

## Chapter One

### BIOLOGY AND ECOLOGY

Noel B. Solis\*

For the culture of any species to evolve from tradition or art to science, basic information on the biology of the species is required.

This paper reviews current information on *Penaeus monodon* including taxonomy, morphology, distribution, and bionomics and life history. The last covers reproduction, development of embryo, larva up to adult, spawning, food and feeding, and physiology.

Problems that have cropped up with the intensification of prawn culture, e.g. discharge of pesticides from grow-out ponds, are highlighted. Other conflicts such as the conversion of mangroves and other estuaries, considered nursery grounds of various marine fauna including *P. monodon*, into fishponds; overexploitation of wild spawners with no stock assessment data; and indiscriminate throwing away of other prawn and finfish fry from wild collections in favor of *P. monodon* fry could adversely affect the ecology of mangroves and other marine ecosystems.

### TAXONOMY

The genus *Penaeus* Fabricius (1798) was placed on the Official List of Generic Names in Zoology as Name No. 498 upon the discovery and description of *Penaeus monodon* by John Christ Fabricius in 1798 (Mohamed 1970). With the revision of the specific name *monodon* by Holthuis, the two species have become stabilized and the name *P. monodon* is generally accepted for the present species (Hall 1961, Mohamed 1970, Motoh 1981). No subspecies are currently recognized for this species and *P. monodon manillensis* (Villaluz and Arriola 1938) proved to be based on an abnormal specimen of *P. semisulcatus* (Mohamed 1970, Motoh 1981).

---

\*Research Associate of SEAFDEC Aquaculture Department

## Definition

The taxonomic definition of the giant tiger prawn is as follows:

Phylum Arthropoda

Class Crustacea

Subclass Malacostraca

Order Decapoda

Suborder Natantia

Infraorder Penaeidea

Superfamily Penaeoidea

Family Penaeidae Rafinesque, 1815

Genus *Penaeus* Fabricius, 1798

Subgenus *Penaeus*

Species *monodon*

Scientific name: *Penaeus (Penaeus) monodon* Fabricius, 1798.

It has four synonyms:

*Penaeus carinatus* Dana, 1852

*P. caeruleus* Stebbings, 1905

*P. monodon* var. *manillensis* Villaluz

and Arriola, 1938

*P. bubulus* Kubo, 1949

The FAO names are giant tiger prawn (English), crevette geante tigre (French), and camaron tigre gigante (Spanish).

The term shrimps and prawns are common English names used synonymously due to the absence of systematic basis to mark a distinction (Wickins 1976, Holthuis 1980). In an attempt to clarify the issue, Holthuis (1980) traced the origin of the names shrimps and prawns and its usage in various countries. In general, shrimps refer to the smaller animals and prawns to the larger ones, while according to Food and Agriculture Organization (FAO) Convention, shrimps refer to marine

penaeids while prawns refer to freshwater palaemonids. In the present view, the term prawn will be used following the accepted usage at SEAFDEC Aquaculture Department.

Considerable taxonomic works on the Penaeidae have been published throughout the world, many providing detailed information to interested workers. Motoh (1977) also compiled various common and vernacular names of commercially important penaeid prawns and shrimps.

For the identification of *P. monodon* postlarvae, Motoh and Buri (1981) published a key for penaeid postlarvae from Panay Island, Philippines; so did Prawirodihardjo et al (1975) in Indonesia, while Rao and Gopalakrishnan (1969) identified *P. monodon* and *P. indicus* juveniles in India.

## MORPHOLOGY

The morphological features of *P. monodon* have been described in detail by workers from various countries, among whom are Bate 1888; Blanco and Arriola 1937; Villaluz and Arriola 1938; Kubo 1949; Holthuis 1949; Racek 1955, 1957, 1972; Hall 1956, 1961, 1962; Dall 1957; Cheung 1960; Racek and Yaldwin 1971; Motoh 1981; and Motoh and Buri 1984.

The following description includes important features sufficient for the identification of this species. The shell is smooth, polished, and glabrous. The rostrum extends beyond the tip of the antennular peduncle, is sigmoidal in shape, and possesses 6-8 dorsal and 2-4 ventral teeth, mostly 7 and 3, respectively. The carapace is carinated with the adrostral carina almost reaching the posterior margin 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 prominent and almost horizontal. The antennular flagellum is subequal to or slightly longer than the peduncle. Exopods are present on the first four pereopods but absent in the fifth. The abdomen is carinated dorsally from the anterior one-third of the fourth, to the posterior end of the sixth, somites. The telson has a median groove but without dorso-lateral spines. Figure 1 shows the various parts of *P. monodon* and the technical terms with taxonomic importance.

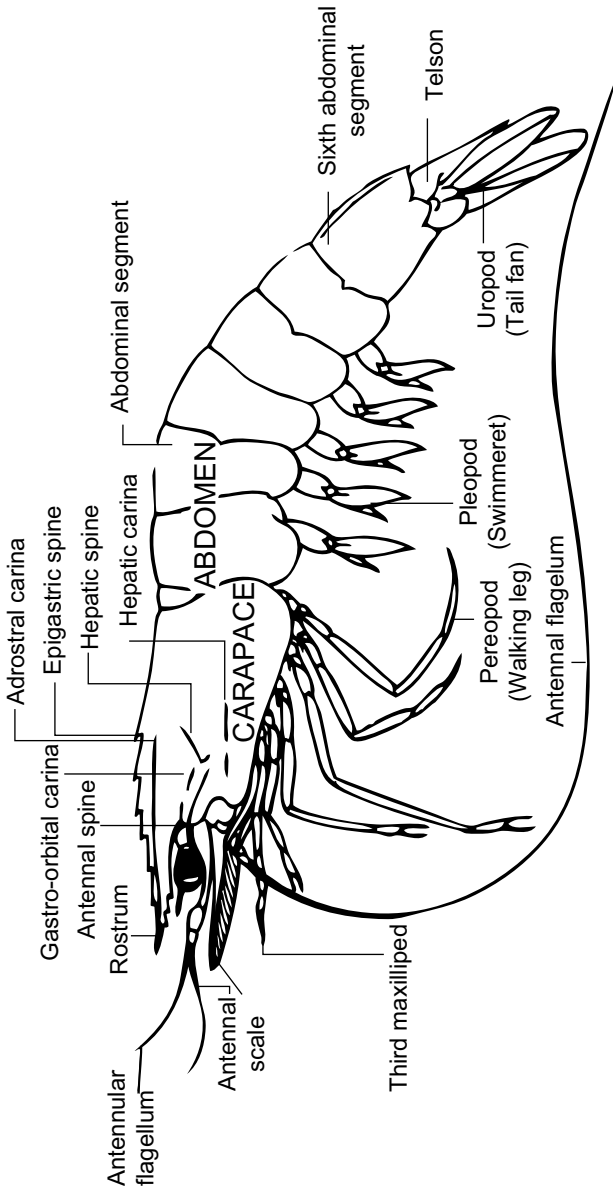


Fig. 1. Lateral view of *P. monodon* showing important parts (Motoh 1981)

A live giant tiger prawn has the following characteristic coloration: carapace and abdomen are transversely banded with red and white, the antennae are greyish brown, and the pereopods and pleopods are brown with crimson fringing setae. In shallow brackish waters or when cultured in ponds, the color changes to dark and, often, to blackish brown (Motoh 1981).

## DISTRIBUTION

The giant tiger prawn is widely distributed throughout the greater part of the Indo-Pacific region, ranging northward to Japan and Taiwan, eastward to Tahiti, southward to Australia, and westward to Africa (Racek 1955; Holthuis and Rosa 1965; Motoh 1981, 1985).

In general, *P. monodon* is distributed from 30°E to 155°E in longitude and from 35°N to 35°S in latitude with the main fishing grounds located in tropical countries, particularly Indonesia, Malaysia, and the Philippines (Motoh 1985, Figure 2).

The fry, juvenile, and adolescent inhabit shore areas and mangrove estuaries, while most of the adults inhabit deeper waters down to 162 m (Motoh 1985). Distribution is sparse as evidenced by a few prawns collected at any one time.

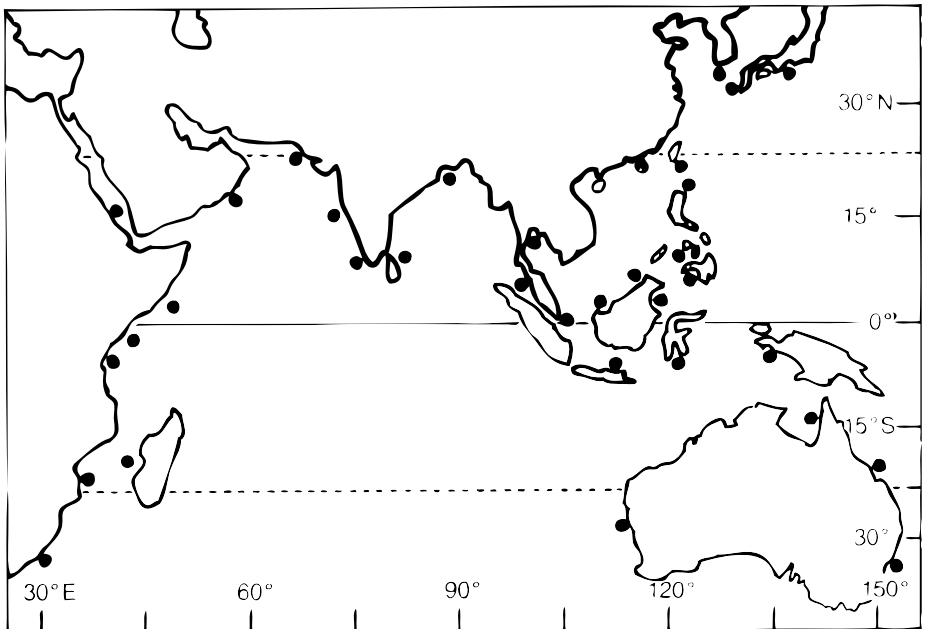


Fig. 2. Geographic distribution of *Penaeus monodon* (Motoh 1981)

## BIONOMICS AND LIFE HISTORY

### Reproduction

*P. monodon* is heterosexual. The female attains a relatively larger size than the male. The sexually mature prawn can be distinguished by the presence of the external genital organs: a joined petasma, a pair of appendix masculina on the exopods of the second pleopods, and a genital opening on the coxa of the fifth of pereopod for the male. In females, the thelycum is situated between the fourth and fifth pereopod with the genital opening on the coxa of the third pereopod.

