Vol. 115, No. 5 The American Naturalist May 1980

GEOGRAPHIC ANALYSIS OF THERMAL EQUILIBRIA: A CONCEPTUAL MODEL FOR EVALUATING THE EFFECT OF NATURAL AND MODIFIED THERMAL REGIMES ON AQUATIC INSECT COMMUNITIES

Robin L. Vannote and Bernard W. Sweeney

Stroud Water Research Center of the Philadelphia Academy of Natural Sciences,
Avondale, Pennsylvania 19311

Submitted June 6, 1978; Accepted January 24, 1979

Insects are often the dominant macroinvertebrates in stream and river communities (Hynes 1970; Cummins 1974). Although the species composition within insect groups performing the same ecosystem function (e.g., leaf shredder, algal grazer, filter feeder, etc.) differs among rivers separated geographically (Ross 1963; Hynes 1970), a notable similarity exists at the generic and/or familial level (Schmid 1955; Ross 1963). This worldwide resemblance of component insect fauna probably results from geographic similarities in the physical and trophic structure of rivers, because (i) specific climates rarely produce unique landforms or channel morphology (Leopold et al. 1964), and (ii) the composition and caloric content of food materials is similar among similar size streams in different geographic regions (Boyd and Goodyear 1971; Cummins and Wuycheck 1971).

Water temperature is one important parameter that can differentiate tributaries both within and among drainage systems. Temperature affects growth, metabolism, reproduction, emergence, and the distribution of aquatic insects. (See Hynes 1970; Precht et al. 1973; Wieser 1973 for general reviews.) In addition, the species composition of insect communities has been shown to change with temperature both seasonally (within a stream reach, Vannote 1973), microgeographically (along the length of a given river, Ide 1935; Sprules 1947), and macrogeographically (among drainage systems, Beatty and Beatty 1968). Thus, the magnitude and pattern of historical, annual, seasonal, and diel temperature fluctuations may be important in selecting and maintaining the array of insect species in a given reach of stream (Smith 1972; Lehmkuhl 1974).

An insect community in a natural river contains numerous species, many of which find thermal conditions suboptimal relative to other rivers in their geographic range. Recent studies of insect communities in White Clay Creek (39°53′ N; 75°47′ W) show a high degree of intraspecific variation with respect to adult body size and fecundity for several aquatic insect species (Sweeney 1976*a*, 1976*b*, 1978; Sweeney and Schnack 1977; Vannote 1978). This variation appears mainly to be a phenotypic response to diel and seasonal temperature fluctuations (Sweeney and Schnack 1977; Sweeney 1978). The amplitude of diel fluctuations and the magnitude and rate of seasonal temperature change varies with the size and location of a river in temperate regions (Thibault 1971; Smith 1972). Climatic changes (altitude and/or latitude) also affect the pattern of river temperatures. Although river insects have evolved under the constraints of a thermally fluctuating system, they show little ability to compensate or acclimate to environmental temperatures (Sayle 1928; Pattee 1955; Lawton 1971; Stockner 1971; Keister and Buck 1974; Sweeney and Schnack 1977; Sweeney 1978).

Our purpose here is to focus on the ecophysiological response of aquatic insects to the thermal variation of rivers. We intend to (i) synthesize new and published data into a conceptual model describing the ecological aspects of thermal variation, (ii) develop a working hypothesis to describe the energetics and developmental dynamics involved in regulating the geographic distribution of aquatic insects, (iii) provide a new perspective for establishing guideline criteria for river management, and (iv) outline the possible role of long-term climatic trends to the development and evolution of river insect communities.

THERMAL HETEROGENEITY OF RIVER SYSTEMS

River discharge during periods of no surface runoff is maintained largely by groundwater accrual along headwater channels. Thermal regimes of headwater tributaries are dominated by the temperature of groundwater outflow. In the continental United States groundwater is generally within 1° C of mean annual air temperature of a region, varies little seasonally, and exhibits a well-defined latitudinal gradient (e.g., ranging from 25° C in southern Florida to 3° C in Maine; fig. 1). Thermal variation both within and between drainage systems reflects alteration of regional groundwater temperature by the interaction of climate, channel geometry, riparian vegetation, and other watershed characteristics.

River drainage systems consist of a network of channels differing in thermal regime and order (size). *Order* refers to Strahler's (1957) modification of Horton's (1945) stream classification system: headwater streams having no tributaries are designated first order; two first-order streams join to form a second order; two second orders form a third, etc. The order of a tributary does not change upon confluence with a stream of a lower order than itself. Among White Clay Creek tributaries, for example, the total degree days (>0° C) accumulated annually remains relatively constant (ca. 4,270), but the seasonal variance in the thermal regime increases with river order (fig. 2). Diel variation also increases with order up to intermediate-sized (orders 4–5) rivers, but a decrease occurs in larger tributaries due to the combined effect of the large volume and high specific heat of water (fig. 3). For a given altitude, the relationship between river order and thermal regime changes with latitude (fig. 4). Thus, a fourth-order river at 39° N latitude may be similar thermally to a fifth-order tributary at 50° N or a second-order one at 30° N.

Although natural river systems are characterized by thermal fluctuations, the spatial and temporal pattern of temperature change appears highly structured and reasonably predictable. Figure 5*a* and 5*b* show that the total annual heat accumulation for a river of specific size and altitude is also predictable given its latitudinal

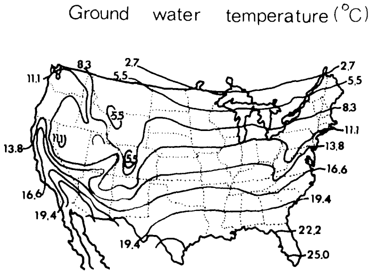


FIG. 1.—Isotherm lines of groundwater temperature for the continental United States (after Collins 1925).

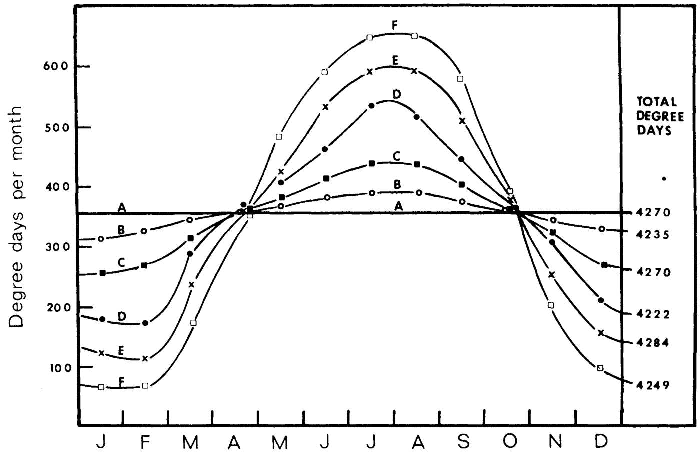


FIG. 2.—Distribution of monthly degree-day accumulations at various recording stations along White Clay Creek. Total degree-days are the annual sum of monthly records for each station. *A*, outflow of groundwater; *B*, woodland spring seeps; *C*, first order spring brooks; *D*, second order streams; *E*, third order stream (upstream segment); *F*, third order stream (downstream segment).

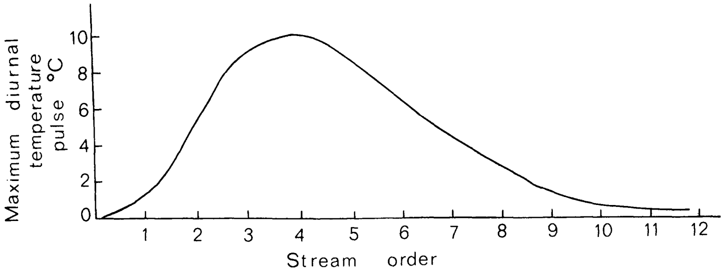


FIG. 3.—Maximum diurnal change in temperature as a function of stream order in temperate North America. Data are from unpublished White Clay Creek studies and water resource reports of the United States Geological Survey (U.S.G.S.).

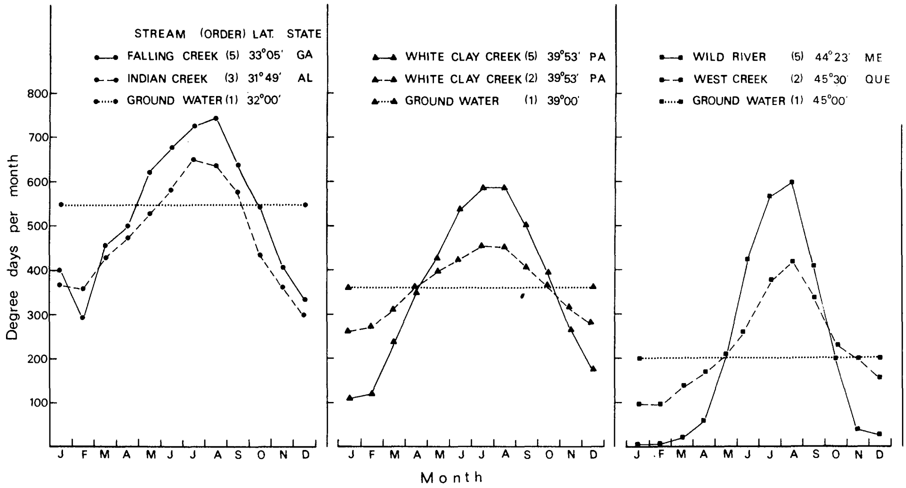


FIG. 4.—Distribution of monthly degree-day accumulations for groundwater and various streams along a latitudinal gradient in eastern North America. Data for Indian Creek, Falling Creek, and Wild River were taken from U.S.G.S. water resource reports; West Creek temperatures are from MacKay (1969).

coordinate. More importantly, the relationship between annual degree days and latitude does not change significantly with longitude (e.g., regression lines for Atlantic and central United States were not significantly different; analysis of covariance, $p > .05$).

Because temperature greatly affects many population parameters of aquatic insects (e.g., egg and larval diapause, embryonic development, larval growth and metabolism, etc.), perhaps the most important aspect of a river's thermal regime is its temporal predictability. We used Colwell's (1974) algorithm to analyze a continuous 10-yr temperature record on White Clay Creek for elements of predictability both within seasons and over the entire water year. Predictability (P) was further partitioned into two components: constancy (C, temporal uniformity) and contingency (M, temporal variability but in an ordered sequence). The analysis indicated both annual and seasonal predictability for the 10-yr record (table 1). Our P values were statistically significant ($p < .001$) from zero (no predictability) using the G statistic outlined by Colwell (1974). Component analysis revealed that summer and winter temperatures were predictable due to high constancy. In contrast, high predictability during seasons of rapid temperature change (e.g., spring and fall) was attributed to high levels of contingency.

