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The Larval Stages of the Malaysian Penaeid Shrimp (*Trachypenaeus fulvus* Dall, 1957) Reared in the Laboratory

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Abstract

Larvae of the brown rough shrimp, *Trachypenasus fulvus*, were successfully reared from egg to first postlarval stage. Spawning took place in seawater of 31 $^{\circ}/_{00}$ salinity at a temperature of 27°C. The rearing water had temperatures and salinities that ranged from 25.5 to 27°C and 28 to 31 $^{\circ}/_{00}$. The nauplius, protozoea, mysis and first postlarva were observed approximately 14, 57, 176 and 412 hours after spawning, respectively. The larvae developed through six naupliar, three protozoeal and four mysis substages before reaching the first postlarval stage. The size and morphology of all substages are described.

Introduction

The generic separation of penaeid protozoea, mysis and postlarval stages of the Gulf of Mexico was first attempted by Cook (1966). Penaeid larvae from the coast of Pakistan could be identified by Haq and Hassan (1975). However, like Cook's key, Paulinose's key should be viewed with caution since the materials were largely from plankton samples rather than from 'aboratory-reared larvae.

The program of culturing penaeid larvae from eggs of known parentage was first initiated in 1983 by the Department of Zoology of the University of Malaya, as part of a larger research project to investigate the population dynamics and ecology of penaeid larvae in

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the Straits of Malacca. This paper, on the brown rough shrimp, *Trachypenaeus fulvus*, is the first of a series which describe the larval development of Malaysian penaeid shrimp, through laboratory rearing from the egg to the first postlarval stage.

Materials and Methods

Gravid female shrimp were caught at sea by short duration trawls in spawning grounds some 5 km off the town of Bagan Sungai Buloh in the state of Selangor.

The shrimp were transported to the laboratory in a woodpolystyrene box within 3-5 hours after capture. They were transferred into spawning tanks which were plastic bins containing 40 l filtered seawater of 31 °/ ∞ salinity (one shrimp to a bin). The water was moderately aerated using an airstone at the bottom of the bin. Sodium EDTA was added at a concentration of 10 ppm.

Hatched larvae were concentrated using a light source. The larvae were then collected and transferred into 20-1 larval-rearing tanks with a stocking density of not more than 250 nauplii/l. The rearing tank was an inverted aspirator whose bottom was removed. The mouth was stoppered with a rubber bung through which an air tube was passed to supply aeration.

The chained diatom, *Thalassiosira* sp., was introduced into the larval rearing tanks as food during the last naupliar stage at a concentration of approximately 12,000 cells·ml⁻¹. Algal cell concentration was increased and maintained at 30,000-45,000 cells·ml⁻¹ through the protozoeal and mysis stages. In addition, baker's yeast was fed to the mysis stages at a concentration of 0.5-1 mg·l⁻¹. Artemia nauplii were only introduced at the postlarval stage.

Half the total volume of rearing water was exchanged daily with fresh seawater. During the rearing process, samples of larvae were taken periodically and fixed in 5% neutralized formalin. Samples of nauplii were taken at 2-hour intervals. After the naupliar stage, larvae were taken out for observation and preserved at least thrice daily.

The following measurements were taken from preserved larvae with the aid of an eye-piece micrometer: total length (TL), from the tip of the rostrum to the tip of the telson excluding the caudal/telson spines; carapace length (CL), from the post-orbital margin to the midposterior margin of the carapace; carapace width (W), the greatest width across the body (for nauplius only); and rostral length (RL), from the base of the rostrum to its tip measured laterally. All measurements were in microns (μ m).

The appendages of the nauplius were examined *in situ* usually unstained. For other larval stages, whole specimens were transferred into cavity blocks and washed through two alchohol solutions (50 and 70%) before they were stained in a solution of one part saturated solution of chlorazol black in 95% alchohol (CB) and three parts polyvinyl lactophenol (PVL). The stain was added in drops (6-10) to the last alcohol wash and stained for 4-10 hours depending on the size of the specimens. Dissections of the appendages were then performed in a very diluted staining solution (1 part CB: 30 parts PVL). Dissected appendages from the same individual were then arranged and mounted in the same fluid. Observations and illustrations were made under a binocular microscope with the aid of an Olympus drawing tube.

The spawner, identified using Hall's taxonomic key (Hall 1962), and its larvae from laboratory culture were deposited in the Department of Zoology of the University of Malaya.

Results

Approximately 2 hours after spawning, the spherical and translucent eggs had a mean diameter of $356 \pm 5 \,\mu\text{m}$ (n = 22). Its perivitelline space was wide and the morula within measured $184 \pm 4 \,\mu\text{m}$ (n = 15). The morula soon developed into an embryonic nauplius surrounded by an embryonic membrane. About 14.5 hours after spawning, the nauplius emerged by breaking through the embryonic and egg membranes.

