



Drift and benthic population structure of the mayfly *Rhithrogena semicolorata* (Heptageniidae) under natural and hydropeaking conditions

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Abstract

Are stream insects able to control their entry into the drift under all flow conditions? Do changes in streamflow patterns modify the typical drift patterns? Which larval instars are most affected by fluctuating flows? In order to document these questions, we studied the diel patterns in the drift density and size-structure of the heptagenid mayfly *Rhithrogena semicolorata* (Curtis, 1834) under natural and intermittent hydropeaking conditions in a mountain stream, i.e., up- and downstream of a hydroelectric power plant with hypolimnetic releases. Under natural conditions, drift exhibited a diel periodicity either during low flow periods ($1 \text{ m}^3 \text{ s}^{-1}$) and snowmelt floods ($5 \text{ m}^3 \text{ s}^{-1}$), nocturnal drift density being clearly higher. Larger individuals were found to drift at night. On the other hand, peak flows flushed many larvae downstream during the day. Smaller individuals were more affected by passive dislodgement, which resulted in a shift towards larger individuals in the size-composition of the benthic populations. When flow raised from 1 to $11 \text{ m}^3 \text{ s}^{-1}$, the catastrophic drift occurring during the day depleted the benthos, and the nocturnal (active) drift was suppressed. However, the nocturnal drift was preserved when flow only raised from 5 to $10 \text{ m}^3 \text{ s}^{-1}$.

Introduction

Drift is the downstream transport of aquatic organisms under the effect of current velocity. Although a debate remains to conclude whether some species actively enter the water column or are passively flushed from the stream bed (Wilzback, 1990), drift is usually assumed to be chiefly a behavioural (active) process in stream invertebrate species, which would allow the regulation of benthic production and the colonization of downstream areas. Numerous field observations have demonstrated that the drift of various stream insects showed a diel periodicity, with high drift density at night and low drift density during the day. In terms of size structure, the largest individuals were found to preferentially enter the drift at night. These remarkable patterns thus strengthened the hypothesis that most insects can actively control their entry into the drift. Specifically, it was assumed that selective pres-

sure from visually-cued predatory fish explained this size-structured pattern (LeRoy Poff et al., 1991). Nevertheless, some questions need further consideration. First, are aquatic insects able to control their entry into the drift under all flow conditions? For example, sudden rises in river flow due to hydropeaking operations are known to decrease both the density and biomass of benthic invertebrates downstream from hydroplant outlets (Hauer & Stanford, 1982; Irvine, 1985; Moog, 1993) by increasing the intensity of bed scour (Cobb et al., 1992; Death & Winterbourn, 1994; Gore et al., 1994), which leads to a high catastrophic drift (Crisp & Robson, 1979; Gore et al., 1989). Second, do changes in diel streamflow patterns modify the typical drift patterns (diel variations in drift density and size-structure)? Whether catastrophic drift (sensu Culp et al., 1985, i.e. generated by any disturbance) occurring during the day may affect the nocturnal drift (or 'behavioural drift', sensu Waters, 1965, i.e. influenced

by variations in luminosity) was not established. Finally, if drift patterns are closely linked to the benthic population structure (Waters, 1972), we suspect that widely fluctuating flows should affect the abundance and size composition of benthic populations through catastrophic drift, because it is likely that some larval instars are more prone to dislodgement than others.

The setting for our study is quite interesting : a hydroelectric power plant preserves the natural flow of a mountain stream, which is only supplemented by water releases diverted from a nearby reservoir when peak demands of electricity must be satisfied. This hydroplant generates high daily fluctuations in river flow several times a day, but maintains the natural conditions when it is inoperative. These exceptional conditions were thus used to measure the above mentioned topics through a field study. We focused on the Ephemeroptera *Rhithrogena semicolorata* (Curtis, 1834), because Heptagenidae mayflies are basically well adapted to fast flowing habitats. Such lotic species are therefore likely to constitute adequate model organisms for the assessment of passive vs. active drift and their consequences upon the benthos, with reference to discharge conditions. Moreover, heptagenids commonly occur within lotic invertebrate assemblages, where they may often represent a significant proportion of the overall density and biomass.

