

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

Original

The impacts of increasing current velocity on the drift of *Simulium monticola* (Diptera: Simuliidae): a laboratory approach / S., Fenoglio; Boano, Fulvio; T., Bo; Revelli, Roberto; Ridolfi, Luca. - In: THE ITALIAN JOURNAL OF ZOOLOGY. - ISSN 1125-0003. - STAMPA. - 80:3(2013), pp. 443-448. [10.1080/11250003.2013.820798]

Availability:

This version is available at: 11583/2513854 since:

Publisher:

Taylor & Francis

Published

DOI:10.1080/11250003.2013.820798

Terms of use:

This article is made available under terms and conditions as specified in the corresponding bibliographic description in the repository

Publisher copyright

(Article begins on next page)



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

Journal:	<i>Italian Journal of Zoology</i>
Manuscript ID:	TIZO-2013-0016
Manuscript Type:	Original Paper
Date Submitted by the Author:	06-Feb-2013
Complete List of Authors:	Fenoglio, Stefano; Università del piemonte orientale, DISIT Boano, Fulvio; Department of Environment, Land and Infrastructure EngineeringPolitecnico di Torino, Bo, Tiziano; Università del piemonte orientale, DISIT Revelli, Roberto; Department of Environment, Land and Infrastructure EngineeringPolitecnico di Torino, Ridolfi, Luca; Department of Environment, Land and Infrastructure EngineeringPolitecnico di Torino,
Keywords:	Hydrological variations , Simuliidae , drift, artificial stream, current velocity

SCHOLARONE™
Manuscripts

1
2
3
4 1 **The impacts of current velocity increases on the drift of *Simulium monticola***

5
6 2 **(Diptera: Simuliidae): a laboratory approach**

7
8 3
9
10 4 S. FENOGLIO^{1*}, F. BOANO², T. BO¹, R. REVELLI², L. RIDOLFI²

11
12
13
14
15
16
17 7 ¹ Department of Science and Innovation Technology, Università degli Studi del
18 8 Piemonte Orientale, Via Teresa Michel 11, I-15121 Alessandria, Italy.

19
20
21 9 ² Department of Environment, Land and Infrastructure Engineering, Politecnico di
22 10 Torino, Corso Duca degli Abruzzi 24, I-10129 Torino, Italy.

23
24
25
26
27
28 12 Correspondence: S. Fenoglio, Department of Science and Innovation Technology,
29 13 Università degli Studi del Piemonte Orientale, Via Teresa Michel 11, I-15121
30 14 Alessandria, Italy. Tel: +39 0131-360201, Fax: +39 0131-360243. Email:
31 15 fenoglio@unipmn.it.

32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50 22 **Keywords:** Hydrological variations, Simuliidae, drift, artificial stream, current velocity

51
52 23 **Running title:** Drift of Simuliidae in laboratory conditions

1
2
3
4 25 **Abstract**
5

6 26 Current velocity and the associated physical forces are among the most important
7
8 27 factors shaping lotic benthic communities. The current increase in the frequency and
9
10 28 intensity of flow alterations, especially related to hydroelectric use or irrigation,
11
12 29 represent a key element of riverine environment deterioration. Numerous studies have
13
14 30 investigated the effect of current velocity increases on the macrobenthic fauna,
15
16 31 underlining that, in most cases, these increases lead to enhancement in the drift, i.e. the
17
18 32 abandonment of the substrate by macroinvertebrates. The purpose of this study is to
19
20 33 examine the drift propensity of *Simulium monticola* (Diptera: Simuliidae) under
21
22 34 different water velocities. Simuliidae are one of the most characteristic components of
23
24 35 fast flowing environments in rivers. Experiments were conducted in an artificial stream
25
26 36 in the laboratories of Politecnico di Torino, analysing the drift of organisms at different
27
28 37 current velocities. Velocity increases significantly contributes to explain the observed
29
30 38 variability of drift: interestingly, we evidenced an inverse relationship between velocity
31
32 39 and drift propensity, with low amounts of drifting organisms at higher velocities. This
33
34 40 tendency was absolutely not related with size of Simuliidae larvae: comparing size of
35
36 41 drifting organisms with velocity no significant correlations were detected. We
37
38 42 hypothesize that the tendency to enter the drift was due to behavioural reasons, and
39
40 43 related to the preference for high water velocities. Our findings support the hypothesis
41
42 44 that increases in water velocity can cause complex changes in the drift of the
43
44 45 macrobenthic community, increasing the propensity for some species to leave the
45
46 46 substrate and decreasing it for some other.
47
48
49
50
51
52
53
54
55
56
57
58
59
60

