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EFFECT OF TEMPERATURE ON THE HATCHING TIME OF PARTHENOGENETIC EGGS OF FIVE *ECDYONURUS* SPP. AND TWO *RHITHROGENA* SPP. (EPHEMEROPTERA) FROM AUSTRIAN STREAMS AND ENGLISH RIVERS AND LAKES

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SUMMARY

(1) Unfertilized (parthenogenetic) eggs of *Ecdyonurus picteti* from the Herrnalmbach and the Seebach (Austria), *E. venosus* from the Seebach and the River Brathay (England), *E. dispar* from Windermere, Lake Ennerdale and the River Lune (England), *E. insignis* from the River Eden (England), *E. torrentis* from the River Lune, *Rhithrogena cf. hybrida* from the Seebach and *R. loyolaea* from the Herrnalmbach were obtained from females which had been reared from mature larvae and kept separate from males. The eggs were kept at constant temperatures (range *c.* 2·0–*c.* 21·0 °C) in the laboratory. Some eggs of all species developed parthenogenetically, but most females produced eggs which did not develop and the hatching success of the parthenogenetic eggs was less than 2% in most experiments.

(2) Hatching time (days after start of the experiment 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 5·1–17·2 °C for *E. picteti*, 4·0–19·8 °C for *E. torrentis* and 5·3–19·8 °C for *E. venosus*. The relationship between hatching time and temperature could not be studied in the other species because few eggs hatched.

(3) The hatching time for parthenogenetic eggs was always longer than the equivalent time for fertilized eggs of the same species. Information on parthenogenesis in Ephemeroptera is briefly reviewed and discussed.

INTRODUCTION

Parthenogenesis occurs in several European and American species of Ephemeroptera (e.g. Degrange 1960; Huff & McCafferty 1974; Mingo 1978), but there is a paucity of detailed information on factors influencing the duration of the embryonic development of parthenogenetic eggs. The effect of temperature on the hatching time of fertilized eggs of twelve species and twenty populations of Ephemeroptera has already been described in detail (summarized in Humpesch & Elliott 1980). The aim of the present study was to obtain similar quantitative data for parthenogenetic eggs of five *Ecdyonurus* spp. and two *Rhithrogena* spp. from different localities near Lunz (Austria) and Windermere (England).

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These results are then compared with those obtained from experiments with fertilized eggs of the same species from the same localities (see Humpesch 1980; Humpesch & Elliott 1980).

MATERIALS AND METHODS

Eggs of *Ecdyonurus* spp. and *Rhithrogena* spp. were obtained from adult females which had been reared from mature larvae and kept separate from males. The laboratory experiments were performed in cooled incubators or climate cabinets under different constant-temperature conditions and photoperiods (using artificial light). The eggs from one female were either all used in one experiment or divided into two batches, one of which was fertilized (see Humpesch 1980), while the other was kept unfertilized. Therefore the numbers of eggs per experiment given in the Appendix table do not represent the number of eggs per female.

The experimental techniques for rearing the eggs are described in detail in Humpesch (1980). A large number of experiments were unsuccessful with no eggs hatching (see Table 1), and details of the successful experiments are given in the Appendix table. Information on the localities is given in Humpesch (1980) and Humpesch & Elliott (1980).

RESULTS

As eggs of *Ecdyonurus dispar* from Lake Ennerdale, *E. picteti* from the Herrnalmbach and *E. venosus* from the River Brathay did not develop, no parthenogenetic development can be recorded for these populations. Parthenogenetic development occurred in some eggs from the remaining populations (Table 1). The percentage of eggs that hatched at each temperature ranged from 0–39% and was less than 2% in most experiments (see Appendix table). These values are well below those obtained for fertilized eggs (cf. values in Humpesch 1980; Humpesch & Elliott 1980).

