Osteological development of the feeding apparatus in early stage larvae of the seabass, *Lates calcarifer*

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Abstract The osteological development of the feeding apparatus was examined in early stage larvae of laboratory-reared seabass, *Lates calcarifer*. At initial mouth openings 40 hours after hatching, the larvae were equipped with the fundamental elements forming the oral cavity, such as the trabecular roof, the lower branchial and hyoid arches forming the floor, the quadrate and symplectic-hyomandibular cartilages making up the sides, and the maxilla and Meckel's cartilage bordering the jaws. The cleithrum appeared almost simultaneously. The mechanics of creating a negative pressure in the oral cavity, which results in a "sucking" mode of feeding, were elucidated from these elements. During a period from 50–60 to 100–110 hours after initial mouth opening (HAMO), new elements such as the premaxilla and jaw teeth appeared, and the ossification of existing elements started. The new elements apparently enabled the larvae to "grasp" food organisms, in addition to the already existing and increasing sucking ability, from 100–110 HAMO.

Key words. — *Lates calcarifer*; larval development; feeding function; ossification.

Development of the morphological structures, particularly those of the jaw apparatus, involved in the feeding of early-stage fishes have been investigated by various authors (Berry, 1964; Aleev, 1969). However, with the advent of staining techniques developed by Dingerkus and Uhler (1977) for both cartilage and bone, much interest has centered on the osteological development of fish larvae. Although a number of more recent studies described the ontogenetic development of bony elements related to feeding (Kohno et al., 1983; Matsuoka, 1985; Watson, 1987; various studies by Potthoff, see Potthoff and Tellock [1993]), none of these investigated the mechanics of feeding or the feeding mode. The mechanics and functional development of feeding in larvae and juveniles were discussed by Otten (1982, for the cichlid, *Haplochromis elegans*) and Matsuoka (1987, for the sparid, *Pagrus major*), based on the development of both bones and muscles. In adult fishes, the design and mechanics of bones and muscles concerned with feeding have been well documented for various species (Alexander, 1970; Gosline, 1971; Liem, 1980; Osse and Muller, 1980; Lauder, 1983; Gerking, 1994).

The seabass, *Lates calcarifer*, is an important species for aquaculture and sport-fishing in Southeast Asia and Australia, with seed production having been successfully conducted in these areas (Anonymous, 1986; Copland and Grey, 1987). The success of mass seed production of the species has generated ample material for early life history studies, such as the development of external features (Kosutarak and Watanabe, 1984), changeover of energy sources (Bagarinao, 1986; Kohno et al., 1986), nutritional requirements (Walford et al., 1991) and development of the digestive tract (Walford and Lam, 1993). Although the osteological develop-

ment of seabass larvae and juveniles was investigated by Kohno et al. (1992), the bony, feeding-related elements described were limited to the jaw apparatus and no discussion on the mechanics of feeding was included.

In the present study, the development of bony elements related to feeding, namely the neurocranium, jaws, suspensorium, hyoid and branchial arches, and opercular bones, as well as that of the fins, was described ontogenetically in the early-stage larvae of the seabass. Based on morphological development, the mechanics of feeding and changes in feeding mode with age are discussed.

Materials and Methods

The eggs used in this study were obtained from spawners induced by hormonal treatment and reared at the Igang Station, Iloilo, Philippines, of the Southeast Asian Fisheries Development Center—the Aquaculture Department (SEAFDEC AQD). Eggs spawned on 12 June, 1994, were transported to the Tigbauan Research Station in Iloilo and placed in 400 *l* hatching tanks. Hatching occurred at 13:30 the following day, with hatched larvae then being transferred to a 500 *l* larval rearing tank at a density of about 60 ind./*l*. The larval rearing methods followed those described by Parazo et al. (1990), the water temperatures ranging from 26–28°C and salinity from 30–31 ppt, during the experiment.

Random sampling of five larvae at a time was done at irregular intervals from hatching to 196.5 hours after hatching, with a total of 75 larvae being utilized for the study. Samples were initially preserved in neutralized 5% formalin and later cleared and stained following the procedure of Dingerkus and Uhler (1977).

