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A model for seasonal synchrony in stream mayflies

J. Denis Newbold, Bernard W. Sweeney, and Robin L. Vannote[1]

Stroud Water Research Center of the Academy of Natural Sciences of Philadelphia, 512 Spencer Road, Avondale, Pennsylvania 19311 USA

Abstract. Many mayfly species have synchronous univoltine life histories over broad geographic ranges, but the life-history adaptations underlying their seasonality remain unidentified. We investigated whether simple adaptations in the response of development rate to temperature might account for the observed phenology of adult emergence and the 1- and 2-year life histories of eight mayfly species studied in Piedmont streams of eastern North America between 34°N and 50°N latitude. We present a model consisting of two sequential life-history stages. Development rate in each stage is a linear function of streamwater temperature above a lower threshold but, in the first stage, a developmental quiescence occurs whenever a maximal temperature is exceeded. The five model parameters are assumed not to vary with latitude. Using daily field temperatures, the model simulated several successive generations beginning from an arbitrary day of the year. With parameters fitted from the field data, the model could reproduce both the univoltine life history and the latitudinal variation in the timing of adult emergence for six species. For two additional species, the model reproduced a northward transition to a semivoltine life history. The simulations suggest that nearly all development occurs in spring and autumn during periods of roughly equivalent thermal regime at all latitudes.

Key words: development, Ephemeroptera, geographic, latitude, insects, phenology, temperature.

A large proportion of temperate mayfly species have 1-yr (univoltine) life histories, and many of these maintain the univoltinism over broad latitudinal ranges (Clifford 1982). Typically, the life history exhibits a strong seasonal synchrony, with adult emergence and oviposition restricted to a brief period (e.g., 1–2 wk) in the spring or early summer. The timing of adult emergence varies geographically, occurring earlier in the year at lower latitudes (Brittain 1982). Many studies, both in the field and in the laboratory have established that temperature plays a major role in governing mayfly phenology. Yet little is known about the specific traits that allow mayflies to maintain a seasonally synchronized, univoltine life history over geographic ranges involving large differences in annual average temperature.

Among insects in general, univoltinism is widely considered to depend at least in part on a diapause—a period of suppressed metabolic activity in which growth and morphogenesis cease or are greatly suppressed, even under thermal conditions that are normally conducive to growth and development (Danilevsky 1965, Tauber et al. 1986, Danks 1987). Photoperiod and temperature (among other factors) can regulate the onset and termination of diapause, providing a means of achieving seasonal synchrony, i.e., appropriate phasing of the life cycle within the annual cycle (Andrewartha 1952). Latitudinal clines in the regulation of diapause (e.g., in photoperiod sensitivity) have been implicated as a major factor that allows seasonal insects to persist over large geographic ranges (Taylor and Spalding 1986). In mayflies, however, diapause has been observed experimentally in only a few species (Britt 1962, Bohle 1969, 1972, Elliott 1978, Sweeney and Vannote 1978, Giberson and Rosenberg 1992), and in all cases, only in the egg stage. Egg diapause has also been inferred for other species from field studies, but the eggs of most species with reported univoltine life histories mature in only a few weeks (Clifford 1982). Photoperiod has not, to our knowledge, been reported to influence seasonality in any mayfly species.

Because systematic investigations are lacking, it remains quite possible that larval diapause, photoperiod, or both regulate seasonality in mayflies. Nonetheless, the absence of evidence for either trait raises the question of whether mayflies might achieve seasonal synchrony entirely through direct control of development by temperature. Danks (1987) used the term "direct control" in reference to the normal influences

[1] Present address: 315 Street Road, Kennett Square, Pennsylvania, USA 19348.

that environmental factors, such as temperature and nutrition, have on the development rate of any ectothermic organism, whether seasonal or not. These include periods of dormancy or "quiescence" that are directly induced and maintained by adverse conditions. He distinguished direct control from control by cues, which represents the more complex and specialized adaptations that regulate induction and duration of diapause. Most seasonally synchronized insect life histories involve a combination of cued and direct control; and temperature-based development models are widely used to predict phenology of non-diapause portions of insect life cycles. But the question of whether direct control alone—i.e., acting over the entire life history—might synchronize the life-histories of some seasonal insects, has received very little attention (Tauber et al. 1986, Danks 1987).

We approach the question of seasonal regulation in mayflies by asking whether direct control can explain observed geographic patterns of voltinism and adult-emergence phenology of several species. Direct control by temperature involves a "development curve", which expresses the rate of development as a function of temperature. If the function is linear, the time required to complete development can be expressed as degree-days measured above a threshold temperature. Although univoltinism in mayflies has often been linked to annual degree-day accumulations, seasonal synchrony cannot be attained unless the development curve changes at some point in the insect's life cycle. Given a particular annual thermal regime, a single curve (e.g., a degree-day requirement) applied to the entire life cycle could predict a generation time of exactly one year; but it would do so from any starting date (excluding periods of quiescence) and therefore would not synchronize to a specific phenology. Moreover, temporal and geographic variations in thermal regime would yield variations in generation time, and a single curve provides no homeostatic mechanism to correct generation time to a one-year duration. To our knowledge, direct control of a univoltine life history without diapause has been examined in detail only by Bentz et al. (1991), who showed by simulation modeling that differing (laboratory derived) development curves among a series of six life-history stages could account for the synchronous univoltine cycle of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins.

In this paper we present the hypothesis that univoltinism and seasonal synchrony in some mayfly species arises from a very simple system of direct control by temperature, involving only two life-history stages. Each stage has a linear development curve with a lower temperature threshold, but in the first stage there is also a quiescence that occurs whenever the temperature exceeds an upper limit. We show by simulation modeling that this hypothesis can account for the univoltinism and phenology of adult emergence over the latitudinal ranges of six species, and for a northern shift to a two-year life history of two other species. Compensation for latitudinal variation in temperature is purely phenotypic, requiring no adaptive clines. The hypothesis remains untested by laboratory study, and we consider it only a step toward elucidating the life-history controls of mayflies. However, the model provides a framework of testable assumptions and predictions that can guide further inquiry.

