

DEGREE-DAYS AND THERMAL EFFICIENCY:
A CASE AGAINST THEIR USE IN DESCRIBING
AQUATIC INSECT GROWTH AND THERMAL OPTIMA

Michael J. Benton¹
Division of Ecology
Department of Biological Sciences
University of Calgary
Calgary, Alberta T2N 1N4 Canada

Received 16 December 1987, 7 April 1988

ABSTRACT: The use of degree-days to describe the thermal units necessary for larval aquatic insect development is widespread in the literature. Degree-day requirements are often based on constant experimental temperatures or mean field temperatures, even though natural thermal regimes generally exhibit diel and seasonal fluctuations which may profoundly affect growth patterns. Threshold growth temperatures are often extrapolated from development times at constant temperatures or simply assumed to be 0°C. Growth thresholds may in fact vary among closely related species, among developmental stages of the same species, or even among conspecific populations occupying thermally similar habitats. Because: 1) growth rates may respond nonlinearly to temperature, 2) the amount of time spent at high temperature can drastically affect growth, and 3) threshold temperatures for growth often vary among developmental stages, populations, and species, the degree-day approach often serves little purpose in the description or prediction of actual growth patterns in natural populations of aquatic insect larvae.

Degree-days have also been used to calculate thermal efficiency in insect egg and larval development, and thermal efficiency has been employed as an indicator of selection for particular thermal optima. However, evidence extrapolated from the literature shows no relationship between thermal efficiency and adaptiveness when mortality and fecundity factors are considered.

* * *

DISCUSSION

Degree-days have often been used to describe the number of thermal units required to complete all or part of insect larval development. Generally, degree-day requirements for eggs and larvae decrease as the developmental temperature increases up to some critical limit, then begin to increase as biochemical disruption occurs (Ward and Stanford, 1982; Wright et al., 1982; Brittain et al., 1984; Williams and Richardson, 1984), although this pattern is not universal (e.g. Hawkins, 1986). Regardless, developing insect larvae are likely to exhibit growth patterns that are responsive to thermal parameters other than total heat units, and which may differ among various life stages, populations, or species. Thus, the degree-day method often sheds little descriptive or predictive light on insect growth patterns as they occur under natural thermal regimes.

Thermal sums as growth predictors/descriptors have shortcomings in at least two important areas:

First, the minimum temperature required to induce growth and development among closely related species, among developmental stages of a single species, or among conspecifics occupying separate but thermally similar habitats is not necessarily constant. Mackey (1977)

* * * * *
¹Present address: Dept. of Biol. Sci., Univ. of Cincinnati, Cincinnati, OH 45221
Evolutionary Theory 8: 155-161 (May, 1988)

The editors thank C.A. Tauber and two other referees for help in evaluating this paper.
© 1988, Biology Department, The University of Chicago.

has shown that developmental zeroes among 25 species of chironomids range from -4°C to 12°C . Corbet (1957) proposed that in odonates the minimum temperatures required to induce growth may be different for various larval body sizes. In this way, small larvae that begin growing earlier in the year at colder temperatures may "catch up" to larger larvae that begin growing later at higher temperatures, thus explaining the lack of size variation in adult odonates. In contrast, Sweeney and Vannote (1981) argued that above a certain threshold temperature growth commences in all size classes of some mayfly species and proceeds uninterrupted to adulthood. This may account for the size variation often observed in a single adult mayfly cohort. However, Hawkins (1986) found that initiation of growth in some Ephemera nymphs differed by as much as four months among populations occupying streams of similar water temperature.

