Size Variation and the Distribution of Hemimetabolous Aquatic Insects: Two Thermal Equilibrium Hypotheses

Abstract. *Adult body size and fecundity of a number of hemimetabolous aquatic insects depend largely on thermal conditions during the larval period. Small adults and reduced fecundity result when temperatures are either warmed or cooled with respect to more optimal thermal conditions. Temperature apparently affects adult size by altering the larval growth rate and the timing and rate of adult tissue development for each larva. The data suggest a new interpretation for the geographic distribution of aquatic insects.*

Recent studies of natural and experimental populations of hemimetabolous stream insects indicate that intraspecific variation in adult size and fecundity reflects mainly seasonal and geographical differences in stream temperatures during larval growth (*1, 2*). Our data suggest that (i) for each species, an "optimum" temperature regime for larval growth can be defined as one that permits an insect to achieve maximum adult weight and fecundity, and (ii) modifying the optimum pattern of temperatures by rearing insects in warmer or cooler environments affects the bioenergetic and developmental aspects of larval growth and results in lower individual adult weight and fecundity. These results are used to formulate two hypotheses concerning the importance of temperature to both size variation (*3*) and the geographical distribution of hemimetabolous aquatic insects in temperate regions.

Laboratory studies (*4*) designed to evaluate thermal effects revealed that "summer species" (*5*) reared at cool temperatures (Table 1) and "winter-spring species" (*6*) reared at warm temperatures (Table 2) produced small adults with fewer eggs relative to control animals growing at ambient White Clay Creek (WCC) (*7*) temperatures. These data also show that WCC temperatures produced the largest and most fecund adults for species whose distribution places the creek at or near the latitudinal center of their geographic range (*8*). *Centroptilum rufostrigatum* McDunnough, a more northern species, and *Ephemerella funeralis* McDunnough, which is distributed southward to Georgia, were the only test species not achieving maximum size in WCC temperatures. For most species, the correlation between adult size and larval growth rate predicted by existing ecological models for metamorphosis of other aquatic organisms was not seen (*9*). For example, in *C. rufostrigatum*, both the highest and lowest growth rates resulted in small adults (Fig. 1A).

The reduced adult size of summer species reared under cool regimes (Table 1) suggests that maximum size of aquatic insects is not necessarily associated with the coldest environments. We further tested this hypothesis by transferring larvae of three winter-spring species [*Isonychia bicolor* (Walker), *Ephemerella subvaria* McDunnough, *Leptophlebia cupida* (Say)] to low temperatures as White Clay Creek began warming in the spring. These transfer experiments also

Table 1. Mean adult dry weight (± standard error) and fecundity for several summer species of hemimetabolous aquatic insects reared under one natural (WCC) and five experimental temperature regimes. Three temperatures (maximum, average, minimum) describe each thermal regime for a given species. Maximum and minimum values represent an average of the three highest and three lowest temperatures, respectively, observed on thermograph records of each experiment; average values were calculated from hourly readings taken from continuous temperature tracings. Missing data indicate thermal regimes under which larvae did not successfully metamorphose. Each species was tested for differences in mean body weight among treatments (thermal regimes); results were significant for all species (Student-Newman-Keuls test, $P < .05$). The number of eggs per average-sized female was estimated by regression equations describing fecundity as a function of female dry weight for each mayfly species (*16*).

