Egg Development of Non-Diapausing Exopterygote Aquatic Insects Occurring in Europe

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Mit 5 Figuren und 2 Tabellen

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Dedicated to Univ.-Prof. Dr. W. KÜHNELT on the occasion of his 80th birthday.

Introduction

A life cycle is defined as the sequence of morphological stages and physiological processes that link one generation to the next. The components of this cycle will be the same for all members of a species, and can generally be described qualitatively. In contrast, the qualitative and quantitative details of the variable events that are associated with the life cycle make up a "life history", which can vary between individuals or populations of one species.

Life-history information can be obtained through enumeration, measurements, categorization, and observation. With these methods, population densities, sizes, life-cycle stages, and the behaviour of organisms at any point in time can be determined. When performed over a period of time, the values obtained for these variables provide estimates of various life-history parameters; e. g. rates of recruitment, growth, mortality, reproduction, development and dispersal. When these parameters are considered in a temporal context, two additional life-history features emerge: voltinism and phenology. The former relates to the frequency with which a life cycle is completed, the latter involves both the seasonal timing of life-cycle processes and population synchrony of these processes (Fig. 1).

Temperature, nutrition and photoperiod are the most important environmental factors that are discussed. In the present account, temperature is chosen only because general principles can be deduced from a relatively large quantitative data base for non-diapausing exopterygote aquatic insects occurring in Europe (e. g. Ephemeroptera, Plecoptera, Odonata). Therefore other important abiotic factors (e. g. dissolved oxygen, pH, current, substrate) and biotic factors (e. g. predation, competition) have not been included here, as well as the interactions of some of these factors.

The present review is restricted to the egg stage only, because this is the least understood of major life stages, even though it is the key to the better interpretation of life-histories (CLIFFORD, 1982).



Fig. 1: Processes and variables involved in the study of life histories. (From BUTLER, 1984.)

Fecundity

The recruitment of a new cohort through oviposition and subsequent hatching marks the beginning of a new generation. Recruitment is one of the more difficult life-history variables to study. Adult emergence can be monitored by a number of means, including qualitative trapping with light, or quantitative sampling with emergence traps. Then the potential number of eggs laid can be estimated from a knowledge of fecundity. Although information on fecundity is available for many species of Ephemeroptera, Plecoptera and Odonata (references in CORBET, 1962, 1980; ILLIES, 1968; QUENTIN, 1968; HYNES, 1976; ZWICK, 1980; BRITTAIN, 1982) most information is for only a few females of each species and usually the size of the females is not given. This is unfortunate because fecundity usually increases with increasing size of the female.

The relationship between fecundity and body length has been shown to be well described by a power law ($Y = aL^b$ where a and b are constants). But information of such a relationship is scarce apart from values given for two ephemeropteran species [*Baetis rhodani* (BENECH, 1972; ELLIOTT & HUMPESCH, 1980), *Ecdyonurus venosus* (HUMPESCH & ELLIOTT, 1984; see Fig. 2)]. When the flight period is long in both species, the females that emerge early are larger and more fecund than those that emerge later (see also Fig. 2). It remains to be demonstrated what are the real causes of this difference in size and hence in fecundity. SWEENEY & VANNOTE (1978) reported that the adult size and fecundity of exopterygote aquatic insects

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Fig. 2: Relationship between fecundity (number of eggs per female) and total length (mm) of *Ecdyonurus venosus* from Seebach, using data from a summer generation (\oplus) and a winter generation (\bigcirc): (a) On arithmetic scale with curvilinear regression line (Y = 0.101 L^{3.77}); (b) On log/log scale with linear regression line (log Y = log 0.101 + 3.77 log L). (From HUMPESCH, 1984.)

depends largely on thermal conditions during the larval growth period. They hypothesized that the geographical distribution of some of these insects may be limited at least partially by lowered fecundity in habitats with increasingly cold or warm temperature cycles.

It is still not known how many emerging females actually return to a particular habitat and successfully lay eggs, or how many eggs or egg masses have been laid. Therefore the effect of variations in recruitment is still not clear.

