Dispersal in drift-prone macroinvertebrates: a case for density-independence

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SUMMARY

1. Studies of dispersal of macroinvertebrates in streams and rivers tend to be focused on drift, whilst benthic movements are usually considered to be less important.
2. Field-enclosure experiments with the mayfly *Baetis rhodani* indicate that net dispersal in this species is simply a proportional loss of individuals from the benthos.
3. Neither net upstream or downstream movements exhibited evidence of density-dependence in the form of curvilinear relationships between initial and final densities.
4. The net number of animals moving upstream did not differ significantly from the net number moving downstream.
5. The probable mechanisms behind density-independent dispersal are discussed, as are the implications for our understanding of population dynamics in relation to invertebrate drift.

Keywords: *Baetis rhodani*, density-dependence, invertebrate drift, stony stream, upstream movements

Introduction

Dispersal from one habitat patch to another is one of the cornerstones of modern ecological theory, and underpins the large body of work devoted to the study of population dynamics (Hanski & Gilpin, 1997; Hassell, 2000). Studies of dispersal of the aquatic stages of macroinvertebrates within lotic systems are very common in the literature. Rapid colonisation and movement of animals between habitat patches on many scales appears to be a key component of the dynamics of many benthic macroinvertebrate populations (e.g. Allan, 1995; Anholt, 1995; Mackay, 1992; Speirs & Gurney, 2001). The physical properties of water mean that animals are more easily entrained within it than they are in air (Denny, 1993; Vogel, 1994), and the unidirectional nature of flow in streams and rivers means that studies of dispersal in streams generally focus on invertebrate drift. The economic

importance of salmonid fishes, which tend to feed predominantly on drifting prey, has also played a part in stimulating studies of drift. Movement on or within the streambed is also considered, especially in studies of colonisation, but the consensus is that the most important dispersal mechanism for benthic macroinvertebrates is likely to be drift (Mackay, 1992; Allan, 1995).

The importance of density-dependent processes in shaping the patterns of dispersal that we see in lotic systems has been debated for more than quarter of a century (e.g. Walton, Reice & Andrews, 1977; Bohle, 1978; Ploskey & Brown, 1980; Turner & Williams, 2000). Its presence or absence has also been used to differentiate between two theories regarding drift. Both Müller's (1954) colonisation cycle and Water's (1961) production-compensation model attempt to explain the phenomenon of drift. The former asserts that upstream flight by adults compensates for larval dispersal; the latter argues that downstream drift represents production in excess of carrying capacity. Evidence for the colonisation cycle is equivocal, and evidence supporting the latter is scarce (Allan, 1995). The presence of density-dependent dispersal has been

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used as the key differentiating process for these two concepts. More specifically, a curvilinear response between number in the benthos and numbers in the drift should be expected if the production-compensation model is the dominant process at work.

The influence of density-dependence upon dispersal, and in particular on drift, of lotic macroinvertebrates has been examined both directly and indirectly in a number of studies. However, as with drift in general, density-dependence or its absence should be addressed at an appropriate level. Organisms found in the drift can be assigned to one of a number of groupings based on their propensity to enter the drift (Elliott, 1971a; Wilzbach, Cummins & Knapp, 1988; Rader, 1997), and this classification seems the best starting point for consideration of both drift and upstream dispersal. Here I focus on the dispersal of one of the most important of the drifting groups, the highly motile and locally abundant *Baetis rhodani* (Pictet). This species forms a large part of the drift in Northern Europe (Elliott, Humpesch & Macan, 1988) and ecologically equivalent species (usually in the same genus) can be found in most biomes.

Previous studies aimed at elucidating the importance of density-dependence have tended to focus on one of two methodologies: field based observations or manipulations and experimental channels or tanks.

The current study was designed to incorporate the most desirable features of both these approaches to examine the relationship between benthic density and both up- and downstream movements in *B. rhodani*. Therefore, field enclosures were used to constrain experimental animals and thus allow accurate determination of benthic densities, whilst not divorcing the situation from natural conditions.