Description of larval stages

FIRST NAUPLIUS - N1 STAGE

TL=248 \pm 7 μ m (235-259 μ m); W=134 \pm 4 μ m (129-141 μ m); n = 15.

Viewed dorsally or ventrally, the body shape is pyriform which is typical of most penaeid nauplii. A black ocellus, which persists throughout the naupliar stage, is present anteriorly on the longitudinal axis of the body.

A pair of spinous setae is at the caudal end. On the ventral surface a blunt labrum is present. The anterior half of the body bears three pairs of appendages: the first antennae, the second antennae and the mandibles (Fig. 1a). The second antennae and mandibles are biramous, the endopods being shorter than the exopods. Setae on all appendages are smooth, i.e., they do not bear setules.



Fig. 1. Nauplius of *T. fulous*, ventral view: a, first nauplius; b, second nauplius; c, third nauplius; d, fourth nauplius; e, fifth nauplius; f, sixth nauplius (anl = first antenna; an2 = second antenna; ck = cophalic knobs; fo = frontal papillae; mn = mandible).

SECOND NAUPLIUS - N2 STAGE

TL = 261 ± 8 μ m (255-267 μ m); W = 133; n = 2.

The general body form is similar to N1 larva but slightly elongated. The number of caudal setae remains 1+1. A pair of small knob-like protuberances is present on the anterior margin of the cephalic region (Fig. 1b). Plumose setae are present and in all subsequent substages.

Setation of the appendages is:

First antenna: Three terminal setae (1 long plumose + 2 short smooth), 3 short smooth ventro-lateral setae and 1 short smooth dorso-lateral seta (Fig. 2b).

Second antenna: Endopod. with 3 terminal setae (2 long plumose + 1 short smooth) and 2 short smooth ventro-lateral setae. Exopod with 3 terminal setae (2 long plumose + 1 short smooth) and 3 long plumose ventro-lateral setae (Fig. 2h).

Mandible: As in N1, except all setae are plymose.

THIRD NAUPLIUS - N3 STAGE

TL = $267 \pm 3 \mu m$ (263-274 μm); W = $135 \pm 3 \mu m$ (133-141 μm); n = 15.

This substage is distinguished from the N2 stage by a more elongated body and caudal setae which numbered 2+2 or 3+3 (Fig. 1c).

Setation of the appendages is:

First antenna: Three terminal setae (2 long plumose + 1 medium plumose), 3 ventro-lateral setae (2 short smooth + 1 short plumose) and 1 short smooth dorso-lateral seta (Fig. 2c).

Second antenna: As in N2. (Fig. 2i). Mandible: As in N2.

FOURTH NAUPLIUS - N4 STAGE

TL = $287 \pm 14 \ \mu m$ (274-306 μm); W = $144 \pm 4 \ \mu m$ (141-149 μm); n = 4.

The body has become more slender posteriorly. The caudal end bifurcates, having a setal formula of 4+4 (Fig. 1d). Posterior to the labrum, other cephalic appendages appear as ventral swellings. The ocellus persists and the medial cephalic knobs become more prominent. The bases of the mandibles have become swollen.

Setation of the appendages is:

First antenna: As in N3 with addition of 1 dorso-lateral seta (Fig 2d).

Second antenna: Endopod with 3 terminal setae (2 long plumose + 1 medium plumose) and 2 short smooth ventro-lateral setae. Exopod with 3 terminal seta (2 long plumose + 1 short smooth) and 4 long plumose ventro-lateral setae (Fig. 2j).

Mandible: As in N2.

FIFTH NAUPLIUS - N5 STAGE

TL = $306 \pm 6 \ \mu m$ (302-314 $\ \mu m$); W = $142 \pm 7 \ \mu m$ (125-149 $\ \mu m$); n = 15.

The number of caudal spines has become 6+6. The longer spines have become plumose, bearing short and spike-like sctules. Two frontal papillae are present, lateral to the medial cephalic knobs (Fig. 1e). The following features have become more pronounced: the cephalic knobs, the caudal furcae, the basal swellings of the mandibles and the developing maxillae and maxillipeds.

Setation of the appendages is:

First antenna: Three terminal setae (2 long plumose + 1 short smooth), 3 short ventro-lateral setae (2 smooth + 1 plumose) and 1 very short, smooth dorso-lateral seta (Fig. 2e). Tiny spinules present at tip.

Second antenna: Endopod with 4 terminal setae (3 long plumose + 1 short smooth) and 2 short smooth ventro-lateral setae. Exopod with 4 terminal setae (2 long plumose + 1 medium plumose + 1 short smooth) and 4 long plumose ventrolateral setae (Fig. 2k).

Mandible: As in N2.

