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The relationship of egg size and incubation temperature to embryonic development time in univoltine and multivoltine aquatic insects

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SUMMARY

1. We used published data to investigate the combined influence of egg size and incubation temperature on embryonic development time for a broad assortment of aquatic insects at four different incubation temperatures (10, 15, 20 and 25 °C).
2. Embryonic development time (EDT) was positively correlated with egg size at each of the four temperatures, but with different relationships for univoltine and multivoltine aquatic insects. The relationships of embryonic development time to egg size expressed in degree-days did not significantly differ in slope ($P > 0.50$) or intercept ($P > 0.05$) for either univoltine or multivoltine aquatic insects at each of the four temperatures.
3. The relationship of embryonic development time (degree-days) to egg mass in multivoltine aquatic insects ($\mathrm{EDT} = 885 \times {}^{0.19}$, $P < 0.0001$, $r^2 = 0.48$) is similar in slope and intercept to that for other oviparous animals (i.e., zooplankton, fish, amphibians and reptiles), and to the relationship of embryonic development time to neonate mass in mammals. Univoltine species on average require 3–5 times longer to develop ($\mathrm{EDT} = 14190 \times {}^{0.29}$, $P < 0.001$, $r^2 = 0.29$) than most other animals of equivalent egg mass, but the relationship of embryonic development time to egg mass is similar in slope to that of most other animals. Together, these relationships provide a basis for evaluating differences in embryonic development time among aquatic insects.

Keywords: degree-days, hatch, multivoltine, thermal requirements, univoltine

Introduction

Understanding variability in embryonic development time among aquatic insects remains a central problem in freshwater biology because of the importance of this life history process to insect ecology, particularly relating to interspecific relationships. Factors known to influence embryonic development time in aquatic insects include photoperiod, geographic location and, especially, incubation temperature (Howe, 1967; Sweeney, 1984; Jackson & Sweeney, 1995; Pritchard, Harder & Mutch, 1996). The time required for development is often expressed in degree-days, yet it remains unclear how the cumulative thermal requirements for embryonic development change with temperature. The cumulative thermal requirements for embryonic development are thought to increase, decrease or remain constant over a range of temperatures, depending on the species (Pritchard *et al.*, 1996).

Insights regarding the variability in thermal requirements across temperatures for embryonic development time in aquatic insects may be gained from a recent study of embryonic development time in other aquatic ectotherms. Gillooly and Dodson (2000) have shown that the cumulative thermal requirements for embryonic development are nearly equivalent across a broad range of temperatures (5–15 °C) for fish,

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amphibians and zooplankton, and that considerable variability in embryonic development time among species is explained by differences in egg size. To date, no such broad scale analysis of embryonic development time in aquatic insects has defined the thermal requirements for development across a range of temperatures, nor revealed the influence of egg size on embryonic development time at even a single incubation temperature.

In this study, we evaluate the relationship of egg size to embryonic development time for aquatic insects across a range of incubation temperatures. First, we investigate the relationship of embryonic development time to egg size for a diverse assortment of aquatic insects incubated at four different temperatures (10, 15, 20, 25 °C). As egg development is often thought to be delayed in species with relatively long, seasonal life cycles (Clifford, 1982), we explore this relationship independently for univoltine and multivoltine species to evaluate possible differences between these two groups. Next, we assess the relationship of embryonic development time to egg size as a function of degree-days across this range of temperatures for both univoltine and multivoltine species. We conclude by comparing the relationship of embryonic development time to egg size and incubation temperature in aquatic insects with the relationship in other taxonomic groups including fish, amphibians and zooplankton.

Methods

Data used in the analyses of embryonic development time were collected from published studies of 34 aquatic insect species that span a broad range of taxonomic orders, climate zones, egg sizes and incubation temperatures (Coleoptera: one species; Diptera: two families, seven species; Ephemeroptera: three families, three species; Heteroptera: two families, two species; Odonata: two families, six species; Plecoptera: eight families, 13 species; Trichoptera: two families, two species) (Appendix 1). An attempt was made to include data for as many species as possible from all major orders.

