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Effects of Diet on Larval Development of *Thor floridanus* (Decapoda, Caridea) in the Laboratory*†

Abstract—*Thor floridanus* larvae maintained in laboratory culture at 24–26°C and 31‰ salinity were subjected to four diets: a) no food, b) algae (approximately half-and-half mixture of *Monochrysis lutheri* and *Phaeodactylum tricornutum*), c) live *Artemia* nauplii, and d) mixed diet (diets b and c together). Twenty-seven newly hatched larvae received each diet. None of the starved larvae molted and all died within nine days. Of those larvae fed only algae, 22% survived through metamorphosis to postlarvae, whereas only 4% of those fed only *Artemia* nauplii survived through metamorphosis. More of the larvae which were fed the mixed diet survived to the postlarval stage than was recorded with any other diet; 48% completed metamorphosis. Development of algae-fed larvae was significantly slower than that of larvae fed the mixed diet, and there also appeared to be a slight (but non-significant) trend for algae-fed larvae to pass through more molts prior to metamorphosis than did those larvae fed the mixed diet. These results are discussed in relation to the results of other studies concerning the dietary requirements of caridean shrimp larvae.

Introduction

Live *Artemia* nauplii have become so widely accepted as food for decapod larvae in laboratory culture that diet, as a factor influencing survival and development of larvae, has been largely ignored. Three important exceptions are the experiments of Broad (1) concerning the effects of different diets on larval development of *Palaemonetes* (Caridea, Palaemonidae), Chamberlain's (2, 3) studies of effects of diet on larvae of four crabs (Brachyura, Xanthidae), and Regnault's (4) recent qualitative and quantitative analysis of the effects of diet on larval development of *Hippolyte inermis* (Caridea, Hippolytidae). The objective of the present study was to examine grossly the responses of larval *Thor floridanus* Kingsley (Caridea, Hippolytidae) to qualitatively different diets.

Broad (5) described eight zoeal stages and a postlarval stage in the complete larval development of *T. floridanus* reared in the laboratory. He reared the larvae with four different algal diets, but he had too few larvae to attempt culture with animal tissue as food. Dobkin (6) discovered that two species, one with the long larval development described by

Broad (5) and the other with an abbreviated larval development, had been confused as the same species in Florida waters. He suggested that the form with long larval life be considered as *Thor floridanus* and the form with abbreviated development as *Thor* sp. until the necessary taxonomic review could be accomplished to establish their correct status. In the present study, *T. floridanus* refers to the form with long larval life.

Methods and Materials

An ovigerous female *T. floridanus* was collected at Beaufort, N. C., on 17 August 1970. Salinity at the collection site was 31.5‰. The shrimp was transported to the Virginia Institute of Marine Science and was kept, but not fed, in a glass bowl of seawater (31‰). The larvae hatched during the night of 20–21 August 1970 and were placed in the experimental situations during the following morning.

T. floridanus larvae were placed singly in small plastic vials containing 15 ml of seawater (31‰). The vials were then placed individually in compartments of plastic boxes, and the boxes were set in a water bath maintained at 24–26°C. Twenty-seven larvae were exposed to each of the following four diets: a) no food, b) algae (approximately half-and-half mixture of *Monochrysis lutheri* and *Phaeodactylum tricornutum*), c) live *Artemia* nauplii (California Brine Shrimp, Inc., Menlo Park, California) hatched in seawater, and d) mixed diet (diets b and c together). Larvae were fed fixed amounts of concentrated algae and/or *Artemia* nauplii as appropriate. The quantitative composition of each diet was not determined, but the amounts given always provided an abundance of food organisms. In the case of the algae, the concentration given was always such as to color the water slightly. There was little noticeable mortality (other than the predation by *T. floridanus* larvae) among the *Artemia* nauplii in the two diets containing nauplii. Fresh nauplii were hatched daily for the diets, and in both cases most nauplii survived the 24 hour period during which they were presented as food to the *T. floridanus* larvae. No attempt was made to control the growth of bacteria in the culture water or to determine the extent, if any, of the contribution of bacteria to the nutrition of *T. floridanus* larvae.

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Evidence of deaths and ecdyses among the larvae was sought by examining each vial under a binocular dissecting microscope once daily. Afterwards, the larvae were transferred to clean vials and fed where appropriate.

Results

The results, although quite limited because of the small number of experimental animals which were available, show several features of interest with regard to the nutritional requirements of *T. floridanus* larvae. Both algal cells and *Artemia* nauplii were ingested. The number of shrimp that completed larval development, and the number of molts and days required to reach the post-larval stage, varies with the diet (Tables I, II). None of the starved larvae molted and all had died by the ninth day, so the "no food" series was excluded from the tabulations. One to several larvae in each of the other diet series survived through metamorphosis. Lowest survival (4%) occurred among *Artemia*-fed larvae, intermediate survival (22%) among algae-fed larvae, and highest survival (48%) among larvae fed the mixed diet (Table I). Both the algae and the *Artemia* nauplii contributed nourishment to the larvae.

