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Egg development in *Hexagenia limbata* (Ephemeroptera:Ephemeridae) from Southern Indian Lake, Manitoba: temperature effects and diapause

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Abstract. Egg development was investigated for *Hexagenia limbata* (Serville) from Southern Indian Lake (SIL) in northern Manitoba, Canada. The SIL population is located near the northern range limit of *H. limbata*, and some important differences in hatching dynamics were seen in comparison with southern populations. Hatching success and egg development time were related to temperature, as reported in the south, but the developmental threshold temperature for the SIL population was near 8°C, 2° lower than previously reported. Storage of the eggs at 8°C resulted in slow but measurable development rather than low-temperature quiescence as expected, leading to inconsistent degree-day estimation among temperature treatments. Following storage at 8°C, both egg development rate and hatching success increased with increasing temperature. However, hatching success was improved by increasing the time the eggs spent in storage, ranging from only 50% hatch in unstored eggs to >90% hatch in eggs stored for ~6 mo. In addition, a bimodal hatching response was seen in the eggs; about half of the eggs deposited by individual females hatched immediately under favourable conditions, and the remainder hatched after exposure to cold (4°C). A lower developmental threshold than previously reported and a previously undescribed egg diapause may enable *Hexagenia limbata* to persist near the northern extent of its distribution.

Key words: *Hexagenia limbata*, egg-hatching, temperature responses.

Hexagenia limbata (Serville) is a burrowing mayfly found in lakes and rivers over much of North America (McCafferty 1975, Edmunds et al. 1976). Development of eggs and nymphs is temperature dependent, and the life cycle ranges from <6 mo in Utah irrigation canals (Edmunds et al. 1976) to >3 yr at the extreme northern edge of their distribution (Giberson 1991). The egg stage may be completed in as little as 2-3 wk under summer conditions (≥20°C: Neave 1932, Hunt 1953, Flattum 1963), or it may extend over weeks or months at cooler temperatures (Flattum 1963, Hudson and Swanson 1972). The developmental threshold temperature, the temperature below which no development occurs, was previously believed to be ~10°C for all stages (Hunt 1953, Heise et al. 1987). Recently, however, development of large individuals of *H. limbata* from Southern Indian Lake (SIL), Manitoba, a new reservoir located near the northern limits of the species, has been reported at 8°C (Giberson and Rosenberg 1992).

Intraspecific variation in development rates in *Hexagenia* often results in life cycles that are complex and difficult to interpret. Nymphal cohorts frequently overlap, which makes them difficult to distinguish using standard size-frequency analysis. Local populations may also show mixed life cycles, in which some individuals complete development in a year or less, while others lag behind by several months (e.g., Horst and Marzolf 1975, Heise et al. 1987). Overlapping cohorts and mixed cycles result from the year-to-year differences in emergence timing of adults, which in turn relate to the developmental variability of the immatures. Previous interpretations of the life cycle focused on nymphal development, but large variations in voltinism may be attributed to timing of egg development as well. Eggs deposited early in the season, when temperatures are warm, may hatch quickly, enabling substantial nymphal growth in the first season. Eggs deposited later in the season, however, may not hatch before winter; several months may pass before hatching and the start of nymphal growth. The alternating 14/24 mo cycles found for *H. limbata* in Lake Winnipeg and Lake Dauphin in Manitoba (Flannagan 1979, Heise et al. 1987), for example, are a result. An understand-

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ing of the dynamics of egg development, therefore, is crucial to the understanding of the life cycle of *Hexagenia.*

In this paper, temperature effects on hatching parameters of *H. limbata* are examined on eggs collected from SIL. The implications of these effects, including a previously undescribed egg diapause, on life-history strategies will also be discussed.

Methods

Site description and collection of adults

Southern Indian Lake is located in northern Manitoba, Canada (56°38'-57°40'N, 99°45'-98°10'W). The lake, a reservoir impounded in 1976, is surrounded by permanently frozen soils (permafrost) and has an annual ice-free period of about 5 mo (Newbury et al. 1984). *Hexagenia* adults were collected from two sites: 1) near the inflow of the Churchill River into SIL, and 2) a shallow bay just south of the main flow through the lake and ~30 km east of the inflow.

