Chamberlain, 1961

CHESAPEAKE BAY INSTITUTE
The Johns Hopkins University

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D. W. Pritchard
Director

PREFACE

Because of the unique properties of estuaries, both physical and biological, many of the methods and concepts used in biological studies in the open ocean are not applicable in estuarine work. One of the biological properties of estuaries making them distinct from the open ocean is the relative abundance of planktonic larvae. These larvae play an important role in many aspects of estuarine ecology. Some areas of study most affected are discussed below.

Gross trophic relations in estuarine plankton are quite different from those occurring in marine plankton. Copepod populations are generally considered of primary importance in studying trophic relations in oceanic plankton; however, in estuaries it is probable that during much of the year planktonic larvae are far more important in grazing and total biomass than are copepods or any other holoplanktonic form. This might be expected since estuaries are restricted and generally support a large bottom fauna, many species of which spawn at about the same time of year and release great numbers of planktonic larvae. The observed retention of larvae in estuaries (Pritchard, 1952; Bousfield, 1955) further increases their concentration.

The relationships between phytoplankton and planktonic larvae are extremely complex, concerning as they do not only the limits imposed on the phytoplankton population by

grazing, but also the influence of the phytoplankton on the developmental pattern of the larvae. For example, in some decapods (Broad, 1957) the time required for larval development is dependent on the phytoplankton to which they are exposed. This relationship then becomes important in the dynamics of estuarine bottom communities since in these communities it has often been found that the time of larval metamorphosis is of great importance in the success of the new year class.

Basic to all of the above studies is the ability to identify planktonic larvae. At the present time a great many planktonic larvae have not been discribed. Detailed descriptions are also of importance to decapod systematics. Gurney (1942) remarks, "...until our knowledge of these larvae is very much more complete than it is now the evidence to be drawn from them is weak, (but) it should hardly need to be argued that the larval stage must ultimately be taken into account." With this consideration in mind research was begun in the laboratory on the larval ecology of estuarine members of a family in the Brachyura, the true crabs.

This report concerns research on aspects of the development of some larval crabs of the family Xanthidae hatched and reared in the laboratory. Portions of this study were supported by a Summer Research Fellowship from Woods Hole Oceanographic Institution, a Summer Research Grant from the National Science Foundation awarded through Duke Marine Laboratory at Beaufort, North Carolina, and a

research contract between the Biology Branch, Biological Sciences Division, Office of Naval Research and the Chesapeake Bay Institute, The Johns Hopkins University.

INTRODUCTION

Brachyuran ontogeny consists of a series of discrete stages in the development of the individual from the time of emergence from the egg until the form of the adult is assumed. As is common in marine invertebrates, these stages are named for genera which were erected with the belief that larvae taken from the plankton were previously undescribed adults. These stages are: prezoea, (sometimes completed before hatching) in which the larvae are covered with the embryonic cuticle; zoeae, a number of stages characterized by rudimentary pereiopods (the walking legs of adult crabs) and swimming by means of maxillipeds (accessory mouth parts in the adult); megalopa, a post-larval stage in which the pereiopods are well developed and the maxillipeds are no longer modified as swimming appendages. From the megalopa, the individual moults to a virtually adult-like form, the first crab stage. The zoeal stages are entirely planktonic, the megalopa swims readily but can crawl, and, in the Xanthidae, the crab stages do not swim at all.

Two descriptions of the larvae of Neopanope texana sayi have been published. Birge (1883) described various stages in the development of the larvae to the first crab stage. Due to difficulties in culturing the zoeae, his study was based largely on material collected from the plankton. Thus the first stage was obtained by hatching the eggs and was kept alive until it moulted to the second

stage. The second stage was then collected from the plankton and kept alive until it moulted to the third stage, and so on. This method was inherently poor since the complete larval development of no other decapod crustacean in the plankton with which he worked was known at that time. Birge described a prezoea, second zoea, third zoea, later zoea, last zoea, and at least four megalopal stages before metamorphosis to the first crab stage. Between each of these stages he describes many moults, some making little or no change in form. Birge gives no details of his culture methods or food of the zoeae.

Hyman (1925) was also unsuccessful in his attempt to raise the larvae through the zoeal stages. His description of larvae taken from the plankton differs significantly from that of Birge. He found a prezoea and four zoeal stages with only one moult between each stage. Hyman gives no information on the food of the larvae he studied.

In the description presented here, differences are noted in zoeae raised from known adults of the same species both in the same and in widely separated areas. It is hoped that this information will indicate the sort of diversity that can be expected in larvae of this species taken from the plankton.

Nothing has been published on the feeding of larvae of Neopanope texana. Several papers are concerned with the feeding of other crab zoeae, however. Lebour (1922, 1923) published studies on the food of larval Brachyura based on plankton collections and laboratory cultures. Lebour found

diatoms, mollusc larvae, echinoderm larvae and crustacea (including zoeae) in crab zoeae taken from the plankton. From these studies she concluded that the main food of crab zoeae was diatoms. She also stated that zoeae in the laboratory feed on organic detritus on the bottom of culture jars. Later (Lebour, 1928; Gurney, 1942) she found the best diet for culturing zoeae to be diatoms and living animal food.

Studies on feeding were undertaken with two objectives in mind. First, the food onwhich the larvae could develop had never been described since the larvae had never been reared. Second, the number of larval stages in some decapods (Broad, 1957 b; and Templeman, 1936 a, 1936 b) is known to be dependent on diet and the same phenomenon is thought to be true in others (Heegaard, 1953).

METHODS

Larvae of various Xanthid crabs were hatched in the laboratory from eggs carried by adult females collected by hand and by dredging in the vicinity of Beaufort, North Carolina. On hatching the larvae were removed and placed in polyethylene containers, fingerbowls, or Petri dishes. In every case where comparison is made between sets of cultures under different conditions, the culture dishes were the same.

The water used in culturing (salinity of 30‰ ± 2‰) was filtered through a stainless steel mesh with openings of 60 micra thus any nannoplankton existing in the water was available to the zoeae. The cultures were examined every day and the food and water in each culture changed. Once a week the culture dishes were sterilized with Clorox. Contaminating colonies of fungi and bacteria were rarely found. Upon detection these containers were sterilized with an ultraviolet germicidal lamp before being reused.

The temperature of some of the cultures was maintained at 21° ± 1.5° C with a water bath. The air temperature at the other cultures was recorded continuously with a thermograph and found to be 30° ± 2° C.

In various experiments larvae were fed nauplii of the brine shrimp Artemia salina, and clumps of the algae Nitzschia closterium, (Bacillareae) and Dunaliella euchlora, (Chlorophyta).

Larvae from individual cultures representing each stage were preserved in 3% formalin in sea water for morphological study. Appendages of the preserved specimens were removed by dissection with fine tungsten needles. Drawings were made with the aid of a Zeiss drawing attachment.

The species discussed here are Neopanope texana sayi (Smith,1869) Rathbun, 1898; Hexapanopeus angustifrons (Benedict and Rathbun, 1891) Rathbun, 1898; and Piluminus sayi Rathbun, 1897. These designations were confirmed by Dr. F. A. Chace of the United States National Museum. Since only one species in each genus is being discussed, the above species are referred to by generic name alone. It should be understood that these references refer only to the above species and not to the entire genus.

RESULTS

Feeding

Preliminary results (Chamberlain, 1957) indicated that the rate of larval development of Neopanope might be dependent upon the food source. There was an indication that larval development was more rapid in the presence of animal food than when only algae were available. The following experiment was designed to examine this relation more thoroughly.

Newly hatched larvae of Neopanope, Hexapanopeus and Piluminus were isolated in Petri dishes and divided into four groups, each with a different diet: (1) nauplii of Artemia, (2) nauplii of Artemia plus the algae Nitzschia and Dunaliella, (3) the algae Nitzschia and Dunaliella, and (4) no food. The food and water in each culture were changed every day. Figure 1 shows the duration of larval development through the zoeal stages of the experimental groups for the three species. It can be seen from this figure that in each species, zoeae which were fed both algae and Artemia required almost twice as much time for development as those fed only Artemia. No overlapping in developmental times was found between larvae maintained on the two diets.