As the hatching success at different temperatures was very low for *Ecdyonurus dispar*, *E. insignis*, *Rhithrogena cf. hybrida* and *R. loyolaea*, these species were not used for the subsequent analyses. Although there were only a few results for *E. torrentis* and *E. venosus*, an attempt was made to analyse the data in the same way as the data for *E. picteti*. The relationship between the time required (Y days after the start of the experiment) for 10, 50 and 90% of the eggs to hatch and water temperature (T °C) over a mean temperature range of 5·1–17·2 °C for *E. picteti*, 4·0–19·8 °C for *E. torrentis* and 5.3–19·8 °C for *E. venosus* was found to be curvilinear on an arithmetic scale and linear on a logarithmic scale (e.g. Fig. 1(a), (b)). Therefore the relationship between hatching time (Y days) and water temperature (T °C) was given by the regression equation

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

or in logarithmic form

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

where a and b are constants. The regressions were a good fit to the data and F-values from the variance ratio were highly significant ($P < 0{\cdot}01$). The proportion (r^2) of the variance of Y due to the regression of Y on T was $\geqslant 0{\cdot}92$ for *E. venosus* and $\geqslant 0{\cdot}98$ for *E. picteti* and *E. torrentis*. Therefore at least 92% of the variability in the time required for hatching was accounted for by variations in temperature, which was clearly the major

TABLE 1. Summary of the following information on experiments with the unfertilized (parthenogenetic) eggs of *Ecdyonurus* spp. and *Rhithrogena* spp. in the laboratory: species and locality where collected, if experiments were successful (some eggs hatched) or unsuccessful (no eggs hatched), number of experiments (n), water temperature (T °C) at which the experiments were performed

Species	Locality	Experiments	n	T °C (mean ± S.E.) and n (if > 1)
E. dispar (Curt.)	Ennerdale (lake)	unsuccesful	4	3·9 ± 0·06, 8·8 ± 0·03, 14·9 ± 0·07, 19·9 ± 0·10
	Windermere (lake)	successful	1	20·2 ± 0·03
		unsuccessful	9	3·9 ± 0·06, 8·7 ± 0·02 (2), 14·1 ± 0·07, 15·0 ± 0·08, 19·8 ± 0·01, 20·2 ± 0·03 (3)
	River Lune	successful	2	14·1 ± 0·06, 20·1 ± 0·03
		unsuccessful	4	3·9 ± 0·06, 8·7 ± 0·03, 20·1 ± 0·03 (2)
E. insignis (Etn.)	River Eden	successful	3	8·7 ± 0·02, 14·5 ± 0·03, 19·9 ± 0·08
		unsuccessful	1	3·9 ± 0·06
E. picteti Meyer-Dür	Herrnalmbach (stream)	unsuccessful	4	3·5 ± 0·02, 5·2 ± 0·10, 13·2 ± 0·01, 17·3 ± 0·03
	Seebach (stream)	successful	19	4·6 ± 0·03, 5·1 ± 0·01 (2), 6·4 ± 0·01, 6·8 ± 0·09, 8·0 ± 0·03, 10·0 ± 0·05 (6), 14·6 ± 0·05, 15·0 ± 0·03 (4), 17·2 ± 0·05 (2)
		unsuccessful	17	1·9 ± 0·08, 3·5 ± 0·03 (2), 4·6 ± 0·03, 5·2 ± 0·05, 8·0 ± 0·03, 10·0 ± 0·05 (4), 13·0 ± 0·01 (3), 19·8 ± 0·02, 20·0 ± 0·03 (2), 20·4 ± 0·02
E. torrentis Kimm.	River Lune	successful	4	4·0 ± 0·08, 8·8 ± 0·04, 14·6 ± 0·03, 19·8 ± 0·10
E. venosus (Fabr.)	River Brathay	unsuccessful	4	3·9 ± 0·06, 8·7 ± 0·03, 14·5 ± 0·02, 19·9 ± 0·08
	Seebach (stream)	successful	16	3·6 ± 0·03, 4·4 ± 0·03 (2), 5·3 ± 0·16, 8·2 ± 0·01, 10·1 ± 0·16 (3), 15·0 ± 0·02 (2) 17·2 ± 0·06 (2), 19·8 ± 0·02 (3), 20·4 ± 0·04
		unsuccessful	50	2·1 ± 0·09 (4), 3·5 ± 0·05, 4·5 ± 0·28 (3), 5·2 ± 0·07 (3), 5·8 ± 0·21 (2), 6·4 ± 0·15 (3), 8·1 ± 0·08 (3), 8·8 ± 0·18, 10·1 ± 0·20 (12), 13·0 ± 0·10 (3), 15·0 ± 0·03 (9), 15·9 ± 0·04, 17·3 ± 0·05, 19·7 ± 0·02, 20·4 ± 0·03 (3)
R. cf. hybrida Etn.	Seebach (stream)	successful	7	5·2 ± 0·04, 6·3 ± 0·09, 8·1 ± 0·02, 10·1 ± 0·02, 15·1 ± 0·03 (3)
		unsuccessful	24	2·1 ± 0·15, 3·2 ± 0·14, 4·5 ± 0·03, 5·2 ± 0·06 (3), 6·2 ± 0·12 (2), 6·7 ± 0·09 (2), 8·0 ± 0·01, 10·1 ± 0·05 (4), 12·9 ± 0·02, 15·1 ± 0·02 (2), 17·2 ± 0·08, 19·6 ± 0·06 (2), 20·4 ± 0·03 (3)
R. loyolaea Navas	Herrnalmbach (stream)	successful	8	3·8 ± 0·05, 4·6 ± 0·03, 5·0 ± 0·04, 5·2 ± 0·04 (4), 6·5 ± 0·03
		unsuccessful	25	2·1 ± 0·06 (3), 5·0 ± 0·04, 8·4 ± 0·04 (2), 10·0 ± 0·05 (4), 13·2 ± 1·11 (3), 15·1 ± 0·03 (5), 17·4 ± 0·05 (3), 20·6 ± 0·06 (4)

