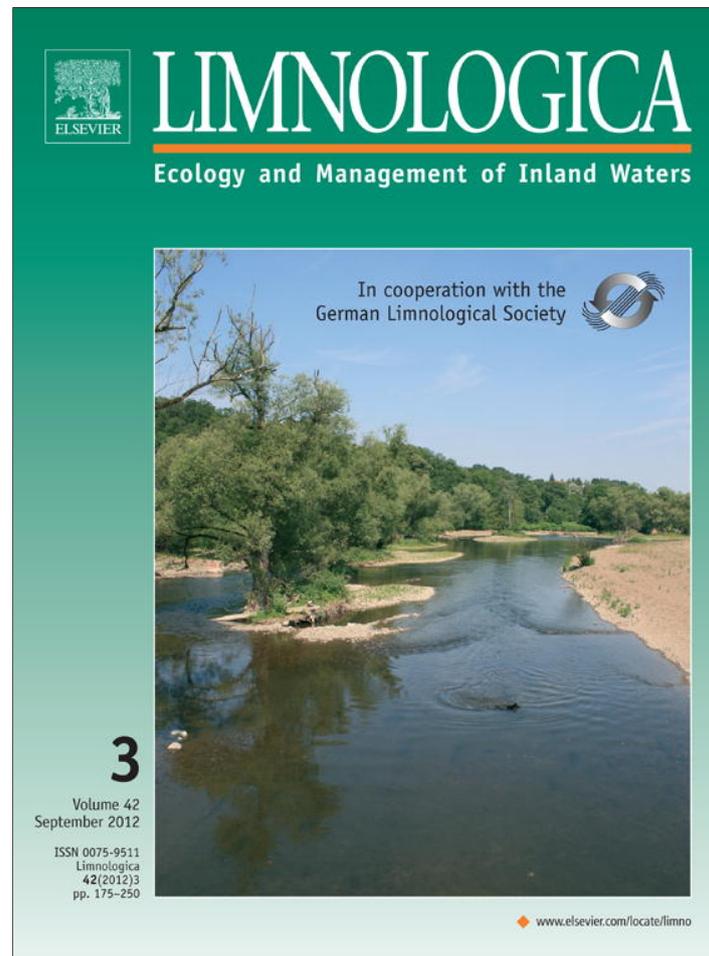


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Mobility of lowland stream Trichoptera under experimental habitat and flow conditions

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ABSTRACT

The species-specific mobility of six species of lowland stream Trichoptera was studied in flume experiments with different habitats and current flows. The test species were selected according to their occurrence along the environmental gradient from more natural towards highly disturbed sandy, lowland streams of the North-West European plain. Two groups of species were distinguished, three species occurring more frequently towards the natural end versus three occurring more frequently towards the disturbed end of the stream disturbance gradient. Experiments were conducted in a temperature and light controlled environment in indoor, re-circulating, man-made stream channels with four replicate gutters each. The bottom of each gutter held ten trays filled with five selected habitat materials (two trays each), which provided refugia and food. Three flow treatments with constant current velocities of 10, 30, or 50 cm/s were applied. Movements were scored based on visual observations of the position of each individual at fixed time points. The first day after release, individuals moved around very actively; this 'release effect' was removed from further analyses. The trichopteran species occurring near the more natural end of the disturbance gradient exhibited significantly less mobility (on average 10–15% of individuals actively moved around) than the species from the more disturbed end of the gradient (on average 30–40% of individuals actively moved around). The first group of trichopteran species also spent significantly longer times in the leaves habitat compared to the other three species, which moved more or less independent of habitat. With increasing current velocity, all test species moved more frequently, particularly the species from the more disturbed end of the gradient. This could indicate behavior to avoid dislodgement. The mobility of all species exceeded the mobility needed to use habitat resources of food and shelter, both present in excess. Therefore, short-term movement could also be (partly) a random behavior. Overall, the more tolerant species from the disturbed end of the gradient showed more mobility and flexibility than the species occurring under more or less natural stream conditions. This was consistent with the hypothesis that mobility is an adaptation of tolerant, ubiquitous species. Mobility is an adaptation of r-strategists.

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Introduction

Distribution of stream macroinvertebrates can be driven by a number of abiotic factors, like temperature (Williams 1980), water chemistry (Hart et al. 1996), flow (Lancaster et al. 1990), and physical structures that offer shelter/refuge (Lancaster et al. 1996). Furthermore, biotic factors can be involved, such as predation (Hildrew and Townsend 1980), food availability (Kohler 1985), and competition (Hildrew and Giller 1994). Over the last decades, the main focus in many of these distribution studies was the habitat (Poff and Ward 1989; Allan 1995). Habitat preferences were shown to be based mainly on current, substrate, and food (Hynes 1970; Allan 1995). Water current is regarded a primary

factor that controls the availability and suitability of substrate patches (Buss et al. 2004). Substrate provides both shelter and food; food generally comprises detritus and its associated bacteria and fungi (Ward and Cummins 1979). Buffin-Bélanger et al. (2006), Lancaster et al. (2006), Lancaster (2008), and Rice et al. (2008) have reported that small-scale macroinvertebrate movements were influenced by near-bed hydraulics and microtopography.

Recently, several studies have reported that macroinvertebrates despite their habitat preference are distributed over multiple habitat patches (Buffin-Bélanger et al. 2006; Negishi and Richardson 2006; Lancaster 2008). Movements of macroinvertebrates across heterogeneous patches can be considered a trade-off between expending energy for movement and gaining resources, like higher quality food and/or shelter (refuge). Patches that provide high quality food can attract certain consumers; for example, detritivores are attracted to certain types of leaves (Dobson and Hildrew 1992). Individuals move around to seek these high food quality

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patches, and remain there when one is located; the first results in a higher mobility, the second in an increased residence time in the respective patch (Kohler 1985; Olden et al. 2004). Movement of stream macroinvertebrates is also described as a negative phototactic response (Bishop and Hynes 1969; Müller 1974), especially in the presence of predators (Townsend 1980). To find shelter in the presence of predators increases mobility, e.g. daytime activity of mayflies (Söderström 1987) or escape behavior (Sih and Wooster 1994), and prolongs the residence time when a refugium is found.

Research on anthropogenic disturbances, particularly the effects of stream canalization, has been strongly focused on the roles that key habitat conditions might play in structuring the stream ecosystem and its functioning (Townsend and Hildrew, 1994) and in regulating the distribution patterns of its inhabitants. Most of these studies were performed on a large spatial scale and over a long term period. Consequently, these studies did not take into account the short-term mobility of macroinvertebrates. However, mobility on a small spatial scale can play a decisive role in the occurrence of species under stress. In recent years a lot of attention has been paid to the links between macroinvertebrate movements and the refuge function of physically undisturbed habitat patches in streams during disturbance and recovery processes (Pickett and White 1985; Pulliam 1988; Lancaster and Hildrew 1993; Olden et al. 2004). Due to these habitat refuges, macroinvertebrate assemblages can recover from flow disturbances within the time frame of one generation of the respective species, not involving immigration from nearby streams or stream sections (Badri et al. 1987; Hildrew et al. 1991).

