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**The impacts of current velocity increases on the drift of *Simulium monticola* (Diptera: Simuliidae): a laboratory approach**

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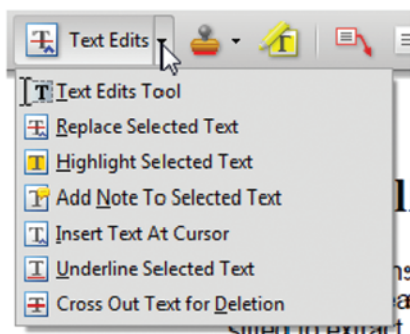
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## The impacts of increasing current velocity on the drift of *Simulium monticola* (Diptera: Simuliidae): a laboratory approach

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### Abstract

Current velocity and associated physical forces are among the most important factors shaping lotic benthic communities. The recent increase in the frequency and intensity of flow alterations, especially related to hydroelectric use or irrigation, represent a key element of riverine environment deterioration. Numerous studies have investigated the effect of current velocity increases on macrobenthic fauna, underlining that, in most cases, these increases enhance the drift, i.e. the abandonment of the substrate by macroinvertebrates. The purpose of this study is to examine the drift propensity of *Simulium monticola* (Diptera: Simuliidae) under different water velocities. Simuliidae are one of the most characteristic components of fast-flowing environments in rivers. Experiments were conducted in an artificial stream in the laboratories of Politecnico di Torino, analysing the drift of organisms at different current velocities. The observed variability of drift appears to be related to velocity increases: interestingly, we evidenced an inverse relationship between velocity and drift propensity, with low amounts of drifting organisms at higher velocities. This tendency was not related to the size of Simuliidae larvae: when comparing the size of drifting organisms with velocity, no significant correlations were detected. We hypothesized that the tendency to drift was mainly behavioural rather than catastrophic, and related to the preference for high water velocities. Our findings support the hypothesis that increases in water velocity can cause complex changes in the drift of the macrobenthic community, increasing the propensity for some species to leave the substrate and decreasing it for others.

**Keywords:** Hydrological variations, Simuliidae, drift, artificial stream, current velocity

### Introduction

One of the most intriguing and debated topics in stream ecology is the study of the relationship between the distribution of lotic organisms and the characteristics of their environment (Allan & Castillo 2007). In particular, stream invertebrates are generally thought to be distributed according to environmental factors that operate at different spatial scales, from regional to local and microhabitat scales (Heino et al. 2003). On a large scale, studies investigating the distribution of macroinvertebrates among and within rivers underline the importance of factors such as water chemistry (Collier et al. 1998), temperature (Vannote & Sweeney 1980) and land use (Eyre et al. 2005). At the smaller, microhabitat scale the distribution of invertebrates is mainly shaped by biotic factors, such as competition and

predation (Fairchild & Holomuzki 2005), and abiotic factors, such as coarse particulate organic matter availability (Murphy & Giller 2000; Fenoglio et al. 2005), substratum characteristics (Minshall 1984; Bond & Downes 2000) and flow velocity (Lancaster 1999). In particular, flow velocity and the associated physical forces are among the most important factors affecting organisms in lotic environments (Allan & Castillo 2007): this factor influences macroinvertebrate distribution both indirectly (controlling substratum size and food resource availability) and directly (as a physical force). Many studies highlighted that increases in current velocity, for example on the occasion of increases in river discharge, led to severe population losses and changes in community structure and composition (Statzner & Higler 1986; Holomuzki & Biggs 2000). In particular, it

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is well known that increases in velocity are frequently associated with increases in drift density (Brittain & Eikeland 1988; Mackay 1992). Reid and Thoms (2008) reported that near-bed water velocity is clearly the most important hydraulic variable influencing both assemblage composition and taxon richness of benthic communities while, in contrast, velocities in the transverse and vertical directions appear to have minimal influence on invertebrate distributions.

