RESEARCH ARTICLE

WILEY

Flow amplitude or up-ramping rate? Quantifying single and combined effects on macroinvertebrate drift during hydropeaking simulations, considering sensitive traits

Lisa Schülting[1] | Florian Dossi[1] | Wolfram Graf[1] | Diego Tonolla[2,3]

[1]Department of Water, Atmosphere and Environment, Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Science Vienna, Vienna, Austria

[2]Institute of Natural Resource Sciences, Zurich University of Applied Sciences, Wädenswil, Switzerland

[3]eQcharta GmbH, Wädenswil, Switzerland

Correspondence
Lisa Schülting, Department of Water, Atmosphere and Environment, Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Science Vienna, Gregor-Mendel-Straße 33, Vienna 1180, Austria.
Email: lisa.schuelting@boku.ac.at

Abstract

The hydrological regime of many alpine rivers is heavily altered due hydroelectric power generation. Hydropeaking operation produces frequent and irregular discharge fluctuations. Depending on the operational changes of flow amplitude and/or up-ramping rate as well as on river morphology, hydropeaking can lead to quick and strong variations in hydraulic stress affecting stream invertebrates and causing increased drift. In the present flume experimental study, we analyzed trait-specific drift reactions to single and combined effects of increased flow amplitude and up-ramping rate. We analyzed taxa according to their hydraulic habitat preference and flow exposure, as these traits seem to be indicative toward hydropeaking. The results show that the sudden increase in discharge and related flow velocity led to increased macroinvertebrate drift proportions in hydropeaking treatments, which differed significantly to parallel control runs (mean drift proportion in all hydropeaking setups: 13% compared to 5% in controls). Increasing flow amplitudes led to an increase in drift for most taxa and traits. This was particularly significant for taxa associated with lentic areas. The effect of the up-ramping rate on macroinvertebrate drift was nonsignificant but showed strong interactive effects with the flow amplitude, especially for taxa dwelling on the substrate surface. Our results therefore indicate that discharge-related parameters, such as flow velocity, primarily affect macroinvertebrate drift and the importance of the up-ramping rate increases, if certain discharge-related thresholds are exceeded. Vice versa, a reduction of the up-ramping rate at hydropeaking events with high flow amplitudes may reduce the effect on macroinvertebrate drift. Flow-exposed (surface) and flow-sensitive (lentic) taxa showed distinct drift reactions following hydropeaking treatments, which were significantly higher compared to effects on taxa associated to lotic and interstital habitats. Therefore, we conclude that both traits (hydraulic and vertical habitat preference) have proven as promising for analyzing hydropeaking effects. The trait classifications should be extended to a higher number of taxa and to different life stages as these may show different drift patterns.

1 | INTRODUCTION

Flow acts as a driving force determining physical habitats and the associated biotic composition within riverine ecosystems (Bunn & Arthington, 2002) because stream organisms have evolved behavioral and morphological traits as well as life history strategies in direct response to natural flow regimes and extreme flows (Arthington, Bunn, Poff, & Naiman, 2006; Lake, 2000; Poff et al., 1997). Many Alpine rivers are found to be subject to significant alterations of the flow regime due to hydroelectric power generation. Storage hydropower plants use the potential energy of water stored at high elevations for rapid electricity production on demand, to provide grid stability by supplementing unsteady power production from solar and wind power plants. This operational mode produces frequent and irregular discharge fluctuations, referred to as "hydropeaking" (HP) (Bratrich et al., 2004; Bretschko & Moog, 1990; Bruno, Siviglia, Carolli, & Maiolini, 2013). Generally, HP events are characterized by three distinct phases of 1) an increase in discharge, 2) a flow peak, and 3) a flow decrease (Greimel et al., 2016). Alterations induced by HP include sudden modifications of the wetted width, water depth, flow velocity, and bottom shear stress. Additionally, hydropeaking can lead to an altered thermal regime as well as to changes in the sediment dynamics (Baumann & Klaus, 2003; Hauer, Holzapfel, Leitner, & Graf, 2017; Schmutz et al., 2015; Zolezzi, Siviglia, Toffolon, & Maiolini, 2011).

Jones (2014) suggests that flow management focusing on avoiding thresholds that limit productivity and decrease biodiversity in HP affected rivers ("ecopeaking") may support ecological functioning, while hydroelectrical energy production and flexibility are not or only partly restricted. For this purpose, it is required to gain profound knowledge on environmental flows and their direct link to effects on biological indicators such as macroinvertebrates (Ramos, Formigo, & Maia, 2018).

Several HP-related parameters have found to trigger benthic invertebrate drift, stranding, or changes in community composition (e.g., Smokorowski, 2021). Main hydraulic characteristics for the description of HP patterns are: (1) the mean and maximum flow fluctuation rate (i.e., the rapidity of flow increase and decrease), (2) the flow amplitude ($Q_{max} - Q_{min}$), (3) the flow ratio (Q_{max}/Q_{min}), and (4) the duration of the event (Greimel et al., 2018). Further, (5) the frequency, (6) periodicity, and (7) timing of HP constitute essential aspects in the ecological assessment of HP impacts (Kjaerstad, Arnekleiv, Speed, & Herland, 2018; Meile, Boillat, & Schleiss, a. J., 2011; Puffer et al., 2015).

An increasing body of literature on HP -induced effects on aquatic macroinvertebrates has been compiled in the recent years. Many of these studies have observed community patterns of affected river stretches, such as macroinvertebrate density, diversity, and population structure. Hydromorphological habitat alteration due to HP is reported to lead to a reduction in biomass as well as a decrease of flow-sensitive and support of flow-tolerant taxa (Bretschko & Moog, 1990; Cushman, 1985; Kjaerstad et al., 2018; Leitner, Hauer, & Graf, 2017; Mihalicz, Jardine, Baulch, & Phillips, 2019). Organism drift induced during flow increase due to high hydraulic stress leads to low macroinvertebrate abundance below dams (Elgueta et al., 2021; Gibbins, Batalla, & Vericat, 2010; Lauters, Lavandier, Lim, Sabaton, & Belaud, 1996; Timusk, Smokorowski, & Jones, 2016). If the animals are forced to enter the drift unintentionally by dislodgement, it is referred to as "passive" or "involuntary drift" (Brittain & Eikeland, 1988; Gibbins, Vericat, & Batalla, 2007; Waters, 1972). While "behavioral" or "active" drift is mostly triggered by biotic factors, such as predatory pressure or food availability, passive drift is caused by physical disturbance (Brittain & Eikeland, 1988; Minckley, 1964; Naman, Rosenfeld, & Richardson, 2016). Depending on the flow amplitude as well as on the river morphology, HP can lead to a strong increase in discharge-related parameters (e.g., flow velocity, water depth) and hydraulic stress acting on the organisms. With increasing discharge, the organisms must invest increasing energy to avoid passive drift. In consequence, a strong link between these parameters and macroinvertebrate drift has been described in numerous studies (Brooker & Hemsworth, 1978; Elliott, 1967; Gibbins et al., 2007; Miller & Judson, 2014; Poff, DeCino, & Ward, 1991; Timusk et al., 2016).

Even though rarely quantified, the up-ramping rate (i.e., the rapidity of flow increase) is regarded as an additional parameter determining the effect of HP on macroinvertebrate drift. Fast flow increases lead to limited time for organisms to seek shelter and hence increases the risk of drift (Bruder, Tonolla, & Schweizer, 2016; Gabbud, Bakker, Clémençon, & Lane, 2019; Kjaerstad et al., 2018; Parasiewicz, Schmutz, & Moog, 1998; Schülting, Feld, Zeiringer, Huđek, & Graf, 2018; Smokorowski, 2010; Timusk et al., 2016; Tonolla, Bruder, Schweizer, & Barcelo, 2017).

Macroinvertebrate taxa and life stages show differing sensitivity to HP in terms of propensity to drift. The lateral and vertical distribution of taxa within a river section can provide indications about the flow tolerance of taxa and their hydraulic habitat preference. Flow exposed taxa (i.e., associated to substrate surface located in high-flow areas like the middle of the stream) have adaptations to resist high flow velocities. Specific taxa can withstand different flow velocity thresholds and exposure time to increased discharge (Oldmeadow, Lancaster, & Rice, 2010; Statzner & Holm, 1989; Waringer, 1989), suggesting that ecological and behavioral traits (e.g., presence of claws/hooks, body shape,. the ability to quickly crawl into the interstices, etc.) affect drift responses to rapid discharge changes (Timusk et al., 2016).

Several studies suggest that biotic assessment of flow alterations is most effective when based on trait-specific sensitivity (Kjaerstad et al., 2018; Rader, 1997; Timusk et al., 2016; Tupinambás, Cortes, Hughes, Varandas, & Callisto, 2016). To address existing knowledge gaps regarding HP impact and assessment, we analyzed trait-specific drift reactions to single and combined effects of flow amplitude and up-ramping rate. We classified taxa according to their distribution along lateral transects (from lentic habitats on the river margin to lotic habitats in the stream center) and their vertical distribution (association to the interstices or substrate surface, indicating the flow exposure of taxa as well as the preference and adaptation to flow) as these features seem strongly relevant in terms of HP sensitivity and propensity of macroinvertebrates to drift (Kjaerstad et al., 2018; Naman et al., 2016).

Quantifying the effects of above mentioned hydraulic parameters in situ is challenging due to the variation in local characteristic and interacting external influences on biota (Hayes et al., 2019; Melcher et al., 2017; Pearce et al., 2019). Flume setups are common approaches to disentangle and quantify effects from multiple variables, since these allow precise control of the setting and a reduction of confounding factors (Bruno, Cashman, Maiolini, Biffi, & Zolezzi, 2016; Carolli, Bruno, Siviglia, & Maiolini, 2011; Imbert & Perry, 2000). To test the short-term reactions of macroinvertebrate assemblages at HP unaffected streams, we therefore used an experimental setup in artificial flumes, with macroinvertebrate drift as response variable (see also Schülting et al., 2018; Schülting, Feld, & Graf, 2016). We hypothesized that HP -induced macroinvertebrate drift will increase with increasing flow-amplitudes and up-ramping rates. Further, we expected stronger drift responses for taxa associated to the substrate surface and low adaptation to flow.

2 | MATERIAL AND METHODS

2.1 | Sampling of donor populations

Donor populations were sampled at the Bodingbach (Strahler order 4), a meta- to hyporhithral brook near the facility. This hydro-morphologically near-natural stream is located in the Northern Limestone Alps and drains into the Ois River (BMLFUW, 2007; Fink, Moog, & Wimmer, 2000). Macroinvertebrate samples were taken before each experimental run, using a hand net (25×25 cm frame size, 500 μm mesh size). To include taxa with different traits, we took four single samples (each covering an area of 25×25 cm) along a transversal transect from the margin to the in-stream area. The four single samples were pooled in a closable bucket. For each experimental run, this procedure was repeated six times to collect the test organisms for six flumes.

