

PRELIMINARY RESEARCH NOTE

EFFECT OF CONSTANT TEMPERATURE ENVIRONMENTS ON EGG DEVELOPMENT OF *ENALLAGMA BOREALE* SELYS (ZYGOPTERA: COENAGRIONIDAE)

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E. boreale has a flight period extending from the beginning of June to the end of August. Females were captured during mating and allowed to lay their eggs (endophytic oviposition) under laboratory conditions. Large quantities of eggs were placed at the following experimental temperatures: 15°, 17.5°, 20°, 22.5°, 25°, 27.5° and 30°C. The equation of the development of eggs in relation to temperature was fitted to transformed data by the method of multiple regression and finally expressed in a theoretical form, as suggested by PRADHAN (1946. Proc. natn. Inst. Sci. India 12: 385-404). A developmental index, the "optimal temperature of development", the "developmental threshold" and a "developmental-hatching threshold" are defined and analysed. The ecological significance of these entities is stressed.

INTRODUCTION

In the lower Laurentides, 80 km North of Montreal, Canada (46° North, 74° West), *Enallagma boreale* Selys is present in fairly large number and can be mainly found in dystrophic lakes although it can also develop in eutrophic lakes and dystrophic bogs (LEBUISS, 1971). This species is one of the first Zygoptera to emerge in the spring in the study area. The flight period extends from June 1 to August 24, mating occurring from June 10 to July 14 (LEBUISS, 1971). However, this species is more abundant in the Laurentian Shield and in Northern Québec.

Temperature is known to influence development of Odonata and to be, with photoperiod, the principal physical factor in diapause (CORBET, 1954, 1955,

1956a, 1956b, 1958, 1962; GOWER & KORMONDY, 1963; LUTZ, 1968; LUTZ & JENNER, 1964; SCHALLER, 1957, 1960, 1962, 1965, 1968; SCHALLER & MOUZE, 1970). However very little has been done to know the effect of temperature on the development of eggs of Odonata. According to CORBET (1962), "it can be assumed that eggs showing direct development have a positive thermal coefficient for growth, that is to say their rate of development increases with a rise of the ambient temperature".

The present work investigates the effect of constant temperature environments on the egg development of *E. boreale* in order to determine the thresholds of development and the optimum temperature range.

METHODS

Constant temperature environments were maintained by means of Hotpack refrigerated incubators model 352700 with a temperature range of 2° to 50°C ($\pm 0.5^\circ\text{C}$). Constant temperatures selected were 15°, 17.5°, 20°, 22.5°, 25°, 27.5° and 30°C. Photoperiod was of 13 hours of light a day with Sylvania F15T12-D fluorescent tubes connected to Canadian General Electric Time Switch type TSA-47.

Male and female adults were captured in the field and allowed to mate in the laboratory. Aquaria provided with water and necessary plant material were used for the endophytic oviposition. Eggs were collected after oviposition periods and immediately placed under constant temperature environments. Hatching of the eggs was observed thrice a day during the time the experiment took place.

RESULTS

For the whole experiment a total of 1073 eggs were used of which 766 succeeded to hatch to first instar larvae, after going through a short prolarval period. Temperature affected survival of eggs differently. At 15°C, there was a 100 per cent mortality or complete failure to hatch (Tab. I). At 17.5° and 20°C, there was approximately 75 per cent mortality while survival was 100 per cent at 22.5°, 25° and 27.5°C. However, at 30°C, a mortality of 3.5 per cent was observed. From Figure 1, it appears that the developmental-hatching threshold, which can be defined as the lowest constant temperature at which complete development from oviposition to the hatching process will occur (JOHNSON, 1940), is approximately 17°C.

The mean duration, from oviposition to hatching, varied from 11 days at 27.5°C to 61 days at 17.5°C. The optimum temperature appeared to be situated around 27.5°C, where the time required to hatch was minimal (Tab. I). The mean incubation period in relation to the constant temperatures of the experiments is illustrated in Figure 2. Over the range of temperatures studied, the

Table I
Development and mortality of eggs of *Enallagma boreale* at various constant temperatures

No. of eggs	Temperature (°C)	Mean time from oviposition to hatching (days)	Standard deviation	% mortality
100	15.0	—	—	100.0
82	17.5	61.00	—	75.4
153	20.0	32.35	2.67	75.0
48	22.5	19.35	0.91	0.0
416	25.0	14.42	0.84	0.0
71	27.5	11.06	0.23	0.0
203	30.0	14.20	0.81	3.5

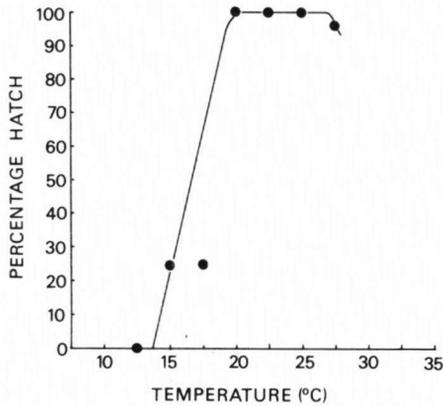


Fig. 1. Percentage hatch of *Enallagma boreale* eggs incubated at various constant temperatures.

regression equation is $\log_e y = 14.68 - 0.88 t + 0.0159 t^2$, where y represents the mean duration of egg development, t represents the temperature of incubation (°C) and e is equal to 2.7182. This equation can also be written in the following arithmetic form: $y = e^{(14.68 - 0.88 t + 0.0159 t^2)}$. So, below the optimal temperature conditions, eggs showing direct development have a positive thermal coefficient for growth. Above these optimum temperatures, however, eggs have a negative thermal coefficient.

