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Larval Development of Palaemonid Prawn, Palaemon (Palaemon) debilis Dana from the Ryukyu Islands*

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ABSTRACT The study of the larval development of the brackish and fresh waters palaemonid prawn, *Palaemon (Palaemon) debilis* was carried out under laboratory conditions. From hatching to the first juvenile, the larvae undergo about eight molts, passing through seven zoeal and a megalopal stages. Two types of megalopal stage appeared during the course of rearing. Details of these are described and illustrated, and also the eggs and spawning ecology are briefly mentioned.

Palaemon (Palaemon) debilis Dana is known from the Red Sea and the Western Indian Ocean eastward to the Southern China including Taiwan, Ryukyu Islands, New Caledonia and the Hawaiian and Tuamotu Islands (Holthuis, 1950, 1969)^{1),2)}; its ecological distribution was already discussed in the previous paper (Shokita, 1975)³⁾.

The post-embryological development of the genus *Palaemon* from Japanese and its adjacent waters has been studied in the following species: *P. paucidens* (Yokoya, 1931)⁴⁾, *P. serrifer* (=*P. macrodactylus*?) (Yokoya, 1957; Utsunomiya & Maekawa, 1959)^{5),6)}, *P. modestus* (Kwon & Uno, 1968)⁷⁾, *P. serrifer, P. pacificus. P. ortmanni* and *P. macrodactylus* (Kurata, 1968)⁸⁾; however, there is no detailed investigation of the larval development of *P. (P.) debilis.*

This paper describes and illustrates the complete development of the larvae of P. (P.) debilis, together with some ecological informations obtained by myself in the Ryukyus.

Material and Method

The study of the larval development of Palaemon (Palaemon) debilis was

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made at the Yaeyama Branch of the Ryukyu Fisheries Experimental Station, Ishigaki Island in June of 1971. A female with eyed eggs, collected at the mangrove swamp in Ishigaki Island, was kept in a circular plastic jar with the size of 36 cm in diameter and 30 cm in depth containing sea water of 17.7‰ salinity until the eggs were hatched. Hatched larvae were reared in the abovementioned jar containing sea water of 34.8‰ salinity, and newly-hatched *Artemia salina* nauplii were fed to the larvae.

The water temperature measured at 10 a.m. ranged from 25.0° to 29.4° , with a mean of 27.0° . Body length was measured from the postorbital margin to the posterior edge of the telson, exclusive of terminal setae. Size of eggs is shown by the average of ten eggs.

Results

Field observation: Palaemon (Palaemon) debilis is essentially an estuarine dweller and an euryhaline species, inhabiting from the coastal water to freshwater. When the plankton net was towed at the Kabira Bay and coastal water of Ishigaki Island, the free-swimming larvae were sometimes found in the samples. After the larvae metamorphosed into the young in brackish or marine waters, a large number of young were observed to migrate to the estuarine areas. In Ishigaki Island the berried females occurred during all years in 1972, with a peak period in summer.

This species shares the habitat with P. (P.) concinnus, Macrobrachium grandimanus, M. equidens and M. formosense, which are all amphidromous species with numerous small eggs and lead a free-swimming larval life in brackish or marine waters.

Number and size of eggs: The pre-eyed egg is relatively small, measuring 0.78×0.61 mm on an average of 100 eggs from ten specimens. As the egg development proceeds the size of eggs becomes slightly larger in comparison with that of pre-eyed eggs, measuring 0.87×0.66 mm on an average of 100 eggs from ten specimens (Table 1).

The number of incubated eggs varied from 65 to 617, with a mean of 274 from 86 specimens. The relation between the body length (X) and the number of eggs (Y) in *P. (P.) debilis* is shown in Fig. 1.

Larval development: Under laboratory conditions the larvae passed through 7 zoeal and a megalopal stages before they reached the first juvenile stage.

