THEORETICAL AND PRACTICAL PROBLEMS INVOLVED IN DETERMINATION OF UPSTREAM FLIGHT COMPENSATION IN LOTIC AQUATIC INSECTS

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ABSTRACT

Lotic aquatic insects face a severe problem in maintaining their population in the upper reaches of a stream because of downstream drift. Stream current tends to move individuals downstream. Over time, the population in the upper reaches may be impoverished, causing an eventual local extinction. Upstream flight compensation has been proposed as a mechanism to enable aquatic insects to maintain population in the upper reaches of a stream.

Upstream flight compensation may allow regeneration of this upstream population. However, studies to date have neglected to take into account habitat heterogeneity and patchiness of population distribution. Problems involved in determination of upstream flight compensation are discussed and methods to overcome these problems in determination of upstream flight compensation are discussed.

DISCUSSION

Lotic aquatic insects often face a severe problem in maintaining their population in the upper reaches of a stream because of the phenomenon of downstream drift. Whenever an individual loses contact with the substrate surface, either actively or passively, the stream current will tend to move that individual downstream. Over time, the population in the upper reaches of the stream can be impoverished due to downstream drift of nymphs and eggs causing an eventual local extinction. For example, Russev (1973) calculated that eggs of *Palingenia longicauda* (Olivier) laid in the Danube River will drift downstream about 300 to 2000 m and that the species would be driven from Bulgaria to the Black Sea in a period of 100 to 500 y without some method of overcoming this downstream drift.

There are three obvious possible mechanisms available to the insect to overcome this problem of downstream population shift. First, a significant number of the insects may simply never release the substrate enough to be affected by the downstream current. This option seems highly unlikely in most instances. Over long periods of time, spates and unexpected floods in most lotic habits are likely to occur of such severity that large numbers of individuals are washed from their microhabitats (cf. Thomas, 1975).

Second, the nymphs may actively swim or move upstream to compensate for any population loss from by downstream movement caused by the current (Hynes, 1970; Elliott, 1971). This probably occurs to a greater or lesser extent with many species, although obstacles such as cascades or locally unfavorable habitat may impede this process, as may extremely cold temperatures in the upper reaches of the stream which can possibly lessen the motility of the nymphs (Thomas, 1975).

The third option, which was postulated by Müller (1954) as part of his "Besiedlungskreislauf" or "colonization cycle" theory, is for the adults to fly upstream before oviposition to effect a continuous repopulation of the upper reaches. This can be simply a random dispersal event or, as has been postulated by several researchers, a directed upstream movement of adults before oviposition, known as upstream flight compensation. Upstream flight compensation is postulated for those situations in which random dispersal flight, because of low population densities or low species vagility, is insufficient to maintain a healthy population in the upper reaches of a stream.

Several studies have been published which purport to show the presence (or absence) of upstream flight compensation in different mayfly species (*e.g.*, Bengtsson, *et al.*, 1972; Madsen, *et al.*, 1973; Gyselman, 1980). The usual method of determination of this phenomenon involves two-sided traps (usually sticky traps) over the stream by which the differential between upstream and downstream flight of adult aquatic insects can be measured. Significantly greater numbers of adults caught on the downstream side of the trap in comparison to the upstream side is usually interpreted as evidence of upstream flight compensation (fig. 1).

This paper deals with some theoretical (and practical) problems involved in attempting to determine the extent of upstream flight compensation in lotic aquatic insects which need to be addressed in interpreting the results of these previous studies and in designing future studies of upstream flight compensation.

These problems are all a result of the possibility of patchiness of the local habitat and the resulting heterogeneous distribution of the fauna. Localized heterogeneous distribution of a species in a stream can produce restricted discrete areas of adult emergence which can in turn produce misleading results when data to determine the presence or absence of upstream flight compensation is analyzed.

The benthic substrate in lotic situations is usually quite heterogeneous locally, even when it appears to be quite uniform at first glance. In a rocky stream, boulders may be interspersed with gravel of different sizes, with sand, and with cobble patches. In a sand-bottomed stream, logs or debris may provide locally diverse habitats, and the sand itself may be loose and shifting, or packed to various degrees of firmness. The current speed often differs drastically among localities very close together because of depth, bottom structure, distance from the bank, and other factors. Thus, stream morphology very often causes the occurrence of different microhabitats in close proximity to one another and along the length of the stream. Any particular species is likely to be linked to a particular type or types of microhabitats and while appearing to be distributed widely over the stream habitat will, in reality, be distributed quite patchily, confined to particular microhabitats (Cummins, 1966; Barber and Kevern, 1973; Ward, 1975, 1976; Corkum, *et al.*, 1977; Brittain, 1978; Shelly, 1979; Ciborowski, 1983; Ciborowski and Clifford, 1983). Emergence of adults often occurs from these scattered but localized patches.

