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Biology and Ecology of *Penaeus monodon*

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Abstract The giant tiger prawn, *Penaeus monodon*, the largest and most commercially important species among penaeids reaching 270 mm in body length or 260 g in weight, is suitable for culture in ponds and offers high market prices. This species occurs mainly in Southeast Asian waters, though it is quite widely distributed from 30°E to 155°E longitude and 35°N to 35°S latitude. Mating and spawning generally take place at night. The maximum number of eggs spawned at a time is more than 800,000. The life history is classified into six phases: embryo, larva, juvenile, adolescent, Subadult, and adult. The biological minimum size is 37 mm carapace length for males and 47 mm CL for females. The food consists mainly of small crustacea, mollusks and annelids. The adult is a predator of slow-moving benthic macroinvertebrates, or opportunistic in feeding behavior. This prawn is relatively eurythermal and euryhaline, growing rapidly to a large size. The life span may be one and a half to two years, and the female may live for a longer period than the male. In general, the female is larger than the male.

Introduction

The giant tiger prawn, *Penaeus monodon* Fabricius, is one of the largest penaeid prawns in the world, reaching some 270 mm in body length, and is of commercial importance in markets.

Recently in Southeast Asian countries, enthusiasm for natural and artificial propagation of both fry and adult giant tiger prawn has been growing rapidly among government and private agriculturists due to strong demand with higher prices in the national and international markets. On the other hand, their habitats such as shore areas and mangrove waters are under destruction in several areas. Therefore, it is important to understand the principal characteristics of the species.

The world crustacean catches in recent years have been about 1.6 million tons. Shrimps and prawns comprise about 1 million tons, of which almost 75% appear to be penaeids.

Identity

Penaeus (Penaeus) monodon Fabricius, 1798

Synonyms

Penaeus carinata Dana, 1852
P. tahitensis Heller, 1862
P. semisulcatus exsulcatus Hilgendorf, 1879
P. coerulus Stebbing, 1905
P. monodon var. *manillensis* Villalluz and Arriola, 1938
P. bubulos Kubo, 1949
P. monodon monodon Burkenroad, 1959

FAO names

Giant tiger prawn (English)
Crevette géante tigrée (French)
Camarón tigre gigante (Spanish)

Description

The rostrum, extending beyond the tip of the antennular peduncle, has 6 to 8 (mostly 7) dorsal and 2 to 4 (mostly 3) ventral teeth, and is sigmoidal in shape. The adrostral carina reaches almost to the epigastric spine. The carina reaches to the posterior edge of the carapace. The gastro-orbital carina occupies the posterior one-third to one-half distance between the post-orbital margin of the carapace and the hepatic spine. The hepatic carina is predominant and the anterior half is horizontal. The antennular flagellum is sub-equal to, or slightly longer than the peduncle. The 5th pereopod has no exopod. The abdomen is carinated dorsally from the anterior one-third of the 4th to 6th somites. The 4th and 5th somites each has a small lateral cicatrice, and the 6th, 3 lateral cicatrices. The telson is unarmed (Fig. 1).

Color in life is as follows: Carapace and abdomen are transversely banded with red and white. The antennae are greyish brown. Pereopods and pleopods are brown and fringing setae red. Upon entering shallow brackish waters or when kept in ponds, the color changes to dark brown and often to blackish.

Distribution

The giant tiger prawn is widely distributed throughout the greater part of the Indo-West Pacific region: South Africa, Tanzania, Kenya, Somalia, Madagascar, Saudi Arabia, Oman, Pakistan, India, Bangladesh, Sri Lanka, Indonesia, Thailand, Malaysia, Singapore, Philippines, Hongkong, Taiwan, Korea, Japan, Australia, and Papua New Guinea (Fig. 2). In

