

Exact compensation of stream drift as an evolutionarily stable strategy

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The colonization cycle hypothesis predicts that adults of stream-dwelling insects preferentially disperse in the upstream direction in order to compensate for larval drift. Upstream biased dispersal has indeed been shown in many, albeit not all, natural populations. Based on a recently published analysis, we develop a simple stochastic model for the competition of genotypes with different dispersal strategies in a stream habitat. By means of an invasion analysis, we show that exact compensation of larval drift by upstream biased adult dispersal is an evolutionarily stable strategy. Exact compensation means that, on average, the net movement of individuals from birth to the time of reproduction is zero. At the population level, we show that, in general, upstream biased dispersal is not necessary for persistence, unless the reproductive rate is very low. Under all conditions, however, populations of exact compensators attain highest sizes or persistence times, respectively. Although selection pressure towards exact compensation is arguably very general in populations subject to stream drift, trade-offs or constraints might change the outcome of selection. Therefore, the analysis presented in this paper has to be viewed as a null model for optimal dispersal behavior in stream habitats.

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Drift is a characteristic determinant in the ecology of lotic invertebrates (reviewed by Waters 1972, Brittain and Eikeland 1988). Stream ecologists have long discussed the need for some mechanism to compensate for drift-induced downstream displacement. The persistence of upstream populations despite continuous drift has particularly intrigued investigators and recently has been termed the “stream drift paradox” (Hershey et al. 1993, Williams and Williams 1993, Anholt 1995). Almost half a century ago, Müller (1954) proposed that adults of amphibiotic insects fly upstream for oviposition and thereby compensate for the downstream displacement of their larvae in a process termed the “colonization cycle”. Subsequently, upstream movements of aquatic stages have been suggested as an additional drift-compensating mechanism (e.g. Schuhmacher 1969, 1970), especially for holoaquatic organ-

isms lacking an aerial stage (Minckley 1964, Meijering 1974, Williams and Moore 1982). Field research in the last four decades has yielded numerous examples of upstream biased adult dispersal (e.g. Roos 1957, Schwarz 1970, Madsen et al. 1973, Svensson 1974, Light and Adler 1983, Zwick 1990, Hershey et al. 1993; for review see Müller 1982) or active upstream movement under water (e.g. Minckley 1964, Bishop and Hynes 1969a, Elliott 1971a, Bird and Hynes 1981a, Bergy and Ward 1989; for review see Söderström 1987). In other cases, however, no compensatory behavior could be found (e.g. Elliott 1967, Bishop and Hynes 1969b, Schuhmacher 1970, Bird and Hynes 1981b, Williams and Williams 1993).

When discussing the “stream drift paradox”, one must distinguish between the evolution of individual behavior and its consequences at the population level.

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Some confusion has arisen because this distinction has not always clearly been made in the past. For example, by mixing up the two perspectives, some of the older literature (e.g. Pearson and Kramer 1972, Neves 1979) implicitly evokes group selection arguments (Anholt 1995). Essentially, however, most of the discussion following Müller (1954) has focused on the population consequences of drift and drift compensation (losses due to drift). In this context, several workers have pointed out that no upstream bias in adult dispersal is necessary for maintaining populations when fecundity is high (Brittain and Eikeland 1988, Wilzbach and Cummins 1989, Allan 1995) or when reproduction or drift are locally density dependent (Waters 1961, 1972, 1981, Allan 1995). The viability of randomly dispersing populations has recently been confirmed theoretically by Anholt (1995) and Speirs and Gurney (in press). From an evolutionary point of view, however, optimal dispersal behavior has to be analyzed from an individual perspective. Selective advantages for upstream dispersing individuals have occasionally been suggested (e.g. Otto and Svensson 1976, Light and Adler 1983, Allan 1995). In Anholt's (1995) simulation study genotypes with upstream biased dispersal drove randomly dispersing competitors to extinction.

In the present paper, we aim to further develop the theory on dispersal behavior in lotic systems by focusing on the mean net movements of animals along the stream. Using the framework developed by Anholt (1995), we conduct an invasion analysis in order to determine the evolutionarily stable dispersal strategy (i.e. the optimal upstream bias). Inspired by Müller's (1954) original idea, we have been led to the hypothesis that, on average, individuals should *exactly* compensate for drift by upstream biased dispersal. That is, the mean net movement of individuals from birth to the time of reproduction should be zero. We thereby quantify and formalize previously verbal arguments on drift compensation. Further, we explore the consequences of drift compensation behavior for the persistence of populations.

