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THE LARVAL DEVELOPMENT OF *PALAEEMONETES KADIAKENSIS*
M. J. RATHBUN IN THE LABORATORY

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The larval phase in the development of fresh water decapod crustaceans is often shortened or suppressed. In European shrimps of the genus *Palaemonetes*, Boas (1889) and Sollaud (1923) have shown differing modes of development in closely related forms that inhabit brackish and fresh water. Sollaud and Gurney (1942) have related the number of larval forms to the size of the egg. Sollaud believes that eggs of *Palaemonetes varians* (= *P. v. macrogenitor* Boas; = *P. v. lacustris* Sollaud) that are in excess of 0.8 mm. in length hatch as advanced larvae. Gurney finds that development in decapods is normal when eggs are "up to about one hundredth" of the adult length but points out that evidence of the normal (*i. e.* complete) larval development of a palaemonid in fresh water is lacking.

The eggs of *Palaemonetes kadiakensis* M. J. Rathbun are 1.4 mm. long or about one twenty-fifth of the adult length. During the summers of 1959 and 1960 we reared this species through metamorphosis in the laboratory starting with eggs carried by adult females. The complete larval phase lasted about three weeks. There were six discreet larval forms or stages. Thus, the development of a fresh-water shrimp, *P. kadiakensis*, with large eggs is normal in that it resembles Faxon's (1879) description of the development of *Palaemonetes vulgaris*, Broad's (1957) account of the development of *P. pugio*, and our (unpublished) observations of larval development of *P. intermedius*.

This paper is an account of the events of metamorphosis in *Palaemonetes kadiakensis* observed in our laboratory, The Franz Theodore Stone Laboratory at Put-in-Bay, Ohio. We extend our thanks to Dr. L. S. Putnam, Director, and to Dr. C. E. Dambach, Director of the Natural Resources Institute of The Ohio State University, for the use of facilities and to Mr. Ronald A. Engel for assistance in collecting.

METHODS

Adult *P. kadiakensis* were collected from several sites in Sandusky Bay and waters tributary or adjacent to it in Ottawa and Erie Counties, Ohio. The shrimp were kept in aquaria of Lake Erie water in our laboratory and were fed macerated parts of any of several local fishes, mainly whole, common emerald shiners, *Notropis atherinoides*.

Ovigerous females were examined periodically to determine if the eggs were ready to hatch. Those with eggs containing advanced embryos were isolated in culture dishes until the eggs hatched. Some of these females then were placed in aquaria with two to four sexually mature males. By this expedient, second clutches of fertilized eggs were obtained from a few females. These females were held in isolation until the second clutches of eggs hatched or were removed from the pleopods by the shrimp.

All the larvae treated were obtained from eggs hatched in the laboratory. Individual larvae were isolated in four-inch, stacking aquaria (finger bowls) and fed daily either day old *Artemia salina* nauplii or, in a few instances, raw Lake Erie plankton. Each larva was inspected daily under a low magnification, stereoscopic microscope (10 to 40 X). For inspection the larvae were removed to depression slides by a large bore pipette. The form of the larva and the presence of

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exuviae were noted at this time. The bowls then were emptied, rinsed refilled with lake water and fresh food added. Otherwise, treatment of larvae was that previously described (Broad, *l. c.*).

The larvae were reared at temperatures that varied between 18.5 and 24 degrees C. Periodic sampling of the water in bowls containing larvae indicated continuous oxygen saturation.

Drawings were made (by J. H. H.) of anesthetized, living larvae. A camera-lucida was used to insure correct representation of proportions. The figures of individual appendages are camera-lucida drawings made from appendages teased from alcoholic specimens and mounted in glycerin jelly.

RESULTS

Twenty female *P. kadiakensis*, on which counts of total larvae released in the laboratory were possible, hatched 760 larvae (range, 11 to 82; mean, 38; standard deviation, 19.27). These data pertain to the number of larvae hatched, not to total eggs carried, but are considerably lower than Meehan's (1936) report of 154 eggs carried by one female presumably of this species, the only other datum of fecundity. The late eggs were measured with a jeweler's caliper (spring gauge) and were uniformly 1.4 mm. long by 1.1 mm. wide, almost exactly the size of *Palaemonetes exilipes* [= *P. paludosus* (Gibbes)?] eggs reported by Gurney (*l. c.*, p. 55).

Two females that had released young in the laboratory produced second clutches of eggs in aquaria with mature males and carried these eggs until they hatched. The incubation periods of these two clutches fertilized in the laboratory were 24 and 28 days.

We observed six different larval forms. The first of these is a protozoa; the other five are zoeae. The postlarva is a juvenile shrimp and marks the end of metamorphosis. We have found it convenient to refer to these forms by Roman numbers and to restrict our use of Arabic numbers to molt cycles. It should be pointed out that our form I larva customarily might be called a first stage larva; our form II would be the second stage, and so on to our form VI which has also been called a sixth stage larva.

The larvae emerge from the egg still encased in the protozoal cuticle. Detailed descriptions of hatching of *P. vulgaris* and *P. paludosus* have been given by Burkenroad (1947) who found the protozoal cuticle intact but lifted slightly from the underlying zoeal cuticle upon hatching. We believe that this is also true of *P. kadiakensis* and note that Burkenroad's description was erroneously interpreted by Broad (*l. c.*) in describing the first zoea or protozoa of *P. pugio*. We call the protozoa of *P. kadiakensis* form I.