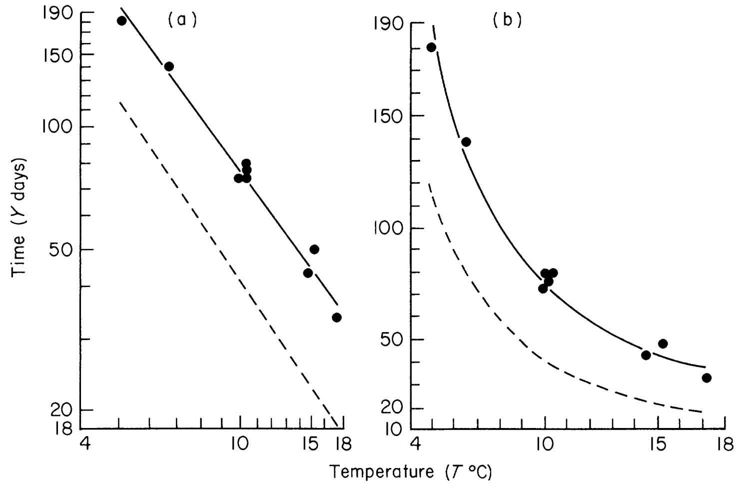

FIG. 1. Relationship between the time required (*Y* days) for 50% of the eggs of *Ecdyonurus picteti* to hatch and temperature (*T* °C) in the laboratory: (a) On log/log scale with linear regression line. (b) On arithmetic scale with curvilinear regression line. Points and solid regression lines: unfertilized (parthenogenetic) eggs; broken regression lines: fertilized eggs (from Humpesch 1980).

factor affecting the time required for hatching in the laboratory. Variations in photoperiod (see Appendix table) had no obvious effect on hatching time.

The values of the constants *a* and *b* from the regression equation for 50 and 90% of eggs hatched were significantly different ($P < 0{\cdot}05$) for *E. picteti* and *E. torrentis*, but were not significantly different ($P > 0{\cdot}05$) between both species and *E. venosus* (Table 2). The latter result may be due to the low number of experiments.

Estimates were made of the actual number of days required for 10, 50 and 90% of the eggs to hatch at 5, 10, 15 and 20 °C (Table 3). The difference in the hatching time varied from a markedly high value of about 15 weeks at 5 °C to about 7 weeks at 10 °C, 5 weeks at 15 °C and 3 weeks at 20 °C. Table 3 also shows that with increasing temperature, the decrease in the number of days required for 50 and 90% of the eggs to hatch was nearly the same for the three species.