Larvae which were not fed did not moult and did not survive more than 2 or 3 days. Those fed only unicellular algae did not moult and did not survive more than about 10 days. The group fed algae and Artemia completed zoeal

Table 1

Duration in days of each zoeal stage when cultured with different diets.

Diet	*Neopanope* stages				*Hexapanopeus* stages				*Piluminus* stages			
	1	2	3	4	1	2	3	4	1	2	3	4
Artemia	3-4	2	1-2	5	3	4	3	4	5	2-3	4	4-5
Artemia plus algae	6-8	5	3-6	9	5	7	6	9	8-9	4-5	7	8
Algae	9-10*				9*				8-9*			
No food	2-3 *				3*				2*			
Sample size	10				5				10			

* Died after this time

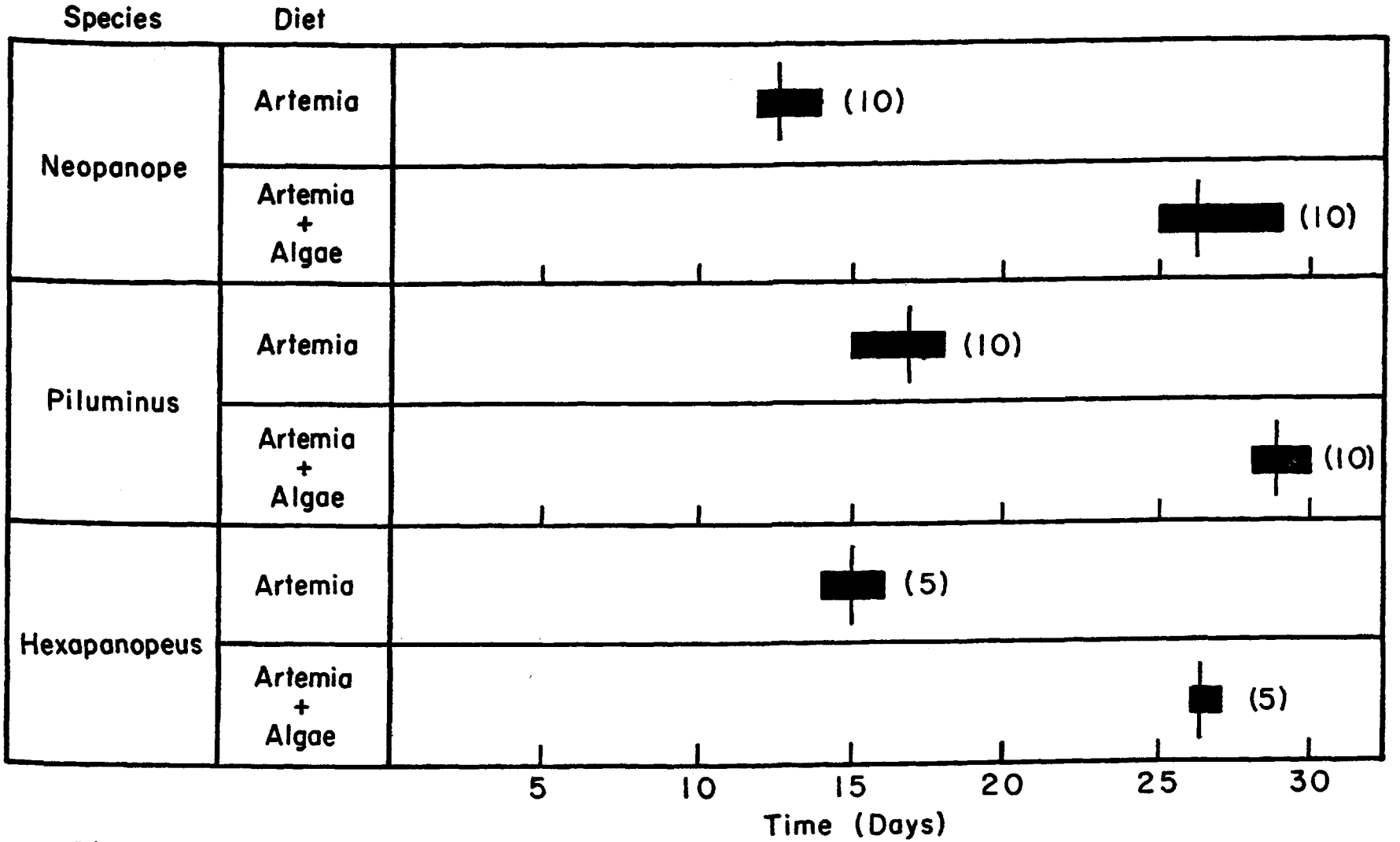

Figure 1. Duration of larval development through the zoeal stages when cultured with different diets. Horizontal bars represent ranges. Vertical lines represent means. Numbers are sample size.

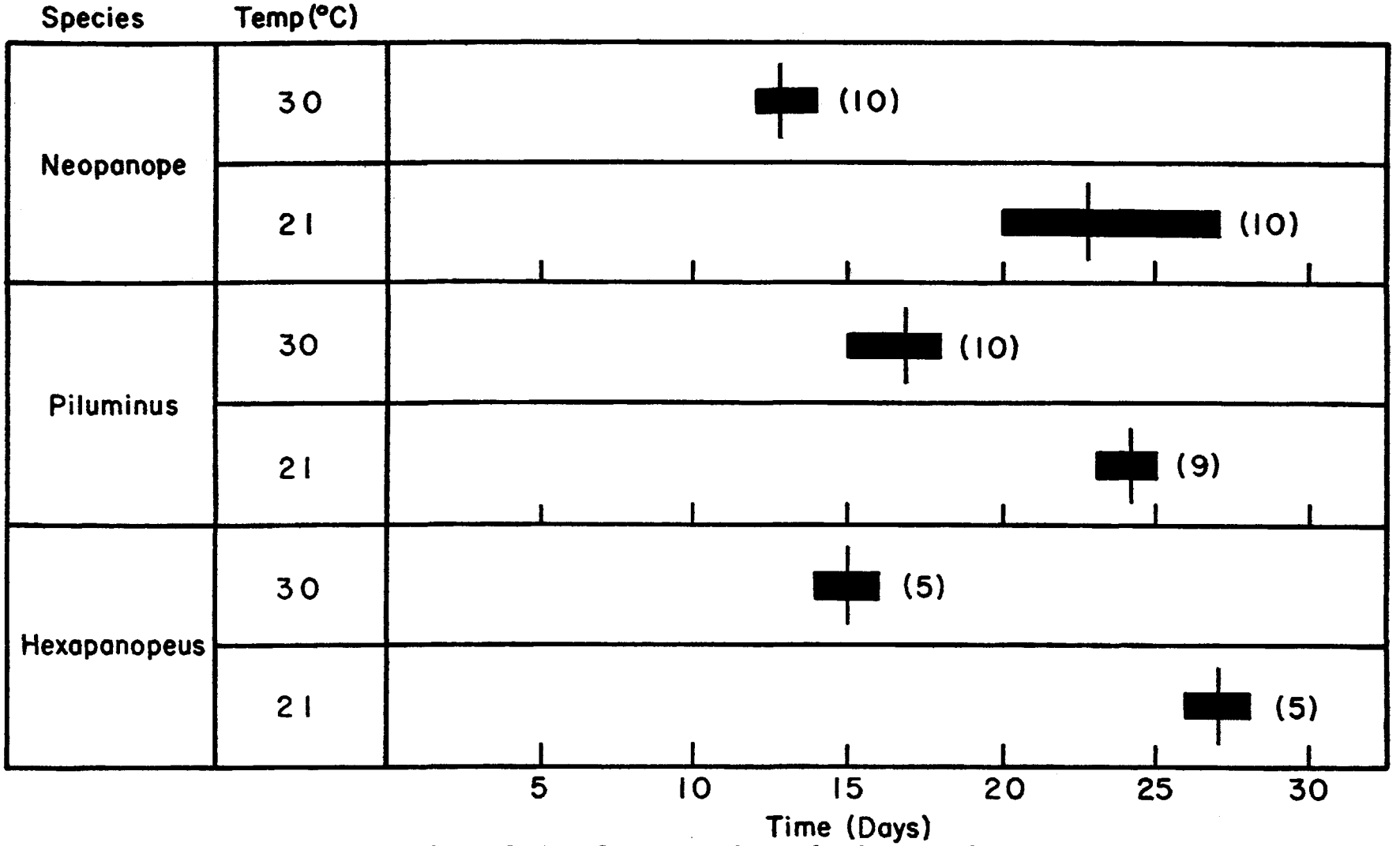

Figure 2. Duration of larval development through the zoeal stages when cultured at different temperatures. Horizontal bars represent ranges. Vertical lines represent means. Numbers are sample size.