50 **Introduction**

51 One of the most intriguing and debated topic in stream ecology is the study of the
52 relationship between distribution of lotic organisms and characteristics of their
53 environment (Allan & Castillo 2007). In particular, stream invertebrates are generally
54 thought to be distributed according to environmental factors that operate at different
55 spatial scales, from regional to local and microhabitat systems (Heino et al. 2003). At
56 large scale, studies investigating the distribution of macroinvertebrates among and
57 within rivers underline the importance of elements such as water chemistry (Collier et
58 al. 1998), temperature (Vannote & Sweeney 1980) and land use (Eyre et al. 2005). At
59 small, microhabitat scale the distribution of invertebrates is mainly shaped by biotic
60 factors, such as competition and predation (Fairchild & Holomuzki 2005), and abiotic
61 factors, such as coarse particulate organic matter availability (Murphy & Giller 2000;
62 Fenoglio et al. 2005), substratum characteristics (Minshall 1984; Bond & Downes 2000)
63 and water velocity (Lancaster 1999). In particular, current velocity and the associated
64 physical forces are among the most important factors affecting organisms presence in
65 lotic environments (Allan & Castillo 2007): this factor influences macroinvertebrate
66 distribution both indirectly (controlling substratum size and food resources availability)
67 and directly (as physical force). Many studies underlined that increases in current
68 velocity, for example in occasion of river discharge enhancements, led to severe
69 population losses and changes in community structure and composition (Statzner &
70 Higler 1986; Holomuzki & Biggs 2000). In particular, it is well known that increases in
71 velocity are frequently associated with increases in drift density (Brittain & Eikeland
72 1988; Mackay 1992). Reid and Thoms (2008) reported that near-bed water velocity is
73 clearly the most important hydraulic variable influencing both assemblage composition

1
2
3
4 74 and taxa richness of benthic coenoses while, in contrast, velocities in the transverse and
5
6 75 vertical directions appear to have minimal influence on invertebrate distributions.
7

8
9 76 Simuliidae, also denominated blackflies, are a Diptera family with world-wide
10
11 77 distribution, that comprises species with blood-eating and disease-vector adult females
12
13 78 (Crosskey 1990). Blackfly larvae are the dominant suspension filter feeders in most
14
15 79 running water environments: they are passive filterers, that rely on current to capture
16
17 80 most of their food (Chance & Craig 1986). For this reason, blackfly larvae inhabit fast
18
19 81 flowing currents, that assure high amount of transported material. At large scale, some
20
21 82 studies evidenced that the occurrence of Simuliidae can vary among ecoregions and
22
23 83 seasons, according to different parameters such as temperature and percentage dissolved
24
25 84 oxygen (McCreadie & Adler 1998), chlorophyll concentration in the water and in the
26
27 85 seston (Morin & Peters 1988), and river order (Malmqvist et al. 1999). At a smaller
28
29 86 scale, it is well known that the main environmental factor controlling Simuliidae larvae
30
31 87 distribution is water current velocity (Phillips 1957; Malmqvist 1994). In an interesting
32
33 88 study about Simuliidae larvae behaviour, Kiel (2001) reported that positioning and
34
35 89 looping (i.e.: little adjustments or position changes, based on the creation of new silk
36
37 90 pads) were affected by current velocity and underlined that drift could be an important
38
39 91 mechanism of re-colonisation or repositioning for these organisms.
40
41
42
43

44 92 Aim of this study was to analyse the propensity of Simuliidae larvae to enter the drift in
45
46 93 different hydrological conditions, i.e. at different water velocities. We hypothesized that
47
48 94 these rheophilic organisms may show an evident diminution of drift propensity at high
49
50 95 water velocities, on the contrary to what happens for most invertebrate taxa; we also
51
52 96 tested if the relationship between drift propensity and water velocity was related to
53
54 97 organism dimension.
55
56
57
58
59
60

98

99 **Materials and methods**

100 Simuliidae larvae were collected in the upper Po river, in a third order reach near
101 Sanfront (Italy, Cuneo district, UTM: X 367154, Y 4946144). General characteristics of
102 the site are reported in FENOGLIO et al. (2007). Larvae were collected with a hand net
103 (250 μm mesh), sorted in the field, stored in refrigerated containers and immediately
104 brought to the laboratory. In the experiments, we utilized *Simulium monticola*
105 (Friederichs 1920), an orophilous species with European distribution, that inhabits
106 streams and small rivers between 200 and 700 m a.s.l. (Rivosecchi 1978).