To evaluate the relative power of our computed values, we created a theoretical 10-yr temperature record displaying an annual amplitude identical to White Clay Creek (i.e., 0°–20° C) but with reduced (and perhaps unrealistic) variance (e.g., the 10-yr record for any given date varied only ± 1° C). This data set yielded a P value of .66, which is about 20% higher than P values obtained for White Clay Creek. These results suggest that White Clay temperatures in 8 out of 10 yr would be very similar for a given date. The pattern and variance of annual stream

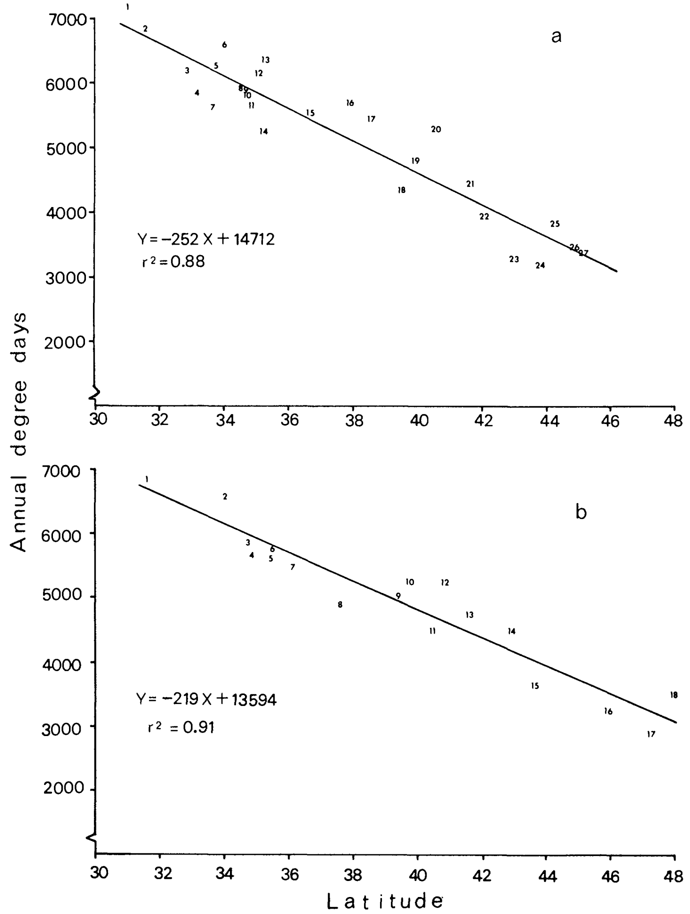


FIG. 5.—*a*, Total annual degree-day (>0° C) accumulation as a function of latitude for various rivers of the eastern United States. Base flow discharge of selected rivers was between 1.2 and 4.6 m^3 s^{-1}. *1*, Satilla River, Ga.; *2*, Conecuh River, Ala.; *3*, Coosawhatchee River, S.C.; *4*, Falling Creek, Ga.; *5*, Alcovy River, Ga.; *6*, Black River, S.C.; *7*, Coosa River, Ala.; *8*, Enoree River, S.C.; *9*, Bear Creek, Ala.; *10*, Conawuga River, Ga.; *11*, Flint Creek, Ala.; *12*, Sugar River, N.C.; *13*, Second Broad River, N.C.; *14*, Second Broad River, S.C.; *15*, North Fork Holston River, Va.; *16*, Jackson River, Va.; *17*, Rappahannock River, Va.; *18*, North Fork Potomac River, Md.; *19*, Brandywine River, Pa.; *20*, Schuylkill River, Pa.; *21*, Quinebang River, Conn.; *22*, Tioga River, N.Y.; *23*, Kayaderosseras Creek, N.Y.; *24*, Independence River, N.Y.; *25*, Sheepcot River, Maine; *26*, St. Regis River, N.Y.; *27*, Clyde River, Vt. *b*, Total annual degree-day (>0° C) accumulation as a function of latitude for various rivers of north and south central United States. *1*, Conecuh River, Ala.; *2*, Coosa River, Ala.; *3*, Bear Creek, Ala.; *4*, Flint Creek, Ala.; *5*, Duck River, Tenn.; *6*, Buffalo River, Tenn.; *7*, Big Sandy River, Tenn.; *8*, Rough River, Ky.; *9*, Embarras River, Ill.; *10*, Big Walnut River, Ind.; *11*, Big Creek, Ill.; *12*, Eel River, Ind.; *13*, DuPage River, Ill.; *14*, Rock River, Wis.; *15*, Kikapoo River, Wis.; *16*, Escanaba River, Minn.; *17*, Trip Rock River, Mich.; *18*, Kawishini River, Minn.

TABLE 1

Calculated Parameters of Predictability* for an Actual and Theoretical Ten-Year Data Set of Daily Average Stream Temperatures

	White Clay Creek†			Theoretical‡		
Season	*P*	*C*	*M*	*P*	*C*	*M*
Full Year	.51	.03	.48	.66	.03	.64
Winter	.51	.27	.24	.67	.38	.29
Spring	.50	.13	.37	.66	.16	.50
Summer	.54	.39	.15	.66	.48	.18
Fall	.46	.09	.37	.66	.17	.49

*See Colwell's (1974) algorithm. Predictability (P) has two separable components, constancy (C) and contingency (M). Maximum predictability (e.g., $P = 1.0$) could result from complete constancy (e.g., $C = 1.0$), complete contingency (e.g., $M = 1.0$), or a combination of constancy and contingency (e.g., $C = .75, M = .25$). In this analysis, complete constancy would imply the thermal regime was the same for each season. In the case of complete contingency, thermal regime varies from season to season, but the pattern is the same for all years.

†Ten-yr continuous record of daily average temperature for a third-order tributary.

‡Theoretical 10-yr record; temperatures vary seasonally but the range of temperatures on any given date is limited to ± 1° C (e.g., the 10-yr frequency record for May 15 was 2, 6, 2 for 14°, 15°, and 16° C, respectively).

temperatures apparently lowers the maximum attainable P value. For example, we observed experimentally that even an ideal 100-yr data set with low variance (e.g., only ± 1° C for any date) produces a P value of only about .85.

The above analysis suggests that natural stream systems exhibit a pattern of "predictable variability" with respect to temperature. We view thermal heterogeneity and its predictable quality as an important ecosystem attribute leading to the development and maintenance of a highly structured community of aquatic poikilotherms (see discussion below).

THERMAL EQUILIBRIUM HYPOTHESIS

Our main hypothesis is that the stability (ability of a subpopulation to recover from serious reductions in numbers by environmental perturbations or fluctuations) of a subpopulation within the geographic range of many lotic species mainly reflects a dynamic equilibrium between temperature and individual growth, metabolism, reproductive potential, and generation time (fig. 6). A thermal regime is viewed as optimum when an individual's body weight and fecundity is maximized (e.g., fig. 6, pathway *b*). We hypothesize that an equilibrium location, the geographic region where individual weight and fecundity is maximized, coincides closely with the location of greatest subpopulation biomass. Geographic range extension away from an optimum area (e.g., fig. 1, pathway *a* or *c*) is associated with temperature-induced changes in the rate and efficiency of energy use, developmental processes, and generation time.

According to our hypothesis, subpopulations in nonoptimum habitats are characterized by low population density and small individuals with reduced

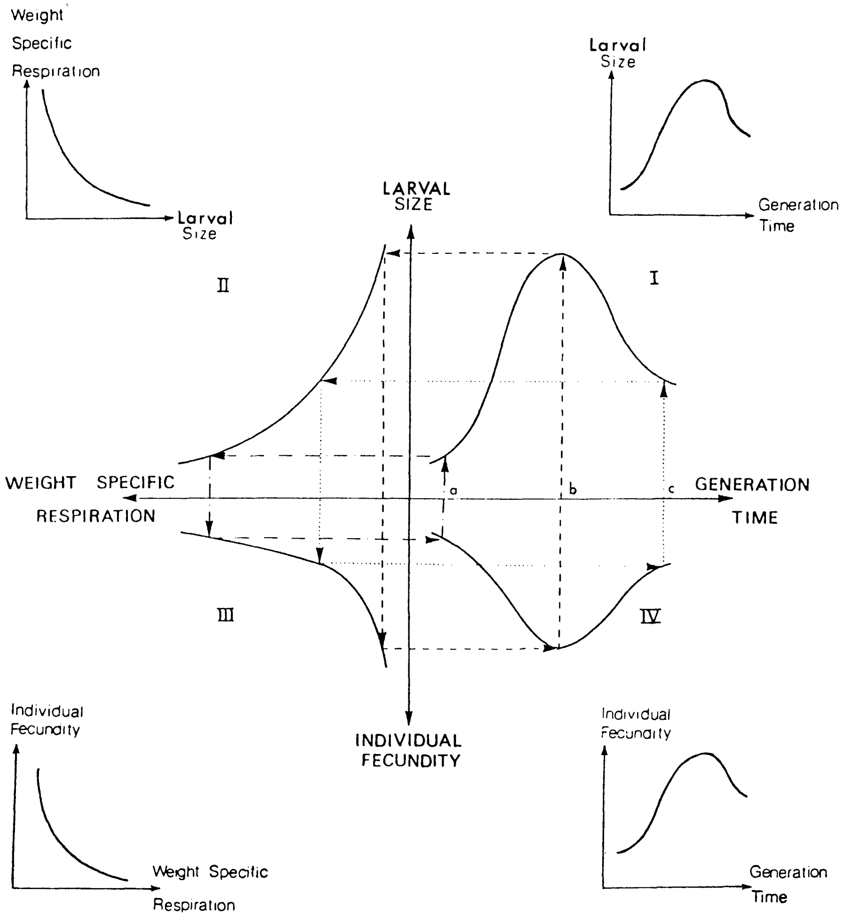


FIG. 6.—A thermal equilibrium model, based on experimental data for White Clay Creek, indicating the population interactions between bioenergetic (growth and metabolic rate) and developmental (fecundity and generation time) parameters for insects reared in optimum and nonoptimum thermal regimes. The individual components of the model are described at the periphery of each quadrat (e.g., the inverse relationship between weight-specific respiration and larval size; quadrat II.) Pathway *b* (an optimum thermal regime) shows that maximum larval size is associated with an intermediate generation time, low weight-specific respiration, and high adult fecundity. Larval size and adult fecundity are intermediate in cold, nonoptimal regimes (pathway *c*). Generation time is shortest in warm regimes (pathway *a*), but high respiration cost and accelerated development of adult tissues (wing pads, reproductive system) results in small larvae and reduced adult fecundity.

fecundity. The ability of these subpopulations to control and/or exploit ecosystem resources is reduced by both the small size and lower density with respect to the total community. The competitive position of these species in the community hierarchy is lowered and the probability of competitive extinction due to environmental fluctuations (natural or induced) is increased. The local extinction of a subpopulation theoretically occurs when individual fecundity approaches zero. A species in nature is probably eliminated wherever recruitment falls below the critical threshold needed to maintain the competitiveness of the subpopulation.

This hypothesis has been synthesized from bioenergetic and developmental studies of insect communities in White Clay Creek, Chester County, Pennsylvania. These data were obtained under an array of natural and experimental temperature regimes and are used here to develop the "thermal equilibrium" concept. Methods and materials for data collection are outlined in detail elsewhere (Sweeney 1976*a*, 1978; Sweeney and Schnack 1977; Vannote 1978). A brief report describing certain aspects of the above hypothesis has been published elsewhere (Sweeney and Vannote 1978).

GROWTH-METABOLISM-FECUNDITY: INTRASPECIFIC AND INTERSPECIFIC VARIATION

The growth and emergence pattern of many "winter-spring" species in White Clay Creek is exemplified by *Ephemerella subvaria* McDunnough; see fig. 7. (Larvae of "winter-spring" species hatch from eggs in late summer or early fall but grow mainly during winter and spring.) The large range of body sizes observed at any date during larval growth of this mayfly is due probably to a nonsynchronous egg hatch as well as differential growth rates among and within the sexes. Adult metamorphosis within the subpopulation is reasonably synchronous, with the largest nymphs of each sex emerging first. Average size of adult males and females decreases progressively throughout the emergence period. All larvae are exposed to a wide range of temperatures during growth and development. The synchronous emergence suggests that adult tissue maturation is initiated almost simultaneously in all larvae (size independent) when vernal temperatures first begin exceeding a critical threshold. This would partially explain the synchrony of adult metamorphosis as well as the progressive decrease in adult weight during the emergence period.

