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**Egg Development of Non-Diapausing  
Exopterygote Aquatic Insects Occuring  
in Europe**

By

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Mit 5 Figuren und 2 Tabellen

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

By UWE H. HUMPEsch

Mit 5 Figuren und 2 Tabellen

(Vorgelegt in der Sitzung der mathem.-naturw. Klasse am 14. Dezember 1984 durch das  
w. M. WILHELM KÜHNELT)

*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).

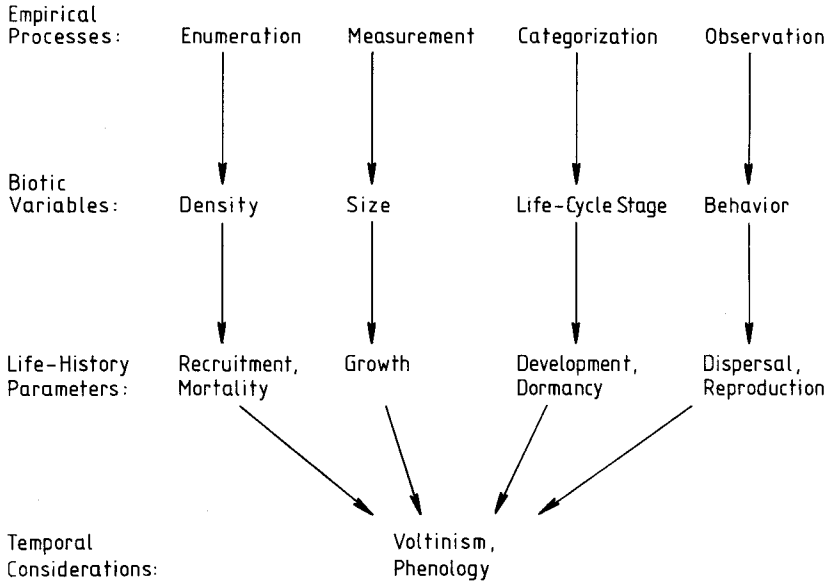


Fig. 1: Processes and variables involved in the study of life histories. (From BUTLER, 1984.)

### 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 & HUMPECH, 1980), *Ecdyonurus venosus* (HUMPECH & 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

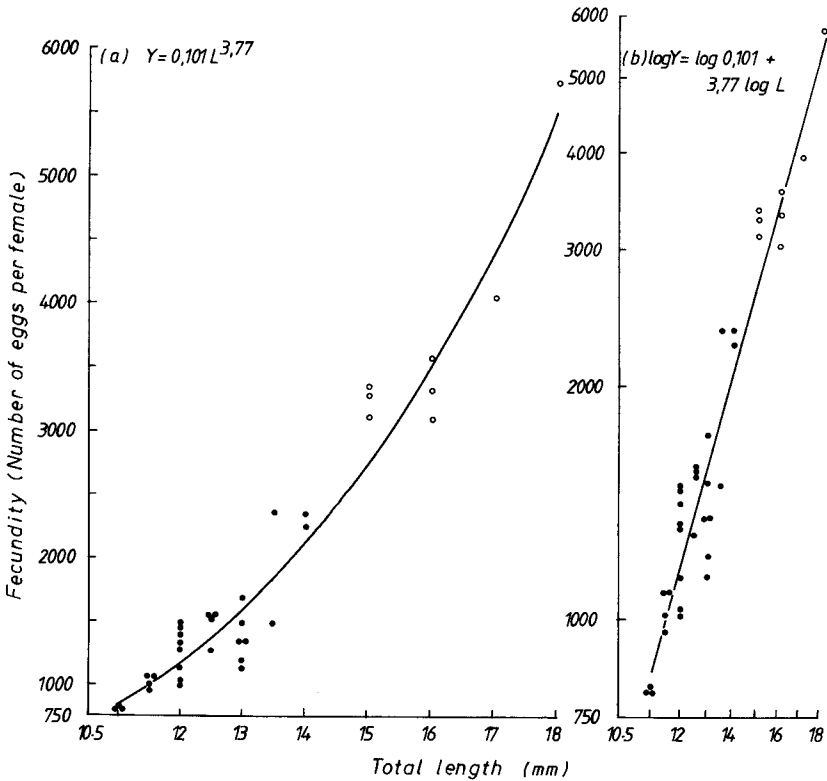


Fig. 2: Relationship between fecundity (number of eggs per female) and total length (mm) of *Ecdyonurus venosus* from Seebach, using data from a summer generation (●) and a winter generation (○): (a) On arithmetic scale with curvilinear regression line ( $Y = 0.101 L^{3.77}$ ); (b) On log/log scale with 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° 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 distribution of these species. Furthermore these species are probably most vulnerable to elimination or enhancement because of climatic change or anthropogenic 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 thermophilic 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 ( $T^{\circ}\text{C}$ ) 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  $5^{\circ}\text{C}$  and  $15^{\circ}\text{C}$  ( $T^{\circ}\text{C}$  in parenthesis indicates that no hatching occurred at this temperature; an asterisk indicates that eggs were fertilized artificially).