107 The experiments were performed in a flume at the Giorgio Bidone Hydraulics,
108 DIATI, Politecnico di Torino. The structure of the flume is made of stainless steel with
109 plexiglas walls and bottom, and it is 11.8 m long with a width of 0.44 m (Fig. 1). Water
110 is pumped in an inlet tank at the upstream end of the flume, flows through the channel,
111 and then falls in a V-notched weir which allows to measure the flow rate. A sluice gate
112 at the downstream end of the channel allowed the regulation of water velocity and
113 depth. The mean velocity was calculated as the ratio between the measured flow rate
114 and the channel flow area. A rectangular slab of stone was placed in the central part of
115 the channel and it was used as substratum for the Simuliidae. The stone was 44 cm wide
116 in order to fit the channel width, and its thickness and length were 3 and 60 cm,
117 respectively. A layer of coarse gravel particles was placed at the upstream end of the
118 stone slab to avoid flow detachment at the stone edge and to ensure the development of
119 a rough-wall boundary layer, thus better reproducing the flow conditions of a gravel bed
120 stream. Finally, a metallic wire net (mesh = 250 μm) was placed at the downstream end

1
2
3
4 121 of the flume so that the nappe was forced to pass through it before entering the weir and
5
6 122 the drifting larvae could be collected and counted.
7

8
9 123 We performed a total of seven experiments, each time following the same
10
11 124 experimental protocol which included an initialization phase followed by a sequence of
12
13 125 steps of velocity variations. Thus, each experiment was conceived to assess the response
14
15 126 of drift to different hydrodynamic conditions, and the adoption of a constant protocol
16
17 127 among the different experiments allowed us to test the repeatability of the measured
18
19 128 drift propensities. During the initialization of each experiment, the pump was switched
20
21 129 on and a known number of Simuliidae were placed on the stone using laboratory
22
23 130 volumetric plastic pipettes. During this first phase, lasting approximately 40-45 minutes,
24
25 131 initial velocity was kept constant, to allow the settling of the larvae. In this first phase, a
26
27 132 number of larvae were transported through the channel and collected in the downstream
28
29 133 net. These individuals were discarded and were not included in the analysis. After all
30
31 134 the larvae were placed on the stone, the initial number of larvae (N_0) at the beginning of
32
33 135 the experiment was recorded. The experimental protocol was composed of a varying
34
35 136 number of steps that are summarized in Table 1. During each step, the mean flow
36
37 137 velocity was increased approximately 0.1-0.2 m/s (by varying the sluice gate opening
38
39 138 and/or the flow rate) and was then kept constant for approximately 20-30 min. This
40
41 139 duration was much longer than the time required for the establishment of steady flow in
42
43 140 the flume, so the flow properties could be considered almost constant for the whole step
44
45 141 duration. After this time elapsed, the net was replaced and the number of drifted larvae
46
47 142 (ΔN) was recorded together with the corresponding flow mean velocity (U) and step
48
49 143 duration (Δt). The experiment then continued with the following steps, and it ended
50
51 144 when the mean velocity reached the value of approximately 1.1-1.2 m/s. At the end of
52
53
54
55
56
57
58
59
60

1
2
3
4 145 the experiment the pump was switched off and the larvae still attached on the stone and
5
6 146 flume bottom were collected and counted. The relationship between the number of
7
8
9 147 drifting Simuliidae and flow characteristics can be better investigated by choosing
10
11 148 proper quantities to quantify the drift. We thus evaluated the drift propensity, which
12
13 149 represents the probability per unit time of a larva to enter the drift, as

14
15
16 150
$$k = \frac{\Delta N}{N \Delta t} \quad (1)$$

17
18

19 151 where ΔN is the number of drifted larvae during a velocity step of duration Δt , and N is
20
21 152 the number of larvae attached to the stone at the beginning of the step. The drift
22
23 153 propensity k is a measure of the tendency of the larvae to detach from the substratum
24
25 154 and enter the drift, and its inverse $1/k$ represents the average time between two
26
27 155 successive entries in the drift.

28
29
30 156 All collected larvae were stored in 75% ethanol. A sub-sample ($n = 150$ individuals)
31
32 157 was later measured in the laboratory with an ocular micrometer mounted on a Nikon
33
34 158 SMZ1500 stereomicroscope (to an accuracy of 0.01 mm): the following two measures
35
36 159 were taken from each individual: a) head capsule width, b) total length.

37
38
39 160 In the experiments, we used water that had been stored for more than a month in the
40
41 161 tanks of the laboratory. The absence of organic matter is not a factor that may have
42
43 162 appreciably influenced behavioural drift: given the short time elapsed in each
44
45 163 experiment, we are confident that concentration and availability of food are not so
46
47 164 important factors in our study, also because it is known that locomotory activity and
48
49 165 drift of Simuliidae are largely independent of food concentration (Ciborowski & Craig
50
51 166 1989).

