THE EFFECT OF TEMPERATURE ON EGG DEVELOPMENT IN ZYGOPTERA: A PRELIMINARY DISCUSSION

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A brief review of the study of embryonic development in relation to temperature in Zygoptera is presented. Such concepts as the threshold, the minimum effective temperature limit, the upper effective temperature limit, the limits of tolerance for development, the developmental units and the mathematical formulations of the velocity curve are analyzed. A brief discussion of the influence of temperature on the development of *Enallagma boreale* Selys, *E. ebrium* (Hagen), *E. vernale* Gloyd, *E. hageni* (Walsh) and *Ischnura verticalis* (Say) (Zygoptera: Coenagrionidae) in the lower Laurentides of Quebec is also presented.

INTRODUCTION

The environment of living organisms is the summation of all conditions sur-rounding them such as weather, food, other animals and a place in which to live (ANDREWARTHA & BIRCH, 1954). Poikilothermic animals are particularly affected by weather which may be defined as the condition of the atmosphere at a particular time and place in terms of temperature, moisture, pressure, and so on. Of these sub-components of weather, temperature has received the most attention, attracting biologists at least as far back as 1734 when Réaumur (BELEHRADEK, 1935) recognized a relationship between temperature and the activities of organisms. More recently, the effects of temperature on different activities of poikilothermic animals have been reviewed by LOTKA (1925), UVAROV (1931), FRY (1947), ALLEE *et al.* (1949), ANDREWARTHA & BIRCH (1954) and BURSELL (1974).

In this paper, the influence of temperature on the embryonic development of Zygoptera is discussed especially with regard to two mathematical models that have been used to describe the relationship between temperature and rate of development, and in relation to the ecological strategies adopted by five coenagrionid species: *Enallagma boreale* Selys, *E. vernale* Gloyd, *E. hageni* (Walsh), *E. ebrium* (Hagen) and *Ischnura verticalis* (Say).

EMBRYONIC DEVELOPMENT IN ODONATA

According to ANDO (1962), CORBET (1962, 1980) and CORBET *et al.* (1960), egg development in Odonata is either direct or delayed. The duration of direct development has been shown to vary between 5 and 40 days (JOHANNSEN & BUTT, 1941; ASAHINA, 1950; GARDNER, 1950, 1951a, 1951b, 1953, 1954, 1955; BICK, 1951; CORBET, 1955, 1957; GARDNER & MACNEILL, 1950; HODGKIN & WATSON, 1958; AGUESSE, 1959; ANDERSON, 1972). In the case of delayed development two types can be recognized: The first one is represented by eggs laid during the summer and developing to full-grown embryos before the onset of winter (CORBET, 1956; ANDO, 1962; TAI, 1967; BOEHMS, 1971; SAWCHYN & CHURCH, 1973; INGRAM, 1976); the second one is represented by eggs laid in late summer or early autumn and overwintering in a stage prior to katatrepsis (ANDO, 1962; SAWCHYN & GILLOT, 1974; DEACON, 1981). In the second indirect type, development is completed after a period of 80 to 230 days (CORBET, 1980).

Many authors such as BALFOUR-BROWNE (1909), LAMB (1925), KRULL (1929), LIEFTINCK (1933), GRIEVE (1937), MARTIN (1939), BICK (1951), KORMONDY (1959), CORBET (1962, 1980), MIYAKAWA (1971), and BATH (1890) have shown that the incubation period for embryonic development varies greatly not only in different species but also in the same species with eggs laid at the same time. The incubation period of the eggs of some species was also observed to vary in relation to the time of year at which they were laid (LUCAS, 1900; GARDNER, 1950, 1951b; ROBERT, 1958; CORBET, 1962); for example, eggs laid in mid-summer hatched directly while those of the same species laid in the autumn overwintered.

