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Larval development – Pattern of penaeid larval development and generic characters of the larvae of the genera *Penaeus*, *Metapenaeus* and *Parapenaeopsis*

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The general pattern of penaeid larval development is discussed and the diagnostic characters of the nauplius, protozoea, mysis and postlarva I belonging to the genera *Penaeus*, *Metapenaeus* and *Parapenaeopsis* are described and illustrated. Inter-specific differences among the larvae belonging to the same genus are not clear.

Apart from the 8 species of prawns, *Penaeus monodon, P. indicus, P. semisulcatus, Metapenaeus dobsoni, M. affinis, M. monoceros, M. brevicornis* and *Parapenaeopsis* *stylifera* whose larvae have been described in detail in this bulletin, the complete larval development of a number of species of penaeid prawns has been traced from eggs spawned in the laboratory in many parts of the world. The larval stages of *Penaeus Japonicus* (Hudinaga, 1942, *Japanese J. zool.*, 10 (2): 305-393[1]) *P. orientalis* (Oka, 1967, *Bull. Fac. Fish. Nagasaki Univ.*, 23: 71-87[2]), *P. latisulcatus* (Shokita, 1970, *Biol. Mag. Okinawa*, 6(8): 34-36[3]), and *Metapenaeus joyneri* (Lee and Lee, 1968, *Publ. Haewundae Marine Lab.* 1: 1-18[4]) from Japan, *Penaeus monodon* (Villaluz et. al., 1969, *Philippine J.Sci.*, 98 (3-4): 205-233[5]) from Philippines, *Metapenaeus bennette* (Morris and Bennet; 1951, *Proc. Linn. Soc. N. S. W.* 76: 104-82[6]), *Penaeus esculentus* (Fielder et. al. 1975, *Aust. J. mar. Freshw. Res.*, 26: 155-175[7]) from Australia, *Penaeus merguiensis* (Raje and Ranade, 1972, *J. Indian Fish. Ass.*, 2 (1&2): 1-16)[8] and *Metapenaeus monoceros* (Raje and Ranade, 1972 *J. Indian Fish. Ass.*, 2 (1 & 2): 30-46)[9] from India, *Penaeus trisulcatus, Parapenaeus longirostris* and *Sicyonia carinata*) Heldt, 1938, *Annl, Inst. Oceanogr. Monaco*, 18 (2): 31-206[10]), from the Mediterranean sea and *Penaeus setiferus* (Heegaard, 1953, *Publ. Inst. mar. Sci. Univ. Tex.*, 3 (1): 73-105[11]), *Penaeus duorarum* (Dobkin, 1961, *U. S. Fish. Wild. Ser. Fish. Bull.*, 61: 321-349[12]) *Penaeus aztecus* (Cook and Murphy, 1971, *U. S. Fish.Wildl. Ser. Fish. Bull.*, 69 (1): 223-239[13]), and *Sicyonia brevirostris* (Cook and Murphy, 1965, *Tulane Studies in Zoology*, 12 (4): 109-127[14]) from the Gulf of Mexico, have been described. A detailed study of the larval characters of the 8 Indian species presented in this Bulletin, and comparing them with the descriptions of the other species referred to above, has resulted in a clear understanding of the general pattern of development of the morphological features of the nauplius, protozoea, mysis and postlarval stages of the penaeid prawns and has brought to light certain generic characters by which the larvae belonging to the genera *Penaeus, Metapenaeus* and *Parapenaeopsis* could be identified. The earlier work of Cook (1966, *U. S.Fish. Wildl. Ser. Fish. Bull.*, 65 (2): (437-447)[15] on the generic characters of the penaeid larvae of the Gulf of Mexico region does not cover the typically Indo-Pacific genera. *Metapenaeus* and *Parapeneopsis* which are [of great commercial importance in the latter region. This lacuna was partly filled by the work of Haq and Hassan (1975, *Pakistan J. zool.* 7 (2): 145-159[16]), who have described some of the generic characters of the larvae belonging to the genera *Penaeus, Metapenaeus* and *Parapenaeopsis* from Pakistan waters. However, during the present study we have found additional morphological features which appear to be characteristic of these three genera. Further we have found for the first time some characters by which even the nauplius stage of these three genera can be distinguished. The larvae of different species belonging to the same genus, however, are so similar that specific identification of the larvae is not possible, except for some stages of *Metapenaeus*. A summary of our observations on penaeid larval development is presented here.

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EGG STAGE

A very narrow perivitelline space (about 15 microns in width) appears to be characteristic of the eggs of all the species of *Penaeus* described so far. The eggs of *Metapenaeus* species (except *Metapenaeus dobsoni*) possess a narrow perivitelline space of 20 to 30 microns in width. The eggs of *M.dobsoni* are peculiar in having a very wide perivitelline space which is about 85 microns in width. The perivitelline space of the eggs of *Parapenaeopsis stylifera* is 60 microns wide. The diameter of the yolk mass was more or less the same (0.22 - 0.24 mm) in all the 8 species of penaeid eggs studied by us, the differences in the egg diameter being due to differences in the width of the perivitelline space which develops only after fertilization. The differences observed in the duration of the embryonic stage were due to differences in the rearing temperature; the eggs of *M. brevicornis* hatched out in 9 hours while the eggs of *P.indicus* took 16-17 hours to hatch out, the rearing temperature being 29.2 to 30.8° C in the former case and 24.4 to 26.8°C in the latter.

NAUPLIUS STAGE

The nauplii of all the penaeids studied passed through 6 nauplius substages which could be distinguished on the basis of the number of furcal setae as follows:-

Stage:	N I	N II	N III	N IV	N V	N VI
Furcal setae:	1+1	1+1	3+3	4+4	6+6	7+7

In N III the inner pair of furcal setae are very minute and ventrally placed and could be easily overlooked when viewed from the dorsal side. Similarly in N IV the outermost pair of setae is minute and placed a little dorsally and could be missed when viewed from the ventral side.

In N V the outermost pair is minute and placed a little dorsally on the lateral margin and could be missed when seen from the ventral side. This may account for the variation in the number of nauplius substages recognised by the earlier workers. While the first 4 nauplius substages are passed through rapidly (3 to 6 hours) the larvae linger for a longer time in N V (10 to 12 hours) and N VI (15 to 24 hours).