SIXTH NAUPLIUS - N6 STAGE

TL = $378 \pm 20 \mu m$ (361-416 μm); W = 148 $\pm 9 \mu m$ (133-165 μm); n = 15.

The number of caudal setae has become 7+7. The body is further elongated at the posterior end which tapers to a distinct "waist", before fanning into the caudal furcae (Fig. 1f). The medial cephalic knobs, the frontal papillae, the caudal furcae and the basal swellings of the mandibles have all shown advanced development. The maxillae and the maxillipeds, which are now external, bear numerous short setae. A rudimentary carapace is observed in older individuals.

Appendage characteristics are:

First antenna: Basal portion segmented. Four terminal setae (2 long plumose + 2 short smooth), 3 short ventro-lateral setae (2 smooth + 1 plumose) and 2 short smooth dorso-lateral setae (Fig. 2f). Tiny spinules present at tip.

Second antenna: Endopod with 4 terminal setae (3 long plumose + 1 medium plumose) and 3 short smooth ventro-lateral setae. Exopod segmented, with 5 terminal setae (2 long plumose + 1 medium plumose + 2 short smooth) and 5 ventro-lateral setae (4 long plumose + 1 short smooth) (Fig. 21).

Mandible: As in N2.

FIRST PROTOZOEA - Z1 STAGE

TL = 765 \pm 33 μ m (706-808 μ m); CL = 303 \pm 8 μ m (209-314 μ m); n = 21.

This is the first feeding stage. It is characterized by a broad anterior portion and a long narrow posterior portion forked at its caudal end (Fig. 3A).



Fig. 3. Protozoea of *T. fulvus*, dorsal view: A, first protozoea; B, second protozoea; C, third protozoea.

The body is loosely covered by an almost-round carapace. For the first time, the larva bears a pair of sessile compound eyes anteriorly beneath the carapace. An ocellus between the compound eyes persists throughout the protozoeal stage. Frontal papilla from the previous naupliar stage protrudes from each compound eye, while the cephalic knobs have disappeared. The labrum bears a spine on its anterior margin. The mandibles, maxillae and maxillipeds (except the third maxillipeds) are well-developed and functional.

The post-carapace region consists of 6 thoracic segments, one abdominal segment and a large unsegmented portion. The latter consists of a yet unsegmented abdomen and a forked telson which bears 7 pairs of spinous setae. These setae are plumose, bearing fine and short setules.

Appendage characteristics are:

First antenna: Consists of 3 major segments; first or basal segment made of 4-5 subsegments, bearing 1 short seta on last subsegment; second segment with 1 short seta at mid-position, 1 long + 1 short setae at distal margin; third or terminal segment with 1 lateral and 5 terminal setae (1 extremely long) (Fig. 4a). All setae filamentous and smooth. Terminal spinules present.

Second antenna: Protopod 2-segmented, without seta. Endopod 2-segmented; proximal segment with 1 pair of plumose setae each on lateral and terminal margins; distal segment with 4 long plumose + 1 short, smooth terminal setae. Exopod 9-segmented; fourth to eighth segments with 5 plumose ventro-lateral setae; fourth and sixth segments with 2 plumose dorso-lateral setae; terminal segment with 5 plumose setae (Fig. 4b).



Fig. 4. Appendages of first protozoea of *T. fulvus:* a, first antenna; b, second antenna; c, right and left mandibles; d, first maxilla; e, second maxilla; f, first maxilliped; g, second maxilliped. Mandible: Endopod and exopod are lost. Masticatory surface consisting of lower molar process and upper curved incisor process; molar with numerous small teeth; incisor with few but larger teeth + 1 spinous seta bearing setules on a single row (pectinate) (Fig. 4c).

First maxilla: Protopod unsegmented, with 2 lobes on inner margin; proximal lobe with 5 long pectinate setae + 2 long plumose setae; distal lobe with 4 strong pectinate setae. Endopod 3-segmented; first segment with 3 plumose setae; second with 1; third with 4. Exopod unsegmented, knob-like, with 4 long plumose setae (Fig. 4d).

Second maxilla: Protopod unsegmented, with 5 lobes on inner margin; first to fifth lobes with 8, 4, 4, 4, 3 plumose/pectinate setae, respectively. Endopod 4-segmented; first to fourth segments with 2, 1, 2, 3 plumose setae, respectively. Exopod unsegmented, with 5 plumose setae; posterior seta thick and extremely long (Fig.4e).

First maxilliped: Protopod 2-segmented; proximal segment(coxa) with 4 plumose setae; distal (basis) with 12. Endopod 4-segmented; first to fourth segments with 3, 1, 2, 5 plumose setae, respectively. Exopod unsegmented, with 7 plumose setae (Fig. 4f).