Hatching of eggs and duration of embryonic development

Until recently there was no detailed work on the effects of temperature on hatching and embryonic development in the laboratory or the field. Information is now available for eleven species of Ephemeroptera, three species of Plecoptera and one species of Odonata (Table 1). Although most species hatch within the range $3-21^{\circ}$ C, there are interspecific differences in the range within which eggs hatch (Fig. 3): *Rhithrogena loyolaea* has a lower upper limit of c. 10° C, while *Baetis rhodani*, *Capnia atra* and *Coenagrion puella* have a higher upper limit of >25° C. The lower limit of *Coenagrion puella* is c. 12° C, that of *Rhithrogena semicolorata* c. 5° C. A narrow range of temperature for hatching (e. g. *Rhithrogena loyolaea*, *Coenagrion puella*) may limit, at least partially, the geographical distributon of these species. Furthermore these species are probably most vulnerable to elimination or enhancement because of climatic change or anthropogene alterations of the thermal regime.

Intraspecific differences in the temperature range within which eggs hatch do not occur in *Baetis rhodani* and *Capnia atra*, but in *Ephemerella ignita* (Fig. 3), the range for the Lahn population differed markedly from that obtained for the Wilfin Beck population. This intraspecific geographic variation may represent a phenotypic response to environmental conditions or genetic differentiation among populations.

The maximum percentage of eggs that hatch in the laboratory is over 90% for two *Baetis* spp., *Ephemerella ignita*, *Taeniopteryx nebulosa*, *Nemurella picteti*, *Capnia atra* and *Coenagrion puella*, but is less than 50% for three species of *Rhithrogena* and five species of *Ecdyonurus* (Table 1). This low hatching success probably also occurs in the field and may be as important as fecundity, as mentioned earlier, in the interpretation of abundance and population dynamics.

There is a clear relationship between hatching success and water temperature in some species (Fig. 3) in the sense that hatching success remains uniformly high at intermediate temperatures and then decreases at lower or higher temperatures. The fact that such a relationship could not be established for *Ecdyonurus* spp. and *Rhithrogena* cf. *hybrida* may be partly due to the artificial insemination in the experimental procedure (Table 1). The ability of several species to develop near 0° C may provide additional evidence for an evolutionary history associated with cool habitats. The remarkable exception is *Coenagrion puella*, a species occurring mainly in ponds, where eggs did not develop at <12° C. This obvious thermophylic species may be typical of species well adapted to the lenitic habitat.

The duration of embryonic development in non-diapausing exopterygote aquatic insects, occurring in Europe, is inversely related to temperature. This relationship is adequately described by a power law or a hyperbolic function (Table 1). Both models are summarised by a general equation $[Y = a/(T-t)^b$ where a, b and t are constants]. If t = 0, then the equation is a two parameter power law $(Y = aT^b)$. If b = 1 and t is the threshold temperature at which the development rate is theoretically zero, then the equation is identical to the two-parameter hyperbolic curve [Y = a/(T-t)], with the constant a, equal to the number of degree days above t°C required for hatching. The general equation has been successfully Table 1: Summary of the following information on egg hatching in eleven species of Ephemeroptera, three species of Plecoptera, and one species of Odonata: locality where the eggs were obtained, the approximate temperature range ($T^{\circ}C$) over which the eggs hatched, the maximum percent of eggs that hatched, the equation relating hatching time to temperature, whether or not the adequacy of the equation has been tested in the field and the mean number of days for 50 % of the eggs to hatch at 5° C and 15° C ($T^{\circ}C$ in parenthesis indicates that no hatching occurred at this temperature; an asterisk indicates that eggs were fertilized artificially).

	Locality (Country)	T° C	Max. % hatched	Equation	Tested in field	Days for 50 % hatch		Refer- ence
						at 5° C	at 15° C	
Ephemeroptera B. rhodani	Breitenbach (FRG) Wilfin Beck (GB) Lissuraga (F)	(0.0) 6.8-20.0 3.0-22.0 7.5-25.0 (27.5)	c. 96 99 99	not known power-law power-law	no yes no	- 65 65	- 15 15	1 2 3
B. vernus	Breitenbach (FRG)	(0.0) 6.8-20.0 (24.0)	> 94	not known (diapause)	no			1
R. cf. hybrida	Seebach (A)	4.5-20.1	33*	power-law	yes			
R. loyolaea	Herrnalmbach (A)	1.9-10.2 (20.6)	33*	power-law, hyperbola	no			
R. semicolorata	Wilfin Beck (GB) River Lune (GB)	(4.5) 5.8-19.9		power-law	yes	154	19	
E. dispar	Windermere (GB) Ennerdale (GB)	3.9-20.3		power-law	yes	180	25	5
	River Lune (GB)	4.4-20.1	21*	not known	no			5
E. insignis	River Eden (GB)	(3.9) 8.7–19.9	13*	power-law	no		20	5
E. picteti	Herrnalmbach (A) Seebach (A)	3.5-17.3 (20.6) 3.5-20.4	13* 30*	power-law power-law	no yes	155 115	23	5 5
E. torrentis	River Lune (GB)	3.9-19.5	29*	power-law	no	138	19	5
E. venosus	Seebach (A) River Brathay (GB)	3.6-20.6 3.9-19.9	17* 48*	power-law power-law	no no	175 166	28 21	5 5
Eph. ignita	Lahn (FRG)	(5.0) 7.2-16.0 (22.0)	> 90	not known (diapause)	yes			6
	Wilfin Beck (GB)	5.9-19.8		hyperbola	yes			
Plecoptera T nebulosa	Ø. Heimdalsvatn (N)	2.0-23.7	99	power-law		60	19	
N. picteti	Pool at Finse (N) Bellman Ground	4.0-20.0	not known	power-law		50	15	
	Beck (GB)	5.9-19.8		power-law				
C. atra	Lomma (N) Ø. Heimdalsvatn (N) Bigasjavrit (N)			power-law				
Odonata C. puella	Herzogenburg (A)	(3.5) 12.0-28.0	100	power-law	yes		48	12