Table 2

Duration in days of each zoeal stage at 30° C and 21° C.

Species	Temperature	Zoeal Stage 1	2	3	4	Total Duration Mean	Range	Sample size
Neopanope	30°	3-4	2-3	1-2	5	12.8	12-14	10
Neopanope	21°	7	4	2-7	7-9	22.7	20-27	10
Piluminus	30°	5	2-3	4-5	4-5	16.9	15-18	10
Piluminus	21°	6-8	4-7	4-7	6	24.2	23-25	9
Hexapanopeus	30°	3	4-5	3	4-6	15.0	14-16	5
Hexapanopeus	21°	5-6	8	5	8-9	27.0	26-28	5

development in about 26 days. Larvae fed only Artemia reached the megalopal stage in about 13 days. Table 1 shows the duration of the four intermoults for each species.

Some individuals of each species at each zoeal stage, having been fed only Artemia nauplii until that stage, lived only a few days when the diet was changed to algae. Individuals similarly changed from a diet of Artemia nauplii to the mixed diet (Artemia and algae) continued development at about the same rate as those that had been reared entirely with a mixed diet.

In every instance of completed larval development, there were four zoeal stages. No individual was found to have moulted without undergoing a change to the next zoeal stage. Also, no individual was found to have undergone change without moulting. No prezoeal stage was found in this study.

Temperature effects

Larvae of Neopanope, Hexapanopeus and Piluminus were reared on a diet of Artemia nauplii at 30° ± 2° C and 21° ± 1.5° C. Figure 2 shows the time for development to the megalopal stage for the three species at these temperatures. In each species it is clear that the higher temperature results in a shorter period of larval development. Table 2 shows the duration of the four intermoults for each species at the two temperatures at which cultures were maintained. It can be seen from this table that the increased rate of development at the higher temperature was not the result of an effect upon any particular larval stage.

Mortality

Of the 240 isolation cultures of Xanthids reared at 30° C with Artemia as food, approximately 80% survived. For Neopanope 160 isolation cultures were attempted. Twenty-seven (16.9%) died. Over half of these died in the moult from the fourth zoea to the megalopa. The mortality of each stage is given in Table 3.

The larvae taken for isolation cultures from the culture dish in which they had hatched were not picked at random. Only those swimming actively were taken. This selection probably lessened the early mortality in the isolation cultures. In mass cultures mortality during the first few days was very high.

Table 3

Mortality of *Neopanope* in isolation cultures at 30° C with *Artemia* as food.

Stage or moult	Mortality	% of 160 individuals
1st zoea	8	5.0
1st to 2nd stage moult	0	0.0
2nd zoea	1	0.6
2nd to 3rd stage moult	0	0.0
3rd zoea	0	0.0
3rd to 4th stage moult	3	1.9
4th zoea	0	0.0
4th stage to megalopa moult	15	9.4
megalopa	0	0.0
megalopal stage to first crab moult	0	0.0
Total	27	16.9%

DISCUSSION

In preliminary work at Woods Hole, Massachusetts, eggs from two female Neopanope hatched as prezoeae which moulted to the first zoeal stage in a very short time (15 seconds to 5 minutes). From 30 adult Xanthids including 11 Neopanope at Beaufort no larvae hatched as prezoeae. Both Birge and Hyman state that in their studies larvae hatched as prezoeae and did not moult for several hours. These differences may well be due to a variation in the salinity of the water in which the eggs were hatched. Sandoz and Rogers (1944) found that the eggs of Callinectes sapidus hatched as prezoeae in water of very high or very low salinity, but all hatched as first zoeae in the salinity range 23‰ to 32‰. Unfortunately where Neopanope is reported to have hatched as prezoeae the salinity is not reported.

In contrast to Birge's description of "a large number of moults, some moultings making little or no change in form" between the "many" stages of the zoeae of Neopanope, only one moult between each of four zoeal stages was invariably found in the present study. Hyman also found only four stages in the plankton with only one moult between each, but states that his "observations are not numerous enough to justify a dogmatic statement." Broad (1957 b) found in two species of the shrimp Palaemonetes that the number of stages in larval development was dependent on diet. His larvae grew more rapidly and underwent fewer stages when fed animal food than when fed

a diet that included plant food. Templeman (1936 a) found that in the lobster Homarus americanus, reducing the amount of food occasionally resulted in an 'extra' larval stage. Sandoz and Rogers (1944) reported that in Callinectes sapidus the duration of the early zoeal stages was longer and the zoeae smaller when 'poorly nourished'. Their study, however, was based on mass cultures. Since zoeae eat other zoeae, results of mass culturing are difficult to interpret. Lebour (1928) considered the number of larval stages constant and used it as a key character for the British species of the Brachyura.

In the present study zoeae fed only algae died without moulting. Those fed animal food plus algae took twice as long to develop as those fed only animal food but did not differ in number of zoeal stages. Thus it is felt that in nature the number of zoeal stages in Neopanope, Hexapanopeus and Piluminus is four and is not dependent on diet. This conclusion is based on the assumptions that the algae and Artemia used were representative of plant and animal food and that variations in temperature and salinity do not affect the number of zoeal stages.

In the laboratory Xanthid zoeae ingest living and dead Artemia nauplii, clumps of algae, and detritus. Zoeae were observed to select to some extent. Sand, wood, etc. are always rejected even though of suitable size, as are Artemia and algae on occasion. Green Dunaliella and apparently intact Nitzschia were occasionally seen with the feces. While algae are definitely not required

in the nutrition of these zoeae, the role of algae is difficult to assess. The experimental evidence indicates that algae are of little nutritive value but are inimical to most rapid development. Since zoeae fed only algae lived longer than starved zoeae, these algae are probably not toxic. Either the zoeae cannot digest these algae or the zoeae require some factor not present in or obtainable from the algae. The results can be explained by a restriction of intake of valuable nutrients by ingestion of nutritionally inert material. This has been postulated by Broad for Palaemonetes. He found that including algae in the diet of his larvae resulted in longer developmental times and increased number of larval stages.

Even if the above role of algae in the nutrition of decapods proves to be generally the case, the reasons for it are likely to remain obscure until large scale nutritional and biochemical experiments have been carried out. Its significance, if general, is obvious. Complex trophic relations between decapod larvae and herbivores and phytoplankton may be found. Thus, a phytoplankton bloom may retard development of zoeae and a following increase in herbivores accelerate it.

DESCRIPTION OF THE LARVAE OF
Neopanope texana sayi

The following description is based on larvae reared from the egg in the laboratory. Several specimens of each stage hatched from 10 adults collected at Beaufort and 2 adults from Woods Hole were examined to get an indication of the diversity of morphological characteristics. A comparison of the setation of these zoeae showed that the variation among individuals hatched from the same sponge was as great as the variation between zoeae from Beaufort and Woods Hole.

