INTRODUCTION

The technology on artificial propagation of fishes, especially of commercially important marine species have made a tremendous progress in the past two decades in Japan. The rapid strides on the rearing techniques of marine fishes are the reflect, in large part, of the change of national fisheries strategy from exploitation to intensive aquaculture, so called farming fisheries, with the advent of 200 miles economic zone. At the same time, a need has arisen to establish the rational resources management scheme for fish stocks in coastal waters, based on basic biological data gained from rearing experiments on individual fish species.

While the techniques of fish rearings are thus in progress, many problems are still remained to be resolved in artificial production of the larvae in the hatcheries, and subsequent release of the hatchery-bred fries to improve natural stock size. In the larval rearing, for instance, effective timing and prey density of initial feeding, optimum size and developmental stage to wean from living food, and transfer from indoor facilities to floating cage system are all primitive yet most critical factors to establish the production techniques for stable harvest in the hatchery. Regarding fries raised in the hatchery, little is known about suitable developmental stage or fish size and sites for releasing. Rational methods to evaluate the fish "quality" are also prerequisite for effective utilization of the raised fishes for both intensive and extensive aquaculture.

As for field investigation, larval growth and development in succession are nearly unknown due to the difficulties of sampling.

Part of these technical constraints commonly encountered in the successful rearing procedures of marine fishes from newly hatched larvae to juveniles may be overcome by obtaining detailed information about not only development of morphological characters but also development of various organs and behaviour differentiation of the fish larvae.

The objective of this study is to describe the developmental sequence of morphogenesis, organogenesis and behavioural aspects of the larvae of eight commercially valuable fish species, raised under laboratory conditions. These characteristics are consid-

ered to be deeply implicated mutually to exhibit the different life modes of the species. Hence, comprehensive knowledge on larval development is needed to understand their biological features in the developmental stages and behavioural aspects which are useful for both artificial production and ecological investigation of fishes in the field. Observations on swimming performance were also made to know the relationship between morphological development and behavioural changes of the larvae.

CHAPTER I. MATERIALS AND METHODS

Rearing of larvae and juveniles

Larvae and juveniles used in this study were reared from egg stage to designed developmental stages of juvenile or young under laboratory conditions. A few specimens caught randomly in the wild also used to compare with the reared ones. Materials reared in this study were as follows; *Engraulis japonica* (Houttuyn), *Plecoglossus altivelis* Temminck et Schlegel, *Seriola quinqueradiata* Temminck et Schlegel, *Oplegnathus fasciatus* (Temminck et Schlegel), *Lateolabrax japonicus* (Cuvier), *Epinephelus akaara* (Temminck et Schlegeli), *Acanthopagrus schlegeli* (Bleeker), *Pagrus major* (Temminck et Schlegeli), *Evynnis japonica* Tanaka, *Hexagrammos otakii* Jordan et Starks, *Paralichthys olivaceus* (Temminck et Schlegeli) and *Limanda yokohamae* (Gunther).

Firstly the eggs used for rearing experiment were obtained by natural spawning techniques or artificial fertilization, and then the viable eggs were maintained in an incubation tank until they hatched out. Newly hatched larvae were then transferred to rearing tanks which capacitating 500 l (circular) to 1,000 l (circular or rectangular) at a stocking density between 5,000 and .SRO 30,000 individuals/m^3 depending on species. The details of rearing characters of experimental duration, temperature and parental sources in each species were summarized in Table 1.

Post-larvae were initially fed with laboratory-cultured roti fer, *Brachionus plicatilis* O.F.Muller cultured with *Chlorella*

Table 1. Records of species used, duration, temperature and egg source of rearing experiment in this study

species	duration	WT(°C)	methods of obtaining eggs
Engraulis japonica	Aug. 7-Oct. 8, 1981	17.7-26.6	Ns
Engraulis japonica	Jul. 5-Oct.14, 1985	19.8-26.9	Ns
Engraulis japonica	Jun.29-Oct.11, 1986	20.5-27.2	Ns
Engraulis japonica	Jun.30-Sept.22,1986	21.4-26.6	Ns
Plecoglossus altivelis	Oct.23-Nov. 4, 1974	17.2-20.3	Af
Plecoglossus altivelis	Oct.10'81-Feb.28'82	10.1-21.6	Af
Seriola quinqueradiata	Apr.29-Jun.18, 1982	19.6-22.1	Af
Oplegnathus fasciatus	Jun.11-Aug.30, 1976	18.8-27.3	Ns
Oplegnathus fasciatus	Jun. 6-Aug.13, 1977	21.0-26.7	Ns
Lateolabrax japonicus	Nov.29-Mar.11, 1978	14.2-19.4	Af
Lateolabrax japonicus	Dec. 6-Mar.12, 1979	13.6-19.5	Af
Epinephelus akaara	Aug. 5-Oct.3, 1985	25.9-27.0	Ns
Acanthopagrus schlegeli	May 21-Aug.29, 1976	18.8-26.3	Ns
Acanthopagrus schlegeli	Jun.17-Aug.16, 1983	19.4-25.7	Ns
Acanthopagrus schlegeli	Jun. 2-Oct.31, 1985	18.8-26.2	Ns
Evynnis japonica	Oct.22-Nov.30, 1978	9.6-22.6	Ns
Pagrus major	May 19-Jun.16, 1977	17.3-24.4	Ns
Pagrus major	Jun.17-Aug.14, 1981	19.4-25.7	Ns
Pagrus major	May 13-Jun.15, 1982	16.6-23.0	Ns
Pagrus major	May 23-Jun.28, 1983	19.1-21.5	Ns
Hexagrammos otakii	Dec.8'81-May 7 '82	10.0-17.5	Ns
Paralichtys olivaceus	Mar.12-Jun.10, 1984	8.0-18.0	Ns
Limanda yokohamae	Jan.17-May 5, 1987	10.9-14.5	Af

Ns,Natural spawning; Af,artificial fertilization.

species for 3 to 5 weeks, in succession *Artemia* nauplii, and copepod, *Tigriopus japonicus* Mori were given with overlapping the feeding duration. Density of the rotifers ranged between 2 and 10 animals/ml in the rearing water column, and that of *Artemia* and copepods were approximately 5 to 20 animals/l. The weaning was done with minced flesh consisting of *Euphausia* species, anchovy, *Engraulis japonica* and sand lance, *Ammodytes japonicus*. Formula pellet was also used supplementary to the minced meat.

Fish larvae were usually cultured in standing water system for the first 3 to 4 weeks, then the running water system was employed for the remainder of the rearing experiment. The volume of water flow increased with larval growth. Residue and feces on the bottom of rearing tank were siphoned everyday. Water temperature

was usually measured at morning (8:30-9:00) and recorded. The salinity of sea water used for experiment fluctuated somewhat, but was generally in the range 25-32. A gentle aeration was provided through the airstone in the tank during the course of rearing experiment.

Preservation and measurement of the specimens

Specimens of larvae, juveniles and young were sampled in series, and at random from the rearing tank for further observations and measurement. The collected specimens were preserved in seawater (25-32) formalin solution ; larvae were generally preserved in 5% formalin solution and 10% solution for juvenile and more developed stages. The preserved specimens were stored under dark conditions at ambient room temperature. The measurement of fish specimens was carried out by profile projector with combination of electronic micrometer with precision of 0.001 mm for the smaller specimens than about 25 mm. The larger one than 25 mm were measured by using caliper with precision of 0.5 mm. No correction factors of shrinkage by formalin preservation were employed for all specimens measured.

Morphometric and meristic observations

Observations based on serially collected specimens were made on morphological development, pigmentation, fin development and squamation for the external organs, and development of the digestive tract was also observed with larval growth. Fin development and squamation were inspected after the specimens were stained by Alizarin Red-S under dissecting and/or huge-power microscopes. All fin rays of paired and unpaired fins were enumerated for the segmentation and branching.

As for scale development, several developmental stages are assigned to observe the sequence from first appearance to full coverage on the body surface by scale row and squamated area.

Development of the alimentary canal is also observed from larval to juvenile stages for its morphological appearance of bending or convolution. Rose Bengal was occasionally used to observe the developmental process of the alimentary canal.

The following meristic characters were measured to evaluate the growth and developmental sequence and allometric growth; preanal length (PL):tip of snout to tip of the anus, standard

length (SL):tip of snout to end of the notochord for larvae, and to the base of the caudal fin for more developed larvae, total length (TL):tip of snout to the end of the caudal fin.

Proportionality of preanal length to total length is calculate with special references to predict morphologically the stable phase of development in the internal organs, particularly on the digestive tract.

Behavioural observations

Behavioural observations were focused on the time to rest and to move for pre-larvae and early post-larvae. Feeding incidence, which representing the ratio of larvae contained the food in their guts, was determined using cultured Brachionus plicatilis for the initial feeding larvae as their growth progressed. Swimming performance of larvae was traced to evaluate the swimming speed when they orientated normal swimming manners in the rearing tanks. The pantagraph was equipped on the rearing tank to record the swimming path of the larvae reared in the tank on paper. Observation of larval swimming was conducted at least 10 individuals. The swimming speed was determined by the swimming distance traveled and the time to require.

CHAPTER II. DEVELOPMENT OF MORPHOLOGICAL CHARACTERS AND BEHAVIOUR

The change of morphological characters exhibits prime appearance in the development of different fish larvae. To know the developmental sequence on external and internal organs as well as behavioural aspect is of importance to ascertain the implication of development in various organs. These information and growth performance, involving allometric growth are also prerequisites to comprehend the ecological significance of morphological and behavioural development of different fish species on their early life stages. In this chapter diagnostic development of the external and internal organs is described with their growth.

Engraulis japonica

Morphological development and growth

The preserved eggs were oval in shape, averaging 1.21 ± 0.06 mm in length and 0.63 ± 0.02 mm in width (mean ± SD, n=35 each) at a salinity of 31. Naturally spawned eggs in captivity varied widely in length and width; 0.9-1.67 mm for length and 0.58-0.7 mm for width. The eggs hatched after 20.5 hrs at 29.6 °C, after 31 hrs at 24 °C and salinity of 31, and after 52 hrs at 17.5°C and salinity of 31.

Newly hatched larvae measured 2.76 ± 0.19 mm SL (Fig.1A). The length of newly hatched larvae were similar to those reported by Uchida (1958a) and Azeta (1981). One day after hatching, the mouth was open and yolk was partly absorbed (Fig.1B). Two day after hatching the yolk was completely absorbed and mouth became functional at temperatures of 23-25 °C (Fig.1C). The notochord started to flex in larvae of about 7.0 mm SL (Fig.1D). The tip of the snout was pointed during the larval stages but became rounded when the fish reached a length of about 20 mm SL. Afterwards the snout tip became markedly rounded as the fish grew (Fig.1M-R). During the larval stages, the end of the maxillary was located beneath the orbit. With growth of the larvae the maxillary extended behind, reaching the region of the anterior portion of the operculum. External appearance resembled closely to that of the adult after they attained about 30 mm SL.

Daily mortality of unfed larvae increased rapidly one day after hatching, and the larvae did not survive over 5 days after hatching. Growth of unfed group increased steadily until they absorbed the yolk sac, thereafter gradual decrement in length was seen until they died (Fig.2).

The growth of larvae during the initial phase of the rearing experiment is shown in Fig. 3. The overall daily increment was 0.43 mm. Daily growth increment in rearing trials was based on observation period of over 55 days and the results ranged between 0.41 to 0.64 mm/day (Fig.4). In contrast, the wild specimens determined by otolith analysis grew at a rate of 0.4 to 0.69 mm/day during their larval life in coastal waters in Japan (Tsuji,1985; Mitani,1988), and 0.68 to 0.76 mm/day for the highest growth rate and 0.37 to 0.41 mm/day for the lowest in the Korean waters (Kim and Kim, 1986). Overall growth from newly

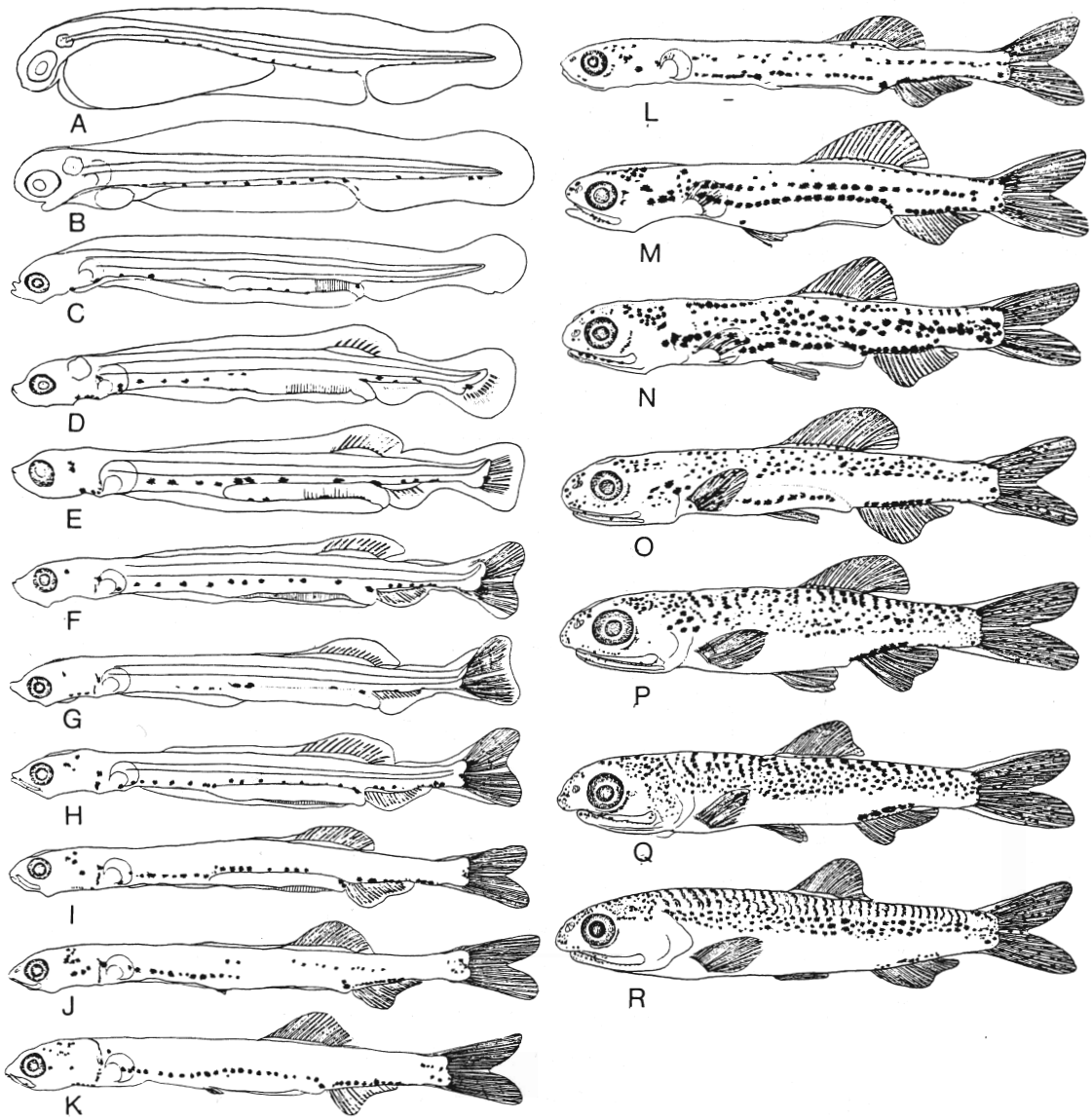


Fig.1. *Engraulis japonica*. Development of larvae and juveniles. A,2.7mm SL; B,3.2mm SL; C,5.6mm SL; D,7.2mm SL; E,8.0mm SL; F,8.5mm SL; G,9.4mm SL; H,10.2mm SL; I,11.0mm SL; J,15.5mm SL; K,19.5mm SL; L,20.0mm SL; M,20.6mm SL; N,23.6mm SL; O,24.8mm SL; P, 30.0mm SL; Q,37.0mm SL; R,43.9mm SL.

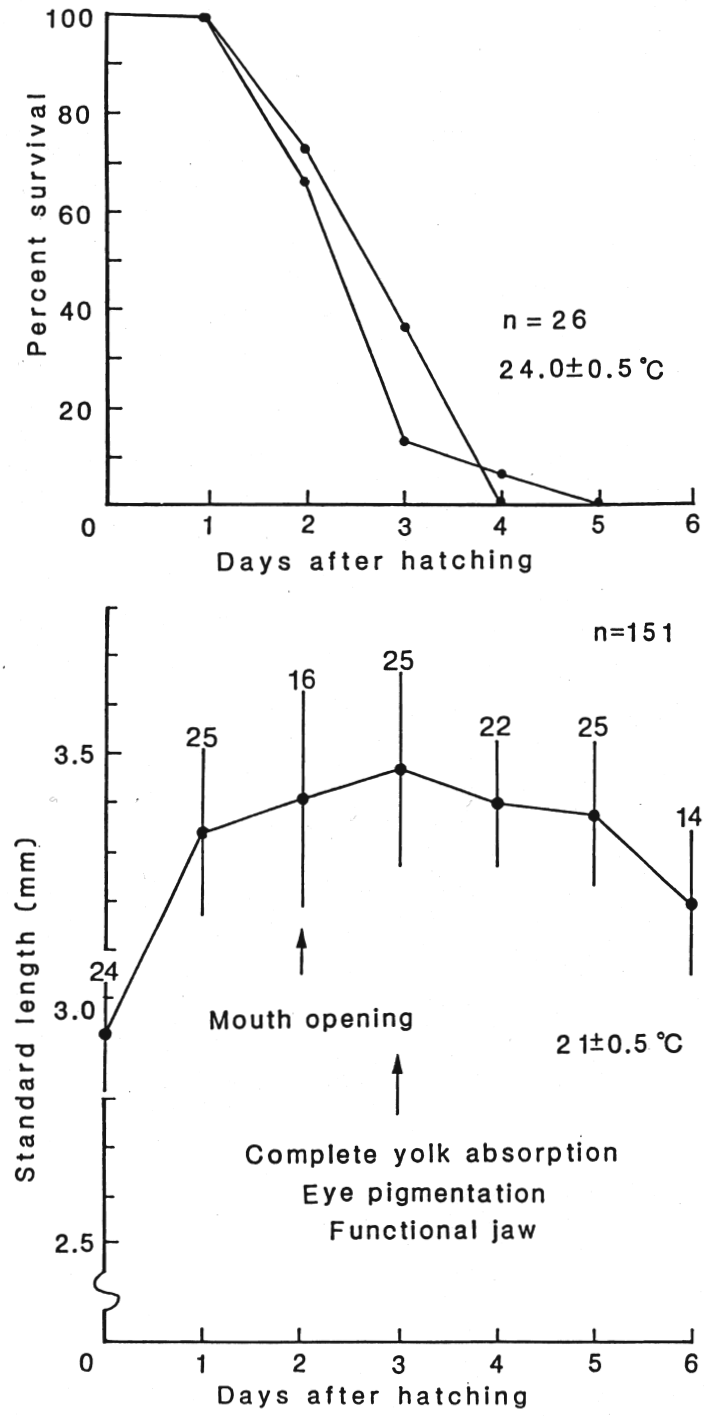


Fig.2. *Engraulis japonica*. Daily mortality (upper) and growth and morphological development (lower) of larvae under unfed conditions.

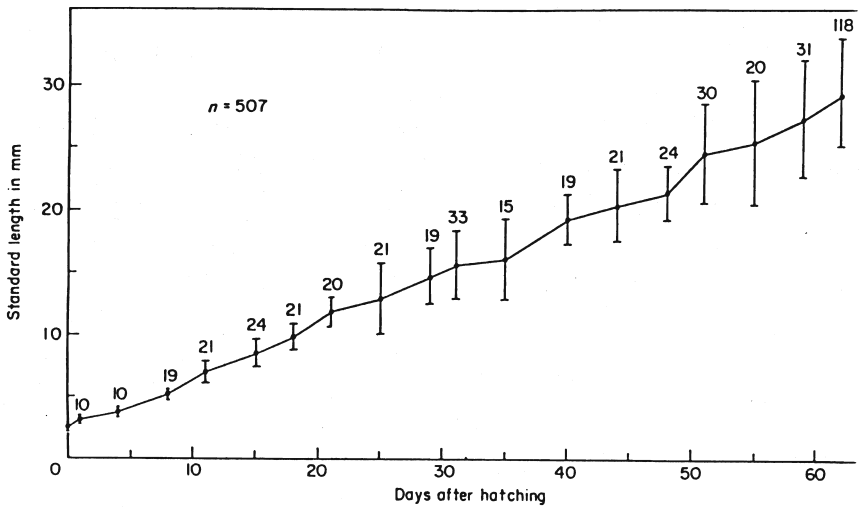


Fig.3. *Engraulis japonica*. Growth of larvae and juveniles reared in a 500 *l* tank(WT=22.7 °C; ranging 17.6 °C to 27.1 °C; S=30.8; ranging 30.0 to 31.6). Dots=mean values obtained from samples taken at random. n=total number of specimens measured. Vertical bars=standard deviation. Numbers at each bar indicate sample size.

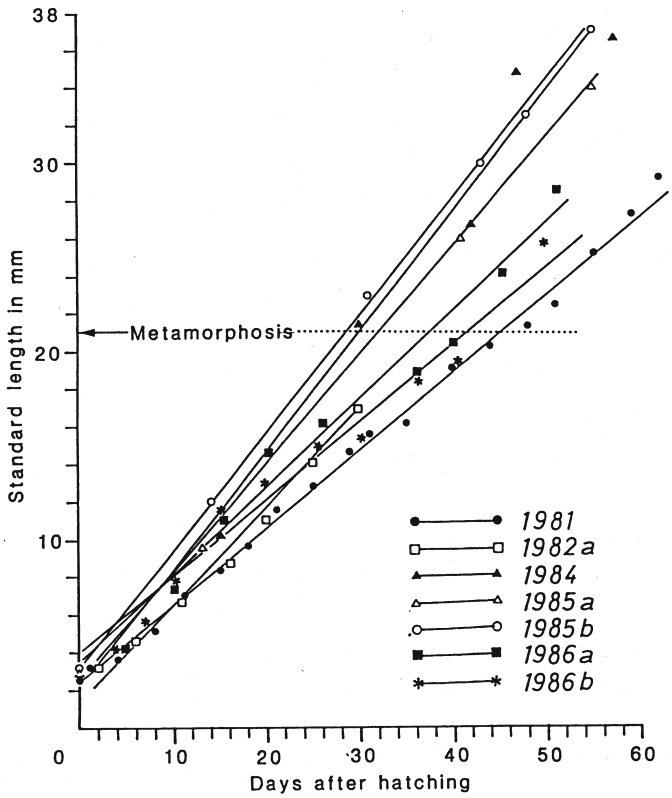


Fig.4. *Engraulis japonica*. Linear description of the initial growth curve of laboratory-reared specimens during 60 days.

hatched larvae to the adult in captivity was reported by Fukuhara and Takao (1988).

Concerning allometric growth, preanal length averaged 74% SL or 71% TL at hatching and increased to 80% SL or 75% TL when larvae were 10 mm SL and 9.0 mm TL (Fig.5). The ratio then decreased markedly to about 60% TL and gradually to 70% SL for specimens less than 20 mm SL (22 mm TL). The ratio became constant at about 60% TL and 72% SL. The relation between total length, standard length and preanal length are shown in Fig.6 for fish between 3.0 mm to 60 mm TL. They are described in linear regressions.

Fin development

Newly hatched larvae exhibited an extended fin-fold which was present until the larvae attained a standard length of 8.5 mm (Fig. 1F). Remnants of the larval fin-fold disappeared completely in larvae of 11.0 mm SL (Fig.1I). A fan-shaped pectoral fin without rays appeared at 3.2 mm SL, 2 days after hatching. Ventral fin buds were present at 15.5 mm SL, 25 days after hatching (Fig.1J). The hind margin of the caudal fin developed in the following sequence; rounded (Fig.1A-C), truncated (Fig.1E), emarginated (Fig.1F-H), and furcated (Fig.1I-R). Furcation of the caudal fin margin became deeper as the larvae grew. The principal fin rays began to ossify in larvae 7.3 mm SL. Fin rays first developed in the caudal fin and then subsequently in the dorsal, anal, ventral and pectoral fins (Figs.7,8). Fin ray development was completed at 7.2 mm SL for the caudal, at 9.5 mm SL for the dorsal, at 10.4 mm SL for the anal, at 16.5 mm SL for the ventral, and 21.0 mm SL for the pectoral fins.

Thus the transformation from the larvae to the juvenile stage occurred at 21.0 mm SL (25.2 mm TL). This differs when compared with wild specimens in which fin rays were fully developed in larvae of more than 19.0 mm TL (Hayashi,1961).

Segmentation of rays began earlier in unpaired fins than in paired fins. Caudal fin rays began to segment at about 8.0 mm SL, dorsal fin rays at 13 mm SL, and anal fin rays at 14.0 mm SL. Fin ray segmentation was completed at about 9.0 mm SL, 16.0 mm SL, 20 mm SL (Fig.7). In the paired fins segmentation of fin rays commenced at 18.0 mm SL for the ventral fins and 21 mm SL for the pectoral fins and finished at about 20 mm SL, and 25 mm SL

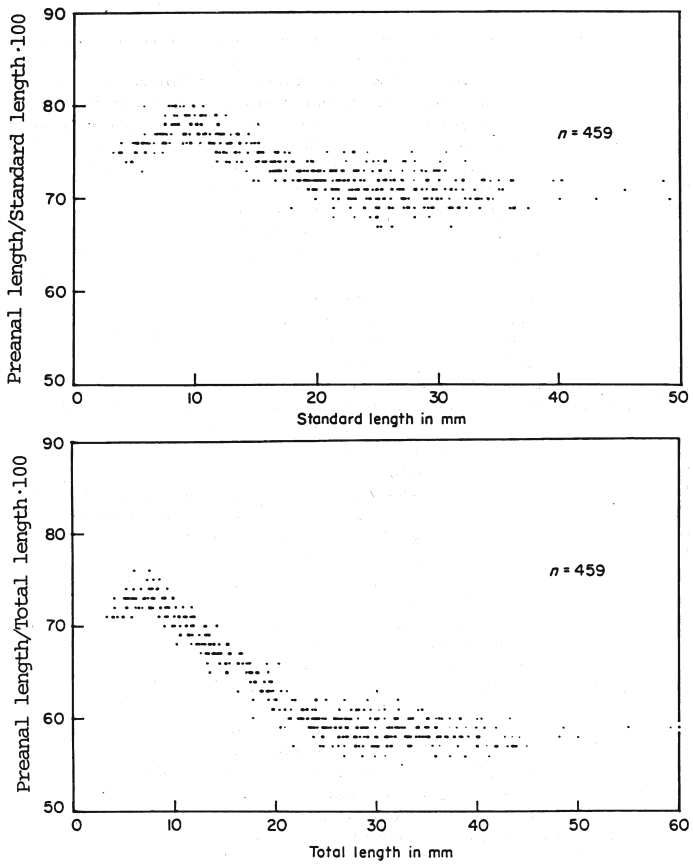


Fig.5. *Engraulis japonica*. Allometric growth of larval and juvenile stages. Preanal length/standard length to standard length (upper), and preanal length/total length to total length(lower). n=number of observations.

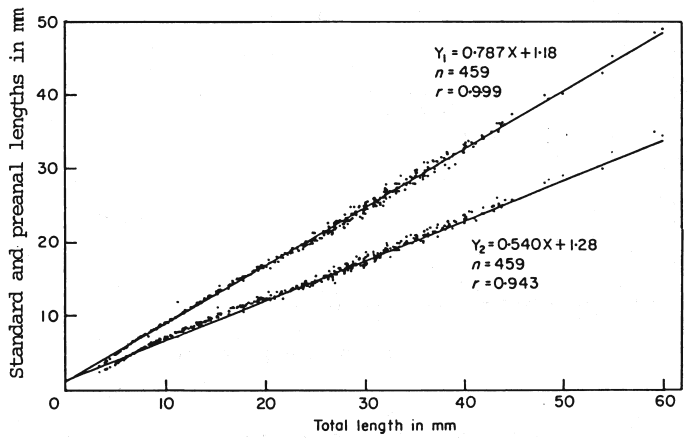


Fig.6. *Engraulis japonica*. Relationship between total length (X), standard length(Y_1), and preanal length(Y_2). n=number of measurement; r=coefficient of correlation.

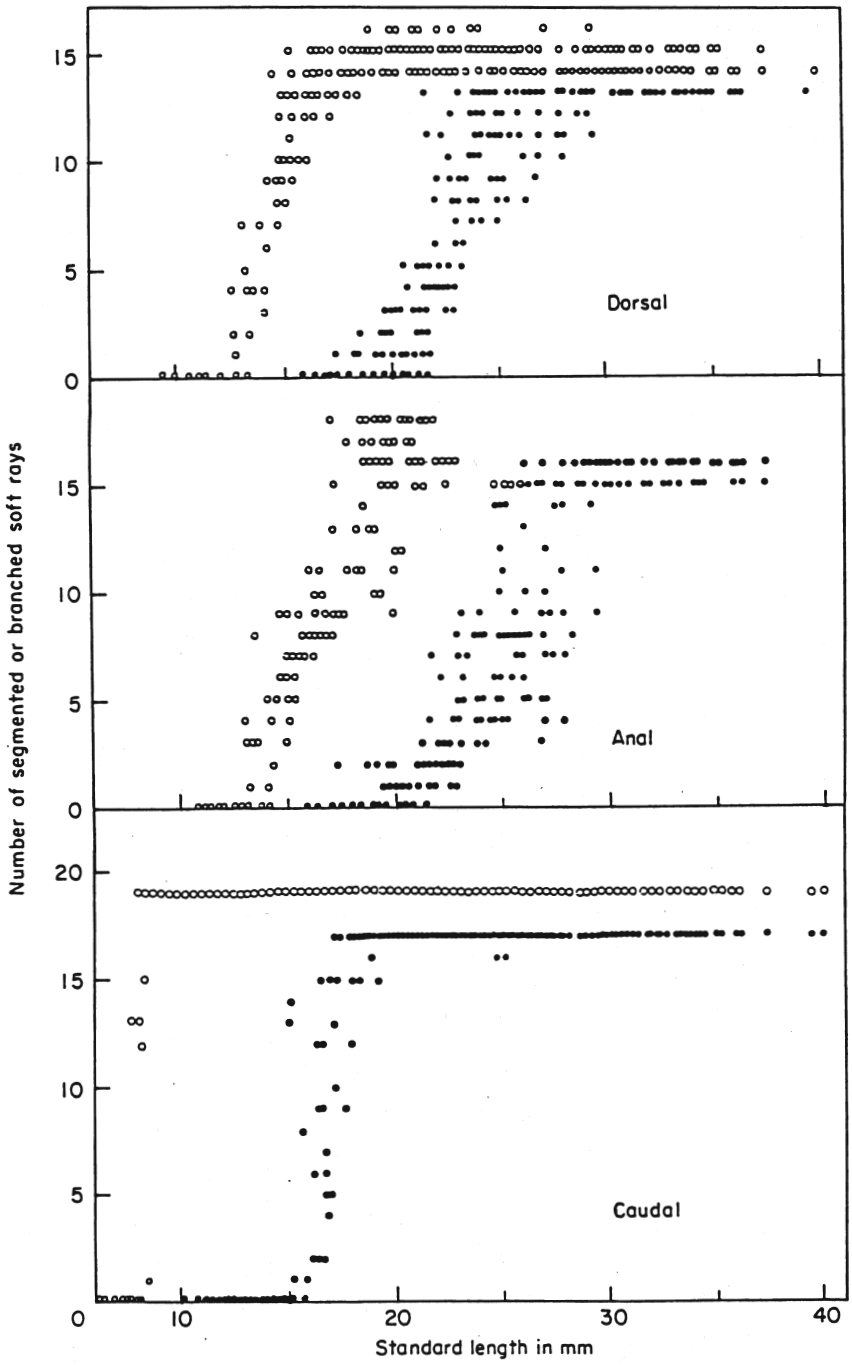


Fig.7. *Engraulis japonica*. Development of fin rays with growth in the unpaired fins. Each circle represents a single observation. Open circles show number of segmented rays and closed circles show number of branched rays.

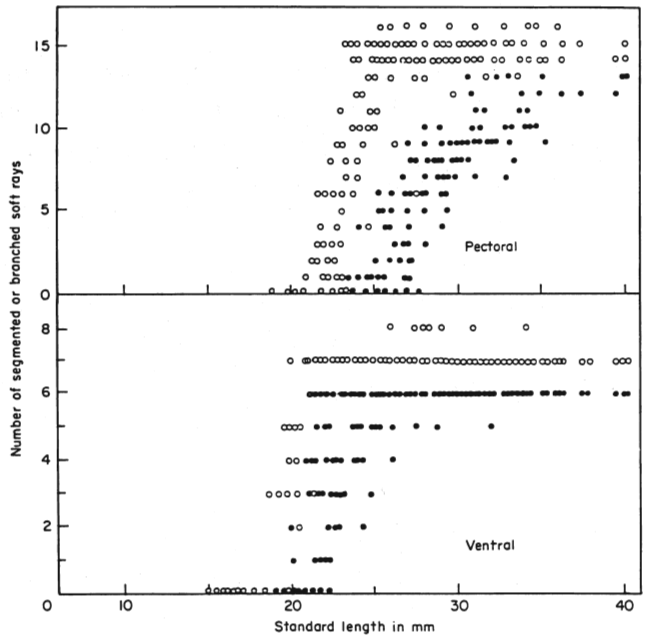


Fig.8. *Engraulis japonica*. Development of fin rays with growth in the paired fins. Symbols in the figure are similar to those in Fig.7.

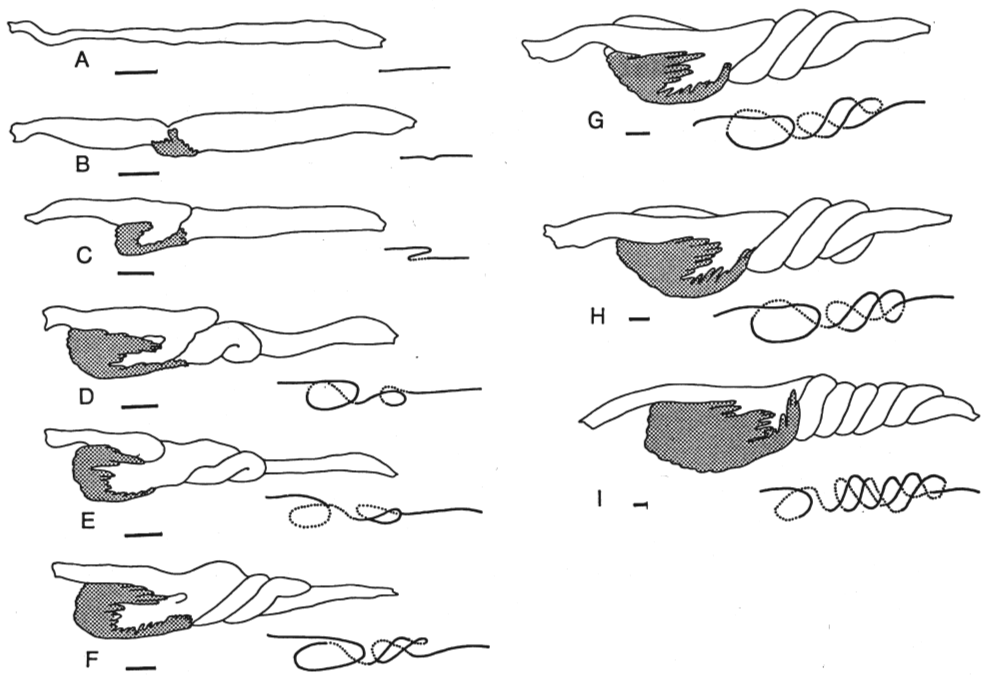


Fig.9. *Engraulis japonica*. Developmental sequence of the alimentary tract in the reared and wild specimens. Dotted area shows the location of the pyloric caeca. Scales depict 1.0 mm.

(Fig.8).

Branching of soft rays began after segmentation was finished in the unpaired fins. The duration of the segmentation and branching of soft rays in the paired fins overlapped as shown in Fig.8. Soft ray branching began at approximately 15 mm SL for the caudal, 20 mm SL for the dorsal and anal, and 20 mm SL for the ventral, 25 mm SL for the pectoral fins. The completion of branching was observed at about 18 mm SL, 25 mm SL, 28 mm SL for the unpaired fins, and 23 mm SL and 34 mm SL for the paired fins. Thus all fins completed segmentation at 25 mm SL, and branching at 34 mm SL.

Pigmentation

Newly hatched larvae had 10 to 13 melanophores on the surface near the abdomen (Fig.1A). Eyes were not pigmented. Melanophores were added continuously to the ventral surface. Eye pigmentation started in 2 days old larvae and several melanophores appeared at the posterior portion of the eyes but were scattered until the larvae were 20.0 mm SL (Fig. 1K). As larvae developed, several melanophores were distributed along the midline of the body surface, and a patch of melanophores, which formed around the caudal fin base, gradually increased in size. In 40 days old larvae, 20.6 mm SL a series of melanophores extended from the pectoral fin base to the caudal peduncle along the ventral surface (Fig. 1M). Melanophores on the midline of the body surface became numerous and those on the ventral surface grew larger. At 45 days after hatching (23.6 mm SL) numerous melanophores were distributed evenly over the body surface (Fig.1L). In the rayed portion of the caudal fin, several melanophores appeared after the larvae reached 20.0 mm SL. When specimens were 50 days old (about 25 mm SL) numerous melanophores were distributed on the body surface, except for on the margin of the ventral surface. Also, some pigment appeared around the eyes, lower jaw and snout (Fig.1M). The number of melanophores on the ventral surface decreased as development proceeded, whereas those on the dorsal surface became more extensive as the fish grew. A little pigment remained at the base of the anal fins (Fig.1 O-R). Sixty-two days after hatching, melanophores appeared on the scales, forming stripes on the dorsal surface (Fig.1R).

Development of the digestive tract

Sequence in development is shown in Fig.9. The digestive tract appeared to be straight during the larval stage (Fig.9A). Then bending of the alimentary canal and pyloric caeca appeared when they reached the morphological transformation from larvae to juvenile (Fig.1B). The alimentary canal bent deeply, and convoluted with larval growth (Fig.1C,D). As development proceeded, the convolution of the digestive tract became complicated for its morphological characters, and the pyloric caeca developed in number and coverage on the intestinal surface (Fig.1E-I). Fig.10 depicts the relationship between developmental stage of alimentary canal and standard length for the reared and wild-caught specimen. Convoluted digestive tract was observed after the larvae reached the juvenile stage. Size variation of each developmental stage became greater with increasing larval length. Defined difference in completion of the alimentary canal was found between the reared and wild specimens observed. The reared fish, which were fully matured were not able to reach the developmental stage I.

The fish size of 20 mm SL exhibited the straight tube was comparable to that observed for the wild-caught specimen in Taiwan (Shen,1969). Hongchao (1984) described the development of alimentary canal based on reared specimens which was comparable to stage A to H in my observation. Unfortunately, not available to compare due to no description of larval size.