INFLUENCE OF TEMPERATURE ON
EGG DEVELOPMENT IN ODONATA

Temperature is generally recognized by odonatologists as the main factor influencing the rate of embryonic development. Nevertheless, supporting data are scarce even though research on the influence of temperature on incubation and embryogenesis dates back to about a century ago. BEUTENMULLER (1890)

was one of the first to mention the influence of temperature on egg development, but like the great majority of earlier investigators (WARREN, 1915; WILSON, 1917-1918; KRULL, 1929; KENNEDY, 1936; and GRIEVE, 1937, for example, with CALVERT (1929) and ASAHINA (1950) as exceptions) he did not mention the temperatures prevailing during his experiments. Since 1962, research on egg development, performed under various conditions of temperature, has been reported by GARDNER (1951b), CORBET (1956, 1957, 1962), FISCHER (1958), HODGKIN & WATSON (1958), AGUESSE (1959), SCHALLER (1960, 1961, 1962, 1968, 1972), CHUTTER (1961), ZEHRING et al. (1962), GOWER & KORMONDY (1963), LUTZ & PITTMAN (1970), SCHALLER & MOUZE (1970), BOEHMS (1971), SAWCHYN & CHURCH (1973), SAWCHYN & GILLOTT (1974, 1975), DEACON (1975, 1979, 1981), INGRAM & JENNER (1976), HASSAN (1977), TENNESSEN & MURRAY (1978). A program to examine the influence of temperature on the rate of development of zygopteran eggs was initiated by RIVARD et al. (1975). This will be discussed later in this paper. As a result of these studies we are able to make some generalizations on such phenomena as the lethal limits to the temperature range, the pattern of increase in development rate with temperature, the threshold temperature for reactivation of diapause eggs, and the effects of temperatures to which eggs are submitted during embryogenesis on the types of larval development that can be observed (MASSEAU & PILON, 1982a, 1982b).

The general form of the temperature-development curve

There are upper and lower limits to the temperature-development curve, above and below which development does not occur (Fig. 1A). Between these lower and upper limits the duration of complete development decreases generally with an increase in temperature (Fig. 1A, C-D). The reciprocal of the duration of development multiplied by 100 is an expression of the rate, speed or velocity of development (Fig. 1A, E-H), which increases with a rise of temperature up to a maximum level (Fig. 1A, G) before decreasing near the upper effective tempera-ture limit (Fig. 1A, G-H). When taking into consideration not only the velocity of development (Fig. 1A) but also the percentage of individuals accomplishing their development successfully (Fig. 1B), the concept of optimum range can be defined as the "temperature range at which the relatively greatest percentage of individuals accomplished their development within the relatively shortest period" (PEAIRS, 1927; UVAROV, 1931). E. boreale was found to have its optimum range situated between 20° and 27.5°C (RIVARD et al., 1975), E. ebrium between 22.5° and 30°C (PILON, 1982), E. vernale between 22.5° and 30°C (PILON, 1982), E. hageni between 17.5° and 30°C (MASSEAU & PILON, 1982a) and I. verticalis between 22.5° and 32.5°C (FRANCHINI & PILON, 1983) (Table I).

HODSON & AL RAWY (1956) developed their concept of hatching-survival threshold when they noticed that eggs incubated at temperatures outside the optimum range, although successfully completing their embryonic development had a high larval mortality rate. The fact that temperatures outside the optimum

range could have an unfavorable influence on later development could be important in the ecology of Odonata, but no such data exist in the odonatological literature. However, from preliminary rearing of *Libellula julia* Uhler in our laboratory we believe that this effect occurs at temperatures above 30°C.

Mathematical formulation of the velocity curve

DAVIDSON (1942, 1944) proposed the use of the logistic curve to analyze temperature-speed of development data in preference to other formulae, and ANDREWARTHA & BIRCH (1954) established use of this model in spite of some drawbacks in its use. The formulation is the well known:

$$100/y = K/1 + e^{a-bx}$$

where y represents the time required for complete development at temperature x; K is a constant representing the upper asymptote; e = 2.718282; a indicates the relative position of the origin of the curve on the abscissa; and b is a constant representing the degree of acceleration of development.

PRADHAN (1946) proposed a somewhat different formulation to describe the effect of temperature on the velocity of development:

$$Y = Y_o \, e^{-1/2ax^2}$$

where Y is the developmental index (100/y) at temperature t; Yo, the highest value of the developmental index; e = 2.718282; a, is a retardation constant (negative acceleration); and x = T-t where T is the temperature corresponding to Yo and t the temperature corresponding to Y.

