudal peduncle, and higher relative growth coefficients, while the latter had parr marks which appeared only temporarily or never appeared, a slimmer body and caudal peduncle, and a more gradual and continuous change in morphology. Coho and chum developed squamation and formed circuli on scales considerably earlier than masu and pink salmons.

Despite several papers devoted to developmental terminology (Koo, 1962; Bakkala, 1970; Balon, 1975), life mode (Healey, 1980, 1982; Kubo, 1980; Beacham and Murray, 1986) and early growth (Shiraishi and Uchida, 1957; Kanno and Hamai, 1969; Okada and Nishiyama, 1970; Kaeriyama, 1980, 1986; Kaeriyama and Bunya, 1982) in *Oncorhynchus*, still relatively little is known about morphological changes during early life. In this study, morphological changes including squamation and scale formation during early development of four species of *Oncorhynchus*: masu (*O. masou*), coho (*O. kisutch*), chum (*O. keta*) and pink (*O. gorbuscha*) salmons were studied.

Materials and methods

Eyed salmon eggs of the four species were collected in 1983 from: the Shiribetsu River (Hokkaido) on September 15 (masu), the Miyagi Prefectural Freshwater Experimental Station on October 29 (coho), the Ohkawa River (Miyagi) on October 11 (chum) and the Shari River (Hokkaido) on September 10 (pink). All these eggs were transported to the Kesennuma Ohkawa Salmon Hatchery from October 31 to December 13, and reared at a constant water temperature of 11.0±0.1°C. Eggs hatched on November 8 (masu), December 13 (coho), November 22 (chum) and November 20 (pink). Alevins were kept in incubator cages from hatching to emergence. After emergence, juveniles were reared in 500 liter tanks, and were fed with dry fish meal twice a day.

Every week after hatching, 20 specimens of each species were fixed in 10% formalin and preserved for at least 90 days. After preservation, fork length (FL), head length, eye diameter, upper jaw length, caudal peduncle length, body depth, and caudal peduncle depth were measured using an ocular micrometer under a dissecting microscope and vernier caliper. Relative growth length (RGL) is defined as the ratio of the length at a particular stage of development to the hatching length. Total, yolk, and tissue weights were measured using an electronic balance. Scales for circuli counts were collected from the body just below the dorsal fin, and two or three rows above the lateral line. Squamation is defined as the time at which the scales are first formed prior to the appearance of circuli.

Results

Developmental process. Morphological stages of the developmental process are summarized in Table 1.

Among the four species, parr marks appeared earliest in coho, second in chum, and thirdly in masu salmon. Pink salmon at no time in their life exhibited any parr marks. Fork and relative growth lengths at the appearance of parr marks were 28 mm and 1.7 in masu, 28 mm and 1.6 in coho, and 33 mm and 1.5 in chum salmon. Parr marks of chum salmon began to disappear with the appearance of guanine 97 days after hatching (72 mm FL, 3.3 RGL).

Coho was the first species to emerge from the gravel bed and to begin exogenous feeding, while chum, masu and pink salmons followed in this order. Though there was no significant difference in relative growth lengths (about 1.8) at emergence, fork lengths and days after hatching differed among the species. The period from emergence to complete absorption of yolk was regarded as a mixed feeding phase (endogenous and exogenous nutrition). It was shortest in chum (9 days), followed by coho (10 d), masu (16 d) and pink (22 d) salmons.

Coho and chum developed squamation considerably earlier than masu and pink salmons. Fork and relative growth lengths were 41 mm and 2.3 in coho, 52 mm and 2.3 in chum, 46 mm and 2.8 in masu, and 57 mm and 3.3 in pink salmon.

At hatching, all alevins still had a finfold. As development progressed, the finfold started to disappear, dorsal and anal fins separated 26 days after hatching in masu, 22 d in coho, 19 d in chum, and 28 d in pink salmon, and the finfold completely disappeared first in chum (61 days, 52 mm FL, 2.3 RGL), then in coho (100 d, 59 mm, 3.4), masu (107 d, 51 mm, 3.1) and pink (110 d, 59 mm, 3.4) salmons.

Thus, early development in these four species reared in a constant water temperature environment seems to be divided into two rates: fast developing (chum and coho salmons), and slow developing (masu and pink salmons).