2.2 | Experimental facility

The experiments were conducted in 2017 from 19th of March to 25th of April at the "Hydromorphological and Temperature Experimental Channels" (HyTEC) in Lower Austria. The HyTEC experimental facility is located approximately 600 m downstream of Lake Lunz (600 m.a.s.l.) and is fed with nutrient-poor lake water from 0.75 and 10 m depth. The water is pumped into two separate basins in which the lake water from both depths is mixed.

Discharge and ramping rates can be programmed for each pipe with a control unit (Siemens Simatic S7-300), measured with ultra-sonic sensors (Rittmeyer RISONIC 2000, Sensor Typ A) and automatically adjusted via electrically controlled pipe gate valves. The manipulation can be adjusted separately for each mixing basin to allow for conducting simultaneous control runs. Downstream the experimental facility, the water is released into the outflow of the lake. For further technical details, please refer to Auer, Fohler, Zeiringer, and Führer (2014); Auer, Zeiringer, Führer, Tonolla, and Schmutz (2017). The outflow of each basin is represented by three flumes (i.e., steel construction with plywood, acrylic sheets as side, and ground elements), which were installed in parallel (Figure 1). Please also see Schülting et al. (2016, 2018). Since the control unit allows controlling the hydrological setting within the mixing basins but not in the flumes directly, flow velocities, depths, and speed of the water level changes had to be measured for different discharge and ramping setups in each flume to guarantee equal conditions for each flume. To achieve comparable thermal conditions between experiments and sampling location, the lake water was mixed with 50% epilimnic and 50% hypolimnic lake water. Water temperature mean deviation between the Bodingbach and the experimental facility was 1.1°C ± 0.8.
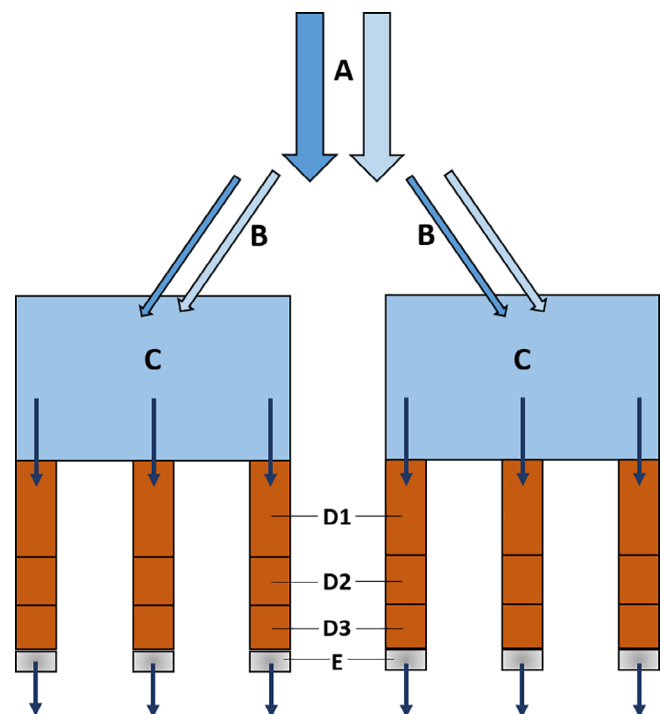

FIGURE 1 Schematic overview of the experimental setup. (a) Pipelines taking water from the deep and upper layer of Lake Lunz indicated by dark and light blue colour, (b) diversion into separate pipes, (c) mixing basins, (d) flumes (D1 and D3: buffer zones, D2: experimental area), and (e) exchangeable drift net [Color figure can be viewed at wileyonlinelibrary.com]
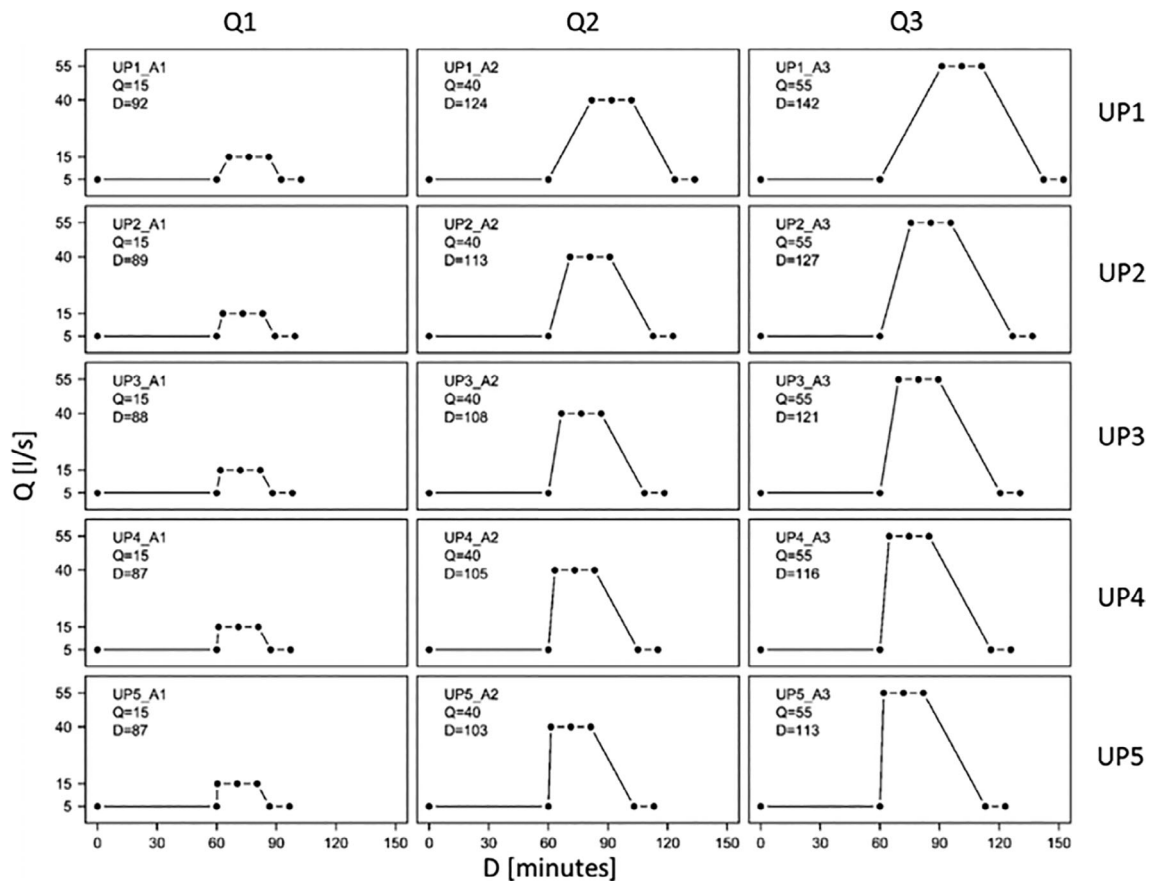
FIGURE 2 Experimental treatment setups and IDs (composed of UP 1–5: up-ramping rate setup and Q 1–3: peak discharge setup), Q: Discharge (l/s), D: duration in minutes (adaptation period to end of down-ramping). Controls consisted of constant discharge of 5 L/s and the same timeline as each corresponding treatment

Each flume has a width of 0.5 m and a length of 3 m. The bottom of each flume was covered with an approximately 15 cm thick sediment layer collected from the nearby River Ybbs (30% akal, 60% micro- and 10% mesolithal). Exchangeable drift nets with a mesh size of 500 μm were installed at the outlets of the flumes. See Schülting et al. (2016) and Schülting et al. (2018) for more details.

2.3 | Experimental setups to quantify the effects of flow amplitude and up-ramping rate

In total, 15 different HP treatments were tested, consisting each of a combination of a specific discharge and up-ramping setup (Figure 1). HP treatments were chosen following an extensive literature research (e.g., Hauer et al., 2017; Lauters et al., 1996; Miller & Judson, 2014; Moog, 1993; Munn & Brusven, 1991; Parasiewicz et al., 1998; Perry & Perry, 1986; Valentin, Wasson, & Philippe, 1995). The most common discharge ratios (between base flow and peak flow) reported in HP field studies were between 1:2 and 1:12. Thus, for the setup of the flume experiments discharge ratios of (Qmin/Qmax) 1:3, 1:8, and 1:11 were chosen, corresponding to base flow of 5 L/s and the peak discharges Q1: 15 L/s, Q2: 40 L/s, Q3: 55 L/s in each flume. Ramping rates are usually reported as flow related measures (e.g., [m³/s]/min);

however, these information are ecologically less relevant and not very useful for installing experimental simulations, in comparison to stage-metrics such as change in water level per time unit (Greimel et al., in review). To estimate a realistic range of up-ramping rates for the flume experimental setup, we therefore used unpublished modeling data (SuREmma project report in German: Greimel et al., 2017; see also Hauer et al., 2017). Based on these, five different up-ramping rates were chosen (UP1: 0.3 cm/min, UP2: 0.6 cm/min, UP3: 1 cm/min, UP4: 2 cm/min, UP5: 5 cm/min). The down-ramping rate was programmed to be always 0.3 cm/min as fish stranding risk seems to be reduced below this value (Hayes et al., 2019; Tonolla et al., 2016), and data for benthic invertebrates regarding stranding are largely missing.

At each experimental run, three flumes (mixing basin 1) served as treatment and the other three flumes (mixing basin 2) as control. Each experimental treatment was repeated twice, whereby HP and control channels were exchanged, thus resulting in six experimental units for each treatment setup and six corresponding controls. In total, 30 experimental runs and 90 experimental treatment units as well as 90 control units (15 treatment setups × 3 flumes × 2 runs and 15 corresponding control setups × 3 flumes × 2 runs). Detailed information about the experimental setups and single runs is listed in Table S1. Simultaneous control runs were conducted with constant

base flow of 5 L/s, using the same timeline as the corresponding treatments.

For inoculation, the flumes were closed, so that stagnant flow conditions were achieved. The six buckets containing the macroinvertebrate samples collected in the brook were then randomly distributed between the flumes and then carefully introduced manually. Organic substrate within the samples was removed. After the inoculation, the flow was re-established with a base flow of 5 L/s for 60 minutes to enable an adaptation of the animals. The adaptation time of 60 min was selected based on preliminary experiments that showed a drift decreased during the first 20 minutes after the introduction of the animals into the flume and was followed by a constant, low drift.