An analysis of the dispersion of the residuals around the zero residual value when the formulae proposed by DAVIDSON and PRADHAN (Fig. 2) are applied to our data for *I. verticalis* indicates that DAVIDSON's formulation is somewhat superior to PRADHAN's. The same conclusions are to be drawn when comparing the two formulations in the case of *E. boreale, E. ebrium, E. vernale* and *E. hageni.*

Threshold of development

This is the physiological zero of earlier workers and can be defined according to PEAIRS (1927) and UVAROV (1931) "as the temperature at which, on the descending scale, the development definitely ceases, and at which, on the ascending scale, the development is initiated" (Fig/ 1A). This, however, does not correspond to the lower lethal limit as described by SALT (1961)..

The experimental determination of this threshold is difficult because it involves a small amount of development at a very slow rate (UVAROV, 1931). Most authors have evaded this difficulty by proposing various indirect methods to calculate it. PEAIRS (1927), SHELFORD (1927), BODENHEIMER (1928), DAVIDSON (1944) and VARLEY *et al.* (1973) proposed as the theoretical threshold of development the point at which the extrapolated straight line portion of the temperature-velocity curve intersects the temperature axis. An alternative method is to extrapolate the velocity curve allowing for deviation from the
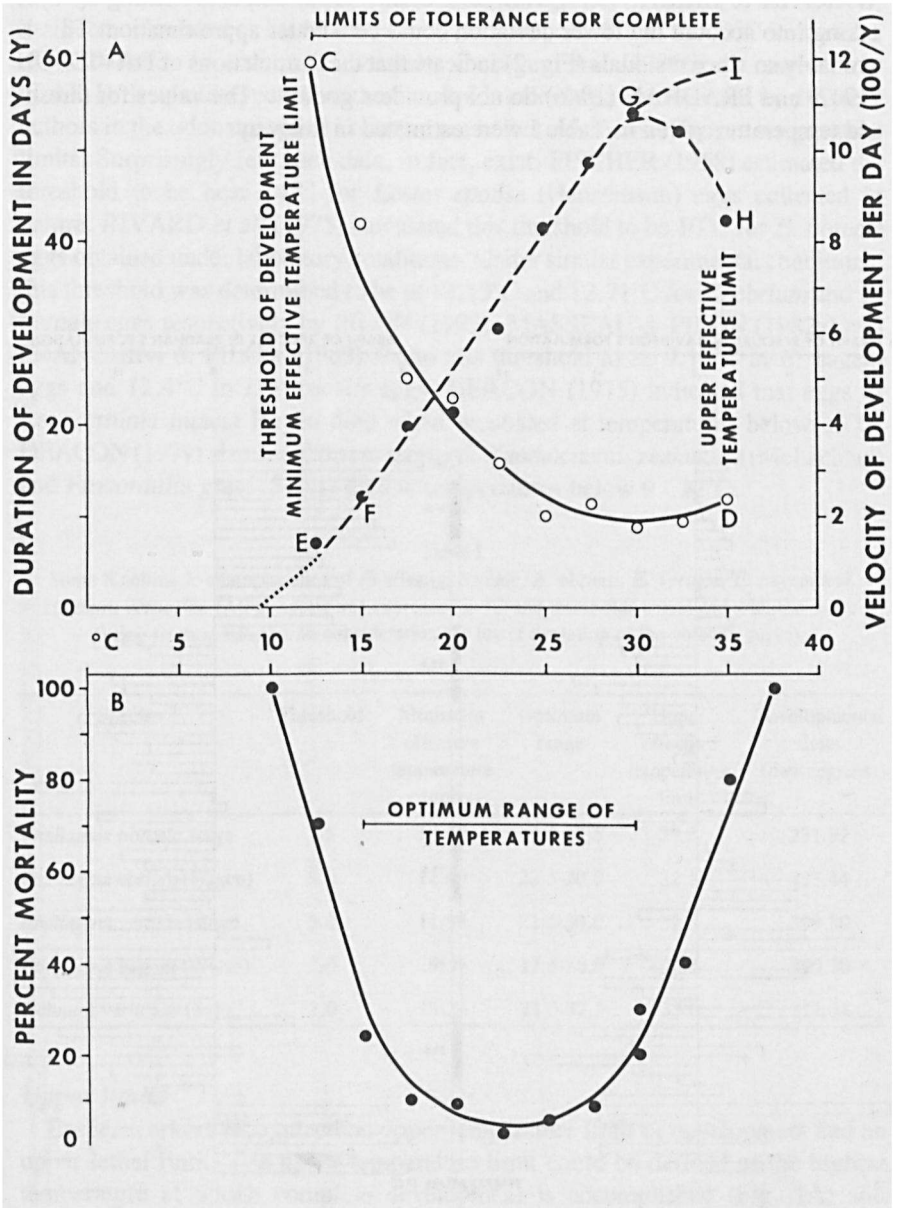
Fig. 1. Theoretical effect of temperature on the duration and velocity of development (A), and on the mortality rate of a development stage (B) of an hypothetical poikilothermic organism.

