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R. G. Stross

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LIGHT AND TEMPERATURE REQUIREMENTS FOR DIAPAUSE DEVELOPMENT AND RELEASE IN *DAPHNIA*

R. G. STROSS

Department of Zoology, University of Maryland, College Park, Maryland

Abstract. The light and thermal requirements for diapause development and release in *Daphnia pulex* were determined for the ephippia from a pseudo-sexual strain cultured in the laboratory and from an autumnal diapausing, bisexual strain in Paul Lake, Michigan.

Light was essential for termination of diapause in the laboratory-cultured strain regardless of the temperature or duration of ephippia storage. Ephippia from the lake population were activated by light, but prolonged storage in constant dark eliminated the requirement for light, and thereby implicated photoperiodic control of diapause release.

The laboratory population completed diapause development within a period of 3 to 6 weeks when stored in constant dark at 22°C. Storage at 3.5°C in constant dark prolonged diapause. In the Paul Lake strain, low temperature was a requirement for diapause development, and at 3.5°C the eggs were in diapause for a period of 5 or 6 months.

The contrasting light and thermal requirements are discussed in the context of environments regulating the duration of diapause in summer and winter diapausing populations of *Daphnia*.

INTRODUCTION

The termination of diapause in *Daphnia* and other Cladocera is stimulated by a number of environmental components. Low temperatures may be necessary for the normal release of ephippial (diapausing) eggs from a state of arrested growth, a fact known in the 19th century (Weismann 1879). The requirement may not be universal, however, as shown by Wood (1932) and Wood and Banta (1933, 1937) for both *Moina* and *Daphnia*. A recent discovery that light breaks the diapause of ephippial eggs (Pancella and Stross 1963) adds a second potential stimulus to diapause termination in nature and one other stimulus known to regulate the life-cycle of *Daphnia*. This paper considers the effects of both light and low temperature stimuli on diapause release in resting eggs of *Daphnia*.

Autumn-produced ephippial eggs of *D. pulex* may require exposures of 3 to 6 months of low temperatures to terminate diapause (Vollmer 1912). Vollmer showed that as winter progressed, increasingly larger numbers of eggs hatched when transferred from storage at 3.0°C to incubation at 15.0°C; 2.0% of eggs hatched in early November and 30.0% hatched in early March of the following year. A temperature of 10°C was reported to permit egg dormancy to be broken. Weismann (1879) achieved an early release of some autumn-produced eggs of the same species following a 1-day exposure to sub-zero (°C) temperatures of brine. However, in another study, freezing did not hasten termination of the dormant state (Vollmer 1912).

Wood and Banta (1933, 1937) reported that ephippial eggs of *D. longispina* renewed active

development without exposure to temperatures lower than that of parent cultures. The ephippia were collected from laboratory cultures and incubated at culture temperatures of 19 to 22°C. Yields of young ranged from 26 to 45% of the incubated eggs. When ephippia were aerated or transferred frequently to new medium, the hatch was as large as 65%. In their studies, a specific stimulus releasing diapause was not identified.

Exposure to low temperature was unnecessary for the release of diapause in laboratory-cultured ephippia of *D. pulex* (Pancella and Stross 1963). Ephippial eggs renewed active development when exposed to constant white light. Autumn-produced ephippia collected in November from a lake also responded to light when tested in December. However, activation by light occurred only after the ephippia were soaked in a solution of sodium hypochlorite.

This paper is a continuation of that work to determine if light is essential for the release of diapause. It also determines if low temperature may provide a natural substitute for the hypochlorite treatment.

METHODS AND MATERIALS

Ephippia for the experiments were gathered from two populations of *D. pulex*. One source of supply was cultured from specimens obtained from the Connecticut Valley Biological Supply House, Southampton, Massachusetts, in 1960. A second group of ephippia was collected from a small lake in the Upper Peninsula of Michigan (Paul Lake; T. 45N R. 8E S36). The ephippia are extremely buoyant and are concentrated by the wind in a small area at the margin of the lake.

Collection was made in November 1962, and the ephippia were returned to the laboratory within 48 hours in a darkened Dewar flask. Upon arrival, the material was stored in sealed containers at 3.5°C. Ephippia from a second species, *D. rosea*, comprised 15.0% of the samples from the lake and, although easily recognized, were permitted to contaminate because of the difficulty in separating adequate numbers of one species. All identifications of *Daphnia* were made using the Key of Brooks (1957).