The model outline

For our analysis, we implemented a model similar to Anholt's (1995), but with some slight modifications. We use an individual-based, discrete-time stochastic approach for simulating the dynamics of an isolated insect population with aquatic larvae along a stream which we assume to be subdivided into a series of identical reaches. The population is either genetically homogeneous or consists of two competing genotypes that differ in the degree of upstream bias during dispersal. In each generation, the population undergoes

the successive steps of larval drift, adult dispersal flight (which may be upstream biased), oviposition and locally density dependent population regulation. The latter is assumed to be operating among the larvae within the reaches of their birth before the next drifting event. In the whole paper, dispersal will be used as a synonym for adult flight. Individuals drifting or flying beyond the boundaries of the stream are assumed to be lost from the population. The simulation is carried on until the population or one genotype has gone extinct or until a maximum number of generations is reached. Unlike Anholt (1995), we do not finish simulations when the population size is reduced to one half because we found that for certain parameter combinations, especially for high drift and dispersal probabilities, stable populations can exist far below this threshold (simulations not shown).

In the following, the number of reaches will be denoted by Z . Each reach is assumed to have a constant carrying capacity K . In the beginning of the simulation, all reaches are uniformly filled up to their carrying capacity. Drift and flight are modeled for each individual separately as successive reach-wise steps of movement with fixed probabilities D and F (for drift and flight, respectively). Therefore, the probability of drifting exactly one reach is $D(1-D)$ and the general probability of drifting n reaches is $D^n(1-D)$. This is equivalent to drawing the final number of reaches traversed by a drifting individual from a geometric distribution (McLay 1970, Elliott 1971b) with mean $D/(1-D)$. Dispersal flight is handled analogously. Active upstream movement by larvae is not included explicitly. However, drift in the model may be viewed as representing the net effect of all under water movements. The direction of flight is determined stochastically once per individual by means of the variable B that specifies the probability of flying upstream (so $B > 0.5$ implies an upstream bias and $B < 0.5$ a downstream bias).

The expected number of offspring P_{n+1} in a reach with P_n individuals (in the case of competing genotypes this is the sum of the individuals of both genotypes within the reach) is calculated by using the following difference equation (see Gabriel and Bürger 1992):

$$P_{n+1} = e^r P_n (1 + a P_n)^{-\beta} \quad \text{with} \quad a = \frac{e^{r/\beta} - 1}{K}, \quad (1)$$

where r denotes the population's intrinsic growth rate and β measures the strength of density dependence. We only analyze the case $\beta = 1$ which is a discrete form of logistic growth. The actual number of offspring is then drawn from a Poisson distribution with the mean value obtained from eq. (1).

Derivation of a formula for exact compensation

The conditions for exact compensation of larval drift by adult dispersal can easily be calculated if edge effects are neglected and an infinitely long stream is considered. Indeed, this approach should be valid for all systems unless the number of reaches is very small. Drift causes on average a downstream displacement of $D/(1-D)$ reaches; flight adds on average $(1-B)F/(1-F)$ to downstream and $BF/(1-F)$ to upstream movements. Exact compensation means that, on average, downstream and upstream movements are balanced. (Of course, stochasticity will cause variation in the actual degree of compensation.) Therefore, the condition for exact compensation is

$$\frac{D}{1-D} + (1-B)\frac{F}{1-F} = B\frac{F}{1-F}.$$

Assuming $D < 1$ and $F < 1$ and solving for B yields B^* , the probability of upstream flight leading to exact compensation for given values of F and D :

$$B^* = \frac{1}{2} + \frac{D(1-F)}{2F(1-D)}. \quad (2)$$

The second term of eq. (2) represents the amount of upstream bias. B^* is always between 0.5 and 1. Unbiased dispersal ($B^* = 0.5$) occurs only when $D = 0$; in this case there is no drift to be compensated for. Whenever there is a positive drift probability, compensation requires upstream biased dispersal ($D > 0$ implies $B^* > 0.5$). If there is as much drift as dispersal, then all dispersal has to be in the upstream direction ($D = F$ implies $B^* = 1$; for $D > F$ eq. (2) yields $B^* > 1$; however, because B is a probability, the best strategy in this case is also $B^* = 1$). B^* can be reduced by either increasing the flight probability F or decreasing the drift probability D . In both cases, B^* approaches 0.5 for $D \rightarrow 0$ or $F \rightarrow 1$. In the following, $B = B^*$ will be referred to as exact compensation, $B < B^*$ as undercompensation, and $B > B^*$ as overcompensation.

