Development of Swimming and Feeding Functions in Larval *Pagrus major*

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Abstract　Developmental sequences of characters concerned in swimming and feeding functions were investigated in the laboratory-raised larvae of *Pagrus major*. The finfold of early larvae was completely separated at 6.50 mm in notochord length (NL). The vertical fins developed earlier than the paired fins; the formation of dorsal, anal and caudal fin-supports and fin-rays started by 5.90 mm NL and their principal adult complements were attained by 6.50 mm NL, whereas an adult complement of fin-rays was attained at 9.40 mm NL in the pectoral fins and not attained by 10.15 mm NL, the largest size we examined, in the pelvic fins. In the vertical fins the development of the caudal fin preceded that of the dorsal and anal fins. The flection of the notochord end started at around 5.00 mm NL and was completed at about 6.50 mm, at which the angle of flection was $40° \sim 50°$. The body became increasingly deep in relation to NL up to about 6.50 mm NL, after which the depth maintained an almost steady ratio to NL. These patterns of development suggest that the larvae of *P. major* shift their mode of swimming from less active larval movement to active caudal propulsion at sizes between 5.00 mm and 6.50 mm NL.

As for feeding-related characters, the premaxillae appeared at 4.35 mm NL and came to occupy most of the upper jaw margin as in adults at about 7.00 mm NL. The formation of teeth started earlier on the upper and lower pharyngeals than on the premaxillae and dentaries. However, a more or less abrupt increase in number of teeth occurred at about 7.00 mm NL irrespective of regions. Observations on these characters indicate that the larvae of *Pagrus major* change their mode of feeding from swallowing to biting at sizes between 5.00 mm and 7.00 mm NL.

Incorporating these findings and our observations on the behavior of larvae, three stages may be recognized according to the mode of swimming and feeding in *Pagrus major* larvae. They are: 1) the early stage with less active swimming and feeding by swallowing prey (to about 5.00 mm NL); 2) the transitional stage (to about $6.50 \sim 7.00$ mm NL); and 3) the advanced stage with swimming by caudal propulsion and feeding by biting prey (about $6.50 \sim 7.00$ mm NL and larger).

The red seabream, *Pagrus major* (Temminck et Schlegel), is a common sparid species in Japanese waters. With the development of its farming through success in mass production of seedlings, a great deal of knowledge has been accumulated concerning the morphological and ecological features during larval stages (e.g., Tanaka, 1971, 1980; Fukuhara, 1976; Kitajima, 1978; Shirota, 1978a, b; Fukuhara and Kishida, 1980; Mori, 1980). However, there is no report on the osteological development of this species except for Matsuoka (1982), nor is there information on the osteological aspects of the functional development of its larvae. This study aims to describe the development of several osteological and morphological characters concerned in swimming and feeding func-

tions of *P. major* larvae, and discusses their implication to the functional development of the larvae.

Material and methods

The specimens used in this study include a daily-sampled series of 108 hatchery-reared larvae, $2.09 \sim 11.50$ mm in notochord length (NL) $11 \sim 30$ days after hatching, produced at the Kanagawa Prefectural Fisheries Experimental Station in 1981, and a young individual, 92.1 mm in standard length (SL), collected off Choshi, Pacific coast of central Honshu, Japan, on April 21, 1981. The larval specimens were originated from eggs spawned naturally in a large spawner tank at the station. They were reared at water temperatures of $18.7° \sim 23.2°C$
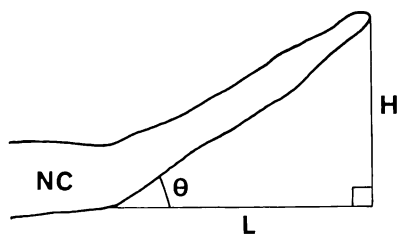
Fig. 1.　Diagram showing the measuring method of the flection angle of the notochord end in *Pagrus major* larvae.　The angle θ was calculated by: Tan θ = H/L.

(mean 21.3°C), fed *Brachionus plicatilis*, at a density of 20~30 individuals/m*l* water, up to the 15th day after hatching, and then *Artemia salina* nauplii and *B. plicatilis* were offered at a volume ratio of 75 : 25.

All specimens were fixed in 5% (larvae) or 10% (young) formalin.　The ratio of NL to total length (TL) in these formalin-fixed specimens was not perfectly constant, but could be approximately expressed by Mori's (1980) equation (TL=1.225SL−0.939).　Thirty-four specimens, 3.70~10.15 mm NL, were stained for

Table 1.　Acquisition of fin-ray and pterygiophore counts in 34 larvae and one young of *Pagrus major*.　NL: stained state; TL: formalin-fixed state, calculated from NL (see Material and methods).　Cart., cartilaginous; Os., ossifying; Sec., secondary.

