# Estimation of intergenerational drift dispersal distances and mortality risk for aquatic macroinvertebrates

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### Abstract

Estimates of the total lifetime dispersal capacity of individuals comprising invertebrate drift in streams and rivers have proved very difficult to determine empirically. Here we use recent data on dispersal in the amphipod *Gammarus pulex* L. to illustrate a method for estimating the total distance an individual is likely to travel downstream during the period between hatching and its first reproductive episode. For the system we consider, this estimate is on the order of 1.5 km. This method may be useful in future explorations of the ecological relevance of within-stream displacement and population persistence. Furthermore, we are able for the first time to estimate an upper bound for the mortality risk associated with entering the drift, which, for the *G. pulex* population under consideration, is less than 1% for individual drift events. We suggest that this risk may not be nearly as high as had previously been thought. These mortality and distance estimates may illustrate a fundamental difference between dispersal in lotic systems and those in other habitats, in that the mean dispersal distance is of much higher ecological relevance than that of rare long-distance events.

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 (Palmer et al. 1996; Hanski and Gilpin 1997; Bilton et al. 2001). Studies of dispersal of the aquatic stages of macroinvertebrates within lotic (flowing water) systems are very common in the literature. Rapid colonization and movement of animals between habitat patches on several spatial scales appears to be a key component of the dynamics of many benthic invertebrate populations (e.g., Mackay 1992; Allan 1995; Anholt 1995; Speirs and 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 downstream transport of benthic invertebrates in the water column.

Movement on or within the streambed has also been considered, especially in studies of colonization, but the consensus is that the most important dispersal mechanism for benthic invertebrates is likely to be drift in the water column (Mackay 1992; Allan 1995; Malmqvist 2002). Consequently, the literature is filled with studies describing the number of animals involved and how far they travel in a single drift event when in the water column. Current evidence suggests that, although some of the animals found in the water column originate from a large area upstream from the sampling point, the majority travel only a relatively short distance at a time (McLay 1970; Elliott 1971; Larkin and McKone 1985; Elliott 2002*c*). However, we are still lacking reliable data on the distance that individual animals might travel downstream during their lifetime, which will involve many drift events.

Here we present some simple calculations, using recently published data from the literature on drift in the amphipod *Gammarus pulex* (L.), which enables us to estimate the total downstream displacement of animals. Furthermore, we estimate an upper bound for the probability of mortality associated with an individual drift event and assess the implications of both of these figures for our understanding of dispersal and population processes in lotic systems.

## The model

*Assumptions*—The following model rests on several simplifying, but not particularly restrictive, assumptions concerning the system in which the population of macroinvertebrates lives. We consider a small stream of infinite extent that is characterized hydraulically by constant depth, width, and water velocity along its length. The velocity–depth profile of the system is not considered explicitly in the model, but when the model is parameterized from empirical data we implicitly assume that this profile matches that of the field site.

*Distance estimate*—Our starting point is the proportion of time an individual animal will spend in the water column. If the density of individuals in the water column is maintained by a process of continuous movement between the water column and the benthos (Speirs and Gurney 2001), then the proportion of time an individual spends in the water column (irrespective of how frequent drift events are, or how long they might last) is given by

$$P = \frac{Y\delta}{X} \tag{1}$$

where $P$ is the proportion of time an individual spends in the drift. $P$ is thus determined by drift density $Y$ ($m^{-3}$) multiplied by the depth of water over the streambed $\delta$ (m), all over the total benthic population density $X$ ($m^{-2}$). Detailed methods for obtaining an estimate of $P$ from experimental data are given in Web Appendix 1 at http://www.aslo.org/lo/toc/vol_48/issue_6/2117a1.pdf.

We next consider the intergeneration time $T_{gen}$ (s), the average time between hatching (considered here to be the point at which drifting can first occur) and first reproductive episode. If $T_{gen}$ is known, then we can calculate the total time an individual is likely to spend in the drift between hatching and its first reproductive episode $T_{drift}$ (s) by:

$$T_{drift} = T_{gen}P \tag{2}$$

In turn, this total time spent in the water column can be divided by the average time spent in the water column per drift event $\bar{t}$ (s) to give an estimate of the total number of drift events between hatching and first reproductive episode:

$$N_{drift} = \frac{T_{drift}}{\bar{t}} \tag{3}$$

If we know the mean distance traveled per drift event $\bar{d}$ (m), then we have all the information we need to be able to calculate the total intergenerational downstream displacement $D_{gen}$ (m):