TABLE I. Synthetic medium for incubating ephippia

Component	Quantity
NaHCO ₃	50.0 mg
MgSO ₄	10.0
CaCl ₂	80.0 mg
Double distilled water	1000 ml

The cultures of the laboratory strain were maintained in a synthetic pond medium (Table I) and fed suspensions of *Chlamydomonas reinhardtii* Dangeard, I. U. strains #89 or #90 as reported earlier (Pancella and Stross). They were exposed to constant light and temperatures of 21.0°C. The ephippia were collected at intervals of 2 days, placed with pond medium in vials, and stored in complete darkness at temperatures of the maternal cultures unless stated otherwise.

The ephippia were tested in groups of 50 or 100 per beaker in 50 ml of either synthetic pond medium (laboratory population), or in water from Paul Lake. The safelamp consisted of a 40-W tungsten bulb filtered with one layer each of a red and a deep blue cellophane.

Incubation in the laboratory was in constant light of 65 ft-c incident light from 20-W "day-light" fluorescent lamps. Controls were housed in light-proof containers. Temperatures were controlled at 3.5 ± 0.5°C, 12.0 ± 0.1°C and 21.0 ± 1.0°C. Each experiment was continued for 80 or 100 days unless otherwise stated.

The presoaking of ephippia with hypochlorite was described previously (Pancella and Stross 1963).

Hatching yields were determined by the number of young *Daphnia* present at daily intervals; these were removed at the time of observation. They are reported as a percentage of the eggs hatching. Either 100 or 200 eggs were used in each replicate unless otherwise stated; the number of eggs was said to equal the normal complement of two per ephippium.

RESULTS

Characteristics of the two populations

In culture, the two populations of *D. pulex* differ in the development of ephippial eggs. When cultured in constant light, the laboratory population produces large numbers of ephippial eggs at, and following maximum densities of the population. When most of the population has died, a number of the old females again reproduce by "summer" eggs which add young to the population. Rates of feeding seem to regulate both density of population and rate of ephippial production. Evidence that the laboratory population is pseudosexual is circumstantial: all members of a culture were observed to produce ephippia. Morphological characteristics, given by Banta (1925), also describe this population.

The lake population was maintained in culture under the same conditions in a reproductive state, but only rarely was an ephippium found in the beakers. In the lake, ephippia are produced in autumn only, to judge from the following observations. The plankton was sampled intensively from May through November, the ice-free period, during the years 1954-56. Collections after mid-September were made on the first and third weekends of October and the second weekend of November. Much of the reproduction was in the form of ephippial eggs in early October. Only ephippial eggs were found in later samples. The buoyant ephippia drifted to a localized segment of shore line where many remained afloat or were deposited temporarily on stones at the water's edge. They were conspicuous when the lake was visited on the third weekend of October. The annual persistence of diapause and localization of the ephippia were evident from visits to Paul Lake during November 1959-63.

The ephippia and the enclosed diapausing eggs are different for the two populations. Some of the ephippia from the laboratory population float at the surface, often as a result of the mother having molted there, but these may submerge if forced beneath the surface film. The eggs, green in color while the ephippium is retained by the mother, very quickly become golden-yellow following liberation.

Ephippia from the lake (both species) are extremely buoyant and resist efforts to sink them. Nearly all of the ephippial eggs from the lake are green, even when collected from the lake shore in early November. One month later a small number have become golden-yellow and small puncta of a heme-red pigment may be seen scattered

across the surface of the egg beneath the hyaline layer. The golden-yellow color is characteristic of nearly all eggs by the following April, but a few still retain a greenish cast. The color transformation is of interest because young hatched from lake ephippia are pink, owing to the globules of red pigment distributed in the soft tissues. All young are pigmented, even those few which hatched in November and early December. The pigment is lost from the young after a day or so of life at 21.0°C.

Laboratory population: light requirement for diapause release

In previous experiments, ephippial eggs from the laboratory population of *D. pulex* were stimulated to hatch by exposure to white light (Pancella and Stross 1963). A small number of young, usually not more than 2%, hatched in dark-controls.

A safelamp, as described, was used when preparing the ephippia for incubation and when examining beakers for hatching of young. The restricted use of light eliminated hatching in the dark controls.