To date, there has been little research examining the short-term, species-specific movement of stream macroinvertebrates across their heterogeneous stream bottom environments. Allan (1995) stated that the distance a stream animal travels per hour remains a mystery, though it can be important for our understanding of species distributions. Negishi and Richardson (2006) concluded that empirical data on routine, inter-patch movements that occur within hours to one day without strong environmental triggers (disturbance or recovery) are lacking, and suggested that the behavior displayed by stream macroinvertebrates might have a large stochastic component. Being distributed over heterogeneous patches raises the question whether short-term movement is solely related to resource availability, in the form of food and shelter (either because of predators or disturbances), or that it is a much more random behavior. This study aimed to better understand the role of short-term, small-scale movements of six species of lowland stream Trichoptera in relation to habitat and current. The key question we addressed was whether short-term movement either depends on habitat type and/or flow velocity, biological factors, like species adaptations, or if it is more stochastic. The ability or morphological adaptations of species to move more randomly between habitats might increase (i) survival rate as more or higher quality food resources can be located and/or (ii) the chance of being present in a refuges at the time of disturbance. In this line of reasoning we asked whether species occurring in more disturbed lowland streams were more mobile in comparison to species occurring more often in natural lowland streams.

Methods

Test species

The advantages of studying Trichoptera are that they live in lowland streams, comprise many species with considerable differences in ecology and distribution, and are easy to handle in the laboratory. We selected six species with similar habitat and food preferences and comparable behavior but a different

ecological distribution. The selected species represent positions along the gradient between natural and eutrophied, channelized lowland streams of the North-West European plain. All of these trichopterans live in organic habitats, like patches of leaves, particulate organic matter, or coarse detritus, in the upper courses of sandy lowland streams. This is one of two dominant habitats (organic matter and sand) in these lowland streams. The species were selected based on their representativeness for this stream type, comparability in traits, and practical ease to handle. The selection of the six trichopteran species was based on an extensive analysis of lowland streams in the Netherlands (Verdonschot and Nijboer 2004), comprising a multivariate analysis based on 949 samples taken in heavily degraded to near natural lowland streams. It showed a gradual distinction between natural lowland streams at one end of the gradient and degraded streams on the other end. We selected the trichopteran species as representatives of the conditions along this gradient. The species order along the gradient runs from *Micropterna sequax* (McLachlan, 1875), *Chaetopteryx villosa* (Fabricius, 1798), *Halesus radiatus* (Curtis, 1834) (all three closer to the natural end), to *Limnephilus lunatus* (Curtis, 1834), *Anabolia nervosa* (Curtis, 1834), and *Mystacides longicornis* (Linnaeus, 1758), all three closer to the disturbed end of the gradient. Further criteria were that the species had to be mobile, non-predatory, case-building, and not too rare. The latter criterion facilitated the field collection of large numbers of specimens; case-building species are easier to handle in the laboratory; non-predatory trichopterans have been shown to select their habitat and preference based primarily on the factors we wanted to study: flow, habitat, and food resources. Instars IV and V of *H. radiatus*, *M. sequax*, and *C. villosa*, were collected from the near natural lowland streams, known as Coldenhoven and Seelbeek, located in the central part of the Netherlands. *A. nervosa*, *L. lunatus*, and *M. longicornis*, were collected from three different channelized streams in the same area. Five of the test species belonged to the family of Limnephilidae (*M. sequax*, *C. villosa*, *L. lunatus*, *A. nervosa*, *H. radiatus*) and one to the closely related family Leptoceridae (*M. longicornis*); both families belong to the Limnephiloidea. We collected 300–400 specimens per species. Specimens were kept in the laboratory in an artificial rearing-stream with a variety of organic materials (detritus, leaves, twigs, water plants) and minerals (fine-to-coarse mineral sand). The larvae were maintained at a current velocity of 5–10 cm/s, a constant water temperature of 12 °C, and a day:night light regime of 16:8 h. Extra food was added weekly; the food consisted of fresh leaves, detritus, and wheat fragments. Experiments were performed with instar V larvae.

Artificial channels and habitat material

The experiments were conducted in four indoor, recirculating, stream mesocosms. Each mesocosm comprised four parallel channels for studying four replicate treatments. Water flow could be manipulated. Water level was maintained at 8 cm, with 3 cm of freely flowing water above habitat refuges with a thickness of 5 cm. A water depth of 3 cm is common in small, upper courses of lowland streams with average flow. Each channel was 3.2 m long and 15 cm wide, and was divided into 16 compartments of 13.4 cm × 14.3 cm. The bottom of each compartment consisted of a tray (depth 5 cm, contents 400 cm³) with a cover plate (Fig. 1). The trays of the first and last 3 compartments were empty, and the cover plates were closed to prevent access. The trays of the other 10 compartments were filled with habitat material; these were habitat compartments. The cover plates of the habitat compartments had a central opening (diameter 5.1 cm) to provide access to the tray and its specific habitat material. Specimens could enter a tray from above and reach the habitat material through this central opening. In this setup, the tray and its material acted as a refuge. All cover plates, and

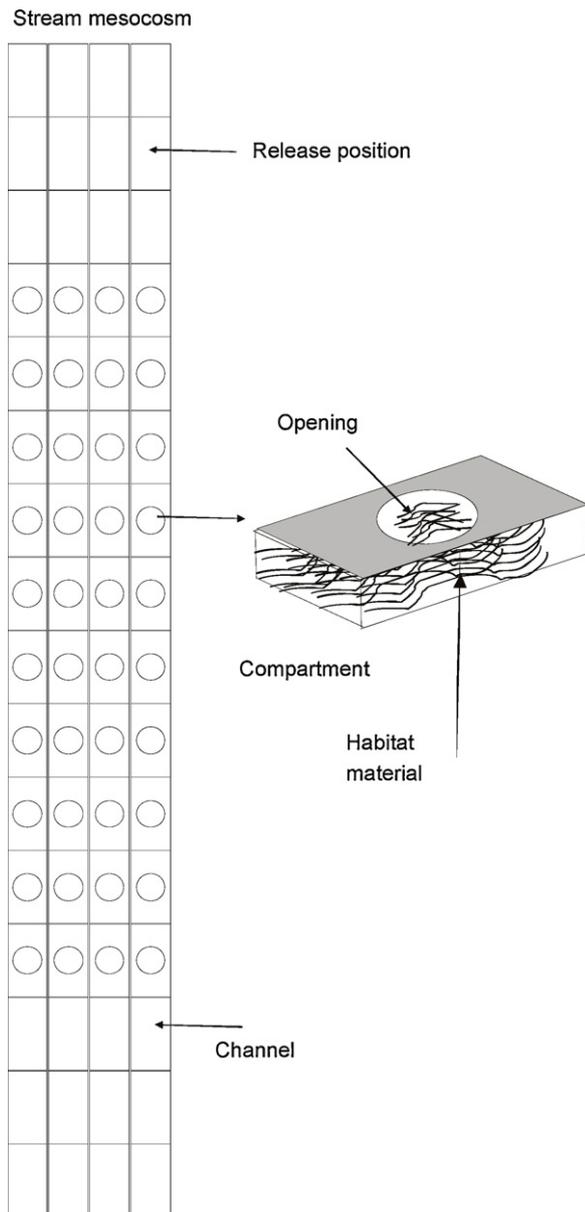


Fig. 1. Experimental set-up.

thus, the whole channel bottom, had a rough surface that consisted of sand grains glued to the tops of the plates; this imitated a natural, flat, sandy, stream bottom. Overall, this set-up allowed the test trichopterans to move around on the channel bottom (cover plates, with sand grains to provide roughness and grip) from one refugium (tray) with food (habitat material) to another. The planar channel structure provided fully comparable flow conditions along all ten habitat compartments. The cover plates shielded the habitat trays from the current and ensured that the protection from flow (the habitat tray) was equal for each habitat.

