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Chapter · January 1980

DOI: 10.13140/2.1.1.1095.2965

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From: ADVANCES IN EPHEMEROPTERA BIOLOGY
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(Plenum Publishing Corporation, 1980)

IMPORTANCE OF BEHAVIOUR TO THE RE-ESTABLISHMENT OF DRIFTING
EPHEMEROPTERA

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ABSTRACT

Experiments with mayfly larvae in a laboratory stream revealed significant differences among settling capabilities of four species. Quantitative measures of overall settling capacity, contribution of morphology and that of behaviour were derived for comparative purposes. Importance of behaviour to re-establishment was greater in species which frequently show diel drift periodicities than those which do not. Although morphological differences between species were large, mean size of nymphs was more important in determining rates of return of dead animals. Intraspecific variations in the ability of drifting individuals to become re-established may partially account for changes in the relative distribution of populations over time.

INTRODUCTION

Several workers have investigated the pattern in which invertebrates released into running water return to the substrate (Madsen 1968, McLay 1970, Elliott 1971, McKone 1975). All have found that a fixed proportion of animals introduced into the water column settle to the bottom for every unit of time or distance which passes. The greater the current velocity, the longer

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re-establishment takes or the farther the animals travel before all have settled. Elliott (1971) observed that live animals settle more quickly than dead individuals, and that settling capabilities differ between species. Elliott attributed this to behavioural dissimilarities since settling rates did not vary among dead individuals of different species.

Our study was conducted to evaluate settling rates of four mayfly species and to estimate the relative importance of behaviour to the settling ability of each.

METHODS

All experiments were conducted in an artificial stream which was housed within an environmental chamber maintained at 5°C. The elliptical stream was constructed of Plexiglass and powered by an Archimedes' screw (Ciborowski *et al.* 1977). Individuals released in the stream settled and remained only where a 15 x 30 cm area of sieved gravel (16-23 mm) was placed on the stream bottom. Water depth was 28.5 cm.

The settling ability of four widespread species of Ephemeroptera was tested. *Baetis vagans* McDunnough, *Ephemerella subvaria* McDunnough, *E. invaria* (Walker) and *Paraleptophlebia mollis* (Eaton) were all common or abundant at a collection site near the Forks of the Credit, Peel County, Ontario. Experiments were conducted with *E. subvaria* nymphs in November, 1976 and with all four species in March, 1977. Experiments consisted of introducing 50 live nymphs into the stream and recording the number suspended within the water column at one-minute intervals until 90 percent of the individuals had settled. This was determined by counting the number of animals which passed a fixed point in the stream during a time interval required for a hypothetical individual to complete one circuit of the stream at a particular current velocity.

Independent trials were run for each species at mean current velocities of 10, 15, 20, 25, and 26.8 cm/sec. Three replicates were conducted at each velocity. Individuals from each trial were killed in Kahle's fluid and experiments were repeated with the dead insects. Mean head widths of the four species at time of testing are given in Table 1.

RESULTS

Rates of settling for each trial were determined by using regression analysis to predict the relationship between the natural logarithm of the number of animals no longer in suspension and the estimated number of times individuals had passed over the substrate.

Table 1. Significance of regressions and analyses of covariance of rS against current velocity for 4 mayfly species. Equations taken the form: $rS = A \cdot (\text{current velocity})^{-B}$.

SPECIES		A	B (95% C.I.)	F _{reg.}	F _{cov.}	MEAN HEAD WIDTH (mm) (95% C.I.)
<i>E. subvaria</i> (Nov.)	Live	23.96	1.9583±0.2302	733.02***	45.79***	1.62±0.04
<i>E. subvaria</i> (Nov.)	Dead	12.05	2.0638±0.3814	296.45***		
<i>E. subvaria</i> (Mar.)	Live	12.08	1.8678±1.2371	23.08*	9.50**	1.99±0.04
<i>E. subvaria</i> (Mar.)	Dead	0.22	0.6427±0.5688	12.93		
<i>E. invaria</i>	Live	4.03	1.5631±0.5380	85.46**	23.89***	1.12±0.03
<i>E. invaria</i>	Dead	0.22	0.7550±0.5886	16.66*		
<i>B. vagans</i>	Live	2.81	1.2583±0.7272	30.32	429.57***	0.80±0.03
<i>B. vagans</i>	Dead	0.27	1.0386±0.6250	27.96*		
<i>P. mollis</i>	Live	1.54	1.5232±0.2981	264.35***	38.46***	0.74±0.02
<i>P. mollis</i>	Dead	1.31	1.6519±0.6793	59.87**		
All species	Live				65.51***	
All species	Dead				27.54***	

* P <0.05

** P <0.01

*** P <0.001

The slope of each regression was the instantaneous settling rate (r_s) for that trial.