A more complete appreciation of diversity awaits extensive statistical and genetic studies which have never been carried out for the larvae of the Brachyura. A comparison with the descriptions of Faxton (1880, first zoea only), Birge (1883), and Hyman (1925) is included in the text to increaseits usefulness.

Setation on the appendages is indicated here by a formula giving the number of setae for each segment and the variation, if any, for each segment. Formulae are used for maxillae and maxillipeds. On maxillae the setae numbers always refer to the segments in the same order, proximal to distal: coxopodite, basipodite and endopodite. Since the endopodite is composed of two segments, the two are enclosed within parentheses. Dashes separate segments and a variation in the observed number of setae on a segment is indicated by two numbers giving the extent

of this variation separated by a virgule (/). Thus the formula 6/7-8/9-(1-5/6) indicates: 6 or 7 setae on the coxopodite, either 8 or 9 setae on the basipodite, an endopodite consisting of two segments, the first (more proximal) bearing 1 seta and the second (more distal) bearing 5 or 6 setae. This example is the setation formula for the first maxilla of the third zoea and is shown, labeled, on Plate VII, Figure 5. The formula for each appendage is explained in the description of the first stage in which it occurs. An 'x' is used to complete a formula taken from a description or drawing in the literature in which all of the appendage is not described or figured. A '?' is similarly used when the number of setae is not clear. Anatomical structures of the appendages are indicated on Plates VII, VIII, and XIV.

FIRST ZOEA

The eyes are not movable at this stage. Length from tip of rostrum to tip of dorsal spine is about 1.2 mm.

Cephalothorax - Plate I. All of the zoeal stages have a long rostrum and dorsal spine and very short lateral spines. In proportion to the size of the zoea in the various stages, the lengths of these spines do not change appreciably.

First Antenna - Plate II, Figure 2. No divisions are apparent at this stage. Three or 4 setae are born terminally. Faxton shows 4 setae, Birge shows 2 and 3, and Hyman shows 3.

Second Antenna - Plate II, Figure 1. Smooth to tip with the exception of a small single seta placed laterally near the base. This is the 'exopodal hair' of Birge and Hyman.

Labrum - Single lobed and bearing many setules. The labrum does not change appreciably during larval development.

Mandible - Plate II, Figure 5. Slightly indented anteriorly, conforming to the labrum. No palp is apparent at this stage.

First Maxilla - Plate II, Figure 3. Coxopodite bearing 6 setae. Basipodite bearing 5 setae. Endopodite with two segments, the proximal bearing a single seta, the distal bearing 6 setae. The setation formula is 6-5-(1-6). Faxton shows the setation 4-2-(0-5). Birge shows 5-5-(1-6) but describes 4-6-(1-6). Hyman shows 5-5-(0-6).

Second Maxilla - Plate II, Figure 4. Coxopodite bearing 5 to 8 setae. Basipodite bearing 5 to 9 setae. Endopodite bearing 7 or 8 setae. Scaphognathite bearing 4 or 5 setae and many setules. The setation formula is 5/8-5/9-7/8-4/5. Faxton does not show this appendage. Biege shows 4-7-5-5. Hyman shows 3-5-6-4.

First Maxilliped - Plate II, Figure 7. Precoxa with a medial and lateral lobe, the medial one bearing a single seta. Protopodite bearing 10 setules. Endopodite with 5 segments bearing setae (from proximal to distal segments) 2/3-2-1-1/2-4/5. Exopodite with two segments, the first

bearing no setae, the terminal segment bearing 4 swimming setae. The setation formula is 1-10-(2/3-2-1-1/2-4/5)-(0-4). Faxton and Birge do not show the precoxa. Faxton shows x-0-(1-2-0-0-3)-(0-4). Birge shows x-8-(1-1-1-2-4)-(0-4) but describes x-8-(1-1-1-1-4)-(0-4). Hyman shows x-0-(0-2-1-2-3)-(0-4).

Second Maxilliped - Plate II, Figure 8. Precoxa bearing no setae. Protopodite bearing 4 setae. Endopodite with three segments bearing setae (proximal to distal) 1-4-4/5. Exopodite with 2 segments, the first bearing no setae, the second with 4 swimming setae. The setation formula is 0-4-(1-4-4/5)-(0-4). Faxton and Birge again do not show the precoxa. Faxton shows setation x-0-(0-0-3)-(0-4). Birge shows x-6-(0-1-4)-(0-4). Hyman shows 0-0-(0-0-3)-(0-4).

Third Maxilliped - Rudimentary, about 25 micra in length.

Pereiopods - Rudimentary, but all 5 pairs are evident. The first pair are about 20 micra in length and are not chelated at this stage.

Abdomen - Six segments, the sixth being fused with the telson. The pleopods are evident as slight ventro-lateral swellings, posteriorly placed on the second through the fifth segment. The first five segments all have two setules on their dorsal posterior margins. Short mid-lateral projections occur on the second and third segments. Short ventro-lateral projections occur on the second through the fifth segments. The telson (Plate II, Figure 6) is bicornuate. Each cornu bears three setae on its medial

margin. These setae all bear setules, the inner pair bearing 5 or 6 longer setules on their medial margins. Each cornu bears a short spine on its mid-dorsal surface. Previous authors have not described the abdomen in detail. Hyman, however, does mention "3 minute spines placed laterally and dorsally" instead of the one described here.

SECOND ZOEA

The eyes are now movable. Length from tip of rostrum to tip of dorsal spine is about 1.5 mm. Plate III.

First Antenna - Plate IV, Figure 2. There are now 4 or 5 setae on this appendage. Birge shows 2 setae on one drawing and 3 on another. Hyman shows 4 setae.

Second Antenna - Plate IV, Figure 1. No change except in size.

Mandible - Plate IV, Figure 3. No change except in size.

First Maxilla - Plate IV, Figure 5. This appendage now bears a single epipodal hair. This is not shown by Birge or Hyman. Setation now 6/7-6/7-(1/2-6). Birge does not show this appendage. Hyman shows 6-7-(1-6).

Second Maxilla - Plate IV, Figure 4. Setation is now 7/9-8/9-7-8/11. Birge does not show this appendage. Hyman shows 9-7-7-11.

First Maxilliped - Plate V, Figure 1. Setation is now 1-7/9-(3-2/3-1-2-4/5)-(0-6). Birge shows 6 swimming setae on the exopodite. Hyman does not show the precoxa. The other setae are shown x-6-(2-2-2-2-4)-(0-4) but he describes not 4 but 6 swimming setae on the exopodite.

Second Maxilliped - Plate V, Figure 2. Setation is now 0-4-(1-1-4)-(0-6/7). Birge and Hyman do not show the precoxa. Birge shows x-0-(0-1-4)-5/6. Hyman shows x-4 (1-1-4)-6/7.

Third Maxilliped - No change except in size. It is still uniramous and is now about 60 micra in length. Birge does not mention this appendage. Hyman states that it is biramous.

Pereiopods - The five pairs are about 50 micra in length. The first is not chelated. Birge describes only 2 pairs at this stage. Hyman states that the first pair is chelated and implies that 5 pairs are present.

Abdomen - There are now three setules on the posterior dorsal margin of the first segment. The fifth segment is fused with the telson. A pair of prominent median setules is now present at the junction of the cornua of the telson (Plate V, Figure 3). The spines present on the abdomen of the first zoea are now more prominent. The pleopod buds are slightly more evident.

THIRD ZOEA

Length from tip of rostrum to tip of dorsal spine is about 2.0 mm. Plate VI.

First Antenna - Plate VII, Figure 2. No change except in size. Four or 5 setae are born terminally. Birge shows 5 to 7 setae. Hyman shows 4 setae.

Second Antenna - Plate VII, Figure 1. A small bud is now present at the location of the basal seta which is still

present. Both Birge and Hyman give this description.