Adult body size and fecundity are also affected indirectly by changes in the proportion of assimilated energy needed for maintenance metabolism. If maintenance costs increase with temperature at a rate disproportionate to overall assimilation (Sweeney and Schnack 1977; Sweeney 1978), then the growth potential of larvae may be reduced at high temperatures due to insufficient energy. Weight specific respiration of *Ephemerella subvaria* is highly dependent on temperature (fig. 8). Metabolic rates for most larvae remain within a well-defined "activity range" (e.g., between 0.6 and 1.9 μl O_2 mg^{-1} h^{-1}) despite increasing temperatures during the winter-spring growth period. This quasiequilibrium for metabolism results from (i) an inverse relationship between weight-specific respiration and body size, (ii) a positive effect of increased temperatures on respiration, and (iii) substantial growth during the period of rising vernal temperatures (Vannote 1978). Figure 9 shows how the growth of an individual theoretically tends to compensate for the stimulatory effect of increased temperatures on respiration rate. This compensatory mechanism may have arisen through selection for individual larvae whose growth rates are adjusted to predictable thermal patterns. The critical growth increment needed to remain within the "activity range" is relatively greater for small versus large larvae. The potential for a small individual to

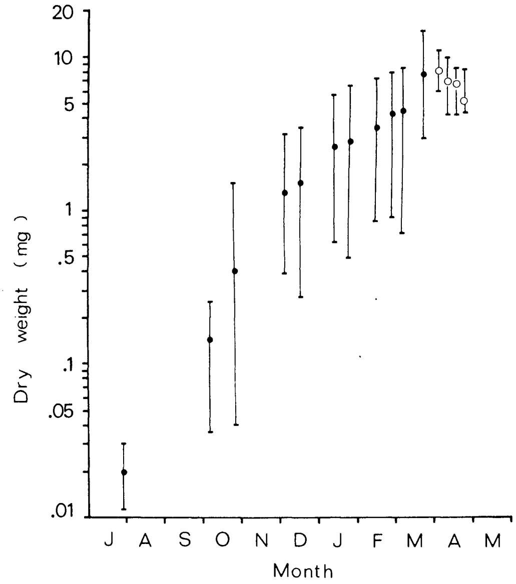


FIG. 7.—Population growth and adult emergence of *Ephemerella subvaria* in a third-order tributary of White Clay Creek. Vertical bars depict the range of values; solid dots (●) and open circles (○) show mean size of larvae and adults, respectively.

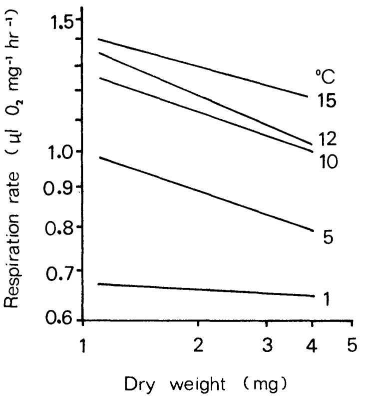


FIG. 8.—Weight specific respiration of *Ephemerella subvaria* at five constant temperatures. Regression equations ($\log Y = b \log X + \log a$) describing respiration rate (Y) as a function of larval dry weight (X) were: 1° C, $Y = -.018X - .175, F_{1,16} = .1$; 5° C, $Y = -.168X + 0, F_{1,89} = 13.7$; 10° C, $Y = -.171X + .112, F_{1,41} = 29.5$; 12° C, $Y = -.236X + .154, F_{1,15} = 5.7$; 15° C, $Y = -.123X + .160, F_{1,24} = 27.1$.

increase substantially in size during rising vernal temperatures is reduced because a greater portion of assimilated energy is required for maintenance (Vannote 1978). Thus, small *Ephemerella subvaria* larvae in early February emerge as small adults in April.

The above discussion emphasizes the outcome of "natural field experiments" where various individual larvae of a given cohort are out of phase temporally and

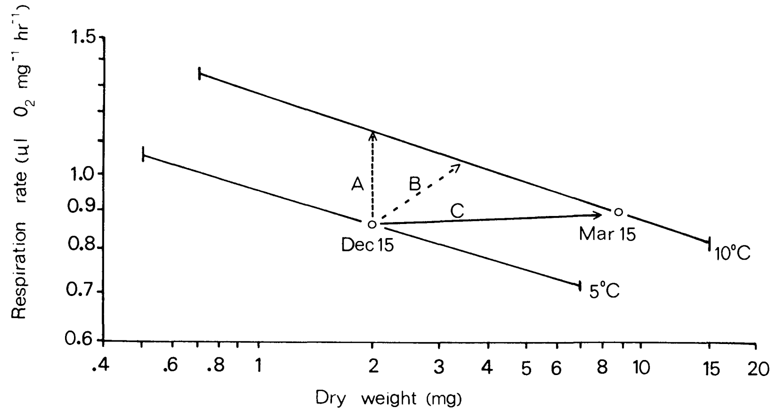


FIG. 9—Diagram outlining the weight-specific metabolism of *Ephemerella subvaria* as stream temperatures warm from 5° to 10° C. The December 15 and March 15 data points represent the average larval weight in the White Clay Creek population. Vectors *A* and *B* depict the theoretical increase in weight-specific respiration that might result from no winter growth and intermediate winter growth, respectively. Vector *C* shows how winter growth of the natural population keeps respiration rates in quasiequilibrium.

exposed to different thermal regimes during growth. Laboratory experiments on other aquatic species (i.e., *Isonychia bicolor* (Walker), *Ameletus ludens* Needham and *Ephemerella dorothea* Needham) confirms the observation that "trailing larvae" of winter-spring species (the last larvae of a cohort to hatch and begin growth) experience warmer temperatures during larval growth, metamorphose at or near the end of the emergence period, and produce the smallest adults of the generation (Sweeney 1976*b*, 1978; Vannote 1978). These data suggest that adult body size is inversely related to ambient stream temperatures during larval growth. This observation is critical to understanding size variation and the distribution of aquatic insects, because river temperatures vary both temporally and spatially.

In White Clay Creek, headwater streams are cooler in the spring and summer but warmer in the winter relative to larger downstream tributaries. Subpopulations of the mayfly *Ephemerella dorothea* emerging from a cool and a warm tributary of White Clay Creek exhibit marked differences in adult size (fig. 10). Note that adults emerging late in the cool stream are small and approach the maximum size of adults from the warm stream. We suggest that this results because individuals emerging late in the cool stream experience a thermal regime similar to individuals emerging early in the warm stream. Reduced adult size in warm tributaries has important ecological implications because the relationship between egg production and female dry weight appears linear for *Ephemerella dorothea* as well as for most other aquatic insect species (fig. 11). Thus, any factor reducing size affects recruitment and the competitive ability of the subpopulation.

Our studies of *Ephemerella subvaria, Ephemerella dorothea*, and many other species suggest that rapid shifts in energy use occur in response to thermal variation (i.e., seasonal changes in temperature within a tributary and/or spatial

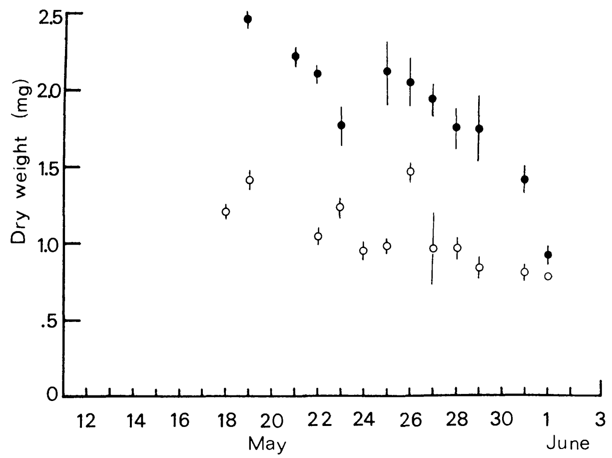


FIG. 10.—Progressive decrease in size of *Ephemerella dorothea* adults emerging from a cool (●) and warm (○) tributary of White Clay Creek. Maximum vernal temperatures are 14.5° and 18.5° C for the two tributaries.

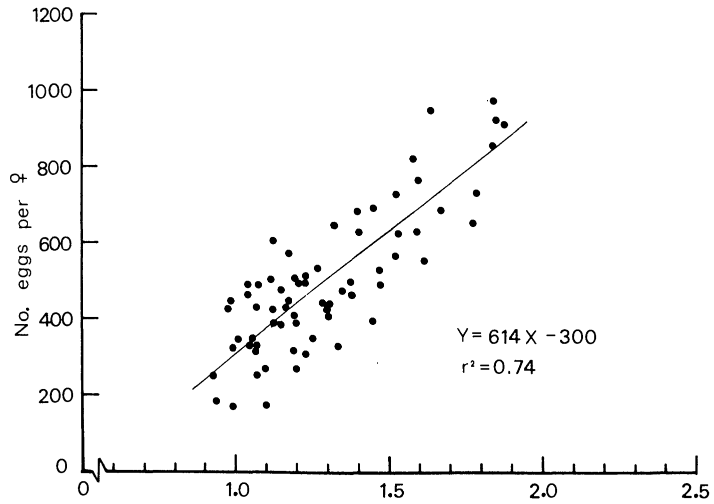


FIG. 11.—Weight-specific egg production for *Ephemerella dorothea* females emerging from a third-order tributary of White Clay Creek.

changes within a drainage system). Because adult body size and fecundity are inversely related to temperature for individuals within a single cohort, one expects a priori that incrementing ambient winter temperatures would result in early emergence and diminished adult size and fecundity for most "winter-spring" species.

The effect of increased winter temperatures on emergence date and adult size was evaluated for *Ephemerella subvaria*. Larvae of this species were collected in midwinter (stream temperature range 0°–5°C), sorted by size, and kept in small

TABLE 2

Results of Midwinter Growth Experiments for Four Size Classes of Female *Ephemerella subvaria* Larvae

Thermal Regime	Size Class	W_i	W_f	No. Days	GR*
9.5 ± 1° C	1	1.62 ± .30	3.42 ± .96	97	.007
	2	2.54 ± .18	3.98 ± .29	95	.004
	3	2.91 ± .23	4.08 ± .37	85	.004
	4	3.57 ± .32	4.74 ± .50	93	.003
15.5 ± 1° C	1	2.44 ± .22	3.57 ± .28	56	.006
	2	3.03 ± .18	3.91 ± .60	53	.005
	3	3.91 ± .35	5.36 ± .27	53	.006
	4	4.61 ± .42	5.77 ± .24	53	.004
White Clay Creek†	1	2.48 ± .26	6.57 ± .50	94	.010
	2	3.10 ± .19	5.54 ± .42	94	.006
	3	3.89 ± .32	8.01 ± .34	93	.007
	4	4.58 ± .47	10.83 ± .57	93	.009

Note.—Initial larval weight (W_i) and final adult weight (W_f) are in mg. The duration of each experiment (no. days) was calculated from day 1 until the first adult emergence. The instantaneous growth rate (GR) was calculated by GR = ($\ln W_f - \ln W_i$)/no. days.