$$D_{gen} = N_{drift}\bar{d} \tag{4}$$

By simple substitution it is easy to show that

$$D_{gen} = T_{gen}P\frac{\bar{d}}{\bar{t}} \tag{5}$$

Given this simple relation between variables, examination of Eq. 5 suggests that changes in $\bar{d}$ or $\bar{t}$ may have profound effects on our estimate of $D_{gen}$, and that errors in our measurement of either may lead to widely differing estimates of total downstream dispersal distance. However, recent data suggest that for any single drift event, the mean time spent in the water column by many drifting animals is, for a wide range of velocities, constant (Elliott 2002b,c). This means that, although both $\bar{d}$ and $\bar{t}$ can be considered functions of velocity $u$, i.e.,

$$\bar{d}(u) = u\bar{t}(u) \tag{6}$$

If time spent in the water column is constant, then

$$\bar{t}(u) = \bar{t} = \text{constant} \tag{7}$$

and assuming that the ratio $\bar{d}/\bar{u}$ is also constant (i.e., there

is a linear relation between water velocity and mean drift distance, evidence for which is provided by Elliott [2002b,c]), then we can see that

$$\frac{\bar{d}}{\bar{t}} = u \tag{8}$$

We can now return to Eq. 5 in a new form:

$$D_{gen} = T_{gen}Pu \tag{9}$$

This suggests that, within a given velocity range for which Eq. 7 remains true, the total downstream displacement is solely the product of three variables: intergeneration time; proportion of the benthos found in the water column; and mean water velocity. Thus, given our assumption of constant $\bar{t}$, variation in drift distance or time in the water column has no effect on $D_{gen}$ for a given velocity, as long as the relation between drift distance and time in the water column remains constant.

*Mortality estimate*—Given that we are now able to estimate the number of drift events an individual might be expected to experience in the time between hatching and its first reproductive episode, we can also try to estimate an upper bound for the probability of death associated with these events.

Our starting point here is the probability of surviving all the drift events between hatching and an individual's first reproductive episode $P(\text{survival}_{T_{gen}})$. However, to proceed further we must make some additional assumptions about the population under consideration. Our first assumption is that the population is closed, and at equilibrium (that is, there is a balance between births and deaths with no immigration or emigration), such that the population remains stable over time. Second, we assume that there are no other sources of mortality other than from drifting. In this case mortality from drifting may come from predation within the water column (e.g., drift-feeding fish, net-spinning caddisflies) and losses from the system where individuals drift into unsuitable habitats (e.g., estuaries, lakes). In addition, two further assumptions are made to simplify the analysis: that females produce young with a 50 : 50 sex ratio that is maintained at all times in the population; and that these females produce all of their offspring in one short reproductive episode.

Because of our assumption of equilibrium population conditions we can, as a first approximation, assume that each individual produces on average one male and one female offspring that survive to reproduce. The probability of survival is assumed to be the same for both surviving offspring and therefore we will concentrate on one (females). Hence, we can easily calculate the probability of survival that leads to an expectation that only one of these female offspring will survive to reproduce. Thus, for a female that produces $n$ offspring, of which half (on average) will be female, the probability that one of these female offspring will survive to reproduce is

$$P(\text{survival}_{T_{gen}}) = \frac{1}{n/2} = \frac{2}{n} \tag{10}$$

and the probability of survival for a single drift event (assuming each individual experiences $N_{drift}$ drift events) is

Table 1.   Parameter values and sources for data used to produce predictions from the model. Estimate indicates value taken from literature; Derived indicates the value was obtained from equations detailed in the Sources column.