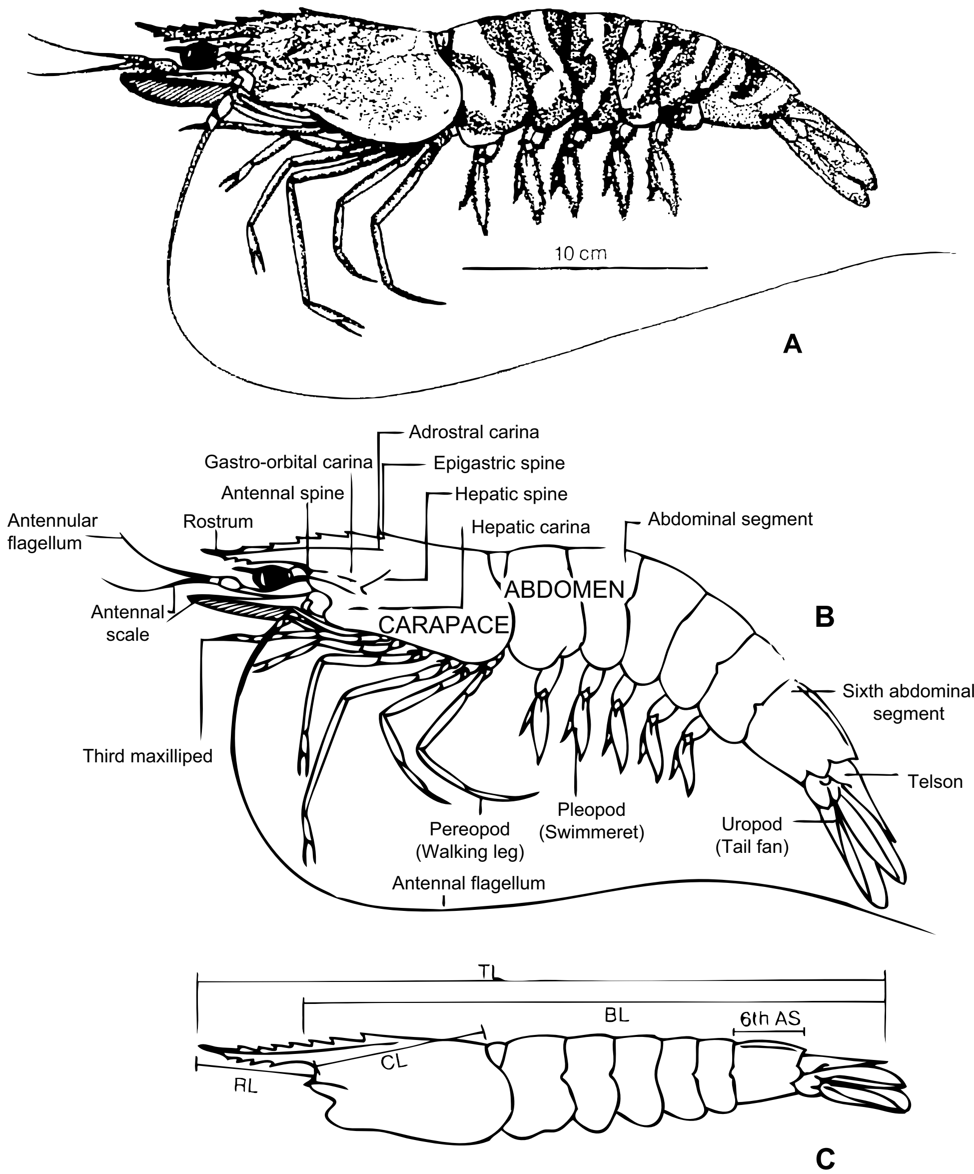

Fig. 1. A: Adult female of *Penaeus monodon;* B: External anatomy of *P. monodon; C:* Methods of measurement of *P. monodon* (RL, rostrum length; CL, carapace length; TL, total length; BL, body length; 6th AS, length of 6th abdominal segment).

general, *P. monodon* is distributed from 30°E to 155°E longitude and from 35°N to 35°S latitude. However, the main fishing grounds are mostly located in tropical countries, particularly in Indonesia, Malaysia and the Philippines.

The fry, juveniles and adolescents inhabit surface waters such as shore areas and mangrove estuaries, while most of the adults inhabit waters down to about 160 m.

Bionomics and life history

Reproduction

Sexuality. *Penaeus monodon* is heterosexual. The sexes can be distinguished by external characters (genital organs): petasma and a pair of appendix masculina in male and thelycum in female (Fig. 3). The petasma is situated between the 1st pleopods and the appendix masculina on the exopods of the 2nd pleopods, while the thelycum is between the 4th and 5th pereopods.

A pair of genital openings in the male is situated on the coxae of the 5th pereopods (walking legs) and in the female on the coxae of the 3rd pereopods.

Females attain a relatively larger size than males.

Morphological development

Embryo (Fig. 4). Viable eggs of *P. monodon* are spherical, yellowish green in color and somewhat translucent, ranging from 0.27 to 0.31 mm with an average of 0.29 mm in dia-

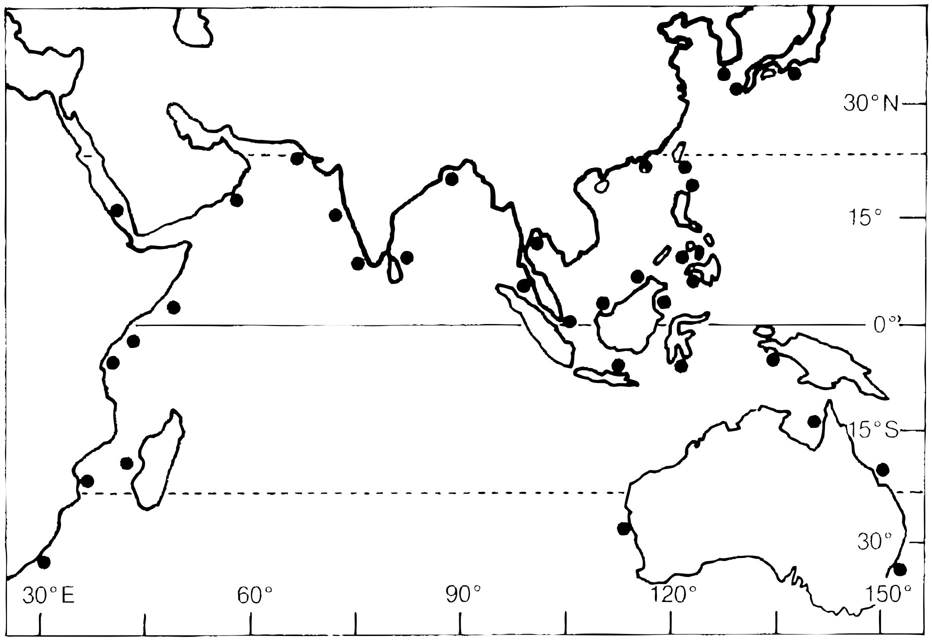

Fig. 2. Geographic distribution of *Penaeus monodon.*

meter. In still water, the eggs sink slowly to the bottom. The 2-celled, 4-celled, morula and embryonic nauplius stages develop approximately 0.5, 1, 1.8 and 11 hours, respectively, after spawning. Before hatching, the embryonic nauplius is observed to move intermittently inside the egg.