We selected organic and mineral habitat materials that were commonly found in lowland streams (Verdonschot and Nijboer 2004). The organic material was derived from fresh leaves (oak; *Quercus robur*) and divided into 3 size classes (1) coarse organic material ("leaves" consisting of whole leaves or leaf parts >2.0 mm); (2) fine organic material ("detritus" consisting of fractionated leaves of 0.25–2.0 mm); and (3) very fine organic material (organic sediment further indicated as "organic silt" consisting of fractionated oak leaves <0.25 mm). The organic

material had a high food quality; on average, the carbon (C) content was 507–523 g/kg and the nitrogen (N) content was 1186–1615 mmol/kg. This C/N ratio approached that of fresh *Alnus glutinosa* leaves (Balseiro and Albariño 2006). The mineral material was divided into 2 classes: (1) fine mineral material ("sand" with a grain size 0.25–2 mm); and (2) coarse mineral material ("gravel" with a grain size >2 mm). Different combinations of these five habitat material types were considered different "treatments". All five habitat treatments were provided twice. The five habitat treatments were randomly distributed among the upstream and downstream compartments of each channel, and in each new experiment.

Experimental set-up

All four channels of each of the four mesocosms were used in each experiment (Fig. 1). Thus, each experiment was performed with 4 replicates. Twenty individuals of each species were tested simultaneously in each channel (in total, 80 individuals/experiment). Each individual was used only once in an experiment. No mortality occurred during the experiments. Specimens were not individually marked. Before the start of an experiment, all individuals were positioned at the 2nd cover plate (recall that the first three cover plates were closed), upstream of the habitat compartments. The water remained calm (approximately 5 cm/s) to allow all specimens to settle on the cover plate. In each experiment, one flow treatment was applied, with a constant current velocity of 10, 30, or 50 cm/s. These three velocities spanned the average range of velocities that occurred under normal flow conditions in a natural lowland stream (Verdonschot and Nijboer 2004). The movement patterns of trichopterans were scored based on visual observations at daytime of the positions of individuals at 4, 8, 16 h, and at 1, 2, 4, and 6 days after release. The positions were classified as follows: (1) present in a habitat compartment (no response), (2) moving upstream, (3) moving downstream, (4) clinging to the channel bottom (cover plate), (5) floating in the water column, and (6) present at the end of the channel. The presence in the habitat tray was checked by visual observation of the tray content through the tray opening.

Data collection and statistics

To test the degree of mobility of the species and whether individuals increased or decreased their mobility over the whole observation period under constant flow of 10 cm/s, we counted the number of individuals present outside the habitat patches (trays) at each observation time point. The proportion of individuals of single species and of groups (the three species occurring more frequently towards the natural end versus the three occurring more frequently towards the disturbed end of the stream disturbance gradient) present outside the habitat patches were modeled by logistic regression and compared pairwise by likelihood ratio tests (McCullagh and Nelder 1989).

To test whether species stayed longer in specific habitats, which would lower the proportion of actively moving individuals, we calculated the proportion of individuals found in the same habitat over consecutive observation time points again under constant flow conditions of 10 cm/s. This habitat–time interaction was tested with multinomial logistic regression (McCullagh and Nelder 1989) to determine whether the frequency of movement reduced over time.

We considered three classes of habitat occupancies, defined as: (1) preference, when F_{hi} (fraction of individuals in a occupied habitat) > F_x (fraction on the move) > F_{ot} (fraction present in any other habitat); (2) subpreference when $F_{hi} = F_x$, and (3) independence when $F_{hi} < F_x < F_{ot}$. The difference in mobility, or the reverse (habitat residence), between species or between groups was tested by

Table 1
Habitat–time interactions of 6 trichopteran species over 6 days of observation (multinomial logistic regression, $P > 0.05$ was considered insignificant).

Time interval (day)	<i>C. villosa</i>	<i>H. radiatus</i>	<i>M. sequax</i>	<i>A. nervosa</i>	<i>L. lunatus</i>	<i>M. longicornis</i>
0.17–0.33	0.000**	0.000**	0.000**	0.000**	0.000**	0.000**
0.33–0.67	0.000**	0.000**	0.001**	0.000**	0.000**	0.000**
0.67–1	0.023*	0.009**	0.020*	0.000**	0.000**	0.000**
1–2	0.131	0.023*	0.021*	0.000**	0.000**	0.000**
2–3	0.159	0.047*	0.630	0.000**	0.015*	0.000**
3–4	0.179	0.015*	0.800	0.000**	0.012*	0.000**
4–5	0.171	0.048*	0.676	0.000**	0.012*	0.000**
5–6	0.458	0.073	0.789	–	–	–

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

comparing the total number of movements among all individuals for each species or group over the time period ranging from day 1 to day 6. These numbers were compared pairwise between species with the Fisher exact test, under the null hypothesis there was no difference between species (Fisher 1954). In addition, the proportion of individuals per habitat was compared and tested between species with the Fisher exact test.

To test the effect of current velocity on mobility, we counted the number of individuals on the move for each of the current velocities, and used logistic regression to analyze the relationship. The same approach was used to examine the proportion of individuals per species that were drifting for each of the 3 current velocities. The resulting models were pairwise compared by using likelihood ratio tests (McCullagh and Nelder 1989). All analyses were performed with Genstat (GenStat, Release 11.1 (PC/Windows), VSN International, Hemel Hempstead, UK). The significance of all tests was set at $P = 0.05$.

Results

Degree of mobility

C. villosa and *H. radiatus* occurred significantly more frequently outside the habitats during the first 24 h after release (20–40%) compared to the subsequent days (10–20%) (Likelihood ratio test; $P < 0.01$). *M. sequax* occurred least outside the habitats (~10% during the first 24 h and 0–10% on the following days). *A. nervosa* was rather mobile; over the whole period of observation, 25–40% of individuals occurred outside the habitats. *L. lunatus* and *M. longicornis* were very mobile during the first 24 h, when 45–80% of individuals occurred outside the habitats. After the first day, active movement decreased significantly in these species ($P < 0.01$), but still 20–50% of individuals continued moving around the subsequent days.