The form I larvae (Pl. I, Figs. 1-13) are about 4.4 mm. long. The stalked eyes

EXPLANATION OF PLATE I

The recently hatched, form I larva of *Palaemonetes kadiakensis* and the appendages of the left side.

- FIG. 1. Entire larva, scale A.
- FIG. 2. Telson and sixth pleonic somite, scale A.
- FIG. 3. Antennule, scale B.
- FIG. 4. Antenna, scale B.
- FIG. 5. Mandible, scale B.
- FIG. 6. Molar and incisor processes of mandible, scale C.
- FIG. 7. Maxillule, scale B.
- FIG. 8. Maxilla, scale B.
- FIG. 9. First Maxilliped, scale B.
- FIG. 10. Second Maxilliped, scale B.
- FIG. 11. Third maxilliped, scale B.
- FIG. 12. First pereiopod (cheliped), scale B.
- FIG. 13. Second pereiopod (cheliped), scale B.

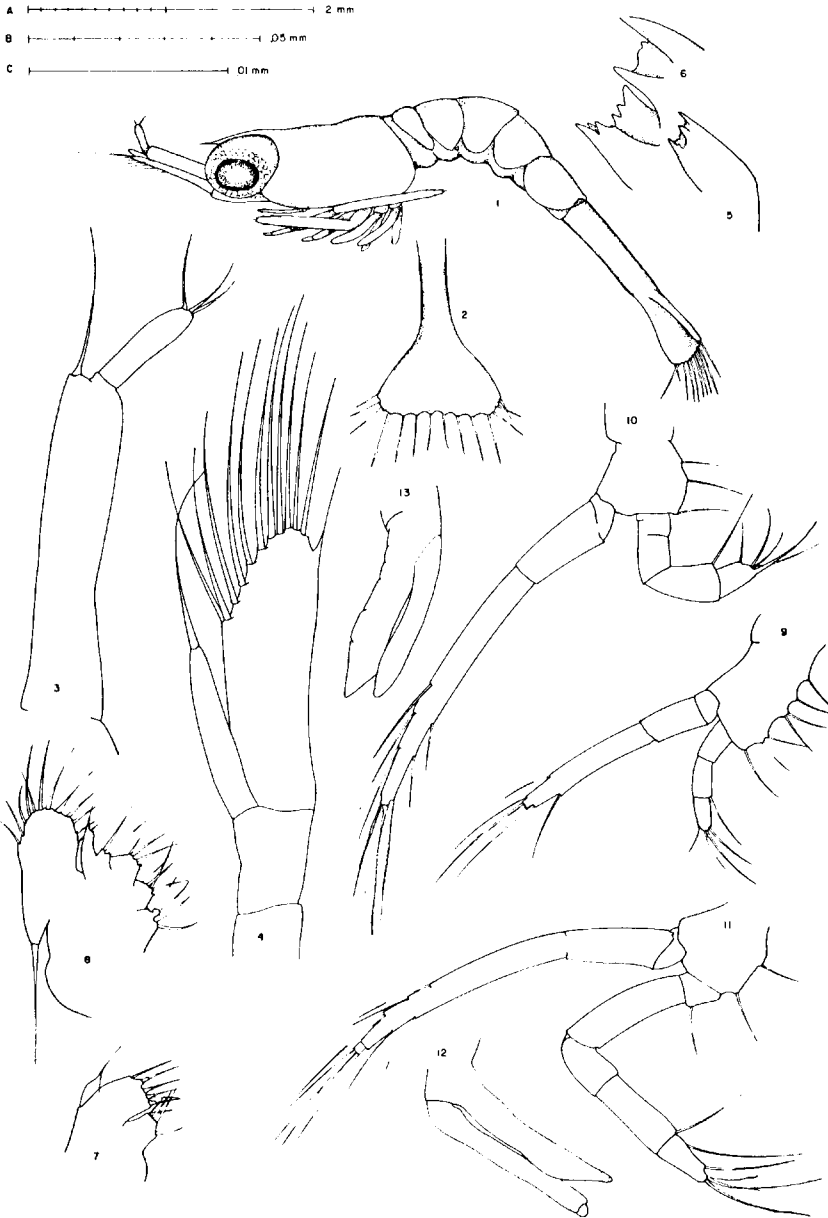


PLATE I

PLATE I

The larval development of *Palaemonetes kadiakensis*. M. J. Rathbun in the laboratory

of subsequent larval forms are compressed beneath the protozocal carapace. Spines and teeth are absent from the carapace, rostrum, and abdomen. There are six abdominal somites, the last of which joins the fan-shaped telson without an intervening articulation. The rostrum is short and projects forward about to the anterior margin of the eyes. The telson (Fig. 2) bears the customary 14 spines.

The antennules (Fig. 3) are simple, uniramous appendages with a long basal segment and a short (upper) flagellum. The basal segment bears a long, plumose seta, and the flagellum a few *aesthetes*. The antennal basis (Fig. 4) consists of two segments and bears a simple flagellum, tipped by a long seta, and an unsegmented scale with marginal setae on the tip and inner border. The spine of the antennal scale is well-formed but terminates in a short seta. The mandibles (Figs. 5, 6) have strong molar and incisor processes and lack palps.

