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EFFECT OF TEMPERATURE ON THE HATCHING TIME  
OF EGGS OF THREE *RHITHROGENA* SPP.  
(EPHEMEROPTERA) FROM AUSTRIAN STREAMS  
AND AN ENGLISH STREAM AND RIVER

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SUMMARY

(1) Eggs of *Rhithrogena semicolorata* from the Wilfin Beck and River Lune (England), *R. cf. hybrida* from the Seebach (Austria) and *R. loyolaea* from the Herrnlmbach (Austria) were kept at constant temperatures in the laboratory. The percentage of eggs that hatched at each temperature varied from 0 to 26% for *R. semicolorata*, 1 to 33% for *R. cf. hybrida* and 0 to 48% for *R. loyolaea*. These variations were related to temperature in two species; i.e. no hatching below 5 °C and maximum values at 15.8 °C for *R. semicolorata*, few eggs hatching above 10 °C and maximum values in the range 1.9–5.2 °C for *R. loyolaea*.

(2) Hatching time (days after fertilization for 10%, 50% and 90% of the eggs to hatch) decreased with increasing temperature and the relationship between the two variables was well described by a power-law within the ranges 5.9–19.9 °C for *R. semicolorata*, 4.5–20.4 °C for *R. cf. hybrida* and 1.9–8.4 °C for *R. loyolaea*. The relationship for *R. loyolaea* was also well described by a hyperbola, but both models were not applicable above 8.4 °C because hatching time in this species then increased with increasing temperature. There were interspecific differences in hatching times for the three species, but the times for 50% and 90% of eggs hatched were not significantly different for the two populations of *R. semicolorata*.

(3) The length of the period over which eggs were hatching was remarkably short;  $\leq 9$  days for *R. semicolorata* and *R. cf. hybrida*, c. 35 days for *R. loyolaea*.

(4) There was good agreement between hatching times estimated from the power-law equations and those obtained in field experiments with *R. semicolorata* and *R. cf. hybrida*.

(5) Quantitative information on the hatching times of twelve species and twenty populations of Ephemeroptera is briefly summarized and discussed. The various mathematical models used to describe the relationship between temperature and hatching time in eggs of poikilotherms are briefly reviewed and it is concluded that the general equation for a hyperbola and power-law is frequently an adequate empirical model.

INTRODUCTION

The species of the genus *Rhithrogena* are generally widespread and abundant in torrential streams and rivers. *Rhithrogena semicolorata* (Curt.) occurs in South and Central Europe, Britain and Denmark, but is not found in the North European region of the Soviet Union

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or in Scandinavia (Sowa 1975a). *Rhithrogena loyolaea* Navas and *R. cf. hybrida* Etn. are Central European species and their larvae are restricted to cold streams. *Rhithrogena loyolaea* occurs in the upper regions of the Carpathians, Alps and Pyrenees, whilst *R. cf. hybrida* is found only in the lower regions of the Carpathians and Alps (Pleskot 1951; Thomas 1970, 1975; Sowa 1975a, b).

The life history of *R. semicolorata* has been frequently described (summarized by Macan 1979), but little is known about the life histories of *R. loyolaea* and *R. cf. hybrida* (Sowa 1975b). These descriptions are based on measurements of larvae collected at appropriate intervals and on the capture of the adults, but nothing is known about the development of the eggs and the newly-hatched larvae. Recent work in the laboratory on the development of eggs of species in the following European genera of Ephemeroptera has shown that the interpretation of life histories from field data has not always been correct: *Baetis* (Bohle 1969; Elliott 1972; Benech 1972), *Ephemerella* (Bohle 1972; Elliott 1978) and *Ecdyonurus* (Humpesch 1980).

The aim of the present study was to obtain quantitative information on the hatching of *Rhithrogena* spp. by rearing eggs from different localities and different populations in streams near Lunz (Austria) and Windermere (England). The experiments were chiefly performed in the laboratory but a small number of field experiments were also attempted to discover if the laboratory results were applicable to *Rhithrogena* spp. in the field.

## MATERIALS AND METHODS

Oviposition by *R. semicolorata* in the Wilfin Beck and the River Lune was observed on several occasions. Swarming for oviposition usually occurs in the late afternoon and evening. The female flies upstream and descends to the water surface, releasing a few eggs by dipping the tip of the abdomen at intervals whilst flying over the water. She seems to prefer sites where the current is fast. After several visits to the water surface, all the eggs are released and the female usually falls on the water surface. The eggs sink to the bottom and are dispersed over a wide area.

### *Laboratory experiments*

Eggs of *R. semicolorata* were obtained from females that were about to oviposit in the Wilfin Beck, a small stony stream on the west shore of Windermere in the English Lake District (stream described by Elliott 1973). Twenty females were caught in June and July 1967, and each female was forced to oviposit on a wet glass slide. The eggs stuck to the slide to form roughly a monolayer of attached eggs. Four slides, each covered by one egg mass, were placed in transparent plastic tubes closed at each end with nylon sifting cloth (aperture 75  $\mu\text{m}$ ), and the four tubes were placed in a constant-temperature tank (described in detail by Elliott 1978). The water in each tank was stirred and aerated by compressed air, and maintained within  $\pm 0.1\text{--}0.2$  °C of a constant temperature. Oxygen concentration was always over 85% saturation and the eggs were illuminated by daylight. The eggs were examined every week and every 3 days when hatching commenced. The newly-hatched larvae were removed and counted, and when hatching had apparently ceased, the slides were examined for a further 28 days to ensure that no more eggs hatched.

Eggs of *R. semicolorata* from the River Lune near Scoutgreen, England (river described by Macan 1976), *R. cf. hybrida* from the Seebach near Kazim, Austria (stream described

by Humpesch 1979a, b), and *R. loyolaea* from the Herrnalmbach, Austria (stream described by Humpesch 1979a), were fertilized artificially and kept in cooled incubators or climate cabinets under different constant-temperature conditions and photoperiods (using artificial light). The experimental techniques are described in detail by Humpesch (1980). Eggs hatched in nearly all laboratory experiments above 5 °C with *R. semicolorata* from Wilfin Beck and River Lune, but in experiments below 5 °C the eggs developed but did not hatch. For *R. cf. hybrida* from Seebach and *R. loyolaea* from Herrnalmbach, eggs hatched only in eleven of twenty-five experiments and thirty-seven of eighty experiments respectively. The hatching success of eggs of *R. loyolaea* was very poor at temperatures above 10 °C. (Details of the months in which the eggs were fertilized, the water temperature, photoperiod, number of eggs used and percentage that hatched in each experiment, and the hatching period are given in the appendix table.)