Adults were collected by hand-picking and sweeping shoreline vegetation with a net at each site during the peak of the emergence period in 1987. Specimens were identified in the laboratory, and eggs for the study were obtained by artificial fertilization.

Artificial fertilization technique

Two *Hexagenia* species occur in SIL: *H. limbata* and *H. rigida.* Males are easily separated by the shape of the penes, but females cannot be distinguished (McCafferty 1975). Therefore, the method of Friesen (1981) was used to ensure that fertilized eggs of *H. limbata* were obtained for the experiments. Two thousand to four thousand eggs (depending on female size, Giberson 1991) were stripped from each of 15 female *Hexagenia* subimagos at 20°C, and the eggs from each female were separated into three groups in separate petri dishes containing a few drops of Yaeger's solution (formula given in Friesen 1981). Mating does not occur until the imaginal stage, but eggs from subimagos are viable, so subimagos were used to ensure that the females had not previously mated (Hunt 1951, Friesen 1981). Terminal abdominal segments of individual male *H. limbata* were macerated and mixed with eggs in one group of petri dishes, and those from male *H. rigida* were macerated and mixed with the second group; the third set was left without fertilization. The mixtures were allowed to stand for 10 min, then dishes were filled with filtered lake water.

The developing embryo could be seen through the chorion under a dissecting microscope within three or four days after fertilization. Five days after fertilization, the eggs were examined closely for development. Egg masses in dishes fertilized by *H. limbata* males that showed little or no apparent development at this time either were unsuccessfully fertilized or resulted from crossing *H. limbata* males and *H. rigida* females; no eggs hatched in unfertilized dishes. Successful fertilization by *H. limbata* was noted in four dishes. Eggs from the successful crosses were separated into groups of 50, and were added to 50-dram vials containing filtered lake water, for storage and later treatment at different temperature combinations. Each treatment included 12 vials: three replicate vials of 50 eggs from the four successful male : female pairings.

Storage procedure

Friesen et al. (1979) determined that *H. rigida* eggs from southern Manitoba (49°53'N, 97°09'W) could be stored at 8°C, 2°C below the developmental threshold, for up to a year with little or no change in hatching parameters. Development of *Hexagenia limbata* eggs had also been reported to cease below 10°C (Flattum 1963), so eggs were expected to store well at 8°C. Eggs were cooled in 4°C stages (4 d each) to 8°C (Friesen 1981), and stored at 8°C until the start of treatments. Storage was necessary because eggs were collected from SIL during the summer, but treatments could not begin in the Winnipeg laboratory until winter.

Treatments

Treatments were designed to simulate temperature conditions encountered at SIL, so that comparisons could be made with concurrent field studies (Giberson 1991). The treatment design is shown in Figure 1, and explained in detail below. Treatments were run in controlled environment chambers (temperature fluctuations <0.5°C), and in constant light. Vials were examined under a dissecting microscope; newly