Methods

Study sites

Sampling locations consisted of 44 streams on 11 river systems in eastern North America between 34°N and 50°N latitude and mostly in the Atlantic drainage. River systems were selected at intervals of about 1.5° latitude. Streams ranged from 1st through 5th order (sensu Strahler 1957). With minor exceptions, sites were chosen to meet the following criteria: (1) a diverse stream insect fauna; (2) location within the Atlantic drainage and below 500 m elevation; (3) intact and natural riparian vegetation along most of the upstream length, including tributaries; (4) temperature and hydrologic regimes and water quality determined largely by natural processes (i.e., little or no industrialization or urban development, no significant thermal discharges, and no impoundments); (5) drainage basin geology conducive to moderate or high productivity (e.g., sedimentary or metamorphic rock, rather than granitic batholith).

Determining dates of adult emergence

For this investigation we define the date of adult emergence at a given site as the beginning of the flight period, i.e., the first date when adults of a given population emerge. Field sites were visited periodically throughout the year,

when larvae were collected and dry mass of each individual was determined. Collections were made at least once every 2 wk during the final growth and emergence periods of the study species. Adult emergence date was determined either by direct observation of adults in the field or by collecting mature larvae (with dark wingpads) and rearing them in the laboratory to the adult stage at temperatures similar to field conditions. If adults emerged in the laboratory within 1 wk of collection, the beginning of laboratory emergence was taken as the emergence date. If no direct information on adult emergence was available for a species at a site, then emergence date was taken as the date corresponding to the maximum average size (biomass) of larvae observed at the end of the growth period, because larval size for all of the species studied exhibited a gradual decline during the emergence period. Final determination of emergence date for a species from these various sources of data was made by an experienced field entomologist (D. H. Funk, Stroud Water Research Center) who also eliminated any estimates that were uncertain by more than about 14 d. The latter decisions involved some subjectivity so, to avoid bias, these judgments were made prior to any data analysis. Except for one case of an obvious discrepancy, no revisions of the original judgments were made after data analysis began.

The eight mayfly species reported in this study were those from the field collections that satisfied the following criteria: (1) the life history duration was 1 yr or more throughout the known range; (2) the egg stage had no known diapause; (3) collections were sufficient to estimate emergence dates over a latitudinal range of at least 10 degrees or from at least ten different sites; and (4) there were no uncertainties with respect to species identification at any of the sites. Identifications were verified through morphological examination of voucher specimens from each of the study sites, and, for a number of species, by electrophoretic examination of 25–30 enzyme loci. For example, *Eurylophella temporalis* was excluded from this study because electrophoretic data revealed the presence of morphologically cryptic species (Funk et al. 1988).

Temperatures

Thermographs (Ryan Model J) were installed in all streams except for a few for which data were supplied by the U.S. Geological Survey. Thermographs were left in the stream for at least 1 yr and checked monthly. Charts were changed every 2–3 mo, when calibrations were verified by mercury thermometer. For a few streams, short gaps in thermograph records were filled in by interpolation from thermograph data from nearby streams. Mean daily temperature was approximated as the average of the daily maximum and minimum temperatures.

For modeling purposes, daily temperatures from each site were smoothed by fitting them to the first several terms of a Fourier series, i.e.,

$$T = \frac{1}{2}A_0 + \sum_{i=1}^{6} [A_i\cos(i2\pi t) + B_i\sin(i2\pi t)] \quad (1)$$

where T is the smoothed mean daily temperature (°C), t = (Julian day of year)/365, and A_o, A_i, and B_i are coefficients (e.g., Gillet and Long 1974). For graphical purposes only (e.g., Fig. 1), we also smoothed latitudinal trends as follows: For each Fourier coefficient (e.g., A_0) we obtained an estimate of the coefficient (A_0*) as a function of latitude from a quadratic regression of all the individual site-estimates versus latitude. Then a grid (1-d by 0.5-degree) of latitudinally and temporally smoothed temperature estimates (T*) was generated from Equation (1) using the functions for A_0*, A_1*, etc. Fifty percent of the smoothed estimates were within ±1.4°C of the observed mean daily temperatures and ninety percent were within ±3.8°C. The isotherms appearing in the figures were generated from the grid using the "Contour" procedure of the SAS system (SAS Institute 1990).

Results

Latitudinal patterns of adult emergence dates

For all eight species, southern populations emerged before northern populations. Regressions of emergence date on latitude are presented in Table 1 as: (1) a standardized emergence date (ED_s), or the value of the regression line at a latitude of 39°52'N (White Clay Creek, southeastern Pennsylvania) and (2) the slope (b), which represents the number of d that emergence is delayed for each degree of northward latitude. Curvilinear (quadratic) regressions in no case produced significant improvement ($p > 0.05$, extra-sums of squares principle, Draper and Smith 1966).