Growth. Changes in the average fork lengths after hatching are shown in Fig. 1. Growth rates decreased suddenly at the emergence from the gravel bed when the fishes changed their food sources from endogenous to exogenous. Growth of *Oncorhynchus* during early life is exponential and may be expressed by the following equation: $L_t = L_0 e^{at}$ (LeBrasseur and Parker, 1964; Brett et al., 1969; Shelbourn et al., 1973; Kaeriyama, 1986) where t is days after hatching, L_t is the fork length at t days after hatching, and L_0 and a are the calculated fork length at hatching and specific growth rate, respectively. As shown by the growth equations in Fig. 1 ($r > 0.9$, $p < 0.01$), specific growth rates were very high before emergence, but subsequently decreased, except in pink salmon. Before emergence, the specific growth rate of coho was the highest of the four species, followed in order by chum, masu and pink salmons. After emergence, the growth rate was somewhat higher in pink salmon than in the others, which were all about equal.

Body proportion. The ratios of body part to fork length during development are shown in

Table 1. Developmental stages of masu, coho, chum and pink salmons. days, days after hatching; FL, fork length; RGL, ratio of length at developmental stage to that at hatching.

Stage		Masu	Coho	Chum	Pink
At hatching	(mmFL)	17	18	22	18
Appearence of	(days)	30	24	27	—
parr marks	(mmFL)	28	28	33	—
	(RGL)	1.68	1.59	1.46	—
Emergence	(days)	56	33	45	56
	(mmFL)	32	30	39	32
	(RGL)	1.94	1.71	1.73	1.82
Absorption	(days)	72	43	54	78
of yolk	(mmFL)	34	32	43	42
	(RGL)	2.06	1.82	1.90	2.39
Squamation	(days)	101	71	61	106
	(mmFL)	46	41	52	57
	(RGL)	2.76	2.33	2.30	3.30
Disappearance	(days)	107	100	61	100
of fin fold	(mmFL)	51	59	52	59
	(RGL)	3.09	3.35	2.30	3.35

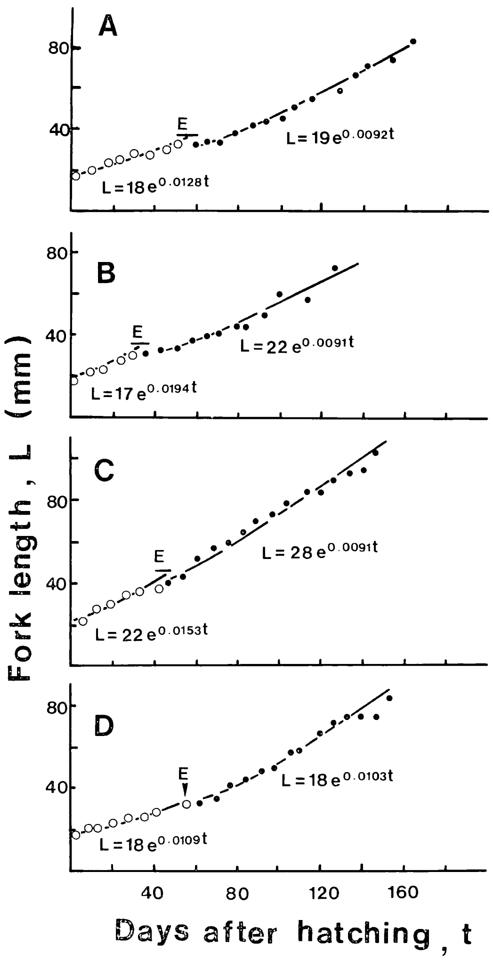

Fig. 1. Changes in the average fork length in masu (A), coho (B), chum (C) and pink (D) salmons reared in freshwater. E, emergence.

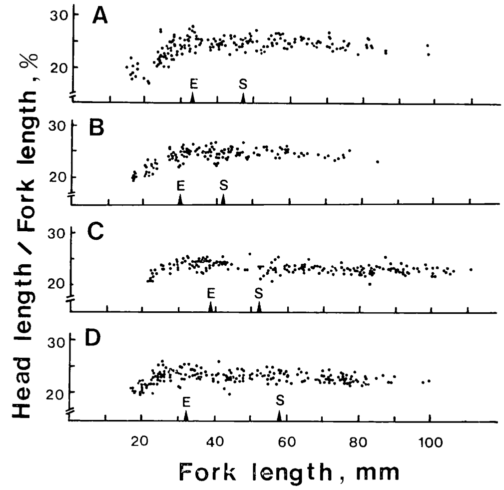

Fig. 2. Changes in the head length as percentage of fork length in masu (A), coho (B), chum (C) and pink (D) salmons. S, squamation; E, emergence.

