Incipient motion and drift of benthic invertebrates in boundary shear layers

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ABSTRACT: The present study aimed to identify threshold shear stresses to cause benthic invertebrates to drift in boundary shear layers. Laboratory experiments were carried out in a small tilting flume, 10 cm wide and 3 m long with a closed recirculation system and a fixed sand bottom of uniform grain size. Benthic invertebrates from different orders (Achaeta, Gastropoda, Crustacea, Ephemeroptera, Odonata, Megaloptera, Trichoptera) were collected from a lowland river (Spree, Germany) and kept in aquariums to adapt to the laboratory conditions. Individuals were placed in the flume at low flow conditions, before gradually increasing the discharge until drift occurred. Photos were taken from the side through the flume walls to capture the behaviour and strategies of the organisms to cope with the flow. Photos against millimeter grid graph paper in the background were taken for each individual in order to quantify the body height and length exposed to flow. Subsequently, velocity and shear stress profiles were measured above the drift location with an Acoustic Doppler Velocimeter (ADV, Nortek Vectrino). Bed shear stresses were determined by extrapolation of the Reynolds shear stress profiles in subcritical flow conditions. For supercritical flow conditions, a simple particle tracking velocimetry was applied to determine velocity profiles. Bed shear stress was then estimated from fitting of a log-law. Results are presented in tabular form, containing the average drift shear stress and drift velocity for 15 taxa commonly found in lowland rivers. Drift shear stresses, which can be interpreted as abiotic 'absence' criteria of the species, were in most cases exceeding the conditions of preferential habitats and incipient motion threshold of the sediments. However, it was observed that sudden changes in the angle of flow attack (e.g. by burst events or surface waves) or direct interaction with sediment motion (animals hit by moving grains or erosion of the grains serving as anchorage) were key factors triggering invertebrate drift.

Keywords: Ecohydraulics, Invertebrate drift, Boundary shear layer, Shear stress, Habitat modelling

1 INTRODUCTION

Benthic invertebrates are important components of stream ecosystems because they transform organic material, the principal energy inputs in lowland streams, into body tissue used by higher trophic levels (Orth and Maughan, 1983). Hydrodynamic processes shape stream ecosystems and affect benthos in different ways; directly by altering their 'performance' (movement, respiration) and indirectly by influencing abiotic and biotic variables of their environment, e.g. substratum and food supply (Hart and Finelli, 1999). Quantification of invertebrate dynamics depending on flow is difficult and the majority of previous research was directed towards more universal preferential habitat models, like 'CASIMIR' (Bratrich and Jorde, 1997) or 'PHABSIM' (Waddle, 2001). A qualitative suitability of the habitat for the organisms is determined based on average hydraulic and morphologic quantities such as mean water depth, velocity or median grain size, and linked to the ecological preference of the species. Habitat models have been proved of high practical value, e.g. for river restoration purposes and species reintroduction (Gore et al., 1998). Nevertheless, it is desirable to model invertebrate dynamics in higher detail and refined spatial and temporal scales. Extended advection-diffusion models provide a basis for such an approach (Hart and Finelli, 1999). The development of such a mechanistic model is the aim of a current bilateral research project on hydraulic-ecological interaction in meander bends, carried out at IGB. The challenge

lies in relating invertebrate behavior and population dynamics to physical parameters of the flow. We started here with a simple individual-based behavioural aspect, which is triggered by abiotic factors: benthic invertebrate drift due to hydraulic stress in a boundary layer. Peak stresses, that organisms are no longer able to sustain and cause their detachment from the bed, are interpreted as a hydraulic 'absence' criteria. The experiments in this study aimed to identify 'drift-related bed shear velocities' $u_{*,d}$ and 'effective drift velocities' $U_{\perp,d}$, to which animals are exposed. We did not consider biotically driven 'voluntary' drift, i.e. as a response to predation risk or competition, or search for alternative food sources (Gibbins et al., 2004). Experiences from this preliminary study are currently implemented in the framework of large-scale field experiments on the River Spree, to be conducted in summer 2010.

2 REVIEW: HYDRAULIC-STRESS DRIVEN DRIFT EXPERIMENTS

The majority of studies linking flow conditions to benthic invertebrates in running waters have been dedicated to define their preferential conditions. It is common practice to perform in situ quantitative sampling of invertebrates (e.g. Merigoux and Doledec, 2004), with a subsequent determination of local hydraulic conditions using the standard FST hemisphere method proposed by Statzner and Müller (1989). Hemispheres of different density but identical shape and size (marked by numbers from 1-24) are exposed to the near-bed flow on a horizontal flat plane. The heaviest hemisphere being moved by the flow-induced drag represents the prevailing flow conditions. The hemispheres were calibrated in a flume, with shear stresses determined from vertical velocity profiles measured with a propeller meter, and a logarithmic law fitting procedure (Statzner et al., 1991).

