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Embryonic Development of *Metanephrops thomsoni* (Bate, 1888) (Crustacea, Decapoda, Nephropidae)

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The embryonic development of *Metanephrops thomsoni* from the East China Sea was studied. The developmental stages were divided into ten stages according to the morphological characteristics of the embryonic appendages. The shape of the eggs was nearly globular in the early stages and became gradually oval-shaped with increasing size after the appearance of eye pigmentation.

INTRODUCTION

The red banded lobster *Metanephrops thomsoni* (Bate, 1888) is distributed on the sandy bottom mud at a depth of around 200 m on the continental shelf from the western part of Japan to the Philippines across the East China Sea (Miyake, 1982). Although this species is caught on a commercial basis for its edible meat by trawlers in the East China Sea, few biological studies have been carried out.

Decapod crustaceans excluding the Dendrobranchiata incubate their eggs by attaching them to their pleopods (Barnes, 1974). A few studies on the attached eggs have been performed for some decapods (e. g. Herrick, 1895 ; Matsuura and Takeshita, 1985). For the present species, *M. thomsoni,* changes in the diameter, shape and color of attached eggs at only two stages, just after egg extrusion and just before hatching, have been described (Uchida and Dotsu, 1973). However, its embryonic development has not been reported.

In this paper, the first attempt is made to classify the developmental stages of the embryos of *M. thomsoni* according to the morphological characteristics of the appendages.

Furthermore, changes in the egg size of this animal during the incubation period are also described.

MATERIALS AND METHODS

Ovigerous females of *Metanephrops thomsoni,* caught by bottom trawlers in the East China Sea during the period between February 1983 and November 1984, were

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preserved in 10 % formalin. Eggs attached to the pleopods were carefully removed using a small pair of forceps. Five eggs were randomly sampled from each female and were dissected in 50 % ethylene glycol under a stereomicroscope. The appendages of the embryos were observed and drawings of them were made with the aid of a camera lucida. Characteristics of external morphology of the embryo were examined in order to clarify the stage of embryonic development using a profile projector. The yolked area appeared opaque and the embryo appeared translucent when eggs were observed with the profile projector. The percentage of the area occupied by the embryo in the profile view showed a close relationship to the developmental stage of the embryo. Hence, the area of the embryo in the egg profile revealed by external observation can be used as an easy method for determining the stage of development.

The incubated eggs of *M. thomsoni* were oval in shape and the width was nearly equal to the height. The lengths and the heights of 50 eggs from each female were measured at the inner egg membrane with the profile projector. Measurements were also made at the outer egg membrane for comparison with the results obtained with other species. All eggs were measured when the clutch size was less than 50. The cubic dimension ($l \times h \times h$) was calculated from the length (l) and the height ($h \fallingdotseq$ width) of the egg and the geometric mean, $\sqrt[3]{l \times h \times h}$, was considered to be the standard egg diameter in this study. The ratio of the height to the length, h/l, was also calculated in order to investigate the changes in egg shape.

RESULTS

Developmental Stages of Embryos

The embryonic development of *Metanephrops thomsoni* was divided into ten stages, A to J, based on the morphological characteristics of appendages and the profile area of the embryo revealed by external observation.

Stage A

No embryonic development visible.

Stage B (Fig. 1 : 1, 2)

Initiation of embryo development. Embryo thin and egg almost completely occupied by opaque yolk mass in profile view. Inner egg membrane present. Optic lobes indistinct. Antennules, antennae and mandibular buds present. Antennule rod-shaped with 2 to 3 terminal processes. Antenna bifurcated, outer branch with 4 to 6 terminal processes. Abdomen bifid at extremity, nearly reaching labrum.

Stage C (Fig. 1: 3-7)

Embryo thicker than at previous stage. Translucent embryo area about 2 % of whole egg in profile view. Each appendage covered with embryonic cuticle. Carapace formation initiated, as in illustration. Optic lobes defined more sharply, with a rounded appearance. Mandible bilobed. Maxillae I and II present, inner margin of maxilla I uneven, maxilla II bilobed. Bifurcated maxillipeds I to III present, exopods and endopods rod-shaped and not bearing processes. Abdominal segmentation initiated.

