

THE EFFECTS OF EXTENDED PHOTOPERIODS ON THE DRIFT OF THE MAYFLY EPHEMERELLA SUBVARIA MCDUNNOUGH (EPHEMEROPTERA : EPHEMERELLIDAE)

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Abstract

Field drift studies indicated that the nocturnal drift density of *E. subvaria* nymphs was greater in early May than in early November.

Laboratory studies showed that the number of individuals appearing in the drift was a linear function of the duration of the preceding photoperiod. Nymphs had a greater propensity to drift when they were not in a state of active growth than when they were growing. The tendency of individuals in a single laboratory population to drift was observed to change under conditions of constant temperature and randomized photoperiod. This suggests that the shift was due to some internal physiological change rather than to an external cue.

It is suggested that drift in *E. subvaria* functions as a method of relocation from fast-water areas to slow-water pools and stream margins. Redistribution to these areas may reduce mortality incurred during spring run-off and during emergence.

Introduction

The importance of light intensity in controlling the diel periodicity of invertebrate behavioural drift is well established (Müller, 1966; Holt & Waters, 1967; Elliott, 1967). Drift normally remains at a relatively low, constant level during daylight hours (Chutter, 1975) and increases following a reduction in light intensity below a certain critical level (Bishop, 1969; Chaston, 1969; Ciborowski, 1976).

The intensity and pattern of drift during darkness is dependent largely on the particular behavioural response

of the organism. Müller (1965) showed that the nocturnal drift pattern of *Baetis rhodani* was directly related to the length of the dark period, however the effect of daylength on subsequent nocturnal drift has not been elaborated. This study examines the effect of extended photoperiods on the drift of the mayfly *Ephemerella subvaria* McDunnough.

Methods and materials

Ephemerella subvaria nymphs were collected for both life history analyses and experimental purposes from a riffle on the East branch of the Credit River, near the Forks of the Credit, Peel County, Ontario, Canada.

Specimens were collected from mid-October, 1974 to June, 1975 and from September 1975 until the beginning of November, 1975. Samples were taken at weekly intervals during the months of September, October and November and biweekly during other months. All individuals were preserved in Kahle's fluid. Head width measurements were made using a Wild dissecting microscope at 25 x magnification with an inset ocular micrometer.

Field investigations were conducted on May 2-3 and on November 1-2, 1975 to determine nocturnal patterns and seasonal variation in the drift of *E. subvaria*. A square-mouth drift sampler (Anderson, 1967) with an opening of 625 cm² and 256-micron mesh was secured in fast water approximately 35 cm deep and 1.5 m from the stream bank. Current velocities at the net mouth were determined with a Gurley Pygmy current meter at the beginning and end of each study.

Studies began at least 30 minutes before sunset and continued for a period of 6 hours after sunset. Catchment jars were changed at 30-minute intervals throughout each experiment and the contents preserved in Kahle's fluid. All samples were completely sorted in the laboratory at 12 x magnification using a Wild dissecting microscope.

Laboratory experiments were carried out in a controlled-environment room using an artificial stream driven by a plexiglass paddlewheel. A depth of 10 cm of dechlorinated tap water was used throughout. Mean current velocity in the stream was 10 cm/sec over a 20 x 30 cm area of gravel substrate (pebbles 16-23 mm diameter). The rest of the stream channel was bare. A removeable drift net was located 2 cm downstream from the substrate.

One hundred and fifty live *E. subvaria* nymphs, transported from the field in wide-mouth vacuum bottles containing river water, were introduced into the stream on October 30, 1974 and maintained under simulated natural photoperiods for 3 days. The nymphs were then subjected to a randomized series of continuous light exposures ranging from 3 to 140 hours in length. Photoperiods used were of the following durations: 3 hours, 5 hours, 6 hours and one-hour increments up to 16 hours, and 20 hours, 40 hours and 20-hour increments up to 140 hours. Following each light period, the stream was darkened and the drift net placed in the stream. Thereafter, the net was changed at 30-minute intervals over a 6 hour period. Trapped individuals were stored in enamelled trays containing aerated water, and returned to the stream at the conclusion of each trial.