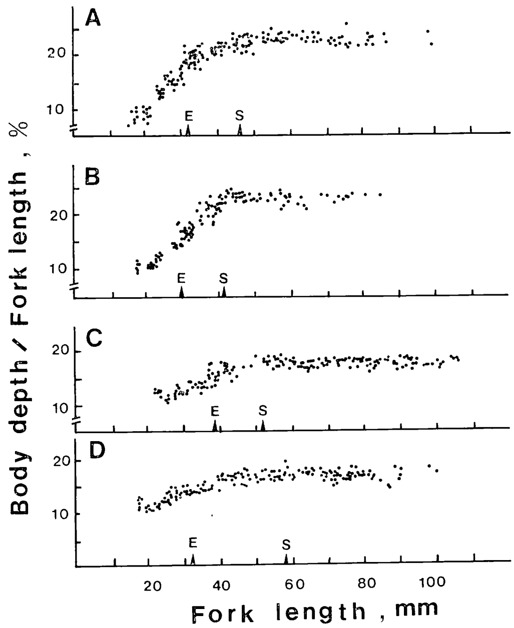

Fig. 3. Changes in the body depth as percentage of fork length in masu (A), coho (B), chum (C) and pink (D) salmons. S, squamation; E, emergence.

Figs. 2–6.

No significant differences were recognized among the four species in the ratio of head to fork lengths (Fig. 2). Head length was 20% FL at hatching. It gradually increassed with growth to 24% FL by emergence, and subsequently remained relatively constant.

The ratio of body depth to fork length was about 10% FL at hatching, and increased during subsequent development (Fig. 3). It was maximized during emergence and squamation, and subsequently remained constant. Maximum values differed considerably among the four species: For masu and coho salmons they were high (21–23% FL), but for chum and pink salmons they were low (about 17% FL).

Changes in the ratio of eye diameter to fork length could be divided into two types (Fig. 4). One is exhibited by masu and coho salmons, where the ratio started to become larger after hatching,

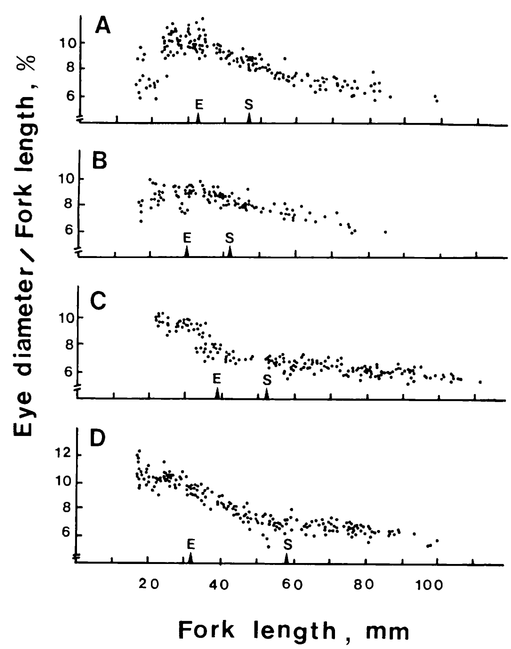

Fig. 4. Changes in the eye diameter as percentage of fork length in masu (A), coho (B), chum (C) and pink (D) salmons. S, squamation; E, emergence.

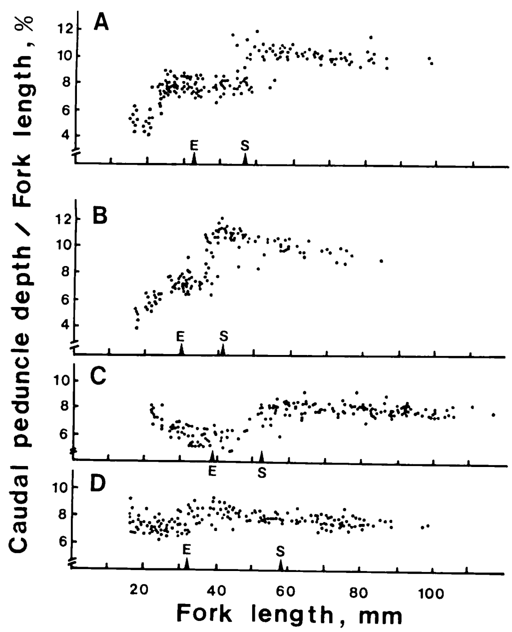

Fig. 5. Changes in the caudal peduncle as percentage of fork length in masu (A), coho (B), chum (C) and pink (D) salmons. S, squamation; E, emergence.