Osteological and morphometric observations were made on the specimens using a microscope equipped with a micrometer eyepiece. The appearance and development of osteological features were observed for the neurocranium, upper and lower jaws, suspensorium, hyoid arch, upper and lower branchial arches, opercular bones and fins. Measurements included the following: head length, measured from the anterior tip of Meckel's cartilage to the posterior midsection of the cleithrum; length of suspensorium, from the anteroventral tip of the quadrate to the posterodorsal corner of the symplectic-hyomandibular cartilage; lengths of ceratohyal-epihyal cartilage, basibranchial, premaxilla and maxilla; and the distance between the posterior end of Meckel's cartilage and the anterior tip of the hyoid arch.

In this study, all references to time were standardized and expressed as hours after initial mouth opening, HAMO (40 hours after hatching). Negative values of HAMO indicate events which occurred prior to mouth opening. All specimens used in this study were deposited in the Museum, Tokyo University of Fisheries (MTUF-P (L) 106).

Results

Osteological development

Jaws. — The first jaw element to appear was Meckel's cartilage, at −15.5 HAMO, the anterior tip being located midway between the eyes (Fig. 1A). The tip position subsequently advanced with age, being located ahead of the anterior margin of the eyes at 0 HAMO. The posterior end of Meckel's cartilage, which was articulated with the suspensorium, was observed to bend downward at 9.5 HAMO (Fig. 1B). An anterodorsally-directed projection was formed on the posterodorsal part of Meckel's cartilage at 35.5 HAMO (Fig. 1C). Initial ossification of Meckel's cartilage was first evident at 58 HAMO, with the dentary, angular and retroarticular ossifying on the anterior and posterior halves, and postero-ventral end of Meckel's cartilage (Fig. 1D), respectively. With larval growth, ossification continued, with Meckel's cartilage becoming more slender.

Of the upper jaw elements, the bony maxilla appeared first, at 9.5 HAMO (Fig. 1B). The short, bony premaxilla formed in front of the upper part of the maxilla at 58 HAMO (Fig. 1D) and subsequently developed downward so as to exclude the maxilla from the border of the gape (Fig. 1E).