52
53
54
55 167

56
57 168 **Results**
58
59
60

1
2
3
4 169 In each experiment a varying number of larvae left the stone substratum and entered the
5
6 170 drift, resulting in a progressive decrease of the number of Simuliidae individuals on the
7
8 171 substratum. All the experiments exhibit a clear decreasing trend, with a steep initial
9
10 172 decrease followed by milder variations. We detected a significant correlation between
11
12 173 drift propensity (k) and current velocity (Pearson correlation test, $r = -0.44$, $p < 0.05$ Fig.
13
14 174 2). In order to verify the possible influence of the larval density on drift propensity, we
15
16 175 also analyzed the relation between k_0 and the initial number of individuals N_0 . Since no
17
18 176 correlation was found ($R^2 < 0.1$), we conclude that variations in drift propensity between
19
20 177 the experiments were not significantly related to differences in density of Simuliidae
21
22 178 individuals on the substratum. The effect of flow velocity on drift propensity was also
23
24 179 investigated by means of an analysis of the single experiments, and Table 2 reports
25
26 180 calculated values of Pearson correlation coefficient $\rho_{k,U}$ between drift propensity and
27
28 181 mean velocity for the seven experiments. Values range between -0.3 and -0.7, indicating
29
30 182 a significant inverse relationship between drift propensity and velocity. Analyzing the
31
32 183 relationships among the two morphometric parameters measured, we detected a
33
34 184 significant correlation between total length and head capsule width (Pearson correlation
35
36 185 test = 0.83, $p < 0.001$, Fig. 3). For this reason, in the subsequent analysis, we only
37
38 186 employed total length as a concise indicator parameter of growth. Comparing size of
39
40 187 drifting Simuliidae with water velocity in different occasions no significant correlation
41
42 188 were detected (Pearson correlation test = -0.112, $p = \text{n.s.}$ – Fig. 4).

48 **Discussion**

49
50 190 Many studies evidenced that increases in current velocity can lead to decreases in
51
52 191 densities and composition of macroinvertebrate communities (Perry & Perry 1986)
53
54 192 reporting increases in drift during periods of elevate discharge and water velocity
55
56
57
58
59
60

1
2
3
4 193 (Borchardt 1993; Tockner & Waringer 1997; Gibbins et al. 2010a; Gibbins et al.
5
6 194 2010b). Moreover, Poff and Ward (1991) performed field experiments to investigate
7
8 195 responses of benthic invertebrates drift to flow manipulation, and realised that drift
9
10 196 density generally augmented following flow increases for most taxa. Simuliidae seems
11
12 197 to present a different picture. Living as filter feeders in flowing waters, they prefer
13
14 198 elevate current velocities that provide ample supply of food, and are able to colonize
15
16 199 fast flowing environments by using attaching silk pads and by orienting their body
17
18 200 parallel to the current, so that this streamlined posture reduces drag coefficients. This
19
20 201 preference for high current velocity was confirmed in our laboratory experiments: in our
21
22 202 study, we observed that the relative number of Simuliidae larvae entering the drift
23
24 203 decreased as a result of velocity increases, with lowest values recorded at highest
25
26 204 velocities. We can hypothesize that drift could be a strategy for *S. monticola* to avoid
27
28 205 unfavourable local conditions linked to low current velocity: it is likely that the
29
30 206 preference of filterers, such as Simuliidae, for high velocity conditions can be related to
31
32 207 both higher feeding efficiency and reduced predation pressures in high flow velocity
33
34 208 situations (Hart & Merz 1998). Interestingly, we also noticed no significant correlation
35
36 209 between size of drifting larvae and flow velocity: this finding underlines the biological
37
38 210 nature of drift, that is not a simple, passive mechanical removal but a complex
39
40 211 phenomenon influenced by behavioural and physiological constraints. Changes in flow
41
42 212 conditions can have complex and different effects in the drift patterns of the
43
44 213 macrobenthic community: at faster flows most taxa show greater propensity to enter the
45
46 214 drift while other, for example Simuliidae, minimize their drift propensity. Recent
47
48 215 studies underlined the importance to improve our knowledge about hydraulic
49
50 216 requirements of stream macrobenthos, especially because of the growing anthropic-
51
52
53
54
55
56
57
58
59
60

1
2
3
4 217 induced alterations of river regimes (Dolédéc et al. 2007). In this context, current
5
6 218 velocity is almost certainly one of the most important environmental variables shaping
7
8 219 composition and abundance of benthic communities (Nelson & Lieberman 2002), and
9
10 220 therefore the biological effects of anthropic alterations of flow should be carefully
11
12 221 considered.
13
14
15
16

223 **Acknowledgements**

17
18
19 224 We are grateful to A. Demaria and S. Bernardi for help in field samplings and
20
21 225 laboratory experiments and B. Maiolini for taxonomical help. This study was supported
22
23 226 by Fondazione Cassa di Risparmio di Alessandria CRAL grants.
24
25
26
27