The reproductive system of male and female *P. monodon* is shown in Figure 3. The following description is based on the studies of Motoh (1981, 1985).

*Male genital organ.* The internal reproductive organ of the male consists of paired testes, vasa deferentia, and terminal ampoules located in the cardiac region dorsal to the hepatopancreas. The testis is translucent and composed of six lobes, each connected in the inner margins leading to the vas deferens. The vas deferens consists of four portions, namely: the short narrow proximal vas deferens, a thickened larger median portion or the medial vas deferens, the relatively long narrow tube as the distal vas deferens, and the muscular portion referred to as terminal ampoule. The terminal ampoule contains the spermatophore and opens at the base of the coxopod of the fifth pereopods.

The spermatozoa of *P. monodon* are minute globular bodies composed of the head of about 3 microns in diameter and a short spike.

The petasma is a pair of endopods of the first pleopods formed by the interlocking hook-like structures. The appendix masculina is oval and is located on the endopod of the second pleopod.

*Female genital organ.* The internal reproductive organ of the female consists of paired ovaries and oviducts. The ovaries are bilaterally symmetrical, partly fused, and extend almost the entire length of the mature female. It is composed of the anterior lobe located close to the esophagus and the cardiac region of the stomach; the lateral lobes located dorsal to the

hepatopancreas; and the abdominal lobe which lies dorso-lateral to the intestine and ventro-lateral to the dorsal abdominal artery. The oviducts originate at the tips of the sixth lateral lobe and lead to the external genital opening at the coxopods of the third pair of pereopods.

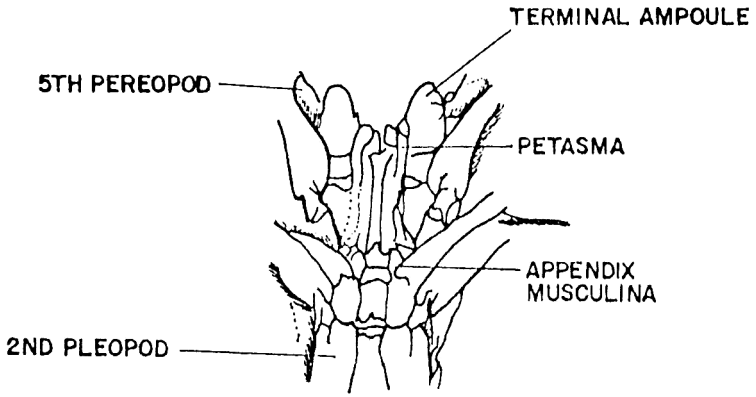
The thelycum, located between the fifth pair of pleopods, consists of an anterior and a pair of lateral plates. It receives the spermatophores during mating. In penaeids, the thelycum may be classified as closed or open type, and *P. monodon* belongs to the closed type.

Motoh (1981) compared the detailed internal reproductive organs of *P. monodon* with those of *P. setiferus* and *P. indicus*.

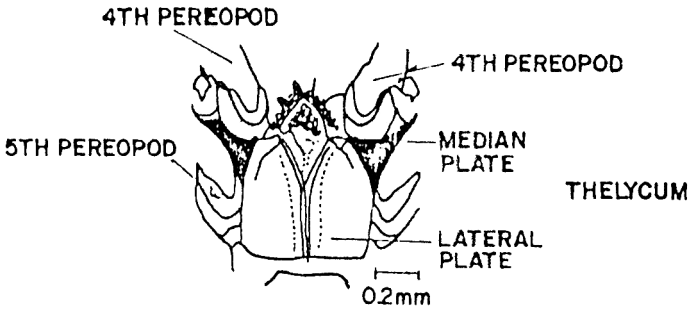
*Sexual maturity.* Motoh (1981) defined sexual maturity as the minimum size at which spermatozoa are found inside the terminal ampoule of the males and inside the thelycum in the females. The later indicates that copulation or the transfer of spermatophores from the male to the thelycum of the female has taken place. On this basis, Motoh (1981) reported that wild *P. monodon* males possess spermatozoa at 37 mm carapace length (CL) (about 35 g body weight or BW) and females at 47 mm CL (about 67.7 mm BW) although pond-reared prawns were mature only at 31 mm CL (about 20 g BW) and 39 mm CL (about 41.3 g BW), respectively. Primavera (1980) reported the presence of spermatozoa in both pond-reared and wild *P. monodon* males of 40 g body weight (38.5 mm CL), a minimum of 63 weight (about 46 mm CL) for wild females, and about 40 g body weight (41 mm CL) for pond-reared prawns.

From the viewpoint of reproduction, Primavera (1985) emphasized the importance of gonadal maturation and the presence of fully developed spermatozoa with tail or spike. Motoh (1981) reported that sperms without tail were observed in wild *P. monodon* males of smaller size or about 37 mm CL, while Primavera (unpubl.) recently made mention of 10-month old pond-reared *P. monodon* with immature (spikeless) sperm.

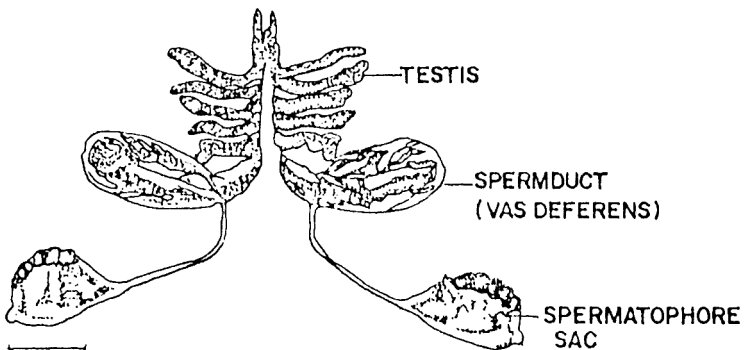
*Ovarian maturation stages.* The maturation of the ovary has been categorized into five stages, the classification of which is based on ovum size, gonad expansion, and coloration (Villaluz et al 1969, Primavera 1980, Motoh 1981, Tan-Fermin and Pudadera, in press). Figure 4 illustrates the stages of ovarian development in *P. monodon*.



EXTERNAL GENITALIA OF MALE



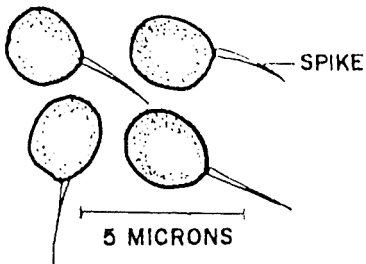
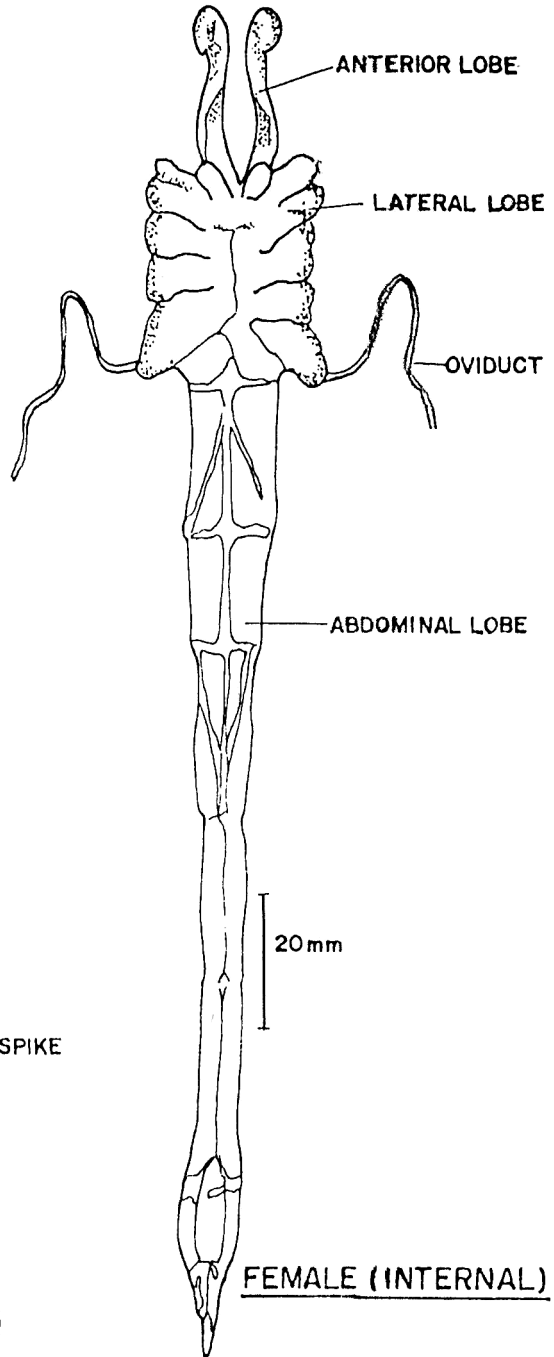
EXTERNAL GENITALIA OF FEMALE



MALE (INTERNAL)

Fig. 3. Reproductive system of *Penaeus monodon* (Motoh 1981)





MATURE SPERMATOZOA  
( X 200 magnification)

FEMALE (INTERNAL)

*Stage I and V (undeveloped and spent stages).* Ovaries are thin, transparent, and not visible through the dorsal exoskeleton. Histological studies show that the ova averaging 36 microns are covered with a layer of follicle cells and the larger ones have nucleus and yolk granules (Motoh 1981). Tan-Fermin and Pudadera (in press) described Stage I as the perinuclear stage composed of perinuclear oocytes (46-72 microns) negatively stained with AB-PAS and Sudan Black. Oocytes bigger than 55 microns are enveloped by a single layer of follicle cells.