In the present study larval development was completed in 14 to 29 days (Table I). Broad (5) reported that *T. floridanus* larvae molted once about every two days, and development through metamorphosis required approximately 16 days in his study.

The rate of larval development was influenced by diet. Comparison of the means and ranges of days required by *T. floridanus* to reach the postlarval stage (Table I) indicates that development of algae-fed larvae was slower than that of larvae fed the mixed diet. This difference was shown to be significant at the 1% level with a Student's *t* test (12) ($t = 4.49$, $df = 17$). The retardation in the rate of development of algae-fed larvae did not become evident until the fifth molt (Table II). The first four larval molts occurred at approximately the same time for algae-fed larvae, for *Artemia*-fed larvae, and for larvae fed the mixed diet. Survival of *Artemia*-fed larvae through metamorphosis was too low to allow a comparison of total time for development. However, beginning with the fifth molt de-

velopment time of the *Artemia*-fed larvae appeared intermediate between that of the algae-fed larvae and those fed the mixed diet. It is perhaps at this time that animal tissue, or simply larger food particles, become important to the nutrition of *T. floridanus* larvae.

Broad (5) reported that metamorphosis of *T. floridanus* larvae occurred at the eighth molt. However, in the present study some larvae were observed to metamorphose at the sixth, seventh, eighth, ninth, and tenth molts, but most often at the seventh or eighth (Table II). There also appeared to be a slight trend for algae-fed larvae to pass through more molts prior to metamorphosis than did larvae fed the mixed diet (Tables I, II). However, a modified *t* test (12) showed no significant difference between the mean numbers of molts of algae-fed larvae and larvae fed the mixed diet ($t' = 0.78$, 5% level = 2.54).

Discussion

Most studies of the effects of diet on larval development of decapods, like the present, have been concerned only with qualitatively different diets. Only a few investigators have made any attempt to measure the quantitative composition of one or more of their diets (4, 11). The others apparently followed the general methodology utilized in the present study.

Among decapod larvae which have been cultured in the laboratory to date, only those of *Thor floridanus* (5, present study) and *Hippolyte inermis* (4) have been successfully reared to postlarvae on diets consisting only of algae. Broad (5) found *Nanochloris* sp. and *Nitzschia closterium* to be adequate food for *T. floridanus* larvae, but the larvae derived less nourishment from *Thorocomonas* sp. and little or none from *Chlamydomonas* sp. In the present study a mixture of *Monochrysis lutheri* and *Phaeodactylum tricornerutum* was found to provide adequate nourishment for *T. floridanus* larvae. Regnault (4) found that of six uni-algal diets prescribed (*Dunaliella bioculata*, *Monochrysis lutheri*, *Phaeodactylum tricornerutum*, *Platymonas* sp., *Skeletonema costatum*, and *Chaetoceros costatus*) only *Dunaliella*, *Monochrysis*, and *Phaeodactylum* had any nutritive value for *H. inermis* larvae, and of these only *Monochrysis* provided sufficient nourishment to allow survival of a few animals through metamorphosis.

Most larval decapods tested to date appear to require animal tissue in their diets and are able to derive little, if any, nutritive value from algae (1-4, 7-10). As a rule, survival is highest and development most rapid among larvae fed only animal tissue (usually *Artemia* nauplii). However, mixed diets of plant and animal material also may provide adequate nourishment for decapod larvae, but such diets generally result in decreased survival and retarded development (1-4) and may cause additional instars (1). Broad (1) suggested that algae were nutritionally inert as far as most decapod larvae were concerned, and that ingestion of algae restricted a larva's intake of *Artemia* nauplii. He then hypothesized that

TABLE I

Comparison of survival and development of *Thor floridanus* larvae reared in the laboratory with different diets

	Diet		
	<i>Artemia</i>	Algae	Mixed
Initial no. of larvae	27	27	27
Survival to postlarva (No.)	1	6	13
(%)*	4	22	48
Molts to postlarva (Mean)	9	7.7	7.2
(Range)	—	6-10	6-8
Days to postlarva (Mean)	21	22.3	16.3
(Range)	—	18-29	14-22

* expressed as nearest whole percent

TABLE II

Comparison of survival and molting of *Thor floridanus* larvae reared in the laboratory with different diets (initially 27 first-stage larvae in each diet series) (Z = zoea; PL = post-larva)