Larva (Figs. 5, 6). The larval stage of *P. monodon* consists of 6 nauplius, 3 protozoea, 3 mysis, and 3 or 4 megalopa substages, and the time required for each stage are about 1.5 days, 5 days, 4 to 5 days, and 6 to 15 days, respectively. Swimming is by antennal propulsion in the nauplius, antennal and thoracic propulsion in the protozoea, thoracic propulsion in the mysis, and abdominal propulsion in the megalopa. Occurring offshore, they are planktonic in behavior. The protozoea and mysis are collectively called zoea. Furthermore, the megalopa as well as earlier juvenile stages are called postlarvae traditionally or fry for commercial purposes. The body of the megalopa is transparent with a dark brown streak from the tip of the antennular flagellum to the tip of the telson. The 6th abdominal segment is relatively longer than the carapace length. The carapace length of the megalopa varies between 1.2 and 2.2 mm. *P. monodon* enters nursery grounds during the last substage of the megalopa.

Juvenile (Fig. 6). During the earlier juvenile stage, the body is partly transparent with a dark brown streak on the ventral side similar to the megalopa. For convenience, they are traditionally called postlarvae or fry in the earlier stage and fingerlings in later stages.

They differ from the megalopa as follows: relatively shorter 6th abdominal segment compared to the carapace length, greater body size, completion of rostral spines and gill system, and benthic behavior. The ratio of the length of the 6th abdominal segment to the carapace length is still greater (about 0.65) than that in the adolescent (about 0.58).

In the middle stage reaching about 2.7 mm in carapace length (CL), the body becomes blackish in color and the rostrum has 6 dorsal and 2 ventral spines. When it reaches about 3.7 mm CL, the body becomes more blackish and bulky and the rostrum has 7 dorsal and 3 ventral spines which is the same in adults. The carapace length varies from 2.2 to 11.0 mm. They crawl using pereopods and swim using pleopods; the former become the main locomotive organ and the latter may be regarded as supplementary and used for rapid movement, both functioning through to the adult stage in the same manner. Juveniles inhabit brackish water areas as nursery grounds.

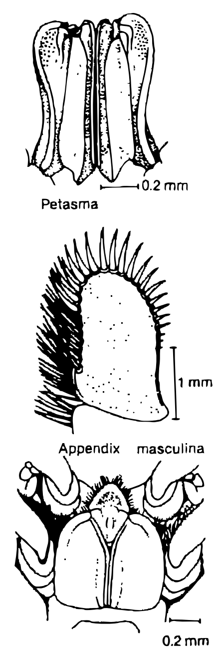

Fig. 3. Genital organ of *Penaeus monodon.*

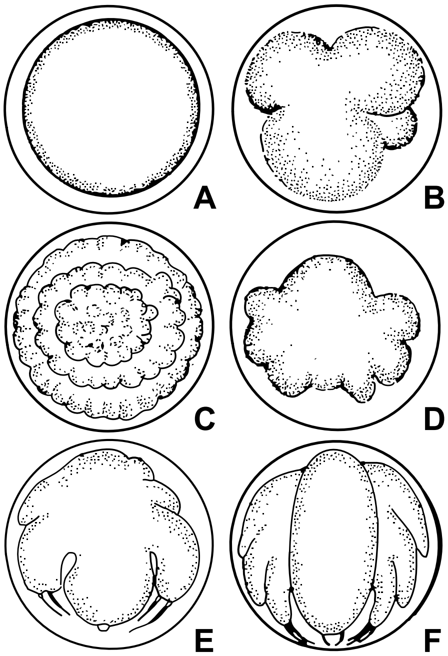

Fig. 4. Eggs of *Penaeus monodon* at various embryonic developmental stages. A: newly spawned egg; B: 4-cell stage (about 1 hr after spawning); C: morula stage (about 1.8 hr after spawning); D: early embryonic nauplius; E: late embryonic nauplius; F: embryonic nauplius immediately before hatching.

Adolescent. The body proportion is almost the same as that in the adult or slightly greater with the ratio of the length of about 0.58. The sexes can now be identified, beginning at 11 mm CL. The carapace length of the adolescent varies between 11 to 34 mm. The minimum size of males possessing a jointed petasma is about 30 mm CL, and the minimum size of females possessing adult-like thelycum is about 37 mm CL.

Subadult. This stage begins at the onset of sexual maturity i.e., minimum-sized males possessing spermatozoa in terminal ampoules, and minimum-sized females possessing spermatozoa inside the thelycum through copulation.

A sex size disparity occurs at almost 30 mm CL, and hereafter the size of females becomes greater than males. They migrate from nursery to spawning grounds. During this stage, first copulation takes place between males with minimum CL of 37 mm and females of 47 mm in the estuarine or inner littoral areas before migrating to deeper water.

Adult. This stage is characterized by the completion of sexual maturity. Males possess spermatozoa in the paired terminal ampoules, and in fact there are no sexual differences from Subadult males apart from size increment and different habitat. Females start to spawn mostly offshore, whereas some spawn in shallow water. A second and other copulations may occur in majority of individuals. Their major habitat is the offshore area at depths of about 160 m.

The maximum size of males recorded is 71 mm CL, whereas the maximum recorded length of females is 81 mm CL, reaching 270 mm in body length or 260 g in weight. Carapace length varies between 37 and 71 mm in males and 47 and 81 mm in females.

