EFFECTS OF TEMPERATURE AND SALINITY ON LARVAL DEVELOPMENT OF GRASS SHRIMP, *PALAEMONETES VULGARIS* (DECAPODA, CARIDEA)[1,2]

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ABSTRACT

Larvae of *Palaemonetes vulgaris* were reared in the laboratory in a factorial experiment employing three temperatures (20°, 25°, and 30°C) and six salinities (5, 10, 15, 20, 25, and 30‰). Temperature and salinity exerted significant effects at the 1% level on survival of larvae through metamorphosis. The temperature-salinity interaction was also significant, but at the 5% level. Lowest survival occurred in 5‰ at all temperatures. In higher salinities, survival at 20° and 25°C was similar (>60%) but was significantly less at 30°C in most salinities. Temperature and salinity also influenced the rate of larval development. Development at 20°C required nearly twice the time as that at 25° and 30°C, but a retarding influence of salinity was slight and evident only at low salinities (5 and 10‰). Considerable variation in the number of larval instars was observed among animals which survived to the postlarval stage. Metamorphosis occurred as early as the fifth molt and as late as the twelfth. Salinity and temperature-salinity interaction had no detectable influence on the number of instars, but the effect of temperature was significant at the 1% level. Larvae reared at 25°C passed through fewer molts prior to metamorphosis than did those reared at 20° and 30°C. Comparing survival, rate of development and number of instars, optimal conditions for larval development occurred at a moderate temperature of about 25°C over a wide range of salinity (10 to 30‰).

The grass shrimp, *Palaemonetes vulgaris* (Say), ranges at least from Barnstable County, Mass., to Cameron County, Tex., (Williams, 1965) and is one of the most abundant estuarine decapods in this range. In the laboratory, Nagabhushanam (1961) found the species to be nearly euryhaline, tolerating salinities from 3 to 35‰. More recently, Bowler and Seidenberg (1971) found *P. vulgaris* to be less tolerant of low salinities (⩽3‰) but more tolerant of high salinities (36 and 40‰) than its congener, *P. pugio*. In the York River, Va., these authors found that the percentage of the *Palaemonetes* population made up by *P. vulgaris* decreased markedly with decreasing salinity, and in North Carolina, Knowlton and Williams (1970) found *P. vulgaris* only in waters of 15 to 35‰ salinity.

Only Knowlton (1965, 1970) has studied the effects of temperature and salinity on *P. vulgaris* larvae, and his results were limited by the small number of experimental animals he used. The objectives of the present study were to determine the effects of temperature and salinity on survival and development of *P. vulgaris* larvae reared through metamorphosis in the laboratory.

MATERIALS AND METHODS

The experimental design was a 3 × 6 factorial using temperatures of 20°, 25°, and 30°C and salinities of 5, 10, 15, 20, 25, and 30‰. Test media were prepared by diluting seawater with

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distilled water, and temperature control baths were modified from Reed (1969). Each bath was equipped with a thermostat, two 125-w heaters, a maximum-minimum thermometer, and an air stone to circulate the water. A grate suspended in each bath supported the culture vessels. The baths were placed inside a cold room maintained at 11°C, where a 60-w bulb controlled by a timer provided 14 hr of light every 24 hr, approximately coincident with times of natural daylight. Although the temperature regimes are referred to above and throughout the paper as 20°, 25°, and 30°C, the observed temperatures (mean ± one standard deviation) were 20.3°C ± 0.7°C (range, 18.3° to 21.1°C), 25.4°C ± 1.0°C (range, 22.8° to 26.7°C), and 30.6°C ± 0.5°C (range, 29.4° to 31.7°C), respectively.