For HP experiments, the discharge was gradually increased (up-ramping phase) until the peak flow was reached (peak flow phase). Peak flow was maintained for 20 min after which the discharge was reduced again to base flow (down-ramping phase). The drift nets were emptied into separate sampling containers after each phase. During peak flow the nets were emptied twice, each after 10 minutes. Drift in the parallel control runs was collected simultaneously to the drift collected during treatments. At the end of each experiment, the substrate was turned over to the bottom of each flume manually at high flow to wash out the remaining animals. Possibly, a very low and negligible number of single individuals may have been missed after each run; however since the cleaning treatment was always the same, the bias should be constant throughout the experiments. After the experiments, the samples were fixed with formaldehyde (final concentration 4%).

Besides the constant inflow measurement in the pipes (see above), flow velocity and water depth (h) were measured separately before the drift experiments, for each discharge setup and in each flume. Thereby, experiments were not disturbed. Flow velocity was measured using a micro propeller (Höntzsch FT25GFE-MN20/100/P6; average over 30 sec) at approximately 40% water depth (measured from the sediment surface; v_{40}) and near (2 cm above) the sediment surface (v_0). All measurements were taken at nine points distributed equally in the experimental area of the flumes. Table 1 reports measured and calculated discharge-related parameters for all three discharge setups and the control.

All samples were taken to the laboratory for identification. The samples were identified (following Glöer et al., 1994; Tachet, Richoux, Bournaud, & Usseglio-Polatera, 2000; Bauernfeind & Humpesch, 2001; Waringer & Graf, 2011), sorted, and counted in the laboratory. The taxonomic level of identification was based on Ofenböck, Moog, Hartmann, Stubauer, and Leitner (2018). Ephemeroptera, Plecoptera, and Trichoptera were identified to the lowest possible level. Most other groups were identified to family level. The different systematic units were then counted.

2.4 | Response variable and statistical analyses

Drift proportions were calculated to express the short-term response of macroinvertebrates to HP, representing the number of drifted specimens divided by the total number of specimens in each flume. The drift proportions were calculated for each experimental unit for all specimens, on trait level and for selected taxa.

$$\text{drift proportion}: \frac{S(UR) + S(P) + S(DR)}{S(UR) + S(P) + S(DR) + S(\text{not drifted})}$$

S: sum of specimens, UR: upramping, P: peak, DR: downramping.

Statistical and graphical analyses were conducted using R version 3.6.2. We tested for normality and variance homogeneity using the Shapiro–Wilk test (Shapiro & Wilk, 1965) and Levene's test (Levene, 1960), respectively. Since assumptions for parametric tests such as t-test or ANOVA were not met for all data, the nonparametric Mann–Whitney U and Kruskal–Wallis tests with a level of significance of 0.05 was performed for testing differences between the experimental setups.

To identify interactive effects between the up-ramping rate and flow amplitude, we additionally computed Bayes factors for all main effects and interaction contrasts in an ANOVA design. The resulting Bayes Factors (BF) calculated for the different models were interpreted based on Kass and Raftery (1995). Hedges' g was calculated to interpret and discuss the different treatment effects for the selected taxa (Hedges, 1981). Hedges' g is a measure of effect size and indicates the way in which an experimental group differs from a control group.

2.5 | Trait classifications of taxa

Two different trait categories were analyzed in the present study: (1) The association of taxa to lentic versus lotic habitats (i.e., hydraulic

TABLE 1 Mean and standard deviation (SD) of hydrological/hydraulic parameters measured or calculated for each discharge setup (Q1, Q2, and Q3) and controls

	Controls	Q1	Q2	Q3
Peak discharge (l/s)	5	15	40	55
Discharge ratio	1:1	1:3	1:8	1:11
Amplitude (Δh in cm)	0.0	3.8	7.8	9.4
h at peak flow (cm)	6.72 ± 1.55	10.50 ± 1.18	14.47 ± 1.17	16.13 ± 1.76
v_0 at peak flow (m/s)	0.09 ± 0.06	0.27 ± 0.08	0.46 ± 0.15	0.54 ± 0.13
v_{40} at peak flow (m/s)	0.13 ± 0.05	0.41 ± 0.06	0.73 ± 0.12	0.84 ± 0.12
Mean shear stress[a] (N/m^2)	0.07 ± 0.07	0.51 ± 0.28	1.48 ± 0.93	1.95 ± 1.01

[a]The shear stress was calculated using an empirical approach according to Whiting and Dietrich (1990).

			Mean	Sd.	Min.	Max.
Control	Vertical habitat preference	Interstitial	0.03	0.03	0.00	0.14
		Surface	0.05	0.03	0.00	0.15
	Hydraulic habitat preference	Lentic	0.05	0.03	0.00	0.15
		Lotic	0.06	0.05	0.00	0.26
HP	Vertical habitat preference	Interstitial	0.06	0.05	0.00	0.24
		Surface	0.13	0.07	0.02	0.33
	Hydraulic habitat preference	Lentic	0.14	0.09	0.00	0.42
		Lotic	0.10	0.06	0.02	0.23

TABLE 2 Trait-specific drift responses (mean, standard deviation, minimum and maximum drift proportions) to hydropeaking simulations compared to controls

habitat preference) represents the taxa-specific adaptation to flow velocity. Taxa inhabiting habitat patches characterized by high current own behavioral or morphological adaptations to exploit habitats in high hydraulic stress, whereas taxa inhabiting lentic areas lack those adaptations (Statzner & Holm, 1989). (2) The association of taxa to interstitial or surface habitats (i.e., vertical habitat preference) represents the individual exposure to flow and therefore the likelihood of being affected by substrate-near hydraulic forces (Rader, 1997).

2.5.1 | Hydraulic habitat preference

For the classification of taxon-specific preferences for lentic or lotic habitats, 28 single samples were taken from Bodingbach along seven transects from the shore to the middle of the stream. Flow velocities (v_0, v_{40}) and water depth were measured at each sampling point.

The distinction between lentic and lotic habitats was carried out using a decision tree based on the recorded flow velocities and water depth as well as the distribution of two antagonistic taxa *Allogamus auricollis* and *Rhithrogena* sp., respectively. *A. auricollis* is known to prefer low-flow shore habitats (Waringer, 1989), while typical habitats of *Rhithrogena*-species are characterized by faster flow velocities (Céréghino, Legalle, & Lavandier, 2004; Schmedtje & Colling, 1996). Additionally, a principal component analysis (PCA) was conducted to identify and visualize respective community patterns. Based on the results of the regression tree, the PCA and the distribution of flow velocity values, each sampling location and the associated taxon was then assigned to the classes "lentic" or "lotic."

Each taxon that occurred with a relative abundance ≥70% in lentic or lotic habitats was associated to the respective group. To identify statistically significant associations of taxa to a group, we further performed a multilevel pattern analysis (i.e., Indicator Species Analysis) based on the Indicator Value Index (Dufrêne & Legendre, 1997).

2.6 | Vertical habitat preference

To indicate the flow exposure of present taxa, the animals were classified according to their association to "interstitial" or "surface" habitats. The vertical habitat preference was classified based on expert knowledge (RHEOPHYLAX working group, 2021). Taxa and trait classification are listed in Table S2.

3 | RESULTS

3.1 | Donor populations and adaptation period

In total, 89 taxa and 70,166 specimens were collected and used within the experimental approach. The number of specimens per experiment ranged from 137 to 776. To account for that bias, we consistently used drift proportions as a response variable for all analyses. Details on the total abundances as well the community structure within each experimental setup are listed in Figures S1 and S2.

During the adaption period, minor drift proportion variations among some taxa were observed, yet all differences between control and HP flumes were not significant. Particularly high drift proportions were observed for Baetidae and Elmidae in the adaptation period. In contrast, Leptophlebiidae showed almost no drift during the adaption period.

3.2 | General and taxa-specific drift responses following hydropeaking treatments

Sudden increase in discharge, shear stress, water depth, and flow velocity (Table 1) following HP treatments significantly increased ($p < 0.01$) the macroinvertebrate drift proportions (0.13 ± 0.7) by a factor of 2.6 compared to parallel control runs (0.05 ± 0.02), which further significantly differed between discharge setups ($p < 0.05$; Figure 3, left).

In the controls, mean drift proportions did not exceed 0.06 (Q1: 0.04 ± 0.03; Q2: 0.06 ± 0.02; Q3: 0.04 ± 0.02). In the HP treatments, mean drift proportions showed an increasing trend from low to high discharge setups (Q1: 0.07 ± 0.03; Q2: 0.14 ± 0.07; Q3: 0.17 ± 0.06). Drift proportions at Q2 were significantly higher than Q1 and drift proportions at Q3 were also significantly higher compared to Q2 (both $p < 0.01$). Differences between drift during Q2 and Q3 were nonsignificant.