The life history phases of *P. monodon* are summarized in Table 1, and the diagram of its life history is shown in Fig. 7. As mentioned earlier, the nursery ground of the giant tiger prawn is in the estuaries which include wide brackish water rivers (mostly upstream and middle portion), mangrove swamps and interior portions of enclosed bays. These areas are exposed to wide fluctuations of physico-chemical conditions, such as water temperature and salinity, so that juveniles and adolescents should have high tolerance to those conditions for their survival. Within those nursery

Table 1. Life history phases of the giant tiger prawn, *Penaeus monodon.*

Phase	Begins at	Duration	Carapace length (mm) Male	Carapace length (mm) Female	Mode of life	Habitat
Embryo	Fertilization	12 hours	0.29[a]		Planktonic	Outer littoral area
Larvae	Hatching	20 days	0.5-2.2		Planktonic	Outer/inner littoral area
Juvenile	Completion of gill system	15 days	2.2-11.0		Benthic	Estuarine area
Adolescent	Stability of body proportion, development of outer genitalia	4 months	11-30[b]	11-37[c]	Benthic	Estuarine area
Subadult	Commencement of sexual maturity, first copulation	4 months	30-37[d]	37-47[e]	Benthic	Inner/outer littoral area
Adult	Completion of sexual maturity	10 months	37-71[f]	47-81[f]	Benthic	Outer littoral area

[a]Egg diameter, [b]Minimum size with jointed petasma, [c]Minimum size with adult-like thelycum, [d]Minimum size with spermatozoa in terminal ampoules, [e]Minimum size with spermatozoa in thelycum. [f]Maximum size ever found

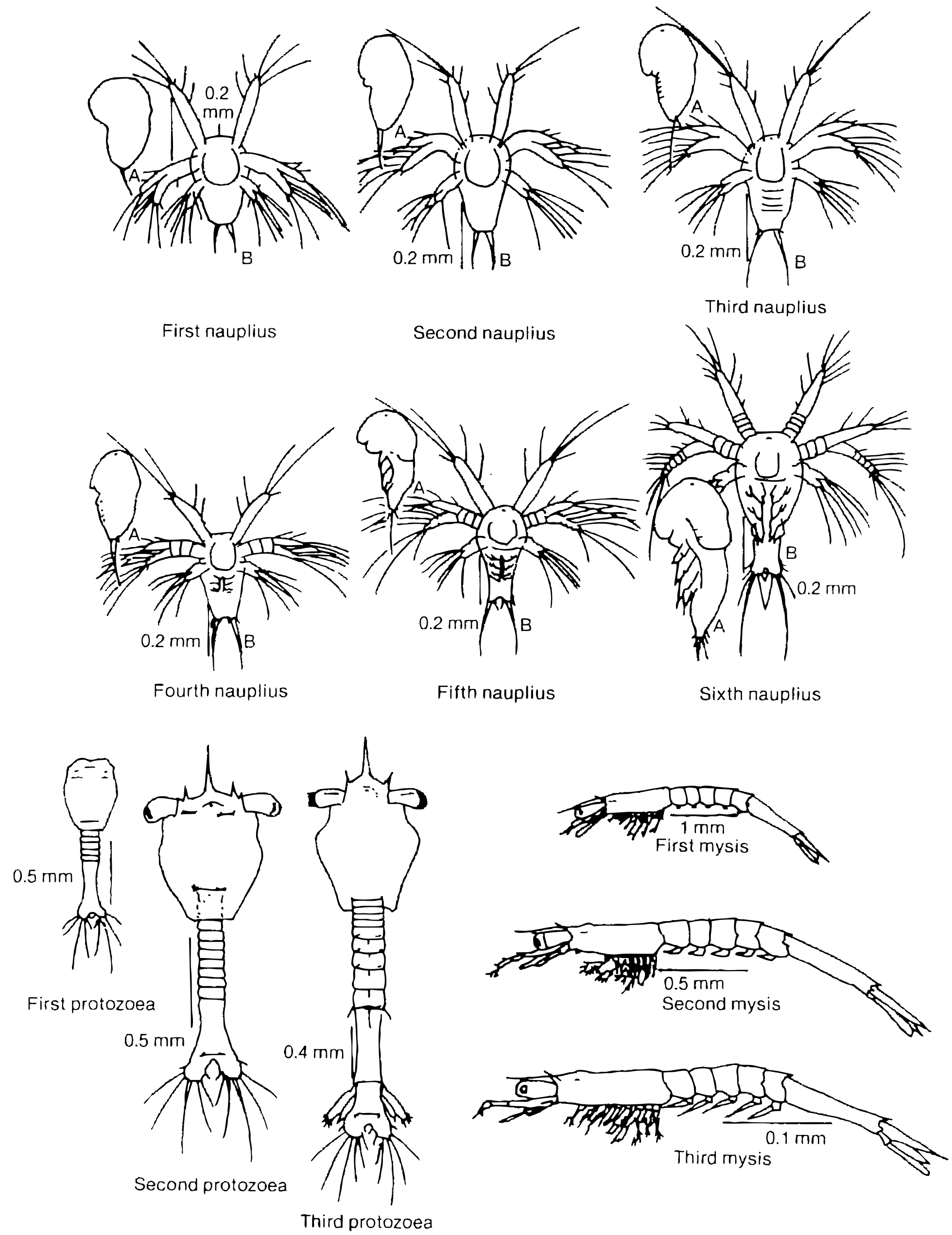

Fig. 5. Larval stages of *Penaeus monodon.* A, lateral view; B, ventral view.

grounds, however, the pressure of predators, particularly big finfishes, is generally not strong unlike in the open sea, and more nutrients are available. The mean monthly temperatures fluctuate between 26.3 and 31.2°C, and salinities between 20.0 and 28.9 ppt; both are extremely and suddenly decreased to about 20°C and 4 ppt, respectively, after a heavy rain.