#### *Field experiments*

Five glass slides, each covered by one egg mass from a female *R. semicolorata*, were placed in small plastic tubes closed at each end with nylon sifting cloth (aperture 75 µm). Each plastic tube was placed in a heavy metal tube that was wedged between large stones in a swift flowing section of the Wilfin Beck. The eggs were laid and placed in the stream on the 5 July 1966, and were inspected at weekly intervals. A maximum and minimum thermometer was placed near the five tubes and was read and reset under water in each week. Oxygen concentration was measured with a Mackereth (1964) meter and was always over 85% saturation.

One experiment was performed with *R. cf. hybrida* in the Seebach (techniques are described in detail by Humpesch (1980)) and two experiments with *R. loyolaea*. Although the eggs of *R. loyolaea* developed but did not hatch after being incubated for a period of about 4 months in Seebach and Herrnalmbach, none of the experiments were successful because the nets were eventually washed away in spates.

## RESULTS

### *Rhithrogena semicolorata and R. cf. hybrida*

#### *Laboratory experiments*

The number of eggs used at each temperature varied considerably in the range 126–2292 (see appendix table). The percentage of eggs hatching varied considerably with temperature for *R. semicolorata* (Fig. 1). An overall range of 16–26% hatched at 15.8 °C but the percentage decreased to about 4–11% at 5.9 °C and 12–25% at 19.8 °C. In experiments below 5 °C, the eggs developed to stage 11 (for the description of the stages, see Bohle (1969)), but did not hatch after being incubated for a period of about 13 months. The percentage of eggs hatching at each temperature ranged from about 1–33% for *R. cf. hybrida*, and there was no evidence that temperature was responsible for these variations in hatching success (see appendix table).

As the methods of analyzing the experimental data are described in detail by Humpesch (1980), only a brief account is given here. The relationship between the time required (*Y* days after oviposition or fertilization) for 10%, 50% and 90% of the eggs to hatch and water temperature (*T* °C) over the temperature range of about 4.5–20.4 °C for *R. cf. hybrida* and 5.9–19.9 °C for *R. semicolorata* was found to be curvilinear on an arithmetic scale and linear on a logarithmic scale (e.g. Fig. 2(a), (b)). Therefore the relationship

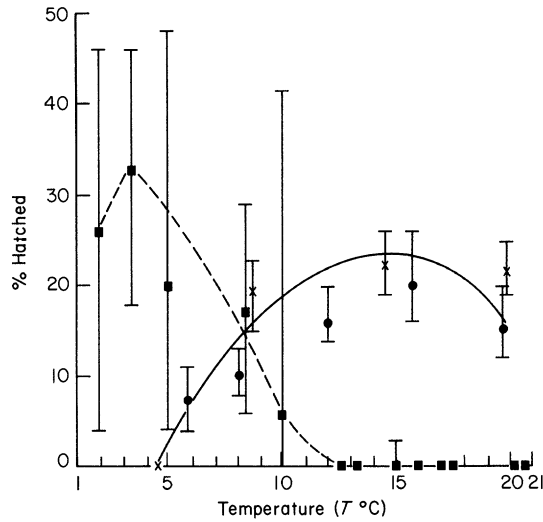


FIG. 1. Percentage of eggs hatching at each temperature for *Rhithrogena semicolorata* (solid line) from Wilfin Beck (●) and from River Lune (×), and for *R. loyolaea* (broken line) (■); each value is the mean with the range and the curves were fitted by eye.

between hatching time ( $Y$  days) and water temperature ( $T$  °C) was given by the regression equation:

$$Y = aT^{-b} \quad (1a)$$

or in logarithmic form

$$\log_e Y = \log_e a - b \log_e T \quad (1b)$$

where  $a$  and  $b$  are constants. The regressions were a good fit to the data and  $F$ -values

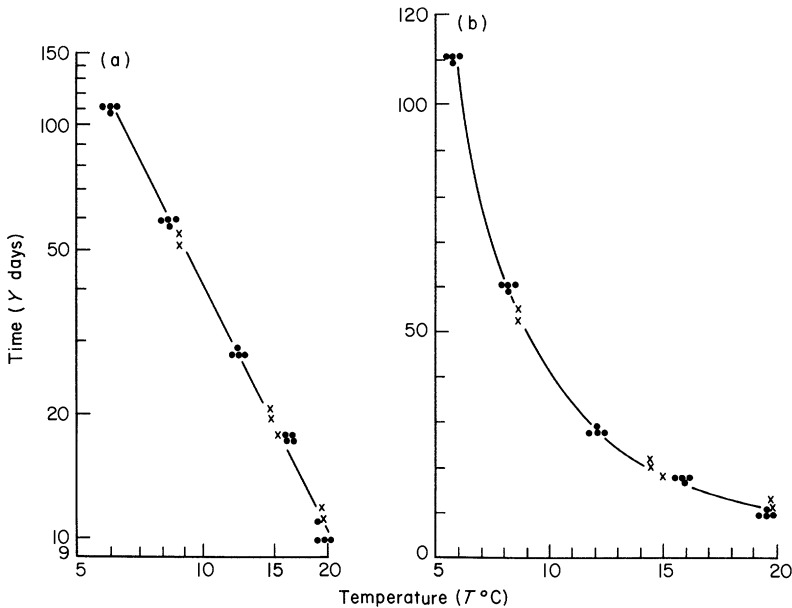


FIG. 2. Relationship between the time required ( $Y$  days) for 50% of the eggs to hatch and temperature ( $T$  °C) in the laboratory, using pooled data for *Rhithrogena semicolorata* from Wilfin Beck (●) and River Lune (×): (a) On log/log scale with linear regression line. (b) On arithmetic scale with curvilinear regression line.

from the variance ratio were highly significant ( $P < 0.001$ ). The proportion ( $r^2$ ) of the variance of  $Y$  due to the regression of  $Y$  on  $T$  was always  $\geq 0.98$ , and therefore at least 98% of the variability in the time required for hatching was accounted for by variations in temperature, which was clearly the major factor affecting the time required for hatching in the laboratory. Therefore the hatching time was apparently unaffected by variations in the time of the year when fertilization occurred or by variations in photoperiod (see appendix table).

The values of the constants  $a$  and  $b$  from the regression equations for 10%, 50% and 90% of eggs hatched differed between the two species (Table 1). For *R. semicolorata* the values of  $a$  and  $b$  for 50% and 90% of eggs hatched for the Wilfin Beck population were not significantly different from those obtained for the River Lune population. It was therefore possible to calculate one regression equation for eggs of *R. semicolorata* from the Wilfin Beck and River Lune by using the pooled results for 50% and 90% of eggs hatched (see Fig. 2(a), (b)). The value of the constant  $b$  from the regression equation for 10% of eggs hatched was significantly different between the two populations, and both regression lines were significantly different from the regression line for pooled data for 10% of eggs hatched. Therefore it was not valid to calculate a pooled regression line for 10% of eggs hatched.