Significant differences between the up-ramping setups were only evident at experimental runs with high peak discharges (Q3; Figure 3; Table 1). At discharge treatment Q3 up-ramping rates >1 cm/min showed mean drift proportions of 0.22 ± 0.06, whereas drift proportions at up-ramping rates ≤1 cm/min were 36% lower (0.14 ± 0.04; $p < 0.01$). In the other discharge treatment groups, the differences between different up-ramping groups were not significant.
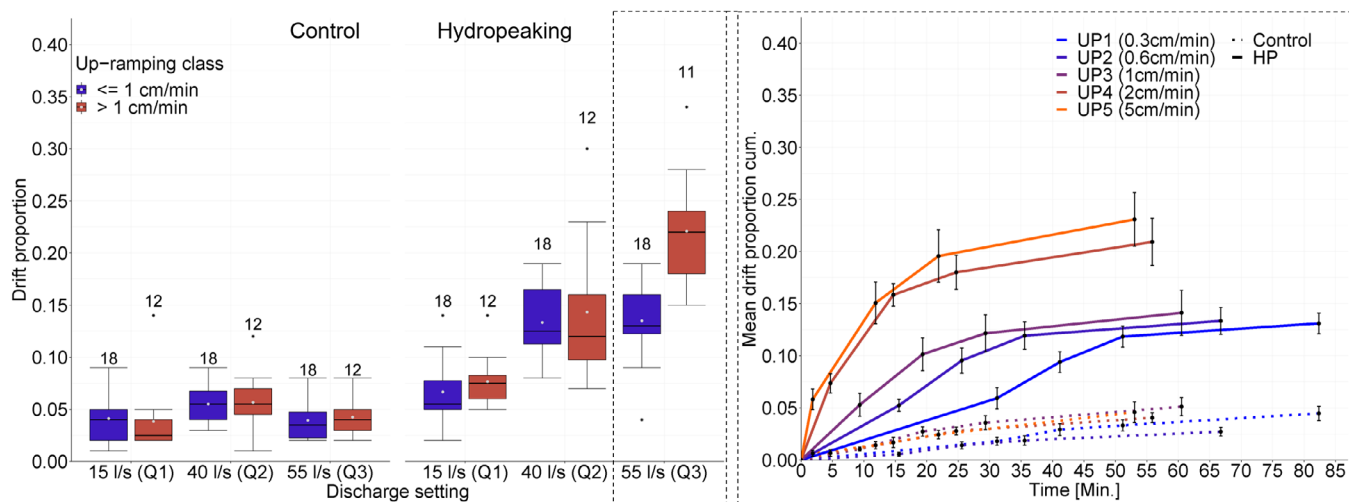
FIGURE 3 Drift proportions displayed for hydropeaking treatments (see Figure 2) and controls, split between discharge treatments and up-ramping rates (grouped: ≤1 cm/min; >1 cm/min); right: mean cumulated drift proportions calculated for each phase during the experiment for the discharge treatment Q3 (mean values and error bars are indicated for each phase from up-ramping, first peak phase, second peak phase, and down-ramping), split between all up-ramping treatment groups (UP1 – UP 5) [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 4 Effect sizes compared between the different discharge setup for most common taxa in the dataset. Dotted lines separate small effects (0.2–0.5), medium effects (0.5–0.8) and large effects (>0.8). Negative values indicate that drift was higher in the controls. Left: Differences between discharge setups; right: Differences between up-ramping setup during the highest discharge setup Q3 [Color figure can be viewed at wileyonlinelibrary.com]
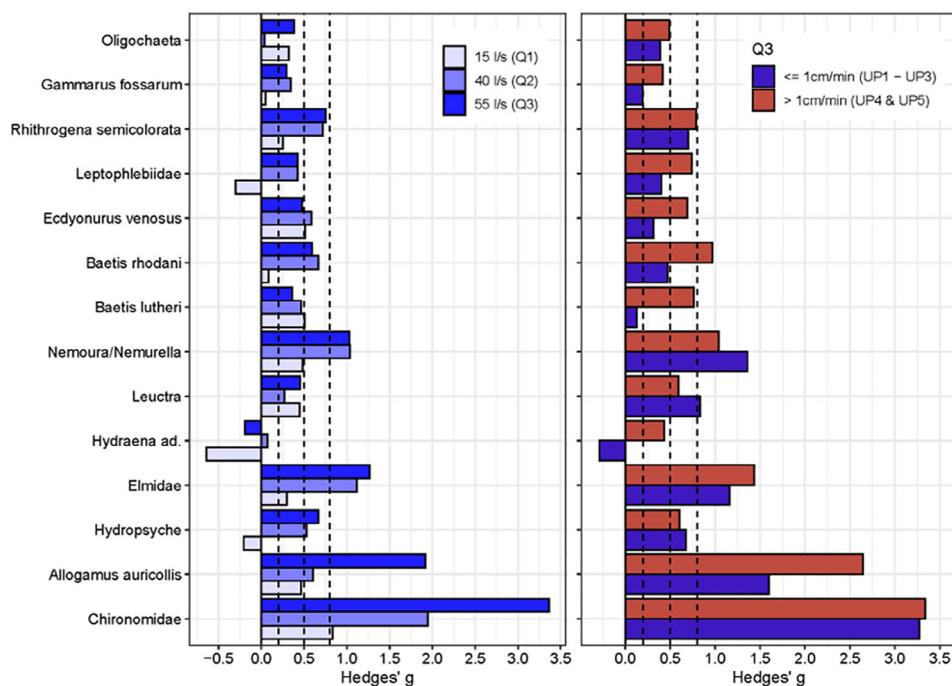
At the highest discharge treatment (Q3), the drift proportions showed an increasing trend from the lowest (0.3 cm/min) to the highest (5 cm/min) up-ramping rate (Figure 3, right). However, despite the minor tendency at up-ramping rates of ≤1 cm/s (Q3_UP1 to Q3_UP3), no differences of the cumulated drift proportions were evident at any stage, whereas up-ramping rates faster than 1 cm/min (UP4 and UP5) resulted in significantly higher cumulated drift proportions. Significant differences of cumulated drift proportions were found between UP1 and UP2 compared to UP4 and UP5 ($p < 0.05$), and drift during UP3 differed significantly from UP5 ($p < 0.01$).

Highest drift proportions were measured during the flow increase (i.e., up-ramping phase) and during the first 10 minutes of the peak in all setups. Differences between drift in the different up-ramping setups became evident during the peak, while after the up-ramping phase the drift proportions were still similar between all setups (Figure 3, right).

Drift proportions in HP treatments varied widely among selected taxa, yet all significantly exceeded those of the corresponding controls ($p < 0.01$), except for *Gammarus fossarum* (Crustacea) and *Hydraena* sp. Adults (ad) (Coleoptera), which showed no significant differences

between treatment and control runs. Comparably low responses were evident for *Leuctra* sp. (Plecoptera) and Oligochaeta (Figure 4, left). Large effects were recorded for Chironomidae, *Allogamus auricollis* (Trichoptera), Elmidae (Coleoptera), and by *Nemoura/Nemurella pictetii* (Plecoptera). Most taxa only showed small treatment effects at Q1, like *Baetis rhodani* and Elmidae, whereas at Q2 and Q3 for most taxa, a medium to large treatment effect was evident (Figure 4, left). Within discharge setup Q3, most taxa showed higher drift response during fast up-ramping (UP4 and UP5) except for *Hydropsyche*

sp. (Trichoptera), *Leuctra* sp., and *Nemoura* sp./*Nemurella pictetii*, which showed opposite patterns (Figure 4, right). More detailed information on taxa-specific drift is provided in Table S2.

3.3 | Trait-specific responses

3.3.1 | Classification of taxa according to their hydraulic habitat preference

The results of the decision tree, based on *Rhithrogena* sp. and *A. auricollis* abundance as well as v_0, v_{40} and water depth (h) as independent variables, identified the v_{40} as pivotal variable and show a clear distinction between both taxa at 0.24 m/s (Figure 5).

As additional validation of these results, a PCA analysis was performed based on the entire benthic communities and flow velocities from each sample (Figure 6, left). Based on these results, sampling locations 1 and 2 were classified as "lentic" and sampling locations 3 and 4 as "lotic." All tested abiotic parameters (v_0, v_{40}, h) show significant differences between both groups, whereby v_{40} shows the strongest discrimination (Figure 6, right).

Taxa that occurred in lentic or lotic samples with relative abundances of more than 70% were classified accordingly. 19 taxa were identified as associated to lentic habitats, and 29 taxa were associated to lotic habitats. All taxa and trait classifications are listed in Table S2. Additionally, an indicator species analysis was performed by which 21 taxa with significant association to one of the groups (lentic or lotic) were identified. Taxa with significant association to lentic habitats were Leptophlebiidae, *Allogamus auricollis*, *Halesus* sp., *Habrophlebia lauta*, *Ephemerella mucronata*, *Ephemera danica*, *Pisidium* sp., *Radix* sp., and *Oreodytes sanmarkii* ad., whereas taxa significantly
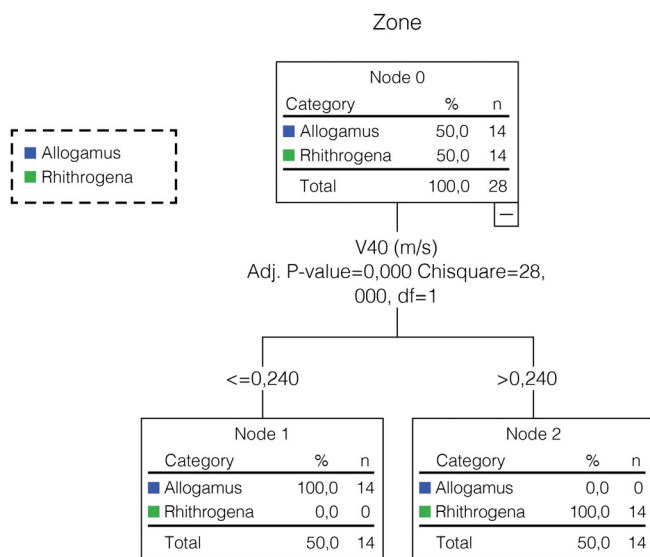

FIGURE 5 Decision tree based on the recorded flow velocities and water depth as well as the distribution of two antagonistic taxa Allogamus auricollis and Rhithrogena sp [Color figure can be viewed at wileyonlinelibrary.com]
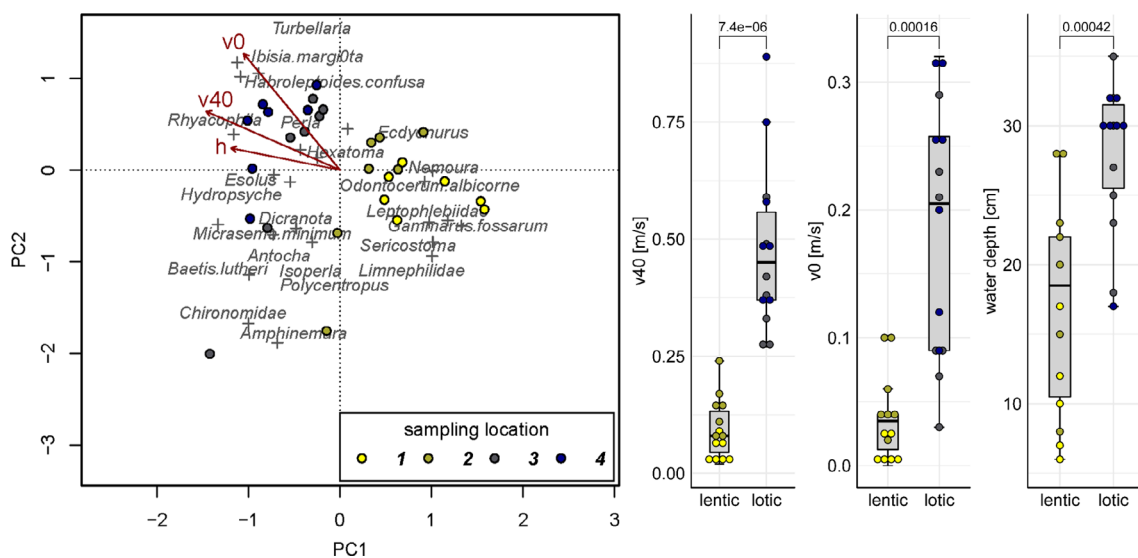

FIGURE 6 Principal component analysis (PCA) showing similarity of taxa composition between the different transect sampling points, where sample location 1 is closest to the shore and sample location 4 is in the middle of the stream. Taxa that have not been displayed in the graph for visual reason are marked as "+." Right: Box- and dot plots displaying the measured values of abiotic variables (v_{40}, v_0, h) at the different sampling locations compared between lentic (zone 1 and 2) and lotic (zone 3 and 4) habitats [Color figure can be viewed at wileyonlinelibrary.com]

associated to lotic habitats were *Rhyacophila* s.str.sp., *Hydropsyche* sp., *Hydropsyche tenuis*, *Baetis* sp., *Baetis lutheri*, *Baetis alpinus*, *Epeorus* sp., *Rhithrogena semicolorata*, *Protonemura* sp., *Hydraena* sp. ad., *Ibisia marginata*, and Simuliidae Gen. sp.