Development of behaviour

Yolk sac larvae were floating motionless in the water column, but occasionally their drifting was interrupted by abrupt locomotion which was in its appearance similar to the "continuous swimming" described for *Engraulis mordax* by Hunter (1972). Fig.11 depicts the time spent for swimming activity movement in fed and unfed larvae. During the first 2 days of the larval life, anchovy larvae rest more than 90% of the observation time. After 3 days from hatching the active time of larvae fed on rotifers was greater than that of the starved ones. In feeding larvae, the active time increased sharply after yolk absorption. During most of the time the activity pattern was pretty uniform showing little variation between measurement. The active time for unfed larvae peaked at 4 days after hatching. Activity did not exceed

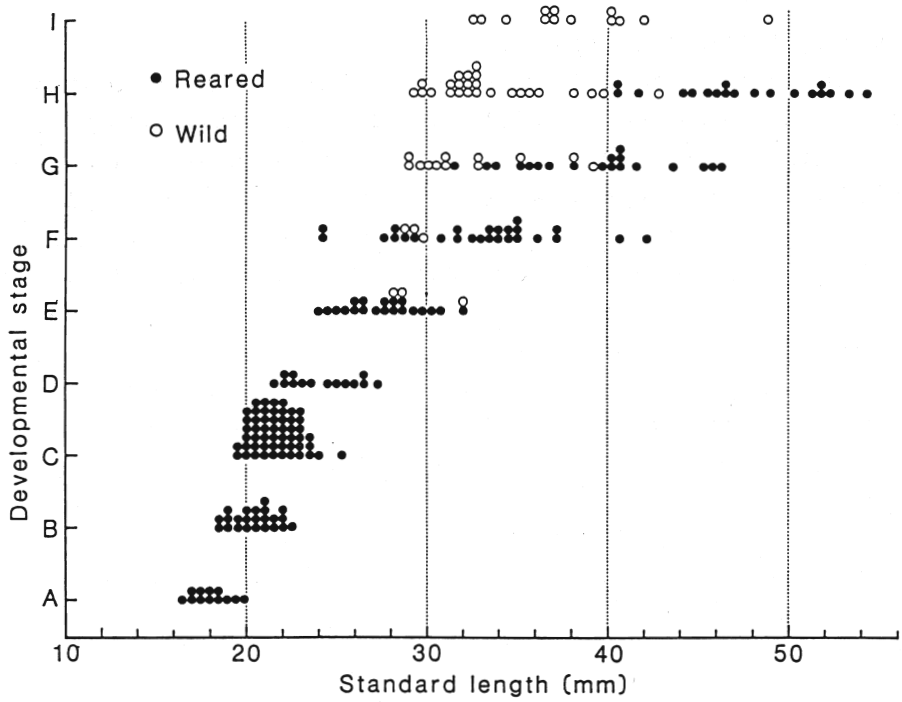


Fig.10. *Engraulis japonica*. Developmental stage of the alimentary canal in the reared and wild specimens plotted against standard length. Refer to Fig.8 for the developmental stages.

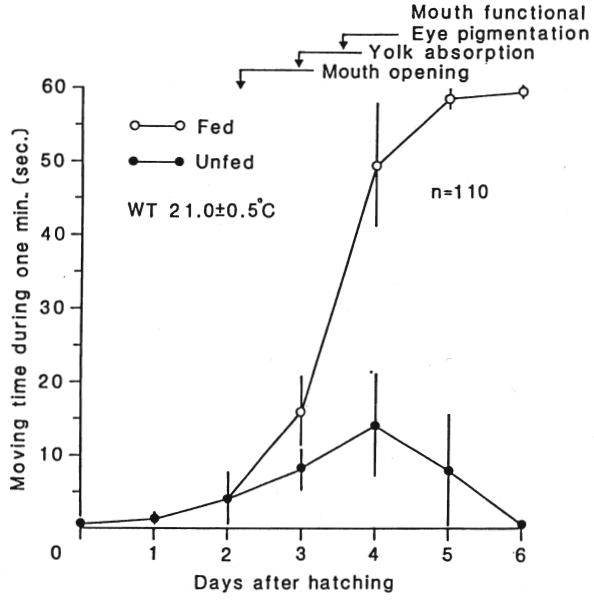


Fig.11. *Engraulis japonica*. Development of swimming activity in fed (open circles) and unfed (closed circles) anchovy larvae during the first 6 days of their life. Each point indicates mean standard deviation of 10 observations.

15% of the time unit (one minute) and decreased markedly thereafter.

Feeding incidence was increasing over the experimental days as depicted in Fig.12. Laboratory-reared *Brachionus plicatilis* were used as food with densities of 4 to 6 individuals/ml. Yolk sac larvae did not contain any rotifers in their stomach even 2 days after hatching. Rotifers were first observed in 20% of the examined guts when larvae were 3 days old. At that time the yolk was completely absorbed. Feeding incidence reached its maximum at day 5 after hatching when the swimming activity reached its maximum level.

Plecoglossus altivelis

Morphological development and growth

Larval size averaged 6.05 ± 0.59 mm SL and 6.16 ± 0.34 mm TL (mean ± SD,n=33) at the time of hatching.(Fig.13A). The length of newly hatched larvae was slightly smaller than that described by Iwai (1962), and relatively larger than those of Uchida (1958). The newly hatched larvae were comparatively longer than older larvae with relatively small head. 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 the anus averaged 73% TL. Proportional measurements of preanal length relative to total length are given in Fig.14. Hypural bone started to develop when larvae attained at 8.5-9.0 mm SL (Fig.13B). The development of the hypural bone occurred earlier in specimens of this study compared to those larvae investigated by Uchida (1958b) at a total length of 12.5 mm. The notochord flexion occurred in our specimens at about 15 mm TL (Fig.13C) which were similar size to those reported by Uchida (1958b). 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 between 15 mm to 20 mm SL (Fig.13D). At this stage the body height increased more rapidly than total length (Fig.13E).

The proportional length of distance between the snout and anus became constant after fish reached about 45 mm TL (Fig.13F-I, Fig.14). Conical teeth appeared on the upper jaw of larvae

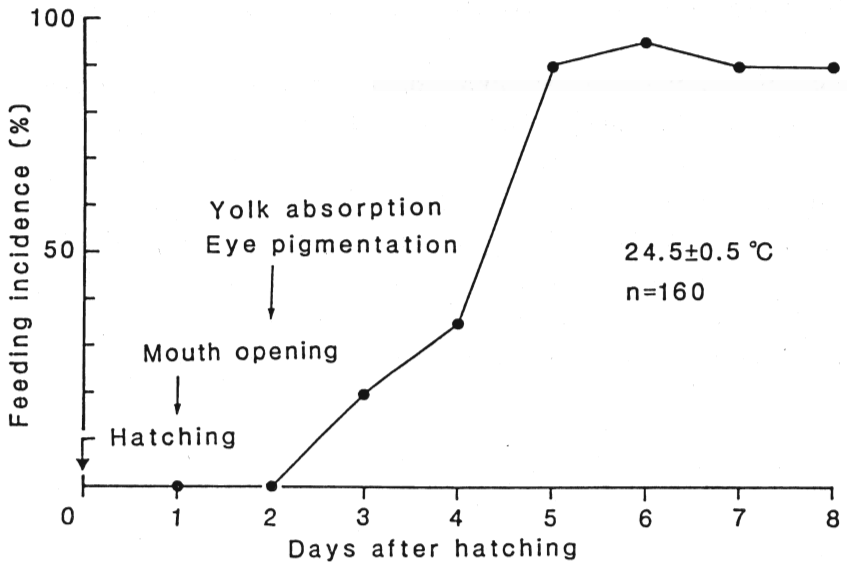


Fig.12. *Engraulis japonica*. Feeding incidence of larvae exposed to prey densities of 4 to 6 rotifers/ml during the first 8 days after hatching. n=total number of observation.

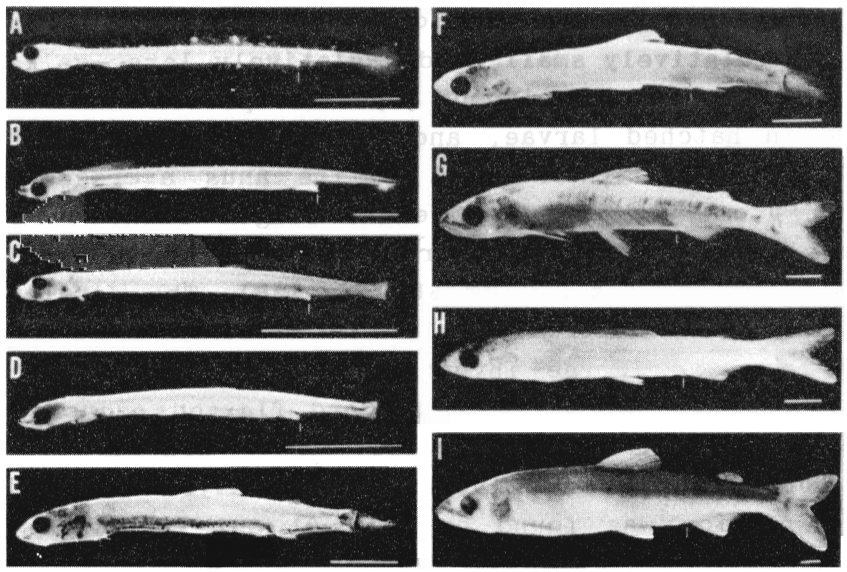


Fig.13. *Plecoglossus altivelis*. Characteristic appearance of various developmental stages reared in the laboratory. A,newly hatched larva (5.7mm SL); B,8.8mm SL; C,13.7mm SL; D,15.5mm SL; E,25.7mm SL; F,36.0mm SL; G,46.5mm SL; H,47.3mm SL; I,86.0mm SL. White bars inserted into figures denote the length of 1.0mm in A,B and 5.0mm in figures C to I. Vertical lines indicate the position of the anus.

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-caught specimen (Iwai,1962). 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 the wild-caught specimens comb-like teeth were described in larvae that had already reached a size larger than 55.0 mm SL (Miyazaki Univ.,1983).

Only few mortality was seen for unfed larvae until they absorbed the yolk sac, and steep decline was detected afterwards. Larvae could not survive beyond 2 days after oil globule absorption (Fig.15).

The growth of larvae investigated in this study is shown in Fig.16. The relationship between standard length and age in days after hatching could be expressed by a linear regression (Fig.17). Preanal length was 72-74% of the total length for newly hatched larvae, and reached about 77% of TL in 10 mm 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 leveled at approximately 62% of the total length (Fig.14).

Fin development

The primordial fin-fold was present in hatched larvae and remained until larvae had reached about 9.0 mm SL (Fig.13B). There was no remnant of larval fin-fold just prior to the anus when larvae reached 26 mm SL (Fig.13E). The caudal fin margin shaped rounded until the notochord started to flex at about 13-14 mm SL (Fig.13C,D). At that stage the caudal fin rays began to ossify.

Fan-shaped pectoral fins without rays developed at hatching. The pectoral fin rays began to develop at larval size 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

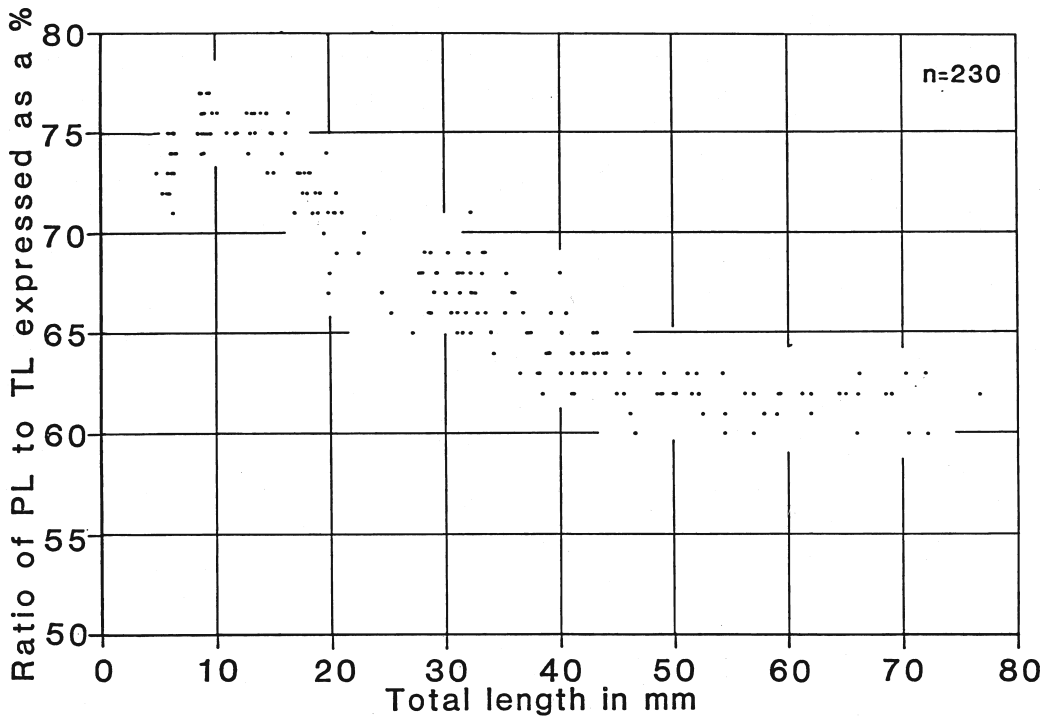


Fig.14. *Plecoglossus altivelis*. Ratio of preanal length (PL) to total length (TL) plotted against total length. n=sample size.

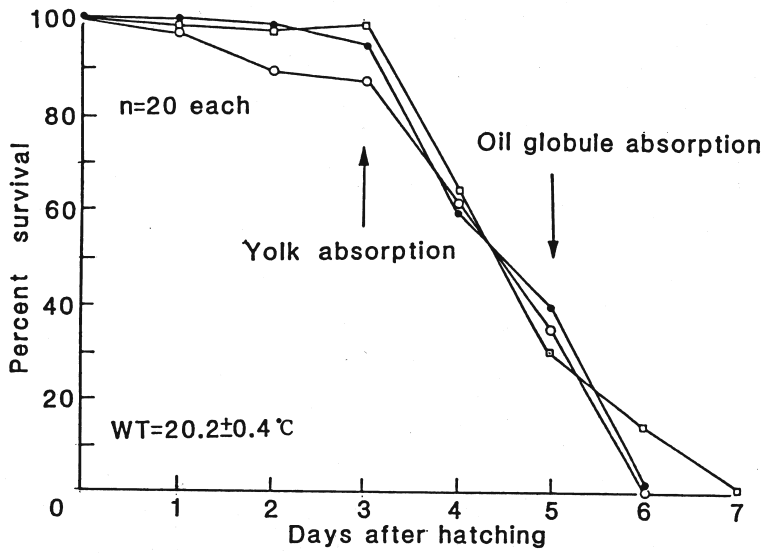


Fig.15. *Plecoglossus altivelis*. Daily mortality of unfed larvae with increasing days after hatching in triplicate experiments. n=number of larvae at the start; WT=water temperature.

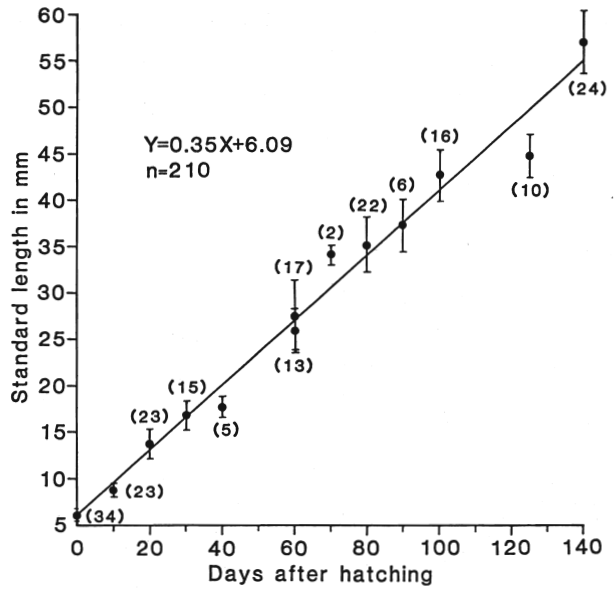


Fig.16. *Plecoglossus altivelis*. Growth in length of larvae and juveniles reared in the laboratory. n=total number of specimens measured. Each point indicates mean standard deviation of individual samples; sample size indicated on brackets; line calculated regression.

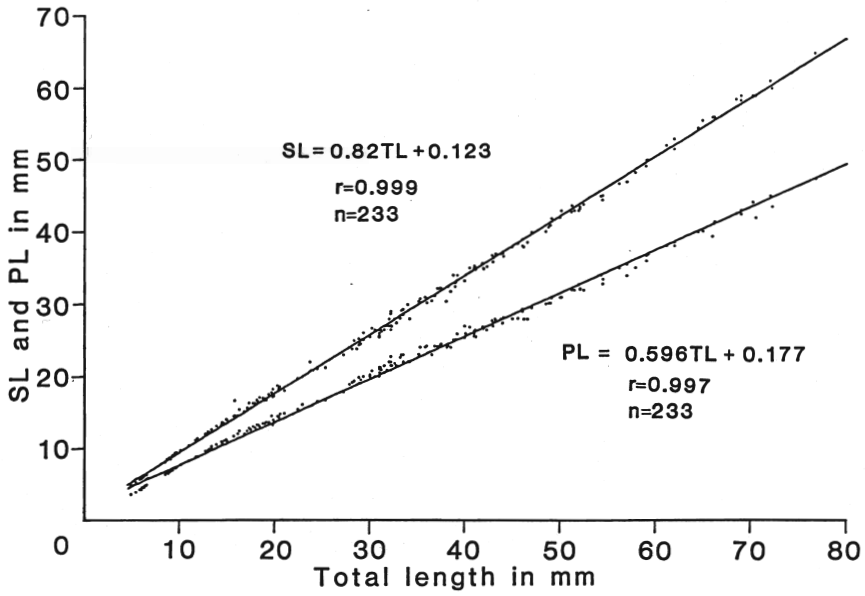


Fig.17. *Plecoglossus altivelis*. Relationship between total length (TL) standard length (SL) and preanal length (PL). n=number of measurements; r=coefficient of correlation.

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 larvae to the early juvenile stage did occur at about 27 mm SL. The larval size at morphological transformation varied largely compared to those of 57 mm TL mentioned by Uchida (1958b).

Fig.18 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. 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).

Pigmentation

Newly hatched larvae and post-larvae were scantily pigmented as shown in Fig.13 (A-D). Few melanophores were arranged serially only along the gut (Fig.13D). No marked changes in the distribution of melanophores were observed until larvae attained 25.7 mm SL (Fig.13E). Larvae of 25 mm to 36 mm SL (Fig.13 E,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.13G,H).

Squamation

The sequence of squamation and relationship between develop-

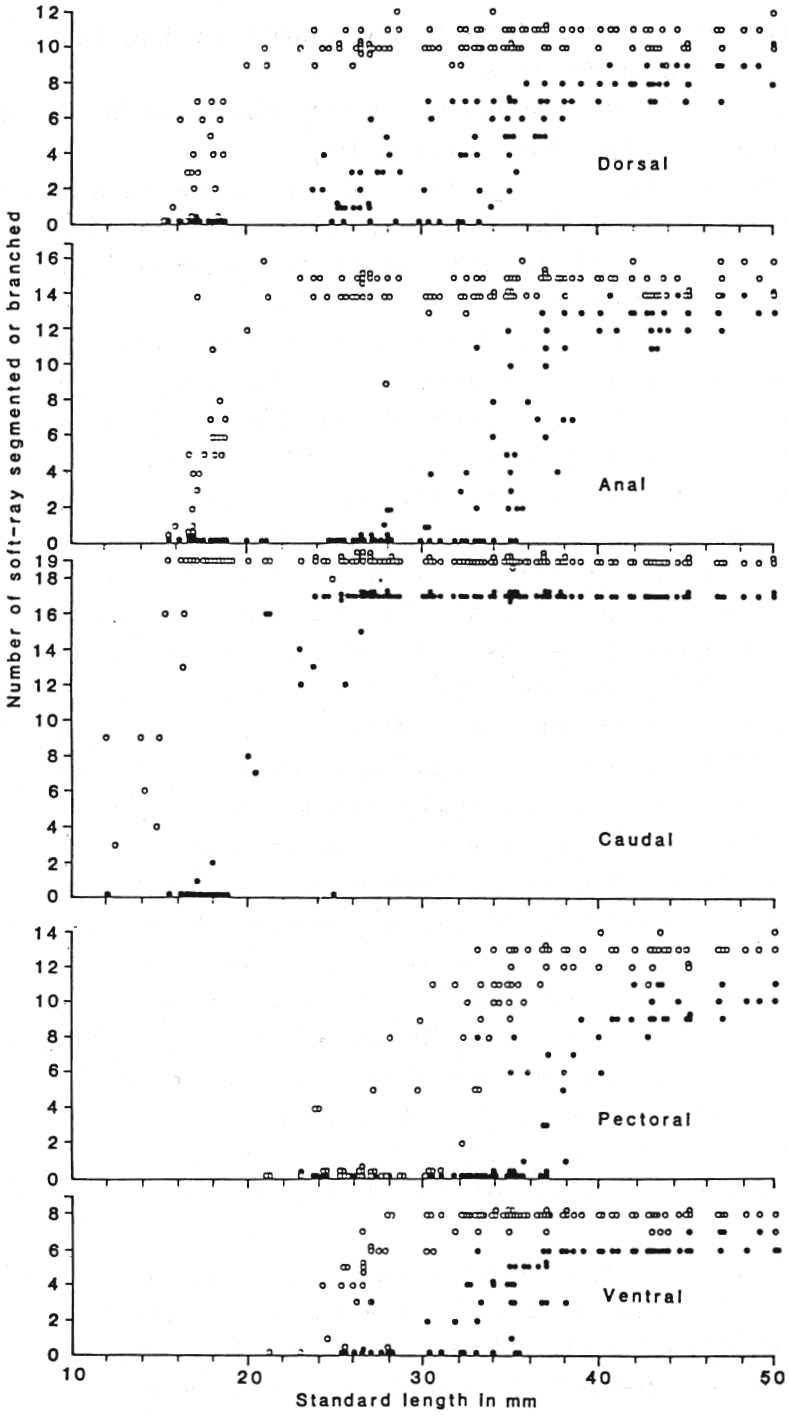


Fig.18. *Plecoglossus altivelis*. Segmentation (open circles) and branching (closed circles) of soft rays in the unpaired and paired fins in relation to growth in length.

mental stage and larval length are shown in Fig.19. Each stage was characterized as follows;
Stage A, Scale first appeared along the lateral line on the posterior part of the caudal peduncle.
Stage B, The sequent development of scale pattern occurred antero-posteriorly. The anterior end reached the vertical of the adipose and the anal fin, and almost the base of the caudal fin for its posterior section.
Stage C, The scale developed now along the forward directed parts of the body. The posterior portion of the scale surface reached the vertical line of the forward located part of the dorsal fin.
Stage D, Scales were formed more rapidly anteriorly, toward the head and less rapidly toward the dorsal and ventral sides, the operculum for the anterior end. At this stage the caudal peduncle and the base of the caudal fin were completely with scales.
Stage E, The caudal portion of the body was now fully squamated. The nape and breast regions were still devoid of scales. Small patches of scales appeared just prior to the ventral fin.
Stage F, Only the nape was left without scales. However the base of fin-ray of the caudal fin was also covered with scales.
Stage G, Juveniles were now fully squamated.

The maximum size of larvae of which individuals occurred without any scales was about 38.0 mm SL, and the smallest larva observed that had already scales was about 36 mm SL, corresponding to an age of about 90 days. The squamation proceeded with larval development, the smallest larva completely squamated measured 56 mm in SL, and was 140 days old after hatching. Larvae larger than 64 mm in SL had finished the squamation process. Therefore, it can be assumed that squamation occurred between 36 mm and 56 mm SL for the fish group that started to develop scales early and about 38 mm to 64 mm SL for those who started at a later date.

In contrast to specimens caught in the wild (Miyazaki Univ.,1983), the appearance of scales was found when fish attained a standard length of about 4 cm. They rapidly squamated during the growth period between 4 cm and 6 cm SL. All specimens over 7 cm were fully squamated. No marked difference was found for the extent of squamated area and pattern between reared and wild specimens. Takashima (1976) described cultured specimens that had scales appearing first at about 30 mm TL, attaining this

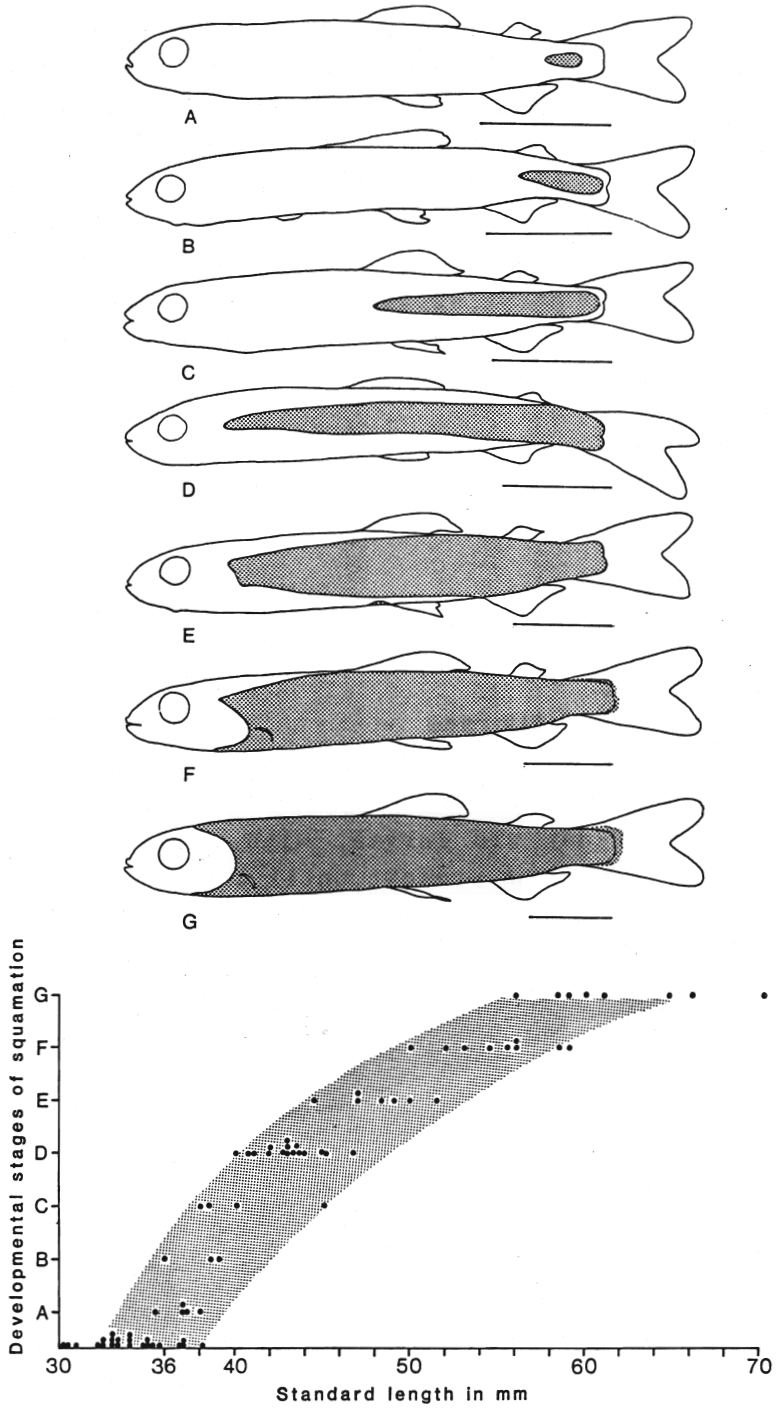


Fig.19. *Plecoglossus altivelis*. Developmental sequence of squamated area on the body surface with larval growth (upper), and relationship between its developmental stages and fish length (lower).

size at an age of 90 days after hatching. The size of first at squamation started differed remarkably from the observations under our rearing conditions. The difference is probably attributable to the environmental conditions in the culture facility, especially with regard to water temperature. Larvae, which first formed scales in this study measured 36 mm SL (or 43 mm TL) during the same time period of about 90 days. In other words, it takes approximately 90 days for larvae to start squamation under rearing conditions, although larval size may differ depending on other environmental factors.

Seriola quinqueradiata

Morphological development and growth

The fertilized eggs were spherical, ranging from 1.08 mm to 1.18 mm in diameter (mean=1.15 mm, n=50). The diameter of eggs were slightly smaller in this study than those of 1.19-1.27 mm with averaging 1.25 mm described by Uchida (1958c). Newly hatched larvae had a sizable yolk sac with an anteriorly located oil globule (Fig.20A), averaging 3.37 mm in standard length (n=16). Subsequent increments of larval length are shown in Fig.21. The mouth was open in 2-day old larvae, with a mean of 3.9 mm SL (Fig.20C). The yolk sac was present until 3 days after hatching.

The cartilaginous hypural elements began to differentiate when the larvae attained 6.4 mm SL (Fig.20F). No specimens had formed hypural elements by day 10. The hypural elements were evident in 20 out of 35 larvae by day 15, and in all 56 specimens by day 18. The notochord flexion occurred in larvae as small as 6.0 mm SL. While there was no occurrence in 10-day old larvae, notochord flexion was observed in 18 out of 35 larvae by day 15 and in all larvae by day 18.

The teeth first appeared in the upper jaw of larvae measuring 4.6 mm SL (Fig.20D), and on the both jaws after larvae reached 6.1 mm SL. The nostril was single during much of the larval stage. Separated nostrils appeared on 4 larvae of 30 specimens (7.5 mm to 7.75 mm SL) by day 20. The nostrils were separated in all 30-day old specimens. The preoperculum spines elongated characteristically after notochord flexion (Fig.20F-H).

Larvae reared in the laboratory grew relatively slowly through the larval stage, but more rapidly after transformation and

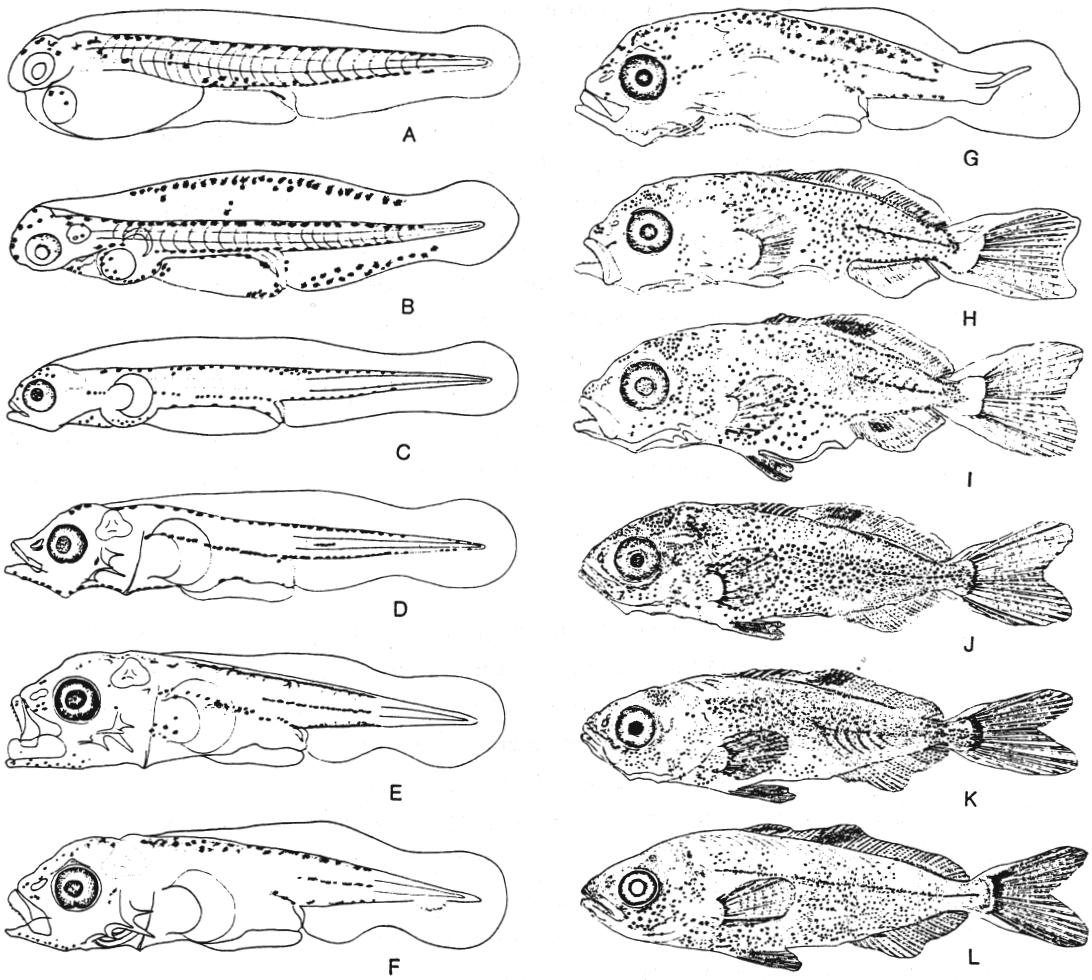


Fig.20. *Seriola quinqueradiata*. Morphological development of larvae and juveniles. A,3.5mm SL, newly hatched larvae; B,3.7mm SL,1 day old; C,4.1mm SL,2 days old; D,4.6mm SL,5 days old; E,5.9mm SL,10 days old; F,6.4mm SL,15 days old; G,7.0mm SL,18 days old;H,8.9mm SL,25 days old; I,12.2mm SL,27 days old; J,19.3mm SL,30 days old; K,21.0mm SL,34 days old; L,25.8mm SL,40 days old.

during the juvenile stage. The growth was expressed by the equation $SL=3.27\ e^{0.048X}$, where SL is standard length and X represents days after hatching (Fig.21). In addition to the morphological change from larvae to juvenile which occurred from 9.85 mm to 13.5 mm SL, variation in fish length became larger than before (Fig.21).

Standard length measurements were employed to examine the development and growth in comparison to other morphometric characters and further observations. The relationships between total length and both standard length and preanal length are shown in Fig.22 for fish ranging from about 3.5 mm to 70 mm SL. These relationships are described with linear regressions (Fig.22).

Relative preanal length ranged from about 50 to 60% of TL during the larval stage, and from about 50 to 60% TL after about 11.0 mm TL (Fig.23). The proportionality of preanal length is bounded on the developmental transit from post-larvae to juveniles.

Fin development

Newly hatched larvae had a prominent larval fin-fold. Fan-shaped pectoral fins without rays developed 16 to 21 hrs after hatching at about 21 °C (Fig.20A). The primordial fin-fold formed from the occiput during larval stages and gradually moved posteriorly during post larval stages (Fig.20A-H).

The marginal shape of the fin-fold changed markedly after notochord flexion: rounded until 7.6 mm SL, truncated from 6.8 mm to 7.8 mm SL and emarginated from 7.0 mm to 20.2 mm SL. Newly transformed juveniles were characterized by the emargination of the caudal fin (Fig.20I). The ventral fin buds appeared early in 15 days old larvae as small as 5.9 mm SL. Rays first appeared in fins in the following sequence: caudal, anal, dorsal, pectoral and ventral fins. The full complement of rays in all fins as present in larvae ranging in size from 9.85 mm SL (12.4 mm TL) to 13.5 mm SL (17.0 mm TL). Therefore, morphological transformation from larva to juvenile had been completed for laboratory-reared specimens from 9.85 mm to 13.5 mm SL. Segmentation of fin rays first occurred in the caudal fin at 6.25 mm SL, subsequently in the pectoral fin at 6.6 mm SL, ventral fin at 6.9 mm SL, anal fin at 7.8 mm SL and dorsal fin at 10 mm SL. The completion of segmentation in the fin was achieved at 7.8 mm SL in the caudal, 10.0

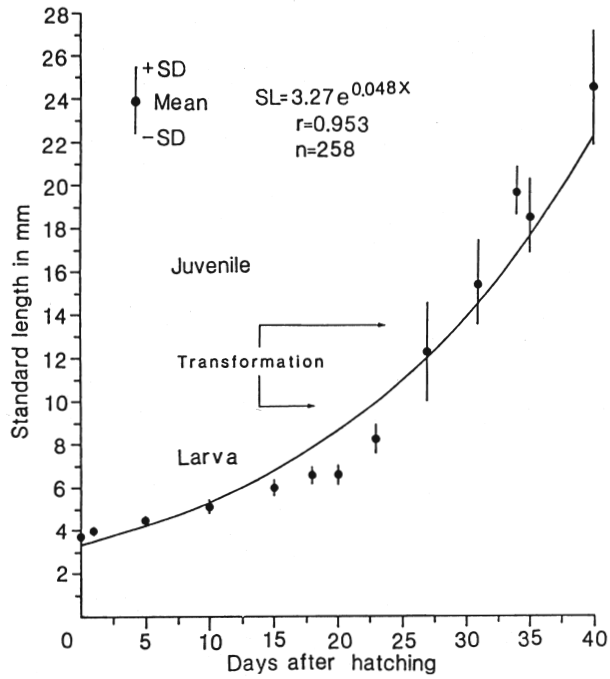


Fig.21. *Seriola quinqueradiata*. Growth of larvae and juveniles reared in the laboratory at a temperature of 19.6 °C to 22.1°C. r=coefficient of correlation; n=number of specimens measured. Transformation represents the duration of morphological transformation from post-larvae to juvenile.

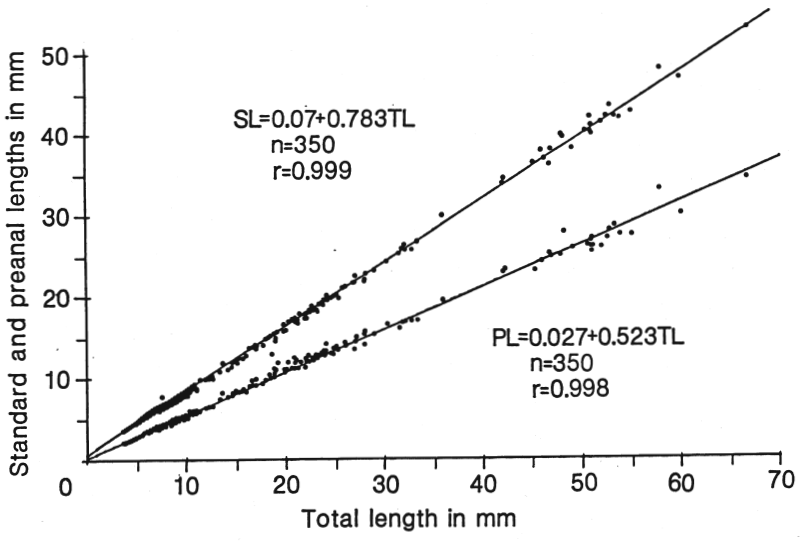


Fig.22. *Seriola quinqueradiata*. Standard length (SL) and preanal length (PL) plotted against total length (TL) in larvae and juveniles.