Differences in the number of species included reflect the availability of embryonic development time data and/or egg size data for each order. Embryonic development time was defined as the mean time to hatch in studies of individual eggs, or as the mean time to 50% hatch in studies where embryonic development time was determined for masses of eggs.

The relationship of egg volume and incubation temperature to embryonic development time was evaluated for eggs ranging in volume from the egg of the ephemeropteran, *Baetis rhodani* (1.0×10^{-3} mm^3) to the egg of the belostomatid, *Abedus indentatus* (5.0 mm^3). Embryonic development time (days) across this size range was assessed for aquatic insect eggs incubated at one or more of four constant temperatures (10, 15, 20 and 25 °C) (Table 1). Temperatures outside of this range were not considered because data for five or more species of univoltine and multivoltine species were not available. In some instances, embryonic development times of individual species were interpolated at one or more of these four temperatures from fitted lines of the relationship of embryonic development time to incubation temperature. We also expressed embryonic development times in terms of degree-days for comparison to other taxonomic groups.

Species were categorized as having a univoltine (one generation per year) or multivoltine (> 1 generation per year) life cycle based on species descriptions in studies of embryonic development time when available, or from synthesis articles and books (Needham, Traver & Hsu, 1935; Merritt & Cummins, 1984; Elliott, 1988; Lillehammer *et al*., 1989; Jackson & Sweeney, 1995; Pritchard *et al*., 1996). Species described as univoltine were also occasionally described as semivoltine (one generation per 2 years) in studies at different geographical locations. The univoltine species considered here generally occur in temperate or subarctic climate zones and display synchronous, seasonal reproduction (exception: *Euthyplocia hecuba*, a univoltine tropical mayfly) as is typical of univoltine species (Clifford, 1982). The univoltine species in this study include species from the orders Ephemeroptera, Odonata, Plecoptera and Trichoptera. Conversely, the multivoltine species considered here generally occur in subtropical or tropical regions and display aseasonal, asynchronous reproduction, as is typical of multivoltine species (Clifford, 1982) (exception: *Aedes sticticus*). While the holarctic Dipteran *Aedes sticticus* has been described as univoltine (Trpis, Haufe & Shemanchuk, 1973), we place it in the multivoltine category because embryonic development is aseasonal and proceeds without delay in water (egg diapause occurs when eggs are dry).

Multivoltine species considered here include species from the orders Coleoptera, Diptera and Heteroptera.

Egg sizes were generally obtained from studies different than those from which embryonic development time data were obtained because egg sizes were rarely recorded in studies of embryonic development time (Appendix 1). Egg volumes were calculated from egg dimensions for spherical and ellipsoidal eggs using appropriate volume equations. To allow comparisons with a range of other taxonomic groups, egg volumes were converted to egg mass assuming a density of 1.0 g mL^{-1}. Data relating embryonic development time to egg size in aquatic insects were analyzed using least squares linear regression on double log-transformed data. Differences in the slopes and intercepts of regression lines were evaluated using analysis of covariance (Zar, 1996).

Results

Embryonic development time increased exponentially with egg size at each of the four temperatures (10, 15, 20 and 25 °C), but with different relationships for univoltine and multivoltine aquatic insects. (Figs 1a–

Table 1 Egg sizes and embryonic development times at four different incubation temperatures for 34 species of aquatic insects. Each species' life cycle categorization is shown after the species' name as U (univoltine) or M (multivoltine). Data sources are listed in Appendix 1. Asteriks indicate temperatures at which development time was not available for a species