Effects of habitat on mobility

The habitat–time interaction was significant for the species coming from the more disturbed end of the environmental gradient (*A. nervosa*, *M. longicornis*, *L. lunatus*), indicating low habitat preference (Table 1). The individuals of these species continued moving between habitats over time and did not remain significantly longer in a specific habitat. The mobility of *H. radiatus*, *M. sequax*, and *C. villosa* was significantly lower (for this group on average 10–15% of the individuals actively moved around) compared to the former (30–40%) (Fischer exact test). The habitat–time interaction for the first 24 h was also significant for these species (except at exactly 24 h after release for *C. villosa*). After the first 24 h, only *H. radiatus* moved between habitats at almost all observation time points; the other two species showed less active movement and high habitat preference (Table 1). In this analysis, we observed a ‘release

effect’: high mobility occurred shortly after release (within 24 h). Therefore, the first 24 h of observation was omitted from all further analyses.

Habitat preference

H. radiatus, *M. sequax*, and *C. villosa* remained significantly longer in the leaves habitat (Fig. 2). *H. radiatus* was found significantly less often in sand and organic silt; *C. villosa* was found significantly less often in sand; and *M. sequax* showed subpreference in detritus, sand, and gravel. Finally, *C. villosa* showed subpreference in gravel. *A. nervosa*, *L. lunatus*, and *M. longicornis* were relatively independent from all habitats. Nonetheless, *A. nervosa* showed subpreference in detritus, and *L. lunatus* in leaves. *A. nervosa*, *L. lunatus*, and *M. longicornis* were found significantly less often in all other habitats; however, *M. longicornis* was more often found in the habitats of leaves and detritus and less often in the mineral habitats.

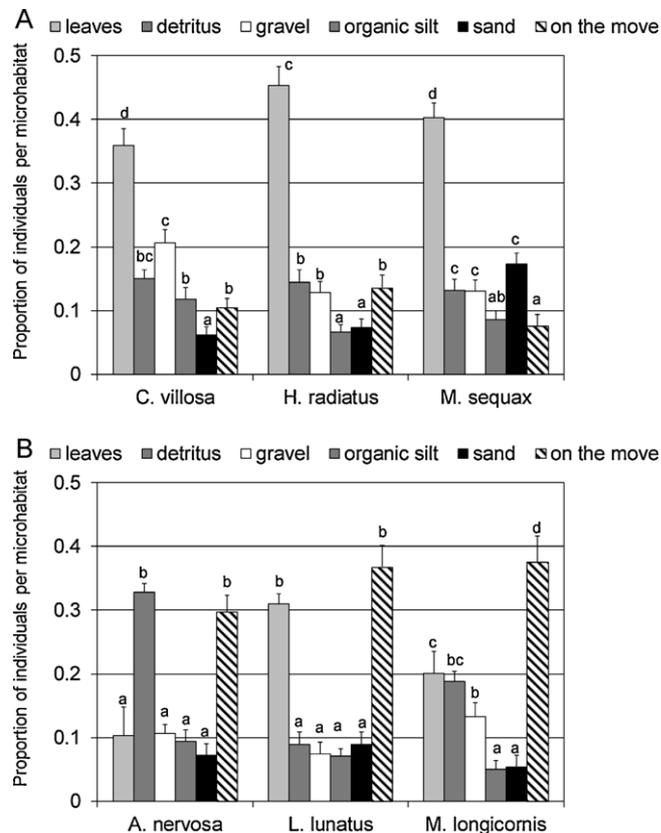


Fig. 2. Mean proportions of individuals (± 1 SD) of (A) restricted distributed species and (B) widespread species that were found in 1 of the habitats or on the move. Different letters indicate significant differences (Fisher exact test, $P < 0.05$).

Table 2
Mean proportion of individuals found in each habitat for 6 trichopteran species.

Habitat	Leaves	Sand	Detritus	Gravel
<i>C. villosa</i>	0.3573 c	0.06289 a	0.1473 ab	0.2054 b
<i>H. radiatus</i>	0.4489 d	0.07265 a	0.1431 ab	0.1259 a
<i>M. sequax</i>	0.4031 cd	0.16931 b	0.1248 ab	0.1334 a
<i>A. nervosa</i>	0.1029 a	0.07256 a	0.3350 c	0.1073 a
<i>L. lunatus</i>	0.3107 c	0.08983 a	0.0916 a	0.0738 a
<i>M. longicornis</i>	0.1998 b	0.05442 a	0.1922 b	0.1345 ab

Different letters indicate significant differences between species within a habitat (Fisher exact test, $P < 0.05$).

Differences between species habitat preferences were also examined. Among all the species, *A. nervosa* was least frequently found in the leaves habitat, and *H. radiatus* and *M. sequax* were significantly more frequently found in leaves (Fischer exact test) (Table 2).

Effects of an increase in current velocity

At current velocities of 10 cm/s and 30 cm/s, significantly (likelihood ratio test; $P < 0.05$) more *A. nervosa* individuals actively moved around, and significantly less *M. sequax* and *L. lunatus* individuals were observed outside a habitat (Fig. 3). At 50 cm/s, most *A. nervosa* individuals continued to actively move around, but high numbers of *H. radiatus* and *M. longicornis* also showed active movement. In contrast, *M. sequax* individuals move around significantly less than the other species.

The proportion of individuals drifting increased significantly (likelihood ratio test; $P < 0.05$) for *C. villosa* (Fig. 4). A comparable increase is shown by *H. radiatus*, but this was not significant. Both *M. sequax* and *A. nervosa* drifted significantly more at a current of 50 cm/s. *M. sequax* entered drift least frequently of all species tested, and also the number of drifting *A. nervosa* was limited. While *L. lunatus* and *M. longicornis* drifted significantly less at a current of 10 cm/s, overall both species entered drift most frequently of all species tested.

Discussion

Flume limitations and release effects

Flume experiments cannot one-to-one be extrapolated to the natural conditions in a stream. For example, in our experiments the stream bottom consisted of glued sand, while in a natural lowland stream it consists of a continuously shifting substrate. Nonetheless, despite some experimental limitations flumes are ideal systems to

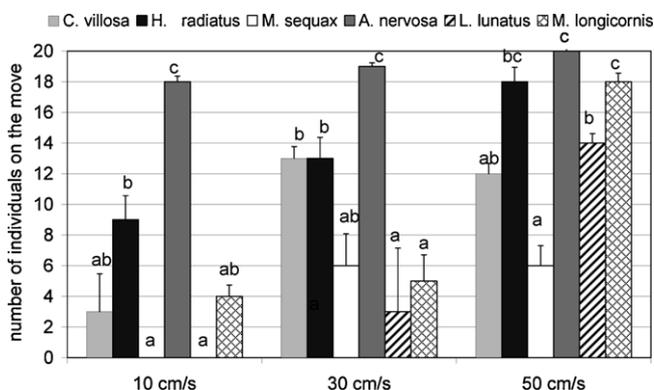


Fig. 3. Mean number of individuals (± 1 SD) on the move at different current velocities. Different letters indicate significant differences between species (likelihood ratio test; $P < 0.05$).