228 **References**

- 29
30 229 Allan JD, Castillo M. 2007. Stream Ecology. Structure and function of running waters.
31
32 230 Dordrecht, The Netherlands: Springer.
33
34 231 Borchardt D. 1993. Effects of flow and refugia on drift loss of benthic
35
36 232 macroinvertebrates: implications for habitat restoration in lowland streams. Freshwater
37
38 233 Biology 29:221-227.
39
40 234 Brittain JE, Eikeland TJ. 1988. Invertebrate Drift - A review. Hydrobiologia 166:77-93.
41
42 235 Chance MM, Craig DA. 1986. Hydrodynamics and behaviour of simuliid larvae
43
44 236 (Diptera). Canadian Journal of Zoology 64:1295-1309.
45
46 237 Ciborowski JJH, Craig DA. 1989. Factors influencing dispersion of larval black flies
47
48 238 (Diptera: Simuliidae): effects of current velocity and food concentration. Canadian
49
50 239 Journal of Fisheries and Aquatic Sciences 46:1329-1341.
51
52
53
54
55
56
57
58
59
60

- 1
2
3
4 240 Collier KJ, Wilcock RJ, Meredith AS. 1998. Influence of substrate type and physico-
5
6 241 chemical conditions on macroinvertebrate faunas and biotic indices of some lowland
7
8 242 Waikato, New Zealand, streams. *New Zealand Journal of Marine and Freshwater*
9
10 243 *Research* 32:1-19.
11
12 244 Crosskey RW. 1990. *The natural history of Blackflies*. Chichester, United Kingdom:
13
14 245 John Wiley and Sons.
15
16 246 Dolédec S, Lamouroux N, Fuchs U, Méricoux S. 2007. Modelling the hydraulic
17
18 247 preferences of benthic macroinvertebrates in small European streams. *Freshwater*
19
20 248 *Biology* 52:145-164.
21
22 249 Eyre MD, Pilkington JG, McBlane RP, Rushton SP. 2005. Macroinvertebrate species
23
24 250 and assemblages in the headwater streams of the River Tyne, northern England in
25
26 251 relation to land cover and other environmental variables. *Hydrobiologia* 544:229-240.
27
28 252 Fairchild MP, Holomuzki JR. 2005. Multiple predator effects on microdistributions,
29
30 253 survival, and drift of stream hydropsychid caddisflies. *Journal of the North American*
31
32 254 *Benthological Society* 24:101-112.
33
34 255 Fenoglio S, Bo T, Agosta P, Malacarne G. 2005. Temporal and spatial patterns of
35
36 256 coarse particulate organic matter and macroinvertebrate distribution in a low-order
37
38 257 Apennine stream. *Journal of Freshwater Ecology* 20:539-547.
39
40 258 Fenoglio S, Bo T, Cucco M, Malacarne G. 2007. Response of benthic invertebrate
41
42 259 assemblages to varying drought conditions in the Po river (NW Italy). *Italian Journal of*
43
44 260 *Zoology* 74:191-201.
45
46 261 Gibbins C, Batalla RJ, Vericat D. 2010a. Invertebrate drift and benthic exhaustion
47
48 262 during disturbance: response of mayflies (Ephemeroptera) to increasing shear stress and
49
50 263 river-bed instability. *River Research and Applications* 26:499-504.
51
52
53
54
55
56
57
58
59
60

- 1
2
3
4 264 Gibbins CN, Vericat D, Batalla RJ. 2010b. Invertebrate drift-velocity relations and the
5
6 265 limits imposed by substrate stability and benthic density. *Journal of the North-American*
7
8 266 *Benthological Society* 29:945-958.
9
10 267 Hart DD, Merz, RA. 1998: Predator prey interactions in a benthic stream community: A
11
12 268 field test of flow-mediated refuges. *Oecologia* 114:263–273.
13
14 269 Heino J, Muotka T, Pascola R. 2003. Determinants of macroinvertebrate diversity in
15
16 270 headwater streams: regional and local influences. *Journal of Animal Ecology* 72:425-
17
18 271 434.
19
20 272 Holomuzki JR, Biggs BJF. 2000. Taxon-specific responses to high flow disturbance in
21
22 273 streams: implications for population persistence. *Journal of North American*
23
24 274 *Benthological Society* 19:670-679.
25
26 275 Kiel E. 2001. Behavioural response of Blackfly Larvae (Simuliidae, Diptera) to
27
28 276 different current velocities. *Limnologia* 31:179-183.
29
30 277 James ABW, Dewson ZS, Death RG. 2008. The effect of experimental flow reductions
31
32 278 on macroinvertebrate drift in natural and streamside channels. *River Research and*
33
34 279 *Applications* 24:22-35.
35
36 280 Lancaster J. 1999. Small-scale movements of lotic macroinvertebrates with variations in
37
38 281 flow. *Freshwater Biology* 41:605-619.
39
40 282 Malmqvist B, Zhang Y, Adler PH. 1999. Diversity, distribution and larval habitats of
41
42 283 North Swedish blackflies (Diptera: Simuliidae). *Freshwater Biology* 42:301-314.
43
44 284 Mackay RJ. 1992. Colonization by lotic macroinvertebrates - A review of processes and
45
46 285 patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 49:617-628.
47
48 286 Malmqvist B. 1994. Preimaginal blackflies (Diptera Simuliidae) and their predators in a
49
50 287 central Scandinavian lake outlet stream. *Annales Zoologici Fennici* 31:245-255.
51
52
53
54
55
56
57
58
59
60

