THE EFFECTS OF TEMPERATURE AND PHOTOPERIOD
ON THE DURATION OF LARVAL DEVELOPMENT IN THREE SPECIES
OF ODONATA

by

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B.Sc. (Hons). The University of Canterbury, 1967

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in the Department
of
ZOOLOGY

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
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Date 14th September 1971
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Corbet has recognised two ecological types of Odonata from temperate regions. He has termed these "spring" and "summer" species, depending upon the presence of a diapause in the final instar. Species possessing a diapause in the final instar are by definition spring species. Corbet believes that spring and summer species represent stages in the colonisation of high latitudes from the tropics. He considers that spring species represent the final stage in adaptation to cold climates, because the diapause confers cold resistance on the final instar, and synchronises the short adult life after the relatively long larval period caused by the low temperatures.

This study tested several hypotheses arising from Corbet's scheme: (1) Corbet's assumption that spring species develop more slowly (i.e., have lower thermal coefficients for development) at high temperatures than summer species; (2) Corbet's assumption that spring species are more tolerant of low temperature than summer species, and (3) the hypothesis proposed in this study that spring species make the most general use of photoperiod in regulating development.

The nymphs of three species of Odonata, Enallagma boreale, Leucorrhinia glacialis and Libellula quadramaculata, were reared under a number of combinations of temperature (10, 15, 20, 25 °C) and photoperiod (6, 9, 12, 15, 18 hr).

Enallagma boreale, the summer species, developed more rapidly than the two spring species at every temperature. This
result supports Corbet's hypothesis that summer species have higher thermal coefficients for growth than do spring species, but does not support his hypothesis that spring species are more tolerant of low temperatures.

Photoperiod significantly affected the rate of development in *Leucorrhinia glacialis* and *Libellula quadrimaculata* at 10 °C and 15 °C, but *Enallagma boreale* was not affected by photoperiod at any temperature. This result supports the hypothesis that species from high latitudes (spring species) are more likely to utilise photoperiod in regulating development.

Preliminary results suggest that *Leucorrhinia glacialis* is capable of continuously variable growth rate response to photoperiod. This is the first time that this response has been recorded in an arthropod.
INTRODUCTION

The time taken to complete larval development varies considerably between species of Odonata. The most rapid development has been observed in tropical species, such as members of the Family Lestidae, which may complete larval development within a few months (Corbet, 1963). On the other hand, temperate members of the Families Cordulegasteridae and Gomphidae probably require four years for development, and a few other species may take even longer (Corbet, loc. cit.).

Although the environmental temperature clearly affects the rate of growth, it is not the sole determinant. Calvert (1929), and Hodgkin and Watson (1958) have shown that species have different thermal coefficients for growth, that is, differ in their capacity to respond to increasing temperature. The latter authors showed that species inhabiting temporary pools had higher thermal coefficients for growth than slow-growing species from upland streams.

In tropical species, the thermal coefficient for growth and the environmental temperature probably determine the larval growth rate (Corbet, 1963). In temperate species, however, the duration of larval development is affected by additional factors, involving variable responses to both temperature and photoperiod (Corbet, loc. cit.; Lutz and Jenner, 1964; Lutz, 1968). Little is known of how these additional factors operate, although one of their functions appears to be to synchronise emergence of the adult at the end of the long larval period (Corbet, loc. cit.).
On the basis of their methods of synchronisation, Corbet (1954, 1956) has recognised two ecological types of dragonflies from temperate regions. He has termed these "spring" and "summer" species, depending upon the position of a diapause stage in the life history.

Spring species by definition possess a diapause in the final instar (Corbet, 1956, 1963). Because of the position of the diapause, spring species are also characterised by a short and relatively early emergence period. Summer species lack the final instar diapause. Consequently, the latter do not have the short and early emergence characteristic of the spring species. However, compared with tropical species, emergence in summer species is relatively synchronised. To explain this, Corbet (1956) has suggested that an ascending series of lower temperature thresholds may regulate entry to the final instar, commencement of metamorphosis, and emergence.

Corbet (loc. cit.) points out that the success of this system requires the thresholds for successive developmental stages to be widely separated, which precludes species with high thermal coefficients for growth. Therefore it is likely to be developed only in summer species which have a slow rate of growth (i.e. low thermal coefficient for growth). Consequently, Corbet has divided summer species into two additional categories: (a) those which require two or more years to complete a generation, and (b) those which require only one year.