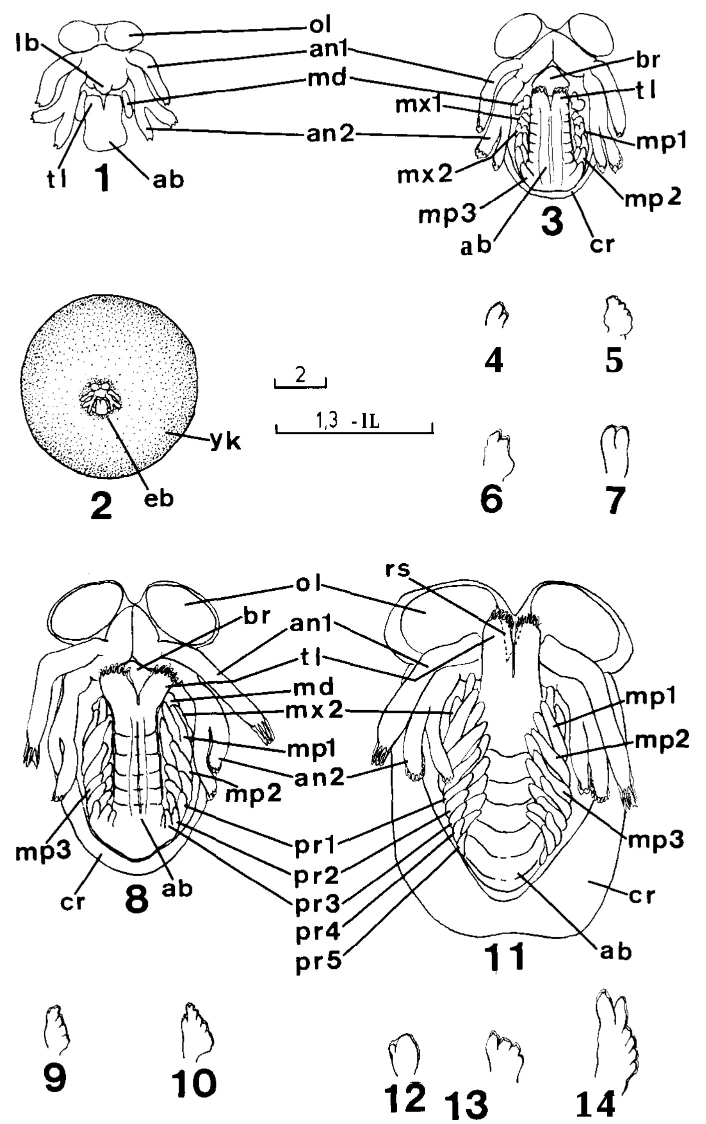

Fig. 1. Developmental stages B, C, D and E of *Metanephrops thomsoni* embryo. 1, 2 : stage B ; 3-7 : stage C ; 8-10 : stage D ; 11-14 : stage E. 1, 3. 8, 11 : embryo in ventral view ; 2 : embryo in relation to the egg (outer and inner egg membranes removed) ; 4, 12: mandible; 5, 9, 13: maxilla I; 6, 10, 14 : maxilla II ; 7: maxillipeds I-III. ab: abdomen ; anl : antennule ; an2 : antenna ; br : brain ; cr : carapace ; eb : embryo ; lb : labrum ; md : mandible ; mpl 3 : maxillipeds I - III ; mxl : maxilla I ; mx2 : maxilla II ; ol : optic lobe ; prl 5 : pereopods I-V ; rs : rostrum ; tl : telson ; yk : yolk. Scales 0.5 mm.

Region of telson distinctly bilobed, each lobe with 4 to 6 terminal processes, partially overlaying the brain.

Stage D (Fig. 1 : 8-10)

Translucent embryo area about 7 % of whole egg in profile view. Antennule with 3 to 4 terminal setae. Antenna1 exopod and endopod with 8 to 9 and 3 terminal processes, respectively, processes of exopod increasing in number on inner margin in subsequent stages. Maxilla I, covered with maxilla II and maxillipeds, not visible externally. Maxilla I flattened, 4-lobed, one lobe as endopod with outer marginal tapered protuberance. Maxilla II flattened, exopod, endopod, basal endite and coxal endite present, terminal surface of endopod uneven, basal and coxal endites bilobed. Biramous buds of pereopods I to III present. Telson with 6 to 7 terminal processes on each lobe, overlaying the brain.

