Verh. Internat. Verein. Limnol.	20	2605—2611	Stuttgart, Dezember 1978

Preliminary notes on the effect of temperature and light-condition on the time of hatching in some Heptageniidae (Ephemeroptera)

UWE HUMPESCH

With 3 figures in the text

Introduction

PLESKOT (1951) has described the distribution and flight period of Heptageniidae from the running-water bodies in Lunz. The species belonging to the genera *Ecdyonurus* and *Rhithrogena* differ in their distribution according to the temperature: in cold streams, only *Ecdyonurus picteti* (new name refer to PUTHZ 1975) and *Rhithrogena loyolaea* are to be found, in the warmer Seebach predominate *Ecdyonurus venosus* and *Rhithrogena* cf. *hybrida,* in addition to which *Ecdyonurus picteti and Ecdyonurus zelleri* occur.

The commencement, duration and termination of the flight period is characteristic both for a species and for a species population in a water body with particular thermal properties: Herrnalm — *Ecdyonurus picteti* (August, September); *Rhitrogena loyolaea* (July, August to mid-September); Seebach — *Ecdyonurus picteti* (April to July, single individuals in September); *Ecdyonurus venosus* (end of April to September); *Rhithrogena* cf. *hybrida* (May to August).

These investigations are concerned with the complex question of the origin of the differences in the developmental pattern. Initially, the processes of and times required for embryonic development of *Ecdyonurus picteti* (Herrnalm and Seebach), *E. venosus* (Seebach), *Rhithrogena loyolaea* (Herrnalm) and *R.* cf. *hybrida* (Seebach) were studied under varying light and temperature conditions. (Owing to the limited time available, only the species *Ecdyonurus picteti* from Seebach will be discussed in detail).

Results

Constant temperatures

The embryonic development depends on temperature that is that with increase of temperature the duration of development decreases. This has also been established for *Baetis rhodani* (BOHLE 1969; ELLIOTT 1972; BENECH 1972) and for *Baetis alpinus* (HUMPESCH 1979). The development proceeds without periods of dormancy. Such periods have been recorded for *Baetis vernus* and *Ephemerella ignita* (BOHLE 1972).

Ecdyonurus picteti was studied at the following temperatures: 20 °C (n = 4 clutches), 17 °C (n = 5), 15 °C (n = 2), 13 °C (n = 6), 10 °C (n = 7), 6 °C (n = 1) in May and June.

Of all the functions tested (BOTTRELL 1975; WINKLER in prep.) the BELEHRADEK-function (BELEHRADEK 1935) gave the best fit for all the results.

Linear model: $\frac{1}{D} = a\,(T - b)$: 88.77 % of the variance explained.

Regression parabola:

D- and T-values logarithmed: 96.56 % of the variance explained.

D-value logarithmed: 96.48 % of the variance explained.

BELEHRADEK-function: $D = a\,(T - b)^c$: 98.69 % of the variance explained.

Log-BELEHRADEK-function: 96.55 % of the variance explained.

Catenary-curve: $D = a \cosh [c\,(T - b)]$: 98.47 % of the variance explained.

Exponential representation: $D = ae^{bt}$: 95.3 % of the variance explained.

Logistic curve: $D = a\,(1 + e^{b - ct})$: 98.61 % of the variance explained.

For a temperature range from 6—20 °C, the lengths of the time between fertilization and the first, median and last day of hatching can be obtained from Fig. 1. The durations of the embryonic development at 10 °C, 15 °C and 20 °C was the same for eggs laid naturally and for eggs fertilized artificially.

The number of eggs produced by a female varied between 1200—7500 (Fig. 2, egg dimension: length 0.16—0.20 mm, width 0.12—0.19 mm). Values for hatching success per female at temperatures ranging from 6—20 °C approximated 25 %. For *Baetisca rogersi*, using the same method of fertilization, at a temperature of 22—24 °C, PESCADOR & PETERS (1974) obtained values of between 1.4 % and 5.9 %, for *Stenonema femoratum*, using another type of artificial fertilisation at a temperature of 18 °C, HUFF & MCCAFFERTY (1974) obtained a value of 95 %. The latter value agrees approximately with those presented for clutches of *Baetis rhodani* from the field for temperatures ranging from almost 4.4 to 15 °C, by BOHLE (1969), ELLIOTT (1972) and BENECH (1972). For temperatures below 4.4 °C and above 15 °C, lower hatching success was recorded by ELLIOTT (1972). (No hatching success can be presented for eggs of *Ecdyonurus* from the field, as the total number of eggs per female was not known.)

