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Delayed Egg Hatching and Semivoltinism in the Nearctic Stonefly *Megarcys signata* (Plecoptera: Perlodidae)

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ABSTRACT

Delayed egg hatching can influence the survival of aquatic insects by reducing exposure to competitors, predators, parasites, or unfavorable environmental conditions. We examined egg development in a Colorado population of the stonefly, *Megarcys signata* (Plecoptera: Perlodidae), whose larvae inhabit high altitude streams in the Rocky Mountains of western North America. Five-thousand fertilized eggs were collected from 40 different females and incubated in the East River, Gunnison County, Colorado, until late fall, at which time unhatched eggs were transported to incubation chambers in Ithaca, New York. We used three different combinations of photoperiod and temperature (10L:14D, 4°C; 10L:14D, 8°C; 8L:16D, 8°C) in an attempt to induce hatching. Eggs in the treatments with temperatures elevated above normal winter temperatures in the East River (8°C) began developing after 6 months, whereas eggs in the treatment most closely simulating natural stream conditions (4°C) did not hatch after 10 months of incubation. Our data indicate that this population of *Megarcys signata* has an extended egg stage that persists for almost a year, and that it is semivoltine at these elevations of 2885 and 2895 meters.

KEYWORDS: Delayed hatching, diapause, life history, stonefly, voltinism.

INTRODUCTION

The ability of aquatic insects to remain in the egg stage for extended periods permits them to survive harsh periods when fitness gained by metamorphosing to a subsequent stage is less than survival in the egg stage (Cohen, 1970). Since there are a number of mechanisms that enable insect eggs to remain viable for several months, years, or even decades (Tauber et al., 1984), this stage plays a critical role in determining the voltinism, life history, and ecological dynamics of aquatic invertebrates (Hairston et al., 1995). In cold, high altitude environments where conditions for growth and development may vary considerably or are restricted to a few warm months during summer, timing of egg development and hatching are critical to the success of many aquatic insects.

The success of stoneflies in such habitats depends largely on specialized traits in their life history that enable them to persist during harsh winter conditions. Following egg development of stoneflies in high altitude streams is difficult,

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because field sampling is restricted to a few months when ice and snow are absent. As a result, most descriptions of egg biology and life history patterns of these species have been inferred from studies on growth and development of larval stages. Previous reports on the life history of the perlodid stonefly, *Megarcys signata* (Hagen), obtained from benthic larval sampling suggested that eggs of this species hatched shortly after oviposition and that its life cycle was no more than one year (univoltine) (Cather & Gaufin, 1975; Allan, 1982; Peckarsky & Cowan, 1991). In this note we report the results of field and laboratory experiments that were designed to examine egg development in *M. signata*, and use these data to provide new information on its voltinism and life history.

Like many predaceous stoneflies, *M. signata* larvae are usually found under large stones in riffles where they feed on benthic invertebrates (Peckarsky, 1991a). Their diet consists of larval Diptera (Chironomidae and Simuliidae) and mayfly nymphs (Baetidae and Heptageniidae: Cather & Gaufin, 1975; Peckarsky, 1985; Peckarsky & Penton, 1989). Larvae grow rapidly throughout the autumn reaching sufficient sizes to become predatory by September (Allan, 1982). They overwinter as late instars and by early summer they molt to their final instar. Last instars emerge by crawling out of the water and metamorphosing under streamside vegetation or rocks. Males and females mate along the stream bank on logs or rocks, and females oviposit in the stream throughout the emergence period, which extends from June – August in streams near the Rocky Mountain Biological Laboratory (Taylor et al., 1998).

