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Flight Behaviour of Merolimnic Insects from the Leutra River (Thuringia, Germany)

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Abstract

1. The flight behaviour of adult merolimnic insects was studied on the first order limestone stream Leutra (Thuringia, Germany) using sticky traps. The focus of the present study was on testing the colonisation cycle hypothesis of Müller (1954) and on the small-scale dispersal of adult merolimnic insects.

2. A high number of sticky traps was used to guarantee a proper statistical analysis of the data and exclude effects of the heterogeneous environment on flight behaviour.

3. The flight behaviour of *Leuctra hippopus*, *Nemoura cambrica*, *Nemoura flexuosa*, *Protonemura nitida*, *Protonemura praecox* (Plecoptera), and *Baetis rhodani* (Ephemeroptera) was studied.

4. Specific flight corridors were observed for *P. praecox*, *Nemoura* spp., *L. hippopus* and *B. rhodani*.

5. Comparison of the catches on sticky traps set perpendicular to the water showed no significant flight upstream in any of the taxa studied. Thus, the results do not support the hypothesis of the colonisation cycle.

Keywords: stream, colonisation cycle, aquatic insects, flight corridors, dispersal, Plecoptera, Ephemeroptera.

Introduction

Flight behaviour of merolimnic insects over streams results in different movement components during insect life cycles. Petersen et al. (1999a) suggest a model for dispersal including a movement inland after emergence to mate, feed and rest and a subsequent return of the females to oviposit, whereas males do not move back to the stream. The present paper deals with two aspects of aquatic insect flight over and near the stream, to test the occurrence of predominant upstream flight and examine spatial patterns of flight.

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Drift of aquatic organisms in streams leads to a loss of individuals but over the longer term populations in the upper region of streams do not decrease in abundance (Gyselman, 1980). The reasons are still unclear. There are three possible strategies of compensation for the loss of individuals by drift: the upstream movement of the nymphs, upstream flight by adults (Müller, 1954) and the better development of offspring in areas of lower population density, and Waters' (1972) excess production hypothesis. In the present study the second of these was tested.

There is some direct and indirect support for predominant upstream flight by adults especially for egg-bearing females (Müller, 1954; Roos, 1957; Lehmann, 1970; Madsen & Butz, 1976; Zwick, 1990; Hershey et al., 1993). Other studies (Madsen et al., 1973; Bird & Hynes, 1981; Jones & Resh, 1988; Petersen et al., 1999b) produced little or no evidence for drift compensation through upstream flight.

A very important factor explaining these divergent findings certainly is the patchy structure of the environment and a related heterogeneous distribution of the animals (Hubbard, 1991). Thus the distribution of adult merolimnic insects is strongly influenced by the distribution of emergence sites, for example mossy stones in the case of stoneflies. The side of a sticky trap facing an emergence site inevitably will catch many more insects than the side facing away. In the present study this difficulty is avoided by setting a high number of traps along an extended reach of stream. This provided replicate catches from the same positions in the stream cross-section and made a better statistical analysis possible than in previous studies using only 1–4 catching devices (Göthberg, 1972; Madsen et al., 1973; Madsen & Butz, 1976; Bird & Hynes, 1981; Gullefors, 1987; Jones & Resh, 1988; Williams & Williams, 1993). Furthermore the species observed, the particular localities and the methods used might affect the results of studies of the flight behaviour.

The horizontal and vertical distribution of flying Plecoptera and Ephemeroptera was examined on a small spatial scale above the water and on the banks of the stream. Large-scale studies have shown distribution peaks near the stream, e.g. Jackson and Resh (1989), Göthberg (1972) and Sode and Wiberg-Larsen (1993) for Trichoptera, Petersen et al. (1999a) for several taxa and Kuusela and Huusko (1996) and Griffith et al. (1998) for Plecoptera.

The design of sticky traps used in this study provided a single methodology for the investigation of both major questions.

Study Site

The Leutra south of Jena in Thuringia, Germany, is a first-order stream rising at an altitude of 400 m a.s.l. in a limestone area. It meanders for 12 km through pastures and woodland, with a continuous wooded riparian zone. Average discharge is $0.0324\,m^3\,s^{-1}$. The study reach was partly canalised in 1938 but since then natural riparian vegetation has again developed within 6 m on either side. The trees include typical riparian species, *Alnus glutinosa* (L.) Gaertn., *Fraxinus excelsior* L. and *Salix* spp.

