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LARVAL DEVELOPMENT OF THE CRUSTACEAN *THOR FLORIDANUS* KINGSLEY[1, 2]

BY A. C. BROAD[3]

Duke University Marine Laboratory, Beaufort, North Carolina

Three tiny, ovigerous, female shrimp were found in August, 1954, among sea squirts and coral near the shore of the Duke University Marine Laboratory at Beaufort, N. C. These individuals were placed in separate bowls of sea water in the laboratory and held until the eggs hatched. The adults were then preserved

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and later identified as *Thor floridanus* by Dr. Fenner A. Chace, Jr. This species has not since been encountered at Beaufort.

The larvae were reared through metamorphosis in the laboratory. These larvae, while resembling those obtained from Bermuda plankton and assigned to the genus *Thor* by Lebour (1940), differed from Lebour's material in size and color and from her reconstructed developmental sequence in both number and structure of intermolts. Since the present larvae are undoubtedly those of *T. floridanus*, the species to which inference assigns Lebour's material, two alternatives are suggested: the two groups of larvae belong to different taxonomic groups; or the larvae belong to the same species but their development varies in accordance with geographic location or other external factors.

The author wishes to acknowledge with thanks his indebtedness to Professor C. G. Bookhout, under whose guidance and direction this work was done. Thanks are also due Dr. T. R. Rice for cultures of algal cells fed to larvae, and Dr. Chace for identification of adults.

METHODS.—Ten larvae from the same clutch of eggs were placed in each of several clean finger bowls of untreated sea water. The larvae were fed clumps of cells from uni-algal cultures made from T. R. Rice's pure stocks of *Chlamydomonas* sp., *Thorocomonas* sp., *Nannochloris* sp. (Chlorophyta), or the diatom, *Nitzschia closterium*. Each individual received the same food throughout its life.

Each larva and bowl was examined daily under a dissecting binocular microscope. Only the presence of all or parts of exuviae was accepted as evidence of ecdysis. Water was changed and food added after each inspection.

Living larvae, anesthetized in a dilute urethane-sea-water solution, were drawn with the aid of a camera lucida. Individual appendages were studied from alcoholic specimens which had been anesthetized, killed in formalin and partially dehydrated in a graded series of alcohols to prevent distortion of the exoskeleton.

RESULTS.—The three females produced respectively 108, 125 and 207 living first zoea larvae. The eggs hatched at night and the parent shrimp molted shortly afterward. One of the three females produced a second clutch of eggs immediately following the post-incubatory ecdysis.

The larvae usually survived the first molt whether they had been fed or not. Twenty-three individuals, out of a total of 30 which were not fed, molted once. None of these molted twice and all died within five days. Of 20 larvae fed *Chlamydomonas*, 12 molted once, none molted twice, nor did any live longer than five days. Forty larvae were fed *Thorocomonas*. Although none of these metamorphosed, five individuals completed the larval phase of development. Twenty first zoeae were fed *Nannochloris*. All of these survived the first molt, and seven lived through metamorphosis. Survival among 40 larvae fed *Nitzschia* was influenced by the removal of specimens for preservation and study. Thirty individuals lived through one molt, and two were left after metamorphosis.

The first molt occurred on the second or third day after hatching. The frequency of subsequent ecdyses among those larvae which survived was one molt every 1.9 to 2.0 days. The final larval form was attained after the seventh molt. Metamorphosis occurred at the eighth ecdysis.

First zoea (Fig. 1–5): length 1.6 mm. Carapace with pterygostomian spine; antero-ventral margin of carapace behind this spine with 3 serrations or teeth. No true rostrum, the carapace terminating anteriorly in a broad flat point between the sessile eyes. Dorsal organ in mid-dorsal line above posterior margin of orbit. Dorsal papilla in mid-dorsal line near posterior margin of carapace. Abdomen of 6 somites, without spines. Abdominal somite 6 continuous with telson. Telson roughly triangular with terminal corners truncated and posterior margin notched medially; bearing 14 terminal spines.