Simuliidae (blackflies) are a Diptera family with worldwide distribution, with aquatic pre-imaginal stages and blood-eating adult females (Crosskey 1990). Blackfly larvae are the dominant suspension filter feeders in most running water environments: they are passive filterers that rely on the current to capture most of their food (Chance & Craig 1986). For this reason, blackfly larvae inhabit fast-flowing environments that assure a high amount of transported material. On a large spatial scale, some studies indicate that the occurrence of Simuliidae can vary among ecoregions and seasons, according to different parameters such as temperature and percentage of dissolved oxygen (McCreadie & Adler 1998), chlorophyll concentration in the water and in the seston (Morin & Peters 1988), and river order (Malmqvist et al. 1999). At a smaller scale, it is well known that the main environmental factor controlling Simuliidae larvae distribution is water current velocity (Phillips 1957; Malmqvist 1994). In an interesting study about Simuliidae larvae behaviour, Kiel (2001) reported that positioning and looping (i.e. little adjustments or position changes, based on the creation of new silk pads) were affected by current velocity, and underlined that drift could be an important mechanism of re-colonisation or repositioning for these organisms.

The aim of this study was to analyse the propensity of Simuliidae larvae to enter the drift in different hydrological conditions, i.e. at different water velocities. We hypothesized that these rheophilic organisms may display a reduced drift propensity at high water velocity, in contrast to what happens for most invertebrate taxa; we also tested if the relationship between drift propensity and water velocity was related to the size of the organism.

## Materials and methods

Simuliidae larvae were collected in the upper Po River, in a third-order reach near Sanfront (Italy, Cuneo district, UTM: X 367154, Y 4946144). General characteristics of the site are reported in Fenoglio et al. (2007). Larvae were collected with a hand net (250- $\mu$ m mesh), sorted in the field,

stored in refrigerated containers and immediately brought to the laboratory. In the experiments, we utilized *Simulium monticola* Friederichs, 1920, an orophilous species with European distribution that inhabits streams and small rivers between 200 and 700 m above sea level (a.s.l.) (Rivosecchi 1978).

The experiments were performed in a flume at the Giorgio Bidone Hydraulics, DIATI, Politecnico di Torino. The flume was made of stainless steel with plexiglas walls and bottom, and it is 11.8 m long with a width of 0.44 m (Figure 1).

Water is pumped in an inlet tank at the upstream end of the flume, flows through the channel, and then falls in a V-notched weir, which allows the measurement of discharge. A sluice gate at the downstream end of the channel allowed the regulation of water velocity and depth. The mean velocity was calculated as the ratio between the measured flow discharge and the channel flow area. A rectangular slab of stone was placed in the central part of the channel and it was used as substratum for the Simuliidae. The stone was 44 cm wide in order to fit the channel width, and its thickness and length were 3 and 60 cm, respectively. A layer of coarse gravel particles was placed at the upstream end of the stone slab to avoid flow detachment at the stone edge and to ensure the development of a rough-wall boundary layer, thus better reproducing the flow conditions of a gravel bed stream. Finally, a metallic wire net (mesh = 250  $\mu$ m) was placed at the downstream end of the flume so that the nappe, i.e. the sheet of water over-topping the weir, was forced to pass through it before entering the weir and the drifting larvae were collected and counted.

We performed a total of seven experiments, in late springtime of 2009, each time following the same experimental protocol, which included an initialization phase followed by a sequence of steps of velocity variations. Thus, each experiment was conceived to assess the response of drift to different hydrodynamic conditions, and the adoption of a constant protocol among the different experiments allowed us to test the repeatability of the measured drift propensities. During the initialization of each experiment, the pump was switched on and a known number of Simuliidae were placed on the stone using laboratory volumetric plastic pipettes. During this first phase, lasting approximately 40–45 minutes, initial velocity was kept constant, to allow the settling of the larvae. In this first phase, a number of larvae were transported through the channel and collected in the downstream net. These individuals were discarded and were not included in the analysis. After all the larvae were placed on the stone, the initial number of larvae ( $N_0$ ) at the beginning of the experiment was