In N I the A1 bears terminally 2 long seta and a minute setal rudiment on the inner ange, and a long lateral seta on the outer distal marle gin; this latter seta is actually dorsolateral in poisition; on the inner lateral margin there are 2 or 3 small setae which are actually ventrolateral in position; all the setae during this stage are non-plumose; they may have very short bristles which appear to be the developing setules. In N II the setae become plumose and the outer of the two long terminal setae and the outer disto-lateral seta are reduced in size and the minute setal rudiment develops into a short seta. In N III this latter seta becomes longer than the outer terminal seta and the outer distolateral seta becomes very thin and small. In N IV the inner terminal seta lengthens further and the thin outer distolateral seta disappears. In N V the inner terminal seta grows in length but is still shorter than the long middle terminal seta. In N VI 2 additional setae and a minute setal rudiment are added on outer distolateral margin. The 2 distolateral setae and the short outer terminal one appear to be actually aesthaetes. The A1 becomes indistinctly segmented in the proximal half in N VI.

In the A2 exopod also the pattern of development of the setae is similar in all the species. In N I there are 5 long setae along the inner and distal margin.

In N II the 4th seta from the proximal end acquires a characteristic bend distally and the seta is bifurcate beyond this bend in all the species observed during the present investigations. The bifurcate nature of this particular seta is retained in all the subsequent nauplius substages. The bifurcate seta was noted by Renfro and Cook (1963, *U. S. Fish wildl Ser. Fish. Bull.*, 63 (1): 165-177)[17] in the later nauplius substages of *Xiphopenaeus kroyeri*, as a variation. But it is invariably present in the nauplius of all the species studied here. An additional seta of A2 exopod was noticed to be bifurcate as a variation but the 4th seta was always bifurcate. The significance of the bifurcate nature of this seta is not clear. Perhaps, it may have some function associated with swimming and floating of the nauplius. For every naupliar moult the number of setae on the exopod increases atleast by the addition of one setal rudiment to the outer distal end or the transformation of a setal rudiment into a seta. In N IV, V and VI a short proximal seta is added to inner margin. The A2 exopod becomes indistinctly segmented from N IV onwards.

In the A2 endopod also the pattern of development of the setae is similar in all the species. In N I the endopod bears 2 short inner lateral setae and 2 long terminal setae and a minute setal rudiment on inner terminal angle. The latter becomes larger in N II and becomes a short seta in N III. A 4th terminal seta is added in N VI. In N VI the distal of the 2 lateral setae becomes longer and a short seta may be added to the base of this seta.

Md has 3 long terminal setae on the exopod and endopod in all the nauplius substages in all the species. From N IV a basal swelling develops; in N VI this swelling is very prominent and the cutting teeth of Md can be seen developing inside it. In N VI the endopod becomes empty and transparent.

Rudiments of Mx1, Mx2, Mxp1 and Mxp2 first appear in N III under the cuticle and become free in N V and acquire rudimentary setae in N VI.

The relative length of the inner lateral setae on A1 and the distribution of the disto-lateral setae (aesthaetes) on the outer margin of A1 in N VI provide certain diagnostic characters for distinguishing the nauplius belonging to the genera *Penaeus, Metapenaeus* and *Parapenaeopsis*. The nauplii of the 3 genera could be characterised as follows:-

Penaeus: A1 (Fig. 1,a) has only two inner lateral setae in N I to N IV, the distal seta being very long, a minute proximal seta may be added in N V or N VI; the very long distal seta is characteristic of the genus. Of the 3 distolateral aesthaetes the most distal is terminal while the other 2 are subterminal, the middle one being equidistant from the terminal and proximal ones.

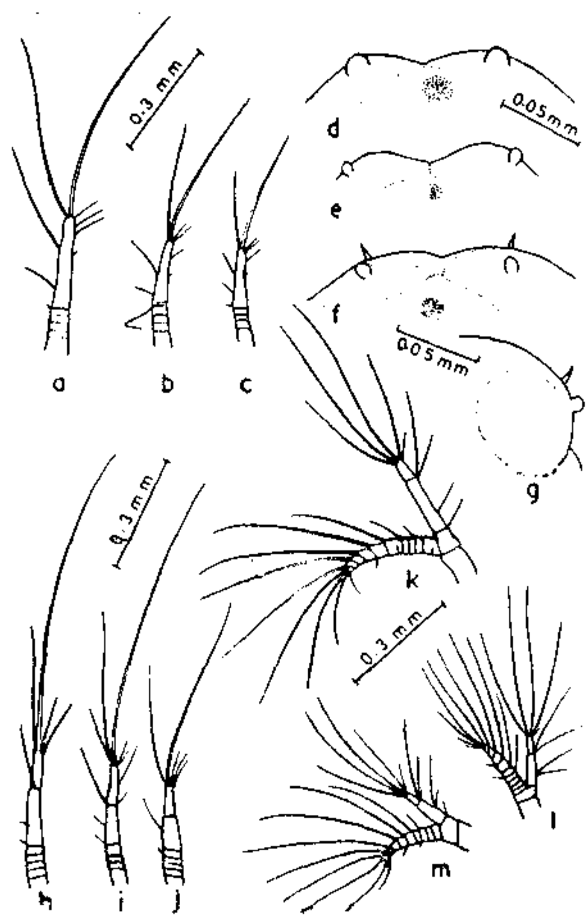

Fig. 1 A1 of Nauplius VI: a - *Penaeus;* b - *Parapenaeopsis;* C - *Metapenaeus*. Frontal organ (Ventral view) of protozoea I: d - *Penaeus;* e - *Parapenaeopsis;* f - *Metapenaeus;* g - lateral view of frontal organ of *Metapenaeus*. A1 of protozoea I; h - *Peneus;* i - *Parapenaeopsis;* j - *Metapenaeus*, A2 of protozoea I: k - *Penaeus;* l - *Parapenaeopsis;* m - *Metapenaeus*.