Alternating temperatures

As the eggs in Seebach were exposed to fluctuations in temperature (Fig. 3 A), the results gained from cultures under constant temperature conditions cannot be directly transferred to the field situation.

Consequently, the influence of the diurnal temperature changes on the duration of the embryonic development was also examined. For such, a range of temperatures which approximated that of the Seebach, was chosen (Fig. 3 B, 3 C).

In a fluctuating temperature development took place within a period shorter than that derived from integrating developmental velocities obtained by the fit function $\frac{1}{D} = a\,(x - b)^c$ (WINKLER in prep.). Thus, it appears that there exist special physiological mechanisms, which accelerate the speed of development under conditions of changing temperatures and which exceed a simple summation of temperature effects.

The average values recorded for the hatching success in these experiments were similar to those obtained under constant temperature conditions and approximated 25 %.

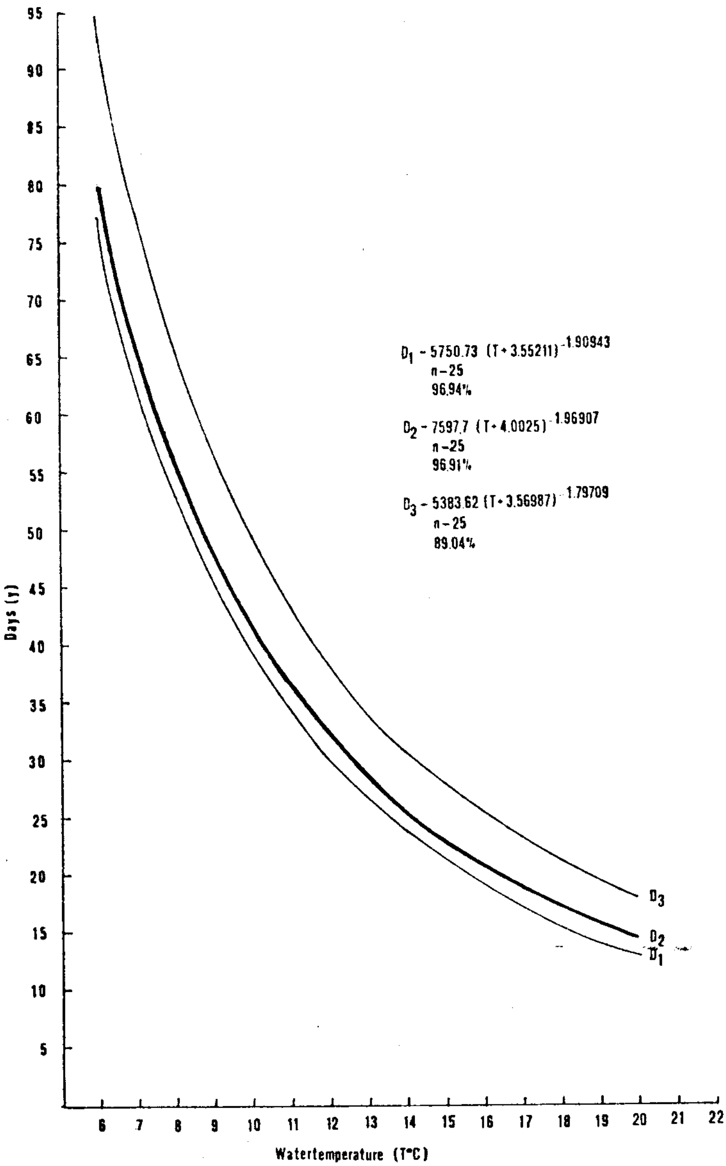


Fig. 1. *Ecdyonurus picteti*/Seebach: Relationship between the duration of embryonic development and the constant water temperatures (X T °C) in the laboratory. D_1 = first hatching day, D_2 = middle hatching day, D_3 = last hatching day.