Stage E (Fig. 1 : 11-14)

Translucent embryo area about 12 % of whole egg in profile view. Isosceles-

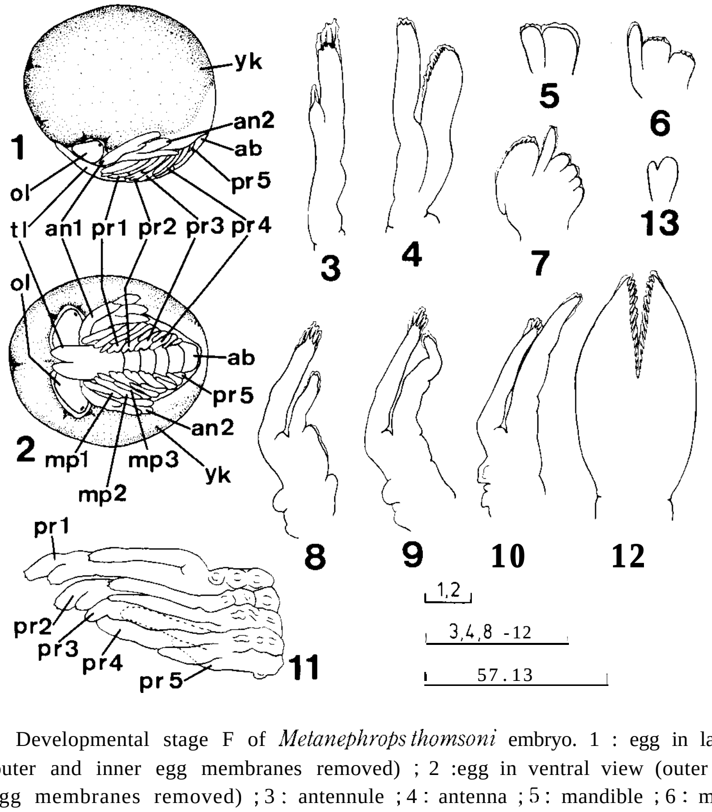

Fig. 2. Developmental stage F of *Metanephrops thomsoni* embryo. 1 : egg in lateral view (outer and inner egg membranes removed) ; 2 :egg in ventral view (outer and inner egg membranes removed) ; 3 : antennule ; 4 : antenna ; 5 : mandible ; 6 : maxilla I ; 7 : maxilla II ; 8 : maxilliped I ; 9 : maxilliped II ; 10 : maxilliped III ; 11 : pereopods I-V and buds of epipods and gills ; 12 : telson ; 13 : pleopod. Abbreviations as for Fig. 1. Scales 0.5 mm.

triangular rostrum present. Antenna1 exopod with 9 to 10 processes. Mandible, covered with maxillae and maxillipeds, not visible externally, inner lobe larger than outer one. Exopod and endopod of maxilla II remarkably developed. Exopods of maxillipeds I to III with a few processes at apex. Biramous buds of pereopods I to V present, endopod of pereopod V situated under pereopod IV. Abdominal segmentation advanced. Telson rectangular, extending beyond antennular base.

Stage F (Fig. 2)

Translucent embryo area about 21% of whole egg in profile view. Carapace formation indistinguishable at this stage and in subsequent stages. Black eye pigment present, optic lobes differentiated into eyes. Antennular endopod present with a terminal seta, exopod with 4 terminal setae surrounded at base by cuticular sheath. Antenna1 endopod more slender than exopod. Inner lobe as mandibular palp unsegmented. Endopod, basal and coxal endites of maxilla I differentiated distinctly with several terminal processes. Endopod of maxilla II more slender than exopod, flattened exopod developed into scaphognathite with about 10 processes on outer anterior margin. Exopod of maxilliped I longer than endopod, unsegmented with 4 terminal setae, endopod with a few processes at apex, basal and coxal endites differentiated, uniramous bud of epipod present. Exopod of maxilliped II as for maxilliped I, endopod shows faint segmentation, uniramous bud of epipod present. Exopod of maxilliped III shorter than endopod, other characters as for first two maxillipeds, endopod as for maxilliped II, buds of epipod and gill present. Endopods of pereopods I to V with a few terminal processes, endopods of pereopods I to III slightly bifid at extremity, buds of epipods and gills of pereopods I to V present. Abdomen with five somites and telson. Biramous pleopods present on abdominal somites II to V. Telson with 11 to 13 processes on each inner lateral margin, the process at apex of each furca being largest.

Stage G (Fig. 3)

Translucent embryo area about 31 % of whole egg in profile view. Eye-stalk differentiated indistinctly. Antennular exopod with 5 terminal setae. Antenna1 exopod more flattened, developed into antenna1 scale with 12 to 13 setae on inner lateral margin. Molar lobe of mandible swollen. Endopod, basal and coxal endites of maxilla II with several terminal processes, scaphognathite with about 20 marginal processes. Uniramous buds of epipods of maxillipeds I to III now roundish, gill buds of maxilliped III differentiated as 2 arthrobranches. Exopods of pereopods I to V with 4 to 5 terminal setae, endopods show faint segmentation with a few processes at apex, each terminal rift of endopods of pereopods I to III progressed, buds of epipod and gill now roundish, pereopods I to IV with an epipod and 2 arthrobranches, pleurobranches of pereopods I to IV undifferentiated, a podobranch present on each of pereopods II to V. Abdominal somite VI differentiated indistinctly. Telson broad and leaf-like, extending beyond eye lobes, each furca with 14 processes on inner lateral margin, a large process present on medial notch.

