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DEVELOPMENT OF SWIMMING AND FEEDING FUNCTIONS IN LARVAE AND JUVENILES OF THE RED SNAPPER, *LUTJANUS ARGENTIMACULATUS**

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Development of swimming-and feeding-related characters and swimming speed was examined in laboratory-reared larvae and juveniles of the red snapper, *Lutjanus argentimaculatus*. In larvae smaller than about 4 mm in total length (TL), mechanical supports of fins were in a primordial stage of development. However, swimming speed increased rapidly in larvae of 3–4 mm TL, although the moving mode was mainly sudden, short-distanced hopping. Mechanical development of jaws, branchial arches and digestive tract had started by about 4 mm TL. Appearance and numerical completion of fin-supports and fin-rays were observed in 4–8 mm TL larvae. During this larval stage, no remarkable increase of swimming speed was observed, the swimming mode being inactive with frequent rushed behavior. Development of feeding-related characters went on continuously until about 9 mm TL, and the stomach and pyloric caeca were differentiated at about 7 mm TL. Fin-supports developed in size and started ossifying in larvae and early juveniles of 8–16 mm TL, during this stage, no remarkable change of mean swimming speed was detected, whereas the maximum swimming speed increased. Rapid increase of swimming speed, which would be supported by the completion of swimming-related characters, was observed in juveniles of 16–20 mm TL and larger.

Key words: *Lutjanus argentimaculatus*, Functional development, Swimming speed, Ossification

Introduciton

Red snapper, *Lutjanus argentimaculatus*, is a common lutjanid distributed in Indo-Pacific waters (Allen, 1985; Allen and Talbot, 1985). This species is of importance to both coastal fishery and aquaculture. Therefore, in order to elucidate the early life history of the species, many studies have been carried out on the changeover of energy resources (Doi *et al.*, 1994a), development of external morphology (Doi *et al.*, 1994b) and development of feeding ability (Doi *et al.*, 1997). Regarding the osteological development of lutjanid larvae and juveniles, some features of fin-supports have been observed (Richards and Saksena, 1980, for *L. griseus*; Mori, 1984, for *L. vitta*). Recently Potthoff *et al.* (1988) described overall osteological development in wild-caught larvae and juveniles of *L. campechanus*. However, on *L. argentimaculatus*, no osteological development is described, nor is there information on the functional development. The purpose of this study was to describe the osteological development of swimming- and feeding-related characters in the laboratory-reared larvae and juveniles of the red snapper, *L. argentimaculatus*. The development of digestive tract was also described, and the change of swimming speed with growth was examined under the rearing-condition.

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Materials and Methods

All the larval and juvenile materials used in this study were raised at the Eastern Marine Fisheries Development Center (EMDEC), Department of Fisheries, Rayong, Thailand in 1991–1992. The spawning inducement and larval rearing methods were described by Singhagraiwan and Doi (1993).

For osteological observations, 75 larvae and juveniles of 2.65–36.40 mm in total length (TL), sampled from a rearing trial conducted in July–August 1992, were cleared and stained by the method of Dingerkus and Uhler (1977). The following measurements and counts were made after staining under a dissecting microscope with an ocular micrometer: total length, mouth width, number of fin-supports and fin-rays, number of teeth on jaws and pharyngeals, and notochord angle. For the measurement of TL of juveniles, a digital caliper was also employed. In this study, the TL was given as preserved state using the equation, TL (preserved) $=0.985\times$TL (stained) -0.131, and rounded to the nearest 0.05 mm. Drawings of osteological elements were prepared with the aid of camera lucida.

A total of 175 larvae and juveniles of 2.50–35.05 mm TL, sampled from a rearing trial in November–December 1991, was used for the observations of digestive tract. The digestive tract was dissected and observed under a dissecting microscope. The digestive tract of several larvae immediately after hatching were supplementally observed in fresh state.

Moving distance of larvae and juveniles traced for one minute was defined as swimming speed (cm/min) in this study. Measurements of the swimming speed were carried out by using two series of larvae reared in March–April 1992.

In one series, a group of about 15 larvae of the same age was transferred gently with water to a plastic container (25 cm in bottom diameter, about 5 cm in water depth) and the moving route was traced individually on a transparent sheet placed on the top of the container. The trace was repeated for 10 different larvae. After the traces, the larvae were sampled and the mean TL was measured. These data were not pooled but considered as variations at the age or mean larval TL of the group. A total of nine groups (90 individuals, 2.45–9.20 mm mean TL's, collected at different intervals) was observed in this series.

In the other series, the moving speed was observed individually for 156 larvae and juveniles of 6.85–26.50 mm TL in a polycarbonate tank with 36 cm in diameter and about 10 cm in water depth. The tracing method of the moving route was the same as above. These larvae and juveniles were sampled immediately after the trace, and the TL was obtained by individuals. A kilvimeter was used for measurement of the moving distance traced.

The TL of the larvae and juveniles, which were measured in fresh state, were converted to TL in preserved state using the equation,

$$\text{TL (preserved)}=0.779\times\text{TL (fresh)}^{1.06}.$$

Terminology followed Potthoff (1975), Kohno *et al.* (1983), Kohno and Taki (1983) and Fujita (1989).

Results

Swimming-related characters

Flexion of notochord end: The smallest specimen examined, 2.65 mm TL, had a straight notochord. The largest specimen retaining this state was 4.70 mm in TL. Notochord flexion started at 5.05 mm TL and became complete by about 7 mm TL.

Caudal fin-supports and fin rays: First visible element of the caudal complex other than the notochord was a cartilaginous bud of hypural 1 in a 3.70 mm TL specimen. Cartilaginous buds of parhypural and hypural 2 were first observed at 4.05 mm TL. In addition, a 4.15 mm TL specimen

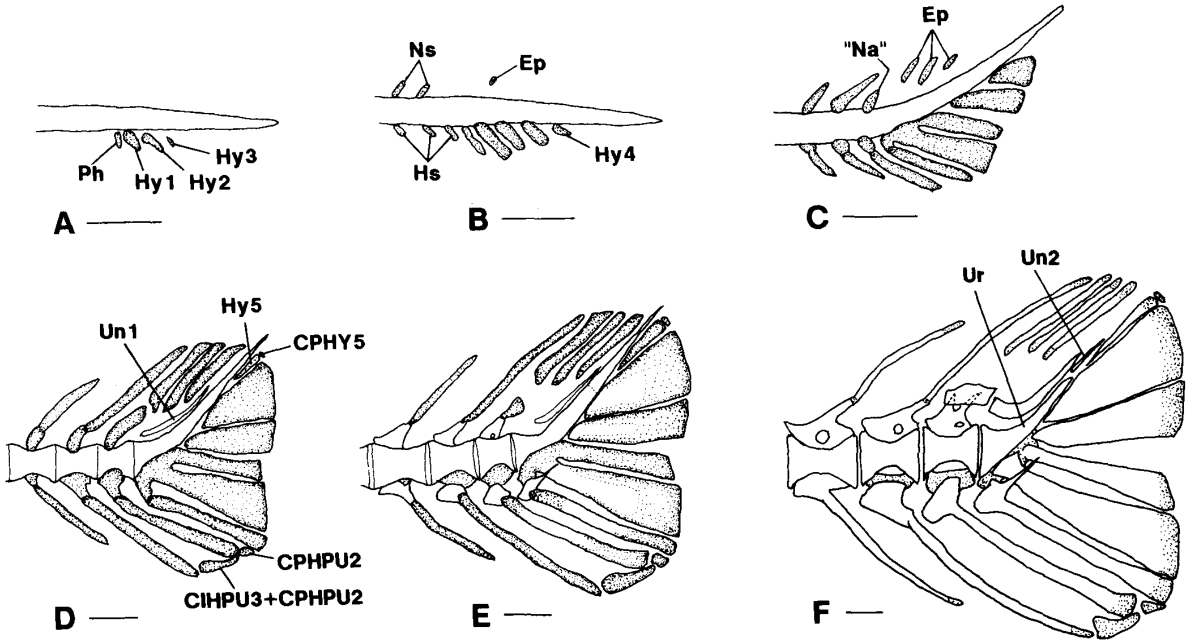

Fig. 1. Development of caudal fin-supports in *Lutjanus argentimaculatus.* A: 4.15 mm TL. B: 4.70 mm TL. C: 5.60 mm TL. D: 10.65 mm TL. E: 15.35 mm TL. F: 23.40 mm TL. Stippled area, cartilage; open area except for notochord, ossification. CIHPU 3, interhaemal spine cartilage of preural centrum 3; CPHPU 2, post-haemal spine cartilage of preural centrum 2; CPHY 5, post-hypural 5 cartilage; Ep, epural; Hs, haemal spine; Hy 1–5, hypurals 1–5; "Na", specialized neural arch; Ns, neural spine; Ph, parhypural; Un 1–2, uroneural 1–2; Ur, urostyle. Scale bars: 0.2 mm.