				Incubation temperature (°C)			
Order	Family	Species	Egg volume (mm^3 × 10^3)	10	15	20	25
Coleoptera	Dytiscidae	*Dytiscus alaskanus* M	2925.26	22.6	12.5	8.6	6.1
Diptera	Chironomidae	*Chironomus decorus* M	1.44	6.5	3.5	2.0	1.6
Diptera	Chironomidae	*Chironomus plumosus* M	10.47	11.8	6.1	3.7	***
Diptera	Culicidae	*Aedes sticticus* M	20.12	25.3	11.5	8.0	6.3
Diptera	Culicidae	*Anopholes quadrimaculatus* M	10.74	20.5	8.0	3.8	1.9
Diptera	Culicidae	*Txoorhynchites brevipalpis* M	24.40	***	7.3	3.2	1.8
Diptera	Culicidae	*Aedes vexans* M	13.13	23.5	10.3	5.9	4.0
Diptera	Culicidae	*Aedes aegypti* M	10.04	***	***	7.2	4.0
Ephemeroptera	Baetidae	*Baetis rhodani* U	1.08	24.4	16.0	8.5	***
Ephemeroptera	Ephemeridae	*Hexagenia rigida* U	3.30	***	41.4	15.3	8.9
Ephemeroptera	Heptageniidae	*Ecdyonurus venosus* U	1.59	55.0	28.0	17.0	***
Heteroptera	Belostomatidae	*Abedus indentatus* M	5000.00	52.1	27.8	17.2	11.6
Heteroptera	Gerridae	*Gerris paludum insularis* M	70.52	***	31.7	17.8	7.2
Odonata	Libellulidae	*Diplacodes bipunctata* U	13.44	***	***	15.0	***
Odonata	Libellulidae	*Diplacodes haematodes* U	21.78	***	42.0	21.0	13.0
Odonata	Libellulidae	*Orthetrum caledonicum* U	24.87	***	33.0	18.0	9.5
Odonata	Coenagrionidae	*Enallagma vernale* U	23.03	***	54.8	29.3	***
Odonata	Coenagrionidae	*Enallagma ebrium* U	23.03	***	56.4	25.6	***
Odonata	Coenagrionidae	*Coenagrion puella* U	12.00	***	47.8	24.9	15.1
Plecoptera	Capniidae	*Capnia atra* U	2.81	23.0	15.0	12.0	***
Plecoptera	Capniidae	*Mesocapnia oenone* U	2.68	50.6	39.9	33.6	***
Plecoptera	Chloroperlidae	*Chloroperla tripunctata* U	9.34	87.9	73.0	63.9	***
Plecoptera	Leuctridae	*Leuctra hippopus* U	2.01	32.3	25.5	21.6	***
Plecoptera	Nemouridae	*Nemoura cinerea* U	10.30	30.0	22.0	17.0	***
Plecoptera	Nemouridae	*Protonemura meyeri* U	3.23	28.6	18.0	15.3	***
Plecoptera	Nemouridae	*Protonemura praecox* U	4.18	33.5	23.7	18.6	***
Plecoptera	Perlidae	*Dinocras cephalotes* U	28.26	124.6	66.7	42.7	***
Plecoptera	Perlidae	*Perla marginata* U	8.37	***	98.5	48.2	***
Plecoptera	Perlodidae	*Perlodes mortoni* U	31.52	***	91.0	***	***
Plecoptera	Polymitarcyidae	*Euthyplocia hecuba* U	38.52	***	112.6	54.8	31.2
Plecoptera	Taeniopterygidae	*Taeniopteryx nebulosa* U	4.38	29.2	19.3	15.0	***
Plecoptera	Taeniopterygidae	*Nephelopteryx nebulosa* U	2.12	***	20.0	***	***
Trichoptera	Limnephfidae	*Apatania fimbriata* U	8.20	23.6	16.9	13.4	***
Trichoptera	Polycentropodidae	*Plectrocnemia conspersa* U	16.40	56.0	21.2	***	***