Stage H (Fig. 4)

Translucent embryo area about 60 % of whole egg in profile view. Eye-stalk differentiated distinctly, pigmented area of optic lobes expanded. Antenna1 endopod

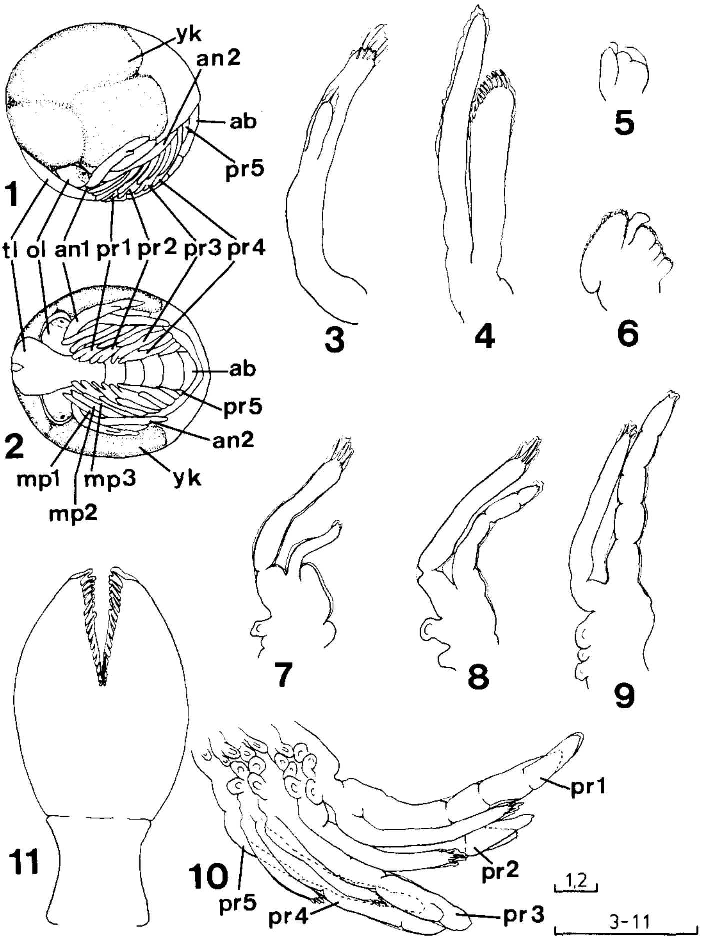

Fig. 3. Developmental stage G of *Metanephrops thomsoni* embryo. 1 : egg in lateral view (outer and inner egg membranes removed) ; 2 : egg in ventral view (outer and inner egg membranes removed) ; 3 : antennule ; 4 : antenna ; 5 : mandible ; 6 : maxilla II ; 7 : maxilliped I ; 8 : maxilliped II ; 9 : maxilliped III ; 10 : pereopods I–V and buds of epipods and gills ; 11 : telson. Abbreviations as for Fig. 1. Scales 0.5 mm.

with 13 to 14 setae, exopod-endopod ratio about two-thirds. Molar lobe of mandible triangular. Scaphognathite with about 30 marginal setae. Epipod of maxilliped I bilobed indistinctly. One pleurobranchial bud present on each epipod of maxillipeds II and III, with no lamella, development of two arthrobranches on maxilliped III advanced. Exopods of pereopods I to V with 4 to 6 terminal setae, segmentation of endopods advanced, each terminal lobe of endopods of pereopods I to III developed into chela, a pleurobranchial bud on each epipod of pereopods I to IV differentiated, each arthrobranch on pereopods I to IV and podobranch on pereopods II to V developed into rod-shaped bud with no lamella. A dorsomedial spine present on each posterior margin