possessed a cartilaginous bud of hypural 3 (Fig. 1A). Hypural 4, neural spines of future preural centra 3 and 4, and haemal spines of future preural centra 2–4 appeared first at 4.45 mm TL. An epural was weakly stained at 4.60 mm TL (Fig. 1B: 4.70 mm TL). Anterior and posterior epurals appeared first at 5.05 mm TL. Specialized neural arch was observed at 5.25 mm TL. Fusion of hypural 1 and 2 at their proximal bases occurred first at 5.40 mm TL. In a 5.60 mm TL specimen, fusion of parhypural and hypurals 1 and 2 at their bases was seen (Fig. 1C). Hypural 5 appeared first at 6.20 mm TL. Cartilaginous buds of CIHPU3+CPHPU2 (interhaemal spine cartilage of preural centrum 3+ post-haemal spine cartilage of preural centrum 2) and CPHPU2 were first observed at 7.10 mm TL. A cartilaginous bud of CPHY5 (post haemal 5 cartilage) appeared first at 10.65 mm TL (Fig. 1D), all cartilaginous elements of caudal complex having appeared by this size.

Urostyle and preural centra 2–4 started appearing at 9.80 mm TL. Uroneural 1 was first perceived faintly as a paired needle-like bones in a 10.65 mm TL specimen (Fig. 1D). Ossification of the hypural 1 started at 13.30 mm TL and the parhypural and hypurals 3–4 at 13.50 mm TL. In a 15.35 mm TL specimen (Fig. 1E), ossification started in the specialized neural arch, neural spines of preural centra 3 and 4, hypural 2 and haemal spines of preural centra 2–4. Uroneural 2 became discernible at 16.55 mm TL. Ossification of the hypural 5 and epurals 1–3 had started by 23.40 mm TL (Fig. 1F).

First discernible caudal fin rays were 9 (5+4) principal rays at 4.95 mm TL. An adult complement of 9+8 principal rays was attained at 5.85 mm TL. Secondary fin rays appeared first at 6.80 and 7.50 mm TL in lower and upper caudal fin lobes, respectively, number of the secondary rays increasing with larval growth.

Dorsal and anal fin-supports and fin rays: Pterygiophores observed first were anteriormost four cartilaginous proximal radials under dorsal fin at 3.70 mm TL and anteriormost five under anal fin at

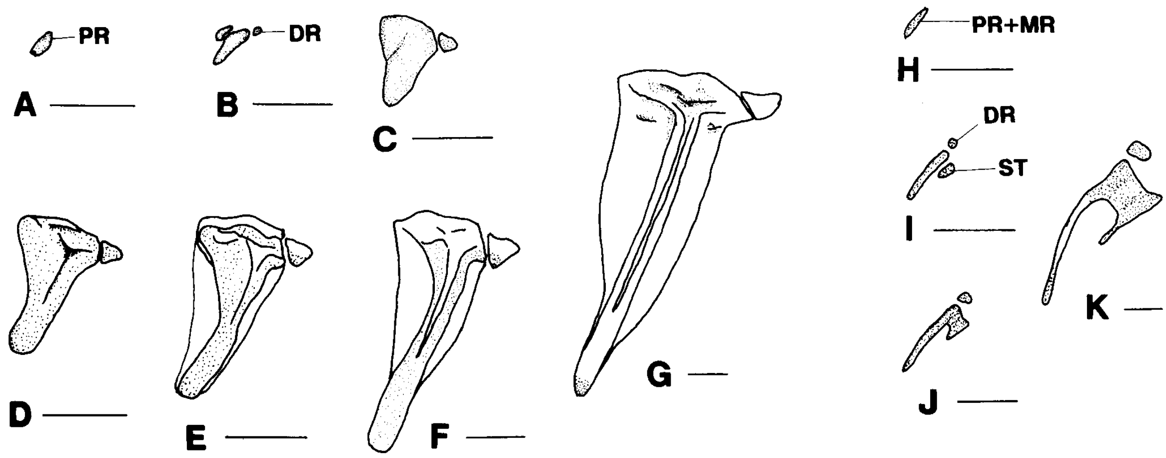

Fig. 2. Development of the first (A–G) and last (H–K) dorsal pterygiophores in *Lutjanus argentimaculatus* A: 3.70 mm TL. B: 3.95 mm TL. C: 4.45 mm TL. D, H: 5.60 mm TL. E, I: 7.10 mm TL. F, J: 10.65 mm TL. G, K: 23.40 mm TL. Stippled area, cartilage; open area, ossification. DR, distal radial; MR, middle radial; PR: proximal radial; ST, stay. Scale bars: 0.2 mm.

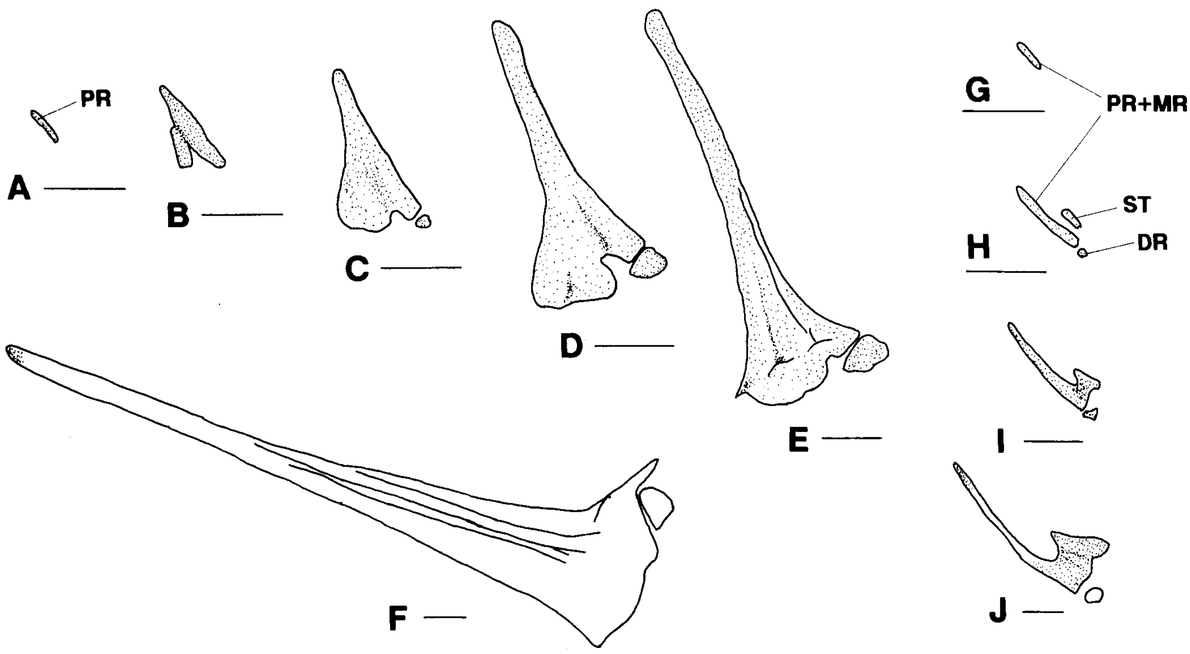

Fig. 3. Development of the first (A–F) and last (G–J) anal pterygiophores in *Lutjanus argentimaculatus*. A: 4.45 mm TL. B: 5.05 mm TL. C, G: 5.60 mm TL. D, H: 7.10 mm TL. E, I: 10.65 mm TL. F, J: 23.40 mm TL. Stippled area, cartilage; open area, ossification. For abbreviations, see Fig. 2. Scale bars: 0.2 mm.