Longevity

Based on data from pond-rearing experiments and size composition of wild specimens, the longevity of *P. monodon* is arbitrarily estimated to be about one and a half years for males and about two years for females. The higher female to male ratio of 1.5 in offshore waters compared to 1.0 in the nursery areas may be a result of the greater longevity of the female. However, more studies on this aspect are highly needed.

Mating*

Mating generally takes place at night, following molting of the female. The courtship and mating behavior may be observed in three distinct phases (Primavera, 1979):

Phase 1: Female above-male below in parallel swimming (Fig. 8A). From a moving or stationary position on the tank

*Descriptions and figures are all cited from Primavera (1979).

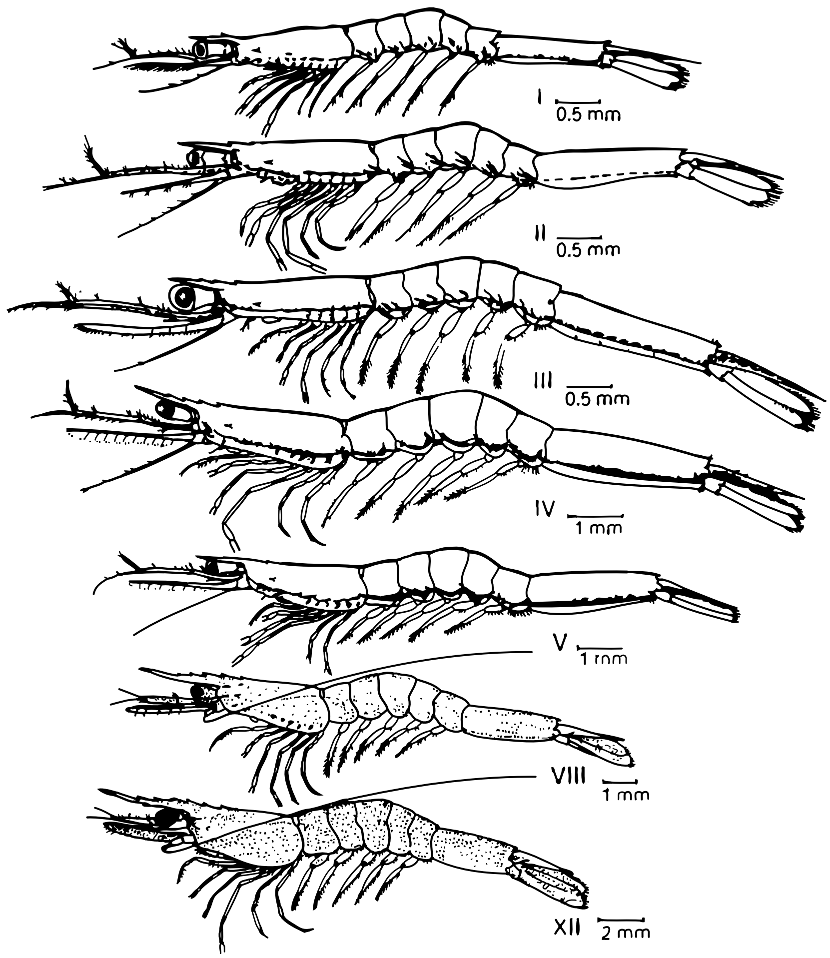

Fig. 6. Morphological development of megalopa (I-III) and juvenile (IV-XII) of *Penaeus monodon.*

bottom, the female swims upwards to a height of 20-40 cm. It moves in a slightly curved line over a distance of 50-80 cm, then changes course, either completely reversing direction or turning at a right angle. These swimming movements are interspersed with rests on the bottom lasting from seconds to a few minutes. While either swimming or resting, the female is approached by one to as many as three males after some kind of initial attraction, the males trailing behind the female as it swims. Eventually the male, or one particular male, in case of many initially attracted to the female, catches up with the female and positions its body directly below the latter. The pereopods of the female hold on to the carapace of the male and help to keep it in position while swimming continues; even later, the pereopods of both partners actively help to maintain the desired positions in the succeeding phases. This phase is the longest and can last up to 2 hours if the male is dislodged from its position below the female by another male or if lengthy rests on the tank bottom intersperse with the swimming activities. It may be as quick as 20 minutes if the male immediately attains the position described in phase 2 below.

Phase 2: Male turns ventral side up and attaches to female (Fig. 8B). Swimming in tandem with the female, the male turns abruptly to a ventral side up position, attempting to align the thoraco-abdominal junction with the posterior thorax of the female. Once the ventral-to-ventral position is achieved, it is difficult for other males to displace the first male and copulation is certain. If unsuccessful, the male immediately returns to the former upright position, still trying to swim parallel to the female, following the latter's every change in direction.

Phase 3a: Male turns perpendicular to female (Fig. 8C). Once the male succeeds in attaching ventrally to the female, it turns perpendicular to the latter, rotating at the point of the posterior end of the thorax. At this junction, the pair may either maintain their position in the water or slowly settle to the bottom.

Phase 3b: Male arches body around female and flicks head and tail (Fig. 8D). Immediately after assuming a position perpendicular to the female, the male curves its body in a U-shape around the thorax of the female and flicks both head and tail simultaneously, as in a squeezing action, up to three times in quick succession. Soon after, the male separates from the female and moves or swims away. The female may also move away.