Obviously, estimates of degree-days necessary for development will vary considerably for the same species depending simply on what threshold temperature for growth is used. Ideally, therefore, growth thresholds will be determined experimentally for a number of larval stages. Unfortunately, growth thresholds are often extrapolated by linear regression, i.e. plotting temperature on the x-axis and development time or growth rate on the y-axis, then using the x-intercept as the developmental zero (Bar-Zeev, 1958, Markarian, 1980, Wright et al., 1982; Williams and Richardson, 1984). Others have estimated growth threshold as the lowest mean temperature at which a difference in consecutive monthly mean body sizes is recorded (Markarian, 1980), while many researchers simply assume the growth threshold is 0°C . Ross and Merritt (1978) reported that by assuming a growth threshold of 0°C , estimates of degree-day requirements for the blackfly Prosimulium mixtum/fuscum range from 240 d°C (Ross and Merritt, 1978) to 1110 d°C (Davies and Syme, 1958), and from 275 d°C (Davies et al., 1962) to 525 d°C (Mokry, 1976) for Simulium venustum. Clearly it is necessary to first properly determine the growth threshold for a specific population and for as many developmental stages as is practical before attempting to evaluate, describe, and predict the effects of temperature on the growth patterns of that population. Because growth may even occur at temperatures below 0°C (Mackey, 1977), some provision must also be made to account for that heat energy. While this admittedly would not apply in freshwater systems, it may apply in brackish, marine, or polluted systems.

Second, growth rate is not usually constant over a range of temperatures above the growth threshold. High temperatures serve to speed enzymatic and hormonal actions, and so accelerate growth and development. But egg development and larval growth of some species may be keyed to "spikes" of maximum temperature rather than to mean temperature (Huffaker, 1944; Sweeney and Schnack, 1977; Sweeney, 1978). Periods of rapid larval development occur during these thermal spikes, while prolonged exposure to the same high temperature may actually reduce the degree of growth stimulation (Shelford, 1927; Headlee, 1940; Sweeney and Schnack, 1977). Thus, such prolonged exposure to high temperature, or early stimulation of adult tissue maturation can lead to early metamorphosis at a reduced adult size and fecundity. By stimulating diapause development, periods of exposure to low temperatures may also shorten maturation time as compared to exposure to constant higher temperature (Schaller, 1968). Other larvae may actually develop more slowly under conditions of fluctuating temperatures (Bradshaw, 1980). So it is clear that the exact nature of a particular thermal regime (e.g. presence or absence of fluctuations,

duration and amplitude of fluctuations), which thermal sums do not reflect, may be extremely important in determining the growth patterns of resident larval populations, and should therefore be part of any complete treatment of the relationship between temperature and growth.

Some of the difficulties and shortcomings of the degree-day approach to optimal growth are demonstrated by data I collected for the siphonurid mayflies Ameletus celer McDunnough and A. similior McDunnough (see Benton, 1987). A. celer was collected from Ford Creek, and A. similior from the headwaters of the Elbow River. Both sites are located in the Bow/Crow Forest in southwestern Alberta, Canada. The headwaters of the Elbow River is a cold, spring-fed site with practically no diel thermal fluctuation and seasonal mean temperatures of from 2°C to 6°C. Ford Creek is a warmer stream with wide daily temperature fluctuations and seasonal mean temperatures of from 0°C to nearly 10°C. However, due mainly to differences in winter water temperatures, the annual degree-day total at the Elbow River site (1304) is nearly as high as at Ford Creek (1386). Despite this similarity, A. similior requires almost twice as much time (approximately 23 months) as A. celer (approximately 12 months) to complete larval development to an adult of about the same size. Degree-day requirements are approximately 1386 for A. celer, but approximately 2752 for A. similior. This is certainly due to the difference in summer thermal regimes. Mean high water temperatures at Ford Creek during June, July and August are nearly double those at Elbow River during the same period, and it is surely this difference which allows A. celer to undergo a period of rapid growth and emerge in a single year. During winter Elbow River, which receives a constant influx of spring water and remains unfrozen, is actually warmer than Ford Creek which freezes over. From December through February, monthly thermal sums at Elbow River are more than two times greater than at Ford Creek. But this is misleading because monthly size-frequency distributions suggest that winter temperatures are probably too low for substantial growth at either site. Thus, degree-day calculations do show some thermal differences between sites during certain months, but specifically how thermal regimes differ is not obvious. Statements about the mechanisms which promote faster growth at Ford Creek cannot be made in sufficient detail from degree-day information alone, and meaningful descriptive and predictive potentials are lost. Fahy (1973) found a different pattern in Baetis rhodani, which developed at the same rate in both constant and fluctuating thermal regimes, while the total degree-days required for development was substantially higher under fluctuating temperature conditions. Ross and Merritt (1978) reported still another pattern. Two successive cohorts of the black fly Prosimulium mixtum/fuscum required the same number of degrees-days to complete development, but the second cohort, which developed under higher ambient temperatures, had a smaller final body size and fewer larval stages (see also Merritt et al., 1982). This was presumably due to the higher thermal maxima to which the second cohort was exposed.