Field experiments

In the Seebach (temperature: 6.2—10.2 °C, average: 8.2 °C) eggs began to hatch after 47 days (refer to Fig. 3 A). In comparison, under conditions of temperature variation (temperature: 5.7—10.9 °C, average 8.4 °C) as already mentioned the first larvae hatched after an interval of 45 days. As expected, both these values were lower than those recorded (50—52 days) for constant tempe-

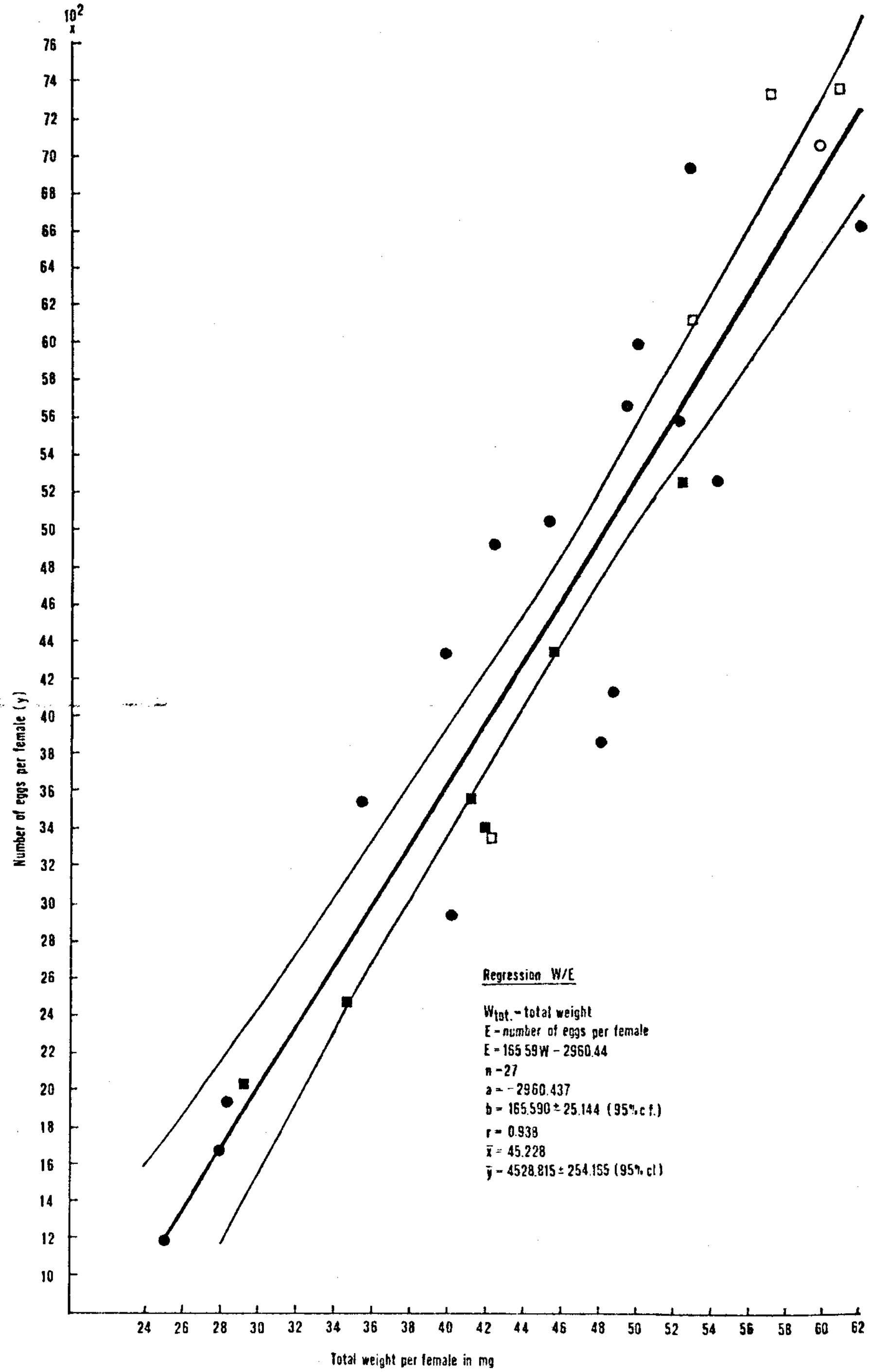
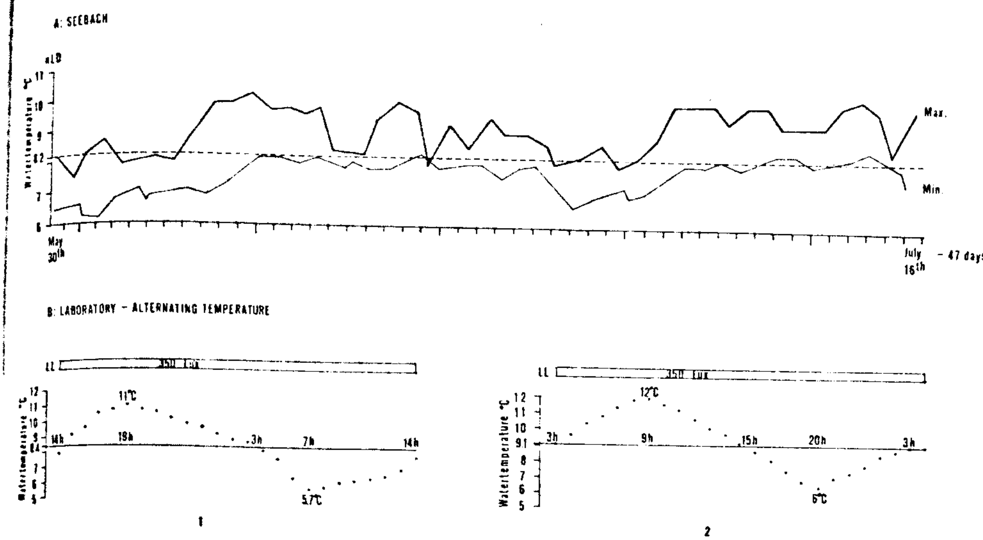