Study area, material and methods

The study was based on the River Oriège, a torrential stream in the French Pyrenees (Fig. 1). A description of the study area has been given in Céréghino et al. (2002). The natural mean flow of the Oriège varied from $1 \text{ m}^3 \text{ s}^{-1}$ in winter and summer to $5 \text{ m}^3 \text{ s}^{-1}$ during the spring thaw. The river channel is covered with water all year round. At 912 m a.s.l., flow in the Oriège River is supplemented by discharge from the Orlu hydroelectric plant (amounts by which flow is supplemented: $5 \text{ m}^3 \text{ s}^{-1}$ in spring to $10 \text{ m}^3 \text{ s}^{-1}$ in winter or summer), which is fed by water diverted from a high-altitude reservoir (Lake Naguilles, 1855 m a.s.l.). Below the outlet, hydropeaking could flush downstream large amounts of fine mineral particulates ('sand', mean diameter $< 2 \text{ mm}$) (Céréghino and Lavandier, 1996), but did not change the composition and morphology of bed paving substrate (i.e. coarse particulates, mean diameter $> 2 \text{ mm}$). Ten sampling sites were selected : a reference site upstream of the hydrostation's discharge point (site 1), and nine sites

below the outlet (sites 2–10). Their characteristics are given in Table 1.

Drift was collected for 24 h periods in June and October 1991, i.e., at the end of spring spates and low flow periods respectively, at site 1 (upstream reference site) and 4 (700 m below the outlet). These two periods allowed to specify whether flow patterns (i.e., hydropeaking representing $+5 \text{ m}^3 \text{ s}^{-1}$ during snowmelt floods in June or $+10 \text{ m}^3 \text{ s}^{-1}$ during low flows in October) had different consequences upon the drift of the species. Moreover, in June, individuals represented the populations which survived the winter conditions and spring spates, whereas in October, we sampled both larvae ending their annual development and young larval populations. Thus, these two periods provided a representative vision of studied populations (see Céréghino & Lavandier, 1996 for life cycle considerations.) However, we acknowledge that it would have been better to repeat the drift collection over a number of consecutive days, in order to validate further or to moderate our conclusions on the observed patterns. Drift samples were collected using a $30 \times 50 \text{ cm}$ drift net (mesh size 0.3 mm) at 1 h intervals. Because of clogging, the sampling period was reduced to 30 min during hydropeaking. Bottom, middle and surface water velocities were measured hourly immediately in front of the net using an OTT® portable flowmeter, to allow calculation of the volume of water filtered. Drift abundance was expressed as number of individuals per volume of water filtered (ind per 100 m^3).

In order to accurately assess the influence of intermittent hydropeaking on the benthic populations (density, biomass, size-structure), five benthic sample-units were also collected at each of the ten sites (1–10) in July 1993 (end of snowmelt floods) and October 1993 (low flow period) using a standard Surber sampler (sampling area 0.1 m^2 , mesh size 0.3 mm). Samples were taken from various substratum types: gravel (2–20 mm), pebbles (20–200 mm) and cobbles ($> 200 \text{ mm}$), and were distributed in proportion to the relative abundance of these substrata (see Table 1). This scheme provided the best quantitative (Surber sampler, all substrata were sampled, replicate sample-units) estimates with a rather low number of samples per site. Significant differences in larval density between site 1 (upstream) and each of the downstream sites were tested using Mann and Whitney non-parametric tests (Dytham, 2003).

All samples were preserved in the field in 5% formalin. *Rhithrogena* larvae were identified in the laboratory, and preserved in 70% ethylalcohol. In-