An analysis of the effect of water temperature (*T* °C) on the length of the hatching period (*Y* days) for 10 to 90% of the eggs to hatch was possible for *E. picteti* but not for *E. torrentis* and *E. venosus* because of the lack of data (see Appendix table). The relationship between the two variables was given by eqn (1), and the values of the constants were $a = 400 \overset{\times}{\div} 3{\cdot}53$ and $b = 1{\cdot}25 \pm 0{\cdot}53$ ($r^2 = 0{\cdot}81$, $P < 0{\cdot}01$). The hatching period for *E. picteti* varied from about 8 weeks at 5 °C to about 1·5 weeks at 20 °C.

DISCUSSION

Parthenogenesis occurs in nearly all orders of insects. Amongst aquatic insects it has not yet been found to occur in Odonata and Heteroptera (Suomalainen 1962; Trembay & Caltagirone 1973), but has been recorded in several species of Plecoptera (Degrange 1960; references in Hynes 1976), Trichoptera (Elliott 1971; references in Malicky 1973) and Diptera (references in Hennig 1973; Glover 1973; Troiano 1978). Information on Ephemeroptera is summarized in Table 4 and for most species, parthenogenetic forms

TABLE 2. Regression equations for the relationship between the time required for hatching of *Ecdyonurus* spp. and water temperature in the laboratory; showing the location where the mature larvae were found, the temperature range (T °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 $\geqslant 0{\cdot}98$ for *E. picteti* and *E. torrentis* and $\geqslant 0{\cdot}92$ for *E. venosus*; all regression equations were highly significant ($P < 0{\cdot}01$))

Species	Locality (Country)	T °C	n	$a \times\!\div$ 95% C.L. 10%	50%	90%	$b \pm$ 95% C.L. 10%	50%	90%
E. picteti	Seebach (Austria)	5·1–17·2	9 (11*)	1574 ×÷ 1·44	1610 ×÷ 1·37	2051 ×÷ 1·33	1·36 ± 0·15	1·33 ± 0·13	1·35 ± 0·12
E. torrentis	R. Lune (England)	4·0–19·8	4	*	2943 ×÷ 1·58	2954 ×÷ 1·97	*	1·71 ± 0·19	1·63 ± 0·28
E. venosus	Seebach (Austria)	5·3–19·8	6	*	3026 ×÷ 2·80	3198 ×÷ 3·87	*	1·45 ± 0·41	1·34 ± 0·54

* See Appendix table.

TABLE 3. Comparison of days required for 10, 50 and 90% of unfertilized and fertilized eggs to hatch: values for unfertilized eggs are either estimated (as 95% C. L. for mean) from equations in Table 2 (*Ecdyonurus picteti*, *E. torrentis*, *E. venosus*), or single values for other species (values for *Rhithrogena loyolaea* at 5·2 °C are ranges); values for fertilized eggs are estimated (as 95% C.L. for mean) from equations in Humpesch (1980) and Humpesch & Elliott (1980); a dash indicates that no data are available, an asterisk indicates a significant difference ($P < 0{\cdot}05$) between values for unfertilized and fertilized eggs