4.45 mm TL. Addition of cartilaginous proximal radials proceeded in posterior direction. At 5.40 mm TL, proximal radials attained the adult complement in number, 21 or 22 in dorsal and 9 in anal fins. Distal radials appeared first at 3.95 mm TL in dorsal fin and at 5.60 mm TL in anal fin. An adult complement in number of distal radials was attained at 7.10 mm TL in both fins. Three predorsal bones developed first in cartilage at 3.95 mm TL.

Detailed developmental sequences of the first and last dorsal and anal fin-supports were traced as below (Figs. 2 and 3).

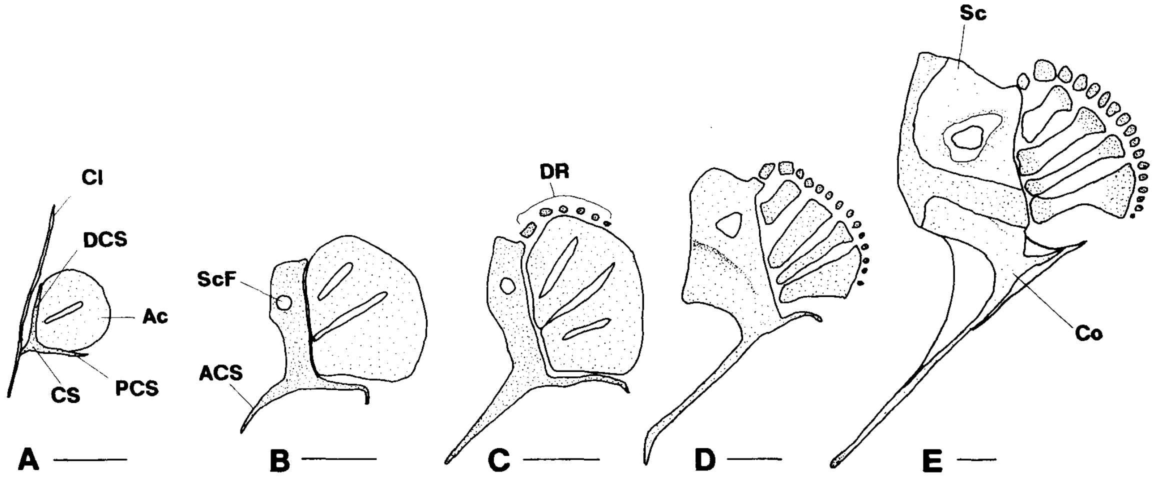

Fig. 4. Development of pectoral fin-supports in *Lutjanus argentimaculatus*. A: 2.90 mm TL. B: 5.60 mm TL. C: 7.10 mm TL. D: 10.65 mm TL. E: 23.40 mm TL. Stippled area, cartilage; open area, ossification. Ac, actinost (blade-like cartilage); ACS, anterior process of coraco-scapular cartilage; Cl, cleithrum; Co, coracoid; CS, coraco-scapular cartilage; DCS, dorsal process of coraco-scaplar cartilage; DR, distal radial; PCS, posterior process of coraco-scapular cartilage; Sc, scapula; ScF, scapular foramen. Scale bars: 0.2 mm.

Anteriormost dorsal proximal radial appeared first as a cylindrical cartilage at 3.70 mm TL (Fig. 2A). Two small cartilaginous balls were visible at 3.95 mm TL, one being postero-dorsal, distal radial, and the other anterior to the proximal radial (Fig. 2B). In larger specimens, the latter cartilaginous element was not visible, but the first proximal radial was more massive and more anteriorly expanded (Fig. 2C: 4.45 mm TL). Ossification started in the central portion of proximal radial at 5.60 mm TL (Fig. 2D). Sagittal bony keels developed anterior and posterior to the proximal radial at 7.10 mm TL (Fig. 2E). The distal radial started to ossify at 10.65 mm TL (Fig. 2F). In a 23.40 mm TL specimen, the proximal and distal radials were totally ossified, in the former T-shaped bony lateral keels being observed on both sides (Fig. 2G).

Last dorsal pterygiophore appeared first as a cylindrical cartilage, future proximal and middle radials, at 5.40 mm TL (Fig. 2H: 5.60 mm TL). A small cartilaginous ball was observed postero-dorsal, distal radial, and postero-ventral, stay, to the proximal+middle radial at 7.10 mm TL (Fig. 2 I). The stay fused with the proximal+middle radial at 7.95 mm TL (Fig. 2J: 10.65 mm TL). Ossification had started at the central part of last pterygiophore by 23.40 mm TL (Fig. 2K).

First and last pterygiophores of the anal fin developed in almost the same manner as in the dorsal fin (Fig. 3), although a small cartilaginous element anterior to the first proximal radial was not perceived in the anal fin. Ossification started at 9.30 mm TL in the anteriormost anal pterygiophore and at 23.40 mm TL in the last one.

Dorsal fin rays observed first were the first and second spines in a 3.95 mm TL specimen. The anal fin rays were first observed at 5.25 mm TL, in which the first and second spines and the following six soft rays had appeared. Fully developed fin ray counts were attained at 6.80 mm TL in the anal fin and 7.10 mm TL in the dorsal fin.

Pectoral fin rays and fin-supports: The smallest specimen examined, 2.65 mm TL, possessed a rod-shaped bony cleithrum, a coraco-scapular cartilage extending dorsally and posteriorly, and a blade-like cartilage with an elliptical crevice at the center (Fig. 4A: 2.90 mm TL). With growth, dorsal process of the coraco-scapular cartilage had expanded to form a broad plate, and a small scapular foramen appeared at the center of the broad plate at 3.95 mm TL. A supracleithrum and a

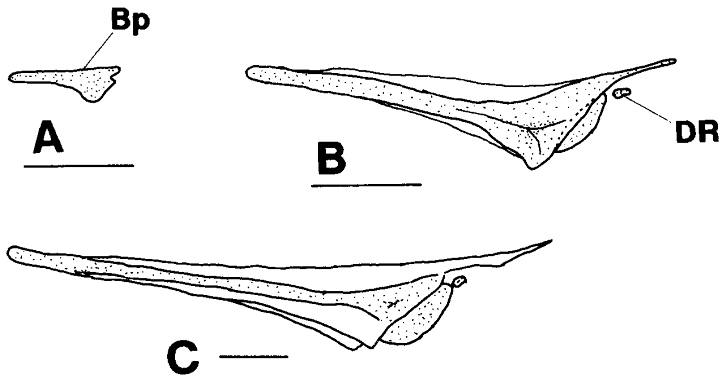

Fig. 5. Development of pelvic fin-supports in *Lutjanus argentimaculatus*. A: 3.95 mm TL. B: 7.10 mm TL. C: 10.65 mm TL. Stippled area, cartilage; open area, ossification. Bp, basipterygium; DR, distal radial. Scale bars: 0.2 mm.

