Influences of Temperature on Development and Survival, Reproduction and Growth of a Calanoid Copepod (*Pseudodiaptomus dubia*)

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Received January 24, 2009; Revised July 28, 2009; Accepted July 31, 2009; Published September 1, 2009

Pseudodiaptomus dubia is a calanoid copepod that is distributed widely in the estuarine-coastal waters of Asia and is a dominant copepod in the shrimp grow-out ponds in southern China. A laboratory culture experiment was conducted to evaluate the influences of water temperature on larval development, survival, and reproduction. Results indicate that within a temperature range from 15 to 35°C, larval development increases as the temperature increases. The water temperature for optimal larval survival rate ranges from 20 to 35°C. Longevity and egg hatching time decrease as the temperature increases from 20 to 35°C. Total fecundity and reproduction frequency increase as the water temperature increases, with the maximum at 30°C. Fecundity and reproduction frequency decrease when the temperature exceeds 30°C. Intrinsic growth rate (r_m) ranges from 0.168 to 0.195 at 25 to 30°C; net reproduction rate (R_0) and finite growth rate (λ) are 163 to 264 and 1.183 to 1.215, respectively, when the temperature is greater than 20 and 35°C; population doubling time (t) varies from 3.556 to 4.128 days at temperatures less than 20 and 35°C. Population generation time (T) is negatively correlated with temperature, with the optimal population growth rate at 25 to 30°C.

KEYWORDS: copepods, growth rate, larval development, *Pseudodiaptomus dubia*, temperature

INTRODUCTION

Temperature is a vital factor that influences mortality[1], instar duration[2,3], molting rate[4,5], and reproduction of copepods[5,6]. Within a suitable range, increases in temperature will increase egg production and growth rate, and shorten reproduction cycle and hatching time. Different species that live in different geographical regions may have specific requirements for temperature. Temperature affects the energy storage and hormone production that control larval development. Molting will not take place until levels of energy and hormone exceed a threshold[7].

Pseudodiaptomus dubia[8], previously reported as *Schmackeria dubia*[9], is a calanoid copepod that is distributed widely in Asian estuarine-coastal waters and is a dominant copepod in the shrimp grow-out

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ponds in southern China. Aside from the morphological characteristics[10], little is known about the effects of environmental factors on the ecology of *P. dubia*. Recently, we reported on the responses of feeding and filtering rates of *P. dubia* to the changes in several environmental factors, including water temperature[9]. Here we report the effects of temperature on reproduction, development, and growth. Findings from this study will provide important insights into the thermal condition that favors mass production of *P. dubia*.

MATERIALS AND METHODS

This experiment was conducted at the Guangdong Ocean University, Guangdong, China between April and June 2006. Previously, we reported the effects of several environmental variables on the filtering and feeding rates of adult *P. dubia*[9]. The objective of the current study was to assess the effects of various water temperatures on the growth and reproduction of *P. dubia* at different development stages.

Experimental Animals

P. dubia were collected from a shrimp farm (water temperature, 30°C; salinity, 27 ppt) in Zhanjiang, southern China. In the laboratory, the copepods were raised at a water temperature between 28 and 30°C, a salinity of 27 ppt, and a light intensity of 160 to 240 $\mu\text{mol m}^{-2} \text{s}^{-1}$ [9]. After the copepods were acclimated to the culture conditions, healthy and energized egg-carrying females were carefully transferred with a pipe to the culture media. Their offspring were used as the experiment animals.

A unicellular golden alga (*Isochrysis zhanjiangensis*) and a diatom (*Chaetoceros müelleri*) provided by the Algal Culture Research Laboratory of Guangdong Ocean University (Zhanjiang, China) were used as food sources. Natural seawater was filtered using a plankton net (mesh size, 200 μm) and boiled to kill all living organisms. Wide-mouth transparent beakers (125 ml) were used as the culture containers.

Larval Selection

Ten milliliters of fresh seawater was added to each of 200 pipettes. Copepods were transferred from the culture media and examined under a microscope. A total of 200 female copepods that were carrying matured egg sacs were then transferred into the 200 pipettes and raised at a water temperature of 30°C, a light intensity of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and a light:dark cycle of 12 h:12 h.