Methods

The study was carried out between March 12 and May 11, 1998. This time was chosen because vegetation is sparse, as trees do not leaf out until mid-May. Vegetation was assumed to affect the spatial distribution as flying insects may avoid dense vegetation patches or may alternatively be attracted by vegetation as food patch or resting place. This will affect the catches especially at the bank-side traps. A further reason was to avoid catching non-merolimnic insects, of which few emerge so early in the year. Sticky traps (Bird & Hynes, 1981) size 1 m × 1 m were used (Fig. 1). The catching surface was 20 µm PE-film coated by transparent insect-glue (F. Schacht GmbH & Co, Braunschweig) on both sides, stretched between two wooden poles. To prevent insects climbing onto the traps from the ground, glue was applied around each pole (Fig. 1). To protect the film from submergence by minor floods they were set 0.3 m above the water or ground surface, respectively.

Twenty transects at 10 m distances along a 190 m reach were selected and a single trap was placed in each in order to avoid interference between adjacent traps. Each trap surface was perpendicular to the direction of stream flow (Fig. 2). The daily catches per trap-side of adjacent traps were checked for pos-

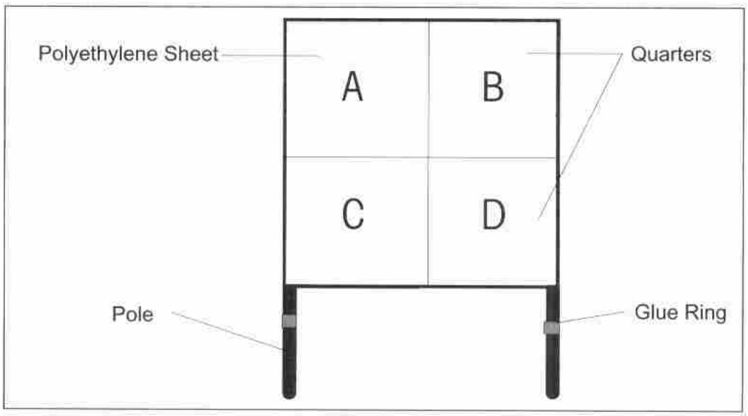

Figure 1. Schematic drawing of the sticky traps.

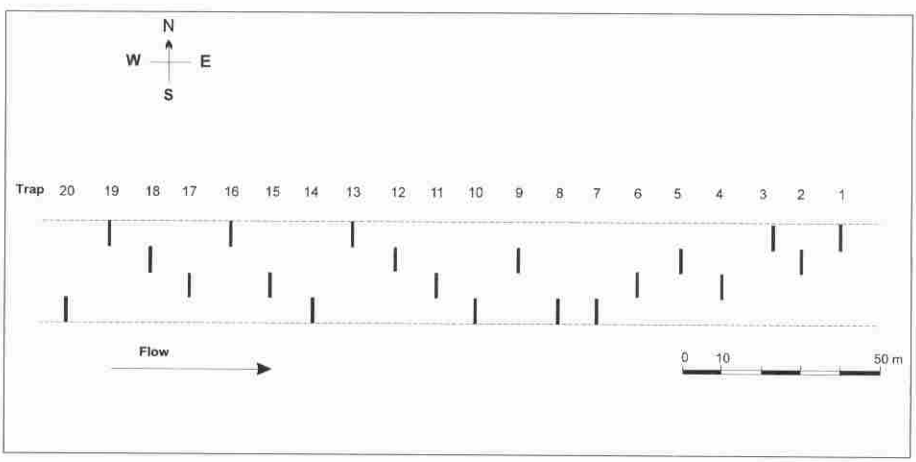

Figure 2. Spatial distribution of the sticky traps along the River Leutra.

sible correlations (Spearman Rank Order Correlation), separately for the downstream and upstream sides, trap by trap, for all species together. The transects were 4 m wide and included the stream plus 1 m of bank on each side. Traps were randomly assigned to each of four possible trap positions along a transect (Fig. 3), so that in total there were five replicate traps in each position.

Sampling was at intervals of two or three days. The stoneflies and mayflies were identified to species or genus. Each individual was sexed and females checked for the presence of eggs.

To test for upstream flight, a ln $(x + 1)$-transformation was first applied, to adjust the data to a normal distribution. The resulting data from upstream facing sides were compared to those facing downstream using a 2-way ANOVA, the factors being trap side and catch date. The high variance resulting from the seasonal fluctuation of adults is eliminated by considering catch date as second factor.