An ovigerous female was collected near Wachapreague, Va., on 12 June 1970. Salinity at the collection site was approximately 30‰. The shrimp was maintained in a glass bowl at 30‰ salinity and 25°C in the laboratory, and larvae were obtained on the day following collection. Active larvae were first placed in mass cultures at room temperature and fed newly hatched *Artemia* nauplii (California Brine Shrimp, Inc., Menlo Park, Calif.). Zoeae to be reared in 5, 10, and 15‰ salinity were acclimated in 15‰ for 4 hr, and those to be reared in higher salinities were maintained in 30‰ for 4 hr. Larvae were then transferred with a large-bore medicine dropper to test media in compartmented plastic boxes. Each box contained 18 compartments in rows of six, and one zoea in 50 ml of media was placed in every compartment. Three salinities were tested per box (i.e., each row of six compartments was a replicate of a particular temperature-salinity combination), and there were six boxes in each of the three water baths. Thus, there were three replicates (one in each of three boxes) of each temperature-salinity combination, and a total of 18 larvae was reared at each condition.

Larvae were transferred to clean boxes with fresh media and fed an abundance of newly hatched *Artemia* nauplii once daily. Molts, deaths, and maximum and minimum temperatures were recorded at this time. Mean temperatures and standard deviations were calculated from the maximum and minimum temperatures. The experiment was terminated after 40 days, when all survivors were in postlarval stages.

RESULTS

A detailed presentation of survival and developmental history of each larva reared in the present study is given in Appendix Table 1.

SURVIVAL

In general, survival was similar (>60%) at 20° and 25°C but was lower at 30°C in nearly all salinities. Survival in 5‰ salinity occurred only at 25°C, where 13 zoeae successfully completed the first molt, and two survived through metamorphosis; in contrast, at 20° and 30°C only two zoeae molted once, and none survived to molt again.

An analysis of variance on arcsin transformations (Steel and Torrie, 1960) of the percentage survival data showed differences in survival between temperatures and between salinities at the 1% level, and the temperature-salinity interaction was significant at the 5% level (Table 1). Student-Newman-Keuls' multiple range tests (Steel and Torrie, 1960) were used to explain the significant differences (Table 2). Perhaps the simplest way of looking at these differences in Table 2 is to compare survival in each salinity under each of the different temperatures, as is shown graphically in Figure 1. Thus, between 20° and 25°C there were significant differences in survival only in 5 and 30‰ salinity. Survival at 25°C, 5‰ was significantly greater than that at 20°C, 5‰, while at 20°C, 30‰ survival was significantly greater than at 25°C, 30‰. Comparing 20° and 30°C, survival at 20°C was significantly greater than that at 30°C in 10, 15, and 25‰. Finally, comparing 25° and 30°C, survival at 25°C was significantly greater than that at 30°C in 5, 10, 15, and 25‰. Highest overall percentage survival (88.9%) occurred at the combination 20°C, 20‰ (Table 2, Figure 1).

TABLE 1.—Analysis of variance for differences in survival of *Palaemonetes vulgaris* larvae through metamorphosis under different conditions of temperature and salinity.

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*
Temperature	2	4,912.0345	2,456.0172	17.8613**
Salinity	5	21,212.5667	4,242.5133	30.8535**
Temperature × salinity	10	3,842.1588	384.2158	2.7941*
Error	36	4,950.1734	137.5048	
Total	53	34,916.9334		

** Significant at 1% level.
* Significant at 5% level.

TABLE 2.—Summary of Student-Newman-Keuls' multiple range tests to explain differences in survival of *Palaemonetes vulgaris* larvae at different temperature and salinity conditions.

Experimental conditions °C	Experimental conditions ‰	Mean (transformed % survival)	Means not overlapped by the same line are significantly different at the 1% level
30	5	0.0	
20	5	0.0	
25	5	16.1	
30	10	24.1	
30	15	31.5	
30	25	38.5	
25	30	52.0	
30	20	58.5	
30	30	58.5	
20	25	58.5	
25	10	62.2	
25	20	62.2	
20	30	65.9	
20	10	66.5	
25	25	67.0	
25	15	70.2	
20	15	70.2	
20	20	73.9	

