

Effect of Temperature on the Time of Hatching in *Baëtis rhodani* (Ephemeroptera: Baëtidae)

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Summary. The period between oviposition and the start of hatching varied from about 17 weeks at 3° C to about 1 week at 22° C, and the length of the hatching period varied from about 34 days at 3° C to about 3 days at 22° C. Regression equations are provided to estimate the lengths of both periods at all temperatures between 3° C and 22° C.

Introduction

Several workers have found that tiny nymphs of *Baëtis rhodani* (Pictet) are present in the benthos for long periods of time (e.g. Macan, 1957; Hynes, 1961; Elliott, 1967). These nymphs may have lived for several months without growing, or they may have only recently hatched from eggs which remained unhatched for long periods. This latter conclusion was confirmed by Illies (1959) who found that eggs of *Baëtis* took up to 297 days to hatch in the laboratory. As the phenomenon of delayed hatching could cause serious errors in calculations of growth rate and production, it is important to discover the length of the period of delayed hatching at different times of the year. This was the chief purpose of the present study.

Materials and Methods

Oviposition occurs underwater. The female lands on a partially submerged stone in rapidly flowing water, folds her wings along the abdomen, then walks under water and appears to search for a suitable oviposition site, usually on the underside of the stone. She always faces the current and swings her abdomen from side to side until a row of eggs is laid in an arc. The female moves slowly forward and thus lays contiguous rows of eggs to form a flat semi-circular plate with its concave edge facing the current. When oviposition ceases, the female may walk out of the water and fly away, but she is usually swept away downstream. As oviposition occurs in daylight, especially in the afternoon, it was possible to collect freshly laid eggs. On three occasions, the female was still on the stone and continued to lay her eggs when the stone was out of the water.

The eggs were counted on the stones which were then enclosed inside bags in the stream or in trays in the laboratory. Each bag was double walled with an inner bag of nylon sifting cloth (aperture 75 μ , 68 meshes/cm) and an outer bag of "Tygan" plastic screening (aperture ca. 1 mm²). The bags and stones were washed

Table 1. Water temperature and number of eggs in each experiment. The numbers of dead embryos and hatched eggs are expressed as percentages of the total eggs in each experiment

Month of oviposition	Laboratory experiments										Stream		
	XI	X	III	X	IV	V	V	VII	VII	X	III	V	
Temperature (° C)	3.0	4.0	5.2	6.8	8.4	10.0	16.9	19.8	22.0	4.4	7.1	14.0	
Mean and range	± 1.6	± 1.2	± 1.3	± 1.2	± 1.5	± 1.3	± 1.0	± 1.2	± 2.3	2.3	4.8	10.4	
										to	to	to	
										8.1	11.6	17.7	
Number of eggs	238	416	796	861	1102	600	786	481	243	896	601	286	
Dead embryos (%)	0.4	0.5	0.1	0.4	0.4	0.2	0.4	0.4	0.8	0.2	0.3	0.7	
Hatched eggs (%)	81.1	88.0	97.0	98.6	98.0	96.0	81.0	78.0	72.0	96.0	99.0	94.8	

in a large bowl every 2 days at temperatures above 6° C and every 4 days at temperatures below 6° C. This procedure removed newly hatched nymphs which were counted and returned to the stream. When hatching had apparently ceased, the bags and stones were regularly examined for a further 16 days, and finally the dead embryos were counted.

There was a continuous flow of water through the trays and the oxygen concentration was over 85% saturation in all experiments. Natural daylight and darkness were used. Maximum and minimum thermometers were read and reset underwater every 2 or 4 days. Temperature was fairly constant in each laboratory experiment but varied considerably in the stream experiments (Table 1). All the 9 laboratory experiments were successfully completed, but only a third of the 9 stream experiments were completed without the bags being either torn open or washed away in spates.

Results

Over 94% of the eggs in each experiment hatched at water temperatures between 4.4° C and 14.0° C, but the percentages were significantly lower at temperatures outside this range (Table 1). There were few dead embryos which were always less than 1% of the total eggs in each experiment. As there was a large variation in the number of eggs which hatched at each temperature, the counts of newly hatched nymphs were expressed as a cumulative percentage of the total number of hatched eggs (= 100%). When these cumulative percentages were plotted against time (Y days after oviposition), they followed the normal probability distribution in each experiment (Fig. 1). An enlarged version of Fig. 1 was used to estimate the number of days required for the hatching of 0.5%, 50% and 99.5% of the total number of hatched eggs. As the counts were made at 2 or 4 day intervals, agreement with the normal distri-