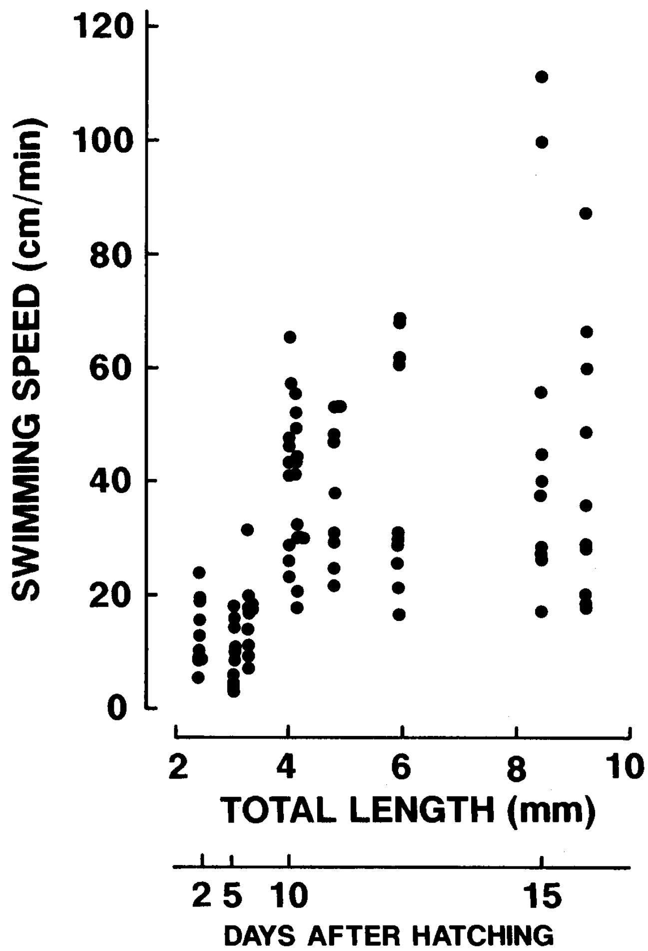

Fig. 6. Relationship between swimming speed and total length in 2–16 days old *Lutjanus argentimaculatus*.

posttemporal appeared first at 3.95 and 4.45 mm TL, respectively. A crevice was observed dorsally to the central crevice of the blade-like cartilage at 4.70 mm TL (Fig. 4B: 5.60 mm TL). At 6.20 mm TL, third crevice positioned ventrally to the first crevice and an uppermost cartilaginous distal radial

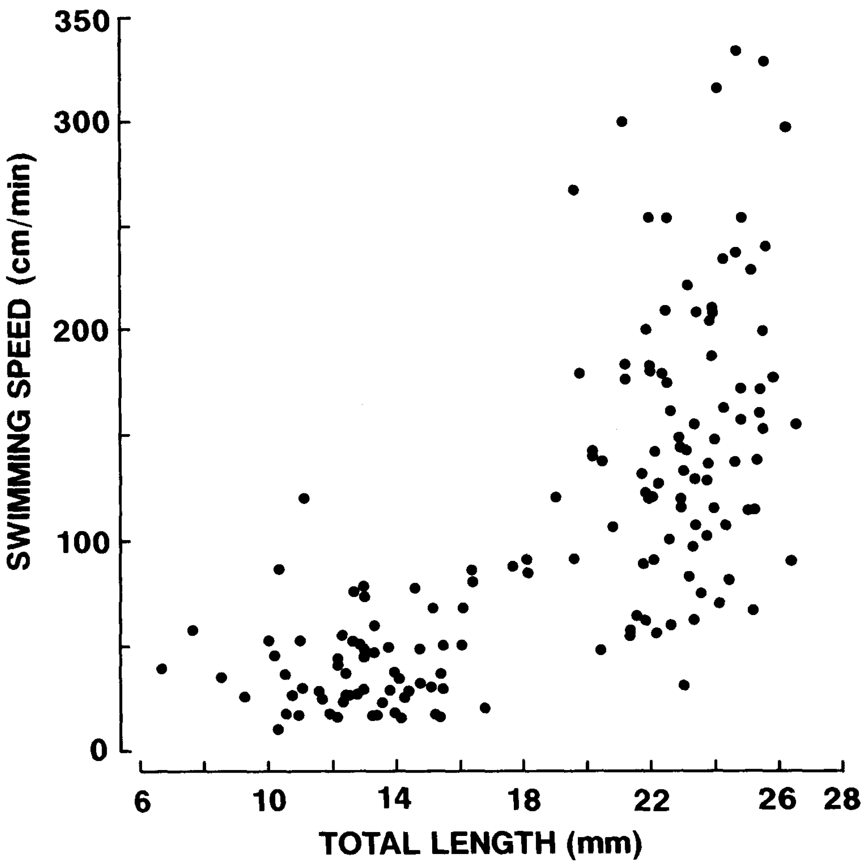

Fig. 7. Relationship between swimming speed and total length in advanced larvae and juveniles of *Lutjanus argentimaculatus*. $N = 156$.

appeared. Number of distal radials increased as larvae grew (Fig. 4C: 7.10 mm TL), its adult complement of 16 or 17 being attained at 13.30 mm TL. The blade-like cartilage was completely divided into four actinosts at 8.35 mm TL (Fig. 4D: 10.65 mm TL).

Dorsal, future scapular, and ventral, future coracoid, parts of the coraco-scapular cartilage started to ossify at 15.35 and 17.95 mm TL, respectively. Ossification of actinosts went on from dorsad to ventrad, the first actinost being ossified at 15.35 mm TL, the second at 18.60 mm TL, and the third and fourth at 19.60 mm TL (Fig. 4E: 23.40 mm TL).

Differentiation of five pectoral fin rays was evident at 5.55 mm TL. An adult complement of 16 or 17 fin rays was achieved at 13.50 mm TL.

Pelvic fin-supports and fin rays: A 3.95 mm TL specimen was the smallest possessing a cartilaginous basipterygium (Fig. 5A). In a 7.10 mm TL specimen, two cartilaginous balls, distal radials, were observed, and ossification of the basipterygium started (Fig. 5B, one distal rasial could not observed from the lateral view). Thereafter, the ossification of the basipterygium proceeded with growth (Fig. 5C: 19.30 mm TL). In a 23.40 mm TL specimen, one cartilaginous distal radial fused with the basipterygium, but the other one was free and supported an inner pelvic fin ray.

Pelvic fin-spine was first evident at 3.95 mm TL and first soft ray at 4.45 mm TL. An adult complement of one spine and five soft rays was attained at 6.20 mm TL.

Swimming speed

Larvae of 2 days after hatching, 2.45 mm in mean TL, stayed on the bottom of the experimental

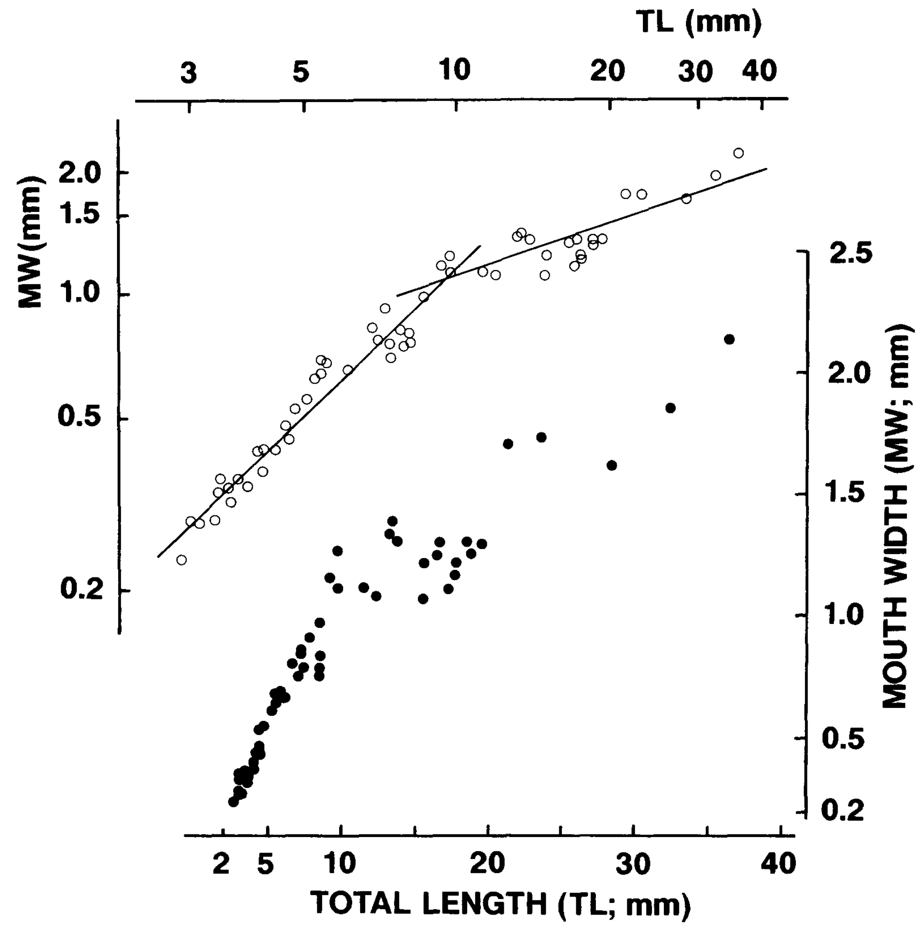

Fig. 8. Relationship between total length and mouth width in *Lutjanus argentimaculatus* larvae and juveniles. Log-log plots of the total length and mouth width are shown in the top. Regression lines: $\ln(MW)=0.413\times\ln(TL)-0.882$ (Range, 2.90–8.75 mm TL; $N=33$; $r=0.963$), $\ln(MW)=1.13\times\ln(TL)-2.51$ (Range, 9.30–36.40 mm TL; $N=23$; $r=0.788$).

