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Abbreviated Larval Development of the Fresh-water Prawn, *Macrobrachium shokitai* Fujino et Baba (Decapoda, Palaemonidae) from Iriomote Island of the Ryukyus*

With 7 Text-figures

Shigemitsu SHOKITA**

Ryukyu Fisheries Experimental Station, Kabira, Ishigaki-shi, Okinawa 907-04, Japan

ABSTRACT Studies on the larval development of the fresh-water prawn, *Macrobrachium shokitai* Fujino et Baba, were carried out under laboratory conditions. The larvae pass through two zoeal stages and one megalopa stage before they molt to juvenile prawns. From hatching to juvenile stage the larvae subsist on the stored yolk without feeding. The newly-hatched larvae have all the appendages of adult form except for uropods, although some zoeal characters still remained. The first zoea has the telson with 35 to 38 plumose setae, very characteristic of this species. The egg is large with the size of 1.43×1.97 mm.

In some fresh-water species of the families Palaemonidae and Atyidae, free-swimming zoeal stages tend to be abbreviated or suppressed during the course of their larval development, hatching as late zoea. Such types of larval development have been recorded by many workers (Boas, 1889; Sollaud, 1923; Mizue & Iwamoto, 1961; Dobkin, 1963; Kwon & Uno, 1968; Fielder, 1970). These species all live in fresh-water and bear a few eggs of large size.

As far as the larval developments of *Macrobrachium* species are concerned, several species are known to pass over normal zoeal stages without abbreviation (Ling & Merican, 1961; Lewis & Ward, 1965; Uno & Kwon, 1969; Kwon & Uno, 1969; Shokita, 1970; Choudhory, 1970; Choudhory, 1971). These species are commonly found in both brackish and fresh-water and bear nemerous small eggs. On the other hand Fielder (1970) reported that *Macrobrachium australiense* had an abbreviated larval life although the number and size of eggs are close to those of marine and

* Contribution No. 6 from the Ryukyu Fisheries Experimental Station, Ishigaki-shi, Okinawa, Japan.

** Present address: Department of Biology, University of the Ryukyus, Naha, Okinawa 903 Japan.

brackish water species.

The present paper provides the morphological descriptions of the first to the fifth molting stages of *Macrobrachium shokitai* and some ecological information obtained by myself in the river of Iriomote Island of the Ryukyus. In this prawn with eggs of large size free-swimming zoeal stages are completely abbreviated or suppressed. So far as is known, this is the first record regarding the complete suppression of free-swimming larval stages of the genus *Macrobrachium*.

MATERIAL AND METHOD

In June of 1970 several berried females were collected in the Urauchi River, Iriomote Island, the southern extremity of the Ryukyu Islands, and transported to the laboratory in small vinyl containers without aeration. One or two female prawns were kept in each jar containing fresh water provided with aeration.

The hatched larvae were transferred into a circular plastic jar (36 cm in diameter, 30 cm in height) containing pure fresh water with moderate aeration, in which they were reared through all the stages to young. The water temperature ranged from 28.0 to 29.3°C during the course of this study. The juvenile prawns were fed with newly hatched *Artemia* nauplii and the shell-fish particles of *Asaphis dichotoma*.

All drawings were prepared by means of a profile projector and a binocular compound microscope. Measurements were made by a low power microscope with an ocular micrometer. Body-length was measured from the postorbital margin to the posterior edge of the telson without setae. Size of eggs shows the average of ten eggs.

RESULTS

Field observation

In the Urauchi River of Iriomote Island, the following species are found: the palaemonid prawns *Macrobrachium formosense, M. lar, M. equidens, M. shokitai* and *Palaemon* (*Palaemon*) *debilis*, the atyid shrimps *Atya moluccensis, Paratya compressa, Caridina typus, C. leucosticta, C. grandirostris, C. serratirostris, C. brevirostris*. Of these *M. shokitai* occurs only in the fresh-water of a good distance from the sea at high altitude of the upper-stream and riverhead areas, where *Caridina brevirostris*, bearing a few but large yolky eggs and completely lacking the free-swimming larval life (unpublished data), is also found. This species is also taken from the Mera River with the similar habitat.

Ovigerous females of *M. shokitai* occur from May to September, and the larvae and juveniles are found toward the beginning of June.

Number and size of eggs

The egg is oval in shape, and largest in size as compared with that of any other

known palaemonid and atyid shrimps of Japan, measuring 1.43×1.97 mm (when freshly laid) on an average (Table 1). As the development proceeds the size of eggs becomes slightly larger in comparison with that of freshly produced eggs (pre-eyed eggs).

The number of eggs carried by the adult female varies from approximately 15

Table 1
Size of females and their eggs in *Macrobrachium shokitai*.

Sp. No.	Pre-eyed eggs		Sp. No.	Eyed eggs	
	Body-length (mm)	Size of eggs (mm)		Body-length (mm)	Size of eggs (mm)
1	31.7	1.99×1.37	1	26.0	2.12×1.67
2	32.5	1.90×1.40	2	26.6	2.34×1.54
3	33.5	1.97×1.46	3	33.5	2.35×1.56
4	35.0	2.04×1.48	4	35.1	2.34×1.60
5	35.6	1.98×1.42	5	35.2	2.29×1.58
6	39.8	1.93×1.43	6	35.3	2.30×1.65
7	40.6	1.93×1.44	7	35.4	2.26×1.51
8	42.8	2.04×1.37	8	36.6	2.16×1.52
9	42.9	2.01×1.46	9	39.5	2.35×1.67
10	43.0	1.01×1.47	10	40.0	2.24×1.50
Average	37.7	1.97×1.43	Average	34.3	2.28×1.58

