A Study of the Life History and Productivity of Hyalella Knickerbokeri Bate.[1]

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Introduction.

My first work with the arthrostracan crustacean, Hyalella knickerbokeri Bate was in the summer of 1920 at the Indiana University Biological Station at Winona Lake, Indiana, and its study was continued throughout the winter of 1920-1921.

The first problem was to determine, if possible, the contribution made by Hyalella knickerbokeri Bate to the food of higher animals. I soon found I could not get very far in my studies until I had worked out the life cycle of the amphipod in some detail.

Hyalella knickerbokeri is widely distributed. It is found in every state but at widely scattered localities. It is especially abundant in southern Canada, southern Minnesota, northern Iowa, Illinois, and Indiana. Miss Weckel ('11) extends its range to Lake Titicaca, Peru, South America. Its distribution is also discussed by Jackson ('12), Weckel ('07), and Della Valle ('93).

Methods.

Hyalella can be collected easily by washing Chara or other water plants in water contained in a small basin. They were then transferred to other vessels. The moving of individuals was done entirely with a small pipette and when the young were extruded they were transferred to a separate dish from that in which the mother was located, one at a time. It was next to impossible to count them when all together in one dish with the mother, due to the continual movement of all of them. Paired individuals were kept in separate dishes where they could be examined at will. The dishes were numbered and the data for each

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pair entered under the same number in my notes as was written upon the dish.

I found that Hyalella would feed upon almost any water plant, but seemed to show a preference for certain ones such as Ceratophyllum, Elodea, and Chara. I also observed amphipods of the species feeding upon certain animal tissue, e.g. a dead dragon-fly nymph, a dead isopod, a dead amphipod, etc. Foods of other species of amphipods are discussed in some detail, by Sexton and Mathews ('13), M. Armand Virè ('03), and Della Valle ('93).

Relation of Reproduction to Season.

All the evidence that I have collected points to the fact that Hyalella has a distinct breeding period, limited to the warmer months. For example, when a hundred or so animals were examined during the first of February, not a single female was found with eggs in the brood pouch nor were there any young, present. The same was true when several hundred adults were examined the first of April. At neither time were any individuals observed mating when they were brought to the laboratory, but the second day after they were collected and in a warm room some fifty-odd pairs were isolated, the male carrying the female in the usual manner when preparing for copulation. These animals were collected on April 6, and on April 8 were noticed pairing. This sudden change in so many animals shows conclusively that both sexes were ripe and ready for mating as soon as conditions (which I believe to be temperature) were suitable, but the time for mating was put off as long as conditions were not favorable. All the females, whether mated or not, could be easily distinguished from the males, because the ova could be distinctly seen and approximately counted as they lay in the ovary which is located in the dorsal thoracic region. The testes appeared as a lighter green than the ovaries and are located approximately in the same position in the male as the ovaries are located in the female. The testes, however, were much more elongated, tapering at each end while the ovaries appeared as a cylindrical green patch ending abruptly at each end. The male ducts according to Kunkel ('18) open by papillae on the ventral side of the last thoracic segment. The oviducts each open at the base of the fifth coxal plate so that when the eggs are deposited they are caught in the marsupium which is formed by certain hair-like projections on the ventral side known as oostegites.

Fifty pairs were isolated the day the male began to carry the female. Of these I succeeded in carrying only three pairs through to the second oviposition. These were pairs 6, 9, and IV, Table 1. In two cases there were twenty-four days and in one case twenty-six days between two successive ovipositions. The dates are found in Table 1.

The young (Table 2) hatch about the twenty-first or twenty-second day after oviposition and remain in the brood pouch from 0-3 days when they are extruded at the time the moult of the female occurs in preparation for the next oviposition. The male may begin to carry the female as early as the seventh day before she moults, three or four days before the young are even hatched. The eggs become easily visible about a week before they are laid. Jackson ('12) succeeded in

carrying one individual through until the young were hatched. From the twentieth day until the twenty-fifth after ovipositoin he was compelled to be absent. On the twenty-fifth day the young were swimming about in the dish. Then, he says "From these observations we see that the eggs were in the pouch twenty-five days, at least, before they