Newly hatched larvae were collected every 2 h; larvae from the time period with the highest hatching rate were transferred to a beaker and used for the experiment.

Experimental Design

There were five temperature levels (15, 20, 25, 30, 35°C), each of which contained 10 replicate groups. Each group within a temperature level consisted of 10 incubation bottles that were further divided into five subgroups, namely A, B, C, D, and E. Each subgroup consisted of two bottles. Each bottle had 125 ml seawater and 10 nauplii added to it. Group A was used to record the development and growth of nauplii and copepodites; Group B was used to record survival rate of nauplii; Group C was used to record survival rate of copepodites. Experimental animals in Groups D and E (four incubation bottles) were used for the reproduction experiment. All animals were fed with *C. müelleri* at an identical concentration of 20×10^4 individuals/milliliter. Incubation was conducted at a salinity of 27 ppt, a pH of 8.0, a light intensity of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and a light:dark cycle of 12 h:12 h.

Growth and Survival Rates

The life cycle of *P. dubia* consisted of 12 stages, including six naupliar stages (NI, NII, NIII, NIV, NV, and NVI), five copepodite stages (CI, CII, CIII, CIV, and CV), and the adult stage. Because *P. dubia* is an egg-carrying invertebrate, eggs in the egg sacs develop into NI before the sacs are detached from the females and the NI nauplii are then hatched. NI nauplii develop into NII within 2–4 min of hatching. Therefore, our observation on larval development began at stage NII.

Developmental stages were monitored every 6 h by randomly taking three to four larvae from Group A bottles. The larvae were staged and returned to the same bottles. When nauplii in Group B reached NVI, they were preserved in formalin. The numbers of survival larvae and prosome length were recorded. When the larvae in Group C reached the adult stage, the numbers of survival and prosome length of females and males were recorded. These data were used to calculate growth and survival rates for the naupliar and copepodite stages.

Survival rate (SR) was calculated using the following equation:

$$SR = \frac{a_1}{10} \times 100\% \quad (1)$$

where a_1 is the live larvae at the end of the incubation. Average growth rate was calculated as

$$\log C = 2.00 \log CL - 5.67 \text{ (nauplii)} \quad (2)$$

$$\log C = 2.87 \log L - 8.03 \text{ (copepodites)} \quad (3)$$

$$G = (C_{i+1} - C_i) / T_i \quad (4)$$

where CL and L are the prosome length (μm) of nauplii and copepodites, C_i is the weight (μg carbon) in stage i larvae, and T_i is the time (days) of stage i larvae.

Reproductivity Experiment

When the adult copepods in Groups D and E started carrying eggs, females and males at a ratio of 1:2 were incubated in six to 10 test tubes containing algal solutions. The hatching rate was recorded every 1–2 days. Incubation was not terminated until all female adults died. These data were used to calculate a reproductivity table that was then used to calculate intrinsic rate of population growth (r_m), finite rate of growth (λ), net reproduction rate (R_0), and generation time (T).

Life parameters of *P. dubia* were calculated following Shen[11] and Tang et al.[12]:

Reproduction rate:

$$R_0 = \sum l_x m_x \quad (5)$$

Generation time:

$$T = \sum x l_x m_x / R_0 \quad (6)$$

Intrinsic rate of population growth:

$$r_m = \ln R_0 / T \quad (7)$$

Finite rate of growth:

$$\lambda = e^{r_m} \quad (8)$$

Population doubling time:

$$t = (\ln 2) / r_m \quad (9)$$

where x is age or time interval, l_x is survival rate at time x , and m_x is birth rate at age x .

All statistical procedures were performed using SPSS software (version 11). Significant tests were performed using the ANOVA procedure. Results were considered significant at $p = 0.05$.

RESULTS

Morphological Development for Nauplii and Copepodites

The major changes in morphology for each stage of nauplii and copepodite are listed in Tables 1 and 2.