Initially appearing jaw teeth were one and two

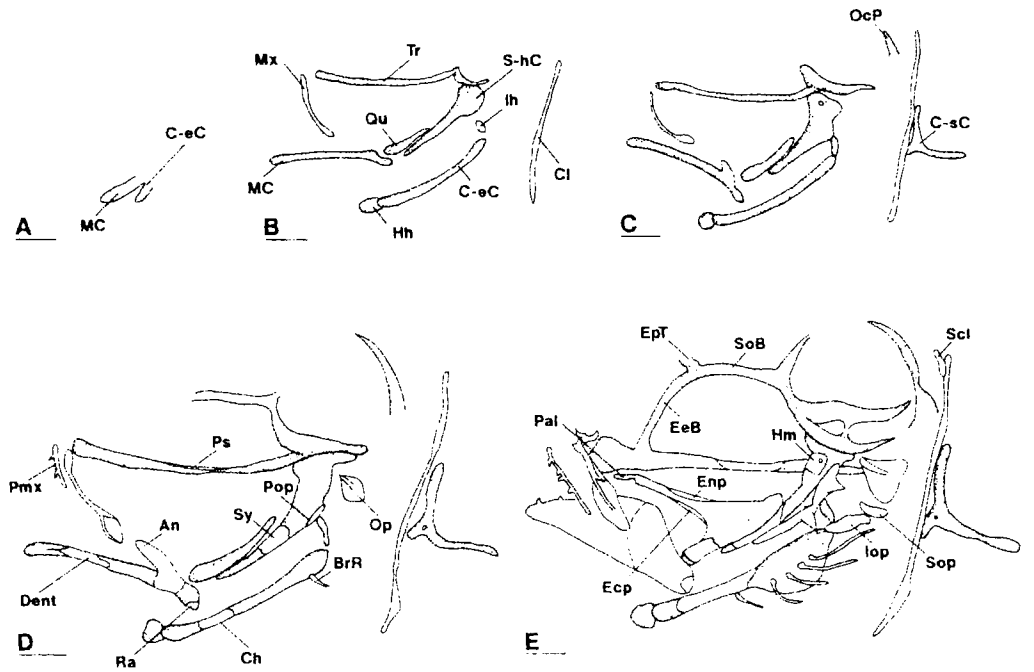

Fig. 1. Development of the feeding apparatus in *Lates calcarifer*. Left lateral views of elements comprising the oral cavity are shown. A) −15.5 hours after initial mouth opening (HAMO) (mean±SD of total length, TL, in fresh state: 2.26±0.02 mm); B) 9.5 HAMO (2.32±0.02 mm TL); C) 35.5 HAMO (2.50±0.01 mm TL); D) 58 HAMO (2.62±0.01 mm TL); E) 104.5 HAMO (2.99±0.02 mm TL). Stippled area, cartilage; open area, ossification. *An*—angular; *BrR*—branchiostegal ray; *C-eC*—ceratohyal-epihyal cartilage; *Ch*—ceratohyal; *Cl*— cleithrum; *C-sC*—coraco-scapular cartilage; *Dent*—dentary; *Ecp*—ectopterygoid; *EeB*—ectethmoid bar; *Enp*—endopterygoid; *EpT*—epiphysial tectum; *Hh*—hypohyal; *Hm*—hyomandibular; *Ih*—interhyal; *Iop*—interopercle; *MC*—Meckel's cartilage; *Mx*—maxilla; *OcP*—occipital process; *Op*—opercle; *Pal*—palatine; *Pmx*—premaxilla; *Pop*—preopercle; *Ps*—parasphenoid; *Qu*—quadrate; *Ra*—retroarticular; *Scl*—supracleithrum; *S-hC*—symplectic-hyomandibular cartilage; *SoB*—supraorbital bar; *Sop*—subopercle; *Sy*—symplectic; *Tr*—trabecula. Scale bars indicate 0.1 mm.

premaxillary teeth in one and four specimens, respectively, out of the five larvae examined at 58 HAMO (Fig. 1D). A single dentary tooth was first evident, in four out of five specimens examined, at 81 HAMO. The number of premaxillary and dentary teeth increased with age, reaching 8–19 and 3–5, respectively, at 156.5 HAMO.

Suspensorium. — The symplectic-hyomandibular cartilage appeared first as an element of the suspensorium at −7.5 HAMO, followed by the cartilaginous quadrate, first observed anterior to the former at 0 HAMO. The suspensorium was articulated ventrally with Meckel's cartilage through the quadrate and dorsally with the auditory capsule through the symplectic-hyomandibular cartilage (Fig. 1B). A small foramen developed first on the upper part of the symplectic-hyomandibular cartilage at 35.5 HAMO (Fig. 1C). Initial ossification, that of the symplectic on the lower part of the symplectic-hyomandibular cartilage, was first evident at 58 HAMO. At 68.5 HAMO, the cartilaginous palatine was first visible, with ossification of the quadrate having begun. The cartilaginous palatine was contiguous with the quadrate, forming a wide, triangular, cartilaginous plate (palatoquadrate cartilage), at 104.5 HAMO, the endopterygoid and ectopterygoid appearing on its upper and lower parts, respectively (Fig. 1E). The hyomandibular started ossifying on the upper part of the symplectic-hyomandibular cartilage at this time.

Hyoid arch. — The ceratohyal-epihyal cartilage appeared first, at −15.5 HAMO. The hypohyal and interhyal cartilages were first formed at