	Locality (Country)	$T^{\circ}\text{C}$	Max. % hatched	Equation	Tested in field	Days for 50% hatch		Reference
						at $5^{\circ}\text{C}$	at $15^{\circ}\text{C}$	
<b>Ephemeroptera</b>								
<i>B. rhodani</i>	Breitenbach (FRG)	(0.0) 6.8–20.0	c. 96	not known	no	–	–	1
	Wilfin Beck (GB)	3.0–22.0	99	power-law	yes	65	15	2
	Lissuraga (F)	7.5–25.0 (27.5)	99	power-law	no	65	15	3
<i>B. vernus</i>	Breitenbach (FRG)	(0.0) 6.8–20.0 (24.0)	> 94	not known (diapause)	no	–	–	1
<i>R. cf. hybrida</i>	Seebach (A)	4.5–20.1	33 <sup>*</sup>	power-law	yes	104	25	4
<i>R. loyolaea</i>	Herrnalmbach (A)	1.9–10.2 (20.6)	33 <sup>*</sup>	power-law, hyperbola	no	202	–	4
<i>R. semicolorata</i>	Wilfin Beck (GB) River Lune (GB)	} (4.5) 5.8–19.9	28	power-law	yes	154	19	4
<i>E. dispar</i>	Windermere (GB) Ennerdale (GB)				yes	180	25	5
	River Lune (GB)	3.9–20.3		not known	no	–	–	5
<i>E. insignis</i>	River Eden (GB)	(3.9) 8.7–19.9	13 <sup>*</sup>	power-law	no	–	20	5
<i>E. picteti</i>	Herrnalmbach (A)	3.5–17.3 (20.6)	13 <sup>*</sup>	power-law	no	155	–	5
	Seebach (A)	3.5–20.4	30 <sup>*</sup>	power-law	yes	115	23	5
<i>E. torrentis</i>	River Lune (GB)	3.9–19.5	29 <sup>*</sup>	power-law	no	138	19	5
<i>E. venosus</i>	Seebach (A)	3.6–20.6	17 <sup>*</sup>	power-law	no	175	28	5
	River Brathay (GB)	3.9–19.9	48 <sup>*</sup>	power-law	no	166	21	5
<i>Eph. ignita</i>	Lahn (FRG)	(5.0) 7.2–16.0 (22.0)	> 90	not known (diapause)	yes	–	–	6
	Wilfin Beck (GB)	5.9–19.8	90	hyperbola	yes	603	96	7
<b>Plecoptera</b>								
<i>T. nebulosa</i>	Ø. Heimdalsvatn (N)	2.0–23.7	99	power-law	no	60	19	8
<i>N. picteti</i>	Pool at Finse (N)	4.0–20.0	not known	power-law	no	50	15	9
	Bellman Ground Beck (GB)	5.9–19.8	96	power-law	no	49	15	10
<i>C. atra</i>	Lomma (N)	} 4.0–24.0 (28.0)	99	power-law	no	42	15	11
	Ø. Heimdalsvatn (N) Bigasjavrit (N)				no	42	15	11
<b>Odonata</b>								
<i>C. puella</i>	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, HUMPECH & ELLIOTT 1980; 5, HUMPECH 1980; 6, BOHLE 1972; 7, ELLIOTT 1978; 8, BRITAIN 1977; 9, BRITAIN 1978; 10, ELLIOTT 1984; 11, BRITAIN, LILLEHAMMER & SALTVEIT 1984; 12, WARINGER & HUMPECH 1984.