| NL (mm) | TL (mm) | Fin-rays | | | | | | | Pterygiophores | | | |
		Dorsal	Anal	Pectoral	Pelvic	Caudal			Dorsal		Anal	
						Upper		Lower	Cart.	Os.	Cart.	Os.
						Sec.	Principal	Sec.				
3.70		0	0	0	0	0	0+0	0	0	0	0	0
3.80		0	0	0	0	0	0+0	0	0	0	0	0
3.90		0	0	0	0	0	0+0	0	0	0	0	0
4.10		0	0	0	0	0	0+0	0	0	0	0	0
4.35		0	0	0	0	0	0+0	0	0	0	0	0
4.40		0	0	0	0	0	0+0	0	0	0	0	0
4.45		0	0	0	0	0	0+0	0	0	0	0	0
4.70		0	0	0	0	0	0+0	0	0	0	0	0
4.95		0	0	0	0	0	3+3	0	0	0	0	0
5.05		0	0	0	0	0	6+6	0	5	0	4	0
5.10		0	0	0	0	0	4+4	0	?	0	0	0
5.45	5.49	0	0	0	0	0	6+6	0	18	0	8	0
5.70	5.79	0	0	4	0	0	7+8	0	16	0	9	0
5.85	5.97	0	0	4	0	0	7+8	0	19	0	9	0
5.90	6.03	4	4	5	0	0	7+8	0	19	0	9	0
6.00	6.14	?	5	5	0	0	8+8	0	20	0	9	0
6.00	6.14	21	10	5	?	0	7+8	0	20	0	9	0
6.10	6.26	?	?	5	?	0	9+8	1	20	0	9	0
6.15	6.32	20	10	7	0	0	9+8	1	19	0	9	0
6.35	6.56	21	10	7	0	0	9+8	1	20	0	9	0
6.40	6.62	21	10	8	?	1	9+8	2	20	0	9	0
6.50	6.73	23	12	8	3	1	9+8	2	20	0	9	0
7.05	7.38	23	12	11	4	2	9+8	3	20	0	9	0
7.30	7.68	23	12	13	4	4	9+8	4	20	0	9	0
7.50	7.91	23	12	14	4	5	9+8	5	20	0	9	0
7.55	7.97	23	12	12	4	3	9+8	3	20	0	9	0
7.75	8.21	23	12	13	5	4	9+8	4	20	0	9	0
7.85	8.33	23	12	14	5	5	9+8	5	20	0	9	0
7.95	8.45	23	12	14	5	5	9+8	4	20	0	9	0
8.35	8.92	23	12	14	5	6	9+8	6	15	5	8	1
8.55	9.15	23	12	14	5	5	9+8	5	15	5	8	1
9.40	10.16	23	12	15	5	8	9+8	8	14	6	8	1
9.80	10.63	23	12	15	5	7	9+8	7	12	8	8	1
10.15	11.04	23	12	15	5	9	9+8	9	12	8	8	1
92.10(SL)		23	12	15	5	9	9+8	10	0	20	0	9
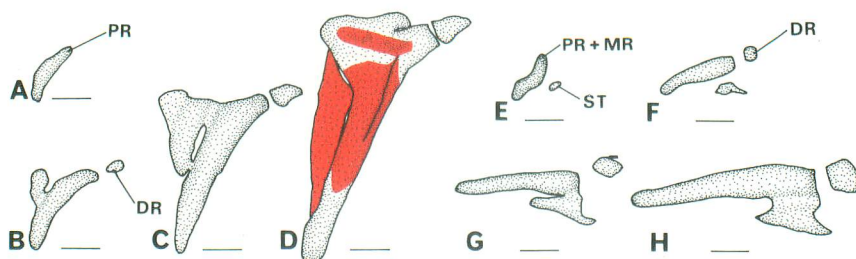
Fig. 2. Development of the first (A~D) and last (E~H) dorsal pterygiophores in *Pagrus major* larvae. Ossifying portions are shown in red. A, E: 6.10 mm NL. B, F: 6.40 mm NL. C, G: 7.95 mm NL. D, H: 10.15 mm NL. DR, distal radial; MR, middle radial; PR, proximal radial; ST, stay. Scale bars: 0.1 mm.
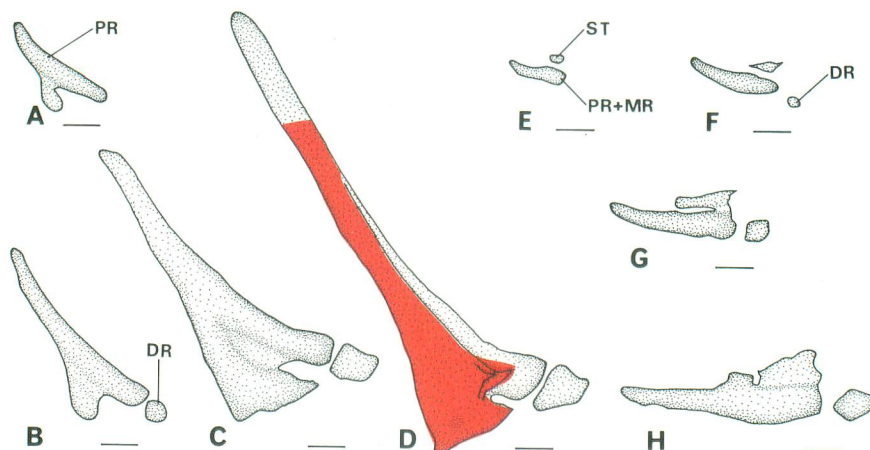

Fig. 3. Development of the first (A~D) and last (E~H) anal pterygiophores in *Pagrus major* larvae. Ossifying portions are shown in red. Drawn from the same specimens as in Fig. 2. For abbreviations, see Fig. 2. Scale bars: 0.1 mm.

both bone and cartilage for osteological observations, following the method of Dingerkus and Uhler (1977). The NL of these specimens tended to increase after staining, at an average rate of 3.78% (N=14). In this paper the NL of all specimens is given as stained state, either calculated from the NL of non-stained specimens (in specimens used for the examination of relationships between NL and the flection angle of notochord end and between NL and greatest body depth) or directly measured (in specimens for all other observations). The TL is given as formalin-fixed state calculated from the NL of stained or formalin-fixed specimens using the above-mentioned equation. TL smaller than 5.50 mm could not be calculated by the equation. Measurements were made under a binocular microscope with an ocular micrometer, read to the nearest 0.05 mm. Methods

for the measurement of the angle of flection of the notochord end are shown in Fig. 1. Counts for rays of the paired fins, and jaw and pharyngeal teeth were made on the left side.