METHODS

The study was carried out during the summer of 1992 at two stream sites in Gunnison County, in western Colorado, USA. The East River site is third-order at 2885m elevation, and the Benthette Brook site is a first-order tributary of the East River at 2895m elevation. Both streams are cold water snowmelt streams that flow through the site of the Rocky Mountain Biological Laboratory (38°57′30″N, 106°59′15″W). The substrate at both sites is a heterogeneous mix of cobble underlain by gravel and fine sediments. Benthette Brook is a shallow fishless stream bordered by willows and open meadows, whereas the East River is a deeper, faster-flowing trout stream with riparian vegetation consisting largely of willows and conifers. Mean and range of water temperatures over the course of the study were 7.3 and 5–14°C for the East River and 6.3 and 5.5–12.5°C for Benthette Brook. Stonefly eggs oviposited by females collected from both streams were used in this study.

Adult *M. signata* were collected during June – August using slit emergence traps placed along the stream edge adjacent to riffles (Moreira and Peckarsky, 1994). Since previous studies reported *M. signata* to emerge at dawn (Peckarsky and Cowan, 1991), traps were checked for newly emerged adults every day at 0800–0900 h MDST. Pairs of newly emerged males and females were placed in individual plastic experimental cages ($20 \times 14 \times 11$ cm) located in the field, provided with 10% sugar solution for food, a small dish of water in which females could oviposit their eggs, and a rock and willow twig for shelter.

All eggs oviposited by each female were placed in 4 cm petri dishes with 45 μm mesh lids and incubated in the East River. Eggs were removed weekly from the stream and checked for hatched individuals and eye-spots (Stark & Szczytko, 1988). By mid September none of the eggs had hatched and there was no morphological evidence of embryonic development. Unhatched eggs were removed from the stream, placed in stream water kept cold with dry ice packs inside a portable cooler, and transported to incubation chambers in Ithaca, New York where experiments were performed to induce hatching.

A total of 5,000 eggs were randomly allocated to treatments in three laboratory incubation chambers with different temperature and photoperiod regimes. In one chamber, we set the temperature at 4°C to simulate winter thermal conditions and late winter photoperiod at 10L:14D. In the second chamber, the photoperiod was also 10L:14D, but the temperature was increased to 8°C to accelerate egg development. The third incubation chamber was set at 8°C, with a shorter daytime photoperiod of 8L:16D simulating winter photoperiod, but summer temperatures. Eggs were reared in 15 × 10 cm plastic cups containing deionized water, with an aquarium pump providing constant aeration. Conductivity of the deionized water was similar to that of the East River (1.1 μS cm-1) and Benthette Brook (1.3 μS cm-1), where the eggs would have been oviposited and hatched. Incubated eggs were checked every two weeks for eye-spots and hatched individuals.

RESULTS

Under natural stream conditions none of the 5,000 fertilized eggs hatched during the oviposition period (summer 1992). There was no eyespot development in any of the eggs, nor were there any signs of fungal infection, osmotic stress, or deterioration in the eggs incubated in the East River through early September 1992. Dissections of fertilized eggs revealed a white fatty embryonic tissue, indicative of early stage developing eggs. We first observed eyespot development in eggs in the incubation chamber with a 10L:14D photoperiod at 8°C in late December 1992, and by 17 January 1993, 25% of the eggs from this chamber had eyespots, and 5% of 1650 eggs had hatched (Table 1). At this time the other two chambers had fewer eggs with eyespots and no eggs had hatched. Hatching and eyespot development continued in all three chambers with the highest rate of development in the chamber with the 10L:14D photoperiod at 8°C. The chamber with winter temperature conditions (10L:14D photoperiod at 4°C) had the lowest egg development rate. By the end of January, 1993 eggs in the two warm chambers developed a fungal infection (most severe at 8 °C and longer photoperiod); and by early May, 1993 the eggs in the coldest chamber became infected, preventing us from determining hatching success or time of hatching for that treatment. By that time 5% of the eggs had eyespots, but none had hatched (Table 1).

Using these laboratory data in conjunction with field sampling of larvae and adults we have constructed a life history diagram, which is characterized by a prolonged egg stage, followed by rapid larval growth during warm summer

TABLE 1. Treatments used to test for diapausing eggs and induce hatching of *Megarcys signata* eggs from three rearing chambers controlling photoperiod and temperature.

