Best wishes,
Jan Ciborowski

Freshwater Biology (1977) 7, 567–572

The effect of current velocity and sediment on the drift of the mayfly *Ephemerella subvaria* Mc~~d~~unnough

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JAN J. H. CIBOROWSKI, P. J. POINTING and LYNDA D. CORKUM Department of Zoology, Erindale College, University of Toronto, Canada

SUMMARY. Experiments conducted in an artificial stream showed that significantly more nymphs drifted from an inorganic substrate at a mean current velocity of 28.5 cm s^{-1} than at 18.5 cm s^{-1}. Drift density, however, was not affected. Disproportionately large numbers of nymphs drifted while current velocities were being increased from 18.5 to 28.5 cm s^{-1}.

Both drift numbers and drift density were greater in turbid water, after the addition of large amounts of inorganic sediment, than under clear-flowing conditions during dark periods but not in the light. The interaction of increasing current velocity and sediment levels resulted in a significantly greater number of drifting nymphs under lighted conditions.

Minor spates which do not seriously disturb the stream bed may initiate significant increases in macroinvertebrate drift.

Introduction

The increases in discharge associated with flooding often disturb the stream bed and result in the displacement of benthic populations (Klyuchareva, 1963; Bailey, 1966; Anderson & Lehmkuhl, 1968; Lehmkuhl & Anderson, 1972; Mackay & Kalff, 1973). Sediment input may also drastically increase during spates and have adverse effects on benthic communities (Tebo, 1955; Chutter, 1969; Nuttall, 1972). The effects of both of these factors may be immediately manifested in increased drift of individuals from the disturbed areas. Logan (1963), Elliott (1967a) and Anderson & Lehmkuhl (1968) related changes in the magnitude of drift to changes in stream discharge, and Elliott (1971) indicated that variations in current velocity were largely responsible for these drift fluctuations. Gammon (1970) and Rosenberg & Snow (1975) have shown that invertebrates may respond to increased sediment input independently of current velocity fluctuations.

The effects of increases in current velocity and sediment input associated with minor spates, during which the stream channel is not seriously disturbed, are not well understood. Because silt load increases with discharge (Brunskill *et al.*, 1973), it is difficult to separate invertebrate drift responses to sediment from responses to current velocity in natural stream systems. In this study an attempt was made to assess the relative importance of each of these factors to the drift of the mayfly *Ephemerella subvaria* McDunnough in an artificial stream in the laboratory.

Methods

Waters & Crawford (1973) and Ciborowski (1976) have studied the life history of *E. subvaria*, a riffle-inhabiting species, found in north-temperate and sub-arctic streams in eastern North America (Allen & Edmunds, 1965). Nymphs hatch in mid-August and

Correspondence: Jan J. H. Ciborowski, Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E1.

growth is linear until the end of November. Little or no growth occurs over the winter, but is resumed in the spring. Emergence occurs from mid-May into June (Ciborowski, 1976).

All experiments were conducted in an elliptical artificial stream 27.5 cm deep, in which dechlorinated tap water was propelled by an Archimedes' screw (Plate 1). The screw was driven by a rheostatically-controlled 1/6 horsepower d.c. electrical motor. Water temperature in all experiments was 5°C and was regulated by the air temperature of the controlled-environment room in which the stream was housed. Gravel substrate (pebbles 16–23 mm diameter) was retained in two removable 15 x 30 x 2 cm stainless steel trays.

Sediment suspension was prepared by mixing potter's clay (Plainsman prepared Red Terra Cotta, type L-10) with distilled water in a Waring blender, and decanting the mixture to remove heavier particles (see Ciborowski, 1976). The suspension was dripped into the stream through a plastic hose leading from a 2-l bell jar.

Experiments were conducted to examine the effects of current velocity, of inorganic sediment and of their interactions on the drift of *E. subvaria* nymphs. The drift was monitored both at a low (basal) and a high level of each factor in a 2 x 2 factorial design. Experiments were run as randomized blocks, five replicates per treatment. The combinations of current and sediment load used were: (1) no sediment and a mean current velocity of 18.5 cm s^{-1} above the substrate (basal levels). (2) 2.68 g l^{-1} suspended clay and 28.5 cm s^{-1} current velocity (high levels). The higher velocity was just less than that which would disturb the substrate particles, whereas the lower velocity was set at 10 cm s^{-1} less than this value. The greater suspended clay concentration approximated the sediment load encountered in a stream flowing through farmland in southern Ontario during an extremely heavy rainfall (Ciborowski, 1976).