			Days required for hatching					
			(a) for unfertilized eggs			(b) for fertilized eggs		
Species	Locality	T °C	10%	50%	90%	10%	50%	90%
E. picteti	Seebach	5·0	155–199*	171–212*	210–257*	105–133	109–120	114–126
		10·0	64–72*	72–80*	87–95*	38–41	40–42	43–45
		15·0	36–43*	41–48*	50–55*	21–23	22–24	24–26
		20·0	24–30*	27–34*	33–38*	14–15	14–16	15–17
E. torrentis	R. Lune	5·0	–	156–222	164–277*	–	124–154	146–194
		10·0	–	51–64	58–82*	–	37–41	41–48
		15·0	–	25–33	29–44*	–	18–20	19–22
		20·0	–	15–21	17–29*	–	10–12	11–13
E. venosus	Seebach	5·0	–	197–436*	219–620*	–	165–185	176–208
		10·0	–	88–130*	113–188*	–	53–56	58–64
		15·0	–	48–73*	64–111*	–	27–29	30–33
		20·0	–	30–52*	39–83*	–	16–18	18–21
E. dispar	Windermere	20·2	21	26	29	14–15	14–15	15–17
E. dispar	R. Lune	14·1	–	193	271	–	211–295	253–370
E. insignis	R. Eden	8·7	–	–	112	–	–	68–78
		14·5	–	–	55	–	–	23–25
		19·9	–	–	16	–	–	11–13
R. cf. hybrida	Seebach	6·3	117	130	154	69–79	73–81	75–93
		15·1	–	40	50	–	23–25	25–31
R. loyolaea	Herrnalmbach	4·5	203	225	250	188–196	202–210	222–234
		5·2	172–250	190–265	208–290	182–190	195–205	215–229

occur, probably sporadically, among bisexual forms (group (a) in Table 4). Degrange (1960) tested fifty-one bisexual species of European Ephemeroptera and found that eggs of twenty-six species were able to develop parthenogenetically. In the present study, all species tested in the laboratory showed a parthenogenetic development, and the present results are the first records for such a development for *Ecdyonurus picteti*, *E. torrentis*, *E. venosus*, *Rhithrogena cf. hybrida* and *R. loyolaea* and agree with the records of Degrange (1960) for *E. dispar* and *E. insignis*. The results of the present study also show that very few females produced eggs which were able to develop parthenogenetically (see Table 1) and this is known for several other species (e.g. Degrange 1960; Friesen & Flannagan 1976). All European species show only an occasional parthenogenesis, but an obligatory parthenogenesis probably occurs in five American species, because males are very rare or have never been found (group (b) (1) in Table 4).

TABLE 4. Summary of information on parthenogenetic development in Ephemeroptera (classification follows Suomalainen 1950)

(a) Occasional or accidental parthenogenesis or tychoparthenogenesis (unfertilized eggs develop occasionally through parthenogenesis)

European: *Siphlonurus aestivalis*, *S. lacustris*, *Baëtis muticus* (= *B. pumilus*), *B. niger*, *B. scambus*, *B. sinaicus* (= *B. subatrebatinus*), *Centroptilum ?lituratum*, *C. luteolum*, *C. pennulatum*, *Cloëon simile*, *C.* sp., *Epeorus alpicola*, *E. sylvicola* (= *E. assimilis*), *Rhithrogena semicolorata* (= *R. semitincta*), *R.* sp., *Ecdyonurus forcipula*, *E. quadrilineatus* (= *Heptagenia lateralis*), *H. sulphurea*, *Ephemerella ignita*, *E. major* (= *E. belgica*), *E. mucronata* (= *E. krieghoffi*), *Caenis luctosa* (= *C. moesta*), *Leptophlebia vespertina*, *Habroleptoides modesta* (= *Habrophlebia modesta*) (all in Degrange 1960); *Ecdyonurus dispar* (= *E. fluminum*), *E. insignis* (Degrange 1960; present paper); *Rhithrogena* cf. *hybrida*, *R. loyolaea*, *Ecdyonurus picteti*, *E. torrentis*, *E. venosus* (present paper).

North American: *Baëtis frondalis*, *B. spinosus* (Bergman & Hilsenhoff 1978), *Stenacron interpunctatum frontale* (= *Stenonema interpunctatum*) (Huff & McCafferty 1974; Mingo 1978), *Stenonema femoratum*, *S. pulchellum*, *S. vicarium* (Huff & McCafferty 1974), *Baëtisca rogersi* (Pescador & Peters 1974), *Hexagenia rigida* (Friesen & Flannagan 1976), *Ephoron album* (Britt 1962).

(b) Normal parthenogenesis

(1) Obligatory parthenogenesis (eggs always develop parthenogenetically).
North American: *Ameletus ludens* (Clemens 1922), *Baëtis ?hageni*, *B. macdunnoughi* (Bergman & Hilsenhoff 1978), *Cloëon triangulifer* (Gibbs 1977).