Much less is known about hydraulic conditions causing the drift of invertebrates. Statzner et al. (1988) present a review of measured velocities from different investigators (Table 1). The hydraulic data contains only point velocities $u(z_{ref})$ at a specific distance z_{ref} from the bed or depth-averaged velocities. Neither bed shear stress, nor effective drift velocities were calculated, and body length l of the organisms is only presented in two of the studies. This makes the results rather difficult to transfer to other sites and conditions. In a later study by Borchardt (1993), the FST method was applied to estimate the critical drift shear stresses of *Ephemerella ignita* and *Gammarus pulex* to 11 (hemisphere 12) and 31

dyn cm^{-2} (hemisphere 15), which equal shear velocities of $u_{*,d}$ = 3.31 and 5.57 cm/s, respectively.

Table 1. Drift data from different sources, summarised in Statzner et al. (1988)

Taxon	u - cm/s	l - mm	Source
Ancylus fluviatilis	240	-	1
Gammarus fossarum	19-38	8-10	2
Gammarus fossarum	> 30	-	3
Gammarus pulex	99	-	1
Ecdyonurus venosus	154	-	1
Ecdyonurus venosus	165-200	9-13	4
Goera pilosa	132	-	1
Tricladida (5 spp.)	96	-	1
Hirudiena (3 spp.)	240	-	1
Gastropoda (6 spp.)	155	-	1
Gastropoda (9 spp.)	75	-	5
Odonata (2 spp.)	77	-	1
Ephemeroptera (10 spp.)	> 179	-	1
Plecoptera (4 spp.)	> 216	-	1
Trichoptera (7 spp.)	159	-	1

[1] 3 mm above flat bed by Dorier and Vaillant (1953/1954)
[2] depth-averaged velocity by Franke (1977)
[3] gravel substrate by Scherer (1965)
[4] 5 mm above flat concrete bed by Butz (1979)
[5] summarised by Dussart (1987)

3 THEORETICAL CONSIDERATIONS

The concept of boundary layers was first introduced in invertebrate ecology by Ambühl (1960) who revealed the importance of the viscous sublayer forming around pebbles in providing shelter zones, but also zones of lower biochemical exchange, e.g. oxygen content. Both features strongly influence invertebrate abundance. The forces acting on the organisms largely depend on animal size, which can be represented by a 'body-length Reynolds number' $Re_l = ul\nu^{-1}$ with the body length l as the length scale, u as a habitat-related velocity scale, and ν the kinematic viscosity of water. Statzner (1988) reported typical body-length Reynolds numbers for lotic invertebrates depending on their life cycle in the range of 1:10 for juveniles, and 1000 or above for adult forms.

With decreasing Re_l, the ratio of lift (directed away from the bottom) to drag forces (directed in main flow direction) generally decreases (Vogel, 1994). Marine zoobenthos species showed a ratio drag:lift of 1:1 to 1:2, but as Re_l for lotic benthos is much lower, Statzner et al. (1988) suggested, that drag prevails over lift. Furthermore, with increasing Re_l, pressure drag (related to the organism's projected area perpendicular to the flow) outweighs friction drag (related to the animal's surfacial area parallel to the flow). To resist these forces, different adaptation strategies are known, of which the most important are: (A) streamlined body shape; (B) formation of drag-minimising

colonies (sheltering of individuals in a group); (C) increase of body weight (e.g. by assimilation of sand grains); (D) active adhesion to the bed by suckers, claws, hooks, silk threads or mucus; (E) migration to zones of lower hydraulic stress; and (F) rheotaxis (drag-minimising body posture). These strategies work on different time-scales, from evolutionary (A) to instantaneous adaptation (F). Of particular interest for this study were the instantaneous to short-time adaptations, (D), (E), and (F), although (A) is implicitly considered by examining invertebrate species with differing body shapes.

