Development of Feeding Ability in Red Snapper 
* Lutjanus argentimaculatus * Early Larvae

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Development of bones in the mouth parts and changes of gut contents were investigated in early red snapper *Lutjanus argentimaculatus* larvae reared with naturally-occurring zooplankton as food. Larvae immediately after initial mouth opening possessed incomplete bony components in the mouth parts. However, the bony elements grew rapidly in size on the day of initial mouth opening, day 0, during which they started feeding. *Acartia sinjiensis* nauplii of 0.10-0.15 mm in total length (TL) were major food organisms at this stage. From day 1 to 2, no conspicuous changes occurred in the size and type of food organisms ingested, although some skeletal elements were added in the mouth part. Many new skeletal elements developed from day 3 to 4, as the size of food organisms in gut increased abruptly. The larvae started feeding on *Oithona dissimilis* copepodids (0.20-0.50 mm TL) and the weight percentages of the copepodids ingested increased thereafter. Early red snapper larvae acquired initial feeding ability by growing the size of a limited number of bony elements in the mouth parts. Further increase in feeding ability was achieved by differentiation of additional bony elements from day 3 to 4.

**Key words:** red snapper, larvae, osteological development, feeding, *Acartia*, nauplii, copepods, food selection

Larval mouth size has been considered as the most important factor restricting the available prey size in marine fishes.1,2) Difficulty in early larval rearing of some marine fish larvae such as groupers (genus *Epinephelus*) and snappers (genus *Lutjanus*) has often been attributed to their small mouth size at the onset of feeding3-6) or from overall early biological natures during the mixed feeding period, which are fragile compared to other species.7-9) As for the feeding-related apparatus of marine fish larvae, osteological development of bones in mouth parts has been described for some species.10-15) However, little information is available at present on the relationship between such morphological development and feeding behavior.

The purpose of this study is to examine the morphological development of characters related to feeding and the feeding ecology in the early stage larvae of the red snapper *Lutjanus argentimaculatus*.

**Materials and Methods**

Red snapper breeders were induced to spawn following the method described by Singhagraiwan and Doi.16) The fish spawned in the evening of September 28, 1993 and the larvae hatched around 14:00 on September 29. They were reared in a 190-m³ tank (mean water depth; 1.2 m) at the Eastern Marine Fisheries Development Center (EMDEC), Department of Fisheries, Rayong, Thailand. Zooplankton, mostly copepodids of *Acartia sinjiensis*, was collected from a 2.5-ha seawater earthen pond using a light trap and introduced to the tank water on the day of larval hatching so as to propagate the nauplii as early larval food.17) Water temperature and salinity of the tank during the observation period of this study, from September 29 to October 6, varied from 30.0 to 32.0°C (mean 30.9°C) and 23-25 ppt (mean 23.4 ppt), respectively. Abundance (individuals/l) of planktonic food organisms in the tank water was observed daily at 10:00 by sub-sampling 20-l of the tank water.

Larval sampling was carried out at different intervals from October 1 when larvae opened the mouth initially (day 0 in this study) to October 6 (day 5). Ten larvae were collected at each sampling, 7:00, 15:00 and 19:00 on day 0, and at 11:00 and 23:00 on days 1-5 for osteological observation. In addition to these specimens, 14-20 larvae were collected at 10:00, 12:00 and 15:00 on day 0, and at 11:00 on days 1-5 for gut content observation. All specimens were preserved in 5% seawater formalin until further treatment. A total of 130 specimens ranging from 2.10 to 4.40 mm in total length (TL) was studied for osteological development and 149 specimens from 2.20 to 3.90 mm TL.
For osteological observation, the specimens were stained for both bones and cartilages following the method of Dingerkus and Uhler. Total length, length of the major bony elements in the mouth parts, and mouth width were measured under a microscope. Mouth gape of early larvae was calculated based on the length of maxilla of the preserved specimen, using the equation:

\[ MG = L \times (\sqrt{6}/2) \]

where, \( MG \): mouth gape at the jaw opening angle of 90°
\( L \): length of maxilla

This equation was derived by referring to Shirota assuming the biased angle of the maxilla to be 30° (Fig. 1). In stained specimens, the TL was calibrated to that in the preserved state using the ratios of calculated preserved TL/stained TL. However, the mouth width and gape measured for stained specimens were also calibrated to those in the preserved state using the equation obtained in this study, TL (preserved) = 0.985 × TL (stained) − 0.131, and rounded to the nearest 0.05 mm. The mouth width and gape of stained specimens were calibrated to those in the preserved state using the ratios of calculated preserved TL/stained TL. However, the illustration and the length of bones were based on measurements of stained specimens without calibration.

