LIFE HISTORY OF PRAWNS — A REVIEW OF RECENT STUDIES WITH SPECIAL REFERENCE TO INDIAN SPECIES

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[The paper contains a brief review of the studies on the life histories of Indian species of prawns chiefly belonging to the family Penaeidae. References to similar work carried out outside India are furnished where significant variations have been observed. The three main larval stages viz., Nauplius, Protozoea and Zoea (Mysis) and their important characteristics, including modes of locomotion, are described. The post-larval development of one species that has been studied in detail (*Metapenaeus dobsoni*) is indicated in outline. Some aspects of the bionomics of these prawns, especially breeding and migration, are also briefly dealt with in view of their relevance in their life cycle.

An outline of the life histories of some Palaemonid prawns of both fresh water and marine habitats is added at the end and the need for well planned investigations in regard to species of such economic value as *Palaemon carcinus* (*Macrobrachium rosenbergii*) is indicated]

The term "Prawn" according to a decision of the Indo-Pacific Fisheries Council (1955) should be applied only to the 3 families Penaeidae, Palaemonidae and Pandalidae. All other decapods with fully developed abdomen and natatory appendages, whether commercially important or not, are to be referred to as 'shrimps'. The vast majority of prawns caught in our commercial fishery belong to the first family Penaeidae and their biology in consequence has stimulated more extensive investigations than that of the others. It should however be recognized that Palaemonidae also includes several species that provide valuable fisheries in different types of environments; fresh water, brackish water (estuaries and back-waters) and the sea and interesting data relating to their fishery and biology have been collected. This paper is written with the limited object of furnishing a brief review of the results of investigations bearing on some aspects of their biology, chiefly their life histories. Similar studies have been carried out in other countries also, notably America, Japan, and Australia, some of them long before they were started in India. In broad outline, so far as is known, the life cycles of prawns of the family Penaeidae follow the same pattern irrespective of their geographical distribution and any one that is fully known may be chosen to elucidate it. This review therefore, is based primarily on Indian work and references to that on foreign species would be made only where significant variations or striking structural peculiarities have been observed.

Historical

The general course of penaeid development from Nauplius to Mysis was traced in

considerable detail by some of the earliest workers in the field such as F. Muller and Claus. They did not know, however, with what genera they were dealing, as it was not possible to establish their identity by linking them with their parents. The publications of many of the later authors (Brooks, Bate and Stephensen) have also not been quite satisfactory in this respect either for lack of illustrations or for the brevity or obscurity of their language. Among the papers published upto about 1924 Gurney (1924) reports that "the only Penaeid larvae which are recognisable with certainty are those of *Gennadas* and *Solenocera*".

The comparatively recent works of Hudinaga (1935), Heldt (1938) and Pearson (1939) have made a remarkable improvement in the situation and we have now excellent accounts of the life histories of several species, Japanese, European and American. Dakin (1938, 1940) and Morris and Bennet (1951) have added to this list the two Australian species *Penaeus plebejus* and *Metapenaeus mastersii*. Gurney, who has made a life-long study of the development of Decapod crustaceans has, among his numerous contributions on the subject, dealt with the larvae of *M. stebbingi* (1927) and *Sicyonia* and *Penaeopsis* (1942). Among Indian species the life history of *M. dobsoni* has been fully worked out (Menon, 1951) and some larval stages of *P. indicus* have been described a few years earlier (Menon, 1937). Notes on post-larvae of several other commercial species will be found in a number of contributions from the C.M.F.R.I. dealing with their bionomics and fishery. So also a number of papers on the development and other aspects of the biology of practically all American species have come out since the publication of Pearson's studies. Two of the most recent of them are Dobkin's (1961) on *P. duorarum*, the pink shrimp and Renfro and Cook's (1962) on *Xiphopenaeus Kroyeri*, the seabob of American waters.

Breeding

Penaeid prawns have so far been observed to breed only in the sea. *Metapenaeus mastersii* is an exception since it spawns in the coastal lakes (Tuggerah) of New South Wales, Australia. Even there two other species *P. pelbejus* and *M. macleayi*, which normally occur together with the former pass out into the open sea for maturation of gonads and breeding. Except for accidental catches of a few larvae in the backwaters, probably carried in by tidal currents and wind, no evidence has been obtained of their breeding in such waters in this country also. Eggs and larvae have been obtained in good numbers in the plankton only from the sea. Mature males of *M. dobsoni* have been caught from the backwaters of Kerala and elsewhere and mature ones of both sexes of *M. brevicornis* were observed in the lower Sunderban area (Rajyalakshmi, 1961). In regard to all other species hardly any specimen of either sex with the gonads well developed or nearly so has been captured from such environments.