Development of characters concerned in swimming function

Dorsal and anal fin-supports and fin-rays. In early stages of larval development the vertical fins were in the form of a continuous, membraneous finfold. The finfold extended dorsally from the nape and ventrally from the anal opening or postero-ventral portion of the yolk, and was continuous at the caudal end. With development, the anterior origins of the finfold receded on both dorsal and ventral sides, and the height of the finfold became lower at the caudal peduncle region. Complete separation of the finfold into dorsal, anal and caudal
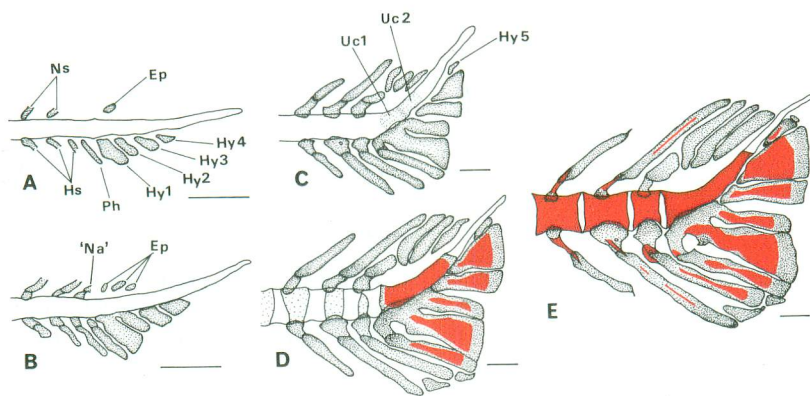
Fig. 4.　Development of the caudal complex in *Pagrus major* larvae.　Ossifying portions are shown in red.　A: 5.10 mm NL.　B: 5.45 mm NL.　C: 6.40 mm NL.　D: 7.95 mm NL.　E: 10.15 mm NL. Ep, epural; Hs, haemal spine; Hy, 1~5, hypurals 1~5; 'Na', specialized neural arch; Ns, neural spine; Ph, parhypural; Uc 1~2, ural centra 1~2.　Scale bars: 0.2 mm.
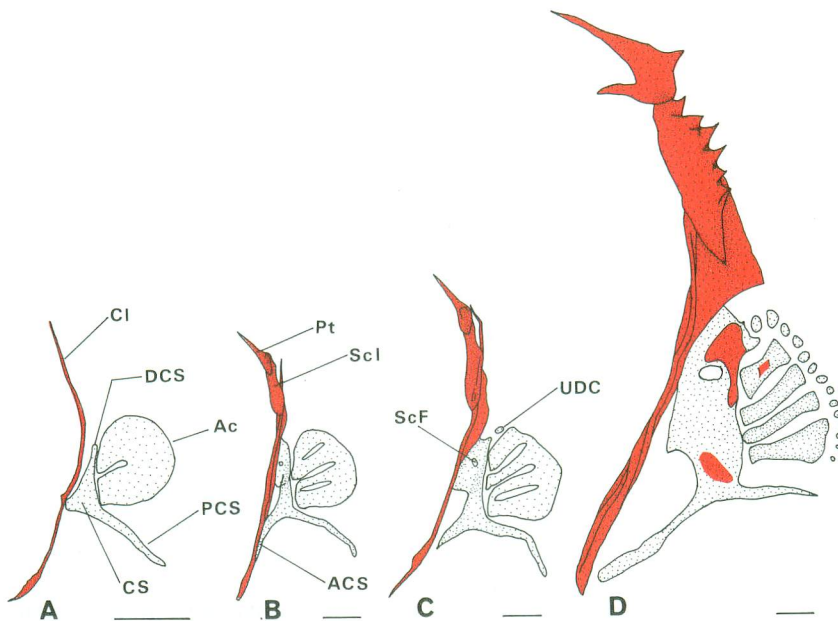
Fig. 5.　Development of the pectoral girdle in *Pagrus major* larvae.　Ossifying portions are shown in red. Postcleithra are removed.　A: 3.70 mm NL.　B: 5.10 mm NL.　C: 6.00 mm NL.　D: 10.15 mm NL.　Ac, actinost (blade-like cartilage); ACS, anterior process of coraco-scapular cartilage; Cl, cleithrum; CS, coraco-scapular cartilage; DCS, dorsal process of coraco-scapular cartilage; PCS, posterior process of coraco-scapular cartilage; Pt, posttemporal; ScF, scapular foramen; Scl, supracleithrum; UDC, uppermost distal cartilage.　Scale bars: 0.2 mm.

fins was first perceived at 6.50 mm NL.

At 4.95 mm NL no components of dorsal and anal pterygiophores were discerned. The pterygiophores observed first were five cartilaginous buds between the 12th and 15th vertebrae under the dorsal fin and four buds

between the 11th and 14th vertebrae under the anal fin at 5.05 mm NL. These pterygiophores were located in areas corresponding to the anterior portion of the soft dorsal fin and the anterior portion of the anal fin. At 5.45 mm NL, 18 pterygiophores, five between the 2nd

and 7th vertebrae and 13 between the 8th and 16th vertebrae, were observed in the dorsal fin, and eight pterygiophores were seen in the anal fin. An adult complement of pterygiophores was recognized at 5.70 mm NL for the anal fin and 6.00 mm NL for the dorsal fin (Table 1).

A detailed sequence of the osteological development of pterygiophores was traced in the first and last elements in both fins. A specimen of 5.90 mm NL was the smallest possessing the first dorsal pterygiophore, which was made up of a cylindrical cartilage, i.e., the proximal radial. There was no change in developmental conditions over 6.10 mm NL (Fig. 2A). This cylindrical proximal radial developed into a Y-shaped radial at 6.15 mm and 6.35 mm NL. In addition to this radial, a small cartilaginous ball, the distal radial, was discerned at 6.40 mm NL (Fig. 2B). The Y-shaped proximal radial grew into an inverted triangular cartilage with an elongate foramen in its center at 7.95 mm NL (Fig. 2C). At 8.35 mm NL ossification was seen in the central portion of the proximal radial. At 10.15 mm NL the anterior proximal keel became totally ossified (Fig. 2D).

The last dorsal pterygiophore first appeared as a cylindrical cartilage, future proximal and middle radials, at 6.00 mm NL. At 6.10 mm NL a small cartilaginous ball, future "stay" (Weitzmann, 1962), appeared posterior to the cylindrical cartilage (Fig. 2E). The distal radial appeared at 6.40 mm NL as a small cartilage (Fig. 2F). At 7.94 mm NL the cartilaginous proximal-middle radial and future stay fused together at their posterior portions (Fig. 2G). At 10.15 mm NL the fusion was almost completed (Fig. 2H). The last pterygiophore did not ossify within the range of the body sizes of our larval specimens.

The first and last pterygiophores of the anal fin developed in the same manner as in the dorsal fin-supports. Several developmental stages of these pterygiophores are shown in Fig. 3.

Formation of dorsal and anal fin-rays was first observed at 5.90 mm NL. Fully developed fin-ray counts were perceived at 6.50 mm NL in both fins.

The developmental sequence in counts of dorsal and anal fin-rays and pterygiophores is shown in Table 1.

