Observations on Upstream Migration by Imagines of Some Plecoptera and Ephemeroptera

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ABSTRACT

The migration of the imagines of some stream insects was investigated with sticky traps. The plecopteran *Brachyptera risi* showed upstream migration; *Nemoura* sp. did not. The ephemeropterans *Caenis rivulorum*, *Baetis* (*rhodani* and *vernus*), and *Ephemerella ignita* all showed upstream migration.

Larvae and nymphs of many stream insects in both the Old and New World are carried downstream by the currents (for a comprehensive review *see* Waters 1972). The causes and effects of this drift have not been completely explained, but one result is that populations in the upper reaches of a stream may be diminished or eliminated. Müller (1954) postulated that gravid females compensate for this loss by flying upstream so that their eggs are laid upstream of the site of emergence.

Roos (1957) has shown by trapping that there is, in fact, an upstream migration of at least certain Trichoptera, but this work has been criticized by, among others, Schumacher (1970) who postulated that this flight is caused by the wind blowing in the same direction as the current. Elliott (1967) has observed that Plecoptera and Ephemeroptera fly with the wind, but we have seen many imagines of Ephemeroptera, Trichoptera, and Simulidae fly upstream regardless of wind direction. This upstream migration normally takes place at sunset, usually in calm weather, and wind can blow the insects off course, or even backwards. Such observations are, however, not quantitative, and they apply to only a small part of the life of the imago. Pearson and Kramer (1972) have observed that the trichopteran *Oligophlebodes sigma* flies upstream after emergence to lay eggs in the uppermost parts of the watercourse; Schumacher (1970) who marked imagines of *Hydropsyche instabilis* and recaptured them in UV light traps above and below the releasing site found no evidence of upstream migration.

METHODS

In our investigations we avoided use of capture methods such as light traps which attract the insects and may influence results. We used a layer of sticky adhesive applied to transparent polyethylene sheets. The adhesive is available as Raupenleim, which is applied to the trunks of fruit trees for protection against ascending caterpillars; Tanglefoot is a North American equivalent. The sheets were set up transversely over the stream, using a wooden frame or wires with one sticky side facing

Table 1. Total numbers and percentage distribution of the catches in one trap on Sugebæk and one trap on Sønderup å. (M—males; F—females)

		Total No.	Upstream		Downstream		Period
			No.	%	No.	%	
Brachyptera risi (Mort.)	M	628	346	16	282	13	7 May–29 Jun
	F	1,541	992	45.7	549	25.3	
Nemoura sp. *cinerea* (Retz.) +	M	879	304	12.3	575	23.3	7 May–29 Jun
flexuosa (Aub.)	F	1,587	583	23.6	1,004	40.7	
Caenis rivulorum (Etn.)	M+F	9,356	7,052	75.4	2,304	24.6	21 Jun–27 Jun
Baetis rhodani (Pict.) +	M	125	93	3.9	32	1.3	11 Jun–27 Jun
vernus (Curt.)	F	2,269	1,467	61.3	802	33.5	
Ephemerella ignita (Poda)	M	9	5	0.2	4	0.1	7 Aug–15 Aug
	F	2,619	2,175	78.2	444	16.0	
subimago	M	54	11	0.4	43	1.5	
subimago	F	99	14	0.5	85	3.1	

upstream and the other downstream. Apparently the insects that we studied do not attempt to avoid these traps. On one trap (1.2 × 4 m) placed across the small stream, Sugebæk, in a wooded valley, we captured nearly 5,000 Plecoptera during the flight season (beginning of May to mid-June). The traps were emptied at intervals of 3 to 7 days and the insects removed by dissolving the adhesive with turpentine.

RESULTS

The plecopteran, *Brachyptera risi,* was caught on both sides of the trap in Sugebæk. This agrees with our direct observations that this species has a highly variable pattern of movement during its 3–4-week period of adult life. Imagines were rarely seen flying upstream, and they often flew away from the watercourse up the sides of the valley. However, despite this more or less random movement, the greater proportion of our captures was on the downstream side of the trap (Table 1), indicating that much of the movement is generally upstream.

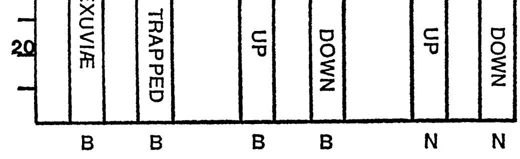

Fig. 1. The percentage distribution of females (white) and males (dotted) of *Brachyptera risi* (B) and *Nemoura* (N). Up and down refers to the part collected on the side of the sheet catching the upstream and downstream migrating part.

Study of exuviae collected along the stream (Fig. 1) indicates that population was 40% females. On the trap it was 71%, showing that the females fly more than the males. On the downstream side of the trap 74% of the catch were females compared with 64% on the other side (Fig. 1). This perhaps indicates that upstream migration is most marked in the female. A χ^2 test of the catches shows that the difference between the two sides is significant (♂ $0.02 > p > 0.01$; ♀ $p << 0.001$).

The valley through which the stream runs is well sheltered, but we measured the wind near the trap throughout our observation period. The direction of the weak winds was nearly always with the current, and as *B. risi* is a poor flyer it is possible that this accounts for the large proportion recorded as flying downstream.