Sp. No.	Pre-eyed eggs			Eyed eggs		
	Body-length (mm)	Size of eggs (mm)	Sp. No.	Body-length (mm)	Size of eggs (mm)	
1	20.9	0.79×0.60	1	20.5	0.80×0.60	
2	21.0	0.77~ imes~0.64	2	21.3	0.92×0.71	
3	21.8	0.81~ imes~0.63	3	21.5	0.89×0.66	
4	21.9	0.80×0.63	4	22.0	0.90×0.68	
5	21.9	0.76~ imes~0.59	5	22.0	0.88×0.66	
6	22.5	0.82~ imes~0.64	6	22.3	0.87×0.64	
7	22.8	0.85×0.63	7	23.0	0.87×0.64	
8	23.5	0.74×0.57	8	23.0	0.88×0.65	
9	27.5	0.72×0.57	9	23.5	0.88×0.64	
10	28.5	0.76×0.59	10	25.4	0.87×0.68	
Average	23.2	0.78×0.61	Average	22.5	0.87×0.66	

Table 1

Size of females and their eggs in Palaemon (Palaemon) debilis.

Times required from hatching to megalopa were 17 days in the shortest period at the mean water temperature of 27.0° C. The major external characters of each stage are described and illustrated below.

First zoea (Fig. 2)

The rostrum is long, straight and unarmed; its tip reaches beyond the antennular peduncle. No spine is present on the carapace. The abdomen consists of 6 segments, the last being fused to a fan-shaped telson. The eyes are sessile.

The antennule is composed of unsegmented peduncle with 2 distal flagella; the inner flagellum is of a long plumose spine; the outer bears l shout and 3 slender terminal aesthetes and l short subterminal seta. The antenna is biramous, consisting of the protopod, scale-like exopod and unsegmented endopod with a long plumose seta and a small spine at its apex. The 4-segmented scale bears 12 marginal setae, and is longer than the endopod.

The mandible lacks a palp. There are 3-4 teeth on the left incisor process, 7-8 teeth on the molar process, and 2 teeth between both processes.

The maxillule consists of inner lacinia with 5 naked distal spines, upper lacinia with 5 distal naked spines, and an unsegmented endopod with a distal spine. The maxilla consists of the protopod, unsegmented endopod and scaphognathite with 5 plumose setae; the endopod bears a distal plumose seta and numerous minute hairs on almost entire margins, and the proximal lobe

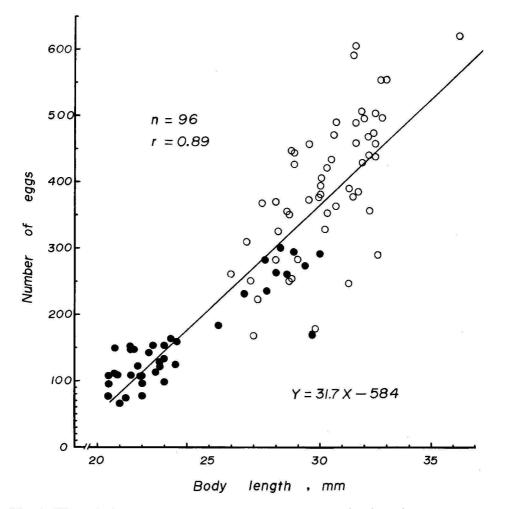


Fig. 1 The relation between the number of eggs (Y) and body length (X) in *Palaemon (Palaemon) debilis* from Ishigaki Island (solid circles) and Okinawa Island (open circles). n = No. of specimens. r = correlation coefficient.

has 2 terminal setae. The protopod is devided into 3 lobes; the proximal two lobes bear 3 terminal plumose setae each, the distal bearing 4 terminal plumose setae.

The first maxilliped is composed of unsegmented protopod with 7 naked setae, 2-segmented endopod with 4 apical plumose and l naked subapical setae, and unsegmented exopod. The exopod is longer than the endopod, with 4 apical and 2 subapical naked setae. The second maxilliped is biramous; the exopod is divided into 9-10 indistinct segments, with 8 apical and subapical setae; the endopod is 3-segmented; the distal segment ends in a strong bristled spine

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accompanying 2 naked basal spine. The third maxilliped is also biramous; the endopod is 3-segmented and ends in a long strong spine accompanying basally 2 medium sized setae: the penultimate segment bears 2 strong bristled and a naked spines distally; the exopod is divided into about 12 indistinct segments, with 8 apical and subapical setae.

The first and second percopods are rudimentary and unsegmented.