Antennule (Fig. 2) simple with a long basal segment which bears distally a long plumose seta on the inner side and an outer flagellum of 1 segment; outer flagellum with 3 club-like aesthetes and a short plumose seta. Antenna biramous; basal segment with a tooth at junction with flagellum; flagellum of 1 short segment with a long plumose seta and a short spine at its distal end; scale consisting of a long proximal and 4 short distal segments with 2 setae externally and 9 long plumose setae around the tip and inside.

Mandible (Fig. 3) with short, 3-toothed incisor process and a toothed molar surface; two small serrate teeth in angle between incisor and molar processes. First maxilla (Fig. 4) with coxa armed with 2 stout teeth and 3 spines; basis with 6 serrate teeth; endopod a 2-jointed palp with 3 setae with stout side bristles and a sparcely bristled terminal spine. Second maxilla (Fig. 5) biramous, the basis 3-lobed, bearing stout spines and bristled setae on the lobes; endopod bearing 3 bristled setae on a lobe near its base, 2 bristled setae on a median lobe, one bristled seta on a lobe near the apex, and 2 bristled apical setae; exopod a flat plate with 3 anterior and one lateral plumose setae.

First maxilliped biramous; basis with 3 inwardly directed setae; endopod of 4 segments each of which bears 1 or 2 setae distally; exopod longer than endopod with 4 apical and 2 sub-apical setae. Second maxilliped similar to first but larger; endopod with 3 apical spines; exopod with 3 apical and 2 sub-apical setae. Third maxilliped biramous; endopod of 4 segments, unlike other maxillipeds, with terminal setae on ultimate and penultimate segments; exopod with 3 apical and 2 sub-apical setae.

First pereiopod biramous, rudimentary, small.

Bright red, stellate chromatophores at distal and proximal ends of antennular peduncle, on labrum, in mid-dorsal line above gastric and cardiac regions, in mid-dorsal line of each abdominal somite, on sternite of thoracic somite 2, on sternite of abdominal somites 3, 4 and 6, anterior to and on each side of anus, and 1 on each side near end of telson. Larvae otherwise colorless.

The first zoea corresponds closely to Lebour's description of the first larval stage. Lebour's larva was 2 mm. or less in length as opposed to 1.6 mm. for the present first larva. Lebour's figure of the first maxilla shows an unsegmented endopod and setation which differs slightly from that of my material in which the enopod is of 2 segments. Setation of the second maxilla differs between Lebour's larvae and the first zoea of *T. floridanus*. Differences in color pattern which apply to all larvae are treated elsewhere.

Second zoea (Fig. 6): length 1.9 mm. Eyes stalked; eyestalks with postero-ventral, red chromatophores. Rostrum flat, broadly triangular, not extending beyond eyes. Carapace with spines and dorsal papillae of previous zoea plus an antennal spine. Telson as before, but with 2 minute terminal spines in the midline.

Antennular peduncle of 2 segments, the proximal segment being over 3 times as long as the distal and bearing 2 setae; distal segment with an inner distal seta borne on a short, bulbous base, and a seta antero-laterally; outer flagellum as before, but the 3 aesthetes are now long. Antennal scale of a long proximal and 3 short distal segments; flagellum without long terminal seta, now ending in a short spine.

Appendages otherwise as before, except as noted. Exopod of first maxilliped with 5 terminal setae. Endopods of second and third maxillipeds now of 5 segments. Rudimentary first pereiopod now quite large. Second pereiopod tiny, biramous, rudimentary.

The second zoea of *T. floridanus* corresponds to Lebour's description of the second larval stage except that Lebour's larva lacks the rudiments of the second pereiopods.

Third zoea (Fig. 7): length 2.0 mm. Telson separate from 6th abdominal somite, no wider posteriorly than anteriorly, with lateral spines about ⅔ the distance from the proximal end and 2 large and 2 minute terminal spines.

Base of antennular peduncle expanded laterally (stylocerite); basal segment with 2 setae on the inside and a distal band of short setae dorso-laterally; ultimate segment with 2 ventro-distal setae, a minute inner flagellum bearing a long seta, an antennular lobe, and a short outer flagellum bearing 2 aesthetes. Antennal scale consisting of a basal and 2 distal segments with 10 long plumose setae.