Metapenaeus: A1 (Fig. 1, c) has 3 short inner lateral setae in all the 6 nauplius substages; the size decreases gradually from the distal to the proximal seta; there is no change in the relative length of these 3 setae fron N I to N VI. Out of the 3 aesthaetes one is terminal and 2 are subterminal and dorsolaterally placed; the middle one is closer to the terminal one than to the proximal one.

Parapenaeopsis: A1 (Fig:1,b) has 3 inner lateral setae in all the 6 nauplius substages. Up to N III, the setae are short, slightly decreasing in length from the distal to the proximal one. But from N IV to N VI the proximal seta becomes thin and greatly elongated. It is directed posterolaterally and is so long that it overlaps its fellow on the other side and is sharply bent in distal 1/3. Pearson (1939, *Bull. U.S. Bur. Fish* 49 (30): 1-73[18]) has shown a thin long proximal inner lateral seta on the A1 of the nauplius of *Trachypenaeus constrictus*. But it is directed anterolateraly and is not as long as in *Parapenaeopsis*. This condition may be characteristic of the genus *Trachypenaeus*, emphasising the close affinity of these 2 genera. Further, the long proximal inner lateral seta is shown in the illustration of the late nauplius substages of *Xiphopenaeus kroyeri* given by Renfro and Coock[17]. It is likely that *Xiphopenaeus* is also phylogenetically close to the general *Parapenaeopsis* and *Trachypenaeus*. This is also borne out by the similarity of the basic pattern of the petasma and thelycum of these 3 genera.

PROTOZOEA STAGE

All penaeid larvae studied pass through 3 distinct protozoea substages. The transition from one substage to the next is marked by abrupt morphological changes. Protozoea I is devoid of rostrum, the eyes are sessile beneath the carapace and the pereopod buds are absent; in protozoea II the rostrum and pereopod buds develop and the eyes become stalked; in protozoea III the first five abdominal segments develop posteromedian dorsal spines, the 5th abdominal segment acquires a pair of posterolateral spines and the uropod buds are present. The intermoult growth of protozoea I, II and III first noticed by Hudinaga[1] in *penaeus japonicus* was observed in all the 8 species studied here. Lee and Lee (1969, *publ. Mar. Lab. Pusan Fish.Coll.* 2 : 19-25)[19] have found that unlike the embryonic and nauplius stages, whose duration is dependant mainly on the rearing temperature, the duration of the protozoea stage is also greatly influenced by the quality of food offered to the larvae. This finding is confirmed by our present studies.

Cook[15] used the following criteria to differentiate the protozoea substages of the penaeid genera: (1) relative length of A1 and A2, (2) nature of cleft of telson, (3) setation of A2 endopod, (4) shape of frontal organ, (5) presence or absence of Mxp3 bud and (6) presence or absence of supraobital spines. Haq and Hassan[15] indicated that the number of segments in A1 and the number of setae on A2 exopod are also of generic importance. During the present study it was found that the following criteria are also useful for distinguishing the genera (1) the disposition of the setae on the caudal furcae, especially that of the outermost pair and the pair medial to the longest pair and (2) the segmentation and setation of the endopod of Mxl and Mx2. On the basis of the above criteria the protozoea stages of the 3 genera *Penaeus, Metapenaeus* and *Parapenaeopsis* could be characterised as follows:

Penaeus: Frontal organs bluntly ronnded, not overhung by frontal horns](Fig.1,d). Rostium long and ventrally bent in protozoea II and III. Supraorbitals bifid in protozoea II (Fig.3,d) and simple in protozoea III. Telson with a shallow wide cleft (Fig.3,a), the outermost lateral setae dorsally disposed, the pair of setae immediately inner to the longest pair of setae, sigmoid in protozoea I. Protozoea III has 8 pairs of telsonic setae (Fig.3,m). In protozoea III posterolateral spines on 6th abdominal segment prominent. A1 and A2 almost equal in length; basal segment of A1 with 5 subsegments in protozoea I and II (Fig.1,h), A1 of Protozoea III 3 segmented (Fig.3,g), A2 endopod has 1+1+2 lateral setae and 5 terminal setae, one short and 4 long, exopod with 11 setae on inner and distal margin (Fig. 1,k). Endopod of Mx1 with 3 segments, the distal one with 5 terminal setae, the middle and basal segments with 2 and 3 inner lateral setae respectively (Fig.2,a). The endopod of Mx2 4 segmented, the distal segment with 3 terminal setae and the other 3 segments each with 2

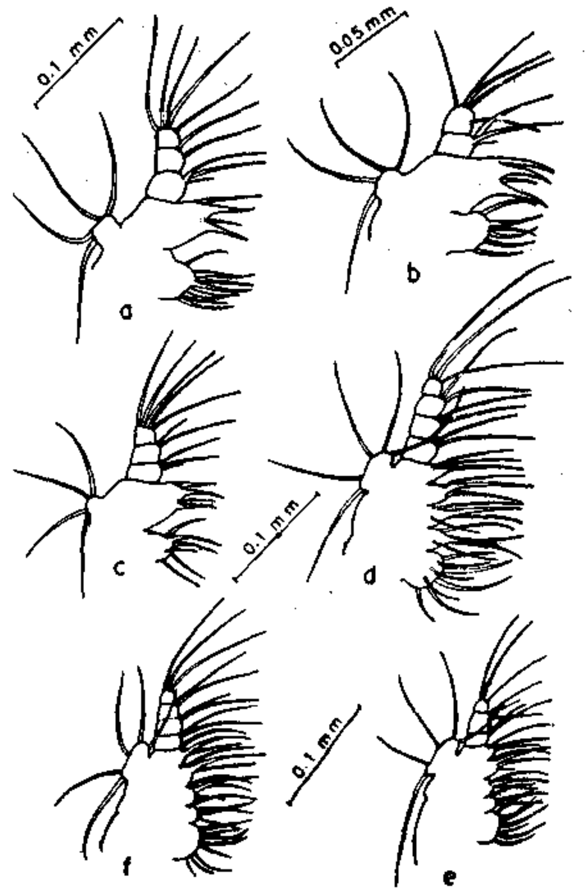

Fig. 2 Mx1 of protozoea I: a - *Penaeus;* b - *Parapenaeopsis;* c - *Metapenaeus.* Mx2 of protozoea I: d *Penaeus;* e - *Parapenaeopsis;* f - *Matapenaeus.*

long setae on inner margin (Fig. 2,d). Mxp3 buds absent in protozoea I and II and present in protozoea III with 2 setae on exopod bud alone (Fig.3,j). The protozoea substages of *Penaeus indicus, P. monodon* and *P. semisulcatus* are so similar that they cannot be distinguished from each other.