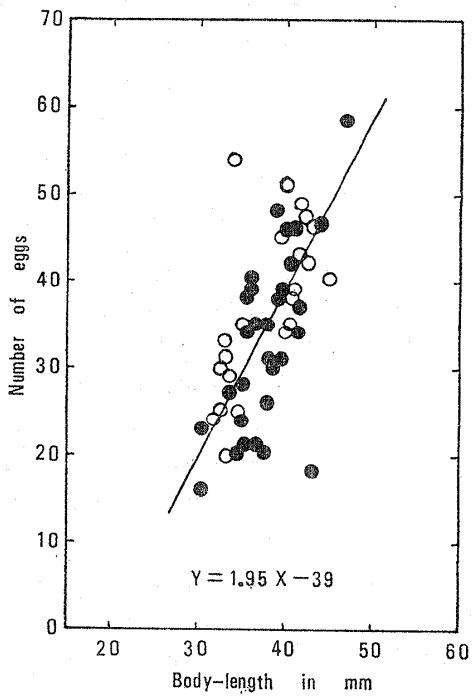

Fig. 1. The relationship between the number of eggs (Y) and body-length (X) in *Macrobrachium shokitai*. Solid circles, eyed eggs; open circles, pre-eyed eggs.

to 58. The relationship between the number of eggs (Y) and body-length (X) may be expressed by the linear formula, $Y=1.95\times-35$ (Fig. 1). There are no great differences in number between the pre-eyed and the eyed eggs, so that most of the produced eggs seem to be carried by the female until hatching.

Larval development

There are two zoea stages and one megalopa stage before they molt to juvenile (the stage names were decided at the suggestion of Dr. H. Kurata of the Nansei Regional Fisheries Research Laboratory, Japan). Most of the first zoea metamorphosed into the second zoea after about 5 hours, into megalopa about 20 hours, and into juvenile about 50 to 58 hours after hatching at the water temperature of 28.0–29.3°C. The larvae take no food until the first juvenile, subsisting only on stored yolk. Major characteristics of larval and juvenile stages are as follows:

First zoea (Figs. 2–7)

Body-length 4.92 mm, carapace length 1.13 mm.

Rostrum strongly curved downwards, reaching middle of antennular peduncle; both upper and lower borders without tooth. Carapace with branchiostegal spine. Abdomen with 6 somites and telson. Telson with 33 to 35 soft plumose setae. Eye sessile, its base with pink chromatophores, one small and the other large.

Antennule simple, with unsegmented peduncle; inner flagellum of a plumose seta; outer flagellum slightly longer, with 4 aesthetes. Antenna biramous; protopod unsegmented; endopod (or flagellum) of numerous joints, slightly shorter than body; exopod (or scale) unsegmented, convex on inner margin, with 35 plumose setae along inner and terminal margins, and an apical spine by far exceeded by round tip of blade.

Mandible without palp, undeveloped; incisor process with 2 teeth; molar process without tooth, very close to incisor process. First maxilla uniramous; upper and lower laciniae each with 2 short spines; endopod simple, palp-like, without spine. Second maxilla plate-like, biramous; endite 3-lobed, lower lobe with a short spine at tip, smaller than the other two lobes bearing no spine; endopod unsegmented, without terminal setae; exopod large with 32 plumose setae around almost entire margin, anterior setae longer than lateral and posterior ones.

First maxilliped biramous, protopod bilobed; endopod unsegmented with 3 terminal setae; exopod twice as long as endopod, bilobed, with 4 apical and subapical plumose setae; epipod small or undeveloped but bilobed. Second maxilliped biramous; endopod 4-segmented, with 3 spines at junction of ultimate and penultimate segments; ultimate segment with lacerated claw; exopod as long as endopod, with 4 apical and 2 subapical plumose setae. Third maxilliped biramous, similar to second maxilliped in general make-up; endopod 5-segmented; exopod with 4 apical and 2 subapical plumose setae.

First and second pereiopods chelate, first slightly shorter than second; cutting edges of chelae without tooth. Third, fourth and fifth pereiopods not chelate. All

pereiopods not functional, lacking exopod.

Pleopods biramous; endopods of 2 to 5 pleopods with appendices internae; endopod and exopod of all pleopods with several setae around apical margin.

Second zoea (Figs. 2–7)

Body-length 5.13 mm, carapace length 1.93 mm.

Differs from first zoea in the following: Carapace with supraorbital, antennal and branchiostegal spines. Rostrum slightly curved downwards, reaching distal