Methods

Experiments were carried out from 28 June to 28 July 2000 in Dale Park Beck (Nat. Grid Ref. SD 353 927), a stony stream in the Lake District. For each of the three trials, six experimental enclosures were placed in one of three riffles in the reach. Stream width in each riffle varied from 1 to 2.5 m, and the bottom consisted of large stones (longest axis 7–30 cm) over smaller stones and gravel. Water depth was between 10 and 15 cm in all riffles.

Enclosures consisted of clear perspex channels with dimensions of $1.40 \times 0.15 \times 0.30$ m ($L \times W \times H$). The enclosures were rectangular in cross-section with solid sides and floor (Fig. 1). Each enclosure incorporated four removable meshes (400 μm aperture) and a 1-mm aperture mesh prefilter. The meshes were positioned such that the enclosures had three sections.

Fig. 1 One of the experimental channels, *in situ*. Water flow is from bottom left to top right of the picture. Dimensions are given in the Methods section.

Of these sections the basal area of the upstream and downstream sections were 0.0615 m^2 (0.41 × 0.15 m) and 0.0645 m^2 (0.43 × 0.15 m), respectively, while the area of the central section was 0.045 m^2 (0.30 × 0.15 m).

Enclosures were anchored to the streambed using stainless steel rods. Natural substrata, cleaned of obvious macroinvertebrates, were placed in the enclosures prior to the addition of the experimental animals. Stones were arranged so as to cover >90% of the surface area of each enclosure. Large larvae, mainly *B. rhodani* with some *B. scambus* (Eaton) and *B. muticus* (L), collected from the reach, were then added to the central sections of the channels.

Densities in the channels were chosen to span the range of natural densities, and varied from 111 to 1556 larvae m^{-2} in the central section (5–70 animals per enclosure). These values are within the range of densities observed for larger *B. rhodani* in the field (Malmqvist & Sjöström, 1987; Huhta *et al.*, 1999; personal observation). Once the animals had been added, the enclosures were left in the stream between 18 and 24 h (depending on the trial, but always including one complete night). After this initial period, the two meshes constraining animals to the central section were removed and the channels left for a period equal to the initial settling period (again, always including one complete night). All meshes were gently cleaned every hour throughout the experimental period to minimise reductions in water velocity within the enclosures because of blocking of the mesh. At the conclusion of the trial, all meshes were replaced, the substrata washed and removed, and the animals in each section collected. Collection was carried out with a medium-bore pipette and animals were preserved in 70% alcohol. Because of disturbance, data for only two of the six enclosures could be collected in the second trial. Table 1 gives details of experimental duration and densities used for each of the three trials.

During each trial, measurements of water velocity 3 cm from surface of the substrata were taken in the downstream section of each enclosure using an OTT C2 flowmeter (OTT Hydrometry Ltd, Lowdham, Nottinghamshire, U.K.) every 6 h. Water temperature was recorded at the same time. All measurements and mesh cleaning that took place during darkness were carried out with a torch fitted with a red filter.

After each trial, the animals were sorted by careful visual examination of each of the entire sample (each divided into small volume subsamples), animals were identified to species and their length measured to 0.1 mm using a binocular microscope fitted with an eyepiece graticule. For specimens where only head capsule width was measurable (13 instances), body length was estimated using the equations given in Meyer (1989). As the mesh aperture used (0.4 mm) was a compromise between excluding smaller nymphs and maintaining water flow within the channels, most samples contained more animals than were originally added to the enclosure. The assumption was made that the individuals added were the largest in the sample and thus animals were ranked by body length (tip of abdomen to head) and animals with head capsule widths less than the mesh aperture were not included in the analysis. The minimum body length included using this ranking method was 2.8 mm (head capsule width approximately 0.403 mm). However, only three individuals of the 468 animals included in the analysis had body length of less than 3.1 mm (head capsule width approximately 0.447 mm). As head capsule width is invariably less than the width of the mesothorax, animals of the sizes selected are unlikely to have originated from outside of the enclosures.