Corbet believes that these categories represent stages in the colonisation of the higher latitudes from the tropics. He regards spring species as the most highly adapted to high latitudes.
Summer species of type (a) also show adaptation to temperate climates, while type (b) appears least modified from the presumed ancestral tropical type.

Corbet's scheme contains several untested premises. First, he assumes that spring species have low thermal coefficients for growth compared with summer and tropical species. He makes this assumption because spring species generally inhabit permanent and relatively cold water, in which high thermal coefficients for growth have little value, whereas tropical species often occupy temporary habitats subject to rapidly rising temperatures (Corbet, 1963). Summer species should have thermal coefficients for growth which fall between those of spring and tropical species.

Second, Corbet (loc. cit.) believes that spring species should exhibit the greatest tolerance of low temperature, beginning with the final instar (the first stage to be overtaken by winter), and progressively extending to the earlier instars. I propose that superior tolerance of low temperature will be reflected by higher growth rates at low temperatures, as well as relatively low temperature thresholds for metamorphosis, emergence, and the induction of diapause or quiescence.

Finally, I suggest that spring species can be expected to show the most general utilisation of, and the most highly developed responses to changes in photoperiod. I propose this hypothesis because the extensive and systematic variation in photoperiod at high latitudes makes it a suitable factor by which to regulate development.

The purpose of this study was to test the following hypotheses: (1) spring species have lower thermal coefficients
for growth than do summer species; (2) spring species are more tolerant of low temperatures than are summer species, which is shown by higher growth rates at low temperatures, and (3) spring species show greater utilisation of photoperiod in regulating development than do summer species.

Three species were chosen for the study: the Zygopteran Enallagma boreale (Selys) and the Anisopterans Leucorrhinia glacialis (Hagen) and Libellula quadramaculata (Linne). E. boreale is a summer species in terms of Corbet's classification, while the Anisopterans are both spring species. No tropical species were included in the study.

MATERIALS AND METHODS.

Field studies were carried out at Marion Lake, situated in south-western British Columbia on the southern slopes of the Coast Mountains (49°19'N, 122°33'W; alt. 305 m). Marion Lake is located in the University of British Columbia Research Forest, about 50 km north-east of Vancouver.

Marion Lake lies within the littoral climatic region, but the lake's typically mild climate is modified by the Coast Mountains in having a heavy winter rainfall (Efford, 1967). The average annual rainfall is 94 inches, 70% of which falls between October and March (Efford, loc. cit.). The average annual temperature is 8.8 °C, with a lowest mean monthly temperature of 1.7 °C (January) and a highest of 16.2 °C (July) (Efford, loc. cit.).

Marion Lake is small and shallow, approximately 800 m long and 200 m across at the widest point, with an average depth of 2.4 m (Efford, 1967). The bottom is comprised mostly of soft
mud and over much of its area supports little vegetation. Beds of *Nuphar variegatum*, *Potamogeton natans*, *Potamogeton epihydrus* and *Equisltum sp.* occur near the shore. Areas of *Isoetes occidentalis* are found in deeper water and patches of *Chara globularis* occur in the large springs in the lake. Sedges and small shrubs are numerous along the shore.

The odonate nymphs were generally found in association with the vegetation, either on the stems of the plants, or in the decaying material around the roots. Few nymphs were obtained from the open sediment. The nymphs used in the rearing experiments were obtained by sweeping the vegetation and substrate with a hand-net. The samples were sorted in the field. No attempt was made to obtain quantitative samples because only *Enallagma boreale* was sufficiently abundant to justify the effort required.

The timing and patterns of emergence were determined by collecting exuvia at weekly intervals from the emergent vegetation. Six areas of approximately 4 m² were located around the lake for this purpose (Figure 1).

The laboratory studies were carried out at the University of British Columbia. The nymphs were reared in photoperiods of 6, 9, 12, 15 and 18 hours at 10 C, 15 C, 20 C and 25 C (all ± 1.5 C). Four 1.22 m X 1.22 m X 0.23 m boxes were built, each divided into 1.22 m long light-proof compartments which were inter-connected to permit the flow through of water. The water was circulated through the boxes from 800-litre reservoirs at approximately 2 litres per minute. Each compartment was fitted with one 1.22 m standard "cool-white" fluorescent lamp with ballast and housing. Five "Intermatic" single-pole, single-throw
Figure 1. Marion Lake: location of the six sites (numbered 1-6) from which the exuvia were collected.
time-switches were used to regulate the photoperiods. Each time-switch controlled four lamps, one from each box.