The telson bears 7+7 plumose setae, the outer two pairs of which are plumose only on the inner margin.

The chromatophores are located on the following portions: the base of the

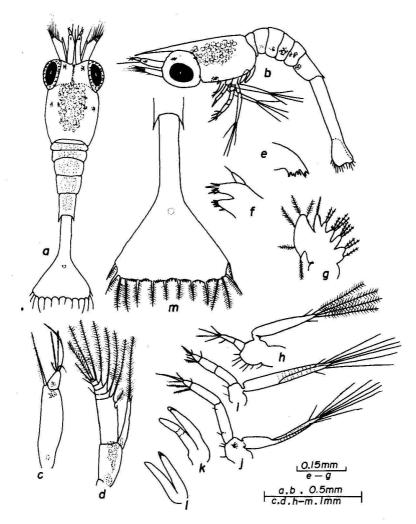


Fig. 2 Palaemon (Palaemon) debilis. lst zoea—a: dorsal view, b: lateral view, c: antennule, d: antenna, e: mandible, f: maxillule, g: maxilla, h: lst maxilliped, i: 2nd maxilliped, j: 3rd maxilliped, k: lst pereopod, 1:2nd pereopod, m: telson.

eye, the tip of the antennular peduncle, the antennal peduncle, the carapace, each abdominal segment and the protopod of the third maxilliped.

Second zoea (Fig. 3)

The major discrepancies between this stage and the preceding are as follows: The eyes are stalked; the supraorbital and pterigostomian spines are present; the antennular peduncle is divided into 2 segments; there is a single dorsal tooth on the carapace.

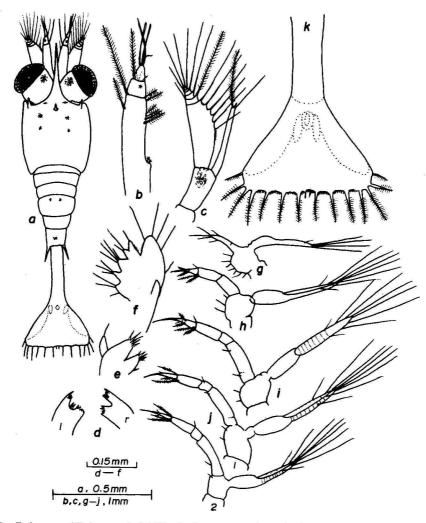


Fig. 3 Palaemon(Palaemon) debilis. 2nd zoea—a: dorsal view, b: antennule, c: antenna, d: mandibles (r and l, right and left mandibles), e: maxillule, f: maxilla, g: lst maxilliped, h: 2nd maxilliped, i: 3rd maxilliped, j: pereopods (1-2, lst and 2nd pereopods), k: telson.

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The left mandible bears 2 teeth between the incisor and molar processes, which teeth are absent from the right.

The first and second pereopods are biramous, bearing strong 4-segmented endopods and natatory exopods.

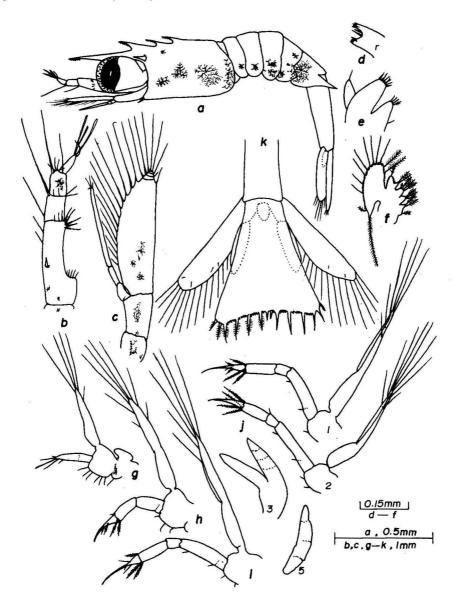


Fig. 4 Palaemon (Palaemon) debilis. 3rd zoea—a: lateral view, b: antennule, c: antenna, d: right mandible, e: maxillule, f: maxilla, g: lst maxilliped, h: 2nd maxilliped, i: 3rd maxilliped, j: pereopods (1,2,3, and 5, lst, 2nd, 3rd and 5th pereopods), k: telson and uropods.