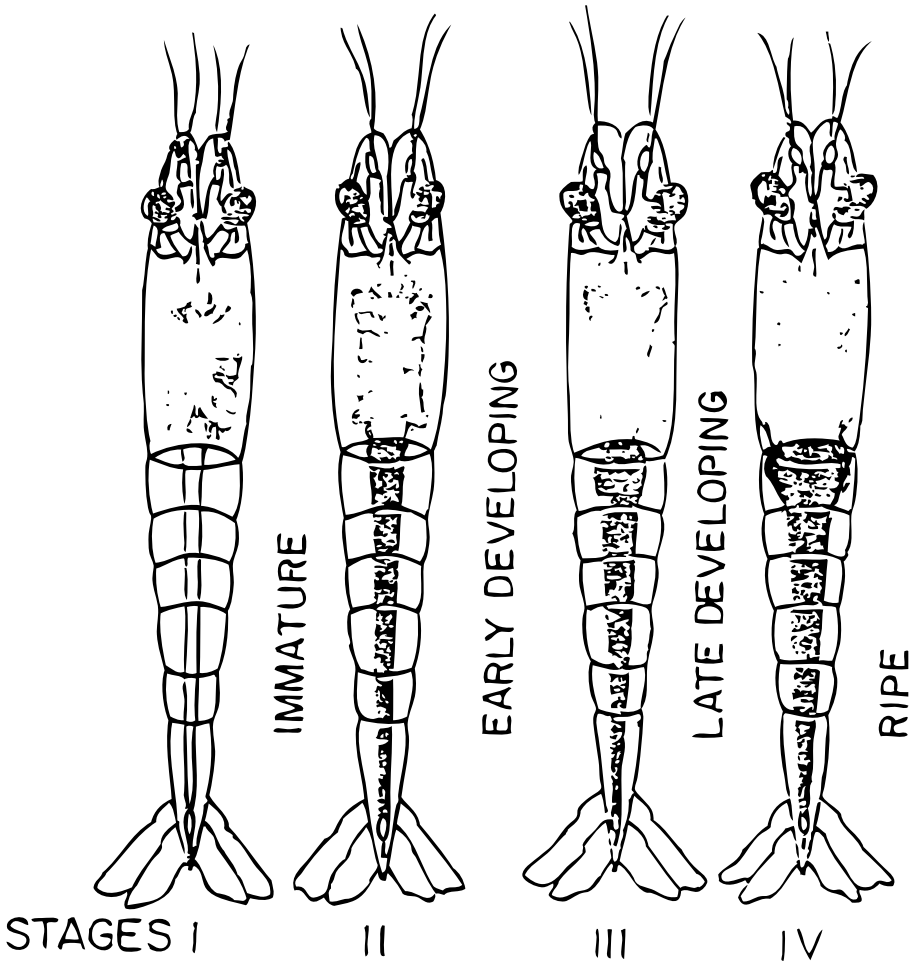


Fig. 4. External appearance of the ovaries of *Penaeus monodon* at different stages of maturity as seen through the dorsal exoskeleton (modified from Primavera 1983)

Similar features are observed in the spent stage which also contains some yolky oocytes, thicker follicle layer, or irregularly shaped perinucleolar oocytes (Tan-Fermin and Pudadera in press).

*Stage II (developing stage).* Referred to as early maturing stage, the ovaries are flaccid and white to olive green in color, and discernible as a linear band through the exoskeleton. The developing ova averaging 177 microns in diameter have yolk granules and cells believed to be nutritive bodies (Motoh 1981). The cells referred by Tan-Fermin and Pudadera (in press) as cytoplasmic inclusions are composed of small granules of glycoproteins, medium-sized globules of lipoglycoproteins, and few large lipid droplets.

*Stage III (nearly ripe stage).* Ovaries have glaucous color with the anterior portion thick and expanded. They are very visible through the exoskeleton, particularly at the first abdominal segment, when viewed against the light (Motoh 1981, Tan-Fermin and Pudadera, in press). The ova average 215 microns in diameter.

*Stage IV (ripe stage).* The ovary classified as ripe (mature) stage is diamond-shaped, expanding through the exoskeleton of the first abdominal segment. The isolated ovary appears dark olive green, filling up all the available space in the body cavity (Primavera 1980). Motoh (1981) reported the presence of a characteristic margin of peripheral rod-like bodies, the apexes of which radiate from the center of the egg. The ova average 235 microns in diameter. Tan-Fermin and Pudadera (in press) characterized this stage to consist mostly of yolky oocytes (288-408 microns) with additional rod-like bodies which contain acid and basic mucopolysaccharides but without lipids.

In some cases, ovaries are observed to be discontinuous, i.e., white in color in either the anterior or posterior portions with olive green color in the opposite ends. This condition is referred to as partially spent ovaries.

At present, these categories are used in the selection of wild spawners and prove to be generally effective. Prawns of Stage IV are used in hatchery operations. In the field, handling of the prawn for visual observation of the ovary color, size, and shape can not be avoided and can be stressful to the animal.

*Fecundity.* The number of eggs spawned varies according to the condition of the spawning female. Estimate of fecundity is mostly undertaken in the laboratory by counting the eggs from aerated spawning tanks.

For wild spawners of *P. monodon*, Motoh (1981) reported 248 000 to 811 000 eggs/spawn. Primavera (1985) mentioned that several researchers have observed lower fecundity. For captive and ablated females, fecundity ranges from 60 000 to 600 000 eggs/spawn because of small body size and uneven development of ovaries. Further detailed discussion on the subject is referred to Primavera (this volume).

In general, larger females produce more eggs than smaller females (Motoh 1981, Primavera 1985, Villegas et al 1986).

## **Morphological Development**

*Embryo.* Eggs are spherical, yellowish green, and very minute, having a diameter ranging from 0.27 to 0.31 mm with an average of 0.29 mm. Eggs tend to sink slowly in still waters. Cleavage to 2-celled, 4-celled, morula, and embryonic nauplius stages occur approximately 0.5, 1, 1.8, and 11 hours, respectively, after spawning (Figure 5). The nauplius in each egg is observed to move intermittently before hatching (Villaluz et al 1969; Kunvankij 1976; Motoh 1979, 1981, 1985).

With significance in hatchery operations, Primavera and Posadas (1981) classified the eggs of *P. monodon* based on morphological criteria and hatching rates.

*Larva.* The larval stage consists of 6 nauplius, 3 protozoa, 3 mysis, and 3 or 4 megalopa substages, requiring about 1.5 days, 5 days, 4-5 days, and 6-15 days, respectively, for development (Villaluz et al 1969; Kunvankij 1976; Motoh 1979, 1981, 1985). Figure 6 illustrates the larval stages of *P. monodon*. Larvae exhibit planktonic behavior offshore with antennal propulsion for swimming in nauplius, antennal and thoracic propulsion in mysis, and abdominal propulsion in megalopa. While the nauplii utilize yolk granules within their body, feeding starts in protozoa and mysis (collectively called zoea) substages. The megalopa with the earlier juvenile stage (traditionally called postlarva or "fry" for commercial purpose) is transparent with, dark brown streak on the ventral side tip of

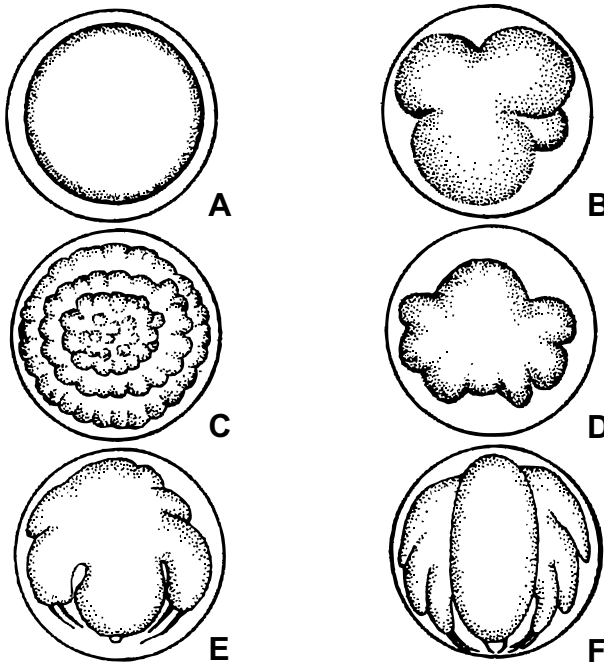
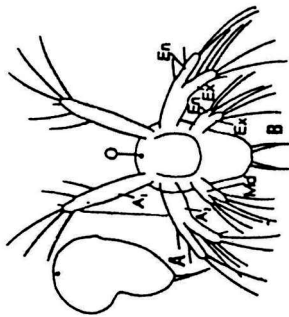