Fig. 2. *Ecdyonurus picteti*/Seebach: Relationship between the number of eggs per female (Y) and the total weight per female (X) in mg. ○ = May 1976, □ = June 1976, ● = May 1977, ■ = June 1977.



C: COMPARISON: CONSTANT – ALTERNATING TEMPERATURE – SEEBACH

	n	Photo-period	Duration for one temperature period	Watertemperature (T°C)			Hatching (1st day)			
				Mean	Min. – Max.	Amplitude	Constant	Expected	Found	%
Alternating temperature	4	LL	24h	8.4	5.7 – 11	2.7	50	49	45	10
	2	LL	24h	9.1	6 – 12	3	45	44	36	20
Seebach	2	nLD	–	8.2	6 – 10.2	2	52	–	47	9.7

Fig. 3. A: Duration of embryonic development in the Seebach. Ordinate: Daily maximum and minimum water temperature (T_{mean} = 8.2 °C); abscissa: Number of days after fertilization; nLD = natural day/night. — B: Program for the alterning temperature for 24 hours: 1. Max. = 11 °C, min. = 5.7 °C, mean = 8.4 °C. 2. Max. = 12 °C, min. = 6 °C, mean = 9.1 °C. Ordinate: water temperature (T °C); abscissa: length of time exposed hours per day. LL = constant light condition. — C: Comparison of duration of embryonic development (first hatching day) under constant and alternating temperature conditions in the laboratory and in the field.

rature conditions. *Baetis rhodani,* in contrast, developed at the same speed in constant and in fluctuating temperature (temperature: 4.8—11.6 °C, average = 7.1 °C) (Elliott 1972). The value for the hatching rate equalled 11 %.

Parthenogenesis

Unfertilized eggs of *Ecdyonurus picteti* developed at all of the temperatures tested (refer to chapter "Alternating temperatures").

The time required for development and for period of hatching (in one clutch) were longer than those determined for the artificially fertilized eggs: the times required for development were found to be approximately one third longer, those for hatching up to five times as long. Values obtained for the hatching rate per clutch lay between 0.1 % and 1 % and thus are considerably lower than those determined for the artificially fertilized eggs. For other species of the genus

Ecdyonurus, DEGRANGE (1960) presents similary low values for the hatching rates. However, other genera of Ephemeroptera also exhibit higher hatching rates (DEGRANGE 1960).