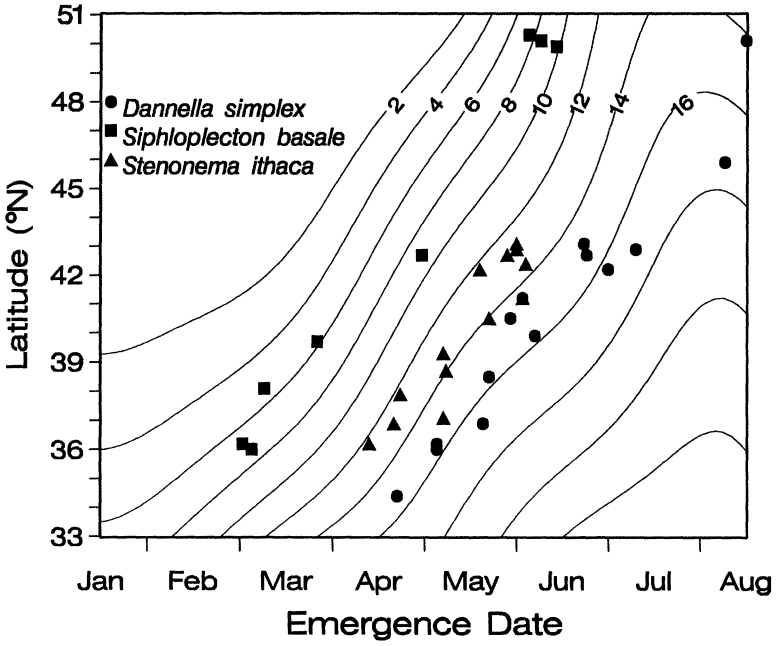

FIG. 1. Dates of adult emergence of three mayfly species on streamwater isotherms. Isotherms were smoothed by time and latitude, as described in the text.

As Figure 1 illustrates, adult emergence for a given species began at about the same temperature at all latitudes. The linear relationships between emergence date and latitude is reflected in approximately linear and parallel isotherms through a range of rising temperatures of roughly 4–14°C. Median temperatures at emergence for the eight species, by comparison, ranged from 7 to 16°C (Table 1). The isotherm slope of 6.5 d per degree latitude (measured at the 10°C isotherm) agrees closely with the median estimate for b of 6.4. The parallel nature of the isotherms (which are greatly smoothed relative to individual site data) shows that pop-

TABLE 1. Linear regressions of emergence date on latitude. Estimated emergence date for latitude, L, is given by $ED = ED_s + b(L - 39.86)$, in which ED_s is the estimated emergence date at 39.86°N latitude (White Clay Creek, southeastern Pennsylvania), and ED and ED_s are expressed as Julian day of year. r^2 is the coefficient of determination. Median emergence temperature represents the median across sites of water temperature (from Eq. 1) on the observed emergence date.

Species	No. of sites	ED_s	b	r^2	Sampled latitudinal range (°N)	Median temperature (°C) at emergence
Siphloplecton basale (Walker)	8	87 (29 Mar)	6.9	0.98	36–50	7.5
Leptophlebia cupida (Say)	19	101 (11 Apr)	6.6	0.83	36–50	10.0
Epeorus pleuralis (Banks)	16	107 (17 Apr)	6.3	0.94	37–50	9.5
Stenonema vicarium (Walker)	14	119 (29 Apr)	6.1	0.89	36–50	12.6
Stenonema ithaca (Clemens and Leonard)	13	132 (13 May)	6.4	0.87	36–43	14.0
Eurylophella funeralis McDunnough	16	138 (19 May)	3.7	0.79	37–50	13.1
Eurylophella verisimilis McDunnough	30	145 (26 May)	4.5	0.86	36–50	15.0
Dannella simplex McDunnough	14	153 (03 Jun)	7.7	0.93	34–50	15.5

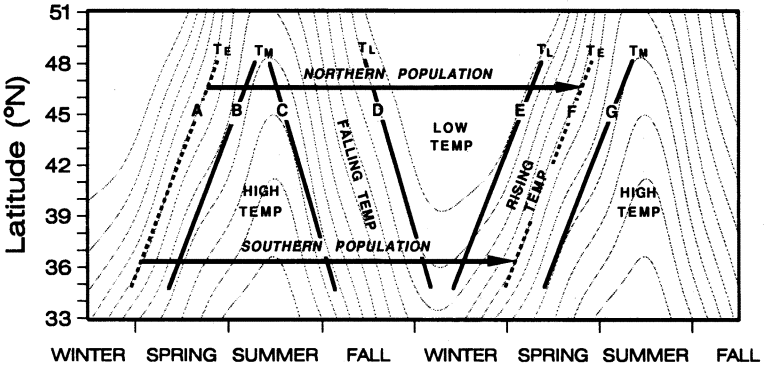

FIG. 2. Schematic of univoltine mayfly development in relation to temperature and latitude. Horizontal lines represent development of a northern and a southern population, respectively. Diagonal lines (*A*–*G*) represent idealized isotherms. T_E = temperature at emergence; T_M and T_L are high- and low-temperature limits of the region of parallel isotherms. Gray lines are actual streamwater isotherms (smoothed as in Fig. 1), from 2° to 22°C by 2°C intervals.

ulations from different latitudes experience similar thermal regimes during the final months of growth and development before emergence.

In the region of parallel vernal isotherms, the number of degree days accumulated between any two isotherms is roughly the same at any latitude. This observation supports the suggestion that a final period of mayfly development may be synchronized as vernal temperatures rise above a critical threshold (Fremling 1973, Brittain 1982, Wright et al. 1982, McCafferty and Pereira 1984, Peters et al. 1987). Emergence would occur after a required number of degree days was accumulated above this threshold. This hypothesis, however, contains the implicit assumption that individuals in a cohort attain some roughly equivalent state of readiness to begin final development during the time when temperatures are below the threshold. Thus, an explanation of mayfly synchrony in terms of temperature must consider development throughout the entire life-history.

Modeling approach

Our objective in constructing a model was to seek the simplest possible description of mayfly development that could generate seasonal synchrony through direct control by temperature. As discussed above, direct control requires a minimum of two successive developmental stages, each represented by a distinct development curve. Simplicity suggests a linear function for each curve, i.e., development would involve two degree-day requirements measured with respect to different thresholds. We investigated such a model and found that although it could produce synchrony at a given site, it was overly sensitive to temperature variations that might occur at a site or between sites in close proximity. More importantly, the model could not accommodate latitudinal variations in thermal regime without the assumption of large genetic clines in degree-day requirements. Although clines in thermal requirements have often been reported (see below), we are unaware of cases in which the variation is as large as the model would require.