4 FLUME EXPERIMENTS

4.1 *Flume conditions*

The flume used in this study, had a glass wall section of a length of 3 m and a width of 10 cm at a maximum depth of 40 cm (see Figure 1). It was tiltable for slopes up to 1/10 with a closed pump circuit enabling to use clean water and to compensate temperature increase due to pump heat by adding cool water. The flume bottom was made of PVC sheets, onto which a layer of uniform sand grains (d_{50} = 0.8 mm) was glued. This layer provided a roughness structure for the animals to attach. Vertical profiles of streamwise velocity $u(z)$ and Reynolds stress $-\overline{u'w'}$ were measured with an ADV (Type 'Vectrino+', Nortek AS, Norway), traversing longitudinally on the flume toprails. A water surface elevation pointer gauge was installed at the entrance of the glass wall section to determine water depth. An electromagnetic currency meter (ECM) integrated in the pipe circuit measured discharge.

Due to the narrowness of the flume, the thickness of the logarithmic layer was only about 3 cm in the test section, the above layers were influenced by side-wall friction resulting in a practically uniform vertical velocity distribution in the centre of the flume.

The maximum bed shear velocity for subcritical flow conditions was $u_* \cong 2.5$ cm/s, which in many cases was too low to drift the invertebrates. The only option was to establish supercritical flow with strong gradients of velocity and bed shear stresses of up to $u_* \cong 8$ cm/s. In supercritical conditions, the experimental runs were more difficult to conduct, as surface waves and associated pressure fluctuations occurred in some runs. As a consequence, ADV measurements could not be carried out for velocities higher than 50 cm/s due to flow separation and air entrainment in the wake of the probe head. In these cases we determined velocity profiles via a simple particle tracking velocimetry (PTV), releasing poppy seeds and taking video records through the sidewalls with a camera speed of 30 frames per second.
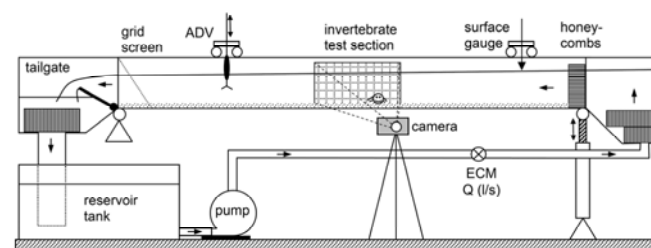

Figure 1: Flume setup, the ADV was traversed longitudinally

4.2 *Invertebrate sampling*

Invertebrates were collected on the River Spree close to Neu-Zittau/Brandenburg, Germany. The Spree is a regulated lowland river with sandy bed, and relatively wide (40 m) and shallow (0.6-1.0 m) cross sections at the sampling location. The estimated cross-sectionally averaged flow velocity was 20 cm/s during the sampling period in August 2009, causing the formation of small ripples in open areas between patches of aquatic macrophytes (predominantly *Sagittaria* spp.). Towards the banks, the bathymetry is shallowing and facilitates colonisation with dense vegetation stands and accumulation of finde sediments. Inverterbrates were collected with Surber nets in sediments and with hand nets from within the vegetation. We deliberately chose large individuals and species to make the handling during the experiments easier. In order to accommodate them to the laboratory conditions, invertebrate individuals were kept in aquariums with their natural substrate, air supply and at a water temperature below 20 centigrade. Individuals were fed ad libitum with living chironomids (for predator species), fragments of macrophytes collected from the river (for shredder species), and with biofilm and algae covering dead wood (for grazer species).

4.3 *Invertebrate test procedure*

For each test run, a single invertebrate was placed with a pair of tweezers at still-water or moderate flow velocities along the flume centreline at mid-flume length. Then discharge was steadily increased until drift occurred or maximum discharge was reached (no drift). The surface pointer gauge was moved following the rising water level to capture the water depth at the instant of drift. It was not possible to use the ADV simultaneously to these runs, as animals often moved quickly towards the flume corners to seek shelter from the

peak stress and velocity in the centreline. Time consuming ADV measurements could only be performed after removal of the invertebrates and at steady flow conditions. The ADV was installed above the location where detachment occurred and the discharge was increased until the water depth at the entrance matched the water depth during drift, as marked by the pointer gauge. The same procedure was used in the supercritical flow tests. In this case, ADV measurements were not possible (see part 4.1) and velocity profiles had to be estimated from the PTV measurements.

Pictures and videos of the invertebrates were taken from the side during the tests using a millimeter grid graph-paper against backlighting through the opposite flume wall. Additional pictures from the top (planview) were taken placing the animals in a Petri dish with a millimeter grid graph-paper below.

Some organisms which did not allow firm attachment to the bed but where constantly moving (gammaridae, crayfish), were tested in still-water conditions only, capturing their moves with a digicam. The image sequences were analysed towards the distance crossed between successive frames to determine their migration/propulsion speed. Additional observations were made during tests with a mobile bed of uniform sand.