Mandible - Plate VII, Figure 3. No change except in size.

First Maxilla - Plate VII, Figure 5. Setation is now: 6/7-8/9-(1-5/6) plus the epipodal seta. Birge does not describe this appendage. Hyman shows the setation: 6-6-(1-6) and states that the epipodal hair is present for the first time at this stage.

Second Maxilla - Plate VII, Figure 4. Setation is now: 8/9-8/10-8-18/19. Birge does not describe this appendage. Hyman shows 7-7-8-17.

First Maxilliped - Plate VIII, Figure 1. Setation is now: 1-9/10-(3-2-1-2-5/6)-0-(7/8). Birge gives 8 swimming setae. Hyman gives 0-10-(2-2-1-2-6)-(0-8/9).

Second Maxilliped - Plate VIII, Figure 2. Setation is now: 0-2/4-(1-1-4)-(0-8/9). Birge gives 8 swimming setae. Hyman gives 0-3-(1-1-5)-(0-8/9).

Third Maxilliped - Slightly larger, no other change.

Pereiopods - About 60 micra in length, not chelated. Neither Birge nor Hyman describes these appendages at this stage.

Abdomen - The sixth segment is now separated from the telson (Plate VIII, Figure 3). It has no spines. The pleopod buds on the second through the fifth segments are now about 50 micra in length. Otherwise like the second zoea.

FOURTH ZOEA

Length from tip of rostrum to tip of dorsal spine is about 2.5 mm. Plate IX.

First Antenna - Plate X, Figure 2. A basal and a subterminal lobe are now evident. Eight or 9 setae are born terminally. Birge describes "3 or 4 joints" and 12 setae. Hyman describes 8 setae.

Second Antenna - Plate X, Figure 1. The simple bud which appeared in the third zoea is now about 30 micra in length. Birge describes this bud as segmented. Hyman states that it is now longer.

Mandible - Plate X, Figure 3. An anterior dorsal palp now appears on the mandible. Both Birge and Hyman mention this palp.

First Maxilla - Plate X, Figure 5. Setation is now: 8/10-10/11-(1-5) plus epipodal hair. Birge does not describe this appendage. Hyman shows the epipodal hair plus: 9/10-9-(1-6).

Second Maxilla - Plate X, Figure 4. Setation is now: 8/9-10/11-7/8-26/28. Birge shows: 8-7-7-19. Hyman shows: 9-11-8-26.

First Maxilliped - Plate XI, Figure 1. Setation is now: 2-10-(3-2-1-2-6)-(0-9/10). Birge shows x-0-(1-1-1-1-4) -(0-10/14). Hyman shows: 2-7-(3-2-1-2-6)-(0-9/12).

Second Maxilliped - Plate XI, Figure 2. Setation is now: 0-4-(1-1-5)-(0-9/10). Birge shows: x-0-(1-0-6)-(0-12/14). Hyman shows 0-5-(0-1-5)-(0-12).

Third Maxilliped - No change except in size, now about 250 micra in length. Both Birge and Hyman state that it is now biramous. Hyman states that 5 segments are now present.
Pereiopods - The five pairs are now 200 to 300 micra in length. The first pair is now chelated. This is also stated by Birge and Hyman.
Abdomen - Pleopods are now longer (about 200 micra on the second segment, about 60 micra on the sixth segment) and biramous on the second through the fifth segments. The telson has not changed (Plate XI, Figure 3). Birge shows no dorsal spines on the telson. Hyman shows the abdomen essentially as above.

MEGALOPA

Length from tip of rostrum to posterior margin of carapace is abour 2.0 mm.
Cephalothorax - Plate XII. The dorsal and lateral spines are no longer present on the now depressed carapace. The rostrum is short and notched.
First Antenna - Plate XIII, Figure 2. This appendage is now segmented. The first segment now bears 4 setae, the second none, the third bears 6 setae distally and a short lateral palp consisting of a single segment bearing 4 terminal setae. The fourth segment bears 5 setae. The fifth and sixth segments are not completely separate. The fifth bears 5 setae and the sixth bears 4 setae. The seventh segment bears 3 terminal setae. The articulations of the second segment allow medial flexion of the appendage.

Second Antenna - Plate XIII, Figure 1. As in the adult, only the endopodite is present. It is divided into 11 segments with segmentation not complete between the sixth and tenth segments. The first segment bears 4 setae, the third 1, the sixth, eighth, tenth, and eleventh, 4 setae. Birge describes "about 11 joints" with "the third or fourth joint from the end" bearing large sense hairs. Hyman describes about 12 segments and does not mention setae.

Mandible - Plate XIII, Figure 3. Only slightly changed from the fourth zoea. The palp is a single segment and bears 4 setae. Both Birge and Hyman describe the palp as three-segmented.

First Maxilla - Plate XIII, Figure 4. Coxopodite with 12 setae. Basipodite with 17 setae. Endopodite with 2 segments, the proximal with a single seta, the distal with four setae. A single epipodal hair is present. Birge does not describe but pictures the setae in the above order as about 14-9-8-6. He shows no epipodal hair but does show 5 basal setae. Hyman does not describe the setae.

Second Maxilla - Plate XIII, Figure 5. Coxopodite with 10 setae. Basipodite with 14 setae. Endopodite with 5 setae. Scaphognathite with 43 setae. Birge shows the setae in the above order as follows: 11-11-0-36. Hyman does not describe the setae.

First Maxilliped - Plate XIV, Figure 1. An epipodite is now present and bears 4 setae. Exopodite with 2 segments,

the proximal bearing a single seta, the distal bearing 3 setae. Endopodite, a single segment bearing 5 setae. The protopodite is 2-lobed, the more distal bearing 17 setae, the more proximal bearing 8 setae. Birge shows the epipodite bearing 21 setae, the exopodite bearing no setae on the proximal segment and 7 setae on the distal segment, the endopodite bearing 7 setae and the protopodite with 5 lobes, the distal three bearing many (65?) setae, the proximal two bearing none. Hyman describes 4 or 5 setae on the distal segment of the endopodite and no others.

Second Maxilliped - Plate XIV, Figure 2. Epipodite with 5 setae. Exopodite with 2 segments, the proximal bearing a single seta, the distal bearing 5. Endopodite with 4 segments bearing setae (proximal to distal) 2-1-7-9. Birge shows the setae in the above order as: 6-(0-5)-(8-0-5-9?) and 2 on the protopodite. Hyman does not describe the setae.

Third Maxilliped - Plate XIV, Figure 3. This appendage is larger and bears more setae than the other maxillipeds. The setation is: epipodite, 21; exopodite proximal segment, 2, distal segment 6; endopodite with 5 segments bearing setae (proximal to distal) 13-9-4-6-9. Protopodite with 5 setae. Birge shows the epipodite with 21 setae, the exopodite with 3(?) segments bearing setae: 9-0-7. Endopodite with 5 segments bearing setae (proximal to distal) 13?-24?-2-6-22? and protopodite with 1 seta. Hyman does not describe the setae.

Pereiopods - Plate XII. These are in the form of the adult with the exception of the chelae which are the same size in this stage. Birge and Hyman give the same description.
Abdomen - Plate XII. Each abdominal segment now has short posterio-lateral projections and no others. The pleopods (Plate XV, Figure 2) are biramous. The exopodites of the pleopods bear setae on the following order (on abdominal segments anterior to posterior): 0-9-10/11-10/12-12-6. Birge describes 18 setae on the pleopods of the second segment, shows 12 setae on the third pair, and 6 setae on the last pair. Hyman gives the same description. The endopodite is a simple palp. The telson (Plate XV, Figure 1) is now a simple plate bearing 2 posterior setules.