container, no constant swimming being observed, but sudden, short-distanced hopping movement by using whole body and pectoral fin occurring. Larvae of 5 and 7 days after hatching, 3.05 and 3.30 mm in mean TL's, also stayed mostly on the bottom but sometimes swam slowly in the middle layer by using the pectoral fins and/or moved suddenly showing the hopping action. The swimming speed of these day 2–7 larvae ($n=30$) varied individually from 3.1 to 31.0 cm/min with a mean of 13.2 cm/min (Fig. 6). Thereafter, the swimming speed increased to 17.5–65.0 cm/min (mean = 38.9 cm/min, $n=20$) in day 11 and 12 larvae of 4.00 and 4.05 mm in mean TL's, respectively, the larvae showing constant swimming, although not so active, in the middle layer of container by beating the posterior half of body weakly and by moving the pectoral and pelvic fins. In these larvae, "rushed behavior", obviously attempting to attack food organisms, was sometimes observed. The swimming mode characterized by inactive slow swimming with rushed behavior was observed up to about 9 mm TL. The swimming speed levelled off at 16.7–64.5 cm/min (40.4 cm/min, 20) in day 13 and 14 larvae of 4.80 and 5.95 mm in mean TL's and slightly increased to 17.0–111.0 cm/min (45.1 cm/min, 20) in day 15 and 16 larvae of 8.45 and 9.20 mm in mean TL's (Fig. 6).

The swimming speed of 6.85–9.35 mm TL larvae observed individually ranged from 24 to 58 cm/min ($n=4$) (Fig. 7), the speed being within an identical level of larvae observed in a group as described

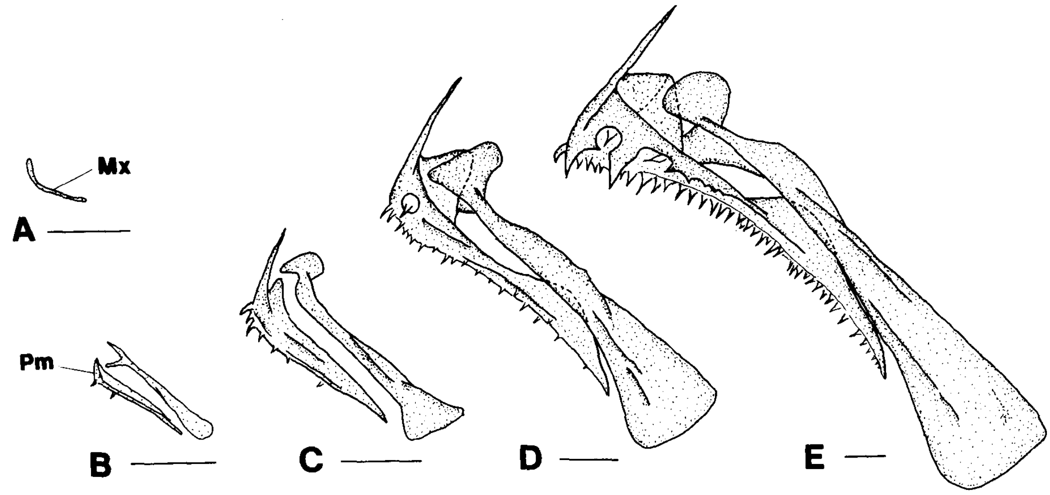

Fig. 9. Development of upper jaw (all bony) in *Lutjanus argentimaculatus*. A: 2.90 mm TL. B: 4.45 mm TL. C: 5.60 mm TL. D: 10.65 mm TL. E: 19.30 mm TL. Mx, maxilla; Pm, premaxilla. Scale bars: 0.2 mm.

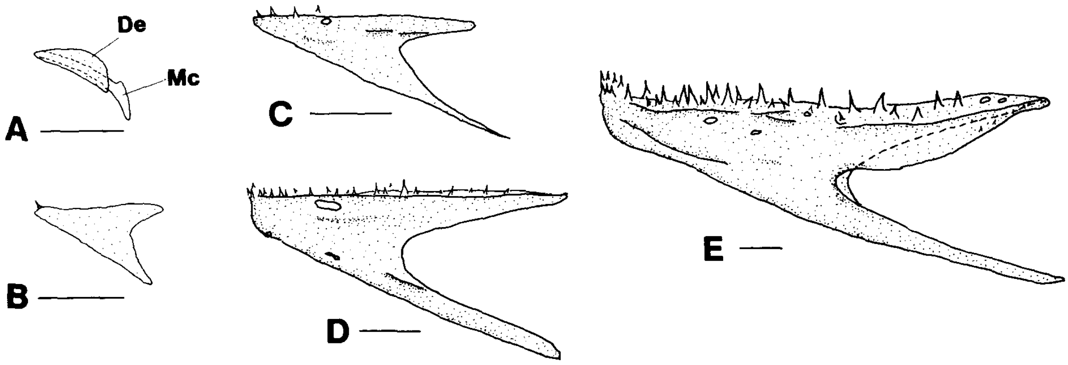

Fig. 10. Development of dentary (all bony except for the Meckel's cartilage) in *Lutjanus argentimaculatus*. A: 3.35 mm TL. B–E, same individuals as B–E, respectively, in Fig. 9. Mc, Meckel's cartilage; De, dentary. Scale bars: 0.2 mm.

above. Larvae and early juveniles of 10.0–15.9 mm TL showed the swimming speed of 10–120 cm/min (mean = 39.3 cm/min, n = 54). In juveniles of 16.0–19.9 mm TL, the swimming speed increased to 20–264 cm/min (101.5 cm/min, 12). During this stage, cruising ability of juveniles had increased obviously. The swimming speed increased continuously thereafter, the speed being 46–301 cm/min (136.0 cm/min, 38) in 20.0–22.9 mm TL larvae and 30–333 cm/min (164.9 cm/min, 48) in 23.0–26.5 mm TL larvae (Fig. 7).

Feeding-related characters

Mouth width: Mouth had opened by 2.90 mm TL with 0.230 mm in width. The mouth width increased with growth, but the growth rate changed at about 10 mm TL, the rate being higher in the larvae smaller than about 10 mm TL (Fig. 8). The regression analysis in logarithmic relation between mouth width and TL indicated a flexion point at 9.55 mm TL and 1.05 mm mouth width.

Jaw structure: Bony maxilla appeared first at 2.90 mm TL (Fig. 9A) and premaxilla at 3.65 mm TL. At 4.45 mm TL, the premaxilla developed an ascending process (Fig. 9B). Dentary was first observed at 3.20 mm TL (Fig. 10A: 3.35 mm TL). Further developmental stages of both upper jaw