Estimates were made of the actual number of days required for 10%, 50% and 90% of the eggs to hatch at 5 °C, 10 °C, 15 °C and 20 °C (Table 2). The period between oviposition or fertilization and 10% eggs hatched varied from about 22 weeks at 5 °C to about 2 weeks at 20 °C. There was a difference in the hatching time between the two species and this varied from a markedly high value of about 7 weeks at 5 °C to about 1 week at 15 °C and 20 °C and less than half a week at 10 °C. With increasing temperature, the decrease in number of days required for 10%, 50% and 90% of the eggs to hatch was not the same for the two species, e.g. *R. cf. hybrida* starts to hatch earlier than *R. semicolorata* at 5 °C, but later at 20 °C.

The length of the hatching period ( $Y$  days) for 10% to 90% of eggs hatched was remarkably short (Table 3) and decreased slightly with increasing temperature. The relationship between the two variables was described by eqn (1). The  $F$ -values from the variance ratio were only significant for *R. semicolorata* from the Wilfin Beck and for the pooled data for *R. semicolorata* and for *R. semicolorata* and *R. cf. hybrida*, whilst non-significant values ( $P > 0.05$ ) were obtained for *R. semicolorata* from the River Lune and for *R. cf. hybrida* from the Seebach. The proportion ( $r^2$ ) of the variance of  $Y$  due to the regression of  $Y$  on  $T$  was between 0.16–0.61. As only 16% to 61% of the variability in time required for 10% to 90% of the eggs to hatch was accounted for by variation in temperature, the latter was not the only factor affecting the length of the hatching period in the laboratory. The values of the constants  $a$  and  $b$  from the regression equations for 10% to 90% of eggs to hatch were not significantly different ( $P > 0.05$ ), neither between the Wilfin Beck and the River Lune population of *R. semicolorata*, nor between *R. semicolorata* and *R. cf. hybrida* (Table 3). It was therefore possible to calculate one regression equation for eggs of the two *Rhithrogena* spp., and conclude that the length of the hatching period for 10% to 90% of the eggs to hatch varied from about 8 days at 5 °C to about 4 days at 20 °C.

#### Field experiments

The number of eggs in each of the five egg-masses of *R. semicolorata* placed in the Wilfin Beck varied from 416 to 581, and the mean percentage of eggs that hatched in each

TABLE 1. Regression equations for the relationship between the time required for hatching of *Rhithrogena* spp. and water temperature in the laboratory; showing the location where the females or mature larvae were found, the temperature range ( $T^{\circ}\text{C}$ ) at which the eggs were kept, the total number of experiments ( $n$ ), the constants  $a$  and  $b$  from the regression equations for 10%, 50% and 90% of eggs hatched (the coefficient of determination ( $r^2$ ) was  $\geq 0.98$  for *R. semicolorata* and *R. cf. hybrida*, and  $\geq 0.75$  for *R. loyolaea*; all regression equations were highly significant ( $P < 0.001$ ))

Species	Locality (Country)	$T^{\circ}\text{C}$	$n$	$a \pm 95\% \text{ C.L.}$			$b \pm 95\% \text{ C.L.}$		
				10%	50%	90%	10%	50%	90%
<i>R. semicolorata</i>	Wilfin Beck (England)	5.9–19.8	20	5121.04 $\pm$ 1.24	3480.76 $\pm$ 1.14	2679.03 $\pm$ 1.06	2.15 $\pm$ 0.09	1.93 $\pm$ 0.05	1.78 $\pm$ 0.03
	River Lune (England)	8.7–19.9	7	3607.83 $\pm$ 1.64	3020.06 $\pm$ 1.40	2551.29 $\pm$ 1.16	1.96 $\pm$ 0.19	1.87 $\pm$ 0.13	1.77 $\pm$ 0.06
	pooled data	5.9–19.9	27	—	3367.08 $\pm$ 1.12	2687.75 $\pm$ 1.06	—	1.92 $\pm$ 0.05	1.78 $\pm$ 0.02
<i>R. cf. hybrida</i>	Seebach (Austria)	4.5–20.1 (20.4*)	9(11*)	926.07 $\pm$ 1.24	892.08 $\pm$ 1.20	827.90 $\pm$ 1.42	1.37 $\pm$ 0.09	1.33 $\pm$ 0.08	1.24 $\pm$ 0.15
<i>R. loyolaea</i>	Herrnalmbach (Austria)	1.9–8.4	25(28*)	279.21 $\pm$ 1.06	297.07 $\pm$ 1.06	314.04 $\pm$ 1.07	0.25 $\pm$ 0.04	0.24 $\pm$ 0.04	0.21 $\pm$ 0.05

\* See appendix table.

TABLE 2. Estimates of the number of days (with 95% C.L.) required for 10%, 50% and 90% of the eggs to hatch at 5 °C, 10 °C, 15 °C and 20 °C

% Hatched $T^{\circ}\text{C}$	10%			50%			90%			20 °C		
	5 °C	10 °C	15 °C	20 °C	5 °C	10 °C	15 °C	20 °C				
<i>R. semicolorata</i>												
Wilfin Beck	160 ± 1.08	36 ± 1.04	15 ± 1.05	8 ± 1.06	155 ± 1.05	41 ± 1.02	19 ± 1.03	11 ± 1.04	154 ± 1.02	45 ± 1.01	22 ± 1.01	13 ± 1.02
River Lune	154 ± 1.22	40 ± 1.09	18 ± 1.06	10 ± 1.10	150 ± 1.15	41 ± 1.06	19 ± 1.04	11 ± 1.06	149 ± 1.06	44 ± 1.03	21 ± 1.02	13 ± 1.03
pooled data	—	—	—	—	154 ± 1.04	41 ± 1.02	19 ± 1.02	11 ± 1.03	153 ± 1.02	45 ± 1.01	22 ± 1.01	13 ± 1.02
<i>R. cf. hybrida</i>												
Seebach	102 ± 1.08	39 ± 1.05	23 ± 1.07	15 ± 1.09	104 ± 1.07	41 ± 1.05	24 ± 1.06	16 ± 1.08	111 ± 1.14	47 ± 1.09	28 ± 1.12	20 ± 1.15
<i>R. loyolaea</i>												
Herrnalmbach	188 ± 1.02	—	—	—	202 ± 1.02	—	—	—	224 ± 1.03	—	—	—

egg-mass was  $27.6 \pm 14.9\%$ . This value is higher than those obtained at  $12.1^\circ\text{C}$  and  $15.8^\circ\text{C}$  in the laboratory experiments (see Fig. 1). One experiment with eggs of *R. cf. hybrida* was performed in the Seebach. There was generally good agreement between the results from the field and laboratory experiments (Table 4) and only a slight disagreement between the times taken for 90% of the eggs of *R. semicolorata* to hatch. Therefore the regression equations calculated from the results of all experiments with the two *Rhithrogena* spp. are probably applicable to the hatching times in the field, and both the number of days required for 10%, 50% and 90% of eggs to hatch and length of the hatching period (10–90% of eggs hatched) can be estimated for all water temperatures from about  $4.5\text{--}20.4^\circ\text{C}$  for *R. cf. hybrida* and  $5.9\text{--}19.9^\circ\text{C}$  for *R. semicolorata*.