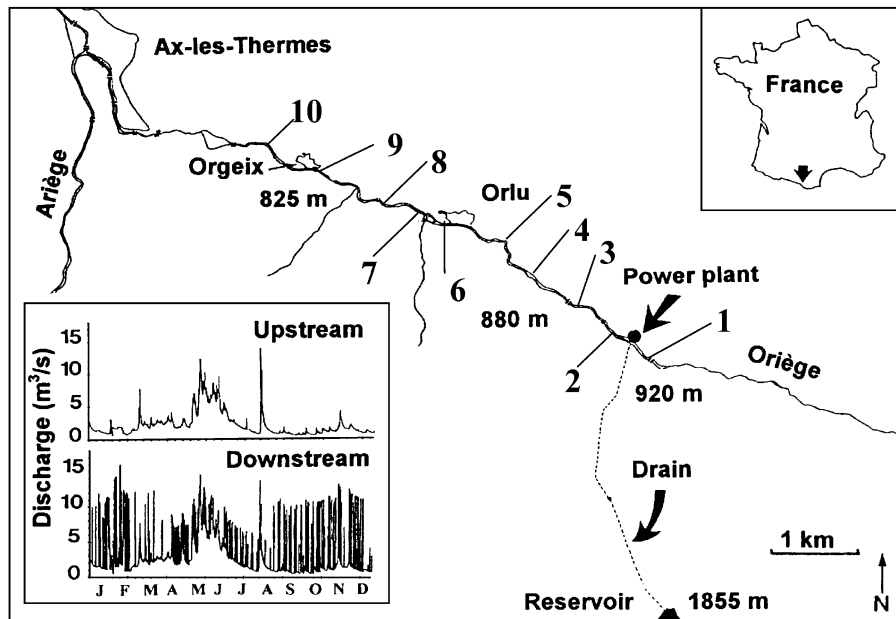


Figure 1. Map of the River Oriège, location of the ten sampling sites (1–10), and hourly discharge ($\text{m}^3 \text{s}^{-1}$) recorded at upstream site 1, and 1500 m downstream from the Orlu power plant.

Individuals were then divided into 0.1 mm interval size classes based on tibia length of the third leg (mm). This size criterion reduced the variability resulting from sexual dimorphism in *Rhithrogena* species. Differences in size-frequency distributions were assessed using Kolmogorov-Smirnov two sample tests (Dytham, 2003). Finally, larvae were dried at 60°C for 24 h and weighed, to allow calculation of the benthic biomass ($\text{mg dry weight per m}^2$) at each site.

Results and discussion

Drift

Above the plant (site 1), drift exhibited a diel periodicity, with low drift density during the day and higher drift density at night (Fig. 2a). Such nocturnal drift can be considered as "behavioural" according to Waters (1965, 1972). At both sampling periods, the size-frequency distribution of individuals drifting at night (i.e., 22 h–6 h in June, 19 h–7 h in October) was significantly different (Kolmogorov-Smirnov two sample tests, $p < 0.05$) from that of individuals drifting during the day. Larger individuals were found to drift at night (see Fig. 2b), which is consistent with the hypothesis of active avoidance of diurnal drift (Allan, 1978).

Overall drift density was higher at site 4 (downstream) than at site 1 (upstream). Drift during the day being low, the impact of catastrophic flows (elevated drift) was easily detected (Fig. 2a). Most larvae were flushed at the beginning and/or at the end of peak flows. The comparison of sampling periods suggested that disturbance was higher in autumn, i.e., when the difference between natural and peak flow was greatest. Moreover, the natural diel periodicity was not observed in October, and drift pulses were only generated by peaking flows below the outlet. Nocturnal drift almost disappeared, suggesting it is related to density-dependent factors (Ghetti & Ravanetti, 1984; Ciborowski, 1987). In June, the flushing action of each peak flow added catastrophic drift (*sensu* Culp et al., 1985) to the daily pattern, but the nocturnal drift was preserved. The size-frequency distribution of drifting larvae did not differ significantly from day to night ($p > 0.05$). The absence of daily patterns in the size composition of the drift in June (Fig. 2b) (which was almost certainly due to the larger amount of individuals drifting during the day below the outlet), and the disappearance of the nocturnal drift in October thus prevented us from assessing which larval instars were most affected by peak flows.