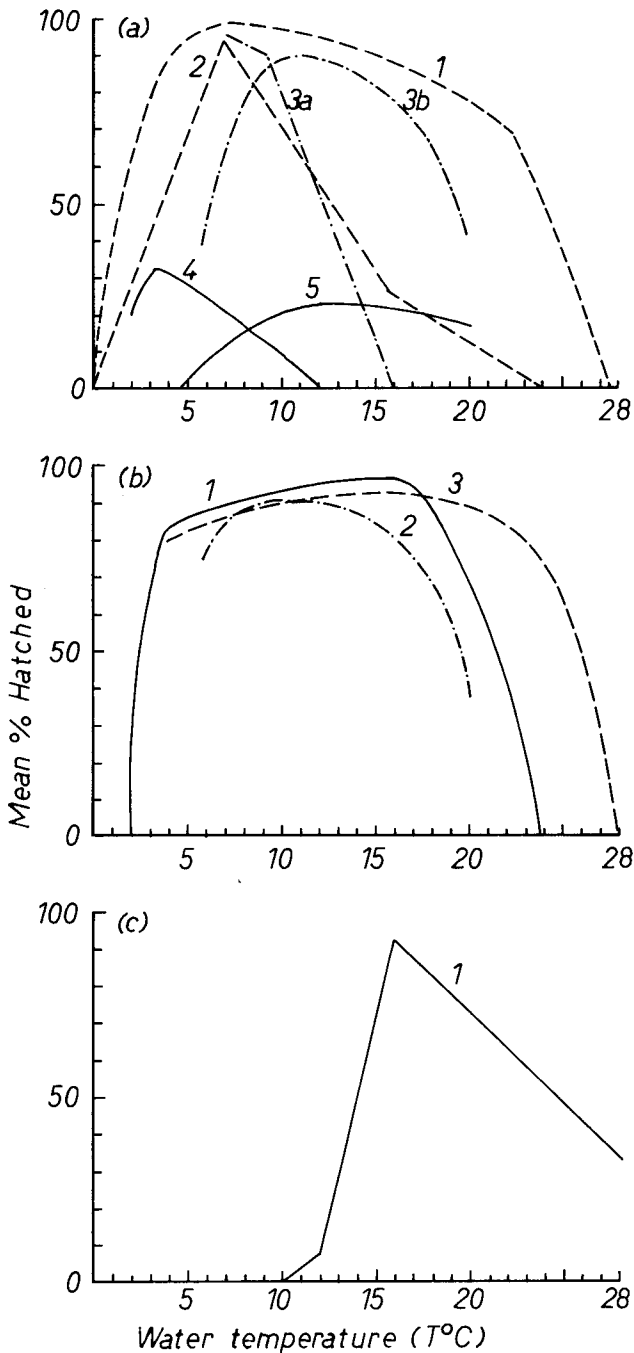


Fig. 3: Comparison of the percentages of eggs hatching at each temperature for European species of (a) Ephemeroptera: (1) *Baetis rhodani* (combined data: BOHLE, 1969; ELLIOTT, 1972; BENECH, 1972); (2) *B. vernus* (BOHLE, 1969); (3) *Ephemerella ignita* [(a) BOHLE, 1972; (b) ELLIOTT, 1978]; (4) *Rhytrogena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