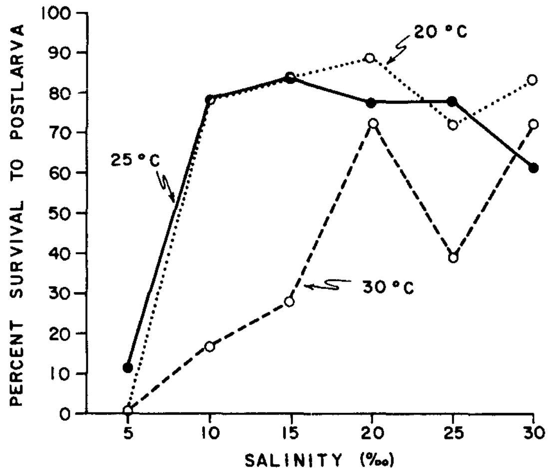

FIGURE 1.—Comparison of survival to postlarvae for *Palaemonetes vulgaris* zoeae reared at different temperatures and salinities.

RATE OF DEVELOPMENT

The effects of temperature and salinity (excluding 5‰) on the rate of larval development are shown in Figure 2. The effect of temperature was pronounced; development at 20°C was much slower than at 25° or 30°C. Mean duration of development (days) ± one standard deviation was 30.2 ± 3.8 (range, 23 to 39) at 20°C, 16.6 ± 2.7 (range, 14 to 25) at 25°C, and 15.7 ± 1.8 (range, 13 to 21) at 30°C. Salinity influenced the rate of development much less than did temperature. Survival in 5‰ salinity occurred only at 25°C, where the larvae in 5‰ generally required about 1 to 4 more days to pass a given stage than did larvae in higher salinities at the same temperature. Development in 10‰ also tended to be slightly slower than in higher salinities, regardless of the temperature (Figure 2). There was little apparent difference among developmental rates in 15 to 30‰. In general, a Q_{10} (20° and 30°C) of about 1.8 was typical of larval development.

Mean duration of instars (Table 3) was inversely related to temperature, reflecting developmental rate. Duration of successive instars tended to increase slightly at 20°C. The second instar was markedly short at 25° and 30°C, and the final instar was of longest duration at all temperatures. Overall mean instar duration (days) ± one standard deviation for animals which completed development was 3.6 ± 0.8 (range, 3 to 7) at 20°C, 2.2 ± 0.7 (range, 1 to 7) at 25°C, and 1.9 ± 0.6 (range, 1 to 4) at 30°C.

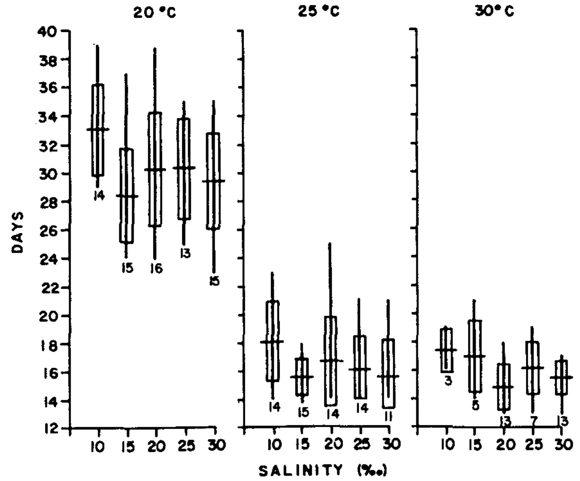

FIGURE 2.—Mean ± one standard deviation and range of days required for *Palaemonetes vulgaris* larvae to reach the postlarval stage at different temperatures and salinities (5‰ excluded) (numbers at the lower end of each range line indicate the number of animals which reached the postlarval stage at those conditions of temperature and salinity).

TABLE 3.—Mean duration (days) of *Palaemonetes vulgaris* larval instars at different temperatures. Final instar treated separately.