Metapenaeus: Rounded frontal organs usually overhung by pointed spine (Fig. 1,f,g); rostrum in protozoea II and III fairly long and ventrally bent. One pair of supraorbital spines present in protozoea II and III, those in protozoea II simple (Fig.3,f). Caudal furcae short and broad, with shallow and moderate cleft, outermost pair of furcal setae slightly ventrally disposed (Fig.3,c); the pair inner to the longest pair not sigmoid; only 7 pairs of setae in protozoea III (Fig.3,o) In protozoea III posterolateral spines on 6th abdominal segment minute. A1 and A2 almost equal in length. Basal segment of A1 with 5 subsegments in protozoea I and II (Fig.1,j), A1 of protozoea III 3 segmented (Fig.3,i). A2 endopod with 1+2+3 lateral setae and 5 terminal setae, 4 long and one medium; exopod with 10 setae on inner and distal margin (Fig.1,m). Endopod of Mx1 3 segmented, the distal segment with 5 terminal setae and the middle and basal segments with 2 and 3 inner lateral setae respectively (Fig 2,c). Endopod of Mx2 with 3 distinct segments, the large middle segment divided into 2 by indistinct segmentation, the distal segment with 3 terminal setae and the rest with 2 lateral setae each (Fig.2,f) Biramous bud of Mxp3 present even in protozoea I; in protozoea III this appendage bears 3 setae on exopod and 2 setae on endopod (Fig.3,l).

The protozoea I of *M. monoceros* differs from that of the other 3 species of *Metapenaeus* in having very minute frontal horns, smaller than the frontal organs; the frontal horns are prominent in *M. dobsoni*, *M. brevicornis* and *M. affinis*. Protozoea II and III of *M. dobsoni* and *M. brevicornis* are devoid of rostral platforms, while in *M. affinis*. and *M. monoceros* the rostral platform is well developed, with rounded anterolateral corners in the former and sharp spine-like anterolateral corners in the latter.

Parapenaeopsis : Frontal organs of protozoea I rounded (Fig.1,e) not overhung by pointed spine. Rostrum short and straight, supraorbital spines absent in protozoea II and III (Fig.3,e). Posterolateral spines on 6th abdominal segment inconspicuous in protozoea III. Cleft in telson deep and wide, the caudal furcae narrow and long, the outermost pair of setae laterlly disposed and separated from the penultimate pair by a wide gap, the pair of setae immediately medial to the longest pair not sigmoid (Fig 3,b). A1 distinctly longer than A2. Basal segment of A1 with 4 subsegments in protozoea I (Fig 1,i) and 3 subsegments in protozoea II, A1 of protozoea III 4 segmented (Fig.3,h). Lateral setae on A2 endopod 2 + 2, terminally with 4 long plumose setae and 1 short hair-like seta, exopod with 10 setae along inner and distal margin (Fig.1,l). Mx1 with 2 segmented endopod (Fig.2,b), the distal segment with 4 terminal setae and one lateral seta in the middle, the basal segment with 3 lateral setae. Mx2 (Fig.2,e) with 3 segmented endopod, distal segment with 3 terminal setae, the middle segment with 2 distolateral setae and one lateral seta springing from the middle of the segment and the basal segment with 2 lateral setae. Biramous bud of Mxp3 present even in protozoea I, in protozoea III this appendage bears 3 setae on the exopod and 2 setae on the endopod (Fig.3,k).

MYSIS STAGE

Unlike the protozoea substages, the transition from one mysis substage to the next appears to be a very gradual one marked only by the increase in body length and the increase in number of setae in many of the appendages. The number of mysis substages appears to vary in the different penaeid genera. Only 3 mysis substages have been observed in all the species of the genus *Penaeus* studied so far(Heldt[10] , Hudinaga[1] , Cook and Murphy [13] , Villaluz[5] , Raje and Ranade[8] , Fielder *et. al*[7] , Silas *et. al*., *Bulletin CMFRI* No.28 [20] , Muthu *et. al*., *Bulletin CMFRI* No.28[21] , Devarajan *et. al*, *Bulletin CMFRI* No.28[22]). But 4 to 6 mysis substages for species of the genus *Metapenaeus* (Morris and Bennet[6] ; Raje and Ranade[9] ; Muthu, *et. al*. 1979 *M. dobsoni*, *Bulletin CMFRI* No.28[23]; Muthu *et. al*. 1979, *M. affinis*, *Bulletin CMFRI* No.28[24] Mohamed *et. al*, 1979 *M. monoceros Bulletin CMFRI* No.28[25]), 7 substages for *Parapenaeopsis* (Muthu *et al*; 1979, *Parapenaeoposis stylifera Bulletin CMFRI* No.28[26]), 4 substages for *Sicyonia* (Cook and Murphy[14]), and 14 substages for *Parapenaeus* (Heldt[10]) have been described.

In the laboratory cultures where the larvae are grown under crowded conditions, the lack of suitable and sufficient food for the larvae and the accumulation of metabolites in the medium may affect the moulting frequency of the larvae and thus lead to variability in the number of substages. Broad (1957, *Biol. Bull.* 112: 144-161[27] ; 1957. *Biol Bull.* 112:162-170[28]) found that the number of zoea stages and the duration of the larval period of the caridean prawn *Palaemonetes Pugio* and *P.vulgaris* increased when the larvae were reared on unsuitable diets. Broad [27] opined that since trophic conditions may vary in nature during the breeding season of the species, a possible response to sub-optimal conditions might be prolonged larval life with a greater number of larval intermoults. Pike and Williamson (1964, *Crustaceana*:6:265-284[29]) also found that under certain conditions larvae of *Pandalus motagui* reared in the laboratory passed through several addifional zoea substages before moulting to megalopa. To what extent the environmental factors contribute to the variability of the number of mysis substages in penaeids is not known at present. In the case of *Sicyonia brevirostris* Cook and Murphy[14] found that the number of substages present in a large volume of planktonic material from the sea was the same as that found among laboratory reared larvae. One of us (M.S.M.) has also recorded 6 mysis substages of *Parapenaeopsis stylifera* from the inshore plankton at Madras; this is in close agreement with the 7 substages observed by us in the mass culture of larvae of *P. stylifera* at the Narakkal Prawn Culture Laboratory. Such observations suggest that the increased number of mysis substages found by us during the laboratory rearing of *Metapenaeus* and *Parapenaeopsis* species may be normal for the respective species even in the natural environment.