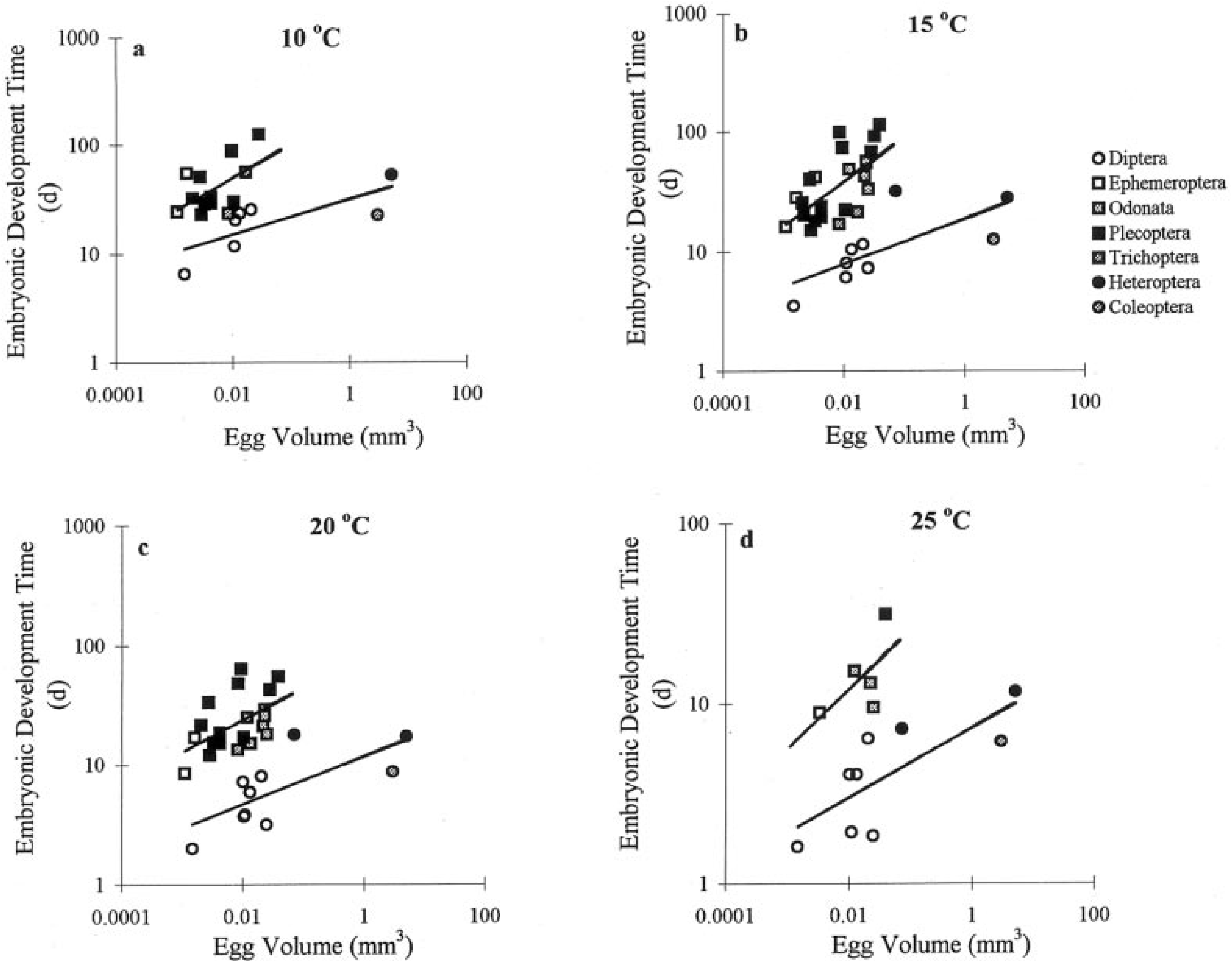

Fig. 1 a–d. The log–log relationship of embryonic development time (d) to egg volume (mm^3) for univoltine (square symbols) and multivoltine (circular symbols) aquatic insects incubated at 10 °C (a), 15 °C (b), 20 °C (c) and 25 °C (d). Lines are fit using least squares linear regression. Equations and statistics for the lines are presented in Table 2. Data sources are listed in Appendix 1.

d). For univoltine species, embryonic development time was significantly correlated with egg volume at 10, 15 and 20 °C (Table 2). For multivoltine species, embryonic development time was significantly correlated with egg volume at all four temperatures (Table 2). While limited data generally prohibited statistical analyses of these relationships within individual orders, the same trend may be observed among the two orders having the most data among univoltine or multivoltine species, namely Diptera and Plecoptera.