### *Rhithrogena loyolaea*

#### *Laboratory experiments*

The number of eggs used at each temperature varied considerably in the range 92–2776 (see appendix table). The percentage of eggs that hatched between  $1.9^\circ\text{C}$  and  $20.6^\circ\text{C}$  ranged from 0% to 48%. Although there was a wide range of values for each temperature, there was clearly an inverse relationship between hatching success and increasing temperature up to about  $10^\circ\text{C}$  (see Fig. 1 and the appendix table). As hatching success was very low at temperatures above  $10^\circ\text{C}$ , the hatching times at these higher temperatures were not used in the subsequent analyses. The times at which 10%, 50% and 90% of the eggs had hatched were used in all analyses, the one exception being the 90% point at  $8.4^\circ\text{C}$ , because technical reasons dictated an elevation of temperature to about  $10^\circ\text{C}$  after the experiments had been running for 5 months. As this alteration probably affected the time at which 90% of the eggs hatched, the value for 90% hatched at  $8.4^\circ\text{C}$  was not taken into consideration for the regression analyses.

The relationship between the time required ( $Y$  days after fertilization) for 10%, 50% and 90% of the eggs to hatch and water temperature ( $T^\circ\text{C}$ ) over the range  $1.9\text{--}8.4^\circ\text{C}$  was well described by a power-law (eqn 1). The regressions were a good fit to the data and  $F$ -values from the variance ratio were highly significant ( $P < 0.001$ ). As the proportion ( $r^2$ ) of the variance of  $Y$  due to the regression of  $Y$  on  $T$  was always  $\geq 0.75$ , temperature was once again the major factor affecting the time required for hatching in the laboratory. Values of the constants  $a$  and  $b$  from the regression equations were significantly lower ( $P < 0.05$ ) than those obtained for *R. semicolorata* and *R. cf. hybrida* (cf. values in Table 1). Estimates were made of the actual number of days required for 10%, 50% and 90% of the eggs to hatch at  $5^\circ\text{C}$  (Table 2). The period between fertilization and 10% eggs hatched was about 27 weeks which is much longer than the corresponding periods for *R. semicolorata* and *R. cf. hybrida*.

The relationship between hatching time and temperature over the range  $1.9\text{--}8.4^\circ\text{C}$  was also well described by a hyperbola (Fig. 3) and therefore the relationship between the rate of development ( $1/Y$ ) and temperature ( $T^\circ\text{C}$ ) was given by the linear regression equation:

$$1/Y = a + bT \quad (2)$$

where  $a$  and  $b$  are constants. Therefore the time taken for development could be expressed in units of degree-days above a threshold temperature. The reciprocal of the regression coefficient ( $b$ ) estimated the total number of degree-days for development to be completed, and the threshold temperature ( $t^\circ\text{C}$ ) was the temperature at which the rate of develop-



TABLE 3. Regression equations for the relationship between the length of the hatching period (10%-90% of eggs hatched) and water temperature in the laboratory; showing the location where the females or mature larvae were found, the total number of experiments (*n*), the constants *a* and *b* from the regression equations, the coefficient of determination (*r*<sup>2</sup>), the level of significance of the regression equations and the estimated values (days with 95% C.L.) for 5 °C, 10 °C, 15 °C and 20 °C

Species	Locality	<i>n</i>	<i>a</i> ± 95% C.L.	<i>b</i> ± 95% C.L.	<i>r</i> <sup>2</sup>	Significance	5 °C	10 °C	15 °C	20 °C
<i>R. semicolorata</i>	Wilfin Beck	20	14.89 ± 1.38	0.33 ± 0.12	0.61	<i>P</i> < 0.001	9 ± 1.13	7 ± 1.06	6 ± 1.07	6 ± 1.10
	River Lune	7	7.61 ± 10.05	0.33 ± 0.87	0.16	<i>P</i> > 0.05	4 ± 2.53	4 ± 1.49	3 ± 1.33	3 ± 1.53
	pooled data	27	18.19 ± 2.28	0.48 ± 0.33	0.27	<i>P</i> < 0.01	8 ± 1.37	6 ± 1.16	5 ± 1.17	4 ± 1.24
<i>R. cf. hybrida</i>	Seebach	9	20.86 ± 7.59	0.56 ± 0.87	0.25	<i>P</i> > 0.05	8 ± 2.11	6 ± 1.63	5 ± 1.88	4 ± 2.25
<i>R. semicolorata</i>	pooled data	36	18.90 ± 2.08	0.50 ± 0.30	0.26	<i>P</i> < 0.05	8 ± 1.32	6 ± 1.15	5 ± 1.18	4 ± 1.25
<i>R. cf. hybrida</i>	Hermalmbach	25	40.80 ± 1.57	0.17 ± 0.34	0.05	<i>P</i> > 0.05	31 ± 1.21	—	—	—
<i>R. loyolaea</i>										

TABLE 4. The number of days (given as a range) required for 10%, 50% and 90% of eggs hatching in the field and estimated values (given as 95% C.L.) obtained from regression equations in Table 1 (*n* is the number of experiments in the field and *T* °C is the mean ± S.E. and range of the water temperature in the field)