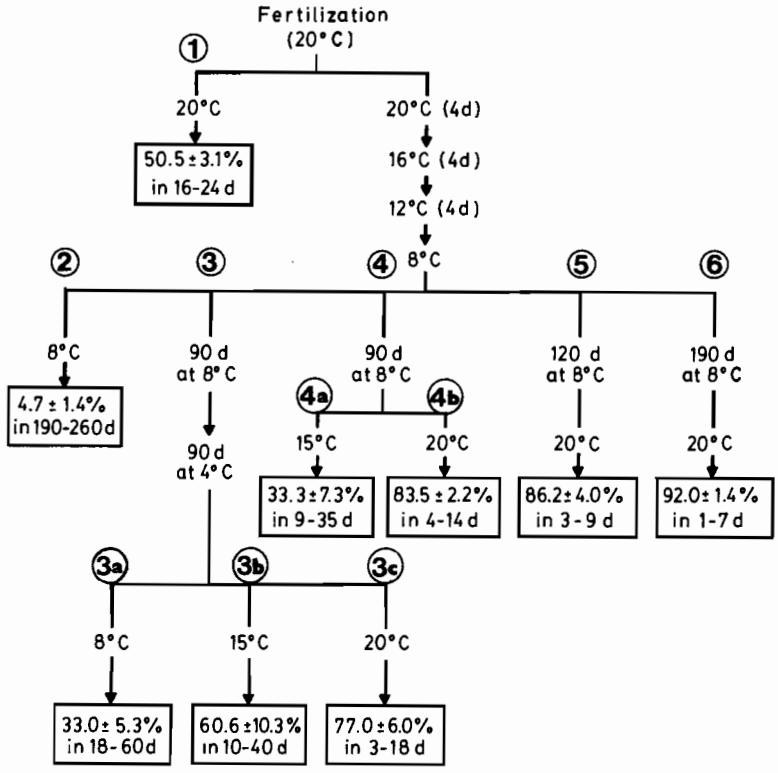

FIG. 1. Egg hatching treatments (circled numbers) and results for *Hexagenia limbata*. Hatching success is expressed as mean % hatch (±1 SE) and development time is the number of days (d) to hatch after warming to final treatment temperature.

hatched nymphs were counted and discarded, and a record was kept of the timing of the hatch.

Treatment 1 (Fig. 1) was originally designed as a control treatment. Eggs were maintained at 20°C at SIL, and were checked daily for 45 d to record hatching success and time to hatch for later comparison with stored eggs. After 45 d, remaining unhatched eggs from the control treatment were inadvertently cooled when they were transported to the Winnipeg laboratory with the eggs stored at 8°C.

Treatment 2 was the "storage" control, established to ensure that 8°C was below the developmental threshold. Eggs were held at 8°C throughout the study period and checked approximately weekly.

In treatments 3–6, eggs were stored at 8°C for at least 90 d before being placed at the various study temperatures (note that 8°C was believed to be below the developmental threshold, so development was expected to be arrested during the storage period). Temperature treatments following storage (Fig. 1) were chosen to simulate conditions observed at different times or locations at SIL:

—Treatment 3: "overwintering at 4°C"—after storage, eggs were cooled to 4°C for a further 90 d, to mimic winter conditions, and then warmed to 8° (Treatment 3a), 15° (3b), and 20°C (3c). Springtime temperatures in SIL were ~8°, mid-summer temperatures in cool areas were ~15°, and those in warm areas were ~20°C.

—Treatment 4: "SIL summer temperatures"—after storage, eggs were warmed immediately to 15° (Treatment 4a) and 20°C (4b).

—Treatments 5 and 6: "warm summer temperatures, varying time in storage"—eggs were maintained at the storage temperature for 120 d and 190 d, respectively, before warming to 20°C.

In all treatments, eggs were examined daily after being warmed to the final treatment tem-

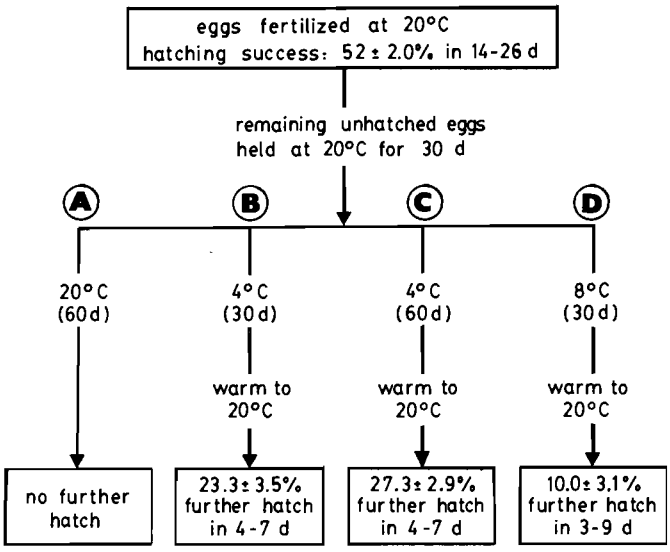

FIG. 2. Summary of *Hexagenia limbata* egg diapause trials. Eggs were allowed to hatch at 20°C, then the remaining unhatched eggs were cooled to mimic overwintering and re-warmed to 20°C. Mean % hatch (±1 SE), and time to hatch after warming (d), are given for each treatment (circled letters).

perature. Treatment differences were analyzed by comparing hatching success (mean % hatch ± 1 SE) and developmental periods (total days required for hatch, days above the threshold temperature, and degree days above the threshold) at the various temperature combinations. Degree days (dd) were calculated using a linear model (Southwood 1978):

$$dd = (T - T_0)d$$

where T = study temperature, T_0 = threshold temperature, and d = days > threshold.