The relationship of embryonic development time to egg size differed for univoltine and multivoltine species both in the length of time required for development and in the variability about these relationships (Figs 2a–b). The embryos of univoltine species required 3–5 times longer to develop than multivoltine species, with the greatest differences occurring at intermediate temperatures. For example, the embryonic development time of a univoltine species with an egg of volume 0.01 mm^3 would be 3.8 times longer at 10 °C, 4.6 times longer at 15 °C and 20 °C, and 4.3 times longer at 25 °C than a multivoltine species. The amount of variability (r^2) explained by the equations describing the relationship at each temperature ranged from 27–41% for univoltine species, and 52–58% for multivoltine species.

When embryonic development time at each temperature (10, 15, 20 and 25 °C) was redefined in terms of degree-days (dd), the relationship of embryonic development time to egg volume did not significantly

Table 2 Relationships of embryonic development time (EDT) to egg volume ($\times$; mm^3) for univoltine and multivoltine aquatic insects cultured at four different constant temperatures. Development time is expressed in units of days for single temperatures, and in degree-days for data combined across all four temperatures. Data sources are listed in Appendix 1

Life cycle	Water temp (°C)	EDT (days =)	P	n	r^2
Univoltine	10.0	$221\times^{0.32}$	0.03	14	0.33
Multivoltine	10.0	$32\times^{0.16}$	0.047	6	0.58
Univoltine	15.0	$209\times^{0.37}$	0.0008	24	0.41
Multivoltine	15.0	$19\times^{0.19}$	0.027	8	0.52
Univoltine	20.0	$78\times^{0.26}$	0.014	22	0.27
Multivoltine	20.0	$12\times^{0.20}$	0.018	9	0.52
Univoltine	25.0	$55\times^{0.33}$	0.26	5	0.39
Multivoltine	25.0	$7\times^{0.19}$	0.018	8	0.57
Univoltine-all	10.0–25.0	$1892\times^{0.29}$	<0.0001	65	0.29
Multivoltine-all	10.0–25.0	$244\times^{0.19}$	<0.0001	35	0.48