Figure 2 illustrates schematically the thermal regime faced by a northern and a southern population of a species superimposed on generalized streamwater isotherms. Adult emergence and oviposition occur at isotherm *A* and, for the next generation, at isotherm *F*, both at temperature T_E. Before emergence, both populations experience approximately the same thermal regime between isotherms *E* and *F*. Individuals of both populations arrive at isotherm *E* at the same age, and must have equivalent developmental status if they are to emerge by isotherm *F*. Yet in the period *A* to *E* they are exposed to very different thermal regimes. For example, by the age of 285 d, individuals of *Stenonema vicarium* from a site at 36°N latitude experience ~4200 degree-days (>0°C), while those from a site at 50°N latitude experience only ~1300 degree-days. Nearly all of the latitudinal difference in degree-day accumulation occurs in the

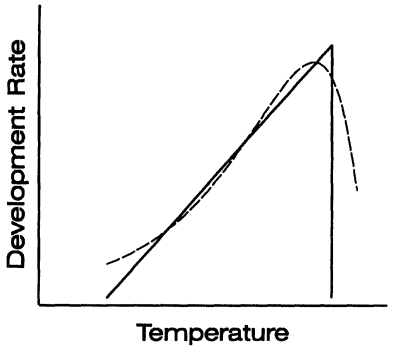

FIG. 3. Linear development rate function with a thermal maximum as in Equation 2 (solid line), superimposed on the asymptotic expansion model of Logan et al. (1976) (broken line).

period between isotherms *B–C*, comprising the hottest portion of the year. If this period *B–C* (delimited by temperatures $>T_M$) were passed in a dormant state (i.e., an estivation), then all populations would experience roughly equivalent degree-day exposure throughout the remainder of the year. Development at any latitude would occur primarily during periods *C–D* and *E–F* under latitudinally uniform thermal conditions, with relatively little development in the cold period *D–E*.

Thus, for the model of mayfly development, we hypothesize a temperature-controlled estivation in stage 1 of a two-stage developmental sequence. The development rate of stage 1 is given by:

$$r_1(j) = \begin{cases} [T(j) - T_{01}]/K_1 & \text{if } T_{01} \leq T(j) \leq T_{max} \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

where $r_1(j)$ is the daily accumulation of development on day j, $T(j)$ is the mean daily temperature on day j, and K_1 is the number of degree-days above the threshold T_{01} required for completion of stage 1. Quiescence (no development) occurs whenever the temperature is below T_{01} or above T_{max}. This function approximates a nonlinear development curve in which the development rate drops rapidly beyond the thermal optimum (Fig. 3). Development of stage 1 is complete when $\Sigma_{j=j_0}^{j_f} r_j(j) \geq 1$, where j_0 and j_f are the dates of starting and completion.

The second stage of development is given by:

$$r_2(j) = \begin{cases} [T(j) - T_{02}]/K_2 & \text{if } T(j) > T_{02} \\ 0 & \text{otherwise} \end{cases} \quad (3)$$

where the parameters K_2 and T_{02} are analogous to K_1 and T_{01}. In this stage, quiescence occurs when the temperature is below the threshold, T_{02}. When development of stage 2 is complete (marking adult emergence and oviposition), stage 1 of the next generation begins. "Completion" of stage 1 refers only to a readiness to begin stage 2. The developmental processes represented by stage 1 (e.g., growth) might continue contemporaneously with stage 2, but we assume that stage 2 represents distinct processes associated with maturation. The complete model involves five parameters, K_1, T_{01}, T_{max}, K_2, and T_{02}, all to be estimated by fitting the model to field data. It assumes that there are no geographic clines in any model parameters.

To test the model, we simulated development for a given species at each site for which we had field-estimates of the date of adult emergence. Simulation of the first generation began on an arbitrary date (e.g., 1 January), and continued to a maximum of 30 generations. Depending on the parameter values and the temperature data for a given site, the model could: (1) produce, after several generations (usually <5), a univoltine life cycle ending on the same date each year; or (2) fail to synchronize with an annual cycle, giving generation times consistently longer or shorter than one year and, hence, progressively changing emergence dates.

This model simulated only one individual in each generation and hence does not explicitly address variability among individuals. But such variability is analogous to starting a generation at an odd time of year so that the ability of the model to synchronize from any starting date implies the ability to resynchronize any degree of temporal spread among individuals within a cohort. For each site, the model used the same annual thermal regime repeatedly, rather than actual regimes from successive years. However, because model parameters were identical across all sites, the variability among sites served as a surrogate for variability among years. Based on 12 yr of record from a 3rd-order reach of the White Clay Creek (39°52'N), temporal variation (in annual degree-days >0°C) is less than the residual site-to-site variation after regressing degree-days on latitude.

Simulations were run iteratively to identify combinations of parameter values that would yield a univoltine life history at all sites, and

TABLE 2. Error and parameter estimates for the development model, and the error obtained when the thermal maximum, T_{max}, was constrained to 14°C and to 16°C.

	T_{01} (°C)	K_1 (°C-days)	T_{max1} (°C)	T_{02} (°C)	K_2 (°C-days)	Error (days)	n	Error when T_{max1} constrained to: 14°C	16°C
Dannella simplex	0	175	11	2	900	7.3	14	7.9	9.0
Epeorus pleuralis	−5	1625	12	6	25	6.9	16	7.2	18.8
Leptophlebia cupida	−5	1500	12	5	65	8.1	19	15.6	30.1
Siphloplecton basale	−5	1425	12	6	10	9.4	8	18.9	10.4
Stenonema ithaca	−5	1150	13	2	460	7.1	13	7.1	7.8
Stenonema vicarium	0	600	12	8	45	7.9	14	8.0	8.0

to find the particular set of parameter values that maximized the agreement between simulated and emergence dates. Approximately 5×10^5 parameter combinations were examined for each species. If a particular set of parameter values failed to yield a univoltine life history for all sites, the parameters were discarded. Otherwise, the squared error of estimation (simulated vs. observed emergence date) was computed and summed over all sites. The reported parameter values are those that minimized the sum of the squared errors (*SSE*). These parameter values were checked using various starting dates to assure that the simulated emergence dates were unique. The reported "error" refers to the minimized root-mean-squared error (i.e., $\sqrt{SSE/n}$, where n is the number of sites). Although we report the estimated parameter values, we caution that these estimates are not robust for two reasons. First, they arise from a model whose validity is hypothetical. Second, as we detail below, it was often possible to constrain one parameter to a selected value and achieve comparable error through compensation by other parameters. Our purpose was not to estimate parameters, but to determine whether there were parameters (or parameter ranges) for which the model could reproduce the observed phenology.