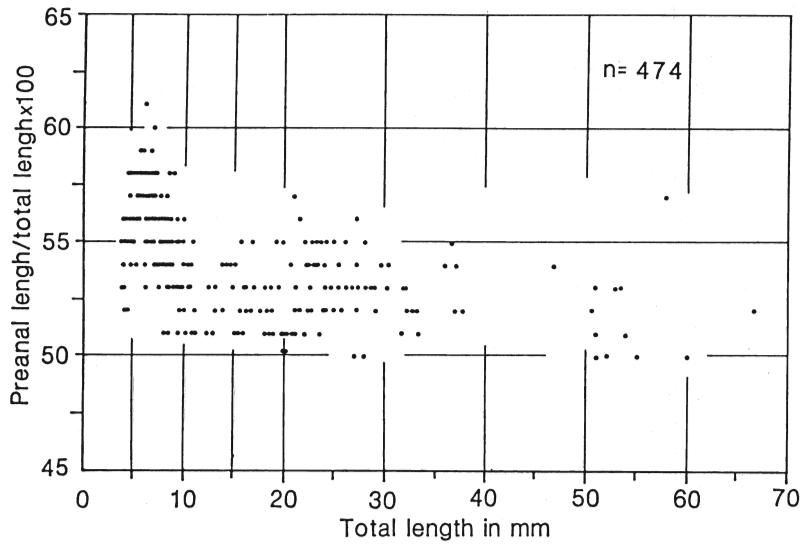


Fig.23. *Seriola quinqueradiata*. Ratio of preanal length to total length expressed as a percentage against total length. n=sample size.

mm SL in the anal, 11.9 mm SL in the dorsal, 12.6 mm SL in the ventral and 16.7 mm SL in the pectoral.

Concerning the branching of soft-ray in each fin, the appearance was first observed at 8.3 mm SL in the caudal, 14.9 mm SL in the ventral, 17.0 mm SL in the pectoral, 20.0 mm SL in the anal and 24.1 mm SL in the dorsal fins. The full complement was observed at 17.0 mm, 16.2 mm, 36.0 mm, 36.1 mm and 46.0 mm SL, respectively (Fig.24).

Pigmentation

Newly hatched larvae had numerous melanophores in a dorso- and ventro-lateral row on each side of the body. A few melanophores could be discerned in the cephalic region, on the oil globule and around the snout (Fig.20A). Between 12 and 24 hrs after larvae hatched, melanophores, which quickly disappeared after preservation, were added along the dorso- and ventro-margin of the finfold, and near the oil globule (Fig.20B). No marked change of pigment pattern was found until fish attained 6.4 mm SL (Fig.20C-F). Melanophores appeared gradually on the lateral surface of the body (Fig.20G), and were distributed heavily on the body surface except for the cheek, thoracic and operculum (Fig.20H). A patch of melanophores appeared in the fin ray por-

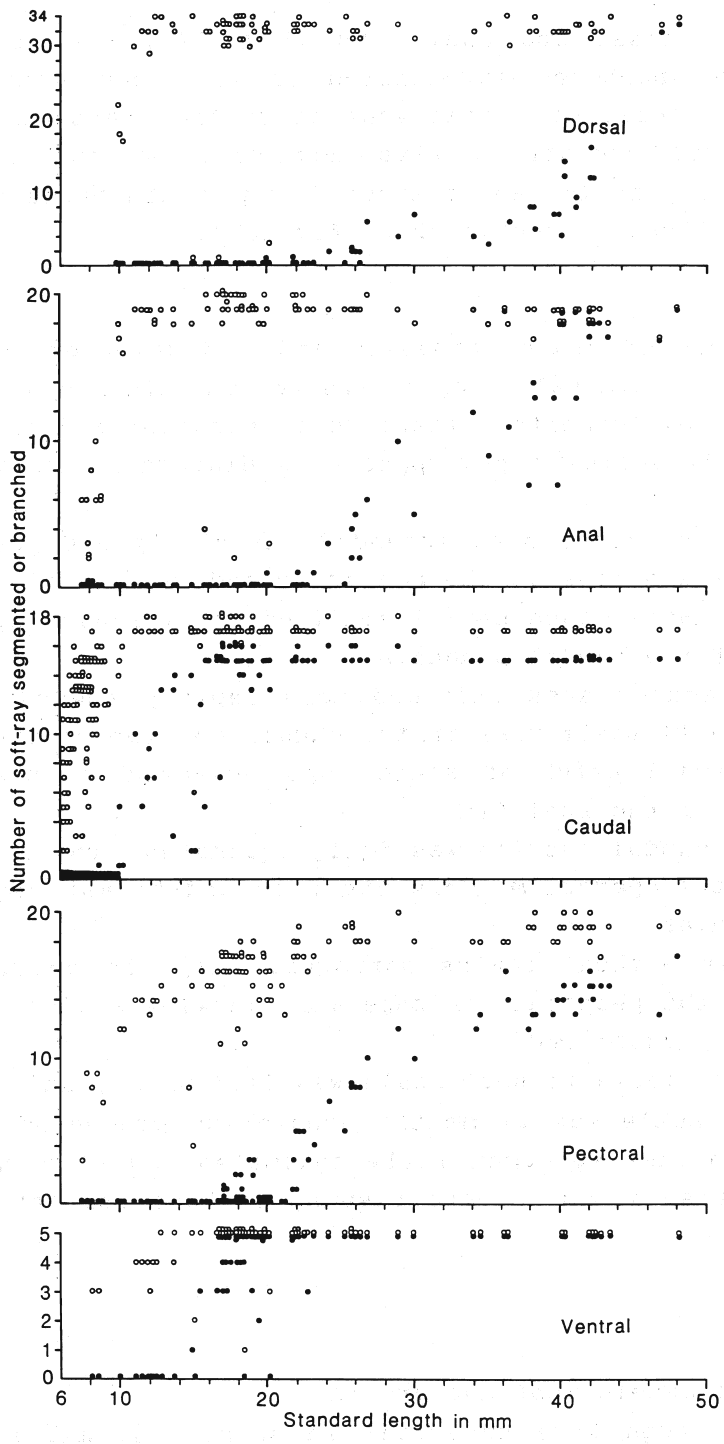


Fig.24. *Seriola quinqueradiata*. Segmentation (open circles) and branching (closed circles) of soft rays in the unpaired fins.

tions of the dorsal and anal fins (Fig.20I,J). As development continued, melanophores intensified on the body surface, more solid on the dorsal half than ventral surface, and increased on the section of procurrent rays and base of the caudal fin (Fig.20K,L). In the larvae of about 26 mm SL the bands of melanophores were slightly identifiable (Fig.20L).

Squamation

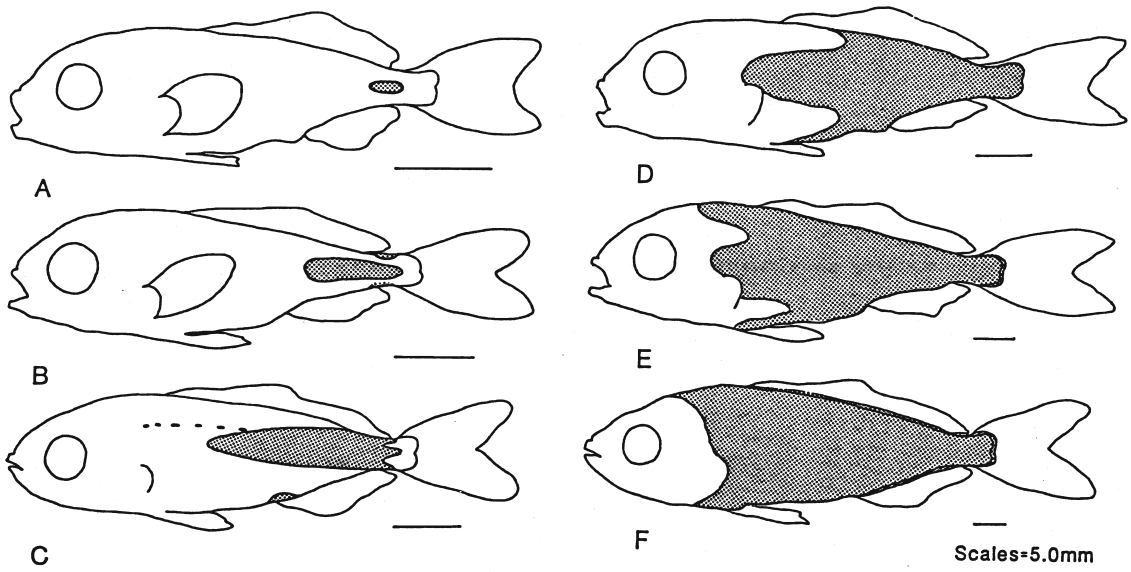
The sequence of scale formation and its developmental stage plotted against larval length are given diagrammatically in Fig.25. Each developmental stages were characterized as follows:
Stage A, A few scales first appeared midlaterally on the caudal peduncle.
Stage B, The squamated area extended anteriorly and posteriorly. Five to six scale rows at the posterior and nine to eleven at the anterior ends were discerned. A small patch of scales appeared on both sides of the caudal peduncle.
Stage C, Squamated area extended more rapidly toward the head, forming 13 to 14 scale rows in the caudal portion of the squamated area. A small patch of scales was observed at the base of anterior and of the anal fin.
Stage D, The caudal section was fully squamated, and the anterior end reached the operculum. Only the nape and breast regions were devoid of scales.
Stage E, Area without scales narrowed. Only the portion around the nape and the pectoral fin base were lacking scales.
Stage F, Fully squamated.

The largest larva without scale was 24.1 mm SL, and the smallest one with scale was 21 mm SL. Squamation proceeded as larvae grew. The smallest specimen fully squamated was 40.2 mm SL, and larvae more than 47 mm SL were assumed to have completed squamation.

Pagrus major

Morphological development and growth

Fertilized eggs were spherical in shape, averaging 0.918 $\pm$ 0.029 mm in diameter (mean $\pm$ SD, n=103). Perivitelline space was narrow and contained a single oil globule. Cultured parent produced various sized eggs spontaneously, which ranged from 0.66 mm



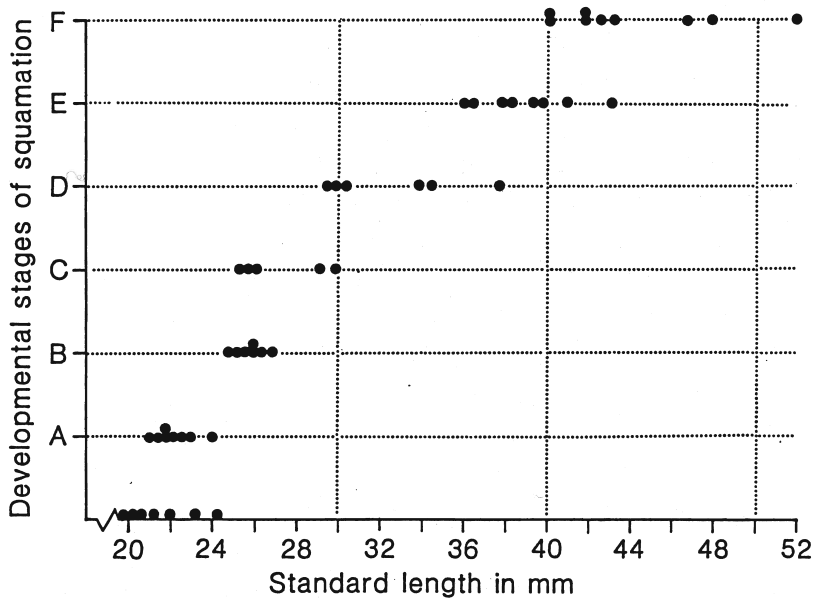


Fig.25. *Seriola quinqueradiata*. Semidiagrammatic illustration of the squamation (upper), and its developmental stages plotted against standard length (lower).

to 1.03 mm in diameter (n=4986). The eggs hatched after 48-50 hrs at about 20 °C. High hatchability was observed at temperatures between 19.05 °C and 29.15 °C and salinity ranging from 27.03 to 34.80 (Apostolopoulos,1976). Newly hatched larvae measured 2.01 ± 0.06 mm TL and 1.93 ± 0.06 mm SL (mean ± SD, n=55). A large yolk sac was present with a single oil globule, located posteriorly (Fig.26A). At about 20 °C the mouth was opened 1st day after hatching, and the yolk was absorbed at 3 days. After yolk absorption, larval survival increased sharply under starved conditions (Fig.27). No marked changes were noted until the larvae attained 5.6 mm SL (Fig.26B). Larvae of 5.6 mm SL, with notochord flexion, had fan-shaped pectoral fins without rays. The end of maxillary was positioned beneath the middle of the orbit. Ossification of the caudal fin region began at 5.6 mm SL. At this size, the hypural bones were developing and some rays were observed in the ventral half of the caudal fin-fold. At a length of about 8.0 mm SL, vertebral column was easily recognizable, and the pectoral girdles were starting to appear (Fig.26E). Ossification of the dorsal and anal fin pterygiophores began at about 10.0 mm SL, and well-developed pterygiophores could be distinguished on 30.0 mm SL specimens (Fig.26K).

Growth of pre-larvae under fed and unfed conditions is shown in Fig.28. Steady increment was observed for the first 4 days. After yolk absorption, unfed group ceased the increment of growth in contrast to those seen in fed group. Even for fed group growth cessation was observed after yolk absorption.

The increase in length of fish staging from larvae to juveniles is presented in Fig.29. Slower growth was seen during larval stage, which lasted initial 25 days following hatching; thereafter fast growth was attained by juvenile. The larval length, and days after hatching was equated by $Y=2.629\ e^{0.0489X}$, where Y=total length, and X=days after hatching. Morphological transformation from larvae to juvenile occurred in the specimens ranging from 7.6 mm to 8.6 mm SL, which was correlated with day 25 to 29. Daily increment was presented by 5% from the equation.

Pertinent to allometric growth, preanal length of newly hatched larvae was 55% TL and decreased rapidly to 32% SL with the absorption of the yolk sac and oil globule. The ratio again increased to 45% TL or 47% TL as the larvae fed, then became constant at 47% to 50% TL when the fish reached the transitional

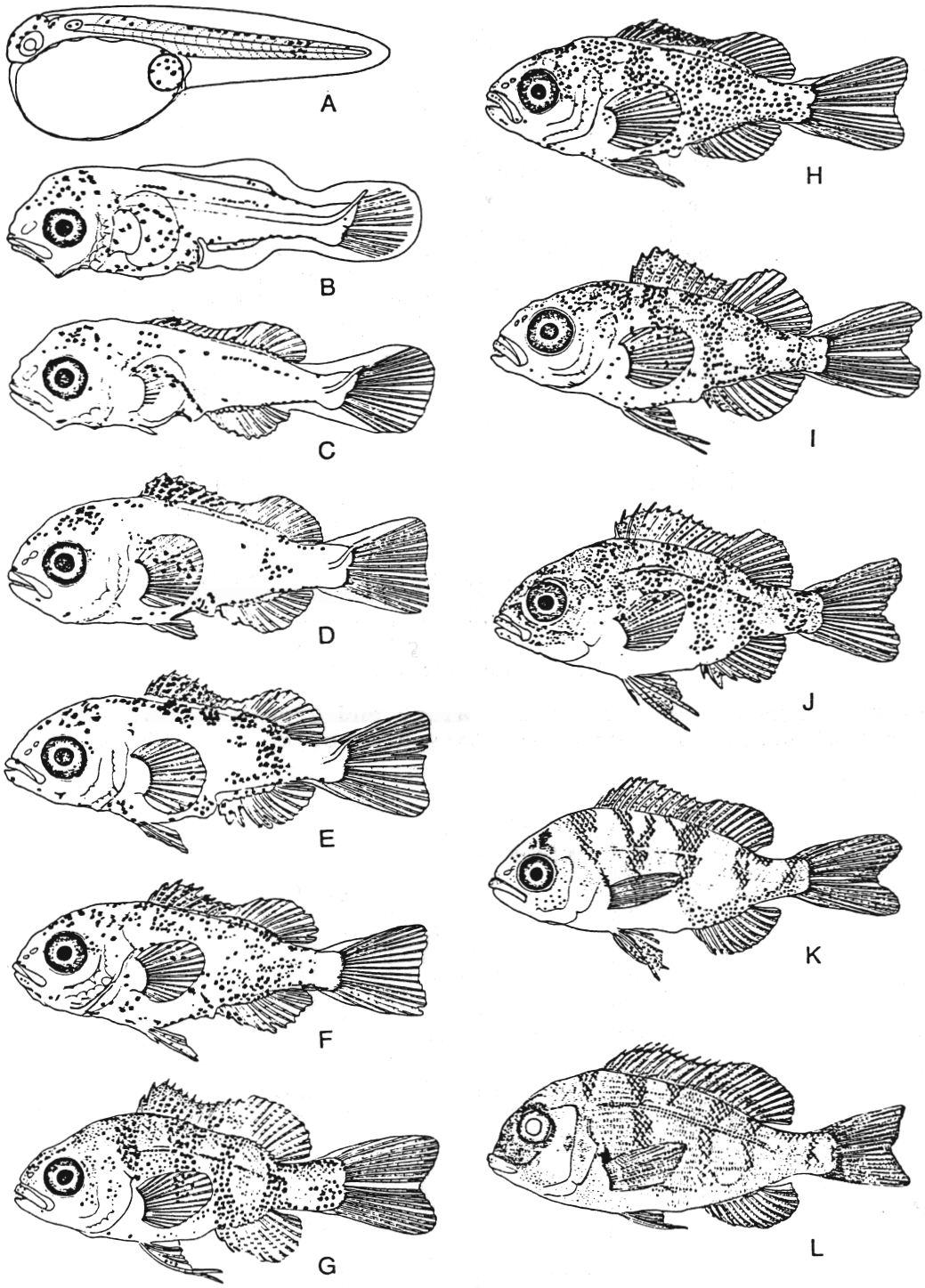


Fig.26. *Pagrus major*. Developmental stages of larvae to young reared in the laboratory. A,2.12mm SL; B,5.6mm SL; C,6.5mm SL; D, 7.6mm SL; E, 8.3mm SL; F, 8.9mm SL; G,10.2mm SL; H,11.8mm SL; I,14.1mm SL; J,19,1mm SL; K,30.8mm SL; L,46.1mm SL.

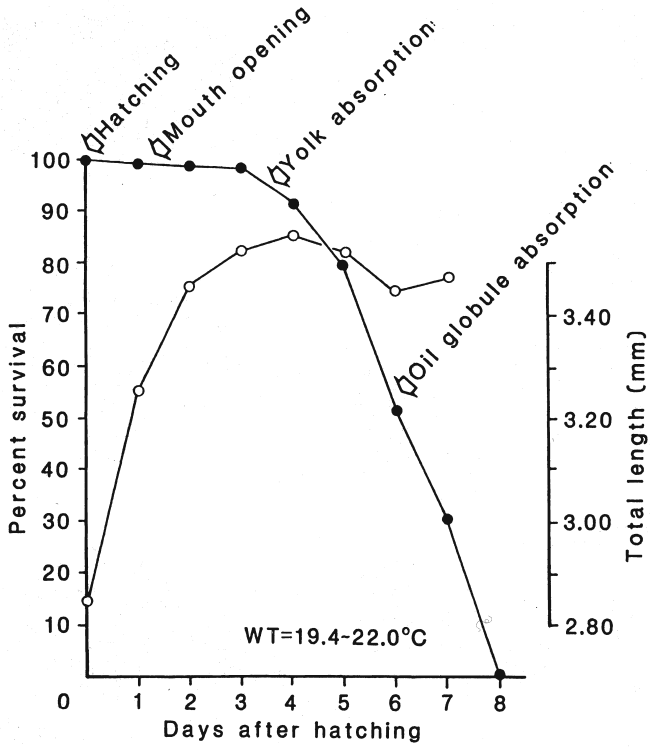


Fig.27. *Pagrus major*. Daily mortality and growth of unfed larvae. Initial number of larvae in starved experiment is 50 individuals.

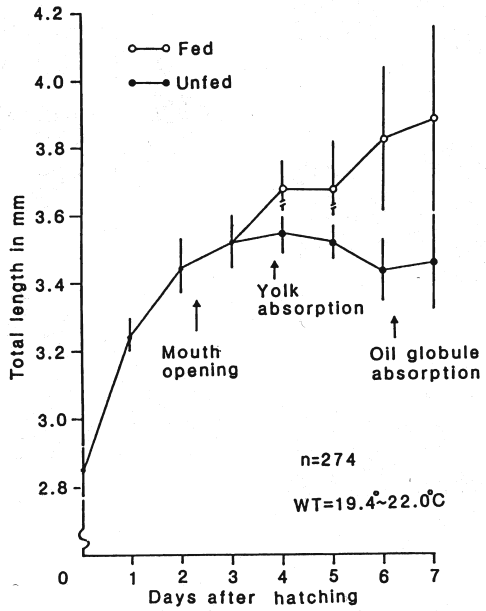


Fig.28. *Pagrus major*. Larval growth in length under fed and unfed conditions. Each measurement indicates mean and standard deviation.

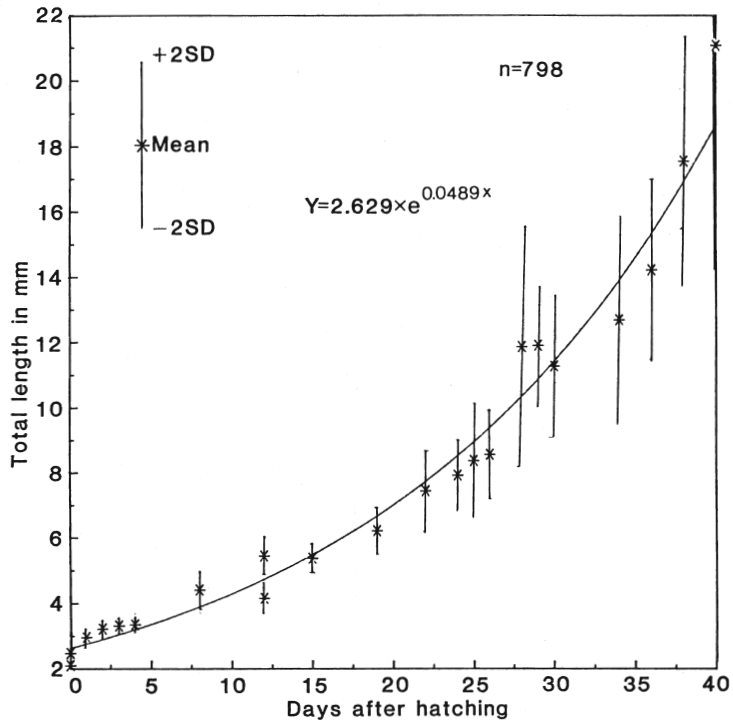


Fig.29. *Pagrus major*. Growth of larvae and juveniles reared in 500 *l* and 1000 *l* capacity tanks under ambient water temperatures ranging from 17.0 °C to 26.0 °C.

phase from larvae to juvenile stage (Fig.30). Other morphometric characters: total length, upper jaw length (Shirota,1978b) and the body height-notochord length relation (Kohno et al.,1983) also revealed constant ratios during the transformation and in newly transformed juveniles.

Standard length was used to examine the development and growth in relation to other morphometric characters. Linear regressions between total length, standard length and preanal length are given in Fig.31 for specimens ranging between 2.2 mm and 27 mm TL.

Fin development

The newly hatched larvae hold the primordial fin-fold from the middle of head the anus (Fig.26A). Unpaired fin began to develop on specimens 6.0 mm to 6.5 mm SL with a change in marginal shape of the fin fold (Fig.26B,C). A truncated-shaped caudal fin was observed for a short period during the transformation to early juvenile stages, ranging from 6.3 mm to 10.3 mm SL (Fig.26E,F).

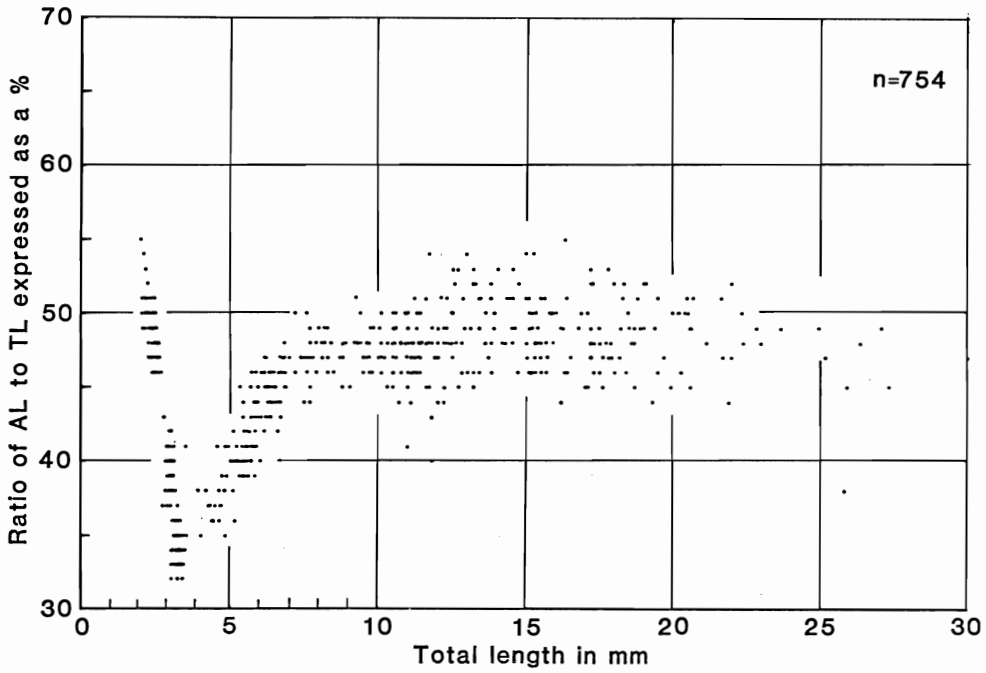


Fig.30 *Pagrus major*. Proportional measurement of preanal length related to total length. n=sample size.

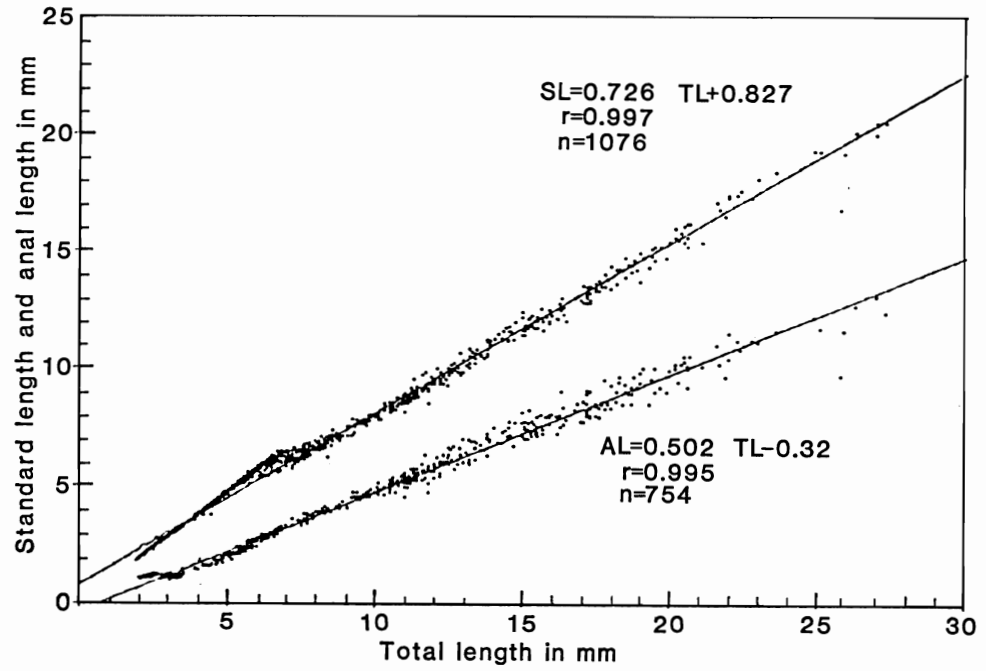


Fig.31. *Pagrus major*. Standard length (SL) and Preanal length (PL) plotted against total length (TL) in larvae and juveniles.

Therefore, the truncated caudal fin was indicative of changing the developmental stages from post-larvae to juveniles. All juveniles ranging from 8.5 mm to 20.8 mm SL had emarginated shaped caudal fin (Fig.26F-J). Adult form of a furcated caudal fin was found on specimens larger than 18.0 mm SL (Fig.26K,L).

The pectoral and ventral fins became pointed and elongated when the developing fish transformed from early juvenile to young stages.

A full complement of fin rays occurred at 7.6 mm SL for the smallest specimens, and at 8.6 mm SL for the largest one, thus the transformation from the larvae to juvenile stage occurred when fish were 7.6 mm to 8.6 mm SL (Fig.26D,E).

Rayed fins developed in the following sequence: caudal, anal, dorsal, ventral and pectorals. After a full complement of soft rays had developed in each fin, segmentation of rays began, earlier in unpaired fins than in paired fins (Fig.32). Caudal fin rays began to segment at about 6.0 mm SL, anal fin at 6.2 mm SL, dorsal fin ray at 6.4 mm SL, ventral fins at 7.0 mm SL and pectoral fins at 7.6 mm SL. The fin rays were fully segmented at 7.8, 8.2, 7.5, 10.3, 18.0 mm SL, respectively.

Branching of soft rays began after segmentation was completed, except for the ventral fins (Fig.32). Soft ray branching began at approximately 11.0 mm SL for the anal, and 12.0 mm SL for the caudal and dorsal fins, 8.0 mm SL for the ventral fins and 11.0 mm SL for the pectoral fins. Branching was completed at 20.5 mm SL for the caudal, 23.3 mm SL for the anal and 26.5 mm SL for the dorsal, 15.6 mm SL for the ventrals and 34.0 mm SL for the pectorals, respectively. Consequently all fins were completely segmented by 18.0 mm SL, and were branched when fish were 34.0 mm SL.

Pigmentation

Newly hatched larvae have melanophores around the cephalic region, on the oil globule located posteriorly in the yolk sac, and scantily along the trunk and caudal region (Fig.26A). By day 3, melanophores appeared on the snout and on the gut. Small melanophores were also serially arranged along the ventral midline between the anus and caudal fin. During the larval stage no marked change in pigment occurred (Fig.26A-C). In the early juvenile stage, the spinous portion of the dorsal fin became

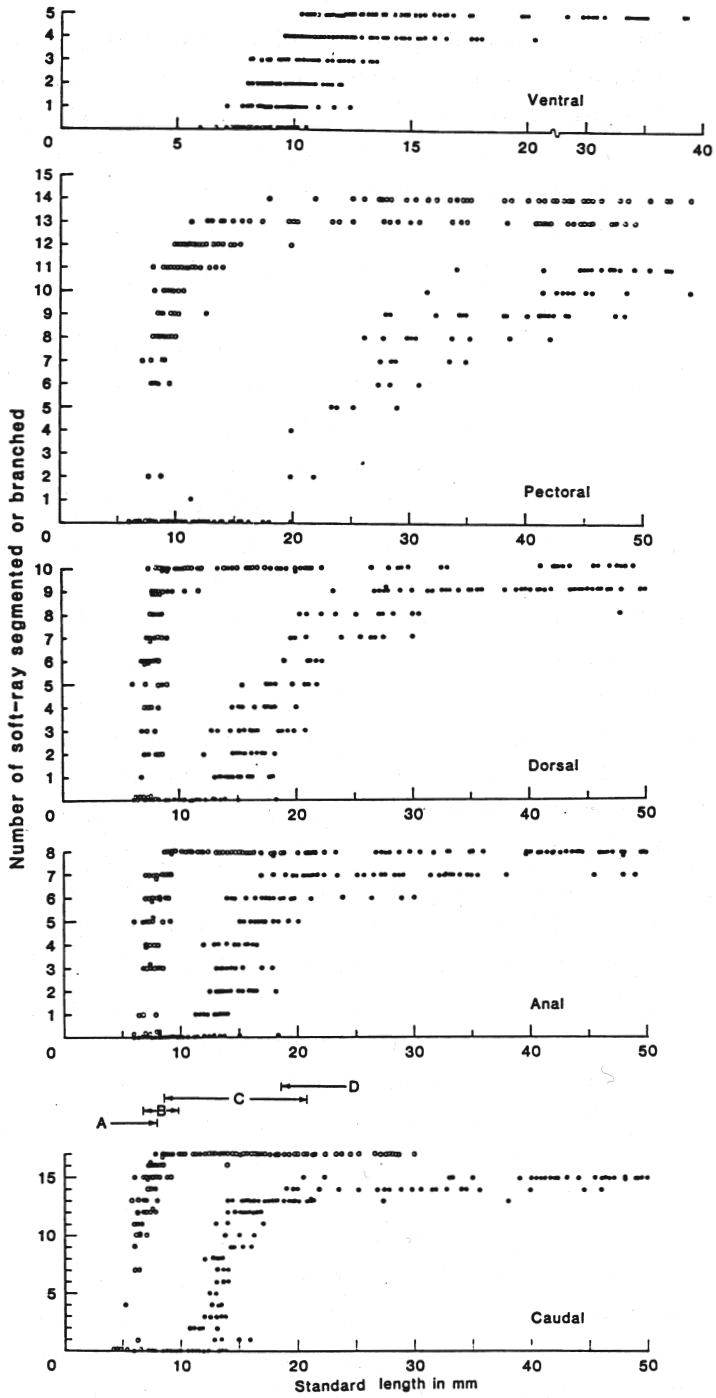


Fig.32. *Pagrus major*. Segmentation (open circles) and branching (closed circles) of soft rays on the unpaired and paired fins. A-D indicate the shape of caudal fin; A,rounded; B,truncated; C,emarginated; D,furcated.

pigmented more intensively, and the number of melanophores increased in the cephalic region (Fig.26D). Relatively larger melanophores, which composed a pigment band in subsequent development, was distributed vertically below the dorsal and at the posterior portion of the anal fin (Fig.26E).

The formation of pigment pattern and its developmental stage plotted against larval length are shown in Fig.33. Each stage is identified by the appearance of the pigment pattern and the number of transverse bands on the lateral surface. The pigment pattern first appeared in larvae about 7.2 mm SL when the melanophores concentrated around the posterior end of the dorsal fin (Fig.32B). Three pigment patches occurred on the nape and the base of spinous dorsal fin (Fig.32C). The pigment pattern formed at the posterior end of the dorsal fin and extended toward the ventral surface (Fig.32D). In larvae measuring 8.0 mm SL, the pigment pattern occurring anterior of the caudal peduncle covered the entire depth of the trunk. A separate, elongated patch of melanophores developed at the base of the soft dorsal fin, and the two became connected by a narrow bridge of melanophores when the larvae attained a length of about 8.0 mm SL (Fig.32E). The pigment pattern was connected at the anal fin base, was elongated posteriorly, and was connected with a small patch located on the caudal peduncle (Fig.32F). The smallest fish with a completely formed pigment band was 9.0 mm SL, and Fig.33 indicates that all specimens larger than 11 mm SL had clearly completed the formation of five distinct stripes (Fig.33G). The commencement of band formation occurred on larvae on day 27; all larvae had completely formed bands after 41 days after hatching.

Squamation

Fig.34 shows the sequence of squamation from first appearance to completion, and relationship between developmental stage of squamation and larval length. Each stage was characterized as follows;

Stage A, A small patch of one scale row appeared in the posterior end on the lateral line.

Stage B, The extension of squamation was seen anteriorly, and two scale rows were found in the central position of its coverage.

Stage C, Coverage area extended antero-posteriorly. There were 2 to 3 scale rows in the center of the scaled area.

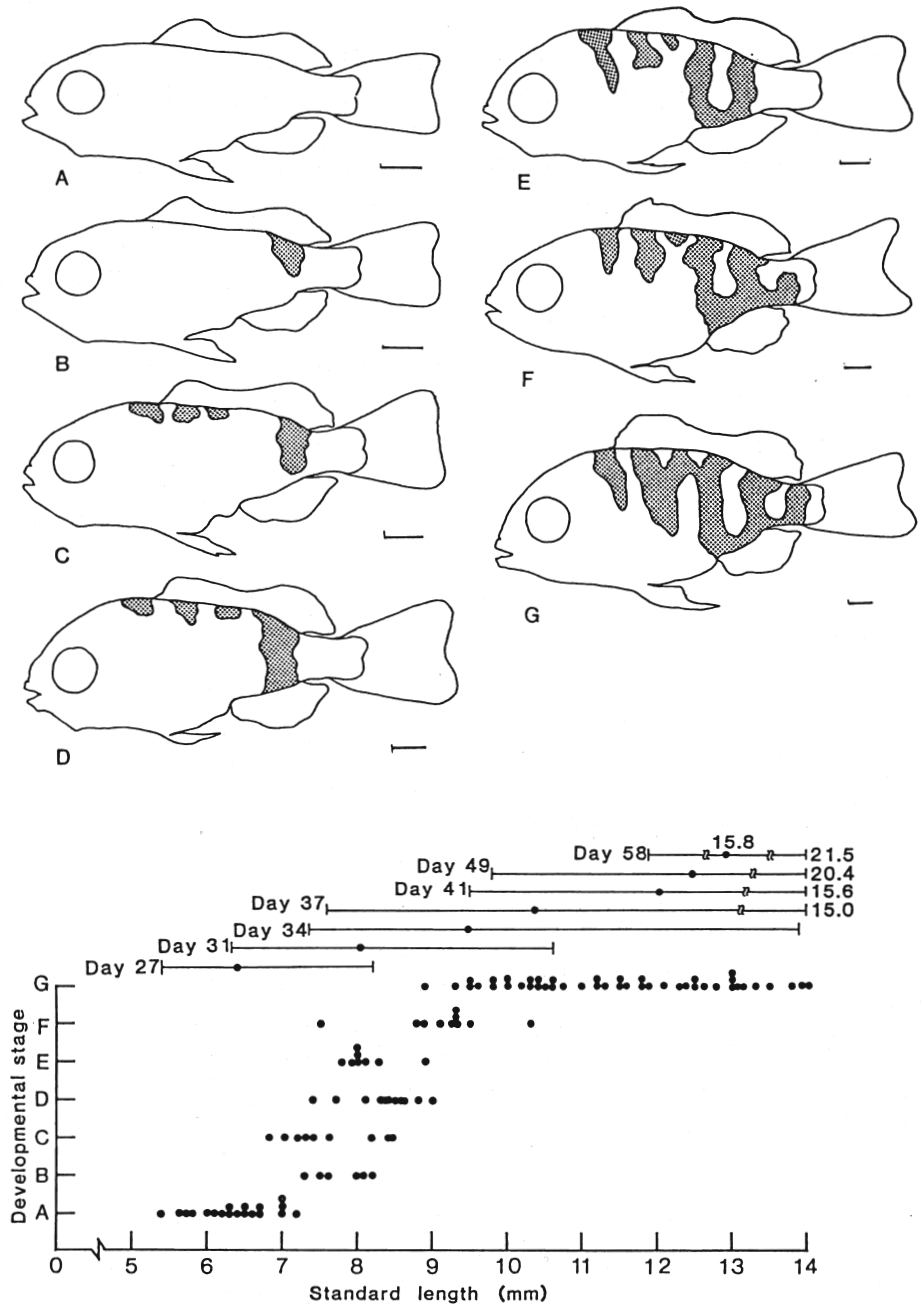


Fig.33. *Pagrus major*. Semidiagrammatic drawing of sequence in pigment pattern distinguished by the number of transverse bands formed on the body surface(upper), and the developmental stages of pigment pattern plotted against standard length (lower). Vertical lines with showing day 27 to 58 indicate the minimum and the maximum of standard length at each day old after hatching; closed circles on the lines denote the mean; scales denote 1.0mm.