The lateral spines of the 5th abdominal segment are strong, projecting posteriorly.

In addition to 7+7 posterior spines, the telson bears a pair of minute median spines.

Third zoea (Fig. 4)

It differs from the previous stage in the following: There are 3 teeth on the dorso-rostral and carapacial margins. The rostrum is straight, reaching the distal end of the antennular peduncle, with 5 minute spines disto-ventrally.

The antenna is biramous; 3-segmented endopod is shorter than the scale.

The scaphognathite of the maxilla bears 12 plumose setae, the ventral of which is the longest. The epipod of the first maxilliped is bilobed but rudimentary.

The rudiments of the third and fifth percopods appear at this stage; the third is biramous, and the fifth simple.

The uropod is biramous, consisting of simple protopod, the exopod with 13 marginal plumose setae and rudimentary nonsetose endopod. The telson is trapeziform, bearing 7 pairs of terminal spines, and is now separated from the sixth abdominal segment.

Fourth zoea (Fig. 5)

This stage is characterized by the fully-developed third and fifth pereopods and the appearence of the rudimentary fourth pereopod. The carapace is almost similar to that in the preceding stage; there are 2 short plumose setae just in front of the distal rostral tooth.

There are 2 spines between the incisor and molar processes in the right mandible, but 3 in the left.

The antennal scale is very similar to that in the adult, bearing 24 plumose setae along inner and terminal margins and a small disto-lateral spine. The 5-segmented endopod is slightly shorter than the scale.

The well developed epipod is 2-lobed, arising from the coxa of the first maxilliped.

The third percopod is biramous, consisting of 4-segmented endopod, functional natatory exopod with 6 apical and subapical plumose setae, and simple protopod. The fifth percopod is simple; the endopod is 4-segmented.

The posterior margin of the telson is slightly cleft, bearing 5 pairs of setae and spines.

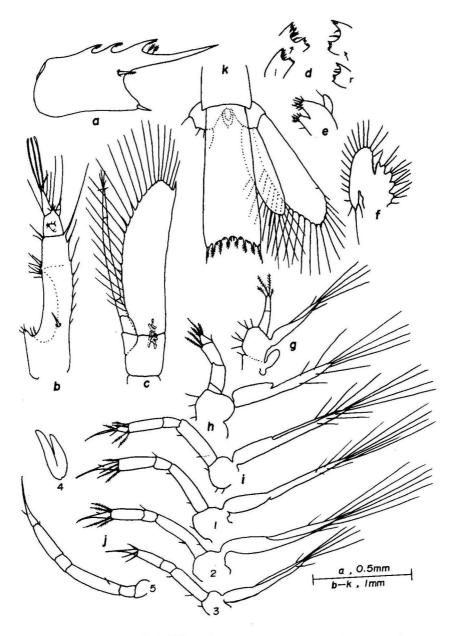


Fig. 5 Palaemon (Palaemon) debilis. 4th zoea — a: carapace, b: antennule, c: antenna, d: mandibles (r and l, right and left mandibles), e: maxillule, f: maxilla, g: lst maxilliped, h: 2nd maxilliped, i: 3rd maxilliped, j: pereopods (1-5, lst,2nd,3rd, 4th and 5th pereopods), k: telson and uropods.

Fifth zoea (Fig. 6)

The noticeable changes between this stage and the preceding are that the fourth percopod is well developed and the bud of pleopod arises from each