For gut content observation, larval specimens were dissected under a dissecting microscope. Index of gut fullness, from 0 (gut empty) to 5 (gut over-full), was estimated following the method of Ohno, and number and total length of food organisms ingested were examined under a microscope. For nauplii of Pseudodiaptomus sp. having a long spine at the posterior end of the body, body length is given as total length. Dry weight of the food organisms was calculated based on their length, referring to the length-dry weight relationships calculated for Acartia clausi and for various copepods. Larval food electivity index was calculated following the equation of Ivlev.

**Results**

**Growth in TL**

The larvae opened the mouth initially around 3:00 on October 1, 1993 (day 0). Mean TL of larvae from 4 to 12 hrs after the initial mouth opening (time after the initial mouth opening; TAIMO) was constant at 2.25 mm (N=10–20) (Fig. 2). The larvae grew to 2.45 ± 0.14 mm TL (N=10) at 16 hrs TAIMO on day 1. They grew more or less linearly thereafter, reaching 3.64 ± 0.16 mm TL (N=20) at 128 hrs TAIMO and 3.92 ± 0.35 mm TL (N=10) at 140 hrs TAIMO on day 5.

**Morphological Development**

**Bones in mouth parts:** Bones in the mouth parts at 4 hrs TAIMO (7:00 on day 0), before the onset of feeding, consisted of the following elements (Fig. 3): thin string-like bony maxilla in the upper jaw; rod-shaped Meckel's cartilage in the lower jaw; rod-shaped hyomandibular-symphotic cartilage and quadrate arranged in parallel in the mandibular arch; small, globular hypohyal, rod-shaped cerato-epihyal and globular interhyal in the hyoid arch; rod-shaped basibranchial (future basibranchials 1–3), small, globular hypobranchials 1–3 and rod-shaped ceratobranchials 1–4 in the branchial arch. No upper branchial arch elements were developed at this stage. As to other
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Fig. 3. Composition of bones in the mouth part of *Lutjanus argentinimaculatus* larvae at 4 hrs after initial mouth opening.

Left: lateral view (top) and its hyoid arch shown separately (bottom). Right: dorsal view of the left branchial arch. Stippled area, cartilage. Open area, ossified portion. B1-3, basibranchials 1-3; C1-4, cerato-branchials 1-4; C-Eh, cerato-epihyal cartilage; Cl, cleithrum; H1-3, hypobranchials 1-3; Hh, hypohyal; Hm-Sy, hyomandibular-symplectic cartilage; Ih, interhyal; Ma, maxilla; Me, Meckel's cartilage; Qu, quadrate; Tr, trabecula. Scale bar: 0.2 mm.

bony, bony cleithrum and anterior part of cartilaginous trabecula were observed (Fig. 3).

The structure and components of these skeletal elements were unchanged in larvae at 16 hrs TAIMO (19:00 on day 0) (Fig. 4A). Among the elements, the Meckel's cartilage and cerato-epihyal were conspicuously large.

In the jaw and opercular elements, the bony components were unchanged by 32 hrs TAIMO (11:00 on day 1). At this time a foramen was formed in the upper part of the hyomandibular-symplectic cartilage in 2 out of 10 larvae (2/10). All larvae had the foramen by 56 hrs TAIMO (11:00 on day 2) (Fig. 4B). The central part of the palatine, which was the first skeletal element newly added after the initial mouth opening, was faintly observed in 6/10 larvae at 44 hrs TAIMO and in all 10 larvae by 56 hrs TAIMO, when the dentary was developed in 3/10, the opercle, 5/10 and the preopercle, 3/10 (Fig. 4B). The dentary appeared in all 10 larvae by 68 hrs TAIMO (23:00 on day 2) and the opercle and preopercle by 80 hrs TAIMO (11:00 on day 3). During 68-80 hrs TAIMO, the postero-ventral process of the maxilla developed, the palatine and quadrate extended and connected with each other (Fig. 4C).