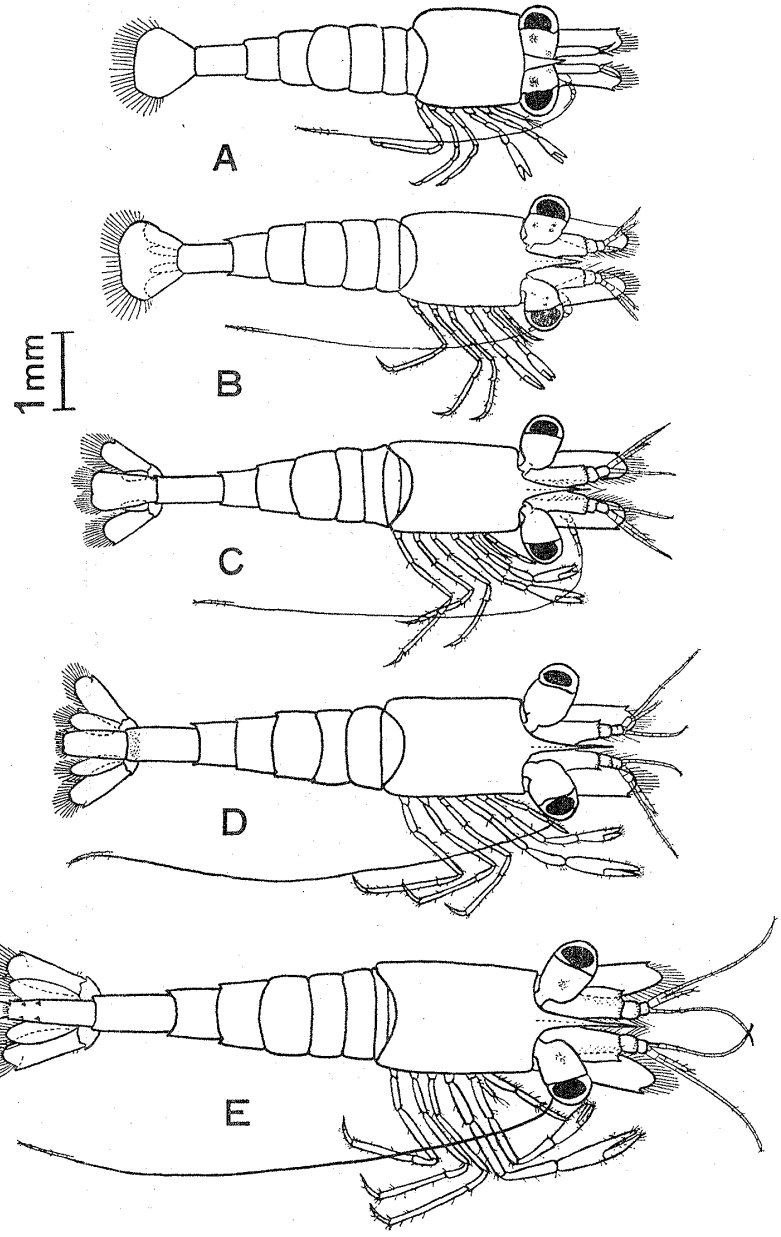

Fig. 2. *Macrobrachium shokitai* Fujino et Baba, dorsal view.——A, zoea 1; B, zoea 2; C, megalopa; D, juvenile 1; E, juvenile 2.

end of first segment of antennular peduncle; upper border with 9 teeth, lower border without tooth. Eye-stalk with 3 pink chromatophores. Telson with 35 plumose setae, outline of uropods often visible under cuticle.

Antennular peduncle 3-segmented; first segment the longest, with a stout stylocerite bearing 3 plumose setae, distolateral angle of the segment with a small spine directed forwards, proximal part of inner margin with a ventral spine; second and third segments of subequal length, much shorter than first. Lower antennular flagellum 4-segmented, upper divided into two rami, inner shorter with 3 terminal aesthetes. Antennal flagellum slightly shorter than body-length; scale about 3 times

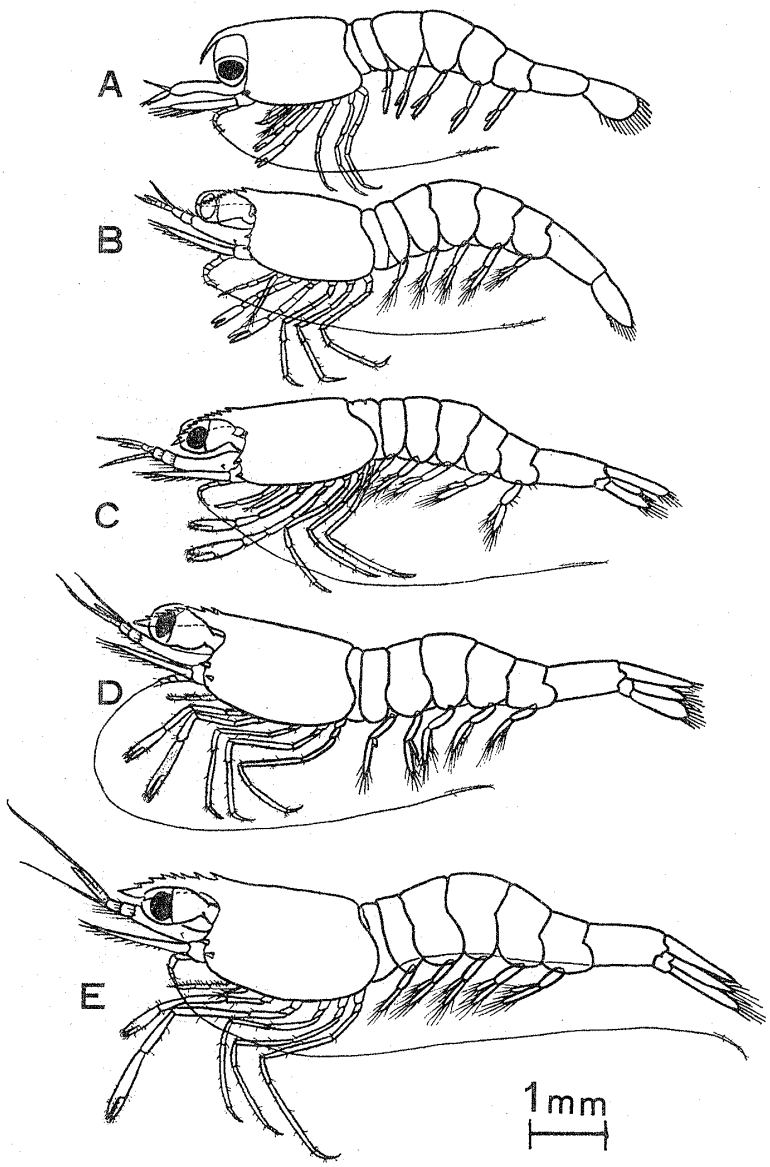

Fig. 3. *Macrobrachium shokitai* Fujino et Baba, lateral view.——A, zoea 1; B, zoea 2; C, megalopa; D, juvenile 1; E, juvenile 2.

as long as wide, with 43 plumose setae.