The experiment was repeated using nymphs collected March 17, 1975. A new order of trials was selected for the replicate, although photoperiods were of the same duration as in the first study.

A third group of nymphs collected December 13, 1975 was placed in the stream and maintained under continuous light for a total of 1215 hours. Drift was then monitored during 6 hours of darkness.

Water temperature in the first experiment was 5°C and in the second and third experiments was 2°C. In each case, laboratory temperatures were within 2 degrees of that in the field at the time of collection.

An ubiquitous growth of an aquatic hyphomycete in the artificial stream provided a food supply in all trials. This was adequate to maintain the last group of nymphs through the winter to maturity.

Least-squares regression analysis was performed on

the photoperiod experiment data to study the relationship between numbers of individuals drifting during darkness and the duration of the preceding photoperiod. Analysis of covariance (Snedecor & Cochran, 1961) was used to test for differences in regression coefficient and intercept between replicates.

Kolmogorov-Smirnov tests of goodness-of-fit (Sokal & Rohlf, 1969) were used to establish whether field and laboratory drift patterns were random and whether they significantly differed from one another.

Results

Head width measurements indicated that *E. subvaria* nymphs in the Credit River grew rapidly throughout the autumn until the end of November (Fig. 1). Little growth was evident during the winter, although individuals did not become dormant. Growth resumed towards the beginning of March and subimagos were first observed emerging from the river on May 10. Further details on the life history of *E. subvaria* are given by Ciborowski (1976).

Field drift densities of *E. subvaria* nymphs (numbers per m³ of water sampled) were much higher in May than in November (Fig. 2b). A large increase occurred after sunset for the May study but not for that in November. The pattern of drift was random in November ($p > .05$) and significantly non-random in May ($p < .05$), maximum density being reached approximately 2 hours after sunset.

Mortality in the two photoperiod experiments was comparable; 121 nymphs were recovered after the first series of trials and 118 after the second. It is assumed that most of the mortality occurred during the beginning of each experiment as a result of handling. Very few dead nymphs were recovered in the drift net, and these were predominantly found during the first few trials of each series.

Linear regression accounted for 62 percent of the variation on the November photoperiod experiment. Closer examination of the data, however, indicated that a relatively low number of individuals drifted in trials conducted before November 26 whereas far more drifted at later dates. Regressions calculated for the early and late portions of the data separately, explained 85 and 93 percent of the experimental variation, respectively (Fig. 3). Slopes of the two regressions were significantly different ($p < .005$).