A striking increase in the number of elements was observed during 80-116 hrs TAIMO (from 11:00 on day 3 to 23:00 on day 4) during which period the premaxilla started to develop in the upper jaw, the angular and retroarticular appeared (10/10) in the lower jaw, the symplectic started ossification on the lower part of the symplectic-hyomandibular cartilage (10/10), the bony endopterygoid appeared (10/10), and the subopercle (5/10) and interopercle (1/10) started to develop (Fig. 4D). At 128 hrs TAIMO (11:00 on day 5), the first jaw tooth on the premaxilla and dentary was discernible in 2/10 and 1/10 larvae, respectively, and the ectopterygoid appeared in 1/10 larva. Until the end of this series of observations, at 140 hrs TAIMO (23:00 on day 5), the premaxilla, subopercle and interopercle were nearly completed, being evident in 9/10 larvae. The first jaw tooth on the premaxilla and dentary, and the ectopterygoid were seen only in more advanced individuals; the ratio of larvae possessing these elements being 5/10, 4/10 and 5/10, respectively (Fig. 4E).

Fig. 4. Early development of jaw, mandibular and opercular bones in *Lutjanus argentinimaculatus*.

A: larva 16 hrs after initial mouth opening (time after initial mouth opening; TAIMO), 2.45 mm TL. A': same as A with the hyoid arch in larva with open mouth. B: larva 56 hrs TAIMO, 2.70 mm TL. C: larva 80 hrs TAIMO, 3.10 mm TL. D: larva 116 hrs TAIMO, 3.35 mm TL. E: larva 140 hrs TAIMO, 4.40 mm TL. Stippled area, cartilage. Open area, ossified portion. An, angular; De, dentary; Ecp, ectopterygoid; Enp, endopterygoid; Hm, hyomandibular; Io, interopercle, Op, opercle; Pal, palatine; Pm, premaxillary; Pro, preopercle; Ra, retroarticular; Sub, subopercle; Sy, symplectic. Scale bars: 0.2 mm.
The components of the hyoid arch were unchanged till 80 hrs TAIMO (11:00 on day 3), although they increased in size (Fig. 5A–C). The small, globular hypohyal consisted of two elements in the ventral view. At 92 hrs TAIMO, 2/10 larvae developed one and two branchiostegal rays, respectively. The percentage of larvae possessing branchiostegal rays and the number of the rays increased thereafter. By 116 hrs TAIMO (23:00 on day 4), all larvae had at least one ray, 2/10 larvae had two rays and 4/10 had three rays (Fig. 5D). The number of branchiostegal rays reached 2–5 at the end of observation for this series of specimens (140 hrs TAIMO), not attaining the adult count of 6 rays (Fig. 5E). At this time, the basihyal was added in 4/10 larvae (Fig. 5E), whereas the urohyal had not been developed in any individuals.

In the branchial arch, the basibranchial 4 (5/10) and ceratobranchial 5 (1/10) in the lower arch, and epibranchial 1 (1/10) and the first upper pharyngeal tooth (7/10) in the upper arch started to develop at 68 hrs TAIMO (23:00 on day 2). These elements developed in all larvae by 92 hrs TAIMO, when epibranchials 2 and 3 were also discernible in all larvae, epibranchial 4 in 4/10 larvae, and pharyngobranchials 2 and 3 in 4/10 and 9/10, respectively. Pharyngobranchials 2 and 3 were completed in all larvae at 104 hrs TAIMO and epibranchial 4 at 116 hrs TAIMO. The first lower pharyngeal tooth appeared in 4/10 larvae at 104 hrs TAIMO and in all larvae at 140 hrs TAIMO. At this time there were two pharyngeal teeth in 9/10 larvae. As to other branchial arch elements, pharyngobranchial 1 was discernible in 1/10 at 128 hrs TAIMO and 7/10 at 140 hrs TAIMO. Pharyngobranchial 4 was not observed in this series of specimens.