*Centroptilum rufostrigatum**			*Tricorythodes atratus**			*Isonychia bicolor**			*Caenis simulans**		*Sigara alternata*†	
Temperature (°C)	Weight (mg)	Eggs per female (No.)	Temperature (°C)	Weight (mg)	Eggs per female (No.)	Temperature (°C)	Weight (mg)	Eggs per female (No.)	Temperature (°C)	Weight (mg)	Temperature (°C)	Weight (mg)
						Thermal regime 1						
13.4			12.3			12.6			12.3		12.6	
13.0	0.91 ± 0.08	289	12.0	1.42 ± 0.07	333	12.3			12.0		12.4	0.80 ± 0.03
12.8			11.9			12.0			11.9		12.2	
						Thermal regime 2						
15.5			14.3			14.7			14.3		14.7	
14.2	1.31 ± 0.08	355	13.3	1.51 ± 0.25	348	13.1			13.3	0.28 ± 0.01	13.2	0.75 ± 0.02
13.1			12.1			12.1			12.1		12.3	
						Thermal regime 3						
18.0			16.6			16.9			16.6		16.9	
14.7	1.46 ± 0.06	380	14.2	1.59 ± 0.22	362	13.8	8.09 ± 0.38	713	14.2	0.90 ± 0.03	13.9	0.90 ± 0.03
13.3			12.1			12.4			12.1		12.5	
						Thermal regime 4						
19.7			17.6			18.5			17.6		18.0	
15.5	1.45 ± 0.14	378	14.5	1.69 ± 0.27	379	14.5	9.62 ± 0.54	885	14.5	0.43 ± 0.02	14.2	1.10 ± 0.03
13.5			12.2			12.6			12.2		12.6	
						Thermal regime 5						
21.2			19.6			20.1			19.6		19.7	
16.4	1.28 ± 0.18	350	14.9	1.71 ± 0.26	382	15.4	9.54 ± 0.56	876	14.9	0.47 ± 0.02	15.2	1.10 ± 0.06
13.7			12.5			12.9			12.5		12.8	
						Thermal regime WCC						
21.3			18.7			20.5			18.7		19.2	
18.5	0.66 ± 0.04	248	17.1	1.72 ± 0.25	384	18.5	9.43 ± 0.83	864	17.1	0.50 ± 0.04	16.8	1.08 ± 0.03
15.9			15.3			16.6			15.3		15.0	

*Order: Ephemeroptera (mayflies). †Order: Hemiptera (aquatic bugs).

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resulted in small adults with reduced fecundity for each species relative to animals reared at natural temperatures (1, 2, 10).

Studies of aquatic insects growing in White Clay Creek have also shown that average adult size and fecundity of most hemimetabolous species decrease linearly from the first to the last day of emergence (1, 2, 10). For example, the average weight and fecundity of *E. subvaria* and *Ephemerella dorothea* Needham females decrease about 40 and 60 percent, respectively, during their 3-week emergence periods in the spring. In mid-winter, we collected larvae of two winter-spring species (*I. bicolor* and *E. subvaria*), sorted the larvae of each species into four size categories, kept the larvae at ambient WCC temperatures, and measured growth, metabolism, emergence, and adult weight for each size category. For both species, the last adults to emerge in a given generation were the smallest larvae at the beginning of spring (2, 10). The warm temperatures of late spring apparently (i) increase the amount of assimilated energy needed for maintenance metabolism, thereby reducing the quantity available for growth and egg production, and (ii) limit the time available for larval growth by stimulating the development of adult tissues and causing metamorphosis to occur before a larva can attain maximum size.

Since adult size variation in stream insects may be a result of the effect of temperature on both the rate and duration of larval growth, the adult weight of polyvoltine species should vary considerably between generations growing at different seasons. Studies of two hemimetabolous mayfly species (*C. rufostrigatum* and *I. bicolor*) and three holometabolous caddisfly species [*Chimarra aterrima* Hagen, *Glossosoma nigrior* Banks, *Dolophilodes distinctus* (Walker)], all of which appear to be cool-adapted (11), indicate that, at White Clay Creek temperatures, adult weights are reduced 50 percent in the summer relative to other seasons. This phenomenon has been observed qualitatively for other species (12).

In White Clay Creek, the pattern of reduced adult size with increased stream temperatures is also observed when two or more congeneric species are compared. For example, the *Ephemerella* complex in the fourth-order tributary of White Clay Creek consists of five species with similar ecosystem function. Larvae of the largest species, *E. subvaria*, complete their growth and the adults emerge from the stream in early April (Fig. 1B). The adult size of congeners decreases progressively from early spring to late summer as each succeeding species grows in a slightly warmer environment (13). Seasonal changes in quality and quantity of food are probably not the critical factors causing the observed size variation of *Ephemerella* mayflies in WCC temperatures (14).