4.4 *Data processing*

For most of the subcritical test conditions, vertical velocity and $-\overline{u'w'}$ Reynolds shear stress profiles were measured (39 runs in total, sampling volume height 3 mm and diameter 6 mm , 10 vertically equidistant points in steps of 3 mm). Here, u' and w' denote the fluctuating velocities in streamwise and vertical direction, respectively, and the overbar denotes temporal averaging. The bed shear stress was determined from linear extrapolation of the $-\overline{u'w'}$ profile to the bed, which then gave the shear velocity $u_* = \sqrt{-\overline{u'w'}}$. In addition, the effective drift velocity $U_{\perp,d}$ was calculated from integrating the velocity profile $u(z)$ over the height between bed level and the height of the invertebrate during flow exposure. In contrast to point velocities at an arbitrary reference level (like the given values in Table 1), effective drift velocities are a better representation of the flow-field around the invertebrates and directly relate to the drag acting on the body.

In supercritical conditions, the trajectories of poppy seeds added to the flow as tracer particles were recorded and analysed by image processing software. Two tests, one at low water depth (10.2 cm) and one at high (14.4 cm) were taken as reference runs and a log-law fitted to the measured points. Equivalent sand roughness and integration

constant were determined and used as parameters for a log-law approach to all supercritical runs at intermediate water depths between the two reference runs.

5 RESULTS AND DISCUSSION

5.1 *Drift stresses and velocities*

The main results of the study are summarised in Table 2, which contains information on the invertebrate taxon test conditions (total number of tested individuals per species, total number of test runs, number of drift incidents in sub- and supercritical flow conditions, body length and height exposed to the flow), hydraulic parameters (drift-related bed shear velocity, effective drift velocity, both with standard errors) and body-length related Reynolds number Re_l calculated by means of the effective drift velocity $U_{\perp,d}$ as velocity scale. In cases when only one or two successful drift incidents were recorded, standard error calculations were omitted.

Four species were not tested in flowing conditions but in a still-water tank (see 4.3). They are listed in the lower part of Table 2 together with their average ($u_{mig,a}$) and maximum ($u_{mig,max}$) migration speed (walking, crawling or swimming). Data of tests with the crayfish *Orconectes limosus* were treated separately for juvenile and adult form, which differed in size and moving performance. The body-length Reynolds numbers of the tested invertebrates were larger than 1×10^3, corresponding to the range of adult forms proposed by Statzner (1988). Only exception is *Hydrachna* sp. which moves slowly and has a small body size. All other collected individuals, even if in larval stage, were relatively large, e.g. the damselfly *Calopteryx splendens* and the dragonfly *Gomphus vulgatissimus*, which were close to their emergence. Subcritical conditions and the associated maximum stresses and velocities (u_* < 2.5 cm/s, u ($z = 5$ mm) = 30 cm/s) were only sufficient to drift *Sialis lutaria* and *G. vulgatissimus*, while all other species resisted these conditions at least once and required further tests in supercritical flows. Some individuals of two species resisted even the maximum possible stresses and velocities in supercritical conditions (u_* = 7.6 cm/s, $u_{z=5}$ = 60 cm/s) and were not drifted, *Hydropsyche* sp. (3 of 3 individuals), a net-spinning caddisfly which was tested without its net, and *C. splendens* (6 of 9 individuals). The latter is consistent with the observations of Dorier and Vaillant (1954/1955), which determined a drift velocity for *Calopteryx* sp. of 77 cm/s (5 mm above the bed). For better

Table 2. Drift-related bed shear velocity, effective and reference drift velocities and body-size data of the tested invertebrate species. The lower block contains the migration speed data of the invertebrates tested in still-water conditions.