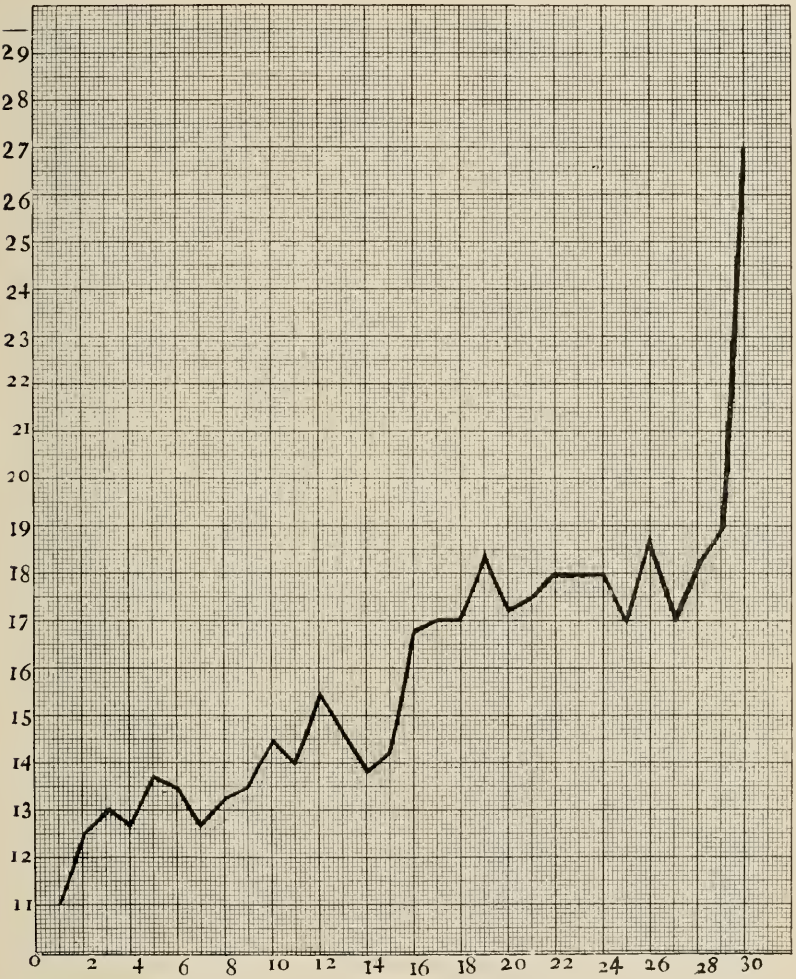

FIGURE 1

Figure 1. The ordinate represents the length of the third joint of the second antenna of the amphipod Hyalella knickerbokeri. The abscissa represents the number in a brood of the amphipods. There is shown a distinct correlation therefore between the age (since any part of an amphipod increases directly with age, the length of any part would represent the age) of an amphipod and the number in a brood.

hatched." I believe my observations and data show clearly that there is an incubation period of about twenty-one days with a brooding period of one to three days after hatching. The twenty-fourth day after the first moult the second oviposition takes place. Therefore, the young cannot be carried more than three days after they hatch for the female moults at that time.

The sequence of events in mating and oviposition is briefly stated as follows: The male carries the female about with him from one to seven days, leaving her when she moults and returning to carry her until