Caudal fin-supports and fin-rays. Five specimens from 3.70 mm to 4.35 mm NL had a straight notochord. No other elements of the caudal skeleton were observed there. A 4.40 mm NL specimen had cartilaginous buds of the parhypural and hypurals 1~3, but hypural 3 was not visible in a 4.45 mm NL specimen. Cartilaginous buds of hypural 4, as well as those of the haemal spines of future preural centra 2~4, the neural spines of future preural centra 3 and 4 and the central epural, became discernible in a 4.70 mm and a 5.10 mm NL specimen (Fig. 4A). In addition to these elements, a 4.95 mm NL specimen had the posterior epural, and a 5.05 mm NL specimen had the anterior and posterior epurals. The specialized neural arch (Potthoff, 1975) of the future preural centrum 2 was first observed in a 5.45 mm NL specimen, in which hypurals 1 and 2 fused together at their proximal bases (Fig. 4B). There was no change in these conditions over 5.85 mm NL. Hypural 5 was added at 5.90 mm NL. Fusion of the parhypural with hypurals 1 and 2 at their bases started at 6.40 mm NL (Fig. 4C). It should be especially mentioned that in this specimen ural centra 1 and 2 were stained light blue, indicating their cartilaginous state (Fig. 4C). These two centra began to fuse together to form a cartilaginous urostyle at 6.50 mm NL. In this specimen cartilaginous distal radials of the haemal spines of preural centra 2 and 3 were observed. At 7.30 mm NL preural centra 2~4 were visible as cartilages. Ossification of hypurals 1~4 was first perceived at 7.55 mm NL, and that of the parhypural, hypural 5 and urostyle at 7.75 mm and 7.95 mm NL (*Fig.* 4D). Ossification of preural centra 2~4 was first seen at 8.35 mm NL. A cartilaginous ball, the distal cartilage, was noticed attaching to the distal end of hypural 5 at 10.15 mm NL (Fig. 4E). In this specimen ossification was observed in all elements except for the specialized neural arch of preural centrum 2 and epurals 1~3 (Fig. 4E).

Principal caudal fin-rays were first discerned at 4.95 mm NL (Table 1). Fin-rays extended obliquely downward during early stages, and then became directed backward as the flection of the notochord end went on. An adult complement of 9+8 principal rays was attained
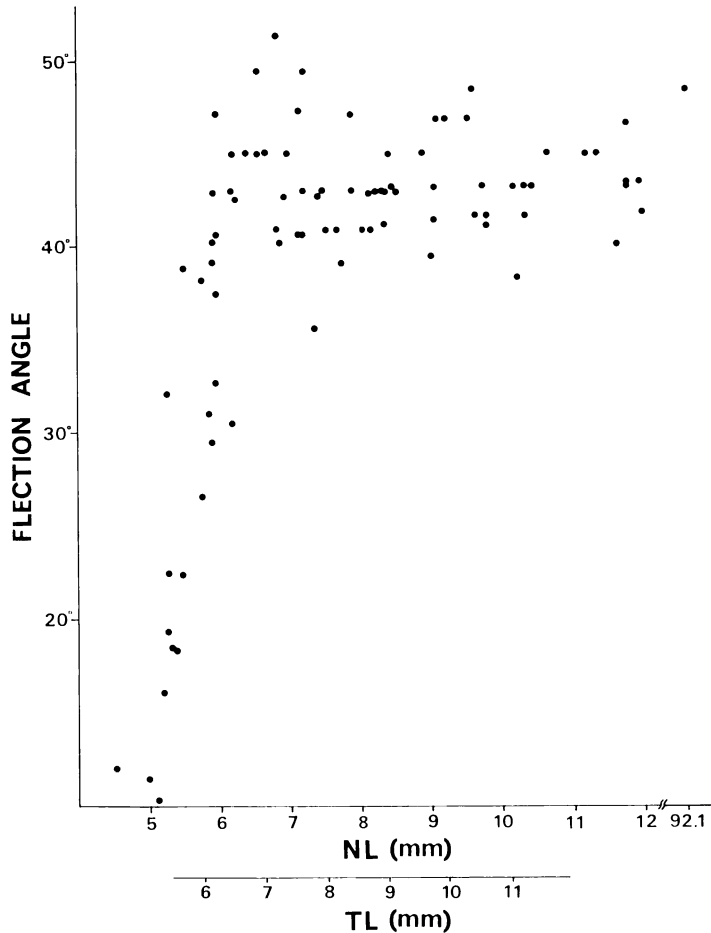
Fig. 6. Relationship between the angle of flection of notochord end and notochord (and calculated total) length in *Pagrus major* larvae.

at 6.10 mm NL (Table 1).

Pectoral fin-supports and fin-rays. A 3.70 mm NL specimen, the smallest we examined, possessed a rod-shaped bony cleithrum, a coraco-scapular cartilage and a blade like cartilage which later grew into actinosts (Fig. 5A). The coraco-scapular cartilage had a long posterior and a long dorsal process. The proximal half of the blade-like cartilage was deeply cleft. A small bony supracleithrum appeared at 4.35 mm NL. A bony posttemporal, an elliptical foramen in the upper part of the blade-like cartilage, and a posterior postcleithrum were discerned at 4.70 mm NL. At 5.10 mm NL, an elliptical foramen was noticed in the upper and lower parts of the blade-like actinost, the anterior and posterior processes of the