TABLE 1
Main Characteristics of Each Stage of Nauplii and Copepodites of *P. dubia*

Nauplii	No. of Seta on Last Segment of Antenna Prima	Body Length (mm)	Copepodite	No. Prosome Segments	No. Abdominal Segments	Length of Thoracic Segment (mm)
NI	Last segment: 4	0.121–0.139	CI	3	2	0.325–0.425
NII	Last segment: 4	0.161–0.17	CII	4	2	0.4674–0.5043
NIII	Abdominal: 1 Last segment: 4	0.190–0.22	CIII	5	2	0.5576–0.63345
NIV	Dorsal: 4 Abdominal: 3 Last segment: 4	0.225–0.25	CIV	5	3	0.79335–0.825 (F) 0.6765–0.76875 (M)
NV	Dorsal: 6 Abdominal: 4 Last segment: 4	0.271–0.30	CV	5	3 (F) 4 (M)	0.933043–1.0332 (F) 0.7995–0.861 (M)
NVI	Dorsal: 8 Abdominal: 4 Last segment: 4	0.305–0.32	Adult	4	3 (F) 4 (M)	1.0947–1.1931 (F) 0.9471–1.04165 (M)

Note: F, female; M, male.

Effect of Temperature on Development Time of Larval *P. dubia*

When water temperature ranges from 15 to 35°C, the development time required for each stage decreases as the temperature increases (Table 2, Figs. 1 and 2). At the nauplius stages, development time is minimal (66 h) at a water temperature of 30 to 35°C. However, it takes 294 h to complete all of the nauplius stages at 15°C. At the copepodite stages, it takes 114 h for copepodite stage I to develop into the adult stage at 35°C, which is 520 h shorter than at 15°C. The entire larval development time is 180 h at 35°C and 928 h at 15°C.

TABLE 2
Development Time (h) of Larvae of *P. dubia* under
Different Temperatures

Larval Stage	15°C	20°C	25°C	30°C	35°C
NII	54	24	18	12	12
NIII	60	24	18	12	12
NIV	60	32	18	12	12
NV	60	32	18	12	12
NVI	60	32	24	18	18
NII–NVI	294	144	96	66	66
CI	80	30	24	18	18
CII	112	42	36	24	24
CIII	128	48	36	30	24
CIV	144	54	42	36	24
CV	170	66	42	36	24
CI–CV	634	240	180	144	114
Sum (h)	928	384	276	210	180

FIGURE 1. The development time of nauplii of *P. dubia* under different temperatures.

Effect of Temperature on the Growth of *P. dubia*

The effect of temperature on prosome length and weight for larvae of the same stage was minor (Tables 3 and 4). This is because prosome length and weight gains were insignificant at the naupliar stage. However, changes in weight at the copepodite stage were significant.

At a temperature range between 15 and 30°C, the growth rate for larvae was consistently higher than that of larvae grown at a low temperature (Fig. 3 and 4). For example, the growth rate for CV at 35, 30, 25, and 20°C was 6.35-, 3.72-, 3.05-, and 2.81-fold higher than the growth rate at 15°C, indicating that at high temperatures, copepodite metabolism accelerated, leading to a higher growth rate.

FIGURE 2. Development time of copepodites of *P. dubia* under different temperatures.

TABLE 3
Effects of Temperature on Development and Growth of the Naupliar Stages of *P. dubia*

Instar	Parameter	15°C	20°C	25°C	30°C	35°C
NII	Prosoma length (μm)	165	170	165	170	170
	Weight (μg C)	0.0582	0.0618	0.0582	0.0618	0.0600
	Development time (days)	2.25	1	0.75	0.5	0.5
	Growth rate (μg C/day)	0.0201	0.0370	0.0517	0.0723	0.0759
NIII	Prosoma length (μm)	220	215	213	214	216
	Weight (μg C)	0.1035	0.09883	0.097	0.0979	0.1
	Development time (days)	2.5	1	0.75	0.5	0.5
	Growth rate (μg C/day)	0.01206	0.0295	0.0390	0.0464	0.0346
NIV	Prosoma length (μm)	250	245	243	238	234
	Weight (μg C)	0.1336	0.1283	0.1262	0.1211	0.12
	Development time (days)	2.5	1.3333	0.75	0.5	0.5
	Growth rate (μg C/day)	0.0160	0.0206	0.0536	0.1028	0.1035
NV	Prosoma length (μm)	285	270	279	284	281
	Weight (μg C)	0.1737	0.1559	0.1664	0.1724	0.17
	Development time (days)	2.5	1.3333	0.75	0.5	0.5
	Growth rate (μg C/day)	0.0209	0.0483	0.0774	0.0957	0.0975
NVI	Prosoma length (μm)	325	321	324	321	319
	Weight (μg C)	0.2258	0.2203	0.2244	0.2203	0.22
	Development time (days)	2.5	1.3333	1	0.75	0.75
	Growth rate (μg C/day)	0.0605	0.0603	0.0527	0.1179	0.1108