Model results for univoltine species

We tested this model for six species that are univoltine throughout their range and have no known diapause. Initial trials produced univoltine life histories and good reproduction of the observed emergence dates. However, for three of the species (*Epeorus pleuralis, Siphloplecton basale,* and *Stenonema ithaca*), the estimated value for T_{max} was much lower than expected, falling in the range of 5 to 9°C. Thermal maxima in this range would allow stage-1 development only in late fall and winter rather than throughout the autumn as we had hypothesized (Fig. 2). We therefore applied a restriction of $T_{max} \geq 11$ to the parameter searches. Among the three species affected, this restriction increased the model error by less than one day. The final model reproduced observed emergence dates with the average error for each species ranging from 7 to 9 d (Table 2). These errors are within the estimated precision of our field-observations of emergence dates. The model-estimated sequence of development is illustrated in Figures 4 and 5 for *Leptophlebia cupida* and *Stenonema vicarium,* respectively.

The final estimates for the thermal maximum of 11–13°C, although plausible, remain lower than we had initially expected on the basis of Figure 2. When $T_{max} = 11$°C, the quiescence would persist until mid October at about 40°N latitude. We therefore conducted additional parameter estimations with T_{max} fixed at 14 and 16°C respectively (Table 2). The error was little affected for three species, but increased to more than 14 d at either 14 or 16°C for the other three species.

The estimated value for T_{01} was negative (−5°C) for four species (Table 2). This does not imply that mayflies develop at such low temperatures, because actual water temperatures can fall only slightly below 0°C. Rather, the significance of the negative threshold is that it allows development to continue at temperatures near zero, a phenomenon that has frequently been observed in aquatic insects (Hynes 1970, Ward

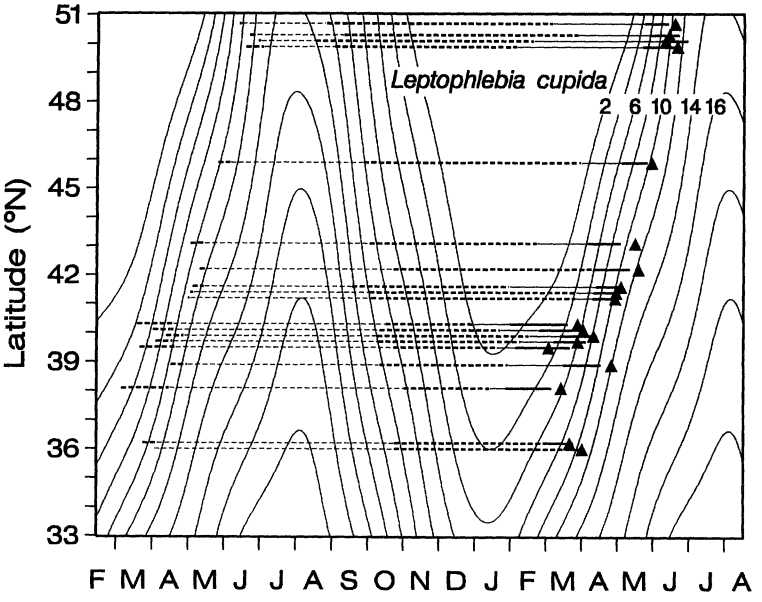

FIG. 4. Simulated development of *Leptophlebia cupida*. Horizontal broken lines represent stage 1. Wide broken lines represent development at temperatures below T_{max}. Thin broken lines are periods of high-temperature quiescence ($T > T_{max}$). Solid lines are stage 2. Narrow solid lines are periods of cold-temperature quiescence ($T < T_{02}$). Wide solid lines are periods of development ($T > T_{02}$). Simulated emergence occurs at right hand terminus. Triangles are emergence observed in field. Some lines and triangles are displaced vertically a maximum of ±0.5 degree to prevent over-plotting. Isotherms as in Figure 1.

and Stanford 1982, Rader and Ward 1990). The value for T_{01} of −5°C estimated for five of the six species represents the lowest value used in the trial simulations. Lower values might have improved the error slightly, but this would have little meaning in comparison to the precision of our field estimates of emergence date. To test whether the negative threshold was required to achieve synchrony, we restricted T_{01} to 0°C. Univoltine cycles were again achieved for all species but with errors ranging up to 12 d.

Limitations of the model became apparent when T_{01} was constrained to zero and, simultaneously, T_{max} was constrained to 14°C or 16°C. For three species (*E. pleuralis*, *L. cupida*, and *Siphloplecton basale*), the error ranged from 19 to 29 d when T_{max} = 14°C, and synchrony could not be obtained when T_{max} = 16°C. All of these species emerge at median temperatures of 10°C or less (Table 1). Table 2 shows that for *Dannella simplex* and *Stenonema vicarium* the error even at T_{max} = 16°C was ≤9 d, while for *Stenonema ithaca* at T_{max} = 16°C and T_{01} = 0°C, the error was 14 d. The latter three species emerge at temperatures between 12 and 16°C. Thus, the model suggests that mayflies emerging early in the spring must have either a long summer quiescence (low T_{max}) or a negative thermal threshold (T_{01} < 0°C) for stage-1 development.