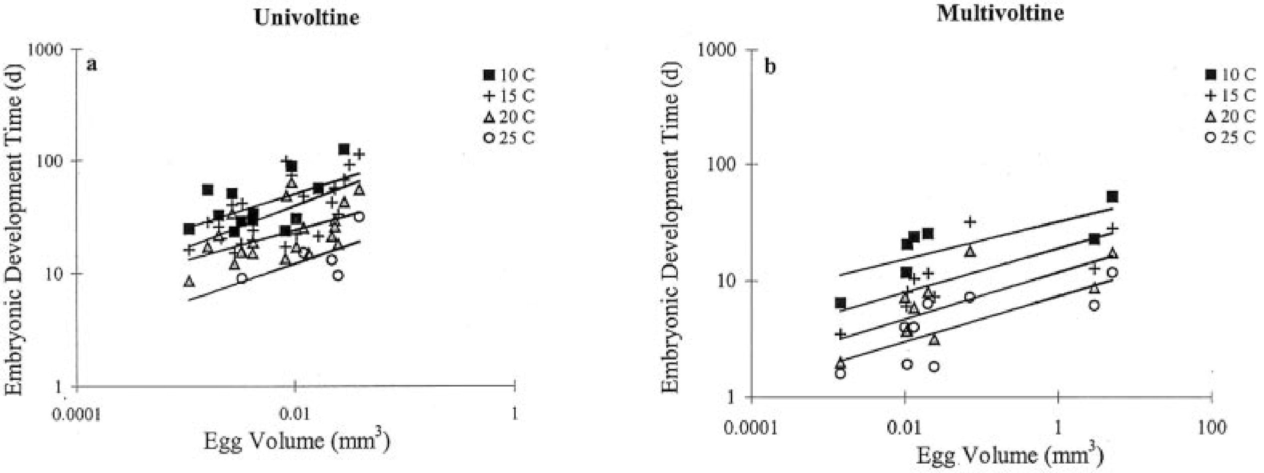

Fig. 2 a–b. The log–log relationships of embryonic development time (d) to egg volume (mm^3) redrawn from Figs 1a–d for univoltine and multivoltine aquatic insects incubated at each of four different temperatures (10, 15, 20 and 25 °C). Lines are fit using least squares linear regression. Equations and statistics for the lines are presented in Table 2. Data sources are listed in Appendix 1.

differ in slope ($P > 0.50$) or in intercept ($P > 0.05$) for either univoltine or multivoltine species at each of the four temperatures. Thus, the relationship of embryonic development time (dd) to egg volume for each group could be estimated with a single equation across this temperature range (10–25 °C) (Table 2).

Discussion

Embryonic development time increases exponentially with egg size across a range of temperatures in aquatic insects. Recent studies comparing embryonic development within particular orders of aquatic insects emphasize differences among species, with little or no mention of the influence of egg size on development time (e.g., Odonata: Pilon & Masseau 1984; Plecoptera: Lillehammer *et al.*, 1989; Pritchard *et al.* 1996). Yet, the influence of egg size on embryonic development time is significant at all temperatures. The difference in embryonic development time (d) between species of different egg sizes is greater at colder temperatures because the relationship of embryonic development time to egg size is expressed on a log–log scale (Figs 1a–b). For example, the difference in development time between the relatively small egg of *Chironomus decorus* and the relatively large egg of *Abedus indentatus* is 46 days at 10 °C, whereas at 25 °C the difference in only 10 days. The increase in development time with egg size may simply reflect the additional time needed to grow larger, rather than differences in mass-specific growth rate, as egg size is positively related to neonate size in most taxonomic groups (Gillooly & Dodson, 2000), including aquatic insects (Plecopterans: Lillehammer *et al*., 1989).

Variation observed in the relationships of embryonic development time to egg size for univoltine and multivoltine aquatic insects is partially explained by the methods we used, and by the relative effects of other environmental influences on embryonic development time in each of the studies (e.g., photoperiod). The necessary use of egg sizes that do not necessarily correspond to those used in the studies of embryonic development time may increase variation as egg size may vary within species (Lillehammer *et al*., 1989). Differences in the quality of data among these published data may also affect the strength of the relationships presented here.

The increase in embryonic development time imposed by larger egg size may help explain interspecific differences in the behaviour or ecology of aquatic insects (e.g., timing of oviposition or emergence). The thermal equilibrium hypotheses proposed by Sweeney and Vannote (1978) suggests that temperature effects on the life history tradeoff between size and fecundity may help explain the dispersal and distribution of aquatic insects, including those from long-term climatic changes. The results presented here further suggest that the longer development time imposed by larger egg size should be included when considering life history tradeoffs with respect to egg production. Differences in embryonic development time among species in the same environment may affect the extent to which each species may exploit that environment.

The relationships of embryonic development time to egg size differed among insects with different life cycles; univoltine species required substantially more time to develop than multivoltine species. The additional time required for hatching among univoltine species may be explained by a period of quiescence or diapause at the egg stage. Egg diapause has been widely recognized among ephemeropterans, plecopterans, trichopterans, but less so among odonates (Merritt & Cummins, 1984; Lillehammer *et al*. 1989; Pritchard *et al*. 1996). Diapause is thought to be adaptive in species as a means by which to synchronize development with favorable weather conditions in seasonal environments (Clifford, 1982; Sweeney, Jackson & Funk, 1995). However, the extent to which diapause occurs in any one order of aquatic insects is not clear as diapause is often difficult to detect and measure in individual species. Generally, diapause is not considered to be restricted to a particular life cycle (i.e., univoltine; Hilsenhoff, pers. comm.). The difference in development time between univoltine and multivoltine species shown here may be an indication of the extent and duration of diapause in univoltine species. However, our analyses are confounded by differences in the taxonomic orders included in the univoltine and multivoltine groups. The availability of data restricted our consideration of univoltine species to ephemeropterans, trichopterans, plecopterans and odonates, whereas multivoltine species consisted of dipterans, heteropterans and coleopterans. As such, we can not exclude the possibility that that the difference in embryonic development time between these two groups is explained by something other than the difference in voltinism.