It is quite likely that the mysis substages of penaeid prawns, like the fureilia stages of euphausids with which they have been equated by Gurney (1943, *Ray. Soc. Lond. Monogr*, 129, 1-306)[30], exhibit the phenomena of "dominant stages" and "skipping of stages". Silas and Matthew (1977, *Proc. Symposium* on *Warmwater Zooplankton*, *Special publ*, NIO, Goa, 171-182[31]) have reviewed these concepts as far as euphausids are concerned and it appears possible that they are applicable to penaeid mysis substages as well.

The flexibility in the development of the mysis substages of penaeids is interesting from another point of view. The ability of some species to moult into a number of mysis substages may have survival value. We found that while rearing the mysis larvae of *P.indicus*, *P.monodon* and *P.semisulcatus*, which had only 3 mysis substages, if the conditions were not optimal, mass mortalities were more frequent, than in the case of the other species such as *M. dobsoni*, *M.affinis*, *M.monoceros* and *P.stylifera* which had 5 to 7 mysis substages. Even in nature when the conditions are unfavourable the larvae of these latter species may linger for a longer time in the plankton by moulting into these 5 to 7 mysis substages and thus gain time till the conditions improve.

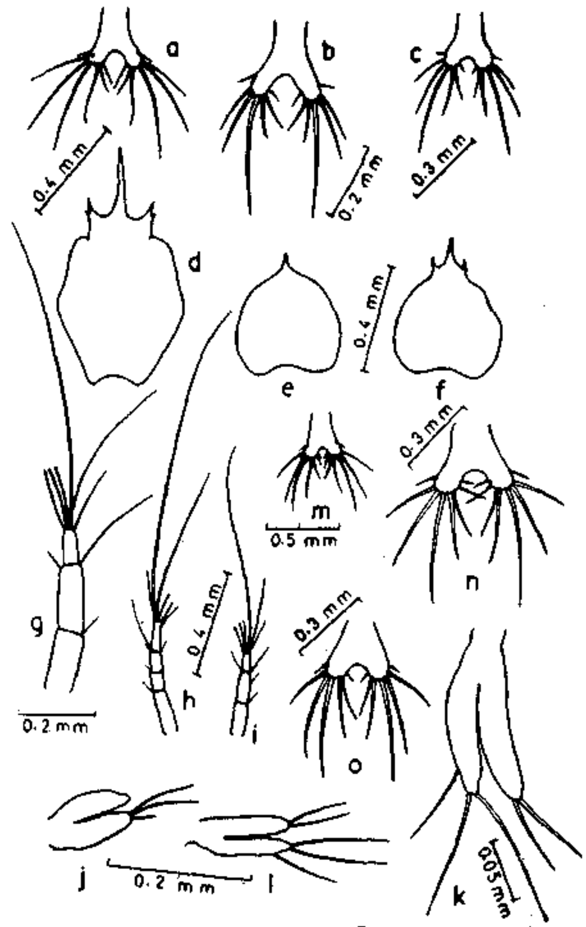

Fig. 3 Telson of protozoea I: a - *Penaeus;* b - *Parapenaeopsis;* c - *Metapenaeus.* Carapace of protozoea II: d - *Penaeus;* e - *Parapenaeopsis;* f - *Metapenaeus.* A1 of protozoea III: g - *Penaeus;* h - *Parapenaeopsis;* i - *Metapenaeus;*. Mxp3 of protozoea III. j - *Penaeus;* k - *Parapenaeopsis;* l - *Metapenaeus.* Telson of protozea III: m - *Penaeus;* n - *Parapenaeopsis;* o - *Metapenaeus.*

Mysis I in all the 3 genera viz *Penaeus*, *Metapenaeus* and *Parapenaeopsis* appears to possess the following features which are not shared by the succeeding substages. (1) the scaphocerite has an outer distolateral seta instead of a spine as in the subsequent substages, (2) Mx1 retains the exopod with 4 feathery setae, (3) Mxp2 has a 4 segmented endopod with 5 terminal setae, in subsequent stages the endopod is 5 segmented and there are

6 terminal setae on distal segment, (4) the protopod of A2 does not bear an anteroventral spine, which is present from mysis II onwards.

Cook[19] used the spination of the carapace and abdomen to identify the mysis stage of the different genera. Haq and Hassen[15] found that the segmentation of the flagellar rudiments of A1 and the segmentation of A2 flagellum are also useful for this purpose. During the present study the following additonal criteria were recognised, (1) Mx1 and Mx2 retain the peculiarities that were noted in the protozoea stage. (2) In Mxp1 the setation of the exopod is constant from the 1st to the last mysis substage and appears to be characteristic for each genus. (3) the number of setae on the exopod and endopod of the pereopods also provide useful criteria for distinguishing the genera. (4) the outer distolateral spine on the exopod of the uropod is also peculiar to each genus. Although Paulinose (1977, *Proc. Symposium of Warmwater Zooplankton, Special publ.* NIO Goa[13]) felt that the structure of the asymmetrical Md during the mysis stage could be used to distinguish some genera, a careful examination of the Md during the present study did not reveal any consistent difference in the 3 genera studied by us.

The mysis stage of *Penaeus, Metapenaeus* and *Parapenaeopsis* could be distinguished on the basis of the following diagnostic characters.