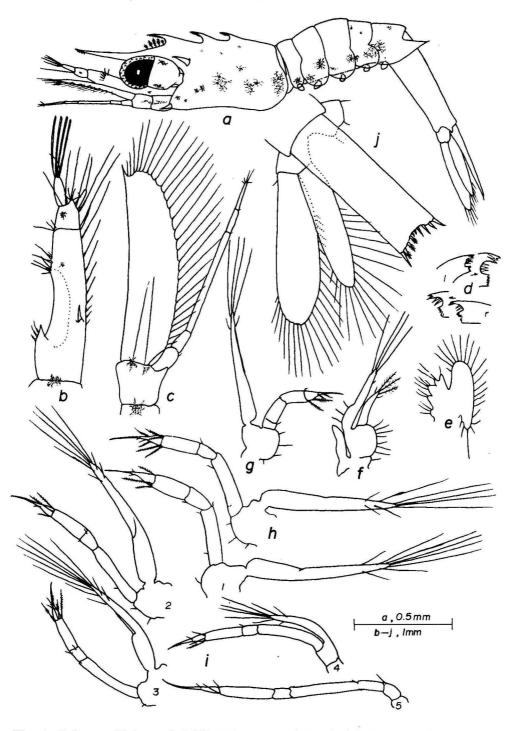


Fig. 6 Palaemon (Palaemon) debilis. 5th zoea—a: lateral view, b: antennule, c:antenna, d: mandibles (r and l, right and left mandibles), e: maxilla, f: lst maxilliped, g: 2nd maxilliped, h: 3rd maxilliped, i: pereopods (1-5, lst,2nd,3rd,4th and 5th pereopods), j: telson and uropods.

abdominal segment excepting the sixth.

The inner flagellum of the antennule has a long terminal plumose seta and the outer flagellum bears a terminal seta and 4 long terminal aesthetes. The endopod of the antenna is 5-segmented and is slightly longer than the scale which is furnished with 28 plumose setae and a disto-lateral spine.

The caridean lobe of the first maxilliped is developed, bearing 3 marginal setae.

The endopod of the fourth percopod is 4-segmented and is slightly more than twice the length of the exopod excluding setae.

The uropodal endopod is subequal to the telson in length but is shorter than the exopod with 24 plumose setae, and has 17 plumose setae. The telson is rectangular; the distal margin is slightly cleft.

Sixth zoea (Fig. 7)

This stage is characterized by the formation of the rudimentary chela of the first two pereopods.

The outer flagellum of the antennule has two bundles of aesthetes: one consisting of 3 aesthetes, placed at proximal third; and another of 4, at distal third.

The maxilla is composed of the 3-lobed protopod, unsegmented endopod with a proximal lobe and scaphognathite with 30 marginal plumose setae. Of 3 protopodal lobes the basal lobe now bears 4 setae, and the remainders have 5 setae each.

The carpus of the 5th pereopod has a spine ventrally, which segment is less than one third the length of dactylus.

Biramous, non-setose pleopods are developed on the first 5 abdominal segments. The telson is narrower toward the posterior end, and has 5 pairs of terminal spines, the outermost of which is the longest and strongest.

Seventh zoea (Fig. 8)

The rostrum is straight, reaching beyond the end of the antennular peduncle, and has the upper border with a pronounced tooth.

The first segment of the antennular peduncle bears a well-developed strong stylocerite, a small disto-lateral spine derected forwards, and stout spine on the proximal part of the inner margin. The 3-segmented inner flagellum is slightly shorter than the outer flagellum. The outer is 3-segmented, bearing

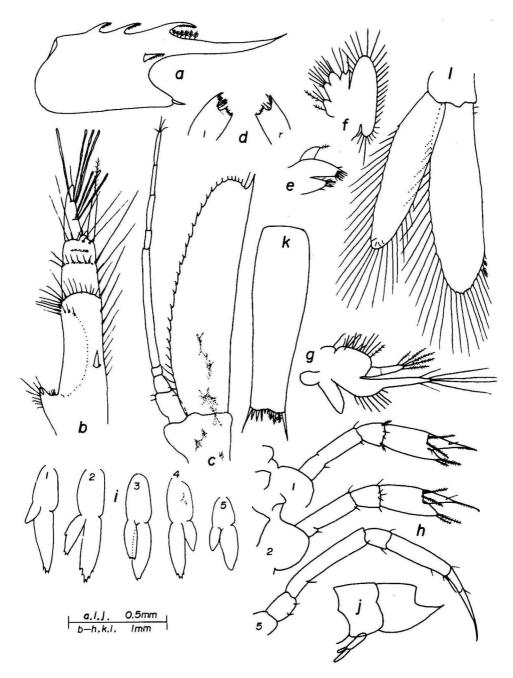


Fig. 7 Palaemon (Palaemon) debilis. 6th zoea — a: carapace, b: antennule, c: antenna, d: mandibles (r and l, right and left mandibles), e: maxillule, f: maxilla, g: lst maxilliped, h: pereopods (1,2 and 5, lst,2nd and 5th pereopods), i: pleopods (1-5, lst,2nd,3rd,4th and 5th pleopods), j: abdominal somite 4 and its pleopod, lateral, k: telson, l: uropod.