coraco-scapular cartilage increased in length, and its dorsal process became a broad plate with a small future scapular foramen (Fig. 5B). The anterior postcleithrum appeared at 5.90 mm NL. At 6.00 mm NL, the upper part of the actinost was separated into two at its proximal end, the coraco-scapular cartilage became broadened, and the scapular foramen was clearly observed (Fig. 5C). A 7.30 mm NL specimen had four cartilaginous actinosts originating from the blade-like plate. At 8.35 mm NL ossification was perceived in the upper (future scapula) and lower (future coracoid) parts of the coraco-scapular cartilage. At 10.15 mm NL, ossification occurred in the dorso-distal portion of future scapula, central portion of future coracoid, and the first (uppermost)
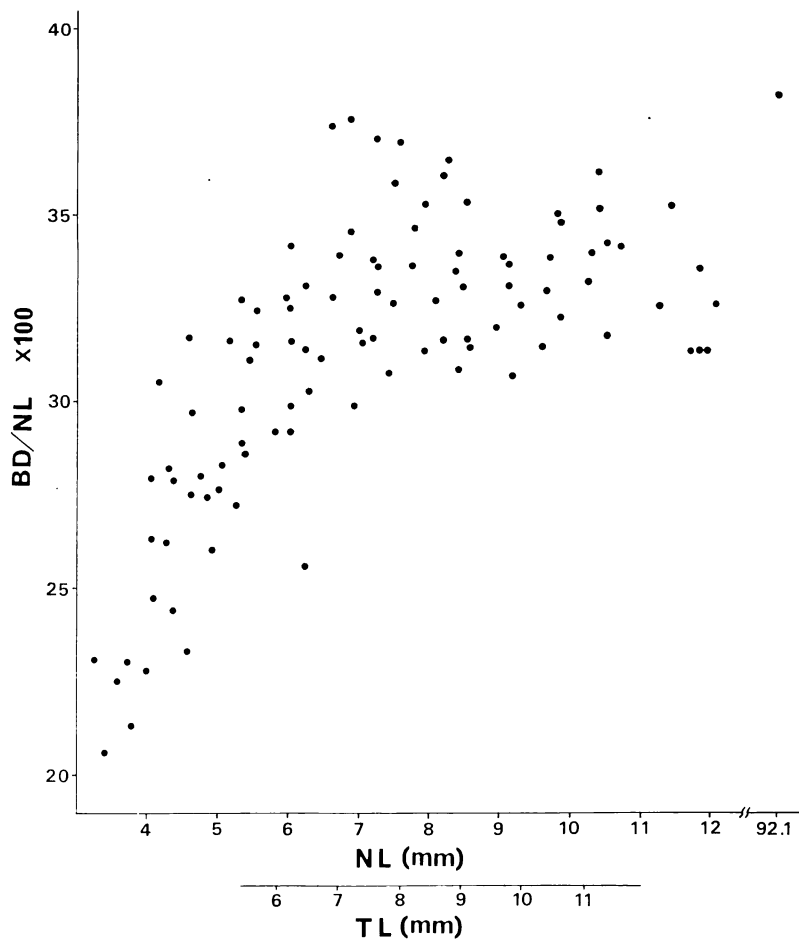
Fig. 7. Relationship between body depth-notochord length ratio and notochord (and calculated total) length in *Pagrus major* larvae.
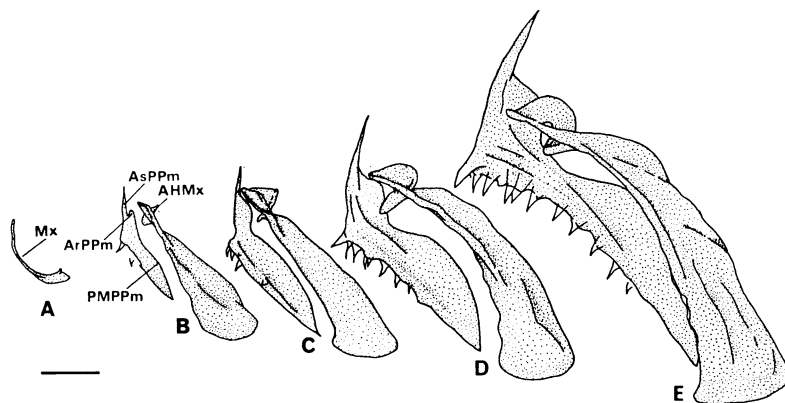

Fig. 8. Development of the upper jaw (all bony) in *Pagrus major* larvae. A: 3.70 mm NL. B: 5.45 mm NL. C: 6.50 mm NL. D: 7.95 mm NL. E: 10.15 mm NL. AHMx, articular head of maxilla; ArPPm, articular process of premaxilla; AsPPm, ascending process of premaxilla; Mx, maxilla; PMPPm, postmaxillary process of premaxilla. Scale bar: 0.2 mm.
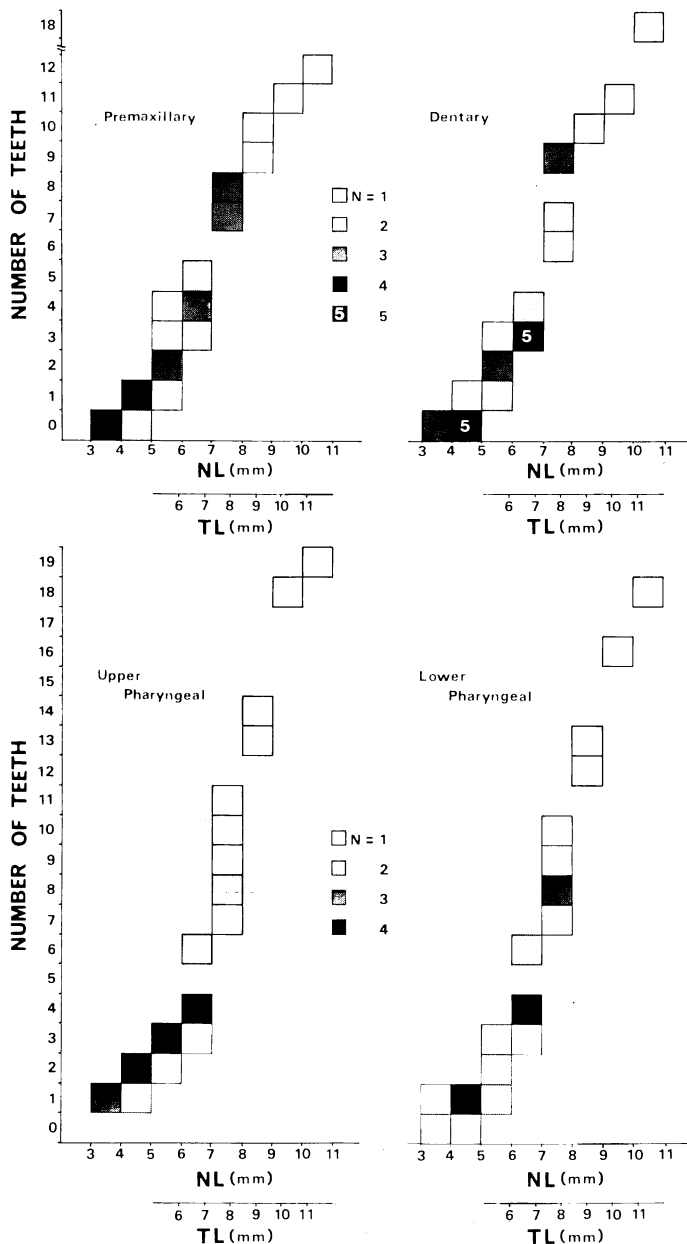
Fig. 9.   Number of jaw and pharyngeal teeth by size-groups in *Pagrus major* larvae.   Tones of shade in the squares indicate number of individuals as designated in the figure.

actinost (Fig. 5D).

Pectoral fin-rays developed from a blade-like finfold.   The first rays to develop were four rays in the dorsal side of the finfold at 5.70 mm NL.   Other rays were added from the dorsal to the ventral portions, and an adult complement of 15 rays was attained at 9.40 mm NL.