Diapause trials

Although no diapause stage had previously been reported for *Hexagenia*, preliminary results from the egg hatching experiments suggested that some *H. limbata* eggs from SIL required exposure to cool temperatures to hatch. When the "control" eggs from Treatment 1 were re-warmed to 20°C after being accidentally cooled to 8°C for 30 d (after >1 mo at 20°C since the last recorded hatch), young hatchlings were observed swimming in the vials. Some of the unhatched eggs were viable, but apparently needed cold stimulation to hatch.

To test for diapause, fertilized eggs were obtained as above from a previously unmated pair of adults that had been reared in the lab from SIL eggs. Fifty eggs were placed in each of 12 vials, and allowed to develop and hatch at 20°C. Vials were checked daily, and newly hatched nymphs were removed from vials and discarded. Hatching success and time to initial hatch were recorded as in Treatment 1 of the egg-hatching experiments (Fig. 1). Thirty days after the last recorded hatch, the groups of vials containing the remaining eggs were then separated into four diapause treatments (Fig. 2), each with three replicates. Vials from the first treatment in the diapause series (Treatment A) were held at 20°C for an additional 60 d to determine whether further hatching would occur during that period without exposure to cold. Eggs in the remaining three treatment series were cooled in 4°C stages (of 4 d each) to 4°C for 30 d (Treatment B) or 60 d (Treatment C), or to 8°C for 30 d (Treatment D) before re-warming to 20°C (Fig. 2). After re-warming, eggs were again checked daily for hatching, and treatments were analyzed by comparing overall hatching success and time to hatch at each temperature combination.

Results

Hatching success

Eggs from individual parent crosses were initially kept separate to determine whether there

TABLE 1. Total number of days, number of days above 8°C, and degree days (dd) >8° and >10°C required for initial hatch of *Hexagenia limbata* eggs exposed to different temperature treatments. Treatment numbers correspond to Figure 1. The 12-d period of cooling to storage temperature and dd accumulated during cooling to storage temperature are included in counts for all except Treatment 1.

Final treatment temperature	Initial treatment	Treatment no.	Total days	Days >8°C	dd >8°C	dd >10°C
20°C	20°C(8°C/30d)	1	16	16	190	160
	8°C/90d	4b	106	16	144	112
	8°C/120d	5	135	15	132	102
	8°C/190d	6	203	13	108	82
	8°C/90d; 4°C/90d	3c	195	15	132	102
15°C	8°C/90d	4a	111	21	159	117
	8°C/90d; 4°C/90d	3b	202	22	166	122
8°C	8°C	2	202	0	96	72
	8°C/90d; 4°C/90d	3a	210	0	96	72

were differences in hatching responses between egg masses. No significant differences in hatching success were found among eggs from different parents (Tukey's multiple comparison test, $\alpha = 0.05$), so results using eggs from different parents were combined and summarized in Figure 1 and Table 1.

Only about half of the eggs held at 20°C (Treatment 1; Fig. 1) hatched within the initial hatch period, although 77–92% of eggs from the same egg masses hatched at that temperature following storage (Treatments 3c, 4b, 5, and 6; Fig. 1). However, after unhatched eggs in Treatment 1 were cooled and subsequently rewarmed, a further 1–19% hatched, resulting in a total mean hatch of about 60% in the control treatment. Hatching success of eggs warmed to 20°C generally improved with increasing time spent at the 8°C storage temperature; 92% of eggs hatched following storage for 190 d compared with 84–86% after 90 and 120 d of storage (Treatments 4b, 5, and 6; Fig. 1).

Egg hatch occurred at all temperatures evaluated except 4°C, although at 8°C (Treatment 2), only about 5% hatched over 202–272 d (including 12 d cooling to storage temperature; Fig. 1). Hatching in this treatment and in Treatment 3a may have been incomplete, however, since the 8°C trials were terminated following an incubator failure on day 272. Cooling to 4°C before warming (Treatment 3) resulted in improved hatch at 8° and 15°C when compared with hatch at 8° and 15°C after storage at 8°C (Treatments 2 and 4a).

Hatching occurred at 8°C, although at that temperature it was extensively delayed and hatching success was low. Therefore, the assumption of a 10°C developmental threshold for the SIL population is incorrect; the threshold is likely near 8°C. Consequently, degree-day estimations for development of *H. limbata* eggs were calculated using both 10°C (literature threshold, for comparisons) and 8°C (experimental threshold).