The species composition in all but three of the 14 enclosures consisted of at least 80% *B. rhodani*, with a few *B. scambus* and *B. muticus*. The three remaining enclosures were those containing 60 individuals in the second trial and 10 and 50 in the third trial (Table 1). The proportion of *B. rhodani* in each was 71.7, 66.7 and 56.0%, respectively. However, analysis of the data set with these three channels excluded made no difference to the pattern of the results and therefore results given are for all 14 enclosures.

Table 1 Experimental duration and densities used for each of the three trials

Trial	Date	Duration (h)	Number of animals added to enclosures
1	29 June – 1 July	18 + 18	5, 10, 20, 30, 40, 50
2	19 July – 21 July	24 + 24	10, 60 (30, 40, 50, 70)*
3	26 July – 28 July	24 + 24	10, 30, 40, 50, 60, 70

*Enclosures disrupted as a result of disturbance: data not collected.

Results

Numbers recovered

The number of nymphs greater than 2.8 mm dropped below the number added in five enclosures in the third trial. The presence of a few emerging nymphs in these enclosures, and the fact that previous trials did not experience reductions, indicates that emergence by winged adults, not escape by aquatic stages, accounts for these losses. Emergence peaks in late July/early August in *B. rhodani* (Elliott *et al.*, 1988). In no cases was this loss greater than 10% of the initial number added to the enclosure.

Net dispersal

The number of nymphs remaining in the central section after the conclusion of the trial was regressed against the initial number of nymphs added to the enclosure (Fig. 2). A power function provided the best fit to the data ($y = 0.592x^{1.0547}$; SE of slope, 0.072; adj. r^2, 0.943; $P < 0.001$), although the slope of the log-linear analogue of this function did not differ significantly from one ($t_{0.05, 12} = 0.764$, $P > 0.05$) suggesting a simple proportional relationship. A proportional relationship between initial density and net dispersal is also supported by a regression of the proportion of the number of animals remaining in the central section against the initial numbers, the slope of which is not significantly different from zero (adj. r^2, –0.083; $P = 0.980$; Fig. 3).

The mean values of the velocities measured for each channel themselves had a mean of 0.246 ms^{-1} ($n = 14$; SD = 0.045; range = 0.143–0.3 ms^{-1}). Plotting
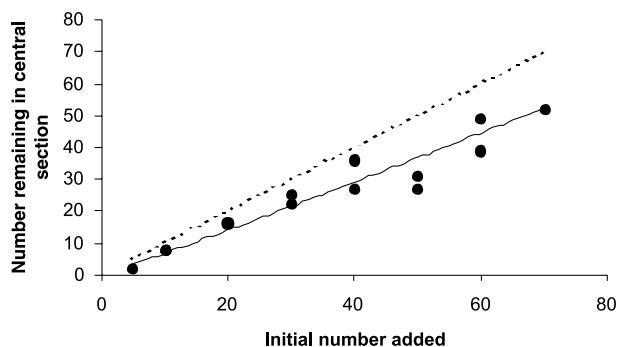

Fig. 2 Net dispersal from the central section of enclosures. Broken line indicates expected relationship if net dispersal was zero. Solid line is a fitted power function ($y = 0.592x^{1.0547}$).
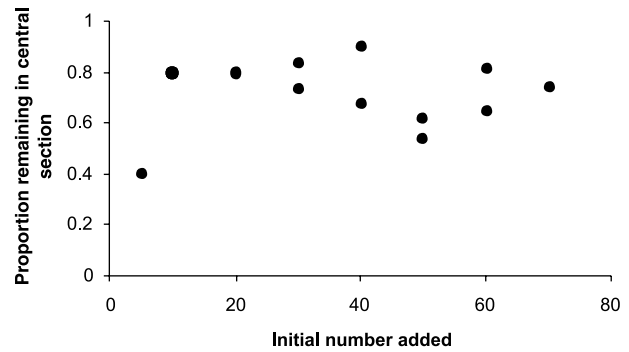

Fig. 3 Proportion remaining of the initial number of animals added to each enclosure against initial numbers.

the residual values from the power function from Fig. 2 against mean current velocity in the enclosure for the whole of the trial indicates that this variable explained less than 0.05% of the total variance (r^2, 0.009; $P = 0.748$). Similar results were seen when the residuals were regressed against geometric mean body length of all the nymphs in the enclosure (0.07% of total variance; r^2, 0.013; $P = 0.703$).