Species	Locality	Month	<i>n</i>	<i>T</i> °C Mean ± S.E.	Range	Days required for hatching					
						(a) in field			(b) in laboratory		
						10%	50%	90%	10%	50%	90%
<i>R. semicolorata</i>	Wilfin Beck Seebach	July	5	14.5	12.1-17.6	14-16	19-23	26-31	15-17	19-20	23-24
<i>R. cf. hybrida</i>		June	1	8.3 ± 0.02	6.6-10.5	51-53	55-56	57-58	48-53	51-56	54-65

ment was zero ( $t = -a/b$ ). These values of the mean number (with 95% C.L.) of degree-days were 3106 (2735–3593) degree-days above  $-11.3 \pm 2.1$  °C for 10% hatched, 3538 (2928–4470) degree-days above  $-12.3 \pm 2.9$  °C for 50% hatched, and 3843 (3058–5170) degree-days above  $-12.1 \pm 4.1$  °C for 90% hatched. Threshold temperatures were slightly different for 10%, 50% and 90% of the eggs hatched, and cannot be re-regarded as true biological thresholds because they were obtained by extrapolation of the regression lines. The three regression lines were highly significant ( $P < 0.01$ ) and the relationship between hatching time ( $Y$  days) and water temperature ( $T$  °C) was therefore given by the hyperbolic equation:

$$Y = D/(T - t) \quad (3)$$

where  $D$  is the total number of degree-days required for hatching. The proportion ( $r^2$ ) of the variance of  $Y$  due to the regression of  $Y$  on  $T$  was 0.73 to 0.89 for the hyperbolic relationship, compared with 0.75–0.86 for the power-law defined by eqn (1), and therefore there was little to choose between the two models.

Both models ceased to be applicable at temperatures just above 8.4 °C (Fig. 3), but the precise end point could not be determined, and at 10.2 °C there was a marked increase in hatching time (above *c.* 10 °C the hatching success was very low: see Fig. 1). The effect of temperature above 8.4 °C was to increase the number of degree-days required for hatching, e.g. the number of degree-days for 50% hatched was constant at 3538 for the range 1.9–8.4 °C, but increased to 6300 at 10.2 °C. As there was only one experiment at 10.2 °C, it was not possible to analyse the relationship between hatching time and temperature at temperatures above 8.4 °C.

The length of the hatching period ( $Y$  days between the times at which 10% and 90% of the eggs hatched) slightly decreased with increasing temperature. An attempt was made to fit eqn (1) to the data, but the regression equation was not significant ( $P > 0.05$ , Table 3). As the  $r^2$  value was only 0.05, temperature was clearly not a major factor affecting the length of the period over which the eggs hatched. The mean ( $\pm 95\%$  C.L.) length of this period was  $35 \pm 1.14$  days (range 20–60 days) for the range 1.9–8.4 °C, and was therefore much longer than the values obtained for *R. semicolorata* and *R. cf. hybrida* (Table 3).

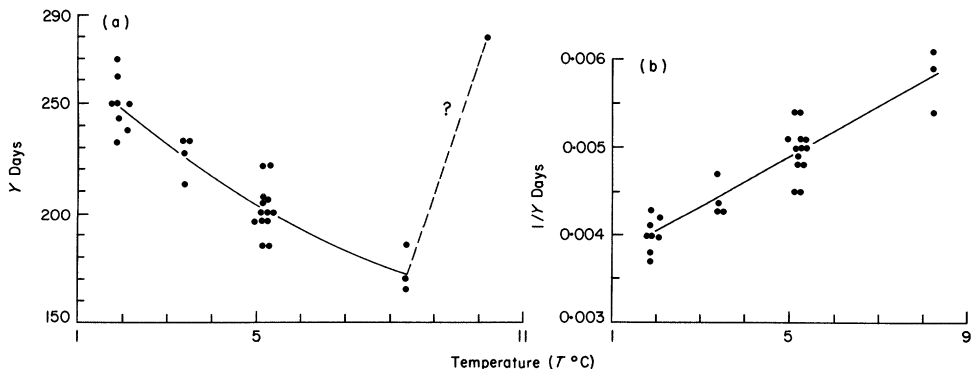


FIG. 3. Relationship between: (a) time required ( $Y$  days) for 50% of the eggs of *R. loyolaea* to hatch and temperature ( $T$  °C) in the laboratory; (b) rate of development ( $1/Y$  days) for 50% of the eggs to hatch and temperature ( $T$  °C).

## DISCUSSION

There is no previous work on hatching times in *Rhithrogena* spp., apart from a note that it took 17 days for eggs of *R. semitincta* (Pictet) (= *R. semicolorata*) to hatch at about 18 °C (Degrange & Perrier 1957). This value is similar to that obtained for *R. semicolorata* in the present study. When hatching commences in *R. semicolorata* and *R. cf. hybrida*, the period over which the eggs hatch is remarkably short at all temperatures with less than 10 days between the 10% and 90% hatching times (Table 3). Similar short times have been reported for *Baetis rhodani* (Elliott 1972) and five species of *Ecdyonurus* (Humpesch 1980), but only at temperatures above about 5 °C and 10 °C respectively. Tiny nymphs of *R. semicolorata* are often found over several months and this observation has been interpreted as an indication of a long hatching period (Macan 1957; Hynes 1961). The results of the present study show that this is incorrect and therefore the most likely explanation is that some nymphs grow very slowly after hatching. The life cycle of *R. semicolorata* and *R. cf. hybrida* takes about 1 year from oviposition to emergence of the adults, whilst *R. loyolaea* takes at least 2 years. Eggs of the latter species rarely hatched at temperatures above about 10 °C and this limitation in egg development is probably one reason for the restricted distribution of this species to cold streams in the Alps, Carpathians and Pyrenees (Thomas 1970, 1975; Sowa 1975a, b).

Detailed studies have now been made on the hatching times of twelve species and twenty populations of Ephemeroptera (Table 5). Hatching of most species usually occurs within the temperature range 3–21 °C with few eggs hatching outside this range. Notable exceptions are *B. rhodani* with large numbers of eggs hatching at temperatures up to 25 °C, *R. loyolaea* with most eggs hatching in a narrow range of 2–10 °C, and *R. semicolorata* with a lower limit between 4.5 °C (none hatching) and 5.9 °C (4–11% hatching, see Appendix). Exact temperature limits for hatching are impossible to determine because, at these limits, the effects of temperature are inextricably confounded with time (Howe 1967). Mean values for the maximum percentage of eggs hatching were over 90% for the two *Baetis* spp., *Ephemerella ignita*, and *Tricorythodes minutus*, but were always less than 50% for the three *Rhithrogena* spp. and five *Ecdyonurus* spp. It was originally suggested (Humpesch 1980) that the low values for the latter species may be due to the artificial fertilization of the eggs in the laboratory (values with asterisks in Table 5), but the values for *R. semicolorata* in the present study were similar for eggs fertilized naturally (Wilfin Beck) and artificially (River Lune). Therefore the low hatching success in these eight species probably occurs in the field and must be taken into account in the interpretation of their life cycles and population dynamics.