3.3.2 | Trait-specific drift responses following hydropeaking treatments

Trait specific mean drift proportions in the HP treatments ranged from 0.06 to 0.14. All trait groups showed significantly higher drift proportions in HP treatments compared to controls (all with $p < 0.01$). Significant differences were evident between lentic and lotic, as well as between surface and interstitial taxa ($p < 0.01$). Lowest drift responses were recorded for interstitial followed by lotic taxa. Surface and lentic taxa showed highest drift proportions under HP. Lentic taxa showed a 2.8 times higher maximum drift proportion (0.42) compared to in the controls (0.15). Maximum drift proportion of surface taxa was 2.2 times higher (0.33) than in the controls (0.15). Maximum drift of lotic taxa was similar in controls and treatments (Table 2).

The strongest reaction to increasing peak discharge was found for lentic (Q1: $\mu = 0.05 \pm 0.03$; Q2: $\mu = 0.15 \pm 0.08$; Q3: $\mu = 0.2 \pm 0.09$) and surface (Q1: $\mu = 0.07 \pm 0.03$; Q2: $\mu = 0.15 \pm 0.05$; Q3: $\mu = 0.16 \pm 0.07$) taxa. Drift responses of taxa associated to interstitial (Q1: $\mu = 0.04 \pm 0.03$; Q2: $\mu = 0.07 \pm 0.06$; Q3: $\mu = 0.07 \pm 0.04$) and lotic (Q1: $\mu = 0.08 \pm 0.05$; Q2: $\mu = 0.11 \pm 0.06$; Q3: $\mu = 0.1 \pm 0.06$) habitat areas showed comparably weak drift responses to increasing peak discharge. Except for lotic taxa, all observed traits showed significantly different drift responses to HP treatments with different discharge setups. For almost all traits, the observed differences were significant between Q1 and Q2 (lentic: $p < 0.01$; interstitial: $p < 0.05$; surface: $p > 0.01$) and Q1 versus Q3 (lentic: $p < 0.01$; interstitial: $p < 0.01$; surface: $p > 0.01$). Only for surface taxa significant differences were found between Q2 and Q3 ($p < 0.05$).

At discharge setup Q3, higher up-ramping rates (>1 cm/min.) led to significantly higher drift proportions in HP treatments for surface ($p < 0.01$) and lentic ($p < 0.01$) taxa (Figure 7). Strongest differences were found for surface taxa with mean drift proportions of 0.22 (±0.06) at up-ramping rates >1 cm/min compared to 0.13 (±0.05) for up-ramping rates ≤1 cm/min. A similar but nonsignificant trend was observed for interstitial and lotic taxa.

3.3.3 | Interactive effects between flow amplitude and up-ramping rate

The combined effect of the amplitude (or peak discharge) and up-ramping rate including the interaction term best described drift patterns for all taxa combined as well as for surface taxa and taxa that were classified as both "surface + lentic." The model including peak discharge alone performed best for all other traits and traits combinations, with especially strong effects (high Bayes factor) for lentic taxa. The up-ramping rate alone never showed a clear evidence for effects (Table 3).

3.4 | Discussion

3.5 | General and taxa-specific drift responses following hydropeaking

Several authors have already stated that passive drift following sudden discharge increases is one of the main causes for reduced abundance and biomass of macroinvertebrates in rivers affected by HP (Brittain & Eikeland, 1988; Céréghino, Cugny, & Lavandier, 2002; Céréghino & Lavandier, 1998; Moog, 1993). The results of this study
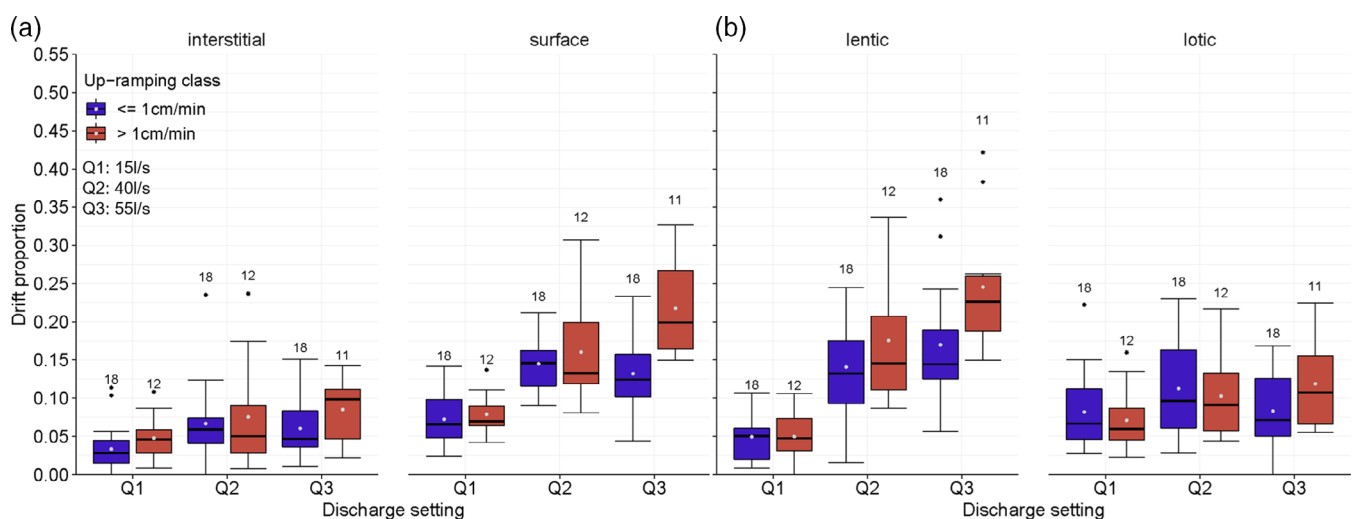

FIGURE 7 Boxplots showing drift proportions for taxa associated to interstitial and surface habitats (a) and for taxa associated to lentic and lotic habitats (b) in the different experimental setups. Data are split between discharge treatments and up-ramping velocities (for graphical reasons grouped: ≤1 cm/min; >1 cm/min) [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Based on a bayes factor (BF) analysis in an analysis of variance (ANOVA) design the table lists the BFs for the models explaining the macroinvertebrate drift response, presented for each examined trait and for all taxa combined. Included model terms were the peak discharge ("Disch"), the up-ramping rate ("Upr.") and the interaction term ("Disch.Upr.")

Trait parameter	Trait	Disch.	Upr.	Disch. + Upr. + Disch.Upr.
All	All	2,412,436	1.2	62,669,108
Hydraulic habitat pref.	Lentic	2,180,833,094	0.2	592,983,337
	Lotic	0.7	0.4	0.54
Vertical habitat pref.	Interstitial	3.4	0.1	0.1
	Surface	4,647,868	0.6	69,822,482
Lateral + Vertical habitat pref.	Interstitial + lentic	209	0.1	1.9
	Interstitial + lotic	8.3	0.1	0.5
	Surface + lentic	70,195,951	0.3	98,898,370
	Surface + lotic	0.2	0.2	0.1

Note: The BFs mean: <1: No effects, 1 to <3: Negligible evidence for H1, 3 to <20: Positive evidence for H1, 20 to 150: Strong evidence for H1, >150: Very strong evidence (Kass & Raftery, 1995)

strongly support this statement. Our data provide evidence that higher hydraulic stress linked to increased discharge triggers macroinvertebrate drift (mean drift proportion in all HP setups: 13% compared to 5% in controls). In field studies, source populations are not defined as in our study, thus different drift measures, such as the drift density are commonly used (Castro, Hughes, & Callisto, 2013; Timusk et al., 2016). Therefore, it is difficult to directly relate the values of this study to field observations; however, Tonolla et al. (in review) have found macroinvertebrate drift to increase two- to three-fold during HP, which corresponds to our results. Timusk et al. (2016), Moog (1993) and White and Wade (1980) have also found similar and even higher drift proportions. Another challenge in comparing specific drift values between this experimental study and findings from field studies relate to the source populations. All specimens in the flume experiments were taken from an unaffected brook, while the populations in established HP stretches are adapted to river-specific HP and morphological conditions.

Our findings showed particularly high drift proportions for Limnephilidae (mainly *Allogamus auricollis*) and Chironomidae (Figure 4). *Allogamus auricollis* is known to depend on lentic habitats (Waringer, 1989) that shows decreased abundance of in HP-impacted river stretches (Graf et al., 2013). This taxon might therefore be particularly vulnerable to further expansion of HP operation. For Chironomid larvae, analog results can be found in literature (e.g., Aksamit, Carolli, Vanzo, Weber, & Schmid, 2021; Kennedy et al., 2014; Kjaerstad et al., 2018) but also contrasting findings have already been published (e.g., Mihalicz et al., 2019; Moog, 1993). Even though highly significant in our study, the results regarding Chironomids are difficult to interpret since this group consists of many differently specialized taxa, which renders generalizations about this family impractical. Nevertheless, our study shows that HP—at least in this particular setup— has an impact on Chironomid species. Considering their abundant and wide distribution, future studies should therefore put more attention on this family to allow tangible statements at the species level. Additionally, considerably high drift was also observed for *Asellus*

aquaticus, *Micrasema minimum*, Polycentropodidae, and *Elmis* sp. (-Table S2). Leptophlebiidae and Leuctridae showed generally low drift responses (Figure 4). They are associated with interstices (Graf et al., 2013) where the effect of increased hydraulic forces (e.g., bottom shear stress and flow velocity) remains low, even during peak events. This is commensurate with different field studies, where abundance of *Leuctra* sp. was not affected by HP (De Jalon, Sanchez, & Camargo, 1994; Graf et al., 2013; Moog, 1993).

Interestingly, both adults and larvae of specific genera of the family Elmidae (mostly *Esolus* sp. and *Limnius* sp.) drifted in low numbers following HP compared to the genus *Elmis*. This further emphasizes the importance of a high identification level. Further, the larval stage and individual size may additionally affect drift responses, with a tendency of younger instars showing larger drift responses (Poff et al., 1991; Schülting et al., 2016; Waringer, 1989). For *Ephemerella mucronata*, for instance, quite low drift responses to HP (8.4%) were observed, whereas *E. major* drifted in high quantities (26.7%) possibly because *E. major* donor populations consisted of much smaller specimens compared to *E. mucronata*.