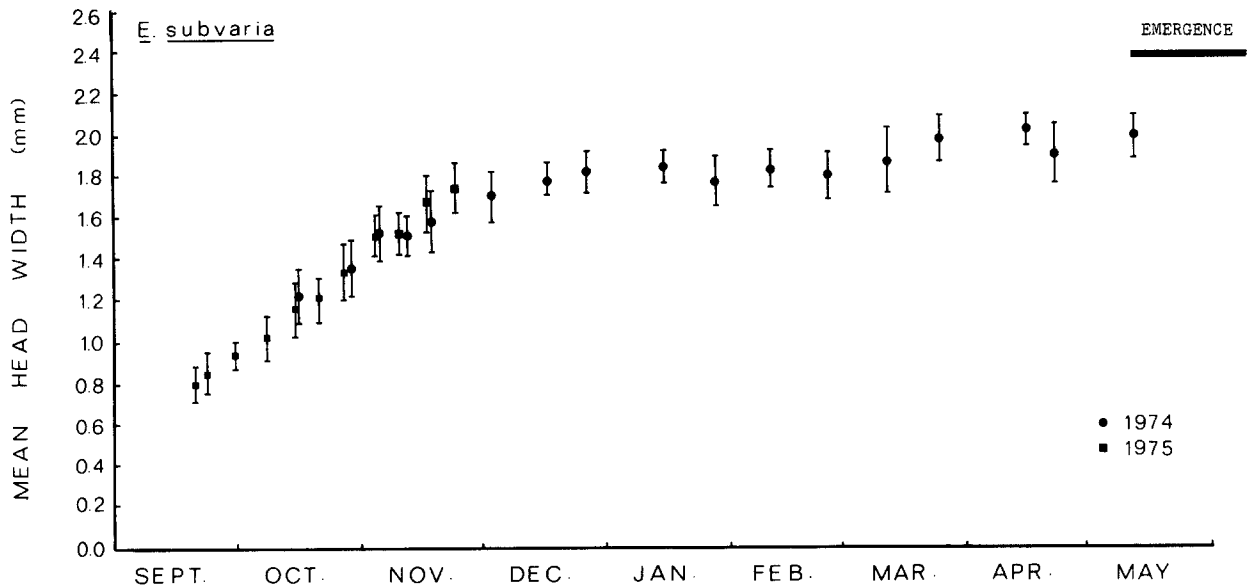


Fig. 1. Mean head width of *E. subvaria* nymphs collected from sample site during 1974 and 1975 \pm 1 standard deviation.

The March photoperiod experiment was terminated at its midpoint following a power failure which disrupted light, water current and temperature controls. Regression of the available data explained 99 percent of the variation. Analysis of covariance indicated that the regression of the March data was significantly different from the early November data in slope ($p < .01$) and from the late November data in intercept ($p < .005$).

Nymphs which entered the drift were not returned to the stream until the end of that trial, and as a result were unavailable to re-enter the drift later on during the same trial. The high numbers drifting early in certain trials therefore seriously reduced the population available to drift in later portions of that trial. Since the regressions may not therefore give a true representation of the response to photoperiod in a natural population, a second series of regressions were performed on the data, whereby the number of nymphs drifting in a 30-minute period were expressed as a proportion of the population remaining on the substrate. In these instances, the slopes of all three curves differed significantly from one another ($p < .005$).

A total of 61 nymphs drifted during 6 hours of darkness following an extended photoperiod of 1215 hours. This was slightly less than the greatest drift intensity observed in any of the other experiments (68 nymphs following a photoperiod of 140 hours during a March trial). The total number of *E. subvaria* nymphs drifting in laboratory

trials was 96, 117 and 267 individuals during early November, late November and March, respectively. Clearly, at least some individuals drifted on more than one occasion in each experiment.

The 30-minute values for drift of trials in each of these data groups were pooled to give an idea of the general distributions of nymphs drifting with respect to time (Fig. 2a). Drift pattern was random for the early November data ($p > .05$) and significantly non-random ($p < .01$) for the other two series. When laboratory and field patterns were compared, the only significant differences were found between the March photoperiod trials and the May field study ($p < .01$). Weighting to allow for reduction of laboratory populations did not significantly change the shape of the distributions.

Discussion

Photoperiod experiments indicated that the intensity of drift of *E. subvaria* nymphs during darkness was a linear function of the duration of the preceding photoperiod. Field evidence also suggests that drift levels rise with increasing photoperiod. Holt & Waters (1967) observed an increase in the nocturnal drift of *Gammarus pseudolimnensis* in a Minnesota stream following continuous exposure of the stream to artificial light for a period of 4 days. Reisen & Prins (1972) found that drift was cor-