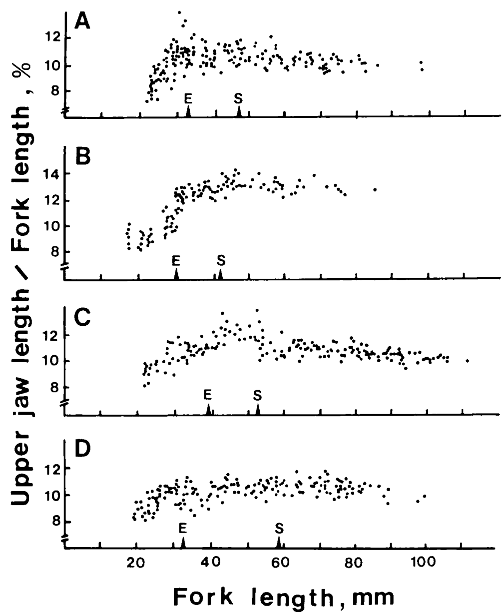

Fig. 6. Changes in the upper jaw length as percentage of fork length in masu (A), coho (B), chum (C) and pink (D) salmons. S, squamation; E, emergence.

reached a maximum value at emergence, and decreased after the inflection; and the other by chum and pink salmons, where it gradually decreased after hatching, inflected at emergence in chum salmon or at squamation in pink salmon, and attained a constant value thereafter.

Changes in the ratio of caudal peduncle depth to fork length could also be divided into two types (Fig. 5). Caudal peduncle depth of masu and coho salmons increased after hatching, leveled off (about 7.8% FL) at emergence, then increased again, reached a maximum (about 10% FL) at about the time of squamation, and finally became constant. On the other hand, those of chum and pink salmons decreased after hatching, and reached a minimum value (6–7% FL) at about the time of emergence. Afterwards, this ratio increased and reached a maximum 2 weeks after emergence in chum salmon (58 mm FL) and at complete absorption of yolk in pink salmon (42 mm FL). It became constant (about 8%) after attaining a maximum value. Caudal peduncle depth changed more markedly in masu and coho than in chum and pink salmons.

The ratio of upper jaw length to fork length was nearly linear and changed only slightly in chum and pink salmons (Fig. 6). However, significant changes were observed in masu and coho salmons. The maximum value was attained at emergence in masu and pink salmons, and at squamation in coho and chum salmons. Subsequently, it was constant.

To summarize, the morphology of the four species changed significantly during the periods of emergence and squamation. Masu and coho salmons developing a deeper body and caudal peduncle, showed more marked morphological changes than chum and pink salmons.

Relative growth. During early development, from hatch to 100–120 days, in the four species, relationships between fork and body part lengths or body weight were expressed as allometric formulae. The initial growth constant (b) and relative growth coefficient (α) of the allometric formulae and the correlation coefficient (r) are shown in Table 2. Masu and coho salmons had higher relative growth coefficients than chum and pink salmons for body depth, eye diameter, interorbital width, and caudal peduncle depth. The growth coefficient in the relationship between fork length and body weight was high (about 3.6) in masu and coho salmons, and low (about 3.3) in chum and pink salmons.

When the relative growth coefficent is $\alpha > 1$, it expresses tachyauxesis; at $\alpha = 1$, isauxesis; and at $\alpha < 1$, bradyauxesis (Kubo and Yoshiwara, 1969; Yamagishi, 1977). Tachyauxesis was observed in growth of body depths of all four species, especially masu and coho salmons; of caudal peduncle depths of masu, coho and chum salmons; and of upper jaw length of coho salmon. Isauxesis was exhibited in the growth of the head and caudal lengths of all four species, upper jaw lengths of all except coho, and caudal peduncle depth of pink salmon. Only eye diameter growth of all four species showed bradyauxesis.

Table 2. Relationships between the fork length (L1) and body measurements (L2) or body weight (W) of masu, coho, chum and pink salmons during early life. b, α, and r show the initial growth constant, the relative growth coefficient and the correlation coefficient, respectively, in the allometric formula ($L2(W) = bL1^{\alpha}$).

