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Early Larval Development of the Penaeid Shrimp, *Trachypenaeus curvirostris* (STIMPSON), Reared in the Laboratory

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Abstract The eggs and early larvae of the penaeid shrimp *Trachypenaeus curvirostris* were reared in the laboratory to describe the morphological character and developmental time. Water temperature ranged from 24.5 to 27.0℃. The eggs hatched out as naupliar larva about 11.6 hours after spawning, and changed to protozoeal larva, which passed through 6 naupliar stages. The closely related species *T. constrictus* has 5 naupliar stages. In comparison with larvae of the genus *Penaeus,* which is distributed with *T. curvirostris* in the shallow waters of Japan, the latter is characterized by the point that the nauplius I and II have no ventrolateral setae on the endopod of the 2nd antenna.

INTRODUCTION

The southern rough shrimp, *Trachypenaeus curvirostris* (STIMPSON, 1860), mainly inhabits the tropical Indo and West Pacific Oceans, and partly penetrates into the Mediterranean through the Suez Canal (HOLTHUIS, 1980). This species extends the distribution most northerly in the family Penaeidae, e. g., to the shallow waters of Hokkaido and Sendai Bay in Japan (YOKOYA, 1933; IGARASHI, 1969; KOSAKA, 1979). In the Inland Sea, the shrimp is extensively caught with a trawlnet and plays an important role of commercial fisheries (YATSUYANAGI and MATSUKIYO, 1951; MAEKAWA and YATSUYANAGI, 1953; HAYASHI, 1974). However, early life history of the shrimp is not studied. Larval development in the genus *Trachypenaeus* are clarified on the roughneck shrimp *T. constrictus* by PEARSON (1939).

This study deals with the early development of *T. curvirostris* reared in the laboratory. Morphological changes in the egg and early larvae (nauplius I ~ protozoea I) are described and compared with other penaeid shrimps.

MATERIALS AND METHODS

On August 1, 1989, gravid females of *T. curvirostris* were collected in the shallow waters of Aki-Nada, the Inland Sea, and immediately transported to the laboratory. Ten gravid females with sticked spermatophore or 'stopper' were placed in a glass aquarium (60 cm×25 cm×35 cm).

The spawning behavior was observed under a dark condition. The larvae after hatching were gathered under the light condition. Thereafter the larvae were maintained in plastic

bottles of 0.5 and 1.0 liter. Water temperature during the rearing period ranged from 24.5 to 27.0℃. Airation of the seawater, 33.4‰ in salinity, was not conducted in these bottles but in the aquarium. Cultured diatoms *Skeletonema costatum* were introduced from the protozoea I.

The eggs and larvae were sampled at a regular interval. The size and morphology were observed with a microscope. Chronology of embryonic development was checked. Body length of the larvae was taken from the tip of the carapace, when present, to the hind end of the telson excluding the furcal spines. The terms of each larval stage were used after Dobkin (1961) and Williamson (1969).

RESULTS

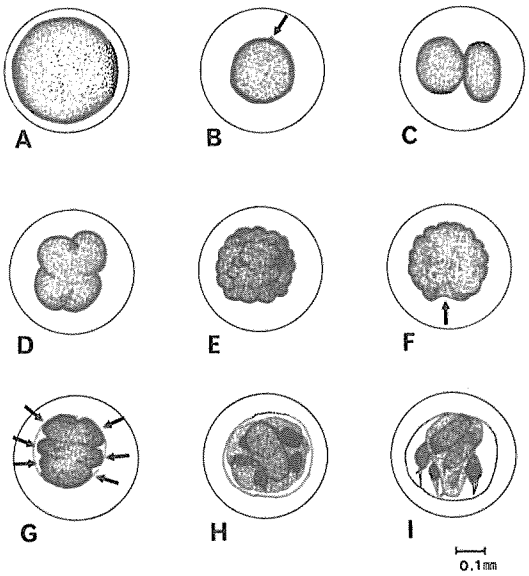

Fig. 1. Eggs of *T. curvirostris* at various embryonic developmental stage.
A : Newly spawned egg.
B : Egg with 2nd polar body.
C : 2-cell stage.
D : 4-cell stage.
E : Morula stage (about 2 hours after spawning).
F : Gastrula stage (about 2.2 hours after spawning).
G : Early embryonic nauplius (about 5 hours after spawning).
H : Late embryonic nauplius (about 8.7 hours after spawning).
I : Embryonic nauplius immediately after hatching.
Arrows indicate 2nd polar body (B), invagination cavity (F) and appendages (G).