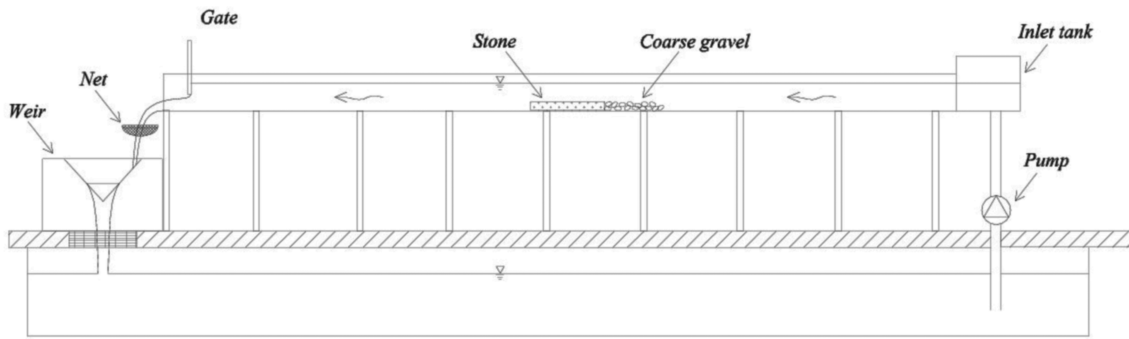


Figure 1. Indoor artificial stream scheme utilised in the study (more explanations in the text).

165 recorded. The experimental protocol was composed  
of a varying number of steps that are summarized  
in Table I. During each step, the mean flow velocity  
was increased approximately 0.1–0.2 m/s (by vary-  
170 ing the sluice gate opening and/or the flow rate)  
and was then kept constant for approximately 20–30  
min. This duration was much longer than the time  
required for the establishment of steady flow in the  
flume, so the flow properties could be considered  
almost constant for the whole step duration. After  
175 this time elapsed, the net was replaced and the num-  
ber of larvae that had drifted ( $\Delta N$ ) was recorded  
together with the corresponding flow mean velocity  
( $U$ ) and step duration ( $\Delta t$ ). The experiment then  
continued in increments following the steps outlined  
180 above, and it ended when the mean velocity reached  
a value of approximately 1.1–1.2 m/s. At the end  
of the experiment, the pump was switched off and  
the larvae still attached to the stone and flume bot-  
tom were collected and counted. The relationship  
185 between the number of drifting Simuliidae and flow  
characteristics can more precisely quantify the num-  
ber of drifting individuals. We thus evaluated the drift  
propensity, which represents the probability per unit  
time of a larva to enter the drift, as

$$k = \frac{\Delta N}{N \Delta t} \quad (1)$$

190 where  $\Delta N$  is the number of drifting larvae during a  
velocity step of duration  $\Delta t$ , and  $N$  is the number  
of larvae attached to the stone at the beginning of  
the step. The drift propensity  $k$  is a measure of the  
tendency of the larvae to detach from the substratum  
195 and enter the drift. The effect of flow velocity  
on drift propensity was tested measuring the tenden-  
cy of the larvae to enter the drift ( $k$ ) at different  
velocity intervals ( $U$ ), by deriving the Pearson coeffi-  
cient. In order to verify the possible influence of the  
200 larval density on drift propensity, we also analysed  
the relation between  $k_0$  (average drift propensity

of each experiment) and the initial number of  
individuals  $N_0$ .

All larvae collected were subsequently stored in  
75% ethanol. To test whether the size of larvae  
205 influenced their propensity to drift, a sub-sample of  
drifting individuals ( $n = 150$  individuals) was later  
measured in the laboratory with an ocular microme-  
ter mounted on a Nikon SMZ1500 stereomicroscope  
210 (to an accuracy of 0.01 mm): the following two  
measures were taken from each individual: (a) head  
capsule width, (b) total length. Then, the relation  
between the size characteristics of drifting larvae  
and flow velocity was analysed by deriving Pearson  
215 correlation coefficients.

## Results

In each experiment a varying number of larvae left  
the stone substratum and entered the drift, result-  
ing in a progressive decrease in Simuliidae remain-  
220 ing attached to the substratum. All experiments exhibit  
a clear decreasing trend, with a steep initial decrease  
followed by moderate variations. Subsequently, there  
was a significant correlation between drift propen-  
sity ( $k$ ) and current velocity (Pearson correlation test,  
225  $r = -0.44$ ,  $p < 0.05$ , Figure 2). No correlation was  
found between initial number of larvae and drift  
propensity ( $r = 0.29$ ,  $p = \text{n.s.}$ ).