Development time

The minimum egg development period (days to first hatch) at constant temperatures ranged from 16 d at 20°C to 202 d at 8°C (Treatments 1 and 2; Fig. 1, Table 1). Eggs in the storage treatments (Treatments 3–6) started to hatch in 106–210 d (including 12 d of cooling to storage temperature; Table 1), depending upon the amount of time spent in storage. Treatments 4b, 5, and 6 were essentially identical except for the amount of time in storage; if the storage temperature had been below the developmental threshold temperature for *H. limbata*, development should not have occurred during storage, and hatching times after warming should have been consistent for given temperatures. However, egg development slowed, but did not cease, during storage at 8°C, and the number of days to initial hatch (following warming) decreased with increasing time in storage in treatments 4b, 5, and 6 (Table 1, Fig. 1).

Conflicting results came from treatments in

which eggs were exposed for a period to 4°C (Treatment 3; Fig. 1). Eggs from Treatments 3b and 3c (90 d at 8°C plus 90 d at 4°C, then warmed to 15°C or 20°C) had a total development period about 90 d longer than those from Treatments 4a and 4b (90 d at 8°C, then warmed to 15°C or 20°C; Table 1). Development was extended by the period of time spent at 4°C, indicating that no egg development occurred at 4°C. However, eggs in Treatments 2 (constant 8°C) and 3a (90 d at 8°C plus 90 d at 4°C, then warmed to 8°C), began hatching after about the same period of time (200–210 d, Table 1), regardless of time spent at 4°C or 8°C. Egg development in this case either occurred at 4°C or was accelerated at 8°C.

Development could not be predicted using the ordinary degree day (dd) accumulation model, because the storage temperature was not below the developmental threshold. Since development occurred at 8°C, the number of dd>10° and dd>8°C appeared to decrease with time in storage. Degree days to first hatch ranged from 72 to 160 >10°C, and from 96 to 190 >8°C (Table 1).

Egg diapause

As in Treatment 1, ~50% of eggs in the diapause trial hatched within 2–4 wk at 20°C (Fig. 2). No additional hatch was recorded at 20°C, at least within the 13-wk period following the end of the initial hatch period (Treatment A). However, in all cases where eggs were cooled subsequently and re-warmed, further hatch occurred. Hatching success following cold treatment was highest after storage at 4°C for 60 d (Treatment C), which prompted an additional hatch of >27% of the original total number of eggs, giving a total hatch of 79%. Storage at 4°C for 30 d (Treatment B) resulted in a further 23% hatch (total 75%), but exposure to 8°C for 60 d (Treatment D) resulted in a further hatch of only 10% (total 62%).

Discussion

In many species of mayflies, both egg hatching success and incubation period are directly related to temperature (Elliott and Humpesch 1980, Brittain 1990, Suter and Bishop 1990). Hatching success is generally highest at some optimum temperature, and decreases at temperatures on either side of the optimum (Elliott and Humpesch 1980, Brittain 1990). Incubation period decreases as temperature increases. The relationship between temperature (T) and incubation time (t) is usually expressed as a power law:

$$t = aT^{-b}$$

where a and b are empirically derived constants (Elliott and Humpesch 1980, Brittain 1990, Suter and Bishop 1990). Prediction of egg hatching times using this relationship requires constant temperatures, which are rarely encountered in field situations. Egg hatching time may also be described in terms of development rate (1/t) with temperature (T), in the form of a logistic curve (Davidson 1944). The advantage of this latter relationship is that for temperatures in the middle parts of the curve, a linear relationship between temperature and development rate exists:

$$1/t = a + bT$$

where a and b are empirically derived constants (Davidson 1944, Rosillon 1988, Giberson and Rosenberg 1992). Incubation time can be predicted, even under changing temperature conditions, by summing the degree days above the developmental threshold: dd>threshold required for development is equal to 1/b, and the derived threshold for predictive purposes is the temperature at which the development (1/t) rate approaches 0 (Rosillon 1988). The true developmental threshold, however, is lower than that derived from extrapolation from the linear model, and development is faster than predicted by the model at temperatures near the lower developmental threshold (Giberson and Rosenberg 1992). Deviations from this response will occur when egg development depends upon an obligatory diapause state (Elliott and Humpesch 1980, Suter and Bishop 1990).