The maxillules (Fig. 7) have bilobed gnathobases and simple, palp-like endopods. The maxillae (Fig. 8) have spinous, multilobed gnathobases. The exopods are gill bailers. Three pairs of biramous maxillipeds (Figs. 9, 10, 11) have raptorial endopods and long, natatory exopods. There are two biramous, rudimentary pereopods (Figs. 12, 13). Other appendages are lacking.

Form II (Pl. II, Figs. 14-21) and subsequent larvae are zoeae. The stalked eyes are free of the carapace. The form II carapace bears branchiostegal and supra-orbital spines. There is a single, dorsal rostral tooth. The telson (Fig. 15), which is now separated from the sixth pleonic somite by a definite articulation, bears 14 large and two minute, median spines. Form II larvae are about 4.7 mm. in length.

There is further development of the appendages. The antennular basis (Fig. 16) consists of three segments the proximal of which bears a weak lateral tooth. An inner flagellum occurs. The antennal flagellum (Fig. 17) is segmented. The spine of the antennal scale is distinct. The first and second pereopods (Figs. 18, 19) are functional appendages with slightly swollen propodi and short, natatory exopods. The remaining pereopods are rudiments; the rudiment of the third (Fig. 20) is biramous; those of the fourth and fifth (Fig. 21), uniramous. The uropods (Fig. 15) are visible through the telson of advanced form II larvae.

All of the appendages of the adult shrimp are visible in the form III larva (Pl. II, Figs. 22-29). These larvae are about 5.4 mm. long. Propodi of first and second pereopods (Figs. 26, 27) bear weak thumbs, that, with the dactyls, form small chelae. Pereiopod three (Fig. 28) is a small biramous appendage with a weak, natatory exopod and a raptorial endopod. Fourth and fifth pereopods (Fig. 29) are functional, uniramous, raptorial appendages carried projecting forward

EXPLANATION OF PLATE II

The form II and form III larvae of *Palaemonetes kadiakensis* and appendages.

- FIG. 14. Entire form II larva, scale A.
 FIG. 15. Telson and sixth pleonic somite, form II, scale A.
 FIG. 16. Antennule, form II, scale B.
 FIG. 17. Antenna, form II, scale B.
 FIG. 18. First pereopod (cheliped) form II, scale B.
 FIG. 19. Second pereopod (cheliped) form II, scale B.
 FIG. 20. Third pereopod form II, scale B.
 FIG. 21. Fourth and fifth pereopods, form II, scale B.
 FIG. 22. Entire form III larva, scale A.
 FIG. 23. Sixth pleonic somite, telson and uropods, form III. Setae of right uropod omitted, scale A.
 FIG. 24. Antennule, form III, scale B.
 FIG. 25. Antenna, form III, scale B.
 FIG. 26. First cheliped, form III, scale B.
 FIG. 27. Second cheliped, form III, scale B.
 FIG. 28. Third pereopod, form III, scale B.
 FIG. 29. Fourth and fifth pereopods, scale B.