Because growth does not always respond linearly with temperature, the use of the degree-day method has been criticized before (Shelford, 1929; Sweeney and Schnack, 1977). This method is often limited to the description of a thermal sum (which may be only one of several factors determining growth responses to temperature) above some growth threshold (which may be neither reliably determined nor constant over the life cycle) at certain constant temperatures (which usually fluctuate on a diel and a seasonal basis under natural conditions). Thus, the actual descriptive and predictive worth of this method for insect growth in

natural habitats is questionable. This is particularly true in fluctuating temperature regimes where it is possible to have similar heat-unit totals among very different thermal environments, and where the duration and magnitude thermal maxima may heavily influence growth.

Aquatic insect growth responses to temperature are not indescribable, but care must be taken to provide sufficient correct information for inferences to be made regarding growth under natural conditions. I believe that, minimally, this information should include: 1) experimentally determined growth threshold temperatures for a number of life stages in each population being studied, 2) a description of the natural thermal regime including average daily minima and maxima and their durations for each month (or less) of the larval life cycle, and 3) experimentally determined growth responses either to fluctuating temperatures which mimic conditions in the natural habitat, or to mean temperatures with short-term exposures to high temperatures which reflect natural maxima in frequency, magnitude, and duration. Such experimentation will require an increase in effort and equipment over constant temperature rearing experiments, but not a prohibitively great one. The result will be more realistic descriptions of how larval growth responds to natural thermal regimes, and more realistic predictions about how similar organisms will respond to similar thermal regimes. Of course, the aforementioned complications of geography remain a possibility, and the effects of photoperiod, nutrition, and other biotic and abiotic factors are undeniable (Brittain, 1982; Ward and Stanford, 1982; Perry *et al.*, 1987). However, once descriptions and predictions are complete in sufficient detail, thermal sums should drop out of the picture as unnecessary and be replaced, perhaps, by time sums required under the specific conditions described.

The number of degree-days necessary for the completion of development has been used as an indicator of thermal adaptation in the eggs and/or larvae of stoneflies (Mutch and Pritchard, 1986), mosquitoes (Pritchard and Mutch, 1985), and dragonflies (Pritchard and Leggott, 1986). These authors argued that a slope of less than zero on a double-logarithmic temperature versus degree-day plot indicated an adaptation to higher temperature, while a slope of more than zero indicated an adaptation to lower temperature within some tolerable range. Assuming that an adaptation is the result of selection toward maximum fitness (= maximum body size and fecundity in "r-selected" organisms such as insects [Pianka, 1970]), this suggests that a temperature treatment which minimizes the thermal unit requirement for egg or larval development is optimal. However, neither the brevity of development nor thermal efficiency alone would seem to be a reliable measure of adaptation (i.e. optimality). Mortality and the effects on subsequent growth and ultimate body size must also be considered. Differences in slope may be a reflection of the temperature ranges over which enzymes and hormones related to growth are active. While one would expect a warm water species to be biochemically more active over a higher temperature range than a cold water species, faster or more thermally efficient development at higher temperatures within that range is not necessarily an indication of adaptation to higher temperatures. The very fact that the normal thermal environment is higher for one species is also evidence for thermal adaptation, but optimality must consider survivorship and fecundity (Stearns, 1976). Wright *et al.* (1982) showed that *Hexagenia bilineata* egg development and larval growth were more efficient at higher temperatures. However, larval survival decreased substantially (from 80% at 15°C to 21% at