The development of pectoral fin-ray count is given in Table 1.

Pelvic fin-supports and fin-rays.   The pelvic girdle was first discerned at 5.90 mm NL.   The girdle remained cartilaginous up to 10.15 mm NL, the largest size we examined.   No detailed observations were made on the developmental
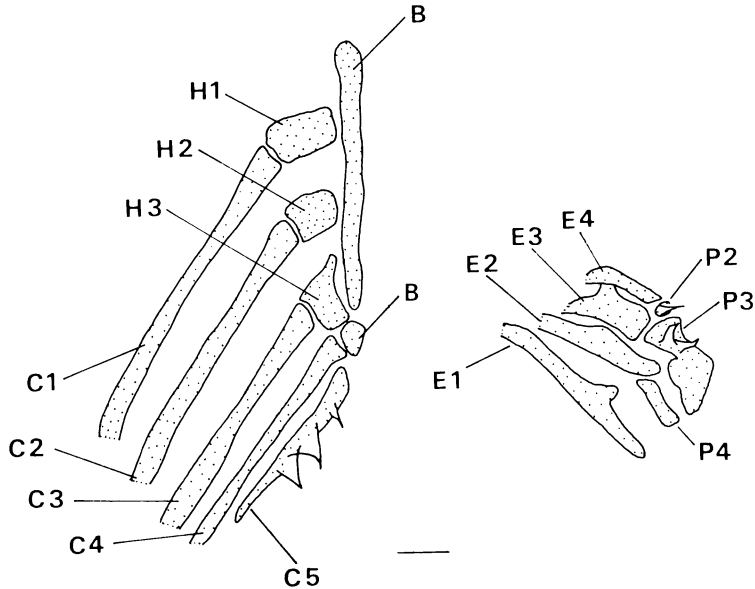
Fig. 10. Left half of the gill-arch (cartilaginous) in a 6.00 mm NL larva of *Pagrus major*. Left: Dorsal view of the lower gill-arch. Right: Ventral view of the upper gill-arch. B, basihyal; C 1~5, ceratohyals 1~5; E 1~4, epihyals 1~4; H 1~3, hypohyals 1~3; P 2~4, pharyngo-branchials 2~4. Scale bar: 0.1 mm.

sequence of the pelvic girdle.

Pelvic fin-rays first appeared at 6.50 mm NL and were fully developed in count at 7.75 mm NL (Table 1).

Flection of notochord end. A 5.15 mm NL specimen was the largest possessing a straight notochord, while the smallest specimen having a flexing notochord was 4.65 mm NL. The flection was completed at about 6.50 mm NL (Fig. 6). Although the angle of flection was not very constant due partially to our measuring method, the flection could be regarded as completed at angles between 40° and 50°.

Greatest body depth. The ratios of the greatest body depth to NL are plotted against each NL in Fig. 7. The depth accounted for a little more than 20% of NL in sizes smaller than 4.00 mm NL. The ratio increased abruptly up to around 6.50 mm NL, and then maintained an almost steady level (Fig. 7).

Development of chasacters concerned in feeding functions

Upper jaw structure. In sizes 4.10 mm NL and smaller, stain uptake was observed only in small bony maxillae (Fig. 8A). A 4.35 mm NL

larva was the smallest possessing discernible premaxillae. At 4.40 mm NL the articular head of the maxilla was seen, and the premaxillae were rod-shaped with an ascending process. The articular and postmaxillary processes of the premaxilla first appeared at 5.45 mm NL (Fig. 8B). Further developmental stages are shown in Fig. 8C~E.

Teeth. Upper jaw teeth were formed only on the premaxillae. The first premaxillary tooth was observed at 4.40 mm NL. The number of teeth increased in proportion to the increase in NL, with a more or less conspicuous leap at around 7.00 mm NL (Fig. 9). Dentary teeth were first perceived at 4.95 mm NL. A more or less marked leap in the number of teeth was also noticed at about 7.00 mm NL (Fig. 9).

An upper pharyngeal tooth was already present at 3.70 mm NL, the smallest size we examined. Lower pharyngeal dentition started at 3.90 mm NL or larger (Fig. 9). All larval teeth were canine-like within the size range we dealt with (Fig. 10). Number of upper and lower pharyngeal teeth increased with growth, again showing a leap at about 7.00 mm NL (Fig. 9).
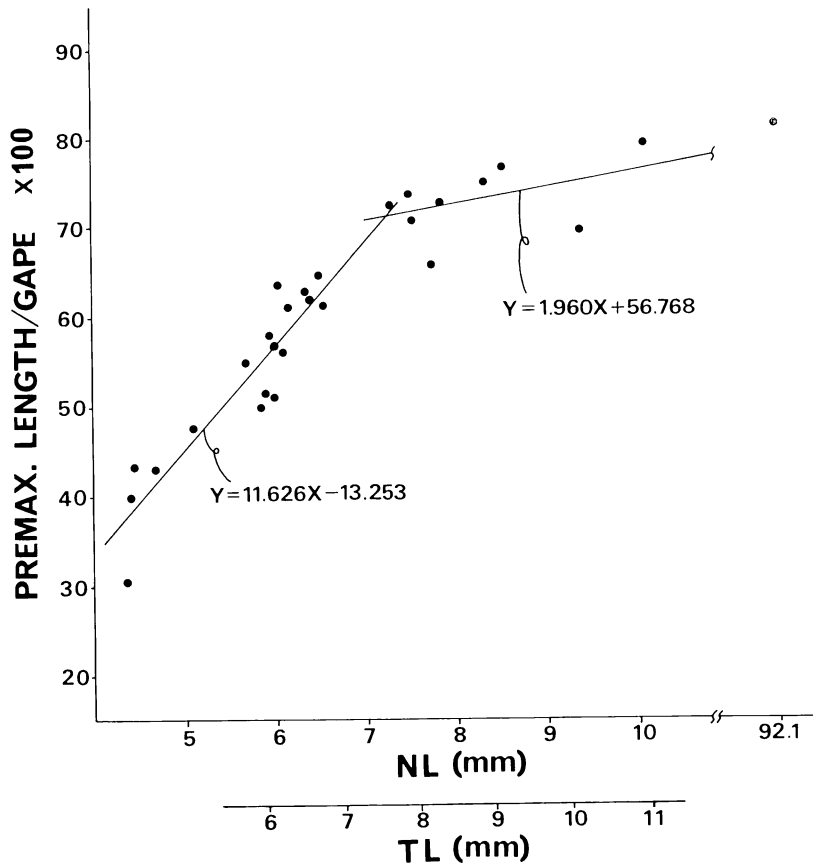
Fig. 11. Relationship between premaxillary length-gape length ratio and notochord (and calculated total) length in *Pagrus major* larvae.

