Development and Early Life History of the Ayu Reared in the Laboratory

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The larval development and growth of *Plecoglossus altivelis* are described based on a series of 268 reared specimens, ranging between 6.1 and 88 mm standard length (SL). Development of morphological characters are described, with special reference to fin formation.

Transformation from the larval to juvenile stage was observed when fish attained about 27 mm SL, 80 to 90 days after hatching. Fin rays completed segmentation at 33 mm SL, and branching at 42 mm SL. Larval growth for 140 days was expressed by linear regression. Relative length of preanal length to total length changed drastically during yolk-sac larva to shortly before transformation, then became constant after 45 mm TL. The importance of organogenesis and morphometric characters with respect to the ecological aspects of early life stages is discussed.

Ayu *Plecoglossus altivelis* is a typical freshwater species which is frequently planted into Japanese rivers. Such activity has already been carried out over a long time period. Recently, large scale artificial propagation and releasing programs have become increasingly important to support the inland fishery. Despite the common occurrence of their species, little is known about its development during early life stages. Embryonic and larval development were briefly described by Uchida,1) Okada,2) Mito3) and Iwai.4) Histophysiological observations on early stages were detailed for wild5) and reared specimen.6) For more than one decade fingerlings were used in teratological studies.7) Takashima et al.8) and Ito et al.9) dealt with the description of meristic characters in reared specimens. Developmental stage in the early life history of landlocked ayu was described by Azuma.10) Quantitative morphological data are a prerequisite for the understanding of the normal occurrence of life pattern, allowing to identify irregularities that might occur during artificial propagation. On the basis of such information the techniques employed to prevent malformations can be easily evaluated.

This report describes some morphological features during development, some morphometric characteristics and the growth of the ayu under laboratory conditions in order to complement available information on the early life history of this species.

Materials and Methods

Fish used in this study were reared during October in 1981 to February in 1982 from artificial fertilization to a size of approximately 88 mm in standard length. At the time of sampling, fish were kept in a 50 m³ tank. The tank was rectangular (10 × 5 × 1 m depth). Water depth was approximately 80 cm. During the rearing period temperature varied between 10.1°C to 21.6°C. Water was supplied to the tank at about 3 l min⁻¹. Initial stocking density was 10 individuals l⁻¹. During the course of development food items offered include rotifer, *Artemia* nauplii and formular pellets. Detailed rearing technique employed to raise larvae in this study was described by Hiramoto et al.* The methods for preserving the specimens, and for measuring body dimensions are identical to those described by Fukuhara and Fushimi.11)

Results and Discussion

Total Length, Standard Length and Preanal Length Relation

Standard length was employed to examine the
development and growth in comparison to other morphometric characters. Overall size from newborn larvae to 80 mm, the relation between total length, standard length and preanal length are shown in linear regression (Fig. 1).

**Description of Larval Development**

Larval size averaged 6.05 ± 0.59 mm SL or 6.16 ± 0.34 mm TL (n=33) at the time of hatching (Fig. 2A). The subsequent growth of individuals is shown in Fig. 4. Newly hatched larvae were comparatively longer than older larvae with relatively small heads. Relatively large yolk sac and fan-shaped pectoral fins without rays were present. The eyes were pigmented in hatched larvae, and the jaw functional. The long distance from the tip of snout to anus averaged 73% TL. Proportional measurements of preanal length relative to total length is given in Fig. 5. Hypural bone started to develop when larvae attained at 8.5–9.0 mm SL (Fig. 2B). The development of the hypural bone occurred earlier in specimens of this study compared to those larvae investigated by Uchida1) at a total length of 12.5 mm. The notochord flexion occurred in our specimens at about 15 mm TL which were similar size to those reported by Uchida1) (Fig. 2C). In 20 days old larvae, the notochord flexion was found only in 21 out of a total of 23 specimens.

No marked changes of most morphological characters were observed in larvae ranging be-
between 15 to 20 mm SL (Fig. 2D). At this stage the body height increased more rapidly than total length (Fig. 2E). The proportional length of distance between the snout and anus became constant after fish reached about 45 mm TL (Fig. 2F-I, Fig. 5).

Conical teeth appeared on the upper jaw of larvae when fish reached a size of 33.0 mm SL, corresponding to an age of 80 days. The larvae bore comb-like teeth on the upper jaw were also found on day 80, at a size of 41.0 mm SL. The indication of forming the comb-like teeth was observed histologically in the 35.5 mm wild specimen.4) The smallest larva exhibiting comb-like teeth on both the upper and lower jaw was observed at 43.0 mm SL, corresponding to an age of about 100 days after hatching. Specimens larger than 51.0 mm SL, showed well-developed comb-
like teeth on both jaws, and had usually reached an age of 140 days. In wild specimens comb-like teeth were described in larvae that had already reached a size larger than 55.0mm SL.16)

The Development of Fins

The primordial fin-fold was present in hatched larvae and remained until larvae had reached about 9 mm SL. There was no remnant of larval fin-fold just prior to the anus when larvae reached 26 mm SL. The caudal fin margin shaped rounded until the notochord started to flex at about 13-14 mm SL. At that stage the caudal fin rays began to develop.