30°C), while final-instar larval size was differentially affected by temperature in each sex. In both sexes, however, larval size was reduced at 30°C. Similar results can be extrapolated for several species of Ephemerella (Sweeney and Vannote, 1981), for Cloeon triangulifer (Sweeney and Vannote, 1984), and for the stonefly Capnia atra (Brittain et al., 1984). It is evident, therefore, that temperatures which may meet one measure of optimality at a particular life stage often will not ultimately maximize fitness, and so cannot be considered truly optimal (Heiman and Knight, 1975).

If an optimum number of degree-days (i.e. one which maximizes growth and fecundity) is calculable, it again would lack descriptive and predictive strength. What such a thermal sum says about an optimal temperature regime is not clear because of changing growth thresholds and the effects of fluctuating temperatures on growth and heat-unit totals. If growth efficiency is of real interest, degree-days provide no description of the ambient conditions that might maximize the instantaneous growth rate by increased growth ratio and/or decreased moult interval (see Benton and Pritchard, 1988), while still producing adults of maximum size and fecundity. Nor do degree-days provide sufficient information to predict what those conditions might be. The most basic problem, however, may be determining just what phenotypic measure of fitness is really most appropriate (Calow, 1979). Even among the Ephemeroptera, a taxon in which fitness is commonly equated to productivity, there is evidence that reproductive efficiency may in fact be more adaptive in some populations (Benton, 1987). Certainly, current evidence suggests that neither a short development time nor thermally efficient development is necessarily indicative of adaptation to a particular thermal regime.

ACKNOWLEDGEMENTS

I thank Gordon Pritchard, Bernard Sweeney, Fred Wrona, Joseph Culp, and William Ross for their remarks on the original version of this paper, and three reviewers for their comments on a later draft.

LITERATURE CITED

- Bar-Zeev, M. 1958. The effect of temperature on the growth rate and survival of the immature stages of Aedes aegypti (L.). Bulletin of Entomological Research 49:157-163.
- Benton, M. J. 1987. Ecology and bioenergetics of two Ameletus (Siphonuridae:Ephemeroptera) populations. Ph.D. thesis. University of Calgary.
- Benton, M. J. and G. Pritchard. 1988. New methods for mayfly instar number determination and growth curve estimation. Journal of Freshwater Ecology 4:361-367.
- Bradshaw, W. E. 1980. Thermoperiodism and the thermal environment of the pitcher plant mosquito, Wyeomyia smithii. Oecologia 46:13-17.
- Brittain, J. E., A. Lillehammer, and S. J. Saltveit. 1984. The effect of temperature on intraspecific variation in egg biology and nymphal size in the stonefly, Capnia atra (Plecoptera). Journal of Animal Ecology 53:161-169.
- Corbet, P. S. 1957. The life history of the emperor dragonfly Anax imperator Leach (Odonata:Aeshnidae). Journal of Animal Ecology 26:1-69.
- Davies, D. M., B. V. Peterson, and D. M. Wood. 1962. The black flies (Simuliidae) of Ontario. Part I. Adult identification and