Other appendages essentially as in second zoea with the following exceptions; Exopod of second maxilla with 4 anterior and one posterior plumose setae. First pereiopod biramous; endopod very short, of 5 segments; exopod long with 3 apical and 2 sub-apical setae. Second pereiopod biramous, rudimentary, large.

Uropod biramous, unsegmented; outer ramus with 6 setae, inner ramus shorter than outer, with 2 minute setae.

The third zoea probably differs from Lebour's third stage in size and development, although she reports considerable variation in regard to both. Lebour's third stage is 2.8 mm. in length as opposed to 2.0 mm. for the third zoea of *T. floridanus*. Lebour's third stage has more pereiopod rudiments and, in larger individuals, suggestions of pleopods. It is generally more advanced than my third zoea.

Fourth zoea. (Fig. 8, 9): length 2.0 mm. Differs only slightly from 3rd zoea. Telson with terminal spines of each side of center notch arranged from lateral to medial: 2 minute spines, 1 large spine, 1 small spine, 1 large spine, and 1 small spine.

Antennular peduncle with longer basal segment imperfectly divided into a long proximal and a short distal segment; lines of separation of peduncle into segments marked by an inner seta and a band of short setae dorso-laterally; ultimate segment of peduncle with 4 setae ventrally at distal end; inner flagellum