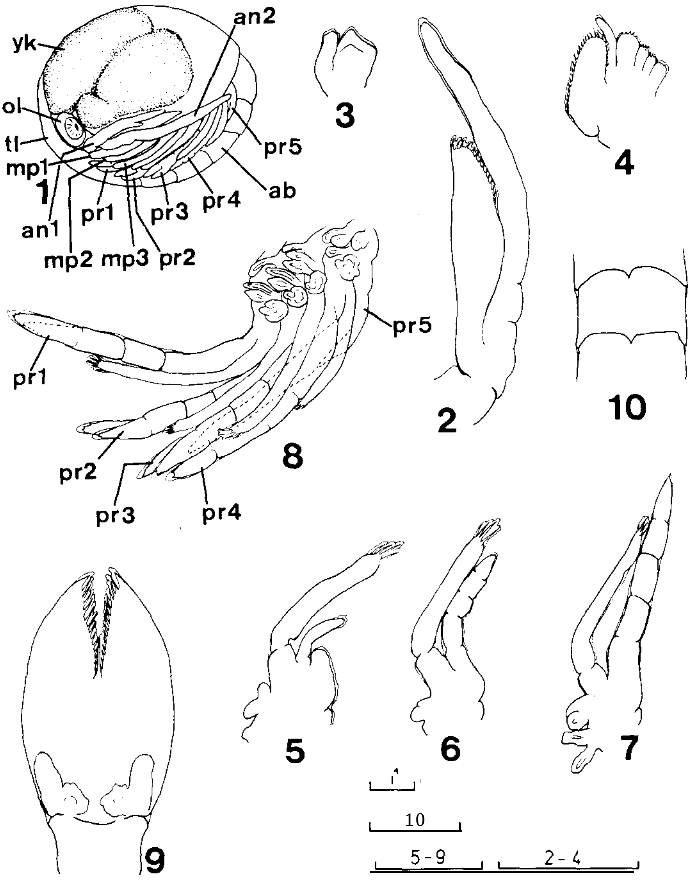

Fig. 4. Developmental stage H of *Metanephrops thomsoni* embryo. 1 : egg in lateral view (outer and inner egg membranes removed) ; 2 : antenna ; 3 : mandible ; 4 : maxilla II ; 5 : maxilliped I ; 6 : maxilliped II ; 7 : maxilliped III ; 8 : pereopods I-V and buds of epipods and gills ; 9 : telson and buds of uropods ; 10 : dorsomedial spines on abdominal somites II-V. Abbreviations as for Fig. 1. Scales 0.5 mm.

of abdominal somites II to V. Biramous buds of uropods visible under cuticle.

Stage I (Fig. 5)

Translucent embryo area about 67 % of whole egg in profile view. Carapace now completed. Antenna1 endopod half of exopod, exopod S-segmented indistinctly, plumose setae of endopod invaginated at base. Segmentation of mandibular palp initiated. Basal endite of maxilla I triangular. Scaphognathite with about 36 marginal plumose setae, each process invaginated at base. Epipod of maxilliped I bilobed distinctly, setae of exopod with barbules, invaginated except at distal end, basal endite with some processes on lateral margin. Endopod of maxilliped II 5-segmented, setae