While the parataxa erected by Aikawa (1929, 1937) have been little used outside of Japan, and have received some criticism (Gurney, 1942), it is felt that in areas where little is known of the larvae of crabs they would be useful. This would be particularly true of plankton surveys in areas where most of the larvae of the crabs present are unknown. His 1937 classification of Neopanope texana sayi is based on Hyman (1925). The present description indicates the following changes should be made.
Telson - Type A_1 rather than A_3. Hyman describes but does not figure 3 dorso-lateral spines on each cornus.
Second Antenna - Type C_1 rather than C_2. This is probably a misprint since C_1 is given in his 1929 account and C_1 is clearly the type shown in Hyman's drawing.

Second Maxilla - Hair formula 2-5 (7)/3-5(8). The number of setae on the endopodite is variable.
Second Maxilliped - Hair formula 5-1-1/4-1-1. The number of setae on the distal segment of the endopodite is variable.

These changes do not affect the placement of Neopanope in Aikawa's parataxon Xanthozoea, but do affect placement within that group. Of greater significance is the observed variability among the zoeae of this species. Indeed if this variability is generally true in zoeae, some of the 'supporting characters' used by Aikawa may prove to be too unstable for use. In the 140 species listed by Aikawa, no variation is noted in the hair formulas. The number of specimens studied in arriving at these formulae is not stated. Lebour states that variation exists (in the number of swimming setae for instance) but it is not clear whether intra - or interspecific variation is being discussed.

From the discrepancies between the later zoea and megalopa shown by Birge and Hyman and those presented here it is questionable if Birge and Hyman were actually working with larvae of Neopanope texana sayi. In the megalopa particularly the form of the appendages and placement and number of setae as shown by Birge are notably different from those presented here. Unfortunately Hyman republished Birge's drawings and his description is not complete enough for extensive comparison.

As was noted previously, both Birge's and Hyman's method of collection from the plankton is subject to error. This is particularly true of the later stages. It may be that future studies of other Xanthid zoeae will reveal the species whose late larval stages were described by Birge and Hyman as Neopanope texana.

The following table shows characteristics of the four zoeal stages which can easily be seen in living or preserved material: Table 4.

Table 4

Characteristics of the zoeal stages in Neopanope

Character	Stage 1	2	3	4
Number of swimming setae on first maxilliped	4	6	7-8	9-10
Number of swimming setae on second maxilliped	4	6-7	8-9	9-10
Length of pleopods on second abdominal segment	not evident	not evident	50 micra	200 micra

SUMMARY

1. Neopanope texana sayi, Hexapanopeus angustifrons, and Piluminus sayi have been reared in isolation from eggs through the first crab stage with about 80% survival.

2. These species hatched in the laboratory as first zoeae and underwent three more zoeal stages and one megalopal stage before metamorphosis to the first crab stage.

3. The duration of the larval stages was twice as long when the zoeae were fed Artemia nauplii plus algae, as when fed Artemia alone. Larvae did not survive when fed algae alone but lived longer than those not fed at all. The mechanism of this inhibition of development by algae is unknown.

4. A morphological description of the larvae of Neopanope texana sayi is given. While no variation in the number of larval stages was found, variations in the zoeae at each stage are described. Some of these variable characters are those frequently used in comparative work on zoeae.

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PLATES

Plate I. First zoea.

Line represents 500 micra. Thoracic appendages not shown.

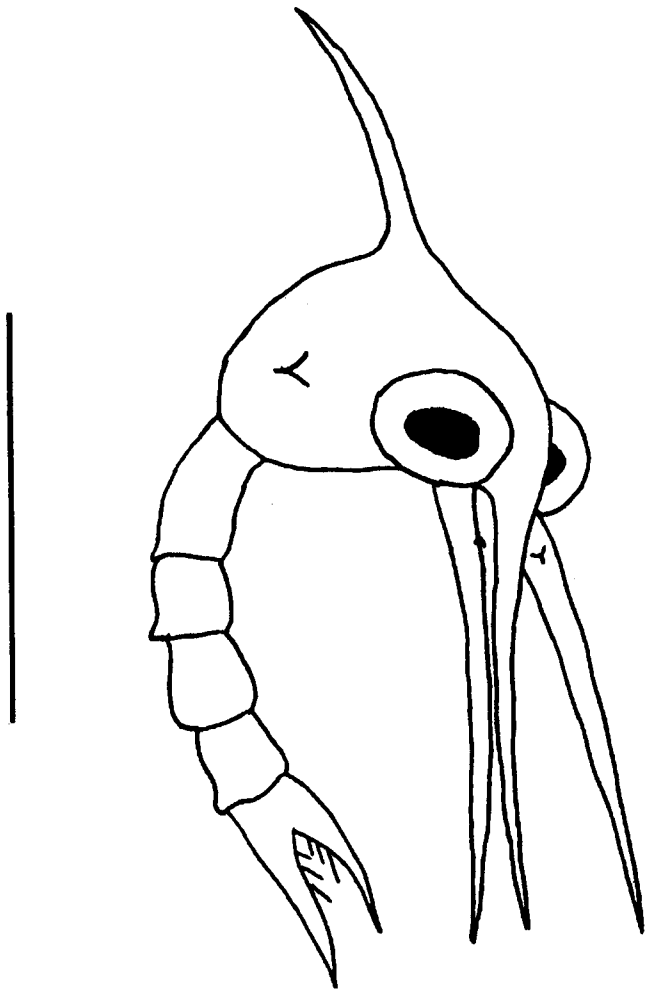

Plate 1

Plate II. First zoea. Line represents 100 micra.

Fig. 1. Second antenna.

Fig. 2. First antenna.

Fig. 3. First maxilla.

Fig. 4. Second maxilla.

Fig. 5. Mandible.

Fig. 6. Telson.

Fig. 7. First maxilliped.

Fig. 8. Second maxilliped.