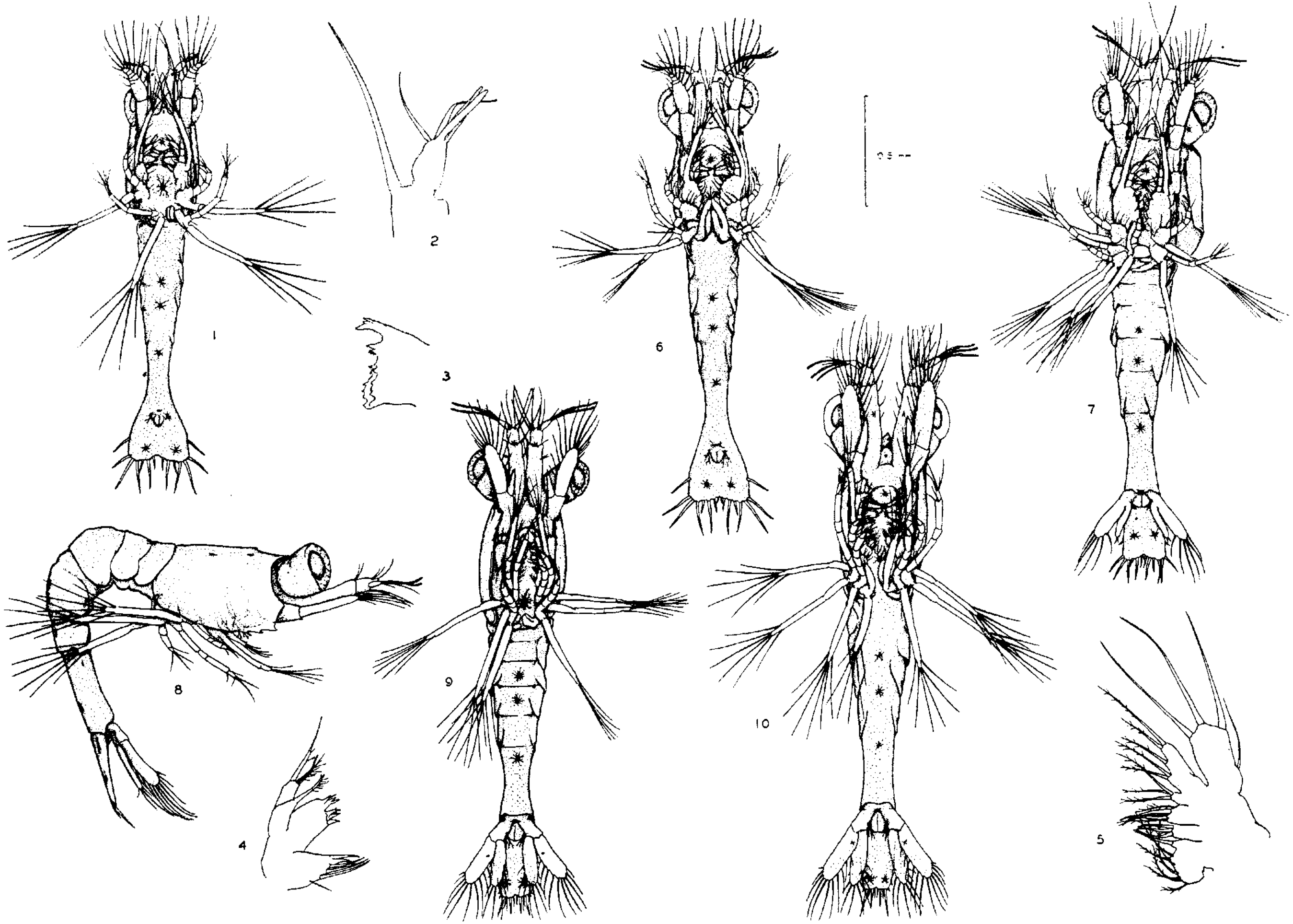

FIG. 1–10. *Thor floridanus.* FIG. 1, 6–10, ×30. FIG. 2–5, ×130. Setules omitted from plumose setae. FIG. 1–5. First zoea. FIG. 1. Entire larva, ventral view. FIG. 2. Tip of antennule. FIG. 3. Mandible. FIG. 4. First maxilla. FIG. 5. Second maxilla. FIG. 6. Second zoea, ventral view. FIG. 7. Third zoea, ventral view. FIG. 8, 9. Fourthzoea. FIG. 8. Lateral view. FIG. 9. Ventral view. FIG. 10. Fifth zoea, ventral view.

essentially as before; outer flagellum with 2 aesthetes and 2 setae. Antennal scale not segmented, bearing a short spine in antero-lateral corner and 13 long plumose setae around the tip and on inside.

First pereiopod stronger than in previous larva, propodus slightly swollen internally. Uropod segmented, endopod and exopod about equal in length; endopod with 2 short spines on outer edge and 7 plumose setae around the tip and on inside; exopod with 10 setae.

The fourth zoea falls within the limits of variation of Lebour's third stage larva except for a more advanced condition of the telson and uropods in *T. floridanus*.

Fifth zoea (Fig. 10): length 2.1 mm. The fifth zoea differs from the fourth in the following: Telson slightly narrower posteriorly with 3 lateral spines on each side and 2 pairs of alternate long and short terminal spines on each side of the slight median notch.

Antennular peduncle with a short, stout tooth about midway of the long basal segment on the ventral side; 4 setae on inside of peduncle; 5 setae ventro-distally; outer antennular flagellum with 3 aesthetes. Antennal scale with 14 plumose setae; antennal flagellum still short, unsegmented, but now without the terminal spine.

First pereiopod with propodus swollen. Second pereiopod biramous; endopod rudimentary with 2 short apical setae; exopod long with 4 apical and 2 sub-apical setae. Third pereiopod a uniramous rudiment.

Uropodal endopod with a single short spine in posterolateral corner and 8 plumose setae; exopod with a short spine in postero-lateral corner and 10 to 12 plumose setae around the tip and inside.

The fifth zoea, although smaller, bears some resemblance to Lebour's fourth larval stage but yet does not have the last two decapodal legs or pleopods.

Sixth zoea (Fig. 11): length 2.8 mm. Telson longer than previously, tapered slightly, median notch in terminal end very small, spines as before.

Antennule unchanged. Basis of antenna with spines on ventral side, at articulation with flagellum and at articulation with scale; inner ramus separated into a short peduncle and a longer flagellum, not equal to scale; scale with 15 plumose setae.

First pereiopod with propodus forming a small thumb in opposition to dactylus. Second pereiopod with endopod of 5 segments, the propodus with a short thumb. Third, fourth and fifth pereiopods long uniramous rudiments.

First to fifth pleopods minute, uniramous buds. Uropodal endopod with 10 setae; exopod with 13 setae.

The sixth zoea of *T. floridanus* is intermediate in development between Lebour's fourth and fifth stages, but about equal in length to her fourth.

Seventh zoea (Fig. 12): length 3.0 mm. Telson essentially as before but longer and narrower posteriorly. Anal spine stronger.