Mandible without palp, interval between incisor and molar processes rather wide. Endopod of first maxilla bilobed; upper lacinia with 5 and lower 4 short spines. Second maxilla almost similar to that in the preceding stage; exopod with 37 plumose setae.

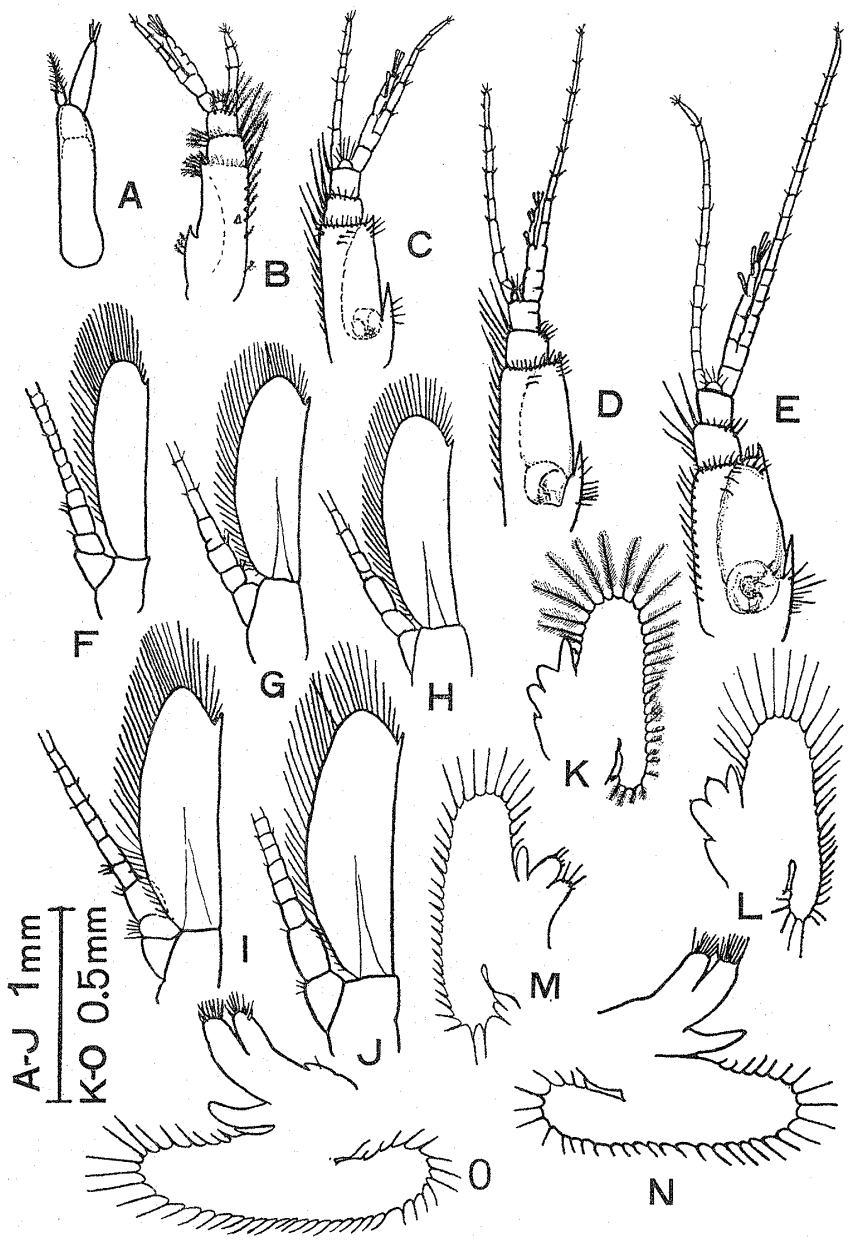

Fig. 4. *Macrobrachium shokitai* Fujino et Baba.——A–E, antennules; A, zoae 1; B, zoea 2; C, megalopa; D, juvenile 1; E, juvenile 2; F–J, antennae; F, zoea 1; G, zoea 2; H, megalopa; I, juvenile 1; J, juvenile 2; K–O, maxillae; K, zoea 1; L, zoea 2; M, megalopa; N, juvenile 1; O, juvenile 2.

First, second and third maxillipeds almost similar to those in the former stage.

First and second pereiopods almost similar to those in first zoea. Remaining pereiopods fully developed.

Endopods and exopods of pleopods with plumose setae.