The effect of flow velocity on drift propensity  
was also investigated by means of an analysis of  
each experiment. For each of the seven experiments,  
230 Table II reports calculated values of  $\rho_{k,U}$ , i.e. the  
Pearson correlation coefficient between drift propen-  
sity and flow velocity. The velocity of each step  
(reported in Table I) was used to calculate the value  
of the correlation coefficient of each experiment  
235 (Table II).

Values range between  $-0.3$  and  $-0.7$ , indicating a  
significant inverse relationship between drift propen-  
sity and velocity. Analyzing the relationships between  
the two morphometric parameters measured, we  
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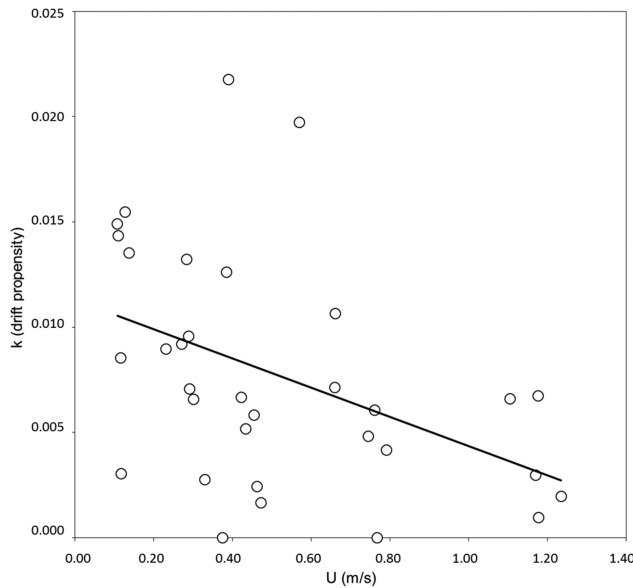


Figure 2. Relationship between drift propensity and mean flow velocity.

Table I. Summary of the number of larvae and characteristics of flow velocity in the experiments.

Experiment	Total number of larvae $N^0$	Mean velocity $U$ (m/s)
1	45	0.14 – 0.23 – 0.33 – 0.38 – 0.47 – 0.77
2	103	0.12 – 0.30 – 0.46 – 0.75 – 1.18
3	51	0.29 – 0.43 – 0.79 – 1.23
4	122	0.11 – 0.29 – 0.46 – 0.76 – 1.11
5	425	0.13 – 0.28 – 0.42 – 0.66
6	1000	0.12 – 0.27 – 0.39 – 0.66 – 1.18
7	204	0.11 – 0.39 – 0.57 – 0.89 – 1.17

Table II. Results of the analysis of drift propensity data for the seven experiments.

Experiment	$k_0$ ( $h^{-1}$ )	$\rho_{k,U}$ (-)
1	0.24	-0.7
2	0.20	-0.4
3	0.28	-0.7
4	0.58	-0.6
5	0.78	-0.7
6	0.72	-0.3
7	1.50	-0.3

$k_0$ : average drift propensity,  $\rho_{k,U}$ : correlation coefficient between drift propensity and velocity.

detected a significant correlation between total length and head capsule width (Pearson correlation test = 0.83,  $p < 0.001$ , Figure 3). For this reason, we only used total length as a concise indicator parameter of growth, and the resulting correlations between

drifting Simuliidae with water velocity for each experiment were not significant (Pearson correlation test =  $-0.112$ ,  $p = n.s.$ , Figure 4).