straight line format (dotted line in Fig. 1A). Clearly, deviation of the curve near its lower end from the straight line has an important bearing on the position of the threshold of development on the temperature axis (PEAIRS, 1927; SHELFORD, 1927; UVAROV, 1931; DAVIDSON, 1942, 1944; PRADHAN, 1946; ANDRE-WARTHA & BIRCH, 1954; VARLEY et al., 1973) and curve fitting by eye, taking into account the lower deviation could be a better approximation. This is probably so since residuals (Fig. 2) indicate that the formulations of DAVIDSON (1942) and PRADHAN (1946) do not provide a good fit. The values for threshold temperature given in Table I were estimated in this way.
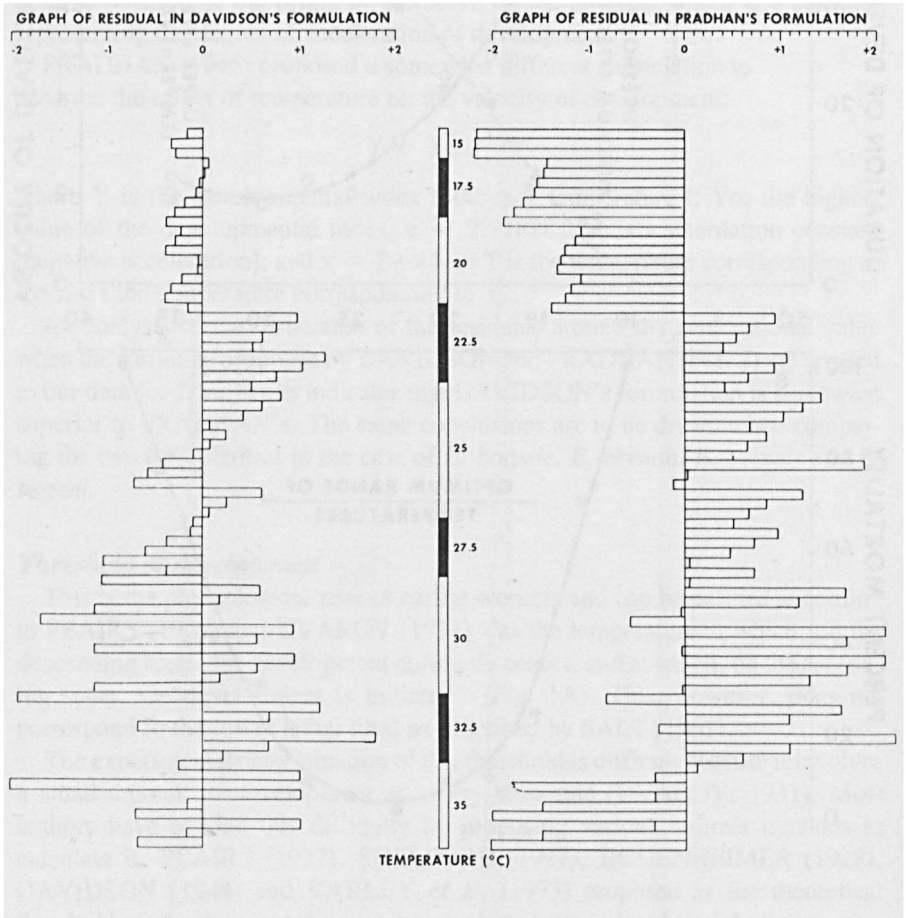

Fig. 2. Dispersion of residuals around the zero value in *Ischnura verticalis* (Hagen) according to Davidson's and Pradhan's formulations.