References: 1, BOHLE 1969; 2, ELLIOTT 1972; 3, BENECH & VIGNES 1972; 4, HUMPESCH & ELLIOTT 1980; 5, HUMPESCH 1980; 6, BOHLE 1972; 7, ELLIOTT 1978; 8, BRITTAIN 1977; 9, BRITTAIN 1978; 10, ELLIOTT 1984; 11, BRITTAIN, LILLEHAMMER & SALTVEIT 1984; 12, WARINGER & HUMPESCH 1984.



Fig. 3: Comparison of the percentages of eggs hatching at each temperature for European species of (a) Ephemeroptera: (1) Baetis rhodani (combined data: BOHLE, 1969; ELLIOTT, 1972; BENECH, 1972); (2) B. vernus (BOHLE, 1969); (3) Ephemerella ignita [(a) BOHLE, 1972; (b) ELLIOTT, 1978]; (4) Rhithrogena loyolaea (HUMPESCH & ELLIOTT, 1980); (5) R. semicolorata (HUMPESCH & ELLIOTT, 1980); (b) Plecoptera: (1) Taeniopteryx nebulosa (BRITTAIN, 1977); (2) Nemurella picteti (ELLIOTT, 1984); Capnia atra (BRITTAIN & LILLEHAMMER & SALTVEIT, 1984); (c) Odonata: (1) Coenagrion puella (WARINGER & HUMPESCH, 1984).

fitted to data for fourteen species and twenty-two populations. A hyperbolic curve was the best model for *Ephemerella ignita* and an adequate model for *Rhithrogena loyolaea*, while the power law was more suitable for the remaining twelve species (Table 1). An example of the good fit of the power-law model is given in Fig. 4.



Fig. 4: Relationship between the time required (Y days) for 50 % of the eggs of *Ecdyonurus* venosus from Seebach to hatch and water temperature (T°C) in the laboratory: (a) On arithmetic scale with curvilinear regression line (Y = 2593 T^{-1.68}); (b) On log/log scale with linear regression line (log Y = log 2593 -1.68 log T). (From HUMPESCH et al., 1982.)

The values of constants a and b were similar between populations of the same species (*Baetis rhodani*, *Rhithrogena semicolorata*, *Ecdyonurus* dispar from lakes, *Nemurella picteti*, *Capnia atra*), eggs of the populations of these species develop at similar rates in different localities and do not exhibit significant geographical variation in response to the duration of embryonic development to temperature. Therefore the regression equations appear to be valid for different populations.

The value of constant b was similar between two populations of *Ecdyonurus picteti* and between different species (*Baetis rhodani* and *Rhithrogena* cf. *hybrida; Taeniopteryx nebulosa, Nemurella picteti* and *Capnia atra*), but their a-values were different. This intra- and interspecific difference means, that the effect of temperature on the rate of

change in the hatching time is similar, but the rate of development at the same temperature is different.

The majority of species of Ephemeroptera showed a difference in the values of both constants a and b, and therefore there is a marked inter- and intraspecific difference in the embryonic development. This means that the time for embryonic development at a given temperature is different between species or/and geographically separated populations (e.g. eggs of Ecdyonurus venosus obtained from a population in a cold environment took longer to develop at a given temperature than eggs from warmer habitats or in Ecdyonurus dispar significant differences in hatching time at identical temperatures occurred when lake and river populations were compared). Therefore the regression equations obtained for these populations and species seem to be restricted to themselves only, the reason for this difference might have evolved through an effective isolation by geographical segregation, but one should always consider the possibility that cryptic species may be involved.