Instar	Temperature (°C)		
	20	25	30
	Days	*Days*	*Days*
I	3.0	2.0	2.0
II	3.1	1.4	1.0
III	3.1	2.0	1.2
IV	3.2	2.0	1.9
V	3.5	2.1	1.9
VI	3.8	2.1	2.0
VII	3.9	2.1	2.0
VIII	3.5	2.4	2.0
IX	3.7	[1]2.2	[1]1.8
X	[1]4	[1]2	--
XI	--	[1]2	--
Final	5.0	3.3	2.9

[1] Based on five or fewer larvae.

VARIATION IN NUMBER OF INSTARS

Most larvae metamorphosed at the 7th, 8th, or 9th molt, but there was much variation in number of instars. Metamorphosis occurred at the 5th through the 12th molts, and one zoea passed through 12 zoeal instars but never reached the postlarval stage.

The effects of temperature and salinity (excluding 5‰ because only two postlarvae were obtained there) on the number of larval stages are shown in Figures 3 and 4. Sample sizes were unequal, so an approximate method, the analysis of unweighted means (Snedecor, 1956) was employed to indicate significant effects (Table 4). The effect of salinity was not significant, although there appeared to be a slight tendency

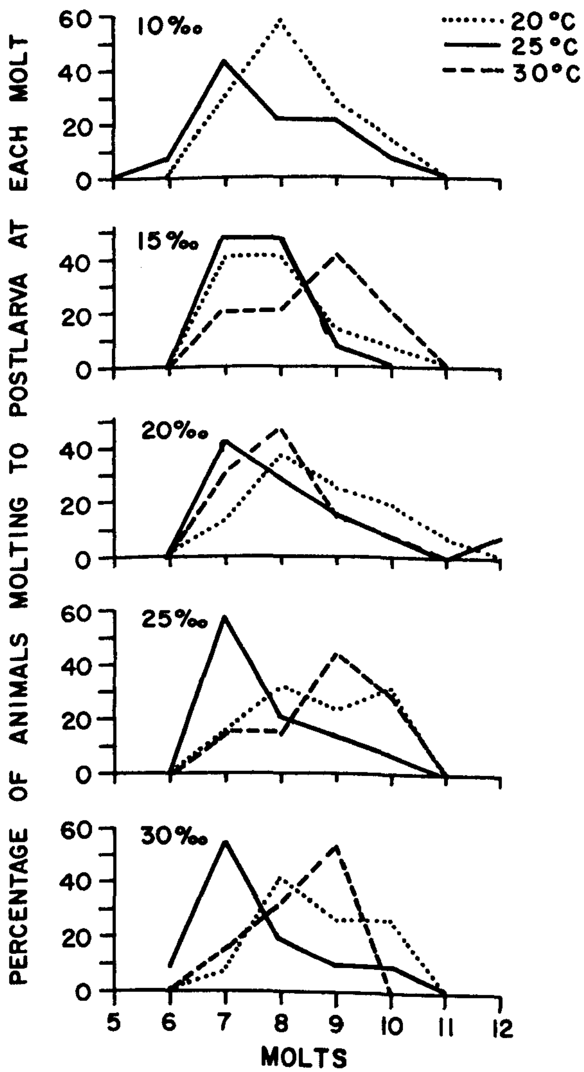

FIGURE 3.—Percentage of animals molting to postlarva at each molt under different conditions of temperature and salinity.

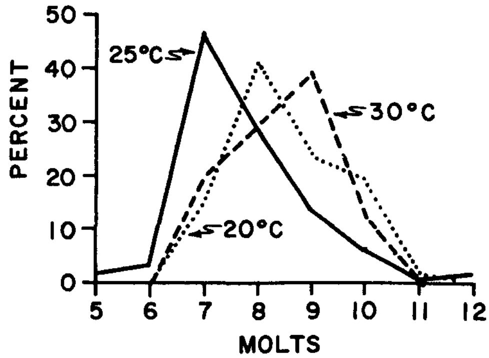

FIGURE 4.—Percentage of animals molting to postlarva at each molt under different temperatures.

for fewer instars in 15‰ than in other salinities. The temperature-salinity interaction also was not significant. However, the influence of temperature was significant at the 1% level, and mean numbers of instars ± one standard deviation were 8.5 ± 1.0 at 20°C, 7.8 ± 1.1 at 25°C, and 8.4 ± 1.0 at 30°C. A multiple mean test showed no difference between the mean numbers of larval instars passed at 20° and 30°C but indicated that animals reared at 25°C passed through significantly fewer instars in larval development.