Molt		Artemia	Algae	Mixed
Z I to Z II	Survival No. (%)*	27(100)	26(96)	26(96)
	Age, days Mean	2.6	2.2	2.2
	Range	2-3	2-3	2-3
Z II to Z III	Survival No. (%)	25(93)	26(96)	26(96)
	Age, days Mean	4.8	4.2	4.4
	Range	4-7	4-5	4-6
Z III to Z IV	Survival No. (%)	18(67)	26(96)	25(93)
	Age, days Mean	6.7	6.3	6.4
	Range	6-8	6-7	6-8
Z IV to Z V	Survival No. (%)	16(59)	22(82)	23(85)
	Age, days Mean	8.8	8.9	8.4
	Range	8-10	8-13	8-10
Z V to Z VI	Survival No. (%)	10(37)	17(63)	19(70)
	Age, days Mean	11.1	12.2	10.5
	Range	10-12	10-17	10-13
Z VI to PL	Survival No. (%)	0(0)	1(4)	1(4)
	Age, days Mean	—	21	15
	Range	—	—	—
Z VI to Z VII	Survival No. (%)	6(22)	11(41)	15(56)
	Age, days Mean	13.8	15.3	12.7
	Range	12-15	13-18	12-17
Z VII to PL	Survival No. (%)	0(0)	3(11)	8(30)
	Age, days Mean	—	18.7	15.8
	Range	—	18-22	15-17
Z VII to Z VIII	Survival No. (%)	4(15)	5(19)	4(15)
	Age, days Mean	17.0	19.2	15.5
	Range	14-20	18-20	14-19
Z VIII to PL	Survival No. (%)	0(0)	0(0)	4(15)
	Age, days Mean	—	—	18.5
	Range	—	—	17-22
Z VIII to Z IX	Survival No. (%)	2(7)	2(7)	0(0)
	Age, days Mean	20.5	22.0	—
	Range	19-22	21-23	—
Z IX to PL	Survival No. (%)	1(4)	1(4)	0(0)
	Age, days Mean	25	25	—
	Range	—	—	—
Z IX to Z X	Survival No. (%)	0(0)	1(4)	0(0)
	Age, days Mean	—	26	—
	Range	—	—	—
Z X to PL	Survival No. (%)	0(0)	1(4)	0(0)
	Age, days Mean	—	29	—
	Range	—	—	—

* Expressed to nearest whole percent

the above-mentioned effects of the mixed diet were due simply to a reduction in the quantity of suitable food ingested by the larvae. Chamberlain (2) supported this hypothesis, and Knowlton (11) recently presented evidence favoring it. Knowlton fed *Palaeomonetes vulgaris* larvae various amounts of *Artemia* nauplii, and he found that low food levels resulted in increased mortality, increased duration of development, and increased number of molts when compared to high food levels. Regnault (4) also found that in mixed diets *Dunaliella* and *Monochrysis* appeared to restrict intake of *Artemia* nauplii by *H. inermis* larvae, but he noted that survival of larvae fed a mixed diet of *Phaeodactylum* + *Artemia* nauplii appeared to be slightly greater than that of the larvae fed only *Artemia* nauplii.

In the present study, survival of larvae fed a mixed diet of algae and *Artemia* nauplii was considerably higher than that seen among algae-fed and *Artemia*-fed larvae, and it was evident that both the algae and the *Artemia* nauplii contributed nourishment to the larvae. The very low percent survival of *Artemia*-fed larvae compared to that seen among algae-fed larvae and larvae fed the mixed diet suggests that *Artemia* nauplii may be less suitable food for *T. floridanus* larvae than are certain unicellular algae. It should be emphasized, however, that since lack of animals prevented repetition of the experiment, it is possible that the extremely low survival seen here among larvae fed only *Artemia* nauplii does not reflect the true importance of animal tissue in the nutrition of *T. floridanus* larvae. Further, development of larvae fed the mixed diet was significantly more rapid than that of larvae fed only algae, and there was a slight (but statistically non-significant) tendency for larvae fed the mixed diet to undergo fewer molts than did algae-fed larvae. These results suggest that the *Artemia* nauplii may have supplied some substance, perhaps an amino acid (8), which, while not essential for development, promoted survival and accelerated development. Regnault (4) suggested that unicellular algae were suitable food for *H. inermis* larvae until the second larval molt, at which time animal tissue began to be required. It is interesting that, at about the same time, the larval yolk reserves became exhausted.

Perhaps the *Artemia* nauplii replaced the yolk in supplying some substance which is not available from algae.

From the foregoing discussion it is evident that there are differences in the physiology of nutrition among larvae of different species of caridean shrimp. Specifically, larvae differ with regard to degree of requirement for animal food and degree of ability to utilize algae as food. Such differences may even occur at different stages of development of the same larva. Much more study will be necessary before the physiological and ecological significance of such differences in dietary requirements may be understood.

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