E. subvaria nymphs were collected from a sample site near the Forks of the Credit, Peel County, Ontario. Individuals for three experiments were collected each morning and transported to the laboratory in wide-mouth, vacuum bottles containing river water. Nymphs were maintained until required under constant light at 5°C in enamelled trays containing aerated river water.

Two hundred and fifty undamaged individuals were introduced at once into the stream, directly above the Archimedes' screw. The nymphs were carried along the stream channel by the current until they became established in the substrate trays. Mean settling time for the population was approximately 20 min. Nymphs suffered no apparent damage from being carried through the screw portion of the channel.

One hour after the introduction of the population, a drift net with removable catchment jar was placed in position immediately downstream from the substrate trays. This marked the beginning of the 'factor-adjustment' period during which clay suspension was continuously added and the current velocity gradually increased in appropriate trials.

At the conclusion of the factor-adjustment period (15 min), the catchment jar was changed and the number of trapped nymphs recorded. Thereafter, the jar was changed at 30-min intervals for the next 6 h.

Trials were conducted with and without illumination, i.e. 'lighted stream' and 'darkened stream'. During darkened stream trials, the lights were extinguished at the conclusion of the factor-adjustment period. In lighted stream trials, the lights were extinguished 3 h following the factor-adjustment period.

At the conclusion of a trial, all nymphs were removed and the stream was drained, rinsed, and refilled with refrigerated dechlorinated tap water. Substrate gravel was rinsed thoroughly and stored at 5°C until next required.

Experiments were run continuously (three per day) between 9 and 25 November 1975, a total of forty trials being completed. Throughout this period all nymphs were in a state of linear growth, a phase in which drift behaviour of this species is assumed to be homogeneous (Ciborowski, 1976).

Results

A large number of nymphs generally appeared in the drift during the factor adjustment period. The numbers of drifting nymphs then

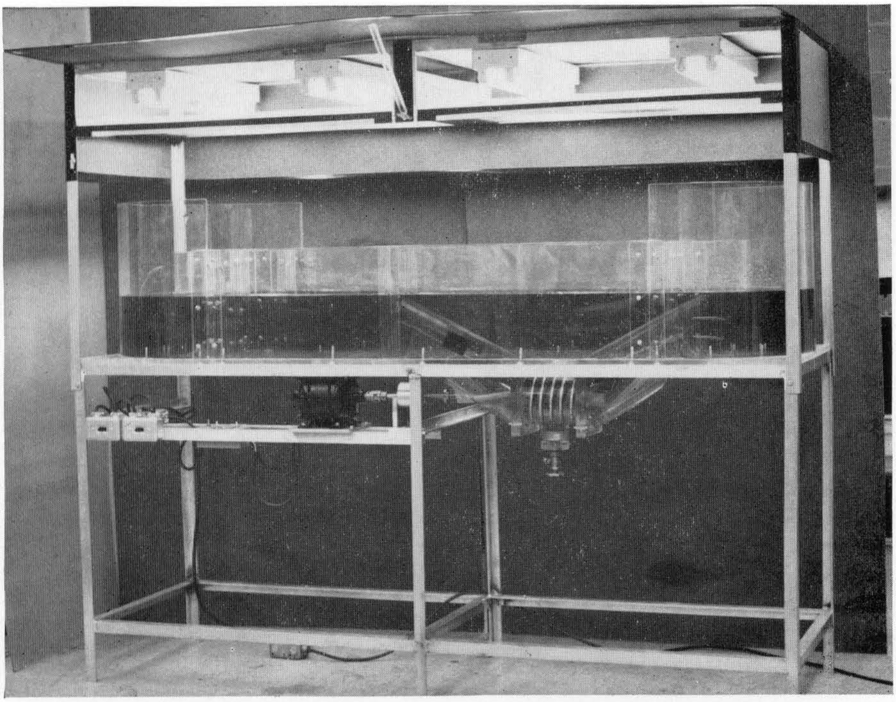

PLATE 1. Artificial stream used for laboratory experiments.

TABLE 1. Significance of effects of current velocity and sediment on numbers of drifting *E. subvaria* nymphs. Detailed copies of the analyses are available on request

Period	Increase in current	Increase in sediment	*C x *S	Current	Sediment	C x S
Factor-adjustment	4.71†	0.78	4.35†	—	—	—
Light	—	—	—	1.12	1.88	1.88
Dark	—	—	—	5.03†	5.96†	0.33
Total	—	—	—	16.24‡	47.80‡	0.83

*C denotes increase in current; *S denotes increase in sediment.
† $P < 0.05$.
‡ $P < 0.005$.
— indicates test not applicable.

gradually decreased in succeeding 30-min intervals under light conditions. Drift numbers rose again with the onset of darkness and decreased towards the end of the trial.