Invasion analysis with competing genotypes – finding the evolutionarily stable upstream bias

To test whether exact compensation can evolve under natural conditions, we carried out an invasion analysis with competing genotypes. The ability of the exactly compensating genotype to either invade an established population or to resist invasion by other genotypes was determined in simulations where it initially occupied either 10% or 90% of the carrying capacity of each reach. We measured the proportion out of 1000 replica-

tions in which the exact compensator drove its competitor to extinction (i.e. its fixation probability). Simulations were performed with all possible competitors (their upstream biases B lying between 0.0 and 1.0 in steps of 0.1) under all combinations of drift and dispersal probability (D and F ranging from 0.1 to 0.9 in steps of 0.1). The fixation probability of the exact compensator was always higher than its initial proportion of the total population. (Slight deviations occurred only at very high values of D and F , probably due to the order of events in the simulation.) The results were unchanged when dispersing individuals were prevented from leaving the stream. Indeed, this setting did not prevent losses due to flight because dispersing individuals piled up near the boundaries where they were reduced by density dependent regulation. In summary, exact compensation of drift by upstream biased flight has to be considered as an evolutionarily stable dispersal strategy.

Figure 1 demonstrates the invasion of a resident population by the exactly compensating genotype. In Fig. 1a, the resident has an upstream bias below the optimal value. The invader first occupies the upstream end of the stream and from there successively spreads over all reaches. If, on the other hand, the upstream bias of the resident is too high, the invader first becomes dominant at the downstream end and starts its occupation of the whole stream from there (Fig. 1b). Hence, overcompensation of drift is as detrimental for the fitness of a genotype as is undercompensation.

Figure 1 highlights the importance of keeping, on average, a constant position in the stream, which is the intuitive idea behind the colonization cycle hypothesis. The resident population in Fig. 1a does not compensate for drift during its dispersal flight and therefore has an inherent tendency to shift towards the downstream direction. In the absence of competing genotypes the resident genotype could in general make up for this shift by enhanced reproduction in the upstream reaches (see below). However, this possibility does not exist in the presence of an exactly compensating invader with the same reproductive potential (the same intrinsic growth rate r) who reoccupies these reaches already before the reproductive step. In this case, the invader successively takes over the reaches of the stream which are not completely recolonized by the resident after drift. Consequently, the latter is gradually displaced from the system (analogous for Fig. 1b).

The influence of drift compensation on population persistence

The question of how stream invertebrate populations persist in spite of drift originally led Müller (1954) to the formulation of the colonization cycle hypothesis. In

order to test whether compensation of drift by upstream biased dispersal is able to reduce extinction risk, we calculated the amount of upstream bias that maximizes the number of generations before the population dies out. Figure 2a shows the optimal probability for upstream flight in terms of population persistence in dependence on dispersal probability F , and compares it with the exactly compensating value B^* predicted by eq. (2). For each simulated data point, the number of generations before extinction was determined for all B s between 0 and 1 in steps of 0.1 in order to find the value of B yielding the highest persistence time. This procedure was then repeated 100 times and the final optimal B calculated as the mean of the optimal B s from these 100 replications. The high degree of agreement between the two curves clearly demonstrates that