The developmental sequence of the aforementioned bones in the mouth part is summarized in Fig. 6. No skeletal element was added for more than 24 hours after the initial mouth opening. Some new bones started development on day 2, and then drastic increases in the number of elements occurred in a short period during days 3–4. The major skeletal elements which had appeared at the initial mouth opening, namely: maxilla, Meckel's cartilage, hyomandibular-symphotic cartilage, cerato-epihyal and fused basibranchial 1–3, increased in length rapidly during 4–16 hrs TAIMO (7:00–19:00 on day 0) and relatively slowly thereafter (Fig. 7).

**Mouth size:** The mouth width at 4 hrs TAIMO was 0.172 ± 0.014 mm. Then it increased almost linearly, reaching 0.192 ± 0.027 mm at 16 hrs TAIMO, 0.273 ± 0.015 mm at 56 hrs TAIMO and 0.426 ± 0.025 mm at 140 hrs TAIMO (Fig. 8).

The mouth gape, estimated from the length of the maxilla, was 0.151 ± 0.024 mm at 4 hrs TAIMO. The gape increased rapidly until 16 hrs TAIMO, reaching 0.214 ± 0.016 mm (Fig. 8). The increase in mouth gape was slow until about 56 hrs TAIMO, the gape being 0.216 ± 0.014 mm at this time, and accelerated thereafter, reaching 0.451 ± 0.059 mm at 40 hrs TAIMO.

**Food Organisms and Larval Feeding**

Propagation of food organisms in the tank water: The food organisms occurring in the tank water were composed mainly of nauplii and copepodids of *Acartia sinjiensis*, *Oithona dissimilis*, *Lonshipsia* sp. and *Pseudodiaptomus* sp. (Table 1). Species other than *A. sinjiensis* seem to have been introduced unintentionally to the tank water which was pumped from the sea and partly from the pond. Total abundance of nauplii was 215.4 individuals/l on day 0, decreased rapidly to 22.1 individuals/l on day 4, and then increased slightly to 45.6 individuals/l on day 5 (Table 1). Nauplii of *A. sinjiensis* was the most abundant with 75.7 individuals/l comprising 35.2% of total nauplii on day 0, but decreased rapidly to 1.3 individuals/l on day 3, and then kept at a very low level (1.1–1.3 individuals/l).
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Fig. 7. Increase in length of major bony elements which were present at initial mouth opening in *Lutjanus argentimaculatus*.

Fig. 8. Increase in mouth width and gape in *Lutjanus argentimaculatus* larvae.
Open circles with dotted line: mouth gape. Solid circles: mouth width.

Table 1. Abundance (individuals/l) of planktonic food organisms in a 190-m³ larval rearing tank