Length of premaxilla. The length of the premaxilla in relation to the gape increased with growth, at a higher ratio up to about 7.00 mm NL (regression coefficient: 11.626) and at a lower ratio in larger larvae (regression coefficient: 1.960) (Fig. 11).

Discussion

Swimming function. The developmental process of the characters taking part in the swimming function of *Pagrus major* larvae can be epitomized as follows and schematically represented as in Fig. 12. In all fins, both the appearance and completion in number of principal elements of fin-supports precede those of fin rays, except for the completion of the pelvic fin elements. The development of the vertical fins precedes that of the paired fins. In the vertical fins, the caudal fin in turn develops

earlier than the dorsal and anal fins. The flection of the notochord end occurs a little later than the formation of the principal caudal fin-supports and fin-rays. The separation of the finfold into the three vertical fins and the inflection point in the body depth-NL ratio occurred at 6.50 mm NL.

Fish larvae at the finfold stage are generally described as moving by undulating the body, with the finfold forming a dorso-ventral extension of the body that adds to the amount of surface pressed against the water (Gosline, 1971). According to our observations, however, the finfold larvae of *Pagrus major,* unlike those of *Plecoglossus altivelis, Paralichthys olivaceus, Limanda yokohamae,* etc., do not exhibit undulating or anguilliform body movement. They only stand still in stagnant water or orientate themselves at the same position in slow-flowing

Dorsal:	fin-rays	5.90 (6.03) O——● 6.50 (6.73)	
	fin-supports	5.05 (-) O————● 6.00 (6.14)	
Anal:	fin-rays	5.90 (6.03) O——● 6.50 (6.73)	
	fin-supports	5.05 (-) O————● 5.70 (5.79)	
Caudal:	fin-rays	4.95 (-) O————● 6.10 (6.26)	
	fin-supports	4.40 (-) O——● ca 5.00 (-)	9.40 (10.16)
Pectoral:	fin-rays	5.70 (5.79) O——————————————●	
	fin-supports	————————————————● 7.30 (7.68)	
Pelvic:	fin-rays	6.50 (6.73) O————● 7.75 (8.21)	
	fin-supports	5.90 (6.03) O————————————	
Greatest body depth/NL		■ ca 6.50 (6.73)	
D, A, C separation		▼ 6.50 (6.73)	
Notochord end flection		ca 5.00 (-) O————● ca 6.50 (6.73)	

Mode of swimming	less active swimming	transitional stage	caudal propulsion

NL (mm)	4	5	6	7	8	9
TL			6	7	8	9	10

Mode of feeding	swallowing	transitional stage	biting

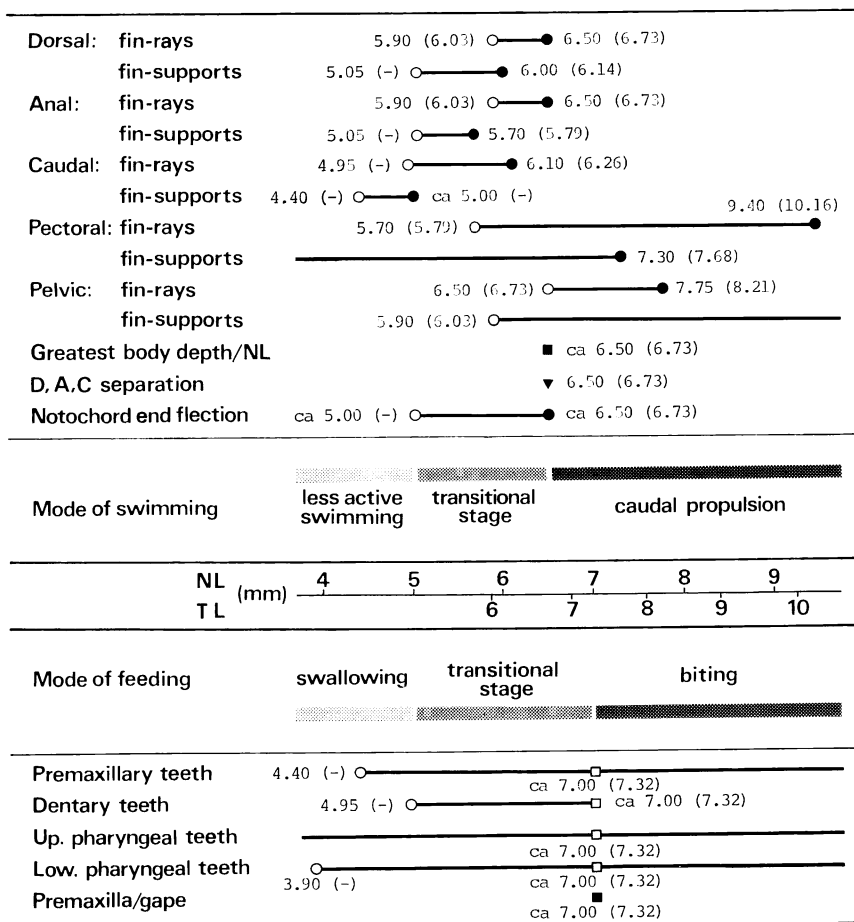|		
Premaxillary teeth	4.40 (-) O————————□ ca 7.00 (7.32)	
Dentary teeth	4.95 (-) O————————□ ca 7.00 (7.32)	
Up. pharyngeal teeth	————————□ ca 7.00 (7.32)	
Low. pharyngeal teeth	3.90 (-) O————————□ ca 7.00 (7.32)	
Premaxilla/gape	■ ca 7.00 (7.32)	

Fig. 12. Schematic representation of the development of swimming and feeding functions in *Pagrus major* larvae. Numerals are NL followed in parentheses by TL (TL smaller than 5.50 mm could not be calculated (−)). Open circle, appearance of element or phenomenon; soild circle, completion in number of elements or of phenomenon; solid square, inflection point of ratio; solid triangle, completion; open square, abrupt increase in number; D, A, C separation, separation of finfold into dorsal, anal and caudal fins.

water, without showing any appreciable movement of the body. We failed in finding how the larvae keep their position against the weak current. Hunter (1981) showed several examples of swimming modes in fish larvae, but under none of his examples comes the swimming mode of the finfold larvae of *P. major*. Nor have we observed any movement similar to the "abrupt swimming" by reaction of body muscles described by Rosenthal and Hempel (1970) in the larvae of some clupeoids.