We reared *E. subvaria* in experimentally warm thermal regimes typical of late spring in White Clay Creek (Table 2) and observed early adult emergence at a body weight similar to the late spring species *E. dorothea* (Fig. 1B). Egg production of *E. subvaria*, however, was lower than *E. dorothea*, because *E. subvaria* eggs are large and egg size remains approximately constant despite large changes in adult size.

We use our data to develop two temperature-dependent hypotheses concerning size variation and the distribution of aquatic insects.

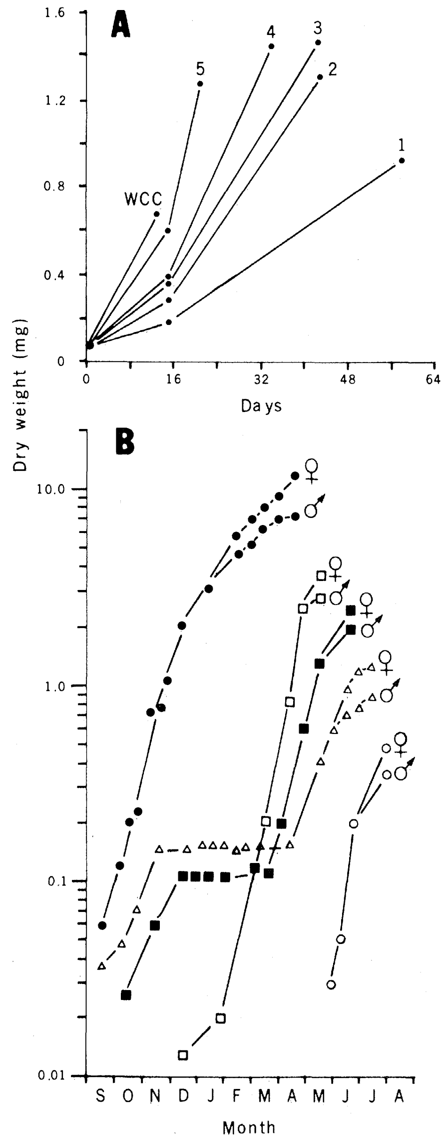
1) Maximum adult size reflects an equilibrium between several developmental processes that appear to be temperature-dependent. These processes include (i) the rate and duration of larval growth and (ii) the specific time in larval development that adult structures (15) begin maturing and the rate of this maturation process. In an optimum temperature regime, adult structures develop only after the larva has grown substantially, and adult development, once initiated, proceeds at a rate that allows time for larval growth (or energy storage) before metamorphosis. It appears that nonoptimum regimes (warmer or cooler) lead ultimately to a disequilibrium between larval growth rate and the timing of metamorphosis.

2) A species distribution both locally within drainage systems and over large geographic areas is limited, in part, by lowered fecundity as adult size gradually diminishes in streams of increasingly cold or warm temperature cycles. This hypothesis suggests that (i) austral and boreal subpopulations of a given species will have smaller, less fecund adults than more central subpopulations; (ii) gradients of size and fecundity will be observed for subpopulations within a drainage network because seasonal patterns

Table 2. Mean adult dry weight (± standard error) and fecundity for several winter-spring species of Ephemeroptera (mayflies) reared under four thermal regimes: WCC, ambient water temperatures of White Clay Creek; about 2°C warmer than White Clay Creek, following both diel and seasonal changes in temperatures; about 5°C warmer than White Clay Creek; and constant 15° ± 0.5°C. Differences in mean body weight among treatments were significant for all species (Student-Newman-Keuls test, $P < .05$). The number of eggs was estimated as in Table 1 (17).