DISCUSSION

Few previous studies have been concerned with the effects of temperature and salinity on *Palaemonetes* larvae. Sollaud (1919) reared larvae of *P. varians microgenitor* in the laboratory and found, as I did for *P. vulgaris,* that development was retarded at low temperatures and in low salinities and that more instars were passed at the lower than at the more moderate temperature tested. According to Broad and Hubschman (1962), development of larvae of *P. intermedius*, *P. pugio*, and *P. vulgaris* was unaffected by salinity above 20‰, but below 10‰ survival was poor. In the present study, survival in 5‰ was very poor, but in salinities of 10 to 30‰ at low and moderate temperatures (20° and 25°C), survival was high. More recently, Knowlton (1970) conducted a factorial experiment similar to mine, but he used only five larvae in each temperature-salinity combination. Knowlton (1970) found that at 20° and 25°C *P. vulgaris* larvae seemed to tolerate the entire range of salinity tested (15 to 35‰) equally well, with highest survival among larvae reared at 25°C. Lowest survival occurred among larvae reared at 30°C, where no larvae exposed to the low salinities (15 and 20‰) completed development. The results of the present study were fairly similar, except that some larvae survived through metamorphosis at 30°C in all salinities but 5‰. However, Knowlton's (1970) values for mean duration of larval life (37.3 ± 2.0 days at 20°C, 30.7 ± 2.0 days at 25°C, and 31.1 ± 4.3 days at 30°C) were considerably greater than corresponding values in the present study (30.2 ± 3.8 days, 16.6 ± 2.7 days, and 15.7 ± 1.8 days, respectively). Similarly, his values for mean instar duration were greater than values determined here.

The number of larval instars varied from 8 to 16 in Knowlton's (1970) study, while in the present study the observed range was 5 to 12. Knowlton (1965, 1970) also found that the number of larval instars increased with increasing

TABLE 4.—Summary of analysis of variance for differences in number of larval molts for *Palaemonetes vulgaris* larvae at different temperatures and salinities.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Total	14	4.0364		
Temperature	2	2.2770	1.1385	10.8017**
Salinity	4	0.5398	0.1349	1.2798 n.s.
Temperature X salinity	8	1.2196	0.1524	1.4459 n.s.
Error	[1]167		[1]0.1054	

** Significant at 1% level. n.s. Not significant.
[1] See Snedecor (1956) for computation of the error mean square in the method of unweighted means.

temperature. In contrast, larvae in my study passed through fewer instars at the moderate temperature (25°C) than at higher or lower temperatures, and at each temperature larvae required fewer molts to reach the postlarval stage in my study than in Knowlton's (1970). Similarly, Ewald (1969) found that *Tozeuma carolinense* larvae passed through fewer instars at 25°C than at 15° and 20°C. He also reported that there were marked differences in the numbers of instars among *T. carolinense* larvae from different populations. Perhaps a similar effect was partially responsible for differences between the numbers of *P. vulgaris* larval instars observed by Knowlton (1970) and by me.

The final zoeal instar was of greater duration than the other instars in both Knowlton's (1970) study and in mine, but the reason for the delay of this molt is not known. However, Hubschman (1963) reported that the X organ-sinus gland complex does not become functional as the primary molt regulator in *Palaemonetes* until after metamorphosis. He suggested that perhaps the rapid larval molting cycle was under the hormonal control of some type of larval molting gland, the existence of which remains speculative. The longer duration of the final zoeal instar thus may reflect transfer of control over molting from some unknown larval molt-regulating mechanism to the X organ-sinus gland complex, or breakdown of the larval regulatory mechanism prior to assumption of molt-regulating function by the X organ-sinus gland complex, or other internal reorganization prior to metamorphosis.