Drift and upstream movement

A simple comparison of numbers in the upstream section with those in the downstream one indicated that there was no significant difference in the net movement of animals upstream from the central section and those moving downstream (paired *t*-test: $t_{0.05, 13} = -0.117$, $P = 0.908$).

In order to examine whether net dispersal, up- or downstream, was density dependent, I regressed the number of animals (number + 1) found in either the upstream or downstream section against the initial number added to the central section (Fig. 4). Again, a power function provided the best fit to the data (upstream: $y = 0.285x^{0.797}$; SE of slope, 0.203; adj. r^2, 0.547; $P = 0.002$; downstream: $y = 0.470x^{0.665}$; SE of slope, 0.170; adj. r^2, 0.543; $P = 0.002$), but this time density was only able to explain around 60% of the variance. As before, the slope of the log-linear analogues of these two functions did not differ significantly from one (upstream: $t_{0.05, 11} = -1.00$; $P > 0.05$; downstream: $t_{0.05, 11} = -1.971$; $P > 0.05$). Examination of residuals from this function for both up- and downstream sections indicated that the ability of water velocity and body size to explain the remaining variance was negligible.
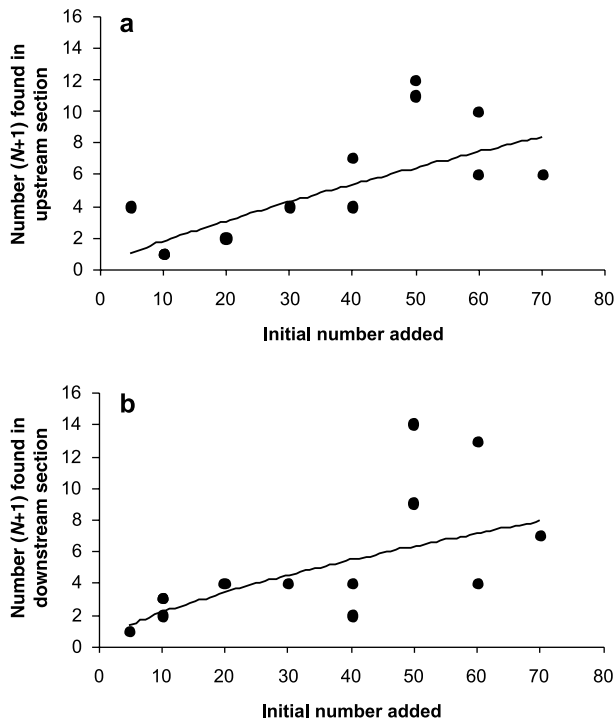
Fig. 4 Net dispersal into the (a) upstream and (b) downstream sections of the enclosures. Initial number added refers to animals placed in the central section of each enclosure (see Methods). Solid lines are fitted power functions [$y = 0.2845x^{0.7968}$ and $y = 0.4702x^{0.6647}$ for (a) and (b), respectively].

Fig. 5 The effect of experimental duration. Comparison of slopes for 18 h (filled circles, solid line) and 24 h (open circles, broken line) trials. Lines are fitted power functions (18 h trials: $y = 0.4037x^{1.1773}$; 24 h trials: $y = 0.9182x^{0.9331}$).

The effect of experimental duration

As trials 2 and 3 lasted for 12 h longer than trial 1, I regressed the number of nymphs found in the central section against the initial number added as before, but this time treated trial 1 and trials 2 and 3 combined as separate data sets (Fig. 5). Comparison of the slopes of these two regression lines showed no significant differences using either linear regressions ($t_{0.05, 6, 8} = -0.326$; $P > 0.05$) or the log-linear analogues of power functions ($t_{0.05, 6, 8} = 1.491$; $P > 0.05$). Thus, experimental duration appears to have had no effect on the results.