The nymphs were reared singly in 9.5 cm diameter X 7.0 cm deep transparent plastic containers, which were floated in the water circulating through the boxes. The water in the containers was renewed at 3-4 week intervals.

The nymphs were fed white worm (Enchaetraids) by hand once per day until satiated. All were initially fed daily, but later the 15 C nymphs were reduced to three feedings per week, and the 10 C nymphs to two feedings per week. Records were kept of food consumption by representative nymphs. The nymphs were checked for ecdysis, emergence and deaths at the time of feeding.

The development of the eggs was also studied, using the apparatus in which the nymphs were reared. The eggs of the two exophytic (oviposition) species, Leucorrhina glacialis and Libellula quadramaculata, were obtained by capturing laying females and inducing them to continue laying. This was done by dipping the tip of the abdomen in water. Females of the endophytic Enallagma boreale were provided with plant stems on which to lay.

ORIGINS, DISTRIBUTIONS AND PATTERNS OF EMERGENCE.

Seven species of Odonata are known from Marion Lake. These are the Anisopterans Plathemis lydia (Drury), Leucorrhina glacialis (Hagen), Libellula quadramaculata (Linne), Aeshna interrupta (Walker), and the Zygopterans Enallagma boreale (Selys), Ischnura cervula (Selys) and Lestes dryas (Kirby). The adult of a fifth Anisopteran has been observed on the wing, but has not been identified.
The feature of the odonate fauna of the southern coastal region of British Columbia, as exemplified by the species found at Marion Lake, is the overlapping of boreal and austral faunas, which is much more marked than in any other part of Canada. This appears due to the cool summers of this region, which permit southward extension of boreal species, and the long summers and mild winters, which permit the existence of certain austral species.

*L. glacialis*, *L. quadramaculata*, *A. interrupta*, *L. dryas* and *E. boreale* belong to the General Boreal fauna (Walker, 1927), and all are widely distributed in the Hudsonian and Canadian Zones (see Klugh and McDougall, 1924). These species all have trans-continental distributions. In addition, *L. dryas* and *L. quadramaculata* are circumpolar in distribution.

*P. lydia* and *I. cervula* belong to the Austral fauna (Walker, 1927). *P. lydia* inhabits the Transition and Upper Austral Zones and hence has an interrupted distribution in Canada. *I. cervula* belongs to the Western Austral or Sonoran fauna and is therefore restricted to southern British Columbia and Western Alberta in Canada.

From the standpoint of origin, the Marion Lake species, other than *I. cervula*, belong to holarctic genera, or to holarctic sections of genera (Walker, loc. cit.). *I. cervula* represents a northward extension of the Sonoran fauna.

*E. boreale*, *L. glacialis* and *L. quadramaculata* are therefore all boreal in distribution and holarctic in origin. *E. boreale* is the most widely distributed species of *Enallagma* in Canada and is the commonest *Enallagma* in the far north (Walker, 1953). In fact,
E. boreale is probably the most abundant Odonate in the northern part of the continent, and it may also range farthest north. It has been recorded from Palmer, Alaska (61 30'N); Dawson, Yukon (64 N) and Fort Norman, North West Territories (61 N) (Walker, loc. cit.). The records are not sufficient to compare L. glacialis and L. quadramaculata, but it is clear that both species are abundant at high latitudes. L. quadramaculata is generally distributed through Canada and Alaska, except in the Arctic Zone (Walker, 1927). Walker records that it was the commonest of the few species of Anisoptera that occurred at Prince Rupert, where L. glacialis was also common.

E. boreale is the earliest of the Marion Lake species to emerge (Table 1). In 1969 and 1970 emergence began about the middle of May and continued until mid-August. With L. glacialis it has the longest emergence period of the species at Marion Lake. The unsynchronised pattern of emergence, resulting from the lack of a final instar diapause, shows that E. boreale is a summer species.