Leptophlebia cupida			*Ameletus ludens*			*Ephemerella subvaria*			*Ephemerella funeralis*		
Temperature (°C)	Weight (mg)	Eggs per female (No.)	Temperature (°C)	Weight (mg)	Eggs per female (No.)	Temperature (°C)	Weight (mg)	Eggs per female (No.)	Temperature (°C)	Weight (mg)	Eggs per female (No.)
					Thermal regime WCC						
16.7			14.3			14.5			18.2		
6.5	9.21 ± 0.29	2054	5.8	3.85 ± 0.22	402	5.4	6.57 ± 0.50	533	7.8	3.52 ± 0.63	775
2.1			2.1			2.1			2.1		
					Thermal regime WCC + 2°C						
15.9			12.1			15.9			18.1		
8.5	9.26 ± 0.39	2065	7.5	3.51 ± 0.41	364	8.5	4.84 ± 0.26	430	9.7	3.53 ± 0.15	777
5.4			5.4			5.4			5.4		
					Thermal regime WCC + 5°C						
13.3			14.3			13.5			17.8		
10.2	7.55 ± 0.49	1072	10.6	3.31 ± 0.27	342	9.5	3.98 ± 0.28	375	11.7	3.92 ± 0.10	830
8.8			8.8			8.5			8.8		
					Thermal regime 15°C						
15.5			15.5			15.5			15.5		
15.0	6.16 ± 0.26	1407	15.0	2.24 ± 0.17	223	15.0	3.57 ± 0.29	355	15.0	4.42 ± 0.23	898
14.5			14.5			14.5			14.5		

Fig. 1. (A) Growth curves for female larvae (*18*) of the mayfly *Centroptilum rufostrigatum* reared at different temperatures. The last data point for each curve represents adult weights; all other points are for larvae. Numbers at the end of each curve correspond to thermal regimes (Table 1). Standard errors for adult weights are given in Table 1; those for larval weights can be found elsewhere (*2, 10*). (B) Growth curves for five *Ephemerella* mayfly species in a fourth-order tributary of White Clay Creek. Each data point represents the mean of at least 100 larvae: ●, *E. subvaria* McDunnough; □, *E. dorothea* Needham; ■, *E. verisimilis* McDunnough; △, *E. deficiens* Morgan; and ○, *E. serrata* Morgan.



of warming and cooling vary from small headwater streams to large rivers; (iii) few, if any, natural subpopulations will have average body size or egg counts approaching low experimental values obtained in the laboratory because a species will probably be displaced by another better-adapted species in streams at or near the geographic thermal boundaries; and (iv) in order to maintain competitive egg production, southern or northern extension of a species range may require movement of subpopulations into cooler (for example, low-order or high-altitude streams) or warmer tributaries (for example, high-order, or low-altitude streams) for a summer-growing species and conversely for species adapted for winter growth.

These observations may help in interpreting the significance of long-term climatic changes to the dispersal and distribution of aquatic insects. For example, we view glaciation in North America as a process that gradually eliminated boreal subpopulations of a given species (through competitive displacement of species with lowered fecundity) but increased the potential for dispersal southward by austral subpopulations. At any time during the Pleistocene, a species might appear to be in thermal equilibrium when in reality the various subpopulations throughout the range would be in a state of flux with respect to individual size and fecundity.

Our results may be critical to evaluating the affects of thermal pollution, since warming the seasonal cycles of a river by 2° to 3°C might eliminate species by affecting body size and fecundity. The loss of species would reduce community diversity unless replacement species, adapted to the new conditions, are available regionally. Monitoring adult size and fecundity of aquatic insects may prove useful in assessing the impact of sublethal alteration of natural temperature patterns.

Finally, a geographically uniform set of data on larval growth rate, adult size, and fecundity for several species of aquatic insects is needed to test and refine our hypotheses. These types of data would also contribute to the development of ecological models for insect growth as well as the ecological aspects of insect metamorphosis.