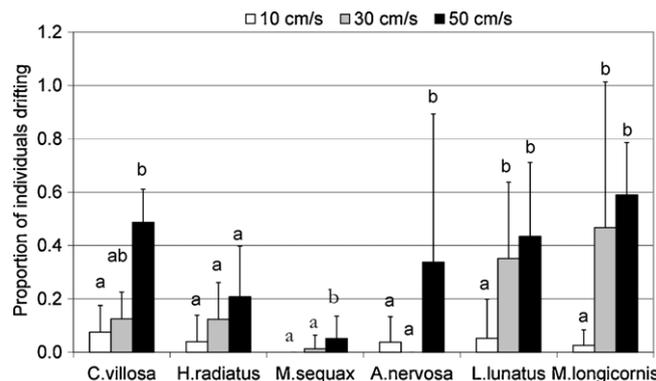


Fig. 4. Mean (± 1 SD) proportions of individuals that drifted at current velocities of 10, 30, and 50 cm/s. Different letters indicate significant differences (likelihood ratio test; $P < 0.05$).

test hypotheses on the level of individual animals at a small spatial scale and over short time periods. With such knowledge, future studies could determine whether organisms move in their natural environment as they do in experimental conditions.

The first 24 h after release, most individuals moved around and were very active. This ‘release effect’ may be the expression of three different types of behavior: (1) finding shelter or refugia and food after a disturbance, (2) coping with the stress related to the catch and/or release manipulation or (3) accommodation/orientation behavior. It was clear that ‘release effects’ should be excluded from the other responses in these experiments. After removing the ‘release effect’, we found that all species more or less moved between habitats, but at different rates.

Habitat preference and resource utilization

In our experiments, high quality food quality and shelter were readily available. Nevertheless, we observed active movement. The reason for active movement can be twofold: habitat preference and resource exploitation or be stochastic.

Habitat preference would reduce the frequency of movement. Habitat preference reflects finding and remaining in a preferred resource of food or shelter. This behavior results in maximal resource use. Individuals only leave the habitat patch in response to decreasing food quality or availability, competition, the arrival of predators, or a negative impact of a change in environmental conditions, such as an increase in water flow. In our experiments, the only factors that would drive individual movement were food quality and behavioral drivers. Food quality was not expected to deteriorate over the duration of the experiments, which would mean that behavioral drivers represented the stronger factor. All the trichopterans in the present study were both shredders and collector-gatherers. Among these, the species from the more natural end of the environmental gradient showed in the experiments a preference for leaves, but the other 3 species did not show any significant preference. This indicated that for the latter food quality was probably equivalent among the different organic habitat types that we implemented. Furthermore, we observed subpreference of *M. sequax* and *C. villosa* to sand and gravel. The three species from the disturbed end of the gradient frequently moved from potential food habitats (organic) to non-food habitats (mineral). Thus, food was an important, but not the only factor underlying habitat preference in the species tested.

Physical habitat structures may be preferred because they serve as refugia and facilitate survival (Sedell et al. 1990). Stream margins, deep pools, interstitial zones, macrophyte patches, and leaf accumulations can be flow refuges (Bishop 1973; Williams 1984). Lowland streams have a sandy substrate, but lack interstitial zones.

Furthermore, sandy substrates are subject to frequent scour, and thus, are not ideal refuges (Palmer et al. 1992). Therefore, in lowland streams, coarse particulate organic matter (CPOM) represents an important potential refuge. The distribution, quality and quantity of these flow refuges are variable in space and time, because CPOM may be discharged from the habitat. Consequently, CPOM habitat refuges are frequently disrupted during high flow events (Webster et al. 1999). Only habitats that can withstand high flows provide sufficient shelter, like accumulations of twigs and branches, macrophyte stands, complex root structures at the stream margins, and leaf dams (Bilby 1981). It is not known whether individual organisms can differentiate between stable and unstable CPOM habitats, like leaf accumulations versus leaf dams. However, the function of a habitat as refuge, at least within our experimental conditions, was less relevant, due to the lack of peak flows or predators.

Habitat preference may also represent sheltered resting behavior. The same triggers as accounted for resource use behavior would induce individuals to leave, except that food scarcity would be replaced by hunger. Sheltered resting can be important for individual fitness. Negative phototactic species typically seek leaf packages that provide shaded or dark areas. In this study, the species from the more natural end of the gradient tended to show more shelter seeking or negative phototactic behavior than the other species. However, shelter was equivalent in all habitats. Therefore, food was expected to be a more important driver than shelter. Indeed, in the experiments the organic habitats were more often occupied than the mineral habitats. The importance of shelter in the habitat preference behavior could be tested further in follow-up experiments by providing habitats comprised of non-edible leaves.

The role of drift

In general, the direction of movement of mobile trichopterans can be longitudinal (upstream, downstream), lateral (e.g. nearing bank structures), or vertical (entering the water column by swimming or drifting or crawling deep into microhabitat patches). Most movement can be regarded as active, even actively entering drift. Upstream movement, or positive rheotaxis, requires active, non-random movement and costs energy, and importantly it may be a compensatory mechanism for downstream drift. Only dislodgement by drag or lift forces is truly passive. In this study, it was found that with increasing current velocity, the number of individuals entering drift increased. Drift densities can increase or decrease with increasing flow (Poff and Ward 1991), depending on near bed flow, streambed topography (Buffin-Bélanger et al. 2003), habitat conditions (Poff and Ward 1991), food availability (Kohler 1985), photoperiod (Ciborowski 1979), and species or species group. The species tested here drifted more at higher flows, which was consistent with the observation of Winterbottom et al. (1997). They studied patch scale colonization and also found a relationship between drift and flow rates.

Downstream drift can also be of considerable importance as a pathway for colonizing new areas (Townsend and Hildrew 1976; Bird and Hynes 1981; Allan 1995). It contributes to the resilience of stream ecosystems (Fenoglio et al. 2002). Because upstream depletion is rarely documented (Neves 1979), downstream movement and drift must be compensated by active upstream movement (Kopp et al. 2001). Hershey et al. (1993) concluded that, based on quantitative data in *Baetis*, the distances that individuals moved upstream were equal to the distances that they had drifted downstream. Those experiments showed that individuals chose a direction of movement, and thus, movement was not random. The variability in species responses to flow observed in these experiments indicated that other environmental or biological factors played a role in the tendency to drift. In our conditions, competition and predation was low or absent. Thus, the variable drift

responses could be attributed to species specific differences in functional morphology and intrinsic behavior. Drift occurred more frequently in species which were more often found in more or less disturbed streams in comparison to those from more natural streams. This suggests that mobility increased the risk of being dislodged. Nonetheless, it should be noted that it also increases the chance of finding a more suitable environment.