L. quadramaculata typically begins emerging two weeks after E. boreale, in late May or early June. Emergence is restricted to about 30 days (Table 1), and more than 75% of the annual population emerges in the first week of the emergence period (1969 and 1970). The close synchronisation of emergence is the result of the diapause in the final instar. L. quadramaculata therefore has a life history of the spring type.

L. glacialis begins emerging at the same time as L. quadramaculata. Except for E. boreale, these two species are the earliest to emerge of the Marion Lake species. The pattern of
Table 1. The patterns of emergence of *E. boreale*, *L. glacialis* and *L. quadramaculata*. Each figure is the number of exuvia collected from an area of 24 m² in the interval prior to the date given.

<table>
<thead>
<tr>
<th>Year</th>
<th>Day/Month</th>
<th>L. quad.</th>
<th>L. glac.</th>
<th>E. boreale</th>
</tr>
</thead>
<tbody>
<tr>
<td>1962</td>
<td>12/5 13/5 14/5 3/6 11/6 21/6 1/7 8/7 18/7 27/7 6/8 22/8 29/8 6/9</td>
<td>- 114 13 4 1 - 3 - - - - -</td>
<td>- 50 14 43 5 1 4 2 - 4 23 32 19</td>
<td>40 110 18 123 46 3 4 50 16 4 1 2 -</td>
</tr>
<tr>
<td></td>
<td>13/5 23/5 30/5 6/6 13/6 20/6 4/7 11/7 19/7 1/8 9/8 15/8 22/8 12/8</td>
<td>- 2 24 3 2 1 - - - - - - -</td>
<td>- 5 2 1 1 1 4 1 28 23 27 15</td>
<td>132 80 77 44 45 59 67 47 2 5 - - -</td>
</tr>
<tr>
<td></td>
<td>23/5 30/5 5/6 12/6 20/6 28/6 5/7 12/7 19/7 7/8 16/8 23/8</td>
<td>- - 2 1 - 1 - - - - - -</td>
<td>- - 2 2 1 - 3 5 11 15 8</td>
<td>85 133 29 46 17 49 41 175 176 7 1</td>
</tr>
</tbody>
</table>
emergence of *L. glacialis* is quite different from those of either of the other two species. It is characterised by two peaks, one at the beginning of emergence, and the second about two months later. Because a (facultative) diapause occurs in the final instar, *L. glacialis* is presumed to be a spring species.

**THE REARING EXPERIMENTS**

Table 2 presents the growth rate data obtained for the three species under the various combinations of temperature and photoperiod. The data were obtained from fourth to penultimate (12th or 13th) instar nymphs. Individual nymphs were reared for periods ranging from a minimum of a month at 25 C and 20 C, to 14 months at 15 C and 10 C. Each figure, excluding the means of all observations, is the mean time in days taken to complete two ecdyses at the specified temperature and photoperiod. The unbracketed values were calculated from the observed number of days taken to complete two ecdyses. The bracketed values for *L. glacialis* and *L. quadramaculata* were calculated from the total number of ecdyses that occurred during the pooled time the nymphs were reared. This procedure was necessary because at 10 C and 15 C many of the nymphs of these two species failed to complete two ecdyses during the study. Where both bracketed and unbracketed values are presented, the former are more representative because they account for every nymph, including those which failed to complete one ecdysis during the experimental period.

**The effect of temperature on the growth rate.**

The mean of the total number of observations at each temperature was used as the measure of the growth rate response
<table>
<thead>
<tr>
<th>Temperature</th>
<th>E. boreale</th>
<th>L. glacialis</th>
<th>L. quadramaculata</th>
</tr>
</thead>
<tbody>
<tr>
<td>25 °C 18 hr.</td>
<td>11.5</td>
<td>23.3</td>
<td>26.9</td>
</tr>
<tr>
<td>15</td>
<td>14.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>12.4</td>
<td>18.9</td>
<td>20.1</td>
</tr>
<tr>
<td>9</td>
<td>12.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>14.4</td>
<td>20.8</td>
<td>16.3</td>
</tr>
<tr>
<td>Mean of all observ.</td>
<td>13.0</td>
<td>21.1</td>
<td>21.4</td>
</tr>
</tbody>
</table>