- distribution with descriptions of six new species. Proceedings of the Entomological Society of Ontario 92:70-154.
- Davies, D. M. and P. D. Syme. 1958. Three new Ontario black flies of the genus Prosimulium (Simuliidae). Part II. Ecological observations and experiments. Canadian Entomologist 90:744-759.
- Fahy, 1973. Observations on the growth of Ephemeroptera in fluctuating and constant temperature conditions. Proc. R. Ir. Acad., Section B 73:133-149.
- Hawkins, C. P. 1986. Variation in individual growth rates and population densities of ephemereid mayflies. Ecology 67:1384-1395.
- Headlee, T. J. 1940. The relative effects on insect metabolism of temperatures derived from constant and variable sources. Journal of Economic Entomology 33:361-364.
- Heiman, D. R. and A. W. Knight. 1975. The influences of temperature on the bioenergetics of the carnivorous stonefly nymph, Acronuria californica (Banks) (Plecoptera:Perlidae). Ecology 56:105-116.
- Huffaker, C. B. 1944. The temperature relations of the immature stages of the malarial mosquito Anopheles quadrimaculatus Say, with a comparison of the developmental power of constant and variable temperatures in insect metabolism. Annals of the Entomological Society of America 37:1-27.
- Mackey, A. P. 1977. Growth and development of larval Chironomidae. Oikos 28:270-275.
- Markarian, R. K. 1980. A study of the relationship between aquatic insect growth and water temperature in a small stream. Hydrobiologia 75:81-95.
- Merritt, R. W., D. H. Ross, and G. J. Larson. 1982. Influence of stream temperature and seston on the growth and production of overwintering larval black flies (Diptera:Simuliidae). Ecology 63:1322-1331.
- Mokry, J. W. 1976. Laboratory studies on the larval biology of Simulium venustum Say. Canadian Journal of Zoology 54:1657-1663.
- Mutch, R. A. and G. Pritchard. 1986. Development rates of eggs of some Canadian stoneflies (Plecoptera) in relation to temperature. Journal of the North American Benthological Society 5:272-277.
- Perry, W. B., E. F. Benfield, S. A. Perry, and J. R. Webster. 1987. Energetics, growth, and production of a leaf-shredding stonefly in an Appalachian Mountain stream. Journal of the North American Benthological Society 6:12-25.
- Pianka, E. R. 1970. On r- and K-selection. American Naturalist 104:592-597.
- Pritchard, G. and M. Leggott. 1987. Temperature, incubation rates and origins in dragonflies. Advances in Odonatology 3 (in press).
- Pritchard, G. and R. A. Mutch. 1985. Temperature, development rates and origins of mosquitoes. In: Lounibos, L. P., J. R. Rey, and J. H. Frank (editors), Ecology of mosquitoes: proceedings from a workshop. Florida Medical Entomology Laboratory, Vero Beach.
- Ross, D. H. and R. W. Merritt. 1978. The larval instars and population dynamics of five species of black flies (Diptera:Simuliidae) and their responses to selected environmental factors. Canadian Journal of Zoology 56:1633-1642.
- Schaller, F. 1968. Action de la temperature sur la diapause et le developpement de l'embryon d'Aeschna mixta (Odonata). Journal of Insect Physiology 14:1477-1483.
- Shelford, V. E. 1927. An experimental investigation of the relations of the coddling moth to weather and climate. Bulletin of the Illinois Natural History Survey 16:311-440.
- Shelford, V. E. 1929. Laboratory and field ecology. Williams and

- Wilkins, Baltimore.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51:3-47.
- Sweeney, B. W. 1978. Bioenergetic and developmental response of a mayfly to thermal variation. *Limnology and Oceanography* 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. 1981. Ephemerella mayflies of White Clay Creek: bioenergetic and ecological relationships among six coexisting species. *Ecology* 62:1353-1369.
- Sweeney, B. W. and R. L. Vannote. 1984. Influence of food quality and temperature on life history characteristics of the parthenogenetic mayfly, Cloeon triangulifer. *Freshwater Biology* 14:621-630.
- Ward, J. V. and J. A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* 27:97-117.
- Williams, H. and A. M. M. Richardson. 1984. Growth energetics in relation to temperature for larvae of four species of necrophagous flies (Diptera:Calliphoridae). *Australian Journal of Ecology* 9:141-152.
- Wright, L. L., J. S. Mattice, and J. J. Beauchamp. 1982. Effect of temperature and sex on growth patterns in nymphs of the mayfly Hexagenia bilineata in the laboratory. *Freshwater Biology* 12:535-545.