Penaeus: Carapace with prominent supraorbital (Fig.4,a) pterygostomial and hepatic spines, antennal spine absent. Abdominal segments 3 to 6 with dorsomedian spines, 5th and 6th segments each with prominent posterolateral spines, the dorsomedian spines on segments 3-5 are variable in size and may be absent on segments 3 and 4 in mysis II and III. Mx1 with 3 segmented endopod with 5 terminal setae on distal segment, 2 lateral setae on middle segment and 3 lateral setae on basal segment, Mx2 with a 4 segmented endopod, with 3 terminal setae on distal segment and 2 lateral setae on each of the 3 other segments. Mxp1 (Fig.4,g) with 10 - 12 setae on exopod. Endopod of pereopods (Fig.5,a,d) with short lateral setae exopod of pereopods with 2+4+2 or 1+4+2 distal setae. Uropod with outer margin of exopod (Fig.5,g) produced into a very prominent distolateral fixed spine beyond which the fringing setae are arranged, the outermost member of this series of setae is shorter than the distolateral spine and is nonplumose. Only 3 mysis substages; mysis I with minute pleopod buds; in mysis II the pleopod buds are well developed with a constriction in the middle; in mysis III the pleopods become clearly 2 segmented. The mysis substages of *P. Indicus, P. monodon* and *P. semisulcatus* are so similar that they cannot be distinguished from one another.

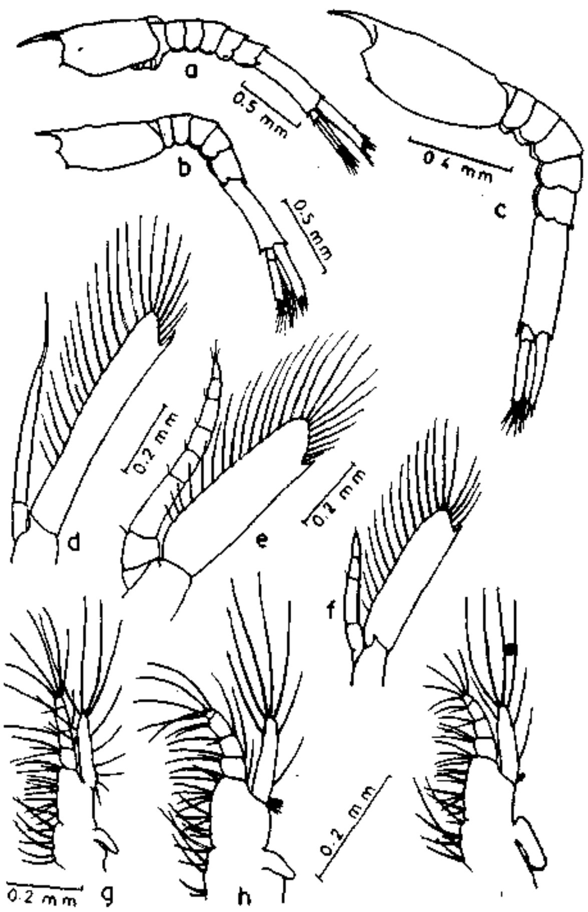

Fig. 4 Lateral view of carapace and abdomen of Mysis 1: a - *Penaeus;* b - *Parapenaeopsis;* c - *Metapenaeus.* A2 of last Mysis: d - *Penaeus;* e - *Parapenaeopsis;* f - *Metapenaeus.*

Metapenaeus: Carapace without supraorbital spine (Fig.4,c), but with antennal and pterygostomial spines, hepatic spines usually absent in mysis I but appear in later substages. Only abdominal segments 5 and 6 with dorsomedian spines; no lateral spines on any segment. Mx1 with 5 terminal setae on distal segment, 2 on middle segment and 3 on basal segment. Mx2 endopod with 4 indistinct segments bearing 3 terminal setae on distal segment and 2 lateral setae on each of the other 3 segments. Mxp1 with 7 setae on exopod and 2-3 small hairs proximal to the outermost seta (Fig.4,i). P1-P5 with a long outer lateral seta on endopod from mysis II onwards, exopod of P1-P5 with 2+4+2 distal setae (Fig.5,c and f). On exopod of uropod the distolateral spine which is a continuation of the outer margin is absent in mysis I and is very small in subsequent stages, being shorter than the outermost movable non-plumose seta (Fig.5,i). May have up to 6 mysis substages.

Mysis I of *M. brevcicornis* can be distinguished from that of the other 3 species of *Metapenaeus* by the presence of distinct though small supraorbital spines on the carapace. Mysis I of *M. dobsoni* has a minute pair of supraorbital spines on the anterior border of carapace, the dorsomedian spine on the fifth abdominal segment is minute. In *M. affinis* and *M. monoceros* the supraorbital spines are totally absent in mysis I and the dorsomedian sipne on 5th abdominal segment is large and well developed.

Parapenaeopsis: Carapace with small supraorbital spine at least in mysis I; hepatic spine absent in all mysis stages; antennal and pterygostomial spines present (Fig.4,b). Abdominal segments 5 and 6 with dorsomedian spines; mysis I may have a vestigial posterolateral spine in the lower half of the 5th abdominal segment; no lateral spines on 6th abdominal segment. Mx1 with short and stumpy 2 segmented endopod with 4 terminal setae and one lateral seta on distal segment and 3 lateral setae on basal segment. Mx2 with short and stumpy 3 segmented endopod with 3 terminal setae on distal segment and one lateral and 2 distolateral seta on middle segment and 2 distolateral setae on basal segment. Mxp1 with 7 setae on exopod and a cluster of hair like setules proximal to the outermost seta (Fig.4,h). P1-P5 with a very long outer lateral seta on endopod from mysis I onwards (Fig.5,b,e), exopod setae increasing in number from 3+4+3 in mysis I to 6+4+6 in last mysis substage. Exopod of uropod lacks the fixed distolateral spine in all mysis substages (Fig.5,h), the outermost member of the fringing setae on the exopod is nonplumose. May have 7 or more mysis substages.

