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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

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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

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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 envi-30 ronmental 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 fac-35 tors 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

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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

- 70 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-
- 75 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 per-
- 80 centage 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 control-
- 85 ling 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

90 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 inverte-

100 brate 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-µm 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 125 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 135 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 140 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 145 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 proto-150 col 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 155 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 160 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

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

recorded. The experimental protocol was composed 165 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 varying the sluice gate opening and/or the flow rate) and was then kept constant for approximately 20-30 170 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 this time elapsed, the net was replaced and the num-175 ber of larvae that had drifted (ΔN) was recorded together with the corresponding flow mean velocity (U) and step duration (Δt) . The experiment then continued in increments following the steps outlined above, and it ended when the mean velocity reached 180 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 bottom were collected and counted. The relationship between the number of drifting Simuliidae and flow 185 characteristics can more precisely quantify the number of drifting individuals. We thus evaluated the drift propensity, which represents the probability per unit time of a larva to enter the drift, as

$$k = \frac{\Delta N}{N \,\Delta t} \tag{1}$$

190 where ΔN is the number of drifting larvae during a velocity step of duration Δt, 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 substra195 tum and enter the drift. The effect of flow velocity on drift propensity was tested measuring the tendency of the larvae to enter the drift (k) at different velocity intervals (U), by deriving the Pearson coefficient. In order to verify the possible influence of the larval density on drift propensity, we also analysed the relation between k0 (average drift propensity

of each experiment) and the initial number of individuals N0.

All larvae collected were subsequently stored in 75% ethanol. To test whether the size of larvae influenced their propensity to drift, a sub-sample of drifting individuals (n = 150 individuals) was later measured in the laboratory with an ocular micrometer mounted on a Nikon SMZ1500 stereomicroscope (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 correlation coefficients. 215

Results

In each experiment a varying number of larvae left the stone substratum and entered the drift, resulting in a progressive decrease in Simuliidae remaining 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 propensity (*k*) and current velocity (Pearson correlation test, r = -0.44, p < 0.05, Figure 2). No correlation was found between initial number of larvae and drift propensity (r = 0.29, p = 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, Table II reports calculated values of $\rho_{k,U}$, i.e. the Pearson correlation coefficient between drift propensity 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 (Table II).

Values range between -0.3 and -0.7, indicating a significant inverse relationship between drift propensity 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 <mark>N⁰</mark>	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	$\rho_{k,U}$
	(11)	(-)
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 veloc-250 ity 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 255 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 260 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 265 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 con-270 firmed 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. 275 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 280 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 285 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 290 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).

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- 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 require-
- 310 ing 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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