The use of these models for the determination of the hatching time in the field as a method for identification and separation of cohorts requires that the predictions obtained from laboratory experiments under constant temperature conditions are applicable to the field. This extension of constant-temperature laboratory data to field development of eggs has been successful for seven species (Table 1) and it has also been demonstrated that in two Ecdyonurus spp. and one Rhithrogena sp. both the hatching time and the rate of development were similar for constant and fluctuating temperatures in the laboratory (Fig. 5).



Water temperature(T°C)

Fig. 5: Relationship between time required (Y days) for 10% of the eggs of Ecdyonurus venosus from Seebach to hatch and the arithmetic mean of fluctuating water temperature $(T^{\circ}C)$ in the laboratory: (a) On arithmetic scale with curvilinear regression line (Y = 2093 T^{-1.63}); (b) On log/log scale with linear regression line (log Y = log 2093 –1.63 log T). Crosses: Hatching time for eggs at constant temperatures. (From HUMPESCH, 1982.)

The duration of hatching decreases with increasing temperature in some species (e. g. Baetis rhodani, Ecdyonurus spp., Rhithrogena semicolorata, Ephemerella ignita, Nemurella picteti) but seems to be independent of temperature in other species (e. g. Rhithrogena cf. hybrida, R. loyolaea, Coenagrion puella; see Table 2). Despite the variation within and between species, the period over which 80-99%eggs hatch is remarkably short, <10 days in some species (e. g. for Baetis rhodani, Rhithrogena cf. hybrida) and <30 days for other species if $T > 5^{\circ} C$ (Table 2). Therefore there appears to be a high degree of population synchrony at hatching and this may have an important impact on the population structure and life cycle analysis. Most of the observations on delayed appearance or prolonged seasonal occurrence of small larvae have been interpreted as an indication for delayed hatching,

Table 2: Summary of the following information on the hatching period of ten species of Ephemeroptera, one species of Plecoptera and one species of Odonata: locality where the eggs were obtained, the equation relating length of the hatching period to temperature, percentage of eggs hatched, and mean number of days required for these to hatch at 5° C and 15° C.

	Locality	Equation	D: e	Refer- ence		
	_		%	at 5° C	at 15° C	
Ephemeroptera						
Bactis rhodani	Wilfin Beck	power-law	99	15	4	1
Rhithrogena						
cf. <i>hybrida</i>	Seebach		80	8	5	2
R. loyolaea	Herrnalmbach		80	31	-	2
R. semicolorata	Wilfin Beck, River Lune	power-law	80	8	5	2
Ecdyonurus dispar	Windermere, Ennerdale	power-law	80	27	2	3
E. insignis	River Eden	power-law	80	_	3	3
E. picteti	Herrnalmbach	power-law	80	24	3	3
•	Seebach	power-law	80	8	2	3
E. torrentis	River Lune	power-law	80	26	2	3
E. venosus	Seebach, River Brathay	power-law	80	27	2	3
Ephemerella ignita	Wilfin Beck	power-law	80	25	4	3
Plecoptera						
Nemurella picteti	Bellman Ground Beck	power-law	80	35	1 9	4
Odonata						
Coenagrion puella	Herzogenburg	none	94	_	~10	5

References: 1, ELLIOTT 1972; 2, HUMPESCH & ELLIOTT 1980; 3, HUMPESCH 1980; 4, ELLIOTT 1984; 5, WARINGER & HUMPESCH 1984.

but it is more probable from the work on egg development that they are the result of inadequate sampling or slow growth in the early instars. However, there is some evidence for other species of Ephemeroptera (BRITTAIN, 1982), Plecoptera (HYNES, 1976; ZWICK, 1980, 1981) and Odonata (CORBET, 1980) that parents may produce eggs with delayed (and perhaps asynchronous) development. Quantitative data for this topic are sparse, in spite of the fact that asynchronous hatching could have great adaptive value in many environments.

Conclusion

The data presented in this review clearly show that there is a need for similar information on other exopterygotes, and especially endopterygote aquatic insect species and populations. This information is essential for the interpretation of life histories, the identification of cohorts, the study of spatial pattern and movements, the construction of life tables and the estimation of rates of growth, mortality and production. The quantitative information on the effects of temperature on the hatching time and hatching success also indicate that voltinism should be viewed as a lifehistory variable at the population level rather than as a characteristic of a species.