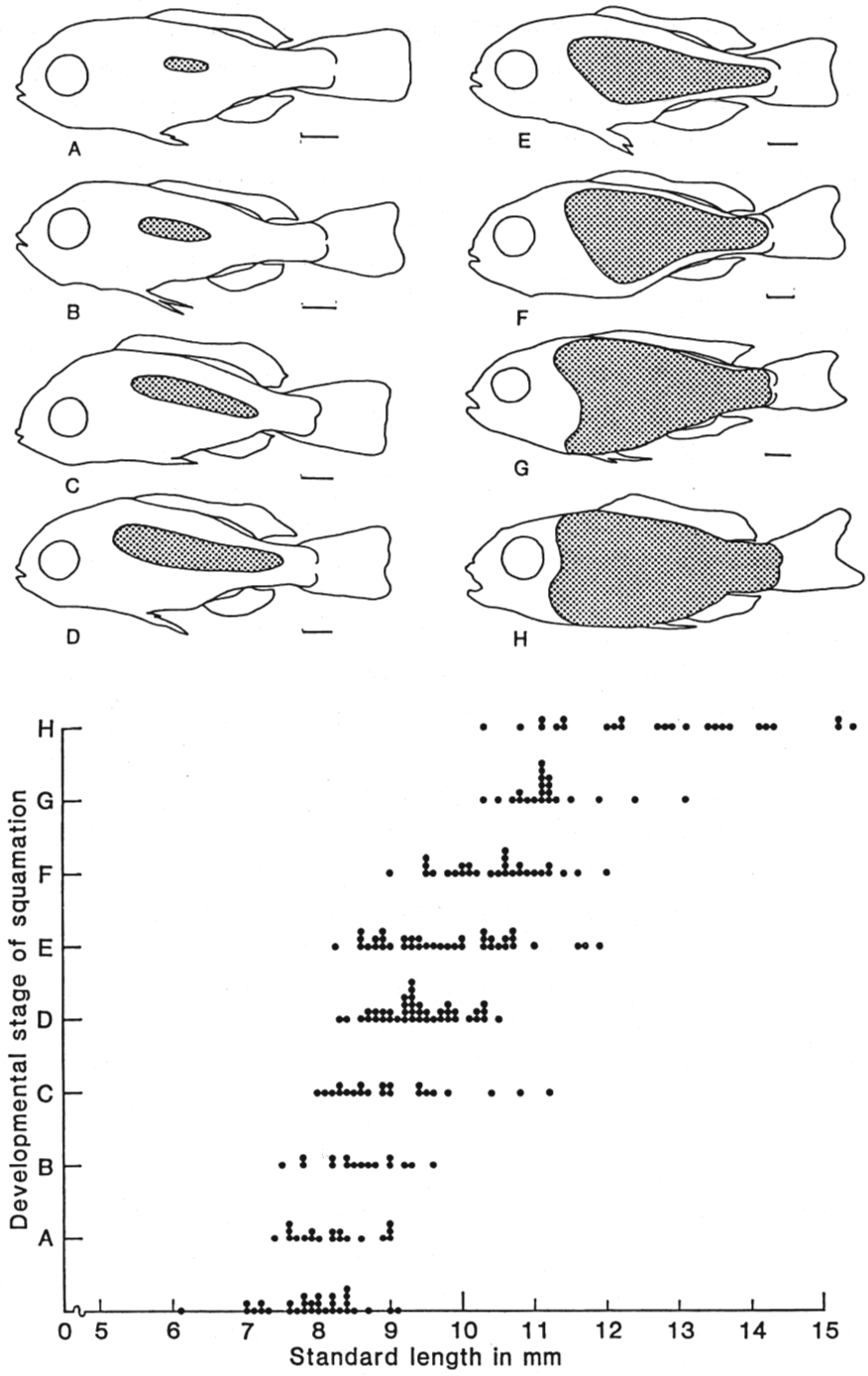


Fig.34. *Pagrus major*. Diagrammatic illustration of squamation (upper), and its developmental stages in relation to standard length (lower).

Stage D, The anterior end of squamation reached the operculum, and the caudal peduncle posteriorly. 3 to 4 scale rows were seen.
Stage E, The squamated area extended to each direction, and about half body surface was squamated.
Stage F, Scales were seen only in marginal portion of the lateral surface. Almost squamated for the caudal peduncle.
Stage G, The nape, posterior position of the dorsal fin, base of the caudal fin and anal fin base were devoid of scales.
Stage H, Fully squamated.

The larva without scale measured 9.1 mm SL, and 7.4 mm SL for the minimum size of larva with scale. Larval size of the equivalent stage in squamation varied from 2.0 mm to 3.0 mm. As to the larval size of completion the smallest larva with full squamation was 10.3 mm SL, and larger specimens than about 14 mm SL finished the scale coverage on the body surface.

Development of the digestive tract

The sequence of development and relationship between its developmental stage and larval length are shown in Fig.35. The digestive tract during larval phase was convolved (Fig.35A) until larvae attained 7.5 mm SL. The pyloric caeca appeared, and posterior portion of the digestive tract was curved slightly (Fig.33B) when larvae reached the size of 5.5 mm to 9.1 mm SL, corresponding to the transformation from the larval to juvenile stages. The specimens over 10 mm SL had well-developed pyloric caeca, and the digestive tract angled posteriorly, just in front of the rectum (Fig.34C). As development proceeded, pyloric caeca elongated and the shape of digestive tract became deeply rounded and curved (Fig.35D).

Development of behaviour

Because the larvae were buoyant due to their yolk sacs, they were concentrated in the surface layer of the tank and were at the mercy of water movement caused by aeration.

Spontaneous movement and/or swimming behaviour were observed after yolk was absorbed. About one day after yolk absorption, fed larvae started to move actively during a one-minute observation period, and continued to move for the most of the observation time after absorption of the oil globule. Conversely, movements of unfed larvae declined sharply (Fig.36).

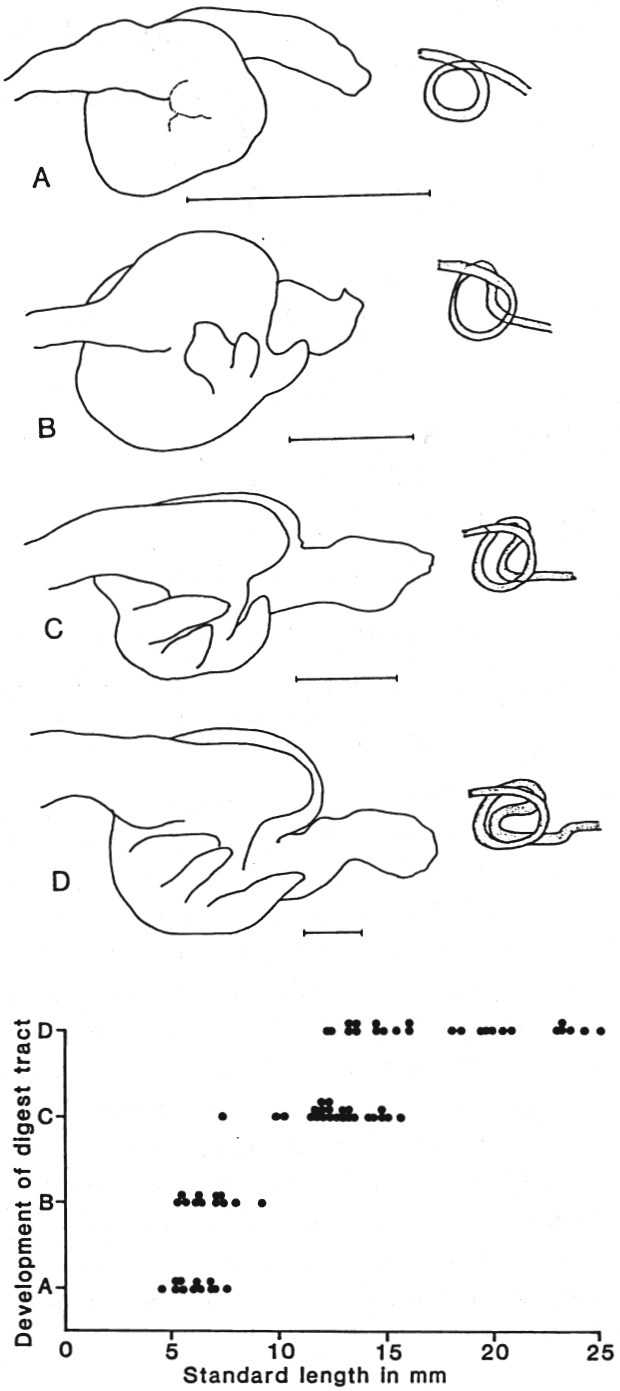


Fig.35. *Pagrus major*. Schematic illustration showing development of digestive organs. Scales denote 1.0mm (upper), and relationship between developmental stages and standard length(lower). Scales denote 1.0 mm.

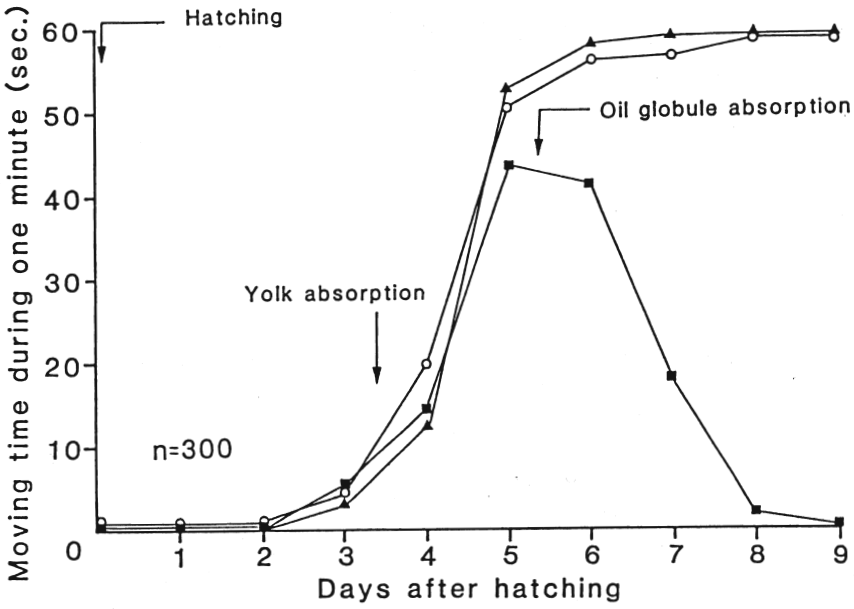


Fig.36. *Pagrus major*. Increment of moving time during one minute observation with larval growth. Closed triangles fed in ambient temperature averaged at 18.4 °C(range; 15.4°C-19.8°C). Open circles indicate fed, and closed squares for unfed conditions, respectively at a constant temperature of 17.0 ± 0.5 °C.

Swimming speed increments are provided in Fig.37. Swimming speed, which was measured both before and after feeding, was less than 50 cm/min; 1 SL/sec during larval phase. It subsequently increased to more than 100 cm/min; 3 SL/sec during the transitional phase from post-larvae to juvenile. Concurrent rises in swimming speeds of about 200 cm/min, corresponding to 4 SL/sec were noted for the metamorphosed fish. Fast swimming was observed in low prey density than high prey density populations as also noted for herring (Rosenthal and Hemple,1970), plaice (Wyatt,1972) anchovy (Hunter and Thomas, 1974), and porgy (Fukuhara, 1983b). The majority of survivors remained near the bottom of the rearing tank when they reached juvenile stage. Concealment and cannibalism were observed among the bottom dwellers. Thus, a shift in swimming mode occurred with the transformation from larvae to juveniles.

Acanthopagrus schlegeli

Morphological development and behaviour

Fertilized eggs were spherical in shape, and contained a

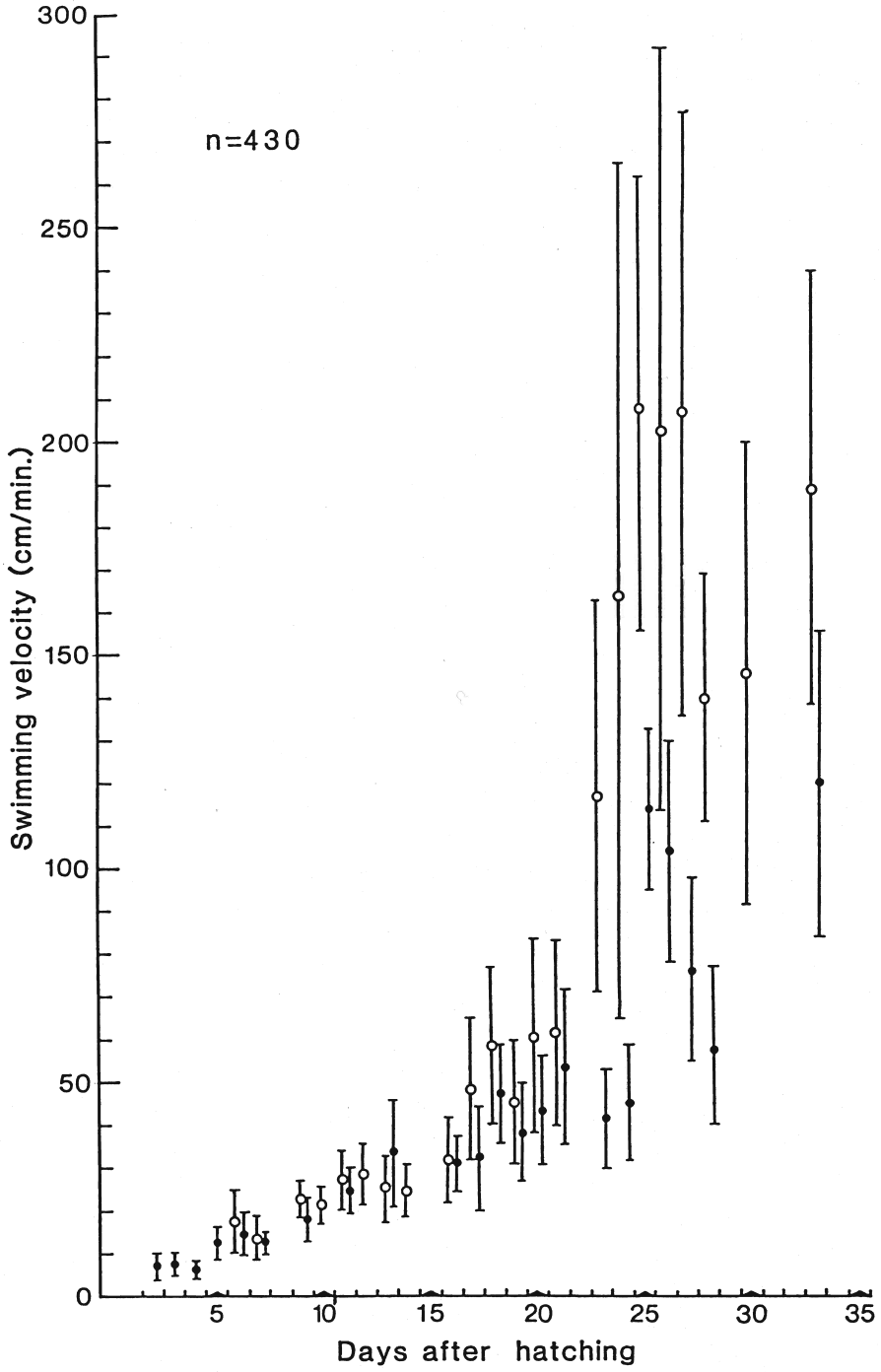


Fig.37. *Pagrus major*. Increase in swimming speed with growth of larvae before (open circles) and after (closed circles)feeding. Each point and vertical lines show the mean of 10 measurements and the standard deviation, respectively.

single oil globule. Perivitelline space was narrow. Naturally spawned eggs averaged 0.902 mm in diameter, with a range of 0.832 mm to 0.965 mm (n=114, SD=0.027). The eggs hatched 2 days after spawning at an incubation temperature of 17.2 °C. New-born larvae were 2.097 mm ± 0.054 SL (n=20,mean ± SD) and 2.179 mm ± 0.056 TL (n=20,mean ± SD), and had a nearly spherical yolk sac with an oil globule at an anterior position (Fig.38A). The size of newly hatched larvae was slightly larger than those described by Kasahara et al.(1960) and Xiaowei et al.(1980). The mouth opened 3 days after hatching, with some yolk and oil globule still remaining. These were absorbed completely at 4 days and 5 days after hatching, respectively. Fed larvae began to feed on given prey of rotifers in a rearing tank prior to complete yolk absorption. The optic vesicles became larger in size as the larvae grew (Fig.38A-F). Cartilaginous hypural elements appeared in larvae as small as 4.74 mm SL, aged 11 (Fig.38F), and larvae formed the hypural elements increased with their growth. On day 17 all observed larvae finished the formation of the hypural elements. Notochord flexion began on day 13 after hatching. Myomeres changed its shape after the hypural elements began to develop (Fig.38G). The nostril started to separate at about 23 days after hatching, and completed this process in all specimens observed by day 33. The preopercular spines developed in larvae of 6.1 mm SL, and increased markedly in number after they reached the stage of metamorphosis (Kim et al.,1971). Transformation to the juvenile stage occurred at a length of 9.0 mm to 11.0 mm SL.

Fed larvae grew steadily and no growth was observed in unfed larvae after yolk absorption (Fig.39). Slight retardation of growth was perceived even for fed larvae when the energy source changed from endogenous to exogenous.

Larval growth for the initial 120 days is presented in Fig.40. Overall growth could be expressed by the equation, $Y=2.83 + 0.15X + 2.47\times10^{-3}\times X^2$, where Y=standard length, and X=days after hatching. Larvae metamorphosed at about 9.0 mm SL, corresponding to day 28 after hatching.

The proportion of preanal length to total length was increased sharply with 30% to 50% in the early stage of larval life ranging from about 3.0 mm and 20 mm TL, then levelled off at a value of 50% TL afterwards (Fig.41). The relationships between total length, standard length and preanal length could be expressed by

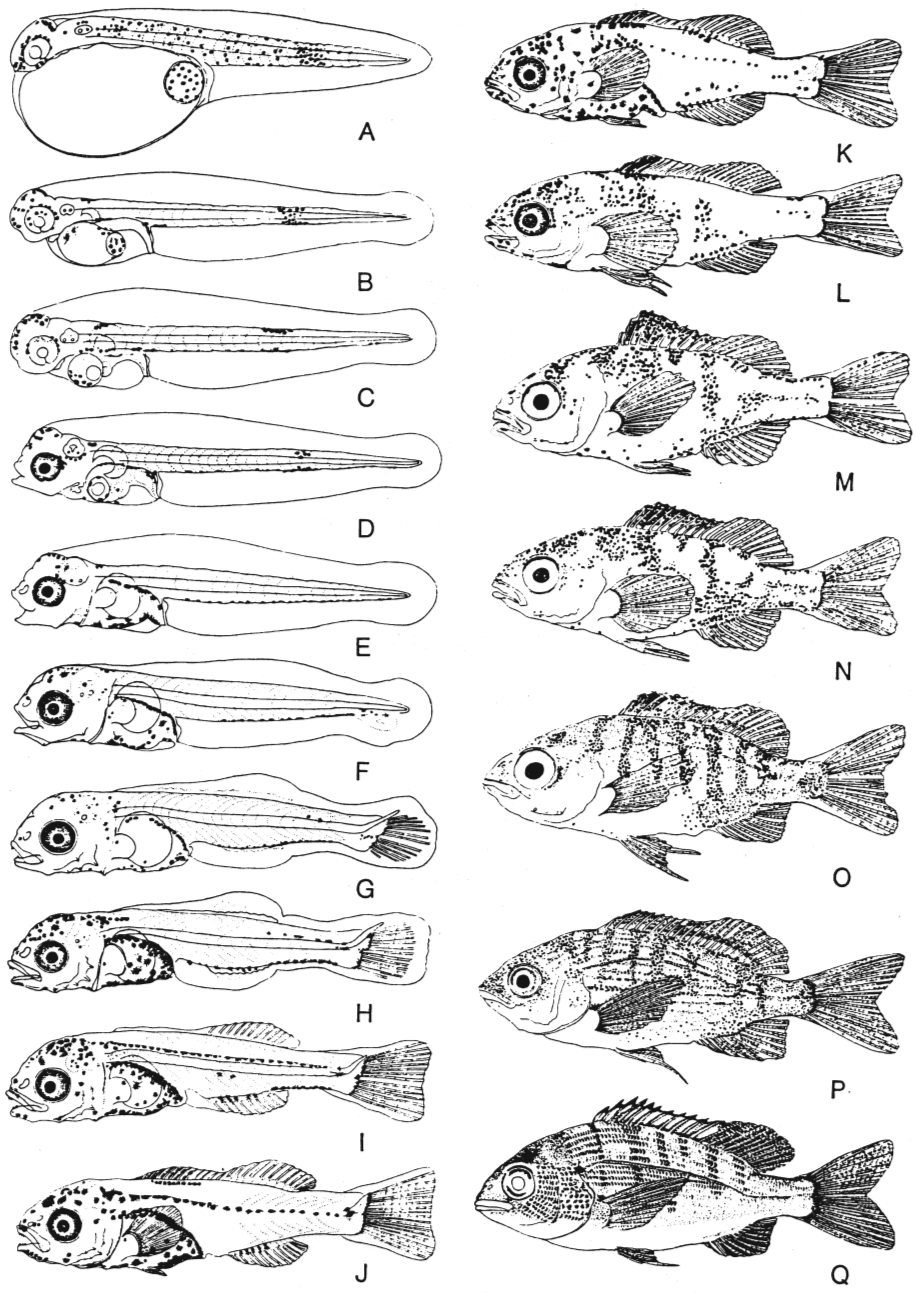


Fig.38. *Acanthopagrus schlegeli*. Morphological development from larvae to young stages. A,2.05mm SL; B,2.80mm SL; C,2.95mm SL; D, 3.09mm SL; E, 3.46mm SL; F,4.74mm SL; G,6.1mm SL; F,4.74 mm SL; G,6.1mm SL; H,6.7mm SL; I,7.8mm SL; J,9.3mm SL; K,11.1 mm SL; L,12.0mm SL; M,12.4mm SL; N,13.9mm SL; O,17.8mm SL; P,28.7mm SL; Q,73.6mm SL.

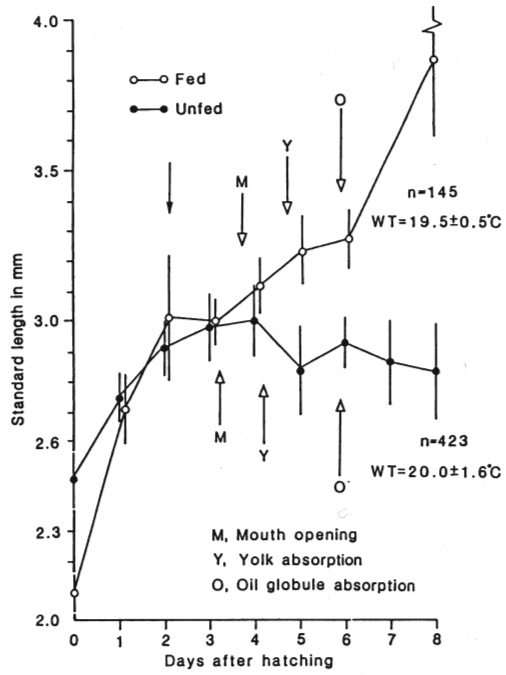


Fig.39. *Acanthopagrus schlegeli*. Growth in length of fed and unfed larvae for the initial 8 days. Points indicate mean and bars represent standard deviation.

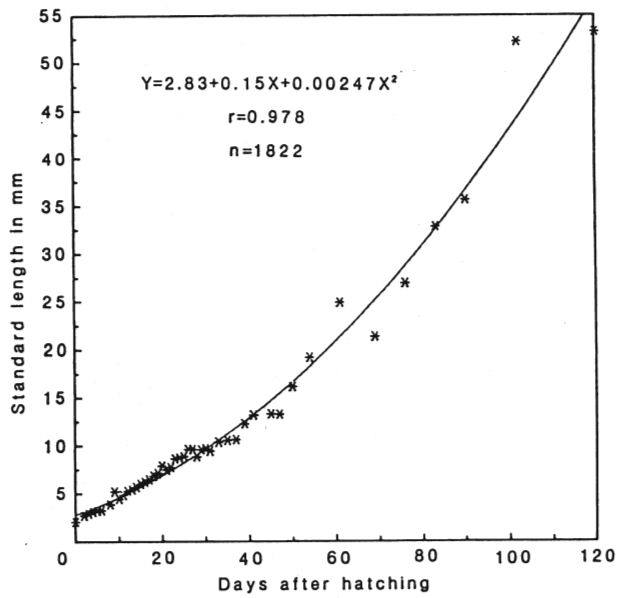


Fig.40. *Acanthopagrus schlegeli*. Growth of larvae for the first 120 days after hatching at temperature ranging from 18.8°C to 25.9°C. r=coefficient of correlation; n=sample size.

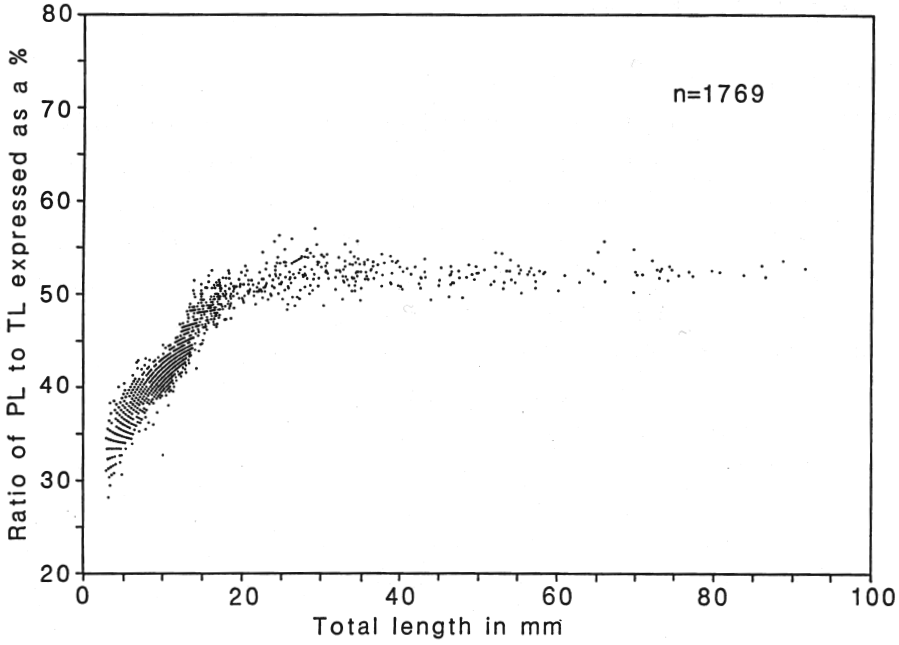


Fig.41. *Acanthopagrus schlegeli*. Proportion of preanal length (PL) to total length (TL). n=sample size.

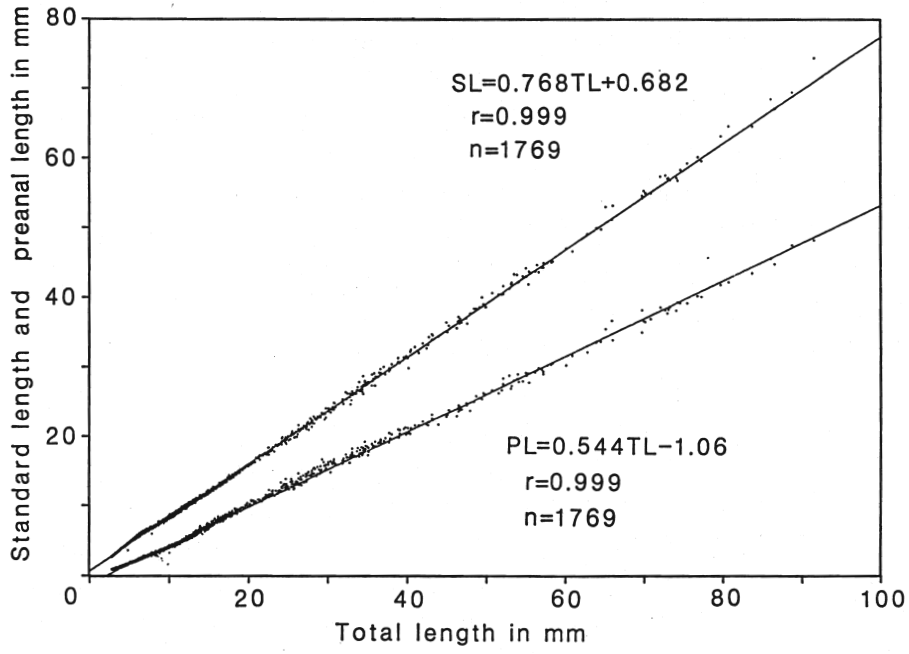


Fig.42. *Acanthopagrus schlegeli*. Standard length (SL) and preanal length (PL) plotted against total length (TL) in the reared specimens.

linear regression (Fig.42).

Fin development

Developmental changes in the primordial fin-fold were similar to those of *Pagrus major*, primordial fin-fold was replaced by the respective unpaired fins at the transitional phase from post-larvae to juvenile when the larva attained 7.8 mm SL (Fig.38I). The cartiliginous hypural elements were developed in larvae 4.74 mm SL (Fig.38F). Some segmented rays could be distinguished in the caudal fin for larger larvae than 6.1 mm SL (Fig.36G). The caudal fin was well-developed in larvae 7.8 mm SL (Fig.38I). At the same time, the hind margin of the caudal fin changed rapidly from a rounded shape to truncate form (Fig.38G-I). This feature can be used for rough estimates on developmental stages. The pectoral fins also changed their shape from a round to a triangular form. The initially triangular ventral fins appeared to be falcated.

Development of segmentation and branching of fin rays were plotted against standard length of fish (Fig.43). Segmentation of the unpaired fins was completed when the larvae reached a standard length of about 9.0 mm SL. The difference in standard length of fish specimens between the first appearance of segmented rays and the completion of segmentation was 3.0 mm in the case of the unpaired fins. This size difference of larvae was equivalent to a five day period in the rearing experiment.

Branching of rays in unpaired fins began shortly after the larvae had attained a standard length of about 10 mm when segmentation was almost completed. Anal and caudal fin branching was completed at about 20 mm SL. No further increase in the number of branching of the dorsal fin was observed, when the larvae attained a size of 30 mm SL.

The segmentation and branching of the soft rays in the pectoral fin levelled off to a constant number when the fish reached 30 mm SL. Development of ventral fins was peculiar in that the branching occurred almost concurrently with segmentation within a narrow range of fish size (9-12 mm SL), whereas in the other fins branching occurred distinctly later than segmentation. Thus the development of the ventral fin was completed considerably earlier than that of the others.

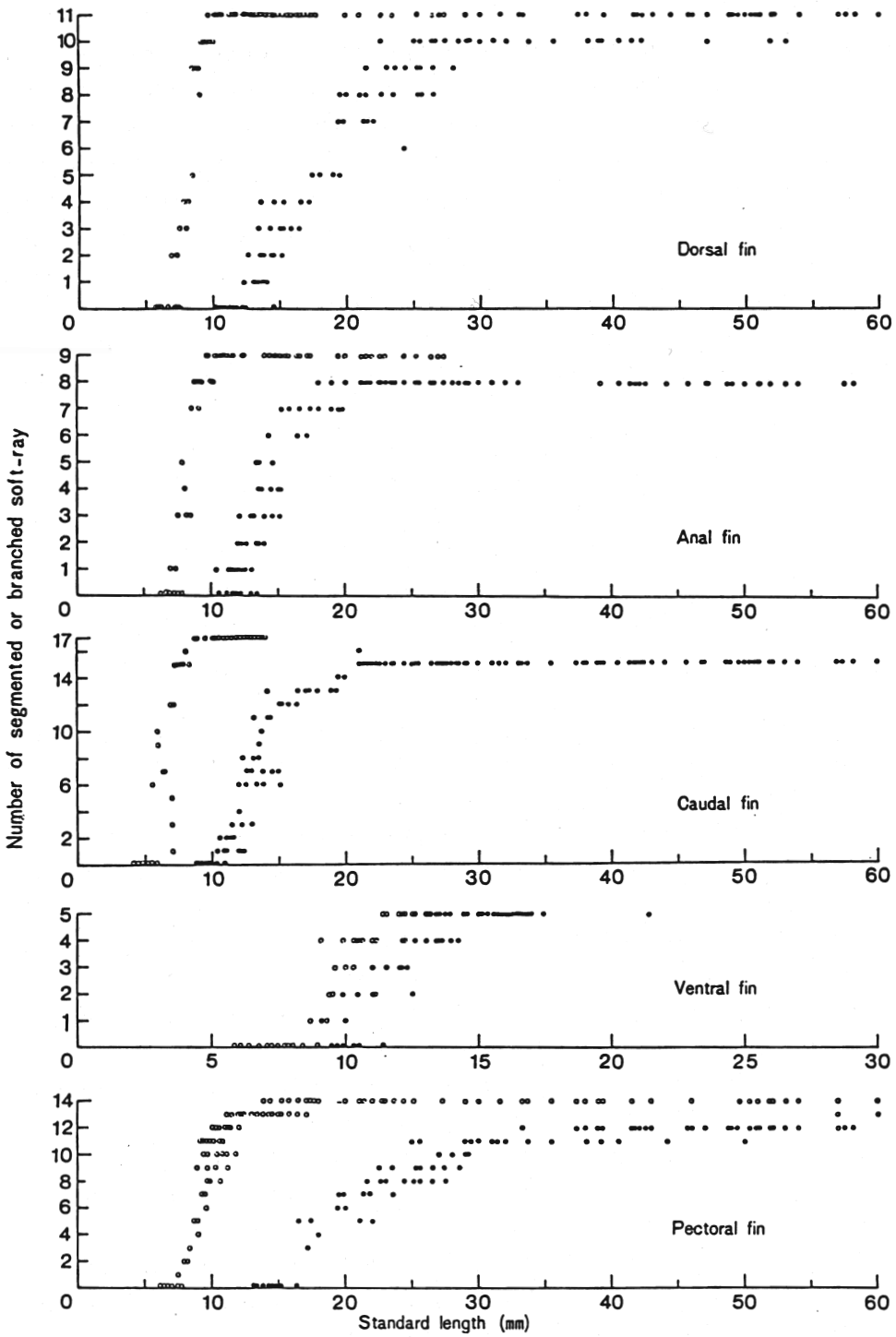


Fig.43. *Acanthopagrus schlegeli*. Segmentation (open circles) and branching (closed circles) of soft rays in the unpaired and paired fins.

Pigmentation

Newly hatched larvae had melanophores around the eyes, hind brain, on the oil globule and evenly in the trunk and caudal region. A band of melanophores was present on the tail at hatching (Fig.38A), and remained until the larvae were about 3.0 mm SL, 4 days old (Fig.38D). Serially arranged melanophores developed along the ventral midline of the tail. The melanophores became larger and more numerous in the gut area, especially in larvae between 6.7 mm and 9.3 mm SL (Fig.38H-J). Relatively heavy pigment appeared in the head region and serially along the mid-lateral surface of the body after larvae reached 7.8 mm SL, 20 days old (Fig.38I,J).

A maximum of 7 to 8 transverse stripes are formed on each side of the body surface in specimens larger than 15 mm SL (Fig.38 O). The transverse stripes are most clear to be distinguished in the late juvenile stage. Their sequence from first appearance to full development, and its stage plotted against larval length are shown diagramatically in Fig.44. The first stripe appeared dorsally at the anterior end of the trunk, and the formation proceeded posteriorly. Each stage might be defined as follows:

Stage A, Melanophores are concentrated in the anterior base of the dorsal fin forming a transverse stripe, which tapers ventrally.

Stage B, The second stripe appeared between the 4th and 7th spine of the dorsal fin, and extended dorso-ventrally further than the first.

Stage C, The third stripe appeared at the anterior position of the caudal region between the 1st and 3rd soft ray of the dorsal fin. This stripe covered the whole depth of the trunk extending posteriorly along the base of the anal fin.

Stage D, The fourth stripe appeared between the first and second, and is narrower than the other stripes already present.

Stage E, The fifth stripe appeared between the 8th and 9th spine of the dorsal fin. This is the last one formed on the trunk, and is as wide as the fourth.

Stage F, The sixth stripe appeared at posterior end of the caudal peduncle. This is the second stripe in the caudal region and is continuous anteriorly with the third stripe along the ventral margin.