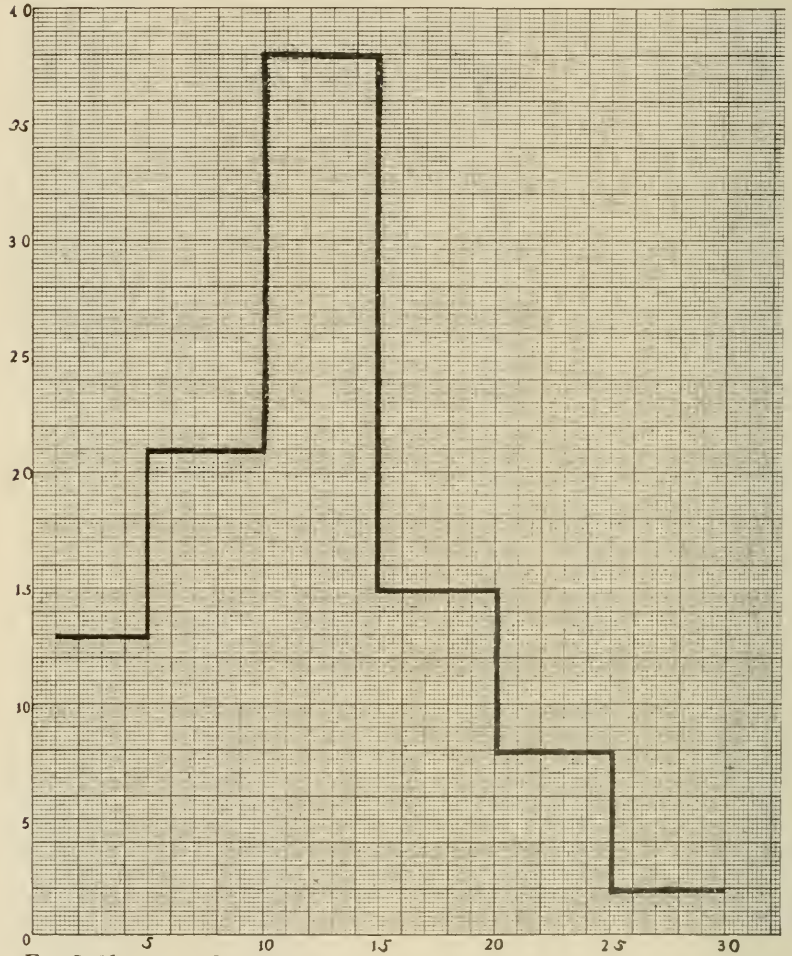

FIGURE 2.

Figure 2. The ordinate represents number of broods. The abscissa represents the number in a brood. This figure represents broods extruded between June 27 and August 14, 1920. Very few animals were breeding at the beginning of the observations recorded here.

copulation takes place which usually occurs during the next twenty-four hours after the female moults. Oviposition then follows copulation directly and the female breaks away from the male's grasp either before or during oviposition.

Seasonal Distribution of Number in Brood.

Preliminary measurements indicated that the third joint of the peduncle of the second antenna is in direct proportion to the length, which in turn has a direct correlation with the age of the animal. I

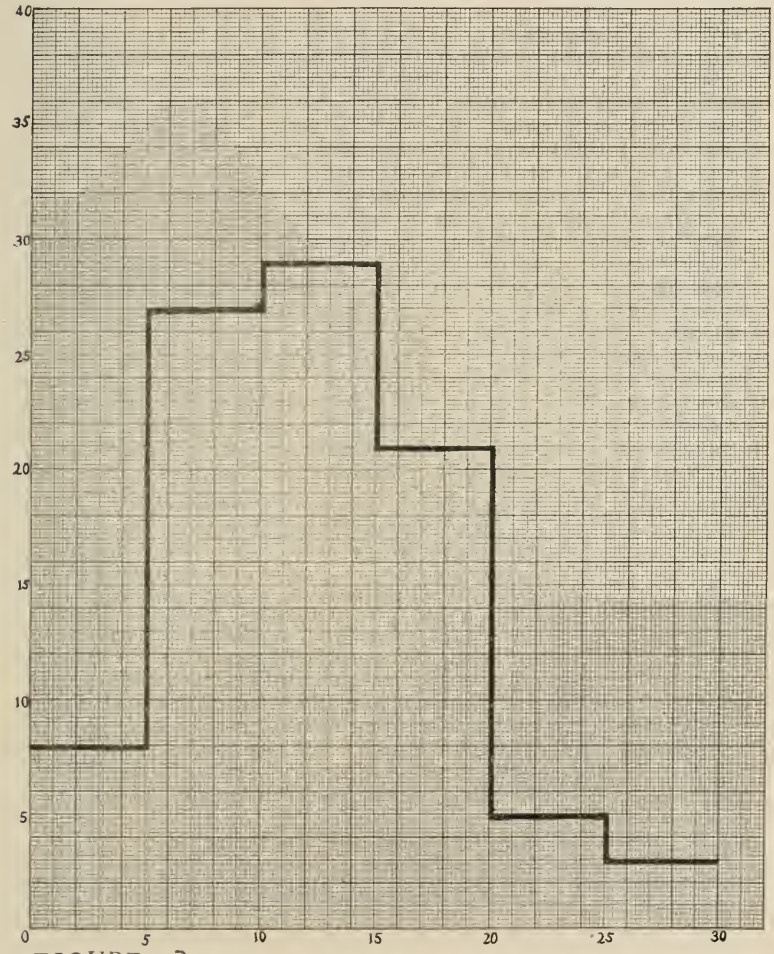

FIGURE 3.