As illustrated in Figures 4–5, the simulated completion of stage 1 often differed by several months at sites of similar latitude. This variation reflects site-to-site differences in water temperatures (which are invisible in the figures because the isotherms are smoothed), but it does not impair synchronous initiation of stage-2 development so long as the completion of stage 1 occurs when temperature is below the threshold for stage 2 (T_{02}). The negative stage-1 thresholds reduce the influence of temperature on the duration of stage-1 development (as discussed further below), increasing the likelihood that stage 1 can complete within the period of below-threshold temperatures.

Semivoltinism at higher latitudes

Two other species that we studied, *Eurylophella funeralis* and *Eurylophella verisimilis* switch from univoltinism to semivoltinism at higher

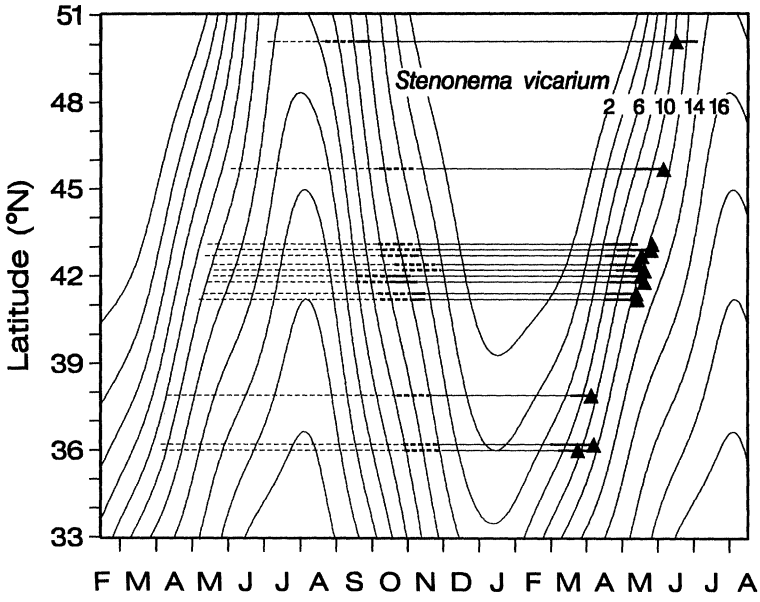

FIG. 5. Simulated development of *Stenonema vicarium*. Symbols and lines as in Figure 4.

latitudes, as inferred from seasonal patterns of larval size distributions. We examined the ability of the model, without modification, to reproduce this life-history transition. In conducting the parameter search, we accepted only parameter combinations that produced semivoltinism at the northernmost sites and univoltinism at the southernmost sites. Within this restriction we determined the parameter values that minimized the error in emergence dates, regardless of the predicted voltinism at intermediate latitudes (i.e., this allowed the life cycle duration of 1 or 2 yr to be incorrectly specified at some sites). For both species, the model was able to simulate a northward transition to semivoltinism. For *E. verisimilis*, the predicted transition occurred between approximately 43° and 45°N latitude (Fig. 6), in agreement with field observations, but the error of this model was 23 d (Table 3). The error for *E. funeralis* (Table 3) was smaller (9 d) but the predicted transition (not shown) of 43°–46°N was north of the observed transition (40°–42°N). Also, the estimated value of T_{max} was only 9°C, which, as discussed above, may be implausibly low. (With T_{max} fixed at 11°C, the transition occurred between 46° and 50°N and the error was 10 d.) These discrepancies do not seem sufficient to reject the model as an explanation for the northward transition to semivoltinism. If this explanation is correct, then such transitions would represent a purely phenotypic response, involving no local genetic adaptation.

Discussion

Seasonal synchrony and physiological time

We have shown that a very simple model for direct control of mayfly development could

TABLE 3. Model error and parameter estimates for two *Eurylophella* species, and latitudes of transition from univoltine to semivoltine life history.

	T_{01} (°C)	K_1 (°C-days)	T_{max} (°C)	T_{02} (°C)	K_2 (°C-days)	Error (days)	Uni/semivoltine transition		
							n	Simulated (°N)	Observed (°N)
Eurylophella funeralis	0	600	9	4	250	9.2	16	43–56	40–42
Eurylophella verisimilis	0	675	11	13	80	23.0	30	43–46	43–46

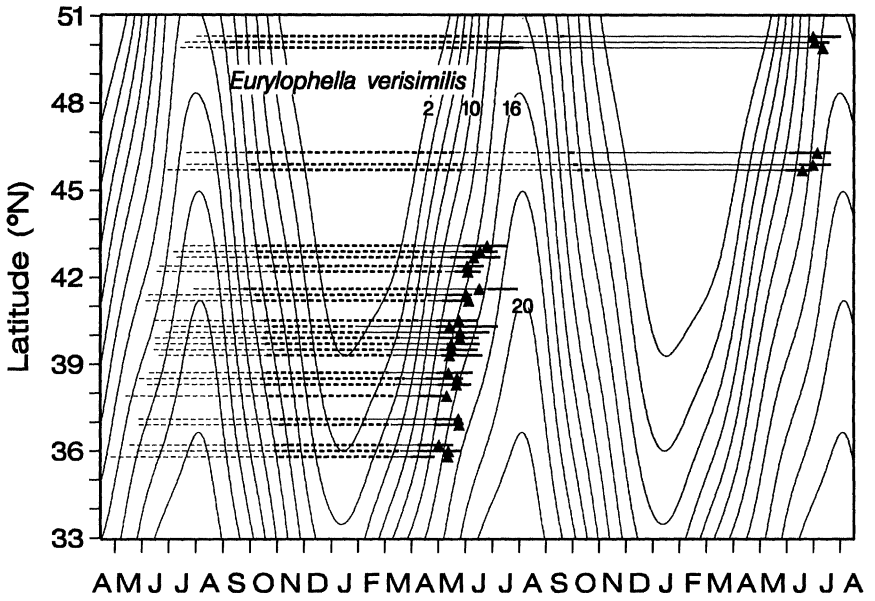

FIG. 6. Model simulations for *Eurylophella verisimilis* showing transition to semivoltinism. Symbols and lines as in Figure 4.