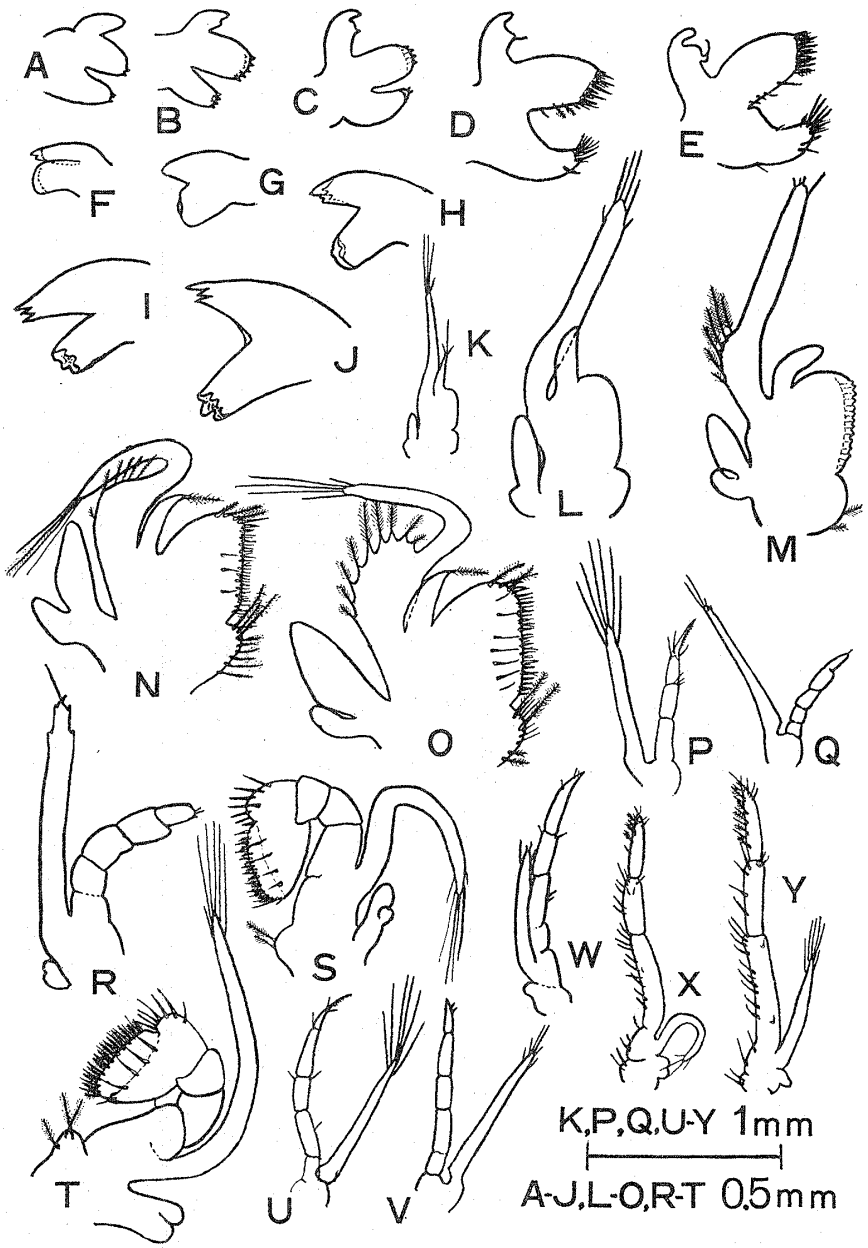

Fig. 5. *Macrobrachium shokitai* Fujino et Baba.——A–E, maxillules; A, zoea 1; B, zoea 2; C, megalopa; D, juvenile 1; E, juvenile 2; F–J, mandibles; F, zoea 1; G, zoea 2; H, megalopa; I, juvenile 1; J, juvenile 2; K–O, first maxillipeds; K, zoea 1; L, zoea 2; M, megalopa; N, juvenile 1; O, juvenile 2; P–T, second maxillipeds; P, zoea 1; Q, zoea 2; R, megalopa; S, juvenile 1; T, juvenile 2; U–Y, third maxillipeds; U, zoea 1; V, zoea 2; W, megalopa; X, juvenile 1; Y, juvenile 2.

Megalopa (Figs. 2–7)

Body-length 5.50 mm, carapace length 1.45 mm.

Carapace and rostrum similar in shape to those in the preceding stage. Telson with 33 to 35 plumose setae, as long as 6th abdominal somite. Uropod biramous, unsegmented; exopod with a small terminal spine and 30 to 32 plumose setae; endopod small or undeveloped, without setae.

Antennular peduncle of 3 segments; basal segment with a strong stylocerite and a statocyst. Outer flagellum with 2 apical and one subapical aesthetes. Antennal