Second maxilliped: Protopod with 2 plumose setae on coxa and 3 on basis. Endopod 4-segmented; first to fourth segments with 2, 1, 2, 5 plumose setae, respectively. Exopod unsegmented, with 6 plumose setae (Fig. 4g).

Third maxilliped: Small, with terminal setae only.

SECOND PROTOZOEA - Z2 STAGE

TL = 1,148 ± 64 μ m (1,058-1,294 μ m); CP = 363 ± 13 μ m (345-392 μ m); RL = 41 ± 4 μ m (35-47 μ m); n = 14.

The second protozoea is distinguished from the first protozoea by a pair of stalked compound eyes, a short rostrum and a fully segmented abdomen (Fig. 3B). The frontal papillae persists on the inner margin of each eye.

The postcarapace body consists of 5 thoracic segments, 6 abdominal segments and a forked telson fused to the last abdominal segment. Each telson furca bears 7 spines.

Appendage characteristics are:

First antenne: Segmentation and setation as in **21**, with additions of 2 terminal setae on second segment and 1 lateral seta on distal segment (Fig. 5a). Terminal spinules present.

Second antenna: As in Z1, except exopod with 10 segments.

Mandible: Asymmetry in setation; the right mandible with 1 pectinate seta, left mandible 5 (Fig. 5b).

First maxilla: As in Z1, except protopodal lobes with 7 plumose/pectinate setae each (Fig. 5c).

Second maxilla: Protopod with 10, 4, 5, 5, 4 plumose/pectinate setae on first to fifth lobes, respectively. Endopod and exopod as in Z1 (Fig. 5d).

First maxilliped: As in Z1, except coxa with 6 plumose setae (Fig. 5e).

Second maxilliped: As in 24 (Fig. 5f).

Third maxilliped: Small, bilobed and bearing few terminal setae.

Perelopode: Budlike, without setae.

THIRD PROTOZOEA - 23 STAGE

TL = 1,576 ± 45 µm (1,512-1,648 µm); CL = 445 ± 19 µm (408-463 µm); RL = 53 ± 5 µm (47-63 µm); n = 15.

The third protozoea is distinguished from the second protozoea by abdominal spines, biramous uropods, a demarcation between the last abdominal segment and the telson, and 8 pairs of telson spines (Fig. 3C).



Fig. 5. Appendages of second protozoea of T. *fuluus*: a, first antenna; b, right and left mandibles; c, first maxilla; d, second maxilla; e, first maxilliped; f, second maxilliped.

Frontal papillae persist on the eyes. Dorso-median spines are at the posterior margins of the first to fifth abdominal segments. A pair of spines is present on the postero-lateral margins of the fifth and sixth abdominal segments. The sixth segment also bears a pair of spines on its ventro-lateral margin. The uropod is blade-like, bearing 6 and 3 terminal setae on its exopod and endopod, respectively.

Appendage characteristics are:

First antenna: Consisting of 4 segments; first segment with 1 smooth seta; second segment with 2 setae (1 smooth + 1 plumose); third segment with 6 setae (3 smooth + 3 plumose); fourth segment with 7 setae (5 smooth + 2 plumose) (Fig. 6a).

Second antenna: As in Z2.

Mandible: Right mandible with 2 pectinate setae; left 6 (Fig: 6b).

First maxilla. As in Z2, except proximal and distal lobes of protopod with 7 and 8 plumose/pectinate setae, respectively (Fig. 6c).

Second maxilla: Endopod and exopod as in Z2. Protopod with 12, 4, 6, 6, 4 plumose/pectinate setae on first to fifth lobes, respectively (Fig. 6d).

First maxilliped: Basis and endopod as in Z1. Coxa with 7 plumose setae; exopod 9 (Fig. 6e).

Second maxilliped: Coxa with 3 plumose setae; basis 4(5); exopod 7. Endopod with 3, 1, 2, 5 setae on first to fourth segments, respectively (Fig. 6f).

Third maxilliped: Not fully developed; Protopod present. Endopod and exopod unsegmented, bearing 3(4) setae each (Fig. 6g).

Pereiopods: Protopod present with 2 rami. Seta absent.



Fig. 6. Appendages of third protozoea of *T. fulvus:* a, first antenna; b, right and left mandibles; c, first maxilla; d, second maxilla; e, first maxilliped; f, second maxilliped; g, third maxilliped.

FIRST MYSIS - M1 STAGE

TL = 2,030 ± 50 μ m (1,959-2,134 μ m); CL = 560 ± 21 μ m (541-612 μ m); RL = 116 ± 12 μ m (94-133 μ m); n = 13.

The larva shows some semblance of the adult prawn for the first time (Fig.7A). Unlike the protozoes, the thorax is now covered entirely by the carapace. Five fully-developed perciopods now function as the main natatory appendages. The first and second antennae have assumed the adult form and function as tactile organs and in orientation.