To obtain high resolution of the spatial distribution the sticky traps were quartered (Fig. 1). Since the traps were set in four positions across the stream it was possible to compare catches between eight quarters horizontally, while vertical distribution was determined pairing upper (A, B) with lower (C, D) quarters (Fig. 3). Kruskal–Wallis ANOVA was used to compare quarters horizontally whilst a t-test was used for vertical comparison. To eliminate the effect of seasonal variation these analyses were performed on the relative proportion of the total daily catch and not on the numbers caught. SPSS (SPSS Inc.) and Sigma Stat. (SPSS Inc.) were used for statistical analyses.

Wind velocity was measured continuously, whereas wind direction was recorded twice a day, both 1 km east of the study site at a 8 m high building in the Leutra valley. Direction was recorded by simply watching a 100 mm piece of wool, velocity with an Anemometer (Testovent 4400, Testoterm Company). The anemometer output was stored on an analog chart recorder. The River Leutra offered optimal conditions for the present study since the position of its straight narrow valley ensures that the wind close to the stream blows either directly upstream or downstream. The wind direction was spot checked for every sticky trap for five days and identical at each trap and on each occasion. This formed the basis for quantifying the effect of wind on flight direction. The influence of wind direction on the detected flight direction was tested by comparing the daily proportion caught at the downstream side of each trap during the two occurring wind directions (Mann–Whitney test), for all four taxa. The influence of the wind velocity on the total numbers caught was tested by linear regression.

Results

Compensation flight

During the observation period seven Plecoptera and three Ephemeroptera species were present at the sticky traps (Table 1). Four taxa (*Protonemura praecox*, *Nemoura* spp., *Leuctra hippopus* and *Baetis rhodani*) were abundant enough for statistical analysis (Table 1). Females of *Nemoura cambrica* and *N. flexuosa* could not be separated, and the data were therefore combined. *P. praecox* was investigated over its entire flight period.

There was no significant difference between upstream and downstream catches of *Protonemura praecox*, *Leuctra hippopus* and *Baetis rhodani*, even when males, females and egg-bearing females were analysed separately (Table 2). However, both males and egg-bearing females of *Nemoura* spp. were caught in significantly higher numbers on the upstream trap sides (Table 2).

The proportions of insects caught on up- and downstream trap sides did not differ ($P > 0.05$) between periods of continual west wind (downstream direction) and changing wind direction (east and west). Wind velocity only influenced the total daily catch. There were significant positive regressions between the mean total numbers caught per trap and wind velocity during the catching period in *P. praecox* and *L. hippopus*, and a negative in *Nemoura* spp. Captures of *B. rhodani* were independent of wind velocity (Table 3).