The relationship of embryonic development time to egg size among aquatic insects transcends many obvious species-specific differences (e.g., complete or incomplete metamorphosis). The slopes of the lines relating embryonic development time to egg size for univoltine (0.26–0.37) and multivoltine species (0.16–0.20) at all four temperatures are also similar to those for zooplankton (0.25–0.30), fish and amphibians (0.27–0.34), reptiles (0.15–0.18) and even to neonate size in mammals (0.28) (Fig. 3) (Gillooly & Dodson, 2000). The relationships of embryonic development time to egg size in aquatic insects also vary across a range of temperatures in much the same way as those for zooplankton, fish and amphibians. The relationship of embryonic development time (dd) to egg size did not differ significantly in aquatic insects from 10–25 °C, while this same relationship did not differ significantly from 5–15 °C among fish and amphibians, or zooplankton (Gillooly & Dodson, 2000). In both cases, the cumulative thermal requirements for embryonic development on average were equivalent across these temperature ranges. The similar nature of the relationship of egg size to embryonic development time across temperatures in aquatic insects to those of other taxonomic groups may indicate the

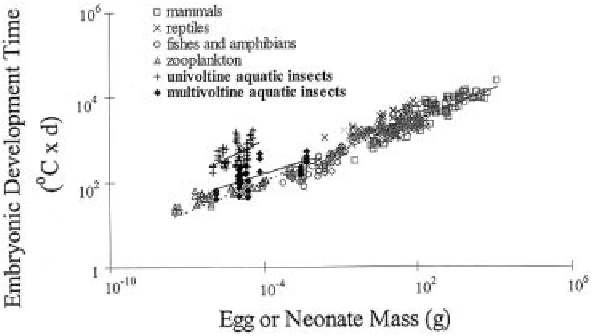

Fig. 3 The log–log relationship of embryonic development time to egg mass (or neonate mass in the case of mammals) for univoltine aquatic insects ($\mathrm{EDT} = 14190 \times {}^{0.29}$, $n = 64$, $P < 0.001$, $r^2 = 0.29$), multivoltine aquatic insects ($\mathrm{EDT} = 885 \times {}^{0.19}$, $n = 35$, $P < 0.0001$, $r^2 = 0.48$), and for zooplankton, fish, amphibians, reptiles and mammals (perforated line, $\mathrm{EDT} = 1030 \times {}^{0.24}$). The relationship for zooplankton, fish, amphibians, reptiles and mammals is reproduced with permission from Gillooly and Dodson (2000). Lines are fit using least squares linear regression. Data sources for aquatic insects are listed in Appendix 1.

factors controlling the rate of embryonic development in aquatic insects are the same as in other taxonomic groups. The relationship of embryonic development time to egg size for multivoltine species was nearly indistinguishable from the general relationship of Gillooly and Dodson (2000) that includes several other taxonomic groups (Fig. 3), but the relationship for univoltine insects is different from most other animals. Simply stated, a multivoltine aquatic insect egg requires about the same number of degree-days to hatch as a zooplankton, fish, amphibian, reptile or mammal species of similar egg or neonate (for mammals) size. However, the relationship for univoltine insects fell well above the lines of other taxonomic groups, highlighting the exceptional nature of this group among animals. Embryos of univoltine insects require 3–5 times longer to develop than other animals of similar egg size.