Diapaused eggs which had been stored in the dark at 21°C for periods ranging from 51 to 182 days hatched in large numbers during their exposure to constant light which lasted for periods of 27 to 83 days (Table II). A total of 763 young

TABLE II. Hatching response of diapaused eggs of *D. pulex* laboratory population, to constant light at 21.0°C following storage in constant dark at 21.0°C for various time intervals

Age of ephippia (days)	Number	Incubation period (days)	Total hatch	
			Light	Dark
51.....	300	35	95 ^a	0
66.....	300	27	156	0
84.....	300	83	160	0 ^a
126.....	300	83	254	0 ^a
182.....	300	31	98	0
Total....			763	0

^a200 ephippia only

hatched from 1,400 ephippia. No young hatched from 1,300 ephippia maintained in the dark.

Response to light and cold storage.—Rates of hatching of ephippia from the laboratory population following storage at 3.5°C suggest that low temperature delays release from diapause, but permits synchronous activation if storage is sufficiently long. Ephippia stored at 22°C in constant dark for a period of 3 to 6 weeks hatched within 96 hours following exposure of the ephippia to light

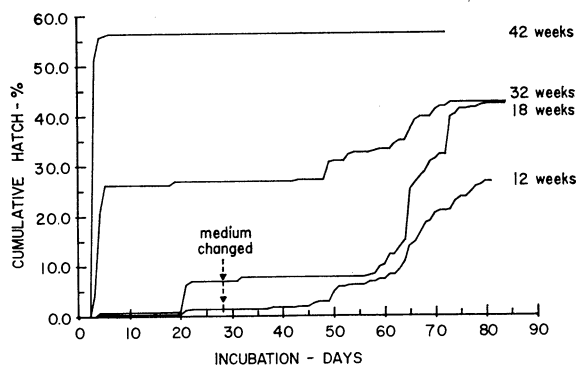


FIG. 1. Hatching of ephippial eggs of *D. pulex*, laboratory population in constant light at 21.0°C following storage in constant dark at 3.5°C for the indicated number of weeks.

(Pancella and Stross 1963). Ephippial eggs stored at 3.5°C in constant dark for 12 and 18 weeks, and, then incubated at 21.0°C, began to hatch after 10 days exposure to continuous illumination, but the majority hatched only after 50 days of exposure (Fig. 1). A storage period of 32 weeks resulted in prompt hatching following the transfer to light. The synchrony of hatching was even greater following 42 weeks of storage. In this test, 51.0% of the eggs hatched within 72 hours following light exposure. In all of the other tests at 21°C the initial hatch occurred between 72 and 96 hours of incubation.

Ephippia 42 weeks of age were also incubated in light, at 3.5 and 12.0°C. Average yields at each of these temperatures were $48.0 \pm 3.3\%$ and $59.7 \pm 4.1\%$, respectively, and they were considered not significantly different from the yield of $56.3 \pm 7.9\%$ obtained at 21.0°C.

Additional containers of 25 ephippia each were exposed only once to 1.0 hour of light at an intensity of 100 ft-c. In one pair of beakers incubated at 21°C, 22.0% of the eggs hatched, while in a second pair of beakers incubated at 12.0°C, 45.0% of the eggs hatched. The difference in yield at the two temperatures has a Q_{10} of 1.86. Hatching at 21°C occurred within 72 and 120 hours following exposure to light. At 12°C all but 1.0% of the young hatched within 164 and 192 hours.

The sensitivity of eggs to light following protracted storage at low temperature is shown in the response of the dark controls. Hatching occurred in the beakers incubated in the dark (except for inspection with safelight), although to a much smaller degree than in the light. After 42 weeks of storage, the hatch in the controls was $9.7 \pm 2.4\%$ at 3.5 and 12.0°C, and $2.3 \pm 2.0\%$ at 21.0°C.

The hatching in the controls was caused by exposure to light from the safelamp. A final experiment was carried out with ephippia that were stored and incubated at 3.5°C. After 48 weeks storage, the ephippia were transferred to incubation in the dark and maintained in the dark until day 22 of incubation. They were exposed only infrequently to the safelamp following that day for the 100 days of incubation. No hatching was observed. In the light, the yield was 48.7% (a value which demonstrated retention of egg viability for nearly 1 year).