TABLE 4
Effects of Temperature on Development and Growth of Copepodite Stage of *P. dubia*

Instar	Parameter	15°C	20°C	25°C	30°C	35°C
CI	Prosoma length (μm)	420	375	360	380	375
	Weight (μg C)	0.2195	0.1596	0.1423	0.1657	0.16
	Development time (days)	3.3333	1.25	1	0.75	0.75
	Growth rate (μg C/day)	0.04424	0.1274	0.2000	0.2355	0.1824
CII	Prosoma length (μm)	504.3	479.7	492	492	467
	Weight (μg C)	0.3669	0.3188	0.3423	0.3423	0.3
	Development time (days)	4.6667	1.75	1.5	1	1
	Growth rate (μg C/day)	0.0587	0.1997	0.1960	0.1647	0.1902
CIII	Prosoma length (μm)	615	614.225	613.45	565.8	558
	Weight (μg C)	0.6408	0.6682	0.6963	0.5070	0.49
	Development time (days)	5.3333	2	1.5	1.25	1
	Growth rate (μg C/day)	0.0828	0.2133	0.3185	0.3353	0.3510
CIV	Prosoma length (μm)	741.075	744.15	768.75	701.1	677
	Weight (μg C)	1.0822	1.0949	1.114	0.9261	0.84
	Development time (days)	6	2.25	1.75	1.5	1
	Growth rate (μg C/day)	0.0837	0.2465	0.2687	0.4387	0.6829
CV	Prosoma length (μm)	848.7	861	848.7	848.7	836
	Weight (μg C)	1.5842	1.6495	1.5842	1.5842	1.52
	Development time (days)	7.0833	2.75	1.75	1.5	1
	Growth rate (μg C/day)	0.1114	0.4246	0.4517	0.5261	0.8189

Note: Body lengths for CIV–CV were based on the body length of males.

FIGURE 3. Effect of temperature on growth rate of *P. dubia* nauplii.

FIGURE 4. Effect of temperature on growth rate of *P. dubia* copepodites.

Effects of Temperature on Larval Survival Rate

The effects of temperature on the survival rate of juvenile *P. dubia* were significant (Fig. 5 and Table 5). Within the suitable range, the larval survival rate at high temperatures was always higher than that at low temperatures. The survival rates for both nauplii and copepodites were highest at a temperature of 30°C and were 80 and 67.5%, respectively, and decreased when the temperature exceeded 30°C. The survival rate for nauplii at 30 and 35°C was significantly higher than at 15 and 20°C ($p < 0.05$); the survival rate for copepodites at 20 and 35°C was significantly higher than at 15°C ($p < 0.05$), with the survival rate at 30°C 1.45-fold of that at 15°C. The most suitable growth temperature for *P. dubia* ranged from 20 to 35°C.

Effects of Temperature on Reproduction

The life span and hatching time for *P. dubia* decreased as the temperature increased, and were lowest at 35°C (41 and 1.02 days, respectively), which were about 64 and 60% less than those at 20°C (Table 6). When the temperature ranged from 20 to 30°C, the total larval production and reproduction time increased as the temperature increased, but decreased when the temperature exceeded 30°C. The highest average larval production and reproduction frequency appeared at 30°C, accounting for 480 individuals/female and 30 times of reproduction, followed at 25°C. Therefore, the optimal reproduction temperature ranged from 25 to 30°C.

Effects of Temperature on Reproduction and Growth Parameters

The intrinsic growth rate, finite growth rate, and net growth rate were 0.195, 1.215, 264, respectively, at 30°C (Tables 7 and 8), followed by 25°C (0.168, 1.183, and 163) and 35°C (0.079, 1.082, and 3.3). At temperatures between 25 and 30°C, the population doubling time was 3.556 to 4.128 days, which were less than those at 20 and 35°C. However, the generation time decreased as the temperature increased, with the shortest at 25°C (15.36 days) and longest at 20°C (58.5 days). The optimal temperatures for population growth ranged from 25 to 30°C.