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Zusammenfassung

Als Lebenszyklus kann die Folge von morphologischen Stadien und physiologischen Prozessen verstanden werden, die von einer Generation zur nächsten führen. Die einzelnen Teile dieses Zyklus sind für alle Individuen einer Art dieselben und können im allgemeinen qualitativ beschrieben werden. Die Lebensgeschichte machen die qualitativen und quantitativen Besonderheiten der Variablen aus, die mit dem Lebenszyklus eng verknüpft sind. Die Lebensgeschichte kann für die Individuen oder Populationen einer Art verschieden sein (Fig. 1).

Von den Faktoren, die die Parameter der Lebensgeschichte wesentlich beeinflussen, werden die Temperatur, Nahrung und Photoperiode am häufigsten diskutiert. In der vorliegenden Übersicht, die sich im wesentlichen mit der Dauer der Embryonalentwicklung von nichtdiapausierenden exopterygoten Wasserinsekten beschäftigt, wurde der Faktor Temperatur deshalb herausgegriffen, weil über dessen Einfluß ein verhältnismäßig großer quantitativer Datensatz zur Verfügung steht, so daß über den Einzelfall hinaus generellere Prinzipien abgeleitet werden können.

Fekundität

Die Beziehung zwischen Fekundität und Körperlänge kann durch eine Potenzfunktion ausgedrückt werden (Fig. 2). Bei Arten mit langer Flugzeit sind die Weibchen, die früher schlüpfen, größer und haben mehr Eier, als die die später im Jahr schlüpfen. Nach Sweeney & VANNOTE (1978) hängt die Körpergröße und damit die Fekundität teilweise von den thermischen Bedingungen während des Larvenwachstums ab. Die geographische Verbreitung einer Art kann daher, zumindest teilweise, dort beeinflußt werden, wo die thermischen Gegebenheiten eine herabgesetzte Fakundität bedingen.

Schlüpferfolg und Dauer der Embryonalentwicklung

Die Ergebnisse, die von elf Ephemeropteren-, drei Plecopterenarten und einer Odonatenart stammen, zeigen, daß die meisten Arten im Temperaturbereich von 3 bis 21° C schlüpfen. Die unteren und oberen Temperaturgrenzen und das Temperaturoptimum für das Schlüpfen können intra- und interspezifisch verschieden sein (Fig. 3). In den unterschiedlichen Temperaturansprüchen für das Schlüpfen manifestiert sich möglicherweise die Entwicklungsgeschichte einer Art.

Die Beziehung zwischen den Variablen Dauer der Embryonalentwicklung und Temperatur kann durch eine Potenzfunktion oder durch eine Hyperbel beschrieben werden (Tabelle 1; Fig. 4). Bei fünf Arten entwickelten sich die Eier verschiedener Populationen mit denselben Raten, bei zwei Populationen und mehreren Arten war der Einfluß der Temperatur auf die Entwicklungsrate gleich, die Rate selbst bei ein und derselben Temperatur jedoch verschieden, bei den verbleibenden Arten waren keine Übereinstimmungen festzustellen. Die mathematische Beschreibung der besprochenen Beziehung macht die Prognostizierung des Entwicklungsablaufes für bestimmte Temperaturen möglich, was in Hinblick auf die Abschätzung einer möglichen Auswirkung der thermischen Beeinflussung eines Gewässers durch Kühlwasser wichtig erscheint (HUMPESCH et al., 1982).

Der Zeitraum in dem 80–99 % der Eier eines Geleges schlüpfen ist relativ kurz und bei einigen Arten ebenfalls temperaturabhängig (Tabelle 2).

Die quantitativen Daten über den Tempratureinfluß auf Fekundität, Schlüpferfolg und Dauer der Embryonalentwicklung machen deutlich, daß der "Voltinismus" als Lebensgeschichten-Paramter auf dem Populations- und nicht auf dem Artniveau gesehen werden sollte.