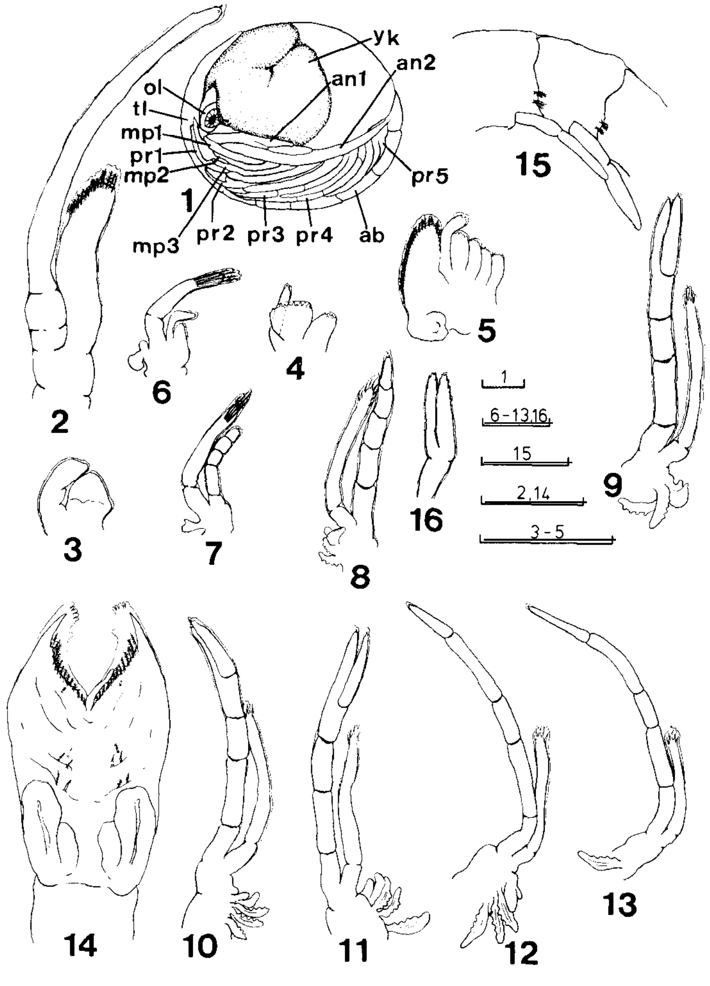

Fig. 5. Developmental stage I of *Metanephrops thomsoni* embryo. 1 : egg in lateral view (outer and inner egg membranes removed) ; 2 : antenna ; 3 : mandible ; 4 : maxilla I ; 5 : maxilla II ; 6 : maxilliped I ; 7 : maxilliped II ; 8 : maxilliped III ; 9 : pereopod I ; 10 : pereopod II ; 11 : pereopod III; 12 : pereopod IV; 13: pereopod V ; 14 : telson and buds of uropods ; 15 : pleuron of abdominal somite. Abbreviations as for Fig. 1. Scales 0.5 mm.

of exopod with barbules, invaginated excluding distal end, pleurobranchial bud on epipod differentiated more sharply with no lamella. Exopod of maxilliped III with 9 terminal setae, endopod 5-segmented, gill buds well developed, arthrobranches with lamellae but pleurobranches with no lamella. Exopods of pereopods I to V with 5 to 8 terminal setae, endopods 5-segmented, propodi and dactyli of pereopods I to III distinctly differentiated into chelae, each gill bud of pereopods I to V well developed with lamellae except for pleurobranches. Pleura of abdominal somites II to V

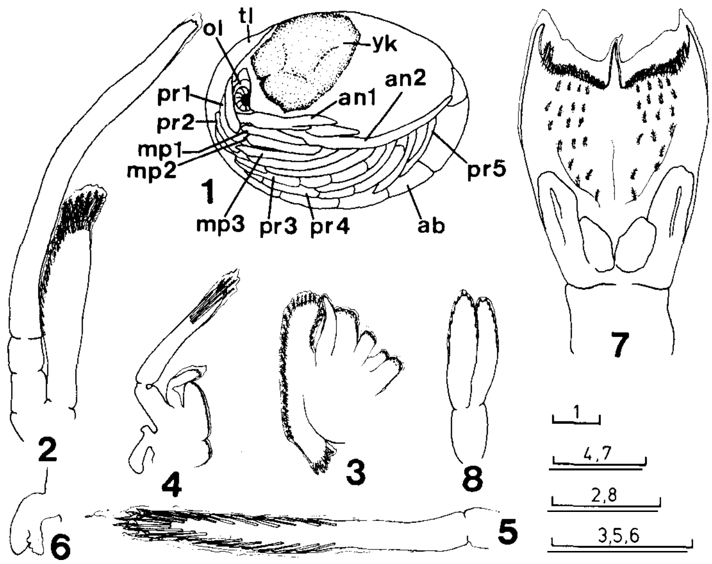

Fig. 6. Developmental stage J of *Metanephrops thomsoni* embryo. 1 : egg in lateral view (outer and inner egg membranes removed) ; 2 : antenna ; 3 : maxilla II ; 4 : maxilliped I ; 5 : exopod of maxilliped III and pereopods I-V ; 6 : epipod and pleurobranch of maxilliped III and pereopods I-V; 7: telson and buds of uropods; 8 : pleopod. Abbreviations as for Fig. 1. Scales 0.5 mm.

developed into triangle with 2 plumose setae. Pleopods on somites II to V further developed, exopods and endopods uneven on lateral margin with 6 to 10 processes. Each furca of telson tapered to a point, expanding to each side with 13 to 14 invaginated plumose setae on inner lateral margin, some plumose setae scattered on dorsal surface, as in illustration. Biramous buds of uropods visible.

Stage J (Fig. 6)

Translucent embryo area about 83 % of whole egg in profile view. Antennal scale with about 30 plumose setae. Scaphognathite with about 40 marginal setae. Basal endite of maxilliped I well developed with about 20 processes on lateral margin. Exopods of maxilliped III and pereopods I to V with 15 to 22 plumose setae, each plumose seta invaginated except at distal end. Each pleurobranchial bud on epipod of maxilliped III and pereopods I to IV with lamellae. Pleopods on abdominal somites II to IV with about 15 processes. Telson with many plumose setae on dorsal surface, as in illustration.

Egg Size

The frequency distribution of egg diameters measured at the inner egg membrane of *M. thomsoni* had one mode throughout all embryonic stages (Fig. 7). This fact shows that the eggs of a single clutch grow simultaneously.