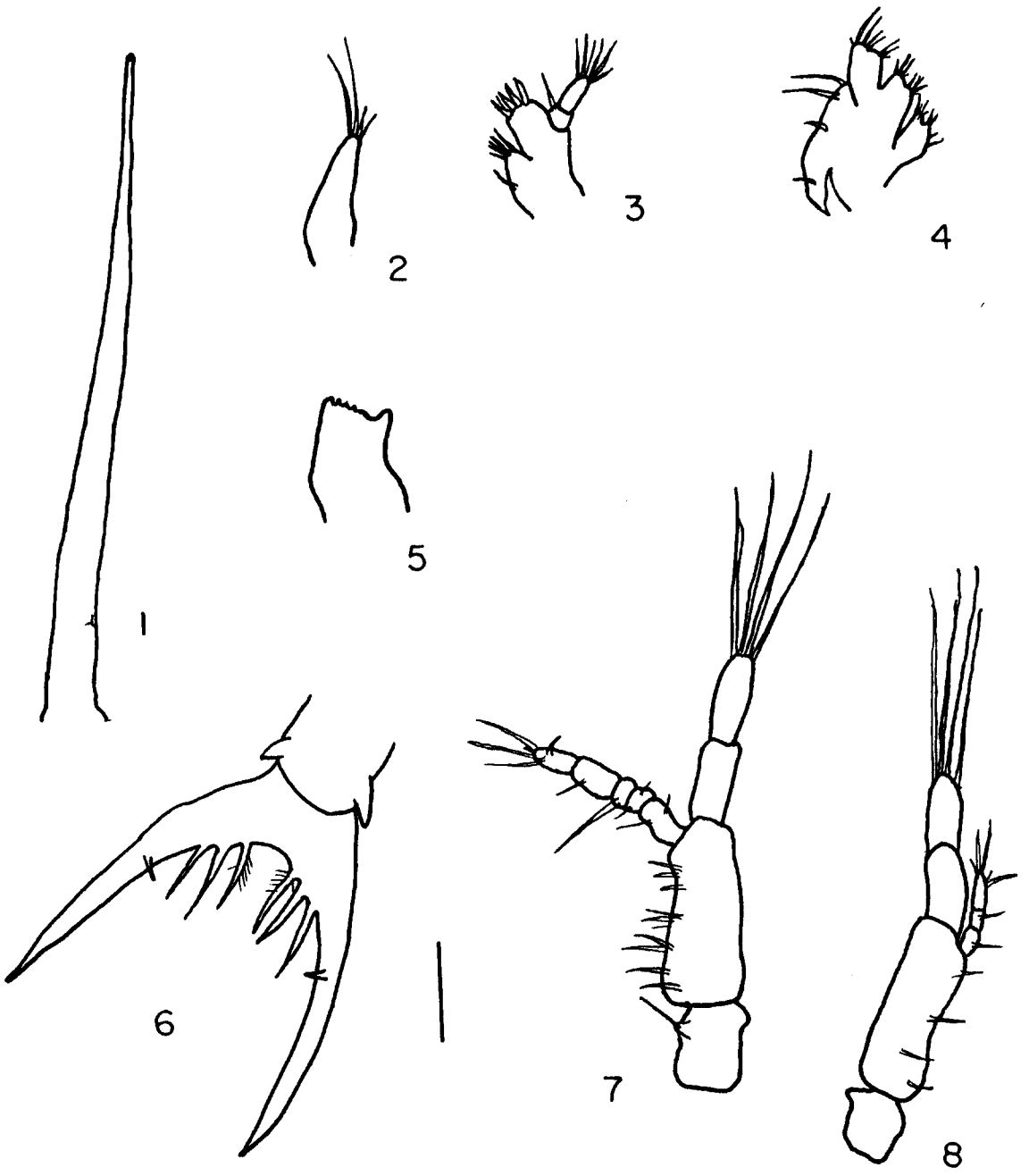

Plate II

Plate III. Second zoea.

Line represents 500 micra. Thoracic appendages not shown.

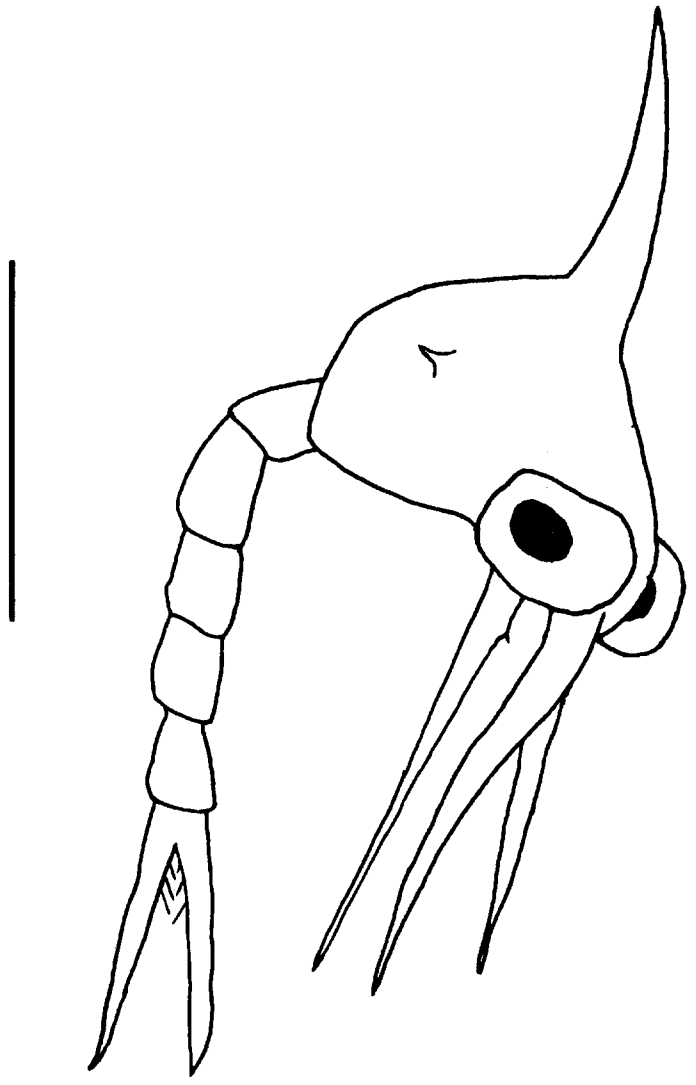

Plate III

Plate IV. Second zoea. Line represents 100 micra.

Fig. 1. Second antenna.

Fig. 2. First antenna.

Fig. 3. Mandible.

Fig. 4. Second maxilla.

Fig. 5. First maxilla.

1

2

3

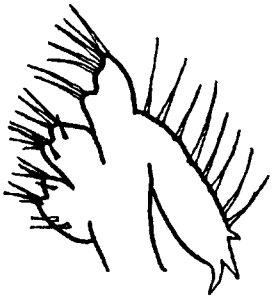

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Plate IV

Plate V. Second zoea. Line represents 100 micra.

Fig. 1. First maxilliped.

Fig. 2. Second maxilliped.

Fig. 3. Telson.

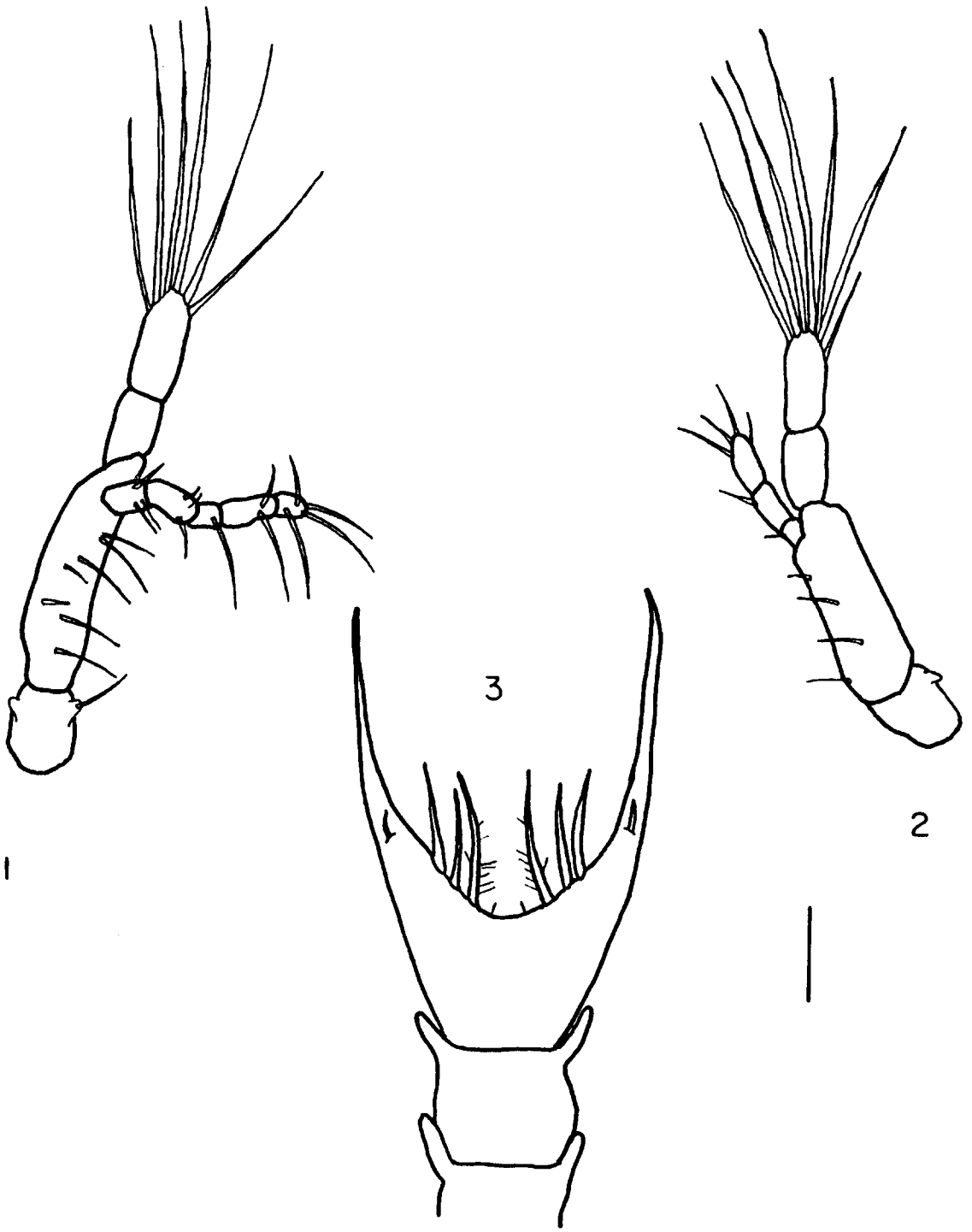

Plate V

Plate VI. Third zoea.