| Parameter | Definition | Value | Derivation | Source |
|---|---|---|---|---|
| $a_n$ | Slope from regression of nocturnally sampled benthic density against drift density | $3.578 \times 10^{-3}$ m$^{-1}$ | Estimated | Reanalysis of data from Elliott (2002*a*) |
| $\delta$ | Mean water column depth | 0.1 m | Estimated | Elliott (2002*a, b*) |
| $\bar{t}$ | Mean time spent in the water column per drift event | 8.0 s | Estimated | 12 May 1996 (Elliott 2002*b*) |
| $\bar{d}$ | Mean distance traveled per drift event | 2.25 m | Estimated | 12 May 1966 (Elliott 2002*b*) |
| $u$ | Mean water velocity 0.01 m from streambed | 0.281 m s$^{-1}$ | Estimated | 12 May 1966 (Elliott 2002*b*) |
| $P$ | Proportion of time spent in the water column | $3.577 \times 10^{-4}$ | Derived | Eq. A6 |
| $T_{gen}$ | Time between hatching and first reproductive event | $15.552 \times 10^6$ s | Estimated | 180 days at 10°C (Hynes 1955; Welton and Clarke 1980) |
| $T_{drift}$ | Total time in water column during time $T_{gen}$ | 5562.95 s | Derived | Eq. 2 |
| $N_{drift}$ | Number of drift events during time $T_{gen}$ | 695 | Derived | Eq. 3 |
| $D_{gen}$ | Total downstream displacement during time $T_{gen}$ | 1563 m | Derived | Eq. 9 |
| $n$ | Total number of offspring produced per female | 500 | Estimated | (Hynes 1955; Welton and Clarke 1980) |
| $P(\text{survival}_{T_{gen}})$ | Probability of surviving time period $T_{gen}$ | 0.004 | Derived | Eq. 10 |
| $P(\text{survival})$ | Probability of surviving one drift event | 0.9921 | Derived | Eq. 11 |
| $P(\text{mortality})$ | Probability of mortality for one drift event | 0.0079 | Derived | Eq. 12 |

$$P(\text{survival}) = \left(\frac{2}{n}\right)^{1/N_{drift}} \qquad (11)$$

Thus, the probability of mortality during a single drift event is given by:

$$P(\text{mortality}) = 1 - P(\text{survival}) \qquad (12)$$

Hence, within the limits of our assumptions, the probability of mortality during a single drift event is simply a function of female lifetime reproductive output $n$, and the number of drift events an individual undertakes in the period $T_{gen}$. If we further decompose $N_{drift}$ we can see that

$$P(\text{mortality}) = 1 - \left(\frac{2}{n}\right)^{\bar{t}/T_{gen}P} \qquad (13)$$

This tells us that $P(\text{mortality})$ is an inverse function of female lifetime reproductive output, raised to the power of the ratio between time spent in the water column per drift event and the total time spent in the water column during the period $T_{gen}$.

*Parameterization*—Here we use data from a comprehensive field study to parameterize the model and to produce predictions regarding $T_{gen}$ and $P(\text{mortality})$ for *G. pulex*. The field study was carried out by Elliott at Bellman Ground Beck, a small stream in the English Lake District (Elliott 2002*a*). Data were collected daily in 1966 and approximately every 3 d in 1967. A small waterfall enabled Elliott to sam-

ple drift from the entire stream cross-section and records were kept of both drift catches and benthic densities upstream from the waterfall. In addition, several experiments to determine drift distances were carried out in 1966 (Elliott 2002*b*). Table 1 gives the values of basic and derived parameters calculated using this field data and other sources from which we obtained basic life-history data for *G. pulex* (Hynes 1955; Welton 1979; Welton and Clarke 1980).

Elliott (2002*a*) shows that the relation between drift density $Y$ (number of animals found per cubic meter of water) and benthic density $B$ (number of animals per square meter of streambed) for *G. pulex* is given by a power function with an exponent not significantly different from unity. Therefore, we can assume that the relation between the number of animals in the water column and the number on the streambed at any instant in time takes the form $Y_{50} \approx a_n B_n$ (see Web Appendix 1). In this case, $a_n$ describes the slope of the regression line between standardized drift density $Y_{50}$ and benthic density sampled at night $B_n$. A linear function was therefore refitted to Elliott's original data, forcing the intercept through zero so that a benthic density of zero gave a drift density of zero ($Y_{50} = 0.1789 \pm 0.0046 B_n$ [mean $\pm$ 95% confidence limit], $n = 365$, adj. $r^2 = 0.753$; Elliott pers. comm.). Simply dividing $a_n$ by 50 rescales it for 1 m$^3$ of water. Estimation of $a_n$ in this way allows us to calculate $P$, the proportion of time spent in the water column using the formulation $P = a_n \delta/(1 + a_n \delta)$ where $\delta$ is depth of the water column (m, see Web Appendix 1). Hence, we can estimate $P$ as $3.577 \times 10^{-4}$ for Elliott's mean water depth of 0.1 m.