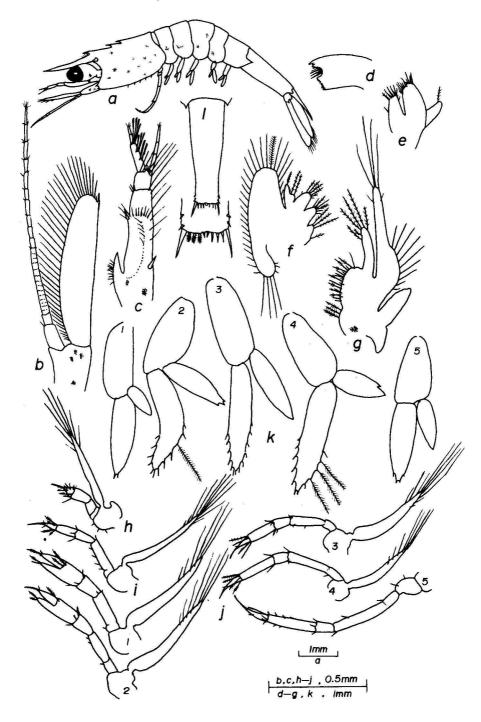


Fig. 8 Palaemon(Palaemon) debilis. 7th zoea—a:lateral view, b: antenna, c: antennule, d:right mandible, e: maxillule, f: maxilla, g: lst maxilliped, h: 2nd maxilliped, i: 3rd maxilliped, j: pereopods (1-5, lst, 2nd, 3rd, 4th and 5th pereopods), k: pleopods (1-5, lst,2nd,3rd,4th and 5th pleopods), l: telson.

groups of 2, 3 and 4 aesthetes on the proximal third, proximal two-thirds, and one thirds to distal end, respectively. The antennal endopod is longer than the scale and is divided into 14 segments; the proximal 4th segment is the longest and is subdivided into indistinct 14 small segments.

The chelae of the first 2 percopods are more developed but not functional as yet. The first 5 pleopods are biramous; the setation of the endopod and exopod are incomplete and not functional.

The telson now bears 2 pairs of disto-lateral spines and 5 pairs of terminal spines.

Megalopa

This stage is characterized by the functional, setose-natatory pleopods. In the course of rearing two types of megalopa were observed. Detailes are described below.

Type 1 of megalopa (Fig. 9)

The carapace bears the supraorbital, antennal and pterigostomian spines, and 2 dorso-mesial teeth. The rostrum is longer than the carapace, with 4 dorsal teeth.

The otolith of the antennule is distinct at the base of the first segment. The rapidly growing antennal endopod is about 4.6 mm long and is divided into 30 segments.

The mandible is devoid of the palp, deeply cleft between the incisor and molar processes; the right incisor process has 4 spinules, and the left 5. The maxillule is similar to the adult shape, consisting of well-developed upper and lower laciniae and an unsegmented endopod; the endopod is cleft at the proximal inner margin. The maxilla also resembles the adult form; both lower and upper endites are elongated, with several setae; the endopod is simple; the scaphognothite bears 41 plumose marginal setae.

The second maxilliped consists of the protopod, bilobed epipod, unsegmented exopod and 5-segmented endopod; the distal 3 segments of the endopod are curved inwards; the distal two segments are widened and bear many terminal small setae. The endopod of the third maxilliped is divided into 3 segments and longer than the reduced exopod.

The percopods are all well developed although reduced exopods are present excepting on the 5th percopod.