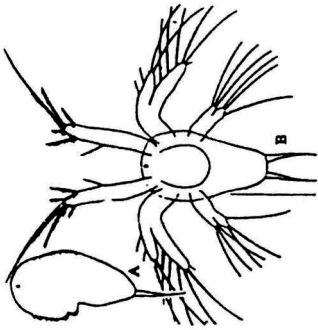
Fig. 5. Eggs of *P. monodon* at various embryonic developmental stages. (A) newly spawned eggs, (B) 4-cell stage (about one hour after spawning), (C) morula stage (about 1.8 hours after spawning), (D) early embryonic nauplius, (E) late embryonic nauplius, (F) embryonic nauplius about to hatch (Motoh 1981)

the antennular flagellum to the tip of the telson. Under laboratory conditions, postlarvae become benthic on the sixth day of the post-larval stage. In natural conditions, the megalopa enters the nursery ground. The carapace length of megalopa varies between 1.2 and 2.3 mm.

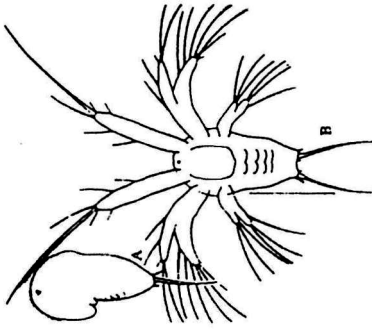
*Juvenile.* The earlier juvenile stage has transparent body with dark brown streak on the ventral side as in the megalopa. Motoh (1985) described the earlier juvenile stages as follows: (1) relatively shorter sixth abdominal segment compared to the carapace length, (2) greater body size, (3) complete rostral spine formula, (4) complete gill system, and (5) benthic behavior.



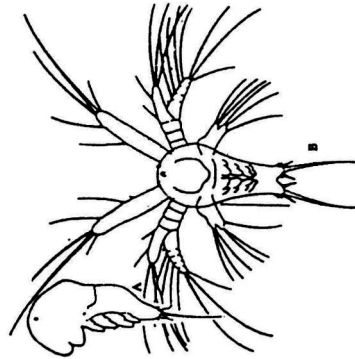
First nauplius, lateral (A) and ventral (B) views. A<sub>1</sub>, first antenna; A<sub>2</sub>, second antenna En, endopod; Ex, exopod; Md, mandible; O, ocellus.



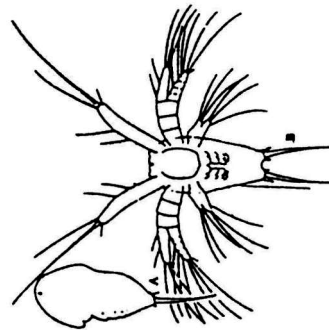
Second nauplius



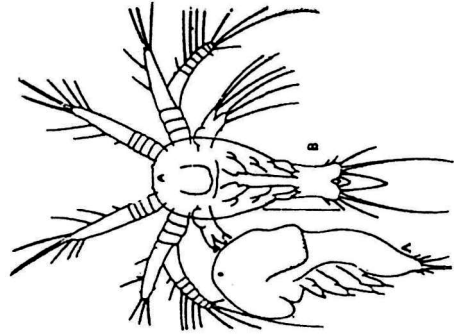
Third nauplius



Fifth nauplius



Fourth nauplius



Sixth nauplius

(Scales represent 0.2 mm.)

Naupliar Substages

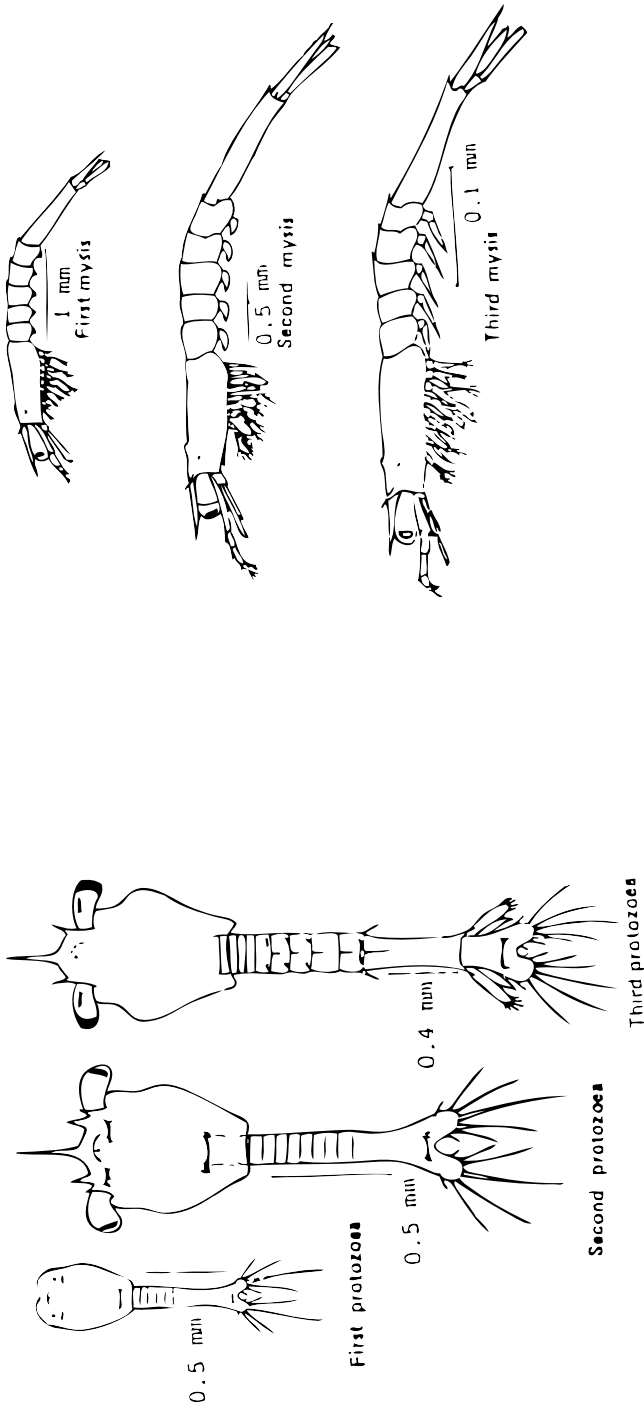


Fig. 6. Larval stages of *P. monodon* (Motoh 1981, 1985)

Substages of Mysis

Protozoal Substages

In the later stage, the body becomes blackish in color and bulky, and the rostrum has 7 dorsal and 3 ventral spines. The juvenile crawls using the pereopods and swims using the pleopods as in adults. The carapace length varies from 2.2 to 11.0 mm.

Motoh (1981, 1985) and Motoh and Buri (1980, 1981) have described the early postmysis stages of the giant tiger prawn.

*Adolescent.* This stage resembles the adult prawn. Sexes are now distinct beginning at 11 mm CL. The minimum size of males possessing a jointed petasma is about 30 mm CL and the minimum size of females possessing adultlike thelycum is about 37 mm CL. The carapace length of the adolescent varies between 11 and 34 mm.

*Subadult.* This stage is the onset of sexual maturity. The male possesses spermatozoa in its terminal ampoules. The thelycum of the female now contains spermatozoa. At this stage (30 mm CL), females grow faster and migration from nursery to spawning grounds begins. In the course of migration, first copulation takes place between males and females having a minimum of 37 mm and 47 mm CL respectively.

*Adult.* This stage has appendages very similar to the subadult and is characterized by the completion of sexual maturity. It differs only with the subadult in size and habitat. Males possess spermatozoa, and females start to spawn offshore although a few spawn in shallow water. A second or more copulations may occur in majority of the species. Major habitat is the offshore area up to about 160 m depth.

The maximum total length recorded was 336 mm (Holthuis 1980), while a mature female of 307 mm from Madagascar was reported by Crosnier (1965) as cited by Mohamed (1970) and 330 mm total length by Racek (1972). In the Philippines, the largest male ever found was 71 mm CL while the female was 81 mm CL with 270 mm body length or 240 g weight (Motoh and Buri 1980). Carapace lengths of adults vary between 37 and 71 mm in males and 47 and 81 mm in females.

The life history phases of the giant tiger prawn are summarized in Table 1, and the diagram of the life history is shown in Figure 7.



## Longevity

There is no reliable method developed to determine the age of an individual prawn. Villaluz et al (1969) believed that the life span of *P. monodon* is one to two years; Motoh (1981) estimated it to be about one and a half years for males and about two years for females. Mohamed (1970) cited Srivatsa (1953) who reported that the life span of prawns (including *P. monodon*) in the Gulf of Kutch is 12-14 months.