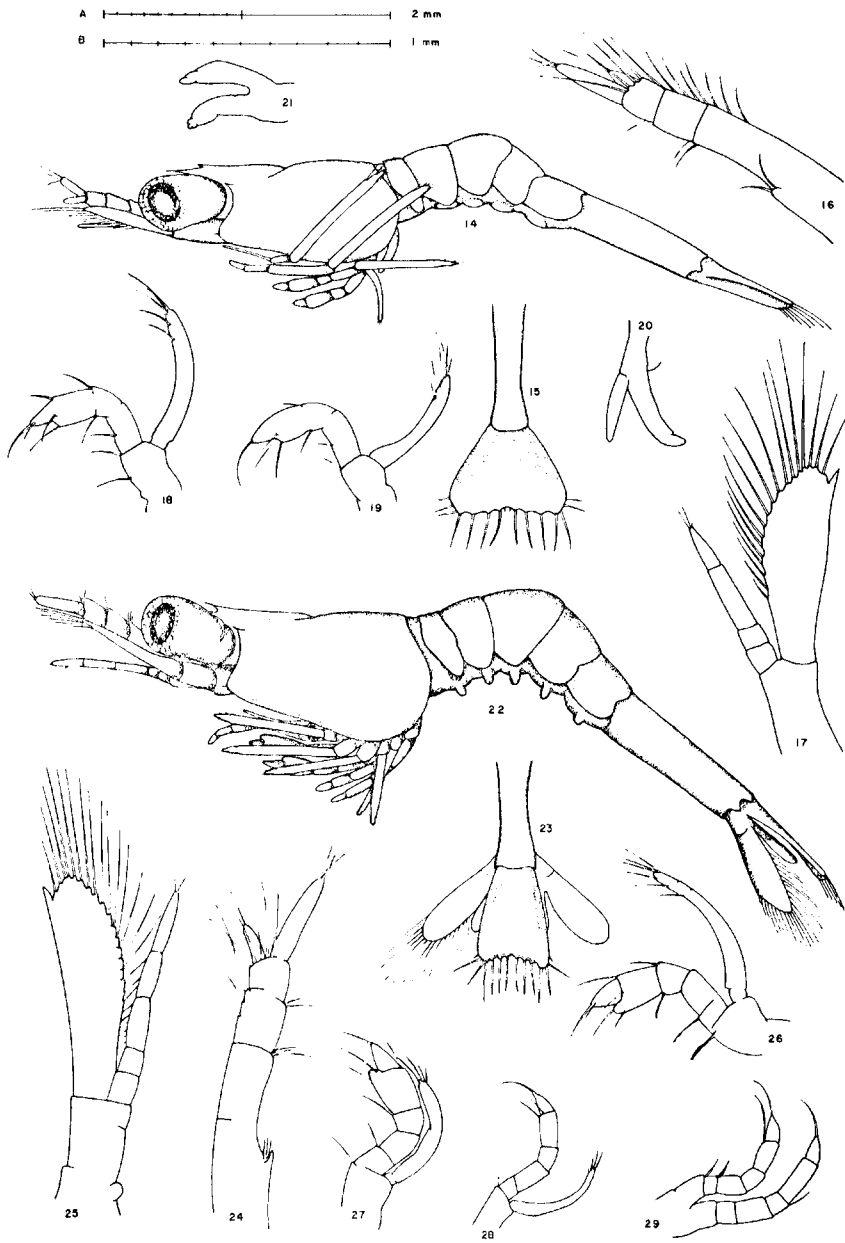


PLATE II

The larval development of *Palaemonetes kadiakensis*. M. J. Rathbun in the laboratory.

beneath the thorax. Pleopod buds appear on the first five abdominal somites. The Uropods (Fig. 23) are biramous with non-setose, rudimentary endopods. The telson bears 14 long spines and is but slightly wider at its terminal end than at its base.

The form IV larva (Pl. III, Figs. 30-41) is about 5.8 mm. long. The upper antennular flagellum (Fig. 32) consists of two segments. The antennal flagellum (Fig. 33) is longer than the scale. The chelae (Figs. 37, 38) are well-developed. The remaining pereopods (Figs. 39, 40, 41) are stronger than in previous larvae. The pleopods are long, biramous rudiments. The endopods of the uropods (Fig. 31) are setose. The telson now has nearly parallel sides. There are small spines on either side near the terminal end and eight terminal spines.

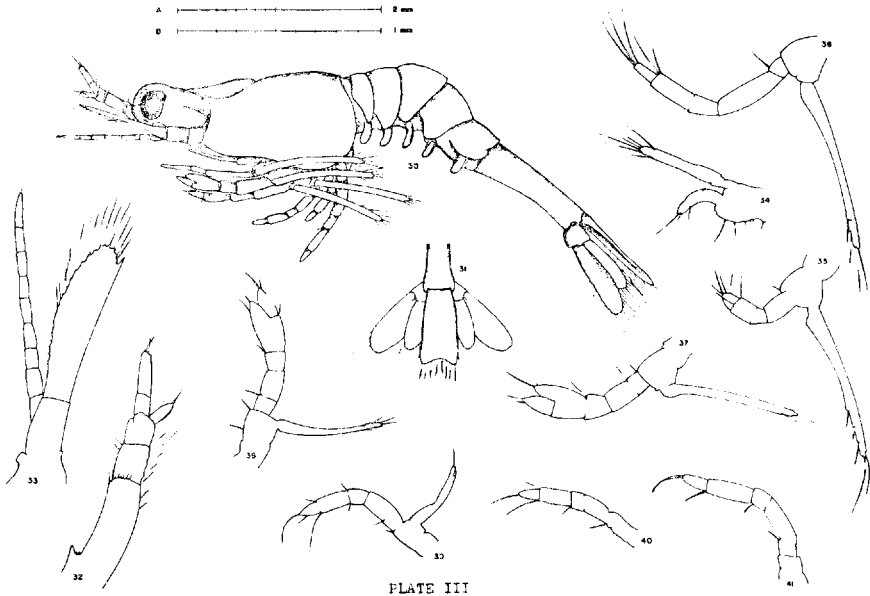


PLATE III

The form IV larva of *Palaemonetes kadiakensis* and appendages.

- FIG. 30. Entire form IV larva, scale A.
 FIG. 31. Telson and uropods, setae of right uropod omitted, scale A.
 FIG. 32. Antennule, scale B.
 FIG. 33. Antenna, scale B.
 FIG. 34. First maxilliped, scale B.
 FIG. 35. Second maxilliped, scale B.
 FIG. 36. Third maxilliped, scale B.
 FIG. 37. First cheliped, scale B.
 FIG. 38. Second cheliped, scale B.
 FIG. 39. Third pereopod, scale B.
 FIG. 40. Fourth pereopod, scale B.
 FIG. 41. Fifth pereopod, scale B.

The larval development of *Palaemonetes kadiakensis*. M. J. Rathbun in the laboratory.

The form V larva (Pl. IV, Figs. 42-52) has two dorsal rostral spines and is about 6.5 mm. long. All appendages are stronger, but the first and second maxillipeds (Figs. 44, 45) have slightly reduced endopods and, presumably, have begun modification to adult form. The pleopods (Fig. 52) are definitely biramous appendages with articular membranes separating basals from the rami. The uropodal endopods (Fig. 43) are now about as long as the telson. The telson is narrower at its terminal end than at its base.

Form VI larvae (Pl. V, Figs. 53–62) resemble the form V larvae but are about 7.1 mm. long. There is often a weak, third rostral tooth. All appendages show further development. The pleopods (Fig. 62) lack setae. The telson (Fig. 54) bears, in addition to the spines of the form V telson, two minute spines in the posteriorlateral corner at each side. Separation of forms V and VI is based largely on this character which is both more easily seen and more reliable than the third rostral tooth.