The mean egg diameter and height/length ratio at each developmental stage are

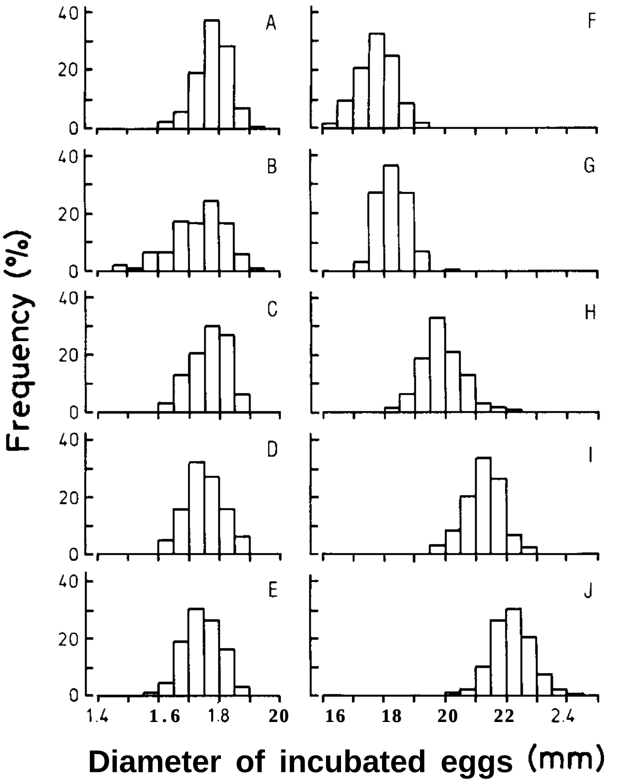

Fig. 7. Size frequency distribution of the diameter of eggs attached to the pleopods measured at the inner egg membrane at embryonic stages A to J of *Metanephrops thomsoni*. Number of samples examined is present in Table 1.

Table 1. Diameter of incubated eggs and their height/length ratio at each developmental stage of *Metanephrops thomsoni* embryos. Geometric mean from length and height is adopted as egg diameter. Oem : *size* measured at the outer egg membrane, Iem: size measured at the inner egg membrane.

Stage	Number of mother animals examined	Number of eggs examined	Egg diameter (mm)		Height/Length	
			Oem Mean SD	Iem Mean SD	Oem Mean SD	Iem Mean SD
A	5	250	1.78±0.05	1.78±0.05	0.95±0.03	0.95±0.03
B	3	150	1.75±0.09	1.73±0.09	0.92±0.04	0.91±0.04
C	2	100	1.81±0.05	1.76±0.06	0.91t0.03	0.91±0.04
D	2	100	1.82±0.06	1.7510.06	0.91±0.04	0.92'0.04
E	5	250	1.7910.05	1.74±0.05	0.91±0.04	0.91±0.04
F	9	450	1.83±0.06	1.78±0.06	0.91±0.04	0.90±0.05
G	3	127	1.86±0.06	1.8310.05	0.86±0.07	0.85±0.06
H	10	457	2.00±0.07	1.99±0.07	0.82±0.06	0.82±0.06
I	5	227	2.13±0.06	2.11±0.06	0.83±0.05	0.82±0.05
J	9	377	2.26±0.07	2.19±0.09	0.84±0.05	0.82±0.05

shown in Table 1. The mean egg diameter was nearly constant from stage A to stage E. However, there was a rapid increase in the mean diameter after stage F when eye pigmentation had appeared in the embryo. The mean height/length ratio was 0.95 at stage A and was nearly constant until stage E. However, the ratio decreased from stage F to stage H, after which it was almost constant again from stage H to stage J. These results show that the eggs of *M. thomsoni* are nearly globular in the early embryonic stages, stage A to stage E, and that they increase remarkably in size and become gradually oval-shaped after stage F when eye pigmentation first appears. The egg volume in stage J, calculated from the mean diameter, was about twice as large as that in stage A.

DISCUSSION

Larval development of *Metanephrops thomsoni* was studied by Uchida and Dotsu (1973), and there are significant differences between our descriptions of the final stage of embryonic development, stage J, and the descriptions of the newly hatched larvae (= prezoea) which they reported. They described the morphology as follows : antennule is unsegmented and rod-shaped; antenna1 scale has 14 plumose setae ; scaphognathite has about 20 plumose setae on terminal lateral margin ; endopod of maxilliped II is rod-shaped ; exopods of maxilliped III and pereopods I to V have no seta ; pleopods have no seta ; buds of uropods appear under cuticle in the following stage. Stage J in the present study, however, was described as follows : antennule has a rod-shaped endopod ; antenna1 scale has about 30 plumose setae ; scaphognathite has about 40 marginal plumose setae ; endopod of maxilliped II is 5-segmented ; exopods of maxilliped III and pereopods I to V have 15 to 22 plumose setae ; pleopods have about 15 marginal processes ; biramous buds of uropod present under cuticle (Fig. 6). Except for the presence of antennular endopod, morphological differences between these two studies may be due to differences of observational criteria and whether or not morphological features visible under the larval cuticle were adopted.