Spawning behavior

The fully matured ovary is dark brownish green and visible from the anterior part of carapace to the posterior of abdomen through exoskeleton. The spawning took place at night, 22:50, and continued about 1 hour. The shrimp laid the demersal eggs by swimming actively from middle to upper parts of the aquarium. During the spawning, five pairs of the pleopods were vigorously moved forward and backward, and the abdomen was sometimes bent.

Egg (Fig. 1)

The viable eggs are spherical, yellowish brown in color and somewhat translucent, ranging from 0.34 to 0.55 mm in diameter. The 2-cell, 4-cell and morula stages were reached approximately 0.75, 1.0 and 2.0 hours after spawning, respectively. The early embryonic nauplius with appendages were observed approximately 5.0 hours after spawning. The late embryonic nauplius with small setae on the tips of appendages were observed approximately 8.6 hours. Just prior to hatching, the embryonic nauplius moved intermittently. The eggs hatched out about 11.6 hours after spawning.

Nauplius I (Fig. 2)

Setal formulae of appendages in the naupliar stages are shown in Table 1.

Individuals of the nauplius I measure from 0.30 to 0.40 mm in body length with a mean of 0.35 mm. An ocellus or 'naupliar eye', which is retained in subsequent naupliar stages, lies on the longitudinal axis of the body near the anterior end. The yellowish brown opaque body has a pyriform shape as viewed from the dorsal or ventral aspect. A pair of spines, about 1/4 to 1/5 of the body length, extends the posterior margin of the body, and the furcal spine formula is 1+1.

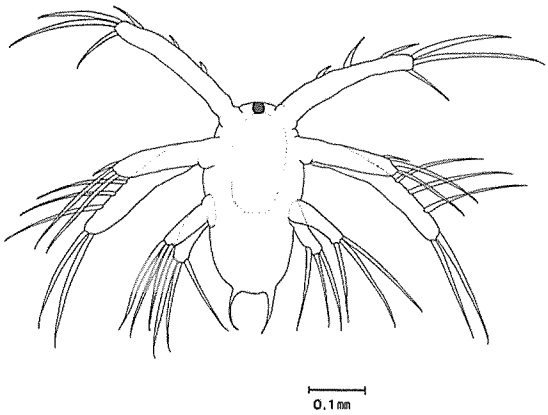

Fig. 2. Nauplius I of *T. curvirostris*. Ventral view.

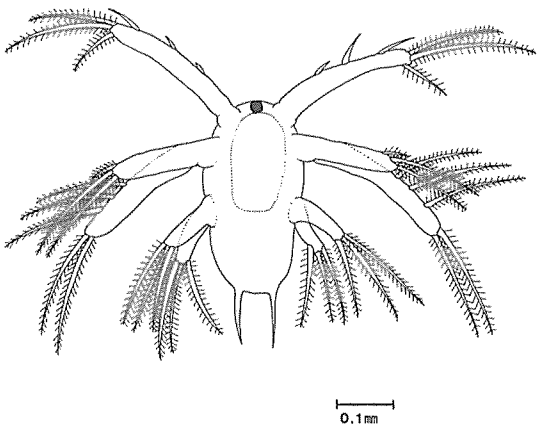

Fig. 3. Nauplius II of *T. curvirostris*. Ventral view.

Three pairs of appendages, notatory in function, are present: 1st antenna, 2nd antenna and mandible. All these appendages are unsegmented and the setae are smooth.