## Discussion

Many studies report that increases in current velocity can lead to decreases in densities and composition of macroinvertebrate communities (Perry & Perry 1986), reporting increases in drift during periods of elevated discharge and flow velocity (Borchardt 1993; Tockner & Waringer 1997; Gibbins et al. 2010a, 2010b). Moreover, Poff and Ward (1991) performed field experiments to investigate the responses of benthic invertebrates' drift to flow manipulation, and demonstrated that drift density generally occurred following an increase in flow for most taxa. The Simuliidae seem to present a different picture. Living as filter feeders in flowing waters, they display a preference for elevated current velocities that provide an ample supply of food, and are able to colonize fast-flowing environments with silk pads to the substrate, clinging to them with the larval posterior abdominal hooks and by orienting their body parallel to the current, so that this streamlined posture reduces drag coefficients. This preference for high current velocity was confirmed in our laboratory experiments. In our study, we observed that the relative number of Simuliidae larvae entering the drift decreased as a result of velocity increases, with the lowest number of drifting individuals recorded at the highest velocities. We hypothesize that drift could be a strategy for *S. monticola* to avoid unfavourable local microhabitat conditions linked to low flow velocity: it is likely that the preference of filterers, such as Simuliidae, for high velocity conditions can be related to both higher feeding efficiency and reduced predation pressures (Hart & Merz 1998). Interestingly, we also noticed no significant correlation between the size of drifting larvae and flow velocity: flow velocity increases did not directly select the size of drifted organisms (as might happen, however, considering sediment particles). This lack of correlation demonstrates that the drift is not (or not only) a process regulated by hydraulic forces, underlining its biological nature. Drift is not a simple, passive mechanical process but a complex phenomenon influenced by behavioural and physiological constraints.

For the experiments, we used water that had been stored for more than a month in tanks of the laboratory. The absence of organic matter is not a factor that may have appreciably influenced behavioural drift: given the relatively short



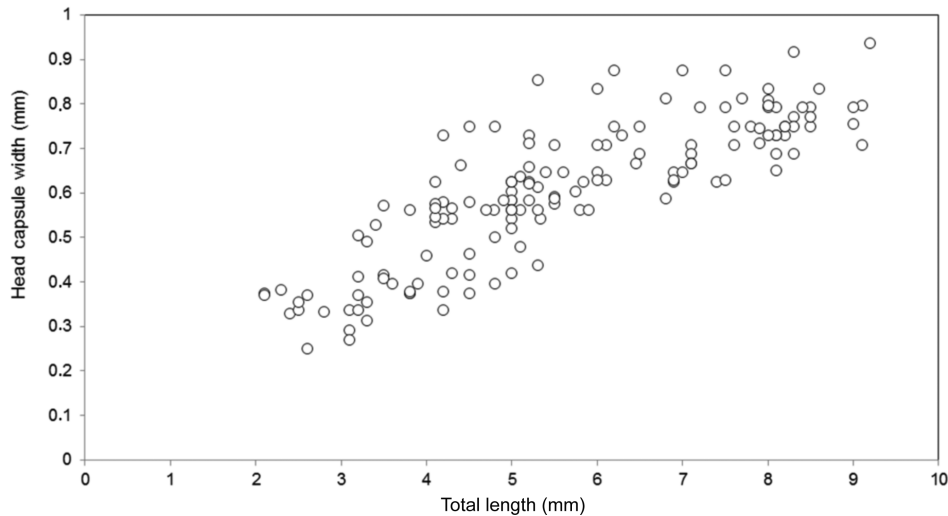


Figure 3. Relationship between total length and head capsule width of *Simulium monticola* larvae. Black line represents linear regression.

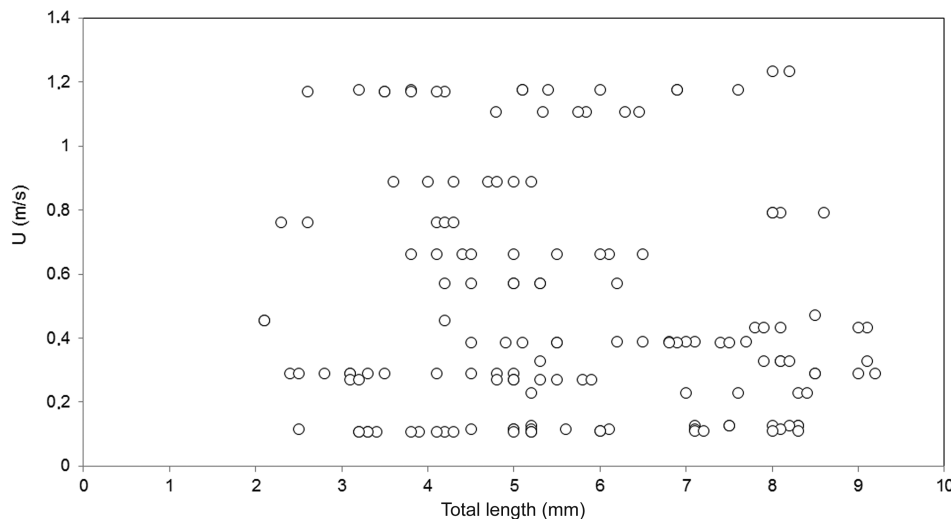


Figure 4. Relationship between total length of *Simulium monticola* larvae and mean flow velocity.