The setose endopods of 2nd to 5th pleopods bear appendices internae with small hooks. The uropodal exopod is longer than the endopod; the disto-lateral

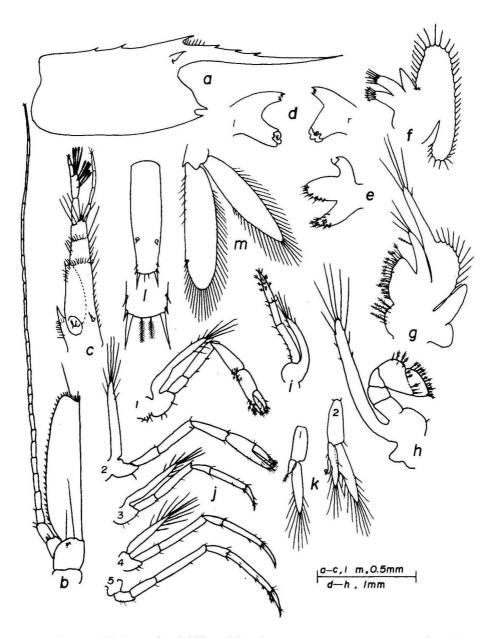


Fig. 9 Palaemon (Palaemon) debilis. Megalopa, type 1 — a: carapace, b: antenna, c:antennule, d: mandibles (r and 1, right and left mandibles), e: maxillule, f:maxilla, g: lst maxilliped, h: 2nd maxilliped, i: 3rd maxilliped, j: pereopods (1-5, lst,2nd,3rd,4th and 5th pereopods), k: pleopods (1 and 2, lst and 2nd pleopods), l: telson, m: uropod.

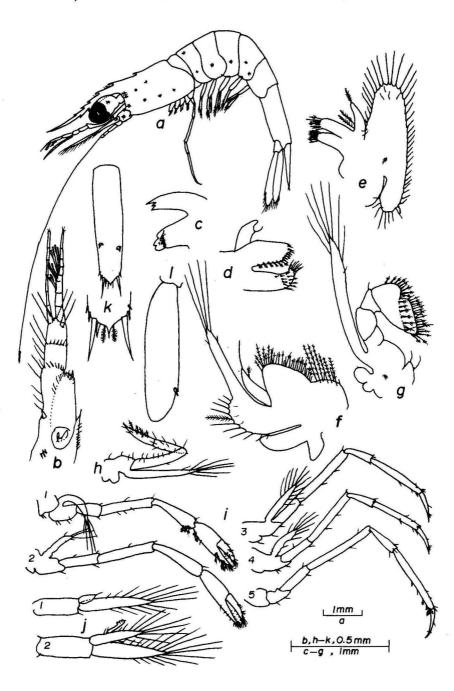


Fig. 10 Palaemon (Palaemon debilis. Megalopa, type 2—a: lateral view, b: antennule, c:right mandible, d: maxillule, e: maxilla, f: lst maxilliped, g: 2nd maxilliped, h: 3rd maxilliped, i: pereopods (1-5, lst,2nd,3rd,4th and 5th pereopods), j: pleopods (1 and 2, lst and 2nd pleopods), k: telson.

angle is pointed to form a stout spine. The telson bears a pair of dorso-lateral small spines at the posterior third and 2 pairs of disto-lateral small spines; the terminal margin has a pair of long strong lateral spines and 2 plumose setae between them.

Type 2 of megalopa (Fig. 10)

In this type the supraorbital spines are completely absent. A tooth is present on the center of the dorso-median line of the carapace. The rostrum is long and somewhat curved downwards, reaching the end of the antennular outer flagellum; the upper border has 5 teeth, and the lower border 2.

The incisor process bears 3 teeth, and is smaller than the molar process, the latter with some blunt teeth.

Degenerated exopods are still present on the first 4 percopods.

The posterior margin of the telson ends in an acute median process, and

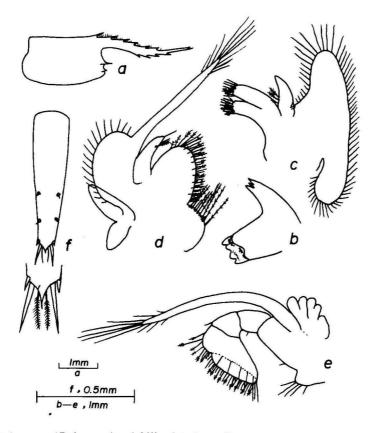


Fig. 11 Palaemon (Palaemon) debilis. lst juvenile — a: carapace, b: right mandible, c: maxilla, d: lst maxilliped, e: 2nd maxilliped, f: telson.

bears 3 spines and 2 plumose setae; the outer spine on each side is strong; less pronounced spine is between the strong lateral spine and the median process only on the left side; the plumose setae are located outside of the median process.