We now consider the intergeneration time $T_{gen}$ (hatching to first reproductive episode) for *G. pulex*, which is around 180 d at 10°C (Hynes 1955; Welton and Clarke 1980), or $15.5 \times 10^6$ s. The product of $T_{gen}$ and $P$ is the total time spent in the water column during time $T_{gen}$, and in this case the parameter $T_{drift}$ is on the order of 5,560 s. Our next step is to calculate the number of drift events during the period $T_{gen}$, for which we require an estimate of $\bar{t}$, the mean time spent in the water column during a single drift event. At Bellman Ground Beck $\bar{t}$ did vary with water velocity, but variation in $\bar{t}$ within the range of velocities examined ($u = $ 0.03 to 0.96 ms$^{-1}$) was only of the order 0.8 s, with $\bar{t}$ equal to $8.0 \pm 0.96$ s (Elliott 2002*b*), and as such we consider $\bar{t}$ to be a constant for this system. As no mean water velocity is available for this system, we assume the values for $u$, $\bar{d}$, and $\bar{t}$ from 12 May 1966 to be representative of typical velocities in the system (Elliott pers. comm). Thus, $N_{drift}$ can be estimated as 695, or somewhere in the region of four drift events per day (24 h). The end result of the preceding calculations is that we can estimate a value for the total downstream displacement of individuals in the population, $D_{gen}$, which is on the order of 1,560 m for a mean stream velocity of 0.281 m s$^{-1}$. Thus, for the population under consideration, the average distance traveled downstream in the drift is just over 1.5 km.

With some confidence we can assume that all *G. pulex* females produce young with a 50 : 50 sex ratio that is maintained at all times in the population (Welton 1979) for our calculation of the probability of mortality associated with drifting. If, as noted above, we also assume that females produce all of their theoretical maximum of 10 broods (Welton and Clarke 1980) of mean 16 young (range 1–43, Hynes 1955) in one short reproductive episode, then an individual might only be expected to produce ~160 (maximum 430) offspring in her lifetime. Since the mortality estimate is an inverse function of female reproductive output (Eqs. 10–12), we take $n$ to be 500, so that our estimates reflect an upper bound for the probability of mortality associated with drifting. From this we can see that the probability of survival during the period $T_{gen}$ is 0.004, and that the probability of survival for a single drift event during this period is 0.992. Thus, our assumptions mean that the overall probability of death is relatively high (1 in every 250 individuals survive), whereas for an individual drift event the probability of mortality is 0.008. Thus, if the risk of mortality during a single drift event were higher than 1 in 125, then the population would decline, even if females were (optimistically) able to produce 500 offspring and there were no other sources of mortality other than when drifting. Because we use an optimistic set of assumptions regarding reproductive output in *G. pulex,* this value is likely to be an overestimate of the true risk of mortality associated with entering the water column. Hence, we speculate that, for *G. pulex* at least, individual drift events are relatively safe, with death occurring at most only eight times in every thousand events. The high mortality associated with drifting is thus not a reflection of the high risk of individual events, but rather the cumulative risk of many (intrinsically low risk) events.

*Caveats*—Our estimation of $P$ is based upon an estimate of the regression slope parameter $a$ (see Web Appendix 1), and hence assumes that the total population from which drifting animals originated can be accurately determined. Using the data we rely on for our parameterization, Elliott (2002*b*) examined the influence of spatial scale of benthic density estimates by applying a weighted averaging method to benthic density according to discharge (which was proportional to velocity) to predict drift densities. He showed that this method failed to improve the fit of the original model that estimated drift density using benthic densities from samples taken from the entire stream section, although estimated drift losses to the local population more than doubled to between 4% and 10% of the estimated benthic density.