Taxon	(1)	(2)	(3)	(4)	$u_{*,d}$ cm/s (5)	$U_{\perp,d}$ cm/s (6)	$u_{z=5}$ cm/s (7)	l mm (8)	h mm (9)	Re_l $\times 10^3$ (10)
Anabolia nervosa	3	11	10	1	1.4 ± 0.3	15.9 ± 3.4	20.3	28-31	6-8	3.3-6.0
Bithynia tentaculata	7	19	7	2	2.1 ± 0.5	30.0 ± 2.8	29.3	10-27	14-18	3.8-5.9
Calopteryx splendens	3	10	1	2	4.9 ± 0.7	39.5 ± 6.5	54.5	18-26	3	5.9-12.2
Calopteryx splendens	6	11	0	0	sustained $u_{*,d}$ = 7.6 cm/s			18-26	3	
Cordulia aenea	1	5	1	1	4.4	38.3	48.1	22	4	8.3
Gomphus vulgatissimus	8	33	15	-	1.5 ± 0.1	14.1 ± 0.8	24.2	14-26	3.5	1.8-3.9
Heptagenia sp.	1	3	0	2	7.2	31.1	59.9	12	2.5	3.7
Hydropsyche sp.	3	3	0	0	sustained $u_{*,d}$ = 7.6 cm/s			16-18	4	
Piscicola geometra	1	4	0	3	5.0 ± 1.7	10.1 ± 3.4	53.5	30	2.5	2.1
Sialis lutaria	1	2	2	-	1.0 ± 0.4	12.5 ± 6.2	19.5	14	3	0.8
Viviparus viviparus	3	15	3	4	4.9 ± 1.2	47.7 ± 8.9	60.6	14-37	13-31	5.5-21.1
Coenagrionidae sp.	2	2	-	2	7.6	34.2	64.5	14	3	4.8

Taxon		(1)	(2)	$u_{mig,max}$ cm/s (11)	$u_{mig,a}$ cm/s (12)		(8)	(9)	(10)
Dikerogammarus villosus		19	13	16.1 ± 0.7	7.1 ± 1.2		10-14	3-5	0.6-1.1
Celicorophium curvispinum		3	2	8.2 ± 0.4	-		8-10	2-4	
Orconectes limosus		2	4	38.7 ± 6.7	3.2 ± 0.5		35-45	20-28	0.9-1.7
Orconectes limosus		1	1	70	8		120	35-45	9.6
Hydrachna sp.		3	3	-	1.8 ± 0.1		4	4	0.06-0.07

(1) Total number of individuals tested for each species; (2) total number of test runs; (3) number of drift incidents in subcrictical conditions; (4) number of drift incidents in supercritical conditions; (5) drift shear velocity and standard error; (6) effective drift velocity and standard error; (7) reference velocity 5 mm above the bed; (8) body-length range of individuals; (9) exposed body-height range of individuals; (10) body-length Reynolds number range, using body-length and effective drift velocity. For still-water tests: (11) maximum migration speed; (12) average migration speed.

comparability to the data of previous studies in Table 1, we added the drift-related velocity $u_{z=5}$ at a reference level 5 mm above the bed. For all tested invertebrate species in Table 2, velocities $u_{z=5}$ are significantly lower than the range 75-249 cm/s reported from previous studies (not considering *G. fossarum*). The discrepancy is reflecting that our samples were adapted to lowland streams with slow flowing or even stagnant waters, while most of the invertebrates in Table 1 are living in steeper gradient and coarser substratum streams and thus are better equipped to sustain high velocities (e.g. *A. fluviatilis*, *E. venosus*, *G. pilosa*). Reported velocities for *G. pulex* and *G. fossarum* range between 19-99 cm/s, which exceeds the maximum migration speed of 8-16 cm/s that we determined in our tests with the comparable Gammaridae species *D. villosus* and *C. curvispinum*. Due to their highly active motions and continuous vertical displacements, the reference-level velocity seems not appropriate to describe their drift threshold. Other taxa in Table 1 are represented as averages over several species (Gastropoda, Trichoptera, Ephemeroptera, Hirudiena) and not directly comparable with our species. Missing information in the source papers about flume conditions and velocity measurements hinder further comparative analysis. Maximum velocities under laboratory conditions reported by Dorier and Vaillant (1953/1954) and Butz (1979) are very high

(200-240 cm/s) and require supercritical flows and steep flumes. Accurate measurements of the near-bed velocities in such conditions are difficult to obtain.

5.2 *Invertebrate behaviour during drift tests*

5.2.1 *Anabolia nervosa* (*tube*-case *wearing* caddisfly)

This caddisfly larvae (Figure 2) are constructing a portable case made of sedge and wood fragments which make them relatively vulnerable to fast flows. Their total frontal area is much increased in comparison with the animals body height. The tube-case was 4-6 mm in diameter and 20-25 mm long, and difficult to be kept in position. At high velocities, *A. nervosa* was pulled out of its case by a few millimeters, then it immediately stopped crawling and pulled the case back into position. *A. nervosa* instinctively moved towards zones of lower shear stresses and velocities (flume corners). Drift occurred during these motions, in both, upstream and downstream facing positions,. Holding abilities by claws was nevertheless strong and enabled reattachment to the bed after short-distance drifts (10-30 cm) without active control by swimming. *A. nervosa* showed decreasing performance from run to run, pointing out that high hydraulic stresses can only be sustained for short

periods (less than a minute) and control of the tube-case was highly energy consuming.