Stochastic movement

All species moved around in the experiments, especially the first day, but also afterwards. *C. villosa*, *H. radiatus* and *M. sequax* moved, on average, twice as less in comparison to *A. nervosa*, *L. lunatus* and *M. longicornis*. These movements out of suited habitats, that provide both food and shelter (as our organic trays did) points to random movement. Under favorable environmental conditions, short-term, active movement most likely represents the search for food and shelter; the alternative is stochastic movement. The latter posed the question of why, after finding a suitable patch, would an individual move towards a new habitat. Moreover, was there always a purpose for short-term movements?

Pearson and Jones (1987) concluded that the immense capacity for movement of macroinvertebrates in chalk streams was remarkable and unnecessary for that environment. The same appears to be true for lowland streams, where abundant organic material provided excess food. Movement always implies an energy cost, but the amount is unclear. Most individual animals will constantly endeavor to maximize their fitness; they will be occupied with maintenance, growth, and survival movements (Dill 1987). Another reason for more stochastic active movements might be to regularly change the aggregation of animals or change the habitat to reduce predator learning and thus, the risk of predation (Charnov et al. 1976). Thus, there is a trade-off between foraging and anti-predation behavior (Dill 1987). Although in this study the trichopteran cases provide camouflage and protection, Wooster and Sih (1992) pointed out that case building trichopterans are preyed upon by both vertebrate and invertebrate predators, particularly the latter. So, stochastic movement as anti-predation behavior would suit our test species. Competition for food or shelter (refuge) could also induce movement and be another factor for random movement.

Mobility in relation to the occurrence along the environmental gradient

In general, our species from the more disturbed end of the gradient were on average 20% more active than the species occurring at the more natural end. More in detail, individual species showed species – specific activity. The greater activity of more tolerant species observed in this experiment suggests that species that are more tolerant to environmental stress may be associated with a higher mobility. Intolerant species will be less mobile. Mobility may provide resilience in more stressful or dynamic environments, because individuals can move away during unfavorable conditions and return when the disturbance stops (Townsend and Hildrew 1994). However, mobility can be an energetically costly avoidance behavior. The benefits of small, random movements for more tolerant species may also be to distribute the risk of being predated or trapped in unfavorable environmental conditions. At the population level, this behavior would ensure survival. Furthermore, patches change continuously due to changes in, for example, current velocity, physical movement of the habitat material, and food quality. The latter can change frequently due to temporal variations in bacterial and fungal growth (Hieber and Gessner 2002), particularly when nutrient levels vary regularly

(Gulis and Suberkropp 2003). Movement of individuals can increase the chances of encountering high quality leaves and detritus.

Flow effects on mobility

We tested the effect of current velocity on mobility. Flow patterns in lowland streams are variable in space and time, even on a daily basis. As a result, organisms experience increasing and decreasing forces of drag and lift (Gordon et al. 2004); they oppose these forces with individual tenacity and an optimal area of attachment (Denny 1988). Increases in flow tend to dislodge organisms (Hart and Merz 1998), and in response, organisms have developed adaptations for increasing attachment to the substrate or reducing their size (Vogel 1994). There is a trade-off between the abilities to move and to attach. Mobile organisms have a smaller attachment area and dislodge easily; but the ability to move rapidly to avoid flow accelerations could also increase survival when refuges are present. Trichopterans tend to move around in areas where current velocity and turbulent kinetic energies are relatively low (Rice et al. 2008). This suggests that they are able to locate velocity gradients. This trait would allow them to exploit pathways that minimize energy loss in opposing drag and lift forces, thereby avoiding dislodgement. Thus, one would expect trichopterans to move little, slowly, and over short distances in response to increasing flow (Lancaster et al. 2006). Surprisingly, in our experiments, all the test species tended to become more active and moved around more frequently when current velocity increased, except for *M. sequax*, which showed a high resistance to flow variation. This may partly be explained by the suggestion of Hart and Merz (1998) that habitats with high flow are likely to create prey refuges. Increased movement with flow acceleration may also indicate the behavior of seeking a place to avoid dislodgement. The variability in species responses to flow we observed, indicated that other environmental or biological factors may also played a role.

Other biological factors

Other biological can refer to body and case morphology, case building, the use of food resources and the instar. The body morphology of *M. sequax*, *H. radiatus* and *A. nervosa* is quite comparable (body length: body width 19:3.5, 22:5, and 18:4, respectively) but the case morphology differs. *M. sequax* demonstrated the lowest flow response. This species also carries the heaviest case (average dry weight 0.43 mg). The case provides resistance to velocity but the animal must be strong to carry the case upstream. The two other species, *H. radiatus* and *A. nervosa*, also have a large body size, but their case is less heavy and largely organic (average dry weight 0.20 and 0.26 mg, respectively).

The narrow and small *M. longicornis* (body length: body width 11.5:1.5), with a mineral case (average dry weight 0.01 mg), could have an advantage of its size and case weight under shear stress conditions. This holds true for the lower but not for the higher velocities. The body morphology of *L. lunatus* and *C. villosa* is more or less comparable (body length: body width 17:3, and 15:3, respectively). *L. lunatus* has a longer but almost full organic case (average dry weight 0.03 mg), while *C. villosa* builds a shorter and mainly mineral case (average dry weight 0.15 mg). At lower velocities *L. lunatus* can be characterized as a somewhat stronger animal but at higher velocities its organic case makes the species more vulnerable. *C. villosa* was less responding, contrary to its case material, and as such it maybe stronger in comparison to *L. lunatus*. In general, *M. sequax* and *M. longicornis* support the hypothesis that not body morphology but case material drives the behavioral response type to velocity or shear stress. Nonetheless, *A. nervosa* showed the opposite.

Not only the case itself but also the need for material to build or maintain the case could induce short term movements. Hansell (1968), Prestidge (1977) and Stuart and Currie (2001) showed that case-repair behavior is not distinguishable from normal case-building behavior. Maintenance and repair could lead to short-term movements.

In the experiments fine and coarse organic particles were offered as food resources. From the species tested it is known that they feed on these particles but also that most are facultative shredders. For example *A. nervosa* also feeds on *Potamogeton* (Jacobsen and Sand-Jensen 1994) and *L. lunatus* also feeds on *Nasturtium officinale* (Jacobsen 1993), thus the species tested can use or even need other kinds of food. Friberg and Jacobsen (1994) indicated that detritivore-shredders, like *Sericostoma personatum*, do not per se prefer leaf litter, but in fact actively select other food items such as filamentous green algae or macrophytes, even when terrestrial leaf litter is abundant. This is most probably to optimize the overall nutritional value. Search for optimizing the food sources can also induce short term movements (Hart and Resh 1980).

It should also be noted that mobility may change depending on instar and the daily light phase. Smaller instars of for example *C. villosa* and *Potamophylax cingulatus* were active for the entire day, whereas final instar larvae showed a strictly nocturnal pattern (Lehmann 1972). As in the experiments last instars were tested, it is assumed that their responses are mutually comparable.