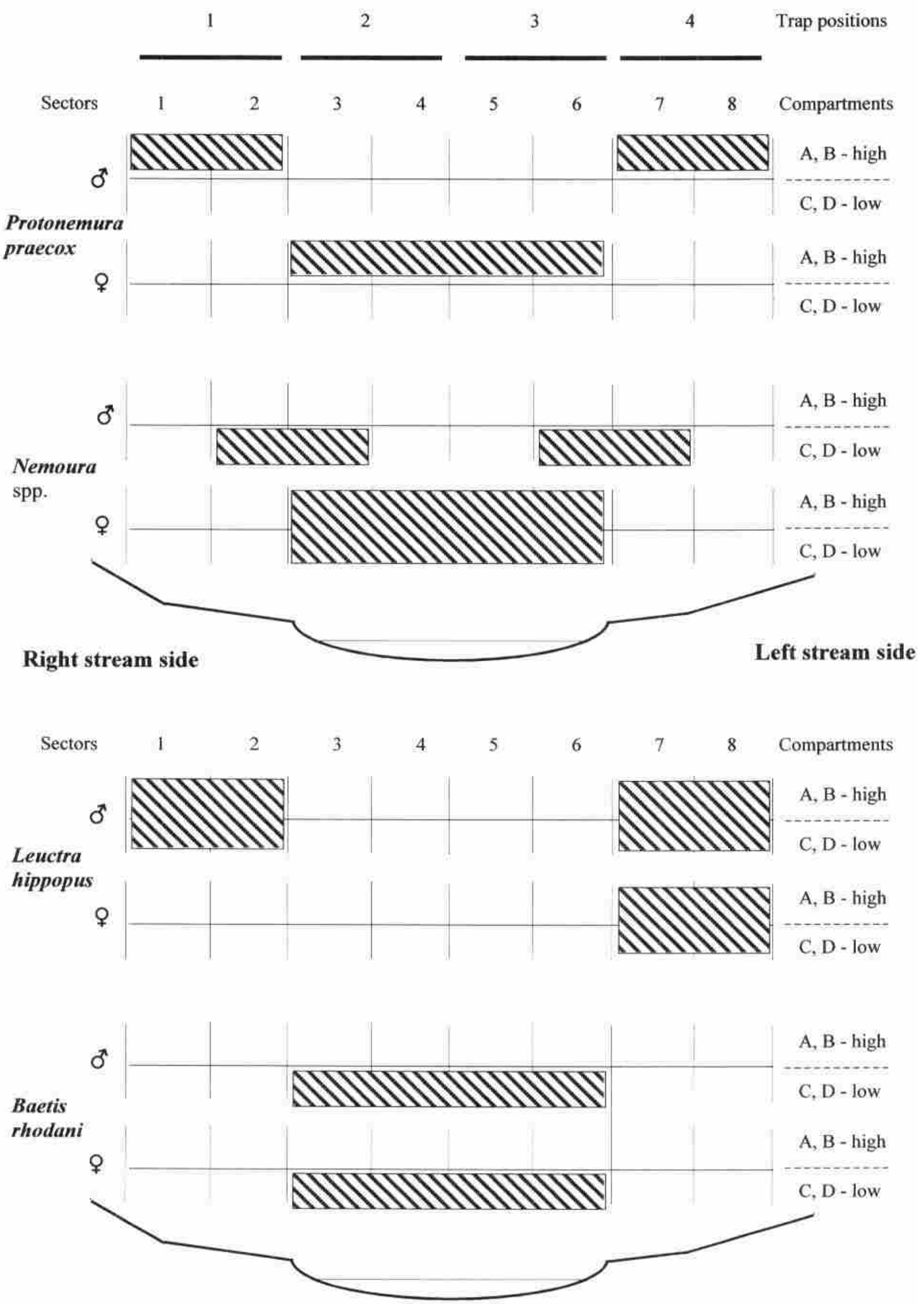

Figure 3. Schematic graph of the predominant flight corridors of: *P. praecox*, *Nemoura* spp., *L. hippopus*, *B. rhodani*. Corridors represented by striped bars. The four trap positions are shown at the top of the graph. For every taxon, the upper graph shows results for males, the lower for females.

Table 1. Taxa caught on the 20 sticky traps along the River Leutra.

Taxon	Total numbers
Plecoptera	
Leuctra hippopus Kempny	4136
Nemoura cambrica Stephens } *Nemoura flexuosa* Aubert }	953
Protonemura praecox (Morton)	4033
Ephemeroptera	
Baetis rhodani (Pictet)	536
other Plecoptera and Ephemeroptera	103

Table 2. Comparison of the numbers caught per flight direction on sticky traps (separately for males (m), females (f); females with eggs (fe), and the total numbers) by 2-way ANOVA.

Taxon	Sex / Egg Status	*N*	Numbers per flight direction: up	down	Significance
Protonemura praecox	m	706	351 (49.7%)	355 (50.3%)	n.s.
	f	761	392 (51.5%)	369 (48.5%)	n.s.
	fe	567	298 (52.6%)	269 (47.4%)	n.s.
	total	2034	1041 (51.2%)	993 (48.8%)	n.s.
Nemoura spp.	m	2935	1297 (44.2%)	1638 (55.8%)	*
	f	3119	1489 (47.7%)	1630 (52.3%)	n.s.
	fe	3479	1457 (41.9%)	2022 (58.1%)	*
	total	9533	4243 (44.5%)	5290 (55.5%)	*
Leuctra hippopus	m	1296	665 (51.3%)	631 (48.7%)	n.s.
	f	1584	807 (50.9%)	777 (49.1%)	n.s.
	fe	1256	564 (44.9%)	692 (55.1%)	n.s.
	total	4136	2036 (49.2%)	2100 (50.8%)	n.s.
Baetis rhodani	m	179	83 (46.4%)	96 (53.6%)	n.s.
	f	357	172 (48.2%)	185 (51.8%)	n.s.
	total	536	255 (47.6%)	281(52.4%)	n.s.