5.2.2 Bithynia tentaculata (faucet snail)

This freshwater snail (Figure 3) inhabits the shallow and slow-flowing zones of lakes and rivers, and grazes on epiphytic algae and biofilm, or filters suspended organic particles from the water column. With its tentacles it senses flow strength and tends to quickly move towards zones of lower hydraulic stress. The shell is less than 15 mm high and 30 mm long resulting in a large frontal area but a well streamlined shape. Drift occurred, when *B. tentaculata* was pulled out of its shell (similar to *A. nervosa*) and the shell aperture was suddenly exposed to the flow increasing the frontal area exposed to the flow and the associated drag on the shell. *B. tentaculata* sustained this stress for 1-30 seconds, before being drifted. Benefits from mucus production were not observed, which was the case for the other tested freshwater snail, *Viviparus viviparus* (part 5.2.9 and Figure 7).

5.2.3 Calopteryx splvendens, Coenagrionida sp. (damselflies)

These damselfly species abundant in River Spree, are typically found in macrophyte stands where they are well camouflaged due to their slender morphology (Figure 4). We collected larvae shortly before emergence, thus having a body length of about 30 mm. Both taxa resisted the highest stresses and velocities reached, and in 85% of all tests they were not drifted at all. In the few drift incidents, the individual was moving towards the flume corners or lifted off the bed by a strong ejection event *C. splendens* applied rheotaxis by keeping the head low, while the abdomen was detached from the bed and legs absorbed near-bed turbulent fluctuations. Swimming movements by sweeping the tail back and forth were only observed for low velocities but not during drift.

5.2.4 Gomphus vulgatissimus, Cordulia aenea (dragonflies)

These dragonfly taxa (Figure 5) live in loose fine sediments close to the banks and are active predators during night. They are not very agile and the physiognomy is adapted to dig into the substrate, where they hide during resting periods. Their claws were not suited well to attach to the grains and drift occurred quickly for all tests in subcritical conditions, often while moving towards the flume corners. For *G. vulgatissimus*, the drift stress is approximately in the range of the incipient motion of the sand used in the tests ($u_* = 1.76$

cm/s) and indicates the adaptation to life in lentic environment. When drifted, *G. vulgatissimus* propelled itself forward by sucking water into the body and expelling it through its anal pore. *C. aenea* has longer legs and a shorter body which allow it to sustain higher stresses than the short-legged *G. vulgatissimus*.

5.2.5 Heptagenia sp. (mayfly)

This mayfly has a streamlined, flat body-shape and relatively short legs which are kept low to the bed (Figure 6). We observed a tendency to move downstream, similar as reported by Butz (1979), but motion stopped at higher velocities when *Heptagenia* sp. fixed firmly to the sand grains.
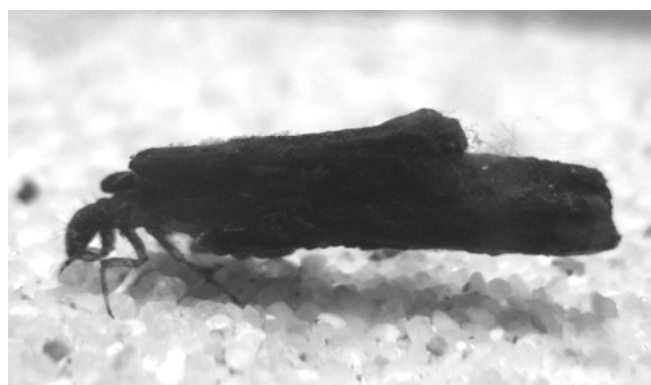

Figure 2 : *A. nervosa* with tube-case (flow from left to right)

Figure 3 : *B. tentaculata* shortly before drift, when shell aperture was exposed to the flow (flow from left to right)
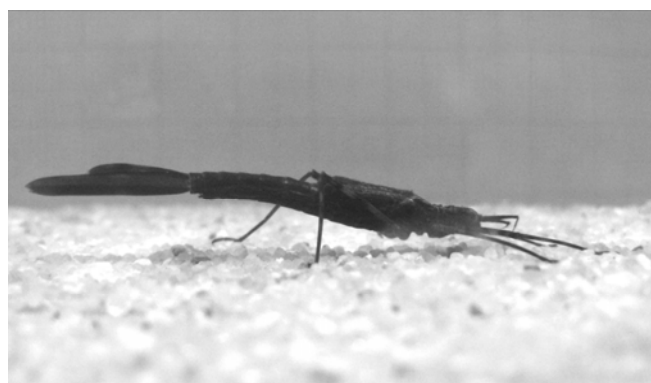