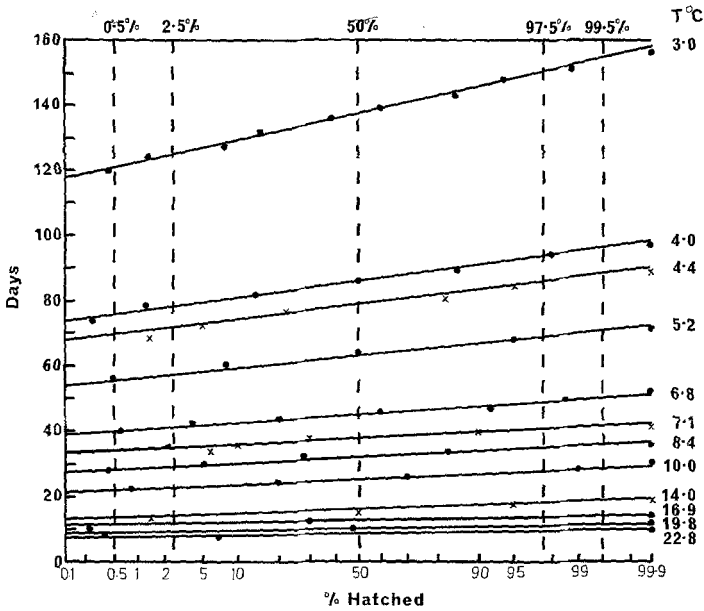


Fig. 1. Time required for eggs to hatch at different temperatures ($T^{\circ}\text{C}$) in the laboratory and in the stream ($4.4, 7.1, 14.0^{\circ}\text{C}$). Ordinate: number of days after oviposition. Abscissa (on probability scale): cumulative percentage of total number of eggs hatched in each experiment

bution was often poor for values outside the range 0.5–99.5%. Therefore it was impossible to estimate accurately the times when hatching started and ended, but the 0.5% and 99.5% points were close estimates. The relationship between the time required for hatching (Y days after oviposition) and water temperature ($T^{\circ}\text{C}$) was linear on logarithmic scales (Fig. 2A) and is given by the regression equation:

$$\log Y = \log a - b \log T$$

or

$$Y = a T^{-b} \tag{1}$$

where constant $b \pm 95\%$ confidence limits = 1.37 ± 0.03 ; and constant $a = 520$ for 0.5% hatched, 593 for 50% hatched, 677 for 99.5% hatched. The length of the hatching period (Y days) also decreased with increasing temperature (Fig. 2B) and the relationship between the two variables is given by Eq. (1) with $a = 97$ and $b = 1.30 \pm 0.14$ for the period over which 95% of the nymphs hatched (2.5–97.5% points); and $a = 112$ and $b = 1.25 \pm 0.12$ for the period over which 99% of the nymphs hatched

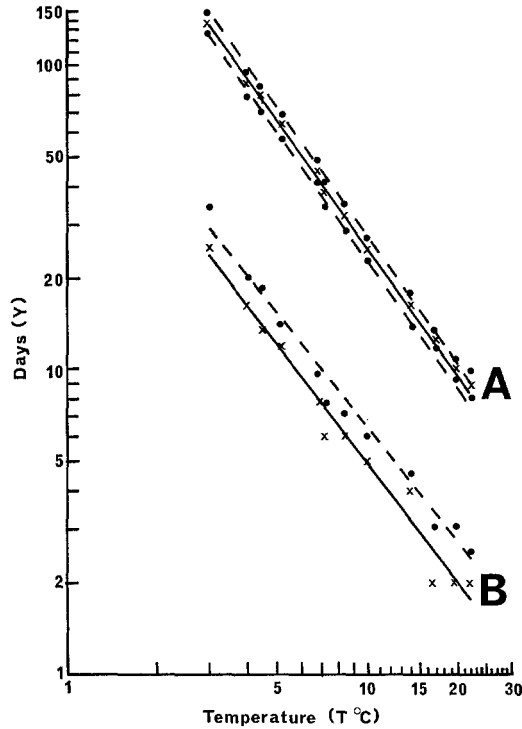


Fig. 2. A Relationship between the time required for hatching (Y days) and water temperature ($T^{\circ}\text{C}$). Crosses and solid regression line are for 50% times, dots and broken lines are for 0.5% and 99.5% times. B Relationship between the length of the hatching period (Y days) and water temperature ($T^{\circ}\text{C}$). Crosses and solid regression line are for period between 2.5% and 97.5% times, dots and broken lines are for period between 0.5% and 99.5% times

(0.5–99.5% points). Therefore the period between oviposition and the start of hatching varied from about 17 weeks at 3°C to about 1 week at 22°C , and the hatching period varied from about 34 days at 3°C to about 3 days at 22°C .

Discussion

In a morphological study of embryonic development in *Baëtis* spp., Bohle (1969) found that 50% of the nymphs of *B. rhodani* hatched after about 43 days at 6.8°C , about 28 days at 8°C , about 13 days at 16 to 18°C , and less than 12 days at 20°C . These values are similar to those obtained in the present study. Although only three stream experiments were successful in the present study, there was good agreement between the results of the stream and laboratory experiments. Therefore the

regression equations calculated from the results of all experiments are applicable to a population of *Baëtis rhodani*, and both the start and length of the hatching period can be estimated for all water temperatures between 3° C and 22° C.

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