* = $P < 0.05$, n.s. = not significant ($P > 0.05$).

There were no negative correlations between catches of adjacent traps. In contrast there was an overall positive correlation ($P < 0.001$) of daily catches on the upstream sides or downstream sides, respectively, of adjacent traps suggesting that catches are not influenced by adjacent traps.

Table 3. Linear regressions of the total numbers (N) caught per trap on mean wind velocity [$m\,s^{-1}$] (WV) during the catching period, SE — standard error of regression coefficient.

Taxon	Regression equation	SE	R^2	Significance
Protonemura praecox	$N = 2.52 \cdot WV + 5.036$	0.782	0.027	***
Nemoura spp.	$N = -12.41 \cdot WV + 33.15$	5.708	0.016	*
Leuctra hippopus	$N = 11.52 \cdot WV + 9.878$	1.443	0.144	***
Baetis rhodani	–		–	n.s.

*** = $P < 0.001$, * = $P < 0.05$, n.s. = not significant ($P > 0.05$).

Spatial distribution

In all taxa, significant differences ($P < 0.001$) were detected in the proportions caught on the eight horizontal quarters. Male *P. praecox* occurred predominantly in the outer sectors but females were more often caught in the central part of the stream (Figs. 3, 4). Male *Nemoura* spp. were caught between riverbank and stream in a position corresponding to the shore line (Figs. 3, 4), whereas maximum catches of female *Nemoura* spp. were above the stream (Figs. 3, 4), which was similar to *B. rhodani* males and females (Figs. 3, 4). Male and female *L. hippopus* were found in higher proportions in the sectors over the banks, the females at the left stream side (Fig. 3, 4).

Captures of *P. praecox*, *Nemoura* spp. males and *B. rhodani* in the upper and lower sectors of the sticky traps differed significantly (Table 4; Fig. 3). More *P. praecox* males and females were caught in the upper sectors (Fig. 3; Table 4) whereas male *Nemoura* spp. and *B. rhodani* males and females were more abundant in the lower sectors (Fig. 3; Table 4). There were no significant differences between the upper and lower sector catches in *L. hippopus* or *Nemoura* spp. female (Table 4).

In summary, the taxa exhibited preferred flight corridors (Fig. 3). Except for *L. hippopus*, females flew above the stream. In contrast, male stoneflies generally flew over the banks or at least along the shoreline, with *P. praecox* predominantly in the upper and *Nemoura* spp. in the lower compartments, but *L. hippopus* was indifferent with regard to height (Fig. 3). Female stoneflies tended to fly above 0.8 m (Table 4) although significantly only in *P. praecox*. Both sexes of the mayfly *B. rhodani* were most abundant at the level 0.3–0.8 m above the centre of the stream (Fig. 3).

Discussion

No predominant upstream flight was present in the four taxa at the Leutra River, which agrees with previous studies (Jones & Resh, 1988; Petersen et al., 1999b). This supports Waters' (1972) excess production hypothesis according to which no predominant upstream flight is necessary to maintain the population in the upper regions. Density dependence at one point in the life cycle coupled with random dispersal by adults, allows populations to persist in upstream regions (Anholt, 1995). Upstream