The carapace has a short toothless rostrum which does not extend beyond the eye. Paired antennal and pterygostomial spines are present. The frontal papillae persist on the eyes.

The postero-lateral margins of the fourth and fifth abdominal segments are notched. Spines are present mid-dorsally on posterior margins of the fifth and six abdominal segments and ventro-laterally on the posterior margin of the sixth segment. A large curved spine appears mid-ventrally between the sixth abdominal segment and the telson. These abdominal spines persist throughout the mysis stage.

The furcae of the telson become less obvious as the intervening notch narrows. The telson bears 8 pairs of spines; 2 pairs are inserted laterally and 6 pairs posteriorly.



Fig. 7. Mysis of T. fulvus: A, first mysis; B, second mysis; C, third mysis; D, fourth mysis.

Appendage characteristics are:

First antenna: Peduncle consisting of 3 segments, bearing 2 unsegmented flagellac; the outer flagellum is longer. First (basal) segment with 1 large midventral spine + 10 plumose setae; second with 7 plumose setae; third with 9 plumose setae. Inner flagellum with 1 short smooth + 1 long plumose setae; outer flagellum with 6 smooth setae (Fig. 8a).

Second antenna: Protopod, endopod and exopod unsegmented. Endopod with 3(4) smooth terminal setae. Exopod blade-like, with 11 plumose setae on margin (Fig. 8b).

Mandible: Right mandible with 3 pectinate setse; left 7 (Fig. 8c).

First maxilla: Protopod with 8 phimose/pectinate setae on proximal lobe; 10 on distal lobe. Endopod and emopod as in Z3 (Fig. 8d).



Fig. 8. Appendages of first mysis of *T. fuluus*: a, first antenna; b, second antenna; cl and c2, right and left mandibles; d, first maxila; e, second maxilla; f, first maxilliped; g, second maxilliped; h, third maxilliped; i, first pereiopod; j, second pereiopod; k, third pereiopod; l, fourth pereiopod; m, fifth pereiopod; n, telson and uropod (vs = ventral spine).

Second maxilla: Protopod with 12, 5, 8, 7, 3 plumose/pectinate setae on first to fifth lobes, respectively. Endopod with 2, 1, 2, 3 plumose setae on first to fourth segments, respectively (as Z1). Exopod unsegmented, with 9 plumose setae (Fig. 8e).

First maxilliped: Coxa with 8 plumose setae; basis 13. Endopod with 4, 2, 2, 5 plumose setae on first to fourth segments, respectively. Exopod unsegmented, with 7 plumose setae (Fig. 8f).

Second maxilliped: Coxa with 2 plumose setae; basis 5. Endopod with 4, 2, 2, 5 plumose setae on first to fourth segments, respectively. Exopod unsegmented, with 5 plumose setae (Fig. 8g).

Third maxilliped: Fully developed. Coxa without seta; basis 1 plumose seta. Endopod with 2, 1, 0, 3, 5 plumose setae on first to fifth segments, respectively. Exopod unsegmented, with 7 plumose setae (Fig. 8h).

Pereiopods: Five pairs of similar form (Figs. 8i-8m). First 3 pairs of almost equal sizes are slightly larger than last 2 pairs. Protopod 2-segmented, without seta. Endopod unsegmented, with 4 (first, second and third pereiopods) or 3 (fourth and fifth pereiopods) plumose setae. Exopods unsegmented, longer than endopods, with 9 plumose setae.

Uropods: Protopod with 2 spines on ventral and outer margins. Endopod and exopod blade-like. Endopod with 7-9 plumose marginal setae. Exopod with 1 outer spine + 11-13 plumose marginal setae (Fig. 8n).

SECOND MYSIS - M2 STAGE

TL = 2,442 ± 135 μ m (2,192-2,716 μ m); CL = 661 ± 21 μ m (612-690 μ m); RL = 138 ± 22 μ m (110-188 μ m); n = 9.

The second and first mysis look alike except that the former has protopodal and exopodal spines on the second antennae and mandibular palps (Fig. 7B). The furcal notch of the telson, which bears 8 pairs of spines, has become less pronounced.

Appendage characteristics are:

First antenna: Peduncle 3-segmented; first segment with or without 1 statocyst + 1 basal spine + 1 mid-ventral spine + 15 plumose setae; second segment with 7 plumose setae; third segment with 10 plumose setae. Inner flagellum with 1 short smooth + 1 long plumose setae; outer flagellum with 9 smooth setae (Fig. 9a).

Second antenna: Basis with 1 spine. Exopod with 1 disto-lateral spine on outer margin + 14 plumose marginal setae. Endopod 2-segmented, without setae (Fig. 9b).