Form VII (Pl. VI, Figs. 63–72) is the postlarva or juvenile shrimp. It differs strikingly from the larvae both in form and behavior. Zocac and protozoae swim by rapid beating of the exopodites of maxillipeds and pereiopods. The normal orientation of larvae is dorsal side down with the anterior end lower than the pos-

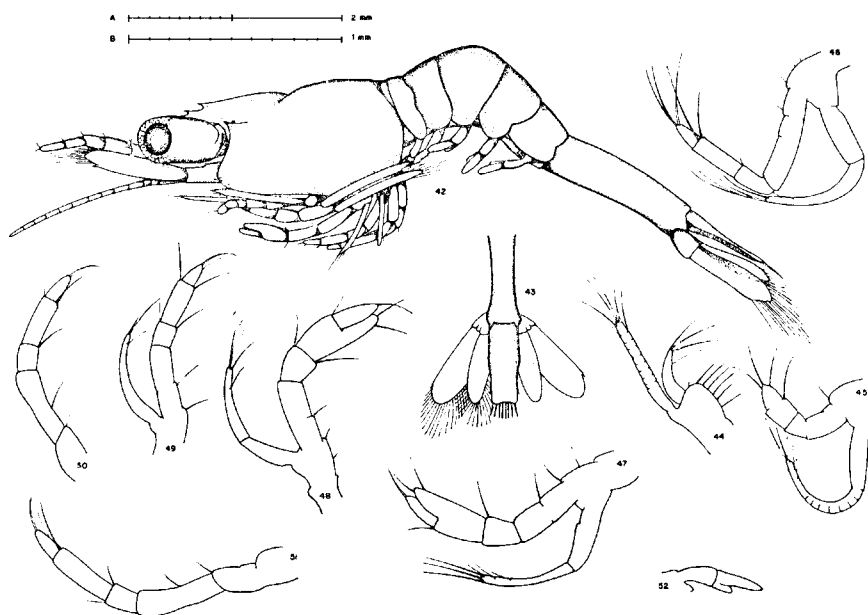


PLATE IV

The form V larva of *Palaemonetes kadiakensis* and appendages.

- FIG. 42. Entire form V larva, scale A.
 FIG. 43. Telson and uropods, setae of right uropod omitted, scale A.
 FIG. 44. First maxilliped, scale B.
 FIG. 45. Second maxilliped, scale B.
 FIG. 46. Third maxilliped, scale B.
 FIG. 47. First cheliped, scale B.
 FIG. 48. Second cheliped, scale B.
 FIG. 49. Third pereiopod, scale B.
 FIG. 50. Fourth pereiopod, scale B.
 FIG. 51. Fifth pereiopod, scale B.
 FIG. 52. Pleopod, Scale B.

The larval development of *Palaemonetes kadiakensis* M. J. Rathbun in the laboratory.

terior. Although other directions of locomotion are possible, larvae usually swim with the posterior end foremost. In spite of a lack of field observations on larvae, their behavior in the laboratory convinces us that they are planktonic.

Postlarvae swim by rhythmic beating of the pleopods. The attitude of form VII individuals is dorsal side up. In swimming the body is level and the anterior end is foremost. Although postlarvae are capable swimmers (as are the adults) they are not planktonic.

Form VII postlarvae (first postlarvae) are about 7.5 mm. long. The rostrum (Fig. 63) barely exceeds half the length of the antennal scale in newly metamorphosed postlarvae. Its upper margin is convex and bears four teeth, all anterior to the orbit. The lower margin is concave and lacks teeth. The carapace is provided with antennal and branchiostegal spines. The placement of the branchiostegal spine, unlike that of the adult, is at the anterior margin of the carapace at the end of the branchiostegal groove.

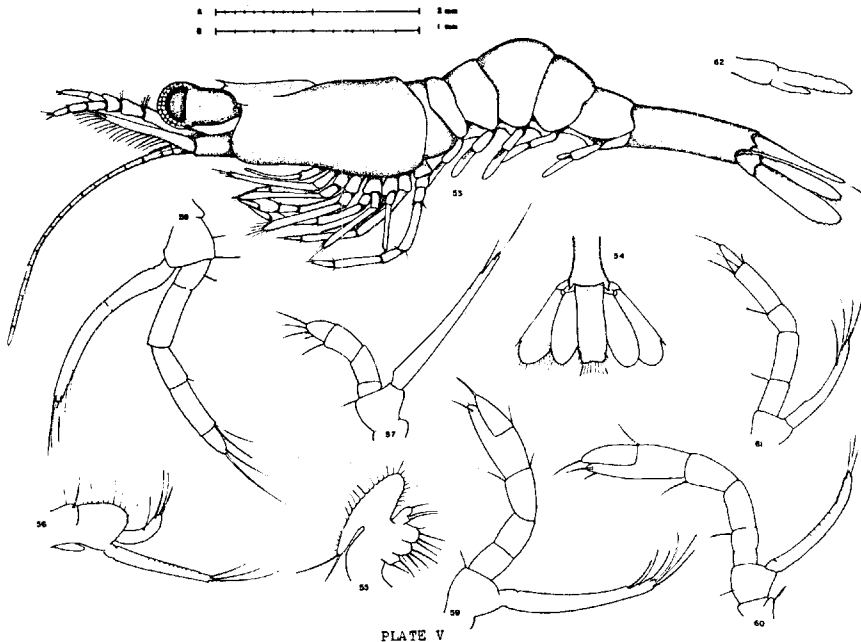


PLATE V

The form VI larva (final larval form) of *Palaemonetes kadiakensis* and appendages.