The relationship between hatching time and temperature could not be described by an equation in four populations, two of which had a diapause in the egg stage (see references in Table 5). In all other populations, the relationship was well described by a hyperbola or power-law. Several mathematical models have been used to describe the relationship between hatching time and temperature in poikilotherms and it is sometimes claimed that these models have a theoretical basis. As this is not generally agreed, it is probably wiser to treat all these mathematical relationships as empirical models until there is strong evidence to the contrary. Popular models are the Van't Hoff and Arrhenius equations, both of which require a constant temperature coefficient ( $Q_{10}$  and  $\mu$  respectively) over a wide range of temperatures. This is frequently not the case and the coefficient remains constant for only a very restricted part of the temperature range over which development occurs (references in Bělehrádek 1957; McLaren 1963; Bottrell 1975). Therefore several

TABLE 5. Summary of the following information on egg hatching in twelve species of Ephemeroptera: locality where the eggs were obtained, the approximate temperature range ( $T^{\circ}\text{C}$ ) over which the eggs hatched, the maximum percent of eggs that hatched and the equation relating hatching time to temperature (an asterisk indicates that the eggs were fertilized artificially)

Species	Locality (Country)	$T^{\circ}\text{C}$	Max % hatched	Equation	Reference
<i>Baetis rhodani</i>	Breitenbach (Germany)	6.8-20.0	c. 96	not known	Bohle (1969)
	Wilfin Beck (England)	3.0-22.0	99	power-law	Elliott (1972)
	Lissuraga (France)	7.5-25.0	99	power-law	Benech (1972)
<i>B. vernus</i>	Breitenbach (Germany)	6.8-20.0	>94	not known	Bohle (1969)
<i>Rhytrogena cf. hybrida</i>	Seebach (Austria)	4.5-20.1	33*	(diapause)	Present paper
<i>R. loyolaea</i>	Hernalmbach (Austria)	1.9-10.2	33*	power-law, hyperbola	Present paper
<i>R. semicolorata</i>	Wilfin Beck, River Lune (England)	5.9-19.9	28	power-law	Present paper
<i>Ecdyonurus dispar</i>	Windermere, Ennerdale (England)	3.9-20.3	38*	power-law	Humpesch (1980)
	River Lune, (England)	4.4-20.1	21*	not known	Humpesch (1980)
<i>E. insignis</i>	River Eden (England)	8.7-19.9	13*	power-law	Humpesch (1980)
<i>E. picteti</i>	Hernalmbach (Austria)	3.5-17.3	13*	power-law	Humpesch (1980)
	Seebach (Austria)	3.5-20.4	30*	power-law	Humpesch (1980)
<i>E. torrentis</i>	River Lune (England)	3.9-19.6	29*	power-law	Humpesch (1980)
<i>E. venosus</i>	Seebach (Austria)	3.6-20.6	17*	power-law	Humpesch (1980)
	River Brathay (England)	3.9-19.9	48*	power-law	Humpesch (1980)
<i>Ephemerella ignita</i>	Lahn (Germany)	7.2-16.0	>90	not known	Bohle (1972)
				(diapause)	
<i>Tricorythodes minutus</i>	Wilfin Beck (England)	5.9-19.8	90	hyperbola	Elliott (1978)
	(U.S.A.)	7.5-23.0	94	power-law	Newell & Minshall (1978)

values of the coefficient may have to be calculated to describe one set of data. In spite of this disadvantage, the coefficient  $Q_{10}$  is still widely used, probably because it is easy to calculate from sparse data! A third model that has received some support for more general physiology is Krogh's 'normal' curve (Krogh 1914) which is basically the Van't Hoff equation in its exponential form with the addition of a third parameter. This model has been used for insect development (Nielsen & Evans 1960) and fish metabolism (Winberg 1956), but other workers have found it inadequate (e.g. Hughes 1970; Bottrell 1975). The equation of Krüger (1961) is also a three-parameter model that is a modified Arrhenius equation. This first group of models basically requires an exponential relationship between development rate and temperature (or the reciprocal of absolute temperature), and if the data do not follow this relationship, then clearly the models are inadequate.

Models in a second group require an estimate of the maximum rate of development or its inverse, the time for development at the optimum temperature. This group includes the 'catenary' curve (Janisch 1928; Huffaker 1944; Messenger & Flitters 1958), an equation by Pradhan (1946) who tried to show that the curve of development rate against temperature could be derived from the normal probability distribution (see especially the criticisms of Howe 1967), and the logistic curve which has been used for eggs of terrestrial insects (Davidson 1944; Birch 1944; Browning 1952) and is strongly advocated by Andrewartha & Birch (1954). These models are not without their critics (see references in Nielsen & Evans 1960; McLaren 1963; Howe 1967) who have shown that they frequently do not fit the data, and who have emphasized the problems of trying to estimate the maximum rate of development or its inverse.

We have tried to fit the models in groups one and two to the data for the eggs of Ephemeroptera species and have found that these models are inadequate when compared with a hyperbola or power-law. Both these models belong to a third group of equations that are summarized in the general equation:

$$Y = a/(T - t)^b \quad (4)$$

where  $a$ ,  $b$  and  $t$  are constants. If  $t = 0$ , then the equation is identical to the two-parameter power-law (eqn (1a)). If  $b = 1$  and  $t$  is the threshold temperature, then the equation is identical to the two-parameter hyperbolic curve (eqn (3) with  $D = a$ ). Equation (4) is sometimes attributed to Bělehrádek (1930, 1935) but belongs to a series of power-law equations that have been used to describe a wide range of relationships in biology and ecology, e.g. allometric growth (e.g. Simpson, Roe & Lewontin 1960), metabolic relationships with body size (e.g. Kleiber 1961; Elliott 1976) and spatial pattern (e.g. Taylor Woiwod & Perry 1978).

The relationship between temperature ( $T^{\circ}\text{C}$ ) and the time taken for 50% of the eggs to hatch ( $Y$  days) has now been studied in eleven species and sixteen populations of Ephemeroptera. Values of the constants  $a$ ,  $b$  and  $t$  in eqn (4) are summarized in Table 6 with species ranked according to values of the exponent  $b$ . *Rhithrogena loyolaea* was the only species with a value of  $b$  less than one for the power-law, and a hyperbola ( $b = 1$ ) was also an adequate model for this species. A hyperbolic curve was the best model for *Ephemerella ignita* and the North American species *Tricorythodes minutus*. The authors who worked on the latter species appeared to be unaware of this because they fit a power-law to the data and did not calculate the number of degree-days required for the eggs to hatch, i.e. 989 degree-days. A power-law was a suitable model for all the remaining species, and  $b$  varied from 1.3 to 2.2 whilst  $a$  varied considerably from 548 to 7881.