South American: *Caenis cuniana* (Froehlich 1969).

(2) Facultative parthenogenesis (eggs may either be fertilized or develop parthenogenetically).
None known.

The percentage of eggs that hatched in each experiment was remarkably low, usually less than 10%. Such low hatching success is now known for twenty-four of the forty-five European and American species known to develop parthenogenetically. Hatching success in the present study was apparently unaffected by the water temperature and the time of the year when females emerged. The percentages of eggs hatching from parthenogenetic eggs were usually much lower than the equivalent values for fertilized eggs (see Humpesch 1980; Humpesch & Elliott 1980). Therefore in these species the effect of parthenogenetic eggs on the establishment of a cohort must be relatively low. Hatching success for the parthenogenetic eggs was usually less than 2% in the present study, but higher values above 10% were obtained for *Ecdyonurus torrentis*, and similar high values have been reported for *Siphlonurus lacustris*, *Baëtis frondalis*, *B. muticus*, *B. niger*, *B. scambus*, *B. sinaicus*, *B. spinosus*, *Centroptilum ?lituratum*, *C. luteolum*, *C. pennulatum*, *Cloeon* sp., *Rhithrogena semicolorata*, *Stenonema femoratum*, *Ephemerella ignita*, *E. mucronata* (Degrange 1960; Huff & McCafferty 1974; Bergman & Hilsenhoff

1978). For species with an obligatory parthenogenesis (group (b) (1) in Table 4), the percentages of eggs hatched were mostly higher than 80%.

The relationship between the time required for hatching in parthenogenetic eggs and water temperature has been examined for the first time in the present study, and has been well described by a power-law within the range of about 4 to 20 °C for *E. picteti*, *E. torrentis* and *E. venosus*. A similar relationship has been found for the effect of temperature on the hatching time of fertilized eggs of the same three *Ecdyonurus* spp. (Humpesch 1980 and see e.g. Fig. 1). A comparison of the values of the constants a and b from the regression equations for 10, 50 and 90% of eggs hatched for eggs of fertilized and unfertilized females shows that while the values of b from the regression equations for the parthenogenetic eggs were not significantly different from those obtained from the equations for fertilized eggs, their a-values were significantly different. Therefore the effect of temperature on the rate of change in the hatching time was similar in both fertilized and unfertilized eggs, but the rate of development at the same temperature was different. When comparisons were made between the hatching times of fertilized and unfertilized eggs, the values for parthenogenetic eggs were always higher, apart from those for *E. dispar* from the River Lune (Table 3).

The length of the period over which eggs of *E. picteti* were hatching varied from about 8 weeks at 5 °C to 1·5 weeks at 20 °C and was always about eight times longer than the corresponding period for fertilized eggs.

It is not known if parthenogenesis occurs in the field for the five *Ecdyonurus* spp. and two *Rhithrogena* spp., and nothing is known about the sex ratio of these species. A change from reproduction by fertilization to parthenogenesis and the influence of the latter on the construction of a cohort requires that: (a) the females must be able to lay eggs without the oviposition-stimulans of mating, (b) the unfertilized eggs must be able to develop, (c) the offspring must be able to maintain a population in the midst of or adjacent to their parental source or sources without being eliminated by competition or hybridization. The first of these requirements has not been observed in the present study, but several authors (e.g. Degrange 1960; Froehlich 1969; McCafferty & Huff 1974; Gibbs 1977; Bergman & Hilsenhoff 1978) have found that unfertilized females of various species readily oviposit when placed in contact with a water surface, and the flight-activity pattern of tropical species with an obligatory parthenogenesis changes from that of bisexual forms (Tjønneland 1970). The second of these requirements was fulfilled by some eggs of all species in the present study but very few females produced eggs that were able to develop parthenogenetically and less than 2% of these eggs usually hatched in the laboratory (see Table 1 and Appendix table). There is no information on the development of larvae hatching from parthenogenetic eggs of these species, but Degrange (1960) reared parthenogenetic larvae in the laboratory and found that unfertilized eggs of *Cloëon simile* developed only into females (= thelytokous parthenogenesis (Suomalainen 1950)), whilst eggs of *Centroptilum luteolum* developed into both males and females (= deuterotokous parthenogenesis (Suomalainen 1950)) with about one male to five females. Information on the sex ratios of adult Ephemeroptera in the field is very rare, but for five European species, similar numbers of males and females were caught in emergence traps in streams in Germany (Sandrock 1978). It is not known if the third of these requirements is fulfilled by parthenogenetic offspring of the *Ecdyonurus* spp. and *Rhithrogena* spp. or by other species with an occasional parthenogenesis. Therefore further studies are required on the development of parthenogenetic larvae, the sex ratio of the parthenogenetic adults and the genetics of their parthenogenesis.