Line represents 500 micra. Thoracic appendages not shown.

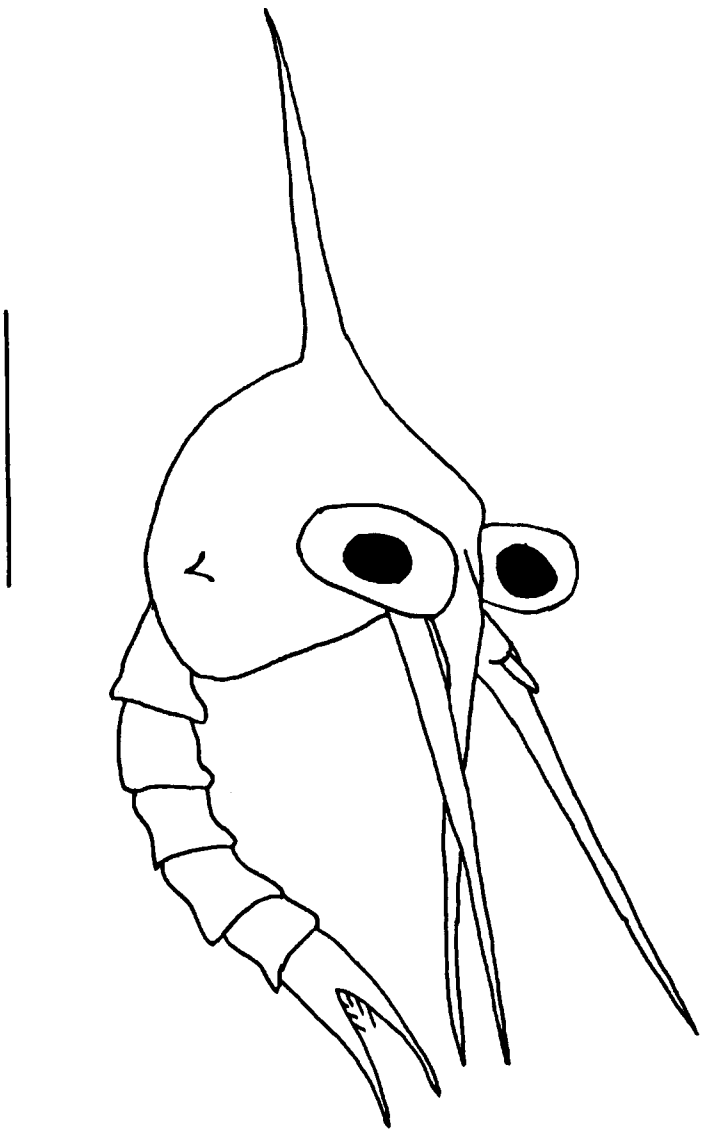

Plate VI

Plate VII. Third zoea. Line represents 100 micra.

Fig. 1. Second antenna.

Fig. 2. First antenna.

Fig. 3. Mandible.

Fig. 4. Second maxilla. Coxopodite, a. Basipodite, b. Endopodite, c. Scaphognathite, d.

Fig. 5. First maxilla. Coxopodite, e. Basipodite, f. Endopodite, g. Epipodal seta, h.

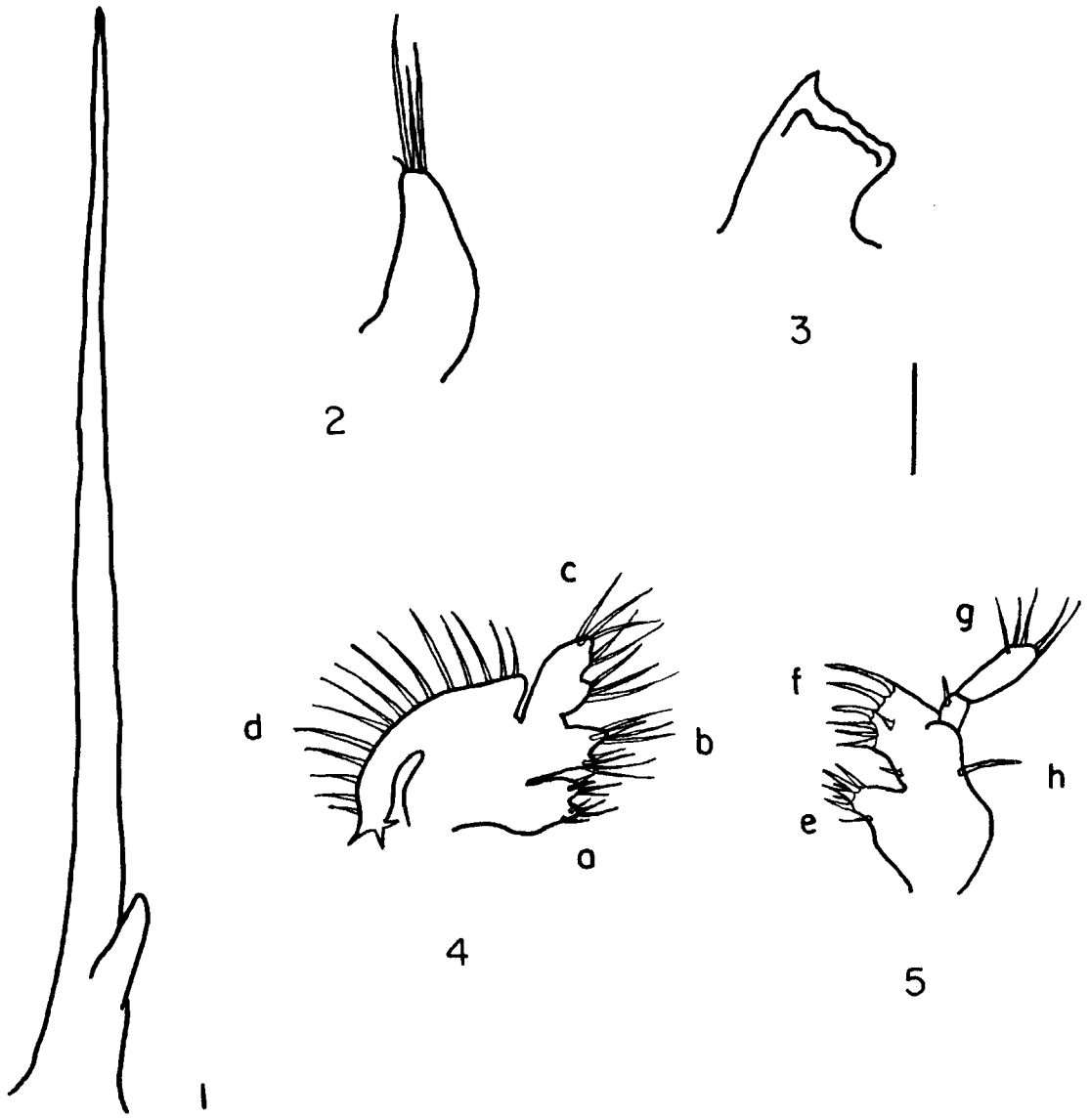

Plate VII