Minimum effective temperature limit

This is the temperature at which complete development is accomplished (Fig. 1A) and below which development is only partial (PARENT, 1969). This corresponds to the developmental-hatching threshold of JOHNSON (1940) and BURSELL (1974). The minimum effective temperature, using TROTTIER's (1971) method, has been calculated to be 12.48°, 12.40°, 11.98°, 9.34° and 11.26°C in the case of *E. boreale*, *E. ebrium*, *E. vernale*, *E. hageni* and *I. verticalis* respectively (Table I). It would appear that the thresholds calculated or estimated by different authors in the odonatological literature are in fact minimum effective temperature limits. Surprisingly few such data, in fact, exist. FISCHER (1958) estimated the threshold to be near 14°C for *Lestes sponsa* (Hansemann) eggs collected in nature. RIVARD *et al.* (1975) calculated this threshold to be 10°C for *E. boreale* eggs obtained under laboratory conditions. Under similar experimental conditions, this threshold was determined to be at 12.15°C and 12.71°C for *E. ebrium* and *E. vernale* eggs respectively by PILON (1982). MASSEAU & PILON (1982a) and FRANCHINI & PILON (1983) found this threshold to be 9.19°C in *E. hageni* eggs and 12.4°C in *I. verticalis* eggs. DEACON (1975) indicated that eggs of *Leucorrhinia intacta* Hagen died when incubated at temperatures below 13°C. DEACON (1979) also noted that embryos of *Xanthocnemis zealandica* (McLachlan) and *Procordulia grayi* (Selys) died at temperatures below 9 - 12°C.

Table I

Some bioclimatic characteristics of *Enallagma boreale*, *E. ebrium*, *E. vernale*, *E. hageni* and *Ischnura verticalis*. (All temperatures expressed in °C and thresholds calculated with the curve fitting method taking into consideration the lower deviation of the velocity curve).

Species	Threshold	Minimum effective temperature limit	Optimum range	Upper effective temperature limit	Developmental units (day-degrees)
Enallagma boreale Selys	7.5	12.48	20.0-27.5	27.5	231.92
Enallagma ebrium (Hagen)	5.0	12.40	22.5-30.0	32.5	383.44
Enallagma vernale Gloyd	5.0	11.98	22.5-30.0	32.5	399.80
Enallagma hageni (Walsh)	2.0	9.34	17.5-30.0	32.5	390.30
Ischnura verticalis (Say)	2.0	11.26	22.5-32.5	35.0	311.38

Upper limits

Earlier workers recognized an upper temperature limit of development and an upper lethal limit. The upper temperature limit could be defined as the highest temperature at which complete development is accomplished (Fig. 1A) and above which only partial development is fulfilled. This is not to be confused with the critical thermal maximum used to measure the sensitivity of aquatic fauna, for example to elevated temperatures (MARTIN & GENTRY, 1974; GARTEN & GENTRY, 1976; GENTRY *et al.*, 1976; MARTIN *et al.*, 1976).

The upper lethal limit on the other hand is defined as the temperature at which, on the ascending scale, development ceases irreversibly and death occurs due to denaturation of proteins (MAYNARD SMITH, 1957), melting of cellular lipids and phosphatides (HOUSE *et al.*, 1958) or irreversible physiological disturbances. UVAROV (1931) was doubtful whether there was a distinction between the upper temperature limit of development and the upper lethal limit but it seems that there is a narrow range between the upper temperature limit of development where the organism is still viable and the upper lethal limit which comes gradually as the metabolic balance is more and more upset (BURSELL, 1974).

The upper temperature limit has been estimated to be between 26° and 30°C in *S. vicinum*, a species characterized by eggs with delayed development (BOEHMS, 1971). RIVARD *et al.* (1975), PILON (1982), MASSEAU & PILON (1982a) and FRANCHINI & PILON (1983), investigating species with eggs developing directly, estimated this limit to be above 27.5°C in *E. boreale*; above 32.5°C in *E. ebrium*, *E. vernale* and *E. hageni*; above 35°C in *I. verticalis* (Table I).

Temperature summation

Botanists were the first to develop this theory with regard to the relation between temperature and development. Applied entomologists have long been interested in this approach because it allowed the prediction of events, such as date of emergence or the duration of a given stage of a pest species. SIMPSON (1903) was among the first to develop the theory of thermal constant expressed in units of "day-degrees" from the hyperbola (Fig. 1A, C-D) according to which the completion of a given stage of an organism's development required an accumulation of a definite amount of heat energy above a threshold of development. The development of the reciprocal of the hyperbola helped to simplify the calculations later on. The classical papers of GLENN (1922, 1931) and SHELFORD (1927, 1929) on the codling moth illustrated very well the practical application of such a theory in applied entomology and in spite of criticisms by DAVIDSON (1944) and LIN *et al.* (1954), this is still much in use.