The 1st antenna is uniramous and somewhat shorter than the body length. It has 4 short lateral setae, of which one is dorsal, 3 are ventral, and 2 long terminal setae. The 2nd antenna is biramous, the exopod longer than the endopod. The exopod, somewhat longer than the 1st antenna, has 3 long ventrolateral and 2 long terminal setae. The endopod bears 1 short and 2 long terminal setae and has no lateral setae. The mandible is biramous, much shorter than the other appendages (about one-half the length of the 1st antenna). It has 3 long terminal setae on the exopod and endopod, remaining unchanged through all naupliar stages.

The swimming movement is produced primarily by means of the 1st

Table 1. Setal formulae of appendages in the naupliar stages of *T. curvirostris*.

Stage	1st antenna			2nd antenna					Mandible		Furcal spine
				En.		Ex.					
	Ven.	Ter.	Dor.	Ven.	Ter.	Ven.	Ter.	Dor.	En.	Ex.	
Nauplius I	(3*)	2*	(1*)	0	(1*)2*	3*	2*	0	3*	3*	1+1
Nauplius II	(3*)	2	(1)	0	(1)2	3	2	0	3	3	1+1
Nauplius III	(3*)	(1*)2	(1)	(2*)	3	3	3	0	3	3	3+3
Nauplius IV	(3*)	(1*)2	(1)	(2*)	3	3	(1*)3	0	3	3	4+4
Nauplius V	(3*)	(1*)2	(1)	(2*)	3	3	(1*)4	0	3	3	6+6
Nauplius VI	(3*)	(1*)2	(1)	(2*)	3	(1*)3	5	0	3	3	6+6

En.: Endopod, Ex.: Exopod, Ven.: Ventrolateral, Ter.: Terminal, Dor.: Dorsolateral
*: naked setae, ( ): short setae

and 2nd antennae and supplementarily by the mandible.

Nauplius II (Fig. 3)

Individuals of the nauplius II measure from 0.32 to 0.37 mm with a mean of 0.35 mm. A pair of spines, about from 1/3 to 1/5 of the body length, extends from the posterior margin of the body. These furcal spines have much individual variation, which extend straight or slightly curve.

The shape of antennae and mandible are similar to those of the nauplius I. Also all these appendages are unsegmented. The setae are plumose, except for 3 ventrolateral setae of the 1st antenna.

The body shape of the nauplius II is very similar to that of the nauplius I, except the former has plumose setae.

Nauplius III (Fig. 4)

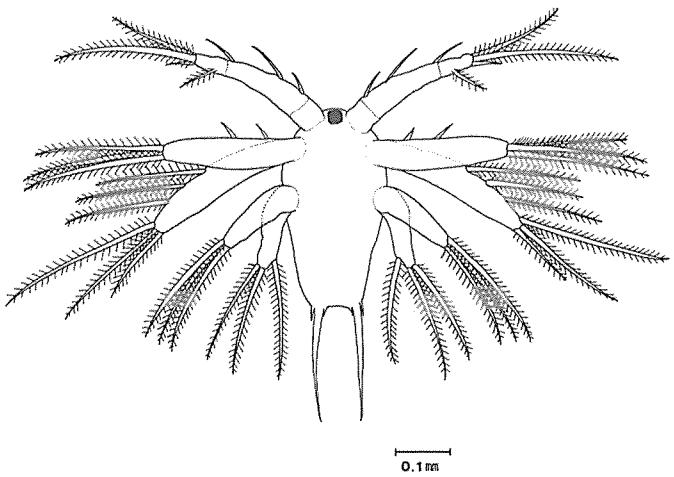

Fig. 4. Nauplius III of *T. curvirostris*. Ventral view.