Inner antennular flagellum longer, but still shorter than outer; outer antennular flagellum with 3 apical aesthetes and a seta and an aesthete which arises midway of the segment. Antennal flagellum of 4 segments, slightly longer than scale.

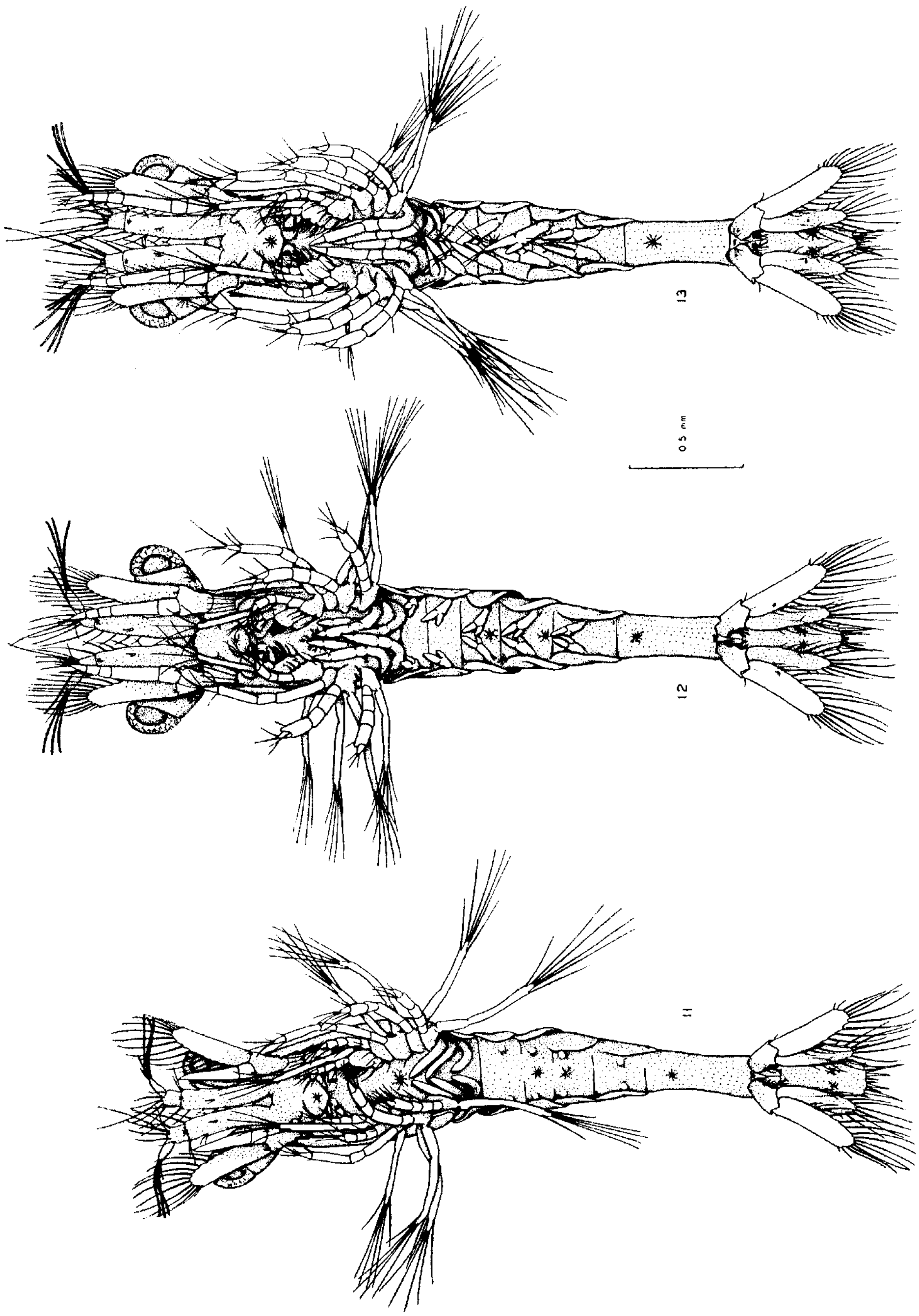

FIG. 11–13. *Thor floridanus.* ×30. FIG. 11. Sixth zoea, ventral view. FIG. 12. Seventh zoea, ventral view. FIG. 13. Eighth zoea, ventral view.