Figure 3. Shows the transition period between time represented in Figure 1 and Figure 4. The time broods were extruded was August 7-14.

measured the aforesaid joints, taking the average length of the joint as the ordinate and the number in a brood as the abscissa, and constructed Figure 1. The figure showed that the number in a brood did increase with the length of the third joint of the peduncle of the second antenna. Therefore, I feel safe in concluding that the number in a brood increases with the age of an animal.

I have not had the good fortune to observe the number of young in two successive broods of the same female. However, Sexton and Mathews ('13) state that in Gammarus chevreuxi, the number of eggs seemed to increase with age, e.g., in the case of one individual the

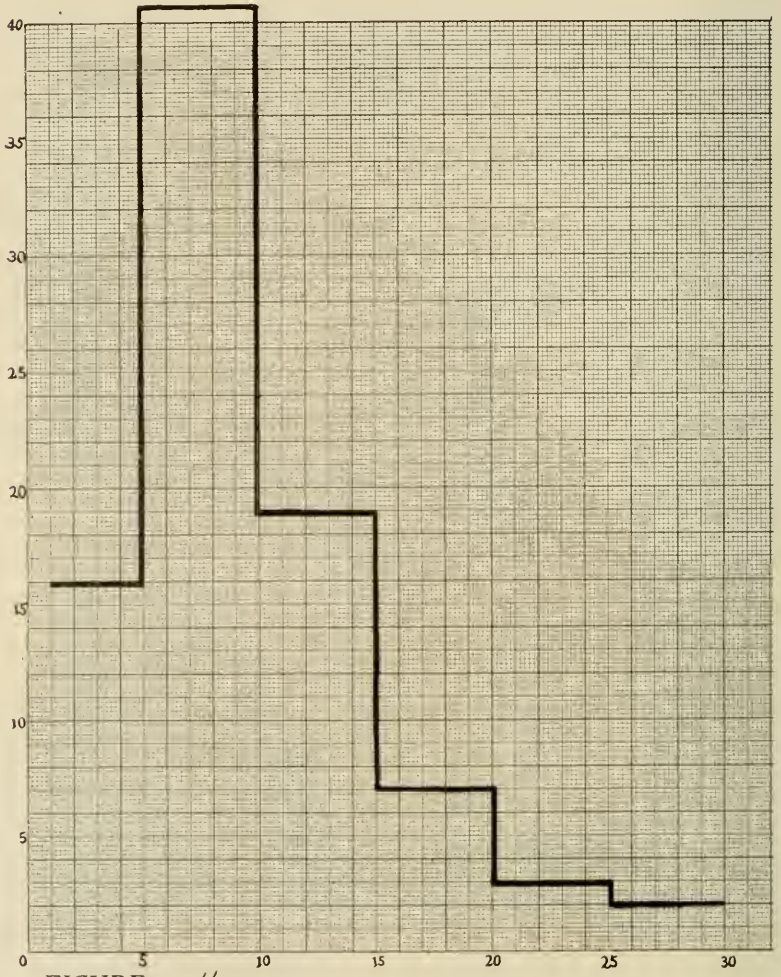

FIGURE 4.

Figure 4. Ordinate and abscissa same as in Figures 2 and 3. Broods extruded between August 16 and September 26.

number of eggs increased from eighteen to forty-four as the age of the animal increased.