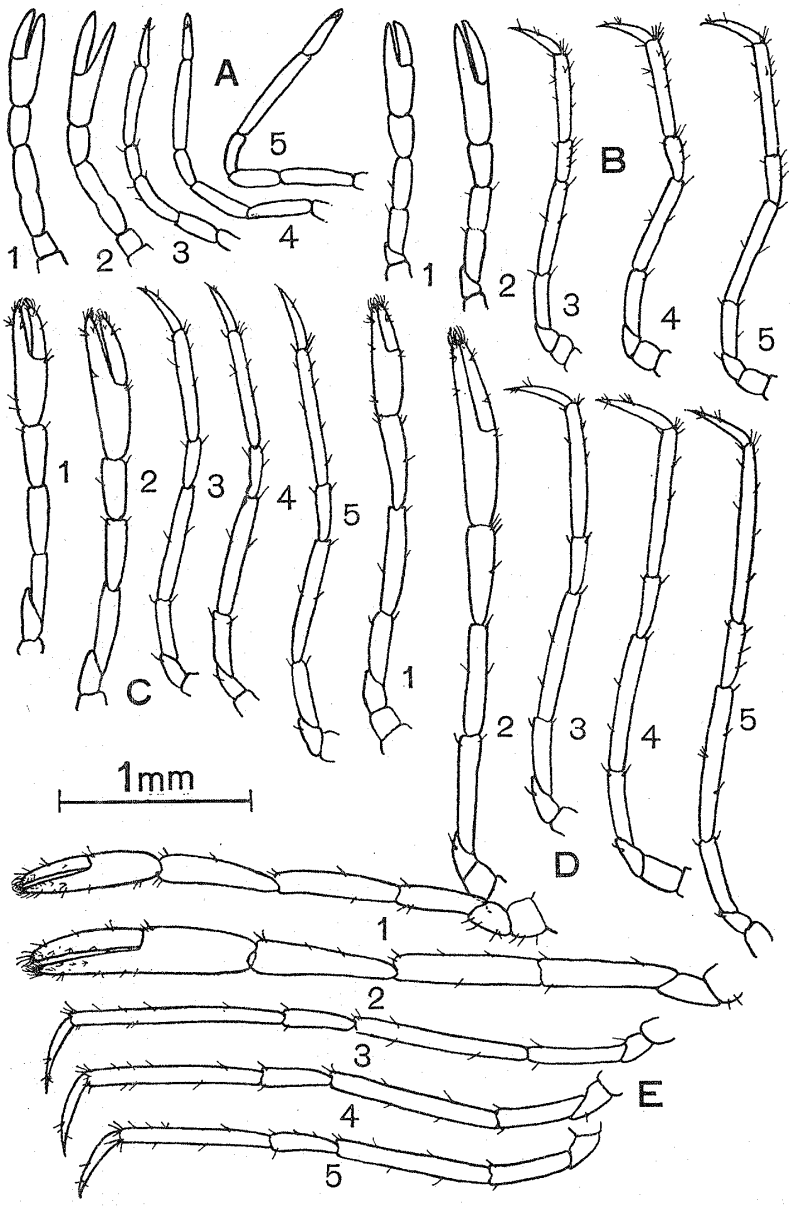

Fig. 6. *Macrobrachium shokitai* Fujino et Baba, perieopods.——A, zoea 1; B, zoea 2; C, megalopa; D, juvenile 1; E, juvenile 2; 1–5, 1st–5th pereiopods.

flagellum approximately as long as body-length; scale with 43 plumose setae.

Mandible somewhat developed; incisor process with 3 teeth. First maxilla almost similar in shape to that of the preceding stage; endopod distinctly cleft. Second maxilla with endite bilobed; lower lobe with 3 long and 3 short setae; endopod