Stage G, The seventh (the third one in the caudal region) appe-

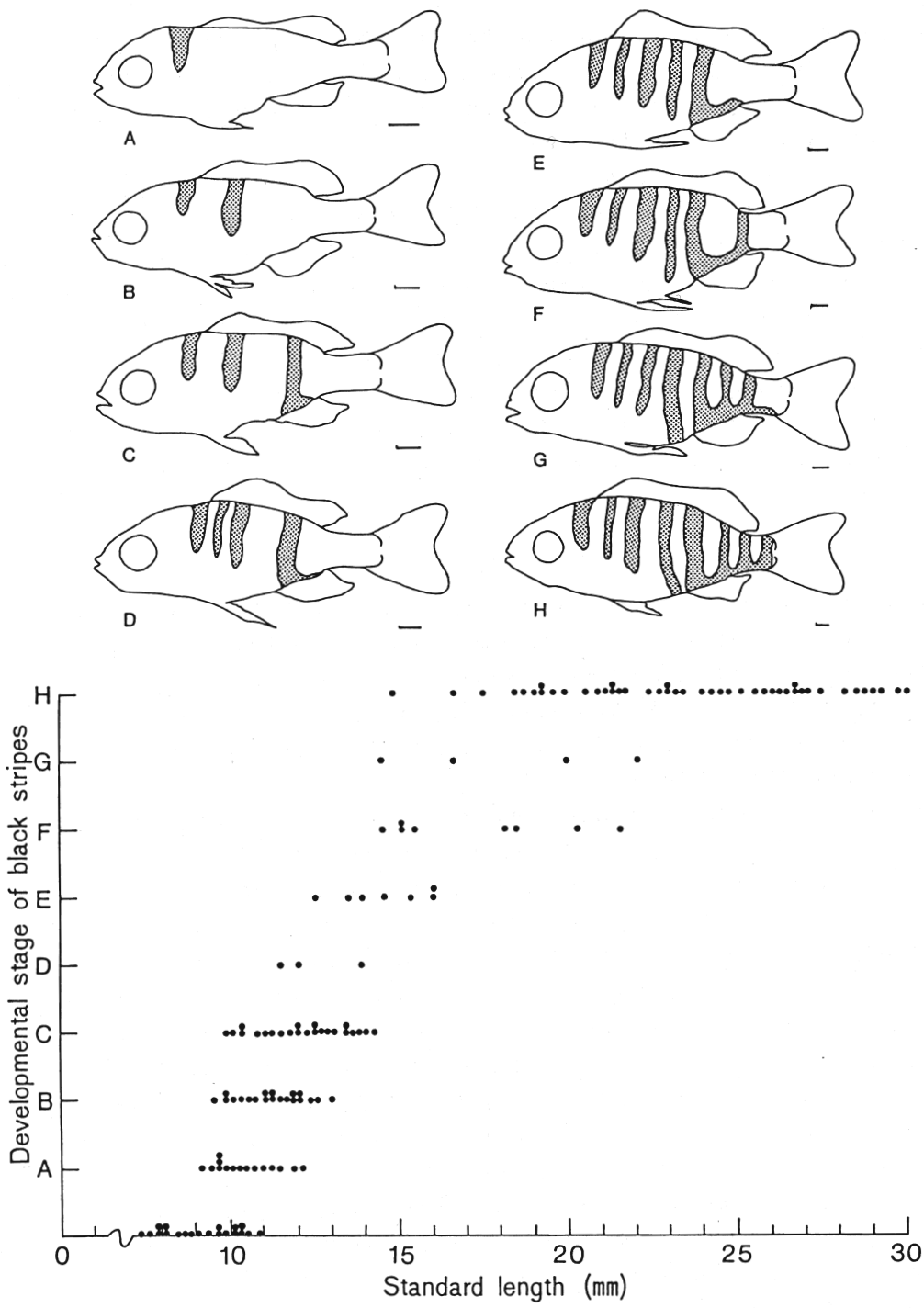


Fig.44. *Acanthopagrus schlegeli*. Semidiagrammatic drawings showing the developmental sequence of black stripes (upper), and its developmental stages plotted against standard length (lower). Scales denote 1.0 mm.

ared between the third one and the sixth stripe.
Stage H, The eighth stripe appeared at the posterior end of the caudal region. All the stripes in the caudal region are connected along the ventral margin.

The largest specimens without any stripe development was 11.0 mm and the smallest one on which first stripe occurred was about 9.0 mm SL. The development of stripes was completed in all the specimens examined when the larvae attained 25 mm SL. In some specimens the number of stripes were not obvious owing to the development of melanophores between stripes. There were a few variations along the edges of the black stripes. In several case, the second stripe branched toward either the dorsal and ventral end, and in other case the fourth stripe branched toward its dorsal end.

Squamation

The sequence of squamation may be divided into seven stages (A-G). This is shown semidiagrammatically in Fig.45 (upper). The characters of each stage was defined as follows:
Stage A, A few scales appeared in the posterior portion of the trunk along the lateral line. No teeth were visible on the exposed portion of the scale.
Stage B, There were 4 scale rows and 3 teeth on each scale. Scale formation extended to each direction on the trunk, anteriorly reaching the posterior end of operculum, and posterior, the central portion of the peduncle.
Stage C, There were 6 to 7 scale rows. The squamation covered anteriorly a part of the operculum, and posteriorly the base of the caudal fin. The squamated area tapered toward the caudal.
Stage D, There were 9 to 10 scale rows. Squamated area was horizontally almost identical with stage C, but extended more dorso-ventrally. About one third of the lateral area of body on each side was covered with scales.
Stage E, There were 11 to 12 scale rows. Squamation reached posteriorly to the hind end of the trunk. Two thirds of the lateral area were squamated.
Stage F, Squamation was almost completed, leaving only the base of the dorsal and anal fin and abdominal portion uncovered.
Stage G, Fully squamated.

The distribution of these developmental stages in relation to

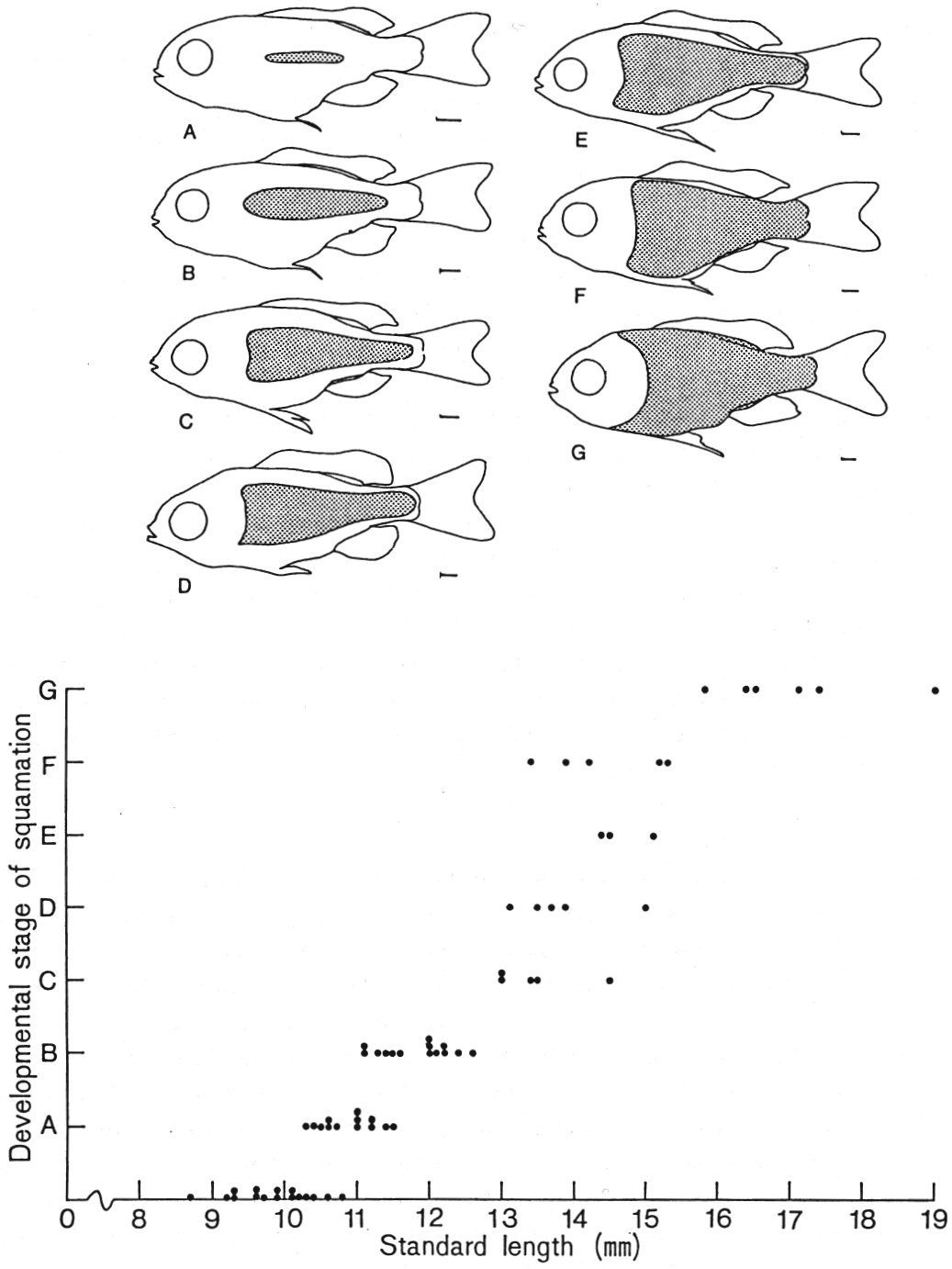


Fig.45. *Acanthopagrus schlegeli*. Semidiagrammatic drawing of squamation (upper), and relationship between developmental stages of squamation and standard length (lower). Scales denote 1.0 mm.

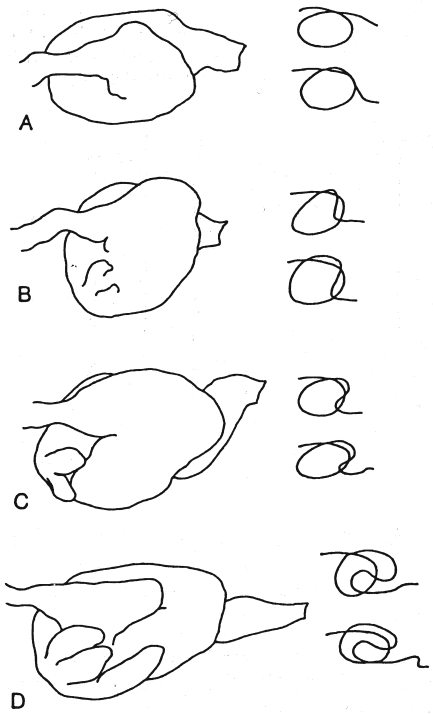
standard length is shown in Fig.45 (lower). The largest larva without scales was about 11.0 mm SL, whereas the first appearance of scale was obserevd in specimens as small as 10.2 mm SL. In all specimens larger than 16 mm SL the squamation was always completed.

Develpment of the digestive tract

The sequence of development of the digestive organs during the larval to juvenile stages and relationships between standard length, age and developmental stage of the digestive tract are also shown in Fig.46. The digestive tract was coiled during larval stages (Fig.46A). Rudimentary pyloric caeca were present, and the posterior portion of the digestive tract assumed a right-angled configuration when the larvae transformed to early juvenile (Fig.46B). The curvature then became more pronounced posteriorly than the previous stage, and the pyloric caeca developed well (Fig.46C). As development proceeded, the pyloric caeca elongated, and the shape of the digestive tract became deeply rounded (Fig.46D). The development of the digestive tract was divided into 4 stages. Stage B, characterized larvae measuring 8.5 mm SL, 25 days old corresponded to the phase of transformation of larvae to juveniles.

Development of behaviour

Newly hatched larvae floated on the water surface of the tank. Usually the head was directed downward, and the larvae moved passively with the water currents caused by aeration. At the end of the yolk-sac period, larval locomotion increased sharply for both fed and unfed groups. Succeeding active swimming was obserevd for fed larvae, and while the movement of unfed larvae declined after the yolk absorbed completely (Fig.47). Vertical movement was dominant during early yolk sac stage, and this gradually transformed into horizontal movement during later stages, as was stated by Rosenthal and Hempel (1970). Active swimming consisting of feeding and searching behaviours differed from those observed in yolk-sac larvae on day 5. Swimming speed of larvae increased gradually as development proceeded during the first 2 weeks, then slightly decreased in the larvae after feeding began and then returned to the speed attained prior to ini tial feeding. A striking increment of swimming speed was detected



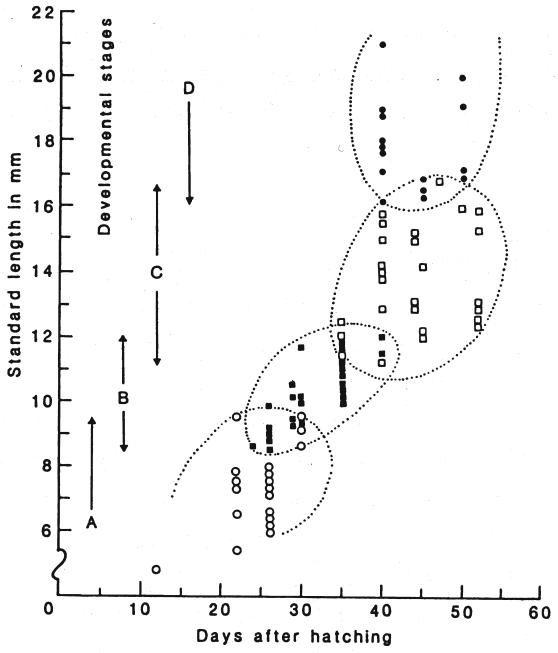


Fig.46. ***Acanthopagrus schlegeli***. Schematic illustration showing developmental stage of the digestive organs (upper), and its developmental stages plotted against standard length (lower).

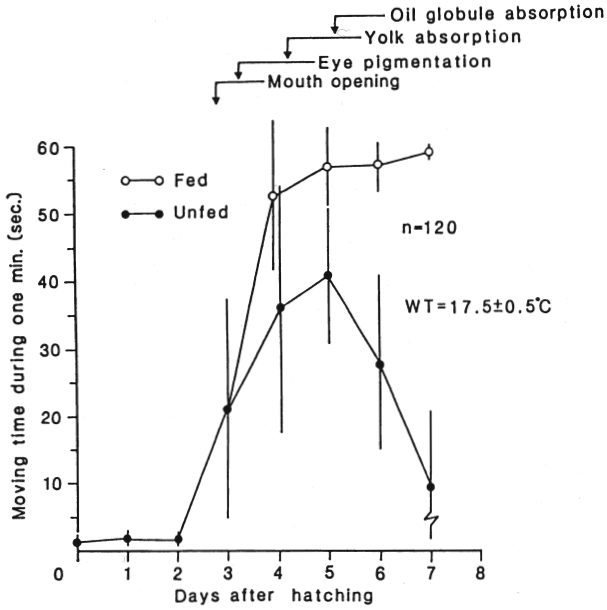


Fig.47. *Acanthopagrus schlegeli*. Locomotion (length of swimming bursts per minute) for the initial 7 days. Each point indicates the mean and standard deviation of 10 measurements is shown by the bars. Note the difference of SD between fed and unfed groups.

for the larvae beyond day 26, as they approached the transformation stage. During larval stage, swimming speed was approximately 1 standard length/sec and 2-2.5 SL/sec up to 26 days (Fig.48).

Hexagrammos otakii

Morphological development and growth

Egg is adhesive demersal, and its diameter ranged from 2.07 mm to 2.21 mm. The egg colour changes variedly with individuals in the reared and wild parents (Fukuhara,1983a).

Newly hatched larvae averaged 7.5 mm SL, ranging from 6.6 mm to 8.8 mm. Incubation time varied largely between 22 and 33 days after fertilization at an ambient temperature of 12.4-16.5 °C. The yolk was large and nearly spherical, with an oil globule at the anterior end at hatching. The yolk and oil globule remained up to 5 days after hatching at an mean temperature of 9.8 °C. The jaw were functional at hatching. The upper jaw extended posteriorly beyond and below the anterior margin of the eye; almost to the anterior margin of the pupil (Fig.49A). The notochord started to flex when larvae attained about 9.0 mm SL (Fig.49B). Teeth

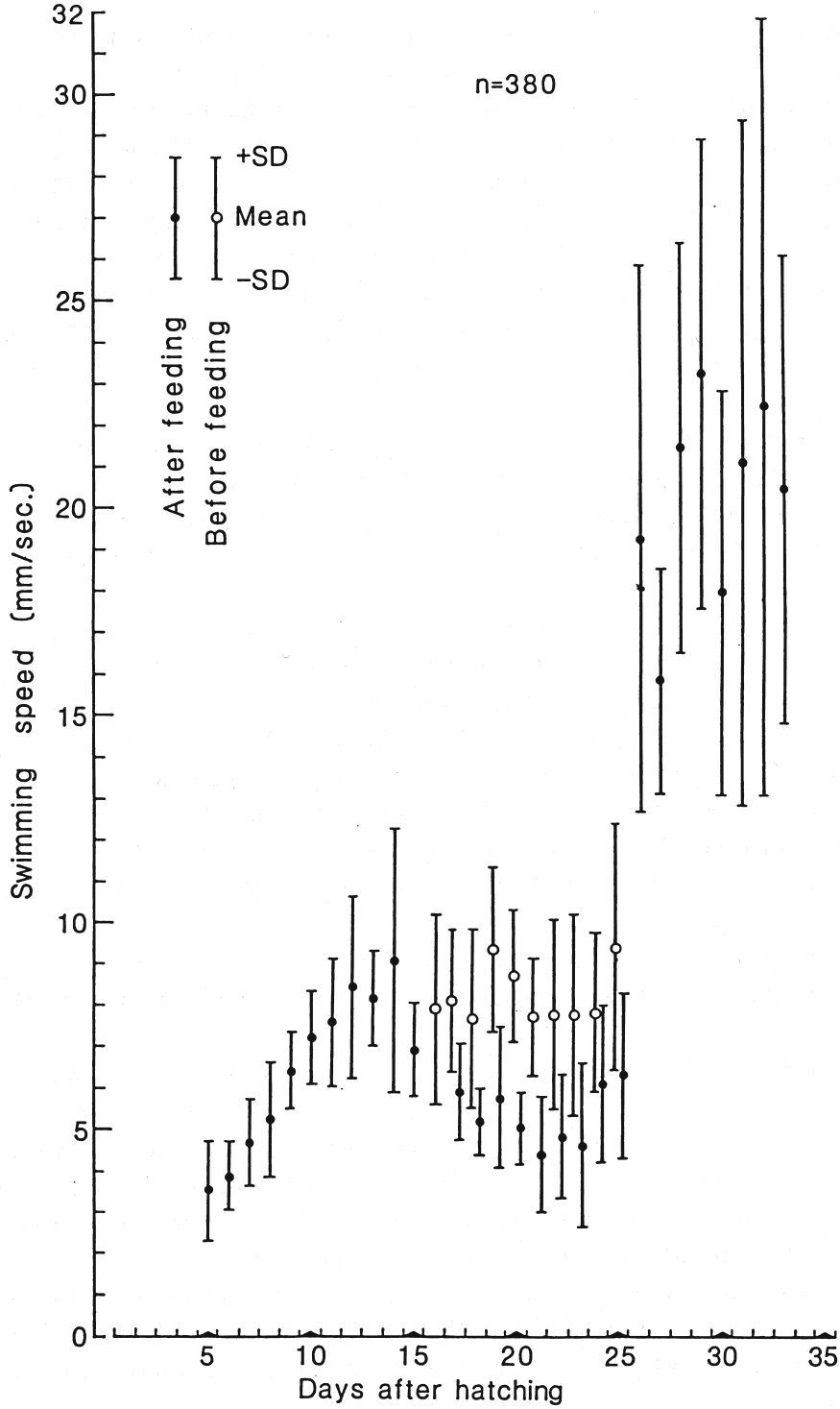


Fig.48. *Acanthopagrus schlegeli*. Increment of swimming speed with larval growth. Each point represents 10 measurements.

appeared on larvae 13.7 mm SL (Fig.49C), and supraorbital flaps on larvae 67 days old, 27.5 mm SL (Fig.49G).

Growth of laboratory-reared larvae is given in Fig.50. Starved larvae could survive 9 to 10 days after hatching at about 14.0 °C, and 12 to 13 days at about 9.0 °C. A slow growth was found during first 40 days and a more rapid increment during the next 60 days. Preanal length, as measured from the snout to the anus, was about 40% SL for larvae from hatching to the yolk absorption stage, then increased rapidly from 40% to 51-58% SL for specimens between 18 mm to 20 mm SL at which the transformation occurred (Fig.51).

Standard length was used to examine the development of *H. otakii* with respect to other morphometric data. The relation between standard length and total length was linear for larvae 7.0 mm to 60 mm length as was that for the preanal length and total length relation (Fig.52).

Comparing wild and reared larvae, the bases of the dorsal and anal fins were first observed at about 12.0 mm TL for wild-caught specimens (Mito,1966), and 10.41 mm TL (9.2 mm SL) in this study reared. Also, the notochord flexion was first found for wild fish at 10.2 mm SL (Nakamura,1936), compared with 9.2 mm SL for the reared. In addition, the fin rays of the dorsal and anal fins first appeared on the wild larvae at 13 mm to 15 mm TL (Nakamura,1936) and at 12.7 mm to 13.3 mm SL (14.2-15.1 mm TL) for the reared.

Accordingly, the striking difference in larval development between wild and reared animals was not considered for the larval stage.

Transformation from larval to early juvenile stage occurred between 14.7 mm SL (18.0 mm TL) and 18.7 mm SL (23.3 mm TL), about 40 days after hatching. In contrast to the wild specimens, Mito (1966) described the complement of the dorsal and anal fin rays for larvae measuring 20 mm TL and Gorbunova (1970) also described the metamorphosis at the same size.

The reared larvae were able to feed by minced fish meat when the larvae transformed to the juvenile stage, and allometric growth of preanal length to standard length became constant.

Fin development

Newly hatched larvae had a fin-fold that invested the trunk

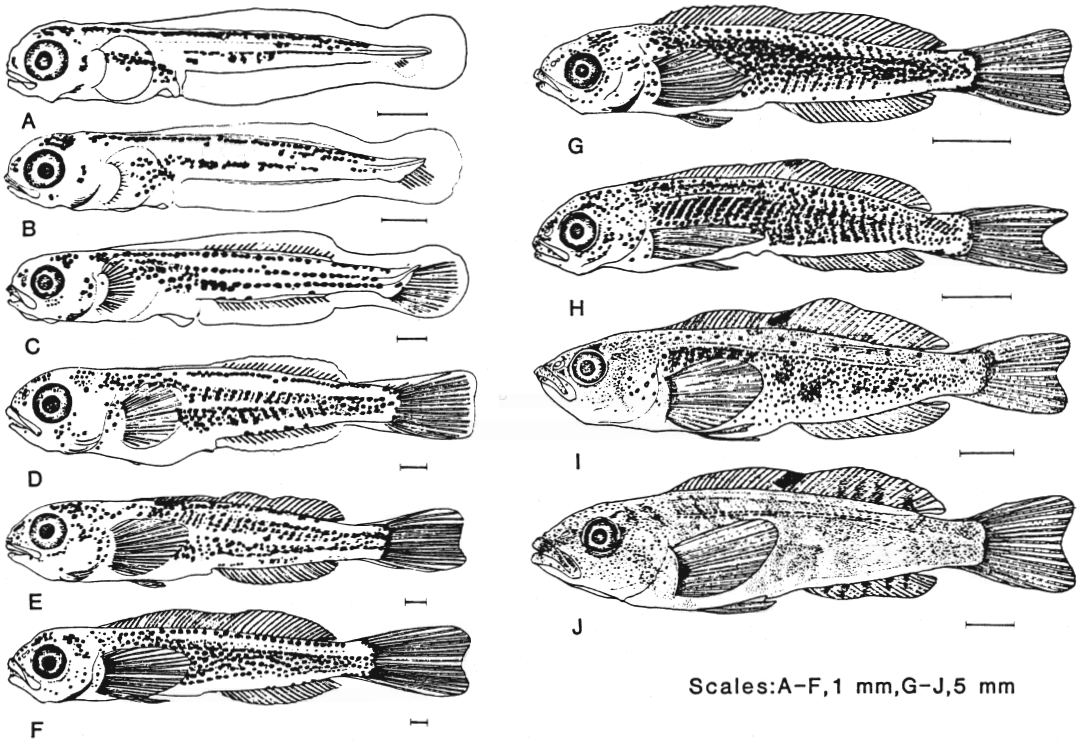


Fig.49. *Hexagrammos otakii*. Developmental stages of larvae and juveniles reared in the laboratory. A,8.6mm SL; B,9.2mm SL;C,13.7mm SL; D,14.5mm SL; E,18.5mm SL; F,21.8mm SL; G,27.5 mm SL; H,31.2mm SL; I, 39.8mm SL; J, 46.7mm SL.

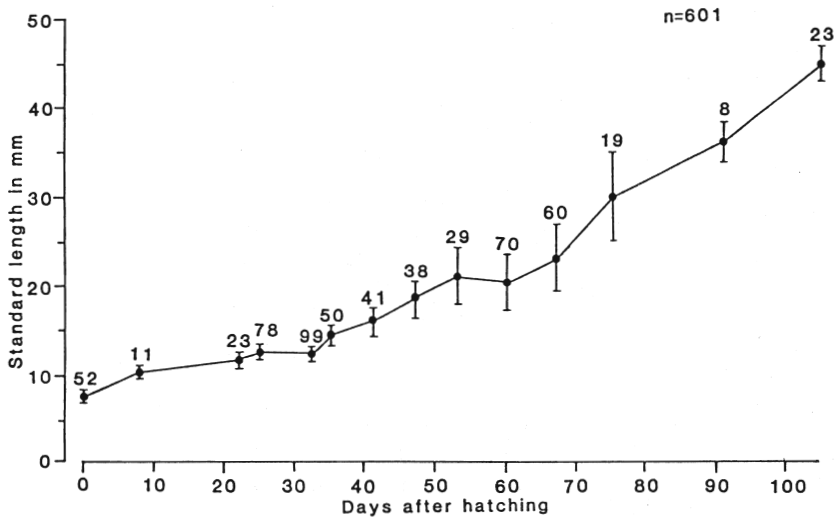


Fig.50 *Hexagrammos otakii*. Growth of laboratory-reared larvae at a temperature of 10°C to 17°C. Each measurement is mean standard length and sample size.

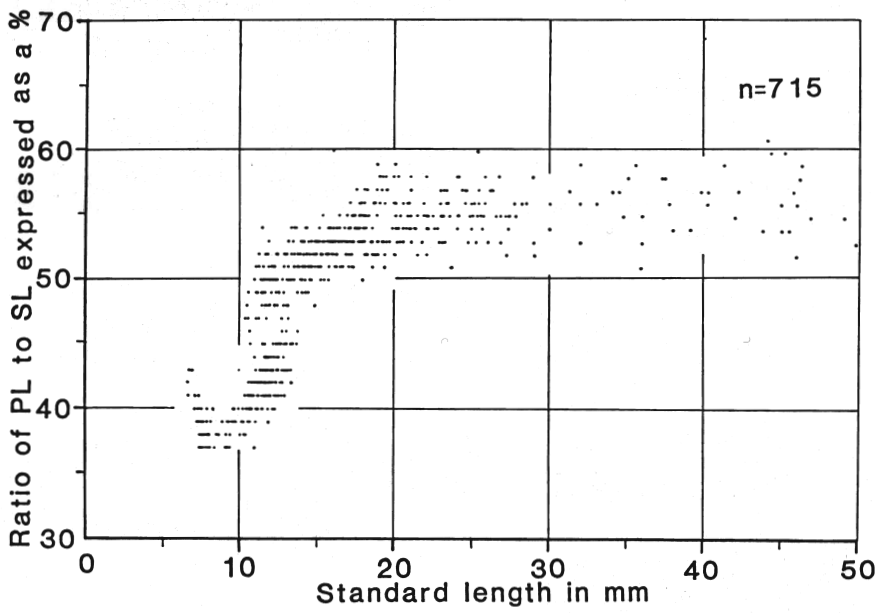


Fig.51. *Hexagrammos otakii*. Allometric growth of preanal length (PL) to standard length (SL) plotted against standard length. n=sample size.

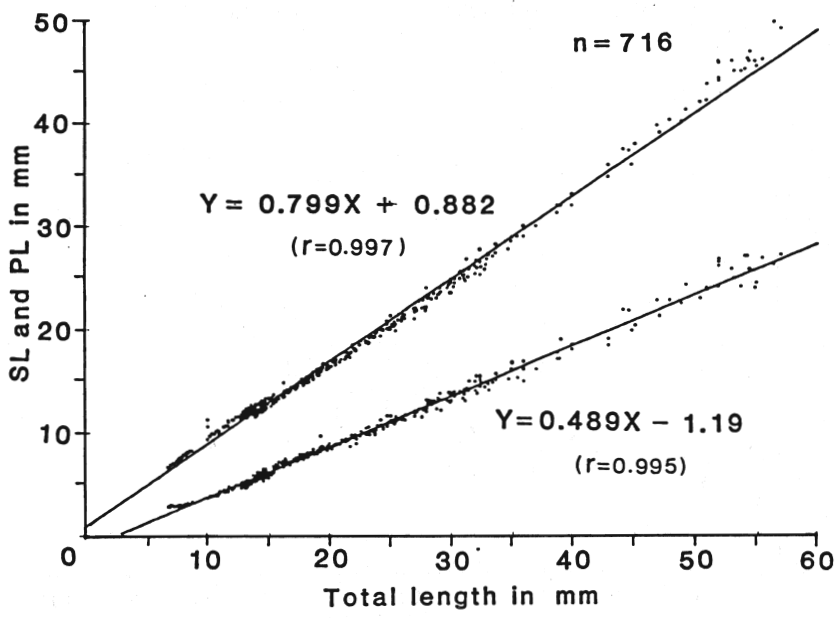


Fig.52. *Hexagrammos otakii*. Relationship between standard length (SL) and preanal length (PL) plotted against total length (TL). n=sample size; r=coefficient of correlation.

and caudal area. No pronounced changes of marginal shape in the fin-fold occurred until larvae grew to 8.6 mm SL, 13 days after hatching (Fig.49A). Fan-shaped pectoral fins without rays were already present at hatching. The cartilaginous hypural elements began to differentiate when the larvae were 8.6 mm SL (Fig.49A), and some rays could be distinguished at 9.2 mm SL when the notochord started to flex. At the same size, fin rays of the pectoral fins and bases of the dorsal and anal fins started to develop (Fig.49B). The primordial fin-fold changed slightly in shape near the caudal peduncle, and developing fin rays were present in the dorsal and anal fins at 13.7 mm SL (Fig.49C). The smallest larva with developing dorsal and anal fin rays was 12.7 mm SL (n=78 specimens). Remnants of the larval fin-fold persisted; the dorsal and anal fins connected with the caudal fin at the anterior portion of the caudal peduncle. The fin-fold just front of the anus was barely present, and the posterior margin of the caudal fin changed from a rounded to a truncated shape. The posterior margin of the caudal fin was rounded for all larvae of 25 days old, and 62% of 100 specimens at 32 days. At 35 days, 94% of 50 specimens had truncated caudal fins. Ventral fin buds were observed on larvae of 14.5 mm SL (Fig.49D). The smallest larva with ventral fin buds was 12.9 mm SL among the 100 observed larvae. Full complements of rays in all fins were observed on larvae 41 days after hatching (Fig.49E). Among 81 41-day old specimens, the smallest larva with complete fin rays measured 14.7 mm SL and the largest without a full complement of fin rays was 18.7 mm SL. The caudal fin then became emarginated. The sequence of fin developments in unpaired and paired fins is given in Fig.53. In the unpaired fins, the caudal fin completed its segmentation of the rays for fish 13 mm to 17 mm SL. The larvae with a full complement of segmentation of more than 21 rays appeared for fish over 19 mm SL for the anal fin compared with 21 mm SL for the dorsal fin. Likewise, in the paired fins the completion of segmentation occurred for the larvae over 20 mm SL, and those of the ventral fins was 17.8 mm SL. The number of soft rays in the pectoral fins ranged from 17 to 19 rays for wild specimens (Quast,1964), compared with 17 to 20 for the reared specimens in this study.

Consequently, the completion of segmentation in all fins started on larva as small as about 20 mm SL. The branching of the rays was identified only in the caudal fin. This started at a

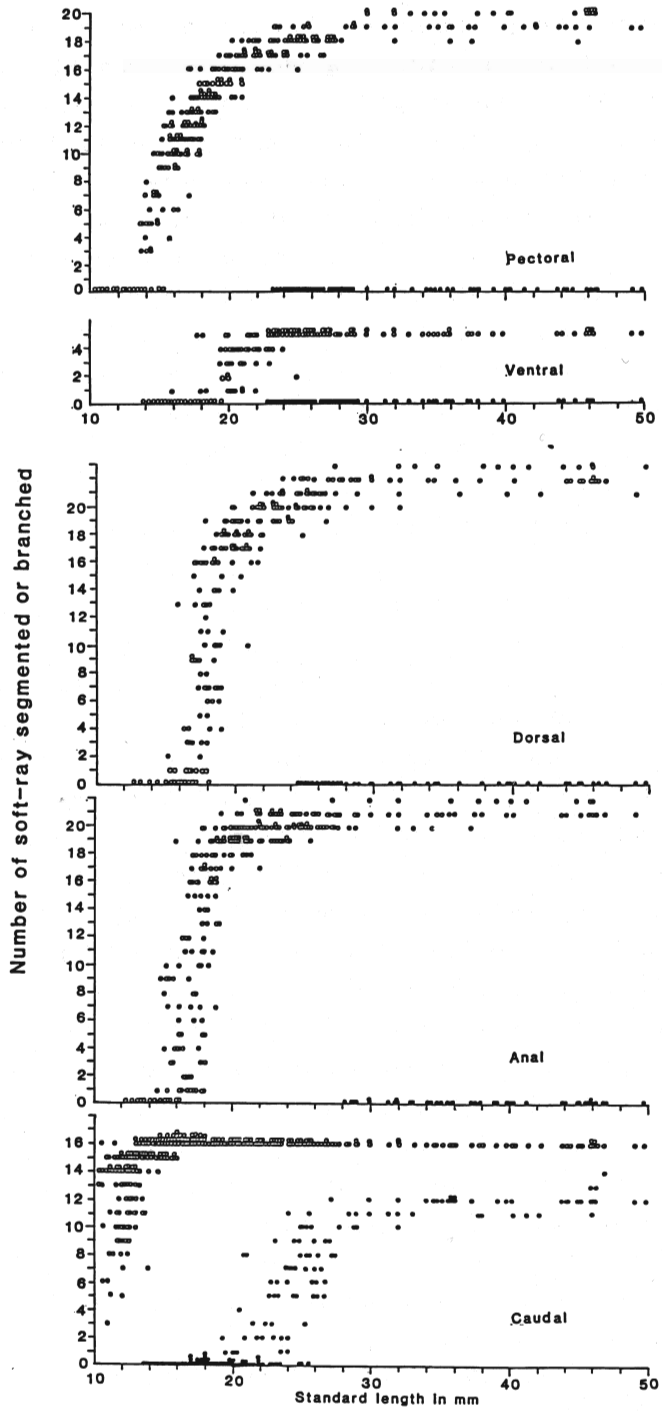


Fig.53. *Hexagrammos otakii*. Segmentation (open circles) and branching (closed circles)of soft rays in the unpaired and paired fins.

size of 19 mm to 24 mm SL. More than 11 rays were branched on the larvae over 30 mm SL.

Pigmentation

Newly hatched larvae had numerous melanophores in dorso-lateral and ventro-lateral lines. Melanophores were present on cephalic and gut regions. The eyes were already pigmented at hatching. No marked changes in the pigmentation pattern were observed until larvae attained 8.6 mm SL (Fig.49A). Melanophores increased in the lateral surface in larvae larger than about 9.0 mm SL (Fig.49B), and the extent and intensity of pigmentation continued to increase in that area as specimens became larger. Melanophores increased in the cephalic region and around the eye as well as the operculum and near the jaws (Fig.49C-F). The lateral surface was heavily pigmented except for the ventral and the base of the caudal fin (Fig.49G,H). Small melanophores appeared near the posterior end of spinous dorsal rays on a specimen 31.2 mm SL (Fig.49H), and coveraged in that portion on larger specimens (Fig.49I,J). Larvae longer than about 40 mm SL invariably had many, small melanophores in the rayed portion of the caudal fin, and 4 to 5 bands of melanophores were distributed in the dorsal and anal fins.

Squamation

The sequence of scale formation is shown diagrammatically in Fig.54 as depicted by nine stages (A-I) of development. Each developmental stage was characterized as:

Stage A, Few scatter scales first appeared simultaneously on the anterior end of the trunk and midlaterally on the caudal peduncle.

Stage B, The squamated area of scatter scales extended anteriorly along the lateral line. Small patches of scatter scales were seen at the dorso- and ventro-surface of the caudal peduncle.

Stage C, The squamated area of scatter scales extended ventrally gradually, and a few scales with ctenii first appeared on the anterior portion of the caudal peduncle.

Stage D, Scatter scales extended dorso-ventrally. The caudal peduncle was completely covered, as was the base of the anal fin. The scale with ctenii extended anterior to the vertical of the spinous rays of the dorsal fin.

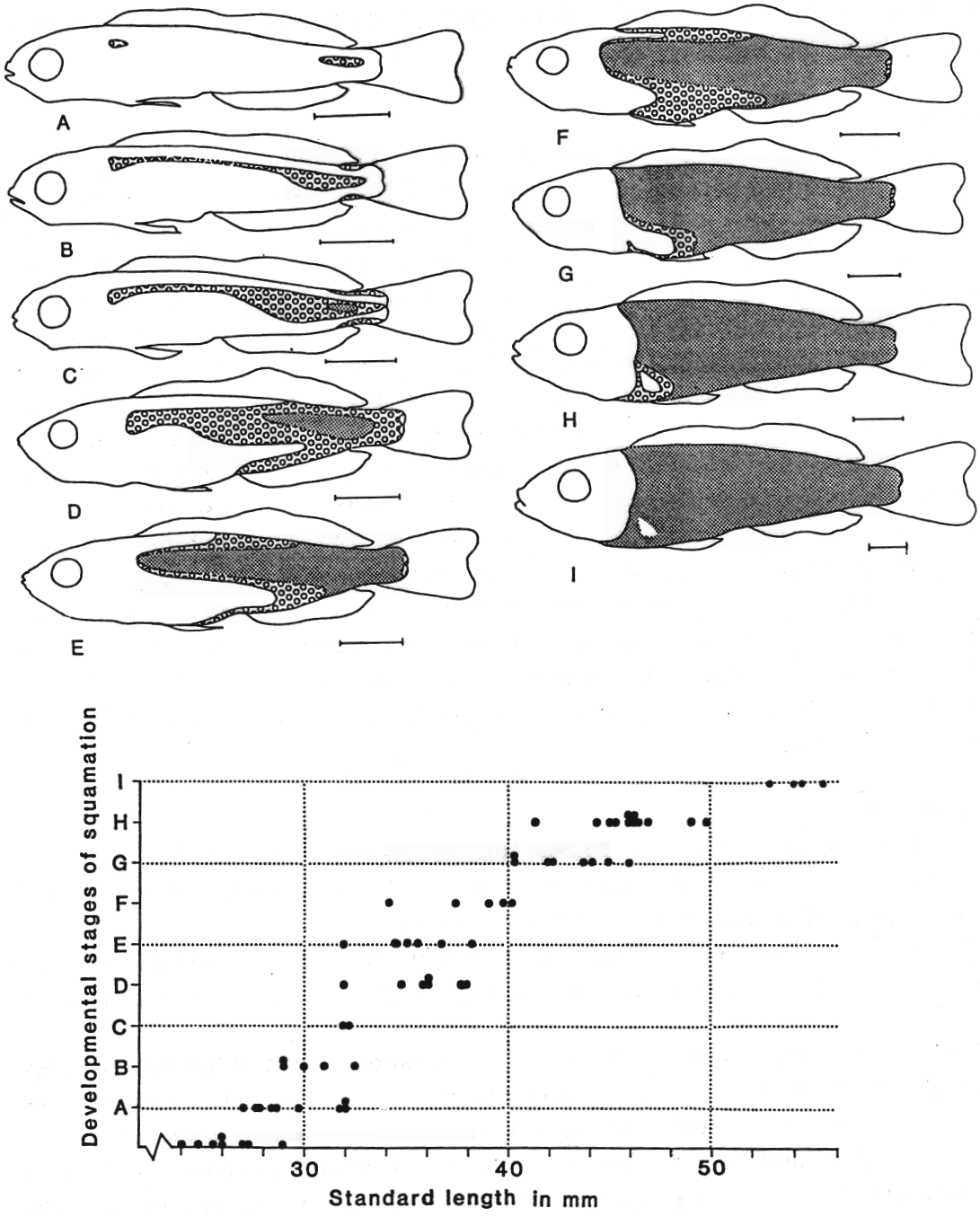


Fig.54. *Hexagrammos otakii*. Sequence of the squamation of laboratory-reared specimens. Open circles and dots indicate squamated areas of scatter scales and ctenoid scales, respectively(upper), and its developmental stage in relation to standard length (lower).