TROTTIER (1971), working on the life-cycle of *Anax junius* Drury stated that an accurate knowledge of the effect of temperature on the rate of development is a necessary step towards an understanding of the ecology of this species. Based on the reciprocal of the hyperbolic equation, he developed a method to determine the minimal accumulated temperature in excess of the threshold required for development (temperature summation).

PILON (1982) demonstrated that eggs of *E. ebrium* required 203.22 day-degrees above 12.1°C to complete their development to hatching and eggs of *E. vernale* 179.87 day-degrees above 12.7°C; MASSEAU & PILON (1982a) calculated that eggs of *E. hageni* required 213.4 day-degrees above 9.2°C while eggs of *I. verticalis* required 141.34 day-degrees above 12.4°C (FRANCHINI & PILON, 1983). However, different methods were used by these authors to determine the threshold of development so that comparisons between species with respect to developmental units required to complete development are difficult. Based on what appeared a more appropriate method to calculate the threshold

and using TROTTIER's (1971) method to calculate the developmental units, we obtained the comparative values shown in Table I.

Egg stage and seasonal regulation in Odonata

In the temperate zone, seasonal regulation is the end result of a process of adaptation by which a species is able to correlate its life cycle with the seasons of the year so that the non-hardy stages are present at the time when conditions are favorable and the hardy life stages present when unfavorable conditions are occurring. Under natural conditions Odonata species vary greatly with regard to seasonal succession and their hardy life stage.

In species in which the egg stage is adapted to survive the unfavourable period, some overwinter as full grown embryos, others in a stage prior to katatrepsis (ANDO, 1962). In either case diapause is obligatory (CORBET, 1956; SAWCHYN & CHURCH, 1973). At 10°C diapause development seems to be completed in 15 weeks in *Lestes sponsa* (CORBET, 1956), but LAPLANTE (1975) found that at -10°C diapause development could be completed in only 14 days in *Lestes unguiculatus* Hagen, *L. forcipatus* Rambur and *L. congener* Hagen, and in 21 days in *L. disjunctus* Selys. This seems to indicate that, as reported by ANDREWARTHA (1952) and CORBET (1956), diapause development proceeds most rapidly at lower temperatures. In such cases, diapause development could be completed by mid-winter and eggs then remain in hibernation until spring temperatures rise again above the threshold for development. This represents one type of seasonal regulation occurring especially in species which emerge in late summer.

Another type of seasonal pattern is illustrated by species which are better fitted to avoid or survive the inclement weather conditions in the adult stage. Some species migrate, as *Anax junius* Drury in Canada (WALKER, 1958), or hibernate as reported by TILLYARD (1917), NEEDHAM & HEYWOOD (1929) and CORBET (1962).

Species hibernating in the larval stage represent a further type of seasonal regulation. In this type, some species overwinter in the final larval instar (CORBET, 1954, 1964) and others in larval instars other than the final one. These two categories were referred to as spring and summer species by CORBET (1954).