The numbers of nymphs drifting during each period were summed for each trial, and replicated analysis of variance tests (ANOVA) were conducted (Sokal & Rholf, 1969). All data were logarithmically transformed and two-way ANOVA was used to estimate the significance of effects of differing current velocities, differing sediment levels and of their interactions on the drift during factor-adjustment periods, during light periods, during dark periods and during the sum of light and dark periods. In addition, three-way ANOVA was performed to test for differences between light conditions as well as the above factors. The results are summarized in Table 1.

Analyses were repeated for all trials to examine the effects of the factors on the drift density (numbers drifting per unit volume of water flowing over the substrate) rather than on the numbers in the drift. In this instance, it was possible to include the drift during the factor-adjustment period as part of the 'total drift' calculations. These results are summarized in Table 2.

Both a greater number and a greater density of nymphs occurred in the drift while the current velocity was being increased than under constant current conditions (Fig. 1). Increasing sediment level, however, did not initially produce a significant change in either the number or density of nymphs drifting (Fig. 2). There was, however, a significant interaction between increasing current velocity and increasing sediment level which affected both the number and density of drifting nymphs.

Sediment levels in the light did not influence either the number or density of nymphs in the drift. During darkness, however, both number and density were significantly greater under high sediment conditions (Fig. 2).

Similarly, only the number of nymphs drifting in darkness was significantly greater at the high current velocity than at the low;

TABLE 2. Significance of effects of current velocity and sediment on density of drifting *E. subvaria* nymphs

Period	Increase in current	Increase in sediment	*C x *S	Current	Sediment	C x S
Factor-adjustment	4.95†	0.92	6.80†	—	—	—
Light	—	—	—	0.00	1.63	1.08
Dark	—	—	—	0.21	9.75‡	0.00
Total	—	—	—	0.00	13.00‡	1.00

*C denotes increase in current; *S denotes increase in sediment.
† $P < 0.05$.
‡ $P < 0.005$.
— indicates test not applicable.

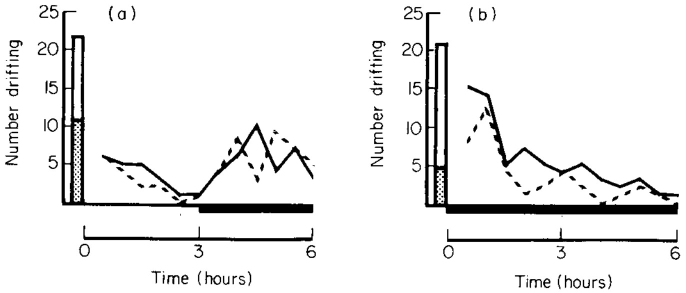

FIG. 1. Distribution of total numbers of drifting *E. subvaria* nymphs at basal (broken line) and increased (solid line) current velocities in (a) lighted, (b) darkened, stream. Columns indicate numbers of nymphs drifting during the factor adjustment period: total column, increasing velocity; stippled portion, basal velocity. Thickened abscissa indicates that stream is in darkness.

drift density, however, did not differ (Fig. 1).

More nymphs drifted during darkness than in the light, and this increase was also reflected in the drift densities.

Discussion

Experiments indicated that more *E. subvaria* nymphs drifted when the current velocity is high than when it is low. The increase in drift number appeared to be proportional to the increase in current, since drift density remained constant at both velocities. Elliott (1967a) hypothesized that current velocity contributes to the magnitude of the drift of a population by dislodging a certain number of individuals. Under conditions of high current velocity, the probability of dislodgement is increased and proportionately more individuals enter the water column. A linear relationship between drift and water velocity would, therefore, be suggested, and this was observed in the present study with *E. subvaria* nymphs. Elliott (1971), however, observed that drift-current velocity relationships in a natural stream were usually linear only after a logarithmic transformation of both variables had been performed. The untransformed relationship for Elliott's (1971) data is, therefore, exponential (when slope > 1). This is probably a reflection of the fact that not only does a greater proportion of a population drift at higher current velocity, but the individuals are also carried a greater distance before they settle (see Elliott, 1967b; Elliott, 1971; McLay, 1970). The distance between the substrates and the drift net in the laboratory experiments with *E. subvaria* nymphs was not great enough to permit any significant degree of settling to occur. Additional laboratory studies on the rate of settling of *E. subvaria* nymphs at various current velocities must be carried out before the relationship between