Paul Lake ephippia: light and temperature response

That light stimulates hatching of *Daphnia* resting eggs from Paul Lake has already been shown (Pancella and Stross 1963). Activation was possible only if ephippia were preliminarily immersed in hypochlorite. A search for a natural stimulus revealed a low temperature requirement for the ephippia of *D. pulex* from Paul Lake.

Ephippia collected from the lake on November 6, 1962 were tested for the effect of both light and temperature on diapause termination. Samples of ephippia were transferred periodically from storage to incubation throughout the following winter and spring. The ephippia were stored in the dark at 3.5°C following return to the laboratory on November 8. One group was placed at 20°C on November 24. The tests were carried out at 20°C and under constant light.

If stored at 20°C, only a few eggs were activated by light during the 100 days of incubation (Fig.

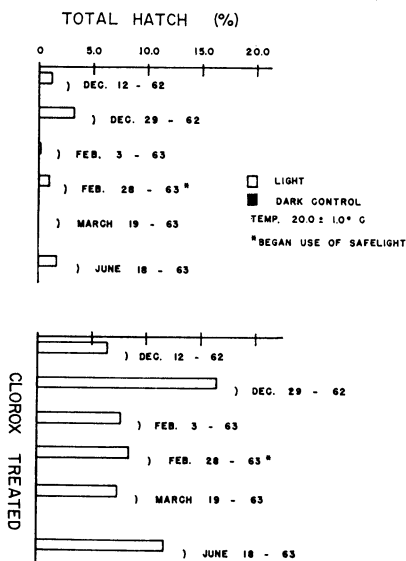


FIG. 2. Hatching of *Daphnia* ephippial eggs from Paul Lake in response to light exposure if eggs stored and incubated at 21.0°C. (See text for further explanation.)

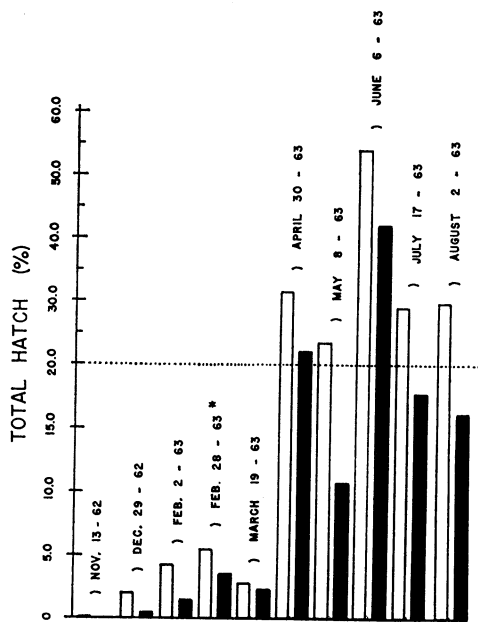


FIG. 3. Hatching of *Daphnia* ephippial eggs from Paul Lake following storage at 3.5°C and incubation at 21.0°C.

2). The number did not exceed 4.0%. A significantly larger number of young hatched from ephippia soaked in a 1% solution of sodium hypochlorite for 5 min, and incubated in light, but it did not exceed 17%. No young hatched in the dark from December to the following June.

The duration of storage at 3.5°C necessary for the normal diapause release of large numbers of ephippial eggs was suggested to be in the range of 5 or 6 months. Release occurred some time between March 19 and April 30 (Fig. 3). Ephippia removed from storage to 21°C on April 30 yielded a 32% hatch in the light-exposed sets and a 22% hatch in the dark. Nearly all young hatched within the initial 10 days. Although the March 19 group was still under incubation in April and May, no young hatched after the initial 10 days. Diapause release could have occurred earlier than April 30 because resting eggs stored in an uncrowded condition (a few hundred in 4 oz. lake water) were already in the process of hatching.

Loss of light and low temperature requirement.—Additional experiments at incubation temperatures less than 21°C showed an inhibitory effect of temperature on hatching rates. These tests also showed the disappearance of a light requirement. On May 8, groups of ephippia were removed from a second storage container and incubated at 12, 18, and 21°C. In continuous light at 12°C, 56.3% of the eggs hatched, but at 18 and 21°C only 23.2% hatched (Table III).