Stage E, The caudal area almost covered with scatter scales or scales with ctenii except for the small area above the anal fin. The scales with ctenii developed toward the head, reaching the operculum.
Stage F, The unsquamated areas were small patches below the dorsal and above the ventral fin. The caudal was almost completely covered with ctenii scales, except for the base of the unpaired fins.
Stage G, The only area devoid of scales was around the base of the pectoral fin. Scales with ctenii were not seen only at the base of the caudal fin and along the abdomen.
Stage H, The body surface was covered with ctenii scales except for a small area around the pectoral fin.
Stage I, Completely squamated.

The largest specimen without scales was 29.0 mm SL. Squamation commenced when fish were 27.0 mm to 32.0 mm SL., and proceeded as they grew. The smallest specimen fully squamated was a larva 53.0 mm SL. From these observations, it is obvious that scale formation occurred during larval development on fish 27.0 mm to 53.0 mm SL. It was assumed that the period of squamation corresponded to fish ages of about 70 to 80 days after hatching based on the growth curve obtained in the rearing experiment (Fig.50).

No comparison of squamation was available between wild-caught specimens and reared individuals due to a lack of squamation information on the wild fish. In rearing experiment (Tange,1980; Yamada et al.,1982), fish changed body colour from greenish to brownish when they attained length of 45 mm to 50 mm. Consequently, the body colour change occurred coincidently with the completion of squamation for the laboratory-reared specimens.

Paralichthys olivaceus

Morphological development and growth

Spawned eggs were pelagic and spherical, and averaged 0.96 $\pm$ 0.035 mm in diameter (n=202). Eggs hatched in 4 days at an incubation temperature of 14 °C. Newly hatched larvae, ranging from about 2.3 mm to 2.7 mm SL (mean $\pm$ SD=2.49 $\pm$ 0.09 mm, n=100), have a sizable yolk-sac with a posteriorly located oil globule (Fig.55A). At about 14 °C, yolk volume, calculated by following equation ; $V=4/3\ \pi(r_1/2)^2 r_2/2$ (r_1, minor axis ; r_2, major axis

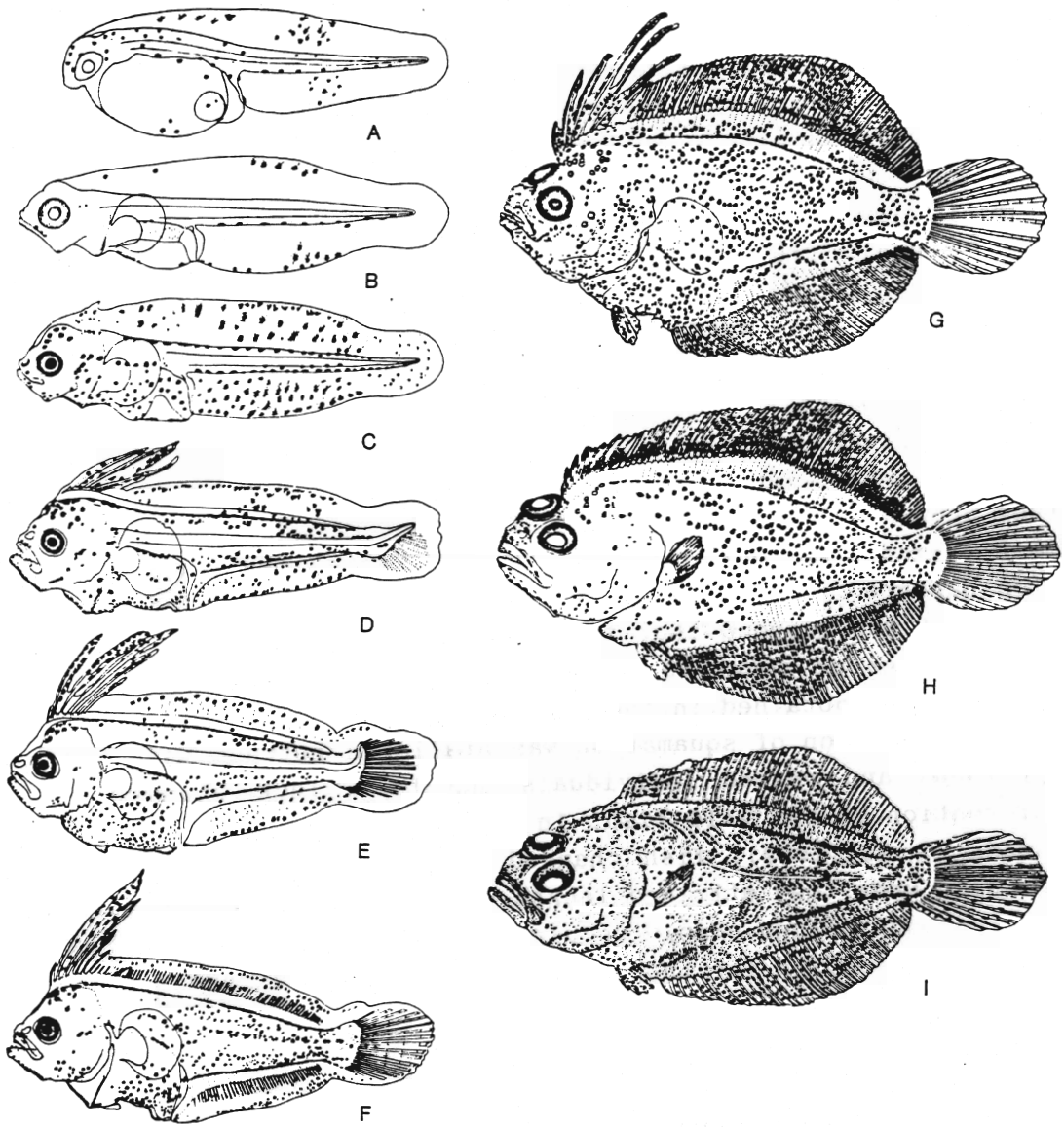


Fig.55. *Paralichthys olivaceus*. Morphological development of larvae and juvenile. A,2.32mm SL; B,3.11mm SL; C, 5.51mm SL; D,7.5mm SL; E,7.5mm SL; F,8.3mm SL; G,9.8mm SL; H,12.2mm SL; I,24.4mm SL.

Rosenthal and Hemple,1970), decreased drastically for a few days and was absorbed completely on day 4 after hatching. With the decreasing yolk volume, the mouth, pectoral fins and eyes became functional (Fig.56). During 3 to 5 days after hatching, the mouth became functional and the yolk sac and the oil globule were completely absorbed (Fig.55B). In the larval stage the end of the maxillary was located beneath the middle of the orbit. Notochord flexion began at about 7.5 mm SL (Fig.55D). Asymmetry of the eyes began at a length of 7.0 mm (35 days old), and the right eye reached the dorsal ridge when the larvae were 8.0-12.0 mm SL (Fig.55G,H). The nostril became separated when larvae were larger than about 10.0 mm SL (Fig.55G). The larvae reared between 16.2 °C and 20.7 °C had separated nares at 9.2 mm to 13.6 mm TL,(aged 26 days) (Kawamura and Ishida,1985). Migration of the eye was completed in the specimens of 10.5 mm SL in the smallest and also in more larger size. The lateral line was distinguishable for newly metamorphosed juveniles (Fig.55I).

In rearing experiments, the smallest size of eye migrated individuals varied widely with size 9.4 mm SL (Hiramoto and Kobayashi, 1979), 12.0 mm SL (Yasunaga, 1971) and 13.5 mm TL

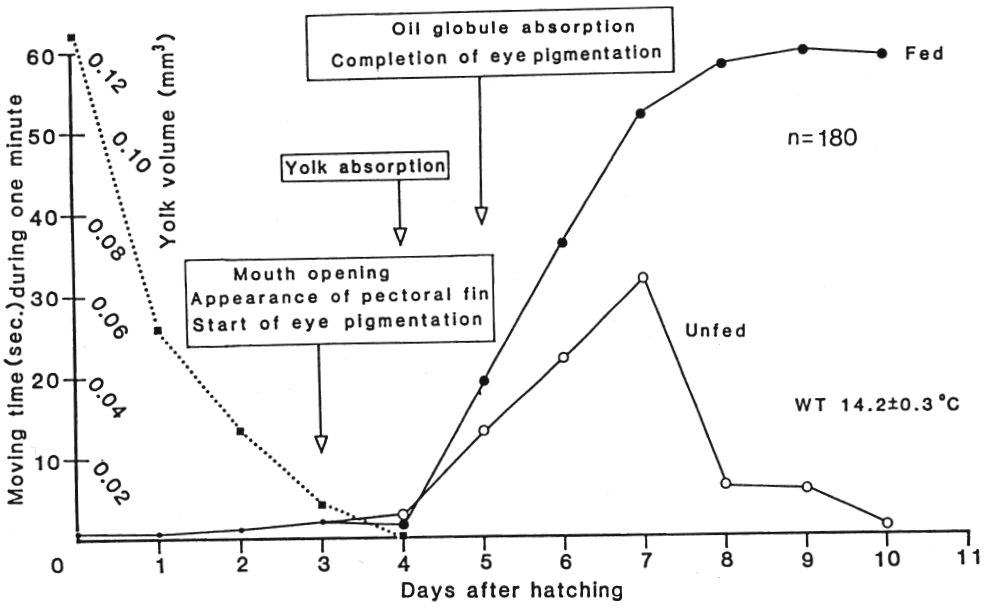


Fig.56. *Paralichthys olivaceus*. The sequence of morphological changes of internal and external organs, and behavioural development for yolk-sac larvae.

(Takahashi,1985) with age, from 25 to 50 days after hatching. On the other hand it was completed for wild-caught specimens when they were more than 14.0 mm TL (Imabayashi, 1980) or about 17.0 mm TL (Okiyama, 1967). No information was available for ascertaining larval size and age during transformation and to metamorphosis. Fig.57 shows the relationships between developmental stages during transformation to metamorphosis determined by eye migration and larval size and age reared at a temperature of about 15.0 °C. The distribution of developmental stage tended to be wider with increasing larval size and ages in day. Mean lengths of each developmental stage were represented at 8.8 mm SL for stage F, at 10.4 mm SL for stage G, at 12.0 mm SL for stage H and 14.3 mm SL for stage I, respectively. Eye migration completed at 10.5 mm SL for the smallest individuals, and 17.0 mm SL for the latest specimens. Metamorphosed fish were first observed for 57 days after hatching, representing 845.7 °C for a cumulative rearing temperature from hatching.

Unfed larvae survived for 10 days after hatching at a temperature of about 14 °C (Fukuhara,1986a). Growth of larvae during the rearing experiment is shown in Fig.58. Newly hatched larvae of 2.49 mm SL grew an average of 15.04 mm SL for a period of 87 days, which showing a daily increment of 0.144 mm. Maximum growth of unfed larvae was about 3.0 mm SL for the initial 7 days. Even for fed larvae, a cessation in growth was recorded just after yolk absorption or oil globule depletion as were also shown in red sea bream (Fukuhara, 1974) the Ayu fish, *P. altivelis* (Tsukamoto and Kajihara, 1984), rabbitfish, *S. guttatus* (Avila and Juario,1987) and flounder, *P. flusus* (Yin and Blaxter,1986).

The relationship between total, standard lengths and preanal length are given in Fig.59. In both regression lines, a flection point was detectable at a vicinity of 9.0-10.0 mm TL, just prior to the onset of eye migration. Furthermore, second flection point was found for the preanal length and total length between 15 mm and 16 mm TL when the newly metamorphosed juveniles appeared. During the 10.0 mm to 15 mm TL interval, the preanal length remained nearly constant, with no increase in length regardless of increment of total length (note coefficient correlation).

Preanal length ranged from 49% to 45% TL at hatching. As the yolk was absorbed completely at about 3.0 mm TL, the preanal length was reduced on the average of 40% TL, and stabilized until

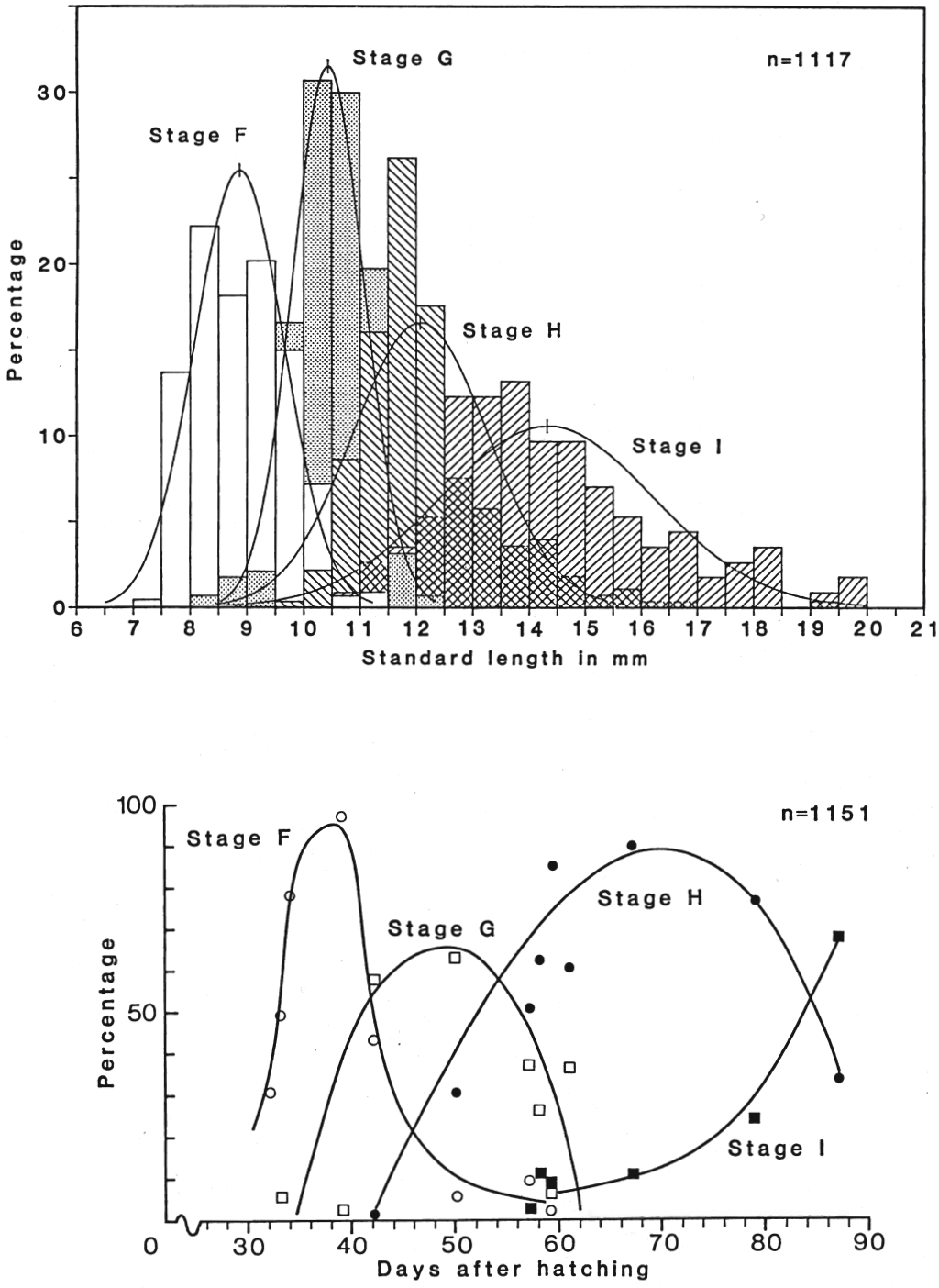


Fig.57. *Paralichthys olivaceus*. Relationship between standard length and developmental stages (upper), and days old after hatching (lower) for larvae reared for 90 days. Refer to Fig.54 for the developmental stages. n=sample size.

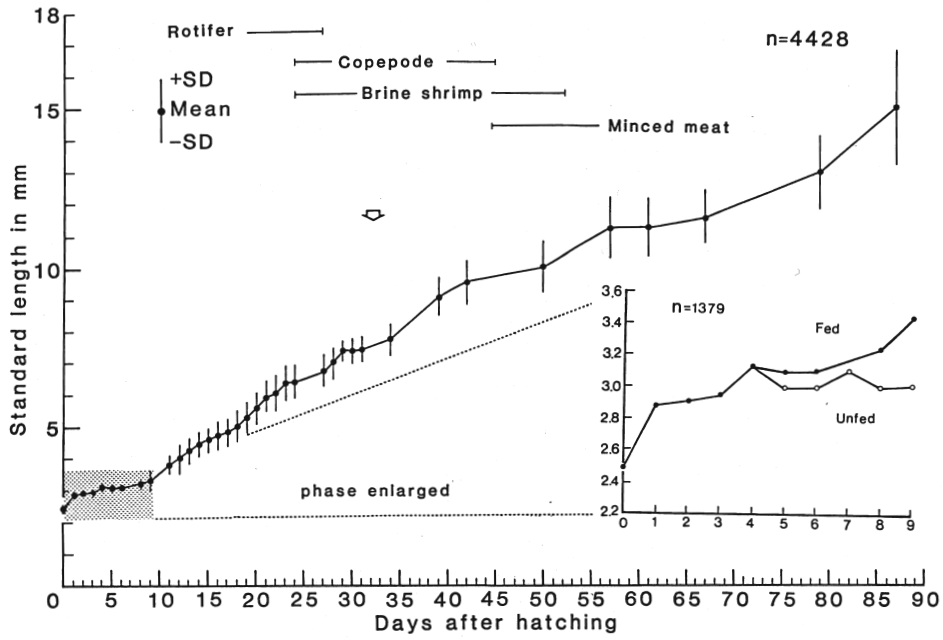


Fig.58. *Paralichthys olivaceus*. Larval growth of larvae from hatching to 90 days old. Initial growth for fed and unfed larvae is shown separately. Arrow indicates start of running water system. n=sample size.

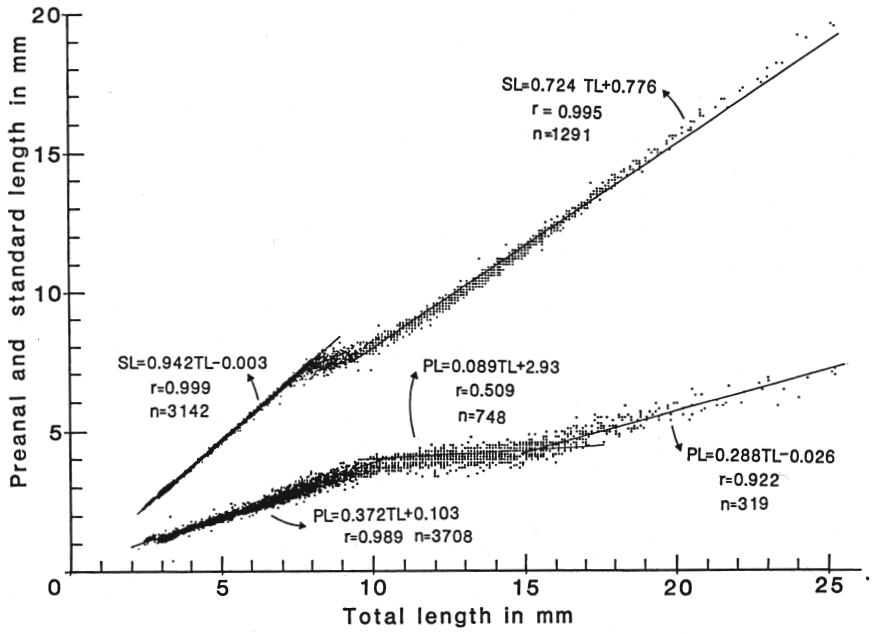


Fig.59. *Paralichthys olivaceus*. Preanal length (PL) and standard length (SL) plotted against total length (TL).

the larvae were about 10.0 mm TL. However the preanal length steeply decreased to 30% TL during transformation of Stages G and H, ranging from about 10 to 15 mm SL. The preanal length exhibited peculiar phase morphometrically during 10 mm to 15 mm SL. Okiyama (1967) also reported the rapid increment of body height during about 8.0-12.3 mm TL. The ratio of PL/TL became constant after metamorphosis again (Fig.60).

Fin development

A widely extended fin-fold surrounded the trunk and caudal areas of newly hatched larvae (Fig.55A). The pectoral fin lacking in rays appeared on the larvae as small as 3.1 mm SL (Fig.55B). That part of the fin-fold on the posterior section of the head exhibited marginal change when the larvae attained a length of 5.51 mm SL (Fig.55C). The cartilagonous hypural elements began to differentiate prior to notochord flexion when the larvae were about 5.5 mm SL. As the larvae grew the spiny armature on the head developed and also lengthen with accompanying fin rays (Fig.55D-F). At 7.5 mm SL (Fig.55D) the ventral fin buds were present and the base of dorsal and anal fins appeared. Segmented

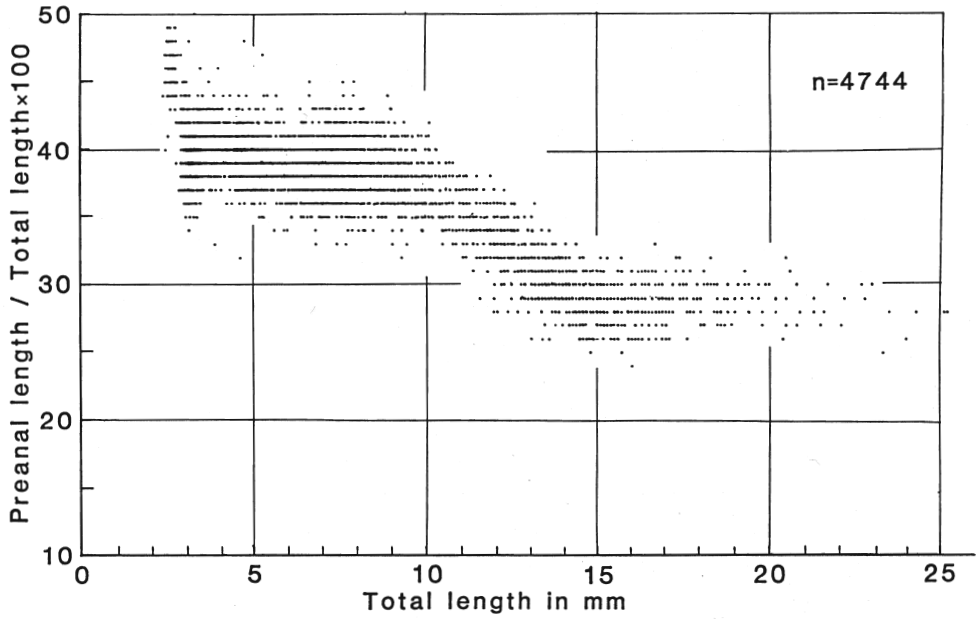


Fig.60. *Paralichthys olivaceus*. Relationship between total length and PL/TL ratio expressed as a percentage. Note two inflection points.

fin rays appeared on the caudal fin of larvae larger than 6.9 mm SL (Fig.55E). The elongate armature on the head decreased in length with the migration of the eye, and had disappeared when the right eye reached the dorsal ridge (Fig.55G,H). Fan-shaped pectoral fins became slender and smaller with larval growth, and fin rays first appeared at a length of 9.0 mm SL. This was later than was observed for the ventral fins. All fin ray development was completed when the smallest larvae were about 11.0 mm SL, and about 12.5 mm SL for the largest. Thus the transformation from the larval to juvenile stage occurred between 11.0 mm to 12.5 mm SL.

The sequence of fin-ray segmentation and branching development is given in Fig.61. Only fin rays that were segmented and branched were counted. Segmentation of fin rays completed at about 9.0 mm SL for the caudal fin, 9.5 mm SL for the dorsal and anal fins, 11.0 mm SL for the ventral fins and 13 mm SL for the pectoral fins. The branching of fin rays of reared specimens was found only in the caudal fin, starting at about 11.0 mm SL and completing at a size over 18.0 mm SL. In wild-caught specimens, the branching of the ventral fins occurred at a size greater than 27 mm SL, whereas branching of the dorsal, anal and pectoral fins began at 41.7 mm SL (Balart,1985).

Squamation

Fig.62 depicts developmental sequence of squamation and the relationship between developmental stage and larval size. Seven stages of squamation were characterized as follows;

Stage A, Scales first appeared as a few rows along the lateral line vertical of the caudal peduncle.

Stage B, Subsequent rapid development of the scale pattern anteriorly toward the operculum, and less rapid dorsally and ventrally.

Stage C, The anterior end of the scale formation reached the operculum along the lateral line. Two rows of scales appeared in the trunk region and six rows at the caudal peduncle.

Stage D, The caudal peduncle squamated completely, consisting of eight scale rows. Maximum 17 to 18 scale rows were observed at the central portion of the body; about half of body surface squamated.

Stage E, Only the nape, breast and base of the dorsal and anal

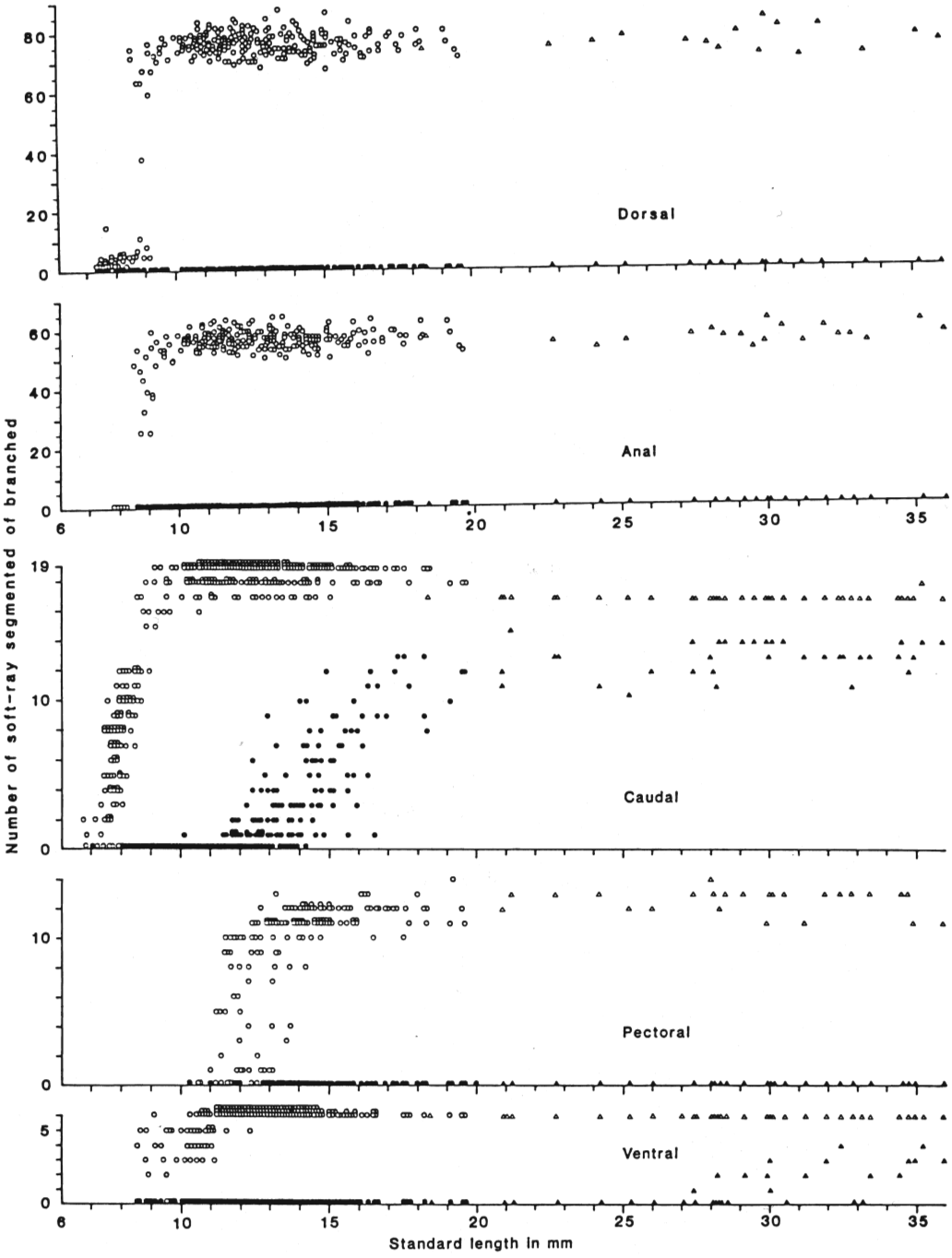


Fig.61. *Paralichthys olivaceus*. Segmentation (open circles and triangles) and branching (closed circles and triangles) for unpaired and paired fins with larval growth. Open and closed circles indicate the reared specimens, and open and closed triangles are wild-caught specimens.

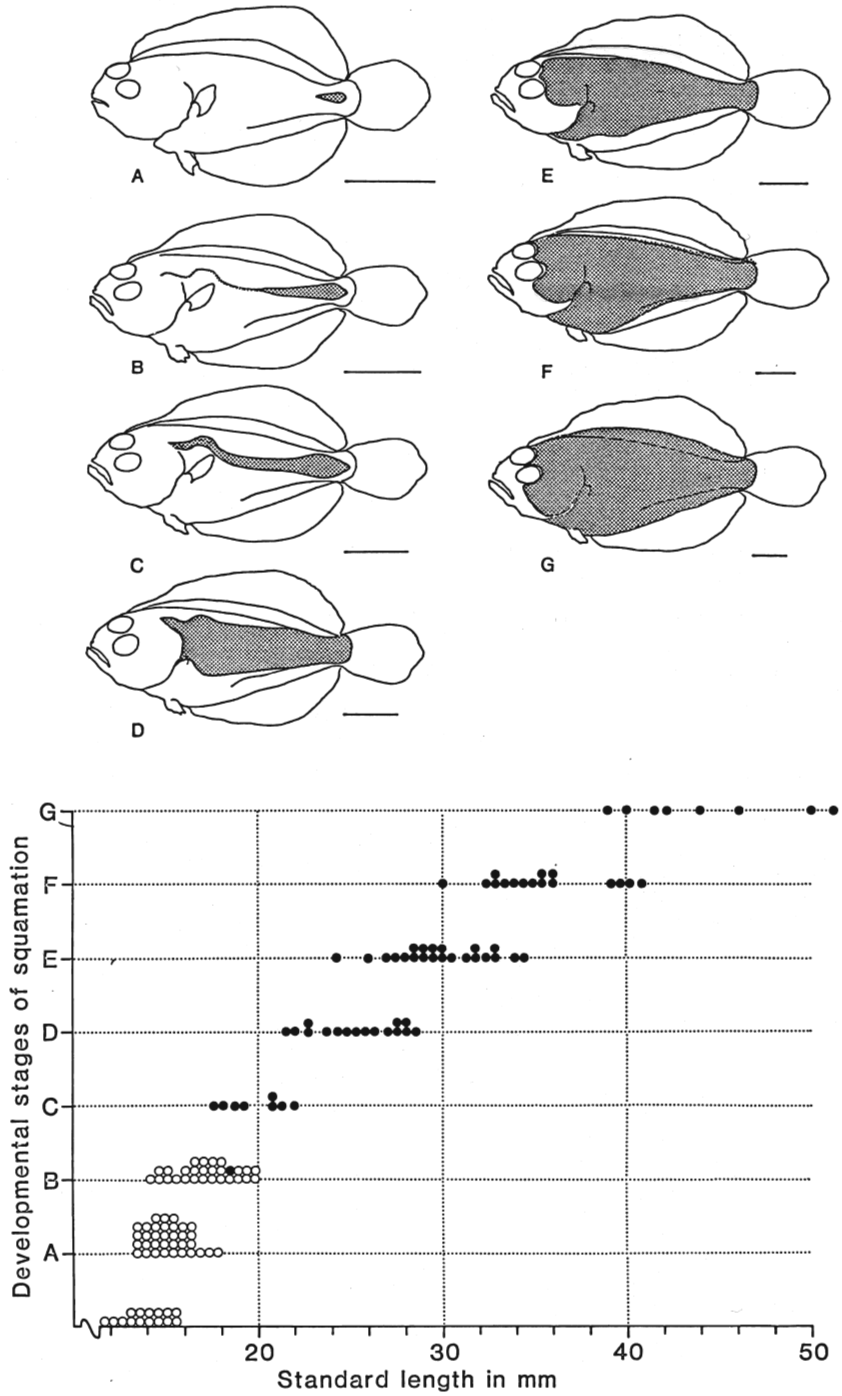


Fig.62. *Paralichthys olivaceus*. The sequence of development in squamation (upper), and its developmental stages plotted against standard length (lower). Open circles indicate reared specimens and closed circles for wild-caught ones. Scales denote 5.0 mm.

fins were devoid of scales.
Stage F, The squamated area extended to the base of the dorsal and anal fins.
Stage G, The trunk and caudal portion were fully squamated. The largest larva without scale was 15.8 mm SL. Squamation began when larvae were 14 mm to 18 mm SL. Full completion was asssumed for larvae after 44.0 mm SL, although the smallest specimen fully squamated was 39 mm SL.

The completion of squamation was observed on the body surface of both sides at 48.2 mm SL larva for wild-caught specimens (Okiyama,1967), and also on the body surface from 20.28 mm to 25.48 mm TL larva reared at temperature from 15 °C to 25 °C (Hsiao-Wei,1965) in the laboratory.

Development of behaviour

Newly hatched larvae were floated during the most of time, and occassionally wriggled for a first 4 days after hatching. After yolk absorption larval activity began to increase; more steap for the fed larvae and gradually for the unfed group (Fig.55). One week after hatching, fed larvae swam most of time. Swimming paths of larvae in the rearing tank were traced for more than one minute every day (Fig.63). Swimming velocities of about 4 mm to 5 mm/sec were recorded for the initial 30 days, and then gradually increased an average of 9 mm to 10 mm/sec. A relatively sharp increment of maximum speed was observed for larvae after 40 days old (10 mm SL long). After that a decrease in swimming speed was observed when larvae more than 47 days old began to inhabit the bottom. However, this trend was not as sharp as those reported for plaice and sole at metamorphosis (Blaxter and Staines,1971). Therefore, calculation of swimming speed in this study was confined to the first 7 weeks of larval life. The larvae of stage H, which had begun to eye migration, usually stayed on the bottom in the tank. In the experiment of swimming performance of this species, rapid increment of swimming velocity was observed for the post-larvae which having no elongated armature, measuring about 5.0-6.0 mm SL. at about 5.0 mm TL.

Sinuous posture is usually found for larvae which have achieved active feeding. S-flex posture is generally observed in marine fish larvae (e.g. Rosenthal and Hemple,1970; Hunter,1980; Houde,1972). In the Japanese flounder, not only was S-flex pos-

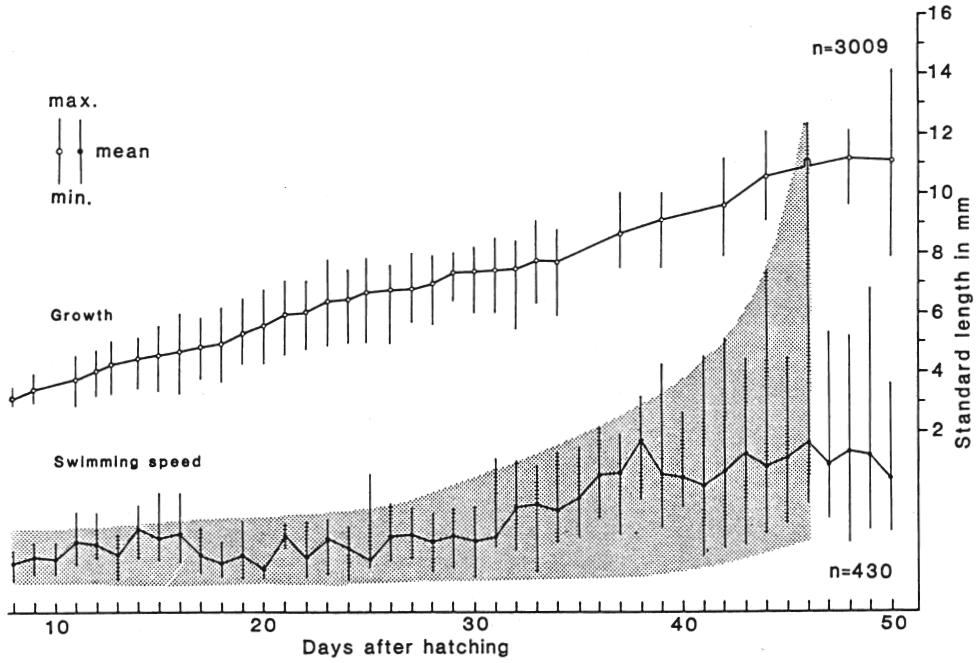


Fig.63. *Paralichthys olivaceus*. Changes of swimming speed plotted against days after hatching. Shadow drawn freehand. n=sample size.

ture observed, but also frequently body bending like omega when larvae reached a stage characterized by elongated armature (Fukuhara,1986a).

Limanda yokohamae

Morphological development and growth

Fertilized eggs are transparent, adhesive and spherical in shape, ranging from 0.743 mm to 0.807 mm in diameter (mean=0.784, SD=0.0265, n=23). The egg diameter determined in this experiment did not differ from that described by Yusa (1960) for the same species. Hatching occurred on day 8 after artificial fertilization at a mean temperature of 11.5 °C. Newly hatched larvae have a large yolk sac (Fig.64A) and range from 3.23 mm to 3.60 mm in SL with an average of 3.46 mm(n=16). Under starvation, 50% of the newly hatched larvae survived until 6 days after hatching, but no larvae survived beyond day 10 to 11 at temperature around 10.7 °C (Fukuhara, 1988).