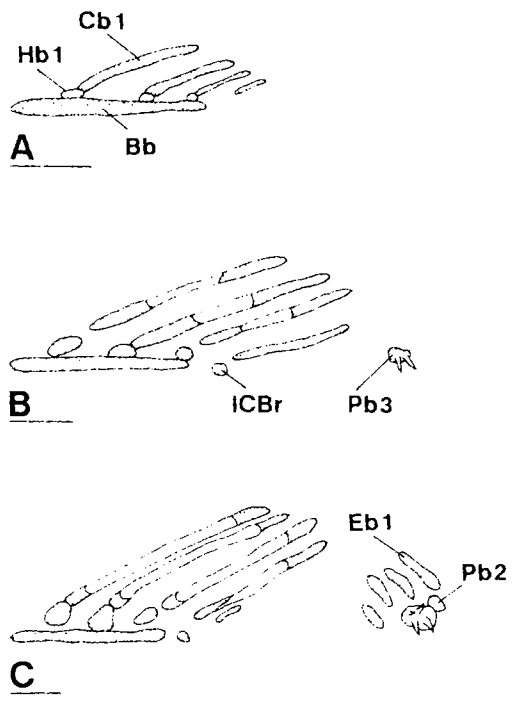

Fig. 2. Development of branchial arches in *Lates calcarifer*. Ventral views of right upper and left lower branchial arches are shown. A) 9.5 hours after initial mouth opening (HAMO); B) 58 HAMO; C) 104.5 HAMO. Stippled area, cartilage; open area, ossification. *Bb*—basibranchial; *Cb1*—ceratobranchial 1; *Eb1*—epibranchial 1; *Hb1*—hypobranchial 1; *ICBr*—isolated cartilage of basibranchial; *Pb2*—pharyngobranchial 2; *Pb3*— pharyngobranchial 3. Scale bars

9.5 HAMO, the hyoid arch being articulated anteriorly with the anterior end of the basibranchial through the former cartilage and posteriorly with the symplectic-hyomandibular cartilage through the latter (Fig. 1B). At 58 HAMO, the ceratohyal started ossifying on the anterior part of the ceratohyal-epihyal cartilage. A single branchiostegal ray was evident (Fig. 1D). Ossification of the interhyal started at 156.5 HAMO, the number of branchiostegal rays having increased to five (in one specimen) or six (in four specimens) at that time. Neither the basihyal nor the urohyal appeared over the duration of the study.

Branchial arch. — The lower arch elements, the cartilaginous basibranchial and anteriormost two ceratobranchials, were the first to appear, at −7.5 HAMO. Ceratobranchials 3–4 and the anteriormost three hypobranchials were added at 9.5 HAMO (Fig. 2A). At 58 HAMO, the isolated basibranchial cartilage was first observed, with ossification of ceratobranchials 1–3 having begun (Fig. 2B). Ceratobranchial 5 was first evident at 68.5 HAMO, with ossification of ceratobranchial 4 beginning at that time. Ossification of ceratobranchial 5 and the basibranchial was first evident at 156.5 HAMO.

The first upper arch element to appear was the cartilaginous pharyngobranchial 3, bearing two teeth, observed at 58 HAMO (Fig. 2B). Four cartilaginous epibranchials and the cartilaginous pharyngobranchial 2 were added at 68.5 and 81 HAMO, respectively (Fig. 2C for 104.5 HAMO). The upper pharyngeal teeth had increased in number with growth, three and four teeth being observed in three and two specimens, respectively, out of the five larvae examined at 81 HAMO. The teeth number increased to 6–7 at 156.5 HAMO.

Opercular bones. — Both the opercle and preopercle appeared at 58 HAMO (Fig. 1D), with the interopercle and subopercle being added at 81 and 104.5 HAMO, respectively (Fig. 1E).

Neurocranium. — The cartilaginous trabecula appeared first at −7.5 HAMO. Contiguous to the trabecula were the cartilaginous ethmoid, auditory capsule and paracordal, appearing first at 9.5 HAMO (Fig. 1B). The cartilaginous occipital process was first evident at 44.5 HAMO, followed by the cartilaginous supraorbital bar at 58 HAMO. The ossification of the parasphenoid had started on the trabecula at the latter time (Fig. 1D). Contiguous with the supraorbital bar, the cartilaginous epiphysial tectum and ectethmoid bar first appeared at 104.5 HAMO.

Fins. — The bony cleithrum appeared first at −7.5 HAMO. The coraco-scapular cartilage, bearing both dorsal and posterior projections, was first evident at 21.5 HAMO. A small, anteriorly-directed projection developed on the anteroventral part of the coraco-scapular cartilage at 35.5 HAMO (Fig. 1C). The bony supracleithrum first appeared at 104.5 HAMO (Fig. 1E). In the caudal fin, three cartilaginous hypurals were first evident at 104.5 HAMO. Thereafter no other fin elements became evident before the conclusion of the study.