References

- BENECH, V. (1972): La fécondité de *Baetis rhodani* Pictet. Freshwater Biology 2, 337–354.
- BENECH, V. & VIGNES, J. C. (1972): Etude expérimentale de l'incubation des oeufs de *Baetis rhodani* Pictet. Freshwater Biology 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). Zoologische Jahrbücher, Abteilung Anatomie und Ontogenie der Tiere 86, 493-575.
- BOHLE, H. W. (1972): Die Temperaturabhängigkeit der Embryogenese und der embryonalen Diapause von *Ephemerella ignita* (Poda) (Insecta, Ephemeroptera). Oecologia 10, 253–268.
- BRITTAIN, J. E. (1973): The biology and life cycle of *Nemoura avicularis* Morton (Plecoptera). Freshwater Biology 3, 199–210.
- BRITTAIN, J. E. (1977): The effect of temperature on the egg incubation period of *Taeniopteryx nebulosa* (Plecoptera). Oikos 29, 302-305.
- BRITTAIN, J. E. (1978): Semivoltinism in mountain populations of Nemurella pictetii (Plecoptera). Oikos 30, 1–6.
- BRITTAIN, J. E. (1982): Biology of mayflies. Annual Review of Entomology 27, 119-147.
- BRITTAIN, J. E., LILLEHAMMER, A. & SALTVEIT, S. J. (1984): The effect of temperature on intraspecific variation in egg biology and nymphal size in the stonefly, *Capnia atra* (Plecoptera). Journal of Animal Ecology 53, 161–169.
- BUTLER, M. G. (1984): Life histories of aquatic insects. In: The Ecology of Aquatic Insects (ed. V. H. Resh & D. M. Rosenberg), 24-55. New York, Praeger.
- CLIFFORD, H. E. (1982): Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. Quaestiones Entomologicae 18, 15-89.
- CORBET, P. S. (1962): A Biology of Dragonflies. London, Witherby. 247 pp.
- CORBET, P. S. (1980): Biology of Odonata. Annual Review of Entomology 25, 189-217.
- ELLIOTT, J. M. (1972): Effect of temperature on the time of hatching in *Baetis* rhodani (Ephemeroptera: Baetidae). Oecologia 9, 47-51.
- ELLIOTT, J. M. (1978): Effect of temperature on the hatching time of eggs of *Ephemerella ignita* (Poda) (Ephemeroptera: Ephemerellidae). Freshwater Biology 8, 51–58.
- ELLIOTT, J. M. (1984): Hatching time and growth of *Nemurella pictetii* (Plecoptera: Nemouridae) in the laboratory and a Lake District stream. Freshwater Biology 14, 491-499.
- ELLIOTT, J. M. & HUMPESCH, U. H. (1980): Eggs of Ephemeroptera. Report of the Freshwater Biological Association 48, 41-52.
- HUMPESCH, U. H. (1980): Effect of temperature on the hatching time of eggs of five *Ecdyonurus* spp. (Ephemeroptera) from Austrian streams and English streams, rivers and lakes. Journal of Animal Ecology 49, 317-333.
- HUMPESCH, U. H. (1982): Effect of fluctuating temperature on the duration of embryonic development in two *Ecdyonurus* spp. and *Rhithrogena* cf. *hybrida* (Ephemeroptera) from Austrian streams. Oecologia 55, 285-288.
- HUMPESCH, U. H. & ELLIOTT, J. M. (1980): Effect of temperature on the hatching time of eggs of three *Rhithrogena* spp. (Ephemeroptera) from Austrian streams and an English stream and river. Journal of Animal Ecology 49, 643-661.

- HUMPESCH, U. H. & ELLIOTT, J. M. (1984): Zur Ökologie adulter Ephemeropteren Österreichs. Archiv für Hydrobiologie 101, 179–207.
- HUMPESCH, U. H. et al. (1982): Ökologische Auswirkungen der thermischen Gewässerbeeinflussung. Oesterreichische Wasserwirtschaft 34, 122-136.
- HYNES, H. B. N. (1976): Biology of Plecoptera. Annual Review of Entomology 21, 135-153.
- ILLIES, J. (1968): Ephemeroptera (Eintagsfliegen). Handbuch der Zoologie 4 (2), 2/5, 1-63.
- QUENTIN, D. S. & BEIER, M. (1968): Odonata (Libellen). Handbuch der Zoologie 4 (2), 2/6, 1–39.
- SWEENEY, B. W. & VANNOTE, R. L. (1978): Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. Science 200, 444-446.
- WARINGER, J. A. & HUMPESCH, U. H. (1984): Embryonic development, larval growth and life cycle of *Coenagrion puella* (Odonata: Zygoptera) from an Austrian pond. Freshwater Biology 14, 385-399.
- ZWICK, P. (1980): Plecoptera (Steinfliegen). Handbuch der Zoologie 4 (2), 2/7, 1-115.
- ZWICK, P. (1981): Diapause development of *Protonemura intricata* (Plecoptera: Nemouridae). Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 21, 1607–1611.

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