## Spawning

Spawning is the release of eggs and spermatozoa by the female prawn into the water for fertilization. The spermatophore which contains the spermatozoa is deposited in the female thelycum during copulation long before spawning. Although there is no report on the actual process observed in the natural condition, the spawning behavior of *P. monodon* has been documented based on laboratory observations (Villaluz et al 1969, Aquacop 1977, Primavera 1980, Motoh 1981). Discussion on spawning behavior is described in detail by Primavera (this volume).

In the Philippines, Villaluz et al (1969) reported that no *P. monodon* spawners below 50 mm CL have been collected in the Panguil Bay area, and concluded that first spawning occurs at 56 mm CL. However, Motoh (1981) reported that spawning females ranged from 47 to 81 mm CL and came in four size groups, namely: 48-50; 60-62, 66, and 72 mm CL. This finding indicates that *P. monodon* spawns four times in its life span and probably has multiple spawnings in a single season (Primavera 1980). In Orissa, India, Rajyalakshmi et al (1985) reported gravid *P. monodon* with size range of 100-250 g (about 54-76 mm CL) off the Paradip Coast.

Specific location of spawning area depends greatly on secondary evidence like the presence of abundant spawners and larval forms. In the Philippines, *P. monodon* spawns in the sea close to the coast (Delmendo and Rabanal 1956) or in the mouth of the bays with water depth of about 20 m but mostly spawns in offshore water to about 70 m (Motoh 1981). Hall (1962) calculated a more specific spawning area of *P. indicus* with *P. monodon* at about 18-36 m deep. In the Paradip Coast, Orissa *P. monodon* spawns at 30-40 m

Table 1. Life history phases of the giant tiger prawn, *P. monodon* (Motoh 1981)

Phase	Begins at	Duration	Carapace length (mm)		Mode of Life	Habitat
			Male	Female		
Embryo	Fertilization	12 hours	0.29* <sub>1</sub>		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* <sub>2</sub> , 11-37* <sub>3</sub>		Benthic	Estuarine area
Subadult	Start of sexual maturity, first copulation	4 months	30-37* <sub>4</sub> , 37-47* <sub>5</sub>		Benthic	Inner/outer littoral area
Adult	Completion of sexual maturity	10 months	37-71* <sub>6</sub> , 47-81* <sub>6</sub>		Benthic	Outer littoral area

\*<sub>1</sub> Egg diameter.\*<sub>2</sub> Minimum size with jointed petasma.\*<sub>3</sub> Minimum size with adult-like thelycum.\*<sub>4</sub> Minimum size with spermatozoa in terminal ampoules.\*<sub>5</sub> Minimum size with spermatozoa in thelycum.\*<sub>6</sub> Maximum size ever found.

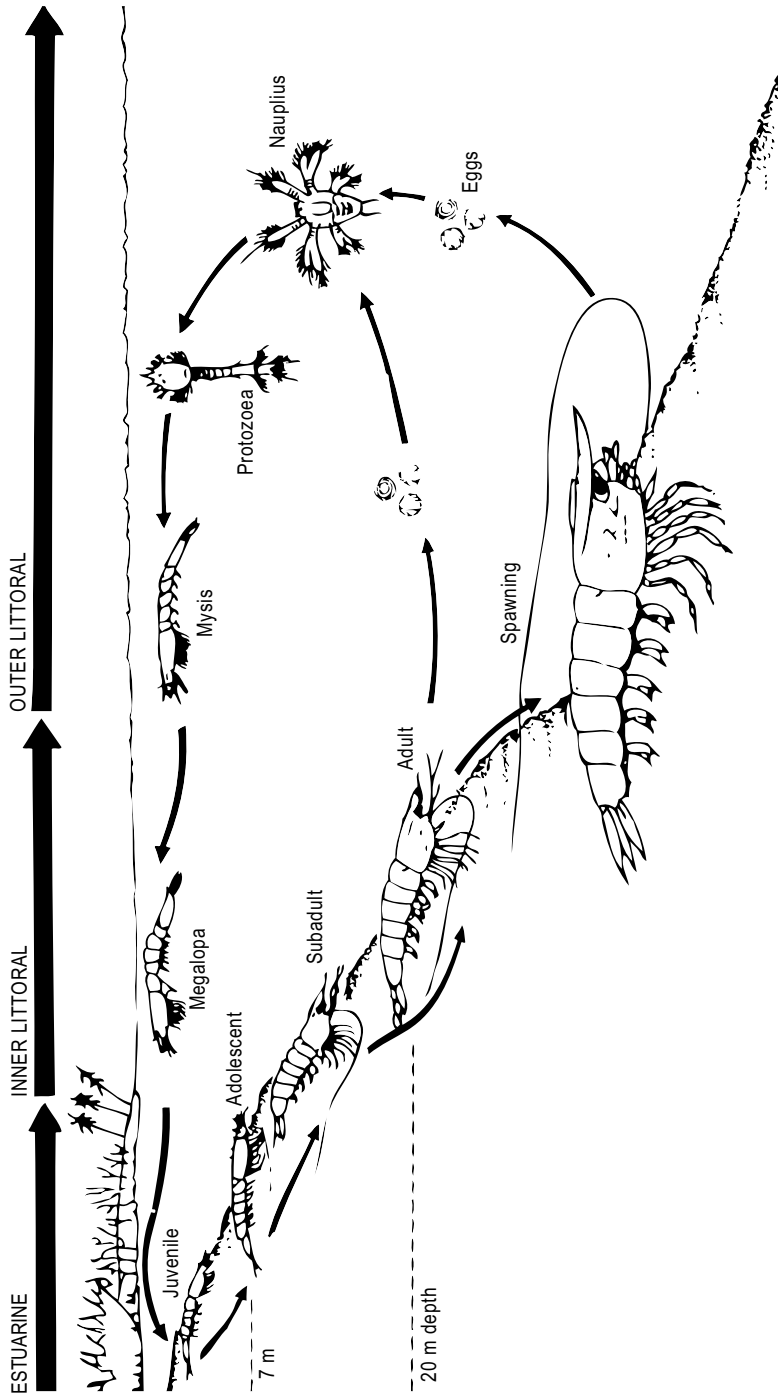


Fig. 7. Diagram of the life history of the giant tiger prawn, *P. monodon*. (Motoh 1981)

(Rajyalakshmi et al 1985), and in the coastal waters of Tungkang, Taiwan at 10-40 m (Su and Liao 1986).

In the Philippines, spawning of *P. monodon* is year-round but there seems to be two peak spawning seasons in a year: February-March or July and October-November although these vary from year to year (Motoh 1981). Hall (1962) reported February to April in Singapore; Rajyalakshmi et al (1985) in October through April corresponding to the post monsoon stability in the water movement and the increasing salinity in Orissa Coast, India; and Su and Liao (1986) from June to December in Taiwan.

### **Food and Feeding Habit**

Hall (1962) generally considered penaeids to be omnivores with *P. monodon* in particular preferring crustaceans, vegetable matter, polychaetes, molluscs, fish, and insects. Thomas (1972) supported this finding and explained that mud and sand found in the gut were accidentally ingested. Villadolid and Villaluz (1951) reported that the fry stage of *sugpo* relishes plankton (*lablab*) food. Marte (1980) reported that *P. monodon* food also consisted of crustacea (small crabs and shrimps) and molluscs, making up 85% of ingested food. The remaining 15% consisted of fish, polychaetes, ophiuroids, debris, sand, and silt. This indicates that the giant tiger prawn is more of a predator of slow-moving benthic macroinvertebrates rather than a scavenger or detritus feeder. Kuttyama (1973) observed that debris composed of mud and organic matter constituted the main portion of the stomach content while crustaceans ranked next in quantity. Similar food items were also observed by Su and Liao (1986). All these findings suggest that *P. monodon* is more of a carnivore with preference for crustaceans particularly when in the natural environment, but it also feeds on other available organisms including algae.

*P. monodon* seems to have increased feeding activity during ebb tide (Marte 1980) and shows some food preferences during seasonal variations of food (Kuttyama 1973). This species feeds by seizing the food with its pinchers and pushing food to the mouth to nibble (Villadolid and Villaluz 1951). Undigested food is defecated four hours after ingestion (Marte 1980).

## Physiology

*Molting.* Growth and the increase in size in crustacea are generally a function of the frequency of molting. Molting can occur anytime but more often at nighttime. Cited in the review by Wickins (1976), some conditions bring about a reduced increment during ecdysis so that the prawn may continue to molt but not grow.

During molting, the cuticle splits between the carapace and intercalary sclerite, paving the way for the cephalothorax and anterior appendage to withdraw, followed by the abdomen and posterior appendage emerging from the old shell with a forceful body flexure. The new cuticle takes about a few hours to harden in small prawns, to one or two days in larger animals (Villadolid and Villaluz 1951, Wickins 1976). Molting prawns characterized by soft shell are sensitive to stress and are good indicators of adverse environmental or nutritional conditions in the culture population (Wickins 1976).

Detailed reviews of the endocrine control of molting and reproduction in prawns were made by Adiyodi and Adiyodi (1970), Mantel and Farmer (1983), Adiyodi (1985), Kleinholz (1985), Skinner (1985), and Truchot (1983). Molting in crustaceans is believed to be controlled by two different hormones, namely: (1) molt-inhibiting hormone (MIH) secreted by the X-organ-sinus gland complex of the eyestalk (Kleinholz 1985, Skinner 1985). Molt-inhibiting hormone inhibits release of ecdysone by the molt gland. Closely associated with molting is reproductive maturation controlled by the gonad-inhibiting hormone (GIH) produced by the neurosecretory cells of the X-organ and transported to the sinus gland for storage and release. Induced gonadal maturation of penaeids through endocrine manipulation, such as eyestalk ablation, influences the molting cycle. Pudadera et al (1985) found marked changes in the internal structure of setae and cuticle throughout the molt cycle so that it is possible to properly time eyestalk ablation for induced ovarian maturation.