Laurentian summer coenagrionids

In the southern range of the northern temperate zone where the "Station de Biologie de l'Université de Montréal" is situated (46°N, 74°W), unfavorable weather conditions prevail from late November to early May. During this period the surfaces of the lakes are covered with ice. In early May temperature rises sharply and favorable conditions occur for about 150 days (temperature of water near surface at or above 10°C) (Fig. 3). Surface water temperature is above 15°C for about 100 days, above 20°C for about 62 days, and above 25 C for about 44 days, the most favorable conditions occurring between mid-June and mid-August at this latitude.
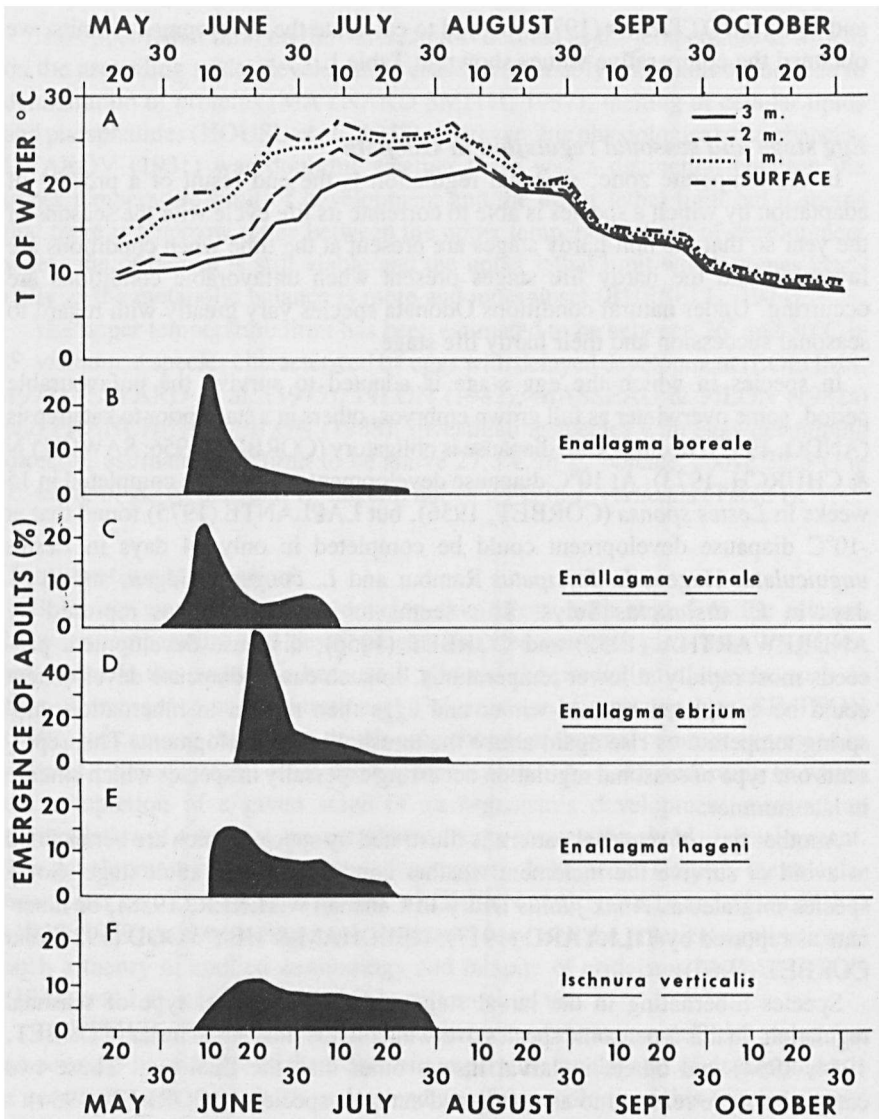
Fig. 3. A. Average water temperature of a typical lake at the biological Station of the Université de Montréal (46°N, 74°W); B-F. Average emergence curves of *Enallagma boreale*, *E. vernale*, *E. ebrium*, *E. hageni* and *Ischnura verticalis* over a two-year period at the Station and in the surrounding lower Laurentides.

Enallagma ebrium and *E. boreale* are summer species with synchronized emergence (KORMONDY & GOWER, 1965; LEBUIS & PILON, 1976; our own personal data). LEBUIS & PILON (1976) classified *E. hageni* as a summer species with asynchronized emergence as are *I. verticalis* (KORMONDY & GOWER, 1965; LEBUIS & PILON, 1976) and *E. vernale* (personal observations) (Fig. 3). Given the environmental temperatures, eggs of all species laid at any

time during the emergence period will complete development well before winter. However, it then becomes important that a cold-hardy larval instar be attained before winter.

Laboratory research on larval stages of Zygopteran species have shown that *E. boreale* probably overwinters in the F-2 larval instar, *E. ebrium* and *E. vernale* in the F-1, and *E. hageni* in the F-2 and F-3 larval instars (RIVARD *et al.*, 1975; FONTAINE, 1977; LEBEUF & PILON, 1977; RIVARD & PILON, 1977, 1978; PILON & RIVARD, 1979; PILON & FONTAINE, 1980; MASSEAU & PILON, 1982a, 1982b; PILON, 1982; PILON & MASSEAU, 1983). *I. verticalis* overwinters in many more larval instars (FRANCHINI, 1979). These findings are in general agreement with the field data of KORMONDY & GOWER (1965) and PAULSON & JENNER (1971) who indicate that coenagrionid larvae overwinter in many larval instars but with peaks in many species at the F-2 and F-1 larval instars.