Character		Masu	Coho	Chum	Pink
Head length	b	0.1366	0.1596	0.2587	0.2046
	α	1.1513	1.1111	0.9705	1.0266
	r	0.9868	0.9947	0.9704	0.9963
Body depth	b	0.0233	0.0150	0.0489	0.0462
	α	1.5670	1.6909	1.2920	1.3128
	r	0.9776	0.9833	0.9939	0.9887
Eye diameter	b	0.1939	0.1315	0.2681	0.3273
	α	0.7773	0.8681	0.6698	0.6270
	r	0.9298	0.9735	0.9858	0.9915
Snout length	b	0.0294	0.0097	0.0217	0.0392
	α	1.2013	1.4545	1.2381	1.1021
	r	0.9840	0.9902	0.9867	0.9730
Interorbital width	b	0.0472	0.0668	0.1173	0.1177
	α	1.1395	1.0514	0.9062	0.9020
	r	0.9635	0.9781	0.9916	0.9828
Caudal peduncle depth	b	0.0201	0.0113	0.0300	0.0677
	α	1.3843	1.5511	1.2161	1.0368
	r	0.9916	0.9762	0.9825	0.9957
Caudal length	b	0.0830	0.1450	0.1310	0.1078
	α	1.1466	0.9886	1.0418	1.0976
	r	0.9917	0.9796	0.9971	0.9965
Upper jaw length	b	0.0962	0.0359	0.0957	0.0679
	α	1.0645	1.3265	1.0239	1.1026
	r	0.9898	0.9915	0.9979	0.9942
Body weight	b	0.0042	0.0042	0.0049	0.0039
	α	3.5986	3.6775	3.2775	3.3811
	r	0.9979	0.9953	0.9993	0.9991

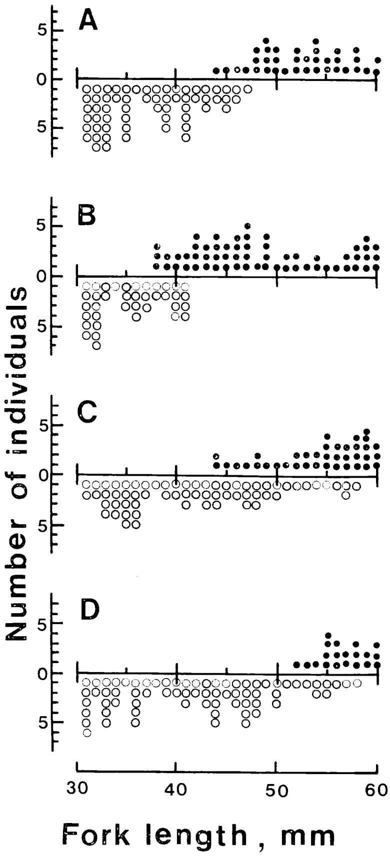

Fig. 7. Distribution of fork length (range: 30–60 mm) as a function of scale development in masu (A), coho (B), chum (C) and pink (D) salmons. Open circles, scale undeveloped; solid circles, scale developed.

Scale formation. The minimum size at scale formation was 38 mm FL in coho, 44 mm FL in chum and masu, and 52 mm FL in pink salmon. The maximum size without scales was 41 mm FL in coho, 47 mm FL in masu, and 58 mm FL in chum and pink salmons (Fig. 7). Therefore, the differences between the minimum size with scales and the maximum size without scales were 3 mm in masu and coho, 6 mm in pink, and 14 mm in chum salmon. Median values between the two were roughly equal to the fork length at squamation (Table 1).

Relationships between the fork length (L, mm) and circuli number (C) of scales are shown in the following formulae and in Fig. 8:

Masu salmon: $C=0.501\ (L-46)^{0.855}$, ($r=0.989$, $p<0.001$)

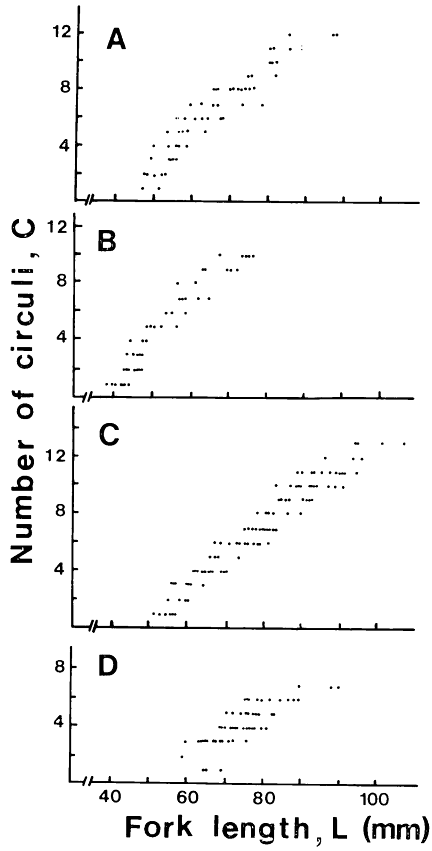

Fig. 8. Relationships between fork length and number of circuli in masu (A), coho (B), chum (C) and pink (D) salmons.