Nevertheless, subtle consequences of peak flows might be addressed through an analysis of benthic

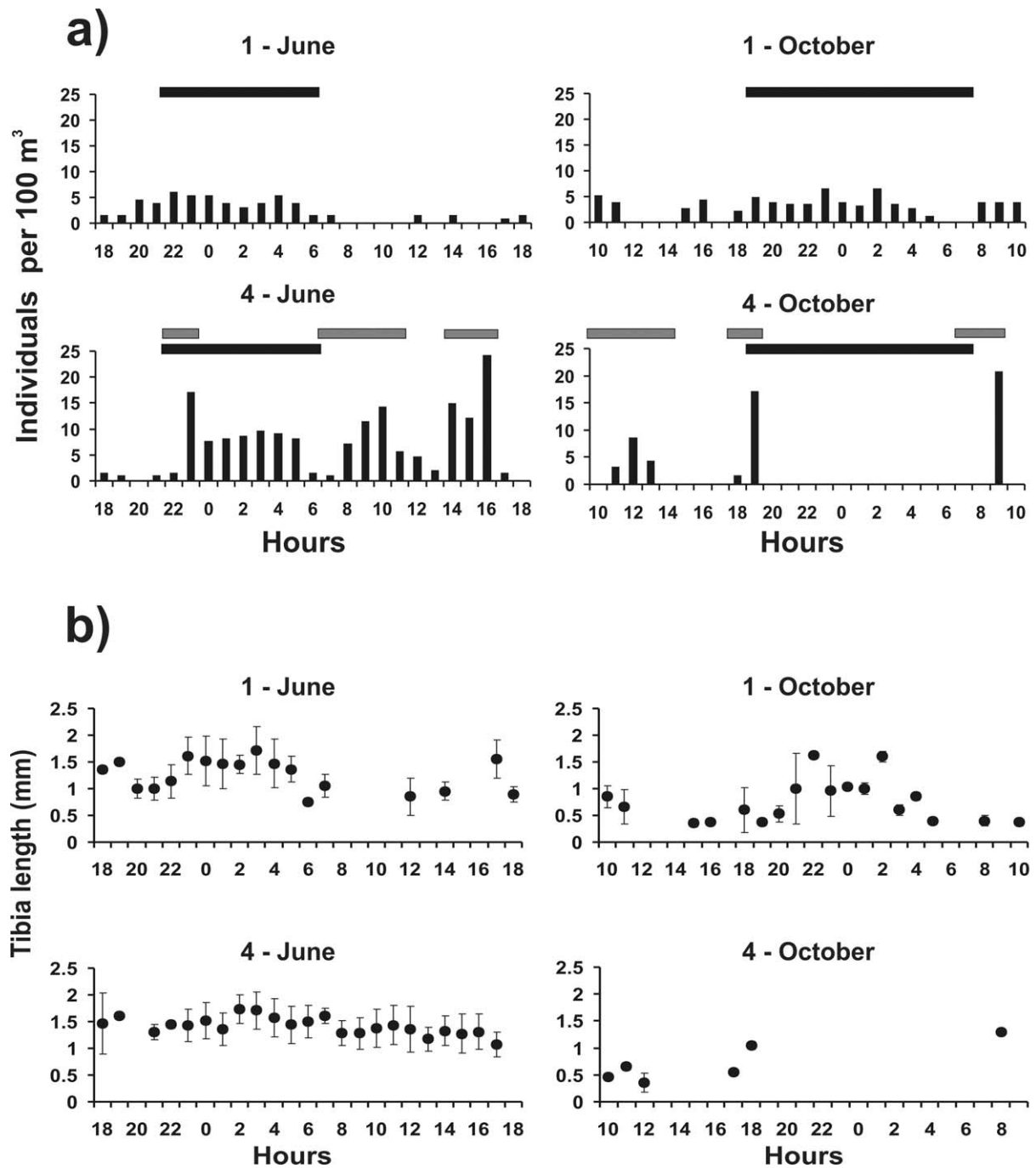


Figure 2. a) Diel variations of drift density at sites 1 (upstream) and 4 (downstream) in June and October 1991, expressed as number of individuals per 100 m³. On the top of the graphs, black solid bars indicate night and grey solid bars indicate periods of power generation. b) Diel variations of mean individual size (mean tibia length \pm SE) over 24 h at the two sites in June and October 1991. Night and hydropeaking periods as in panel (a).

Table 1. Main characteristics of the ten sampling sites 1–10 (measurements under natural conditions).