* Waldbauer growth rate = $(W_f - W_i)/.5(W_f + W_i)$/no. days.

† Maximum, minimum, and average temperature for the entire experiment were 14.5, 2.1, 4.5° C, respectively.

microcosm streams at various experimental temperatures under a natural photoperiod. Fine particulate detritus and periphyton scraped from rocks collected from the natural stream were added to each microcosm stream weekly to assure comparable nutrition for experimental animals. Four size categories of *Ephemerella subvaria* were placed in each of three thermal regimens: 9.5 ± 1°C, 15±1°C, and ambient stream temperature. By increasing winter temperatures to 15°C, adults emerged 6 wk earlier and at a smaller size (6%–44%) relative to adults reared at ambient stream temperatures (table 2). At 9.5°C adult emergence was slightly earlier (2–10 days) and adult size was reduced (22%–46%) relative to the results of ambient temperatures. Adult metamorphosis was synchronous within a specific thermal regime even though larvae varied greatly in size at the beginning and end of the experiment. Results for *Ephemerella subvaria* suggest that high (>9°C) temperatures (i) initiate the development of adult tissue in both small and large larvae at about the same time (although a lower size threshold undoubtedly exists), (ii) reduce the overall growth potential of an individual larva, and (iii) accelerate the rate of adult tissue maturation, leading to early emergence at reduced size.

The above results suggest that a large size difference should occur between winter and summer cohorts of polyvoltine species. We have observed, for example, a 50% or greater reduction in size for summer cohort females of *I. bicolor, Baetis tricaudatus* Dodds, *Centroptilum rufostrigatum* McDunnough, *Chimarra aterrima* Hagen, *Glossosoma nigrior* Banks, *Dolophilodes distinctus* (Walker), and *Rheotanytarsus exinguus* (Johannsen) relative to nonsummer cohorts in White Clay Creek. Fecundity of summer cohort adults is also lower relative to

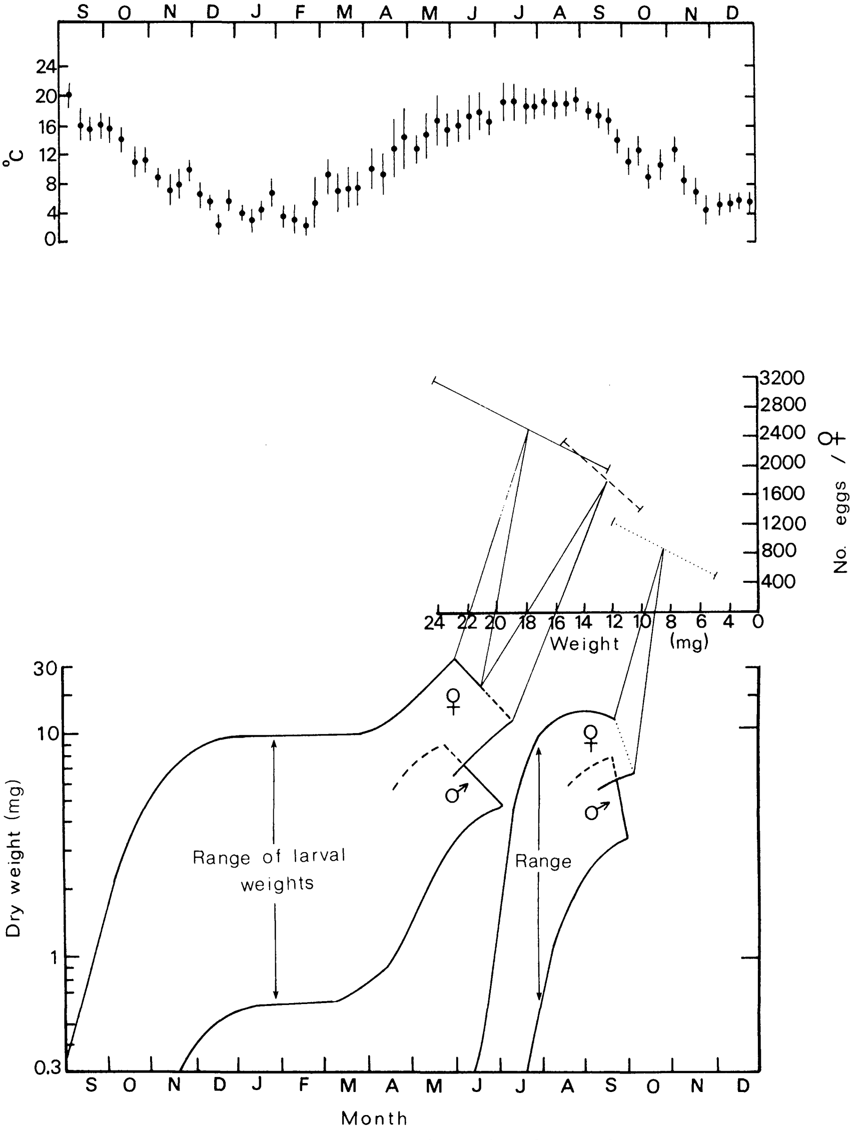


FIG. 12.—Seasonal growth, emergence, and fecundity of *Isonychia bicolor* in a third-order tributary of White Clay Creek. Vertical lines and solid dots show the diel range and weekly mean temperatures, respectively.

other seasons for most polyvoltine species (e.g., fig. 12 for *I. bicolor*). Intercohort size variation has been reported for other aquatic species (Macan 1957; Elliott 1967; Benech 1972; Fahy 1973). Seasonal changes in quality and quantity of food are probably not the critical factors causing the observed size variation of insects in White Clay Creek.

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 prep). 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 prep.).

In a fourth-order subbasin (ca. 800 hectares) of White Clay Creek, at least 49 species of Ephemeroptera (mayflies) have been collected over the past 10 yr (R. L. Vannote, unpublished data). The approximate date of first emergence and average maximum female size for 25 species are reported in fig. 13. The remaining 24 species are still under study. None of the remaining species, however, emerge before June 1 or at a size exceeding 3 mg. These data show that (i) adult size decreases during the spring-summer period for both congeneric species and conspecific cohorts, and (ii) during the summer, the adults of only three species (*Ephemera varia* Eaton, *Hexagenia atrocaudata* McDunnough, and *I. bicolor*) exceed 3–4 mg dry weight. Because at least 20–25 mayfly species emerge during the summer, the predominance of small, polyvoltine species is striking. Many of the large species, whose adults emerge from the creek in April-May-June, emerge in June-July-August from streams at more northern latitudes. We suggest, therefore, that the rate and magnitude of warming in White Clay Creek has either (i) caused large species to emerge by late spring, or (ii) eliminated species that lack an egg diapause, either directly, through increased larval mortality at high temperatures, or indirectly, through reduction of adult fecundity below some critical threshold. It is interesting that many of the larger species in White Clay Creek either over-summer in an egg diapause or require a long (>60 days) period of time for embryonic development.

The pattern of decreased adult size with increased stream temperatures for species with multiple cohorts has also been observed when two or more congeneric species are compared (Sweeney and Vannote 1978). For example, the *Ephemerella* complex in fourth-order tributaries of White Clay Creek usually consists of five species with similar ecosystem function (i.e., consumers of fine particulate detritus and diatoms in riffle and run habitats). Maximum larval growth and resource use for each species occurs at a different time of year (fig. 14). The largest species, *Ephemerella subvaria*, begins larval development in July and completes growth and emerges from the stream as an adult in early April. Adult size of congeners decreases progressively from early spring to late summer as each succeeding species grows in a slightly warmer environment. In addition, the average size of emerging adults decreases within each species during the emergence period (e.g., see fig. 7, *Ephemerella subvaria*). Thus, the last individuals of a species emerge just before, but at a similar size to, the first individuals to emerge of the next species in the series. As shown previously, midwinter exposure of *Ephemerella subvaria* larvae to late spring temperatures results in premature emergence at a size approaching *Ephemerella dorothea* (table 2). Egg production of small *Ephemerella subvaria*, however, is well below that of *Ephemerella dorothea* because egg dimensions remain relatively unchanged within a species despite large variation in overall body size.

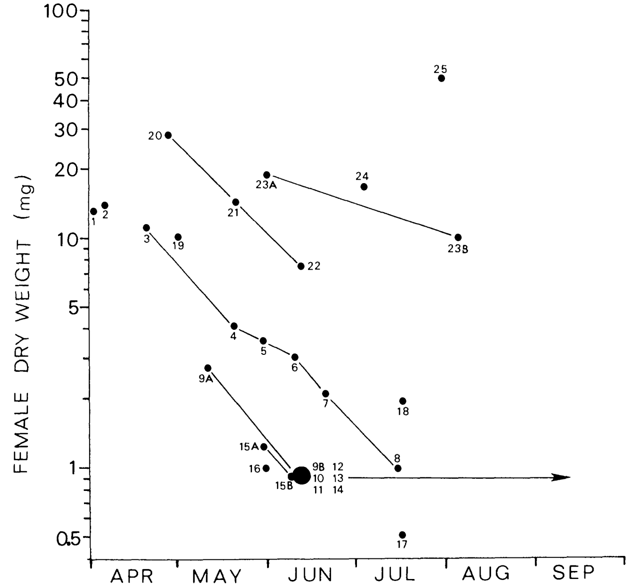


FIG. 13.—Average dry weight of the 10 largest females for several mayfly species emerging from White Clay Creek. Average weight for each species is graphed as a function of average first emergence date. The species included in this analysis are : *1*, *Ameletus ludens* Needham; *2*, *Leptophlebia cupida* (Say); *3*, *Ephemerella subvaria* McDunnough; *4*, *Ephemerella funeralis* McDunnough; *5*, *Ephemerella dorothea* Needham; *6*, *Ephemerella verisimilis* McDunnough; *7*, *Ephemerella deficiens* Morgan; *8*, *Ephemerella serrata* Morgan; *9A*, *9B*, *Baetis tricaudatus* Dodds; *10*, *B. flavistriga* McDunnough; *11*, *B. frondalis* McDunnough; *12*, *B. intercalaris* McDunnough; *13*, *B. palladulus* McDunnough; *14*, *B. pluto* McDunnough; *15A*, *15B*, *Centroptilum rufostrigatum* McDunnough; *16*, *Habrophlebiodes* sp.; *17*, *Caenis simulans* McDunnough; *18*, *Tricorythodes atratus* McDunnough; *19*, *Epeorus pleuralis* (Banks); *20*, *Stenonema pudicum* (Hagen); *21*, *Stenonema rubrum* (McDunnough); *22*, *Stenacron interpunctatum frontale* (Banks); *23A*, *23B*, *Isonychia bicolor* (Walker); *24*, *Ephemera varia* Eaton; *25*, *Hexagenia atrocaudata* McDunnough. Large dot and arrow represent six species that emerge continuously from June through September. Solid lines connect data points for closely related species. Note that *Baetis palludulus* is now considered in synonomy with *Baetis flavistriga*.

Several other examples of resource partitioning among closely related species have been observed in White Clay Creek (Vannote 1973). In each case, seasonal temperature patterns appear to be the critical factor maintaining the temporal segregation. Temperature patterns seem to influence both the stability and number of species in a given complex.