Newly hatched larvae exhibited an open mouth on day 1 after hatching. On day 2 the mouth became functional and few larvae

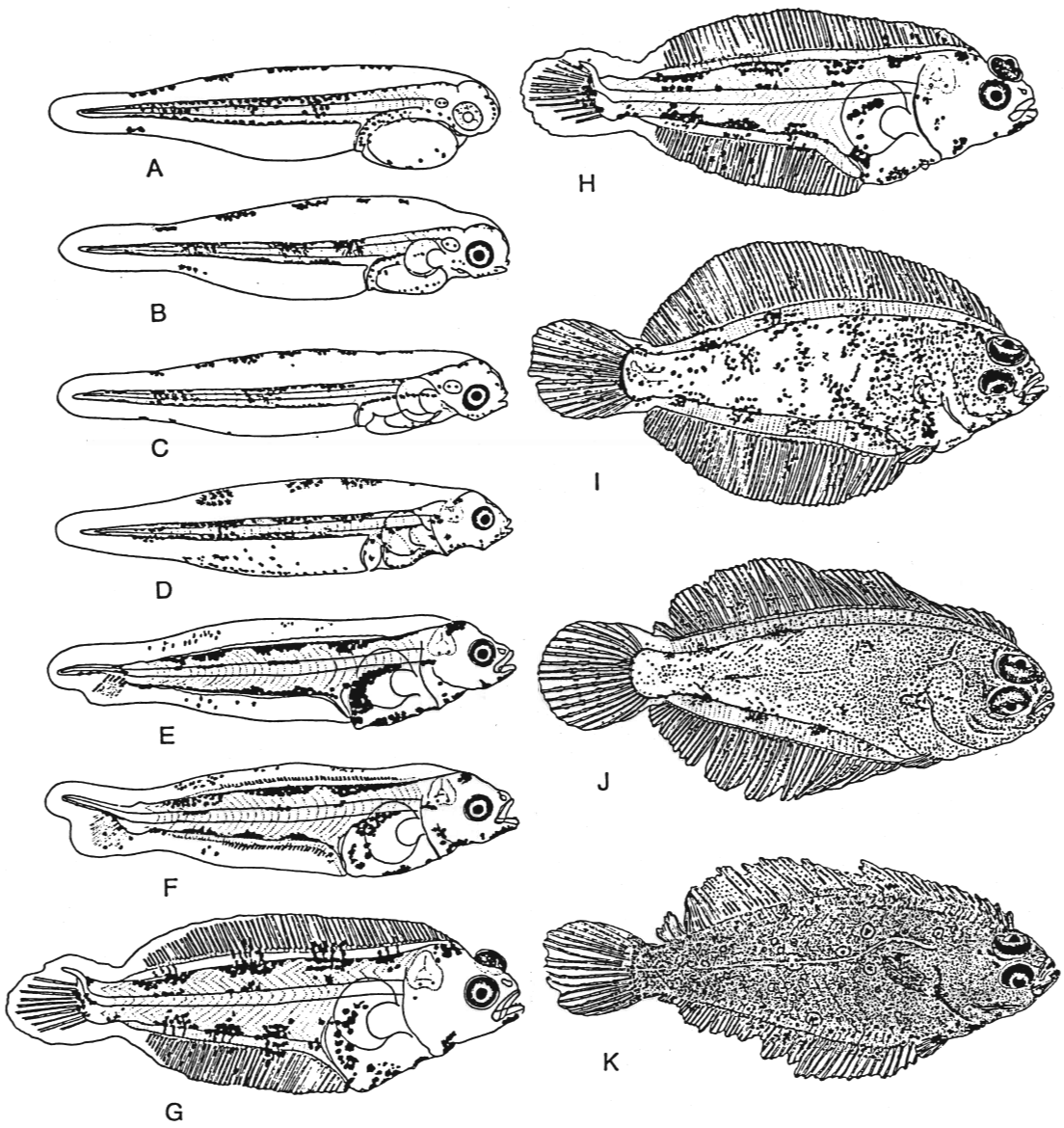


Fig.64. *Limanda yokohamae*. Larval development from newly hatched larvae to young stage. A to H, larval stage; I to K, metamorphosis and young stages. A, 3.4mm SL; B, 4.1mm SL; C, 4.3mm SL; D, 4.8mm SL; E, 8.0mm SL; F, 8.2mm SL; G, 9.4mm SL; H, 9.7mm SL; I, 12.5mm SL; J, 15.6mm SL; K, 21.5mm SL.

started feeding when the yolk was still relatively large (Fig.64B). The yolk was absorbed gradually and completely utilized at day 6 after hatching (Fig.64D). The depth of body muscle became wider with increasing larval length. The cartilaginous hypural bone was first observed in 19 days old larva (Fig.64E). The notochord flexion was discernible when the larvae attained 8.2 mm SL, about 20 days after the hypural element began to form (Fig.64F). The upturned notochord became greater in its angle as the larvae grew (Fig.64G,H). The projected notochord was found in all larvae on day 34, and disappeared in 38 days old larvae. Eyes began to move to an asymmetrical position when larvae attained about 8.8 mm TL, 27 days after hatching. The eye migration was completed in all larvae when they were larger than 11.0 mm SL (Fig.64I). The separated nares were observed when larvae reached 10.7 mm SL. The lateral line was discerned clearly in 70 days old larvae, averaging 18.5 mm SL (Fig.64K). Increment of body height was greater for metamorphosed fish than for larval stages.

Eye migration is a unique development phase in flatfish. Various criteria had been tried to qualify the developmental sequence during metamorphosis. Some difficulties and confusion, however, exist in previous standards to evaluate the sequence of eye migration. To simplify the staging, definitions shown in

Table 2. *Limanda yokohamae*. Stage definition of larvae and juveniles compared with staging of flatfish in previous studies. Alphabetical letters and numbers under author columns refer to staging they used in their respective studies

Stage	Criteria	Ryland (1966)	Minami (1981)
F	Eyes asymmetrical but not visible from the other side	4a	F,G
G	Eyes asymmetrical, eye visible from the other side but pupil not visible	4b	H,I
H	The pupil of the eye visible from the other side, but the pupil of its half not beyond the edge of the head	5	
I	More than half of the pupil beyond the ridge of the head, Completing metamorphosis		J

Table 2 were employed in this study to determine the relationship between developmental stage, age and fish length. The distribution of several developmental stage in surface and bottom waters of the tank, where relative occurrences were plotted against larval age, are shown in Fig.65. Newly metamorphosed fish of Stage I appeared first on day 34 after hatching, when only one larva out of 53 individuals was found to have reached that stage, while 98% of 51 individuals, averaging 9.7 mm SL had complete eye migration on day 43 after hatching. The majority of larvae which swam near the surface belonged to developmental stage F, and no larva of that stage were found after day 38 from hatching. Day degree of 43 to complete the eye migration is comparable to those described by Mututani (1988) at a temperature of 10 °C. The development of bottom dwellers progressed in succession with increasing days from hatching. Larvae which started eye movement trended to settle on the bottom of tank. The similar phenomenon was seen in *P. olivaceus* (Seikai,1985; Fukuhara,1986a).

In Fig.66 shows the size composition of 228 larvae, which commenced eye migration, being 30- to 46-day old, and attaining a total length between 8 mm and 16 mm (7.7-12.8 mm SL). Each developmental stage (G,H and I) overlapped with wide length range is shown. Size variation of the stages became wider with proceeding development. Fish in which eye migration was completed belonged to Stage I, measuring 9.6 mm TL (Minimum) and preceding Stage H, measuring 13.8 mm TL (Maximum). Therefore, metamorphosis occurred between 9.6 mm and 13.8 mm TL.

Contrasted with randomly collected individuals which were captured at the littoral zone during 10 to 16 March 1987 off the laboratory, no marked difference was observed on the relationship between developmental stage and fish length. This obsevation demonstrated that development sequence of laboratory-reared fish was comparable to that of fish randomly caught.

Overall growth of larvae is shown in Fig.67. Growth was slow for the initial phase of larval development, day 15 and day 28, achieving an average daily increment of only 0.2 mm. No increment in length was observed before and during metamorphosis (e.g. days 30 to 45). Thereafter, the growth curve exhibited a relatively sharp rise, with an average daily increment of 0.32 mm. The standard deviation for the average length became definitely larger after metamorphosis than for earlier larval stages. During

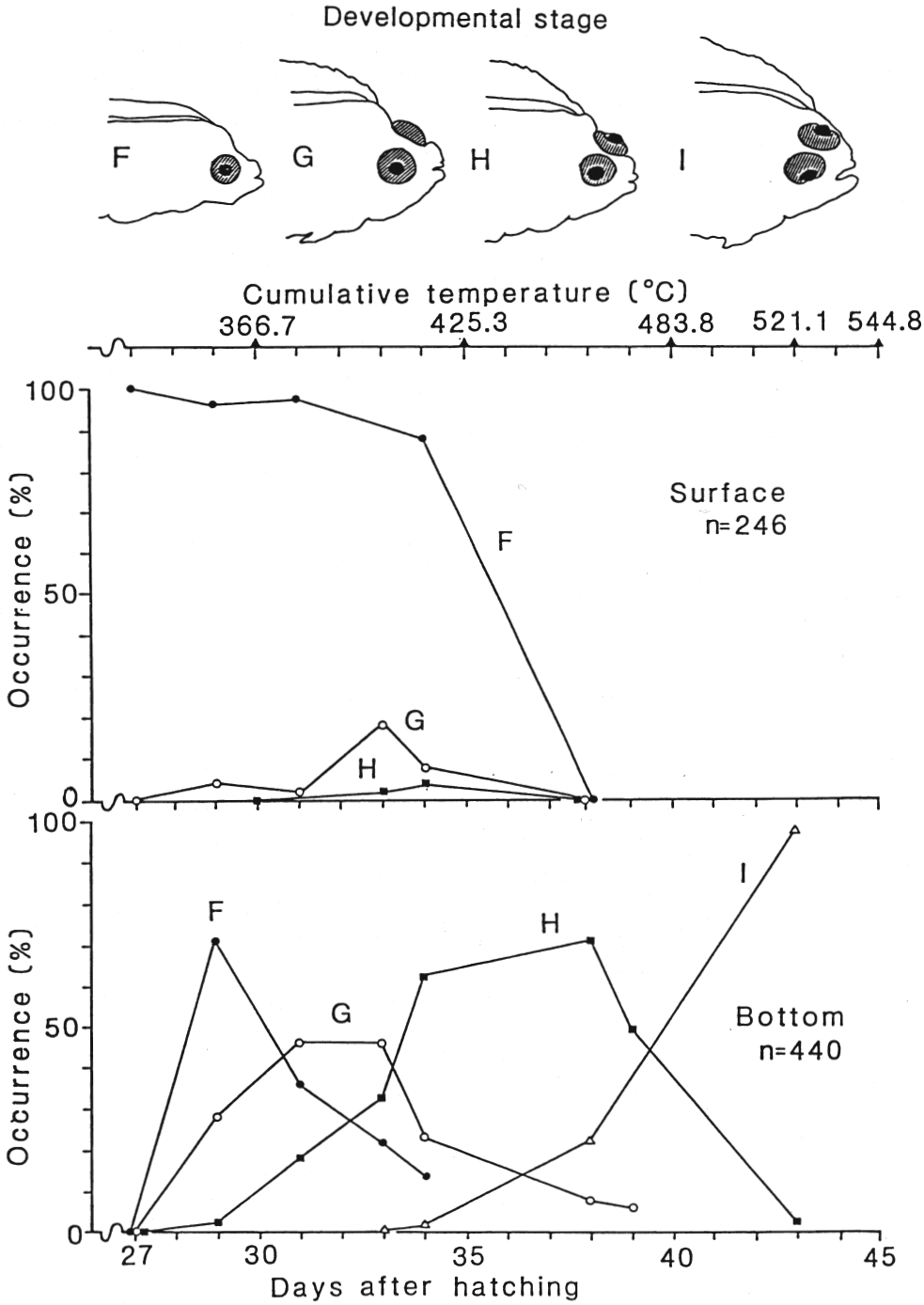


Fig.65. *Limanda yokohamae*. Relationship between larval age in days and developmental stages at surface and bottom in rearing water column. Refer to Fig.62 for the developmental stages. n=sample size.

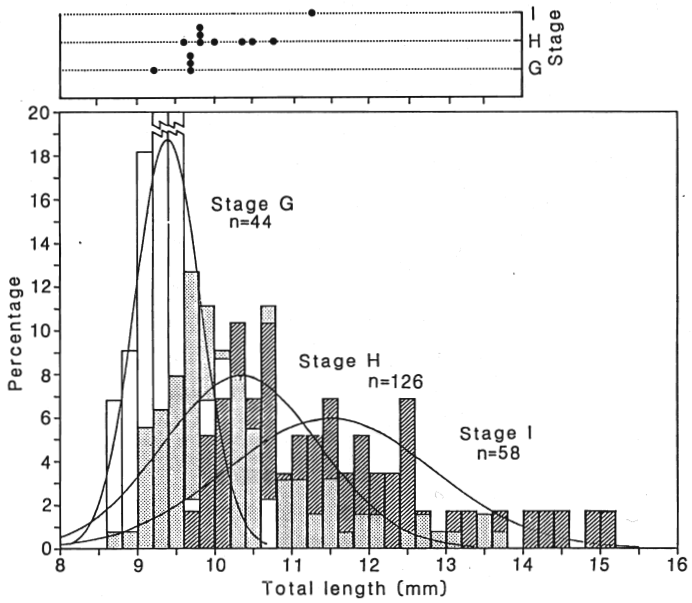


Fig.66. *Limanda yokohamae*. Size distribution of developmental stages G,H, and I in reared individuals. Staging and length relation in randomly collected individuals also shown (closed circles). n=number of specimens sorted to each stage.

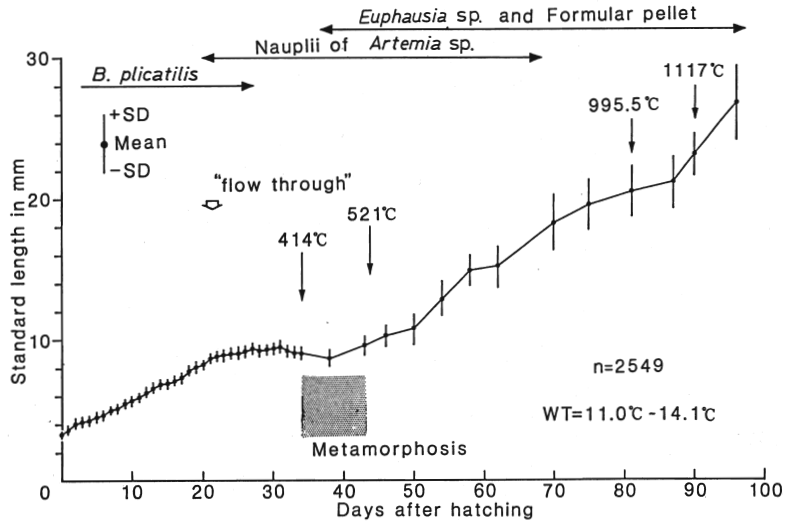


Fig.67. *Limanda yokohamae*. Growth curve of reared larvae and juveniles for 96 days after hatching and prey species given with feeding duration. Open arrow indicates start of running water system and closed arrows show cumulative temperature at each point. Speckled area predicts size range of larvae in which metamorphosis was observed. WT=water temperature; n=number of specimens measured.

the period of metamorphosis, growth in length ceased not only in surface- but also in bottom-dwelling larvae (Fukuhara,1988), a trend observed for both total and standard lengths. Metamorphosis occurred when cumulative temperatures, which summed daily temperature value, ranged between about 410 °C and 520 °C. Fish attained about 20 mm SL when cumulative temperatures reached 995.5 °C. At the given rearing temperature, larvae required a cumulative temperature of 410 °C to commence eye migration.

The relative preanal length changed largely in the larval and metamorphosing stages when the digestive organs began to develop and to differentiate. Proportional preanal length increased steadly from 20 to 35% TL for the early larval stage, and rapidly decreased to 25% TL during metamorphosis. The ratio of preanal length tended to stabilize at 25% TL when the digestive organs were close to adult size (Fig.68).

Standard length was used to examine the development and growth of larvae and juveniles with respect to other morphometric characters. Relationships between standard length, preanal length and total length were expressed by separate linear regression. In both relations, the regression coefficient is higher in larval stages than in juvenile stages. Flection points are clearly discerned during early metamorphosis (Fig.69). Meristic characters also fluctruate largely during metamorphosis.

Fin development

Newly hatched larvae had a prominent larval fin-fold; no pectoral fins were present at hatching (Fig.64A). Fan-shaped pectoral fins without rays developed in 2-day old larvae (Fig.64B). The uniformed fin-fold was present until larvae reached a size of about 8.0 mm SL; this was at a time when the cartilaginous hypural bones and the base of the dorsal and anal fins appeared (Fig.64E). The ossification of a few rays in the dorsal, anal and caudal fins began after larvae attained 8.2 mm SL (Fig.64F). The fin ray development of the dorsal and anal fins progressed from the anterior part to the posterior section with increasing larval length (Fig.64G,H). The rays of the caudal fin segmented first and then the ventral fin buds appeared on larvae, attaining about 9.4 mm SL (Fig.64G). Fin ray development was found to be completed when larvae reached about 12.5 mm SL (Fig.64I). Fin rays in unpaired and paired fins were counted,

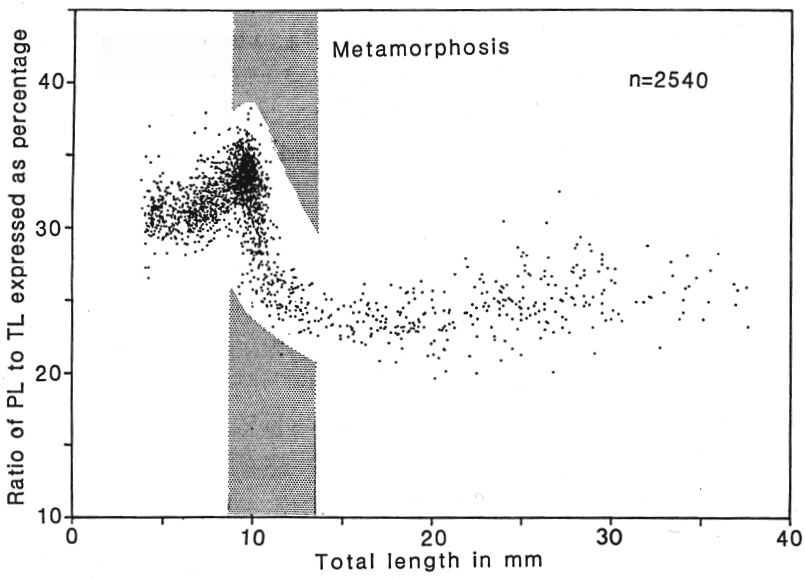


Fig.68. *Limanda yokohamae*. Proportion of preanal length (PL) to total length (TL) for larvae and juveniles reared in laboratory. Specked area indicates range of larval length in which metamorphosis occurred. n=sample size.

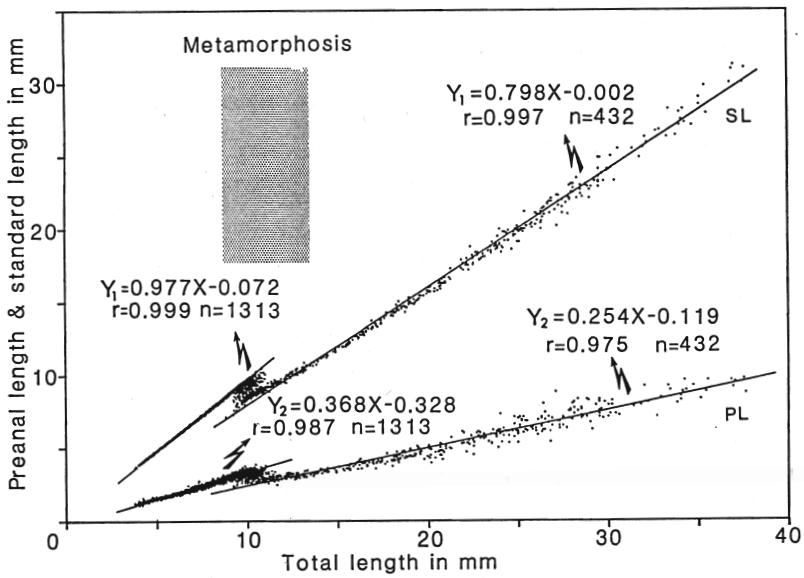


Fig.69. *Limanda yokohamae*. Standard length (SL) and preanal length (PL) plotted against total length. Y1:standard length Y2:preanal length; r=correlation coefficient; n=sample size.

with 68 to 75 in the dorsal fin, 55 to 61 in the anal fin, 18 in the caudal fin, 10 to 11 in the pectoral fin and 6 in the ventralfins. The fin ray numbers varied widely and this variation was greater than in randomly collected individuals (Kato et al.,1974; Minami,1981).

Pigmentation

Newly hatched larvae had numerous melanophores in dorso- and ventro-lateral rows on each side of the body, and small melanophores converged on three sections on the lateral surface of the body. The gut was densely covered with melanophores. A few melanophores were present on the snout and on the yolk sac. The dorsal side of the fin-fold was heavily pigmented in the yolk sac larvae (Fig.64A). Pigment spots increased in number on the trunk, caudal region and the fin-fold as larvae grew larger (between 4.1 mm and 4.8 mm SL, Fig.64B-D). Melanophores appeared along the dorso- and ventro-lateral surface of the body and intensified in colour during post-larval stages (between 8.0 mmm and 9.7 mm SL; Fig.64E-H). Melanophores were widely distributed on the head and trunk regions, when larvae exceeded 12.5 mm SL, and the caudal region and fin-fold were sparsely pigmented when the larvae completed eye-migration (Fig.64I). The body surface was heavily covered with tiny melanophores in metamorphosed fish (Fig.64J), and ocellated pigment pattern were dispersed when the juvenile was more than 20 mm SL (Fig.64K). The pigment development changed its feature distinctly after metamorphosis.

Squamation

Scale first appeared after the larvae completed their eye-migration. The sequence of scale development and relationship between developmental stage of squamation and fish length are shown in Fig.70. Six stages can be characterized as follows:

Stage A, A few scales were seen on the midline of the caudal peduncle. No scales were obserevd on the blind side.

Stage B, Scale appeared in the caudal peduncle and extended their coverage area anteriorly. The anterior end of this area reached the middle of the body. On the blind side, first scales appeared on the caudal peduncle.

Stage C, The scaled area extended along the lateral line, and the anterior end reached the operculum. The squamation progressed

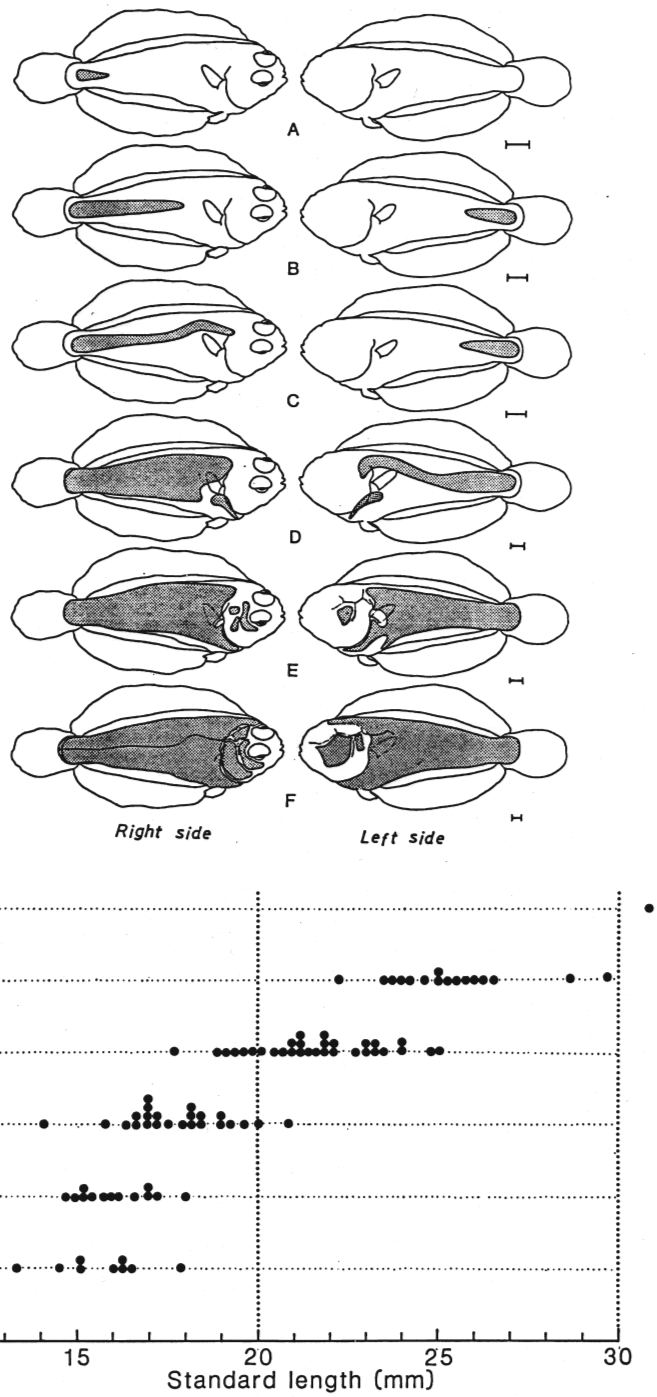


Fig.70. *Limanda yokohamae*. Sequence of squamation in eyed and blind side (upper), and its developmental stage in relation to standard length (lower). Scales depict 1.0 mm.

more slowly in the blind side.

Stage D, The scaled area reached anteriorly the operculum, and posteriorly the base of caudal fin. The caudal peduncle was fully covered with scales. A patch of scales appeared beneath the pectoral fin on either side of the body. On the blind side, the squamated area reached the operculum at the anterior end.

Stage E, At this stage the portion of the nape, the pectoral fin base and the ventral fin margin were the only body areas devoid of scales. The area lacking scales on the blind side was larger than the one on the eyed side.

Stage F, Both side of the body were fully squamated at this developmental stage. The head region was also partly squamted.

Scales first appeared in larvae after they had finished their metamorphosis, and this process occurred in larvae as small as 13.2 mm SL, although most of them were larger. Squamation progressed with increasing larval length. Fully squamated juveniles usually attained a standard length of more than 35 mm SL were assumed to have completed their scale formation.

Development of the digestive tract

The alimentary canal of larvae remained unlooped until the larvae reached 4.8 mm SL. The morphological development of the digestive tract and its developmental stages plotted against larval length are depicted in Fig.71. The coiled digestive tract was formed when larvae attained more than 4.8 mm SL (Fig.71A). Posterior portions of the digestive tract curved deeply as the larvae grew (Fig.71B-E). Rudimentary pyloric caeca appeared first in larvae of about 12.0 mm SL (Fig.71C). The pyloric caeca became larger with the growth of the fish and the configuration of the coiled digestive tract exhibited a convex shape. As the larvae of stage C were corresponded to the metamorphosis or beyond metamorphosis, the appearance of pyloric caeca was indicative of the onset of metamorphosis. All fish larger than 35 mm TL were assumed to have reached the adult-like form of the digestive tract.

Development of behaviour

Newly hatched larvae floated passively near the surface, being at the mercy to the water current due to the aeration in the tank. Occasionally, locomotive activity was observed for a few seconds. Swimming activity increased with larval age, and this

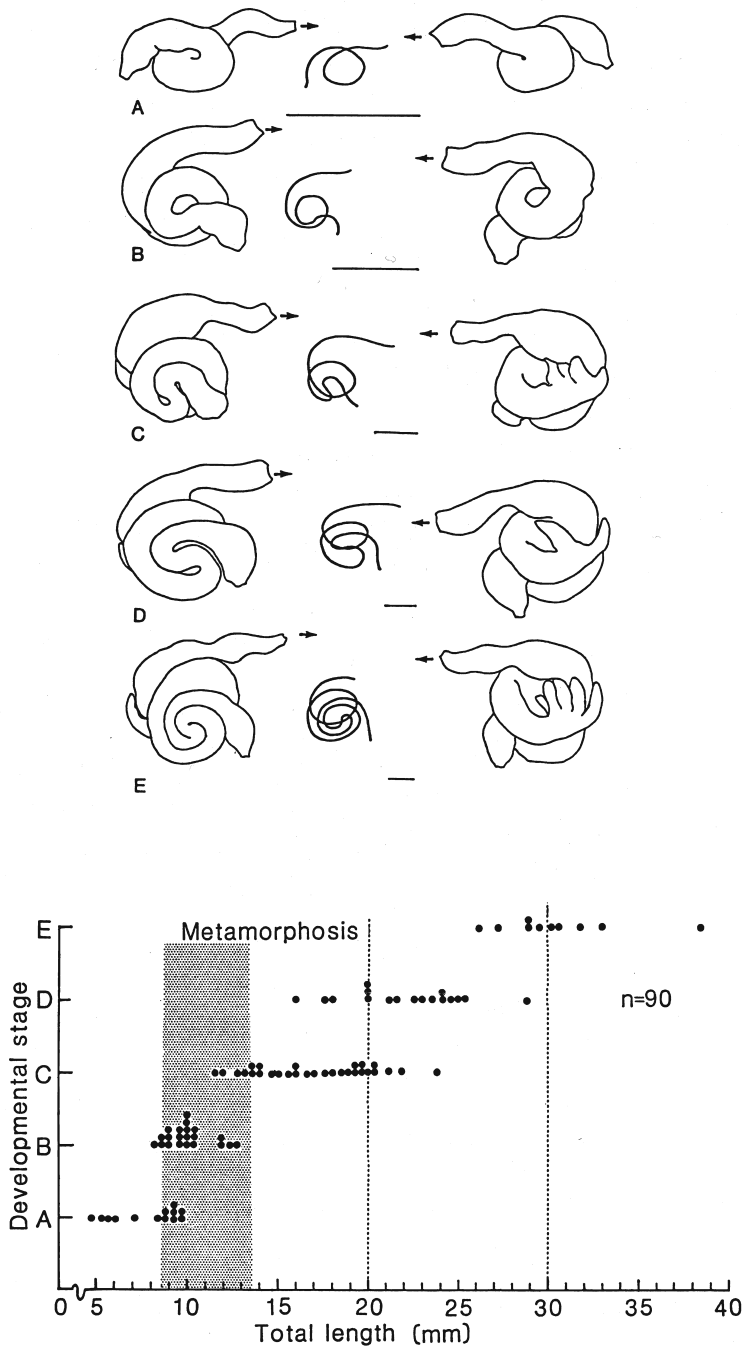


Fig.71. *Limanda yokohamae*. Sequence of development of the digestive tract of larvae and juveniles. Arrows indicate direction to head (upper), and its developmental stages plotted against total length (lower). Scales indicate 1.0 mm.

increase was more rapid for fed than for unfed larvae. The swimming activity of fed larvae levelled off on day 4 after hatching, shortly before complete yolk absorption, whereas that of unfed larvae reached its maximum on day 5 after hatching, with a downward trend thereafter. The feeding incidence of fed larvae increased clearly with swimming activity (Fukuhara, 1988). The development of swimming speed in relation to larval growth from the time onward when larvae started to swim actively is shown in Fig.72. Swimming speed increased gradually with larval growth, but its ratio to standard length is almost stable, varying from 1.4 SL to 1.7 SL. No observations were made for larvae older than 32 days old. Because larvae began to settle on the bottom of the rearing tank before completing eye-migration, which was shown before (Fig.65). The bottom-dwelling fish usually preyed on the feed given to them at the bottom of the tank. They rarely swam in the middle or upper layers after they settled in the tank.

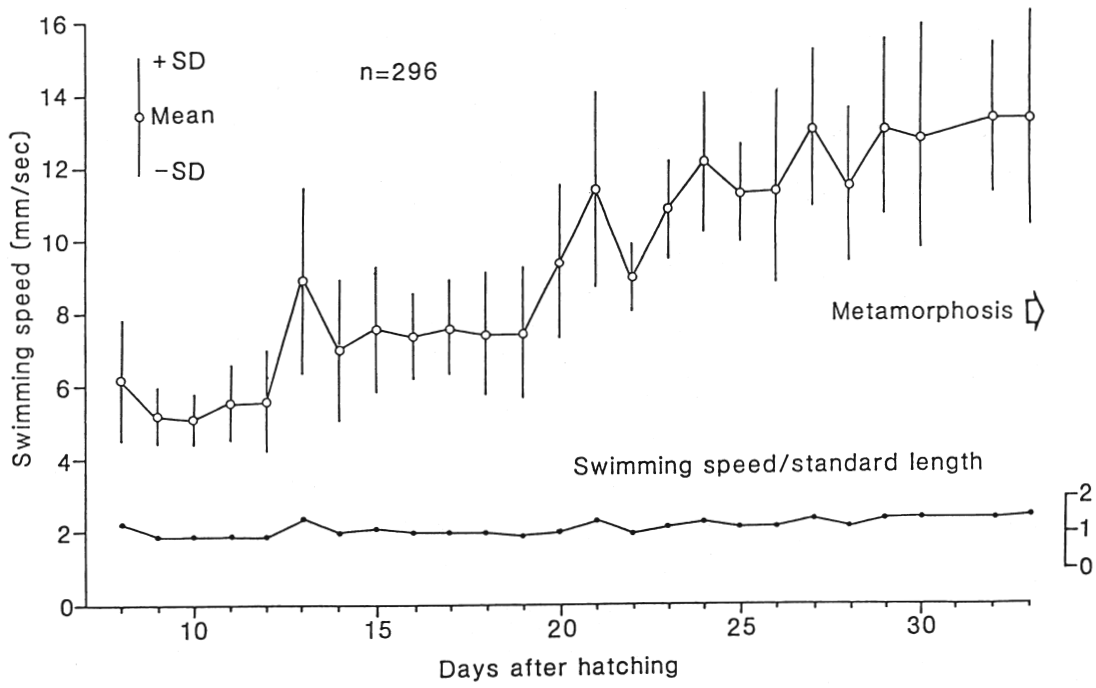


Fig.72. *Limanda yokohamae*. Swimming speed of larvae after initiating active locomotion and its ratio in relation to standard length. n=number of larvae investigated. Arrows indicates the start of metamorphosis.

Discussion

The yolk existence and the completing fin rays with fixed number are prevalently employed to define developmental stages in the early life history of fishes; transfer from pre-larvae to post-larvae for the former, and post-larvae to juveniles for the latter (e.g. Uchida et al.,1958; Watanabe, 1970; Watanabe and Hattori,1971). This definition is useful and realizable from a viewpoint of simplicity for morphological observations involving taxonomical purposes. However, better understanding on biological characters in larval development required comprehensively detailed information on the developmental sequence of various organs, besides fin development, regarding functional and behavioural aspects and their implication during the development. Watanabe (1970) demonstrated with common mackerel, *S. japonicus* implicational significance between morphological development and ecological change to clarify the ecology of the species.

Structural differences of fins were reviewed for the adult from taxonomical and anatomical focuses (Lagler et al.,1962; Norman and Greenwood, 1975; Bond,1979; Moyle and Cech Jr.,1982). However, little is known about the significance of diversity in fin development on early life stage of fishes.

Morphological appearance in fin-fold resemble closely between species at the time of hatching (Fig.73). As larval growth progressed, however, the fin-fold developed distinctly into fixed shape varying greatly with the species (Fig.73). Distinctive fin shapes which being similar to the adult form were exhibited morphologically when these fishes reached the juvenile stage (Fig.74). Marked difference among the species is seen in the developmental process of larval fin-fold; change from continuous to separate shapes. The fin-fold of pelagic species separated discernibly than that of the demersal fish species. After the fishes reached the juvenile stage or beyond the metamorphosis, specific distinction was characterized by hind margin of the caudal fin. Fast-swimming fish group (e.g. *E. japonica*, *P. altivelis* and *S. quinqueradiata*) is characterized by the furcated shape. Slow-swimming group (e.g. *E. akaara* and *H. otakii*) exhibited truncated of emarginated margin, and bottom-dweller such as *P. olivaceus* and *L. yokohamae* had rounded caudal fin. The caudal fin margin furthermore is indicative for staging juvenile in each

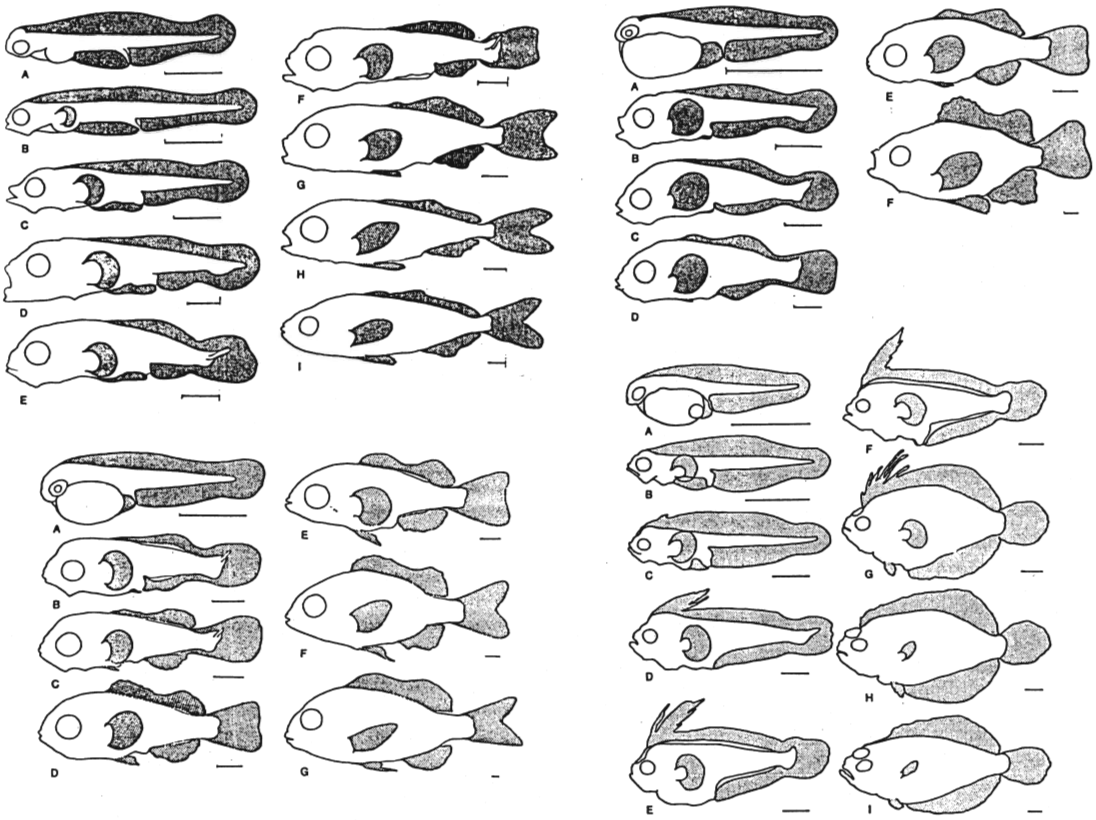


Fig.73. Schematic illustration of morphological development of the fin-fold with special reference to external appearance. *S. quinqueradiata* (upper left); *P. major* (lower left); *O.fasciatus* (upper right); *P. olivaceus* (lower right). Drawn to the same size but not the same scale.