Conclusion

In the experiments carried out in the present investigation, it was demonstrated that the embryonic development of *Ecdyonurus picteti* (Seebach) is temperature-dependent, this means that the larvae will hatch from eggs which have been laid in one water body on different seasons, or in water bodies with different thermal properties in the same season, at different times. It appers that light does not influence the developmental processes.

The duration of development is shorter under conditions of temperature change.

The shortening established in these experiments is unimportant in relation to the time required for the development of a 3 mm larva to the imago established in the laboratory for *Ecdyonurus picteti* three quarters of a year.

However, as the postembryonic development can be influenced by a fluctuation in temperature (FAHY 1973; ROUX 1975), the effect can be considerably greater than in a milieu with a constant temperature. Further investigations should be carried out on the influence of other temperature variables (such as amplitude, frequency etc.) and also their effects on fertility, food uptake and assimilation and other physiological processes.

Acknowledgements

I would particulary like to thank Dr. HANS WINKLER for advice on the statistical questions, Dr. HANS MALICKY for provision of the continuous temperature recordings from the Seebach, Dr. RICHARD SOWA for help in identification of the species and Dr. T. T. MACAN for correct the English. This study was supported by the "Fonds zur Förderung der wissenschaftlichen Forschung" Projekt Nr. 2077.

References

BELEHRADEK, J., 1935: Temperature and living matter. — *Protoplasma Monograph* **8.** Borntraeger, Berlin, p. 277.

BENECH, V., 1972: Etude éxperimentale de l'incubation des oeufs. — *Freshwat. Biol.* **2:** 243—252.

BOHLE, H. W., 1969: Untersuchungen über die Embryonalentwicklung und die embryonale Diapause bei *Baetis vernus* CURTIS und *Baetis rhodani* PICTET (Baetidae, Ephemeroptera). — *Zool. Jb. Anat.* **86:** 493—575.

— 1972: Die Temperaturabhängigkeit der Embryogenese und der embryonalen Diapause von *Ephemerella ignita* (PODA) (Insecta, Ephemeroptera). — *Oecologia* **10:** 253—268.

BOTTRELL, H. H., 1975: The relationship between temperature and duration of egg development in some epiphytic Cladocera and Copepoda from the River Thames, Reading, with a discussion of temperature functions. — *Oecologia* **18:** 63—84.

DEGRANGE, CH., 1960: Recherches sur la reproduction des Ephéméroptères. — Thèses Fac. Sci. Univ. Grenoble 132: 1—193.

ELLIOTT, J. M., 1972: Effect of temperature on the time of hatching in *Baetis rhodani* (Ephemeroptera: Baetidae). — *Oceologia* **9:** 47—51.

FAHY, E., 1973: Observations on the growth of Ephemeroptera in fluctuating and constant temperature conditions. — *Proc. R. I. A.* 73: 133—149.

HUFF, B. L. & McCAFFERTY, W. P. 1974: Parthenogenesis and experimental reproductive biology in four species of the mayfly genus *Stenonema*.— *Wasman J. Biol.* 32 (2): 247—254.

HUMPESCH, U., 1979: Autökologische Untersuchungen zum Entwicklungszyklus einiger mitteleuropäischer Ephemeropteraarten. — 2nd Internat. Conf. on Ephemeroptera.

PESCADOR, M. L. & PETERS, W. L., 1974: The life history and ecology of *Baetisca rogersi* BERNER (Ephemeroptera: Baetiscidae). — *Bull. Florida State Mus., Biol. Sci.* 17 (3): 151—209.

PLESKOT, G., 1951: Wassertemperatur und Leben im Bach. — *Wetter u. Leben* 3 (5—7): 129—143.

PUTHZ, V., 1975: Über einige europäische Heptageniiden (Insecta, Ephemeroptera). — *Rev. suisse Zool.* 82 (2): 321—333.

ROUX, A. L., 1975: Température stabile et température fluctuante. II. Etude comparative de leurs effets sur la durée d'intermue de Gammaridae femelles. — *Verh. Internat. Verein. Limnol.* 19: 3014—3021.

Author's address:

Dr. U. HUMPESCH, Institut für Limnologie, Berggasse 18/19, A-1090 Wien, Austria.