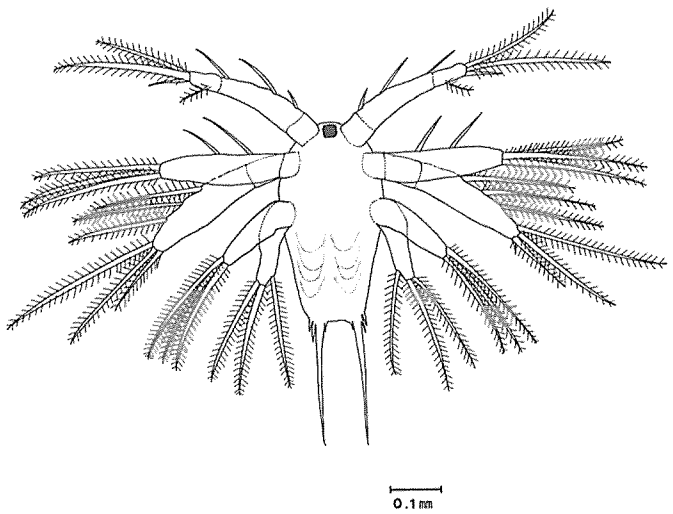

Fig. 5. Nauplius IV of *T. curvirostris*. Ventral view.

Specimens of the nauplius III measure from 0.30 to 0.43 mm with a mean of 0.37 mm. The furcal spine formula increases to 3+3 with the addition of short internal and external spines. The longest spines are about from 2/5 to 1/3 of the body length.

The 1st antenna is uniramous, segmented and somewhat shorter than the body length. It bears 3 short ventrolateral, 2 long and 1 short terminal and 1 short dorsolateral setae. The 2nd antenna is biramous, the exopod longer than the endopod. The exopod, somewhat longer than the endopod. The exopod, somewhat longer than the 1st antenna, has 3 long setae on ventrolateral and terminal. The endopod,

bears 2 short ventrolateral and 3 long terminal setae. The mandible is biramous, much shorter than the other appendages (about one-half the length of the 1st antenna). It has 3 long terminal setae on the exopod and endopod.

Smooth are 3 ventrolateral and 1 short terminal setae of the 1st antenna, and 2 short ventrolateral setae of the 2nd antenna. The others are plumose.

Nauplius IV (Fig. 5)

Specimens of the nauplius IV measure from 0.32 to 0.43 mm with a mean of 0.40 mm. The furcal spine formula increases to 4+4 with the addition of short external spines. The longest spines are about from 1/2 to 1/4 of the body length.

The 1st antenna is uniramous and somewhat shorter than the body length. It has 3 short ventrolateral, 2 long and 1 short terminal and 1 short dorsolateral setae. The 2nd antenna is biramous and segmented. The exopod, somewhat longer than the 1st antenna, bears 3 short ventrolateral, 3 long and 1 short terminal setae. The endopod, equal length to the 1st antenna, has 2 short ventrolateral and 3 long terminal setae. The mandible is biramous, much shorter than the other appendages (about one-half of the 1st antenna). It has 3 long terminal setae on exopod and endopod.

Smooth are 3 ventrolateral and 1 short terminal setae of the 1st antenna, and 2 short ventrolateral setae of the endopod and 1 short terminal setae of the exopod of the 2nd antenna. The others are plumose. Four pairs of ventral appendages, the 1st and 2nd maxillae, and the 1st and 2nd maxillipeds, are visible posterior to the mandibles.

Nauplius V (Fig. 6)

Specimens of the nauplius V measure from 0.37 to 0.47 mm with a mean of 0.43 mm. The furcal spine formula increases to 6+6 with the addition of short internal and external spines. The longest spines are about from 1/2 to 1/3 of the body length.