<table>
<thead>
<tr>
<th>Days after the initial mouth opening</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
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<tr>
<td>Nauplii</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Calanoids</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Acartia sinjiensis</em></td>
<td>75.7</td>
<td>34.1</td>
<td>19.0</td>
<td>1.3</td>
<td>1.1</td>
<td>1.3</td>
</tr>
<tr>
<td>*Pseudodiaptomus sp.*¹</td>
<td>0.5</td>
<td>2.7</td>
<td>8.3</td>
<td>0.0</td>
<td>1.1</td>
<td>1.2</td>
</tr>
<tr>
<td>Cyclooids</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Oithona dissimilis</em>²</td>
<td>69.0</td>
<td>42.0</td>
<td>42.8</td>
<td>21.3</td>
<td>11.1</td>
<td>5.1</td>
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<td></td>
</tr>
<tr>
<td>*Longipedia sp.*³</td>
<td>70.1</td>
<td>0.4</td>
<td>0.6</td>
<td>6.3</td>
<td>8.8</td>
<td>38.0</td>
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<td>Nauplii total</td>
<td>215.4</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Acartia sinjiensis</em></td>
<td>16.0</td>
<td>87.0</td>
<td>129.5</td>
<td>97.3</td>
<td>5.0</td>
<td>58.9</td>
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<tr>
<td><em>Pseudodiaptomus sp.</em></td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.6</td>
</tr>
<tr>
<td>other calanoids</td>
<td>2.1</td>
<td>0.0</td>
<td>1.2</td>
<td>1.3</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Cyclooids</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Oithona dissimilis</em></td>
<td>79.9</td>
<td>97.5</td>
<td>119.4</td>
<td>160.6</td>
<td>107.7</td>
<td>183.6</td>
</tr>
<tr>
<td>other cyclooids</td>
<td>2.1</td>
<td>0.4</td>
<td>0.6</td>
<td>1.3</td>
<td>0.0</td>
<td>1.3</td>
</tr>
<tr>
<td>Harpacticoids</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><em>Longipedia sp.</em></td>
<td>2.6</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>other harpacticoids</td>
<td>0.5</td>
<td>0.4</td>
<td>0.6</td>
<td>0.6</td>
<td>1.5</td>
<td>0.6</td>
</tr>
<tr>
<td>Copepods total</td>
<td>103.0</td>
<td>185.3</td>
<td>251.2</td>
<td>261.0</td>
<td>114.2</td>
<td>245.0</td>
</tr>
<tr>
<td><em>Brachionus sp.</em></td>
<td>2.6</td>
<td>0.0</td>
<td>0.0</td>
<td>1.3</td>
<td>13.0</td>
<td>3.8</td>
</tr>
<tr>
<td>Other zooplankton⁴</td>
<td>2.1</td>
<td>1.1</td>
<td>2.4</td>
<td>1.9</td>
<td>2.7</td>
<td>3.8</td>
</tr>
</tbody>
</table>

¹ Including nauplii of unidentified calanoids.
² Including nauplii of unidentified cyclooids.
³ Including nauplii of unidentified harpacticoids.
⁴ Nauplii of *Balanus sp.*, larvae of polychaetes and gastropods, and *Lorica sp.*

on days 4-5 (Table 1). Naupliar counts of *O. dissimilis* were as high as 69.0 individuals/l on day 0 and decreased relatively slowly to 21.3 individuals/l on day 3 and to 5.1 individuals/l on day 5. Nauplii of *Longipedia sp.*, which occurred in an abundance as high as 70.1 individuals/l on day 0, decreased suddenly to 0.4-0.6 individual/l on days 1-2, and then increased gradually to 38.0 individuals/l on day 5, accounting for 83.3% of the total nauplii. As for other copepod nauplii, those of *Pseudodiaptomus sp.* occurred in low abundance (maximum 8.3 individuals/l on day 2).

Copepods of copepods maintained relatively high abundances, 103.0-261.0 individuals/l during days 0-5, of which *O. dissimilis* and *A. sinjiensis* were major species (Table 1).

As for the other planktonic food organisms, the rotifer *Brachionus sp.*, nauplii of barnacles *Balanus sp.*, larvae of polychaetes and gastropods and *Lorica sp.* occurred in low abundances (Table 1).

Feeding incidence: No larvae had started feeding at 7:00 on day 0 (4 hrs TAIMO). Then, 3 out of 20 larvae were observed to feed on one to two nauplii of *A. sinjiensis* at 10:00 (7 hrs TAIMO) (Fig. 9). The feeding incidence (% of larvae with food in gut) increased rapidly to 40% at 12:00 (N=15) and 95% at 15:00 (20) of the same day. Mean index of gut fullness also increased rapidly, reaching 2.50 at 15:00 (20) on day 0. From day 1 to 5, 95-100% of larvae had food in the gut and the mean index of gut fullness was 2.78-3.75, indicating that most of the larvae fed on a sufficient amount of food organisms during this period (Fig. 9).
Composition of food organisms ingested: At the onset of feeding (10:00 to 15:00; 7-12 hrs TAIMO) on day 0, larvae fed solely or mostly on A. sinjiensis nauplii of 0.10-0.15 mm in total length (TL), which accounted for 85.9-100% in number (Fig. 10) and 64.9-100% in dry weight (Fig. 11) of total food items. Food organisms ingested on day 0 other than A. sinjiensis nauplii were nauplii of O. dissimilis of 0.12-0.16 mm TL.