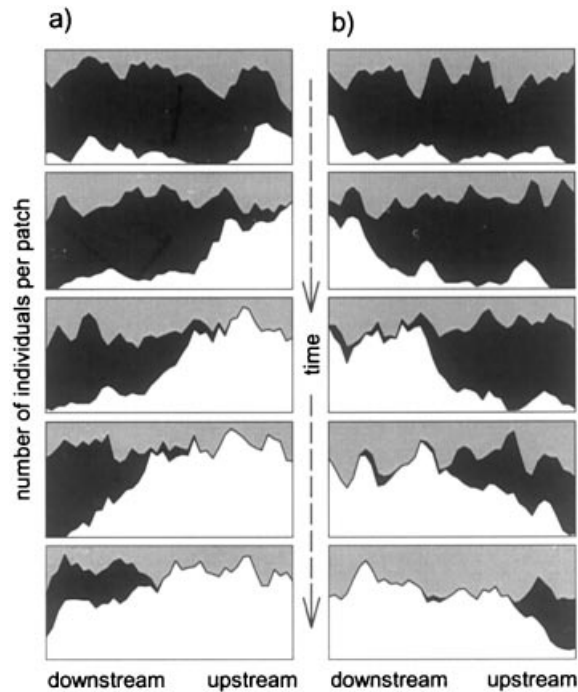


Fig. 1. Invasion and competitive exclusion of an established population by the exactly compensating genotype. The graphs show the distribution of residents (black) and invaders (white) along the stream at various times during the invasion process. At the beginning of each simulation the invader occupied 10% of the carrying capacity of each reach. In a) the upstream bias of the resident is too low and it is therefore gradually displaced from the system via the downstream end ($D = 0.3$, $F = 0.4$, $B_{\text{resident}} = 0.5$, $B_{\text{invader}} = B^* = 0.82$; graphs show the populations after the reproductive step in generations 43, 64, 94, 115, and 141; the invader was fixed after 209 generations). In b) the resident has a too high upstream bias and shifts out through the upstream end ($D = 0.1$, $F = 0.4$, $B_{\text{resident}} = 0.9$, $B_{\text{invader}} = B^* = 0.58$; populations shown after the reproductive step in generations 16, 63, 95, 125, and 154; the invader became fixed in generation 202). Common parameters: $r = 1.0$, $\beta = 1$, $Z = 40$, $K = 20$. Plots were slightly smoothed by calculating for each reach the mean population sizes of itself and the two adjacent reaches. The length of the vertical axes is $25 = K \cdot 1.25$.

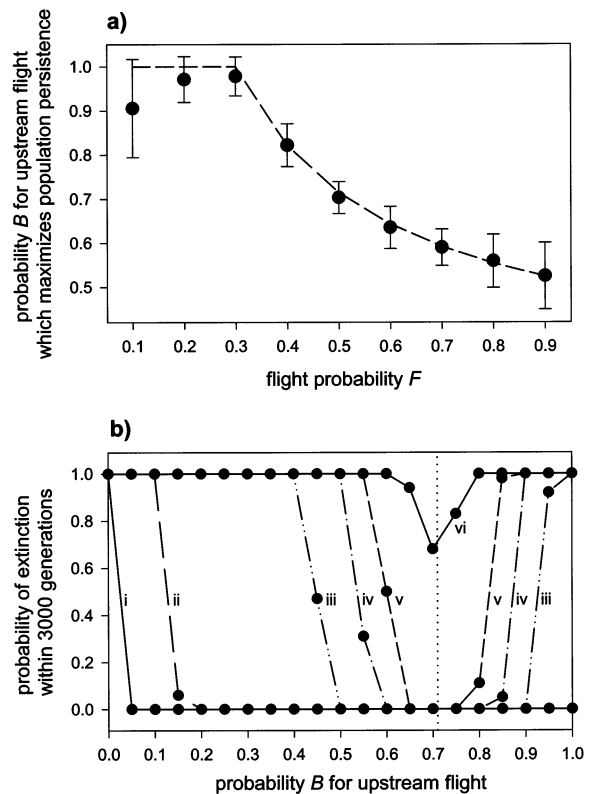


Fig. 2. Exactly compensating upstream biased dispersal maximizes the persistence of genetically uniform populations. a) The probability of upstream dispersal B ($B > 0.5$: upstream bias; $B < 0.5$: downstream bias) which maximizes population persistence plotted against dispersal probability F . Circles represent means \pm standard deviations of these optimal B s obtained from 100 simulation runs each (see text). The dashed line denotes the probabilities of upstream flight leading to exact compensation of drift according to eq. (2). The good agreement between the two plots indicates that exact compensation maximizes population persistence. Parameters: $D = 0.3$, $r = 0.01$, $\beta = 1$, $Z = 100$, $K = 10$. b) Probability of extinction of a single population within 3000 generations plotted against probability B of flying upstream for different intrinsic growth rates r . (i) $r = 1.0$, (ii) $r = 0.5$, (iii) $r = 0.1$, (iv) $r = 0.05$, (v) $r = 0.03$, (vi) $r = 0.01$. The plots center around the exactly compensating probability of upstream flight derived from eq. (2) ($B^* = 0.71$, dotted line) which minimizes extinction risk. Parameters: $D = 0.3$, $F = 0.5$, $\beta = 1$, $Z = 100$, $K = 10$.

exactly compensating upstream biased dispersal maximizes population persistence.