| 20 °C 18 hr. | 25.4       | 26.5        | 31.1             |
| 15          | 20.3       |             |                  |
| 12          | 17.6       | 33.3        | 27.5             |
| 9           | 17.1       |             |                  |
| 6           | 16.9       | 24.2        | 20.3             |
| Mean of all observ. | 18.8 | 26.9 | 26.3 |

| 15 °C 18 hr. | 34.3       | 83.0 (81.2) | 104.8 (111.1) |
| 15          | 24.1       |             | (513.0)       |
| 12          | 29.1       | 104.7 (100.5) | (195.7)     |
| 9           | 31.7       | 132.6 (148.4) | (333.5)    |
| 6           | 30.5       | 103.5 (105.9) | (333.5)    |
| Mean of all observ. | 29.9 | 103.5 | 105.9 |

| 10 °C 18 hr. | 85.4       | 147.4 (139.3) | 162.3 (243.5) |
| 15          | 52.8       |             | (513.0)       |
| 12          | 66.9       | 169.2 (252.7) | (513.0)     |
| 9           | 60.3       |             | (513.0)       |
| 6           | 64.8       | (527.0)     | (333.5)       |
| Mean of all observ. | 63.8 | (229.2) | (333.5) |

Table 2. The growth rate data obtained for *E. boreale*, *L. glacialis* and *L. quadramaculata*. Each figure, excluding the means of all observations, is the mean time in days taken to complete two ecdyses at the specified temperature and photoperiod. Where both bracketed and unbracketed values are presented, the former constitute the basis of the analyses (see page 11).
to temperature (Table 2). Equal numbers of equivalent instar nymphs were reared at each photoperiod in order to reduce biases caused by response to photoperiod.

Table 3 gives for each temperature the ratios of the time taken by each species to complete an instar relative to the time taken by *E. boreale*. It is clear that *E. boreale* develops much more rapidly than either *L. glacialis* or *L. quadramaculata* at each of the temperatures tested. The difference is most apparent at 15°C and 10°C, where *E. boreale* developed between 3.5 and 6.5 times more rapidly than the other two species.

There were no detectable differences in growth rate between *L. glacialis* and *L. quadramaculata* at 25°C and 20°C, but at 15°C and 10°C *L. glacialis* required little more than half the time needed by *L. quadramaculata* to complete one instar.

Discussion.

The data presented in Tables 2 and 3 support the hypothesis that summer species have higher temperature coefficients for growth than spring species. *E. boreale*, the summer species, developed more rapidly than either *L. glacialis* or *L. quadramaculata* at all of the experimental temperatures.

On the other hand, the data do not support the proposal that spring species are more tolerant of low temperatures than summer species. If superior growth rate is taken to indicate superior tolerance of low temperatures, *E. boreale* is clearly the most tolerant of the three species.

Corbet (1956, 1963) believes that spring species represent the final stage in adaptation to cold climates. However, the
Table 3. The growth rate responses of *L. glacialis* and *L. quadramaculata* to temperature expressed as ratios relative to the growth rate of *E. boreale*.

<table>
<thead>
<tr>
<th>Temperature</th>
<th><em>E. boreale</em></th>
<th><em>L. glacialis</em></th>
<th><em>L. quadramaculata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>25 C</td>
<td>1</td>
<td>1.6</td>
<td>1.6</td>
</tr>
<tr>
<td>20 C</td>
<td>1</td>
<td>1.4</td>
<td>1.4</td>
</tr>
<tr>
<td>15 C</td>
<td>1</td>
<td>3.5</td>
<td>6.5</td>
</tr>
<tr>
<td>10 C</td>
<td>1</td>
<td>3.6</td>
<td>5.2</td>
</tr>
</tbody>
</table>

Table 4. The growth rate responses of *L. glacialis* and *L. quadramaculata* to photoperiod expressed as ratios relative to the fastest growth rate shown by each species.

<table>
<thead>
<tr>
<th>Photoperiod - hr.</th>
<th>18</th>
<th>15</th>
<th>12</th>
<th>9</th>
<th>6</th>
<th>18</th>
<th>15</th>
<th>12</th>
<th>9</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. glacialis</em></td>
<td>1</td>
<td>1.2</td>
<td>1.8</td>
<td></td>
<td></td>
<td>1</td>
<td>1.8</td>
<td>3.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L. quadramaculata</em></td>
<td>1</td>
<td>4.5</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>2.1</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
laboratory results leave little doubt that *E. boreale* is better able to develop at low temperatures than are *L. glacialis* and *L. quadramaculata*. Field observations agree with the laboratory results. *E. boreale* is the first species to emerge at Marion Lake and it is probably the most abundant of the three at high latitudes.