Mandible: Palp present. Right mandible with 3 pectinate setae; left 7 (Fig. 9c)

First maxilla: Proximal lobe with 8 plumose/pectinate setae; distal 11. Endopod with 3, 1, 4 plumose setae on first to third segments, respectively. Exopod has disappeared (Fig. 9d).

Second maxilla: Protopod with 12, 5, 8, 7, 3 plumose/pectinate setae on first to fifth lobes, respectively. Endopod with 2, 1, 2, 3 plumose setae on first to fourth segments, respectively. Exopod with 12 plumose setae (Fig. 9e).

First maxilliped: Coxa with 8 plumose setae; basis 14. Endopod with 4, 3, 2, 5 plumose setae on first to fourth segments, respectively. Exopod unsegmented with 8 plumose setae (Fig. 9f).

Second maxilliped: Protopod and exopod as in M1. Endopod 5-segmented, with 4, 3, 1, 2, 5 plumose setae on first to fifth segments, respectively (Fig. 9g).

Third maxilliped: As in M1, except exopod with 8 setae.

Pereiopods: Protopod with 1 plumose seta on basis. Endopod unsegmented, with 7 (first and second pereiopods) or 6 (third, fourth and fifth pereiopods) plumose setae. Early cheliped formation at terminal ends of first to third pereiopods. Exopods with 9(10) plumose setae (Figs. 9h and 9i).

Uropod: Protopod as in M1. Endopod with 14 plumose marginal setse. Exopod with 1 spine + 14 plumose marginal setse (Fig. 9j).



Fig. 9. Appendages of second mysis of *T. fuluus:* a, first antenna; b, second antenna; cl and c2, right and left mandibles; d, first maxilla; e, second maxilla; f, first maxilliped; g, second maxilliped; h, third pereiopod; i, fourth pereiopod; j, telson and right uropod.

THIRD MYSIS - M3 STAGE

TL = $3,032 \pm 138 \ \mu m$ (2,755-3,259 $\ \mu m$); CL = $806 \pm 25 \ \mu m$ (768-855 $\ \mu m$); RL = $168 \pm 9 \ \mu m$ (141-180 $\ \mu m$); n = 14.

Pleopods which are unsegmented and curved anteriorly appear in the third mysis (Fig. 7C). The carapace has a short rostrum, with or without a rostral spine. The posterior margin of the telson, which still bears 8 pairs of spines, has become straight.

Appendage characteristics are:

First antenna: Peduncle 3-segmented; first segment with 1 statocyst + 1 basal spine + 1 mid-ventral spine + 20 plumose setae; second with 8 plumose setae; third with 11 plumose setae. Inner flagellum with 1 long plumose + 2 short smooth setae. Outer flagellum with 9 smooth setae (Fig. 10a)



Fig. 10. Appendages of third mysis of *T. fulvus*: a, first antenna; b, second antenna; c1 and c2, right and left mandibles; d-f, first, second, and third maxillipeds; g-k, first to fifth pereiopods; l, telson and uropod (ep = epipodite; pa = mandibular palp; sc = statocyst).

Second antenna: Protopod unsegmented, with 1 spine. Endopod 4-segmented. Exopod with 1 spine + 22 plumose marginal setae (Fig. 10b).

Mandible: As in M2. Palp unsegmented (Fig. 10c).

First maxilla: As in M2.

Second maxilla: As in M2, except except with 24 plumose setae.

First maxilliped: As in M2, except epipod now present (Fig. 10d).

Second maxilliped: Coxa with 2 plumose setae; basis 6. Endopod as in M2, except fifth segment bearing 6 setae. Exopod unsegmented, with 6 plumose setae (Fig. 10e).

Third maxilliped: Basis with 1 plumose sets. Endopod with 2, 2, 3, 4, 5 plumose setse on first to fifth segments, respectively. Exopod unsegmented, with 8-10 plumose setse (Fig.10f).

Pereiopods: Protopod as in M2. Endopod 5-segmented; first to fifth segments with 1, 1, 0, 3, 2 plumose setae, respectively on first and second pereiopods (Fig. 10g and 10h); 1, 1, 1, 3, 2 setae on third pereiopod (Fig. 10i); 1, 1, 1, 3, 3 setae on fourth pereiopod (Fig. 10j); 1, 1, 2, 3, 3 setae on fifth pereiopod (Fig. 10k); propodus and dactylus of first 3 pairs of pereiopods modified to form a chela. Exopod with 10 plumose setae.

Uropod: Protopod with 2 spines. Endopod with 17-19 plumose setze. Exopod with 1 spine + 17 plumose marginal setze (Fig. 101).

FOURTH MYSIS - M4 STAGE

Mean TL = $3,139 \pm 105 \ \mu m$ (2,968-8,259 $\ \mu m$); CL = $869 \pm 20 \ \mu m$ (834-909 $\ \mu m$); RL = $173 \pm 18 \ \mu m$ (157-204 $\ \mu m$); n = 16.