About 3,000 imagines of *B. risi* from Sugebæk were marked and distributed with half at the lower and half at the higher end of the watercourse. Only a few

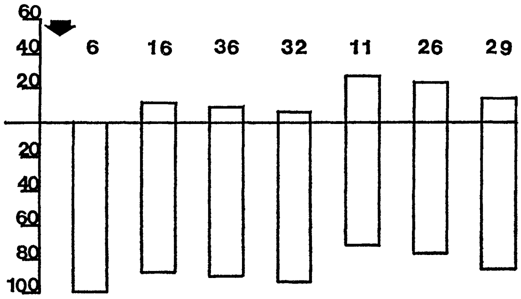

Fig. 2. The percentage distribution of *Baetis rhodani* collected at weekly intervals from the end of July on the two sides of a trap positioned across a little springbrook. The numbers shown above are the totals each week. The arrow indicates the direction of the current.

were reobserved or recaptured. Of the individuals released at the lower end of the stream, 1 was found further downstream, and 24 were found from about 50 to 250 m upstream from the point of release. Of the individuals released at the upper end of the stream, 48 were found mostly near the point of release, and 5 were found farther downstream.

Also in Sugebæk the plecopterans *Nemoura cinerea* and *Nemoura flexuosa* gave results opposite to those of *B. risi* (Table 1). Here the smaller proportion was caught on the downstream side of the trap. If one assumes that the same quantity emerge from the stream above and below the point of trapping, it is possible that the difference in numbers on the two sides of the trap was caused by the wind. We do not know the actual percentage of females in the *Nemoura* population, but the proportion was the same on both sides of the trap (Fig. 1), and this implies no migration of females in any particular direction.

Observations on Ephemeroptera were made on Sønderup å, a river running through a broad meadow. Some of the results are shown in Table 1. The wind blew most often downstream with a deviation of about 10°. In one trap, nearly 10,000 individuals of *Caenis rivulorum* were captured. It was difficult to distinguish the sexes since the delicate insects were ruined by removal from the adhesive, but in one small well-preserved sample we found that 60% were females, all full of eggs. By far the greater proportion was captured on the downstream side of the trap. Strong gusts of wind can blow this species backwards, so that some of the catch on the upstream side was possibly caused by the wind. Both our catches at Sønderup å and our observations on other streams show that this species migrates upstream, but this would be difficult to substantiate without traps, since it occurs during a very short period, often only a few days in the year.

Captures of *Baetis* (*rhodani* and *vernus*) also indicate upstream migration; in addition to the results shown in Table 1 we have similar findings for July and August. Most of the specimens were females. These insects also fly in swarms, which are, however, appreciably smaller than those of *C. rivulorum* and occur over a much longer period. During a single week in August, 2,619 individuals of *Ephemerella ignita* were captured, and the results here also indicate a pronounced upstream migration. This is in full agreement with numerous sightings of this species flying upstream at sunset. The females nearly always fly singly—seldom in swarms—and they are easily recognizable, even at a distance, by the very large egg mass that they carry.

We have also carried out some investigations on migration of *B. rhodani* in a small stream near Vegger. There the trap was positioned right over the stream, where there was good shelter. The results were thus not affected by wind, and the catches made at about 1-week intervals are shown in Fig. 2. It is evident that here also there was an upstream migration.

DISCUSSION

In the stream investigated, *B. risi* showed a complex migration, but the general movement, especially among the females, was mostly upstream.

This was not true of *Nemoura,* and the difference can perhaps be explained by differences in the ecology of the nymphs. Those of *Nemoura,* which live in leaves and under stones, are better protected against the current than the nymphs of *B. risi*, which live on the surface of stones (Madsen 1968). One may suppose, therefore, that only species that are liable to be carried into the drift have a compensatory upstream migration. Our unpublished results from both Sugebæk and a similar stream, Gjessøbæk, show that nymphs of *B. risi* drift in large numbers in these streams while those of *Nemoura* do not.

All the Ephemeroptera that we studied displayed a predominantly upstream migration. Nymphs of *C. rivulorum* live in muddy substrata for most of their life cycle, but the large nymphs move up into the vegetation, and both from there and during the actual emergence process they can drift with the current.

Nymphs of the two species of *Baetis* live on plants and on stones exposed to the current and both occur in the drift, often in very large numbers (Müller 1966). Despite the fact that *E. ignita* lives in places more sheltered from the current than does *B. rhodani*, it also is found in the drift (Madsen 1966).

The upstream migration that has been demonstrated in the Ephemeroptera we investigated may be interpreted as a compensation for the losses arising from drifting of the nymphs.

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On the concept of lake stability[1]

ABSTRACT

A new equation describing the stability of a lake, as conceptually defined by Schmidt, is developed to supply information on the contribution of each lake layer to stability. It is analogous in form to the expression derived by Birge for his concept of direct work of the wind and may be combined with that to yield a curve for direct total work as a function of lake depth.

Birge (1916) defined the *work of the wind* as the minimum work required to overcome buoyancy forces in distributing a given surface heat load within an initially unstratified lake of minimum heat content (generally assumed to be at 4°C), so as to produce an observed density stratification. Schmidt (1928) defined the *stability of a lake* as the additional work that would be required to transform this density distribution into one of new uniformity without further addition or subtraction of heat. Although both of these quantities are only small, varying, and unknown parts of the total wind work performed against viscous forces in generating turbulence, they have enjoyed a long history of significant usage in limnology. Since the formulation of

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