Figure 4 : *C. splendens* in drag-minimising body posture (flow from right to left)

Figure 5 : *G. vulgatissimus* searching for shelter in a flume corner (flow from right to left)

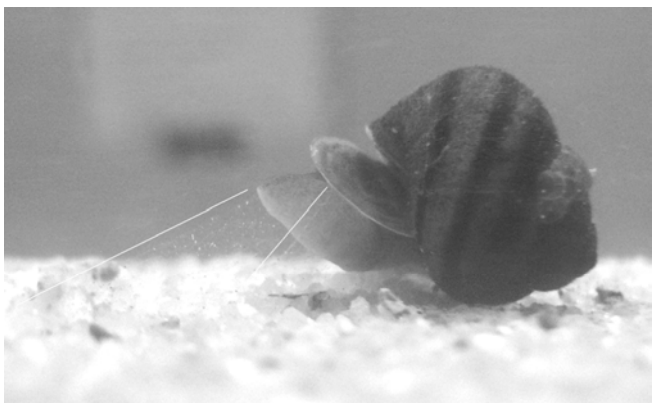Figure 6 : Rheotaxis of *Heptagenia* sp. (flow from right to left)

Figure 7 : Large *V viviparus* shortly before drift, with mucus threads serving as anchorage (half-transparent and indicated by white lines in the Figure, flow from left to right)

5.2.6 *Hydropsyche sp.* (net-spinning caddisfly)

Tests were performed after removal of its net. Nevertheless, *Hydropsyche* was able to resist the maximum possible shear stress by keeping a flat posture supported by short legs, and fixing firmly between the grains. At lower flow velocities, vital search for sheltering zones was observed, e.g. in the transducer drillings of the flume.

5.2.7 *Piscicola geometra* (fish leech)

This fish parasite sustained high velocities by fixing to the bed with its larger posterior sucker, while the oral sucker was freely oscillating in the flow. *P. geometra* was completely stretched (30

mm long) during the tests and sustained high velocities up to 30 seconds, before it released and drifted. Drift was probably influenced by the oscillatory swaying motions induced by the flow.
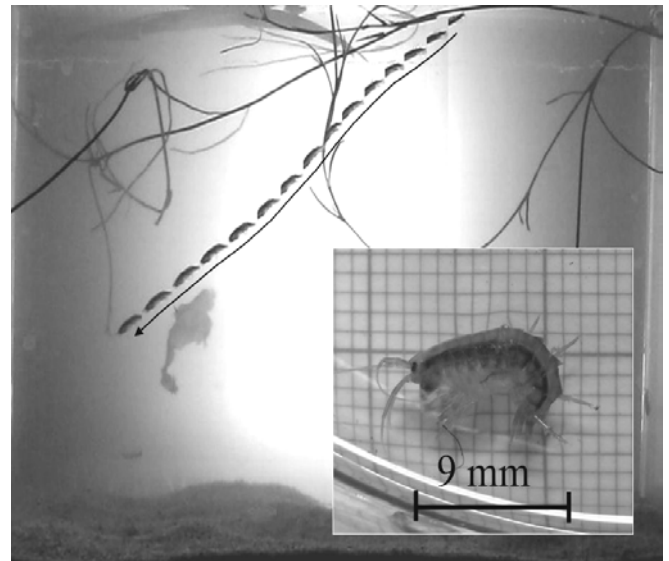

Figure 8 : Swimming trajectory and size of *D. villosus* in a still-water tank shown as an overlay image

Figure 9 : *O. limosus* crawling upstream, body length 37 mm

5.2.8 *Sialis lutaria* (alderfly)

S. lutaria was probably the most active invertebrate tested, crawling swiftly across the substrate and not spending any efforts to fix to the substrate when velocities were increased. Drift occurred practically immediately.

5.2.9 *Viviparus viviparus* (common mud snail)

V. viviparus has a bulbous shell, whose aperture is closed, if needed, by an operculum (apertural lid, Figure 7). *V. viviparus* needed time to adapt to the flume conditions, and in some cases the operculum was opened not sooner than after one minute. Drift in many cases occurred immediately, as the snail did not attach firmly to the bed. The larger adults quickly produced mucus, which served as adhesive anchorage to their foot and significantly increased its ability to resist stresses. We observed that even after detachment of the foot, remaining mucus threads prevented the snail to be drifted.