The fourth mysis has 2 segmented pleopods (Fig. 7D) and a telson with convex posterior margin. The short rostrum does not exceed the eye and bears a single rostral spine. In large individuals an epigastric spine may be present. The pleopods may bear a few short terminal setae but have not assumed their swimming function. The telson bears 6 pairs of posterior and 2 pairs of lateral spines.

Appendage characteristics are:

First antenna: Peduncle 3-segmented; first segment with 1 statocyst + 2 spines + 27 plumose setae; 2nd with 9 plumose setae; third with 12 plumose setae. Inner flagellum unsegmented, with 1 long plumose + 2 short smooth setae. Outer flagellum 2-segmented; first segment with 3 smooth setae; second with 8 (Fig. 11a).

Second antenna: Protopod with 1 spine. Flagellum with 4 free segments. Antennal blade (=exopod) with 1 spine + 24 plumose setae (Fig. 11b).

Mandible: As in 6M3. Palp larger and flattened.

First maxilla: As in M3 (Fig. 11c).

Second maxilla: As in M3, except greatly expanded scaphognathite (=excepd) with 29 plumose setae setae (Fig. 11 d).

First maxilliped: Coxa with 8 plumose setae; basis 15. Endopod with 4, 3, 2, 5 plumose setae on first to fourth segments, respectively. Exopod unsegmented, with 6 plumose setae (Fig. 11e).

Second maxilliped: Coxa with 3 plumose setae; basis 7. Endopod with 4, 3, 1, 2(3), 6(7) plumose setae on first to fifth segments, respectively. Exopod unsegmented, with 6 plumose setae (Fig. 11f).

Third maxiliped: As in M3.

Pereiopods: First, second and third pereiopods identical in segmentation and setation; basis with 1 plumose seta, endopod with 1, 1, 3, 3, 1 plumose seta on first to fifth segments, respectively, and exopod with 8 plumose setae (Fig. 11g). Fourth and fifth pereiopods identical; basis with 1 plumose seta, endopod with 1, 1, 3, 3, 2 plumose setae on first to fifth segments, respectively, and exopod with 10 plumose setae (Fig. 11h).

Uropod: Protopod as in M3. Endopod with 22(23) plumose setae. Exopod with 1 spine + 20 plumose marginal setae (Fig. 11i).



Fig. 11. Appendages of fourth mysis of *T. fulvus*: a, first antenna; b, second antenna; c, first maxilla; d, second maxilla; e, first maxilliped; f, second maxilliped; g, third pereiopod; h, fifth pereiopod; i, telson and uropod.

FIRST POSTLARVA - PL1 STAGE

TL = 3,263 ± 157 μ m (2,950-3,511 μ m); CL = 926 ± 32 μ m (886-980 μ m); RL = 173 ± 15 μ m (141-204 μ m); n = 19.

The postlarva is distinguished from the mysis by numerous lateral setae on the pleopods which now function as swimmerets (Fig. 12a). The exopods of the maxillipeds and perciopods are not degenerated or lost. An epigastric spine is now present on the carapace. The rostrum is short and bears a single, or rarely, 2 rostral spines.

The telson has a wedge-like posterior margin, bearing 2 pairs of lateral spines, 6 pairs of posterior spines and a pair of fine plumose setae between the first and second pair of lateral spines.

Appendage characteristics are:

First antenna: Peduncle 3-segmented; first segment with 1 statocyst + 2 spines + 38 plumose setae; second segment 9 plumose setae; third segment 13



Fig. 12. First postlarva of T. fulcus: a, lateral view; b, first antenna; c, second antenna; d, right and left mandibles; e, first maxilla; f-h, first, second and third maxillipeds; i, third pereiopod; j, fifth pereiopod; k, first pleopod; l, fifth pleopod; m, telson and uropod.

plumose setse. Inner flagellum with 3 segments bearing 4 setse. Outer flagellum with 3(2) segments bearing 14 setse (Fig. 12b).

Second antenna: Protopod with 1 spine. Flagellum with 8 or more free segments, bearing numerous setae. Antennal blade with 1 spine + 28 plumose setae (Fig. 12c).

Mandible: Setation as in M4. Palps unsegmented, bearing 10(11) phymose setae (Fig. 12d).

First maxilla: As in M4, except distal lobe of protopod bearing 13 plumose/ pectinate setae (Fig. 12e).

Second maxilla: As in M4, except fourth lobe of protopod bearing 8 setae, an additional seta on the outer protopodite margin and the scaphognathite bearing 38 setae.

First maxilliped: Coxa with 10 plumose setae; basis 21. Setation of endopod as in M4. Exopod persisting, with 7 plumose setae; (Fig. 12f).