Finally, the relationships of embryonic development time (dd) to egg size in univoltine and multivoltine aquatic insects provide simple expressions for the combined effects of egg size and incubation temperature across a range of temperatures (10–25 °C). These relationships may be useful as tools for estimating embryonic development time in natural systems with variable temperature regimes. These relationships may also provide a basis for examining differences in embryonic development time among species of aquatic insects. Understanding the combined influence of egg size and incubation temperature will help in discerning the relative influence of other environmental influences on individual species.

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Appendix 1: Data references for Table 1

Species	Egg size	Embryo development time
Dytiscus alaskanus (Balfour-Browne)	Aiken (1986)	Aiken (1986)
Chironomus decorus (Johannnsen)	Maier *et al*. (1990)	Maier *et al*. (1990)
Chironomus plumosus (L.)	Merritt and Cummins (1984)	Hilsenhoff (1966)
Aedes sticticus (Meigen)	Trpis *et al*. (1973)	Trpis *et al*. (1973)
Anopholes quadrimaculatus (Say)	Reinert *et al*. (1997)	Huffaker (1944)
Txoorhynchites brevipalpis (Theobold)	Trpis (1972)	Trpis (1972)
Aedes vexans (L.)	Horsfall *et al*. (1973)	Horsfall *et al*. (1973)
Aedes aegypti (L.)	Christophers (1960)	Christophers (1960)
Baetis rhodani (Pictet)	Percival and Whitehead (1925)	Elliott (1972)
Hexagenia rigida (McDunnough)	Needham *et al*. (1935)	Friesen *et al*. (1979)
Ecdyonurus venosus (Fabr.)	Enders and Wagner (1996)	Humpesch (1980)
Abedus indentatus (Haldeman)	Kraus *et al*. (1989)	Kraus *et al*. (1989)
Gerris paludum insularis (Motschulsky)	Mori (1969)	Park (1988)
Diplacodes bipunctata (Brauer)	Rowe (1992)	Rowe (1992)
Diplacodes haematodes (Burm.)	Trueman (1991)	Hawking and New (1995)
Orthetrum caledonicum (Brauer)	Trueman (1991)	Hawking and New (1995)
Enallagma vernale (Gloyd)	Pilon (1982)	Pilon (1982)
Enallagma ebrium (Hagen)	Pilon (1982)	Pilon (1982)
Coenagrion puella (L.)	Banks and Thompson (1987)	Waringer and Humpesch (1984)
Capnia atra (Morton)	Brittain *et al*. (1984)	Brittain *et al*. (1984)
Mesocapnia oenone (Neave)	Brittain and Mutch (1984)	Brittain and Mutch (1984)
Chloroperla tripunctata (Scopoli)	Hynes (1941)	Elliott (1988)
Leuctra hippopus (Kempny)	Percival and Whitehead (1925)	Elliott (1987)
Nemoura cinerea (Retzius)	Lillehammer *et al*. (1991)	Brittain and Lillehammer (1987)
Protonemura meyeri (Pictet)	Strange (1985)	Strange (1985)
Protonemura praecox (Morton)	Degrange (1960)	Elliott (1988)
Dinocras cephalotes (Curtis)	Rosciszewska (1991)	Frutiger (1996)
Perla marginata (Panzer)	Rosciszewska (1991)	Frutiger (1996)
Perlodes mortoni (Klp.)	Percival and Whitehead (1925)	Percival and Whitehead (1925)
Euthyplocia hecuba (Hagen)	Sweeney *et al*. (1995)	Sweeney *et al*. (1995)
Taeniopteryx nebulosa (L.)	Brittain (1977)	Elliott (1988)
Nephelopteryx nebulosa (L.)	Percival and Whitehead (1925)	Percival and Whitehead (1925)
Apatania fimbriata (Pictet)	Enders and Wagner (1996)	Enders and Wagner (1996)
Plectrocnemia conspersa (Curtis)	Hildrew and Wagner (1992)	Hildrew and Wagner (1992)