None of the studies of upstream flight compensation, as yet, has taken this patchiness of distribution into account, although in practice it can have the effect of seriously affecting the results of such a study. The location of the primary area of emergence in relation to the trapping device can strongly bias the perceived direction of mass movement. If, for example, a major emergence occurs just downstream of the trap and little or no emergence takes place upstream, most specimens caught would be on the downstream side of the trap, indicating a resultant overall upstream movement, even if the majority of the individuals actually fly downstream (fig. 2). The seriousness of this problem will be, of course, inversely proportional to the vagility of the species under study. With a single trap or set of traps there is no way to determine if heterogeneity of distribution is present in a significant amount and is affecting the results of the study.

In order to rule out the effects of habitat heterogeneity in determining mass flight movement direction two corollary conditions must be met. First, the sample taken should be from a subpopulation occurring in a single homogenous habitat patch. Second, individuals from other subpopulations should be excluded from the sample to avoid biasing the results.

A method has been developed which, in some cases, will allow these conditions to be met and which will permit adequate determination of the extent of upstream flight compensation. With suitable modifications, it should be adaptable to many other situations as well.

Two sets of traps should be used and only the results of the downstream side of the upstream trap and the upstream side of the downstream trap should be considered. The traps should be close enough together (say 30 m) that the effects of habitat heterogeneity are minimized by the inter-trap distance being much smaller than the flight distance of individual insects. Individuals from outside of the inter-trap area should be excluded from the traps by some method so that only specimens from within the sample block are considered in the determination. With low-flying species a net about two metres high stretching completely across the stream may preclude the passage of most individuals. Considering only those individuals trapped on the inner side of the inter-trap area assures that patchiness of distribution is not a consideration and that the results are not an artifact caused by habitat heterogeneity.

In practice, high-flying species present a special problem in trying to exclude individuals from outside the inter-trap area. Bird and Hynes (1981), recognizing that local air currents could affect results of sticky traps, proposed four traps set right across the stream and down to the water surface. This method may be adaptable for high-flying species. It has the advantage of demonstrating clear movement in one direction when it is present by the decreasing catch in the direction of movement although the effects of habitat heterogeneity are not ruled out completely.

Several traps widely spaced along the length of the stream, all yielding similar results in direction of mass flight movement, would also tend to negate or rule out the possible effects of local habitat heterogeneity.

It is probably impossible in practice to completely rule out the effects of habitat heterogeneity but it should be possible, in most cases, to lessen these effects by careful experimental design and a well-founded knowledge of the habitat, and its local heterogeneity, in which the study is performed.

While the results of previous studies of upstream flight compensation in aquatic insects may well be valid, interpretation of these results should be done keeping in mind the possible effects of localized habitat heterogeneity and the resultant patchiness of distribution which may cause a bias in apparent mass direction of flight. Future studies should be designed to minimize and take into account the possibility of these effects whenever possible.

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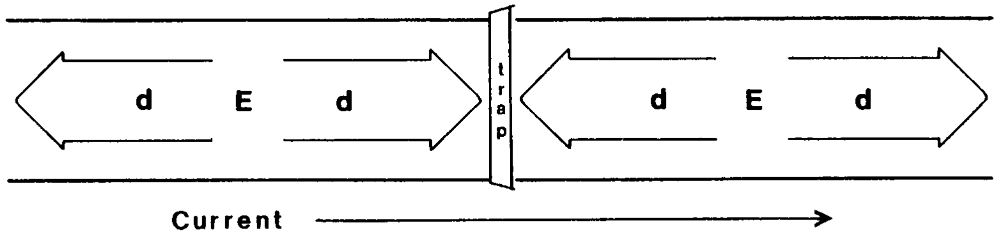

Fig. 1. Traditional view of determination of upstream flight compensation ("e" = place of emergence; "d" = direction of dispersal).

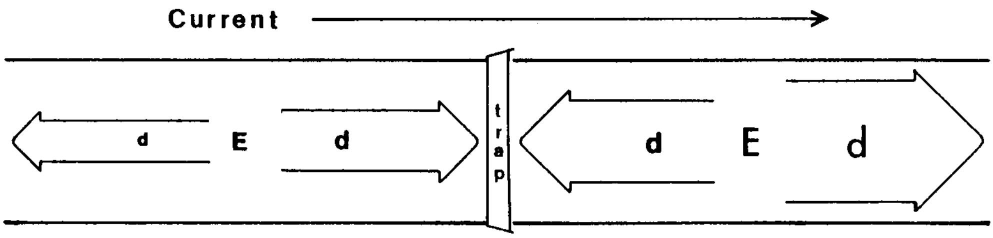

Fig. 2. Habitat heterogeneity can bias results of perceived mass movement direction ("e" = place of emergence; "d" = direction of dispersal).

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