Of course, persistence is also influenced by the population's intrinsic growth rate r . As shown in Fig. 2b, for each value of r exact compensation yields the highest persistence. However, the smaller r is, the smaller becomes the range of strategies around B^* that still prevent extinction. Hence, if the expected number of offspring is made sufficiently large, extinction risk within several thousand generations always becomes negligible in a wide area of parameter space. For larger values of r , a comparison of population sizes after a fixed number of generations (instead of persistence

times) leads to results similar to those shown in Fig. 2a. Thus, exact compensation also maximizes population size. Indeed, there is no fundamental difference between these two criteria: further simulations showed that strategies leading to high densities when r is large also yield long persistence times when r is small.

In summary, we agree with Anholt (1995) that locally density dependent reproduction can contribute to the compensation of drift. However, even genetically homogeneous populations do best with exact compensation by upstream biased dispersal (see Fig. 2b). If the intrinsic growth rate r is small (e.g. under high predation pressure) an upstream bias can actually become necessary for population persistence. In this case, the potential for compensating drift by reproduction is low, whereas upstream biased dispersal works identically in all cases and is an additional source of drift compensation even for high r .

In our simulations, exactly compensating populations attained roughly symmetrical frequency distributions along the stream. In contrast, the distributions of under- or overcompensating populations were heavily biased towards the downstream or upstream end, respectively. This might be an explanation for the high persistence times of exact compensators. Intuitively, populations centered around the middle of the stream should do better than those concentrated near the boundaries, where the risk of drifting or flying out of the system is high.

Discussion

In the present paper, we analyze a simple model for the competition of adult dispersal strategies in a population of stream invertebrates subject to drift and local density dependence. Although the concept of compensation is as old as drift research itself, to our knowledge this idea has never been quantified before. Here, we show that *exact* compensation for drift via upstream biased dispersal is an evolutionarily stable strategy: if there is genetic variability for dispersal behavior, non-compensating genotypes will be gradually displaced by exactly compensating invaders that are able to maintain a stable distribution along the stream (Fig. 1). It is essential to recognize that “exact compensation” in this sense refers to the individual and not to the population level. More precisely, it designates the mean of stochastic individual dispersal behavior: the oviposition site of each female should, on average, coincide with its site of birth. This does not imply, however, that a reach of stream necessarily contains the same number of individuals after dispersal than it did before drift.

Yet, although a population of exact compensators may experience losses due to drift-induced (Wilzbach and Cummins 1989) or other mortality, it does not

change its mean position in the stream. Thereby, the individual strategy of exact compensation simultaneously maximizes the persistence and size of the whole population. In general, we confirm the view of previous workers (Waters 1961, 1972, 1981, Allan 1995, Anholt 1995) that upstream biased dispersal is not necessary for population persistence. However, we also show that, especially at low growth rates caused, for example, by high predation pressure, upstream biased dispersal may become indispensable for survival. Furthermore, we find that overcompensation for drift has the same negative consequences as undercompensation.

Overall, our results are in accordance with the colonization cycle hypothesis. However, our notion of exact compensation is more general than Müller's (1954) original concept: While the classical colonization cycle involves concentration of oviposition in upstream reaches and subsequent depletion of these reaches by drift, in our model both oviposition and emergence of adults may occur along the whole length of the stream. Furthermore, the prediction of exact compensation is independent of the effect drift has on the population as a whole: Several authors have questioned the need for drift compensation because upstream depletion has rarely been documented (e.g. Einsele 1960, Waters 1965, Elliott 1967, Brittain and Eikeland 1988; but see Otto and Svensson 1976, Neves 1979), drifting individuals were viewed as excess production above carrying capacity (Waters 1961, 1965, 1972, 1981), or because of the high fecundity of most stream invertebrates (e.g. Brittain and Eikeland 1988, Wilzbach and Cummins 1989, Allan 1995). However, while all this is true from the point of view of population persistence, our model predicts that individual selection should nevertheless favor exact compensation. In particular, it should be noted that the favored upstream bias B^* in eq. (2) is independent of the population growth rate r . Finally, although active upstream movement by larvae (or holoaquatic organisms) is not explicitly implemented in the model, we expect that the principle of exact compensation can be extended to this situation (see model outline section). The key point is that the average net sum of larval and adult movements is equal to zero. The details of the life cycle should be of minor importance.