TABLE III. Effect of incubation temperature on light activation of eggs from Paul Lake when ephippia removed from constant dark at 3.5°C and incubated at temperatures indicated

Date at start	Ephippia	Incubation temperature (°C)	Total hatch	
			Light % ± SE	Dark % ± SE
May 8	300	12.0	56.3 ± 2.2	16.8
	"	18.0	23.2 ± 2.5	12.0
	"	21.0	23.2 ± 1.4	10.8
June 6	300	3.5	64.8 ± 3.3	61.5 ± 2.5
June 11	"	12.0	59.0 ± 2.2	52.5 ± 2.9
	150	21.0	54.0 ± 3.5	42.3 ± 6.4

In the dark the hatch of 16.8% at 12°C was approximately one-third the percentage (and number) hatching in the light. Smaller, but proportional, numbers hatched in the dark at the two higher incubation temperatures. The inhibitory effect of temperature, and stimulation by light, had largely disappeared when eggs were tested 1 month later (Table III).

The largest percentages of hatching were obtained if the eggs were incubated at the temperature of storage (3.5°C). Ephippia transferred to fresh lake water on May 20, from the crowded and odorous storage containers, hatched in a spectacular way; 72.2% hatched in light-exposed, and 76.3% hatched in dark control beakers. The ephippia were transferred from storage to incubation without exposure to light from the safelamp as a precaution against activating the ephippia. In spite of this, hatching was equivalent in the light and in the dark controls. In July, the yield of young had declined, indicating that some loss of viability may have begun to occur (Fig. 3).

The lowest temperatures prolonged the period of postdiapause development of the embryo *Daphnia*. At 21°C, hatching occurred between days 3 and 4 of incubation. At 12°C, 5 or 7 days were necessary for hatching to begin. And at 3.5°C, hatching required 14 or 16 days of incubation. Most, if not all of the hatch from Paul Lake ephippia was completed within a period of 3 or 6 days following the beginning of hatching.

Strength of diapause in D. pulex and D. rosea.—It should be remembered that the samples from Paul Lake in 1962 were 85.0% *D. pulex* and 15.0% of the contaminant species, *D. rosea*. The small yield of young in tests preceding that of April 30 may have resulted in whole or in part, from the more weakly diapausing egg of *D. rosea*. A number of tests were carried out on ephippia collected from Paul Lake in November 1963. At that time, 25.0% of the ephippia were those of *D. rosea*.

The strength of diapause in the two species was tested in December. Duplicate sets of 15 ephippia each from each of the two species were soaked in hypochlorite and incubated under conditions described above. No eggs hatched in the beakers containing *D. pulex* ephippia. Fourteen young were removed from the two beakers containing ephippia of *D. rosea*, a yield of 46.7%. The tests suggest *D. pulex* to have the more intense diapause. From this information, it seems probable that diapausing eggs of *D. rosea* were the larger contributor to the pre-April hatch of the preceding year.

DISCUSSION AND CONCLUSIONS

The two strains of *D. pulex* contrast sharply in their light and temperature requirements for diapause development and release. An extension of the performance at light and temperatures in the laboratory to field conditions would provide the rudiments for understanding both aestival and hibernal diapause patterns in *Daphnia*.

Reviews of diapause in insects and mites (Andrewartha 1952; Lees 1955; deWilde 1962) and of seed dormancy in higher plants (Evanari 1956; Toole, Hendricks, Borthwick and Toole 1956) outline common modes and specific mechanisms of environmentally regulated dormant intervals in the life-cycles of the respective groups. Within the phenomenon of diapause, Lees includes stages from the life cycles of a large variety of animals in which suppressed metabolism or arrested growth exists. The specific inclusion of the resting eggs of *Daphnia*, as a typical example of diapause, aligns early studies of the *Daphnia* resting egg with the more general field of diapause study. Embryonic diapause in *Daphnia* is readily recognized, owing to shape and size of the eggs and the outermost membrane (ephippium) surrounding the pair of eggs. Reports of hatching within days following separation of the ephippium from the adult (which is when nondiapausing eggs hatch) (Wood 1932) may be considered an example of weak diapause rather than disproof that ephippial egg and diapausing stage are synonymous.