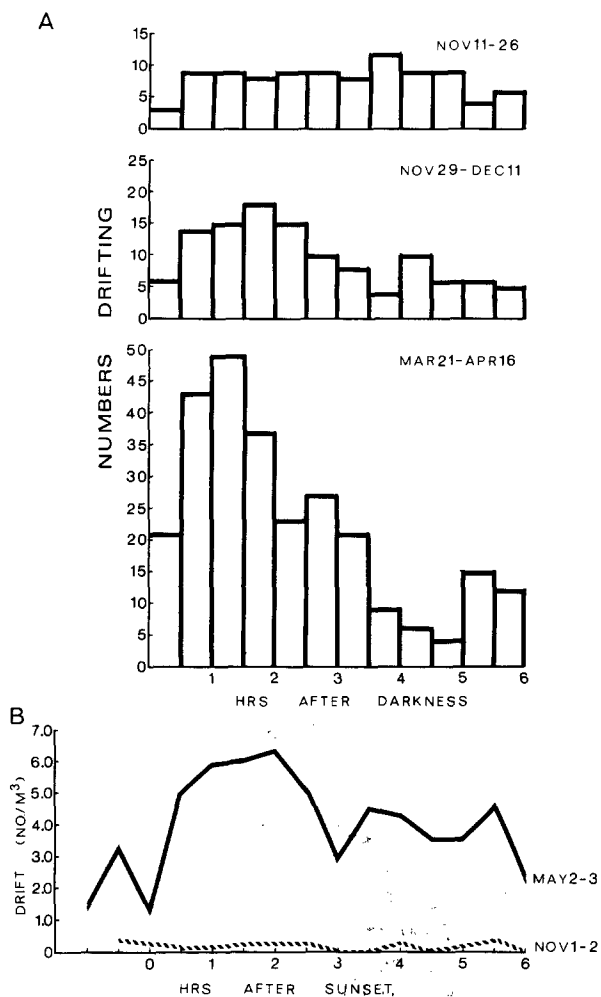


Fig. 2. A: Drift pattern of *E. subvaria* nymphs in laboratory photoperiod experiments. B: Drift density of *E. subvaria* nymphs in east Credit River.

related with total hours of light in a field study, but rejected that variable because of its co-linearity with water temperature.

Numerous other field studies show a general trend of increased drift during the summer months. This is undoubtedly partly due to increased temperatures (Müller, 1963; Waters, 1968; Wojtalik & Waters, 1970; Madsen, 1968) but photoperiod may also have a widespread influence on the magnitude of drift. I found no difference in drift of *E. subvaria* during normal photoperiods at 2°C and 5°C (Ciborowski, 1976).

The magnitude of drift of *E. subvaria* nymphs increased with the-age of the individuals in both laboratory and field studies. A corresponding change in the pattern

of drift was also observed. This change, under laboratory conditions at least, must be due to some behavioural modification of the individuals. Relatively few individuals drifted during initial trials in November while in later trials more nymphs drifted following a photoperiod of equivalent duration. The shift in response corresponded closely with the time at which the change in growth was observed in the Credit River. This suggests an association with the modification of growth pattern. Whether this is the case or not, the behavioural change would have to be either endogenously controlled or regulated by some factor other than light, temperature, or changes in water current, all of which were controlled in the laboratory.

A relatively greater proportion of nymphs drifted in the March experiment than in the latter portion of the November experiment, once diminishing numbers in the substrate had been accounted for. I suggest that the late November experiment represents the response of a population composed of some individuals in each of two behavioural states, corresponding to animals in a state of growth and those in a 'no-growth' phase. Both the regression of drift on photoperiod and the pattern of drift in late November were intermediate between those of the early November and March trials.

Waters (1969, 1972) has suggested that drift may reflect a search for a suitable pupation or emergence site or may be a mechanism to distribute reproductive processes as widely as possible. I propose that the drift of *E. subvaria* is primarily a mechanism of redistribution. Drift levels are initially low for young, growing nymphs located in riffles. With the onset of winter, the propensity to drift increases but short winter photoperiods maintain drift at a low level. As daylength increases towards the spring, large numbers of nymphs would enter the water column and become redistributed.

Ciborowski (1976) observed that drifting *E. subvaria* are incapable of selecting an area of reattachment to the substrate, but that strong thigmotaxis results in an ability to remove themselves from the water column on contact with the substrate. Ciborowski & Corkum (unpublished data) also found that older *E. subvaria* nymphs are less able to remove themselves from the drift at high current velocities than are younger nymphs. Drifting nymphs would therefore tend to become concentrated in relatively slow-water areas, where growth would be completed and from which the subimagos would eventually emerge.