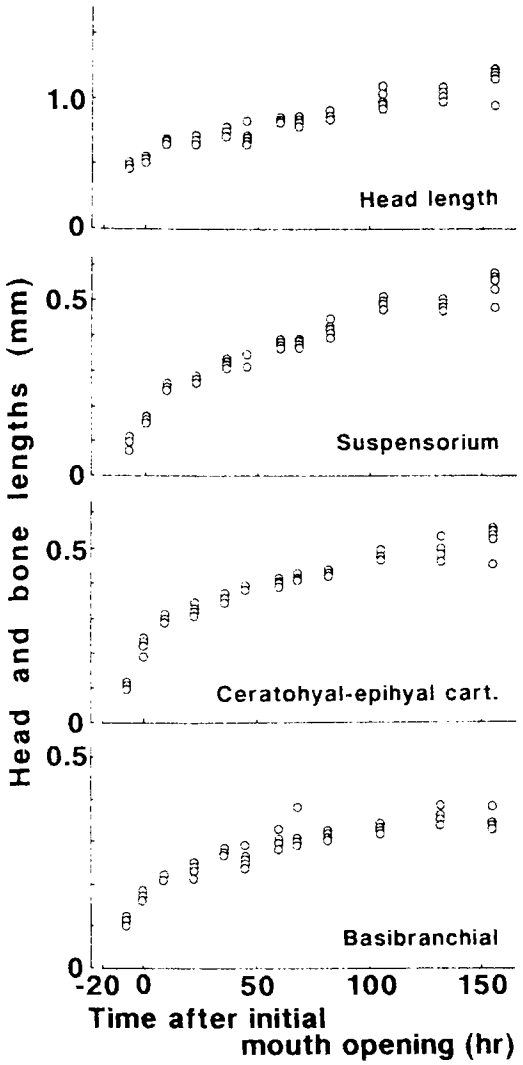

Fig. 3. Changes in head and bone lengths with time after initial mouth opening in *Lates calcarifer*.

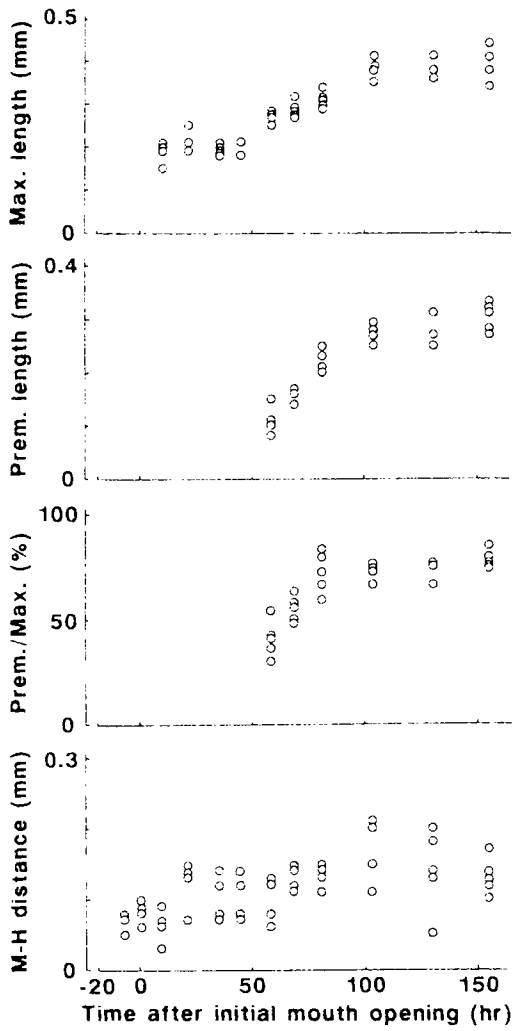

Fig. 4. Changes in maxillary and premaxillary lengths, ratios of premaxillary length to maxillary length and distance between the posterior end of Meckel's cartilage and anterior tip of hyoid arch (M–H distance) with time, after initial mouth opening in *Lates calcarifer*.

Morphometrics

Head length increased linearly with age, the mean±SD being 0.50±0.013, 1.00±0.049 and 1.14±0.102 mm at 0, 104.5 and 156.5 HAMO, respectively (Fig. 3). Asymptotic growth curves for the lengths of the suspensorium, ceratohyal-epihyal cartilage and basibranchial were noted, all becoming stable at about 100 HAMO (Fig. 3).