From an ecological point of view, it is more interesting to consider our data when transformed into a developmental index ($Y = 100/y$). The preceding

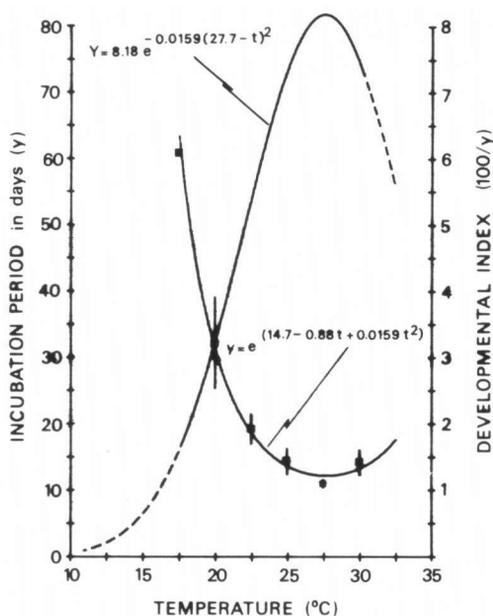


Fig. 2. The duration of the period from oviposition to hatching of *Enallagma boreale* eggs at constant temperatures and the reciprocals of these values (developmental index) plotted against temperature. Square dots represent mean incubation time for each constant temperature experimented while vertical lines crossing them represent the confidence limits of raw data ($P < 0.01$).

equation can then be expressed as $Y = 100 * e^{(-14.68 + 0.88 t - 0.0159 t^2)}$. By a mathematical approach, PRADHAN (1946) demonstrated that the developmental index can also be expressed in the following form:

$$Y = Y_0 * e^{(-0.5ax^2)}$$

where Y = developmental index = $100/y$

Y_0 = highest value of Y

x = $(T_0 - t)$

T_0 = temperature corresponding to Y_0 ($^{\circ}C$)

t = temperature of incubation ($^{\circ}C$)

a = $-(2A)$

A = coefficient of t^2 in the preceding equation

So the last numeric equation, expressed in relation to Pradhan's work, becomes $Y = 8.18 e^{(-0.0159*(27.67 - t)^2)}$. The optimal temperature for development ($27.67^{\circ}C$) and the corresponding developmental index (8.18), from which the minimum duration of incubation can be estimated ($y = 100/8.18 = 12.2$ days),

are easily deduced from this equation. From Figure 2, the developmental threshold (SHELFORD, 1929), which is the temperature above which development begins to be perceptible in amount, can be estimated approximately at 10°C. The developmental threshold is distinct from the developmental-hatching threshold already discussed, since a slight amount of development may occur below 17°C, although the embryo fails to hatch.

DISCUSSION

For *E. boreale*, oviposition has been observed on *Typha*, a little above the water level (WALKER, 1953) or on the leaves of *Nuphar* (ROBERT, 1963). However, according to our observations, eggs are mainly laid along the stems of *Nuphar* at various depths in the water. By this vertical distribution, eggs may be subjected to a vertical gradient of temperature. As indicated by SCHALLER & MOUZE (1970), these differences in temperature of incubation influence the number and the duration of larval instars.

These preliminary results indicate that the most favourable temperatures for egg development range from 22.5° to 30°C. Below optimum conditions, time to develop and mortality increase rapidly. Above 27.6°C, which is the optimal temperature of development, development is also retarded and mortality increases slightly, probably because of the harmful effects of these higher temperatures on biochemical reactions of metabolism.

It has been shown that 17°C is the developmental-hatching threshold for the eggs of this species and that the developmental threshold is 10°C. It must be understood that hatching may occur below the developmental-hatching threshold since eggs will hatch at lower temperatures if they are incubated at temperatures higher than 17°C till just before eclosion. This temperature is known as the hatching threshold (JOHNSON, 1940).

According to the works of JOHNSON (1940) on *Cimex lectularius* L. (Hemiptera), it seems that, even if temperature fluctuations occur in nature, mean temperatures are probably a good guide to the possibility of hatching. The surface water temperature, observed in a lake nearby our field station during the incubation period of eggs of *E. boreale*, was found to vary between 19° and 28°C. The relationship between water temperature of this lake and the favourable laboratory temperatures of the experiment suggest these damselflies are well adapted to their environment. In nature, optimal temperature conditions seem to be realised throughout the incubation period.

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