Coho salmon: $C=1.121\ (L-41)^{0.622}$, ($r=0.987$, $p<0.001$)

Chum salmon: $C=0.473\ (L-52)^{0.826}$, ($r=0.994$, $p<0.001$)

Pink salmon: $C=0.881\ (L-57)^{0.522}$, ($r=0.706$, $p<0.1$)

At squamation, masu and chum salmons had higher relative growth coefficients; but coho and pink salmons had higher initial growth constants than masu and chum, and fork lengths of masu and coho were greater than those of chum and pink salmons. Consequently, the rate of circulus formation during early development was considerably slower in pink salmon than in the others, which exhibited little difference.

Discussion

Generally, development in fishes is a process of adaptation to the environment or habitat during each ontogenetic stage. This is reflected in morphological changes after hatching, but becomes more apparent in the body shape and markings of *Oncorhynchus* after emergence from the gravel bed. At this point, the life modes of the four species diverge: masu and coho do not form schools and remain in the river for one or two years until smolt transformation occurs. On becoming smolts, they usually migrate to the sea (Hoar, 1958; Chapman, 1962; Kubo, 1980; Mayama and Suzuki, 1981; Kawamura, 1983). Chum and pink salmon fry, on the other hand, exhibit schooling behavior and migrate to the sea immediately after emergence (Hoar, 1951, 1958; Kobayashi, 1964; Kaeriyama, 1985, 1986). Accordingly, they can be divided into two life modes: masu and coho as "freshwater types", chum and pink as "marine types".

A correlation can be made between these two life modes and the early life changes in morphology as the locomotor function develops and energy acquisition is required. In the freshwater type, the fish have distinct parr marks, a fatter and deeper body shape, a deeper caudal peduncle, and higher relative growth coefficients. This body form is distinguished as "rotund" by the author. The relative thickness of the body makes it possible to accommodate the mass of muscles, stores of fat and carbohydrate necessary to support the sudden acceleration of fast starts and quick turns (Hertel, 1966; Driedzic and Hochachka, 1978), consistent with their behavioral characteristics such as defending territories (Hoar, 1951; Kubo, 1976; Yamagishi and Nakamura, 1983). Counter to this, the schooling marine type is what the author calls "streamlined" which has gradual or less marked morphological changes and lack parr marks, or if they appear, are exhibited only temporarily.

All the four species examined in this study exhibited significant changes in morphology by the time of emergence, when the growth rate slowed down (Figs. 1–6). Afterwards, the ratios (RGL) of body segment measurements (except head length) to fork length still increased, but nearly stabilized by the squamation stage (Table 1). In chum salmon, squamation was previously found to correspond to the period when ossification began (Kaeriyama, 1986), and that scale formation began considerably earlier in chum than in pink salmon (Okada and Nishiyama, 1970). This study further supported these findings and furnished evidence that scale formation also occurred significantly earlier in chum and coho than in pink and masu salmons. In particular, pink was extremely slow in developing scales (Table 1, Figs. 7, 8). Although it could not be determined whether these differences in the rate of scale formation were attributable to speciation or environmental factors, the author suggests that there is a strong correlation with developmental speed.

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初期生活期のサケ属魚類4種における形態比較と鱗形成

帰山雅秀

サケ属魚類のうち，サクラマス，ギンザケ，サケおよびカラフトマスの仔魚と幼稚魚の発育に伴う形態の変化と鱗の形成を調べ，4種間の比較と相違点について検討した．サケとギンザケの発育速度および鱗の形成速度は他2種に比べて明らかに早かった．4種とも，浮上時には一時的に成長速度が低下し，形態は孵化時から浮上時あるいは幼生鱗形成時まで著しい変化を示した．サクラマスとギンザケは形態の変化が顕著で，パー・マークがよく発達し，体高が高く，尾柄が太く，相対成長係数が高かったのに対して，サケとカラフトマスは比較的連続的で直達的な発育をし，形態の変化が小さく，パー・マークも一時的に出現するか，全く欠いていた．以上のことと4種の初期生活期における生活様式から，サケ属魚類の形態は円筒型（サクラマス，ギンザケ）と流線型（サケ，カラフトマス）に分けられた．

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