Similar size and composition of ingested food organisms were seen on days 1 and 2. The larval gut content consisted of copepods nauplii ranging from 0.10 to 0.17 mm TL, of which A. sinjiensis nauplii were predominant in both number and dry weight, although the percentages decreased slightly, i.e., 90.0% and 73.5% in number, and 86.3% and 64.5% in dry weight, on days 1 and 2, respectively (Figs. 10 and 11). As for the other food organisms ingested, O. dissimilis nauplii were found in larval gut on...
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Day 1, and nauplii of O. dissimilis and Pseudodiaptomus sp. on day 2.

A striking increase in the size range of ingested food organisms was seen on day 3 due to the start of larval feeding on copepods of O. dissimilis (0.20–0.50 mm TL) as well as advanced nauplii up to 0.25 mm TL (Fig. 10). The copepods accounted for only 6.2% in total prey number, but the percentage in dry weight reached 23.5% (Fig. 11). Percentage of A. sinjiensis nauplii decreased to 20.7% in dry weight, while nauplii of O. dissimilis, Pseudodiaptomus sp. and Longipedia sp. occupied 24.5, 31.0 and 0.3%, respectively (Fig. 11). From day 4 to 5, the size range of ingested food organisms increased slightly and copepods of O. dissimilis became predominant in weight (Figs. 10 and 11). On day 5, larvae fed on the copepods up to 0.55 mm TL, which comprised 76.6% in dry weight. As other food organisms, a rotifer (0.17 mm in lorica length) was eaten by a larva on day 4.

Larval food electivity: Ivlev's food electivity index was calculated among the major food items ingested by larva, i.e., nauplii of the four copepod species and copepods of O. dissimilis (Fig. 12). Larvae on days 0–1 showed exclusively strong food preference for A. sinjiensis nauplii, the index being 0.56–0.65, while other food items had negative indices. On day 2, the larvae tended to select nauplii of Pseudodiaptomus sp. as well as A. sinjiensis, the index being 0.25 and 0.75, respectively. Both species are calanoids. Food electivity to nauplii of O. dissimilis (a cyclopoid) was nearly neutral (index: -0.08) and that to nauplii of Longipedia sp. (a harpacticoid) was negative (-1.00). From day 3 to 5, although the number of food items ingested by larvae increased, the larvae continued to select nauplii of A. sinjiensis (0.85–0.96) and Pseudodiaptomus sp. (0.97–1.00) rather than those of O. dissimilis (-0.16–0.38) and Longipedia sp. (-1.00–0.02) or copepods of O. dissimilis (-0.36–0.86).

Discussion

At the initial mouth opening of the larvae, bones in the mouth part consisted of a limited number of primodial elements (Fig. 3), which grew in size rapidly (Fig. 7), thus the size of the mouth increased (Fig. 8). During the period from initial mouth opening to 16 hrs TAIMO, when bone size and mouth size increased, the larvae started feeding (7 hrs TAIMO), with feeding incidence reaching 95% at 12 hrs TAIMO (Fig. 9). No bony elements were added during this period (Fig. 8). These observations indicate that the larvae acquired initial feeding ability by increasing the size of bones in the mouth part, not by the addition of new elements nor the ossification of existing elements.

Among the bony elements in the mouth part, robust rod-shaped bones were seen only in the lower part of the mouth, i.e., Meckel’s cartilage of the lower jaw and the elements comprising the hyoid, mandibular and lower branchial arches. Early development of a series of rod-shaped elements in the lower part of the mouth associated with the cleithrum and muscle system seems to play a principal role in generating negative pressure in the oral cavity for swallowing the prey at the onset of feeding, though the number of elements was incomplete.