Because of the characteristic variability of temperature and salinity in estuaries, success of a particular decapod species may depend on the ability of the larvae to survive frequent exposure to suboptimal temperature-salinity conditions, to settle and/or metamorphose only under those conditions which are suitable for survival of the adult form, and to remain within, be carried into, or return to a given area to replenish the parental population. The number of larval instars may also be important, since ecdyses are critical periods in larval life, and highest mortality of cultured decapod larvae often occurs then (Ong, 1966; Knowlton, 1970; Roberts, 1971). Reduction of the number of premetamorphic molts thus may increase larval survival. So, considering survival, rate of development, and number of instars, it appears that optimal conditions for larval development of *P. vulgaris* occur at a moderate temperature of about 25°C in salinities of 10 to 30‰. Knowlton (1970) also concluded that a temperature of 25°C was optimal over the salinity range tested (15 to 35‰) in his experiment.

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APPENDIX TABLE 1.--Comparison of survival and developmental rates of *Palaemonetes vulgaris* larvae reared at different temperatures and salinities.

Temperature (°C)	Salinity (‰)	Survival		Age (days)		Survival		Age (days)		Survival		Age (days)		Survival		Age (days)	
		%	No.	Mean	Range	%	No.	Mean	Range	%	No.	Mean	Range	%	No.	Mean	Range
		Molt No. 1 Zoea I to zoea II				Molt No. 2 Zoea II to zoea III				Molt No. 3 Zoea III to zoea IV				Molt No. 4 Zoea IV to zoea V			
20	5	11.1	2	4.0	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	100.0	18	3.0	--	100.0	18	6.5	6-9	88.9	16	9.8	9-12	88.9	16	13.5	12-16
	15	100.0	18	3.0	--	100.0	18	6.0	--	100.0	18	9.1	9-10	100.0	18	12.3	12-17
	20	100.0	18	3.0	--	100.0	18	6.0	--	100.0	18	9.0	--	100.0	18	12.0	--
	25	100.0	18	3.0	--	100.0	18	6.0	--	100.0	18	9.0	--	100.0	18	12.0	--
	30	100.0	18	3.0	--	100.0	18	6.0	--	100.0	18	9.0	--	100.0	18	12.0	--
25	5	72.3	13	2.8	2-7	27.8	5	6.2	4-9	22.2	4	9.8	8-13	22.2	4	11.8	10-15
	10	100.0	18	2.0	--	100.0	18	3.8	3-4	100.0	18	5.8	4-6	100.0	18	7.8	7-8
	15	100.0	18	2.0	--	100.0	18	3.1	3-4	100.0	18	5.1	5-6	100.0	18	7.1	7-8
	20	100.0	18	2.0	--	100.0	18	3.2	3-5	100.0	18	5.2	5-7	100.0	18	7.2	7-9
	25	100.0	18	2.0	--	100.0	18	3.4	3-4	100.0	18	5.3	5-6	100.0	18	7.3	7-8
	30	100.0	18	2.0	--	100.0	18	3.3	3-4	100.0	18	5.3	5-6	88.9	16	7.3	7-9
30	5	11.1	2	2.0	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	100.0	18	2.0	--	100.0	18	3.0	--	100.0	18	4.9	4-5	94.5	17	6.9	6-7
	15	94.5	18	2.0	--	88.9	16	3.0	--	83.4	15	4.3	4-5	83.4	15	6.3	6-7
	20	100.0	18	2.0	--	100.0	18	3.0	--	94.5	17	4.1	4-5	94.5	17	6.1	6-7