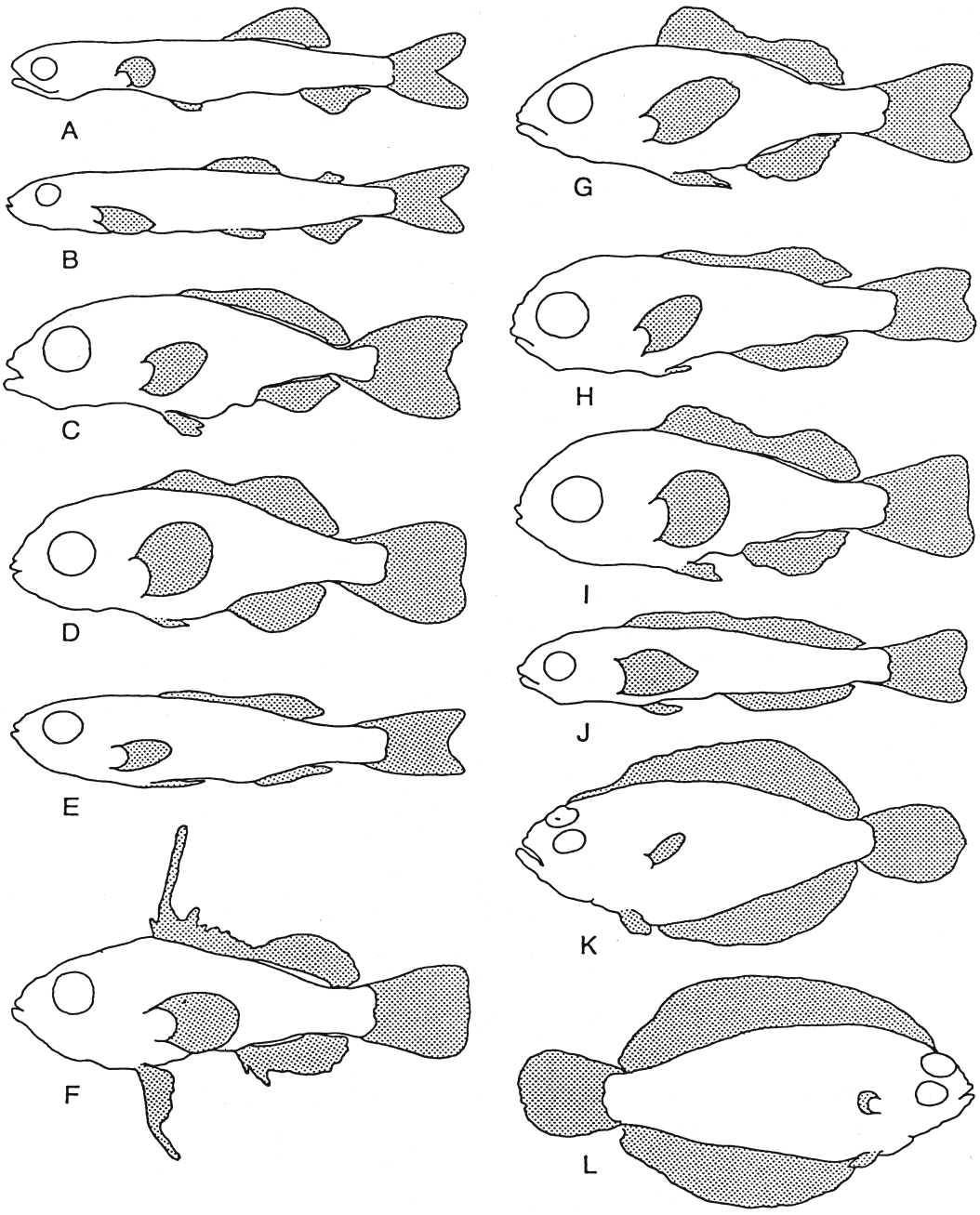


Fig.74. Schematic illustration of external appearance of each fin at the developmental stage of newly transformed juvenile. A, *E. japonica*; B,*P. altivelis*; C,*S. quinqueradiata*; D,*O. fasciatus*; E,*L. japonicus*; F,*E. akaara*; G,*A. schlegeli*; H, *E. japonica*; I,*P. major*; J, *H. otakii*; K, *P. olivaceus*; L, *L. yokohamae*. Drawn to the same size but not the same scale.

species. This indicative character is useful to evaluate roughly the developmental stage in practical rearing activities. Because the character of the caudal fin was observed for a rather short time interval of morphological transformation from post-larvae to juvenile. The pectoral fins also revealed specific features during its developmetal process; rounded pectoral fins changed with larval growth to pointed shape for the most species, but decreased in size or degenerated for pleuronectid fish, *P. olivaceus* and *L. yokohamae*. Likewise, the ventral fins usually changed its shape from triangular form to specific ones of each species; falcate, pointed or rudimentary with larval growth (Fukuhara,1984a).

It therefore is likely that each developmental phase defined by morphological change of fins seems to differ characteristically with various characters and behavioural performance.

Sparid fish increased their swimming speed steadily as they grew after pre-larval stage compared to pleuronectid fish, and the former fish swam faster with a ratio of 3-5 SL/sec (Figs.37, 48) than did the latter one with 1-1.7 SL/sec (Figs.63, 72) when they approached the juvenile stages. In addition, even for the sparid fish swimming speed of black sea bream increased more steeply with its growth than those for the red sea bream (refer to Figs.37, 48).

These lines of evidence suggest that the completion of fin rays may be accompanied by not only morphological changes but also structural development, and consequentially contribute to the behavioural development and ecological change. The different manners in fin development from the yolk sac larvae to juveniles are interpreted to indicate the diversity of biological characteristics. Therefore, to know the sequence of larval development from a functional viewpoint is needed to provide useful information to understand the life mode of different species.

Table 2 shows the common sequence in morphogenesis, organogenesis and behavioural development for the early life history stage of fish investigated in this study. The course of early development of larvae may be divided into three stages; pre-larvae, post-larvae and juveniles in terms of energy source and fin development.

In each developmental stage, organogenesis and behaviour revealed different developmental phase. During the pre-larval to

post-larval stages, various characters commenced to appear and differentiate successively. The change of energy supply from an endogenous to exogenous source had been studied in various larval marine fish species (e.g. Tanaka,1973; May,1971; Houde,1974; Hunter,1980). The transitional period was identified as a critical period that could cause high mortalities during early life history. Iwai (1972) reviewed the diversity of the onset of initial feeding in various species, and stated that yolk-sac larvae which were able to feed on prey successfully had a better survival potential than those starting later. The transitory period of during which the source of energy supply changes from endogenous to exogenous food is very short in *E. japonica* (Fig.11), *P. major* (Fig.27) and *P. olivaceus* (Fukuhara,1986a).

Therefore, a delay in initial feeding of more than 24 hrs after eye pigmentation or yolk absorption is considered critical for the survival rate in these species as were reported for various marine fish larvae; common mackerel (Watanabe,1970), subtropical marine fishes, *A. mitchilli*, *A. rhomboidalis* and *A. lineatus* (Houde,1974), *S. quinqueradiata* (Umeda, 1978) and rabbitfish, *S. guttatus* (Bagarinao,1986; Avila and Juario,1987). The organogenetic development relating the energy source largely depended on temperature regimen (Houde, 1974).

Whereas, *A. schlegeli*, *H. otakii* and *L. yokohamae* were able to use the yolk energy until they initiated the feeding of planktonic food organisms, grunion, *L. tenuis* (May,1971), jack mackerel, *Trachurus symmetricus* (Theilacker,1978), Pacific mackerel, *Scomber japonicus* (Hunter and Kimbrell, 1980), Japanese sand eel, *A. personatus* (Yamashita and Aoyama,1985) and seabass, *L. calcarifer* (Kohno et al.,1986) may have a higher survival potential for yolk sac larvae in terms of energy utilization.

Various organs then began to change in shape and in length intensively for a period from post-larvae to juvenile stage. Therefore, marked changes in qualitative changes of organs and of feeding habit from living to dead stuff occurred coincidently when fish reached the juvenile stage. Fundamental structures were completed in fin rays and in the digestive system for newly transformed juveniles, and initiations of squamation and stripe formation were perceived after the transformation began. Juveniles which fully completed fin ray branching, squamation and stripe formation may exhibit different characteristics than did

they before. Because these characters are central parameters to govern the change of life mode. Developmental transfer from ray segmentation to branching implies increasing complexity of locomotion and resistance to the water movement. The completion of squamation and pigment pattern also implicate the development of functional roles relevant to protecting body surface and concealment.

Elongated structure of the fins disappeared just before or after transformation in *P. olivaceus* and *E.akaara*. The elongated fins are supposed to play a role in sustaining the fish body and protecting from predator during pelagic stage (Moser,1981). As to Lutjanid fish, which also has elongated fins for pelagic juvenile, the elongated fin disappear completely when they reach the benthic juvenile, measuring 34.8 mm SL (Mori,1984).

Accordingly, the disappearance of diagnostic structure of the fins also indicate presumably the shift of habitation.

Concerned with behaviour, active and relatively uniform swimming performance changed gradually to different manners of behaviour; settling in the tank for sparid fish, *E. akaara*, bottom dwelling for pleuronectid fish and schoaling for *E. japonica*. In addition, cannibalism and territory behaviour were observed frequently at this stage for *P. major* (Yamagishi,1969; Fukuhara,1978; Kitajima,1978), *A. schlegeli* (Fukuhara,1977), *L. japonicus* (Masumura,1976; Iwashita,1979), *E. akaara* (Kayano and Oda,1987), *P. olivaceus* (Harada et al.,1966) and *Sebastes schlegeli* (Hoshiai,1977), and ultimately these behaviours consisted in major causes of high mortality in certain species for mass production in the hatchery works.

Furthermore, the ratio of meristic characters, preanal length to total length, fluctuated largely from pre-larval to post larval stages, then achieved a stable value after transformation from post-larvae to juvenile without exception.

Thus, each developmental stage revealed different phase of morphogenesis, organogenesis and behavioural performance. The shift from pre-larvae to post-larvae, and post-larvae to juveniles may be drastical and also critical in the early life stage in terms of morphological development as well as morphometric characters.

Transformation or metamorphosis from post-larvae to juveniles varied conspicuously in fish size and in days old post hatching,

as were also seen in the developmental sequence of the fin, scale, stripes and the digestive tract for all fishes observed, and the variations of their development usually become larger with larval growth (see Figs.33, 44, 71). In addition, the variations of development in various characters ultimately resulted in that growth and behaviour (swimming speed) varied coincidently in their performance (Figs.29, 37). Because larger fish and fish with well-developed organs were beneficial for foraging speed, feeding and swimming activities. This causality must occurred in the wild conditions as well as in rearing conditions.

Tanaka(1973) demonstrated the variations in the differentiation time of the digestive organs for *P. altivelis*. From his observations, it was supposed the differentiation time of the organs was related to age more closely than size at least during the early phase, and seemed to correspond with their functional variations.

Fish size of newly transformed juvenile red sea bream ranged between about 8.0 mm and 13.0 mm SL in the reared and randomly wild-caught specimens as was summarized by Fukuhara (1984b). Metamorphosed size of *P. olivaceus* also varied widely with ranges from 9.0 mm to 19.4 mm TL (Harada et al.,1966; Yasunaga,1971; Ishida and Tanaka,1976; Hiramoto and Kobayashi,1979) for the reared specimens, and ranging from 14.0 mm to 17.0 mm SL for the wild-caught specimens (Okiyama,1967; Imabayashi,1980).

Hence, effect of the morphometric variations on ecological appearances become a central parameter to understand the life mode and response to environmental changes, especially on early stage of larval life in the sea.

Few distinguished difference on developemnt of organs was obsereved between the reared and wild-caught specimens; pigment pattern for red sea bream (Fukuhara and Kuniyuki, 1978), three-line grunt, *P. trilineatum* (Kimura,1987) and the digestive tract for anchovy (Fig.10). Matsuoka (1987) observed the variations in fin structure between reared and wild-caught *P. major*, and postulated the variations might be responsible to that of organogenesis. Blaxter (1975) reviewed the biochemical differences between wild and hatchery fish. He stated that cause of the difference may be attributable largely to environmental factors of prey density, predator, starvation and abiotic conditions between

reared and wild conditions. Further study is desired to clarify the causes for facilitating the rearing techniques of fishes and for taking hold of difference between the reared and wild animals.

Chapter III GENERAL DISCUSSION

1. RELATIONSHIP BETWEEN MORPHOGENESIS AND ORGANOGENESIS

In the previous chapter, the diversity of ontogenetic development in early life stage and characteristics of each developmental stage were described to understand the signification of developmental stage on early life history of different fish species. In this chapter major interests are focused on the relationship between organogenesis and morphogenesis in the developmental stages during larval growth, and its ecological significance on their life. To know the both developments and their mutuality is of importance for understanding biological characters, and a prerequisite for artificial production and management in captivity and in-situ.

1)Morphological and organogenetic changes for larval stage

The first dramatic change of organogenetic characters is the occurrence of yolk absorption and/or oil globule depletion in the early stage of larval life. The change from an endogenous to exogenous source is first critical period for larval survival as mentioned before, and morphologically it reflected on the proportionality of preanal length to body length. The proportional change indicate developmental status of the digestive system. The ratio of preanal length to total length changed remarkably during the period of energetic transition, then proportional value achieved a constant when the fundamental structure of the digestive system were formed with morphological transfer from postlarvae to juveniles.

This finding suggests that organogenetic change of the digestive tract reflects apparently on the appearance of morphological characters. Proportional length of internal organ fluctuated largely during they were developing, and trended to achieve

constant level after the digestive system formed the fundamental structure, which usually observed during transformation as well as newly transformed juveniles.

This implication between organogenesis and morphogenesis is exemplified by some other species. According to Watanabe's investigation (1970), the anus position of larval common mackerel, *S. japonicus* moved anteriorly during the digestive system was developing progressively, and trended to level off after fish reached juvenile stage. Allometric growth of stomach (stomach length/SL) in skipjack tuna, *K. pelamis* revealed a constant ratio of about 30% when they reached the transitional size, 15 mm to 20 mm SL, form post-larave to juvenile, and this evidence was interpreted to show the rapid increase in the function of the digestive organs through the post-larval period (Nishikawa, 1975). Though the length of digestive tract does not increased for yolk sac larvae of *P. olivaceus*, rapid increment of the digestive tract occurred after complete yolk absorption (Yasunaga,1972). In the ayu fish, the alimentary canal changes into an adult form in the larvae measured about 50-55 mm (Matsui,1938; Iwai,1962) at which the PL/TL ratio achieved a constant level (Fig.14).

As approaching the yolk absorption, various organs related to feeding and locomotion begin to differentiate, and ultimately resulted in its morphological change. Appearance of the pectoral fins, eye pigmentation and mouth opening usually occurred prior to complete yolk absorption to compensate foraging food organisms exogenously (Figs.12, 27, 56, Table 3).

The ayu fish not only formed the fundamental structure of the digestive system, but also increased enzyme activity during the transitional stage from larval to juvenile (Tanaka et al.,1972). The differentiation of the digestive tract occurred before complete yolk absorption in the most teleost fish larvae (Tanaka,1969a,b) or rapidly after the yolk absorbed completely in larval rabbitfish (Avila and Juario,1987). Umeda and Ochiai (1973) observed the differentiation of the gastric glands were associated with the digestive function of the stomach in the larval yellowtail.

Smoothly continued fin-fold shaped wavy for its margin with growth, and developed subsequently into separated unpaired fins with primordial rays at the time of morphological transformation from post-larvae to juveniles. Functional structures of fins were

Table 3. Generic summary on development for external and internal organs, and behaviour on early stages of larval life.

STAGING	Pre-larva	Post-larva	Juvenile
MORPHOGENESIS	hatching mouth opening	yolk absorption oil globule absorption	transformation or metamorphosis
BEHAVIOUR	vertical movement → horizontal movement → normal swimming → settling or bottom dwelling (floating → wriggling) (S-flex posture → active feeding)		
FIN DEVELOPMENT	promordial fin-fold (continued) appearance of pectoral fins appearance of ventral fins	forming paired & unpaired fins (separated)	fin rays completion ray segmentation ray branching
SQUAMATION			appearance completion
PIGMENT PATTERN			appearance completion
ALIMENTARY CANAL	straight form	bending or coiling	appearance of pyloric caeca
ENERGY OR FOOD	yolk & oil globule	planktonic organism (rotifer & *Artemia*)	weaning (fish flesh or pellet)

formed after transforming to the juvenile stage; segmentation and branching of fin rays provide flexibility and elasticity of fin ray structure, and considered to increase the efficiency of fin movement which influencing the locomotion (Gosline,1971). Likewise, squamation and pigment pattern, which also developed after fish reached the juvenile, are recognized to play a role of protecting body surface and concealment, respectively (Uchida,1966; Norman and Greenwood,1975; Keenleyside,1979). In considering the functional role of each organ, the development of them may enable the fish to adapt wider changes of environmental conditions. It has been well known that habitation and/or behaviour of juvenile fish differed from those of previous stage in the field investigation; sea bass (Tanaka and Matsumiya,1982), red sea bream (Mori,1980; Tanaka,1985), Japanese flounder (Minami,1982) and mud dab (Yusa,1979) as well as in the rearing experiment (Yamagishi, 1969; Fukuhara,1984a). Therefore, it is reasonable that the change of life mode; habitation, feeding, behaviour and so forth is linked closely with morphological and organogenetic development.

Ecological investigation in the field is restricted to collect serial specimens in order to ascertain developmental sequence and its variation. While, outcome of observations on reared specimens is able to provide these knowledge.

2)Morphological and organogenetic changes for juvenile stage

Fig.75 epitomized the developmental sequence in organogenesis and meristic characters in relation to the morphological transformation, from post-larvae to juveniles. Coincidence of developmental duration was distinctly seen between the onset of constant PL/TL ratio and the transformation. The differentiation of the pyloric caeca and digestive gland was revealed widely at initial phase of the juvenile of various species (Tanaka,1973; Nishikawa,1975 Honma,1983; Ochi et al.,1984).

Concerned with Sparid fish exclusive of *E. japonica*, squamation and stripe development also occurred simultaneously. Squamation occurred intensively after transformation or metamorphosis, and its developmental sequence was associated with those of segmentation and branching of fin rays. In this connection, the period of squamation was comparable to that of fin segmentation for the species ; *O. fasciatus*, *A. schelegel*, *P. major*, *P. oliva-*

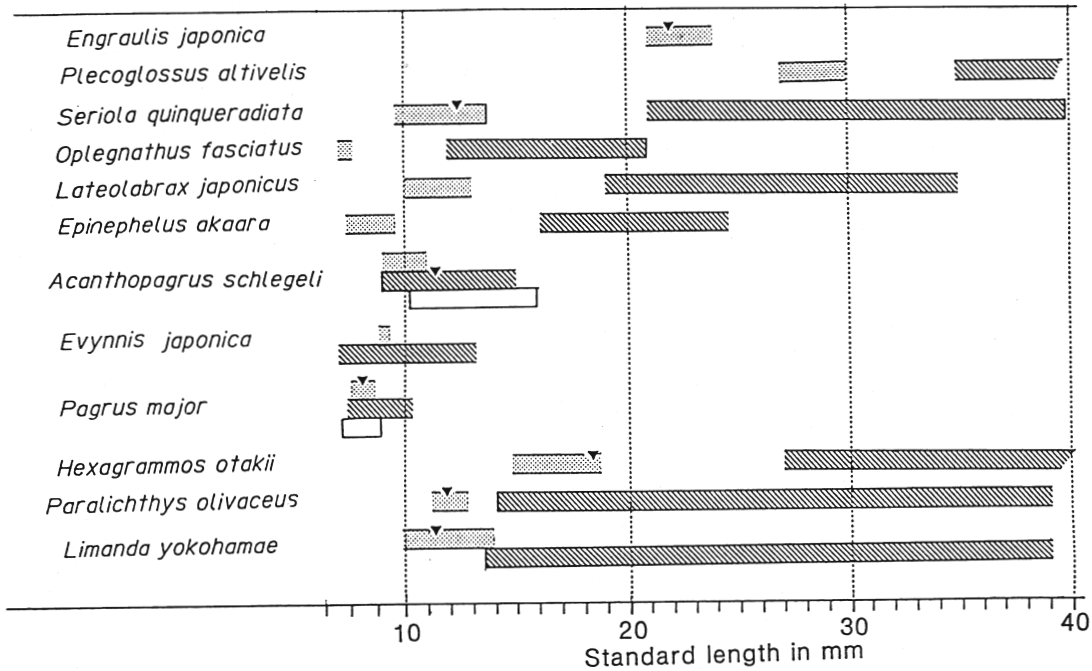


Fig.75. Duration of development in squamation, pigment pattern and morphological transformation from post-larvae to juvenile with different species. Speckled area, morphological transformation; striped area, squamation; blank, stripe formation. Flection point of preanal length to total length is also shown by closed triangles. Refer to the text for the detail of PL/TL ratio.

ceus and *L. yokohamae*, and to fin branching for *S. quinqueradiata*, *L. japonicus* and *H. otakii*.

Additionally, the squamation is assumed to be indicative characters for starting the shift of the habitation in the migrant fishes. The ayu fish change its habitat from estuaries to more brackish waters, namely beginning the anadromous migration when they complete the squamation at about 55 mm SL (Fig.19). As to Japanese sea bass, *L. japonicus* larvae distributed in the sea water area in mid March ascended the fresh water zone in mid April when they attained the mean standard length of 20.1 mm, ranging from 15 to 25 mm SL (Matsumiya et al.,1982). The standard length of ascending behaviour correspond to fish size to complete the squamation (Fukuhara and Fushimi,1982; Fig.75). Kaeriyama and Bunya (1982) found that the squamation of chum salmon, *Oncorhynchus keta* was the most practical criterion of the phasic change from fry to fingerling and habitat change from fresh to saline

waters.

These findings show the ecological significance of squamation to acclimatize new habitation. Therefore, the completion of squamation and fin ray structure is useful information to know the ecological change from a viewpoint of morphogenesis.

Shirota (1978a,b) focused the relationship between upper jaw length and its morphological and ecological significance in various marine fish larvae and found that a marked inflection point on a proportional length of upper jaw to total length is related to the morphological transition and ecological changes. It was similarly reported for chum salmon, *O. keta* that the flection point of upper jaw length to fork length was seen during the transformation from post-larvae to juvenile (Kaeriyama,1986).

Consequently, morphological development linked closely with the development of organogenetic characters during the larvae progressed their growth. The intimate interplay in the development of both characters play a important role to acquire various capability, which resulting in adaptation to new environmental conditions.

2. RELATIONSHIP BETWEEN ORGANOGENESIS AND BEHAVIOUR

In the early life history of fish, the significant of morphological development and organogenesis may be clarified more definitely when both variables are evaluated in contradistinction to the behavioural development. The behavioural development is the most important information to understand the life mode of larvae and juvenile. Numerous studies have conducted on the relationship between behavioural development and organogenesis; sensory organs (Iwai,1980; Kawamura et al.,1984; Kawamura and Ishida,1985) and muscle (Matsuoka and Iwai,1984; Matsuoka,1987). O'Connell (1981) reviewed the functional effects of various organs on behaviour and ecological implications in northern anchovy and other teleosts. However, little is known about knowledge as to implication between organogenetic development and behavioural development in the early life stage.

The object of this section is to consider the relationship between organogenesis and behavioural development and its influence in the life mode of early life stage.

1)Behavioural development and organogenesis of larvae with growth

In the newly hatched larvae, marked change of larval behaviour was seen initially in the time spending to move and to rest. A relatively longer time of rest usually interrupted by a short darting or movement for the pre-larval stage. These manners of larval locomotion were observed vigorously in herring (Rosenthal and Hempel,1970) and northern anchovy (Hunter,1972). Time of movement of yolk sac larvae increased certainly with larval growth. This locomotion change related closely with existence of the yolk sac and the oil globule. The locomotion time increased sharply as the yolk and oil globule were absorbed (Figs.11, 36, 47, 56). After the yolk and/or oil globule were exhausted completely, unfed larvae became inactive rapidly and ultimately deceased. These observations suggest that the yolk sac and oil globule are the origin for locomotive activities. Furthermore, appearance of the pigmented eyes, the pectoral fins and functional mouth are also needful for initiating active movement for the pre-larvae. Moving time of *E. japonica* under unfed conditions (Fig.11) did not rise sharply, about 20% of observation time, as did other species; *P. japonica*, *A. schlegeli* and *P. olivaceus*, and declined rapidly after yolk absorption. This behavioural difference may be attributable to the existence of oil globule, and which indicate that the oil globule is more important energy source for locomotion than the yolk sac.

Fig.76 shows the changes of feeding incidence, percentage of larvae which ingested food organisms in their gut, with increasing locomotive activity for larval *E. japonica* and *L. yokohamae*. For both species, a sharp rise of the feeding incidence was followed by locomotive activity. This finding indicates that initiation of larval movement derived from the requirement of endogenous energy. After larvae shifted swimming manners from vertical to horizontal movement, larval swimming increased steadily with their growth. Swimming performance which differed from species to species is attributable largely to sequence in the fin development. Increment of swimming speed with larval growth is shown in Figs.77 and 78 for *Pagrus major* and *P. olivaceus*, respectively. *P. major* increased their swimming speeds harply compared to that for *P. olivaceus*. The swimming speed of *P. major* is three time greater than did *P. olivaceus* for the maximum. This difference in swimming performance may resulted

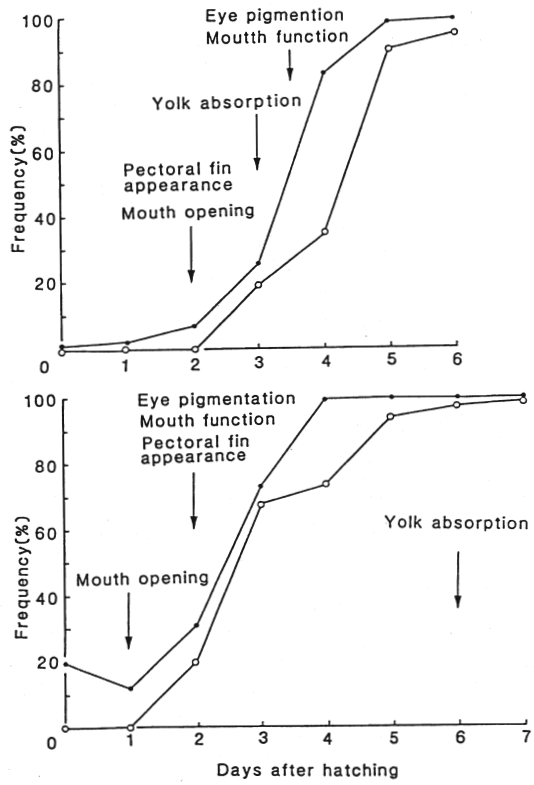


Fig.76. Changes of locomotion activity, feeding incidence and morphological characters during early larval stages in *E. japonica* (upper) and *L. yokohamae*.

from the fin structure. Sharp rise in swimming speed of *P. major* occurred when the continuous fin-fold began to develop into the separate shape. In addition, the caudal fin changed coincidentally its marginal shape from rounded to truncated with increasing swimming speed. Whereas, the swimming speed of *P. olivaceus* increased gradually with growth until they began to settle on the bottom in the tank. No marked change of fin-fold, excepting disappearance of the elongated armature was observed with the morphological development. It is likely that *P. olivaceus* began to settle on the bottom as early as possible to compensate poor swimming ability. In the rearing tank survivors stayed on the bottom at the developmental stage H (Fig.55), before complete eye migration.

Thus, the fin development and structure are assumed to play a important role for swimming activity. According to field observation, larval *P. major* was attacked by predator, Chaetognaths,

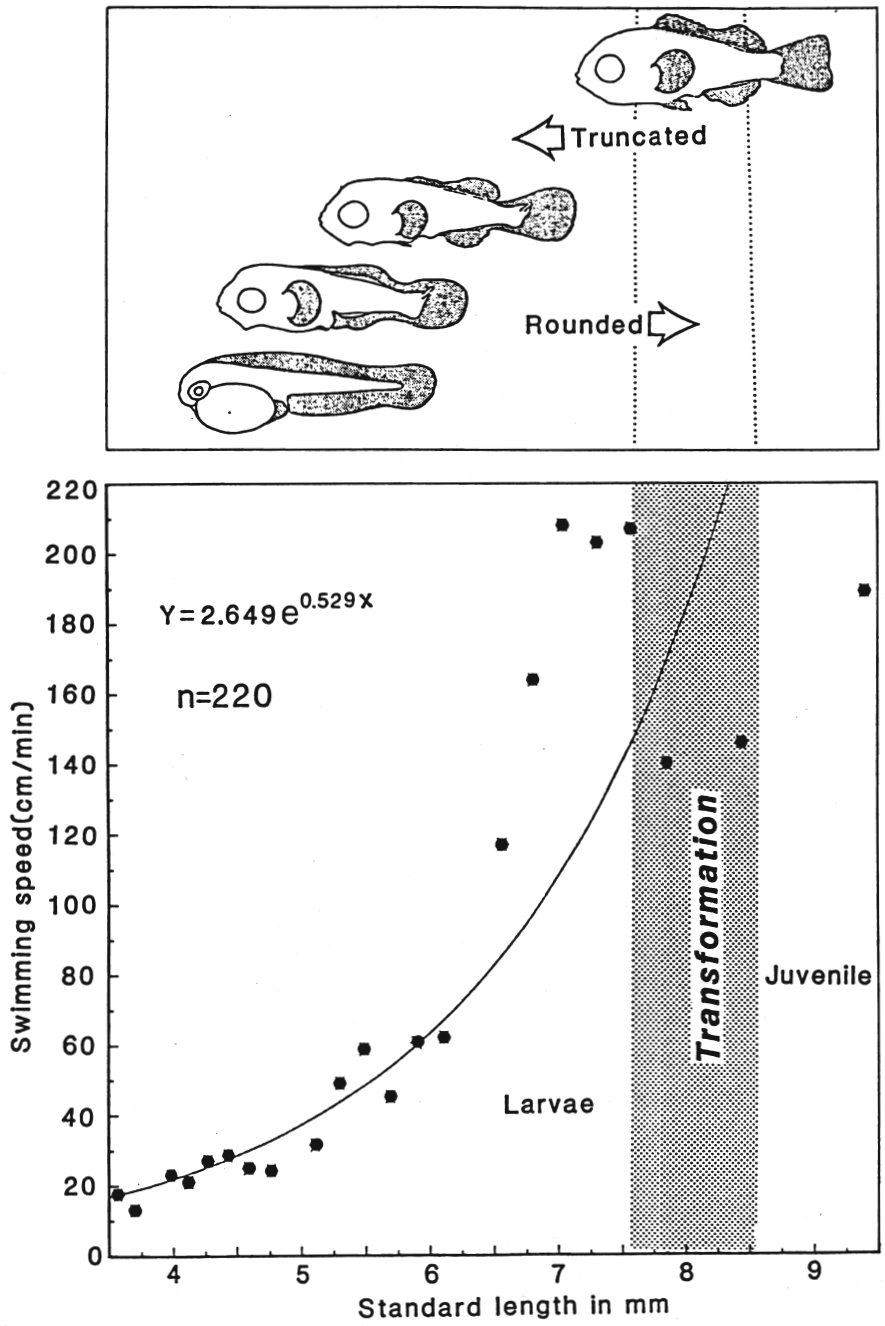


Fig.77. *P. major*. Increment of swimming speed with larval growth in relation to morphological changes of the caudal fin. n=sample size.

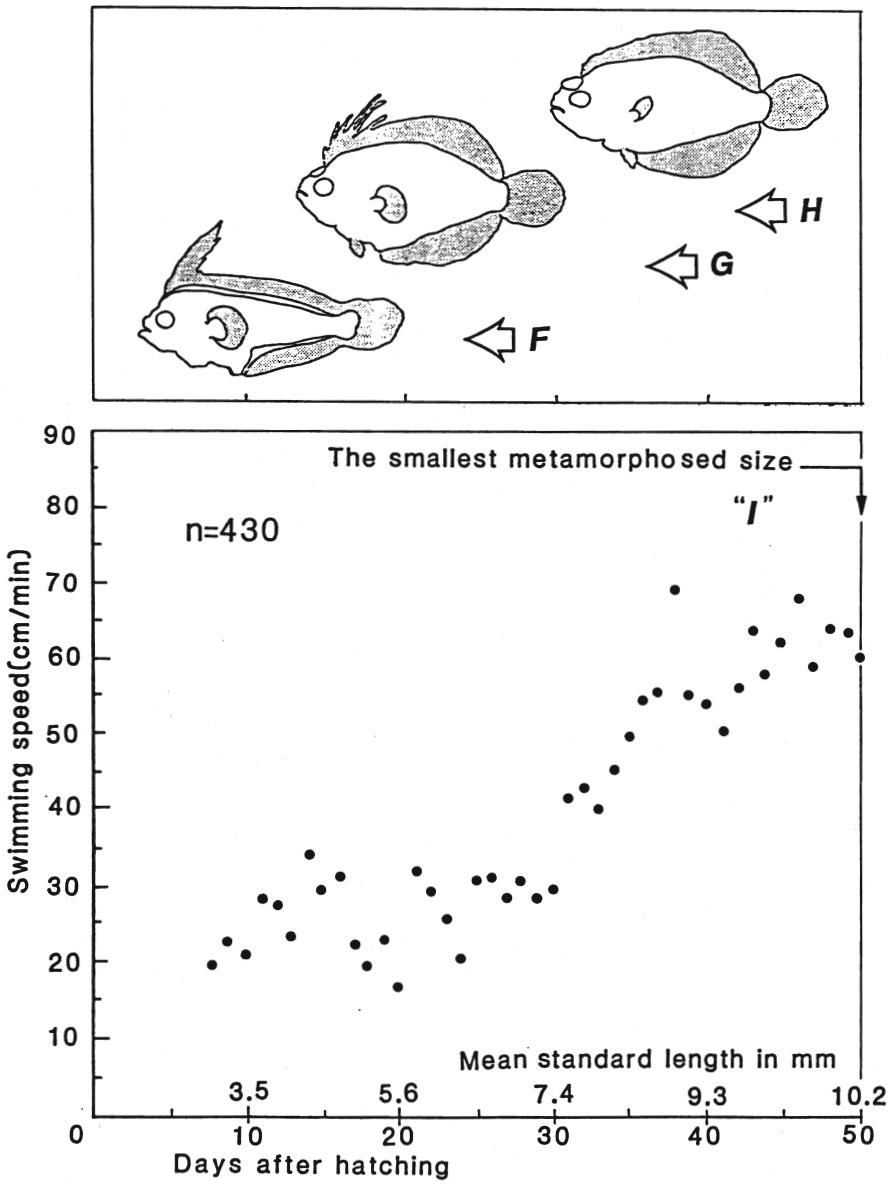


Fig.78. *P. olivaceus*. Increment of swimming speed with larval growth in relation to morphological changes of the caudal fin. F,G,H and I indicate the developmental stages of larvae. Refer to Fig.55 for the detail of the developmental stages. n=sample size.

Sagitta crassa and mullet *Mugil cephalus* in an earthen pond (Fukuhara and Fukunaga,1984), but they were not found in the predator's stomach after reaching the early juvenile stage, about 7.5 mm SL. This evidence indicates partly the increasing capability to avoid the predators as they grew.

Concerning the flatfish, settlement was seen for the larvae when they started eye migration in the field (Minami, 1981; 1982) and in the laboratory conditions. These behaviour of the flatfish are presumably related with strategic adaptation to avoid the predation in the field.

As the fish progressed their growth, pigment pattern seemed to be apparent for some species, and the pigment pattern was usually concerned with behavioural change for a certain period in the early life stage. In the Sparid fish, *P. major* and *A. schlegeli* formed characteristically the pigment pattern when they were staged newly transformed juvenile (Figs.33, 44). The juvenile which formed the pigment pattern shifted habitation from surface to the bottom. In the rearing tank larval P. major began to stay on the bottom when they commenced the formation of the pigment pattern. According to the observation in the semi-natural conditions, the smallest size of the bottom dweller in 150 samplings measured 10.5 mm SL (Fukuhara,1985) at which the stripe formation was finished (Fig.33), and the pigment pattern was not discerned in the larvae swam in the upper layer.

Thus, the stripe formation is indicative for shifting the habitation in the fish which has the stripe during early life stage. Both reared and wild conditions, a phenomenon of coincidence between stripe formation and habitat shift has been well-known in various species (Fukusho,1975; Hoshiai,1977; Zama et al.,1977; Schroder and Zaret,1979).

Consequently, the stripe which is considered to play roles of concealment and specific communication may be a requisite character when they avoid the predator in the new surroundings.

2)Significance of biological information on fish production

Recently artificial fish propagation became increasingly important measures to produce the fingerlings for both intensive and extensive aquaculture. Because the procurement of fingerlings from the wild stock for these activities should be decreased theoretically to conserve the natural populations. As a matter of

fact, the wild catch for the cage culture are regulated for the fingerlings of yellowtail and red sea bream. Therefore, the artificial propagation in the hatcheries must be performed effectively to produce the large number of fingerlings for cage culture and for releasing.

During the course of larval rearing, information on diagnostic characteristics of reared fish is a prerequisite for establishing the effective rearing systems. Optimum time of the initial feeding must be determined by behavioural maneuver of larvae as well as physiological changes of energy source. Food density also largely depends on specific characteristics of swimming activities. Newly hatched larvae like *E. japonica* should be fed immediately with higher prey density after yolk absorption because of poor locomotion activity. On the other hand, the larvae which show active locomotion before yolk absorption could be maintained with lower prey density than that of poor swimming groups. The developing larvae are able to regulate their foraging speed with prey density in the rearing tank (Fukuhara and Kishida,1980; Fukuhara,1983b). In the lower prey condition, the larvae usually swam faster than that in higher density (Wyatt,1972; Hunter and Thomas,1974; Hunter,1981; Munk and Kioerboe,1985). Therefore, the prey density is an important factor in the rearing procedure in terms of saving cost of the prey and water quality control.

Biological characters in larval behaviour described in this study may provide the fundamental information to perform reasonable feeding techniques in rearing commercially important species, and to understand the larval mortality in early stage.

The feeding techniques used to be carried out in mass production are desired to regard the specific characteristics on behaviour for the initial feeding larvae and the increasing swimming ability to search the prey with their growth. As regards ecological investigation, not only developmental stage but also various characters related with behaviour must be considered to determine sampling method, time and location for better understanding different developmental stages. The external organs of fin structure, pigment pattern and squamation provide useful information to clarify the diversity of specific life style as mentioned before.

Restocking activity, so called artificial releasing of hatchery-bred fingerlings is the most important measures to recruit

reared fishes to the natural populations. Despite of vigorous efforts, the effect of the artificial releasing is still unstable and unknown for many species. Various experimentations on releasing techniques have been conducted on optimum fish length, releasing sites and intermediate breeding before liberation. Little trial, however, is conducted to adopt the diagnostic features of designated fish in the releasing procedures. Fish size to be released varied widely with each trials. To determine the optimum fish size, various biological parameters should be regarded with each species in the releasing.

From morphological and behavioural observations, a shift of habitation usually occurred after fish reached the juvenile stage both in the laboratory conditions and in situ. These findings indicate that the fish acquired the capability of adaptation, and required new habitation after reaching the juvenile stage.

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