In conclusion, basic knowledge of the trade-offs between costs and benefits, like predation–anti-predation movements, and resource-competition movements, is needed to further develop evolutionary-based, functional approaches in stream ecology. For example, Tomaszewski (1973) showed that the elongation of the second and third pairs of legs was correlated with mobility. Although portable cases appear to have evolved initially as protection or camouflage for larvae moving to food resources, they also provide ballast, buoyancy, streamlining, structural rigidity, and respiratory efficiency (Mackay and Wiggins 1973). Thus morphological and behavioral adaptations facilitate movement and flexibility. In this study, the more tolerant species showed more mobility and flexibility than the species occurring in more natural stream conditions. Thus, mobility appears to be an adaptation that allows the individual to distribute risks. The risk of leaving a food patch and encountering less suitable patches, being eaten while moving around, or even being washed away by a flood appeared to be less important than the advantages of avoiding food depletion in a patch, being located by a predator, or being outcompeted from a resource. Thus, mobility can be regarded as an adaptation for r-strategists.

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References

- Allan, J.D., 1995. Stream Ecology. Structure and Function of Running Waters. Chapman and Hall, London.
- Badri, A., Giudicelli, J., Prevot, G., 1987. Effects of flood on the benthic macroinvertebrate community in a Mediterranean river, the Rdat (Morocco). *Acta Ecologica-Ecologia Generalis* 8, 481–500.
- Balseiro, E., Albariño, R., 2006. C-N mismatch in the LEaf Litter-Shredder relationship of an Andean Patagonian Stream Detritivore. *J. N. Am. Benthol. Soc.* 25, 607–615.
- Bilby, R.E., 1981. Role of organic debris darns in regulating the export of dissolved and particulate matter from a forested watershed. *Ecology* 62, 1234–1243.