In the deductions that follow we make the following assumptions: 1. That these instars in which larvae normally overwinter are the only cold-hardy instars in the species' life cycle; 2. That the day-degree summation for completion of larval development up to the earliest cold-hardy instar, obtained in the laboratory at one temperature (usually 25°C) and one photoperiod (usually 14 h light:10 h dark), is a thermal constant for larval development in that species; 3. That the threshold for development of larvae is the same as that for eggs of the same species (Table I). Given these assumptions we can predict whether larvae will attain the cold-hardy instar in the field.

For example, FONTAINE & PILON (1979) have shown that 28% of the larvae of *Enallagma ebrium* reared in the laboratory at 25°C have a type of development with ten larval instars, 66% have an 11-instar larval stage, and 6% have a 12-instar larval stage, requiring respectively 68.8, 86.5, and 115.2 days to develop to the F-1 instar. Assumed thermal constants, above the 5.0°C threshold determined for eggs of this species, for these 3 types of larval development to the F-1 instar are, therefore, 1,376, 1,730, and 2,304 day-degrees respectively. We can now predict that larvae of the 10-instar developmental type originating from eggs laid on July 9 would not attain the F-1 larval instar before winter, needing another 119 day-degrees. In the case of the 11-instar type of development, only individuals hatched from eggs laid on June 20 could complete their pre-overwintering development on October 13. Larvae from eggs laid on June 30 and July 10 would lack 246 and 449 day-degrees. Larvae of the 12-instar type of development could not complete their normal prewinter development.

In the case of *E. boreale* we predict that larvae originating from eggs laid on June 10 and 24 would complete their pre-winter development on September 6 and September 26 respectively, but larvae hatching from eggs laid on July 24 could not attain the F-2 larval instar by the end of October.

E. vernale is an occasional species at the Biological Station of the Université de Montréal (PILON & LEBUIS, 1976). Based on the water temperature of the lakes and the bioclimatic characteristics of the species, we predict that it is possible for *E. vernale* to develop to the F-1 larval stage before winter at the

station since the 12-instar type of development requires 1,872.5 day-degrees, the 13-instar type of development 2,082 day-degrees and the 14-instar type of development 2,117 day-degrees. At the Station, from June 1 to October 30, 2,137 day-degrees are available for development with a threshold of 5°C.

In the case of *E. hageni*, MASSEAU & PILON (1982b) estimated in the laboratory that 0.5% of the larval population was of the 9-instar type of development, 24.7% of the 10-instar type of development, 57.4% of the 11-instar type of development, 16.8% of the 12-instar type of development and 0.6% of the 13-instar type of development. According to the available data and based on a threshold of 2°C, only larvae hatched from eggs laid before August could complete their development to the F-2 or F-3 hardy larval stage before winter in the types of development with 9, 10, and 11 instars.

I. verticalis is a versatile species occurring in many types of habitat from early to late summer. Assuming a threshold of 2°C, larvae from eggs laid between June 7 and August 17 could overwinter in F, F-1 and F-2 in the 9-instar type of development, in F to F-4 in type 10, in F to F-4 in type 11, in F to F-6 in type 12. In the case of larvae of type 9 originating from eggs laid on June 7, an abnormally warm summer could produce a second generation as suggested by FRANCHINI (1979).

SUMMARY

An analysis of the limits of tolerance for egg development in Odonata has been discussed in relation to two of the mathematical formulations available in the biological literature. Thresholds and limits are discussed in relation to the findings of RIVARD *et al.* (1975), MASSEAU & PILON (1982a), PILON (1982), and FRANCHINI & PILON (1983) on the egg development of *E. boreale, E. ebrium, E. hageni, E. vernale* and *I. verticalis*. From this review new thresholds for each species and new values for temperature summation are proposed.

A speculative discussion on the development of larval stages in five summer Coenagrionids in the Lower Laurentides is presented. Egg development in these species takes place at the time when optimal weather conditions prevail in the field. However, a certain percentage of the larval population is probably not able to develop to the overwintering stage depending on the type of larval development to which they belong.

As pointed out by TROTTIER (1971) an accurate knowledge of the effect of temperature on the rate of development of the different stages of Odonata is a

necessary step towards an understanding of their ecology. This present paper simply stresses the importance of this statement and the need for further investigations.

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