The 1st antenna is uniramous, segmented, and somewhat shorter than the body length. It has 3 short ventrolateral, 2 long and 1 short terminal and 1 short dorsolateral setae. The 2nd antenna is biramous and segmented. The exopod, somewhat longer than

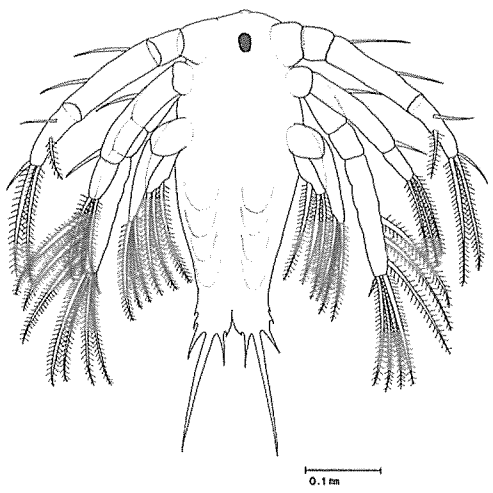

Fig. 6. Nauplius V of *T. curvirostris*. Ventral view.

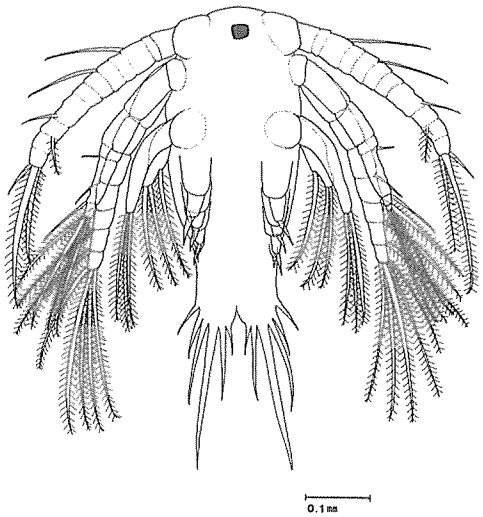

Fig. 7. Nauplius VI of *T. curvirostris*. Ventral view.

the 1st antenna. They bears 3 long ventrolateral, 4 long and 1 short terminal setae. The endopod, somewhat shorter than the 1st antenna, has 2 short ventrolateral and 3 long terminal setae. The mandible is biramous, much shorter than the other appendages (about one-half the length of the 1st antenna). It has 3 long terminal setae on the exopod and endopod.

Smooth are 3 ventrolateral and 1 short terminal setae of the 1st antenna, and 2 short ventrolateral setae of the endopod and 1 short terminal setae of the exopod of the 2nd antenna. The others are plumose. Four pairs of ventral appendages are visible posterior to the mandibles.

Nauplius VI (Fig. 7)

Eighty four specimens of the nauplius VI measure from 0.40 to 0.57 mm with a mean of 0.51 mm. The furcal spine formula remains 6+6. The longest spines are about from 1/2 to 1/3 of the body length.

The 1st antenna is uniramous, segmented, and somewhat shorter than the body length. It has 3 short ventrolateral, 2 long and 1 short terminal and 1 short dorsolateral setae. The 2nd antenna is biramous, and segmented. The exopod, somewhat longer than the 1st antenna, bears 3 long and 1 short ventrolateral, 5 long terminal setae. The endopod, somewhat shorter than the 1st antenna, has 2 short ventrolateral and 3 long terminal setae. The mandible is biramous, much shorter than the other appendages (about one-half the length of the first antenna). It has 3 long terminal setae on the exopod and endopod.

Smooth are 3 ventrolateral and 1 short terminal setae of the 1st antenna, and 2 short ventrolateral setae of the endopod and 1 short terminal setae of the exopod of the 2nd antenna. The others are plumose. Four pairs of ventral appendages show more advanced development.