Progress from ventral attachment (phase 2) to head- and tail-flicking (phase 3b) is very quick, lasting a few seconds. The whole process from the initial upward swimming move-

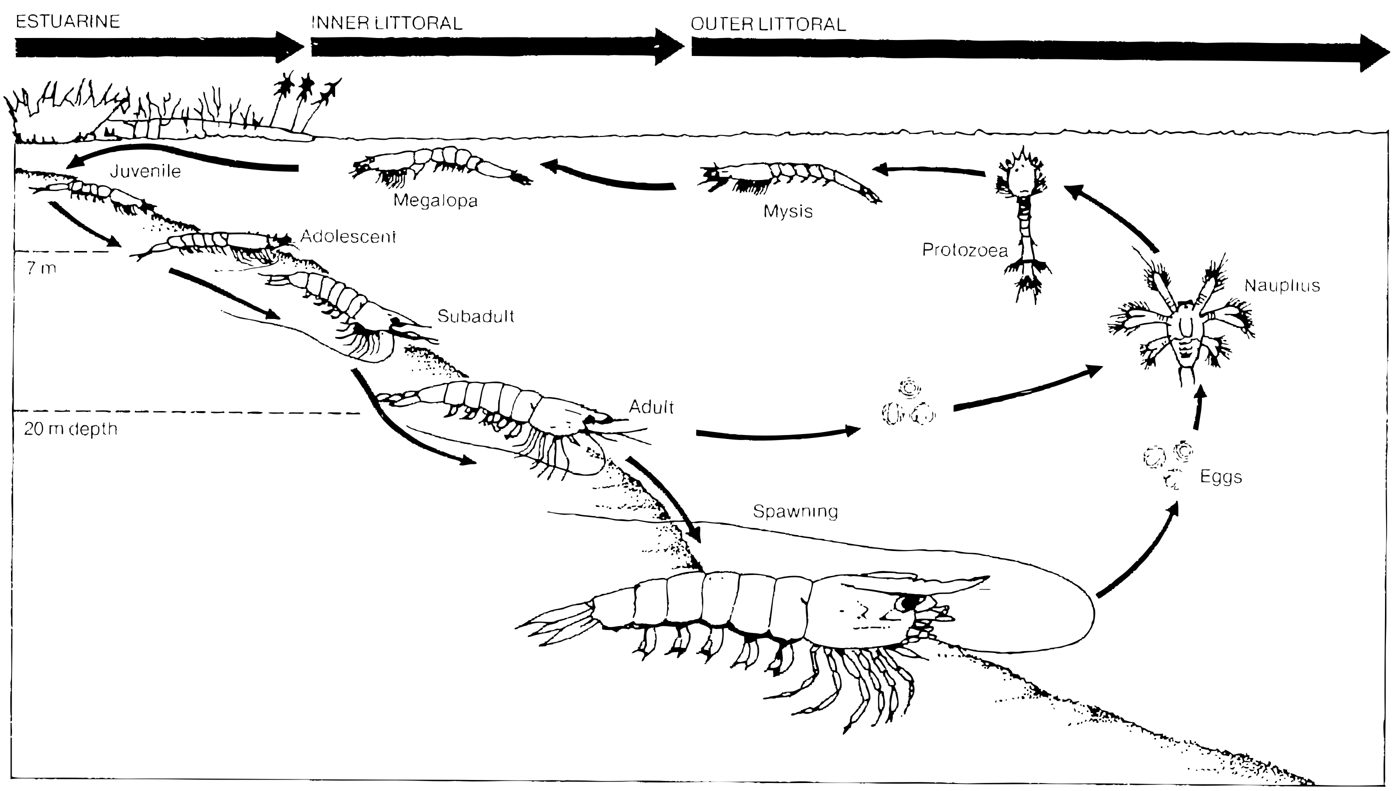

Fig. 7. Diagrammatic representation of the life history of *Penaeus monodon.*

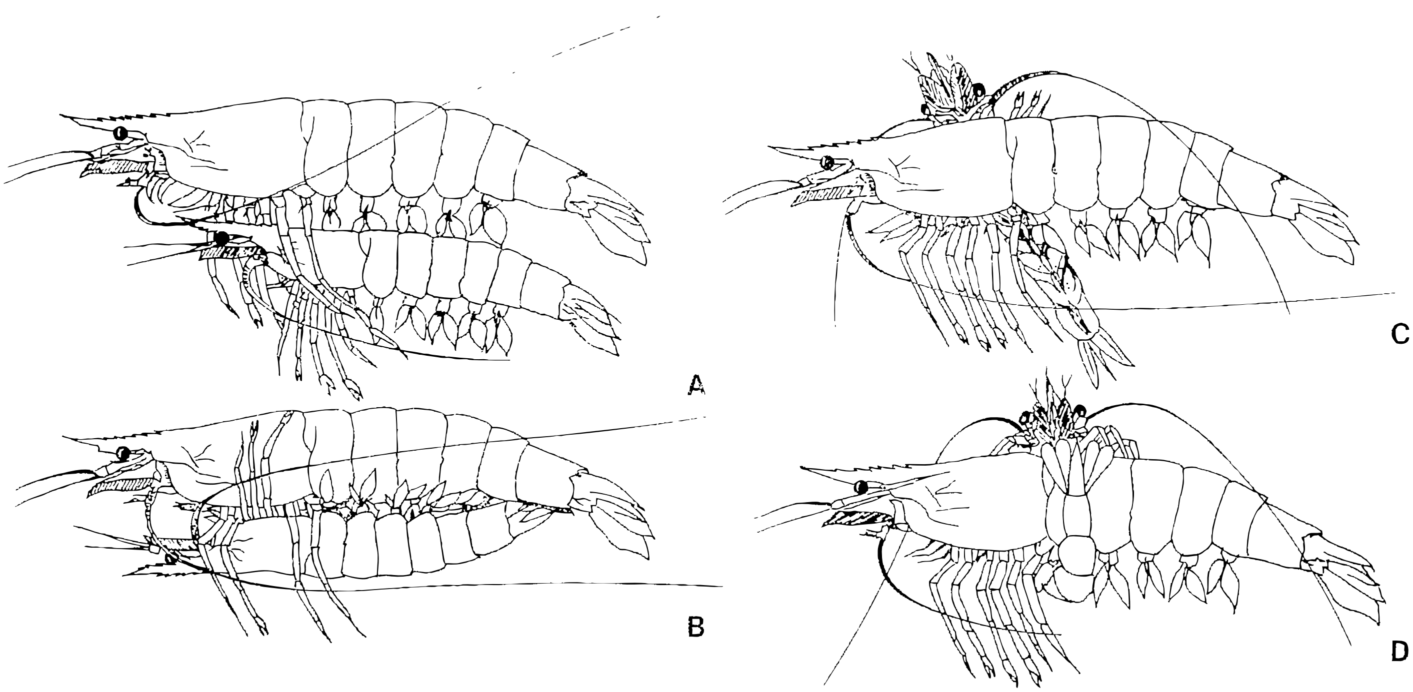

Fig. 8. Courtship and mating behavior of *Penaeus monodon.* A: Female above-male below in parallel swimming (phase 1); B: Male turns ventral side up and attaches to female (phase 2); C: Male turns perpendicular to female (phase 3a); D: Male curves body around female and flicks head and tail simultaneously (phase 3b) (Primavera, 1979).

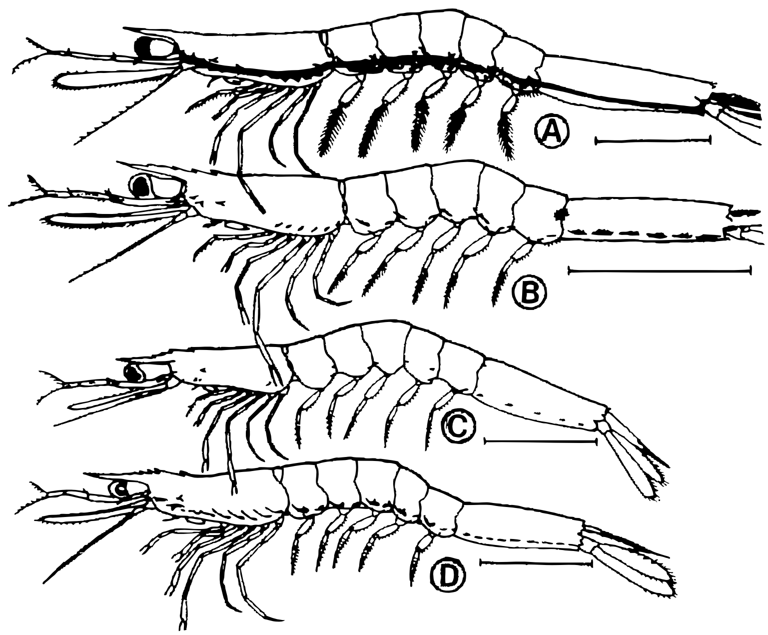

Fig. 9. Lateral view of *Penaeus* postlarvae showing chromatophore patterns. A: *P. monodon*; B: *P. semisulcatus*; C: *P. merguiensis* group; D: *P. japonicus* group. Scales represent 2 mm.

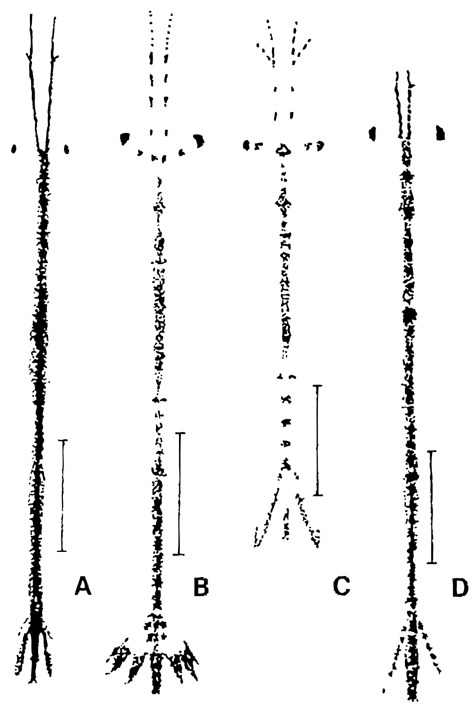

Fig. 10. Dorsal view of *Penaeus* postlarvae showing chromatophore patterns for quick identification. A: *P. monodon*; B: *P. semisulcatus*; C: *P. merguiensis* group; D: *P. japonicus* group. Scales represent 2.5 mm.

ments of the female to the separation of the pair may last from half an hour to 3 hours.

Spawning

Spawning generally takes place at night. While resting on the sandy bottom, the spawner suddenly becomes active, swimming in the water for about one minute, and then starts to spawn while swimming very slowly in the upper or middle part of the water. During spawning, the last three pairs of pereopods are held tightly together and flapped with an open and close movement, presumably to help discharge eggs and spermatozoa, while strongly moving the pleopods for swimming. The eggs are extruded from the paired genital pores located at the base of the 3rd pereopods at the same time as spermatozoa from the thelycum located at the base of the 5th pereopods, looking like greenish smoke and whitish smoke, respectively, blowing backward. It is believed that these discharged eggs are fertilized in the water owing to turbulence generated by the forward and backward movements of the pleopods. As a result, the movement of the pleopods seems to aid not only in swimming but also in fertilizing the eggs spawned. The fertilized eggs remain suspended in the water for a few minutes making the water turbid, and then gradually sink to the bottom. The time required for each spawning is approximately 2 minutes.