generate synchronous univoltine life histories with appropriate phenology over a wide latitudinal range for eight species. Two factors contribute to the ability of the model to synchronize to a specific phenology. One of these is the effect of a threshold temperature in timing the initiation of a given stage of development. As shown in Figures 4–6, the simulated initiation of both stages 1 and 2 often, but not always, occurred at temperatures prohibiting development of the next stage. Thus T_{02} usually synchronized the beginning of stage-2 development and T_{max} often synchronized the beginning of stage-1 development. However, this direct synchronization by thresholds cannot be the only factor responsible for phasing the life cycle within the year. When the life cycle is displaced from its equilibrium phasing (as in the first generation of all simulations), a given stage does not necessarily end within the period of prohibitive temperatures that would allow the threshold to be effective. Moreover, for several of the simulations the entire life cycle was completed without threshold-synchronization. Two examples are shown in Figure 4 (~36 and 42°N), where both stages begin in active development (as thick lines).

The other synchronizing factor in the models involves the effect of rising or falling temperatures on development rate. If development rate increases with temperature, then rising temperatures are strongly synchronizing (Bradshaw 1973, Schmidt 1984). This effect is evident when development is represented on a physiological time scale (Hughes 1963, Taylor 1981). For a linear development curve, physiological time is measured in degree-days and real time is scaled in proportion to $(T-T_0)$, where T_0 is a threshold temperature. Figure 7 represents two individuals with identical degree-day requirements beginning a period of degree-day accumulation in the winter, displaced in (real) time by 1 mo. Although the offset remains constant in physiological time, it grows smaller in real time so that the individuals complete their development within three d of each other. The effect is related to the temperature differential between the beginning and end of the degree-day accumulation: a displacement of 10 d at 1°C above threshold is equivalent to only 1 d at 10°C above threshold.

Falling temperatures produce an opposite, desynchronizing effect, so that insects are subject to both synchronizing and desynchronizing effects at different times of the year. These effects would balance over the annual cycle,

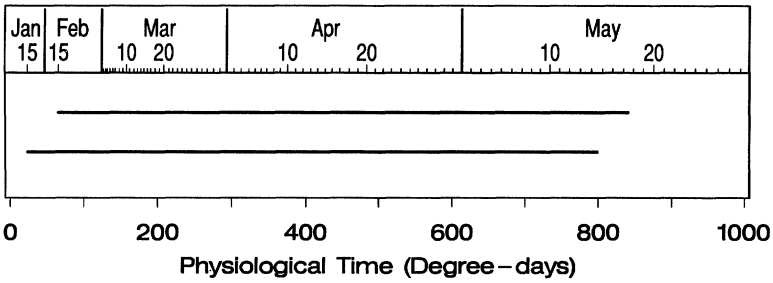

FIG. 7. The synchronizing effect of rising temperatures. Horizontal lines represent development of individuals through a stage requiring 776 degree-days, the upper line being delayed by 42 degree-days relative to the lower line. Calendar dates are located on the physiological time axis according to the degree-days (>0°C) accumulated since 1 January, based on water temperatures from the White Clay Creek, Pennsylvania (39°52'N). The distance between dates increases throughout the spring as the water warms.

with no net synchronizing effect, if the relationship between development and temperature were to remain fixed for the entire life cycle. In Figure 7, this balance would appear as two lines of 1-yr duration, with the real-time displacement being the same at the end of the year as at the beginning. But where two or more developmental stages are involved, development in effect switches from one physiological time scale to another. It is this switching that allows a net synchronizing effect and a consistent life-cycle duration even under varied thermal regimes. In the model, the positive thermal thresholds for stage-2 development enhance the synchronizing effects of rising spring temperatures, whereas the negative thermal thresholds for stage-1 development lessen the desynchronizing effects of autumnal declining temperatures. Both effects occur because the sensitivity of the physiological time scale to temperature fluctuations increases with the thermal threshold. For example, when the threshold is 0°C, the rate of development at 10°C is twice that at 5°C, whereas for a 4°C threshold, the differential in development rates between 5°C and 10°C increases to six fold.

With two or more physiological time scales (in contrast to a single scale), the total amount of physiological time experienced in a year depends not only on the thermal regime, but also on which scale is in effect at any particular time of year. Annual synchrony is achieved when the life cycle reaches a phasing within the year under which the available and required physiological time coincide. This interpretation reflects the point emphasized by Danks (1987, 1991) that seasonal synchrony depends not on individual stages in isolation, but on their interactions within the entire developmental sequence.

Latitudinal gradients, clines, and phenology

Insects exhibit a diverse array of phenological adjustments to latitudinal gradients that involve both phenotypic responses and genetic clines (Danilevsky 1965, Masaki and Sakai 1965). Clinal adjustments may involve control of diapause, e.g., critical photoperiods, or diapause duration (Taylor and Spalding 1986, Hayes et al. 1987, Krysan 1982), or of ordinary development, e.g., thermal thresholds and degree-day requirements (Masaki 1967, Dingle and Baldwin 1983). Considerable evidence suggests substantially more genetic plasticity in the control of diapause than of thermal requirements (Danilevsky 1965, Tauber et al. 1987). Masaki (1967) pointed out that univoltine life histories involving summer dormancy would minimize selection for clines in thermal requirements. Our results support and extend this point, showing not only that total degree-day exposure remains relatively uniform with latitude, but also that geographically disparate populations experience roughly equivalent temperatures at equivalent states of development. Vannote (1978) demonstrated a relationship between body size and respiratory rate in the mayfly *Ephemerella dorothea* which implied that the optimal temperature for growth (as opposed to develop-

ment) increases during the spring, commensurate with the actual rise in streamwater temperature. Our results suggest that this apparent specialization to a specific thermal regime could have evolved regardless of the level of geographic gene flow.