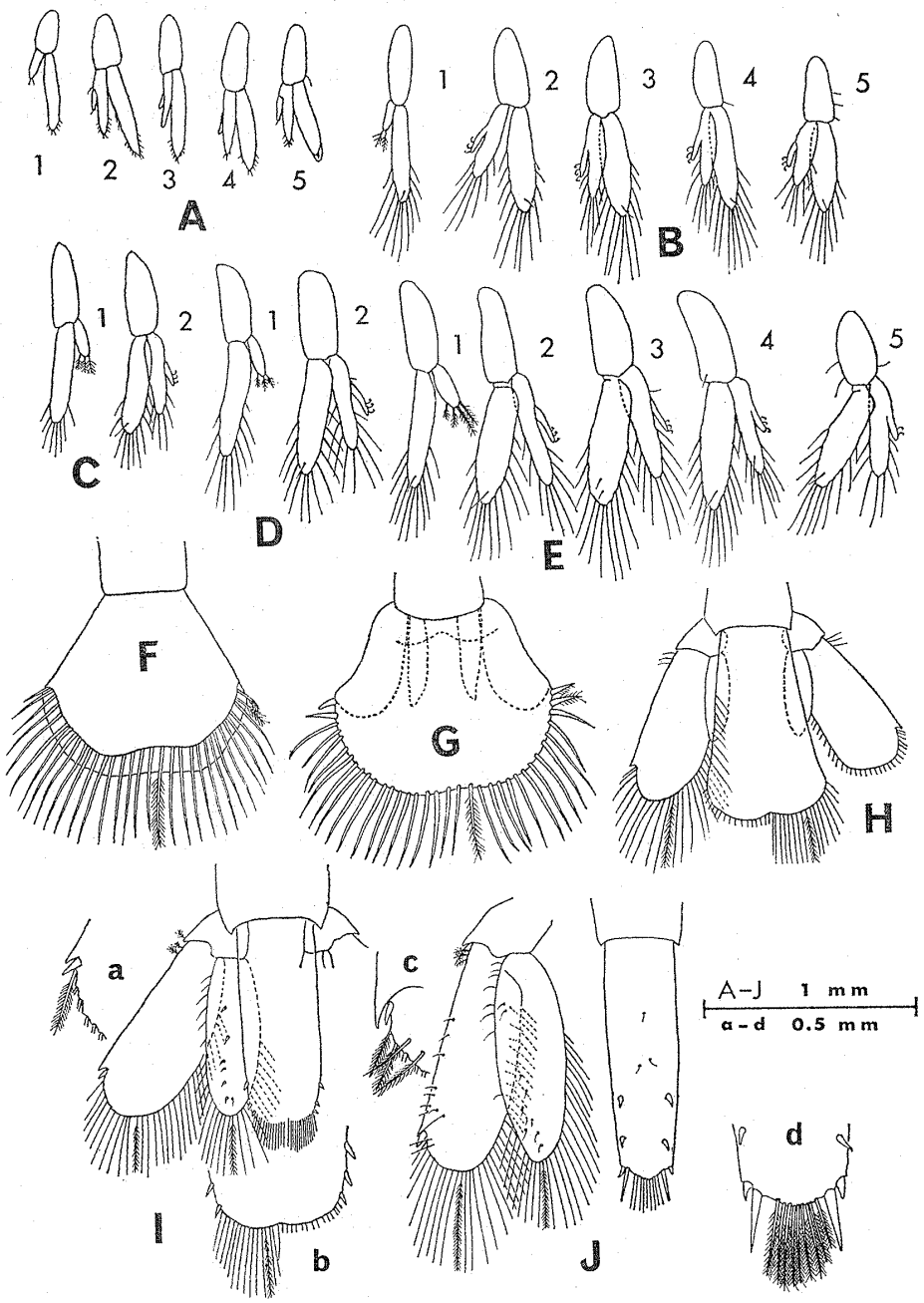

Fig. 7. *Macrobrachium shokitai* Fujino et Baba.——A–E, pleopods; A, zoea 1; B, zoea 2; C, megalopa; D, juvenile 1; E, juvenile 2; 1–5, 1st–5th pleopods; F–J, telsons and uropods; F, zoea 1; G, zoea 2; H, megalopa; I, juvenile 1; J, juvenile 2; a and c, disto-lateral parts of exopods of uropods; b and d, distal parts of telsons.

palp-like, without setae; scaphognathite ear-like, with 34 plumose setae.

Protopod of first maxilliped bilobed; upper lobe with numerous lacerated spines; lower lobe with 2 short plumose setae; caridean lobe well developed, with 6 plumose setae; epipod well developed, bilobed. Second maxilliped somewhat developed; endopod 5-segmented, with 3 short simple setae terminally; epipod small, bilobed. Third maxilliped with 4-segmented endopod; epipod small and undeveloped.

Pereiopods well developed, with sensory hairs. Pleopods fully developed and functional.

First juvenile (Figs. 2–7)

Body-length 5.95 mm, carapace length 1.60 mm.

This is essentially adult in all respects but secondary sex characters. It differs from the previous stages in the following: Carapace with stout antennal and hepatic spines, without supraorbital and branchiostegal spines. Rostrum with 7 dorsal teeth, reaching tip of second segment of antennular peduncle. Telson elongated and a little wider anteriorly, with 3 pairs of lateral spines and 29 to 30 posterior plumose setae. Endopod and exopod of uropods well developed.

Antennula and antenna almost similar to those in the preceding stage except for size and number of segments and plumose setae.

Mandible fully developed; incisor process with 3 teeth; teeth of molar process large, wen-like. Protopod of first maxilla consisting of two laciniae; lower lacinia with 8 apical and 1 subapical spines; upper lacinia with 14 apical and 1 subapical spines and 2 subapical plumose setae; endopod bilobed, lower lobe with an apical seta. Exopod of second maxilla with 36 plumose setae; endite elongated, bilobed, lower lobe with 10 and upper with 9 setae on each distal margin.

Protopod of first maxilliped large, bilobed; lower lobe with 10 plumose setae; upper lobe with 3 plumose and numerous coarse setae; endopod small, with an apical plumose seta; exopod with 4 apical plumose setae, caridean lobe enlarged, with 6 plumose setae around margin; epipod large, bilobed. Second maxilliped with 5-segmented endopod, ultimate and penultimate segments wider than long, with numerous short plumose and coarse spines; coxa with 2 plumose setae, basis without setae; exopod with 4 apical and 2 subapical plumose setae; epipod elongated, bilobed. Third maxilliped with 3-segmented endopod, coarsely setose throughout; exopod with 4 apical setae; epipod small, bilobed; coxa with 2 and basis with 3 setae.

Pereiopods fully developed, second pereiopod especially elongated.

Pleopods resembling those in the preceding stage except for increment of setae.

Second juvenile (Figs. 2–7)

Body-length 6.81 mm, carapace length 1.85 mm.

Rostrum with 7 dorsal and 1 ventral teeth (ventral tooth not always developed), reaching beyond distal end of scaphocerite.

Telson elongated and narrower posteriorly, with 2 pairs of strong dorso-lateral

spines; posterior margin with a pair of long and a pair of medium stout spines at each corner and 9 to 10 plumose setae between spines.

Form of appendages almost similar to that in preceding stage except for the size and number of segments, spines and setae.

Table 2
Three types of larval development and the characters of the first zoea of *Macrobrachium*.

Species	Larval development	Characters of first zoea
M. formosense (Shokita, 1970)	Common type; with 9 zoea stages and 1 megalopa.	Eyes sessile; rostrum straight, without tooth; abdomen of 6 somites plus telson; telson with 14 setae; antennal flagellum shorter than scale, scale segmented; 1st and 2nd periopods biramous and buds.
M. australiense (Fielder, 1970)	Abbreviated type; with 3 zoea stages and 1 megalopa.	Eyes sessile; rostrum straight, without tooth; abdomen of 6 somites plus telson; telson with 14 setae; antennal flagellum shorter than scale, scale segmented; all pereiopods rudimentary and unsegmented, all biramous excepting 5; pleopods of small buds.
M. shokitai (present paper)	Complete suppression type; with 2 zoea stages and 1 megalopa, lacking free-swimming life.	Eyes sessile; rostrum strongly curved downward, without tooth; antenna with long flagellum, scale unsegmented; abdomen of 6 somites plus telson; telson with 35 to 38 setae; all pereiopods uniramous, segmented, without exopod; pleopods biramous.

Table 3
List of species with a few and large eggs among *Macrobrachium*.