The physiological aspect of molting of *P. monodon* has received little attention. Although some works have been done on external factors, e.g., light, temperature, photoperiod, and salinity that may affect molting in penaeid prawns and shrimps (Bishop and Herrnkind 1976, Wickins 1976), no studies have been conducted on *P. monodon*. Meanwhile, Ferraris et al (1986)

reported a high degree of interaction between molting and salinity on osmotic and ionic regulation in *P. monodon*.

*Osmoregulation.* Crustaceans when subjected to change in water salinity have built-in mechanisms to adapt themselves to such change. It can be a mechanical response, such as burrowing, but the more efficient mechanisms are their physiological processes like osmoregulation by the organism. This process has been thoroughly reviewed by Mantel and Farmer (1983), Truchot (1983), Kleinholz (1985), and Skinner (1985). On the other hand, osmoregulation of *P. monodon* has been studied only by a few workers, e.g. Ferraris et al (1986) and Cheng and Liao (1986).

In the life history of *P. monodon*, spawning occurs in offshore waters where the larval stages are subsequently found. Post-larval, juvenile, and adolescent stages inhabit the nursery areas which are subjected to wide variations in salinity, temperature, and other environmental conditions. With proper acclimatization procedure, *P. monodon* postlarvae can also survive in fresh water (Pantastico and Oliveros 1980, Motoh 1981). The subadults and adults migrate to offshore areas where conditions are more or less stable. Behavior and survival are better understood, among others, in terms of the prawn's osmoregulation abilities. These physiological responses can be monitored by the changes in osmolality (or the number of particles such as ions, amino acids in solution) and the ion concentration of the blood (hemolymph) in relation to those of the medium (Ferraris et al 1986).

In the event when there is no osmotic gradient between the medium and the hemolymph, isosmotic point is attained. *P. monodon* in low salinity sea-water responds to osmotic gradient between the blood and external medium by gaining water, losing ions or both (hyperosmotic regulation) (Mantel and Farmer 1983). *P. monodon* juveniles are highly efficient regulators between 103 and 1480 mOsm/kg (30-50 ppt) and adults in over 444 mOsm/kg (about 15 ppt) (Cheng and Liao 1986). Isosmotic point for *P. monodon* juveniles of about 10 g is 730 mOsm/kg (Cheng and Liao 1986) or 676-720 mOsm/kg (26-28.5 ppt) (Ferraris et al 1986); for subadult (about 30 g weight or about 35 mm CL) 724-792 mOsm/kg (26-28.5 ppt) (Ferraris et al 1986); and for adults, 750 mOsm/kg (Cheng and Liao 1986). In general, *P. monodon* have isosmotic concentration at 20-30 ppt.

The isoionic points for *P. monodon* are 352 mEq/l for sodium and 320 mEq/l for potassium (Cheng and Liao 1986); with Ferraris et al (1986) finding chloride between 324 to 339 mM in 10 g prawns.

Relating these findings to the distribution of *P. monodon* in their natural habitat, Cheng and Liao (1986) attributed the abundant distribution of postlarvae to low salinity with due regard to other factors such as being genetically highly euryhaline species.

### Identification of Postlarvae

Wild fry still support the seed requirements of the extensive culture operation. Inasmuch as there are many other *Penaeus* fry during collection, fry gatherers and users often mistakenly identify *P. monodon* fry with that of other penaeids. At present, scanty information has been found on the identification of *P. monodon* fry. Some published articles on the subject are those by Rao and Gopalakrishnan (1969) for the juveniles of prawns in India, Prawirodihardjo et al (1975) on fry of *Penaeus* in Indonesia and Motoh and Buri (1981) on fry along the shoreline of Panay Island in the Philippines.

Morphological characters and color (chromatophore or pigment patterns) are often used in the identification of penaeid postlarvae. The following morphological characters were used by Motoh and Buri (1981) to identify *Penaeus* postlarvae along the coast of Panay Island, Philippines: (1) shape of rostrum, (2) number of rostral spines, (3) relative length of the antennular flagellum, (4) presence of antennal spine, and (5) presence of spinules on the sixth abdominal segment (6th AS). Chromatophore patterns on the 6th AS, telson, and uropods were also utilized, especially with fresh materials.

Compared with larvae and postlarvae of known parentage and reared in the laboratory, Motoh and Buri (1981) distinctly separated the postlarvae of *P. monodon* from *P. semisulcatus*, whereas with the absence of distinct differences in morphological characters for species identification, *P. indicus* and *P. merguensis* were combined as a group, and *P. japonicus*, *P. latisulcatus*, and *P. longistylus* as another group.

*P. monodon*. The postlarvae of *P. monodon* are the largest among the species or groups. The body is slender and the modal CL is 2.6 mm. The rostrum is either straight or slightly bent upward at the tip, usually having five dorsal spines but devoid of ventral spines. The inner (lower) antennular flagellum is twice lower than the outer (upper) flagellum. The 6th AS does not have spinules (Motoh and Buri 1981).

Distinct with fresh postlarvae, chromatophores of dark brownish red extend from the tip of the inner antennular flagellum to the tip of the telson. When viewed microscopically, thirteen chromatophores align ventrally along the 6th AS or are densely distributed to form an almost continuous pattern (Prawirodihardjo et al 1975, Motoh and Buri 1981). The chromatophore on the antero-lateral margin of the 6th AS is absent.

*P. semisulcatus*. The postlarvae of this species are relatively small. The rostrum is usually bent upward and has six dorsal spines and one or no ventral spine. The inner antennular flagellum is about one and a half to two times longer than the other flagellum. The antennal spine is very small or absent (Motoh and Buri 1981).

Chromatophores are not so dense, numbering from six to twelve along the 6th AS. Only the base and the tip portions of the telson and uropods are pigmented (Prawirodihardjo et al 1975, Motoh and Buri 1981). One chromatophore is present at the antero-lateral margin of the 6th AS.

Motoh and Buri (1981) confirmed the similarities between the postlarvae of *P. monodon* and *P. semisulcatus* in the Philippines and that of the specimens from Indonesia.

*P. merguensis* group. The postlarvae of this group, composed of *P. merguensis* and *P. indicus* are the smallest among the other species or groups. The rostrum is long or one and one-half times larger than the CL. About two-thirds of the anterior portion of the rostrum is toothless both dorsally and ventrally, but the remaining portion has three to four dorsal teeth and none below. Antennal spine is absent.

In older postlarvae, the rostrum becomes more bent upward having six to seven dorsal and three to five ventral teeth. As in its adult form, the postlarvae are poorly pigmented,



hence, the species are referred to as white prawns. One prominent chromatophore at the antero-lateral margin of the 6th AS is present (Motoh and Buri 1981).

*P. japonicus* group. The postlarvae of this group represents *P. japonicus*, *P. latisulcatus*, and probably *P. longistylus*. The body is short and bulky. The rostrum is short and does not exceed the tip of the eye. There are five to seven dorsal but no ventral teeth. The inner flagellum is about one and one half longer than the length of the outer flagellum. The carapace has a modal length of 2.0 mm. These postlarvae are often mistaken as smaller post-larvae of *P. monodon* because they have similar longitudinal streaks of dark brown chromatophores. The chromatophores at the 6th AS are more than eight or sometimes countless and are usually absent at the antero-lateral margin (Motoh and Buri 1981).

Chromatophore patterns of different *Penaeus* species shown in Figure 8 and the chromatophore patterns on the 6th AS, telson, and uropods shown in Figure 9 can aid in quick identification of each species or group.

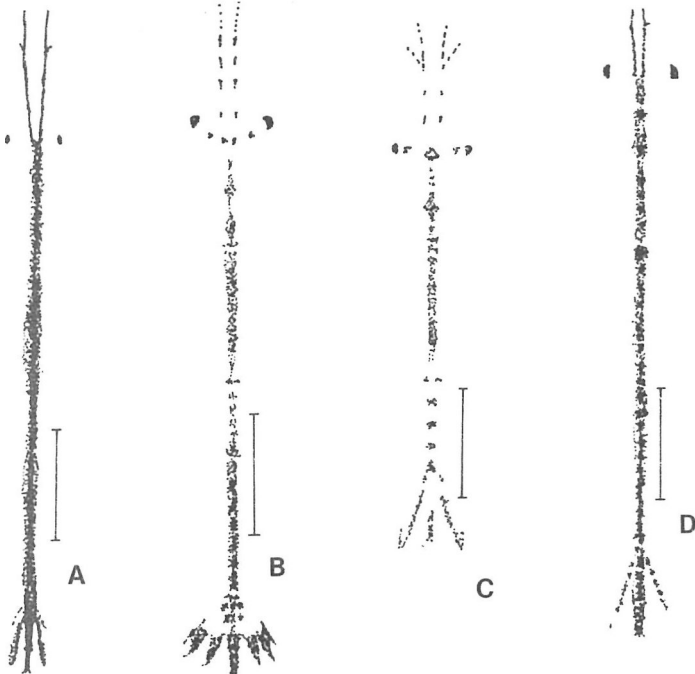


Fig. 8. Dorsal view of postlarval *Penaeus* showing chromatophore patterns for quick identification. (A) *P. monodon* (B) *P. semisulcatus* (C) *P. merguensis* group, (D) *P. japonicus* group. Scales represent 2.5 mm (Motoh 1981)