- Bird, G.A., Hynes, H.B.N., 1981. Movements of immature aquatic insects in a lotic habitat. *Hydrobiologia* 77, 103–112.
- Bishop, J.E., 1973. Observations on the vertical distribution of the benthos in a Malaysian stream. *Freshwater Biol.* 3, 147–156.
- Bishop, J.E., Hynes, H.B.N., 1969. Upstream movements of the benthic invertebrates in the Speed river, Ontario. *J. Fish Res. Board Can.* 26, 279–298.
- Buffin-Bélanger, T., Reid, I., Rice, S.P., Chandler, J.H., Lancaster, J., 2003. A casting procedure for reproducing coarse-grained sedimentary surfaces. *Earth Surf. Proc. Land.* 28, 787–796.
- Buffin-Bélanger, T., Rice, S.P., Reid, I., Lancaster, J., 2006. Spatial heterogeneity of near-bed hydraulics above a patch of river gravel. *Water Resources Research* 42, W04413, doi:10.1029/2005WR004070.
- Buss, D.F., Baptista, D.F., Nessimian, J.L., Egler, M., 2004. Substrate specificity, environmental degradation and disturbance structuring macroinvertebrate assemblages in neotropical streams. *Hydrobiologia* 518, 179–188.
- Charnov, E.L., Orians, G.H., Hyatt, K., 1976. Ecological implications of resource depression. *Am. Nat.* 110, 247–259.
- Ciborowski, J.H., 1979. The effects of extended photoperiods on the drift of the mayfly *Ephemera subvaria* McDunnough (Ephemeroptera: Ephemerellidae). *Hydrobiologia* 62, 209–214.
- Denny, M.W., 1988. *Biology and the Wave-swept Environment*. Princeton University Press, Princeton, NJ.
- Dill, L.M., 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behavior. *Can. J. Zool.* 65, 803–811.
- Dobson, M., Hildrew, A.G., 1992. A test of resource limitation among shredding detritivores in low order streams in southern England. *J. Anim. Ecol.* 61, 69–77.
- Fenoglio, S., Agosta, P., Bo, T., Cucco, M., 2002. Field experiments on colonization and movements of stream invertebrates in an Apennine river (Visone, NW Italy). *Hydrobiologia* 474, 125–130.
- Fisher, R.A., 1954. *Statistical Methods for Research Workers*, 12th ed. Oliver and Boyd, Edinburgh.
- Friberg, N., Jacobsen, D., 1994. Feeding plasticity of two detritivore-shredders. *Freshwater Biol.* 32, 133–142.
- Gordon, N.D., McMahon, T.A., Finlayson, B.L., 2004. *Stream Hydrology. An Introduction for Ecologists*, 2nd ed. John Wiley and Sons, Chichester.
- Gulis, V., Suberkropp, K., 2003. Leaf litter decomposition and microbial activity in nutrient enriched and unaltered reaches of a headwater stream. *Freshwater Biol.* 48, 123–134.
- Hansell, M.H., 1968. The selection of house building materials by the caddisfly larva, *Agapetus fuscipes*. *Rev. Comportement Anim.* 2, 90–101.
- Hart, D.D., Resh, V.H., 1980. Movement patterns and foraging of a stream caddisfly larvae. *Can. J. Zool.* 58, 1174–1185.
- Hart, D.D., Clark, B.D., Jasentuliyana, A., 1996. Finescale field measurement of benthic flow environments inhabited by stream invertebrates. *Limnol. Oceanogr.* 41, 297–308.
- Hart, D.D., Merz, R.A., 1998. Predator–prey interactions in a benthic stream community: a field test of flow-mediated refuges. *Oecologia* 114, 263–273.
- Hershey, A.E., Pastor, J., Peterson, B.J., Kling, G.W., 1993. Stable isotopes resolve the drift paradox for *Baetis* mayflies in an Arctic River. *Ecology* 74, 2315–2325.
- Hieber, M., Gessner, M.O., 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. *Ecology* 83, 1026–1038.
- Hildrew, A.G., Dobson, M.K., Groom, A., Ibbotson, A., Lancaster, J., Rundle, S.D., 1991. Flow and retention in the ecology of stream invertebrates. *Verh. Int. Ver. Theor. Angew. Limnol.* 24, 1742–1747.
- Hildrew, A.G., Giller, P.S., 1994. Patchiness, species interactions and disturbance in the stream benthos. In: Giller, P.S., Hildrew, A.G., Raffaelli, D.G. (Eds.), *Aquatic Ecology: Scale, Pattern, and Process*. Blackwell Scientific Publications, Oxford, pp. 21–62.
- Hildrew, A.G., Townsend, C.R., 1980. Aggregation, interference and foraging by larvae of *Plectrocnemia conspersa* (Trichoptera: Polycentropodidae). *Anim. Behav.* 28, 553–560.
- Hynes, H.B.N., 1970. *The Ecology of Running Waters*. Liverpool University Press, Liverpool.
- Jacobsen, D., 1993. Trichopteran larvae as consumers of submerged angiosperms in running waters. *Oikos* 67 (2), 379–383.
- Jacobsen, D., Sand-Jensen, K., 1994. Growth and energetics of a Trichopteran larva feeding on fresh submerged and terrestrial plants. *Oecologia* 97 (3), 412–418.
- Kohler, S.L., 1985. Identification of stream drift mechanism, an experimental and observational approach. *Ecology* 66, 1749–1761.
- Kopp, M., Jeschke, J.M., Gabriel, W., 2001. Exact compensation of stream drift as an evolutionarily stable strategy. *Oikos* 92, 522–530.
- Lancaster, J., 2008. Movement and dispersion of insects in stream channels, what role does flow play? In: Lancaster, J., Briers, R.A. (Eds.), *Aquatic Insects, Challenges to Populations*. CAB International, Wallingford, pp. 139–157.
- Lancaster, J., Buffin-Bélanger, T., Reid, I., Rice, S.P., 2006. Flow- and substratum-mediated movement by a stream insect. *Freshwater Biol.* 51, 1053–1069.
- Lancaster, J., Hildrew, A.G., 1993. Flow refugia and the microdistribution of lotic macroinvertebrates. *J. N. Am. Benthol. Soc.* 12, 385–393.
- Lancaster, J., Hildrew, A.G., Gjerlov, C., 1996. Invertebrate drift and longitudinal transport processes in streams. *Can. J. Fisheries Aquatic Sci.* 53, 572–582.
- Lancaster, J., Hildrew, A.G., Townsend, C.R., 1990. Stream flow and predation effects on the spatial dynamics of benthic invertebrates. *Hydrobiologia* 203, 177–190.
- Lehmann, U., 1972. Tagesperiodisches Verhalten und Habitatwechsel der Larven von *Potamophylax luctuosus* (Trichoptera). *Oecologia* 9, 265–278.
- Mackay, R.J., Wiggins, G.B., 1973. Ecological diversity in Trichoptera. *Annu. Rev. Entomol.* 24, 185–208.
- McCullagh, P., Nelder, J.A., 1989. *Generalized Linear Models*, 2nd ed. Chapman and Hall, London.
- Müller, K., 1974. Stream drift as a chronobiological phenomenon in running water ecosystems. *Annu. Rev. Ecol. Syst.* 5, 309–323.
- Negishi, J.N., Richardson, J.S., 2006. An experimental test of the effects of food resources and hydraulic refuge on patch colonization by stream macroinvertebrates during spates. *J. Anim. Ecol.* 75, 118–129.
- Neves, R.J., 1979. Movements of larval and adult *Pycnopsyche guttifer* (Walker) (Trichoptera, Limnephilidae) along Factory Brook, Massachusetts. *Am. Midl. Nat.* 102, 51–58.
- Olden, J.D., Hoffman, A.L., Monroe, J.B., Poff, N.L., 2004. Movement behavior and dynamics of an aquatic insect in a stream benthic landscape. *Can. J. Zool.* 82, 1135–1146.
- Palmer, M.A., Bely, A.E., Berg, K.A., 1992. Responses of invertebrates to lotic disturbances, a test of the hyporheic hypothesis. *Oecologia* 89, 182–194.
- Pearson, R.G., Jones, N.V., 1987. Short-term movements of chalk-stream invertebrates. *Freshwater Biol.* 18, 559–568.
- Pickett, S.T.A., White, P.S., 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Inc., Orlando, FL.
- Poff, N.L., Ward, J.V., 1989. Implications of streamflow variability and predictability for lotic community structure, a regional analysis of streamflow patterns. *Can. J. Fisheries Aquatic Sci.* 46, 1805–1818.
- Poff, N.L., Ward, J.V., 1991. Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. *Can. J. Fisheries Aquatic Sci.* 48, 1926–1936.
- Prestidge, R.A., 1977. Case-building behaviour of *Pycnocentroseseria* (Trichoptera: Sericostomatidae). *N. Z. Entomol.* 6, 296–301.
- Pulliam, H.R., 1988. Sources, sinks and population regulation. *Am. Nat.* 132, 652–661.
- Rice, S.P., Buffin-Bélanger, T., Lancaster, J., Reid, I., 2008. Movements of a macroinvertebrate (*Potamophylax latipennis*) across a gravelbed substrate, effects of local hydraulics and microtopography under increasing discharge. In: Habersack, H., Hoey, T., Piegay, H., Rinaldi, M. (Eds.), *Gravel-bed Rivers, From Process Understanding to River Restoration*. Elsevier BV, Amsterdam, pp. 637–660.
- Sedell, J.R., Reeves, G.H., Hauer, F.R., Stanford, J.A., Hawkins, C.P., 1990. Role of refugia in recovery from disturbances, modern fragmented and disconnected river systems. *Environ. Manage.* 14, 711–724.
- Sih, A., Wooster, D.E., 1994. Prey behavior, prey dispersal and predator impacts on stream prey. *Ecology* 75, 1207–1217.
- Söderström, O., 1987. Upstream movements of invertebrates in running waters – a review. *Arch. Hydrobiol.* 111, 197–208.
- Stuart, A.E., Currie, D.C., 2001. Using caddisfly (Trichoptera) case-building behaviour in higher level phylogeny reconstruction. *Can. J. Zool.* 79, 1842–1854.
- Tomaszewski, C., 1973. Studies on the adaptive evolution of the larvae of Trichoptera. *Acta Zoologica Cracoviensia* 18, 1–93.
- Townsend, C.R., 1980. *The Ecology of Streams and Rivers*. Studies in Biology, vol. 122. Edward Arnold, London.
- Townsend, C.R., Hildrew, A.G., 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. *J. Anim. Ecol.* 45, 759–772.
- Townsend, C.R., Hildrew, A.G., 1994. Species traits in relation to a habitat template for river systems. *Freshwater Biol.* 31, 265–275.
- Verdonschot, P.F.M., Nijboer, R.C., 2004. Macrofauna en vegetatie van de Nederlandse beken. Een aanzet tot beoordeling van de ecologische toestand. Wageningen, Alterra, Alterra-rapport 756.
- Vogel, S., 1994. *Life in Moving Fluids*, 2nd ed. Princeton University Press, Princeton, NJ.
- Ward, G.M., Cummins, K.W., 1979. Effects of food quality on growth of a stream detritivore, *Paratendipes albianus* (Meigen) (Diptera, Chironomidae). *Ecology* 60, 57–64.
- Webster, J.R., Benfield, E.F., Ehrman, T.P., Schaeffer, M.A., Tank, J.L., Hutchens, J.J., D'Angleo, D.J., 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. *Freshwater Biol.* 41, 687–705.
- Williams, D.D., 1980. Temporal patterns in recolonization of stream benthos. *Arch. Hydrobiol.* 90, 56–71.
- Williams, D.D., 1984. The hyporheic zone as a habitat for aquatic insects and associated arthropods. In: Resh, V.H., Rosenberg, D.M. (Eds.), *The Ecology of Aquatic Insects*. Praeger, New York, NY, pp. 430–455.
- Winterbottom, J.H., Orton, S.E., Hildrew, A.G., 1997. Field experiments on the mobility of benthic invertebrates in a southern English stream. *Freshwater Biol.* 38, 37–47.
- Wooster, D., Sih, A., 1992. A review of the drift and activity responses of prey to predator presence. *Oikos* 73, 3–8.