	25	100.0	18	2.0	--	100.0	18	3.0	--	100.0	18	4.2	4-5	100.0	18	6.1	6-7
	30	100.0	18	2.0	--	100.0	18	3.0	--	100.0	18	4.2	4-5	94.5	17	6.0	--
		Molt No. 5 Zoea V to zoea VI				Zoea V to postlarva				Molt No. 6 Zoea VI to zoea VII				Zoea VI to postlarva			
20	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	88.9	16	17.4	16-20	0.0	0	--	--	83.4	15	21.4	20-25	0.0	0	--	--
	15	100.0	18	16.2	15-21	0.0	0	--	--	94.5	17	20.1	18-25	0.0	0	--	--
	20	100.0	18	15.4	15-19	0.0	0	--	--	94.5	17	19.1	18-23	0.0	0	--	--
	25	100.0	18	15.2	15-16	0.0	0	--	--	94.5	17	19.1	18-20	0.0	0	--	--
	30	100.0	18	15.1	15-16	0.0	0	--	--	100.0	18	18.7	18-19	0.0	0	--	--
25	5	16.7	3	12.7	12-13	5.6	1	22.0	--	16.7	3	14.7	14-15	0.0	0	--	--
	10	100.0	18	10.0	9-11	0.0	0	--	--	94.5	17	12.4	11-13	5.6	1	15.0	--
	15	100.0	18	9.2	9-10	0.0	0	--	--	100.0	18	11.2	11-12	0.0	0	--	--
	20	100.0	18	9.2	9-11	0.0	0	--	--	94.5	17	11.1	11-12	0.0	0	--	--
	25	94.5	17	9.4	9-10	0.0	0	--	--	94.5	17	11.5	11-13	0.0	0	--	--
	30	88.9	16	9.3	9-11	0.0	0	--	--	83.4	15	11.2	11-12	5.6	1	15.0	--
30	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	94.5	17	9.0	8-11	0.0	0	--	--	66.7	12	10.8	9-11	0.0	0	--	--
	15	66.7	12	8.3	8-9	0.0	0	--	--	55.6	10	10.6	10-11	0.0	0	--	--
	20	88.9	16	8.1	8-9	0.0	0	--	--	83.4	15	10.0	9-11	0.0	0	--	--
	25	100.0	18	7.9	7-9	0.0	0	--	--	94.5	17	9.9	9-11	0.0	0	--	--
	30	94.5	17	7.7	7-8	0.0	0	--	--	88.9	16	9.7	9-10	0.0	0	--	--
		Molt No. 7 Zoea VII to zoea VIII				Zoea VII to postlarva				Molt No. 8 Zoea VIII to zoea IX				Zoea VIII to postlarva			
20	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	83.4	15	25.4	24-29	0.0	0	--	--	38.9	7	29.0	28-30	44.5	8	30.9	29-35
	15	50.0	9	23.3	23-24	33.4	6	26.7	24-30	16.7	3	27.3	27-28	33.4	6	28.3	27-30
	20	83.4	15	22.8	22-24	11.1	2	26.0	24-28	44.5	8	26.4	25-27	33.4	6	27.5	27-28
	25	83.4	15	22.9	22-24	11.1	2	25.5	25-26	50.0	9	26.6	25-28	22.2	4	27.5	27-28
	30	94.5	17	22.1	21-23	5.6	1	23.0	--	55.6	10	25.3	24-27	33.4	6	27.2	26-28
25	5	5.6	1	18.0	--	0.0	0	--	--	0.0	0	--	--	5.6	1	21.0	--
	10	50.0	9	14.7	14-16	33.4	6	16.3	14-17	27.8	5	17.4	16-18	16.7	3	17.3	17-18
	15	50.0	9	13.3	13-14	38.9	7	14.6	14-15	5.6	1	15.0	--	38.9	7	17.0	16-18
	20	55.6	10	13.5	13-16	33.4	6	14.0	--	22.2	4	15.3	15-16	22.2	4	16.8	16-17
	25	50.0	9	13.8	13-16	44.5	8	14.8	14-16	33.4	6	16.2	15-18	16.7	3	16.0	--
	30	27.8	5	13.4	13-14	33.4	6	14.2	14-15	16.7	3	16.0	--	11.1	2	16.5	16-17
30	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	61.2	11	12.9	12-15	0.0	0	--	--	44.5	8	14.6	13-15	0.0	0	--	--
	15	33.4	6	12.7	12-14	5.6	1	15.0	--	22.2	4	14.5	14-16	5.6	1	16.0	--
	20	55.6	10	11.9	11-13	22.2	4	13.0	--	16.7	3	14.0	--	33.4	6	15.0	14-16
	25	66.7	12	11.8	11-13	5.6	1	13.0	--	38.9	7	13.6	13-14	5.6	1	15.0	--
	30	77.8	14	11.6	10-12	11.1	2	13.5	13-14	44.5	8	13.3	12-14	22.2	4	15.3	15-16