The above data suggest that an "optimum thermal regime" probably exists within the geographic range of a species population where both body size and fecundity are maximized. The concept of an optimum thermal regime implies, however, that both higher and lower temperatures reduce fucundity. Experimental results for the mayfly *Centroptilum rufostrigatum* McDunnough support this concept because adult body size is reduced when larvae are reared at both high and low temperatures when food quality and quantity were kept at high levels (fig.

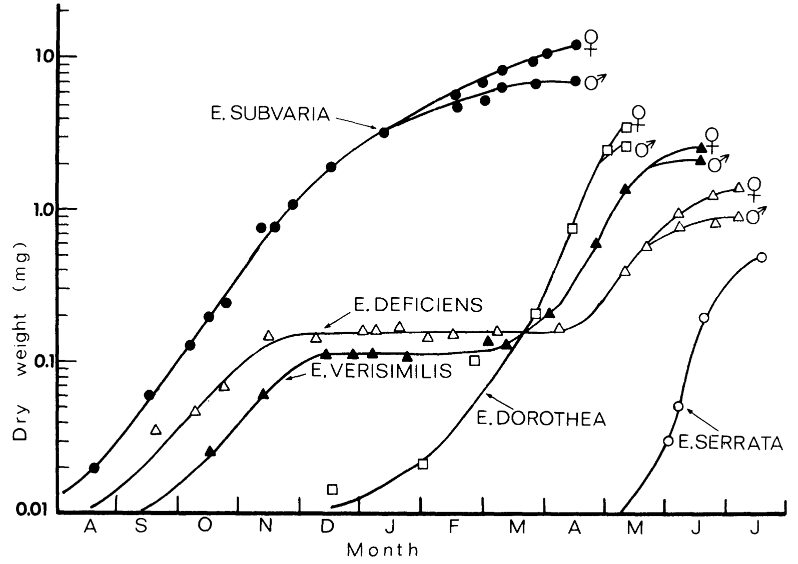


FIG. 14.—Population growth curves for *Ephemerella* species in a third order tributary of White Clay Creek. Each data point is the mean dry weight of larvae for a specific sample data (sample size ≥ 100). ● = *E. subvaria;* △ = *E. deficiens;* ▲ = *E. verisimilis;* □ = *E. dorothea;* ○ = *E. serrata.*

15). (Fine particulate detritus was added to experimental trays at weekly intervals. Algae collected from White Clay Creek was added at the beginning of the experiments and *in situ* production of diatoms remained between 0.05 and 0.10 $\mu g/cm^2$ day for the rest of the experiment [see Sweeney 1976*b*].)

Decreased adult size and fecundity has also been observed for other "summer-active" species reared at cold temperatures (table 3) as well as "winter-active" species reared at warm temperatures (table 4). These studies also show that maximum adult size is usually not associated with maximum larval growth rate. For all species that we have studied, temperature above and below the optimum (i.e., thermal regime that maximizes individual body size and fecundity) appear to suppress larval tissue growth more than adult tissue development, and this leads to the production of small adults. Maximum adult size occurs at intermediate rearing temperatures which apparently optimize the relationship between larval and adult tissue growth.

GEOGRAPHIC DISPERSAL AND THERMAL VARIATION

Because temperature varies both within and between river systems (e.g., fig. 2 and 4, respectively), macrogeographic extension of a species range may require movement of subpopulations into higher or lower order tributaries. For example, southern dispersal of a boreal species might involve movement into cool, low order tributaries (headwater compression) or into streams at increased altitudes. These movements could provide a partial compensatory mechanism for range

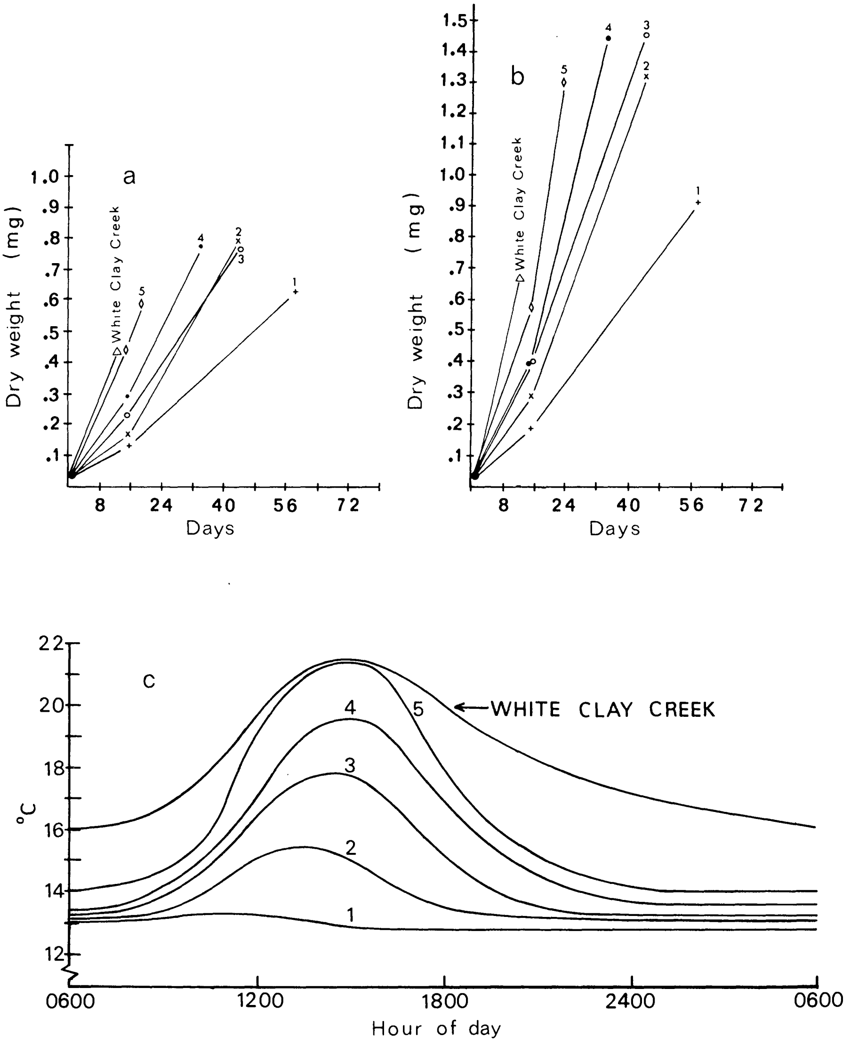


FIG. 15.—Growth curves for *a*, Male and *b*, Female *Centroptilum rufostrigatum* larvae reared at natural stream temperatures (*c*, White Clay Creek) and in five experimental regimes (*c*, 1–5) having diel fluctuations of various amplitudes.

extension along a latitudinal thermal gradient. Spatial shifts would be needed because insects do not acclimate generally (see Keister and Buck 1974 for review) and fecundity must be kept reasonably high for successful invasion into established and highly structured communities while dispersing geographically.

The energetics and developmental dynamics of dispersing within a stream system (i.e., upstream or downstream) or between stream systems (i.e., northern and southern dispersal) by a midlatitude insect species is described in fig. 16. To simplify this conceptual model, we assume (perhaps unrealistically) that during dispersal between streams, the position (i.e., stream order) of the subpopulation

TABLE 3

Results of Growth Experiments for Five Summer Species of Aquatic Insects Reared under One Natural (WCC) and Five Experimental Temperature Regimes

Species	Thermal Regime	Temperature (Max, Mean, Min)	W_i	W_f	No. Days	GR	No. Eggs
Centroptilum rufostrigatum	1	13.4, 13.0, 12.8	.03 ± .01	.91 ± .08	58	.058	289
	2	15.5, 14.2, 13.1	.04 ± .01	1.31 ± .08	43	.081	355
	3	18.0, 14.7, 13.3	.03 ± .01	1.46 ± .06	43	.090	380
	4	19.7, 15.5, 13.5	.04 ± .01	1.45 ± .14	34	.105	378
	5	21.2, 16.4, 13.7	.04 ± .01	1.28 ± .18	19	.182	350
	WCC	21.3, 18.5, 15.9	.04 ± .01	.66 ± .04	13	.215	248
Tricorythodes atratus	1	12.3, 12.0, 11.9	.04 ± .01	1.42 ± .07	64	.055	333
	2	14.3, 13.3, 12.1	.04 ± .01	1.51 ± .25	53	.068	348
	3	16.6, 14.2, 12.1	.16 ± .02	1.59 ± .22	47	.048	362
	4	17.6, 14.5, 12.2	.06 ± .01	1.69 ± .27	36	.092	379
	5	19.6, 14.9, 12.5	.15 ± .03	1.71 ± .26	33	.073	382
	WCC	18.7, 17.1, 15.3	.10 ± .02	1.72 ± .25	31	.091	384
Isonychia bicolor	1	12.6, 12.3, 12.0	.70 ± .07	...	...	...	...
	2	14.7, 13.1, 12.1	.82 ± .05	...	...	...	...
	3	16.9, 13.8, 12.4	.75 ± .04	8.09 ± .38	60	.039	713
	4	18.5, 14.5, 12.6	.77 ± .04	9.63 ± .54	46	.054	885
	5	20.1, 15.4, 12.9	.74 ± .03	9.54 ± .56	42	.060	876
	WCC	20.5, 18.5, 16.6	.76 ± .04	9.43 ± .83	43	.058	864
Caenis simulans	1	12.3, 12.0, 11.9	.04 ± .01	...	...	...	...
	2	14.3, 13.3, 12.1	.04 ± .01	.28 ± .01	62	.031	...
	3	16.6, 14.2, 12.1	.04 ± .01	.38 ± .01	42	.053	...
	4	17.6, 14.5, 12.2	.04 ± .01	.43 ± .02	41	.057	...
	5	19.6, 14.9, 12.5	.04 ± .01	.47 ± .02	36	.068	...
	WCC	18.7, 17.1, 15.3	.04 ± .01	.50 ± .04	34	.074	...
Sigara alternata	1	12.6, 12.4, 12.2	.02 ± .00	.80 ± .03	82	.044	...
	2	14.7, 13.2, 12.3	.02 ± .00	.75 ± .02	79	.045	...
	3	16.9, 13.9, 12.5	.02 ± .00	.90 ± .03	67	.056	...
	4	18.0, 14.2, 12.6	.02 ± .00	1.10 ± .03	58	.069	...
	5	19.7, 15.2, 12.8	.02 ± .00	1.10 ± .03	46	.087	...
	WCC	19.2, 16.8, 15.0	.02 ± .00	1.08 ± .03	42	.094	...

Note.—Maximum and minimum temperatures (° C) represent an average of the three highest and three lowest temperatures, respectively, taken from thermograph records of each experiment. Mean temperatures were calculated from hourly readings taken from continuous temperature recordings. Missing data indicate thermal regimes under which larvae did not successfully metamorphose. Initial larval weights (W_i) are for a representative subsample of larvae (male and female) placed in each treatment; final weights (W_f) are for adult females only. All weights are in mg. The no. of days indicates the amount of time between starting the experiment and the appearance of the first adult female. Instantaneous growth rate (GR) was calculated as mg mg^{-1} day^{-1} using the equation $GR = (\ln W_f - \ln W_i) \div$ no. days. The no. of eggs per average-sized female was estimated by the following regression equations describing fecundity (F) as a function of female dry weight (DW) for each mayfly species: *Centroptilum rufostrigatum*, $F = 165.0\text{DW} + 139.6$, $N = 24$, $r^2 = .70$; *T. atratus*, $F = 171.7\text{DW} + 89.3$, $N = 40$, $r^2 = .59$; *I. bicolor*, $F = 112.4\text{DW} - 195.4$, $N = 45$, $r^2 = .84$. Fecundity for *Caenis simulans* ranged between 95 and 240 eggs per female, but we could not develop an accurate fecundity–dry weight relationship because of the small size of the species. Egg counts on *S. alternata* were not possible because adult females feed extensively prior to oogenesis.