To our knowledge, many aspects regarding the consequences of HP-induced macroinvertebrate drift, especially size-dependency, drift distance of taxa, and mortality could not be revealed by previous nor by our study. Future studies should emphasize the role of the drift and drift composition for the depletion of the benthic community in affected rivers.

3.6 | Trait-specific drift responses following hydropeaking

The trait classifications in this study (vertical habitat preference and hydraulic habitat preference) aimed to express the preference and adaptation to flow. Results of the trait-specific analyses showed that especially taxa preferring lentic conditions as well as taxa associated to the substrate surface, such as *Allogamus auricollis*, *Halesus* sp.,

Ephemerella mucronata, or *Nemoura/Nemurella pictetii*, have higher maximum drift proportions and higher variability in drift responses (for details see Table S2). Taxa of these traits also showed strongly increased drift responses with increasing discharge amplitudes (Figure 7) indicating that those taxa are more sensitive and vulnerable to sudden discharge increases and related hydraulic forces. For surface taxa high up-ramping rates increased drift proportions in combination with the flow amplitude. This indicates that in case of HP waves with strong water level changes (high amplitudes), the surface-dwelling taxa can have enough time to find shelter within the interstices only if the up-ramping rates are low.

Trait-based approaches to assess stressor effects on freshwater ecosystems have a long tradition and have been widely applied in aquatic science (e.g., Naman et al., 2016; Rader, 1997; Statzner, Bêche, & a., 2010). Several macroinvertebrate trait classifications (e.g., feeding type, current preference) can serve as indicators of human pressures in aquatic ecosystems because they reveal relationships between aquatic communities and environmental (e.g., hydrological) gradients (Monk et al., 2018; Statzner et al., 2010; Statzner, Bady, Dolédec, & Schöll, 2005). Both newly applied traits demonstrated promising results regarding stressor sensitivity to HP. The classifications should be extended to a higher number of taxa with life-stages specific consideration; however, these information are unavailable for many taxa (Naman et al., 2016). River-type specific classifications should also be considered as there may be spatio-temporal differences regarding habitat use (Bacher & Waringer, 1996; Fjellheim, 1980; Statzner, 1988; Statzner & Holm, 1989; Waringer, 1989). In a further step, suitable traits should be verified in field situations, by testing if taxa with sensitive traits show reduced abundances in HP-affected river stretches compared to near-natural rivers.

3.7 | Effects of amplitude, up-ramping rate, and interaction effects

Hydrological patterns significantly impact riverine habitat characteristics (e.g., Allan & Castillo, 2007; Poff & Zimmerman, 2009). While the total amount of discharge—in interplay with the river-specific morphology and sedimentology—affects the overall habitat characteristics such as water depth, wetted area, and hydraulic forces, the up-ramping rate specifies the timeframe in which aquatic organisms have to react to the new situation (Greimel et al., 2018). The two hydrological parameters "flow amplitude" and "up-ramping" rate are therefore often stated to be key indicators to assess the intensity of HP events (Smokorowski, 2021).

In our study, the amplitude clearly showed the strongest effect on macroinvertebrate drift. Increasing amplitudes through higher peak discharge in the flumes were linked to increased water depth (Δ up to 9.4 cm), increased flow velocities (v_{40}: Δ up to 0.71 m/s), and increased bed shear stress (Δ up to 1.9 N/m^2), which finally led to an increase in drift over all observed trait groups (Figure 7). This was particularly significant for taxa associated to lentic areas as for this group discharge alone best explained the drift responses to HP (Table 3). The distinct changes in habitat characteristics in lentic areas under HP events appear to have a high impact on the associated benthic community. The rate in which these changes occur—until a certain threshold of hydraulic stress is reached—seems negligible. Considering the frequent discharge fluctuations in HP affected river stretches (Greimel et al., 2016; Meile et al., 2011), especially those taxa that lack adaptations to high current have to invest extensive amounts of energy to avoid downstream displacement and are therefore subject to strong selective pressure.

Our flume experiments further showed that the parameter up-ramping rate never exclusively affected macroinvertebrate drift—regardless the habitat preferences—yet strong synergistic effects were found with the flow amplitude for the whole community as well as for surface taxa as mentioned above. The results suggest that at lower peak discharges, the up-ramping rate has only a negligible impact. Only in experiments with the highest peak discharge (and correspondingly highest maximum hydraulic forces such as flow velocities), a significant trend toward higher macroinvertebrate drift with increasing up-ramping velocities was evident. This indicates that the up-ramping rate affects macroinvertebrate drift if certain discharge-related thresholds are exceeded due to high amplitudes (see also Figures 3 and 7). Vice versa, a reduction of the up-ramping rate in those cases has the potential to mitigate effects on macroinvertebrate drift, since the time to seek for shelter in the interstices is extended (Imbert & Perry, 2000). In future, more research emphasis should be given to taxa and life-stage specific flow preferences and thresholds, which would be valuable for the development of mitigation and stressor-specific monitoring strategies.

Even though experimental setups as well as measured drift responses are in the range of values found in the field, we acknowledge the limitations of our study in regard to its simplifications of the natural environment. For instance, the experiments were designed to mimic a situation in lentic areas and flow velocity presented above correspond to those measured at a permanently wetted area of the river margin. Flow velocities in HP stretches can exceed the ones measured in our experiments by far (Bretschko & Moog, 1990; Parasiewicz et al., 1998; Perry & Perry, 1986). Further, some taxa (such as Chironomidae) would possibly need up to several days for adaptation. We tried to account for this problem by assessing treatment effects (Hedges' g) based on parallel controls to quantify and classify the drift responses. Flow velocity and other discharge-related parameters (bottom shear stress, Froude number) are decisive factors regarding macroinvertebrate drift (Gibbins, Vericat, Batalla, & Buendia, 2016) but also depend on the river morphology. When transferring outcomes related to specific flow amplitudes or discharge ratios to field situations, it is crucial to consider hydraulic characteristics during HP, for example, the changes in flow velocity or water depth, since these may vary strongly depending on morphological characteristics (Hauer et al., 2017; Holzapfel, Leitner, Habersack, Graf, & Hauer, 2016).

4 | CONCLUSION AND OUTLOOK

The extent of taxa responses to HP depends on physiological and behavioral adaptations (e.g., ability to quickly retreat into the substrate), whereby interstitial and flow-tolerant taxa are found to be drifting to a significantly lesser extent, compared to flow-sensitive and surface taxa. HP operation and the corresponding increase in hydraulic force strongly relate to aquatic macroinvertebrate drift, while the drift response was found to mainly depend on hydraulic variables related to the flow amplitude and magnitude. The significance of the up-ramping rate depends on the extent of the hydraulic forces during the up-ramping and peak flow phases. Therefore, HP -operation requires mitigation strategies aiming to reduce hydraulic stress linked to fluctuating discharge and water level and to provide suitable habitats as well as refugia during peak events. A combination of hydrological and morphological mitigation measures therefore seems to be a promising approach. An increased channel width, for instance, leads to decreased water level changes and ramping rates (Hauer et al., 2017; Hauer, Schober, & Habersack, 2013). To our knowledge, biological monitoring data before and after implementation of HP -specific mitigation projects is rarely available (except few field experimental data) and would be a significant gain for the prediction of mitigation effects and planning process.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Lisa Schülting https://orcid.org/0000-0001-8188-3009

REFERENCES

Aksamit, C. K., Carolli, M., Vanzo, D., Weber, C., & Schmid, M. (2021). Macroinvertebrate recovery to varying hydropeaking frequency: A small hydropower plant experiment. *Frontiers in Environmental Science*, *8*, 1–16. https://doi.org/10.3389/fenvs.2020.602374

Allan, J. D., & Castillo, M. M. (2007). *Stream ecology: Structure and function of running waters* (2nd ed.). Dordrecht: Springer.

Arthington, A. H., Bunn, S. E., Poff, N. L., & Naiman, R. J. (2006). The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications*, *16*, 1311–1318. https://doi.org/10.1890/1051-0761(2006)016[1311:TCOPEF]2.0.CO;2

Auer, S., Fohler, N., Zeiringer, B., and Führer, S. (2014). Experimentelle Untersuchungen zur Schwallproblematik - Drift und Stranden von Äschen und Bachforellen während der ersten Lebensstadien. Bundesamtes für Umwelt (BAFU), Schweiz.

Auer, S., Zeiringer, B., Führer, S., Tonolla, D., & Schmutz, S. (2017). Effects of river bank heterogeneity and time of day on drift and stranding of juvenile European grayling (Thymallus thymallus L.) caused by hydropeaking. *Science of the Total Environment*, *575*, 1515–1521. https://doi.org/10.1016/j.scitotenv.2016.10.029

Bacher, I., & Waringer, J. A. (1996). Hydraulic microdistribution of cased caddis larvae in an Austrian mountain brook. *Internationale Revue der Gesamten Hydrobiologie*, *81*, 541–554. https://doi.org/10.1002/iroh.19960810408

Bauernfeind, E., & Humpesch, U. H. (2001). *Die Eintagsfliegen Zentraleuropas - Bestimmung und Ökologie*. Vienna: Verlag NMW.

Baumann, P., and Klaus, I. (2003). Gewässerökologische Auswirkungen des Schwallbetriebes. Bundesamt für Umwelt, Wald und Landschaft (BUWAL). Bern, Schweiz.