FIGURE 5. Effect of temperature on survival rate of *P. dubia*.

TABLE 5
Variance Analysis of Survival Rate of *P. dubia* under Different Temperatures

Variance		SS	df	Ms	F	F _{0.05}
Nauplii	Treatment	0.17	4	0.0425	6.0714*	3.06
	Error	0.035	5	0.007		
	Total variance	0.205	9			
Copepodites	Treatment	0.388	4	0.097	4.4091*	3.06
	Error	0.33	5	0.022		
	Total variance	0.718	9			

* Significant at $p < 0.05$.

TABLE 6
Growth and Production Parameters of *P. dubia* under Different Temperatures

Growth/Reproduction Indices	Temperature (°C)			
	20	25	30	35
Development stage before hatching (days)	16	11.5	8.75	7.5
Reproduction stage (day)	100.2	54	46.5	33.8
Range of longevity (days)	84–119	41–79	37–64	39–45
Average longevity (days)	116.2	65.5	55.3	41.3
Range of total larval production (larvae/female)	72–467	199–447.5	255–583	1–20
Average larval production (larvae/female)	195.13	316.75	480.25	3.88
Reproduction frequency	20	26	30	0.5
Average clutch size	9.58	12.18	16.00	7.75
Hatching time (days)	2.60	2.05	1.2	1.02

TABLE 7
Fecundity Life Table for *P. dubia* at Different Temperatures

Age, x (days)	Survival Rate l_x (°C)				Birth Rate m_x (°C)				$l_x m_x$ (°C)				$x l_x m_x$ (°C)			
	20	25	30	35	20	25	30	35	20	25	30	35	20	25	30	35
1	1	1	1	1	0	0	0	0								
3		0.75	0.8	0.75	0	0	0	0								
6	0.6		0.68	0.45		0	0	0		0				0		
11	0.6	0.63	0.68	0.45	0	0	9.71	3	0	0	6.56	1.35	0	0	72.1	14.9
12	0.6	0.63	0.68	0.45	0	6.67	4.43	0	0	4.17	2.99	0	0	50	35.9	0
13	0.6	0.63	0.68	0.45	0	7.67	8.71	2	0	4.79	5.88	0.9	0	62.3	76.5	11.7
14	0.6	0.63	0.68	0.45	0	5.75	0	0	0	3.59	0	0	0	50.3	0	0
15	0.6	0.63	0.68	0.45	0	9.83	12.3	0	0	6.15	8.29	0	0	92.2	124	0
17	0.48	0.63	0.68	0.45	0	16.3	33.7	0	0	10.2	22.8	0	0	174	387	0
18	0.48	0.63	0.68	0.45	0	0	17.6	1	0	0	11.9	0.45	0	0	214	8.1
19	0.48	0.63	0.68	0.45	0	12.2	14.3	0	0	7.6	9.68	0	0	145	184	0
21	0.48	0.63	0.68	0.45	0	12.5	32.5	0	0	7.81	21.9	0	0	164	461	0
22	0.48	0.63	0.68	0.45	3.38	3.33	18.8	0	1.6	2.08	12.7	0	35.3	45.8	280	0
24	0.46	0.59	0.63	0.45	5.88	14.8	18.8	0	2.67	8.73	11.8	0	64.2	209	284	0
26	0.46	0.59	0.63	0.45	8.88	16.5	37.8	0	4.04	9.71	23.8	0	105	252	619	0
27	0.46	0.59	0.63	0.32	9.75	3.17	17.8	2	4.44	1.86	11.2	0.64	120	50.3	302	16.6
29	0.46	0.59	0.57	0.28	0	12.2	15.8	0	0	7.16	9.02	0	0	208	262	0
31	0.46	0.59	0.52	0.28	14.1	17.7	36.3		6.43	10.4	18.7		199	322	579	
33	0.46	0.59	0.52	0.24	11.6	10.3	18.5	0	5.29	6.08	9.54	0	175	201	315	0
35	0.46	0.55	0.52	0.2	6.38	15	19	0	2.9	8.27	9.8	0	102	290	343	0
37	0.46	0.55	0.46	0.12	9	17.3	25	0	4.1	9.56	11.5	0	152	354	424	0
39	0.46	0.48	0.46	0.1	6.38	13.5	19.7	0	2.9	6.45	9.01	0	113	252	351	0
41	0.46	0.48	0.46	0.05	13.5	15.6	12.7	0	6.15	7.46	5.8	0	252	306	238	0
43	0.46	0.44	0.39	0.05	8.5	13.6	20.7	0	3.87	6	8.12	0	166	258	349	0
45	0.46	0.44	0.39	0.03	5	4.4	22	0	2.28	1.94	8.64	0	102	87.4	389	0
47	0.46	0.37	0.33	0	10.6	15	17	0	4.84	5.52	5.56	0	227	259	262	0
49	0.46	0.29	0.33		7.63	16	13.3		3.47	4.71	4.36		170	231	214	
50	0.46	0.29	0.33		2.63	8.4	5.33		1.2	2.47	1.75		59.8	124	87.3	
52	0.46	0.29	0.33		0	13	9.67			3.82	3.16		199	199	165	
53	0.46	0.24	0.26		10.3	7.8	6		4.67	1.86	1.57		247	98.8	83.3	
56	0.46	0.24	0.26		6.25	15	14.3		2.85	3.59	3.75		159	201	210	
59	0.46	0.24	0.2		13	25.5	18		5.92	6.09	3.53		349	360	209	
61	0.46	0.24	0.13		4	5.33	3		1.82	1.28	0.39		111	77.8	24	
64	0.46	0.24	0		7.67	7.33	0		3.49	1.75	0		223	112	0	
66	0.44	0.21			6.5	7.33			2.83	1.53			187	101		
68	0.42	0.12			3.88	3.67			1.61	0.44			110	29.8		
70	0.42	0.09			5.13	3			2.15	0.27			151	18.8		
71	0.4	0.03			4	0.33			1.6	0.01			114	0.71		
74	0.4	0.03			8.75	2.5			3.5	0.08			259	5.53		
77	0.4	0.03			7	0			2.8	0			216	0		
79	0.4	0			2.63	0			1.05	0			83	0		
84	0.36				19.9				7.15				601			
89	0.34				10.9				3.69				329			
91	0.34				10.5				3.57				325			
94	0.32				6.83				2.19				206			
98	0.32				7.33				2.35				230			
103	0.32				10.7				3.41				352			
104	0.32				2.5				0.8				83.2			
105	0.28				0				0				0			
106	0.28				1				0.28				29.7			