time of each experiment, we are confident that concentration and availability of food were not important, also because it is known that locomotory activity and drift of Simuliidae are largely independent of food concentration (Ciborowski & Craig 1989).

Changes in flow conditions can have complex and different effects on the drift patterns of macrobenthic communities: at faster flows, most taxa display a greater propensity to enter the drift while, in contrast, Simuliidae appear to minimize their drift propensity. Recent studies underlined the importance of improving our knowledge regarding the hydraulic requirements of stream macrobenthos, especially because of the growing anthropic-induced alterations of river

flow regimes (Dolédec et al. 2007). In this context, current velocity is almost certainly one of the most important environmental variables shaping the composition and abundance of benthic communities (Nelson & Lieberman 2002) and, therefore, the biological effects of anthropic alterations of flow should be carefully considered.

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## References

- Allan JD, Castillo M. 2007. Stream ecology. Structure and function of running waters. Dordrecht, The Netherlands: Springer.
- 330 Bond NR, Downes BJ 2000. Flow-related disturbance in streams: An experimental test of the role of rock movement in reducing macroinvertebrate population densities. *Marine and Freshwater Research* 51:333–337.
- 335 Borchardt D. 1993. Effects of flow and refugia on drift loss of benthic macroinvertebrates: Implications for habitat restoration in lowland streams. *Freshwater Biology* 29:221–227.
- Brittain JE, Eikeland TJ. 1988. Invertebrate drift – A review. *Hydrobiologia* 166:77–93.
- 340 Chance MM, Craig DA. 1986. Hydrodynamics and behaviour of simuliid larvae (Diptera). *Canadian Journal of Zoology* 64:1295–1309.
- Ciborowski JJH, Craig DA. 1989. Factors influencing dispersion of larval black flies (Diptera: Simuliidae): Effects of current velocity and food concentration. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1329–1341.
- 345 Collier KJ, Wilcock RJ, Meredith AS. 1998. Influence of substrate type and physico-chemical conditions on macroinvertebrate faunas and biotic indices of some lowland Waikato, New Zealand, streams. *New Zealand Journal of Marine and Freshwater Research* 32:1–19.
- 350 Crosskey RW. 1990. The natural history of Blackflies. Chichester, United Kingdom: John Wiley and Sons.
- Dolédéc S, Lamouroux N, Fuchs U, Mérigoux S. 2007. Modelling the hydraulic preferences of benthic macroinvertebrates in small European streams. *Freshwater Biology* 52:145–164.
- 355 Eyre MD, Pilkington JG, McBlane RP, Rushton SP. 2005. Macroinvertebrate species and assemblages in the headwater streams of the River Tyne, northern England in relation to land cover and other environmental variables. *Hydrobiologia* 544:229–240.
- 360 Fairchild MP, Holomuzki JR. 2005. Multiple predator effects on microdistributions, survival, and drift of stream hypsopsychid caddisflies. *Journal of the North American Benthological Society* 24:101–112.
- 365 Fenoglio S, Bo T, Agosta P, Malacarne G. 2005. Temporal and spatial patterns of coarse particulate organic matter and macroinvertebrate distribution in a low-order Apennine stream. *Journal of Freshwater Ecology* 20:539–547.
- 370 Fenoglio S, Bo T, Cucco M, Malacarne G. 2007. Response of benthic invertebrate assemblages to varying drought conditions in the Po river (NW Italy). *Italian Journal of Zoology* 74:191–201.
- 375 Gibbins C, Batalla RJ, Vericat D. 2010a. Invertebrate drift and benthic exhaustion during disturbance: Response of mayflies (Ephemeroptera) to increasing shear stress and river-bed instability. *River Research and Applications* 26:499–504.