- 1
2
3
4 288 McCreddie JW, Adler PH. 1998. Scale, time, space, and predictability: species
5
6 289 distributions of preimaginal black flies (Diptera: Simuliidae). *Oecologia* 114:79-92.
7
8
9 290 Minshall W, Winger MV. 1968. The effect of reduction in stream flow on invertebrate
10
11 291 drift. *Ecology* 49:580-582.
12
13 292 Morin A., Peters RH. 1988. Effect of microhabitat features, seston quality, and
14
15 293 periphyton on abundance of overwintering black fly larvae in southern Quebec.
16
17 294 *Limnology and Oceanography* 33:431-446.
18
19 295 Minshall GW. 1984. Aquatic Insect-Substratum Relationships. In: Resh VH, Rosenber,
20
21 296 DM, editors. *The Ecology of Aquatic Insects*. New York: Praeger Publisher, pp. 358-
22
23 297 400.
24
25
26 298 Murphy JF, Giller P S. 2000. Seasonal dynamics of macroinvertebrate assemblages in
27
28 299 the benthos and associated with detritus packs in two low-order streams with different
29
30 300 riparian vegetation. *Freshwater Biology* 43:617-631.
31
32
33 301 Nelson SM, Lieberman DM. 2002. The influence of flow and other environmental
34
35 302 factors on benthic invertebrates in the Sacramento River, U.S.A. *Hydrobiologia*
36
37 303 489:117-129.
38
39 304 Perry SA, Perry WB. 1986. Effects of experimental flow regulation on invertebrate drift
40
41 305 and stranding in the Flathead and Kootenai Rivers, Montana, USA. *Hydrobiologia* 134:
42
43 306 171-182.
44
45
46 307 Phillips J. 1957. The effect of current speed on the distribution of the larvae of the
47
48 308 blackflies, *Simulium variegatum* (Mg.) and *Simulium monticola* Fried. (Diptera).
49
50 309 *Bulletin of Entomological Research* 48:811-819.
51
52
53
54
55
56
57
58
59
60

1
2
3
4 310 Poff NL, Ward JV. 1991. Drift responses of benthic invertebrates to experimental
5
6 311 streamflow variation in a hydrologically stable stream. *Canadian Journal of Fisheries*
7
8 312 and *Aquatic Science* 48:1926-1936.

9
10 313 Reid MA, Thoms MC. 2008. Surface flow types, near-bed hydraulics and the
11
12 314 distribution of stream macroinvertebrates. *Biogeosciences Discussions* 5:1175-1204.

13
14
15 315 Rivosecchi L. 1978. Simuliidi (Diptera Simuliidae) Guide per il riconoscimento delle
16
17 316 specie animali delle acque interne italiane. Roma, Italy: C.N.R.

18
19 317 Statzner B, Higler B. 1986. Stream hydraulics as a major determinant of benthic
20
21 318 invertebrate zonation patterns. *Freshwater Biology* 16:127-139.

22
23
24 319 Tockner K, Waringer JA. 1997. Measuring drift during a receding flood: results from an
25
26 320 Austrian mountain brook (Ritrodal-Lunz). *Internationale Revue der gesamten*
27
28 321 *Hydrobiologie und Hydrographie* 82:1-13.

29
30 322 Vannote RL, Sweeney BW. 1980. Geographic analysis of thermal equilibria: a
31
32 323 conceptual model for evaluating the effect of natural and modified thermal regimes on
33
34 324 aquatic insect communities. *The American Naturalist* 115:667-695.

35
36
37 325
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4 326 **Captions to Figures**
5

6 327
7

8 328 Figure 1: Indoor artificial stream scheme utilised in the study (more explanations in the
9
10 329 text).
11
12

13 330
14

15 331 Figure 2: Relationship between drift propensity and mean flow velocity.
16
17 332

18
19 333 Figure 3: Relationship between total length and head capsule width of *Simulium*
20
21 334 *monticola* larvae. Black line represents linear regression.
22
23 335

24
25 336 Figure 4: Relationship between total length of larvae and mean flow velocity.
26
27 337

28
29
30 338 **Captions to Tables**
31
32 339

33
34 340 Table 1: Summary of the characteristics of the experiments.
35
36 341

37 342 Table 2: Results of the analysis of drift propensity data for the seven experiments (k_0 :
38
39 343 average drift propensity, $\rho_{k,U}$: correlation coefficient between drift propensity and
40
41 344 velocity).
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4 345
5
6 346
7
8
9 347 Experiment Total number of larvae Mean velocity
10
11 348 *N*0 *U* (m/s)
12
13 349
14
15 350 1 45 0.14 – 0.23 – 0.33 – 0.38 – 0.47 – 0.77
16
17 351 2 103 0.12 – 0.30 – 0.46 – 0.75 – 1.18
18
19 352 3 51 0.29 – 0.43 – 0.79 – 1.23
20
21 353 4 122 0.11 – 0.29 – 0.46 – 0.76 – 1.11
22
23 354 5 425 0.13 – 0.28 – 0.42 – 0.66
24
25 355 6 1000 0.12 – 0.27 – 0.39 – 0.66 – 1.18
26
27 356 7 204 0.11 – 0.39 – 0.57 – 0.89 – 1.17
28
29
30
31 357
32