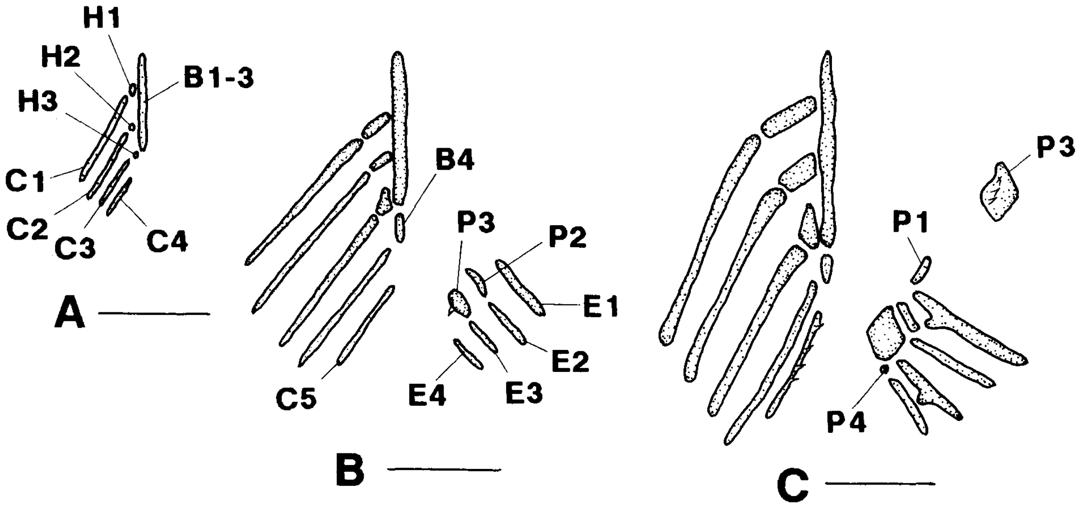

Fig. 11. Development of branchial arches (all cartilage) in *Lutjanus argentimaculatus*. A: 2.90 mm TL, dorsal view of left lower arches. B: 3.65 mm TL, dorsal view of left lower and right upper arches. C: 5.05 mm TL, dorsal view of left lower and right upper arches, and ventral view of pharyngobranchial 3. B1–4, basibranchials 1–4; C1–5, ceratobranchials 1–5; E1–4, epibranchials 1–4; H1–3, hypobranchials 1–3; P1–4, pharyngobranchials 1–4. Scale bars: 0.2 mm.

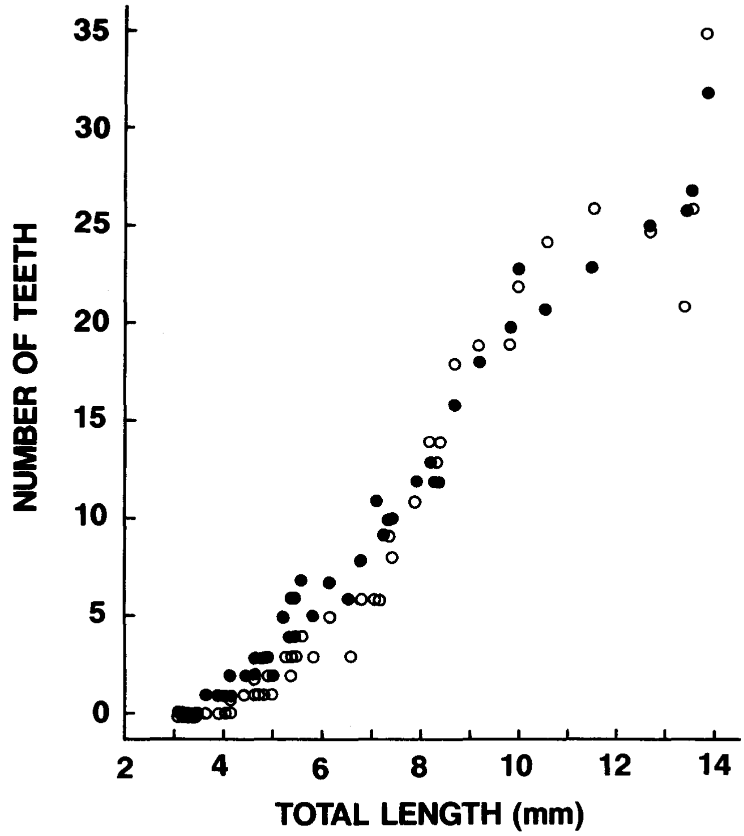

Fig. 12. Increment of jaw teeth number in *Lutjanus argentimaculatus* larvae and early juveniles. Solid and open circles indicate the teeth on premaxilla and dentary, respectively. $N=49$.

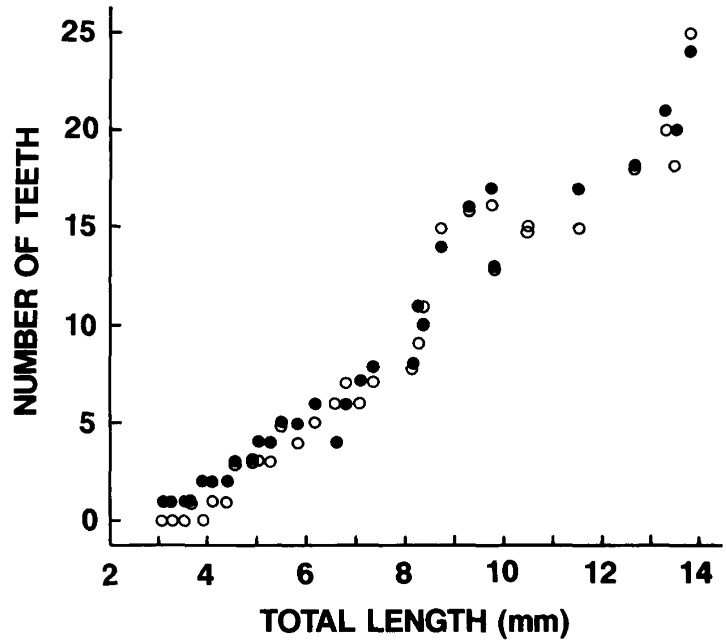

Fig. 13. Increment of pharyngeal teeth number in *Lutjanus argentimaculatus* larvae and early juveniles. Solid and open circles indicate the teeth on upper and lower pharyngeal, respectively. $N = 31$.

and dentary are shown in Figures 9C-E and 10B-E.

Branchial arches: The 2.90 mm TL specimen had the following cartilaginous elements of branchial arch: a rod-shaped basibranchial (future basibranchials 1–3); small, globular hypobranchials 1–3; and rod-shaped ceratobranchials 1–4 (Fig. 11A). No upper branchial arch elements were discernible at this size. Basibranchial 4, ceratobranchial 5 and upper branchial arch elements composed of epibranchials 1–4 and pharyngobranchials 2 and 3 had appeared by 3.65 mm TL (Fig. 11 B). At 5.05 mm TL, pharyngobranchials 1 and 4 were added.

No ossification was observed in the larvae of 10.63 mm TL and smaller. The first ossification was observed in ceratobranchial 5 and tooth plate of pharyngobranchial 3 at 11.55 mm TL. In a 17.55 mm TL specimen, ossification was perceived in ceratobranchials 1–4, pharyngobranchials 2–3 and epibranchials 1–4, and basibranchial 1 was separated from basibranchial 2 + 3. All but basibranchial 4 started ossifying in a 23.42 mm TL specimen.

Teeth: Upper jaw teeth were formed only on the premaxilla. The first premaxillary tooth was observed at 3.70 mm TL. The number of teeth increased as larvae grew with a more or less conspicuous leap at about 9 mm TL (Fig. 12). A dentary tooth was first perceived at 4.15 mm TL. A more or less remarkable leap in the number of teeth was also noticed at 8–9 mm TL (Fig. 12).

An upper pharyngeal tooth was first evident at 3.10 mm TL and a lower tooth at 3.70 mm TL. Number of upper and lower pharyngeal teeth increased with growth, showing a leap at 8–9 mm TL (Fig. 13).