APPENDIX TABLE 1.--Comparison of survival and developmental rates of *Palaemonetes vulgaris* larvae reared at different temperatures and salinities.--Continued.

Temperature (°C)	Salinity (°/oo)	Survival %	Survival No.	Age (days) Mean	Age (days) Range	Survival %	Survival No.	Age (days) Mean	Age (days) Range	Survival %	Survival No.	Age (days) Mean	Age (days) Range	Survival %	Survival No.	Age (days) Mean	Age (days) Range
		Molt No. 9								Molt No. 10							
		Zoea IX to zoea X				Zoea IX to postlarva				Zoea X to zoea XI				Zoea X to postlarva			
20	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	11.1	2	33.0	32-34	22.2	4	34.8	33-36	0.0	0	--	--	11.1	2	38.0	37-39
	15	5.6	1	32.0	--	11.1	2	32.0	--	0.0	0	--	--	5.6	1	37.0	--
	20	22.2	4	30.8	30-31	22.2	4	30.8	30-32	5.6	1	34.0	--	16.7	3	35.0	34-36
	25	27.8	5	29.6	28-31	16.7	3	32.3	31-33	5.6	1	35.0	--	22.2	4	34.0	32-35
	30	27.8	5	28.4	27-29	22.2	4	29.5	28-31	0.0	0	--	--	22.2	4	33.0	31-34
25	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	5.6	1	19.0	--	16.7	3	21.7	20-23	0.0	0	--	--	5.6	1	23.0	--
	15	0.0	0	--	--	5.6	1	18.0	--	0.0	0	--	--	0.0	0	--	--
	20	11.1	2	17.0	--	11.1	2	18.5	18-19	5.6	1	19.0	--	5.6	1	20.0	--
	25	16.7	3	18.7	17-20	11.1	2	19.5	18-21	5.6	1	23.0	--	5.6	1	20.0	--
	30	11.1	2	18.0	--	5.6	1	19.0	--	5.6	1	21.0	--	5.6	1	21.0	--
30	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	16.7	3	16.7	16-17	11.1	2	16.5	16-17	5.6	1	19.0	--	5.6	1	19.0	--
	15	11.1	2	17.0	16-18	11.1	2	17.0	--	0.0	0	--	--	5.6	1	21.0	--
	20	5.6	1	16.0	--	11.1	2	16.5	16-17	0.0	0	--	--	5.6	1	18.0	--
	25	11.1	2	15.5	15-16	16.7	3	16.3	16-17	0.0	0	--	--	11.1	2	18.0	17-19
	30	5.6	1	15.0	--	38.9	7	16.3	15-17	0.0	0	--	--	0.0	0	--	--
		Molt No. 11								Molt No. 12							
		Zoea XI to zoea XII				Zoea XI to postlarva				Zoea XII to zoea XIII				Zoea XII to postlarva			
20	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	15	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	20	0.0	0	--	--	5.6	1	39.0	--	0.0	0	--	--	0.0	0	--	--
	25	5.6	1	39.0	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	30	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
25	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	15	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	20	5.6	1	21.0	--	0.0	0	--	--	0.0	0	--	--	5.6	1	25.0	--
	25	5.6	1	26.0	--	0.0	0	--	--	5.6	1	28.0	--	0.0	0	--	--
	30	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
30	5	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	10	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	15	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	20	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	25	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--
	30	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--	0.0	0	--	--