Table 7 continues

TABLE 7 (continued)

108	0.28	2.8	0.78			84.7
110	0.28	1.6	0.45			49.3
112	0.28	7.2	2.02			226
114	0.28	6	1.68			192
117	0.14	0	0			0
118	0.08	0	0			0
119	0.05	0	0			0
120	0	0	0			0
Total R ₀			119	163	264	3.3

TABLE 8
Life Table Parameters of *P. dubia* at Different Temperatures

Growth Parameters	Temperature (°C)			
	20	25	30	35
Net reproduction rate (R_0)	119	163	264	3.3
Population growth cycle (T)	58.5	30.4	28.6	15.36
Intrinsic growth rate (r_m)	0.082	0.168	0.195	0.079
Population doubling time (t)	8.49	4.13	3.56	8.833
Finite growth rate (λ)	1.085	1.183	1.215	1.082

Effects of Temperature on Generation Survival Curve

The generation survival curve of *P. dubia* was steepest and shortest at 35°C (Fig. 6), but was similar between 25 and 30°C, and longest at 20°C, which corresponded to their life cycle.

DISCUSSION

Effects of Temperature on Juvenile Development and Survival

Water temperature is an important factor that affects the survival, development, and growth of aquatic invertebrates[5,13]. Temperature affects metabolism level and oxygen consumption that, in turn, affect an animal's ability to resist environmental changes. High temperatures can accelerate metabolism and oxygen consumption, leading to excessive use of protein and a low survival rate[14,15,16]. This is in agreement with our findings that indicate significant effects of temperature on development time, survival rate, and growth rates of *P. dubia*. As the temperature increases, the development time required for each larval stage decreases and growth rates increase. The survival rate increases as the temperature increases within the range from 15 to 30°C. However, when the temperature exceeds 35°C, the larval survival rate begins to decline and larval development slows down as the temperature drops. During copepod development, there are three critical stages, i.e., fertilized egg to nauplii, NIII to NIV, and NVI to CI, which are extremely sensitive to environmental changes as evidenced by high mortality. These periods will be prolonged if development slows down, leading to high mortality. At a temperature of 15°C, the entire larval development time is 33 days. This explains the high mortality under low temperatures, which delay larval development significantly. Therefore, temperature is a critical factor that affects the copepod life cycle.