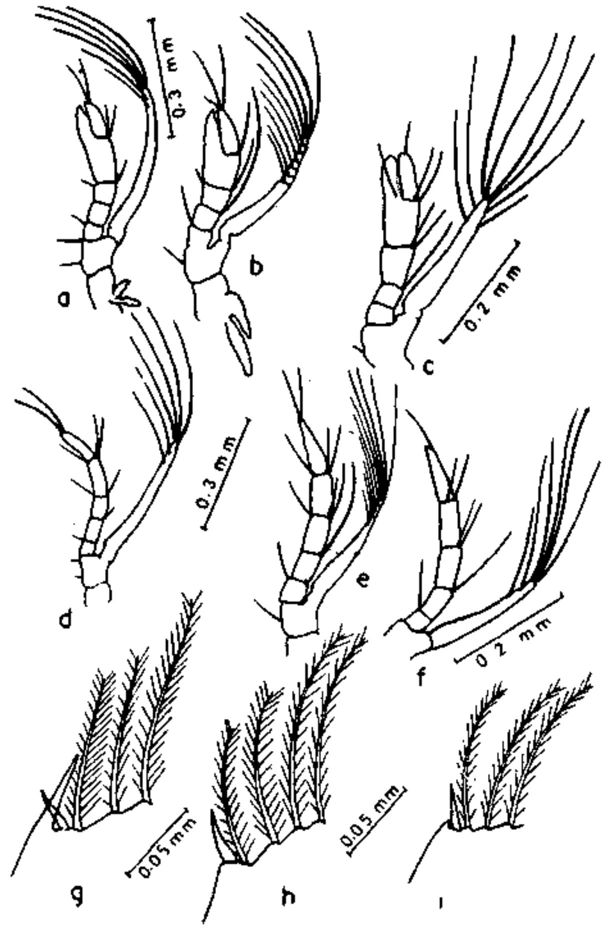

Fig. 5 P1 of last Mysis: a - *Penaeus;* b - *Parapenaeopsis;* c - *Metapenaeus* P5 of last Mysis: d - *Penaeus;* e - *Parapenaeopsis;* f - *Metapenaeus.* Outer distal margin of exopod of uropod of last Mysis: g - *Penaeus;* h - *Para penaeopsis;* i - *Metapenaeus.*

The mysis substages of *Trachypenaeus fulvus* described by Kirkegaard (1969, *Fish. notes Dept. of Harbour and Marine* Queensland,. 3(1): 15-25[33]) from the plankton appear to belong to some species of *Parapenaeopsis* due to the following reasons: (1) in the mysis substages the endopod of Mx1 has 4 terminal setae on distal segment and 1 seta on middle segment, (2) the Mx2 in the mysis stage has an endopod described as typical of *Parapenaeopsis* in the above paragraph.

POSTLARVAL STAGE

Since the number of postlarval stages appears to be very large (about 20) and we cannot say when the postlarval stage ends and the juvenile stage begins, the present discussion is confined to the early (first 1 or 2) postlarval stage. When the last mysis metamorphoses into postlarva I the following changes take place; (1) The pleopods acquire plumose setae for swimming, (2) the exopods of Mxp2 and Mxp3 and P1-P5 lose the plumose setae and become shrunken (3) the endopods of Mx1, Mx2 and Mxp1 become highly reduced (4) the free standing teeth between the incisor and molar processes of the Md are replaced by a sharp cutting edge, the Md palp becomes segmented and setose (5) endopod of Mxp2 becomes recurved and (6) the chelae on P1 to P3 become functional and the long plumose setae on the endopods are lost. But during artificial propagation, the last mysis may moult into 1 or 2 intermediate substages which have setose on pleopods but retain many of the characters of the mysis stage such as the free standing teeth in Md and plumose exopods of Mxp2, Mxp3 and P1 to P5.

The spination of the carapace, abdominal segments and telson proved useful in the generic identification of the early postlarvae. The diagnostic features are given below:

Penaeus: The postlarvae are long and slender. Rostrum long with 1 or 2 dorsal spines, supraorbital and hepatic spines present on carapace, posterodorsal and posterolateral spines present on 5th and 6th abdominal segments (Fig.6,a). Telson with 8 pairs of setae. Scaphocerite long and narrow, broader anteriorly than proximally (Fig.6,g); A2 flagellum shorter than scaphocerite. A1 flagella 2-3 segmented (Fig.6.d) Md palp cylindrical with distal segment smaller than and of same width as, proximal segment (Fig. 7,a).

The postlarva I of *P. indicus, P. monodon* and *P. semisulcatus* are morphologically alike.

Metapenaeus: Postlarvae small, rostrum short with 2 dorsalspines+1 epigastric spine (Fig.6,c). Hepatic spine present but no supraorbital spine. Dorsal spine present only on 6th abdominal segment. no lateral spines on any abdominal segment: Telson with 7 pairs of setae. Scaphocerite uniformly broad in distal and proximal halves (Fig.6.i), A1 flagella 2 segmented (Fig.6,f), Md palp club shaped, distal segment broader than proximal (Fig.7,c). The blunt rostral tip of postlarva I is characteristic

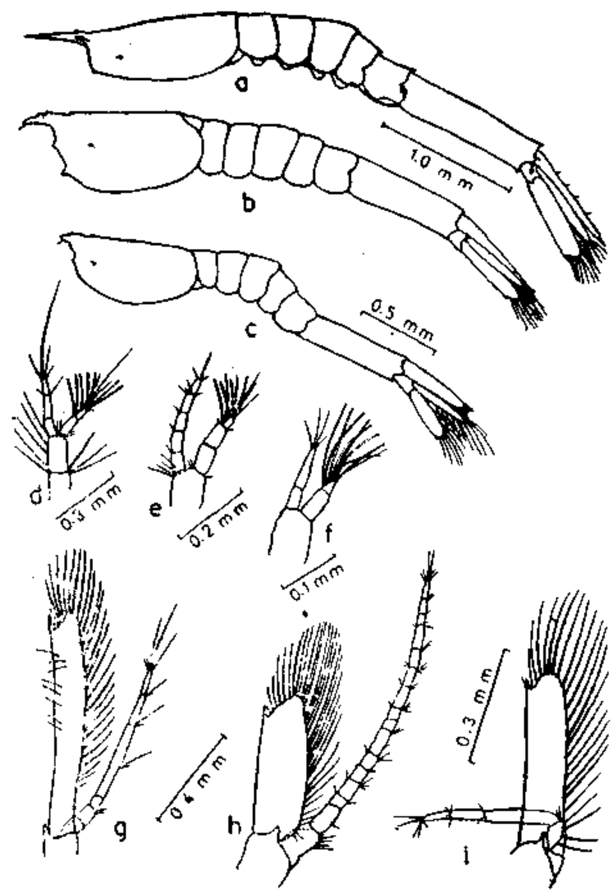

Fig. 6 Lateral view of carapace and abdomen of postlarva - I: a - *Penaeus;* b - *Parapenaeopsis;* c - *Metapenaeus* A1 Flagella of postlarva I; d - *Penaeus;* e - *Parapenaeopsis;* f - *Metapenaeus.* A2 of postlarva I: g - *Penaeus;* h - *Parapenaeopsis;* i - *Metapenaeus.*

of *M. dobsoni;* the rostral tip is sharply pointed in *M. affinis* and *M. monoceros.*