TABLE 4

RESULTS OF GROWTH EXPERIMENTS FOR SEVERAL WINTER-SPRING SPECIES OF MAYFLIES REARED UNDER FOUR THERMAL REGIMES

Species	Thermal Regime	Temperature (Max, Mean, Min)	W_i	W_f	No. Days	GR	No. Eggs
Leptophlebia cupida	WCC	16.7, 6.5, 2.1	.97 ± .05	9.21 ± .29	77	.029	2054
	WCC + 2° C	15.9, 8.5, 5.4	.97 ± .05	9.26 ± .39	64	.035	2065
	WCC + 5° C	13.3, 10.2, 8.8	.97 ± .05	7.55 ± .49	49	.041	1702
	15 ± 1° C	15.5, 15.0, 14.5	.97 ± .05	6.16 ± .26	32	.057	1407
Ameletus ludens	WCC	14.3, 5.8, 2.1	.66 ± .05	3.85 ± .22	71	.024	402
	WCC + 2° C	12.1, 7.5, 5.4	.66 ± .05	3.51 ± .41	54	.030	364
	WCC + 5° C	14.3, 10.6, 8.8	.66 ± .05	3.31 ± .27	54	.029	342
	15 ± 1° C	15.5, 15.0, 14.5	.66 ± .05	2.24 + .17	33	.037	223
Ephemerella subvaria	WCC	14.5, 5.4, 2.1	2.48 ± .26	6.57 ± .50	94	.011	533
	WCC + 2° C	15.9, 8.5, 5.4	2.54 ± .29	4.87 ± .26	94	.006	430
	WCC + 5° C	13.5, 9.5, 8.5	2.41 ± .21	3.98 ± .28	77	.006	375
	15 ± 1° C	15.5, 15.0, 14.5	2.44 ± .22	3.57 ± .29	56	.006	355
Ephemerella funeralis	WCC	18.2, 7.8, 2.1	.87 ± .05	3.52 ± .63	91	.015	775
	WCC + 2° C	18.1, 9.7, 5.4	.87 ± .05	3.53 ± .15	70	.020	777
	WCC + 5° C	17.8, 11.7, 8.8	.87 ± .05	3.92 ± .10	59	.025	830
	15 ± 1° C	15.5, 15.0, 14.5	.87 ± .05	4.42 ± .23	40	.040	898

NOTE.—WCC = ambient water temperature of White Clay Creek; WCC + 2° C = about 2° C warmer than White Clay Creek while following both diel and seasonal changes in temperature; WCC + 5° C = about 5° C warmer than White Clay Creek; and constant 15 ± 1° C. Data on temperature (Max, Mean, Min), initial weight (W_i), final weight (W_f), no. of days, and growth rate (GR) were estimated as described for table 3. The no. of eggs per average-size female was estimated by the following regression equations describing fecundity (F) as a function of dry weight (DW): *L. cupida*, $F = 212.3\text{DW} + 99.4, N = 305, r^2 = .46$, *A. ludens*, $F = 111.6\text{DW} - 27.0, N = 151, r^2 = .52$; *E. subvaria*, $F = 59.3\text{DW} + 143.4, N = 129, r^2 = .44$; *E. funeralis*, $F = 135.5\text{DW} + 299.3, N = 143, r^2 = .33$.

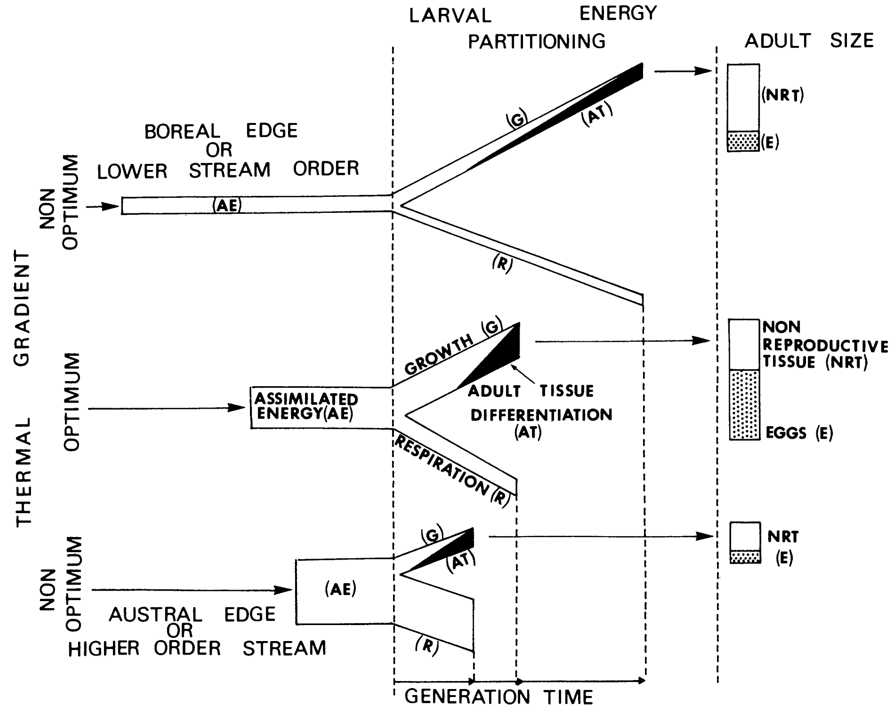


FIG. 16.—Conceptual model describing shifts in developmental rates and energy use by an aquatic insect reared in optimum and nonoptimum thermal regimes. The area of each block depicts the relative amount of assimilated energy (*AE*) partitioned into growth (*G*) or lost through respiration (*R*) during the course of larval development. Blackened growth areas represent adult tissue (*AT*) maturation; generation time is defined as length of the larval growth period. Adult size (area *NRT* + *E*) equals the amount of energy accumulated during larval growth (area *G* + *AT*). Partitioning of adults into nonreproductive tissue (*NRT*) and eggs (*E*) was based on experimental studies of several insect species from the White Clay Creek.

within the drainage network remains constant. The model shows that movement from optimum thermal conditions into warmer (i.e., higher order or more southern) streams may result in (i) increased rate of energy assimilation per individual, (ii) relatively less energy available for growth due to a disproportional increase in maintenance metabolism, (iii) adult tissue maturation (shaded area) beginning earlier in development and proceeding rapidly, thus reducing the time available for larval growth, and (iv) decreased adult body size and egg production due to the short growth period and high maintenance requirements.

Conversely, dispersal from the optimum conditions into colder streams (lower order or more northern) may be accompanied by (i) reduced assimilation rates per individual but similar allocation of energy between growth and metabolism, (ii) adult tissue maturation proceeding slowly, thus increasing the duration of the larval stage, (iii) reduced size due to low temperatures differentially suppressing the developmental rates of adult and larval tissue (i.e., slightly favoring adult tissue maturation), and (iv) reduced fecundity because of reduced size and incomplete conversion of stored materials into eggs at low temperatures. This conceptual model assumes that a constant total amount of energy is assimilated by an individual during its larval growth regardless of geographic location, with changes occurring only in process rates and energy partitioning. This assumption is based on larval energy budgets calculated for several insect species from White Clay Creek that were reared in a wide range of temperature regimes and where food quality and quantity were not limiting (Sweeney 1976*b*, 1978; Sweeney and Schnack 1977; R.L. Vannote, unpublished data).

Using the above models, figure 17 describes the theoretical response of life-history parameters for *Ephemerella dorothea* with (i) movement upstream and downstream from midorder tributaries of White Clay Creek (stream order change), or (ii) northern and southern dispersal to distant drainage systems (latitudinal change). White Clay Creek is about midway between the known northern and southern distributional limits for *Ephemerella dorothea* (Allen and Edmunds 1965). Note that maximum adult size is not correlated with larval growth rate. This is one important aspect of our model that differs from existing ecological models for metamorphosis of other aquatic organisms (see Wilbur and Collins 1973). To our knowledge, data concerning generation time and adult size and fecundity of *Ephemerella dorothea* are not available for subpopulations outside White Clay Creek.

Limited observations on a closely related species, *Ephemerella subvaria*, are consistent with the above hypothesis (fig. 18). These data show increased generation time and decreased adult size in northern populations. Experimental thermal regimes similar to streams beyond the known southern distributional limit yield a short generation time, small adults, and low egg production. Thus, the headwater extremities of first-order streams at 34° N probably represent the absolute limit to the potential southern distribution of this species.

Morphometric and geographic observations for the mayfly genus *Centroptilum* are also consistent with our hypothesis. Distributional records in Edmunds et al. (1976) show only four of 16 eastern North American species with ranges extending into the southeast United States. Our data for *Centroptilum rufostrigatum* suggest that the White Clay Creek population is at or near the southern limit of its range, since individual weights of adult males and females more than doubled when larvae were reared in cooler thermal regimes (fig. 15). Edmunds et al. (1976) report this species as occurring only in eastern Canada. Range extension into the northeast United States is apparently restricted to cool low-order tributaries.

Two of the four southern species of *Centroptilum* have been found only in mountain areas of North Carolina and Alabama. Traver (1932) described one species as being "smaller than any species recorded from the United States or Canada" and doubtfully referred to the specimen as "*C. album* McD.?" Berner (1950) described two small species in northern Florida and noted that nymphs occur mainly in streams that are "spring fed" or the "main spring runs." We suggest that southern populations of *Centroptilum* are compressed into high altitude or low-order streams where annual thermal regimes enable adult body size and fecundity to exceed some lower threshold for continuous recruitment.

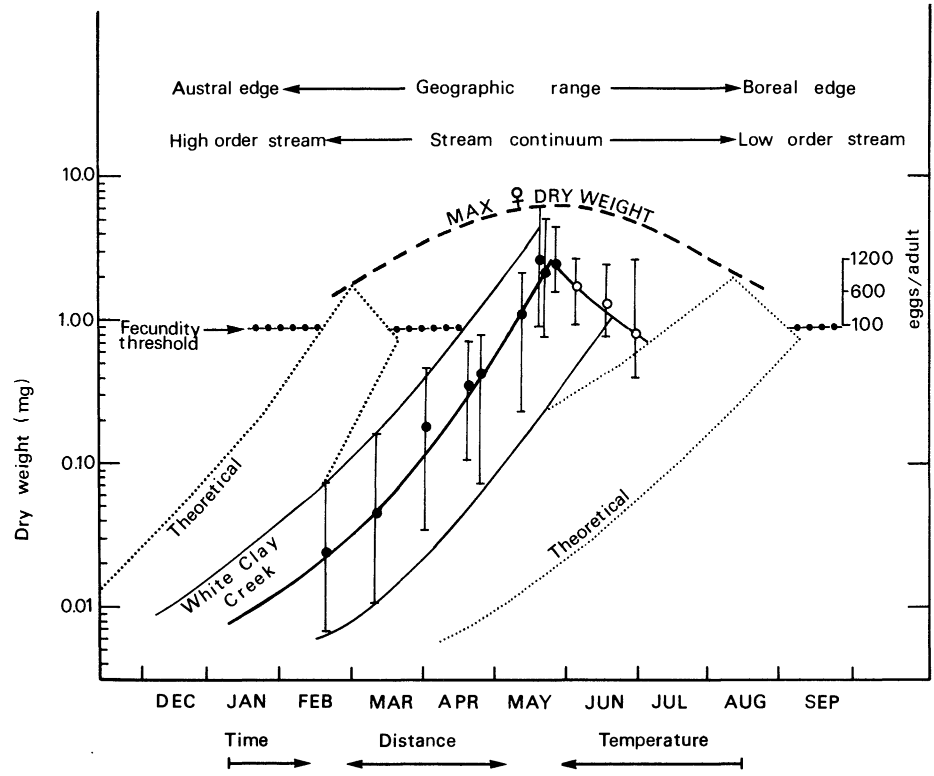


FIG. 17.—Population growth and fecundity (actual and theoretical) of *Ephemerella dorothea* at various locations in its geographic range or along the river continuum.