BMLFUW (2007). Hydrologischer Atlas Österreichs. Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Abteilung Wasserhaushalt. Wien, Österreich

Bratrich, C., Truffer, B., Jorde, K., Markard, J., Meier, W., Peter, A., … Wehrli, B. (2004). Green hydropower: a new assessment procedure for river management. *River Research and Applications*, *20*, 865–882. https://doi.org/10.1002/rra.788

Bretschko, G., & Moog, O. (1990). Downstream effects of intermittent power generation. *Water Science and Technology*, *22*(5), 127–135. https://doi.org/10.2166/wst.1990.0020

Brittain, J. E., & Eikeland, T. J. (1988). Invertebrate Drift - A Review. *Hydrobiologia*, *166*, 77–93. https://doi.org/10.1007/BF00017485

Brooker, M. P., & Hemsworth, R. J. (1978). The effect of the release of an artificial discharge of water on invertebrate drift in the R. wye, Wales. *Hydrobiologia*, *59*, 155–163. https://doi.org/10.1007/BF00036494

Bruder, A., Tonolla, D., & Schweizer, S. (2016). A conceptual framework for hydropeaking mitigation. *Science of the Total Environment*, *568*, 1204–1212. https://doi.org/10.1016/j.scitotenv.2016.05.032

Bruno, M. C., Cashman, M. J., Maiolini, B., Biffi, S., & Zolezzi, G. (2016). Responses of benthic invertebrates to repeated hydropeaking in semi-natural flume simulations. *Ecohydrology*, *9*, 68–82. https://doi.org/10.1002/eco.1611

Bruno, M. C., Siviglia, a., Carolli, M., & Maiolini, B. (2013). Multiple drift responses of benthic invertebrates to interacting hydropeaking and thermopeaking waves. *Ecohydrology*, *6*, 511–522. https://doi.org/10.1002/eco.1275

Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, *30*, 492–507. https://doi.org/10.1007/s00267-002-2737-0

Carolli, M., Bruno, M. C., Siviglia, A., & Maiolini, B. (2011). Responses of benthic invertebrates to abrupt changes of temperature in flume simulations. *River Research and Applications*, *28*, 678–691. https://doi.org/10.1002/rra

Castro, D. M. P., Hughes, R. M., & Callisto, M. (2013). Influence of peak flow changes on the macroinvertebrate drift downstream of a Brazilian hydroelectric dam. *Brazilian Journal of Biology*, *73*, 775–782. https://doi.org/10.1590/S1519-698420130004000013

Céréghino, R., Cugny, P., & Lavandier, P. (2002). Influence of intermittent hydropeaking on the longitudinal zonation patterns of benthic invertebrates in a mountain stream. *International Review of Hydrobiology*, *87*, 47–60. https://doi.org/10.1002/1522-2632(200201)87:1<47::AID-IROH47>3.0.CO;2-9

Céréghino, R., & Lavandier, P. (1998). Influence of hypolimnetic hydropeaking on the distribution and population dynamics of Ephemeroptera in a mountain stream. *Freshwater Biology*, *40*, 385–399. https://doi.org/10.1046/j.1365-2427.1998.00353.x/full

Céréghino, R., Legalle, M., & Lavandier, P. (2004). Drift and benthic population structure of the mayfly Rhithrogena semicolorata (Heptageniidae) under natural and hydropeaking conditions. *Hydrobiologia*, *519*, 127–133. https://doi.org/10.1023/B:HYDR.0000026499.53979.69

Cushman, R. M. (1985). Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. *North American Journal of Fisheries Management*, 5, 330–339. https://doi.org/10.1577/1548-8659(1985)5<330:ROEEOR>2.0.CO;2

De Jalon, D. G., Sanchez, P., & Camargo, J. A. (1994). Downstream effects of a new hydropower impoundment on macrophyte, macroinvertebrate and fish communities. *Regulated Rivers: Research and Management*, 9, 253–261. https://doi.org/10.1002/rrr.3450090406

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2

Elgueta, A., Górski, K., Thoms, M., Fierro, P., Toledo, B., Manosalva, A., & Habit, E. (2021). Interplay of geomorphology and hydrology drives macroinvertebrate assemblage responses to hydropeaking. *Science of the Total Environment*, 768, 144262. https://doi.org/10.1016/j.scitotenv.2020.144262

Elliott, J. M. (1967). Invertebrate drift in a Dartmoor-stream. *Archiv für Hydrobiologie*, 63, 202–237.

Fink, M. H., Moog, O., & Wimmer, R. (2000). *Fliessgewässer-Naturräume Österreichs*. Umweltbundesamt GmbH (Federal Environment Agency Ltd): Wien, Österreich.

Fjellheim, A. (1980). Differences in drifting of larval stages of Rhyacophila nubila (Trichoptera). *Holarctic Ecology*, 3, 99–103. https://doi.org/10.1111/j.1600-0587.1980.tb00714.x

Gabbud, C., Bakker, M., Clémençon, M., & Lane, S. N. (2019). Hydropower flushing events cause severe loss of macrozoobenthos in alpine streams. *Water Resources Research*, 55(12). https://doi.org/10.1029/2019WR024758

Gibbins, C., Batalla, R., & Vericat, D. (2010). Invertebrate drift and benthic exhaustion during disturbance: Response of mayflies (Ephemeroptera) to increasing shear stress and river-bed instability. *River Research and Applications*, 26, 499–511. https://doi.org/10.1002/rra

Gibbins, C., Vericat, D., & Batalla, R. J. (2007). When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events. *Freshwater Biology*, 52, 2369–2384. https://doi.org/10.1111/j.1365-2427.2007.01858.x

Gibbins, C. N., Vericat, D., Batalla, R. J., & Buendia, C. (2016). Which variables should be used to link invertebrate drift to river hydraulic conditions? *Fundamental and Applied Limnology/Archiv für Hydrobiologie*, 18, 191–205. https://doi.org/10.1127/fal/2015/0745

Glöer, P., Meier-Brook, C., & Deutscher Jugendbund für Naturbeobachtung. (1994). *Süsswassermollusken: ein Bestimmungsschlüssel für die Bundesrepublik Deutschland*. Höxter, Deutschland: Deutscher Jugendbund für Naturbeobachtung.

Graf, W., Leitner, P., Moog, O., Steidl, C., Salcher, G., Ochsenhofer, G., … Müllner, K. (2013). *Schwallproblematik an Österreichs Fließgewässern – Ökologische Folgen und Sanierungsmöglichkeiten*. Vienna Available: Dateneerhebung und Analyse Benthische Invertebrtaten. http://hydropeaking.boku.ac.at/

Greimel, F., Grün, B., Hayes, D. S., Höller, N., Haider, J., Zeiringer, B., … Schmutz, S. (in review) PeakTrace: Routing of hydropower plant-specific hydropeaking waves using multiple hydrographs – a novel approach. *River Research and Applications*.

Greimel, F., Neubarth, J., Fuhrmann, M., Führer, S., Habersack, H., Haslauer, M., … Zeiringer, B. (2017). SuREmMa Sustainable river management – Energiewirtschaftliche und umweltrelevante Bewertung möglicher schwalldämpfender Massnahmen. Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Vienna, Austria.

Greimel, F., Schülting, L., Wolfram, G., Bondar-Kunze, E., Auer, S., Zeiringer, B., & Hauer, C. (2018). Hydropeaking impacts and mitigation. In S. Schmutz & J. Sendzimir (Eds.), *Riverine ecosystem management* (pp. 91–110). Cham, Switzerland: Springer.

Greimel, F., Zeiringer, B., Höller, N., Grün, B., Godina, R., & Schmutz, S. (2016). A method to detect and characterize sub-daily flow fluctuations. *Hydrological Processes*, 30, 2063–2078. https://doi.org/10.1002/hyp.10773

Hauer, C., Holzapfel, P., Leitner, P., & Graf, W. (2017). Longitudinal assessment of hydropeaking impacts on various scales for an improved process understanding and the design of mitigation measures. *Science of the Total Environment*, 575, 1503–1514. https://doi.org/10.1016/j.scitotenv.2016.10.031

Hauer, C., Schober, B., & Habersack, H. (2013). Impact analysis of river morphology and roughness variability on hydropeaking based on numerical modelling. *Hydrological Processes*, 27, 2209–2224. https://doi.org/10.1002/hyp.9519

Hayes, D. S., Moreira, M., Boavida, I., Haslauer, M., Unfer, G., Zeiringer, B., … Schmutz, S. (2019). Life Stage-Specific Hydropeaking Flow Rules. *Sustainability*, 11(6), 1–17. https://doi.org/10.3390/su11061547

Hedges, L. (1981). Distribution theory for glass´s estimator of effect size and related estimators. *Journal of Educational Statistics*, 6, 107–128.

Holzapfel, P., Leitner, P., Habersack, H., Graf, W., & Hauer, C. (2016). Evaluation of hydropeaking impacts on the food web in alpine streams based on modelling of fish- and macroinvertebrate habitats. *Science of the Total Environment*, 575, 1489–1502. https://doi.org/10.1016/j.scitotenv.2016.10.016

Imbert, J., & Perry, J. (2000). Drift and benthic invertebrate responses to stepwise and abrupt increases in non-scouring flow. *Hydrobiologia*, 436, 191–208. https://doi.org/10.1023/A:1026582218786

Jones, N. E. (2014). The dual nature of hydropeaking rivers: Is ecopeaking possible? *River Research and Applications*, 30, 521–526. https://doi.org/10.1002/rra.2653

Kass, R. E., & Raftery, A. E. (1995). Bayes factors. *Journal of the American Statistical Association*. 90(430), 773–795. https://doi.org/10.1080/01621459.1995.10476572

Kennedy, T. a., Yackulic, C. B., Cross, W. F., Grams, P. E., Yard, M. D., & Copp, A. J. (2014). The relation between invertebrate drift and two primary controls, discharge and benthic densities, in a large regulated river. *Freshwater Biology*, 59, 557–572. https://doi.org/10.1111/fwb.12285

Kjaerstad, G., Arnekleiv, J. V., Speed, J. D. M., & Herland, A. K. (2018). Effects of hydropeaking on benthic invertebrate community composition in two central Norwegian rivers. *River Research and Applications*, 34, 218–231. https://doi.org/10.1002/rra.3241

Lake, P. S. (2000). Disturbance, patchiness, and diversity in stream. *Journal of the North American Benthological Society*, 19, 573–592. https://doi.org/10.2307/1468118

Lauters, F., Lavandier, P., Lim, P., Sabaton, C., & Belaud, A. (1996). Influence of hydropeaking on invertebrates and their relationship with fish feeding habits in a Pyrenean river. *Regulated Rivers: Research and Management*, 12, 563–573. https://doi.org/10.1002/(SICI)1099-1646(199611)12:6<563::AID-RRR380>3.0.CO;2-M

Leitner, P., Hauer, C., & Graf, W. (2017). Habitat use and tolerance levels of macroinvertebrates concerning hydraulic stress in hydropeaking rivers – A case study at the Ziller River in Austria. *Science of the Total Environment*, 575, 112–118. https://doi.org/10.1016/j.scitotenv.2016.10.011

Levene, H. (1960). Robust tests for equality of variances. *Contributions to Probability and Statistics Essays in Honor of Harold Hotelling*, 2, 278–292.