33 358 Table 1
34
35 359
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

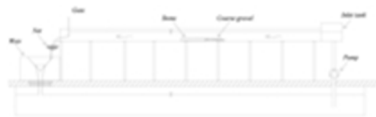
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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

Table 2

For Peer Review Only

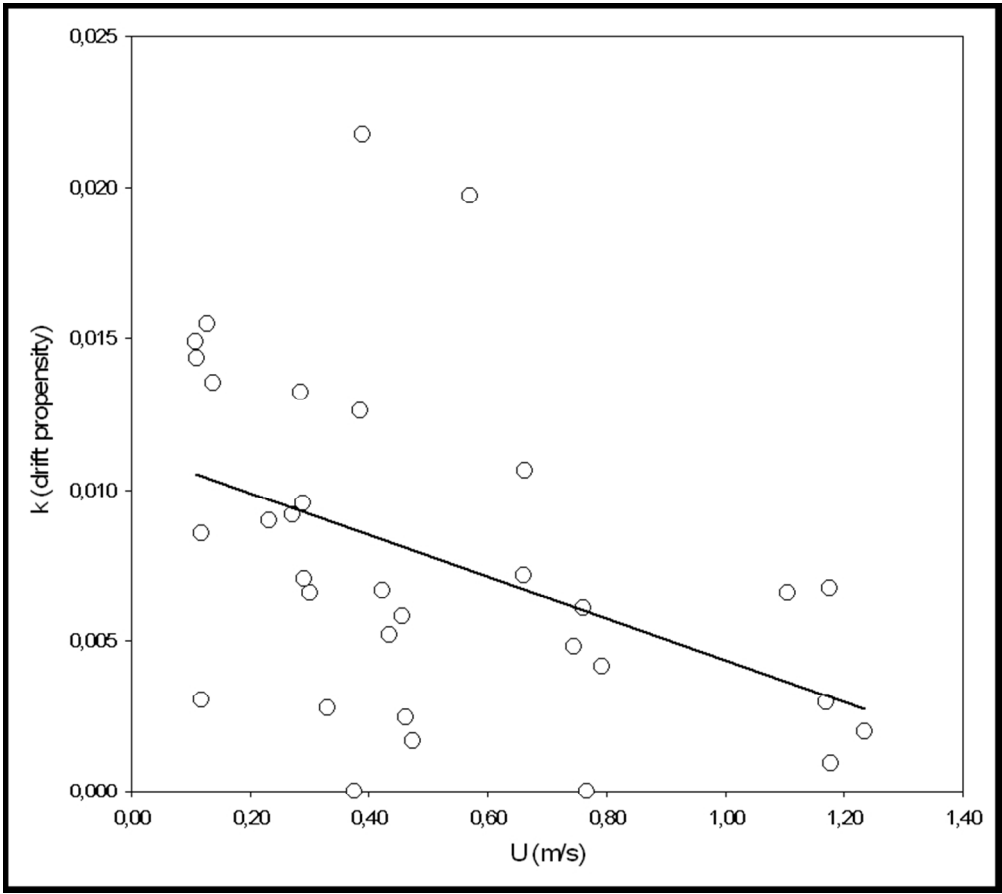
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



15x4mm (300 x 300 DPI)