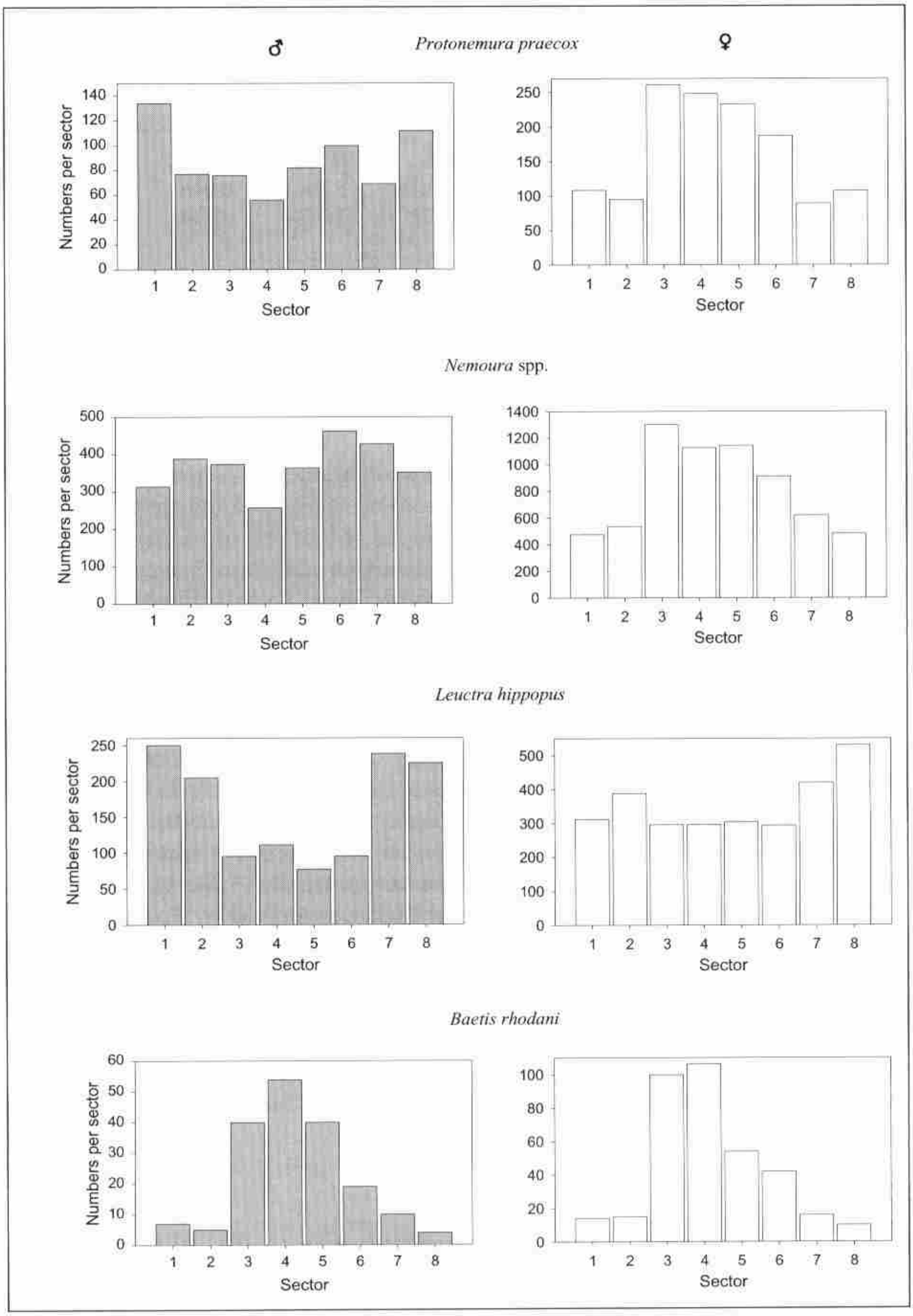

Figure 4. Horizontal distribution of the four investigated taxa along the River Leutra on the 20 sticky traps. Striped bars are males, white bars females, position 1: right stream side and position 8: left stream side, Kruskal–Wallis One-Way ANOVA on Ranks $P < 0.001$ in all taxa.

Table 4. Comparison of the numbers caught at the two height levels of the sticky traps by *t*-test.

Taxon	Sex	Proportion per sector [%] upper	lower	Significance
Protonemura praecox	male	62	38	***
	female	59	41	*
Nemoura spp.	male	44	56	***
	female	54	46	n.s.
Leuctra hippopus	male	45	55	n.s.
	female	56	44	n.s.
Baetis rhodani	male	42	58	***
	female	35	65	***

*** = $P < 0.001$,* = $P < 0.05$; n.s. = not significant ($P > 0.05$).

flight is only profitable for a given specimen if it maximises its fitness by increasing the prospects for offspring survival. This would be the case in reaches of lower larval density and lower intraspecific competition. That may occur in upper regions but not if a high proportion of females oviposits at upstream sites. The development of strong upstream-biased dispersal in a population is therefore counteracted.

Moreover, it is well known that merolimnic insects actively move upstream in the water (Bishop & Hynes, 1969; Brusven, 1970; Elliott, 1971; Townsend & Hildrew, 1976; Pearson & Jones, 1987) and thereby compensate downstream displacements. Elliott (1971) showed a drift compensation of about 30% by upstream movement of larval Plecoptera, Ephemeroptera, Trichoptera, Coleoptera, Diptera and of Crustacea, under certain conditions.