FIGURE 6. Survival curves of *P. dubia* at different temperatures.

Within the experimental range of temperature, there was no difference in body weight between nauplii and copepodites. Previous studies found that adult body weight can attain its maximum under low temperatures[17] and large individuals require a longer period of development[16]. This finding is contradictory to our results, which revealed no significant difference in body length for the same larval stage under different temperatures. We also did not observe an increase in body length with a decrease in water temperature in our experiment.

Effects of Temperature on Reproduction

Chen[18] reported an increase in mating frequency under high temperatures. However, negative effects on the reproduction of copepods have also been reported. For example, Li and Chen[19] indicated in their experiment that the egg production increased as the temperature increased and reached its peak at 24°C, and then decreased with further increase in temperature. McKinnon[20] also found that the body length of a subtropical copepod, *Acrocalanus gibber*, increased with water temperature. These experiments indicate that an optimal spectrum of temperature is species specific[14]. This is in agreement with our results that indicate the importance of temperature to the longevity and reproduction of *P. dubia*. As temperature increases, the longevity and hatching time for *P. dubia* decrease. Total egg production and mating rate increase as temperature increases, but decreases when the temperature exceeds 30°C. Hatching rate and reproduction frequency are at the lowest at 35°C. Therefore, within a suitable temperature range, elevated temperature may promote copepod reproduction, increase egg production, and shorten reproduction cycle and hatching time.

Chen[18] found that at high temperatures, mating individuals increased and mating time decreased. Our experiment indicates that the optimal temperature ranges from 25 to 30°C for population growth and reproduction by *P. dubia*. Intrinsic, finite, and net growth rates are the highest at 30°C. Meanwhile, the individual development and reproduction (clutch size and hatching rate) are also high. At 30°C, it takes 210 h or 8.75 days for NII to reach the adult stage, with a survival rate of 80%, an average longevity of 55.25 days, an average total hatching number of 480.21/female, and a reproduction frequency of 30 with an average hatching of 16 larvae. Under the optimal temperature of 30°C, the net production rate (R_0) is 264, generation time (T) is 28.6 days, intrinsic growth rate (r_m) is 0.195, finite growth rate (λ) is 1.215, and population doubling time (t) is 3.55. These data suggest a very high reproduction capacity of *P. dubia* under the optimal temperature and food conditions.

Banase[21] found that intrinsic growth rate varied among different sizes of invertebrates at the same temperature. Ji et al.[22] found intrinsic growth rate of acarus (*Oligonychus biharensis* Hirstwas) at 35°C also higher than at 25°C, but net reproduction rate and average egg production at 35°C were lower than at 25°C, which led to a conclusion that 25°C is a more suitable temperature for *O. biharensis*. Our results show little difference in intrinsic growth rate at 35°C (0.79) and 20°C (0.082). However, this does not imply that there was no difference in population growth between these temperatures. At 35°C, the reproduction rate of the next generation is 3.875 (Table 8), while the net reproduction rate at 20°C is 119; the average hatching rate is 3.875 larvae/female at 35°C, which is significantly lower than the 195.125 larvae/female at 20°C. It is concluded that population reproduction and growth are significantly better at 20°C than at 35°C.

ACKNOWLEDGMENTS

This study was funded by the Ministry of Science and Technology of China (2006GB2E000224) and Guangdong Provincial Science and Technology Projects (2006A20305003).

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This article should be cited as follows:

Li, C., Luo, X., Huang, X., and Gu, B. (2009) Influences of temperature on development and survival, reproduction and growth of a calanoid copepod (*Pseudodiaptomus dubia*). *TheScientificWorldJOURNAL: TSW Environment* **9**, 866–879. DOI 10.1100/tsw.2009.96.