Recent studies on marine invertebrates (Foraminifera) also suggest that intraspecific variation in sizes may be a phenotypic response to thermal differences occurring throughout the geographic range of many species (Hecht 1976). These data also show that both size and relative abundance of a species generally reach a maximum in the same geographic location (and hence thermal regime). This geographic location is considered "optimal" because the relative abundance of the species is maximized. We have hypothesized for aquatic insect species that maximum size and relative abundance should be correlated, but our definition of "optimal thermal regime" is independent of this hypothesis. Although bioenergetic and developmental data (as used in our model) are not available for Foraminifera, we suggest that the patterns of size variation and geographic distribution observed for these invertebrates tend to support our observations concerning aquatic insects.

THERMAL ASPECTS OF INSECT COMMUNITY DEVELOPMENT

Climatic instability and geographic isolation have been implicated as being important components in the speciation of aquatic insects and the development of order and structure in river communities (Ross 1972). Thermal variation associ-

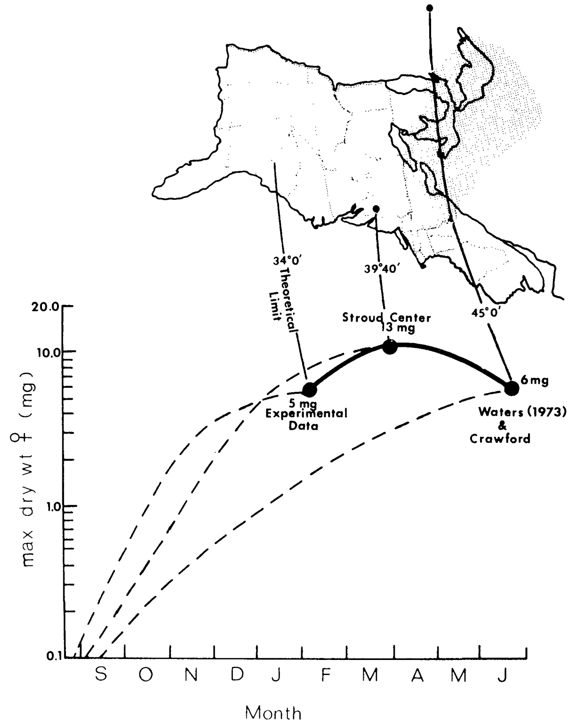


FIG. 18.—Seasonal growth curves and adult body size of female *Ephemerella subvaria* at different points in its geographical distribution. Stippled area represents the known geographic distribution for the species (Allen and Edmunds 1965). Wet weight data from Waters and Crawford (1973) were converted to dry weight by multiplying by a correction factor (.206) derived experimentally.

ated with glacial and interglacial periods was apparently a critical factor in the evolution of large complexes of "sister" species for many North American aquatic genera (Ross and Ricker 1971). Insect fauna of contemporary river communities often contain one or more sets of closely related species within each functional group (e.g., fig. 13 and 19 for White Clay Creek). Functional group refers to a group of species that occupy a similar trophic position in a given habitat and obtain food material in a similar fashion; e.g., "grazer" of benthic periphyton, "shredder" of coarse particulate organic material, "filter feeders" on suspended organic matter, etc. For each species complex, temperature appears to be the critical factor keeping individual subpopulations synchronized and reducing competition by temporal segregation within a given habitat (Vannote 1978).

We view community development as a long-term assembly of numerous species into discrete functional groups. This may lead to efficient annual use of stream resources through spatial, temporal, and trophic specialization. The developmental process entails a highly structured interaction at the following levels of community organization (i) within populations of competing species, (ii) among competing species within functional groups, (iii) between entire functional groups,

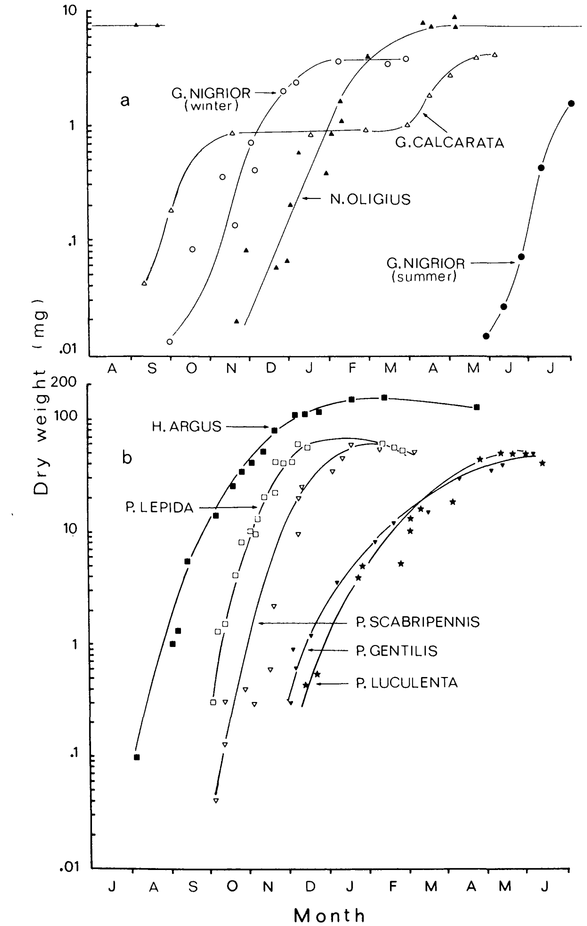


FIG. 19.—Temporal sequencing of population growth for species in two functional groups of aquatic insects in a third order tributary of White Clay Creek. *a*, Caddisfly "grazers" (graze algae off rocks in riffle areas). *b*, Caddisfly "shredders" (consume leaf litter).

and (iv) predator-prey associations. These interactions exert an effect (positive or negative) on the entire community as well as "looping back" to influence the interacting species themselves (Wilson 1976; Levins 1976). For example, aquatic insects that collect fine particulate organic material (i.e., "collectors") are affected positively by the efficiency of species that produce fine particles from coarse particles of organic material (e.g., leaf litter and wood).

Data for White Clay Creek suggest that the development of aquatic insect communities has involved a trade-off between maximum efficiency of resource use and continuous exploitation of available resources (Vannote 1978). A complex of closely related species within a functional group appears to reduce negative feedback at the community level (e.g., minimize competition) while increasing the efficiency of community function. It is difficult to test whether an existing "species complex" represents a high degree of community development or is merely a random gathering from a large pool of closely related and regionally available species. The *Ephemerella* series (fig. 13) in White Clay Creek support the former explanation. Maximum instantaneous growth rates are equivalent for each species despite large differences in the seasonality of population growth. The overlap of maximum production, resource exploitation, and adult emergence by each *Ephemerella* species appears too small for a random event. This is particularly evident since almost 25 species of *Ephemerella* occur near White Clay Creek (table 5). In fact, almost every state in the Atlantic drainage contains about 25 species of *Ephemerella*, but any given stream reach rarely contains more than five. Temperature must be considered a key factor affecting the number and kinds of *Ephemerella* species occurring in a specific stream, especially since our data show most species in the complex to be highly temperature dependent.

We view the *Ephemerella* complex in White Clay Creek as a "point observation" of a much longer developmental process involving population replacement within the community (i.e., evolution at the community level). Addition and extinction of species from a complex may be a response to the following relationships (i) productivity and/or variety of available resources, (ii) accommodation of species through greater resource overlap or specialization to narrow resource segments, and (iii) overall efficiency of the complex in the controlled use of available resources.

Insect communities in streams have developed within the constraints of the physical system. Temperature assumes a major role in synchronizing local subpopulations (e.g., *Ephemerella* species in White Clay Creek) to narrow portions of the resource spectrum (Vannote 1978). This probably reflects paleoclimatic variation during speciation which produced populations having different thermal optima. Annual thermal variation of contemporary streams tends to distribute these optima over the year such that activity periods of closely related species are sequenced temporally. Diel temperature change appears to increase the potential number of species exposed to an optimum temperature during part of each day (Sweeney 1978). The annual and diel predictability of thermal variation is consistent with the development of a diverse but highly structured insect community.