The tolerance to low temperature demonstrated in *E. boreale* is not necessarily a refutation of Corbet's scheme, even though other unusually tolerant summer species probably exist (e.g. *Enallagma cyathigerum* Charp). The results of this study are interpreted to mean that there may have been several pathways of adaptation to high latitudes. The more common pathway, proposed by Corbet, was the development of the diapause stage, possibly by the physiologically less tolerant and adaptable species. The other pathway could have involved the development of greater tolerance, presumably by the physiologically most adaptable species.

*The effect of photoperiod on the growth rate.*

Either an analysis of variance (Li, 1964), or the Mann-Whitney U test (Siegal, 1956) was carried out on the photoperiod data in Table 2. The analysis of variance was applied to the data at each of the four temperatures for *E. boreale*, and to the 25 C and 20 C data for *L. glacialis* and *L. quadramaculata*. The Mann-Whitney U test was performed on the 15 C and 10 C data obtained for *L. glacialis* and *L. quadramaculata*.

There was no significant difference (99% confidence limits) between photoperiods for any of the species at 25 C and 20 C. This was also true for *E. boreale* at 15 C and 10 C. On the other hand,
both *L. glacialis* and *L. quadramaculata* showed significant responses (95% confidence limits) to photoperiod length at 15 C and 10 C.

**Discussion.**

I predicted that summer species would show relatively little adaptation or response to photoperiod compared with spring species. I proposed this hypothesis because summer species, having higher thermal coefficients for growth, and living in relatively warm habitats, have little need of response to photoperiod in regulating growth. The data presented in Tables 2 and 4 support this contention. *E. boreale* showed no detectable growth rate response to photoperiod at any of the temperatures tested, while the spring species showed well-developed responses.

The fact that *L. glacialis* and *L. quadramaculata* responded to photoperiod only at the lower two temperatures is interpreted as additional support for the hypothesis that low temperatures favour the development of photoperiod response.

Both spring species showed a greater response to photoperiod at 10 C than at 15 C, which is also interpreted as support for the above hypothesis. The difference in response is most readily seen in *L. glacialis* (Table 4), for which the ratio between the shortest and the longest photoperiods was more than twice as long at 10 C (1 : 3.8) as it was at 15 C (1 : 1.8).

*L. quadramaculata* is evidently more responsive to photoperiod than *L. glacialis* at equivalent temperatures. This can be seen best at 15 C, where *L. quadramaculata* produced a growth rate ratio of 1 : 4.5 for a 6 hr increment in photoperiod, whereas *L. glacialis* produced ratios of 1 : 1.2 and 1 : 1.5 for increments of the same length (Table 4).
The trends discussed in the previous two paragraphs are not immediately apparent at 10 C, but can be demonstrated by the following analysis. *L. glacialis* developed as rapidly at 10 C 18 hr as at 15 C 6 hr (Table 2). However, *L. quadrarmaculata* required less than half the time for development at 10 C 15 hr (243.5 days) as at 15 C 9 hr (513.0 days). The photoperiod increment was 12 hr for *L. glacialis*, but only 6 hr for *L. quadrarmaculata*.

There can be little doubt that *L. quadrarmaculata* has, on the one hand, a lower thermal coefficient for growth than *L. glacialis*, but is more responsive to photoperiod. While there is the danger of over-interpreting the data, this conclusion agrees with the hypothesis that the higher the thermal coefficient for growth, the less developed the response to photoperiod.

To conclude, comment should be made of the relative influence of photoperiod and temperature on the growth rate. It has been shown for *L. quadrarmaculata* that a 6-hr increase in photoperiod has, at low temperatures, a substantially greater effect on the growth rate than a 5 C rise in temperature. Even in the less responsive *L. glacialis*, a 12-hr increase in photoperiod is as effective as a 5 C rise in temperature. These results suggest that in habitats which experience long periods of low temperatures, photoperiod may be a dominant factor in determining growth rate.

The response of the final instar to the experimental conditions.