Despite the lack of scale effects in this system, it is still useful to estimate the effect of errors in our estimates of benthic densities on model predictions. Because errors in $a$ are additive (Harper and Weaire 1985), variation in our estimates of this parameter can be directly translated into estimates of the variation in our predictions for total downstream displacement and the probability of mortality associated with a single drift event. The procedure for this is simple, but does vary with the method used to estimate $P$. For estimates using $a_d$ the error associated with $D_{gen}$ or $P$(mortality) is simply $a_d$ error as a proportion of $a_d$, multiplied by the relevant variable. For estimates using $a_n$ the error associated with $D_{gen}$ or $P$(mortality) is twice the proportional error of $a_n$. Figure 1 illustrates the variation associated with $D_{gen}$ and $P$(mortality) when we consider the variation associated with our estimate of $a_n$. In this case we have taken the 95% confidence limits for $a_n$ and translated them into the errors associated with our estimate of $D_{gen}$ and $P$(mortality). Thus, the errors associated with $D_{gen}$ are $D_{gen} \pm D_{gen}(2[a_n/\Delta a])$. Although we have used the errors associated with our estimate of $a_n$, the direct translation of errors in estimating 'true' benthic density to errors in predictions means that their influence on any conclusions can be examined relatively easily. As a guide, we recommend that both benthic densities and drift are sampled throughout the stream section of interest, and spatial variation in these estimates quantified. If this spatially separate benthic sampled densities differ significantly, then specific $a$ values should be derived from weighting benthic densities upstream from the drift sampler, dependent on velocity to determine extent of upstream contribution (Elliott 1983; Elliott 2002*a*).

It should also be noted that there are several assumptions underlying our calculations that have particular bearing on the use of this method for other taxa. First, we ignore displacement during the egg stage, a phenomenon that has received little attention in the literature. In the case of taxa such as *Gammarus* where eggs are brooded by the female (Gledhill et al. 1993), or where egg masses are attached to the substratum, this may make little difference to the estimated displacement distances. However, this is unlikely to be the case in groups where eggs are simply released into the water, for instance in common mayfly species such as *Ephemerella ignita* and *Rhithrogena semicolorata* (Elliott and Humpesch 1983). Second, although the mesh aperture size used by Elliott (2002*a*) was 0.265 mm and so is likely
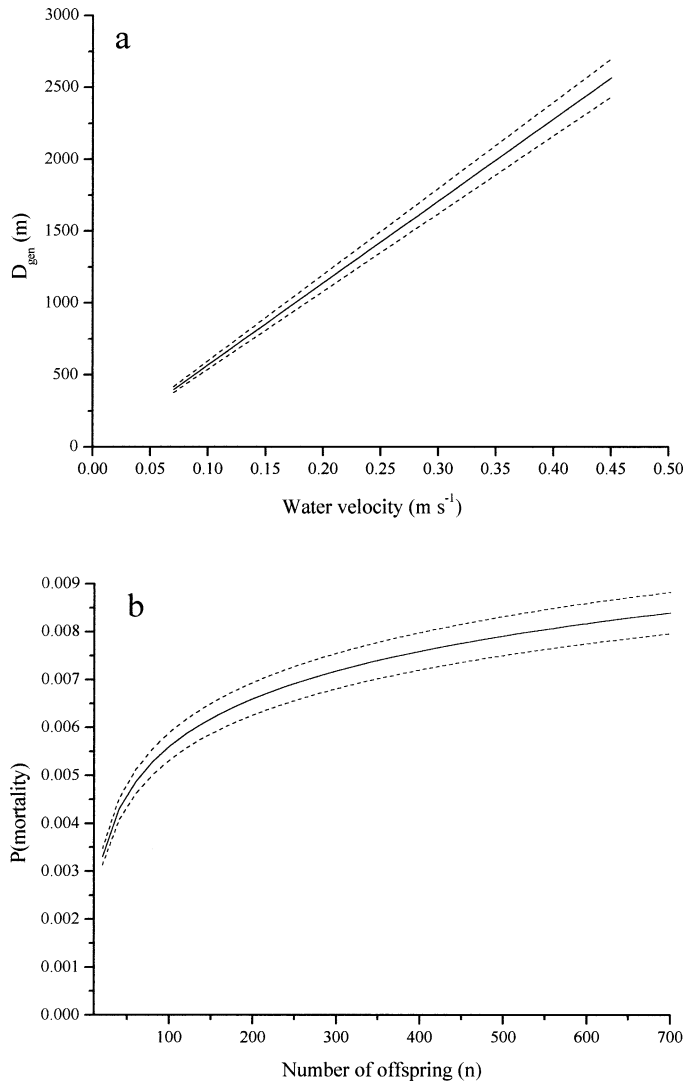
Fig. 1. (a) Estimated cumulative downstream drift distances and (b) probability of mortality associated with one drift event for *Gammarus pulex*. Both estimates are based on a generation time of 180 d. Downstream displacement is plotted as a function of water velocity (in the range over which time in the water column per drift event is constant). The probability of mortality per drift event is plotted against the total number of offspring produced by each female in the population. Broken lines indicate the error associated with the predictions (based on 95% confidence limits of $a_n$).