Replicated least-squares regression analysis was then used to test the relationship between r_s and current velocity for each species. Logarithmic transformations of both variables gave the best regressions in all cases. Slopes of the regressions for live and dead animals of each species were significantly different (analysis of covariance, Table 1).

Visual examination of the curves (Fig. 1) suggests that some species were more capable than others of returning to the substrate at any given current velocity. Analysis of covariance indicated that there were significant differences among species in both live and dead insect trials (Table 1). *B. vagans* and *E. subvaria* (Nov.) had the highest curves (indicating most rapid settling capabilities), *E. subvaria* (March) and *E. invaria* were intermediate, and *P. mollis* was the least able to settle. These trends can be better elucidated by determining the area beneath the curve for each species (integrals of the regression equations). This provides a numerical index of the insects' capabilities of settling over the entire range of current velocities tested, which we call the settling capacity (SC).

Similarly, by calculating the area beneath the curve for dead insect trials of each species, one can determine that portion of the SC due to morphological characters (MC). The area between these two curves (SC - MC) must therefore be the contribution of behaviour to the SC. We term this the behavioural scope for settling (BC) after Fry (1947) who used a similar method to determine physiological tolerances of fishes.

These values permit calculation of the relative contribution of behaviour to the SC of an organism, or behavioural index (BI), i.e. $BI = BC \div SC$.

Table 2 shows the derived values for the four species tested, as well as values calculated from field r_s data of Elliott (1971). Elliott pooled the regressions of his dead invertebrate trials and all indices from his data have been determined using this single value.

Figure 1. Relationships between r_s and current velocity for live (circles: upper curves) and dead (squares: lower curves) individuals of 4 mayfly species. Each point represents geometric mean of three trials.