The prediction of exact compensation is derived from a very simple model. It was obtained solely from analyzing the effects of individual movements (drift and dispersal) and local density dependence. Indeed, the basic idea is very simple and straightforward: Genotypes which do not compensate for drift during their dispersal flight will eventually be displaced from the system by exactly compensating invaders. Accordingly, we feel that the process shown in Fig. 1 is quite robust and general and probably operates in more complex situations as well. We believe, therefore, that selection pressure towards exact compensation is quite universal in benthic stream invertebrates.

However, the ecology of stream invertebrates is certainly much more complex than our simulations. For example, far from being a mere passive process, drift is influenced by a variety of biotic and abiotic factors, such as temperature, food supply, population density, or presence of predators (see review by Brittain and Eikeland 1988). The same is probably true for dispersal flight, although we are not aware of any data on this subject. Streams are not homogeneous habitats, but resources in them may be patchily distributed or exhibit longitudinal gradients. Real-life females might have the additional opportunity of dispersing to neighboring habitats (lateral dispersal). These and other factors might create additional selective forces which are not accounted for in our simulations. Since trade-offs or constraints can change the outcome of selection we do not claim that, in nature, exact compensation occurs in every population.

One can easily think of some factors which might lead to incomplete drift compensation. For example, upstream movement might be associated with costs. This appears to be most likely in holoaquatic organisms, such as gammarids (e.g. Minckley 1964, Meijering 1974, Williams and Moore 1982), isopods (Thomas 1969), snails (Schneider 1993) or waterstriders (Fairbairn 1985) which have to overcome the water current when moving upstream. In insects, the flight direction of weak fliers is sometimes determined mainly by the wind (Brindle 1957, Elliott 1967; but see Russev 1973 for a counterexample of a strong flier). Further, if there is high competition for oviposition sites (as indicated by Bunn and Hughes 1997, Hughes et al. 1998) individuals might tend to use the first suitable site they encounter regardless of the distance already traveled. Exact compensation might also be constrained by incomplete knowledge of drifting distances or by weak dispersal abilities. When dispersal occurs primarily between neighboring streams (lateral dispersal, e.g. Svensson 1974, Bunn and Hughes 1997, Hughes et al. 1998, Petersen et al. 1999), a key assumption of the model, the linearity and isolation of the habitat, is not fulfilled. When drift is associated with high mortality (Waters 1961, Wilzbach and Cummins 1989), the surviving individuals will be those that have drifted least. In this case, no conspicuous compensatory movements are to be expected.

As all the above-mentioned mechanisms might counteract selection for exact compensation, the analysis presented in this paper should be regarded as a *null model* for the optimal dispersal strategy. Nevertheless, it is probable that there is a very general selection pressure towards exact compensation in all populations subject to stream drift. In case of apparent lack of drift compensation in a study population it will be interesting to analyze the factors that are able to overpower this selection pressure.

Despite the large number of studies on drift and dispersal, the data available at present do not allow a definite statement about how often the prediction of our null model actually holds true. Most stream ecologists seem to agree that at the population level, drift compensation is at best partial. For example, Allan (1995) recently summarized: "... the admittedly provisional evidence [does not] support the claim that upstream movement by either aquatic or aerial stages is sufficient to compensate for the apparently great downstream displacement engendered by drift". However, the data leading to this view are not readily transferable to the question of individual behavior: For example, the literature on upstream movement of aquatic stages contains some data on "percentages of drift compensation" which usually lie far below 100% (e.g. 1.6–14.9% (Bishop and Hynes 1969a); 7–10% (Elliott 1971a); 50% (Meijering 1974); 2.1–15.2% (Bird and Hynes 1981a); 11% (Williams and Moore 1982); 8.2% (Benson and Pearson 1987)). However, these values simply represent the ratio of animals caught in the upstream and downstream side of a bidirectional trap and do not include drift-induced mortality (e.g. Wilzbach and Cummins 1989, see above) nor drifting distances. Therefore, while they provide information on the population losses caused by drift, they cannot be used to infer the movement patterns of the surviving individuals.