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APPENDIX

(for successful experiments)

Source of eggs (species and locality where collected) and experimental conditions for hatching in *Ecdyonurus* spp. and *Rhithrogena* spp., showing water temperature (T °C), photoperiod (LL = continuous light, DD = continuous dark, L:D = ratio of hours of light:darkness), 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 (a dash indicates that no data are available and a question mark indicates that the beginning of the hatching period and the value for 10% of the eggs that hatched were not recorded).

			T °C				Number of eggs		Hatched eggs		Hatching
Species	Locality	Month	Mean ± S.E.	Range	Photoperiod	n	Mean	Range	Mean %	Range %	period (days)
E. dispar	Windermere (lake)	July 1978	20·2 ± 0·03	19·4–20·7	LL	1	–	–	–	–	21–33
	River Lune	July 1978	14·1 ± 0·06	13·3–16·1	12L:12D	1	2066	–	1·2	–	74–276
		July 1978	20·1 ± 0·03	18·6–21·0	LL	1	–	–	–	–	35–64
E. insignis	River Eden	June 1978	8·7 ± 0·02	7·9–9·0	12L:12D	1	365	–	1·9	–	109–118
		June 1978	14·5 ± 0·03	14·2–15·2	12L:12D	1	1166	–	5·7	–	57–63
		June 1978	19·9 ± 0·08	19·2–21·1	LL	1	413	–	0·5	–	16
E. picteti	Seebach (stream)	May 1977	4·6 ± 0·03	3·8–6·0	10L:14D	1	–	–	–	–	127–130
		May 1977	5·1 ± 0·01	4·2–6·3	LL	1	2668	–	0·5	–	160–295
		May 1977	5·1 ± 0·05	2·4–7·8	DD	1	1482	–	0·1	–	169–189
		May 1977	6·4 ± 0·01	6·0–7·0	10L:14D	1	1869	–	5·5	–	134–184
		June 1976	6·8 ± 0·09	5·5–8·4	DD	1	1913	–	0·1	–	145–152
		May 1977	8·0 ± 0·03	7·6–9·6	LL	1	1286	–	0·3	–	208–292
		June 1976	10·1 ± 0·02	9·4–11·0	LL	2	2489	2157–2820	0·4	0·1–0·7	68–100
		June 1975	10·0 ± 0·03	9·5–10·6	LL	2	3959	3629–4289	0·4	0·1–0·7	63–101
		May 1976	10·2 ± 0·03	9·8–10·8	LL	1	4071	–	0·6	–	60–106
		May 1975	10·3 ± 0·05	9·8–10·8	LL	1	1818	–	0·1	–	78–79
		June 1975	14·6 ± 0·05	14·2–15·1	LL	1	2557	–	1·4	–	38–63
		April 1977	15·0 ± 0·01	14·6–15·6	LL	2	5744	4657–6830	5·7	0·02–11·3	?–202
		June 1977	15·1 ± 0·03	14·6–16·2	LL	1	1757	–	0·7	–	?–54
		June 1976	15·2 ± 0·02	14·6–15·6	LL	1	2170	–	11·3	–	41–82
		May 1977	17·0 ± 0·03	16·3–17·7	10L:14D	1	2590	–	0·7	–	44–82
		May 1977	17·2 ± 0·05	16·2–18·1	10L:14D	1	1384	–	0·3	–	32–49