TABLE 6. Values of the constants  $a$ ,  $b$  and threshold temperature ( $t$  °C) in eqn (4) and the coefficient of determination ( $r^2$ ) for the relationship between the time required for 50% of eggs to hatch and water temperature in eleven species of Ephemeroptera; the last column notes if the adequacy of the equation has been tested in the field.

Species	Locality	$a \pm 95\%$ C.L.	$b \pm 95\%$ C.L.	$t \pm 95\%$ C.L.	$r^2$	Tested in field
<i>Rhithrogena loyolaea</i>	Herrnalmbach	$297 \pm 1.06$ $3538 \pm 1.21$	$0.24 \pm 0.04$ $1.00 \pm 0.00$	0 $-12.3 \pm 2.9$	0.85 0.85	no no
<i>Ephemerella ignita</i>	Wilfin Beck	$862 \pm 1.15$	$1.00 \pm 0.00$	$3.6 \pm 0.002$	0.99	yes
<i>Tricorythodes minutus</i>	Not given	$989 \pm 9.87$	$1.00 \pm 0.84$	0	0.93	no
<i>Rhithrogena cf. hybrida</i>	Seebach	$892 \pm 1.20$	$1.33 \pm 0.08$	0	1.00	yes
<i>Baetis rhodani</i>	Lissuraga	$548 \pm 1.33$	$1.33 \pm 0.10$	0	0.99	no
	Wilfin Beck	$599 \pm 1.08$	$1.37 \pm 0.03$	0	1.00	yes
<i>Ecdyonurus picteti</i>	Herrnalmbach	$1655 \pm 1.23$	$1.47 \pm 0.09$	0	0.99	no
	Seebach	$1227 \pm 1.14$	$1.47 \pm 0.06$	0	0.99	yes
<i>Ecdyonurus venosus</i>	Seebach	$2592 \pm 1.16$	$1.68 \pm 0.06$	0	0.99	no
	River Brathay	$3516 \pm 1.71$	$1.90 \pm 0.06$	0	1.00	no
<i>Ecdyonurus dispar</i>	Windermere, Ennerdale	$3291 \pm 1.16$	$1.80 \pm 0.06$	0	0.99	yes
<i>Ecdyonurus torrentis</i>	River Lune	$2610 \pm 1.31$	$1.83 \pm 0.11$	0	0.99	no
<i>Rhithrogena semicolorata</i>	Wilfin, Lune	$3367 \pm 1.12$	$1.92 \pm 0.05$	0	1.00	yes
<i>Ecdyonurus insignis</i>	River Eden	$7881 \pm 1.20$	$2.22 \pm 0.07$	0	1.00	no

Therefore there were considerable differences between species, and also intraspecific differences for some species (*Ecdyonurus picteti*, *E. venosus*) but not for others (*Baetis rhodani*, *E. dispar*, *Rhithrogena semicolorata*). More general intraspecific differences in egg development have also been found between populations of *Ephemerella ignita* in Germany and England (Bohle 1972; Elliott 1978) and populations of *E. dispar* from lakes and rivers (Humpesch 1980). These intraspecific differences may be genuine but there is also the possibility that this work was on different species that were not recognized because of taxonomic inadequacies! Although the models summarized in eqn (4) were found to be adequate for the laboratory experiments (cf.  $r^2$  in Table 6), their usefulness increases considerably if they can be used to predict the time of hatching in the field. This has now been tested successfully for six species (Table 6), in spite of the problems of studying hatching of eggs in the field.

Models in a fourth group have been used by some workers and extend the power-law to a quadratic form:

$$\log Y = \log a + b \log T + c(\log T)^2 \quad (5)$$

where  $a$ ,  $b$  and  $c$  are constants. This equation was found to give a better fit than the simpler power-law for the relationship between temperature and the duration of egg development in epiphytic Cladocera and Copepoda (Bottrell 1975), and in *Gammarus pulex* (Nilsson 1977). It is possible that eqn (5) would be a slight improvement on the power-law fitted to the data on eggs of Ephemeroptera. However, polynomials have rarely been helpful in ecology, chiefly because biological processes are inherently multiplicative, not additive (Taylor, Woiwod & Perry 1978).

The power-law has been successfully fitted to a wide range of temperature-dependent rates (see examples in Bělehrádek 1930, 1935, 1957). These include the relationship between temperature and rate of egg development in several aquatic animals, e.g. twelve species of frogs in the genus *Rana* (McLaren 1965a, 1972), two species of fish in the genus *Sardinops* (Lasker 1964), several species of copepods (McLaren 1963, 1965b, 1966; McLaren, Corkett & Zillioux 1969), eight species of amphipods in the genus *Gammarus* (Steele & Steele 1973; Welton & Clarke 1980), two species of Plecoptera (Brittain 1977, 1978) and ten species of Ephemeroptera (references in Table 5). Therefore the power-law appears to be an adequate model for egg development in a wide range of aquatic animals, but can be used as only an empirical model at present. Bělehrádek (1957) has tried to find a theoretical basis for this model from observations that the relationship between temperature and viscosity (but not chemical reaction rate) also follows a comparable log/log relationship. He has suggested that the common feature for all temperature-dependent physiological rates is the movement of hydrated molecules. Although it is generally accepted that the relationship between temperature and enzyme reactions is linear on a logarithmic scale, a considerable amount of biochemical and physiological work is done at single or uncontrolled temperatures and therefore surprisingly little is known about the effects of temperature on the biochemical reactions in insect eggs (Howe 1967). Whether or not these reactions will provide a theoretical basis for power-law relationships, only time will tell.

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## APPENDIX

Source of eggs (species and locality where collected) and experimental conditions for hatching in *Rhithrogena* spp., showing water temperature ( $T^{\circ}\text{C}$ ), photoperiod (LL = continuous light, DD = continuous darkness, L:D = ratio of hours of light:darkness, nLD = natural light/dark cycle); number of experiments at each temperature ( $n$ ), number of eggs at each temperature (mean number per experiment with range), percentage of eggs that hatched at each temperature (mean % per experiment with range), and the period over which the eggs hatched (days after fertilization). Zero values indicate that no eggs hatched and a dash indicates that no data are available