Digestive tract: Intestine was straight in larvae immediately and one day after hatching, irrespective of their body size (Fig. 14A for 2.50 mm TL). In larvae two days after hatching, the middle part of intestine twisted ventrally, the esophagus and rectum were differentiated, and early liver and swim bladder were formed (Fig. 14B for 2.50 mm TL). The mid-gut rotated, although not complete loop, in a 2.95 mm TL specimen (Fig. 14C), the completely looped intestine occurring in 2.75–3.70 mm TL specimens (Fig. 14D for 3.40 mm TL). Anticipated stomach was discernible first at 4.00 mm TL (Fig. 14E for 4.70 mm TL). A conical posterior tip of the stomach was differentiated

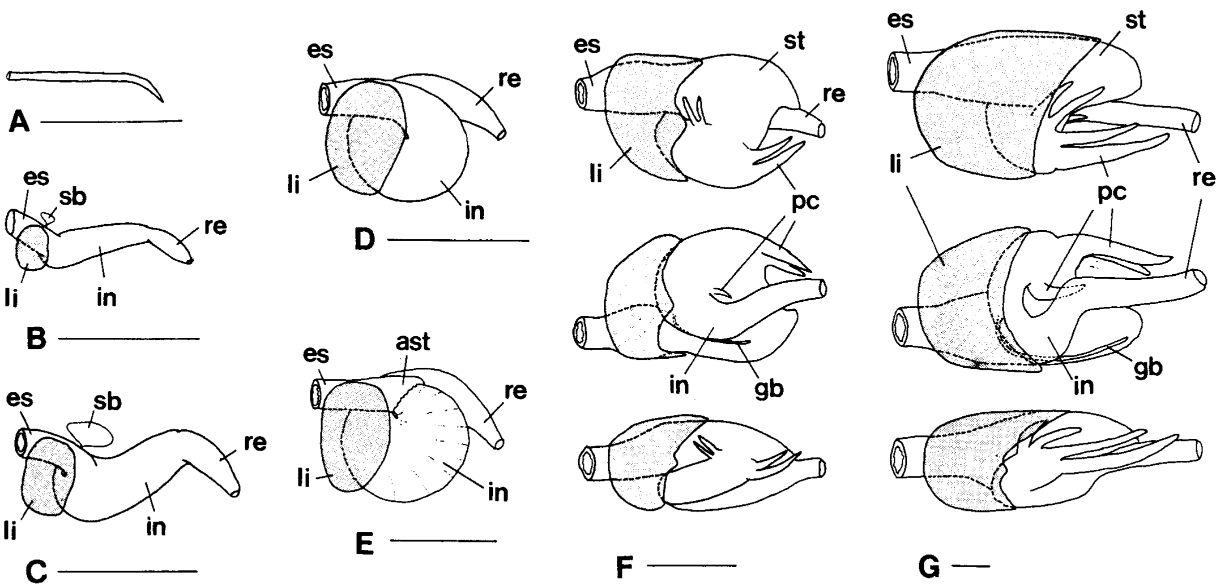

Fig. 14. Early development of digestive tract in *Lutjanus argentimaculatus*. A: 2.50 mm TL (1 day old). B: 2.50 mm TL (2 days old). C: 2.95 mm TL. D: 3.40 mm TL. E: 4.70 mm TL. F: 10.15 mm TL. G: 30.90 mm TL. The lateral view of left side is shown in A–E. In F and G, the lateral view of left side is shown in top, the lateral views of right side in middle and the ventral view in bottom. a, air bladder; ast, anticipated stomach; es, esophagus; gb, gall bladder; in, intestine; li, liver; pc, pyloric caeca; re, rectum; sp, spleen; st, stomach. Scale bars: 0.5 mm in A–E; 1 mm in F; 5 mm in G.

in larvae of 7.05–7.35 mm TL, in which small buds of pyloric caeca were seen. In a specimen of 10.15 mm TL, five pyloric caeca had developed in the connecting portion of stomach and intestine, and a small, string-like gall bladder was found (Fig. 14F). The stomach extended posteriorly to form a large blind sac with round posterior tip in juveniles of 16.15–19.20 mm TL (Fig. 14G for 30.90 mm TL). At this stage, the five pyloric caeca extended their length and the convoluted intestine bent downward anteriorly.

Discussion

Comments on osteological development

Developmental sequence of fin rays in *Lutjanus argentimaculatus* was as follows: dorsal/pelvic-caudal-anal-pectoral in appearance; and caudal (principal rays)-pelvic-anal-dorsal-pectoral in numeral completion. This order is almost the same as in the other lutjanids (Laroche, 1977 for *Rhomboplites aurobens*; Richards and Saksena, 1980 for *L. griseus*; Potthoff *et al.*, 1988 for *L. campechanus*), fishes with spinous dorsal or pelvic fins appearing first being unusual in percoids (Potthoff *et al.*, 1988; Potthoff and Tellock, 1993). Lutjanids, siganids and serranid epinephelines and anthiines have early-forming, elongated dorsal and pelvic fin spines (Leis and Rennis, 1983; Hara *et al.*, 1986; Kohno *et al.*, 1993).

No bony fusion was observed in caudal complex of *L. argentimaculatus* during the ontogenetic development. However, cartilaginous fusion occurred in proximal bases of parhypural and hypurals 1 and 2, this kind of fusion being observed commonly in many fishes (Kohno and Taki, 1983).

Cartilaginous distal radials of dorsal and anal fins originated separately from the proximal cartilage in *L. argentimaculatus*, this having been observed by Kohno and Taki (1983), Kohno *et al.* (1983, 1984) and Potthoff and Tellock (1993). The stay was proved to be a vestigial radial element by Kohno and Taki (1983). The present study supports their view, the stay of a small cartilaginous element having originated separately from the last pterygiophore in early stage larvae of *L. argentimaculatus.*

Generally the anteriormost dorsal and anal pterygiophores supporting two spines by secondary association originate from two pieces of cartilage (Kendall, 1976; Kohno and Taki, 1983; Potthoff and Tellock, 1993). The anteriormost dorsal pterygiophore was formed by fusion of two cartilaginous pieces in *L. argentimaculatus*, whereas the anteriormost anal pterygiophore appeared first as a triangular-shaped cartilage. In the latter, a cartilaginous piece supposed to be present for a short time may fuse with the main cartilaginous body to form the triangular-shaped pterygiophore. Potthoff *et al.* (1988) observed the first anal pterygiophore originated from two pieces of cartilage in *L. campechanus*, whereas the anteriormost dorsal pterygiophore originated from one massive, dorsally expanded cartilage.

Development of swimming- and feeding-ability

Swimming speed of *L. argentimaculatus* larvae ranging from ca. 3 to 4 mm TL increased rapidly with their growth. However, no remarkable osteological characters related to swimming function appeared in larvae smaller than about 4 mm TL. The moving mode of these larvae was not active swimming but mainly sudden, short-distanced hopping, suggesting that the increase of swimming speed would not depend on mechanical development of osteological structure. On the other hand, osteological feeding-related characters had appeared and the larval gut increased its capacity with a loop by 4 mm TL. The size of *L. argentimaculatus* larvae at initial feeding on copepod nauplii was 2.26 mm in mean TL (Singhagraiwan and Doi, 1993). These results indicate that the increase of swimming speed in *L. argentimaculatus* larvae smaller than 4 mm TL would be derived from the increase of feeding activity supported by appearance and development of both osteological and non-osteological feeding-related characters and probably by non-osteological swimming-related characters. Matsuoka (1984) reported the appearance of superficial red fibers shortly before yolk resorption serving early stage larvae to permit further feeding activity in *Pagrus major*.

Appearance and numerical completion of fin-supports and fin rays were observed in *L. argentimaculatus* larvae of 4–8 mm TL except for the pectoral fin ray which completed at 13.40 mm TL. No remarkable increase of swimming speed was, however, observed during this larval stage, the swimming mode being inactive slow swimming with frequent rushed behavior attacking food organisms. Therefore, development of number of fin-supports and fin rays may not contribute directly to increase the swimming speed but to increase the swimming ability such as maneuverability. Development of feeding-related characters such as number of teeth, jaw structure and size of mouth width went on continuously in this larval stage. The anticipated stomach appeared and the stomach with conical posterior tip was differentiated at about 7 mm TL. According to Singhagraiwan and Doi (1993), gut contents of larvae changed drastically in this larval stage as follows: larvae smaller than about 4 mm TL ingested mainly copepod nauplii, which shared more than 88% of total gut contents in number, whereas those larger than about 4 mm TL ingested various food organisms such as rotifers and copepod copepodids, the percentage of copepod nauplii ingested decreasing to 45% and 30% at 5.57 and 6.65 mm TL, respectively; and the size of ingested food organisms increased gradually with larval development. Such improvement in larval feeding function seems to relay not only on the development of feeding-related characters but also on the the increased maneuverability supported by development of fin-supports and fin rays in number.