Meile, T., Boillat, J. L., & Schleiss, A. J. (2011). Hydropeaking indicators for characterization of the upper-Rhone River in Switzerland. *Aquatic Sciences*, 73, 171–182. https://doi.org/10.1007/s00027-010-0154-7

Melcher, A. H., Bakken, T. H., Friedrich, T., Greimel, F., Humer, N., Schmutz, S., … Webb, J. A. (2017). Drawing together multiple lines of evidence from assessment studies of hydropeaking pressures in impacted rivers. *Freshwater Science*, 36, 220–230. https://doi.org/10.1086/690295

Mihalicz, J. E., Jardine, T. D., Baulch, H. M., & Phillips, I. D. (2019). Seasonal effects of a hydropeaking dam on a downstream benthic macroinvertebrate community. *River Research and Applications*, 35, 714–724. https://doi.org/10.1002/rra.3434

Miller, S. W., & Judson, S. (2014). Responses of macroinvertebrate drift, benthic assemblages, and trout foraging to hydropeaking. *Canadian Journal of Fisheries and Aquatic Sciences*, 687, 675–687. https://doi.org/10.1139/cjfas-2013-0562

Minckley, W. L. (1964). Upstream movements of Gammarus (Amphipoda) in doe run, Meade County, Kentucky. *Ecology*, 45, 195. https://doi.org/10.2307/1937129

Monk, W. A., Compson, Z. G., Armanini, D. G., Orlofske, J. M., Curry, C. J., Peters, D. L., … Baird, D. J. (2018). Flow velocity–ecology thresholds in Canadian rivers: A comparison of trait and taxonomy-based approaches. *Freshwater Biology*, 63, 891–905. https://doi.org/10.1111/fwb.13030

Moog, O. (1993). Quantification of daily peak hydropower effects on aquatic fauna and management to minimize environmental impacts. *Regulated Rivers: Research and Management*, 8, 5–14. https://doi.org/10.1002/rrr.3450080105

Munn, M. D., & Brusven, M. A. (1991). Benthic macroinvertebrate communities in nonregulated and regulated waters of the Clearwater river, Idaho, U.S.A. *Regulated Rivers: Research and Management*, 6, 1–11. https://doi.org/10.1002/rrr.3450060102

Naman, S. M., Rosenfeld, J. S., & Richardson, J. S. (2016). Causes and consequences of invertebrate drift in running waters: From individuals to populations and trophic fluxes. *Canadian Journal of Fisheries and Aquatic Sciences*, 73, 1292–1305. https://doi.org/10.1139/cjfas-2015-0363

Ofenböck, T., Moog, O., Hartmann, A., Stubauer, I., & Leitner, P. (2018). *Leitfaden zur Erhebung der biologischen Qualitätselemente, Teil A2— Makrozoobenthos*. Umwelt und Wasserwirtschaft, Wien, Österreich: Bundesministerium für Land- und Forstwirtschaft.

Oldmeadow, D. F., Lancaster, J., & Rice, S. P. (2010). Drift and settlement of stream insects in a complex hydraulic environment. *Freshwater Biology*, 55, 1020–1035. https://doi.org/10.1111/j.1365-2427.2009.02338.x

Parasiewicz, P., Schmutz, S., & Moog, O. (1998). The effect of managed hydropower peaking on the physical habitat, benthos and fish fauna in the river Bregenzerach in Austria. *Fisheries Management and Ecology*, 5, 403–417. https://doi.org/10.1046/j.1365-2400.1998.550403.x

Pearce, J. L., Smokorowski, K. E., Brush, J., Timusk, E., Marty, J., & Power, M. (2019). Unrestricted ramping rates and long-term trends in the food web metrics of a boreal river. *River Research and Applications*, 1575–1589, 1575–1589. https://doi.org/10.1002/rra.3516

Perry, S. A., & Perry, W. B. (1986). Effects of experimental flow regulation on invertebrate drift and stranding in the Flathead and Kootenai Rivers, Montana, USA. *Hydrobiologia*, 134, 171–182. https://doi.org/10.1007/BF00006739

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., … Stromberg, J. C. (1997). The natural flow regime: A paradigm for river conservation and restoration N. *Bioscience*, 47, 769–784. https://doi.org/10.2307/1313099

Poff, N. L., DeCino, R. D., & Ward, J. V. (1991). Size-dependent drift responses of mayflies to experimental hydrologic variation: Active predator avoidance or passive hydrodynamic displacement? *Oecologia*, 88, 577–586. https://doi.org/10.1007/BF00317723

Poff, N. L., & Zimmerman, J. K. H. (2009). Ecological responses to altered flow regimes: A literature review to inform the science and management of environmental flows. *Freshwater Biology*, 55, 194–205. https://doi.org/10.1111/j.1365-2427.2009.02272.x

Puffer, M., Berg, O. K., Huusko, A., Vehanen, T., Forseth, T., & Einum, S. (2015). Seasonal effects of hydropeaking on growth, energetics and movement of juvenile Atlantic Salmon (Salmo Salar). *River Research and Applications*, 31, 1101–1108. https://doi.org/10.1002/rra.2801

Rader, R. B. (1997). A functional classification of the drift: Traits that influence invertebrate availability to salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 1211–1234. https://doi.org/10.1139/f97-025

Ramos, V., Formigo, N., & Maia, R. (2018). Environmental flows under the WFD implementation. *Water Resources Management*, 32, 5115–5149. https://doi.org/10.1007/s11269-018-2137-8

RHEOPHYLAX working group (2021). New biologicaltraits and ecological preferences of European freshwater organisms for freshwaterecology.info

Schmedtje, U., & Colling, M. (1996). *Ökologische Typisierung der aquatischen Makrofauna*. München, Deutschland: Bayerisches Landesamt für Wasserwirtschaft.

Schmutz, S., Bakken, T. H., Friedrich, T., Greimel, F., Harby, A., Jungwirth, M., … Zeiringer, B. (2015). Response of fish communities to hydrological and morphological alterations in hydropeaking rivers of Austria. *River Research and Applications*, 31, 919–930. https://doi.org/10.1002/rra.2795

Schülting, L., Feld, C. K., & Graf, W. (2016). Effects of hydro- and thermopeaking on benthic macroinvertebrate drift. *Science of the Total Environment*, 573, 1472–1480. https://doi.org/10.1016/j.scitotenv.2016.08.022

Schülting, L., Feld, C. K., Zeiringer, B., Hudek, H., & Graf, W. (2018). Macroinvertebrate drift response to hydropeaking: An experimental approach to assess the effect of varying ramping velocities. *Ecohydrology*, 12(1), 1–12. https://doi.org/10.1002/eco.2032

Shapiro, S. S., & Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, 52, 591–611.

Smokorowski, B. K. E. (2010). Effects of Experimental Ramping Rate on the Invertebrate Community of a Regulated River Benthic Invertebrates as Test Organisms. *Proceedings of Colorful River Basin Science Resource Management Global Symposium*, 149–156.

Smokorowski, K. E. (2021). The ups and downs of hydropeaking: a Canadian perspective on the need for, and ecological costs of, peaking hydropower production. *Hydrobiologia*, 849(849), 421–441. https://doi.org/10.1007/s10750-020-04480-y

Statzner, B. (1988). Growth and Reynolds number of lotic macroinvertebrates: A problem for adaptation of shape to drag. *Oikos*, 51, 84–87.

Statzner, B., Bady, P., Dolédec, S., & Schöll, F. (2005). Invertebrate traits for the biomonitoring of large European rivers: An initial assessment of trait patterns in least impacted river reaches. *Freshwater Biology*, 50, 2136–2161. https://doi.org/10.1111/j.1365-2427.2005.01447.x

Statzner, B., & Bêche, L. A. (2010). Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? *Freshwater Biology*, 55, 80–119. https://doi.org/10.1111/j.1365-2427.2009.02369.x

Statzner, B., & Holm, T. F. (1989). Morphological adaptation of shape to flow: Microcurrents around lotic macroinvertebrates with known Reynolds numbers at quasi-natural flow conditions. *Oecologia*, 78, 145–157. https://doi.org/10.1007/BF00377150

Tachet, H., Richoux, P., Bournaud, M., & Usseglio-Polatera, P. (2000). *Invertébrés d'eau douce*. Paris: CNRS.

Timusk, E. R., Smokorowski, K. E., & Jones, N. E. (2016). An experimental test of sub-hourly changes in macroinvertebrate drift density associated with hydropeaking in a regulated river. *Journal of Freshwater Ecology*, 5060, 1–16. https://doi.org/10.1080/02705060.2016.1193064

Tonolla, D., Bruder, A., Schweizer, S., & Barcelo, D. (2017). Evaluation of mitigation measures to reduce hydropeaking impacts on river ecosystems – a case study from the Swiss Alps. *Science of the Total Environment*, 574, 594–604. https://doi.org/10.1016/j.scitotenv.2016.09.101

Tonolla, D., Chaix, O., Meile, T., Zurwerra, A., Büsser, P., Oppliger, S., & Essyad, K. (2016). *Schwall-Sunk – Massnahmen*. Bern, Schweiz: Ein Modul der Vollzugshilfe Renaturierung der Gewässer.

Tonolla, D., Dossi, F., Kastenhofer, O., Doering, M., Graf, W., Hauer, C., & Schülting, L. (in review) Effects of hydropeaking on macroinvertebrate

drift, stranding and community composition: a field experimental approach in three regulated Swiss rivers. *River Research and Applications*.

Tupinambás, T. H., Cortes, R. M. V., Hughes, S. J., Varandas, S. G., & Callisto, M. (2016). Macroinvertebrate responses to distinct hydrological patterns in a tropical regulated river. *Ecohydrology*, 9, 460–471. https://doi.org/10.1002/eco.1649

Valentin, S., Wasson, J. G., & Philippe, M. (1995). Effects of hydropower peaking on epilithon and invertebrate community trophic structure. *Regulated Rivers: Research and Management*, 10, 105–119. https://doi.org/10.1002/rrr.3450100207

Waringer, J., & Graf, W. (2011). *Atlas der mitteleuropäischen Köcherfliegenlarven/Atlas of Central European Trichoptera Larvae.* Dinkelscherben: Erik Mauch Verlag Available at: http://shop.lauterbornia.de/product_info.php?products_id=233&language=en [Accessed July 5, 2018]

Waringer, J. A. (1989). Resistance of cased caddis larva to accidental entry into the drift: The contribution of active and passive elements. *Freshwater Biology*, 21, 411–420. https://doi.org/10.1111/j.1365-2427.1989.tb01373.x

Waters, F. T. (1972). The drift of stream insects. *Annual Review of Entomology*, 17, 253–272. https://doi.org/10.1146/annurev.en.17.010172.001345

White, R. G., & Wade, D. T. (1980). *A study of fish and aquatic macroinvertebrate fauna in the south fork Boise River below Anderson ranch dam with emphasis on effects on fluctuating flow.* Idaho: United States Department of the Interior.

Whiting, P. J., & Dietrich, W. E. (1990). Boundary shear stress and roughness over mobile alluvial beds. *Journal of Hydraulic Engineering*. 116(12), 1495–1511. https://doi.org/10.1061/(ASCE)0733-9429(1990)116:12(1495)

Zolezzi, G., Siviglia, A., Toffolon, M., & Maiolini, B. (2011). Thermopeaking in alpine streams: Event characterization and time scales. *Ecohydrology*, 4, 564–576. https://doi.org/10.1002/eco.132

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.