	1	2	3	4	5	6	7	8	9	10
Elevation a.s.l. (m)	920	900	885	880	860	841	833	830	825	819
Distance from outlet (m)	–700	30	275	700	1550	2250	2800	3125	3500	4375
Slope (%)	2.5	2.6	2.4	1.4	2.1	2.7	1.4	0.9	0.5	0.6
Stream width (m)	8	9.2	12	17	11	11.5	14.3	14.4	21.4	15.3
Mean depth (m)	0.25	0.26	0.45	0.39	0.33	0.39	0.33	0.28	0.29	0.30
Mean bottom current velocity (m s^{-1})	0.60	0.52	0.68	0.30	0.41	0.74	0.28	0.28	0.25	0.26
Substrate composition (%):										
Gravel (2–20 mm)	10	–	5	30	25	5	40	15	30	25
Pebbles (20–200 mm)	60	60	45	60	65	45	60	85	70	65
Cobbles (>200 mm)	30	40	50	10	20	50	–	–	–	–
Number of benthic sample units:										
Gravel	1	–	1	2	1	1	2	1	2	2
Pebbles	2	3	2	2	3	2	3	4	3	3
Cobbles	2	2	2	1	1	2	–	–	–	–

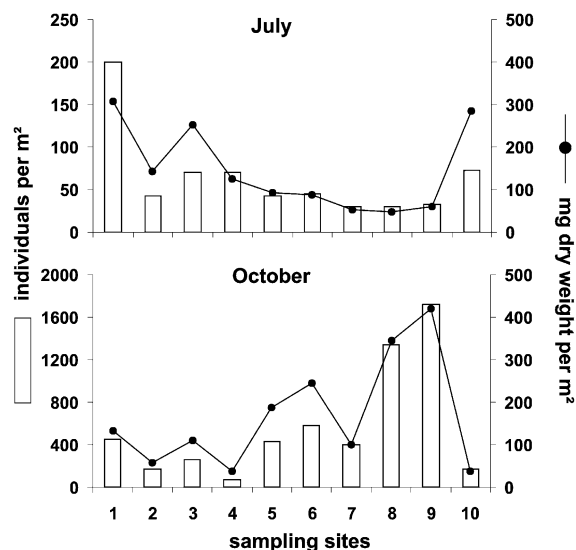


Figure 3. Benthic density (ind m^{-2}) and biomass ($\text{mg dry weight m}^{-2}$) of *Rhithrogena semicolorata* at sites 1–10 in July and October 1993.

populations: it is indeed likely that catastrophic drift pulses may have adversely affected the density and/or biomass and/or the size-structure of benthic populations below the outlet.

Benthos

Downstream changes in the benthic density, biomass, and population structure of *R. semicolorata* are

shown in Figs 3 and 4. In July (end of snowmelt floods), reference site 1 had the highest benthic density (200 ind m^{-2}) (Fig. 3). Density was significantly lower ($p < 0.05$, Mann and Whitney tests) at the downstream sites 2–10. Immediately below the outlet (site 2), it decreased to 43 ind m^{-2} , then ranged between 30 and 73 ind m^{-2} below this point. In October (low flow period), benthic density was significantly lower at sites 2–4 and 10 than at site 1, and significantly higher at sites 8 and 9 (no significant differences between site 1 and 5–7). The number of individuals decreased from site 1 (450 ind m^{-2}) to site 2 (175 ind m^{-2}). The lowest density was recorded at site 4 (73 ind m^{-2}), then it increased towards downstream sites (433 – 1723 ind m^{-2}) and finally decreased at the farthest downstream site 10 (170 ind m^{-2}). Despite slight differences in the longitudinal patterns of benthic density (i.e., the distance affected), these results suggest that intermittent discharges were primarily responsible for the depletion of the benthic population below the outlet (sites 2–10 affected in July, sites 2–4 affected in October). There were differences in the biomass to density ratio between site 1 and each of the immediate downstream sites (Fig. 3). This pattern resulted from longitudinal differences in the frequency distribution of size classes (Fig. 4). Indeed, there were significant differences ($p < 0.05$, Kolmogorov-Smirnov two sample tests) in the frequency distribution of size classes, with a shift towards larger larvae at sites 2–4 or 2–6 depend-