Species	Authors	Size of eggs (mm)	Distribution
M. quelchi	Gurney, 1942	2.5–2.7×1.8–2.0	South America
	Holthuis, 1952	2.5	
M. borellii	Holthuis, 1952	1.1–2.0	South America
M. potiuna	Holthuis, 1952	1.1–1.9	South America
M. brasiliense	Holthuis, 1952	1.8–2.2	South America
M. jelskii	Holthuis, 1952	1.3–2.3	South America
M. cavernicola	Kemp 1924	1.9–2.1×1.4–1.7	India
	Gurney, 1942	2.0×1.5	India
M. pilimanus	Gurney, 1942	1.5–1.6×1.0–1.2	Southeast Asia
	Holthuis, 1950	1.2–1.8	
M. sintangense	Holthuis, 1950	1.0–1.5	Southeast Asia
M. trompii	Holthuis, 1950	?	Southeast Asia
M. australiense	Fielder, 1970	1.1×0.8	Australia
M. asperulum	Shokita (unpublished)	1.6×1.3	Formosa
M. shokitai	Present paper	2.0×1.4	Ryukyu Islands

Table 4
The resistance to salinity of the first and the second larvae of *Macrobrachium shokitai* in the laboratory. Water temperature: 28.0 to 28.5°C.
Abbreviations: +, normal; ±, weakened; −, died.

Times elapsed (in hours)	Salinity (‰)				
	0	30	50	70	100
0	+	+	+	+	+
0.5	+	+	+	+	+
1.0	+	+	+	+	+
1.5	+	+	+	+	±
2.0	+	+	+	±	−
3.0	+	+	+	−	
12.0	+	+	+		

Discussion

The first larvae of *Macrobrachium shokitai* are easily distinguished from those of the other species by the following: Large number of telson setae, absence of the exopods on the pereiopods, the long antennal flagellum and the biramous pleopods. These characters may also be applied to separate them from most of the freshwater palaemonid and atyid larvae. In most of the *Macrobrachium* larvae newly hatched, the antennal scale is segmented distally. On the contrary the first zoea of the present species has the scale unsegmented. At first sight the larvae of *M. shokitai* are characterized by the great number of the telson setae, 35 to 38, whereas 14 telson spines are reported in *M. rosenbergii* (Ling & Merican, 1961; Ling, 1969; Uno & Kwon, 1969), *M. carcinus* (Lewis & Ward, 1965; Choudhory, 1971), *M. nipponense* (Kwon & Uno, 1969), *M. acanthurus* (Choudhory, 1970), *M. australiense* (Fielder, 1970), *M. formosense* (Shokita, 1970), *M. lar* and *M. equidens* (Shokita, unpublished data), etc.

According to Sollaud (1923), the larval development of palaemonid prawns is divided into three types. The first type is basic and common, and bears many small eggs and passes through normal zoea stages without abbreviation. Such species are common from marine to down stream regions. The second is an abbreviated type, which eliminates some zoea stages and bears fewer, larger eggs than the species of the first group. The third type of development is a complete suppression of free-swimming larval life, in which the newly-hatched larva lacks exopods on the pereiopods and has biramous pleopods and a long antennal flagellum. Table 2 shows a comparison among three species which seem to represent the above-mentioned three types as regards the larval development and the characteristics of the first stage larva. *M. shokitai* belongs to Sollaud's third class, and the newly-hatched larvae have the similar appendages as in the adult except for the uropods. Larval development, however, is not entirely suppressed, and the larva grows feeding

on egg-yolk for a time.

Table 3 shows a list of the species which bear a few but large eggs among *Macrobrachium*. The larvae of these species excepting *M. australiense* and *M. shokitai* appear to pass through the abbreviated larval development.

The larval development of *M. shokitai* may be divided into 2 zoea and 1 megalopa stages from the following regards: The first stage has all the maxilliped functional, the eyes sessile and the telson of larval form, which characters are considered to be homologous with those of the normal first zoeae of other prawns. The second stage larva has also some zoeal characters in the mouth parts and the telson. In the first and second stages, swimming (or movement like jumping) was observed to be made by the telson with the large number of terminal setae. In the third stage, the mouth parts are somewhat more developed in comparison with those in the preceding stages, but they still are of larval form. Swimming in this case is mainly done by the pleopods instead of the telson (which is mainly used for swimming until the second stage). Therefore, the third stage larva evidently agrees with "megalopa" stage (Kurata, 1968; Williamson, 1969).

As already mentioned, *M. shokitai* is found restricted to fresh-water, almost at the upper stream and river-head areas. On the other hand, *M. formosense*, *M. lar* and *M. equidens*, which bear numerous small eggs, live in middle stream to brackish water, at a short distance from the sea. The species fitting in Sollaud's first class is found generally in down stream regions, while those of Sollaud's third class in upper stream. Dobkin (1963) suggested that the larvae of species which live in fresh-water for longer periods show a tendency toward condensation of development while those relatively new to this habitat have a longer larval life. From his consideration, it may be said that *M. shokitai* adapted itself to fresh-water earlier than *M. formosense*, *M. lar* and *M. equidens* which pass through a long planktonic larval life.

Such a pattern in the distribution of the adult *Macrobrachium* agrees well with the result of a comparative study on the salinity-tolerance of newly-hatched larvae, reared in the laboratory under different conditions in salinity. The first stage larva of *M. formosense, M. lar* and *M. equidens* died within one or two days when kept in fresh-water (Shokita, unpublished data), while that of *M. shokitai* soon died under 70% to 100% sea-water salinity (Table 4). The larvae of many palaemonid and atyid prawns living in fresh-water require some salinity to grow, but those of *M. shokitai* grow exclusively in fresh-water, and pass through the whole life in fresh-water.

In the geographical distribution, *M. shokitai* seems to be restricted to Iriomote Island and adapted itself to only the upper stream of a few rivers with a considerably advanced zoea of benthonic habit. On the other hand, *M. formosense, M. lar* and *M. equidens* are very widespread species with a long free-swimming larval life in marine and brackish waters.

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