Protozoea I (Fig. 8)

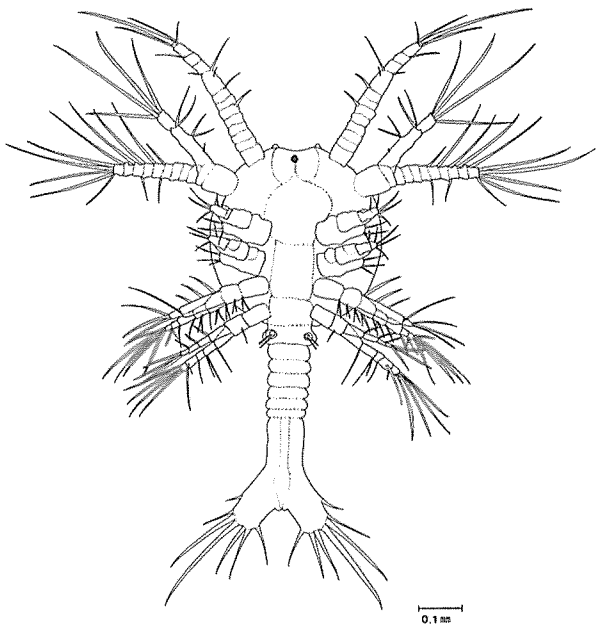

Fig. 8. Protozoea I of *T. curvirostris*. Ventral view.

In this paper, the term "protozoea" is used to the first three post-naupliar stages in the Penaeidea (Williamson, 1969).

Individuals of the protozoea I measure from 0.78 to 0.97 mm in body length with a mean of 0.93 mm. The protozoea I is radically different from the nauplius; the body is divided into two parts. The anterior part is covered by the large carapace. The narrow posterior part is divided into a six-segmented thorax and an unsegmented abdomen. A pair of compound eyes are still present slightly below the anterior end of the carapace.

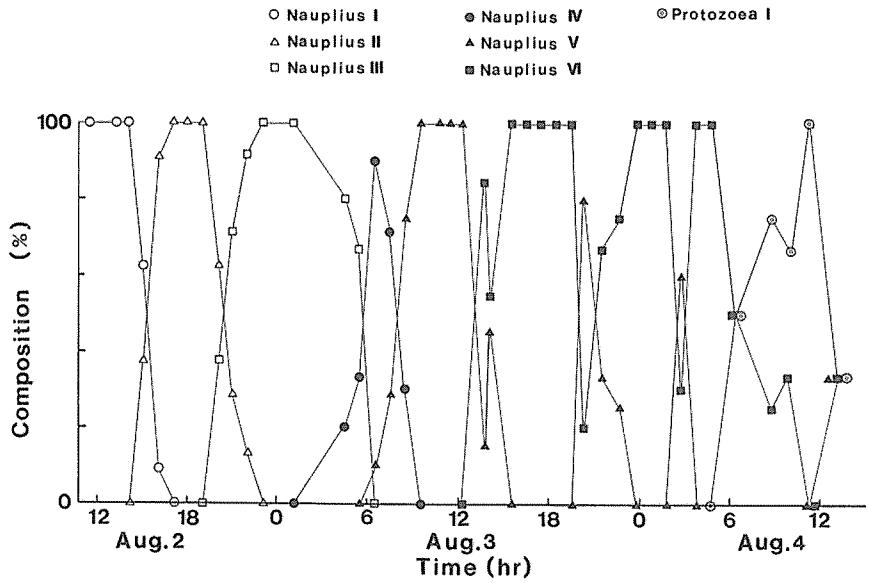

Fig. 9. Change in the larval composition of *T. curvirostris* after hatching.

The maxillae and maxillipeds are functional. The 1st antenna is uniramous. It has 1 short and 3 long ventrolateral, 1 short and 3 long terminal, and 2 short dorsolateral setae. The 2nd antenna is biramous. The endopod, about one-half the length of the exopod, has 1 short and 4 long ventrolateral and 4 long terminal setae. The exopod has 1 short and 4 long ventrolateral, 5 long terminal, and 2 short dorsolateral setae. The mandible has lost the endopod and exopod.

The abdomen terminates in a well-developed telson, each lobe of which has seven furcal spines.

Chronology of larval development

Change in the larval composition of *T. curvirostris* is shown in Fig. 9. The nauplius I was present about 6 hours after hatching. The nauplius II was first noted about 3.4 hours after hatch-out. The naupliar stages molted at a almost regular interval except the nauplius V and VI. The nauplius V and VI, which were present 24 hours, hardly showed a difference in the shape and size between the early and late individuals. The nauplius VI metamorphosed into the protozoea I about 30.9 hours after hatch-out.