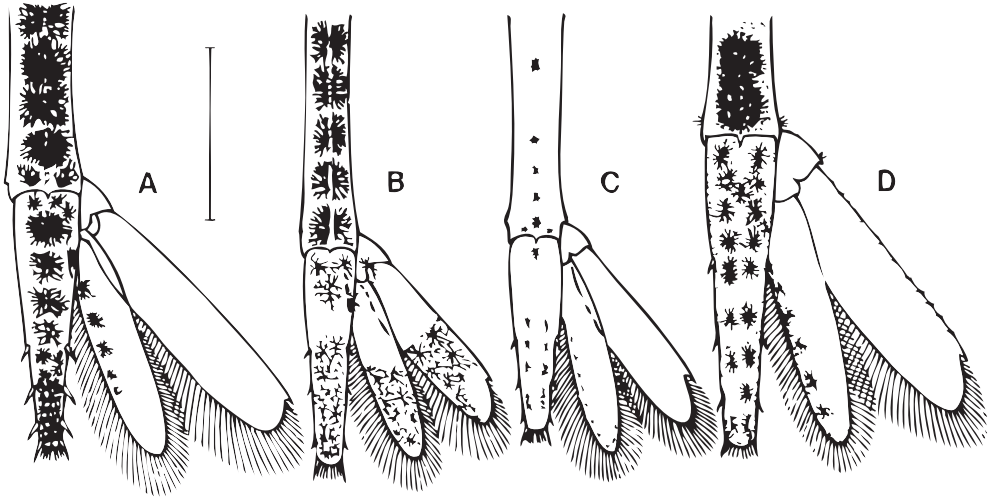


Fig. 9. Dorsal view of the sixth abdominal segment, telson, and uropods of postlarval *Penaeus* showing chromatophore patterns. (A) *P. monodon* (B) *P. semisulcatus* (C) *P. merguensis* group, (D) *P. japonicus* group. Scale represents 1 mm (Motoh 1981)

The following is the key prepared by Motoh and Buri (1981) to identify post-larval *Penaeus* appearing at the shoreline of Panay Island, Philippines.

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

- 1) Rostrum stout and inferior to tip of eye, spinules on the sixth abdominal segment present\*, antennal spine prominently present, carapace slightly longer than sixth abdominal segment .....*P. japonicus* group.  
 Rostrum slender and exceeding tip of eye, spinules on the sixth abdominal segment absent, antennal spine absent or minute, carapace slightly or distinctly shorter than the abdominal segment.....2.
- 2) Inner (lower) antennular flagellum nearly 1.6 times the outer (upper), exceeding the latter by its distal one segment.....*P. merguensis* group.  
 Inner antennular flagellum 1.6 to 2.0 times the outer (upper) 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*.

\*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 sixth abdominal segment less than seven. Antero-lateral chromatophore of the sixth abdominal segment present  
*P. merguensis* group.  
Number of chromatophores on the sixth abdominal segment more than seven. Antero-lateral chromatophore of the sixth abdominal segment present or absent.....2.
- 2) Number of chromatophores on the sixth abdominal segment less than 12. Antero-lateral chromatophore of the sixth abdominal segment present, chromatophores on the middle portion of telson and inner uropods absent  
*P. semisulcatus*  
Number of chromatophores on the sixth abdominal segment more than 12, antero-lateral chromatophore of the sixth abdominal segment absent.  
Chromatophores on the middle portion of the telson and inner uropods present  
3.
- 3) Chromatophores on the sixth abdominal segment dense and thickly continuous  
*P. monodon*.  
Chromatophores on the sixth abdominal segment discontinuous or confluent  
*P. japonicus*.

Common to all workers is the use of morphological characters and color patterns for identification, with Motoh and Buri (1981) also using morphometric measurements in identifying *P. monodon* from *P. semisulcatus* and two other groups, *P. merguensis* and *P. japonicus*.

Motoh and Buri (1981) confirmed the similarities between the post-larvae of *P. monodon* and *P. semisulcatus* in the Philippines and Indonesia.

For detailed descriptions, Motoh and Buri (1981) provided a key with illustrations while Prawirodihardjo et al (1975) tabulated the differences between *P. monodon* and *P. semisulcatus*.

## PROBLEMS AND PROSPECTS

Findings on biology and ecology of *P. monodon* have contributed significantly to its aquaculture. What was before an extrinsic species in the brackishwater pond culture of milkfish is now a cash crop of great demand in intensive monoculture. Fry collection from the wild has intensified to meet the demand for seeds usually for extensive culture while improvement in hatchery techniques has resulted in the proliferation of commercial hatcheries supplying the seeds for intensive culture. Despite these advances, a myriad of problems remain.

First, there is a conflict in the use and management of natural resources. The estuarine areas, rivers, and mangroves which are considered nursery grounds of wild *P. monodon*, are often identified for fishpond development or reclamation for social, commercial, or industrial purposes. This is a complex problem requiring concerted efforts of intergovernmental agencies to formulate and to religiously implement policies on the conservation of natural resources.

Second, there is no conservation effort during collection from the wild of *P. monodon* fry where finfish fry and larvae, other penaeid fry, and crustaceans of potentially high economic value are often discarded indiscriminately. Measures should be taken to return the live fry or larvae of other organisms to the shorewater. Policies on proper management and collection of wild fry should be adopted.

Third, overexploitation of wild stock, especially the spawners of *P. monodon*, is apparent. Stock assessment studies are thus necessary to pave the way for sea ranching open-water stocking in certain protected areas to replenish wild stocks.

For aquaculture scientists, the physiological aspects of the biology of *P. monodon* remain a major area for future research. More baseline information on molting is needed. The manipulation of hormonal and environmental conditions that control frequency and time of molting could improve growth and survival in culture, reproductive maturation for broodstock, and lastly, artificial fertilization techniques beneficial for genetic stock improvement and hybridization studies.

## LITERATURE CITED

- Adiyodi KG and Adiyodi RG. 1970. Endocrine control of reproduction in decapod Crustacea. *Biol. Rev.* 45:121-165.
- Adiyodi R. 1985. Reproduction and its control. In: Bliss DE and Mantel LH, eds. *Integument, pigments, and hormonal processes*. New York: Academic Press; p. 147-215. (Bliss DE, ed-in-chief. *The Biology of Crustacea*; vol. 9)
- Aquacop. 1977. Reproduction in captivity and growth of *Penaeus monodon* Fabricius in Polynesia. *Proc. World Maricult. Soc.* 8:927-945.
- Bate CS. 1888. Report of the scientific result of the exploring voyage of H. M. S. Challenger during the years 1873-76. *Sci. Res. "Challenger"* 24:250-252.
- Bishop JM and Herrnkind WF. 1976. Burying and molting of pink shrimp, *Penaeus duorarum* (Crustacea:Penaeidae), under selected photoperiods of white light and UV-light. *Biol. Bull.* 150:163-182.
- Blanco G and Arriola FJ. 1937. Five species of Philippine shrimps of the Genus *Penaeus*. *Philipp. J. Sci.* 62(2):219-226. plates 1-3.
- Cheng JH and Liao IC. 1986. The effect of salinity on the osmotic and ionic concentrations in the hemolymph of *Penaeus monodon* and *P. semisulcatus*. Maclean JL, Dizon LB, Hosillos LV, eds. *The First Asian Fisheries Forum: proceedings*; 1986 May 26-31; Manila, Philippines. Manila: Asian Fisheries Society; 633-636.
- Cheung TS. 1960. A key to the identification of Hong Kong penaeid prawns with comments on points of systematic interest. *Hong Kong Univ. Fish. J.* 3:61-69.
- Crosnier A. 1965. Les crevettes penaeides du plateau continental Malgache. *Cah. O.R.S.T.O.M. (Oceanogr.)* 3, Suppl. 3:1-158. (cf Mohamed KH 1970).

- Dall W. 1957. A revision of the Australian species of Penaeinae (Crustacea Decapoda: Penaeidae). Aust. J. Mar. Freshwat. Res. 8(2): 136-231.
- Delmendo MN and Rabanal HR. 1956. Cultivation of "sugpo" (jumbo tiger shrimp), *Penaeus monodon* Fabricius, in the Philippines. Proc. IPFC 6(Sect.3):424-431.
- Ferraris RP, Parado-Estepa FD, de Jesus EG, Ladja JM. 1986. Osmoregulation in *Penaeus monodon*: effects of molting and external salinity. Maclean JL, Dizon LB, Hosillos LV, eds. The First Asian Fisheries Forum: proceedings; 1986 May 26-31; Manila, Philippines. Manila: Asian Fisheries Society; 637-640.
- Hall DNF. 1956. The Malayan Penaeidae (Crustacea, Decapoda). Part I. Introductory notes on the species of the genera *Solenocera*, *Penaeus* and *Metapenaeus*. Bull. Raffles Mus. (27):68-90. plates 8-12.
- Hall DNF. 1961. The Malayan Penaeidae (Crustacea, Decapoda). Part II. Further taxonomic notes on the Malayan species. Bull. Raffles Mus. (26):76-119. plates 17-21.
- Hall DNF. 1962. Observations on the taxonomy and biology of some Indo-West Pacific penaeidae (Crustacea:Decapoda). Colon. Off. Fish. Pub. Lond. (17):1-229.
- Holthuis LB. 1949. The identity of *Penaeus monodon* Fabr. Proc. Konink. Ned. Akad. Wet. 52(9): 1051 - 1057.
- Holthuis LB. 1980. Shrimps and prawns of the world; an annotated catalogue of species of interest to fisheries. Rome: Food and Agriculture Organization of the United Nations. 271 p. (FAO Species Catalogue; vol.1).
- Holthuis LB and Rosa H Jr. 1965. List of species of shrimps and prawns of economic value. Rome: Food and Agriculture Organization of the United Nations. 21 p.