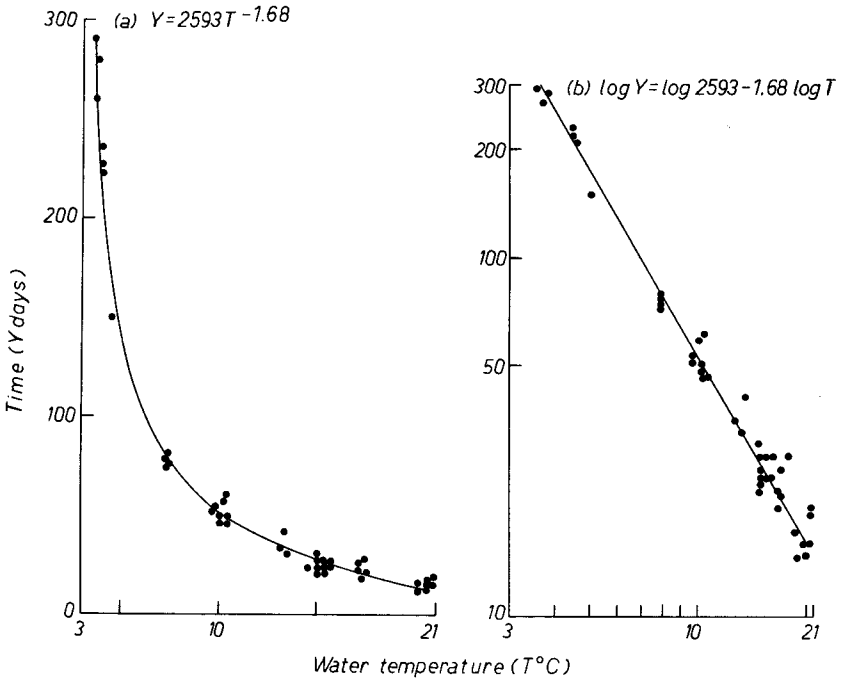


Fig. 4: Relationship between the time required (Y days) for 50% of the eggs of *Ecdyonurus venosus* from Seebach to hatch and water temperature ( $T^{\circ}\text{C}$ ) in the laboratory: (a) On arithmetic scale with curvilinear regression line ( $Y = 2593 T^{-1.68}$ ); (b) On log/log scale with linear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

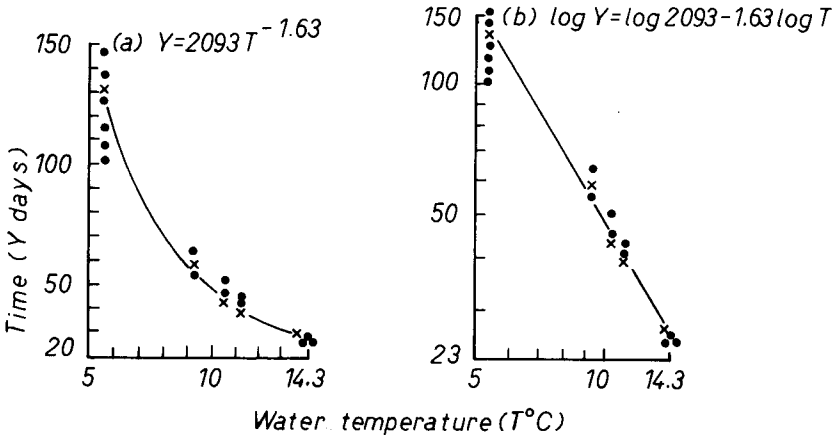


Fig. 5: Relationship between time required (Y days) for 10% of the eggs of *Ecdyonurus venosus* from Seebach to hatch and the arithmetic mean of fluctuating water temperature (T°C) in the laboratory: (a) On arithmetic scale with curvilinear regression line ( $Y = 2093 T^{-1.63}$ ); (b) On log/log scale with linear regression line ( $\log Y = \log 2093 - 1.63 \log T$ ). Crosses: Hatching time for eggs at constant temperatures. (From HUMPECH, 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  $T > 5^{\circ}\text{C}$  (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  $5^{\circ}\text{C}$  and  $15^{\circ}\text{C}$ .

	Locality	Equation	%	Days for % of eggs hatched		Reference
				at $5^{\circ}\text{C}$	at $15^{\circ}\text{C}$	
Ephemeroptera						
<i>Baetis rhodani</i>	Wilfin Beck	power-law	99	15	4	1
<i>Rhithrogena</i> cf. <i>hybrida</i>	Seebach	none	80	8	5	2
<i>R. loyolaea</i>	Herrnalmbach	none	80	31	–	2
<i>R. semicolorata</i>	Wilfin Beck, River Lune	power-law	80	8	5	2
<i>Ecdyonurus dispar</i>	Windermere, Ennerdale	power-law	80	27	2	3
<i>E. insignis</i>	River Eden	power-law	80	–	3	3
<i>E. picteti</i>	Herrnalmbach	power-law	80	24	3	3
	Seebach	power-law	80	8	2	3
<i>E. torrentis</i>	River Lune	power-law	80	26	2	3
<i>E. venosus</i>	Seebach, River Brathay	power-law	80	27	2	3
<i>Ephemerella ignita</i>	Wilfin Beck	power-law	80	25	4	3
Plecoptera						
<i>Nemurella picteti</i>	Bellman Ground Beck	power-law	80	35	19	4
Odonata						
<i>Coenagrion puella</i>	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 (BRITAIN, 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 life-history variable at the population level rather than as a characteristic of a species.

### Acknowledgements

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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 nicht-diapausierenden 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 Fekundität 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 mehrerer 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 Temperatureinfluß auf Fekundität, Schlüpferfolg und Dauer der Embryonalentwicklung machen deutlich, daß der „Voltinismus“ als Lebensgeschichten-Parameter auf dem Populations- und nicht auf dem Artniveau gesehen werden sollte.

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