Our model for mayfly development represents a life-history strategy that requires no clines, either in thermal requirements or in control of dormancy. Purely phenotypic accommodation of latitudinal variation is apparently rare in insects, but has been observed or proposed for a number of insects in which temperature, rather than photoperiod, is a primary cue (Carton and Claret 1982, Nechols et al. 1983, Gutierrez et al. 1986). Pener and Orshan (1980, 1983) reported a summer reproductive diapause in the grasshopper *Oedipoda miniata* that is reversibly controlled by both temperature and photoperiod but, in natural settings, primarily by temperature. It is thus similar to our hypothesized high-temperature quiescence. They argued that this control would lead to appropriately timed autumnal oviposition over both altitudinal gradients and the latitudinal range of the species. Strategies that accommodate large differences in thermal regime through purely phenotypic responses may prove advantageous in the face of rapid global climate change (Sweeney et al. 1992).

A variety of latitudinal trends in body size have been observed in insects (e.g., Masaki 1967, 1972, 1978, Mousseau and Roff 1989). Sweeney and Vannote (1978) predicted that size and fecundity of adult aquatic insects should decrease both north and south of some latitude at which thermal regime is optimal (see also Vannote and Sweeney 1980). This prediction was based primarily on laboratory-derived differential effects of temperature on development and growth rates. In extrapolating these results to latitudinal gradients, they implicitly assumed that insects at lower latitudes would develop under warmer conditions than those at higher latitudes. This assumption, it is now clear, did not take into account the potential of phenological adjustment to compensate for latitudinal gradients. Many species exhibit maximal growth during the final 60–90 d of development during which they may accumulate more than 90% of their final weight. In all species that we examined, this critical growth period occurs under conditions no warmer at the southern limit of the species' range than at the northern limit. If periods of growth correspond to periods of development and both are arrested at high summer temperatures, then we might expect very little effect of latitude on growth at any developmental stage.

Control of mayfly seasonality

The earlier emergence at lower latitudes that we observed is consistent with other studies of mayflies (Clifford et al. 1973, 1979, Saettem and Brittain 1985). The influence of vernal temperatures on emergence date has also been observed among streams of differing thermal regimes within a drainage basin (Ulfstrand 1968, Newell and Minshall 1978, Ban and Kawai 1986, Perry et al. 1986, Rader and Ward 1990), between years of differing temperature in a single stream (Illies and Masteller 1977, Peters et al. 1987) and in laboratory studies (e.g., Nebeker 1971, Brittain 1976, Sweeney 1978, Humpesch 1981, Sweeney and Vannote 1981, Wright and Mattice 1981). Our results support the hypothesis that a threshold temperature initiates a final development stage. This stage might represent the differentiation of adult tissues (Clifford 1970, Svensson 1977, Sweeney and Vannote 1981). Our model places this hypothesis in the context of the entire life cycle, showing that with few additional assumptions it is possible to account for voltinism over a geographic gradient in addition to emergence timing. The model clearly does not rule out more complex or alternative modes of seasonal control, but provides a framework for experimentally identifying and interpreting such alternatives. In particular, it identifies two major issues that any explanation of mayfly seasonality must address. The first is that some adaptation must exist to account for the latitudinal variation in summer degree-day accumulation. The model demonstrates that a high-temperature quiescence may be all that is needed, but an alternative hypothesis is that larvae enter a summer diapause. Indeed, it could be difficult in this case to distinguish between diapause and quiescence. We have used the term quiescence to denote the simple, reversible control by temperature. Diapause, in contrast, cannot normally be terminated simply by a reversal of the cues that induce it (Tauber et al. 1986, Danks 1987). However, diapause is more fundamentally distinguished from quiescence by its physiological basis in neurohormonal control (Tauber et al. 1986), and it has been shown

that such control can act reversibly (Pener and Orshan 1980). Summer diapause in the larval stage is common in Plecoptera (Harper and Hynes 1970). Khoo (1968) found that in *Capnia bifrons*, the diapause was induced by temperatures exceeding 12.5°C and terminated more rapidly at lower temperatures, although photoperiod was involved as well. There is little direct evidence for or against larval estivation in mayflies. Brittain (1976) observed markedly slowed growth of *Leptophlebia vespertina* through the summer months at temperatures exceeding ~15°C. But Clifford et al. (1979) reared *L. cupida* through its entire life cycle at 20°C in approximately 160 d. In this case, however, the population came from a high-latitude (53°31'N) stream with maximum temperatures of ~18°C, i.e., where there would be little or no benefit of a quiescence.

The second major issue identified by the model involves the desynchronizing effect of declining autumn temperatures. The modeling indicated that autumnal control would require very low, probably negative, thermal thresholds. Topp (1990) showed that thresholds as low as −4°C in *Catops nigricans* were important in an annual synchronization that involved both photoperiod and thermal effects. The model of Bentz et al. (1991), which generates univoltism without diapause, also involves autumnal development under very cold temperatures. Alternatively, photoperiod could directly regulate autumnal development, as it does commonly among dragonflies and damselflies (Odonata) (Lutz and Jenner 1964, Lutz 1968, 1974a, 1974b, Norling 1976, 1984, Killian and Lutz 1985, Pritchard 1989). Lutz repeatedly observed that photoperiod could alter developmental rates when insects were maintained at constant temperature, but not when insects were maintained under a natural thermal regime. This strongly suggests a life cycle that is fundamentally regulated by temperature, as we suspect is true for mayflies, with photoperiod acting in a supplementary capacity, becoming important in years of unusual temperatures or in habitats with extraordinary thermal regimes.

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