Treatment	Temperature (°C)	Number of eggs	Eyespots (%)	Hatched (%)	Date
(Control) 10L : 14D	4	~ 1,650	5	0	5/1/92
(Warm dark) 8L : 16D	8	~ 1,650	10	2	1/30/92
(Warm Normal) 10L : 14D	8	~ 1,650	25	5	1/17/92

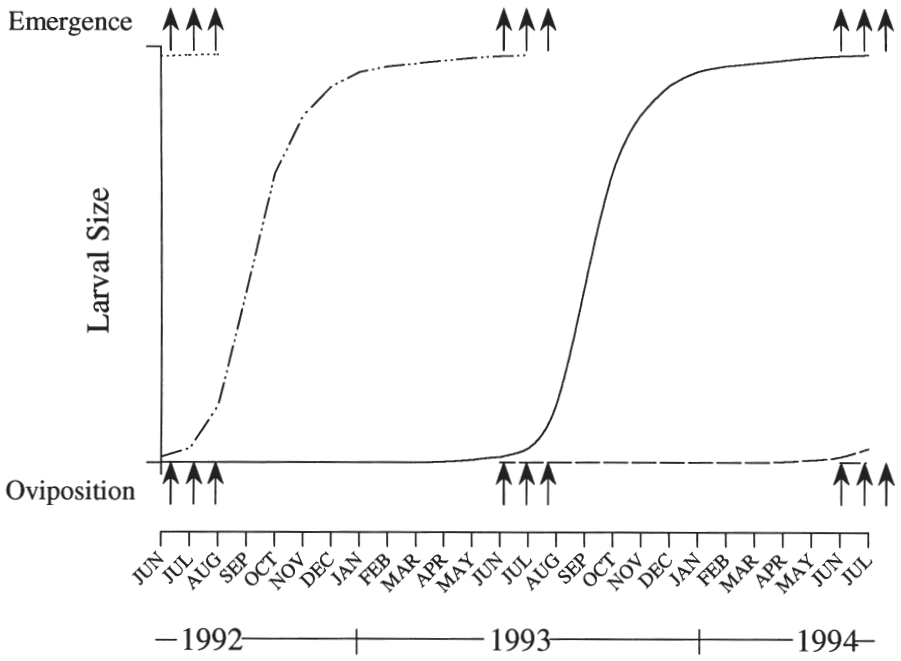


Fig. 1. Schematic representation of the life cycle of *M. signata* based on egg development data, benthic larval samples, and adult emergence for Benthette Brook and East River populations. Solid line represents the development curve for the generation examined in this study. Arrows indicate emergence of adults or oviposition of eggs during the reproductive period. Larval growth pattern adapted from Allan 1982, Table 3.

months, then a slow-growth overwintering period, and finally emergence as adults during the following summer (Fig. 1).

DISCUSSION

The discovery of delayed hatching in populations of *Megarcys* from both streams was unexpected, because univoltinism had previously been inferred from patterns of larval cohort development. Early instars of this species are readily observed several weeks after initiation of the adult flight period (Peckarsky, 1991a), and development of each larval cohort is synchronous with no appearance of multiple larval stages at any time during the larval period. In this study none of the eggs from the 1992 overwintering larval cohort hatched while incubated in the stream over the entire summer; and only when subjected to elevated water temperatures did eye spot development and hatching occur. These field and laboratory egg data along with field observations of larval development (Peckarsky unpublished data)