Size composition of larval stage

The size composition and change in the body length of the each stage are shown in Fig. 10. The nauplius I and II showed one peak in the size composition. Two peaks appeared in that of the nauplius III, and were obviously isolated in the nauplius IV. The smaller group remained in the protozoea I.

No or little increase in the size was observed from the nauplius I and II. Thereafter the increment per molt increased gradually: 5.7~19% from the nauplius II to V, and 82% from the nauplius VI to the protozoea I.

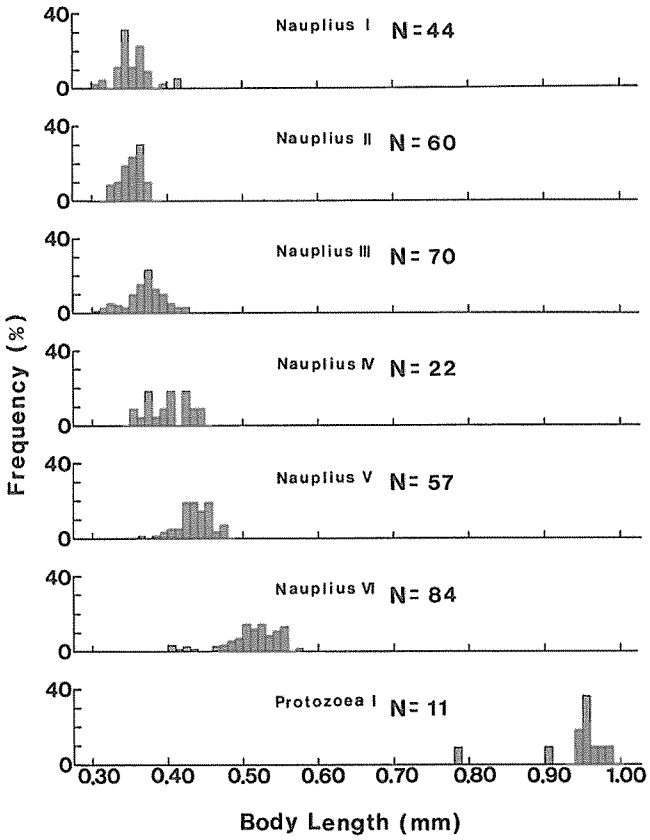

Fig. 10. Size composition in the naupliar and protozoeal stages of *T. curvirostris*.

DISCUSSION

Eighteen species in the genus *Trachypenaeus* are known in the world (Hayashi, 1982). The early development is studied only on *T. constrictus* (Pearson, 1939), which distributes in the tropical West Atlantic Ocean (Chace, 1972). Size, shape and color of the egg is similar between *T. curvirostris* and *T. constrictus*. On the other hand, number of the naupliar stages is six in the former and five in the latter, based on the change of morphological charcters (Table 2). The nauplius I and II in *T. curvirostris* hardly show any difference in the setae formulae of 1st and 2nd antennae, and furcal spines, including the body size. However two stages can be divided on the fact that the setae of appendages becomes plumose after the nauplius II, which is also observed in the penaeid shrimp *Penaeus aztecus* (Cook and Murphy, 1971) and *P. indicus* (Courties, 1976). Pearson (1939) reported that a large number of the embryonic nauplius passed through a series of naupliar molts within the egg because of unruptured egg membrane. It is, therefore, deduced that the nauplius I in *T. constrictus* can be divided into two stages.