The final instar could not be studied in a systematic manner with the apparatus used for this study, but several observations are worth comment. The final instar has to be
studied separately because the development and duration of this instar in some species is evidently affected by complex interactions of temperature and photoperiod which have little bearing on earlier development.

*E. boreale* emerged at all four temperatures, with no detectable differences in success. Temperature appeared to affect the duration of the final instar in the same manner in which it affected the earlier instars. Similarly, photoperiod did not appear to affect the time spent in the final instar.

Most of the *L. glacialis* nymphs reared at 25 C and 20 C reached the final instar but subsequently failed to emerge. This suggests that diapause is obligatory. On the other hand, field evidence suggests that the diapause is facultative. For example, a large number of the final instar were present in Marion Lake prior to the second peak of emergence (Table 1), but many did not take part in this emergence. Corbet (1955, 1956, 1957) showed that *Anax imperator*, which has a pattern of emergence like that of *L. glacialis*, has a facultative diapause in which the instar forgoes diapause if the day length is increasing by more than two minutes per day. It seems likely that *L. glacialis* responds in the same way to changing day length. In other words, the constant conditions in the laboratory probably predisposed the nymphs to diapause, despite apparently being otherwise favourable (e.g. high temperatures and long photoperiods).

Two emergences were recorded at 15 C, and none at 10 C. Many of the nymphs which reached the final instar later died, apparently after having completed metamorphosis. Representative nymphs were removed from both temperatures and reared at higher
temperatures under natural photoperiods. Most of these quickly emerged. It seems probable that temperature was the factor limiting emergence at 15 C and 10 C in the laboratory.

In order to reconcile these results, we must assume that photoperiod is critical in initiating diapause, but has little bearing on emergence once diapause development has been completed.

One emergence was recorded for L. quadramaculata at 15 C. It is likely that this species is also unable to emerge at 15 C and 10 C. However, very few nymphs reached the final instar before the study was terminated. It is also probable that diapause is obligatory in this species. This is suggested by the presence of the final instar in Marion Lake throughout the summer following emergence.

The response of the eggs to the experimental conditions.

The eggs were studied with the expectation that they (1) would show thermal coefficients for development paralleling those of the nymphs and (2) would respond to photoperiod length.

The eggs of L. glacialis and L. quadramaculata obtained before the summer solstice hatched rapidly at high temperatures, with the latter species showing the slightly faster rate of development. L. quadramaculata hatched in approximately 8, 16 and 41 days at 25 C, 20 C and 15 C, and L. glacialis required 10, 20 and 52 days. Both species failed to hatch at 10 C. Photoperiod did not affect development in either species.

The eggs of L. glacialis collected after the summer solstice took 4 - 7 months to hatch, in contrast to the rapid development of the eggs collected earlier. In addition, the eggs at 10 C hatched. It appears that L. glacialis has a facultative diapause
in the egg as well as in the final instar.

The experiments with the eggs of *E. boreale* were unsatisfactory. Most failed to hatch, probably because of the premature decay of the plant material in which they were laid. The hatch obtained suggests that development is slower in this species (i.e. \( \approx 21 \) days at 25 C). The effect of photoperiod could not be assessed.

The results do not support the hypothesis that the eggs respond to temperature and photoperiod in the same manner as do the nymphs. For example, the thermal coefficients for development are reversed for *L. glacialis* and *L. quadramaculata* in the egg stage. Furthermore, both species probably develop more rapidly than *E. boreale*. Finally, the eggs of the spring species showed no response to photoperiod, in contrast with their nymphs.

There are several explanations for these results. At the species level, the differences can be attributed to the habitats in which the eggs develop. The two spring species lay in shallow water, which is subject to drying up and, consequently, to very high temperatures. In this situation, high thermal coefficients for development are an important adaptation for survival. On the other hand, *E. boreale* lays in plant stems in deeper water, where there is little danger of drying out, and where temperatures are lower.

In general, the eggs experience a narrow range of conditions (usually involving high temperatures and long photoperiods) compared with the nymphs. Because the habitat is different, the eggs require a different set of responses from those developed by the nymphs.
Several criticisms of the execution of the study should be noted. The object of the study was to compare summer and spring species. However, while one summer species and two spring species were studied, all three species were boreal in distribution and holarctic in origin. In other words, *E. boreale* is not a typical summer species, at least in distribution, because it occurs at higher latitudes than would be expected of a summer species. *E. boreale* was included in the study with the expectation that it would be difficult to categorise. However, the study consequently lacked a "typical" summer species. *Plathemis lydia* and *Ischnura cervula* were obvious choices, but neither was sufficiently abundant to work with. In the event, *E. boreale* proved informative, but several more typical summer species would complete the comparison.