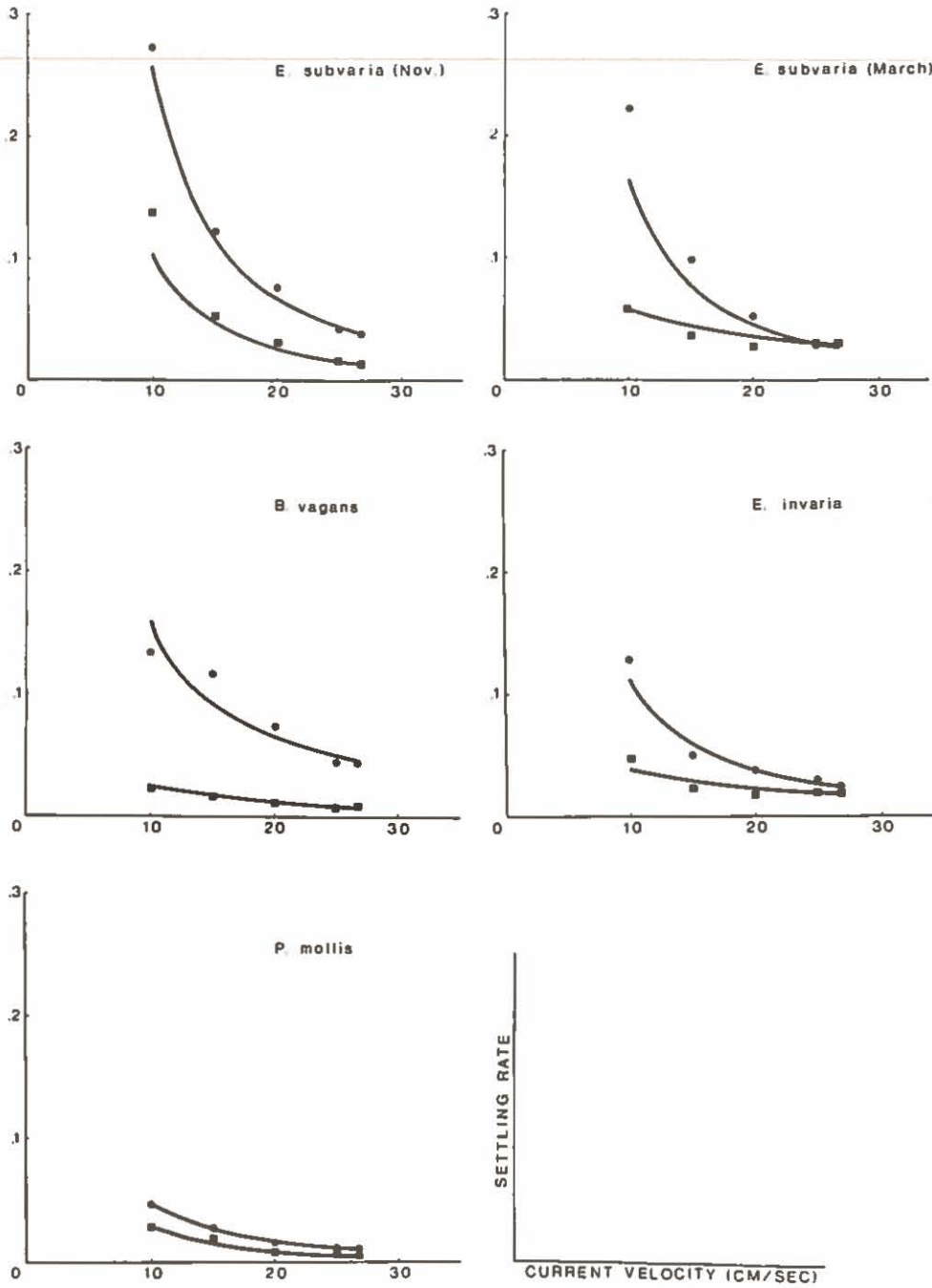


Figure 1

Table 2. Measures of settling capabilities of various species determined from this study and from Elliott (1971); and frequency of diel drift periodicities for North American genera of aquatic invertebrates.

SPECIES	SC	MC	BC	BI	REL. FREQ. OF DIEL DRIFT	
					%	N
This study:						
<i>Baetis vagans</i>	1.35	0.24	1.11	.82	53	40
<i>Ephemerella subvaria</i> (Nov)	1.68	0.64	1.05	.62	47	28
<i>Ephemerella subvaria</i> (Mar)	1.09	0.62	0.47	.43	47	28
<i>Ephemerella invaria</i>	0.83	0.41	0.42	.51	47	28
<i>Paraleptophlebia mollis</i>	0.36	0.21	0.15	.41	25	12
Elliott (1971):						
Amphipoda						
<i>Gammarus pulex</i>	19.12	5.49	13.63	.71	73	11
Ephemeroptera						
<i>Baetis rhodani</i>	18.84		13.34	.71	53	40
<i>Ecdyonurus venosus</i>	10.87		5.37	.49	33*	9
<i>Rhithrogena semicolorata</i>	6.27		0.78	.12	50	6
Plecoptera						
<i>Protonemoura meyeri</i>	6.32		0.83	.13	31**	61
<i>Chloroperla</i> spp.	6.28		0.79	.13	31**	61
<i>Leuctra</i> spp.	6.20		0.71	.11	31**	61
Coleoptera						
Elmidae	5.53		0.04	.01	54	13
Trichoptera						
<i>Agapetus fuscipes</i>	5.49		0.00	.00	20***	5
Diptera						
<i>Simulium</i>	6.07		0.57	.09	18	28
Chironomidae	5.48		0.00	.00	8	52

* for *Stenonema* spp. ** for all Plecoptera *** for *Glossosoma* spp.

To provide a comparative measure of the relationship between BI and behavioural drift tendencies of the taxa studied, we undertook a search of the North American drift literature. We tabulated by genus the total number of published accounts of taxa taken in 56 drift studies. The percentage of these citations for which diel drift periodicities were reported was used as an index of how prevalent behavioural drift is in that genus (Table 2). A Spearman's rank correlation test was performed and showed a significant association ($r = 0.55$, $P < 0.05$) between BI and the relative frequency of diel drift periodicities.

DISCUSSION

There appears to be a general correlation between BI and the reported tendency for the various organisms studied to show diel drift periodicities. *Baetis* spp. and *Gammarus* frequently exhibit strong behavioural drift patterns. Our data indicate that both have high BI and among the greatest overall SC (Table 2). Other animals (*Ephemere*lla, *Ecdyonurus*, *Paraleptophlebia*) are intermediate both in BI and in their reported tendency to drift, whereas Plecoptera, Simuliidae, Chironomidae and Elmidae have conspicuously lower indices and, with the exception of the elmids, are less likely to show diel periodicities (Adamus and Gaufin 1976). Thus, species most prone to drift consistently may also be those best able to remove themselves from the drift. This suggests that behavioural drift may be more than the result of accidental displacement from vulnerable positions on the substrate (Stein 1972).

Our estimates for *E. subvaria* in November and March suggest that SC decreased through time, even though MC remained virtually unchanged. In March, the curve for live and for dead insects intersected at about 26 cm sec⁻¹, and at this point a live insect is no better at settling than its dead counterpart. This contrasts with a much greater estimated point of intersection for the November experiments. We would predict that, given an equal propensity to drift, older and large *E. subvaria* nymphs would tend to become more concentrated in slower water areas than young smaller larvae (perhaps reducing mortality during emergence). In fact, older *E. subvaria* in the laboratory are considerably more prone to drift than are young ones (Ciborowski 1979). Kovalak (1978) however found no differences in relative sizes of *E. subvaria* nymphs among fast and slow water areas in the Pigeon River, Wisconsin; and greater numbers were consistently located in the fast water area at all times of the year. Perhaps differences, if they exist, would be more apparent along a stream margin-to-centre gradient than along an upstream-downstream gradient (Waters 1972).