Fan-shaped pectoral fins without rays developed at hatching. The pectoral fin rays began to develop at larval sizes between 20 mm and 23 mm SL. The buds of the ventral fin appeared on larvae as small as 18 mm SL. The ventral fin buds were present in all larvae over 19 mm SL. Fin ray development was completed at about 18 mm SL for the dorsal fin, and 12 mm and 18.5 mm SL for the caudal and anal fins. In paired fins the complement of fin rays was found at 24 mm and 27 mm SL in the ventral and pectoral fins, respectively. Consequently, metamorphosis, the transformation from the larval to the early juvenile stage did occur at about 27 mm standard length.

Fig. 3 shows the sequence of segmentation and branching of the soft rays in unpaired and paired fins. The segmentation started at a standard length of 11 mm (caudal fin) and 16 mm (anal and dorsal fins), and finished at 15 mm, 21 mm and 23 mm SL, respectively. Segmentation in paired fins started at about 23 mm SL for the pectoral fins and 24 mm SL for the ventral fins, and was completed at a standard length of 33 mm and 28 mm.

Branching of the rays began at approximately 23 mm SL for the dorsal, 28 mm SL for the anal, 18 mm SL for the caudal, 36 mm SL for the pectoral and 30 mm SL for the ventral fins. The completion was observed at about 40 mm, 38 mm, 22 mm SL for the unpaired fins and 42 mm, 37 mm SL for the paired fins. Thus all fins finished their segmentation at 33 mm SL, and the branching of rays at a standard length of 42 mm. Therefore, fundamental structure of fin rays was recognized for the fish measuring over 42 mm SL (51 mm TL), and resulting in development of fin locomotion as mentioned by Gosline.17)

Pigmentation

Newly hatched larvae and post-larvae were scantily pigmented as shown in Fig. 2 (A-D). Few melanophores were arranged serially only along the gut (Fig. 2D). No marked changes in the distribution of melanophores were observed until larvae attained 25.7 mm SL (Fig. 2E). Larvae of 25 mm to 36 mm SL (Fig. 2E, F) showed melanophores which were distributed along the cephalic area, the operculum, around the jaws, and more intensively along the gut, the caudal peduncle and the base of the caudal fin. As development progressed the lateral melanophores became more numerous but were still abundant.
along the dorsal surface area of the larvae, particularly on the posterior half of the body. They were sparsely distributed along the ventral side of the body (Fig. 2G-H).

**Larval Growth**

The growth of larvae investigated in this study is shown in Fig. 4. The relation between standard length and age in days after hatching could be expressed by a linear regression (Fig. 4).

Preanal length from snout to anus distance was 72–74% of the total length for newly hatched larvae, and reached about 77% of TL in 10 to 12 mm long larvae. From this size onward this relationship decreased drastically until fish attained a total length of about 45 mm. After 50 mm TL the PL/TL ratio levelled at approximately 62% of the total length (Fig. 5).

The relative length of the body portion to SL and/or TL was implicated with the development of morphometric characters and functional, ecological aspects in various marine fish larvae. According to Tanaka et al., gastric glands, pyloric caeca and digestive mechanism of protein were converted to subsequent stage of its development during morphological transit from larval to juvenile ayu, which was suggesting the closed relation of morphometric characters and functional aspects. Ito et al. stated that the inflection point of allometric growth in various body dimension occurred for the ayu at 20 mm to 30 mm SL, being a transit phase of larval development.

In the ayu changes of feeding habits from a planktivorous fish to a more herbivorous species is usually reported to occur after about 50–65 mm SL. At the vicinity of this size the fish also changes its habitat from estuarine to more brackish waters. Iwai stated that in the specimens measuring 51 mm SL the intestine was apparently looped and the total length of the alimentary canal was drastically increased as compared to an "unlooped" previous stage of development, and such fish belonged to the stock beginning the anadromous migration. Matsui also described a rapid elongation of the alimentary canal when post-larvae reached 48 to 55 mm SL. Concerning with development of morphological characters during the phase in which the changes of feeding habits and habitat occurred, the branching of all fin rays completed in fish more than about 50 mm TL. The well-developed comb-like teeth were found in fish over 50 mm SL (60.8 mm TL). In addition squamation which was considered to be profitable for a change of habitat, completed at a length of more than 55 mm SL. Coincidently PL/TL ratio achieved a constant values as mentioned before.

These observations in connection with our determinations indicate that differentiation of the internal and external organs is not only linked with the changes of feeding habits and habitat selection but also connected to rapid changes in morphometric characteristics. Therefore the morphometric development of this species can be interpreted to be related to advances in organogenesis and to behavioural changes that occur coincidently at a time when the PL/TL ratio is achieving a constant values.

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