Hatching in Rhithrogena spp.												
Species	Locality	Month when fertilized	T °C		Photoperiod	n	Number of eggs		Hatched eggs		Hatching period (days)	
			Mean ± S.E.	Range			Mean	Range	Mean %	Range %		
<i>R. semicolorata</i>	Wilfin Beck	June 1967	5.9	5.7-6.1	nLD	4	608	508-750	7.5	4-11	99-123	
		June 1967	8.2	8.0-8.4	nLD	4	503	462-561	10.3	8-13	51-69	
		July 1967	12.1	12.0-12.2	nLD	4	412	364-481	16.0	14-20	22-34	
		July 1967	15.8	15.7-15.9	nLD	4	380	320-416	20.3	16-26	12-24	
		July 1967	19.8	19.5-20.1	nLD	4	407	362-463	16.0	12-20	7-19	
		July 1966	14.5	12.1-17.6	nLD (stream)	5	495	416-581	27.6	15-46	14-35	
		June 1978	4.5 ± 0.10	3.5-5.3	DD	3	494	176-1120	0	-	0	
		June 1978	8.7 ± 0.03	7.9-9.5	12L:12D	2	196	149-243	19.5	15-23	52-57	
		June 1978	14.6 ± 0.05	14.2-15.7	12L:12D	2	185	126-244	22.6	19-26	19-26	
		June 1978	15.1 ± 0.08	14.6-15.7	12L:12D	1	578	-	1.0	-	16-22	
<i>R. cf. hybrida</i>	Seebach (stream)	June 1978	19.9 ± 0.08	19.2-21.1	LL	2	384	308-459	21.7	19-25	10-15	
		June 1977	4.5 ± 0.03	3.8-6.0	10L:14D	1	-	-	-	-	106-142	
		May 1977	5.1 ± 0.01	4.2-6.3	LL	1	1944	-	2.1	-	*	
		June 1977	5.2 ± 0.04	2.4-7.8	DD	2	1979	1666-2292	4.9	4-6	92-124	
		June 1976	6.7 ± 0.09	5.5-8.0	DD	1	1798	-	7.4	-	70-77	
		May 1976	10.1 ± 0.02	8.8-11.0	LL	1	1098	-	33.2	-	40-54	
		June 1977	12.9 ± 0.02	12.6-13.1	10L:14D	1	-	-	-	-	29-32	
		June 1977	15.1 ± 0.02	14.7-16.2	LL	1	818	-	1.8	-	23-44	
		June 1977	19.9 ± 0.02	19.0-21.1	LL	1	1468	-	9.8	-	15-30	
		June 1977	20.1 ± 0.03	19.3-20.8	LL	1	1373	-	0.9	-	14-18	
<i>A. loyolae</i>	Herrnalmbach (stream)	July 1977	20.4 ± 0.02	20.0-21.0	10L:14D	1	1718	-	2.3	-	*	
		June 1977	8.3 ± 0.02	6.6-10.5	nLD (stream)	1	-	-	-	-	44-60	
		Sept. 1977	1.9 ± 0.06	0.4-3.6	10L:14D	6	390	967-126	28.6	11-46	210-360	
		Aug. 1976	2.1 ± 0.06	0.6-3.6	10L:14D	1	1964	-	28.7	-	230-310	
		Sept. 1976	2.1 ± 0.06	0.6-3.6	10L:14D	1	1419	-	4.2	-	225-260	

Hatching in *Rhithrogena* spp.

Aug. 1976	3.4 ± 0.02	2.5-5.5	10L:14D	2	1078	1069-1087	25.5	18-33	205-270
Sept. 1977	3.4 ± 0.02	2.5-5.5	10L:14D	2	191	176-206	39.9	34-46	200-275
Aug. 1976	5.0 ± 0.04	0.2-10.3	DD	1	1157	-	29.0	-	180-290
Aug. 1977	5.2 ± 0.04	3.3-7.1	LL	2	289	136-442	23.6	9-38	190-265
Aug. 1977	5.2 ± 0.04	3.3-7.1	LL	2	-	-	-	-	180-255
Sept. 1977	5.2 ± 0.04	3.3-7.1	LL	3	565	167-1162	28.3	3-43	175-255
Aug. 1977	5.2 ± 0.04	2.4-13.2	DD	2	-	-	-	-	190-340
Sept. 1977	5.2 ± 0.04	2.4-13.2	DD	3	855	406-1188	31.9	7-48	170-300
Sept. 1977	8.4 ± 0.04	7.4-12.2	LL	2	618	375-860	17.3	6-29	135-310
Sept. 1977	8.4 ± 0.04	7.4-12.2	LL	1	-	-	-	-	165-330
Sept. 1977	9.9 ± 0.03	9.4-10.4	LL	1	2776	-	0.04	-	188
Sept. 1977	9.9 ± 0.03	9.4-10.4	LL	1	492	-	0	-	0
Aug. 1976	10.0 ± 0.03	9.4-10.6	10L:14D	1	1614	-	0.06	-	249
Sept. 1977	10.2 ± 0.05	8.9-13.1	10L:14D	1	162	-	41.4	-	250-360
Sept. 1977	10.2 ± 0.05	8.9-13.1	10L:14D	3	-	-	0	-	0
Sept. 1976	12.7 ± 0.11	10.0-13.6	LL	2	1004	382-1625	0	-	0
Sept. 1977	13.2 ± 0.03	12.6-13.8	10L:14D	4	-	-	0	-	0
Sept. 1976	15.0 ± 0.03	14.4-16.2	LL	1	1788	-	0	-	198
Sept. 1976	15.0 ± 0.03	14.4-16.2	LL	1	817	-	0	-	0
Sept. 1977	15.1 ± 0.03	14.4-15.4	LL	1	-	-	-	-	297
Sept. 1977	15.1 ± 0.03	14.4-15.4	LL	2	845	274-1416	1.71	0.1-3	170-230
Sept. 1977	15.1 ± 0.03	14.4-15.4	LL	2	182	92-272	0	-	0
Sept. 1976	15.9 ± 0.03	15.3-16.6	10L:14D	1	1857	-	0	-	0
Sept. 1977	17.1 ± 0.05	16.3-17.9	10L:14D	1	117	-	0.9	-	28
Sept. 1977	17.1 ± 0.05	16.3-17.9	10L:14D	2	127	119-134	0	-	0
Sept. 1977	17.1 ± 0.05	16.3-17.9	10L:14D	1	-	-	0	-	0
Sept. 1976	17.4 ± 0.04	16.9-18.5	LL	2	1468	1341-1594	0	-	0
Sept. 1977	20.3 ± 0.06	19.8-21.1	LL	1	1180	-	0.1	-	87
Sept. 1977	20.3 ± 0.06	19.8-21.1	LL	4	489	136-996	0	-	0
Sept. 1977	20.3 ± 0.06	19.8-21.1	LL	2	-	-	0	-	0
Sept. 1977	20.6 ± 0.04	20.2-21.0	10L:14D	4	367	107-952	0	-	0

\* The beginning of the hatching period and the values for 10% and 50% of the eggs that hatched have not been recorded.