Development rate of *Hexagenia* eggs shows a linear response to temperature above a threshold of ~10°C for the species studied (Hunt 1953, Flattum 1963, Friesen et al. 1979, Wright et al. 1982). We sought to evaluate the thermal dependence of egg development for *H. limbata* under conditions found in SIL. Although eggs were collected from relatively few adults, no significant differences in hatching responses were seen among the eggs from different parents, so the responses probably represent those

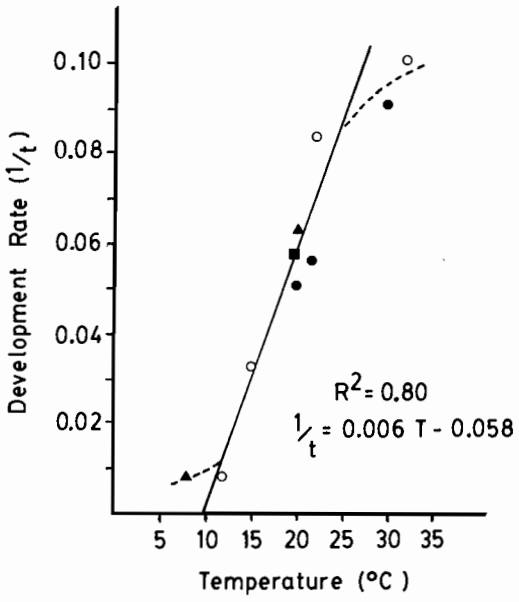

FIG. 3. Relationship between development rate (1/t) and incubation temperature for *Hexagenia limbata* eggs (data from Neave 1932 (■), Hunt 1953 (●), Flattum 1963 (○), and this study (▲).

of the population. The general pattern of decreased development time and increased hatching success with increased temperature was confirmed, although the SIL population differed from southern populations with respect to specific details of the development/temperature response.

Based on egg development studies by Flattum (1963) and Friesen et al. (1979), storage below the reported threshold of 10°C was expected to result in low temperature quiescence, with no further development until eggs were subsequently warmed. Egg hatch could then be predicted as a function of the accumulated dd>10°C. However, the threshold temperature for egg development in the SIL population is below, but probably near 8°C. Consequently, development at that temperature was faster than predicted by the linear dd model, resulting in lower apparent dd requirements following storage of the eggs at 8°C.

Eggs in the 20°C control treatment were not stored, so their hatching times could be compared with other studies reporting incubation temperatures. Eggs from SIL (56°38'–57°40'N) required 160–240 dd>10°C for completion of the initial hatch, compared with 170–190 dd in Lake Winnipeg (50–54°N) and 200–260 dd in some Michigan lakes (42°36'N; calculated from Neave [1932] and Hunt [1953], respectively). These differences in dd for hatching are minor, suggesting that temperature responses of *H. limbata* eggs are fairly constant over a wide geographic area.

Many insect species have shown a trend for the developmental threshold temperatures to decline with increasing latitude (Danks 1987), and the presence of an 8°C threshold in the SIL population appears at first to support this pattern. The assumption of a 10°C threshold for *H. limbata* is based primarily on field data from Hunt (1953), in which growth of nymphs ceased at temperatures below about 48°F (generally approximated as 10°C although 48°F = 8.9°C). Subsequent studies showed good agreement between nymphal development and dd accumulation >10°C, so 10°C has become widely accepted as the developmental threshold temperature for *H. limbata* (Hudson and Swanson 1972, McCafferty and Pereira 1984, Heise et al. 1987). Calculation by linear regression of the derived threshold (one based on the linear dd model) for egg development for *H. limbata* using data from several sources (Fig. 3), including our study, yields a value of 9.8°C. For temperatures in the middle of the temperature range, then, calculation of dd>10°C should be generally valid for prediction of egg hatch over the entire geographic range, including SIL. Development of nymphs from SIL also appeared consistent with a threshold near 10°C for temperatures in the middle range (Giberson and Rosenberg 1992). Therefore, the hypothesis of a lower threshold for the northern population needs to be validated by more detailed work on southern *Hexagenia* populations.