Spawning Ground

The location of the spawning grounds in respect of depth or distance from the coast seems to vary with the adult size and habits of the parents. Small species like *M. dobsoni* and *Parapenaeopsis stylifera*, which shoal in comparatively shallow coastal waters, also spawn there. Eggs and larvae of both have been collected in large numbers upto about 12-13 fathoms; beyond this they are few and are seldom present in offshore plankton. Direct evidence in regard to the spawning grounds of other species from larval distribution is unsatisfactory, but the distribution of adult females with fully ripe ovaries may provide indirect evidence. Catches of the vessels belonging to the Government of India Off-shore Fisheries Station at Cochin made in 20-25 fathoms have occasionally included numerous adult females of *M. monoceros* and *P. indicus* with fully developed ovaries. Recently George and George (1964) have reported the discovery of a concentration of mature *M. monoceros* in 25-30 fathoms off Cochin (75% were females) on a bottom of sand and silt. This together with the absence of their larvae in inshore waters do certainly prove that they liberate their eggs in deeper offshore waters. Australian and American workers have come to similar conclusions in respect of the spawning grounds of *P. pelbejus* and *P. setiferus*. Trapping experiments, followed later by trawling trials, have revealed the existence of females of *P. carinatus*, the largest Indian sea prawn, with mature ovaries in 65-75 fathoms off New South Wales in Australia (Racek, 1959). It may prove useful to the industry and to fishery biologists if similar experiments are

undertaken off the west and east coasts of India too.

Breeding Period

The breeding period is fairly extended in the case of *M. dobsoni* — from November to March. *P. stylifera* breeds from October to December. In regard to the larger *P. indicus* two periods, October-November and May-June, have been observed along the coast of Kerala. On the east coast (Madras) Subrahmanyan (1963) has reported that the species breeds most actively in May, July, August and September. *M. brevicornis* spawns twice a year, March-April and July-August (Rajyalakshmi op. cit).

Eggs

Eggs of Penaeid prawns are shed in the sea unlike those of other groups which remain attached to the abdominal appendages of the mother until they hatch. They sink down and are therefore demersal. Eggs of some species like *M. dobsoni* are buoyant and are easily stirred up by disturbances caused by currents and waves so that large numbers of these eggs are sometimes caught in two nets. Eggs of this species, most of which were in late stages of development when caught were spherical and measured from 0.35 - 0.44 mm. in diameter. No other eggs have been obtained and hence characteristics of other Indian species are yet unknown.

Larval Stages — Nauplius

The eggs hatch rather quickly, 12-18 hours after spawning and the tiny creature that emerges is called the Nauplius. It has a pearshaped unsegmented body with a couple of short setae at the posterior end. A median eye at the front end is quite often visible. It has 3 pairs of limbs, the first of which is uniramous and the other biramous. Mouth and anus are not developed and the larva therefore does not feed, nutrition being obtained from the yolk that is present within the body cells making the animal opaque.

This nauplius sheds its skin a number of times (moults) gradually developing during the process. In *M. dobsoni* only 3 naupliar stages have been observed; in *M. stebbingi* from the suez Canal also there are only 3 stages. In the development of *M. mastersii*, however, Morris and Bennet (1938) have described 4 and are inclined to believe that the full series consists of 8 stages as in *P. trisulcatus*. The number appears to be very variable (6 in *P. japonicus*, 5 in all of the American species studied) and the time taken to complete the whole series is quite short, usually 24-36 hours. The last stage shows considerabe advancement over the first. It looks more slender and is semitransparent and has a shell fold on the dorsal side. At the posterior end of the body there is a well marked bifurcate telson bearing 7 spines of unequal lengths on each lobe. Besides the 3 pairs of appendages possessed by the first stage biramous rudiments of 4 more pairs have developed behind them.

Protozoea

The last nauplius moults into the next phase in the larval development named Protozoea. It is quite different in appearance and is partly covered on the dorsal side by a shield or carapace. On either side of the median eye there is a colourless rudiment of the stalked eye. Behind the appendages of the last nauplius all segments of the thorax are well differentiated. But the abdomen still remains unsegmented (the first segment may be sometimes marked out) and is terminated by the caudal fork with 7 setae on each fork. Both mouth and anus are well developed and the protozoea feeds actively.