5.2.10 *Dikerogammarus villosus, Celicorophium curvispinum* (*crustacea*)

Both Gammaridae species (Figure 8) were tested in a still-water tank, because they were continuously and actively moving and swimming and could not be kept in position in the flume. Their typical motion is to swim for 5-20 cm, often in a bow-like trajectory, then to rest and breath, before to start another swim phase or sinking to the bed in a curled position. Swimming trajectories were recorded and analysed to determine the migration speed.

5.2.11 *Orconectes limosus (freshwater crayfish)*

This invasive crayfish species (Figure 9) was tested in still-water conditions and the average backward- and forward crawling speed as well as the maximum speed by propulsion, were determined. Propulsion is an impulsive rearward motion, which begins with powerful flexing of the abdomen and is followed by streamlining posture and reduction of frontal area and drag coefficient. Data collected on adult and juvenile crayfish are treated separately due to the differences in their performance.

5.2.12 *Hydrachna sp. (freshwater mite)*

Hydrachna sp. is a sphere-shaped freshwater mite, living in the still-water zones along the river banks and inside macrophyte patches. It swims unsteadily by movements of its three pairs of short legs. Swimming trajectories were analysed in still-water conditions and the average migration speed was determined.

6 SUMMARY & CONCLUSIONS

Incipient motion drift shear stresses and velocities were determined for different benthic invertebrate species commonly found in lowland rivers. The data was gained from flume experiments, where invertebrates were exposed to increasing flow velocities until drift occurred. Velocities and Reynolds shear stresses were measured with an ADV. Additionally, pictures of the invertebrates were taken through the flume sidewalls and from the top to capture their strategies to cope with the flow and to quantify their size. The aim of the study was to provide a data set for invertebrate drift conditions linking invertebrate morphology and behaviour to sound hydraulic parameters. We chose drift-related boundary shear velocity and effective drift velocity, which is the average streamwise velocity integrated over the flow-exposed height of the invertebrate, as standard parameters. Priority was set on a wide variety of invertebrate species typical for a German lowland river, instead of focusing on less species but on higher experimental detail (e.g. performing more replicas, considering invertebrate size fractions and life cycle).

Results of the study suggest that invertebrates are able to sustain high stresses and velocities, which are exceeding the in-situ conditions at the sampling location. Drift shear stresses were in many cases higher than the incipient motion threshold for the sediments in Spree ($u_* \cong 2.5$ cm/s), indicating that erosion and sediment transport may be the decisive factors triggering benthic invertebrate drift, which is consistent with results of Gibbins et al. (2004). Incidentally, we studied the behaviour of the damefly *C. splendens* during sediment motion and observed immediate drift, after the invertebrate was hit by moving grains or the grains serving as anchorage were mobilised. It should be kept in mind though, that boundary layers over planar mobile or immobile surfaces do not represent the preferential habitat conditions of most of the invertebrates. However, we used it as a reference habitat to determine parameters which are universal and comparable to other local hydraulic conditions.

It was technically impossible in our experiments, to conduct ADV measurements during the drift tests, in order to link drift with turbulence characteristics; e.g. by bursting motions, which are known to affect the transport of maritime benthic organisms (Denny, 1988). We intend to continue in this direction and already conducted some preliminary laboratory studies on the effect of turbulence on invertebrate drift in coarse substrate. Experiments were conducted in collaboration with project partners at EPFL Lausanne and data are currently analysed and prepared for publication. Experiences from both studies will feed into a series of large-scale field experiments with invertebrates under controllable and manipulated flow conditions in Spree in summer 2010.

INDEX OF VARIABLES

d_{50} - median grain size diameter
h - animal's flow-exposed height
l - animal's body length
Re_l - body-length Reynolds number
$U_{\perp,d}$ - effective drift velocity averaged over flow-exposed animal height
u - streamwise velocity
u_* - bed shear velocity
$u_{*,d}$ - drift-related bed shear velocity
$u_{mig,a}$ - average migration speed
$u_{mig,\max}$ - maximum migration speed
$u_{z=5}$ - reference velocity 5 mm above the bed
u', w' - turbulent intensities of streamwise and vertical velocity components
$-\overline{u'w'}$ - Reynolds shear stress
z - vertical distance from the bed
z_{ref} - reference height from the bed
ν - kinematic viscosity of water

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