First and second pereiopods with endopods chelate. Third, fourth and fifth pereiopods uniramous, long, imperfectly separated into segments, without setae.

First to fifth pleopods biramous rudiments, without setae. Uropod larger than before, endopod with 11 and exopod with 15 setae.

The seventh zoea, although smaller, corresponds quite closely to Lebour's fifth stage larva.

Eighth zoea (Fig. 13): length 3.0 mm. Form essentially unchanged.

Antennular flagella about equal in length; outer with 3 terminal aesthetes and 3 aesthetes arising from midway of the segment. Antennal flagellum of 5 segments.

First and second pereiopods as before. Third, fourth and fifth pereiopods uniramous, of 4 segments, without setae and probably not functional in the larva; carried beneath the thorax between the bases of the other thoracic appendages.

First pleopod with rudimentary endopod, exopod without setae. Second to fifth pleopods with 2 apical setae on exopods, endopods without setae. Uropodal endopod with 12, exopod with 17 plumose setae.

The eighth zoea, although smaller than Lebour's last stage larva, is somewhat more advanced in having setose and presumably functional pleopods.

First postlarva (Fig. 14, 15): length 3.2 mm. Carapace with antennal and pterygostomian spines, a tooth on the antero-ventral margin posterior to pterygostomian spine, dorsal organ and a dorsal papilla just ahead of the posterior end of the carapace. Rostrum flat, broadly triangular, not extending beyond eyes. Pleura of abdominal somites 4, 5 and 6 with a minute tooth in the postero-ventral corner. Anal spine between bases of uropods. Telson a long, truncated triangle with a minute, median point at the posterior end, 3 pairs of short lateral spines, 2 pairs of long terminal spines of which the outer pair are slightly longer, and a pair of slender setae one of which arises from between the terminal spines on each side.

Antennular peduncle of 3 segments, the basal with a short stylocerite bearing 3 setae in its angle and 2 at its base; segmentation of peduncle marked by bands of short setae dorso-laterally; inner antennular flagellum of 3 segments, equal to outer, bearing 2 short apical setae; outer antennular flagellum imperfectly divided into 4 segments, a tuft of 3 aesthetes at junction of segments, ultimate segment with 3 short apical setae. Antennal basis of 2 obliquely separated segments, the outer basal segment with a ventral spine at the articulation with the scale; antennal peduncle of 3 segments, flagellum of many segments, over half as long as body; antennal scale with tip of spine projecting free of blade and 23 plumose setae around the blade.

Mandible large, incisor process with 4 teeth, molar process many-toothed. First maxilla small, armed with many short teeth on basis, endopod short, unsegmented, palp-like with 1 seta. Second maxilla with 3-lobed base, the lobes armed with 5, 7 and 8 long coarse setae; endopod unsegmented with a long and a short apical seta and a long seta on a lobe midway of the segment; exopod flattened, armed anteriorly with 10 plumose setae and posteriorly with a seta.