Diapause development and release must occur in quite different environments if summer and winter intervals are to be regulated. *Daphnia* populations are known to deposit ephippial eggs in three basic patterns that involve both warm and cold periods of the year. In lakes, this stage may be absent (acyclic) or appear in autumn (monocyclic) with remarkable periodicity (Berg 1931). Populations in smaller bodies of water may include more than one such period (polycyclic). Berg found not more than two, sometimes protracted

diapause intervals in Danish lakes, one in late spring or early summer, and a second in autumn or winter. Temperature and photoperiod are, perhaps, the two most obvious components contrasting the environments of summer and winter diapausing eggs.

The laboratory strain of *D. pulex* completed diapause development within a period of 3 to 6 weeks (Pancella and Stross 1963). Wood and Banta (1937) reported a similar experience with the ephippial eggs of *D. longispina*. In both instances, the diapause interval was completed at 21°C. These two instances are in contrast to the protracted period of diapause development that requires low temperatures, as observed elsewhere (Vollmer 1912) and above for the autumnally produced ephippia from Paul Lake. The implication that the thermal requirement for diapause development is determined solely by temperatures at inception of diapause has not been tested in *Daphnia*. Masaki (1956) has shown that aestival and autumnal diapausing pupae of a terrestrial insect (*Barathra brassicae*) complete diapause at different temperatures.

The temperature permitting diapause development in *Daphnia* embryos is related to the light response. In the laboratory strain of *D. pulex*, exposure to light was essential for diapause release. The duration of exposure required for activation was associated with the length of storage in darkness and the temperature of post-diapause incubation. Exposures of 1 hour were found to be as effective as constant light on ephippia stored for 42 weeks in the dark at 3.5°C. However, the temperature of incubation following light exposure was shown to influence the length of exposure required for complete activation with longer exposures required at the higher temperature of incubation. The same effect of temperature was observed in the light controls where brief interruption of light from the safelamp activated larger numbers of embryos at 3.5 and 12.0°C than at 21.0°C. Activation of a small percentage of the eggs with brief exposure to light was possible when ephippia were stored at 3.5°C for periods longer than 32 weeks, if response of controls to light from the safelamp is a suitable criterion.

The development of responsiveness to light during storage is dependent on temperature. An immediate and synchronous response following exposure to constant light was apparent only after storage for 42 weeks at 3.5°C. A similar response required only 3 to 6 weeks storage at 22°C (Pancella and Stross 1963).

The diapausing eggs of the Paul Lake strain

are clearly activated by light but in a manner which suggests that light is not essential for diapause release under conditions of the experiments. Light activation was apparent in diapause-interrupted eggs. Whatever the effect of hypochlorite in interrupting further diapause development, its effectiveness depended on subsequent exposure to light. The activating effect of light was also apparent while the eggs were undergoing the latter stage of diapause development at low temperature. When the ephippia were removed from dark storage in May, a majority (56.3% compared to 16.8%) of the eggs required light for activation. An additional month of storage in constant dark eliminated further need for light. One explanation is that prolonged storage in constant dark eliminates the light requirement, and this is consistent with observations on other arthropods (Paris and Jenner 1959).

The loss of a light requirement suggests that diapausing eggs are under the control of photoperiod and that with constant exposure to darkness, the eggs respond as if exposed to long-day photoperiods or constant light. Although indirect, the evidence for photocontrol of the diapausing embryo is supported by demonstration that diapause in the Paul Lake strain is induced by photoperiod (Stross and Hill 1965).

From the contrast in light and temperature requirements of the strains and suspected similarities between *Daphnia* and insect diapause emerges the idea of two distinct types of environmental control mechanisms. The Paul Lake strain of *D. pulex* is obviously adapted to autumnal diapause in a north temperate latitude where the winter period is many months in duration. Photoperiod could control the synchrony with which the eggs hatch in spring, and flotation could be a specific adaptation to insure maximum exposure under the ice or to the optimum aeration necessary for photocontrol.

The lack of a low temperature requirement in the laboratory strain suggests it to be functional for late spring and summer diapause periods. Surprisingly, the same strain could function in arctic regions, where the winters are extremely long, provided that light is excluded from the eggs. This possibility is suggested by the delaying action of low temperature on diapause development, and by a persistent requirement of light to activate the eggs. Although possibly coincidental, the pseudo-sexual derivation of the diapause eggs is reported to be of widespread occurrence in arctic regions (Edmondson 1955). Specific components of the above model are being tested.

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