The four mayfly species which we examined were of widely different morphological forms. *B. vagans* is a streamlined animal,

E. subvaria and *E. invaria* are thick-bodied, and *P. mollis* is dorsoventrally flattened. We had initially hypothesized that such variety in body shape might differently affect the contribution of MC to the SC of each species. However, variations in MC may be almost completely the result of dissimilarities in the size rather than the shape of the animals tested. MC appeared to be closely correlated ($r = 0.96$, $P < 0.05$) to the mean head width of the animals tested. This relationship, if valid for all aquatic invertebrates, is of significance in interpreting field drift data. Several workers (Clifford 1972, Stein 1972, Waters 1972, Reisen 1977) have reported on variations in the abundance of animals of different sizes in the drift. In instances where behaviour makes a minimal contribution to SC (e.g. Chironomidae, Simuliidae; Table 2) smaller individuals may, rather than being more prone to entrainment in the drift, simply take longer to resettle and are therefore more likely to be captured in a net than larger animals.

Our analysis of settling was concerned only with the influence of a single variable (current velocity) on the settling abilities of mayflies, but this type of analysis need not be so restricted. Luedtke and Brusven (1976), Corkum *et al.* (1977), and Walton (1978) have all shown that different substrate types can also influence the drift and (or) settling of invertebrates. By performing the appropriate series of experiments, substrate type could be added to the analysis as a second independent variable to provide a similar measure of SC and the importance of behaviour. Indeed, any number of parameters could be incorporated and indices defined to give an overall estimate of the importance of behaviour and morphology of a species to its re-establishment on the substrate. Such estimates would be quantitatively comparable to values obtained for other species examined in the same way. Furthermore, regression curves used to estimate indices can be integrated over selected intervals of the independent variables to assess the probability of animals becoming established in particular habitats. Thus, one could predict possible changes in the distribution of animals within a stream as a result of drift and subsequent re-settling.

ACKNOWLEDGMENTS

We wish to thank Drs. P.J. Pointing, W.G. Sprules, H.F. Clifford and Mr. R.L. Baker, all of whom provided valuable suggestions and criticisms of this work. The research was partially funded by grants from the National Research Council of Canada and Erindale College to Dr. P.J. Pointing.

RESUME

Grâce à des expériences réalisées sur des larves d'éphéméroptères dans un cours d'eau de laboratoire, on a découvert que quatre espèces accusent des différences importants dans leur aptitude à s'établir. Des mesures quantitatives de la capacité moyenne d'adaptation ont été prises et l'apport de la morphologie et du comportement évalué aux fins de comparaison.

Le comportement joue un rôle plus important dans le rétablissement des espèces qui accusent des périodicités plus fréquentes que les autres des mouvements de dérivation par vingt-quatre heures. Bien qu'il y ait des différences appréciables de morphologie entre les espèces, la grosseur moyenne des larves acquiert une importance plus grande lorsqu'il s'agit de déterminer le taux de mortalité des insectes. Des variations au sein d'une même espèce dans la capacité de rétablissement des insectes pris individuellement peuvent expliquer en partie les changements qui se produisent dans la répartition relative des populations au cours du temps.

ZUSAMMENFASSUNG

Experimente mit Larven von Eintagsfliegen in einem Laboratoriumsgewässer ergaben bemerkenswerte Unterschiede in Bezug auf das Ansiedlungsvermögen von vier verschiedenen Arten. Zur Vergleichung herangezogen wurden quantitative Meßwerte der Gesamtansiedlungskapazität, morphologische Eigenarten und spezifische Verhaltensweisen. Es zeigte sich, daß die Fähigkeit zur Re-Etablierung für diejenigen Arten von größerer Wichtigkeit ist, die im Verlauf eines 24 Stunden Zyklus gewissen Veränderungen durch Abtriften unterworfen sind, als für solche, die davon unbeeinflusst bleiben. Obwohl große morphologische Unterschiede zwischen den einzelnen Arten bestanden, war doch die mittlere Größe wichtiger bei der Bestimmung der Raten zurückkehrender, toter Tiere. Intraspezifische Variationen der Fähigkeit driftender Einzeltiere, sich wieder anzusiedeln, sind wahrscheinlich zum Teil verantwortlich für Veränderungen in der relativen Verteilung der Populationen über eine bestimmte Zeitspanne hinweg.

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