One apparent anomaly in hatching responses among eggs in the different treatments was seen in the treatment that mimicked overwintering conditions at SIL (Treatment 3). In two of the treatments (3b and 3c, where eggs were warmed to 15°C and 20°C), an extended development period equal to time spent at 4°C indicated that development did not occur at that temperature; this response was expected if the developmental threshold temperature is near 8°C. However, in a third treatment (3a, where eggs were warmed to 8°C), no extension of the development period relating to time spent at 4°C was seen, indicating that development may, in fact, have been occurring at that temperature. It is possible that a sudden rise in temperature in

spring may serve as a cue to speed development at 8°C, particularly since hatching success of eggs exposed to 4°C was also improved at 8°C.

Temperature effects on success of hatching have not been well documented for *Hexagenia*, although Hunt (1953) reported that >90% of naturally fertilized *H. limbata* eggs from Michigan lakes hatched at ~20°C, without exposure to a cold period. In our study, hatching success (post-storage) improved with increasing temperature within the range of study temperatures investigated. Therefore, the optimum temperature for hatch is 20°C or greater. At 20°C, hatching success also improved with increased amount of time in storage, ranging from only ~50% hatch for no storage (Treatment 1) to >90% hatch after more than 190 d in storage (Treatment 6). The poor initial hatch in Treatment 1 was originally attributed to a failure of the artificial fertilization technique. However, hatching success of eggs from the same egg masses was high following low temperature storage. Eggs were viable, but apparently required an environmental cue to stimulate hatch.

A second set of experiments confirmed that the unhatched eggs entered a true diapause, rather than a low temperature quiescence, since they did not hatch until after exposure to a temperature stimulus. Under natural conditions, this sequence would result in a bimodal egg hatching pattern, in which some eggs in an egg mass could hatch immediately if conditions were favourable, and the remainder would enter diapause. Although both diapause and non-diapause eggs may be produced in the same insect species or population, individual females usually lay batches containing either one kind or another (Walker 1980). In SIL *Hexagenia limbata*, individual females produced both diapausing and non-diapausing eggs in the same egg mass.

The egg diapause observed in the SIL population of *H. limbata* appears to be limited geographically. Hunt (1953) recorded >90% hatching success of naturally fertilized eggs in Michigan without cold-treatment. However, anecdotal information in the literature suggests that diapause occurs in other northern populations. Neave (1932) recorded only 50% hatch of *H. limbata* eggs from Lake Winnipeg, Manitoba, and Heise et al. (1987) could not relate the presence of small nymphs of *H. limbata* early in the spring in Dauphin Lake, Manitoba, to an oviposition period during the previous season.

Bimodal egg hatching responses, whether they result from diapause as in the SIL population or from low temperature quiescence, may have a significant effect on interpretation of *H. limbata* life cycles in other locations. In SIL, the presence of diapausing eggs ensured survivorship of a cohort, but had little obvious effect on subsequent growth patterns of the nymphs. Because nymphs grow slowly in SIL, those hatching in August were still tiny by the autumn and subsequent spring, when the remainder of the cohort hatched. Therefore, the two parts of the cohort were virtually indistinguishable by the end of the second year (Giberson 1991). In warmer locations, two egg-hatching periods could result in a splitting of the cohort into two obvious groups if nymphs from early hatching eggs grew substantially before their first winter.

The adaptive significance of this type of diapause is obvious. It presents a "bet-hedging" strategy in the unpredictable conditions that may occur at the limits of distribution of a species. Weather conditions at SIL are highly variable, resulting in some years that provide favourable conditions for *Hexagenia* and other years that are unfavourable (Giberson et al. 1991). Emergence timing and success is strongly associated with weather conditions at SIL, and may vary by several weeks from one year to the next (Giberson 1991). Conditions that result in two widely separated egg-hatching periods can effectively split the cohort. In years of early emergence and oviposition (mid-summer), nymphs hatch early and develop to a sufficient degree for successful overwintering (Giberson 1991). However, late emergence, oviposition, and hatching may result in few survivors in the following spring, because newly hatched nymphs show poor survivorship at low temperatures (Giberson and Rosenberg 1992). In the latter situation, an egg diapause with subsequent spring hatching ensures that at least some members of a cohort will have a good chance of survival, allowing them to persist in the unpredictable environment at the northern edge of their distribution.

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