E. torrentis	River Lune	June 1978	4·0 ± 0·08	2·5–6·2	LL	1	3582	–	0·4	–	?–300
		June 1978	8·8 ± 0·04	7·9–12·0	12L:12D	1	1619	–	32·2	–	63–134
		June 1978	14·6 ± 0·03	13·9–15·6	12L:12D	1	1175	–	39·0	–	23–56
		June 1978	19·8 ± 0·10	17·4–21·1	LL	1	1685	–	11·9	–	17–29
E. venosus	Seebach (stream)	June 1977	3·6 ± 0·03	2·5–5·2	10L:14D	1	1012	–	0·1	–	391
		Aug. 1976	4·4 ± 0·03	3·8–5·2	10L:14D	1	591	–	0·2	–	288
		June 1977	4·5 ± 0·03	1·8–6·0	10L:14D	1	523	–	0·6	–	272–275
		June 1977	5·3 ± 0·16	2·5–9·2	DD	1	1894	–	0·5	–	256–319
		June 1977	8·2 ± 0·01	7·7–8·7	LL	1	1214	–	0·4	–	139–147
		July 1975	9·8 ± 0·02	9·2–10·6	LL	1	994	–	11·3	–	72–179
		July 1976	9·9 ± 0·02	9·6–10·5	LL	1	884	–	3·3	–	73–230
		Aug. 1976	10·1 ± 0·16	9·6–10·6	LL	1	323	–	0·3	–	145
		June 1977	15·0 ± 0·02	14·6–16·5	LL	1	1528	–	0·5	–	62–63
		July 1975	15·2 ± 0·02	14·8–15·7	LL	1	865	–	0·8	–	56–90
		June 1977	17·2 ± 0·06	16·5–18·0	10L:14D	1	1458	–	2·9	–	40–122
		Sept. 1976	17·2 ± 0·03	16·1–17·6	LL	1	506	–	0·2	–	56
		June 1977	19·8 ± 0·02	19·0–20·7	LL	2	1630	1524–1736	1·0	0·1–1·8	?–133
		Sept. 1975	19·8 ± 0·02	19·6–20·2	LL	1	379	–	0·3	–	16
		Aug. 1977	20·4 ± 0·04	19·9–21·2	LL	1	–	–	–	–	33–36
R. cf. hybrida	Seebach (stream)	June 1977	5·2 ± 0·04	2·4–7·8	DD	1	765	–	0·1	–	294
		May 1976	6·3 ± 0·09	3·5–8·5	DD	1	2105	–	0·1	–	119–156
		June 1977	8·1 ± 0·02	7·7–8·6	LL	1	982	–	0·1	–	78
		May 1976	10·1 ± 0·02	8·8–11·0	LL	1	1922	–	0·1	–	65–72
		June 1977	15·1 ± 0·02	14·7–16·2	LL	1	626	–	1·6	–	37–55
		May 1976	15·3 ± 0·02	14·8–15·9	LL	1	1613	–	0·3	–	46–68
		June 1976	15·3 ± 0·03	14·2–15·8	LL	1	862	–	0·2	–	45–50
R. loyolaea	Herrnalmbach (stream)	Sept. 1977	3·8 ± 0·05	2·9–5·2	10L:14D	1	283	–	0·7	–	256
		Sept. 1977	4·6 ± 0·03	4·1–5·1	10L:14D	1	359	–	9·2	–	201–340
		Aug. 1976	5·0 ± 0·04	0·2–10·3	DD	1	1174	–	0·6	–	194–220
		Aug. 1977	5·2 ± 0·04	3·3–7·1	LL	1	–	–	–	–	210–280
		Sept. 1977	5·2 ± 0·04	3·3–7·1	LL	1	653	–	0·5	–	175–210
		Aug. 1977	5·2 ± 0·04	2·4–13·2	DD	1	–	–	–	–	259–332
		Sept. 1977	5·2 ± 0·04	2·3–13·2	DD	1	258	–	1·2	–	234–292
		Sept. 1977	6·5 ± 0·03	6·1–6·6	10L:14D	1	386	–	0·3	–	277