Second maxilliped: Coxa with 3 plumose setae; basis 8. Last 2 segments of endopod recurved (Fig. 12g); first to fifth segments with 5, 4, 1, 7(8), 9-11 setae, respectively. Exopod persisting, with 4-6 plumose setae.

Third maxilliped: Relatively unchanged from M4. Exopod persisting bearing 8-10 plumose setae (Fig. 12h).

Pereiopods: One sets on coxa of all pereiopods. Fourth and fifth pereiopods have lost basial sets. Endopod with 1, 1, 3, 3, 1(2) setse on first to fifth segments, respectively. Exopod persisting, with 10 plumose setse (Figs. 12i and 12j).

Pleopods: Uniramous, with 1 basial spine. Five pairs of plumose setae on first to third pleopods (Fig. 12k); 4 pairs on fourth and fifth pleopods (Fig. 12l).

Uropod: Protopod as in M4. Endopod with 24(25) plumose marginal setae. Exopod with 1 spine + 21 plumose marginal setse (Fig. 12m).

Chronology of Larval Development

Spawning took place at 2230 hours on the same day the female shrimp was caught. Water temperature was 27°C while salinity was 31 ‰.

The eggs hatched approximately 14 hours later. The protozoeal, mysis and first postlarval stages were observed approximately 2, 7 and 17 days, respectively, after spawning. The durations of each stage and its substages are given in Table I. The water temperatures ranged from 25.5 to 27°C and salinities from 28 to 31 $^{\circ}/_{\infty}$.

Discussion

The larvae of *T. fulvus* pass through six naupliar, three protozoeal and four mysis substages before the first postlarval stage. This sequence of development differs from that of *Penaeus japonicus* (Hudinaga 1942), *P. merguiensis* (Motoh and Buri 1979) and *Metapenaeus affinis* (Thomas et al. 1974), where three mysis substages were observed.

Stage	Substage	Cumulative time after spawning day hours min.			Duration of stage (hours)	Duration of substage (hours)
Egg					14.4	
Nauplius	NI		14	25	42.7	3.7
	N2		18	6		2.0
	N3		20	1		4.6
	N4	1	0	39		6.4
	N5	1	7	1		7.5
	N6	1	14	31		18.5
Protozoea	Z1	2	9	1	119.6	72.4
	22	5	9	1		221
	Z3	6	7	28		25.1
Mysia	MI	7	5	36	236.0	46.5
	ME	9	7	6		58.2
	M3	11	17	16		67.8
	M4	14	13	6		63.5
Postlarva	PLI	17	4	36		

Differences in body form, morphology and setation of the appendages between the nauplii of T. fulvus and the above species are either minor or absent. However, one character in the nauplius of T. fulvus has not been described in other genera, i.e., the presence of a pair of cephalic knobs or protuberances. These cephalic knobs are medial in position as opposed to the more lateral position of frontal sense organs also found in T. fulvus and commonly in members of the genera Penaeus (Hudinaga 1942; Motoh and Buri 1979), Metapenaeus (Thomas et al. 1974) and Parapeneopsis (Chong, unpublished data).

In T. fulvus, cephalic knobs first appear in the second nauplius, become distinct only in the fourth or fifth nauplius and disappear in the first protozoea. The frontal sense organs are first observed in the fourth nauplius and persist till the first mysis. In this respect, T. fulvus again differs from members of other genera where frontal organs disappear in the second protozoea.

Definitive characters by which T. fulvus larvae can be separated from other penaeid larvae are found in the protozoeal and subsequent stages. For the protozoeal stage, the most useful character appears to be the setation on the endopod of the second antenna. While protozoeae of the genera Penaeus, Metapenaeus and Parapeneopsis may be distinguished using this character (Haq and Hassan 1975), the protozoea of T. fulvus shows similar antennal setation to those of Parapeneopsis. Indeed, Haq and Hassan (1975) stated that "in their antennal setation the larvae of Parapeneopsis resemble that of Trachypenaeus and Xiphopenaeus reported from the Atlantic." The mysis of T. fulvus also show remarkable similarities with those of the genus Parapeneopsis. In fact, Haq and Hassan's key would have classified the mysis of T. fulvus as belonging to the genus Parapeneopsis!

The following characters in *T. fulvus* contradict those described by Cook (1966) and Paulinose (1982) for *Trachypenaeus*:

- (1) There are five terminal setae, four long and one short, on the antennal endopod of all protozoea instead of four long terminal setae as described by Cook.
- (2) Supra-orbital spines reported as present by Cook are absent in the mysis.
- (3) Postero-lateral spines reported as present by Cook are absent on the fifth abdominal segment of the mysis.
- (4) The rostrum does not reach the end of the eye in the mysis and first postlarva, which is contrary to Paulinose's description.

Hence, existing keys are inadequate to the specific identification of larvae of the genus *Trachypenaeus*.

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