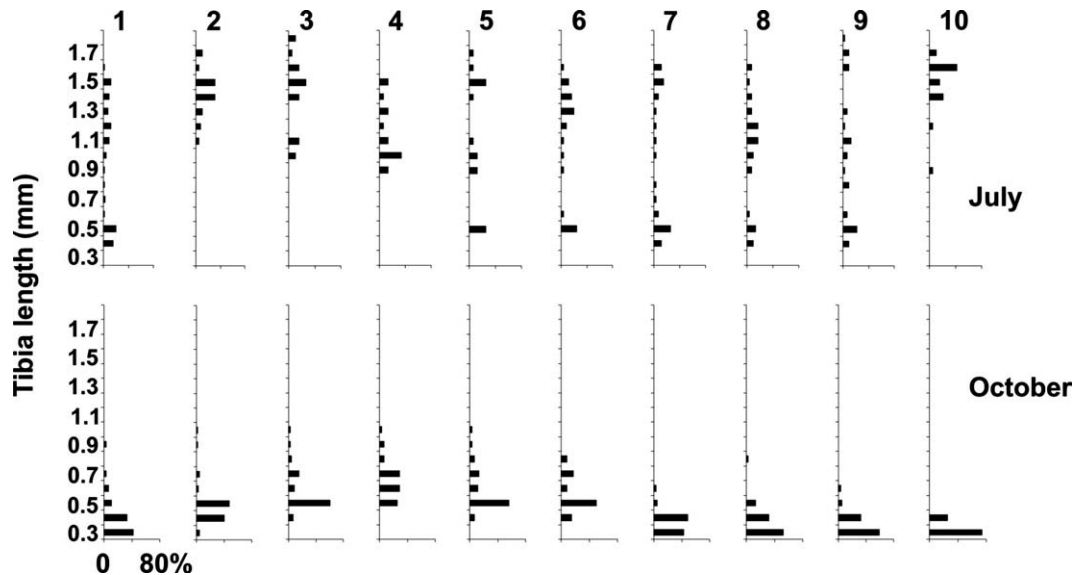


Figure 4. Frequency distribution of measurements of tibia length (3rd leg, mm) of *R. semicolorata* larvae at sites 1–10 in July and October 1993. The left-bottom panel shows the scale which was consistently used.

ing on the considered period (Fig. 4): *R. semicolorata* recovered to the reference population structure at sites 5 and 7 (i.e., 1550 and 2800 m below the outlet) in July and October respectively. These results allow one to specify the extent to which hydropeaking modified the benthic population structure of the species. Intermittent discharges obviously depleted the benthos to the detriment of smaller individuals through catastrophic drift. Nevertheless, under quite similar conditions, Raddum (1985) reported a shift towards smaller benthic individuals in several mayfly and stonefly species in Norway, due to the drift of the largest individuals out of the area. As a possible explanation of our observations, we suggest that harsh hydraulic conditions could have adversely affected smaller larvae during a 'critical period', i.e. when they had not yet established their refuge habitats soon after hatching.

Conclusion

Under a natural flow regime, *R. semicolorata* was able to control its entry into the drift, either during low (autumn, $1 \text{ m}^3 \text{ s}^{-1}$) and high flow (spring, $5 \text{ m}^3 \text{ s}^{-1}$) periods. When sudden rises in discharge were artificially generated (natural flow being supplemented by $5 \text{ m}^3 \text{ s}^{-1}$ and $10 \text{ m}^3 \text{ s}^{-1}$ in spring and autumn respectively), many larvae were flushed downstream during the day. Smaller individuals – which were probably unable to maintain their position under greater

erosive forces and/or did not found refuge habitats – were more affected by passive dislodgement. Indeed, the benthic population was adversely affected both in terms of density and size-composition, with a shift towards larger individuals below the outlet. Catastrophic drift occurring during the day adversely affected (suppressed) the nocturnal active drift when the difference between natural flow and peak flow was the greatest, i.e., when flow was supplemented by $10 \text{ m}^3 \text{ s}^{-1}$ and thus raised from 1 to $11 \text{ m}^3 \text{ s}^{-1}$. Nevertheless, the nocturnal drift was preserved when flow only raised from 5 to $10 \text{ m}^3 \text{ s}^{-1}$. These results support the idea that the amplitude of disturbance is a more important factor than the peak value itself.

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