In some previous works the absence of a compensatory flight was particularly attributed to the special habitats of the species. The results in *Nemoura* spp. (*N. cambrica*, *N. flexuosa*) on the Leutra agree with the finding of Madsen et al. (1973) for *Nemoura* spp. (*N. cinerea*, *N. flexuosa*). These authors argued that no compensatory flight is required in these species because the larvae live in leaf packs and under stones which makes them less prone to drift than, for example, larvae of mayflies which feed in regions of higher current (Schönborn, 1992). *P. nitida* and *P. praecox* are found in similar habitats as *Nemoura* spp. and are also not exposed to high current. Simultaneous drift and nymph density data for the River Leutra to indicate the existence of downstream movement would have been useful but were unfortunately not available.

Another explanation still is that upstream flight remained perhaps undetected because it may have occurred outside the capture area. Imagines are able to move far away from the stream (Madsen et al., 1973; Griffith et al., 1998; Petersen et al., 1999a) and Kuusela and Huusko (1996) could not even detect a decrease in the abundance of *L. hippopus* and other Nemouroidea up to 60 m from the stream. In the present study, flights at a distance of more than 1 m from the stream channel were not recorded and might differ from the near channel flight, which would affect the total net movement of adults.

The absence of a predominant upstream flight in the Leutra contradicts some direct demonstrations of compensatory flight in merolimnic insects (Müller, 1954; Roos, 1957; Lehmann, 1970; Madsen & Butz, 1976; Winterbourn & Crowe, 2001). Because these studies used only few traps, the results represent the conditions at specific points but may not be valid for the entire population. Many factors in the stream and in the terrestrial habitat may influence flight patterns (Petersen et al., 1999b). Wind is one such factor; however, in the present study wind direction had no impact on net flight direction. Studies using up to six sticky traps showed that the results of individual traps differ from the sample total (Bird & Hynes, 1981; Winterbourn & Crowe, 2001). Therefore, data from a high number of sites are needed to detect a general trend among locally strongly variable patterns and to provide the necessary statistical power.

The reason for the significantly higher downstream flight of males and females with eggs in *Nemoura* spp. in the present study is not clear. It may be an artefact resulting from pooling the data of *Nemoura cambrica* and *N. flexuosa*. At least for *N. cambrica* only part of the flight period was sampled and the net downstream flight observed might have been compensated by predominant upstream flight, after the experiment ended.

Differences between female and male flight pattern are in accordance with oviposition in the water for which females should fly over the stream in search of suitable sites. However, only females of *B. rhodani* flew low over the stream. Stonefly females were heterogeneously distributed with height or flew more than 0.8 m above the water (*P. praecox*). This might be because the flight to find suitable foraging localities and to mate masked their ovipositional flight patterns.

Why Plecoptera males seem to avoid the stream centre and why the flight pattern of the mayfly *B. rhodani* differed strongly from stoneflies is unclear and needs further investigation. However, the distribution of *L. hippopus* differed also from the other stoneflies, both sexes flew mainly above the banks. One possible explanation is that the poor flight of *L. hippopus* led them to prefer the banks to avoid falling into stream and become easy prey for predators. Plecoptera generally do not fly well and *L. hippopus* is a poor flyer relative to *P. praecox*. *L. hippopus* showed a saltatory flight, flying only a few meters at a low height, landing and flying again after a short time. In contrast, *P. praecox* flew for much longer distances, and sometimes steeply upwards. The poorer flying ability of *L. hippopus* might also explain why males did not prefer the upper section of the flight corridor monitored, but this must be tested in further studies.

Sticky traps are evidently a highly effective tool to study merolimnic insect flight behaviour. The specimens caught remain at the point where they hit the film, resulting in high spatial resolution, in contrast to Malaise traps (Malaise, 1937). Both sides of the catching film are equal and their catches are therefore comparable. However, the effect of environmental heterogeneity can only be excluded by use of high numbers of traps. Sampling a broader strip of bank side would have required more traps than could be handled in this study, because removing the insects undamaged from the trap is particularly time consuming. Still, the 20 traps used here on a small spatial scale were sufficient for a more detailed statistical analysis of the data than was attempted in other studies (Bird & Hynes, 1981; Gullefors, 1987; Jones & Resh, 1988; Williams & Williams, 1993).

The analysis clearly showed the absence of compensatory upstream flight and differences in the use of flight corridors between the mayfly *Baetis* spp. and the three stoneflies, and between *L. hippopus* and the other stoneflies.

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