- FIG. 53. Entire form VI larva, scale A.
 FIG. 54. Telson and uropods, setae of right uropod omitted, scale A.
 FIG. 55. Maxilla, scale B.
 FIG. 56. First maxilliped, scale B.
 FIG. 57. Second maxilliped, scale B.
 FIG. 58. Third maxilliped, scale B.
 FIG. 59. First cheliped, scale B.
 FIG. 60. Second cheliped, scale B.
 FIG. 61. Third pereopods, scale B.
 FIG. 62. Pleopod, scale B.

The larval development of *Palaemonetes kadiakensis* M. J. Rathbun in the laboratory.

The telson (Fig. 64) is narrow posteriorly and bears a pair of dorsal spines about $\frac{1}{5}$ of the way back. In each posterolateral corner there are three spines, two of which are minute. The posterior margin is smooth, lacks the median tooth of the adult telson, and bears a pair of feathered setae.

Except for the persistence of rudiments of exopodites on the first three pereopods (Figs. 70, 71) the appendages (Figs. 65-72) differ from those of the adult mainly in relative lengths of segments or number of segments of antennular and antennal flagella. The pleopods (Fig. 72), unlike those of the larvae, are setose.

A summary of the molting and developmental history of 436 larvae on which individual, daily observations were made is given in table I. Larvae are treated as two groups: 60 individuals that successfully completed metamorphosis (data

pertaining to these are marked by an asterisk); and the remaining larvae that died or were preserved prior to completion of the larval phase. Differences in molting frequency or in form of larvae were not noted between those individuals fed *Artemia* and those fed plankton.

The first column of the table gives the number of the molt cycle. The protozoal intermolt is part of the first cycle. Columns two and four give the number of individuals prior to and following the molt at the end of the cycle given in column one. Thus, of 436 larvae treated, 378 completed the first molt and 273 successfully

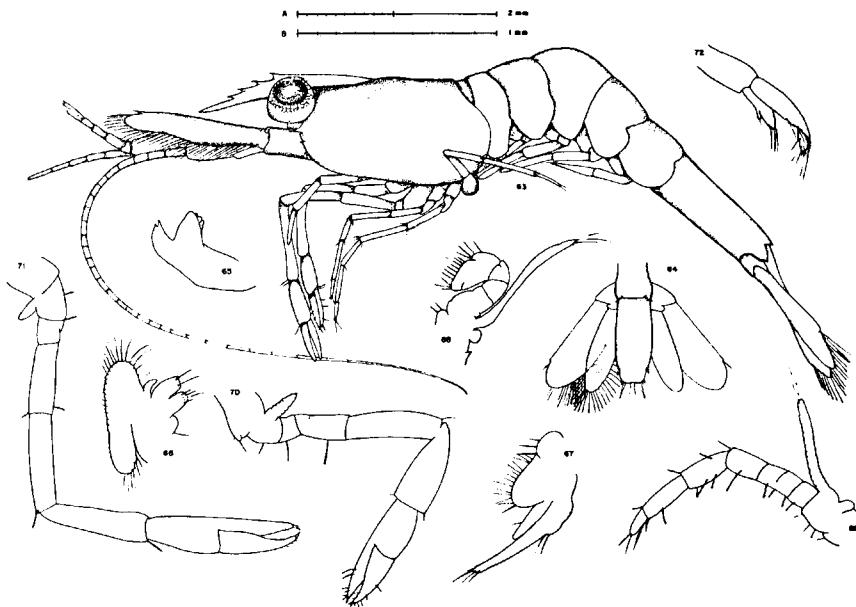


PLATE VI

The recently metamorphosed postlarva (form VII) of *Palaemonetes kadiakensis* and appendages.

- FIG. 63. Entire postlarva, scale A.
 FIG. 64. Telson and uropods, setae of right uropod omitted, scale A.
 FIG. 65. Mandible, scale B.
 FIG. 66. Maxilla, scale B.
 FIG. 67. First maxilliped, scale B.
 FIG. 68. Second maxilliped, scale B.
 FIG. 69. Third maxilliped, scale B.
 FIG. 70. First cheliped, scale B.
 FIG. 71. Second cheliped, scale B.
 FIG. 72. Pleopod, scale B.

The larval development of *Palaemonetes kadiakensis* M. J. Rathbun in the laboratory.

molted twice. Column three gives the form of the larvae in each intermolt period. Columns five, six and seven describe the duration of the molt cycle based on the number of individuals given in column four.

Examination of the data in columns one and three shows a regular sequence of forms from I to IV in which all the larvae advance from one form to the next at each molt. Following the fourth molt cycle, however, variation in the form of larvae of the same molting history is evident. Thus, among fifth intermolt larvae there are forms IV, V and VI individuals as well as larvae intermediate between these and designated as forms IV-V and V-VI. Sixth intermolt larvae may be

in forms V, V-VI or VI. Two individuals metamorphosed at the end of the fifth molt cycle and were form VII (post-larvae) in the sixth intermolt. Most of those individuals that completed metamorphosis did so at the end of the sixth molt cycle, but larval forms V-VI and VI were also found among seventh intermolt shrimp. Only two form VI larvae remained in the eighth intermolt, and these metamorphosed at the following molt.