Parapenaeopsis: Postlarvae stout. Rostrum short and curved (Fig.6,b), tip produced into a blunt tooth from which 2 long ventral plumose setae arise. 2-3 rostral spines+1 epigastric spine. Hepatic spine present. Supraorbital spine absent. No dorsal or lateral spines on 1-5 abdominal segments, dorsal spine present on 6th abdominal segment. Telson with 8 pairs of setae and a posteromedian spine. Scaphocerite short and broad (Fig.6,h), broader proximally than anteriorly; A2 flagellum longer than scaphocerite with more than 10 segments. A1 flagella 3-5 segmented (Fig.6,e). Md palp (Fig.7,b) with a large oval distal segment and a smaller triangular proximal segment.

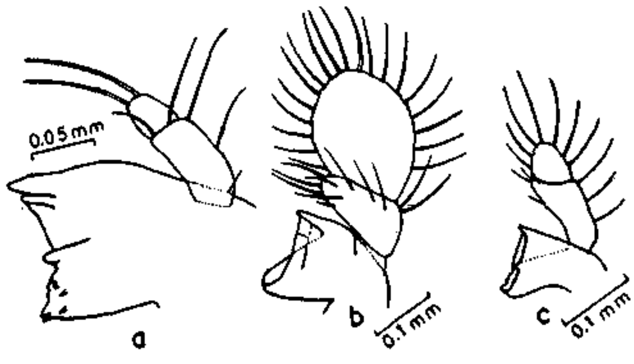

Fig. 7 Md. of postlarva I: a - *Penaeus;* b - *Parapenaeopsis;* c - *Metapenaeus.*

A generic key for the various larval stages is given below:

NAUPLIUS

1 a. The proximal inner lateral seta of A1 longer than the 2 anterior ones and filamentous in N IV to N VI............. *Parapenaeopsis*

1 b. The proximal inner lateral seta of A1 shorter than the 2 anterior ones in N IV to N VI 2

2 a. The anterior most inner lateral seta in A1 very long; the posterior most inner lateral seta absent or rudimentary in N I to N III. In the N VI the 3 aesthaetes on the outer distal margin of A1 equally spaced i. e. the middle one is equidistant from the distal and proximal ones................................ *Penaeus*

2 b. The size of the 3 inner lateral setae on A1 decreases gradually from the anterior to the posterior one. In N VI the 3 aesthaetes on the outer distal margin of A1 not equally spaced, the 2 anterior ones closer to each other than to the posterior one................................ *Metapenaeus*

PROTOZOEA I

1 a. A2 exopod with 11 setae along inner and distal margin, endopod with 1+1+2 lateral setae; outermost furcal seta dorsally disposed ....*Penaeus*

1. b. A2 exopod with 10 setae along inner and distal margin, endopod not with 1+1+2 lateral setae. Outermost furcal seta ventrally or laterally disposed.................2

2. a. A2 endopod with 1+2+3 lateral setae, Frontal horns usually present above frontal organs. Caudal furcae separated by shallow semicricular space, outermost furcal seta slightly ventrally disposed .... *Metapenaeus*

2. b. A2 endopod with 2+2 lateral setae. No frontal horns above the frontal organs, caudal furcae separated by deep ʌ shaped space; outermost furcal seta laterally disposed and widely separated from the penultimate outer seta .. . *Parapenaeopsis*

PROTOZOEA II

1. a. Supraorbital spines absent..................... *Parapenaeopsis*

1.b. Supraorbital spines present......... 2

2.a. Supraorbital spines bifid ....*Penaeus*

2.b. Supraorbital spines simple...*Metapenaeus*

PROTOZOEA III

1.a. Telson with 7+7 furcal setae .... *Metapenaeus*

1.b. Telson with 8+8 furcal setae 2

2.a. A1 4 segmented, supraorbital spine absent .... *Parapenaeopsis*

2. b. A1 3 segmented, supraorbital spine present .... *Penaeus*

MYSIS STAGE

1. a. 5th abdominal segment with a pair of posterolateral spines. Dorsal spines present on 4th, 5th and 6th abdominal segments; sometimes on 3rd segment also .... *Penaeus*

1. b. 5th abdominal segment devoid of posterolateral spines. Dorsal spines present only on 5th and 6th abdominal segment..... 2

2. a. Telson with 7+7 spines. Hepatic spine present in later mysis substages. . ... *Metapenaeus*

2. b. Telson with 8+8 spines. Hepatic spine absent in all mysis substages.......... ... *Parapenaeopsis*

EARLY POSTLARVAE (up to P2)

1. a. 5th abdominal segment with posterodorsal spine................................ *Penaeus*

1. b. 5th abdominal segment without posterodorsal spine 2

2. a. Telson with 7 pairs of spines.............. *Metapenaeus*

2. b. Telson with 8 pairs of spines on either side of a median spine .. *Parapenaeopsis*

REMARKS

It is likely that many of the characters noted under the various larval stages of each genus may have suprageneric significance especially in the nauplius and protozoea stages and when the detailed morphology of the larvae of more penaeid genera are worked out they may throw interesting light on the phylogenetic relationships of the various genera. The following features are likely to be of interest in this connection: (1) the setation of A1 and A2 in the nauplius stage, (2) the number of subsegments present in the basal segment of A1 in the protozoea stage, (3) the segmentation and setation of the endopods of Mx1 and Mx2 in the protozoea and mysis stages and (4) the setation of the exopod of Mxp1 in the mysis stage.