The maxillary length of 0.18±0.019 mm, at the first appearance of the element, 9.5 HAMO, remained stationary until 40 hours (0.20± 0.014 mm at 44.5 HAMO), but increased thereafter, finally stabilizing at around 100 HAMO (0.38±0.019 mm at 104.5 HAMO and 0.39± 0.033 mm at 156.5 HAMO) (Fig. 4). On the other hand, the premaxillary length increased rapidly after its appearance at 58 HAMO (0.11±0.023 mm), finally stabilizing at around 100 HAMO (0.27±0.016 mm at 104.5 HAMO and 0.30±0.026 mm at 156.5 HAMO) (Fig. 4). The ratio of premaxillary length to maxillary length increased rapidly from the first appear-

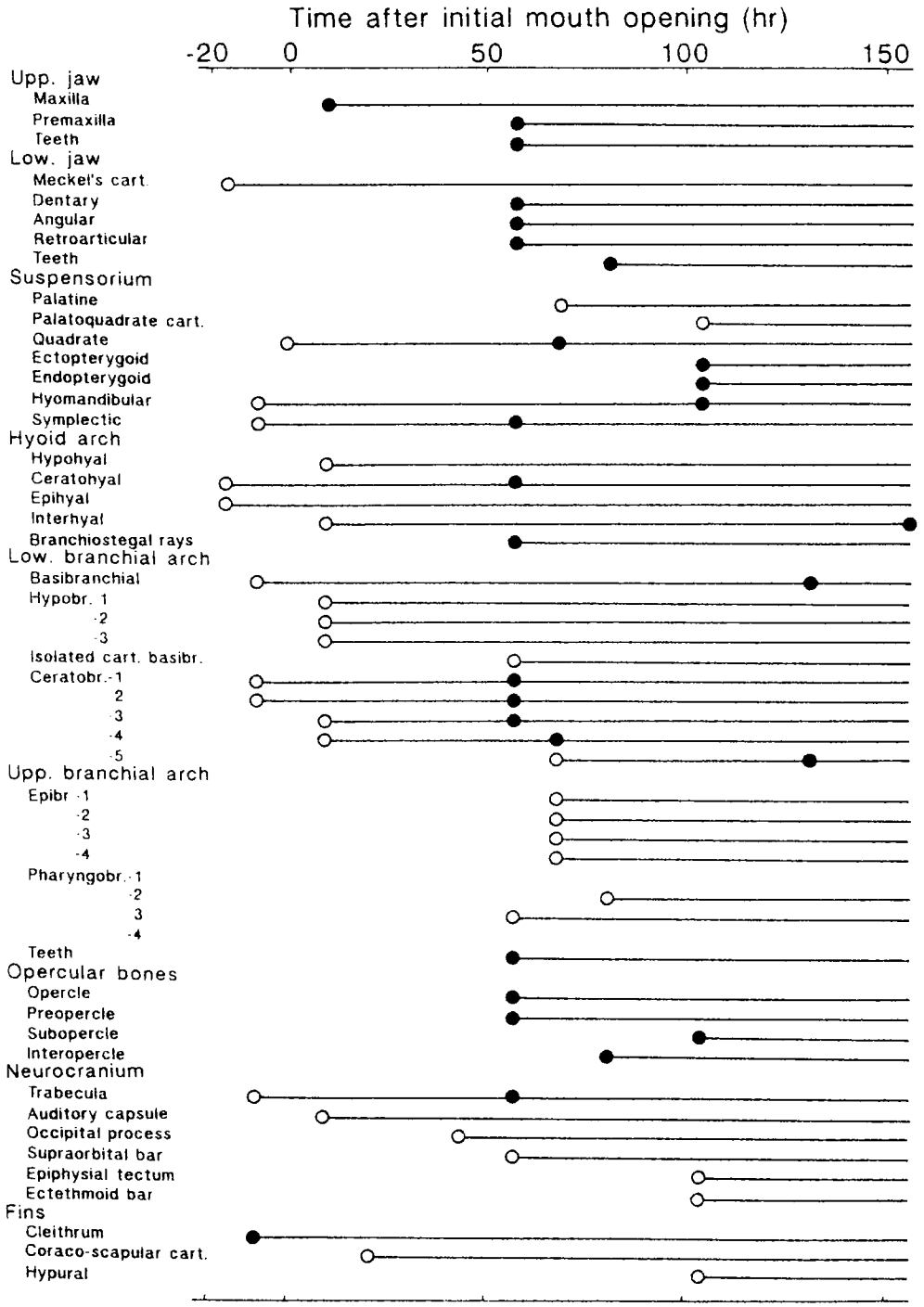

Fig. 5. Schematic representation of the development of elements comprising the oral cavity and fins in *Lates calcarifer*. ○: appearance of cartilaginous element; ●: appearance of ossified bone or beginning of ossification of cartilaginous element.