First maxilliped biramous with a bilobed epipod; coxa and basis armed

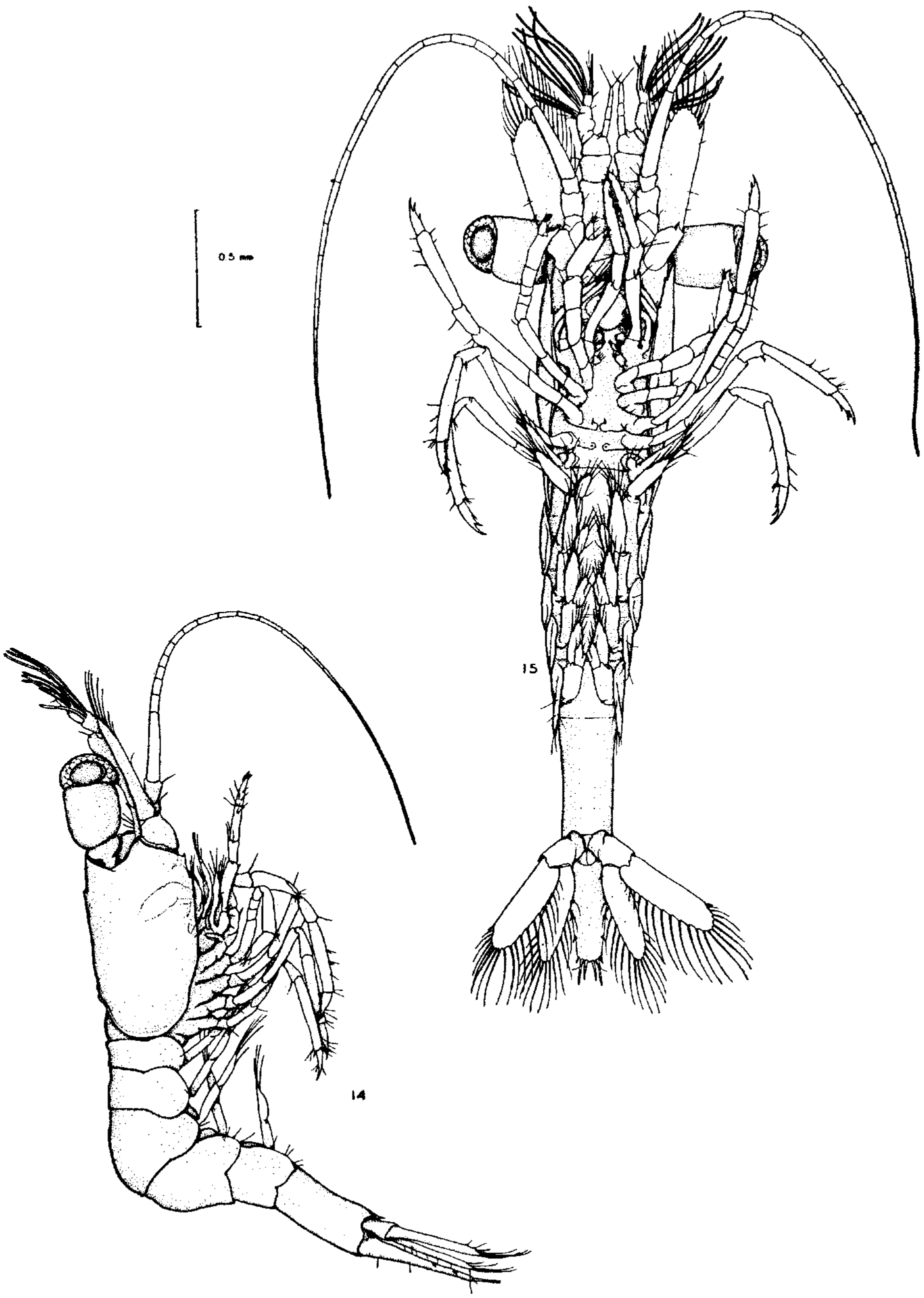

FIG. 14, 15. *Thor floridanus*. ×30. FIG. 14. Postlarva, lateral view. FIG. 15. Postlarva, ventral view.

medially with stout setae or spines; endopod reduced, palp-like, bearing 3 setae; exopod with 3 long plumose setae near proximal end and 4 apical and 2 sub-apical setae. Second maxilliped with coxa and basis armed with stout, inwardly directed setae; endopod of 5 segments, flexed, the segments armed with stout setae which face inward, dactylus with 9 stout setae; exopod longer than endopod, with 4 apical and 1 sub-apical setae. Third maxilliped with rudimentary exopod; endopod of 3 segments, armed with spines and bristles.

First pereiopod chelate, with a short, rudimentary exopod; endopod of 5 segments, dactylus and thumb with bifid, curved tips. Second pereiopod chelate, with a short rudimentary exopod; endopod with carpus of 3 or 4 segments, dactylus and fixed finger bifid at tip. Third, fourth and fifth pereiopods uniramous, dactyls bifid at tip, armed apically with 2 short claws and a short sub-apical spine.