Exact compensation at the individual level is most clearly conceivable in situations resembling the "classical" colonization cycle according to Müller (1954) where oviposition is restricted to the upstream region of the stream and emergence mainly occurs downstream (Dorris and Copeland 1962, Elliott 1969, Schwarz 1970, Lauzon and Harper 1986). Similar patterns arise when migration between two different biotopes is part of the life cycle of the organism under study (Müller 1982 and references therein, Schneider 1993) or belongs to an overwintering strategy (Pearson and Kramer 1972, Mendl and Müller 1978, Müller 1982). Söderström (1987) argued that upstream movement might be selected for for reasons totally different from drift compensation, such as search for optimal pupation, emergence, or oviposition sites. However, whenever these sites are restricted to a small area of the total habitat, exact compensation will result as a quasi-automatic byproduct of this behavior.

When oviposition is not restricted to particular reaches of the stream the pattern is much less clear. Indeed, for this general case, quantitative evidence on the degree of compensation is very limited. The greatest body of literature consists of studies which have merely looked for the presence or absence of some preference for upstream movement. Allan (1995) summarized these efforts by stating that "supporting evidence exists for the colonization cycle, especially that egg-bearing females often fly upstream... However, upstream flight does not seem to be universal". Indeed, empirical

studies on the direction of dispersal have revealed many examples of upstream biased dispersal. Various methods have been applied: direct observations (Russev 1959, 1973, Madsen et al. 1973, and further references therein), bidirectional traps (Roos 1957, Waters 1968, Göthberg 1972, Madsen et al. 1973, Müller 1973, Svensson 1974, Madsen and Butz 1976, Madsen et al. 1977, Neves 1979, Bird and Hynes 1981b, Müller 1982, Solem and Bongert 1986, Dudgeon 1988, Flecker and Allan 1988), mark-recapture experiments (Nishimura 1967, Madsen and Butz 1976), and observation of overrepresentation of mature females in upstream reaches (Lehmann 1970, Madsen and Butz 1976, Lavandier 1982, Zwick 1990). Active upstream movement by larvae of amphibiotic insects has also been found in several studies (e.g. Bishop and Hynes 1969a, Elliott 1971a, Bird and Hynes 1981a; reviewed by Söderström 1987 and Allan 1995 with further references therein). Frequently, the strongest upstream bias is found among egg-bearing females (e.g. Roos 1957, Madsen et al. 1973, Bird and Hynes 1981b) or the last larval instars (e.g. Hultin et al. 1969, Mendl and Müller 1978). Active upstream movement by holoaquatic organisms has been reviewed by Söderström (1987, see references therein). On the other hand, there are also numerous cases where no compensatory behavior has been found (Einsele 1960, Elliott 1967, Bishop and Hynes 1969b, Waters 1969, Hynes 1970, Schuhmacher 1970, Bishop 1973, Madsen et al. 1973, Müller 1973, 1974, Svensson 1974, Bird and Hynes 1981b, Dudgeon 1988, Flecker and Allan 1988, Jones and Resh 1988, Zwick 1990, Williams and Williams 1993). Some authors have interpreted upstream movement under water as simple random movement (Bird and Hynes 1981a, Bergey and Ward 1989 with further references).

However, the information content of these data regarding individual drift compensation is limited: a positive preference for upstream dispersal clearly shows that some compensation is taking place. Yet, it does not by itself indicate the precise degree of compensation. The cases with unbiased dispersal are even more difficult to interpret. Some of them probably represent situations where selection for upstream dispersal is overridden by trade-offs or constraints (e.g. in weak fliers which cannot fly against the wind; Brindle 1957, see above, Elliott 1967). However, one also has to bear in mind that according to our model exact compensation does not necessarily result in spectacular upstream movements: When drift (i.e. the parameter D) is negligibly small (e.g. for caddisflies with stone cases; Hughes et al. 1998, Jackson et al. 1999), or when dispersal distances (i.e. the parameter F) are large, eq. (2) predicts the probability for upstream dispersal to be near 0.5. Then the upstream bias is probably not detectable. Unfortunately, in most studies the data provided are still insufficient to distinguish between these alternative hypotheses.