TABLE I

Molt Cycle No.	No. at Start of Cycle	Larval Form	No. at End of Cycle	Duration of Molt Cycle in Days		
				Range	Mean	Std. Dev.
1	376 60*	I I	318 60*	1-3 2-3*	2.17 2.13*	0.41 0.11*
2	318 60*	II II	213 60*	3-5 2-4*	3.10 3.08*	0.36 0.49*
3	213 60*	III III	119 60*	2-5 3-5*	3.61 3.62*	0.74 0.66*
4	119 60*	IV IV	72 60*	1-8 1-5*	3.36 3.12*	1.05 0.69*
5	6 7 57 60* 1 1	IV IV-V V V V-VI VI	6 5 32 60* 0 0	2-5 2-5*	3.44 3.53*	0.68 0.74*
6	2* 18 4 21 56* 2*	V V V-VI VI VI VII	2* 6 0 6 56* —	included two lines below		
				2-4	3.17	0.55
				2-7*	3.67*	0.84*
7	1 11 17* 41*	V-VI VI VI VII	1 0 17* —	3-4*	3.59*	0.49*
8	2* 15*	VI VII	2* —	3-4*	3.50*	—
9	2*	VII	—			

TABLE I. A summation of the developmental history of larvae of *Palaemonetes kadiakensis* reared in the laboratory. Data marked by an asterisk apply to those larvae that completed metamorphosis. See text and figures for descriptions of larval forms I to VI and the postlarva, form VII.

If only those 60 individuals that completed metamorphosis are considered it is seen that all passed through a sequence for forms I, II, III, IV and V after which some variation became evident. Two individuals remained in form V after the fifth molt and two advanced to the postlarval condition (form VII) directly from form V without an intervening form VI. The two larvae that repeated developmental form V advanced to form VI at the end of the sixth molt cycle when 41 larvae that had gone through a developmental sequence of forms I, II, III, IV, V and VI metamorphosed. At the end of the seventh molt cycle 15 larvae meta-

morphosed. Thirteen of these had repeated form VI in the seventh intermolt, and two had repeated form V in the sixth molt cycle. Two eight intermolt larvae repeated form VI for the second time and metamorphosed at the end of the eighth cycle. Thus, among 60 individuals, metamorphosis occurred after the fifth, sixth, seventh, or eighth molt following a developmental sequence of five or six discrete larval forms, the last of which was sometimes repeated in individuals evidently having completed larval development but not yet ready for the transformation to postlarvac.

Columns five, six and seven of table I summarize the duration of the several larval molt cycles, but these data require further elucidation. The interval between hatching and the first molt probably does not represent a full molt cycle since the protozoal cuticle is lifted clear of the underlying integument at the time of hatching. Secondly, larvae were observed to molt only at night, a factor that may bias data on duration of the period between molts if it follows that molting of larvae is influenced even partially by a diurnal cycle. If we assume that, conditions requisite to molting having been satisfied within the hours at daylight, the actual ecdysis is blocked until the following darkness, the molt cycles described in table 1 may be biased by extrinsic factors. Because of this the molt cycle data are described grossly, and analysis of the periodicity is not attempted.

The duration of molt cycles other than the first, for which a time of origin can not be determined, varies from one to five days among those larvae that survived metamorphosis, although one individual that did not survive the larval phase molted successfully after an intermolt of eight days duration. Means of the molt cycles varied from 3.08 to 3.62 days. There seems to be a slight increase in the length of successive molt cycles, but it should be stressed that these data were obtained under laboratory conditions described above.

Among the larvae that completed metamorphosis the larval phase lasted from 16 to 30 days with a mean larval life of 21.17 plus or minus 2.33 days. One individual raised in 1959, on which a daily record of form was not kept, metamorphosed in 14 days.

DISCUSSION

Meehan (1936) described and figured first and second stage larvae of "*Palae-moneles paludosa*", but his figure of the adult from which the larvae presumably were obtained is of a mature female *P. kadiakensis*. We assume, therefore, that Meehan's description of larvae actually was based on material identical to our form I and form II larvae, although, because of the marked resemblance among early larval forms of *P. kadiakensis*, *P. pugio*, *P. vulgaris* and *P. intermedius*, more precise identification of his material is impossible. We reserve for a forthcoming account of the larvae of *P. intermedius* a discussion of resemblances among the larvae of these closely related species.

The relationship between form and molting of *Palaemonetes* larvae has been discussed by Broad (1957a) who found that differences in form of *P. pugio* larvae of the same age and molting history might be related to the amount of food consumed since hatching. Although no attempt was made to vary the feeding of *P. kadiakensis* larvae, differences in form were noted among both fifth and sixth molt cycle larvae. Thus, six larvae that had completed four molt cycles were in form IV, having failed to develop beyond the form of the fourth molt cycle. Seven of these fifth molt cycle larvae were intermediate between forms IV and V. Differences between forms V and VI, noted among both fifth and sixth cycle larvae, are small and subject to some personal interpretation. We, nevertheless, found ourselves both individually and collectively consistent in our identification of larval form. The occurrence of variation in form among larvae of the same molting history is considered to be real and is interpreted as evidence of independence of molting and development (including growth). We believe that the small number

of fifth and sixth intermolt larvae that differed from the norms of each group reflect the uniformity of the diet and other culture conditions.