The prezoeae and embryonic larvae on the point of hatching of two species of ***Metanephrops, M. andamanicus*** and ***M. challengeri,*** have been described (Berry, 1969 ; Wear, 1976). The embryo just before hatching of these two species and *M. thomsoni* are very similar in morphology. Thus we think that they develop sufficiently in eggs to have chelae on the pereopods I to III and the pleopods of abdominal somites II to V and then hatch at similar developmental stages. The egg size in the final stage, J, of *M. thomsoni* is 2.26 mm (Table 1) and those in the late embryonic stage of ***M. andamanicus*** and ***M. challengeri*** are 2.46 mm and 2.52 mm (mean calculated from Wear, 1976), respectively. In the early stage of development, the mean egg sizes of *M. australiensis* and ***M. boschmai*** are 2.49 mm and 1.80 mm (calculated from Wear, 1976). The egg size of *M. japonicus* from the East China Sea is 2.81 ± 0.06 mm (mean ± SD, n = 50) at equivalent stage ***G*** of *M. thomsoni* and that of ***M. sagamiensis*** from the East China Sea is 2.57 ± 0.10 mm (mean ± SD, n-50) at equivalent stage E of *M. thomsoni* (Hamasaki and Matsuura, unpublished data). These data suggest that the larvae of other species of ***Metanephrops*** will hatch at an advanced developmental stage like ***M. thomsoni, M. andamanicus*** and *M. challengeri*.

Thorson (1950) suggested that marine benthic invertebrates generally had small eggs and planktrophic larvae in low latitudes or in shallow waters, and conversely had large eggs and lecithotrophic larvae in high latitudes and in deeper waters. Among ***Metanephrops*** species, *M. thomsoni* is the only one for which the complete larval development has been studied (Uchida and Dotsu, 1973). The duration of the larval period up to the megalopal stage when benthic life and feeding begin is about four days at 18 to 21°C (Uchida and Dotsu, 1973). These results indicate that the pattern of larval development of ***M.*** *thomsoni* is lecithotrophic which is defined as consuming only yolk without taking food in early larval development before settlement. Considering that ***M.*** *thomsoni* inhabits the sandy bottom mud at a depth of about 200 m (Miyake, 1982), the relationship between the egg size and the developmental pattern of larvae seems to conform to the theory of Thorson (1950). Jenkins (1972) found that ***Metanephrops*** species have been taken at depths of between 50 and 885 m and that the majority of records showed depth greater than 150 m. From these records, it seems very likely that ***Metanephrops*** species live in deep water and have large eggs. Furthermore, much yolk is present in the late embryos and newly hatched larvae of *M. andamanicus* and ***M. challengeri*** and it is suggested that their larvae settle immediately after hatching (Berry, 1969 ; Wear, 1976), so it appears that the lecithotrophy mentioned by Thorson (1950) is a common feature in ***Metanephrops.***

It is a well known fact that eggs attached to the pleopods of decapod crustaceans increase in size during the incubation period due to osmotic uptake of water (Davis, 1964a, 1964b, 1965a, 1965b, 1966). However, there have been few studies which have examined the period when egg size increases during incubation. Wear (1974) studied the change of egg volume with elapsed time for two caridean shrimps, five anomurans and fourteen brachyurans in detail and found that the egg volumes increased more rapidly at about the time of initiation of heartbeat, followed by the first appearance of chromatophores and black eye pigmentation in the embryo. Herring (1974) also described a similar phenomenon in five species of caridean shrimp, *Acanthephyra*. In addition, Mashiko (1982, 1983) reported a remarkable increase in egg volume after pigmentation of the eyes of the embryo in two Japanese caridean shrimps, *Palaemon paucidens* and *Macrobrachium nipponense*. Matsuura and Takeshita (1985) found that the average diameter of incubated eggs increased from the middle of the incubation period in an anomuran crab, *Paralithodes camtschaticus*. The eggs of ***M. thomsoni,*** studied in the present paper, scarcely increased in size during early embryonic development, but grew rapidly after eye pigmentation had appeared in the embryo. An increase in the size of incubated eggs during development, especially during the later stages, may thus be common in decapod crustaceans since it has been observed in various taxonomical groups as mentioned above.

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