Two more Protozoea stages succeed. In the third all abdominal segments are formed and the sixth carries a pair of small biramous wropods. Projecting forwards from the front end of the carapace there is a rostrum and quite often supraorbital spines, both making their appearance in the second stage. In the third the abdominal segments may develop median and lateral spines. The colourless rudimentary paired eyes of the first stage become well developed stalked eyes completely free from the carapace and have dark cornea.

There does not seem to be much variation in the number of protozoea stages in the species studied.

Mysis or Zoea

The moult which the last Protozoea undergoes to change into the Mysis brings about a profound alteration in the shape of the larva, which now has an elongated somewhat laterally compressed body more or less similar to that of the adult prawn.

In addition to the change in shape the functional development of the exopodites of all the thoracic legs and the appearance of pleopods on the abdominal segments are some of the other important characteristics of this stage. The abdominal segments in some genera as in *Gennadas*, may bear prominent spines. The forked telson of the Protozoea has changed into an elongated flat plate with almost parallel sides and a deep cleft on the posterior margin in the earlier stages. This cleft becomes less pronounced later and is obliterated in the last Zoea. Gill rudiments also develop in this phase.

The number of Zoeal stages also varies much. In *M. dobsoni*, *M. stebbingi* and *M. mastersii*, there are three. In *P. trisulcatus*, four stages have been recorded (Heldt, 1938) while in one of the American species viz. *P. setiferus* only two have been observed. *P. duorarum* and *P. japonicus* also pass through three Mysis stages. In *Parapenaeus longirostris* (Heldt 1938) the number seems to be quite large (as many as sixteen).

The mode of locomotion of these three larval stages is quite characteristic and may be briefly referred to here. In both the Nauplius and Protozoea the antenna is well developed and biramous carrying feathery setae on both rami and it is mainly the movements of this appendage together with those of antennules that effect locomotion, aided no doubt by those of the maxillipeds in the protozoea. At the moult to the first Mysis stage the antenna changes so much (the outer branch becomes a long narrow plate called scale much as in the adult) that it is no longer able to function as a locomotor organ. The exopodites of the thoracic legs however are well developed and tipped with feathery setae and are therefore able to take over this function. When the zoea metamorphoses into the post-larval stage 3-4 weeks after spawning and the peraeopods lose their natatory exopodites the pleopods of the abdominal segments become functional and are the principal swimming organs. Referring to this feature Gurney (1942) remarks that "decapod development may, therefore, be regarded as made up of four phases of phylogenetic significance :

Nauplius Protozoea	Antennal propulsion
Zoea	Thoracic propulsion
Post-larva	Abdominal propulsion

First Post-larva

The two striking changes which the moult, at the close of the Zoea stage, effects namely the reduction or loss of exopodites of the thoracic appendages and development of setae on the pleopods adapting them to take over the function of locomotion have been pointed out in the previous para. On the carapace a conspicuous hepatic spine appears on each side. The pleopods, though functional are still uniramous. The cleft on the posterior margin of the telson disappears completely and marginal spines develop on either side of its hinder half which as in Zoea 3, is narrower.

The subsequent development of the post-larvae can be traced by collecting later stages from the plankton of estuaries and back-waters into which they migrate in large numbers. Rearing these larvae in suitable containers in the laboratory is not difficult. This method has the advantage that it would enable one to detect a moult within a few hours after it has taken place and ascertain the extent of development that the post-larva has undergone by the moult. By adopting this method it was possible to etsablish that the first post-larva of *M. dobsoni* measuring about 3.5 mm. in length undergoes a succession of 12 moults before it gets transformed into a juvenile prawn with practically all parts showing the adult specific characters. The rostrum, telson and pleopods of the early postlarva differ greatly from those of the adult and they have been observed to develop progressively and approximate more and more closely to the adult condition after each moult. The entire series of 12 moults was completed within the course of about 7 weeks. In the closely related Australian species *M. mastersii* Morris and Bennet (1951) have noted the rostrum with the full number of teeth developed when the post-larva is about 17 mm. in length and the species thus shows close resemblance to the Indian form.

Habits of Larvae

It has been stated previously that the eggs of Penaeid prawns are demersal and that those of some species are buoyant to some extent making it possible to obtain such eggs in plankton nets when dragged at some depth below the surface. The nauplii hatching out of these eggs, however, soon rise to the surface and are planktonic in habit.