The flection of notochord end started at about 5.00 mm NL and was completed at about 6.50 mm NL. By the time of its completion all of the principal elements of fin-supports and all principal rays of the caudal fin had been formed. As the flection goes on, caudal fin-rays shift their direction from an obliquely downward arrangement to a horizontal arrangement. This change, coupled with the development of the fin-supports and fin-rays, increases forward propulsive force.

The completion of the fundamental adult structures of the caudal fin at about 6.50 mm NL coincides in time with the separation of the finfold into the three vertical fins, the comple-

tion of the formation of dorsal and anal fin elements, and the inflection point in the body depth-NL relationship. The segregation of the vertical fins should be concerned with a change in swimming mode (Gosline, 1971), as should the change in the relative body depth (Aleev, 1963).

All these observations suggest that the larvae of *Pagrus major* begin to change their mode of swimming at about 5.00 mm NL and almost completely shift to locomotion with caudal propulsion at about 6.50 mm NL (6.73 mm TL).

Fukuhara and Kishida (1980) reported that hatchery-raised larvae of *Pagrus major* about 20 days after hatching (about 6.00 mm NL in our case) increased swimming speed. Tanaka (1980) stated that wild larvae larger than 7.00 mm TL showed dodging behavior. Mori (1980) reported that wild larvae larger than 6.00 mm TL became difficult to be caught by a larva net. These observations basically agree with our findings.

Feeding function. The development patterns of the characters concerned in feeding function are summarized in Fig. 12. The formation of the premaxillae was preceded by that of the maxillae, starting at 4.35 mm NL. Jaw teeth began to develop at 4.40 mm NL on the premaxillae and at 4.95 mm NL on the dentaries. Pharyngeal teeth appeared earlier than jaw teeth, by 3.90 mm NL. At about 7.00 mm NL, the ratio of premaxillary length to gape reached an inflection point, and teeth in all regions showed a more or less abrupt increase.

A mouth with poorly developed premaxillae seems to have insufficient function to open and close (see Iwai, 1972), and that with few teeth may be unable to seize prey even if the mouth can be functionally opened and closed. Larvae smaller than about 5.00 mm NL seem to feed by swallowing food organisms. Pharyngeal teeth that are already in existence may play a role in seizing the organisms swallowed and passing them to the gut.

The ability of biting is acquired and increases as the premaxillae and other jaw elements develop and dentition goes on. At about 7.00 mm NL, the premaxillae come to occupy a great part of the upper jaw margin similar to adults and the number of teeth increases more or less abruptly, the larvae seem to acquire, nearly or

quite completely, a biting ability.

In conclusion, the larvae of *Pagrus major* shift their mode of feeding from swallowing to biting, starting at about 5.00 mm NL and reaching completion at about 7.00 mm NL (7.32 mm TL).

This assumption agrees well with our actual observations on the behavior of the larvae; cannibalism becomes noticeable at about 6.70 mm NL and larger. The pattern of changeover in the mode of feeding described in the present study also agrees with conclusions drawn from various aspects of previous studies (e.g., Tanaka, 1971, digestive system; Shirota, 1978a, b, upper jaw length).

Conclusive notes. Larvae up to about 5.00 mm NL are not capable of swimming actively and pursuing and biting food organisms. From this stage, preparation for caudal propulsion and biting commences in the structures concerned. The preparation is completed at about 6 50 mm NL (6.73 mm TL) for caudal propulsion and at about 7.00 mm NL (7.32 mm TL) for biting. Based on these observations, the development of swimming and feeding functions in the larvae of *Pagrus major* may be roughly divided, if we venture to do it, into three stages, i.e., 1) early stage with less active swimming and feeding by swallowing (to about 5.00 mm NL), 2) transitional stage (to about 6.50~7.00 mm NL, 6.73~7.32 mm TL), and 3) advanced stage with swimming by caudal propulsion and feeding by biting (larger than the preceding stage).

Intervals of fish development have been studied and discussed by many authors (see Balon, 1975, 1976, and Richards, 1976, for literature). Kitajima (1978) divided the postlarval stage of *Pagrus major* into two, postlarval stages I and II, with a total length of 6.00 mm as a border, based on morphological changes. This is fundamentally in agreement with our results. There are many approaches to the arrangement of intervals. However, it should be mentioned that the development of larvae is a continuous phenomenon, a mosaic made up of variously overlapped patterns of formation of individual characters.

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マダイ仔魚の遊泳・摂餌機能の発達

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　マダイ仔魚の遊泳・摂餌機能に関与する形質の発達を観察し，機能発達との関連を考察した．

　鰭褶は 6.50 mm NL（脊索長）で完全に分離した．垂直鰭の支持骨・鰭条の発達は対鰭のそれよりも早く，約 5.00 mm NL までに主要な全要素が出現し，垂直鰭のなかでは尾鰭の発達が他よりも早かった．脊索末端の屈曲は約 5.00 mm NL からはじまり，約 6.50 mm NL で完了した．体高・脊索長比は約 6.50 mm NL まで増加し，以後は比較的一定した値を保った．以上から，マダイ仔魚は約 5.00～6.50 mm NL のあい

だで，初期の不活発な遊泳から尾鰭推進に移行するものと推論した．

摂餌に関与する形質では，前上顎骨は約 7.00 mm NL で上顎の主要縁辺を占めるにいたった．顎歯は咽頭歯よりも発達がおくれたが，いずれの場合も 7.00 mm NL 前後であるていどの数の急増がみられた．以上の観察から，仔魚の摂餌様式は 5.00〜7.00 mm NL のあいだで swallowing から biting に移行するものと結論した．

上記を総合すると，マダイの遊泳・摂餌様式は，1）遊泳能力があまりなく，swallowing により摂餌する初期段階（約 5.00 mm NL まで），2）移行期（6.50〜7.00 mm NL まで），3）尾鰭推進と biting を行う発達した段階の 3 期に分けることができる．

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