Fecundity

The carapace of spawners varies from 53.1 to 81.3 mm, and the number of eggs from 248,000 to 811,000. It may be said that the number of eggs spawned increases with carapace length.

Food and feeding habit

The food of *P. monodon* consists mainly of crustacea (small crabs and shrimps) and mollusks, making up 85% of ingested

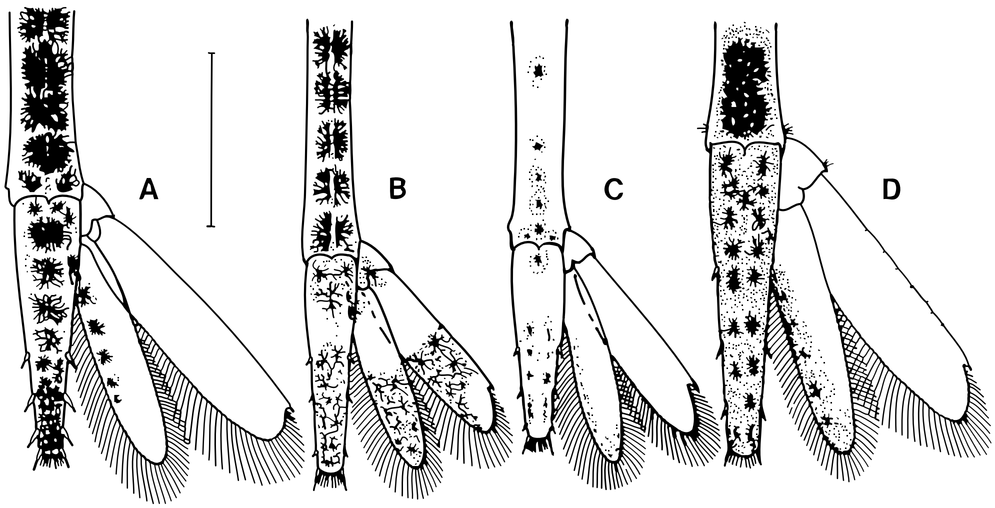

Fig. 11. Dorsal view of the 6th abdominal segment, telson and uropods of *Penaeus* postlarvae showing chromatophore patterns. A: *P. monodon;* B: *P. semisulcatus;* C: *P. merguiensis* group; D: *P. japonicus* group. Scale represents 1 mm.

food. The remaining 15% consists of annelids and others. *P. monodon* is more of a predator of slow-moving benthic macroinvertebrates rather than a scavenger or opportunistic in feeding habit. The feeding habit appears to be associated with the tidal phase (Marte, 1980).

Identification of postlarvae (fry)

It has been observed that fry collectors and concessionaires sometimes mistakenly identify the postlarvae of *P. monodon*. However, identification of the postlarvae can be made based on their morphological characteristics such as shape of the rostrum, number of rostral teeth, relative length of antennular flagella, antennal spine, and presence of dorsal spinules on the 6th abdominal segment. The chromatophore patterns on the 6th abdominal segment and on the telson and uropods are also useful (Figs. 9-11, keys).

Key to the postlarval *Penaeus* appearing at shore waters, based on morphological features

1) Rostrum stout and inferior to tip of eye, spinules on the 6th abdominal segment present[a], antennal spine prominently present, carapace slightly longer than 6th abdominal segment.................................... *P. japonicus* group

   Rostrum slender and exceeding tip of eye, spinules on the 6th abdominal segment absent, antennal spine absent or minute, carapace slightly or distinctly shorter than 6th abdominal segment..2

2) Inner (lower) antennular flagellum nearly 1.6 times the outer (upper), exceeding the latter by its distal one segment.. *P. merguiensis* group

   Inner antenullar flagellum 1.6 to 2.0 times the outer, exceeding the latter by its distal two segments .... *P. semisulcatus*

   Inner antennular flagellum more than 2.0 times the outer, exceeding the latter by its distal three segments .... *P. monodon*

[a]When the number of rostral teeth is less than four, the spinules are sometimes poorly present or absent. In this case, other criteria are useful.

Key to the postlarval *Penaeus* appearing at shore waters, based on chromatophore patterns

1) Number of chromatophores on the 6th abdominal segment less than seven. Anterolateral chromatophore of the 6th abdominal segment present.................................... .... *P. merguiensis* group

   Number of chromatophores on the 6th abdominal segment more than seven. Anterolateral chromatophore of the 6th abdominal segment present or absent..............2

2) Number of chromatophores on the 6th abdominal segment less than 12. Anterolateral chromatophore of the 6th abdominal segment present, chromatophores on the middle portion of telson and inner uropods absent .... *P. semisulcatus*

   Number of chromatophores on the 6th abdominal segment more than 12. Anterolateral chromatophore of the 6th abdominal segment absent, chromatophores on the middle portion of the telson and inner uropods present..3

3) Chromatophores on the 6th abdominal segment dense and thickly continuous.................................. *P. monodon*

   Chromatophores on the 6th abdominal segment discontinuous or confluent.............................. *P. japonicus* group

Recommendations

For the conservation of the nursery grounds and for increasing production of the giant tiger prawn, the following are recommended:

a) Avoid conversion of nursery grounds (brackish water areas) into fishponds or human settlement areas.
b) Ban spreading of chemicals for killing predators in fishponds and nursery grounds.
c) Introduce postlarval *P. indicus* as well as *P. merguiensis* into prawn ponds in addition to *P. monodon* for their cultivation.
d) Keep statistical data on the population of fry and adults of *P. monodon* and other penaeids in relation to their habitat and growth stages.
e) Artificial fertilization to utilize dead or weak spawners and genetic study to produce more suitable prawns might be necessary in the near future.

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