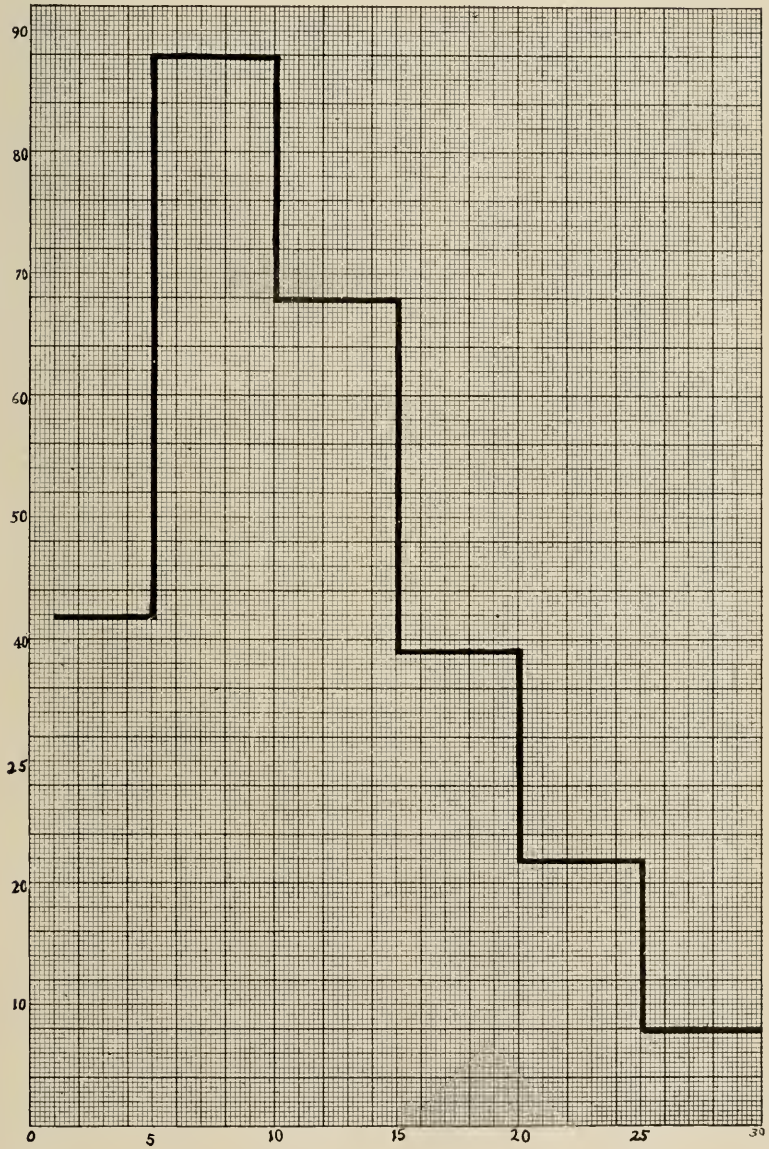

FIGURE 5.

Figure 5. Ordinate and abscissa same as in Figures 2, 3, and 4. Includes all broods extruded between June 27 and September 26, 1920, a total of 293 broods.

The largest number of broods with ten to twelve in a brood occurs early in the season during the last of June to the middle of August (Figure 2), but in the latter part of the season the largest number of broods with five to ten in them are found. (Figure 4.)

Let me suggest that probably the high point of (Figure 2), which represents all those females producing from ten to fifteen in a brood, represents those individuals breeding which were themselves produced the year before. As the season progresses the highest point is changed and the number of individuals producing five to ten reaches the largest number. There is a smaller number in a brood because younger animals are breeding and evidently they themselves were produced early that same season. Summing up then we might say that

1. In the early part of the season there are larger broods, produced as a rule, than during the latter part of the season, therefore

(a) Individuals reproducing in the first part of the season were themselves produced during the previous season and are older than,

(b) Individuals reproducing toward the last of the season which were themselves produced early that same season.

(c) Figure 3 shows the transition stage as occurring during the middle of August. That is, the largest number of broods produced with ten to fifteen in a brood is being reduced both in number and its relative position to the number of broods of five to ten in a brood.

After the females produce from ten to fifteen young in a brood the females seem to gradually die off. (Figure 5.) There could be very few reasons for this.

(a) The females might become barren after reaching a certain age but this is unusual in crustacea and I myself never found it to be true in the hundreds of individuals examined.

(b) Died when a certain age was reached, which is not true as there would be a sudden drop some place in Figure 5 but it is a gradual drop.

(c) The animals might meet with accidents such as being seized and eaten by other animals. This seems to me is the true explanation so that an animal increases in age it has fewer companions its own size and age. Thus an individual seldom, if ever, reaches a size, which in reality represents its age, to produce a brood above the thirty mark.