to have sampled all size classes of *G. pulex*, size data were not recorded and our calculations were not elaborated to incorporate size-related changes in drift distance through ontogeny as found by Allan and Feifarek (1989), although this would certainly be possible, given adequate data. Third, although drift densities for *G. pulex* are not temperature dependent (Elliott 2002*a*), time to maturity in females is (Welton and Clarke 1980), and so the specific displacement will depend on the local temperature of the system under study. For instance, using Welton and Clarke's formulae, females would mature in ~441 d at 5°C and 156 d at 15°C. Using our methods, this gives a range of 3.8–1.4 km for total downstream displacement, and a maximum probability of

mortality during a single drift of 0.0032–0.0091. The relevance of these values is difficult to interpret when we consider the likelihood of a temperate stream holding temperature for over a year at 5°C. Nonetheless, they do suggest the possibility of seasonal or latitudinal changes in the magnitude of lifetime dispersal for species such as *G. pulex*. Finally, our calculations ignore spatial and temporal habitat heterogeneity, by applying our estimates over the whole of the streambed for the entire 180 days. However, mean time in the drift and drift distance appear robust to both seasonal and diel variations in stream parameters (Elliott 1971; Elliott 2002*c*).

## Discussion

If we are to understand the dispersal and subsequent population dynamics of animals living in lotic systems we need to be able to quantify more than the simple net displacement of individuals and populations. The method presented here adds another means of addressing the contribution of downstream transport to net displacement. Although we discuss above some limitations regarding the applicability of this study to other species, we do not in principle see any real obstacles to the implementation of similar calculations as suitable data become available.

The accuracy of our estimates is difficult to judge because of the lack of information on total downstream displacement as opposed to net downstream displacement. The difficulty involved in obtaining estimates of these parameters should not be underestimated, as the effort involved in obtaining the continuous, year-long data set and the large body of drift distance data on which we base our estimates illustrates. As a first approximation, we can compare our estimate of total downstream displacement with a minimum net downstream transport estimate of 2.1 km, on the basis of stable isotope tracers, for the mayfly genus *Baetis* (an equally drift-prone species) in an Alaskan river (Hershey et al. 1993). The figure compares relatively well with our estimate of 1.5 km for total downstream displacement in *G. pulex*, but there are severe limitations to the comparison. Our estimate is for 180 rather than 30 d, and we assume lower velocities in the system, but the main issue is that Hershey et al.'s (1993) figure is for net downstream displacement, which includes possible upstream movements.

To present a simple model that makes the most of current data, but does not overplay our still-incomplete understanding of the processes involved, our calculations have been concerned solely with means. A more powerful approach would be one that acknowledged that all of our parameters would more suitably be described by distributions rather than single values. Equally as importantly, we would expect a correlation structure between some of those distributions; for example, it may be that individuals who have a trend toward shorter displacements in individual drift events also have a trend toward higher rates of drifting. However, there is no evidence to support or refute any such correlations and at present we do not have a sufficiently detailed study of any system to allow such a more complicated model to be plausibly presented. Until such data become available, our

results must be considered as tentative, since one could plausibly construct scenarios where our simple mean-field model gives quite different predictions to a more complex individual-based model.

We explicitly assume that the population we consider is at equilibrium within our system. However, we expect that this is only an approximation to reality and that the appropriate scale at which such an equilibrium can be justified may well be smaller than that of the catchment. More importantly, some systems will exhibit migration between populations, a scenario particularly likely for species with aerial adult stages (e.g., Ephemeroptera, Plecoptera, Trichoptera), but still with some relevance for purely aquatic species such as *Gammarus*. Within a collection of linked subpopulations there are likely to be some that are net sources, and others that are net sinks. The survival of subpopulations within these habitats will not be determined solely by the arguments put forward in this paper, but rather will require migration from other subpopulations (Speirs and Gurney 2001; Humphries and Ruxton 2002). We would also expect that even within a closed system, population dynamic effects or environmental fluctuations will drive temporal variation in population numbers. For these two reasons our assumption of equilibrium population conditions must be viewed as an approximation, the accuracy of which will vary from system to system and can only be resolved by long-term monitoring of populations at large scales.