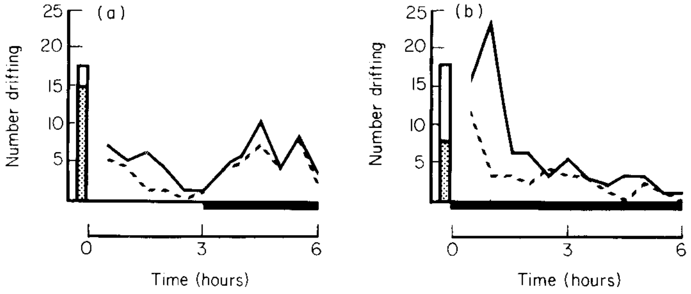

FIG. 2. Distribution of total numbers of drifting *E. subvaria* nymphs under clear-flowing (broken line) and high sediment (solid line) conditions in (a) lighted, (b) darkened, stream. Columns indicate numbers of nymphs drifting during the factor adjustment period: total column, increasing sediment level; stippled portion, no sediment. Thickened abscissa indicates that stream is in darkness.

current velocity and drift can be estimated reliably for a field situation.

Both the number and density of drifting nymphs increased while current velocity was increasing, suggesting that changes in current velocity are more important in determining the magnitude of the drift than the absolute current velocity. Pearson & Franklin (1968) made similar observations on the drift of *Baetis* sp. and Simuliidae larvae. It is likely that as mean current velocity increases, the current regime around substrate particles changes, thus exposing more individuals located on or beneath those particles to currents of differing velocities and increasing the likelihood of dislodgement.

Although the clay-water suspension was decanted, leaving behind the heaviest particles, some suspended sediment did settle on and around the substrate. It is, therefore, difficult to determine whether the drifting nymphs responded to the sediment in suspension or to that which settled on the bottom of the stream channel. Both have been cited as responsible for increases in the drift of invertebrates. Gammon (1970) found that drift levels of macroinvertebrates increased in proportion to the amount of limestone solids added to a stream and suggested that the observed drift was a response to light reduction. Similarly, Pearson & Franklin (1968) ascribed high drift levels of *Baetis* sp. to light extinction as a result of turbidity levels. Conversely, Rosenberg & Snow (1975) attributed high drift levels in a subarctic river to the settling of experimentally added silt.

The suspended sediment concentrations used in the laboratory trials were sufficiently high to reduce light intensity at the substrate to a level which would, theoretically, elicit a behavioural drift response in *E. subvaria* (Ciborowski, 1976), but the plexiglass construction of the laboratory stream permitted substantial light transmission through the sides of the stream. Since drift levels increased only during the dark periods of all experiments and not immediately following the addition of sediment (Fig. 2a) nymphs probably reacted to settled sediment rather than to the filtering effects of the sediment in suspension. The settling particles may have served to render the substrate 'unfavourable' (Tebo, 1955; Chutter, 1969; Hynes, 1973) for the nymphs so that they actively entered the water column during darkness as a means of redistribution to a more favourable habitat. Alternatively, the suitability of the habitat may not have been significantly altered. Nymphs may have simply become more active after darkness (Elliott, 1968; Chaston, 1968) and the sediment coating on the substrate may have increased the difficulty of maintaining a hold on the gravel in the current, thereby increasing the probability of dislodgement.

This difficulty in obtaining a foothold might account for the interaction between increasing current velocity and increasing sediment level. The change in velocity would alter the current regime around individual substrate particles, perhaps inducing individuals to move to other areas out of the current (see Butz, 1973) and, as they are unable to maintain themselves on the coated substrate, some would be swept into the water column.

The drift response to sediment under typical field conditions would depend largely on the type of stream under study. The effect would be more pronounced in a stream which had little autochthonous plant material and of less importance in those which had abundant growths of mosses, algae or macrophytes, which would provide alternate holdfasts for silt-inundated individuals. Elliott (1967b) and Barber & Kevern (1973) have both commented on the effectiveness of macrophytic 'drift sieves' in reducing the amount of drift.

Evidently, short-term spates could significantly affect the drift patterns of *E. subvaria* nymphs, through the effects of both increased current velocity and sediment levels, although the flood itself might not be severe enough to disturb the stream bottom, producing extensive 'catastrophic' drift.

Acknowledgments

The authors acknowledge the assistance of Drs R. J. Mackay and W. G. Sprules for their helpful criticisms during this study.

This research was supported in part by grants from the National Research Council of Canada and from Erindale College to P. J. Pointing.

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(Manuscript accepted 3 May 1977)