Some studies provide evidence for positive correlations between the strength of drift and the amount of upstream dispersal (e.g. Light and Adler 1983). Williams and Williams (1993) found a similar correlation between drift and upstream movement under water. Minckley (1964) reported mass upstream migrations of *Gammarus bousfieldi* taking place after catastrophic drift events. Several authors have discussed that species without upstream biased dispersal are less prone to drift (Madsen et al. 1973, Müller 1973, Svensson 1974, Flecker and Allan 1988). These findings indicate that drift compensation is indeed among the ultimate causes of upstream dispersal.

Very few data exist on the absolute distances traveled by an individual during its life-time. The literature contains a few (rough and greatly diverging) estimates of the distances covered by drift (Russev 1973, Hemsworth and Brooker 1979, Neves 1979, Benson and Pearson 1987, Jackson et al. 1999), upstream movement (see references in Bird and Hynes 1981a), and flight (Zwick 1990 and references therein). Allan (1995) states that in the case of drift "... total distances traveled per animal per hour or night still are a mystery, and one cannot deny the possibility that downstream displacement may be very large". Obviously, obtaining this kind of information is very difficult. For holoaquatic *Gammarus pulex fossarum* Lehmann (1967: 255ff.) concluded that short drift events were balanced by active upstream movement such that individuals remained within short reaches of the stream. To our knowledge, the only study which gives quantitative estimates on net movements of larvae and adults of an amphibiotic insect was conducted by Hershey et al. (1993) on *Baetis* mayflies in an arctic river. Most interestingly, by use of radioactive labeling these authors showed that the amount of upstream dispersal approximately equals a minimum estimate of drifting distance. This is probably the best empirical evidence for exact compensation available.

The discussion above indicates that more work will be needed until final conclusions can be drawn about the significance of exact drift compensation in nature. In particular, data are needed that provide insight into the net movements of individual females. Both direction and distances of drift and dispersal should be measured on a long-term basis, covering the whole life cycle of the organism under study. It is also essential that the spatial scale of the study is sufficiently large. Drift-induced mortality has to be taken into account, because only the drift of surviving individuals needs to be compensated for. Since it will hardly be possible to track individual animals throughout their life-time (over several molts), indirect methods will probably be necessary. Directional traps, the most commonly applied device so far, appear to be inappropriate because they measure neither distances nor mortality. They might also fail to reveal upstream-biased dispersal if

individual insects frequently change flight direction. On the other hand, the radioactive labeling methods applied by Hershey et al. (1993) seem promising. Fairbairn (1985) experimentally depopulated an upstream and a downstream section of his study stream and measured recolonization rates. Molecular techniques (see e.g. Schmidt et al. 1995, Bunn and Hughes 1997, Hughes et al. 1998) are available to test whether the longitudinal distribution of individual genotypes stays constant over the years or whether it gradually shifts downstream. These methods could also be used to examine whether there is genetic variation for dispersal direction in a population.

Astonishingly, the papers by Anholt (1995) and Speirs and Gurney (in press) seem to be the first theoretical work on the “stream drift paradox”, despite the decades-long history of empirical research in this field. These papers together with our analysis will hopefully initiate further, more elaborate analysis. Future models might include additional features such as density dependence in drift and dispersal, costs of drift and dispersal, or a non-homogeneous habitat (e.g. with carrying capacity increasing in the downstream direction). Interesting questions to be asked would be: What is the optimal variance of dispersal distances? Is it possible that several dispersal strategies coexist in one stream? Can the selective advantage associated with exact compensation be quantified? Which factors might lead to the evolution of incomplete compensation?

The concept of exact compensation need not be restricted to freshwater streams. Similar problems should arise for all organisms living in habitats where a directional force favors asymmetric dispersal. Examples might include coastal benthic communities subject to surf or flying insect populations in areas where the wind blows mainly from one direction. Finally, we hope that the results of our null model and its quantified predictions help to stimulate further investigations on dispersal behavior in stream ecosystems.

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