The experimental environment in which the nymphs were reared was not entirely satisfactory. The static system used was subject to the accumulation of waste products, and the growth of bacterial and algal populations. The dissolved oxygen supply undoubtedly declined at the same time. Periodic renewal of the water reduced the problem to some extent, but the process was laborious, and of course did not maintain constant conditions.

It was not possible to determine whether the growth rate of the nymphs was affected by the experimental environment, but it is assumed that the more constant environment produced by a continuous flow system would at least reduce experimental variance.

When assessing the effects of the experimental conditions on the development of the nymphs, we should consider the conditions
previously experienced in the natural habitat. This is particularly important in the case of the final instar, which may have been conditioned to diapause prior to removal from the field. This study did not compare growth rates of earlier instars obtained before and after the summer solstice, nor on either side of the autumnal equinox, both apparently important times in final instar development (Corbet, 1963; Lutz and Jenner, 1964). It is assumed that the development of all but the final instar, depending upon the species, is facultative, but this has to be proved.

The photoperiodic reactions of insects and mites characteristically control alternative pathways of development, such as diapause or form determination (Lees, 1960). The response is therefore of an all-or-nothing nature, involving a critical photoperiod. For example, in *Megoura vicae* the transition from a short day to a long day effect takes place over less than 30 minutes, as the photoperiod is extended from 14½ to 15 hours (Lees, loc. cit.).

A very few insects have been shown to respond to the progression of photoperiod. The response of the final instar of *Anax imperator* to changing photoperiod has already been mentioned. Response of this kind to changing day length has been demonstrated only in two other arthropods, a locust, *Nomadacris septemfasciata*, and a beetle *Anthrems verbasci* (in Corbet, 1963). The present study suggests that both the adult and the final instar of *L. glacialis* are also capable of responding to changing photoperiod.

The results reported in this study are of interest because they suggest that at least one invertebrate (i.e. *L. glacialis*)
is capable of continuously variable responses to changing photoperiod. Unlike normal invertebrate reactions, this response seems similar to the photoperiodic control of testicular growth in birds, where little growth occurs at photoperiods of less than eight hours, but which increases to a maximum in continuous light (Lees, 1960).

Several other species of Odonata appear likely to respond to photoperiod in the manner demonstrated for *L. glacialis*. *L. quadramaculata* is likely to do so. Lutz (1968) has shown that the final four instars of *Lestes eurinus* grow more rapidly at a 14-hr photoperiod than at 11 hr. Preliminary work by Jenner (1969) showed that some of the later instars of several species of Odonata also developed more rapidly at 14 hr than at 11 hr. However, the presence of this response must be confirmed by testing the effects of at least three photoperiods on the rate of development, otherwise the responses may be attributed to the presence or absence of diapause.

It is clear that a number of Odonata are highly responsive to changes in photoperiod. This study shows that the influence of photoperiod is not necessarily restricted to the final instar, or to the egg (through the adult) but, in some species, may affect the rate of development throughout the larval stage. Furthermore, evidence presented in this study shows that photoperiod can have an extraordinary influence on the rate of development at low temperatures, to the extent that photoperiod may be the dominant factor in regulating development at low temperatures in some species. In view of these considerations, it is evident that the photoperiod responses of Odonata of high latitudes warrant further study.
ACKNOWLEDGEMENTS

This study was supported with grants from the Canadian International Biological Program. I wish to express my appreciation of the help, and patience, shown me by my thesis supervisor, Dr. I. E. Efford. I also wish to thank Dr. D. Chitty, who provided helpful criticism of the manuscript, and Mrs Anthea Bryan and Mr. Michael Hoebel, who took care of experiments in my absence. Mrs. Kathryn Calef, Mr. Kanji Tsumura and Mr. Itsuo Yasaki provided technical assistance. Finally, I wish to thank my wife, Mrs. Anita Procter, who helped without complaint throughout the study.
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