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References and Notes

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2. B. W. Sweeney, *Limnol. Oceanogr.*, in press.
3. Dry weight (60°C for 24 hours) is our principal measure of size.
4. Methods and materials for growth studies are described elsewh [B. W. Sweeney, *Limnol. Oceanogr.* **21**, 758 (1976)]. Food quality and quantity were similar for all experimental populations (*2*).
5. Summer species exhibit maximum population growth and resource exploitation from May to September.
6. Larvae of winter-spring species hatch from eggs in the fall but grow mainly during winter and spring. For each test species, larvae were collected from the natural stream in early winter; at least 40 larvae were placed in separate, flow-through plastic trays (45 by 24 by 20 cm) containing substrate. A subsample of larvae was taken from trays at the start of each experiment to estimate mean body weight. No further samples were taken from the trays. Nylon netting was placed tightly over each tray to capture emerging adults. Test animals were always <10 percent grown (relative to the average size of adults in the White Clay Creek population) when the experiments were initiated.
7. A fourth-order tributary of White Clay Creek (39°53′N, 75°47′W) in southeastern Pennsylvania. The abbreviation WCC is used to refer to the experimental temperature regime mimicking conditions in White Clay Creek. When the actual creek is being referred to, the name is spelled out.
8. G. F. Edmunds, S. L. Jensen, L. Berner, *The Mayflies of North and Central America* (Univ. of Minnesota Press, Minneapolis, 1977).
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12. F. P. Ide, *Univ. Toronto Stud. Fish. Res. Lab.* **59**, 1 (1940); V. Benech, *Ann. Hydrobiol.* **3**, 141 (1972); H. F. Clifford and J. Boerger, *Can. Entomol.* **106**, 111 (1974).
13. We have also observed a seasonal decrease in size among three species of *Stenonema* [*S. pudicum* (Hagen), *S. rubromaculatum* (Clemens), and *S. interpunctatum frontale* (Banks)] in White Clay Creek. A similar phenomenon has also been described for three *Ephemerella* [*E. subvaria* McDunnough, *E. invaria* (Walker), and *E. excrucians* Walsh] and two *Paraleptophlebia* [*P. adoptiva* (McDunnough) and *P. mollis* (Eaton)] mayfly species from the Mad River [F. P. Ide, *Univ. Toronto Stud. Fish. Res. Lab.* **50**, 1 (1935).
14. Gross primary production in White Clay Creek averages 4.5 g m^{-2} day^{-1} and weekly averages range from 0.56 to 7.5 g m^{-2} day^{-1} (T. L. Bott, in preparation). Standing crop of detritus (particle size: 0.45 μm to 16.0 mm) averages 248 g of organic matter per square meter for the year and seasonally ranges from 169 to 346 g m^{-2} over the four seasons. Leaf litter detritus (particle size > 16.0 mm) rarely falls below 40 g m^{-2}. Average daily transport of detritus ranges from 0.66 to 3.2 g m^{-3} during the year (R. L. Vannote, in preparation).
15. Wing-bud development can be used to assess the extent of adult tissue synthesis. A threshold body size probably exists for adult tissue development regardless of temperature.
16. Mayfly eggs are fully developed in the larval stage; adult females emerge with their full complement of eggs, mate and oviposit usually within 24 to 48 hours, and die. According to regression analysis, egg production is a linear function of dry weight for adult mayflies. The regression equations, where F is fecundity and W is dry weight, are: *C. rufostrigatum*, $F = 165.0\ W + 139.6$, $N = 24$, $r^2 = 0.70$; *I. bicolor*, $F = 112.4\ W - 195.4$, $N = 45$, $r^2 = 0.84$; *T. atratus*, $F = 171.7\ W + 89.3$, $N = 40$, $r^2 = 0.59$. Fecundity could not be measured for *S. alternata* because adult females feed extensively and more than double their initial weight prior to oogenesis. *Caenis simulans* females contained between 95 and 240 eggs at metamorphosis but we could not accurately define a fecundity-dry weight relationship because of the small size of the species.
17. The equations are: *A. ludens*, $F = 111.6\ W - 27.0$, $N = 151$, $r^2 = 0.52$; *E. funeralis*, $F = 135.5\ W + 299.3$, $N = 143$, $r^2 = 0.33$; *E. subvaria*, $F = 59.3\ W + 143.4$, $N = 129$, $r^2 = 0.44$; *L. cupida*, $F = 212.3\ W + 99.4$, $N = 305$, $r^2 = 0.46$.
18. The effect of temperature on larval growth was similar for males and females (that is, nonoptimum cool or warm temperature regimes produced small adults).
19. This work was supported by grants from the Rockefeller Foundation, the Francis Boyer Research Endowment, and the Stroud Foundation. We thank B. Anderson, B. Cocks, S. Hyatt, and J. Peirson for technical assistance and T. L. Bott and G. W. Minshall for comments on the manuscript. We thank R. K. Allen for confirming the identification of *Ephemerella funeralis*.

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