Additional Observations.

Holmes ('03) in his discussion of sex recognition among amphipods states that the instinct of the males for carrying the females is very strong, and that they cling to them by the first gnathopods even when injured. His point is that the lack of resistance on the part of the female when carried by the male, determines whether she shall be carried by him or not, and not merely her sex. In corroboration of this view I saw a male tugging away at a male who in turn was carrying a female. He pulled and tugged while the two ventral amphipods remained comparatively quiet. If the male carrying the female had not been carrying her, he would not have permitted the other male to carry him, but he clung to his mate in spite of his unusual position.

I had the good fortune to observe the process of copulation several times which was in detail as follows:

On April 15, 1921, I observed a male swimming about with a female which he held in the usual way, but every once in a while, when swimming he braced his pereopods against the dorsal side of the female and then by forcing them backward quickly, produced a short quick jerk of himself but did not seem to effect the female. This he did three or four times, which actions seemed to be a signal for copulation or at least a procedure gone through with before copulation which immediately followed and lasted a period of twenty-five or thirty seconds.

Without changing or releasing his hold of the female with his first gnathopods by which he held her on the dorsal side, he extended the posterior part of his body around the female to her ventral side until his uropods touched the marsupium of the female at its mid-ventral part. He pressed the marsupium with a succession of quick movements with the tips of his uropods, lasting as stated about some twenty-five or thirty seconds. His last thoracic somite just turned past the coxal plates of the female so that the ejected sperm could be quickly swept into the marsupium by the fast moving pereopods of the female. Meanwhile the male did not perceptibly move his pereopods. He next straightened himself into the dorsal position and swam off with the female, but modified the swimming by extending his first gnathopods with which he still clung to the female, pulled the female back as if he were shaking her. He did this several times and the whole process as described above was repeated as many as eleven times. The next morning, April 16, the eggs were deposited in the brood pouch and he no longer swam about with the female. One time I observed a pair copulating while the eggs were passing down the oviduct but usually, as far as I can observe, copulation occurs before the eggs even start down the oviduct.

On April 12, 1921, I observed a male carrying a female which had laid her first egg in the brood pouch. When the second one had passed down she struggled free and from that time 11:12 to 11:52 a. m., a total of forty minutes exactly, she had laid all the eggs. My observations for Hyalella knickerbokeri is the same as Sexton and Mathews ('13) for Gammarus chevreauxi as to the laying of the eggs, for the last one laid was the most posterior and also as they stated an oviduct was clearly seen. I could distinguish it only when the eggs were passing down it.

The ova are of a dark green color and as they left the ovary by means of this small tube, smaller in diameter then the ova, they were pressed out of their usual spherical shape. The eggs passed down both oviducts at the same time. The oviducts were seen to open at the base of the fifth coxal plate.

The incubation period for Hyalella knickerbokeri is, as stated above, about twenty-one days. The eggs remain green for a week or ten days, then turn black. When examined under the binoculars one can see the elongated embryos. About the eighteenth to the twentieth day they become a reddish brown or pinkish and on the twentieth day the red eyes of the embryo can be distinguished very well. Miss Langenbeck ('98) says that the colors of the embryos of Microdentopus gryllotalpa Costa changed color in a similar manner.

The young after hatching may be extruded that same day or any

time up to three days later when the mother moults in preparation for the next oviposition.

Hyalella knickerbokeri swims about restlessly until it comes in contact with any object and then crawls into the crevices and between the branches of plants until as much of it is in contact as possible. There it comes to rest. H. T. Jackson ('12) says of this species that, "They may come to rest curled up in the surface film, the surface tension then producing the contact stimulus." This may be easily observed at any time.

Phototropism.

The influence that light has upon Hyalella is quite noticeable. If a number are placed in a glass dish, they collect almost immediately on the side of the dish away from the windows. There are always some leaving the light and swimming to the other parts of the dish but they eventually get back to the side farthest from the light. C. H. Phipps ('15) says, the stimulus of the direction of rays to which the Amphipods react negatively has a stronger effect than the stimulus of light intensity." Thus we see Hyalellae are positively thigmotropic and negatively phototropic.