- Kleinholz LH. 1985. Biochemistry of crustacean hormones. In: Bliss DE and Mantel LH, eds. Integument, pigments, and hormonal processes. New York: Academic Press; p. 463-522. (Bliss DE, ed-in-chief. The Biology of Crustacea; vol. 9).
- Kubo I. 1949. Studies on the penaeids of Japanese and its adjacent waters. J. Tokyo Coll. Fish. 36(1):1-467.
- Kungvankij P. 1976. Early developmental stages of jumbo tiger shrimp, (*Penaeus monodon*) Fabricius. Thailand Phuket Fisheries Station. 24 p. (PFS Fisheries Contribution; no. 6).
- Kuttyama VJ. 1973. Observation on the food and feeding of some penaeid prawns of Cochin Area. J. Mar. Biol. Assoc. India 15(1):189-194.
- Mantel LH and Farmer LL. 1983. Osmotic and ionic regulation. In: Mantel LH, ed. Internal anatomy and physiological regulation. New York: Academic Press; p. 53-161. (Bliss DE, ed-in-chief. The biology of Crustacea; vol. 5)
- Marte CL. 1980. The food and feeding habit of *Penaeus monodon* Fabricius collected from Makato River, Aklan, Philippines (Decapoda, Natantia). Crustaceana 38(3):225-236.
- Mohamed KH. 1970. Synopsis of biological data on the jumbo tiger prawn *Penaeus monodon* Fabricius 1798. FAO Fish. Rep. 4(57):1251 - 1266. (FAO Fisheries Synopsis; no. 93)
- Motoh H. 1977. An annotated list of scientific and English common names of commercially important penaeid prawns and shrimps. Technical report, no. 2. Tigbauan, Iloilo: SEAFDEC Aquaculture Department. 14 p.
- Motoh H. 1979. Larvae of decapod crustacea of the Philippines. III. Larval development of the giant tiger prawn, *Penaeus monodon* reared in the laboratory. Bull. Japan. Soc. Sci. Fish. 45(10):1201-1216.
- Motoh H. 1981. Studies on the fisheries biology of the giant tiger prawn, *Penaeus monodon* in the Philippines. Technical report, no. 7. Tigbauan, Iloilo: SEAFDEC Aquaculture Department. 128 p.

- Motoh H. 1985. Biology and ecology of *Penaeus monodon*. Taki Y, Primavera JH, Llobrera JA, eds. Proceedings of the first international conference on the culture of penaeid prawns/shrimps; 1984 December 4-7; Iloilo City, Philippines. Iloilo: SEAFDEC Aquaculture Department; 27-36.
- Motoh H and Buri P. 1980. Early developmental stages of the giant tiger prawn, *Penaeus monodon* Fabricius. Res. Crust. (10): 13-34.
- Motoh H and Buri P. 1981. Identification of postlarvae of the Genus *Penaeus* appearing in shore waters. Res. Crust. (11):86-94.
- Motoh H and Buri P. 1984. Studies on the penaeid prawns of the Philippines. Res. Crust. (13-14): 1-20.
- Pantastico JB and Oliveros EN. 1980. Acclimation of *Penaeus monodon* postlarvae to fresh water. Fish. Res. J. Philipp. 5(1):33-38.
- Prawirodihardjo S, Poernomo A, Nurhamid S, Siswono C, Nugroho J. 1975. Occurrence and abundance of prawn seed at Jepara. Bull. Shrimp. Cult. Res. Cent. 1(1):19-26.
- Primavera JH. 1980. Broodstock of sugpo (*Penaeus monodon*) and other penaeid prawns. Extension manual, no. 7. Tigbauan, Iloilo: SEAFDEC Aquaculture Department. 24 p.
- Primavera JH. 1983. Broodstock of sugpo *Penaeus monodon* Fabricius. Extension manual, no. 7, 3rd ed. Tigbauan, Iloilo:SEAFDEC Aquaculture Department. 26 p.
- Primavera JH. 1985. A review of maturation and reproduction in closed thelycum penaeids. Taki Y, Primavera JH, Llobrera JA, eds. Proceedings of the first international conference on the culture of penaeid prawns/shrimps; 1984 December 4-7; Iloilo City, Philippines. Iloilo: SEAFDEC Aquaculture Department; 47-64.
- Primavera JH and Posadas RA. 1981. Studies on the egg quality of *Penaeus monodon* Fabricius, based on morphology and hatching rates. Aquaculture 22:269-277.



- Pudadera R, Llobrera J, Caballero RM, Aquino N. 1985. Molt staging in adult *Penaeus monodon*. Taki Y, Primavera JH, Llobrera JA, eds. Proceedings of the first international conference on the culture of penaeid prawns/shrimps; 1984 December 4-7; Iloilo City, Philippines. Iloilo: SEAFDEC Aquaculture Department; 177.
- Racek AA. 1955. Littoral penaeidae from New South Wales and adjacent Queensland waters. Aust. J. Mar. Freshwat. Res. 6(2):209-241. plates 1-9.
- Racek AA. 1957. Penaeid prawn fisheries of Australia with special reference to New South Wales. Research Bulletin, no. 3. New South Wales: State Fisheries, Chief Secretary's Department. 19 p.
- Racek AA. 1972. Indo-West Pacific penaeid prawns of commercial importance. Pillay TVR, ed. Coastal Aquaculture in the Indo-Pacific Region; papers presented at the Indo-Pacific Fisheries Council Symposium on Coastal Aquaculture; 1970 November 18-21; Bangkok. West Byfleet, England: Fishing News (Books); 152-172.
- Racek AA and Yaldwin JC. 1971. Notes on littoral penaeinae (Crustacea:Decapoda) from the New Guinea area. Proc. Linn. Soc. N.S.W. 95(3):209-214.
- Rajyalakshmi T, Pillai SM, Ravichandran P. 1985. The biology of *Penaeus monodon* in the capture fisheries off Orissa Coast, India in the context of occurrence of natural broodstock. Taki Y, Primavera JH, Llobrera JA, eds. Proceedings of the first international conference on the culture of penaeid prawns/shrimps; 1984 December 4-7; Iloilo City, Philippines. Iloilo: SEAFDEC Aquaculture Department; 175.
- Rao RM and Gopalakrishnan V. 1969. Identification of juveniles of the prawns *Penaeus monodon* Fabricius and *P. indicus* H. M. Edwards. Proc. IPFC 13(2):128-131.
- Skinner D. 1985. Molting and regeneration. In: Bliss DE and Mantel LH, eds. Integument, pigments and hormonal processes. New York: Academic Press; p. 43-146. (Bliss DE, ed-in-chief. The Biology of Crustacea; vol. 9)

- Srivatsa KR. 1953. A survey and comparative analysis of the prawn (shrimp) fishery of the Gulf of Kutch in Saurashtra in Western India. Saurashtra, India: Department of Industries and Supplies, (cf Mohamed KH 1970)
- Su MS and Liao IC. 1986. Distribution and feeding ecology of *Penaeus monodon* along the coast of Tungkang, Taiwan. Maclean JL, Dizon LB, Hosillos LV, eds. The First Asian Fisheries Forum: proceedings; 1986 May 26-31; Manila, Philippines. Manila: Asian Fisheries Society; 207-210.
- Tan-Fermin JD and Pudadera RA. In press. A qualitative and quantitative study of the ovarian maturation stages of the wild giant tiger prawn *Penaeus monodon* Fabricius. Aquaculture.
- Thomas MM. 1972. Food and feeding habits of *Penaeus monodon* Fabricius from Korapuzha Estuary. Indian J. Fish. 19:202-204.
- Truchot SP. 1983. Regulation of acid-base balance. In: Mantel LH, ed. Internal Anatomy and physiological regulation. New York:Academic Press; p. 431-471. (Bliss DE, ed-in-chief. The Biology of Crustacea; Vol. 5)
- Villadolid DV and Villaluz D. 1951. Cultivation of sugpo (*Penaeus monodon* Fabricius) in the Philippines. Philipp. J. Fish. 1(1):68-78.
- Villaluz DK and Arriola FJ. 1938. Five other known species of *Penaeus* in the Philippines. Philipp. J. Sci. 66(1):35-45, plate 4.
- Villaluz DK, Villaluz A, Ladrera B, Sheik M, Gonzaga A. 1969. Reproduction, larval development and cultivation of sugpo (*Penaeus monodon* Fabricius). Philipp. J. Sci. 98(3-4):205-236.
- Villegas CT, Trino A, Travina R. 1986. Spawner size and the biological components of the reproduction process in *Penaeus monodon* Fabricius. Maclean JL, Dizon LB, Hosillos LV, eds. The First Asian Fisheries Forum; proceedings; 1986 May 26-31; Manila, Philippines. Manila: Asian Fisheries Society; 701-702
- Wickins JF. 1976. Prawn biology and culture. Oceanogr. Mar. Biol. Annu. Rev. (14):435-507.