The comparison with the genus *Penaeus* need to be made as follows, because *T. curvirostris* and *P. japonicus* are distributed in the same waters such as the Inland Sea. The nauplius I and II has no ventrolateral setae on the endopod of the 2nd antenna of *T. curvirostris*, while has some ventrolateral setae that of *P. aztecus* (Cook and Murphy, 1971), *P. indicus* (Courties, 1976), *P. esculentus* (Fielder et al., 1975), *P. monodon* (Motoh, 1979), *P. merguiensis* (Motoh and Buri, 1979), *P. canaliculatus* (Choy, 1984), *P. vannamei* (Kitani, 1986-b), *P. chinensis* (Oka, 1967-a), *P. latisulcatus* (Shokita, 1984), *P. californiensis* (Kitani and Alvarado, 1982), *P. stylirostris* (Kitani, 1986-a), *P. duorarum* (Dobkin, 1961), *P. setiferus* (Pearson, 1939), and *P. japonicus* (Hudinaga, 1942). The size of egg is larger in *T. curvirostris* with 0.34 to 0.55 mm in diameter than in *P. japonicus* with 0.29 to 0.32 mm (Hudinaga, 1942), *P. monodon* with 0.26 to 0.28 mm (Motoh, 1979), *P. chinensis* with 0.13 to 0.14 mm (Oka, 1967-b) and so on.

Table 2. Comparison of the morphological characters in the naupliar stages between *T. curvirostris* and *T. costrictus*.

Stage	Characters	*T. curvirostris* (Present study)	*T. constrictus* (PEARSON, 1939)
Nauplius I	Body length	0.30~0.40 mm (m=0.35 mm)	0.24~0.26 mm
	1st antenna	3·2·1	3·2·1
	2nd antenna En.	0·3·0	0·2·0
	Ex.	3·2·0	2·3·0
	Furcal spines	1+1	1+1
Nauplius II	Body length	0.32~0.37 mm (m=0.35 mm)	0.26~0.32 mm
	1st antenna	3·2·1	3·3·0
	2nd antenna En.	0·3·0	2·2·0
	Ex.	3·2·0	3·3·0
	Furcal spines	1+1	2+2
Nauplius III	Body length	0.30~0.43 mm (m=0.37 mm)	0.36 mm
	1st antenna	3·3·1	3·3·0
	2nd antenna En.	2·3·0	2·3·0
	Ex.	3·3·0	3·4·0
	Furcal spines	3+3	5+5
Nauplius IV	Body length	0.32~0.43 mm (m=0.40 mm)	0.38~0.42 mm
	1st antenna	3·3·1	3·3·1
	2nd antenna En.	2·3·0	2·3·0
	Ex.	3·4·0	4·4·0
	Furcal spines	4+4	6+6
Nauplius V	Body length	0.37~0.47 mm (m=0.43 mm)	0.40~0.44 mm
	1st antenna	3·3·1	3·3·1
	2nd antenna En.	2·3·0	2·4·0
	Ex.	3·5·0	4·4·0
	Furcal spines	6+6	7+7
Nauplius VI	Body length	0.40~0.57 mm (m=0.51 mm)	
	1st antenna	3·3·1	
	2nd antenna En.	2·3·0	
	Ex.	4·5·0	
	Furcal spines	6+6	

Setal formulae of 1st and 2nd antennae are in the order of ventrolateral, terminal and dorsolateral. En.: Endopod, Ex.: Exopod, m: mean length.

It is considered that the protozoea I died out probably because cultured diatoms was unsuitable for its molt.

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サルエビ *Trachypenaeus curvirostris* (STIMPSON) の初期幼生の発生過程

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実験室内で産卵したサルエビの卵および孵化した幼生を飼育し，特に初期幼生の形態的特徴と発生時間の観察を行った。その結果，水温 24.5～27.0℃ 下で，産卵後11時間40分にノープリウス幼生として孵化し，ノープリウスVI期を経て，孵化後30時間50分にプロトゾエア幼生となった。これは同属のクビレサルエビ *Trachypenaeus constrictus* (STIMPSON) が5ノープリウス期からなることと異なっている。また日本近海で混在して出現するクルマエビ属 *Penaeus* の幼生と比較すると，本種のノープリウスのI期とII期は第2触角内肢の腹側面に棘を持たない点で区別できる。