First juvenile (Fig. 10)

This stage is very similar to the adult in all respects except for secondary sex characters. The rostrum is very long and slender, somewhat curved upwards in the distal part; the upper border of the rostrum bears 7 teeth, and the lower 4.

The bilobed epipod of the first maxilliped is well developed; the caridean lobe is also fully developed, bearing 17 plumose setae. The epipod of the second maxilliped is devided into 5 lobes.

The telson is elongate and narrower posteriorly, with 2 pairs of dorsal spines of which the one is placed at the distal fifth and the outer at the distal two-fifths. The posterior margin of the telson is medially produced with 2 pairs of spines and a pair of plumose setae; the outer pair of spines is small, the inner greatly developed; the plumose setae are present at the base of the median process.

Stage D		Body-length (mm)	Setation of appendages					
	Duration (day)		Antennal scale	Uropod		Scaphognothite	Caridean lobe	
	(uay)			Endopod	Exopod	Scaphognotinte		
1st zoea	0	2.1	12	-	-	5	-	
2nd zoea	2	2.6	14	-	-	6	-	
Brd zoea	4	3.2	21	0	13	12	-	
4th zoea	6	3.6	24	11	19	19	-	
5th zoea	8	4.2	28	17	24	21	3	
oth zoea	10	5.8	31	26	30	30	8	
7th zoea	13	6.4	40	32	37	36	9	
Megalopa	16-17	6.9	42	33	41	44	11	
lst juvenile	20-24					63	17	

Table 2 Duration, body-length and the setation of some appendages of each stage in *Palaemon* (*Palaemon*) debilis.

Discussion

At first sight the zoeal larva of *Palaemon (Palaemon) debilis* is allied to that of *P. elegans* (Tsunamal, 1963)⁹⁾, but it is distinguished from the latter by the difference of the appearance pleopods and the number of zoeal stage. Similarly, the zoeae of the present species differ from those of *P. serrifer* and *P. pacificus*

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(Kurata, 1968)⁸⁾ in the following regards: The third abdominal segment of P. (P.) debilis is smooth, whereas that of P. serrifer bears weak dorsal ridge. A distolateral spine of the antennal scale is present in P. (P.) debilis, while it is absent in P. pacificus. The zoeal larvae of the present species are also easily distinguished from those of P. ortmanni and P. macrodactylus (Kurata, 1968)⁸⁾ by the form of the third abdominal somite: In the latter two species the dorsal ridge or spine arises from the third abdominal somite. The rudimentary third and fifth pereopods appear first in the third zoea in P. (P.) debilis, whereas in P. pausidens (Yokoya, 1931)⁴⁾, which lives in the freshwater pond and bears large eggs, they are distinct from the second zoeal stage.

In addition to the morphology *P.* (*P.*) debilis can be distinguished from *P. modestus* (Kwon et Uno, 1968)⁷) by the number of larval stages; in the latter species there are 2 zoeal stages, and the newly-hatched larva has biramous pleopods and rudimentary chelate percopods.

It is interesting to note that the zoeal stages of the present species, which is commonly known to inhabit the brackish and fresh-water, are abbreviated one stage as compared with those of *P. pacificus* which is mainly marine. Generally, in some fresh-water species of the families Atyidae and Palaemonidae there is a tendency to bear a few eggs of large size and to hatch as the advanced late larva as compared with the marine ones. For such an abbreviated larval development of the Ryukyuan species the reader is referred to Shokita (1973a, 1973b, 1976)^{10),11),12)}.

The two type of megalops were observed during the rearing. As shown in Fig. 8, one of the types has the supraorbital spines and the incomplete rostrum without lower marginal tooth; the pleopods are setose and functional. The other type (Fig. 9) may be normal, having the well-developed rostrum, the degenerated exopods of the pereopods, and disappearing supraorbital spines.

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