The relocation of individuals in this manner may serve to minimize the likelihood of wash-out during spring

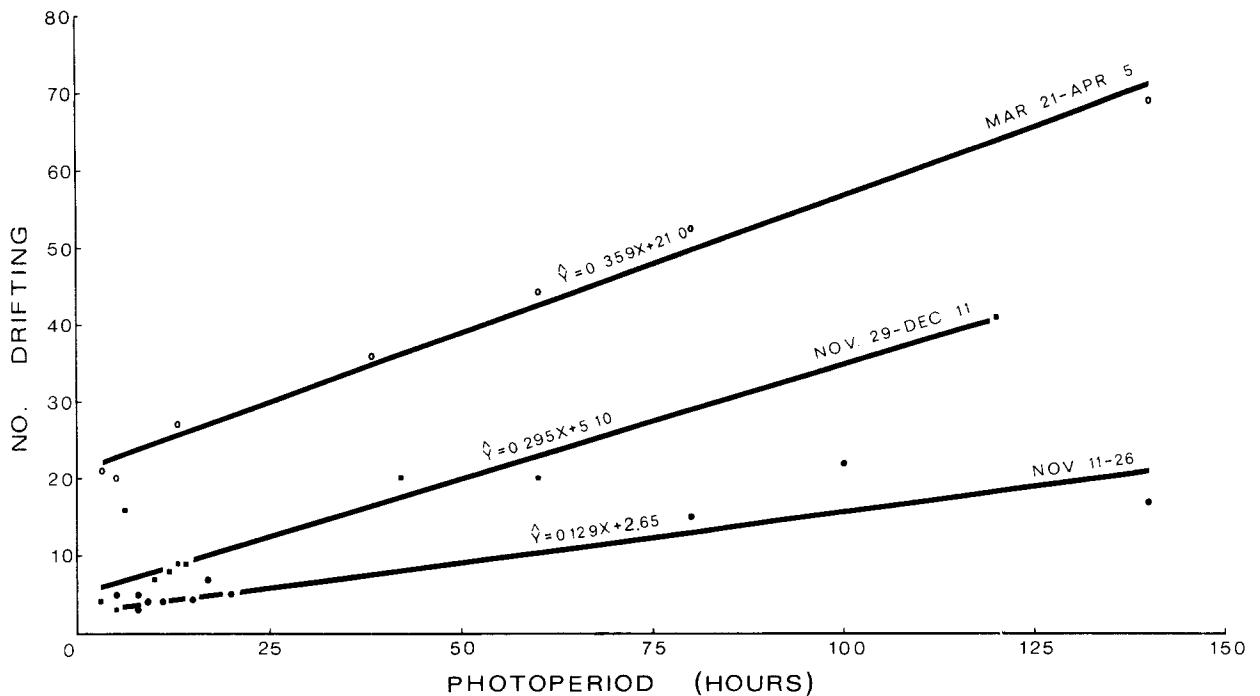


Fig. 3. Relationships between numbers of *E. subvaria* nymphs drifting during 6 hours of darkness and duration of the preceding photoperiod.

run-off. It might also reduce mortality at emergence, since mature nymphs rise and transform directly from the water surface. Further studies on the seasonal distribution pattern of *E. subvaria* nymphs would be required to substantiate this hypothesis.

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Summary

The life history of *Ephemerella subvaria* McDunnough in the Credit River, Ontario, Canada was determined

from head width measurements made on nymphs collected at weekly or biweekly intervals. Nymphs grew throughout the autumn, but not during winter months. Emergence began in mid-May.

Field studies indicated that *E. subvaria* nymphs drifted in low numbers and in a random pattern at night in November, and in much greater numbers and a non-random pattern in May.

Laboratory studies showed that nocturnal drift was a linear function of the duration of the preceding photoperiod. Furthermore, the tendency to drift increased with the age of the nymphs.

A spontaneous change in the tendency to drift was observed in a laboratory population under conditions of constant temperature and randomized photoperiod. This change was associated in time with the observed change in growth rate in the Credit River. A change in pattern of drift from random to non-random was also observed in conjunction with the increased propensity to drift.

It is hypothesized that these responses act to relocate nymphs from riffles to slower-water areas, the benefits from such a change in habitat being a reduced likelihood of wash-out during spring run-off, and reduced mortality during emergence of the nymphs.

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