Swarms of Penaeid larvae, nauplii, protozoae and Zoeae mostly of the same species may be occasionally noticed in the plankton. Though their power of swimming is feeble and are seen drifting about in the direction of currents or winds yet it is believed that such swarms imply a certain ability for the individuals in a swarm to keep together. The first post-larval stage also is planktonic in habit. In the case of *Metapenaeus dobsoni* later post-larvae were quite rare in the plankton from inshore waters and they were obtained in fairly good numbers only from the backwaters. It seems therefore reasonable to infer that older post-larvae abandon their pelagic habit and become benthic. Post-larvae and early juveniles of the king and tiger prawns of Australia (species of *Penaeus*) were dredged from bottom as deep as 53 fathoms, and upto 60 miles from the nearest inlet (Racek, 1959).

Migration of Post-larvae

It is now fairly well known that the post-larvae of most Penaeid prawns, so far studied, migrate into the less saline or brackish waters of coastal lakes, estuaries etc. very early in life. Post-larvae of species that are supposed to spawn in the high seas far away from shore also share this habit and presumably therefore the late larvae and the earliest post-larvae of such species drift shorewards so as to make this migration possible. It is possible that vast numbers of such fry "accumulate in perifluvial areas and at inlets and enter during each ingoing tide in quite dense patches," (Racek, 1959). In the Cochin backwaters they have been collected in considerable numbers throughout the breeding period. Post-larvae of *Metapenaeus dobsoni* entering the backwaters in this manner mostly measure less than 6 mm. and those of *P. indicus* seldom exceed 10 mm. *Metapenaeus monoceros* post-larvae are about the same size as those of *Metapenaeus dobsoni*. Among the commercial species of the south-west coast *Parapenaeopsis stylifera* does not seem to have acquired this habit since their post-larvae have hardly ever been caught from brackish water environments.

The muddy bottom of such localities containing large amounts of animal and plant detritus provide optimum conditions for their growth. After growing for a few months they pass back into the sea where alone their gonads can develop and become ripe. In Australia both the inward migration of post-larvae and the seaward migration of adults have been observed to be subject to lunar periodicity. Observations made here have not provided clear evidence for such periodicity.

It should be stated here that the inward migration of post-larvae does not necessarily imply that it is obligatory for completing the life-cycle of these prawns. Indeed there is good evidence to prove that even if they remain in the sea they may not perish and may be able to grow and become mature. Racek (1959) has referred to the capture of these post-larvae at great distances from the shore, where presumably they remain and grow. Discussing the question of this migration in relation to the American species *P. setiferus* Gunter (1961) observes that "Small shrimp are not killed or precluded by high salinity as if it were poison; they simply do not do well in it, for reasons unknown". Post-larvae of *Metapenaeus dobsoni* have been reared in sea water under laboratory conditions for several months proving thereby that high salinity is not harmful to them.

Growth–Longevity

From what has been said in the preceding section it is clear that the life cycle of most Penaeid prawns is completed in two types of environments. Larvae and early post-larvae are entirely marine in habit. So also the adults with well developed gonads are found only in the sea. Older post-larvae and juveniles, however, are abundant in brackish water environments like coastal lakes and estuaries. The rich prawn fisheries of such areas therefore owe their existence to this peculiar habit. It need not therefore be specially pointed out here that the entire commercial catch from such localities consists of immature juveniles. Observations extending over several years have shown that over 96% of *Metapenaeus dobsoni* caught from backwaters measure less than 70 mm. in length. *Metapenaeus monoceros* similarly grows to about 100 mm. before they return to the sea and *P. indicus*, which occupies the third rank in the *Penaeid* population of the estuaries and backwaters of Kerala rarely grows over 120 mm. in length. The adults of these species normally reach about 115 mm. 150 mm. and 180-190 mm. in length. The rest of the growth therefore takes place in the sea.

By combining the results of experiments and statistical analysis of size data obtained by measuring random samples of catches it was possible to infer that both *M. dobsoni* (Menon, 1955) and *Metapenaeus monoceros* (George, 1959) live for 3 years and *P. stylifera,* which is about equal to the first species in size for about 2 years (Menon, 1953). *Metapenaeus brevicornis* seems to have a life span of 3 years in the Hooghly estuarine system (Rajyalakshmi, 1961). The duration of life of the other species can only be guessed. Both *Metapenaeus dobsoni* and *P. stylifera* become mature and breed in the first year of their life, but *Metapenaeus brevicornis,* the adults of which have been reported to migrate to the lower reaches of the Hooghly estuary for maturing and spawning, seem to become mature when they are about 100 mm. long in the third year of their life.