suggest that this population of *Megarcys signata* has an extended egg stage that lasts for nearly a year, from the time of oviposition (in June–August) until the following summer, which is the first appearance of early instar larvae (Peckarsky, 1991a). We do not suspect that experimental artifacts contributed to the delay in egg hatching. We collected early instar *Megarcys* in field samples during summer 1992, but these could not have hatched from eggs oviposited by the cohort that overwintered as larvae and emerged in 1992. Instead they must have hatched from eggs of earlier cohorts that had delayed hatching for many months. Our data suggest that delayed hatching is obligate at this altitude, with no evidence of a time-dependent cohort split, such as that recorded in other species of stoneflies (Moreira & Peckarsky, 1994), and tipulids (Pritchard, 1980). Although egg diapause and extended egg development is fairly common for stonefly species that have been well studied (Harper, 1973; Stewart & Stark, 1988; Dewalt & Stewart, 1995), this is only the second reported instance of semivoltinism in a North American perlodid. Dewalt and Stewart (1995) reported extended egg diapause and semivoltinism in *Isogenoides zionensis* (Hanson) (Perlodidae).

The significance of this delay in hatching that results in a two (or more) year life cycle for *Megarcys* is unknown. Elliott (1995) suggests that differences in egg development may function as a mechanism to reduce interspecific competition among twelve species of predatory stoneflies coexisting in European streams. While *Megarcys* in these North American streams coexists with another predatory perlodid, *Kogotus modestus* (Banks), temporal displacement of development results in only a brief period of interspecific interference competition (Peckarsky, 1991b; Peckarsky & Cowan, 1991), which would not be affected by egg diapause. A more plausible explanation for the significance of delayed hatching in high altitude stoneflies is that remaining in the egg stage enables populations that emerge any time over the ice-free period to overwinter in a protective state and begin egg development synchronously the following year as soon as conditions are more favorable for larvae. Similarly, Zwick (1996a) has reported that the predatory stonefly, *Dinocras cephalotes* (Curtis) (Perlidae), can extend egg development over more than one year using several warm summer periods to complete embryogenesis. Thus, discontinuous egg development may be adaptive for this stonefly enabling larvae to hatch during favorable conditions. This life history strategy allows this species to persist at the colder extremes of its distribution. Zwick (1996b) has also shown that eggs of a perlid stonefly will diapause for longer than one generation under specific conditions, thus representing a potential egg bank in these streams. We suspect that at high altitude the thermal requirements for *M. signata* eggs to develop immediately may not be adequate from the time they are oviposited to the onset of winter, and that the stimulus (temperature) for development is not reached until the following spring or summer.

In this study we have demonstrated that populations of *M. signata* in the East River have a semivoltine life history. In contrast, previous studies on the life history of *M. signata* have reported that this species is univoltine and has immediately hatching eggs (Cather & Gaufin, 1975; Allan, 1982; Peckarsky & Cowan,

1991). Although voltinism has been shown to be flexible across geographic ranges of other species of stoneflies (Hynes, 1976), key climatological variables were not very different among these studies. All studies of *M. signata* were conducted at approximately the same altitude in these studies (1650–2280, 2610–3535, and 2885–2895 m, respectively), at similar temperatures (5–10, 3–14, 3–13°C, respectively), and were in relatively close geographic proximity (Utah, Colorado, Colorado, respectively).

These three previous studies did not examine egg development time, and life history information was inferred from the presence of early instar larvae in benthic samples during the extended reproductive period when adults were emerging and ovipositing eggs. Only by following egg development we were able to determine that the early instar larvae present in the stream could not have been offspring of the generation emerging that same summer, but were individuals hatching from eggs laid the previous summer. The semivoltine life history of this stonefly could not have been detected from benthic samples alone. This study clearly illustrates the need for studies of aquatic insect life histories to incorporate all stages of the life cycle: egg, larval, and adult in field sampling.

Our data show that at this location *M. signata* produce eggs that do not hatch immediately. Whether *Megarcys* eggs develop slowly, discontinuously, or are in diapause remains unknown since we were unable to perform the detailed experiments necessary to determine the physiological and development state of eggs during development. Although diapause is common among the Plecoptera, egg development is highly variable (Stewart & Stark, 1988), and detailed information on the egg biology of most species is unknown. The ecological and evolutionary implications of the various types of egg development in stoneflies offer a fruitful area for further research.

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