Discussion

In this study, neither net dispersal nor net up- or downstream movement of *Baetis* appears to be density-dependent. Although net movements are not strict measures of separate components of dispersal, examination of both up- and downstream movement in the same enclosure means that conclusions drawn
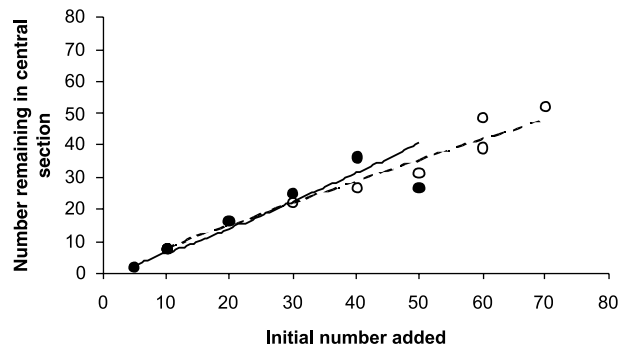
regarding these movements are probably applicable to drift and upstream movements. Restricting immigration from drift in the upstream section and from upstream crawling in the downstream section, combined with the fact that there was a net dispersal of only 28% of animals from the central section, means that compensation for movement in one direction is unlikely to bias the results presented here.

Previous work on drift in general has generated conflicting conclusions regarding the existence of density-dependence. These conclusions are confounded by comparisons between a number of species that are often markedly different in their ecology. Therefore, it would seem prudent to examine trends for taxa grouped according to settlement ability (*sensu* Elliott, 1971a). Thus, studies such as those by Dimond (1967) that examine drift fauna in general, and those that focus on different functional groups (e.g. Hildebrand, 1974; Walton *et al.*, 1977; Turner & Williams, 2000) even if they show similar trends, may have little bearing on a drift-prone species such as *B. rhodani*. There is limited evidence that drift in *Baetis* is density-dependent (e.g. Gyselman, 1979). In comparison, work by Reisen & Prins (1972) (*B. bicaudatus* Dodds), Bohle (1978) (*B. rhodani*), Corkum, Pointing & Ciborowski (1977) (*B. vagans* McDunough), Ciborowski (1983) (*B. tricaudatus* Dodds), and Statzner & Mogel (1985) (mostly *B. buceratus* Eaton), support the idea that drift in this group is a density-independent phenomenon. This work adds weight to the idea that density-dependent movements are not an important process in the dispersal of drift-prone taxa.

Work on upstream movements has focused to some extent on compensation for downstream losses (Söderström, 1987). *Baetis rhodani* undertakes extensive upstream movement shortly before emergence (Hultin, Svensson & Ulfstrand, 1969), but upstream movements are also common before this period (Elliott, 1971b). Results from the field enclosures suggest that upstream movement is sufficient to compensate for numerical losses because of drift, at least in the short term and for relatively small distances. This result is in conflict with a number of other studies (Elliott, 1971b; Elliott *et al.*, 1988) that suggest that compensation by upstream movements never exceeds 40% of the numbers moving downstream (e.g. Bird & Hynes, 1981). However, Richards & Minshall (1988) found that drift accounted for only 52–62% of immigration onto rocks in *B. bicaudatus*, the rest being attributable to benthic crawling. It is also worth noting that previous studies have utilised trapping techniques that tend to redirect invertebrates back on their original course before entering the capture-net. Thus, there may well be a tendency for the animals to alter their behaviour prior to capture, a problem not encountered in this study. However, compensation in terms of numbers does not imply equality in the distances travelled in either direction. Current evidence suggests that drift distance is likely to exceed the distance covered during upstream movement (Elliott, 1971a, b). Nonetheless, we still lack any information on the relative frequency of these two dispersal mechanisms per individual. We may yet find that relatively irregular drift can be compensated by almost continuous upstream movements in many taxa.