First pleopod with a short, rudimentary endopod armed with 2 setae; exopod with 6 setae. Second and third pleopods biramous, setose, endopods bearing a seta on a slight knob which arises about mid-way along the segment. Fourth and fifth pleopods biramous, setose, endopods with *appendices internae*. Uropodal exopod with a tooth in the postero-lateral corner and 19 plumose setae; endopod with 15 setae.

The postlarva is smaller than Lebour's postlarva, from which it differs slightly. Lebour's postlarva lacks pterygostomian spines and denticles on the antero-ventral margin of the carapace. Lebour found a postero-lateral tooth on only the pleura of abdominal somite 5 as opposed to small teeth on somites 4, 5 and 6 in the postlarva of *T. floridanus*.

DISCUSSION.—Only one generalization may be derived from the rearing of *T. floridanus* larvae in the laboratory: some, but not all, species of unicellular algae constitute an adequate diet for survival, molting and metamorphosis. Neither *Nitzschia closterium* nor *Nannochloris* sp. may be considered an optimum diet. The lack of data for larvae reared on a diet containing animal tissue is a serious one. If more larvae had been available, or if the larvae obtained had not all become available at the same time, more experimental culture work might have been possible.

The inference that Lebour's larvae are *T. floridanus* is based on Verrill's (1922) report of this species at Bermuda. Subsequent attempts to obtain it or other *Thor* species there have been unsuccessful (Lebour, 1940). Holthius (1947) includes Bermuda in the distribution of *T. floridanus*, but it is possible that he also refers to Verrill's report.

A positive suggestion of systematic difference between Beaufort *T. floridanus* and the group to which Lebour's larvae belong is found in the differences in color pattern between Lebour's larvae and those hatched from *T. floridanus* eggs. Lebour's larvae were colored "bright red with many chromatophores on a yellow ground, there being two red streaks from the thorax right along the abdomen." The Beaufort larvae were colorless but bore a single row of stellate red chromatophores on the abdomen. These, however, were not so close together as to suggest a continuous stripe or streak of color. Gurney (1942) reviewed the importance of pigment patterns in separating larvae of closely related species and concluded that primary chromatophores are specifically constant in number and position. More recently, Broad (1957) has distinguished two species of *Palaemonetes* during the larval phase on the basis of primary chromatophore distribution.

It is difficult to say how much importance may be attached to the differences in size and the number and form of intermolts between Lebour's larvae and those raised in the laboratory. Gurney (1942) feels that the mode of development is constant for every species. Under laboratory conditions, however, variation in the number, size and structure of larval intermolts, caused by diet, salinity or temperature, has been reported for *Homarus* (Templeman, 1936, 1936a), *Callinectes* (Sandoz and Rogers, 1944) and *Palaemonetes* (Broad, 1957, 1957a). In spite of many reports of abnormal larvae and the provocative suggestions of Heegaard (1953) regarding penaeid development, documentation of variation in development of decapods in nature, in the form of either analyses of the frequency of occurrence of abnormal larvae or careful studies of the development of the abnormal larvae, is lacking. It is the belief of the author that variation in development which may be experimentally induced is also within the capability of the species in nature.

Although the differences between the structure of Lebour's larvae and those of Beaufort *T. floridanus* are not extreme, the difference in size of larvae of similar structure is at least suggestive of taxonomic distinctness. This, if taken in conjunction with the difference in color patterns of the larvae, results in reasonable doubt of the specific identity of Lebour's larvae.

SUMMARY

1. Larvae hatched from eggs carried by three female *Thor floridanus* Kingsley were reared in the laboratory at Beaufort, N. C. These larvae differed in size and color, structure and mode of development from *Thor* larvae, presumably of the same species, from Bermuda plankton.

2. If fed a diet of either *Nitzschia closterium* or *Nannochloris* sp., the larvae metamorphosed at the time of the 8th ecdysis, about 16 days after hatching. The first molt occurred from two to three days after hatching. The frequency of molting was once every 1.9 to 2.0 days.

3. The larvae of *T. floridanus* are described.

4. Because the number of individuals and the limited time during which larvae were available did not permit a greater variety of culture conditions, it cannot be said that the variation in mode of development between present and Bermuda larvae is not within the range of capability of a single species. On the other hand, differences in color and size of larvae of similar structure are suggestive of differences of taxonomic importance.

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