The average number of Amphipods in a brood is 11.27 out of a total of 3,103 young in 275 broods counted. The maximum number in any brood was thirty young and the largest number of broods occurred with seven in a brood.

Summary and Conclusions.

1. Data collected seems to point to the fact that Hyalellae of northern Indiana have a distinct breeding season during the warmer months of the year.

2. The breeding habits of Hyalella knickerbokeri are similar to other amphipods.

3. The female is carried by the male from one to seven days before copulation occurs.

4. The female moults before oviposition and the period between moults is twenty-four to twenty-six days.

5. Copulation lasts about twenty-five to thirty seconds but is repeated ten to twelve different times at intervals of a few minutes.

6. Oviposition follows copulation in the following twelve to twenty-four hours. There are twenty-four to twenty-six days between ovipositions, therefore there are twenty-four to twenty-six days between broods.

7. The incubation period is about twenty-one days.

8. The young are carried in the brood-pouch from one to three days. Then the female moults in preparation for her next oviposition.

9. Preliminary measurements indicated that the length of the third joint of the peduncle of the second antenna is in direct proportion to the life length.

10. The age of an amphipod is correlated directly with the number of young in a brood.

11. The number in a brood increases as the length of the third joint of the peduncle of the second antenna. (Figure 1.)

12. The number in a brood must increase each successive brood or as the animal increases in age.

13. Hyalellae probably live a second summer, for the largest number of broods occurring with ten to fifteen in a brood was toward the beginning of the season. (Figure 2.)

14. Hyalella knickerbokeri is positively thigmotropic and negatively phototropic.

15. The average number of young in a brood was 11.27 individuals.

16. The largest number of broods produced were produced with seven in a brood.

17. The maximum number in any brood counted was thirty young.

18. The total number of young counted was 3,103.

19. The total number of broods observed was 275.

Acknowledgment.

I undertook the studies recorded in this paper at the suggestion of Dr. Will Scott. It is due to his help that it is now completed.

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TABLE I.

Number of Pair	Date ♂ began to carry ♀ W	Date ♀ moulted	Date ♂ carried after moult of ♀	Date eggs were deposited	Date young were hatched	Date young were extruded	Date ♀ was again carried by ♂	Date of second moult	Date of 2nd time carried after moult	Date of second oviposition
Pair 1	April 8	April 9	?	April 10	May 1	May 1	April 24			
Pair 2	April 8	April 11	April 11	April 12	May 2 or 3	May 5				
Pair 3	April 8	April 9	April 9	April 10	May 2	May 4–7				
Pair 4	April 8	April 13	?	April 13	May ?	May 6				
Pair 5	April 8	April 10	?	April 11	April 3?	May 4 & 5				
Pair 6	April 8	April 10	?	April 10	May 1	May 4	April 29	May 5		May 6
Pair 7	Aptil 8	April 10	?	April 10	May 3 6	May 6				
Pair 8	April 8	April 9	?	April 9	April 30	May 1				
Pair 9	April 8	April 12	?	April 13	May 1	May 6	April 29	May 6	May 6	May 7
Pair 10	April 8	April 12	?	April 13	May 3					
Pair 11	April 8	April 13	?	April 13	?	May 4 & 5				
Pair 12	April 8	April 9	?	April 10						
Pair 13	April 8	April 12	April 12	April 13						
Pair 14	April 8	April 10	April 10	April 11						
Pair 15	April 8	April 13	?	April 13		May 6	April			
Pair I	April 7	April 8		April 9	April 29	April 29				
Pair II.	April 7	April 11		April 12	May 2					
Pair III.	April 7	April 10		April 11	May 2-3					
Pair IV.	April 7	April 8		April 9		April 30	April 27	May 2	May 2	May 3
Pair V.	April 7									
Pair VI.	April 7	April 9		April 10						
Pair VII.	April 7	April 10		April 11						
Pair VIII.	April 7	April 9								
Pair IX.	April 7	April 10		April 12						
Pair X.	April 7	April 13		April 13						
Pair XI.	April 7									
Pair XII.	April 7	April 9		April 9						
Pair XIII.	April 7	April 11		April 12	May 2					
Pair XIV.	April 7	April 10								
Pair XV.	April 7	April 11		April 11	May 2	May 4				