- Gibbins CN, Vericat D, Batalla RJ. 2010b. Invertebrate drift-velocity relations and the limits imposed by substrate stability and benthic density. *Journal of the North American Benthological Society* 29:945–958.
- 380 Hart DD, Merz, RA. 1998: Predator prey interactions in a benthic stream community: A field test of flow-mediated refuges. *Oecologia* 114:263–273.
- 385 Heino J, Muotka T, Pascola R. 2003. Determinants of macroinvertebrate diversity in headwater streams: Regional and local influences. *Journal of Animal Ecology* 72:425–434.
- Holomuzki JR, Biggs B. 2000. Taxon-specific responses to high flow disturbance in streams: Implications for population persistence. *Journal of North American Benthological Society* 19:670–679.
- Kiel E. 2001. Behavioural response of Blackfly Larvae (Simuliidae, Diptera) to different current velocities. *Limnologia* 31:179–183.
- 395 Lancaster J. 1999. Small-scale movements of lotic macroinvertebrates with variations in flow. *Freshwater Biology* 41:605–619.
- Mackay RJ. 1992. Colonization by lotic macroinvertebrates – A review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 49:617–628.
- 400 Malmqvist B. 1994. Preimaginal blackflies (Diptera: Simuliidae) and their predators in a central Scandinavian lake outlet stream. *Annales Zoologici Fennici* 31:245–255.
- Malmqvist B, Zhang Y, Adler PH. 1999. Diversity, distribution and larval habitats of North Swedish blackflies (Diptera: Simuliidae). *Freshwater Biology* 42:301–314.
- 405 McCreddie JW, Adler PH. 1998. Scale, time, space, and predictability: Species distributions of preimaginal black flies (Diptera: Simuliidae). *Oecologia* 114:79–92.
- Minshall GW. 1984. Aquatic insect-substratum relationships. In: Resh VH, Rosenber, DM, editors. *The ecology of aquatic insects*. New York: Praeger Publisher. pp. 358–400.
- 410 Minshall W, Winger MV. 1968. The effect of reduction in stream flow on invertebrate drift. *Ecology* 49:580–588.
- 415 Morin A, Peters RH. 1988. Effect of microhabitat features, seston quality, and periphyton on abundance of overwintering black fly larvae in southern Quebec. *Limnology and Oceanography* 33:431–446.
- Murphy JF, Giller P S. 2000. Seasonal dynamics of macroinvertebrate assemblages in the benthos and associated with detritus packs in two low-order streams with different riparian vegetation. *Freshwater Biology* 43:617–631.
- 420 Nelson SM, Lieberman DM. 2002. The influence of flow and other environmental factors on benthic invertebrates in the Sacramento River, USA. *Hydrobiologia* 489:117–129.
- 425 Perry SA, Perry WB. 1986. Effects of experimental flow regulation on invertebrate drift and stranding in the Flathead and Kootenai Rivers, Montana, USA. *Hydrobiologia* 134:171–182.
- Phillips J. 1957. The effect of current speed on the distribution of the larvae of the blackflies, *Simulium variegatum* (Mg.) and *Simulium monticola* Fried. (Diptera). *Bulletin of Entomological Research* 48:811–819.
- 430 Poff NL, Ward JV. 1991. Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. *Canadian Journal of Fisheries and Aquatic Science* 48:1926–1936.
- 435 Reid MA, Thoms MC. 2008. Surface flow types, near-bed hydraulics and the distribution of stream macroinvertebrates. *Biogeosciences* 5:1175–1204.
- 440 Rivosecchi L. 1978. Simuliidi (Diptera: Simuliidae) Guide per il riconoscimento delle specie animali delle acque interne italiane. Roma, Italy: CNR.
- Statzner B, Higl B. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology* 16:127–139.
- 445 Tockner K, Waringer JA. 1997. Measuring drift during a receding flood: Results from an Austrian mountain brook (Ritrodatt-Lunz). *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 82:1–13.
- 450 Vannote RL, Sweeney BW. 1980. Geographic analysis of thermal equilibria: A conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *The American Naturalist* 115:667–695.