For Peer Review Only

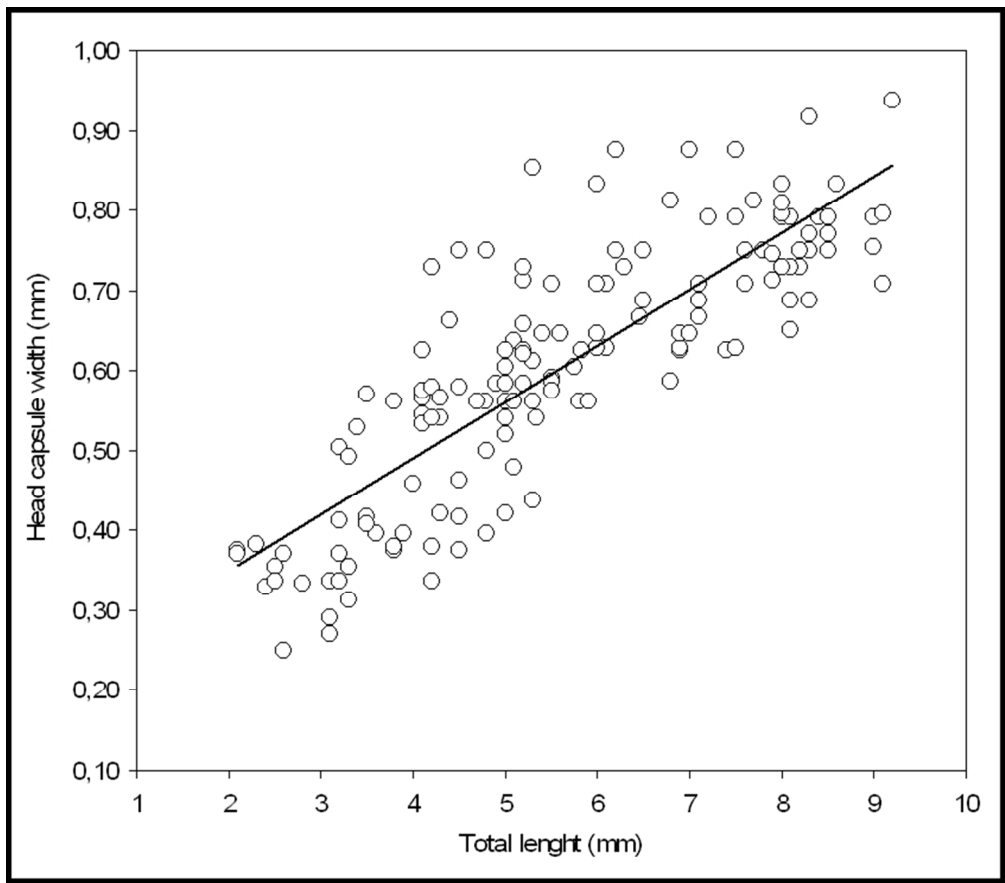
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



226x201mm (96 x 96 DPI)

Only

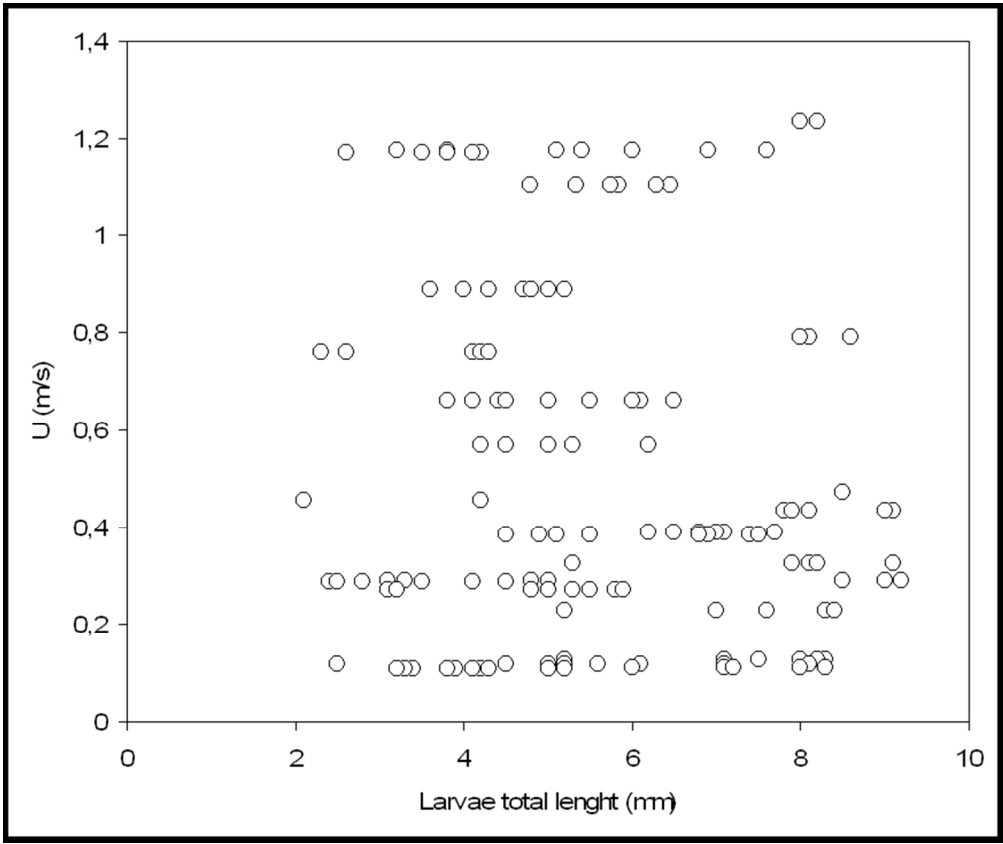
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



223x195mm (96 x 96 DPI)

View Only

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



230x193mm (96 x 96 DPI)

www Only