Swimming-related characters developed well in *L. argentimaculatus* larvae and early juveniles from 8 to 16 mm TL, elements of fin-supports having been robust and some elements having started ossifying. However, the swimming speed was not accelerated when comparing with that of preceding stage, although the maximum speed increased. Regarding the feeding-related characters, some striking changes occurred during this stage. Increasing leaps occurred in jaw and pharyngeal teeth number at about 9 mm TL. Ossification of the branchial arch started on ceratobranchial 5 and pharyngobranchial 3 at 11.55 mm TL. The pyloric caeca, which started to develop at 7 mm TL, became evident at about 10 mm TL. Development of the stomach and pyloric sphincter in *Lates calcarifer* larvae is known to increase pepsin-type enzyme activity associated with a possible exogenous proteolytic enzymes from the autolysis of food organisms, the latter being accelerated by development of the pharyngeal teeth (Walford and Lam, 1993). Size of food organisms ingested became larger in *L. argentimaculatus* larvae and early juveniles of 10.9 mm TL and larger (Singhagraiwan and Doi, 1993). These observations may indicate that the larvae and early juveniles would acquire an ability of higher feeding success and food digestibility, and they allocate the energy uptake into increasing foraging ability, maneuverability and seemingly quick escape ability from predator rather than increasing cruising ability at this stage.

Rapid increase of swimming speed was observed in *L. argentimaculatus* juveniles, 16–20 mm TL and larger. Nearly all elements of fin-supports had started ossification by about 16 mm TL and been almost completed by about 23 mm TL. Ossification in branchial arch elements also proceeded and the stomach increased capacity by extending the blind sac in this stage. In natural waters, where the spawning ground of *L. argentimaculatus* is considered to be in offshore waters (Johannes, 1978), the body size of the species occurring in river estuaries is larger than 16 mm TL, mostly between 19–23 mm TL in eastern Thailand (Doi *et al.*, 1992). These results may indicate that the nearly completed characters pertaining to swimming function would make it possible for *L. argentimaculatus* juveniles larger than about 16 mm TL to acquire swimming or cruising ability strong enough to migrate to coastal waters and to river estuaries. Increase in food storage capacity by enlarged stomach may be helpful in shifting the habitat.

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References

Allen, G. R. 1985. *Lutjanus argentimaculatus* (Forsskål, 1775). In: FAO Species Catalogue, Vol. 6 Snappers of the World. Rome, FAO, pp. 58–60.

Allen, G. R. and Talbot, F. H. 1985. Review of the snappers of the genus *Lutjanus* (Pisces: Lutjanidae) from the Indo-Pacific, with description of a new species. Bishop Museum Press. Honolulu, Hawaii, 87 pp.

Dingerkus, G. and Uhler, L. D. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Tech., **52**: 229–232.

Doi, M., Singhagraiwan, T., Sasaki, M. and Sungthong, S. 1992. Movement, habitat and growth of the juvenile and young red snapper, *Lutjanus argentimaculatus*, released in Phe Bay, eastern coast of the Gulf of Thailand during 1989–1991. Thai Mar. Fish. Res. Bull., **3**: 79–90.

Doi, M., Kohno, H., Ohno, A. and Taki, Y. 1994a. Development of mixed-feeding stage larvae of red snapper, *Lutjanus argentimaculatus*. Suisanzoshoku, **42**: 471–476.

Doi, M., Kohno, H., Taki, Y., Ohno, A. and Singhagraiwan, T. 1994b. Morphological development of eggs, larvae and juveniles of the red snapper, *Lutjanus argentimaculatus* (Pisces: Lutjanidae). J. Tokyo Univ. Fish., **81**: 135–153.

Doi, M., Ohno, A., Kohno, H., Taki, Y. and Singhagraiwan, T. 1997. Development of feeding ability of red snapper *Lutjanus argentimaculatus* early larvae. Fish. Sci., **63**: 845–853.

Fujita, K. 1989. Nomenclature of cartilaginous elements in the caudal skeleton of teleostean fishes. Japan. J. Ichthyol., **36**: 22–29.

Hara, S., Kohno, H. and Taki, Y. 1986. Spawning behavior and early life history of the rabbitfish, *Siganus guttatus*, in the laboratory. Aquaculture, **59**: 273–285.

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

Kendall, A. W., Jr. 1976. Predorsal and associated bones in serranid and grammistid fishes. Bull. Mar. Sci., **26**: 585–592.

Kohno, H., Taki, Y., Ogasawara, Y., Shirojo, Y., Taketomi, M. and Inoue, M. 1983. Development of swimming and feeding functions in larval *Pagrus major*. Japan. J. Ichthyol., **30**: 47–60.

Kohno, H. and Taki, Y. 1983. Comments on the development of fin-supports in fishes. Japan. J. Ichthyol., **30**: 284–290.

Kohno, H., Shimizu, M. and Nose, Y. 1984. Morphological aspects of the development of swimming and feeding functions in larval *Scomber japonicus*. Bull. Japan. Soc. Sci. Fish., **50**: 1125–1137.

Kohno, H., Diani, S. and Supriatna, A. 1993. Morphological development of larval and juvenile grouper, *Epinephelus fuscoguttatus*. Japan. J. Ichthyol., **40**: 307–316.

Laroche, W. A. 1977. Description of larval and early juveniles vermilion snapper, *Rhomboplites aurorubens*. Fish. Bull., U.S., **75**: 547–554.

Leis, J. M. and Rennis, D. S. 1983. The larvae of Indo-Pacific coral reef fishes. Sydney, New South Wales University Press, 269 p.

Matsuoka, M. 1984. Morphometry of the myotomal muscle fibers in larvae and juveniles of the red sea bream. Bull. Japan. Soc. Sci. Fish., **50**: 29–35.

Mori, K. 1984. Early life history of *Lutjanus vitta* (Lutjanidae) in Yuya Bay of the Sea of Japan. Japan. J. Ichthyol., **30**: 374–392.

Potthoff, T. 1975. Development and structure of the pterygiophores in the blackfin tuna (*Thunnus atlanticus*, Pisces, Scombridae). Bull. Mar. Sci., **22**: 205–231.

Potthoff, T., Kelley, S. and Collins, L. A. 1988. Osteological development of the red snapper, *Lutjanus campechanus* (Lutjanidae). Bull. Mar. Sci., **43**: 1–40.

Potthoff, T. and Tellock, J.A. 1993. Osteological development of the snook, *Centropomus undecimalis* (Teleostei, Centropomidae). Bull. Mar. Sci., **52**: 669–716.

Richards, W. J. and Saksena, V.P. 1980. Description of larvae and early juveniles of laboratory-reared gray snapper, *Lutjanus griseus* (Linnaeus) (Pisces, Lutjanidae). Bull. Mar. Sci., **30**: 515–522.

Singhagraiwan, T. and Doi, M. 1993. Induced spawning and larval rearing of the red snapper, *Lutjanus argentimaculatus*, at the Eastern Marine Fisheries Development Center. Thai Mar. Fish. Res. Bull., **4**: 45–58.

Walford, J. and Lam, T. J. 1993. Development of digestive tract and proteolytic enzyme activity in seabass (*Lates calcarifer*) larvae and juveniles. Aquaculture, **109**: 187–205.

ゴマフエダイ仔稚魚の摂餌・遊泳機能の発達

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飼育下のゴマフエダイ仔稚魚について，遊泳と摂餌に関する形質と遊泳速度の成長に伴う発達を検討した。全長 4 mm より小さい仔魚では，鰭は未発達であった。それにもかかわらず，遊泳速度は全長 3～4 mm から増加したが，遊泳様式は主に短距離の移動であった。顎や鰓弓，消化管は全長 4 mm までに発達し始めた。全長 4～8 mm の仔魚では，鰭支持骨と鰭条が出現し始め，また，定数に達した。この段階では，遊泳速度の急激な増加は見られなかった。なお，遊泳行動には，ゆっくりした巡航中に時々“ダッシュ”する様式がみられた。摂餌に関する形質も引き続き発達し，胃や幽門垂が全長約 7 mm で分化し始めた。全長 8～16 mm では，鰭支持骨が大きくなり，また化骨し始めた。この段階では，平均遊泳速度にあまり変化が見られなかったが，最大速度は増加した。遊泳に関する形質の完成に伴う遊泳速度の急激な増加は，全長 16～20 mm あるいはそれ以上の稚魚で認められた。

キーワード：ゴマフエダイ，機能発育，遊泳速度，骨化