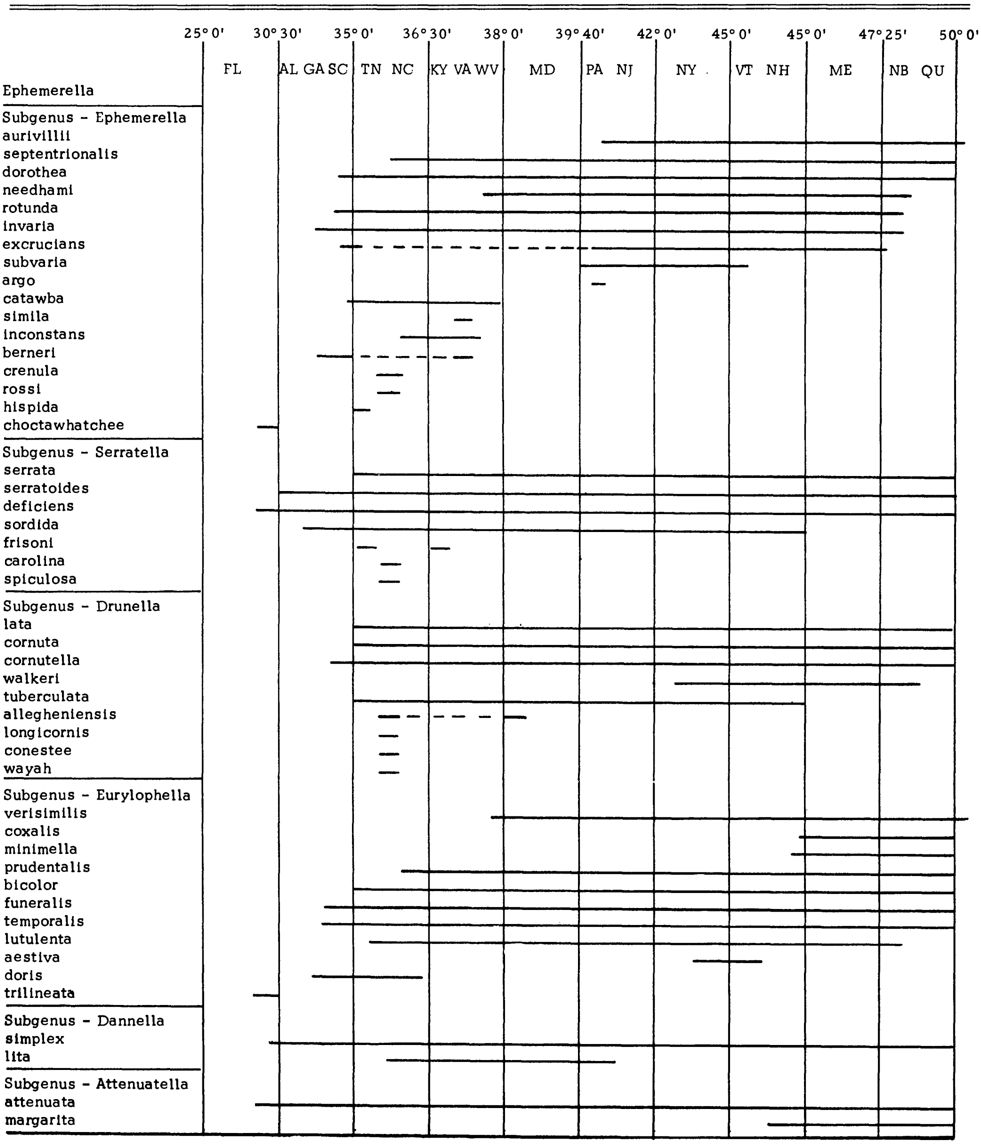
CONCLUSIONS

The case supporting a thermal equilibrium hypothesis for size variation in aquatic insects is compelling. A large body of experimental evidence suggests a rapid bioenergetic and developmental response to temperature. The thermal equilibrium model presented here was developed mainly from bioenergetic and developmental studies of insects in White Clay Creek under a broad array of natural and experimental thermal regimes. Although the data base is highly sitespecific, the generality of our thermal equilibrium model may not be limited since numerous taxa, differing functionally, morphologically, and developmentally, were used for its development.

It is unlikely that temperature is the only factor affecting size variation and the geographic distribution of aquatic insects. It is even more unlikely that temperature should be judged as a factor of only marginal importance. The significance of

TABLE 5

Known Geographic Range of *Ephemerella* Mayflies along the Atlantic Drainage (From Allen and Edmunds 1965)



temperature to aquatic insect life history is indisputable. Temperature assumes a controlling or at least a modifying role in most aspects of insect development. We view local and geographic thermal variation of rivers as a primary force controlling the composition, development, and function of aquatic insect communities. At the population level, thermal patterns may place absolute limits (e.g., high mortality, zero fecundity, etc.) or play a qualifying role (e.g., reduced competitiveness at low population densities, increased susceptibility to predators due to longer larval period, etc.) on a species distribution. At the community level, temperature affects process and production rates and divides the year into seasonal periods for activity by particular species or groups of species. The predictability of stream temperature patterns (diel, seasonal, and annual) are conducive to the development of communities that are both functionally predictable and highly structured.

SUMMARY

Adult body size and fecundity of several species of hemimetabolous aquatic insects were shown to depend largely on thermal conditions during larval growth. We suggest that an ''optimum'' thermal regime exists where adult size and fecundity are maximized; temperature regimes warmer or cooler than the ''optimum'' result in small and less fecund adults. Two hypotheses concerning river water temperatures and size variation of adult insects are described. First, maximum adult size reflects an equilibrium between several developmental processes that appear highly temperature dependent, viz., (i) the rate and duration of larval growth, and (ii) the specific time in larval development that adult structures begin maturing and the rate of this maturation process. Second, a species distribution both locally within drainage systems and over a large geographic area is limited, in part, by lowered fecundity as adult size gradually diminishes in streams of increasingly cold or warm temperature cycles. The importance of river water temperatures to insect community development is discussed.

ACKNOWLEDGMENTS

We thank B. Anderson, D. Funk, S. Hyatt, J. Pierson, C. Staub, and B. Vannote for technical assistance. This work was supported by the Rockefeller Foundation, Stroud Foundation, and the Boyer Endowment Research Fund.

LITERATURE CITED

Allen, R. K., and G. F. Edmunds, Jr. 1965. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae) VIII. The Subgenus *Ephemerella* in North America. Misc. Publ. Entomol. Soc. Am. 4:243–282.

Beatty, A. F., and G. H. Beatty. 1968. Origins and biogeographic affinities of the Odonata fauna of Pennsylvania. Pa. Acad. Sci. 42:110–115.

Benech, V. 1972. La fecondite de *Baetis rhodani* Pictet. Freshw. Biol. 2:337–354.

Berner, L. 1950. The mayflies of Florida. University of Florida Press, Gainesville.

Boyd, A. E., and C. P. Goodyear. 1971. Nutritive quality of food in ecological systems. Arch. Hydrobiol. 69:256–270.

Collins, W. D. 1925. Temperature of water available for industrial use in United States. Pages 97–104 *in* U.S. Geological Survey Water Supply Paper 520–F. U.S. Geological Survey, Washington.

Colwell, R. K. 1974. Predictability, constancy, and contingency of periodic phenomena. Ecology 55:1148–1153.

Cummins, K. W. 1974. Structure and function of stream ecosystems. Bioscience 24:631–641.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Theor. Angew. Limnol. 18:1–158.

Edmunds, G., S. Jensen, and L. Berner. 1976. The mayflies of North and Central America. University of Minnesota Press, Minneapolis.

Elliott, J. M. 1967. The life histories and drifting of the Plecoptera and Ephemeroptera in a Dartmoor stream. J. Anim. Ecol. 36:343–362.

Fahy, E. 1973. Observations on the growth of Ephemeroptera in fluctuating and constant temperature conditions. Proc. R. Ir. Acad., Sect. B 73:133–149.

Hecht, A. D. 1976. Size variations in planktonic Foraminifera: implications for quantitative paleoclimatic analysis. Science 192:1330–1332.

Horton, R. E. 1945. Erosional development of streams and their drainage basins: hydrophysical approach to quantitative morphology. Geol. Soc. Am. Bull. 56:275–370.

Hynes, H. B. N. 1970. The ecology of running waters. University Toronto Press, Toronto.

Ide, F. P. 1935. The effect of temperature on the distribution of the mayfly fauna of a stream. Publ. Ont. Fish. Res. Lab. 50:1–76.

———. 1940. Quantitative determination of the insect fauna of rapid water. Univ. Toronto Stud. Fish. Res. Lab. 59:1–20.

Keister, M., and J. Buck. 1974. Respiration: some exogenous and endogenous effects on the rate of respiration. Pages 469–509 *in* M. Rockstein, ed. The physiology of Insecta. Vol. 6. Academic Press, New York.

Lawton, J. H. 1971. Ecological energetics studies on larvae of the damselfly *Pyrrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). Freshw. Biol. 1(1):99–111.

Lehmkuhl, D. M. 1974. Thermal regime alteration and vital environmental physiological signals in aquatic organisms. Pages 216–222 *in* J. W. Gibbons and R. R. Sharitz, eds. Thermal ecology. I. N.T.I.S. [National Technical Information Service] Conf. 730505.

Leopold, L., M. Wolman, and J. Miller. 1964. Fluvial processes in geomorphology. Freeman, San Francisco.

Levins, R. 1976. Evolution in communities near equilibrium. Pages 16–50 *in* M. L. Cody and J. M. Diamond, eds. Ecology and evolution of communities. Harvard University Press, Cambridge, Mass.

Macan, T. T. 1957. The life histories and migrations of the Ephemeroptera in a stony stream. Trans. Soc. Br. Entomol. 12:129–156.

Mackay, R. J. 1969. Aquatic insect communities of a small stream on Mont. St. Hilaire, Quebec. J. Fish. Res. Board Can. 26:1157–1183.

Pattee, E. 1955. Influence d'un changement de température sur la consommation d'oxygène et phénomène d'accountumance chez quelques larves aquatiques d'insects. Bull. Biol. 4:370–378.

Precht, H., J. Christophersen, H. Hensel, and W. Larcher. 1973. Temperature and life. Springer-Verlag, New York.

Ross, H. H. 1963. Stream communities and terrestrial biomes. Arch. Hydrobiol. 59:235–242.

———. 1972. The origin of species diversity in ecological communities. Taxon 21(2/3):253–259.

Ross, H. H., and W. E. Ricker. 1971. The classification, evolution, and dispersal of the winter stonefly genus *Allocapnia*. Ill. Biol. Monog. 45:1–166.

Sayle, M. 1928. Factors influencing the rate of metabolism of *Aeshna umbrosa* nymphs. Biol. Bull. 54:212–223.

Schmid, F. 1955. Contribution a l'etude des Limnophilidae (Trichoptera). Mitt. Schweiz. Entomol. Ges. 28:1–245.

Smith, K. 1972. River water temperatures—an environmental review. Scott, Geogr. Mag. 88:211–220.

Sprules, W. M. 1947. An ecological investigation of stream insects in Algonquin Park, Ontario. Publ. Ont. Fish. Res. Lab. 69:1–81.

Stockner, J. G. 1971. Ecological energetics and natural history of *Hedriodiscus truquii* (Diptera) in two thermal spring communities. J. Fish. Res. Board Can. 28(1):73–94.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Trans. Am. Geophys. Union 38:913–920.

Sweeney, B. W. 1976*a*. A diurnally fluctuating thermal system for studying the effect of temperature on aquatic organisms. Limnol. Oceanogr. 21:758–763.

———. 1976*b*. The response of aquatic insects to thermal variation. Ph.D. thesis. University of Pennsylvania, Philadelphia.

———. 1978. The response of a mayfly to thermal variation. Limnol. Oceanogr. 23:461–477.

Sweeney, B. W., and J. A. Schnack 1977. Egg development, growth, and metabolism of *Sigara alternata* (say) (Hemiptera: Corixidae) in fluctuating thermal environments. Ecology 58:265–277.

Sweeney, B. W., and R. L. Vannote. 1978. Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. Science 200(4340):444–446.

Thibault, M. 1971. Écologie d'un ruisseau a truites des Pyrénées Atlantiques Le Lissuraga. II-Les fluctuations thermiques de l'eau; répercussion sur les périodes de sortie et la taille de quelques éphéméroptères, plécoptères, et tricoptères. Ann. Hydrobiol. 2:241–275.

Traver, J. R. 1932. *Neocloeon*, a new mayfly genus (Ephemerida). N.Y. Entomol. Soc. J. 40:365–373.

Vannote, R. L. 1973. Effects of natural temperature on invertebrates. Pages 1228–1243 *in* Effects and methods of control of thermal discharges Part 3, 1181–1270. An Environmental Protection Agency report to the Senate Committee on Public Works, November, 1973 [Serial no. 93-114].

———. 1978. A geometric model describing a quasi-equilibrium of energy flow in populations of stream insects. Proc. Natl. Acad. Sci. USA 75:381–384.

Waters, T. F., and G. W. Crawford. 1973. Annual production of a stream mayfly population: a comparison of methods. Limnol. Oceanogr. 18:286–296.

Wieser, W. 1973. Temperature relations of ectotherms: A speculative review. Pages 1–24 *in* W. Wieser, ed. Effects of temperature on ectothermic organisms. Springer-Verlag, New York.

Wilbur, H. M., and J. P. Collins. 1973. Ecological aspects of amphibian metamorphosis. Science 182:1305–1314.

Wilson, D. S. 1976. Evolution at the level of communities. Science 192:1358–1360.