The control of molting in natantians, although imperfectly understood, probably involves activation of the epidermis by a molting hormone demonstrated in brachyurans by Eschaler (1954) and others. In molting cycles of adults this hormonal activation probably occurs at the beginning of the stage which Drach (1939) has called proecdysis or stage D and is followed by an actual separation of the old cuticle from the underlying epidermis and forming new cuticle. Animals, especially crabs, in which this separation of old and new cuticles is evident on gross examination have been called peelers and are in stage D_2 or D_3 of the molt cycle. This condition, which is usually reached late in the cycle, is followed by exuviation. According to Passano (1960) stages D_2 - D_3 persist through about the last 18 percent of the cycle in adult natantians. Proecdysis or activation of the integument may be blocked during earlier stages of the cycle possibly by substances elaborated in neurosecretory cells of the eyestalk. Carlisle (1959), however, has demonstrated molt inhibition and molt acceleration resulting from eyestalk removal in *Palaemon serratus* from different populations. The eyestalk organs known to be secretory in adult decapods have been found in *Crangon allmani* larvae by Dahl (1957), but there is no evidence of their secretory activity even in these larvae.

We have noted separation of old and new cuticle evident as double outlines particularly of uropods and antennal scales in *Palaemonetes* larvae usually on the day following the molt. If, as this indicates, activation of the integument occurs within 24 hours after exuviation, while the next molt does not usually occur for another 24 to 48 hours or more, it must be concluded that stages D_2 - D_3 in larval molt cycles are of much longer relative duration than are the corresponding stages of adult molting. As a corollary it may be stated that the activation of the integument, either by release from inhibition or by a lack of it, occurs shortly after the molt in the larvae of *Palaemonetes*. The observed prolongation of the peeler condition may result from a delay of actual exuviation which seems to be related to a diurnal cycle.

We have noted previously that metamorphosis in *Palaemonetes* larvae, which may occur on any of several days or in any of several molt cycles, seems to bear no fixed relation to completion of larval development since some individuals may skip the last larval form and others may repeat this through several intermolts. These data on *P. kadiakensis* reinforce this argument and suggest a control over the termination of the larval phase not dependent upon either specific molting or developmental history.

SUMMARY

1. From 436 newly-hatched larvae obtained from eggs carried by ovigerous female *Palaemonetes kadiakensis* M. J. Rathbun, 60 postlarval shrimp were reared in the laboratory.
2. These and the remaining larvae passed through all or some of a sequence of six larval forms, but after the fourth form a relationship of form to molting history no longer existed.
3. In the main, larval development of *P. kadiakensis* parallels that of *P. pugio* and *P. vulgaris* but both eggs and larvae of the fresh water shrimp are larger.
4. The larvae molted from five to eight times. The duration of molt cycles other than the first, which begins prior to hatching, was from 3.08 ± 0.49 days to 3.62 ± 0.66 days at least two-thirds of which was spent in the D_2 - D_3 stages of the molt cycle.
5. Metamorphosis to the postlarval condition occurred from 16 to 30 days (21.17 ± 2.33) after hatching and was somewhat independent of prior molting and possibly of prior developmental history.

LITERATURE CITED

- BOAS, J. E. V. 1889. Über den ungleichen Entwicklungsgang der Salzwasser und Süßwasser-Form von *Palaemonetes varians*. Zool. Jahrb. Syst., 4: 793-804.
- BROAD, A. C. 1957. Larval development of *Palaemonetes pugio* Holthuis. Biol. Bull., 112: 144-161.
- 1957a. The relationship between diet and larval development of *Palaemonetes*. *Ibid.*, 112: 162-170.
- BURKENROAD, M. D. 1947. Reproductive activities of decapod crustacea. Amer. Nat., 81: 392-398.
- CARLISLE, D. B. 1959. Moulting hormones in *Palaemon (Leander)*. II. Differences between populations. Jour. Mar. Biol. Assoc., U. K., 38: 351-359.
- DAHL, E. 1957. Embryology of the X organs in *Crangon allmani*. Nature, 179: 482.
- DRACH, P. 1939. Mue et cycle d'intermue chez les Crustacés Décapodes Ann. Inst. Oceanogr., Paris. 19: 103-391.
- ESCHALIER, G. 1954. Recherches expérimentales sur le rôle de "l'organe Y" dans le mue de *Carcinus moenas* (L). Compt. Rend. Acad. Sci., Paris, 238: 523-525.
- FAXON, W. A. 1879. On the development of *Palaemonetes vulgaris*. Bull. Mus. Comp. Zool., 5: 303-330.
- GURNEY, R. 1942. Larvae of decapod crustacea. The Ray Society, London.
- MEEHAN, O. L. 1936. Notes on the freshwater shrimp, *Palaemonetes paludosa* Gibbes. Trans. Amer. Microsc. Soc., 55: 433-441.
- PASSANO, L. M. 1960. Molting and its control. In Waterman, T. H., Ed. 1960. The Physiology of Crustacea. I. Metabolism and Growth. Academic Press, New York.
- SOLLAUD, E. 1923. Le développement larvaire des Palaemonidae. Bull. Biol. France et Belg., 57: 510-603.