The time at which 50% of red snapper larvae started feeding can be estimated from Fig. 9 as 9.5 hrs TAIMO. The length of the bones in the mouth part at this time was calculated from Fig. 7 and compared with those of the red seabream Pagrus major larvae immediately before onset of feeding, which were measured from the drawings of Matsuoka. All the elements examined were shorter in red snapper than in red seabream (Table 2), suggesting that the mouth size at onset of feeding and hence initial feeding ability of the former are smaller and lower than those of the latter. This morphological character together with the comparatively smaller endogenous nutrition reserves of this species at the onset of feeding would make it difficult to rear early larvae of this species with cultured rotifers, Brachionus spp., unlike many other marine fish larvae produced at hatcheries, i.e., red seabream. The sizes of rotifers cultured commonly at fish hatcheries in the tropics is about 0.22 mm in lorica length for B. rotundiformis (the so-called S-strain) and about 0.16 mm for Brachionus sp. (SS-strain). These are a little larger than early stage nauplii of copepods (0.10–0.16 mm TL) that red snapper larvae fed on after 16 hrs TAIMO.

Table 2. Comparison of major bone length in mouth part at onset of feeding between Lutjanus argentimaculatus and Pagrus major larvae

<table>
<thead>
<tr>
<th>Bone</th>
<th>L. argentimaculatus</th>
<th>P. major</th>
<th>Ratio (%) (a/b) × 100</th>
</tr>
</thead>
<tbody>
<tr>
<td>*Bone length in P. major was measured from the drawings in Matsuoka.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maxillary</td>
<td>0.160</td>
<td>0.195</td>
<td>82.1</td>
</tr>
<tr>
<td>Meckel's cartilage</td>
<td>0.255</td>
<td>0.345</td>
<td>73.9</td>
</tr>
<tr>
<td>Ceratocephalic</td>
<td>0.283</td>
<td>0.310</td>
<td>91.3</td>
</tr>
<tr>
<td>Basibranchial</td>
<td>0.188</td>
<td>0.250</td>
<td>75.2</td>
</tr>
<tr>
<td>Hyomandibular</td>
<td>0.176</td>
<td>0.255</td>
<td>69.0</td>
</tr>
</tbody>
</table>

Food selection of early marine fish larvae is known to be affected not only by the biological nature of prey such as size (25, 26) and swimming behavior (27, 28) but also by prey density. (29, 30) Pryor and Epifano (30) have shown that early weakfish Cynoscion regalis larvae did not feed selectively when prey abundance was less than 100 individuals/l. In this study, however, early red snapper larvae showed a clear food selection, in other words a difference of food composition between the tank water and larval gut, among nauplii of copepods even when the total abundance of nauplii was less than 100 individuals/l (Table 1 and Fig. 12). Feeding success rate (percentage of feeding attempts when larvae can capture prey) of first-feeding larvae is not usually 100%, varying depending on fish species and type of food organisms given. (25-28) Early red snapper larvae particularly on day 0 may try to feed on any nauplii they encounter, but they can ingest only certain types of the nauplii that they can capture, i.e., early stage nauplii of A. sinjiensis and presumably those of Pseudodiaptomus sp. From day 1 to 2, some skeletal elements started to develop in the mouth parts (Fig. 6) but no conspicuous change occurred in size or type of food organisms ingested (Fig. 10). During this period, no marked increase in feeding ability was attained, although the size of bony elements increased. Then, from day 3 to 4, many new elements were added (Figs. 5 and 6) and the size of food organisms ingested by larvae increased abruptly (Fig. 10). These findings suggest that the larval feeding ability has been upgraded by the advanced form of skeletal components in the mouth parts as well as the increase in mouth size. Mechanical improvement of the bony structure at this stage, e.g., extension of the posterior process of the maxilla, appearance of upper branchial arch elements, appearance of jaw and pharyngobranchial teeth, etc., seems to give the larvae higher prey capture ability. (14, 15, 33) This study demonstrates that osteological development of bones in the mouth parts supported directly the enhancement of feeding ability in early red snapper larvae.

Acknowledgments

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References

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