Palaemonidae

Palaemon and *Leander* are the 2 genera of the Palaemonidae the species of which contribute to the commercial fishery of India. Species of the former are mostly inhabitants of fresh water, but some are known to pass into brackish water of low salinity presumably for breeding. Species of *Leander* are marine, but ascend into estuarine or other brackish water areas e. g. *L. styliferus* and *L. fluminicola.* Egg-bearing females of Leander species living in rivers and estuaries are reported to pass into the sea for liberation of larvae. *L. fluminicola,* however, seems to free its larvae in estuarine waters (Rajyalakshmi, 1961). Larvae of species of *Leander* and *Palaemon* which have a normal larval development (in some species of both genera the development is abbreviated and the newly hatched larva is in possession of all appendages except the uropods as in *P. lamarrei* (Rajyalakshmi op. cit) hatch out at a stage comparable to the early Mysis stage of Penaeids with eyes not yet free from the carapace. In addition to the head appendages they have 3 pairs of well developed biramous maxillipeds and all the abdominal segments clearly differentiated. The eyes become free in the second stage and the uropods develop in the third. Two more stages may follow at the end of which the larva changes into the post-larva.

Several species of *Palaemon* occur in fresh water throughout the country, most of which may be caught in the commercial prawn fishery. One species *P. carcinus* (*Macrobrachium rosenbergii*) is the largest of all, adults growing upto 1 foot or more in length. It is possibly the most important species from the point of view of the fishery and its life history, so far as known, may be briefly summarised here. The habit of egg-bearing females of this species moving into brackish water when the salinity is low has been referred to. It has a normal larval development, the eggs hatching out into a zoea larva showing all the usual characters of the Caridean first stage larvae. This and the following stage have been described as early as 1938 by Menon. They have been obtained in good numbers from the plankton of the backwaters (Raman 1964). All efforts to secure later stages, from the backwaters or rivers by various methods proved fruitless. Rearing experiments under laboratory conditions also did not succeed. Ling and Merican (1961) have reported from Malaya that eggs hatch in fresh water. It was, however, found that the larvae survived only when a quantity of sea water was added. They have also successfully reared the larvae in their laboratory for a period of 55 days. From their brief remarks on the characters of the larvae towards the close of the experiment it would seem that even then they were true larvae and had not passed into the post-larval stage.

The distribution of juveniles of this species was investigated along the course of one of the rivers joining the Vembanad lake viz. the Pampa of Central Travancore (Raman op. cit). During the months of January and February small juveniles measuring less than 100 mm. (30 - 87 mm.) were found in quite good numbers in a stretch of the river some 10 miles in length around its confluence with the tributary known locally as Manimala river. The river in this stretch is rather deeper than in other parts (upto 12 metres) and the bottom is made up of loose mud with plenty of organic detritus. The discovery of this nursery is interesting and it is possible that similar ones may occur in the other rivers and tributaries connected with the Vembanad lake. Since *M. rosenbergii* is one of the species that could be successfully cultured in ponds the discovery of nursery grounds establishing the possibility of securing adequate numbers of fry is of practical importance. A well planned programme of observations on the same lines along the course of the rivers or streams connected

directly or indirectly with the Vembanad lake seem therefore well worth undertaking.

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Discussion

(The paper was read by Shri M. J. George)

Shri John P. George wanted to know as to how long does it take for the hatched eggs to reach post-larvae stage.

Shri George replied that it takes three to four weeks to attain adult characteristics. Shri Alexander Cherian enquired whether it is necessary that all the post-larvae should come to estuary to complete the life history and what happens if they remain in the sea only.

Shri M. J. George said that very large numbers of these post-larvae are found to enter the estuaries where they subsequently support a lucrative fishery of the juveniles. The juveniles are, however, obtained from the very close inshore waters also in relatively insignificant numbers indicating thereby that they are able to survive in the sea. Alexander Cherian further wanted to know whether the "Konchu" (*Macrobrachiun rosenbergii*) also have to go to sea for breeding. Shri George answered in negative and further explained that it is a freshwater species; but it requires slight saline environment for breeding and hence they are found to descend to the upper reaches of the estuaries where salinity is not very high.