ance of the former (39.9±7.88%), until about 80 HAMO (71.8±8.90% at 81 HAMO). Thereafter the ratio more or less stabilized (77.6±3.82% at 156.5 HAMO) (Fig. 4). Values of the distance between the posterior end of Meckel's cartilage and the anterior tip of the hyoid arch were all

positive, indicating the location of latter ahead of the former (Fig. 4). Distances increased asymptotically with age, though with more or less wide variances (0.07 ± 0.011, 0.08 ± 0.017, 0.16 ± 0.041 and 0.13 ± 0.026 mm at -7.5, 0, 104.5 and 156.5 HAMO, respectively).

Discussion

Mechanics of suction feeding

Within 10 hours following initial mouth opening, the seabass larvae had already been equipped with the fundamental bony elements forming the oral cavity, such as the trabecular roof, some elements of the lower branchial arch and all of the hyoid arch forming the floor, the quadrate and symplectic-hyomandibular cartilages making up the sides, and elements bordering the jaw (maxilla and Meckel's cartilage) (Fig. 5). The cleithrum had also developed (by -7.5 HAMO). These elements, with the exception of the maxilla and cleithrum, were all cartilaginous in nature. Further elements contributing to the oral cavity were not added until 50–60 HAMO, except for the coraco-scapular cartilage and some cartilaginous elements of the neurocranium. Furthermore, ossification of existing cartilage was not observed during this period.

Larvae of the majority of teleostean fish species engulf whole food organisms by suction (Gerking, 1994), such being achieved by the creation of a negative pressure within the oral cavity (cf. Alexander, 1970; Osse and Muller, 1980). The fundamental elements observed in the early-stage larvae of the seabass appeared to function so as to create a negative pressure, the mechanics of which involve the simultaneous occurrence of the following, interlinked movements (Fig. 6; see also Gosline [1971], Otten [1982] and Matsuoka [1987]): 1) the sternohyoideus muscle is contracted; 2) the lower branchial arch moves backward and downward; 3) the posterior ends of the ceratobranchials expand laterally; 4) the anterior end of the hyoid arch is pulled down while its posterior ends expand laterally; 5) the anterior tip of Meckel's cartilage is pulled down owing to the contraction of the geniohyoideus muscle subsequent to the movements of the lower branchial arch; and 6) the posterior ends of Meckel's cartilage and the ventral portion of the suspensorium expand laterally.