It is often argued that it is the few individuals that travel long distances that are likely to be most important to population processes (Palmer et al. 1996; Turchin 1998; Nathan and Muller-Landau 2000; Nathan 2001). However, on the basis of our results for *G. pulex*, we suggest that the situation for invertebrate drift may be slightly different. Our results suggest that, unlike studies into dispersal of propagules or reproductive-age individuals searching for mates where there is one major dispersal event, benthic invertebrates in streams and rivers might experience hundreds of dispersal events in their lifetime. This difference is also illustrated by comparison of our mortality estimates for *G. pulex* with data for mortality during dispersal of aphids. Ward et al. (1998) estimated mortality for bird cherry-oat aphids (*Rhopalosiphum padi*) in Scotland, which disperse once during their lifetime, at 99.4%. Our assumption for total mortality is in accordance with this figure, but individual dispersal events for *G. pulex* are much less risky, with mortality estimated at no more than 0.8%.

In addition, although individual drift distances can vary greatly (McLay 1970; Elliott 1971; Larkin and McKone 1985; Allan and Feifarek 1989; Lancaster et al. 1996), we might justifiably assume that turbulence and streambed heterogeneity mean that the distance traveled by an individual during one drift event is independent of that traveled by the same individual in any other. If this is the case, then we might expect that the variance in downstream displacement distance of the animals drifting from a local section of stream will be relatively small. That is, even though individual drift events show great variance, the sum of these drift distances may well be a relatively narrow distribution. If this is the case, then the mean of this total displacement should be a parameter of high ecological relevance. This

contrasts with organisms (like the aphids discussed above) that have only one dispersal event in a lifetime, where the mean dispersal distance may be a very poor representation of the distribution of individual distances (Andersen 1991; Nathan and Muller-Landau 2000). Students of organisms that disperse only once must thus face the challenge of quantifying dispersal distance for the (ecologically very important) few individuals in the tail of the distribution that move a much greater distance than the mean (Nathan 2001). Here we argue that this should be much less of a concern for those like ourselves studying invertebrate drift, where individual organisms experience many dispersal events during their life.

Our low mortality estimate for single drift events of *G. pulex* suggests that actively entering the drift is likely to be adaptive in a number of situations, from life-or-death situations such as avoidance of benthic predators (Dahl and Greenberg 1996; Lima 1998) to simple patch-search behaviors (Bohle 1978; Kohler 1984, 1985). Thus, on a short-term level, we can explain the use of drift for predator escape and foraging, but we also suggest that a long-term perspective allows for an explanation of diel variations in drift related to avoidance of drift-feeding fish (Flecker 1992; Forrester 1994) and adaptations to minimize accidental dislodgement from the streambed. Somewhat paradoxically, the risk to an individual that enters the drift is low, but the sheer number of drift events during an individual's lifetime means that drifting may present the majority of mortality in a population of benthic animals. The generality of this statement remains to be demonstrated by results from other drifting species; however, we contend that individual drift events may not be particularly dangerous, but that the cumulative effects mean that very few individuals are likely to survive to maturity.

This last point suggests a further possibility. Our mortality estimates assume that drift is a random process with respect to individual animals; however, drift could be selective. For instance, if parasitized or weakened individuals are inherently more likely to enter the drift (as suggested by Wilzbach et al. 1988; but see also Vance 1996), there is the possibility that the cumulative risks associated with large numbers of drift events continuously remove such individuals from the population. However, if these individuals are relatively uncommon in the general population, drift-net samples may not reveal any bias in the number of these individuals in the drift.

Our assumption of population equilibrium also extends to the case where mortality sources other than drift exist (e.g., benthic predators). In this scenario $P(\text{survival}_{T_{gen}})$ will be greater for drift events than that estimated without benthic mortality. Consequently, if $P(\text{survival}_{T_{gen}})$ is greater than expected, then $P(\text{mortality})$ will be less than expected. Therefore, benthic predation, loss of young instars, or eggs, are unlikely to increase our estimate of per-drift mortality and our original assumption gives, as we originally suggested, a conservative maximum estimate for the risk of mortality associated with a single drift event.

The estimates presented here represent a first step toward accurate values for the total downstream displacement likely to be experienced by a particular taxon of benthic macroinvertebrate. We have been unable to find other data sets that include all of the relevant data needed to calculate down-

stream displacement for other species, but with suitable data, and testing of assumptions, the methods used here can be applied easily. However, the generality of this model is still unclear and we thus hope that this work will encourage others to examine total downstream displacement in other groups.

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