Limitations to the channels used in this study may also have some bearing on interpretation of the results. Although hydrodynamic conditions at either end of the channels may have varied because of the presence of the meshes impeding flow and altering turbulence structure (Nowell & Jumars, 1984; Hart & Finelli, 1999), it is unlikely that the effects were the same for both the upstream and downstream ends. Thus, although most individuals were retrieved from the central section it seems unlikely that movement away from the two end sections because of unsuitable hydrodynamic conditions would result in an equal density of animals in these sections as found in this study. A second argument is that the natural distances travelled by both drifting and crawling animals are likely to be greater than the channel in which they were confined (Elliott, 1971a, b). If this is true, then both density-dependent and -independent dispersal are likely to produce a random distribution within the channels at equilibrium (tending to equal density in each section with increasing numbers). However, with net dispersal of approximately 28% in this study, we can infer that density-dependence is unlikely to be the mechanism behind the distributions found, unless the trials did not last long enough for movements to equilibrate. If this is the case, then an equal density at the up- and downstream sections is unlikely, because of asymmetries in movement distance and frequency, a prediction not supported by these results.

There is considerable evidence that mayflies are sensitive to the abundance of epilithic algae, and thus leave patches dependent on resource abundance (e.g. Hildebrand, 1974; Kohler, 1985; Richards & Minshall, 1988). *Baetis* is not commonly thought to compete through direct interactions (Corkum, 1978; Wiley & Kohler, 1981), and so it is possible that the density-dependence may have been apparent if the trials had included manipulations of resource abundance or, alternatively, densities above those occurring naturally. Further exploration of the effects of food density in this type of channel would be an obvious extension of this work.

Because of their small size, and thus ability to enter and leave the channels through the mesh dividers, accurate counts of the smaller *Baetis* present in the channels was not practical. However, given their small size compared with the experimentally added animals, competition for food between the two groups is unlikely to have been particularly strong (Brown, 1961). Even if competition was an important factor, there was nothing in the experimental protocol to suggest that density should differ between sections within channels. In addition, observations also suggested that these colonising animals were not present in high numbers.

By addressing the question of density-dependence, some consideration of whether drift is mediated predominantly by behaviour, *directly* or *indirectly*, is possible. Use of a species that is motile, and that is known to have some control over its settlement from the drift (Elliott, 1971a), means that any dislodgement from the substratum as a result of water current will ultimately be because of the behaviour that placed the animal in a given position in the first place. My work

suggests that downstream dispersal is a simple proportion of benthic density, and the most parsimonious mechanisms for this are dislodgement by water current and/or downstream benthic movement. In order to confirm the former, a positive relationship between water velocity and drift needs to be evident. I was unable to examine this question adequately in the current study as the experimental design necessitated holding water velocity relatively constant whilst manipulating density. However, such a relationship is already widely recognised (see Brittain & Eikeland, 1988) for many drifting animals, although the relationship between current velocity and drift for *Baetis* spp. has rarely been examined, and those studies suggest increased velocity results in a decrease in the number of animals drifting (Corkum *et al.*, 1977; Ciborowski, 1983). This is an area that clearly requires more investigation. Any inference of passive entertainment into the water column does not, however, rule out an active behavioural component of drift. It simply implies that any active component is likely to involve avoidance of high-risk areas and/or influence travel distance once the animal is in the water column.

If dispersal in drift-prone species such as *B. rhodani* is density-independent, then there are likely to be repercussions for our understanding of the life-histories and population dynamics of these species. Many consider that density-dependence at some stage in an organism's life-history is almost certainly a prerequisite for population persistence (Begon, Harper & Townsend, 1996; Royama, 1992; but see also Speirs & Gurney, 2001). Therefore, the search for density-dependence should not be limited to one aspect of the life-history of aquatic macroinvertebrates. Larval blackfly (*Simulium vittatum* Zetterstedt) exhibit density-dependent dispersal away from egg masses (Fonseca & Hart, 1996), and density-dependent mortality of drift may well occur in the presence of drift-feeding fishes (although this could manifest as either a positive or a negative relationship).

In conclusion, this study suggests that, at least in drift-prone species like *B. rhodani*, dispersal is a proportional loss of individuals from the benthos. In addition, within the limits of the experimental system, it suggests that upstream benthic movements may be sufficient to compensate numerically for downstream transport. The current study does not rule out a strong influence of biotic interactions, nor the influence of current velocity on in-stream disper-

sal. However, it does suggest that (i) any search for density-dependence may need to be focused on other stages of these animals' life-histories and (ii) more attention should be paid to the influence of upstream movements on the population dynamics of drift-prone taxa.

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