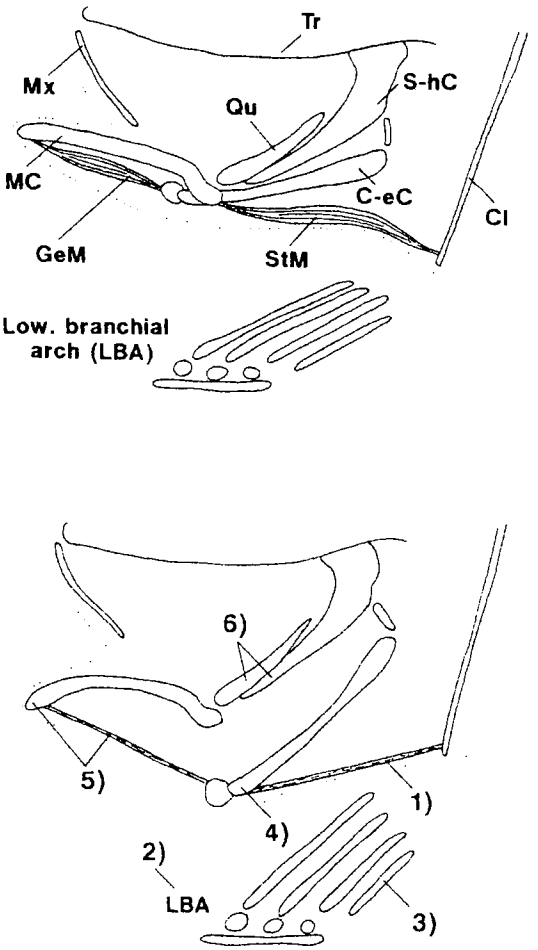

Fig. 6. Schematic drawings showing the mechanics of expansion of the oral cavity in *Lates calcarifer* larvae. Lateral view of elements comprising the oral cavity and ventral view of lower branchial arch in closed (*Top*) and expanded (*Bottom*) states are shown. *C-eC*—ceratohyal-epihyal cartilage; *Cl*— cleithrum; *GeM*—geniohyoideus muscle; *MC*—Meckel's cartilage; *Mx*—maxilla; *Qu*—quadrate; *S-hC*—symplectic-hyomandibular cartilage; *StM*—sternohyoideus muscle; *Tr*—trabecula. See text for movement patterns.

Initial feeding of seabass larvae on rotifers, *Brachionus* sp., had occurred by 12.5 HAMO in 23% of the larvae examined (unpubl. data). The number of rotifers occurring in the digestive

tract of progressively older seabass larvae increases steadily thereafter (Kohno et al., 1986), although in such larvae examined here, neither additional elements appeared nor ossification of existing elements occurred from about 10 to 50–60 HAMO. On the other hand, the size of the existing elements increased rather rapidly during the same period (see Fig. 3). The improvement of larval feeding ability from that at initial feeding to that 50–60 HAMO is thus considered to depend largely on the size-development of the existing elements.

Acquisition of a grasping feeding mode

The period from 50–60 to 100–110 HAMO was characterized by the appearance of new elements and the initial ossification of existing cartilages (Fig. 5). At 58 HAMO, the lower jaw started ossifying, with the premaxilla and associated teeth, upper pharyngeal teeth, opercle and preopercle appearing. New suspensorium and upper and lower branchial arch elements became evident at about 70 HAMO. The lower jaw teeth and interopercle appeared at 81 HAMO, with the maxillary and premaxillary lengths stabilizing by about 100 HAMO. Finally, the subopercle became evident at 104.5 HAMO (Fig. 5), completing the formation of all the oral cavity elements, with the exception of the basihyal and urohyal.

Ossification of the earlier-formed elements and the appearance of new ones implied an improvement in the feeding ability of the larvae, as well as signifying the employment of a new feeding mode (Otten, 1982; Matsuoka, 1987). The newly-acquired features included the premaxilla and jaw teeth, elements enabling the grasping of food organisms (see Gosline, 1971). The acquisition of teeth and a functionally-developed premaxilla paved the way for the progression from merely sucking in prey to both grasping and sucking capabilities. Although no detailed observations were made on the feeding behavior of the seabass larvae in this study, the abilities of the larvae to capture and securely hold food organisms appeared to be greatly improved some 100–110 HAMO and thereafter.

Such improvement in feeding ability is brought about by the following functional enhancement of the structures involved: increased ability to open and close the jaws owing to the development of the premaxilla and ossification of the lower jaw; greater capacity for expansion and contraction of the oral cavity owing to the appearance of the opercular bones; strengthening of the oral cavity by the development of new elements and the ossification of existing ones; and enhanced grasping ability given by the jaw and pharyngeal teeth. The improvement of larval feeding ability from 100–110 HAMO is considered largely dependent on the functional-development of the mouth; this contrasted with earlier observations on the larvae up to 50–60 HAMO, wherein feeding ability was mainly dependent on size-development.

Concluding Notes

Considering the chronological sequence of events, the development in seabass larvae of morphological structures involved in feeding can be divided into three phases. The first phase, from initial mouth opening to 50–60 HAMO, is characterized by the presence of basic oral cavity elements, predisposing the larvae to a "sucking" mode of feeding. The second phase, occurring from 50–60 to 100–110 HAMO, is characterized by the acquisition of new elements and the initial ossification of earlier ones. This phase is considered a transition period, during which the newly-acquired elements develop functionally, allowing the larvae to acquire grasping capabilities in addition to the suction method. The third phase is characterized by improved feeding ability, using both sucking and grasping methods to seize and ingest food organisms. Such improvement, brought about by the completion and ossification of the bony elements involved in feeding, is considered to occur from 100–110 HAMO. The improvement in larval feeding ability during the first phase is considered to be dependent on the size-development of the structures comprising the oral cavity, while that of the third phase is on the functional-development.

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