Effects of hydropeaking on drift, stranding and community composition of macroinvertebrates: a field experimental approach in three regulated Swiss rivers

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Abstract

Hydropeaking operation leads to fluctuations in wetted area between base and peak flow and increases discharge-related hydraulic forces (e.g., flow velocity). These processes promote macroinvertebrate drift and stranding, often affecting benthic abundance and biomass. Our field experimental study – conducted in three hydropeaking-regulated Swiss rivers – aimed to quantify (i) the short-term effects of the combined increase in flow amplitude and up-ramping rate based on macroinvertebrate drift and stranding, as well as (ii) long-term effects based on the established community composition. Hydropeaking led to increased macroinvertebrate drift compared to base flow and to unaffected residual flow reaches. Moreover, stranding of macroinvertebrates was positively related to drift, especially during the up-ramping phase. Flow velocity and up-ramping rate were identified as major determinants for macroinvertebrate drift, while flow ratio and down-ramping rate for stranding. Particularly high sensitivity towards HP was found for Limnephilidae, whereas Heptageniidae seemed to be resistant in respect to short and long-term hydropeaking effects. In the long-term, hydropeaking did not considerably reduce benthic density of most taxa, especially of some highly resistant and resilient taxa such as Chironomidae and Baetidae, which dominated the community composition even though they showed comparably high drift and stranding responses. Therefore, we argue that high passive drift and/or stranding, especially of individual-rich taxa, does not necessarily indicate strong hydropeaking sensitivity. Finally, our results demonstrate the necessity to consider the differences in river-specific morphological complexity and hydropeaking intensity, since these factors strongly influence the community composition and short-term drift and stranding response of macroinvertebrates to hydropower pressure.

Introduction

High-head storage hydropower plants often have detrimental ecological impacts on downstream river ecosystems because of their high-volatile electricity production, which cause severe daily and sub-daily downstream fluctuations in discharge and water levels due to so-called 'hydropeaking' (hereafter, HP; Bruder et al., 2016; Young, Cech, & Thompson, 2011). Those hydropower operations influence the flow regime not only during peak flow. Due to the temporal water storage in the reservoir, the river segment located between storage and hydropower plant experiences relatively constant base-flow conditions, so-called residual flow (hereafter, RF). An increase of 1.2 TWh is forecasted by 2050 in the energy storage capability of the Swiss hydropower reservoirs, corresponding to 20% of today's energy storage capacity (Boes et al., 2021). Consequently, further ecological impacts within riverine ecosystems are expected with an increase in HP operation.

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In alpine rivers, HP often occurs in high frequency and its intensity can be characterized by several hydrological parameters (Greimel et al., 2016; Li & Pasternack, 2021). HP operation in the up-ramping phase often leads to abrupt increase in discharge and related hydraulic forces (e.g., flow velocity, bed shear stress). This can promote unintentional and mechanical dislodgement of aquatic macroinvertebrates (hereafter, MIV) from the substrate and their downstream transport in the water column until passive (e.g., in hydraulic dead zones) or active (behavioral or through morphological adaptations) exit of the drift (Ciborowski, 1987; Naman, Rosenfeld, & Richardson, 2016). The causes for MIV drift by HP operation are manifold and complex and often strongly taxon- and trait-specific (e.g., Kjærstad, Arnekleiv, Speed, & Herland, 2018; Leitner, Hauer, & Graf, 2017). The following parameters are of major importance regarding HP-induced passive MIV drift: up-ramping rate, flow magnitude and amplitude, flow velocity, and to a lesser extent also Froude number and bed shear stress (Bruno, Cashman, Maiolini, Biffi, & Zolezzi, 2016; Bruno, Maiolini, Carolli, & Silveri, 2010; Gibbins, Vericat, Batalla, & Buendia, 2016; Imbert & Perry, 2000; Miller & Judson, 2014; Schülting, Feld, Zeiringer, Huđek, & Graf, 2018a; Timusk, Smokorowski, & Jones, 2016). Moreover, sudden variations in water temperature (i.e., thermopeaking) may induce behavioral MIV drift (Bruno, Siviglia, Carolli, & Maiolini, 2013; Schülting, Feld, & Graf, 2016), and re-suspension of fine sediments increases turbidity and clogging risk (Hauer, Holzapfel, Tonolla, Habersack, & Zolezzi, 2019) further affecting MIV (Bo, Fenoglio, Malacarne, Pessino, & Sgariboldi, 2007; Crosa, Castelli, Gentili, & Espa, 2010; Jones et al., 2012). In addition to drift, stranding is a possible consequence of HP operations. MIV stranding has been documented, also if not unequivocally, to be related to down-ramping rate, flow magnitude, amplitude and rate, flow velocity and the extension of the dewatering area (Kroger, 1973; Perry & Perry, 1986; Tanno, Wächter, & Gerber, 2021; Tanno, Wächter, & Schmidlin, 2016). Tanno et al. (2021) further found a positive correlation between MIV drift and stranding. In a similar vein as for drift, water temperature and turbidity are probably likely to influence stranding. For example, water temperature has been shown to influence stranding risk of fish (e.g., Halleraker et al., 2003). Besides the short-term effects of MIV drift and stranding, long-term effects of altered hydromorphological habitat conditions in HP rivers are reported to affect colonization patterns of benthic populations (Bretschko & Moog, 1990; Cushman, 1985; Kjærstad et al., 2018). Morphological heterogeneity, for instance, is known to be crucial in providing diverse habitats and refuges for MIV communities under HP conditions (Hauer, Holzapfel, Leitner, & Graf, 2017). The complex interplay of drift, stranding and altered hydromorphological habitat conditions caused by HP operation, most likely contribute to reductions in MIV abundance and biomasses (Céréghino, Cugny, & Lavandier, 2002; Céréghino & Lavandier, 1998; Elgueta et al., 2021; Leitner et al., 2017; Moog, 1993). Another possible consequence is the alteration of the MIV community composition due to the evolution of specific behavioral (e.g., mobility, ability to regain a foothold, sinking postures) and morphological (e.g., body shape, hooks) traits as well as life history strategies. HP may, for example, contributes to a selection of rheobiont and rheophilic taxa (Bretschko & Moog, 1990; Cushman, 1985; Ruhi, Dong, McDaniel, Batzer, & Sabo, 2018) against limnophilic taxa or of taxa associated with lentic and substrate surface areas (Graf et al., 2013; Leitner et al., 2017; Ruhi et al., 2018; Schülting et al., 2018a; Schülting, Dossi, Graf, & Tonolla, 2021). Community changes due to HP may consequently affect the local food web structure and the ecological functioning of river systems (e.g., Holzapfel, Leitner, Habersack, Graf, & Hauer, 2017; Pearce et al., 2019).

The complex interactions between MIV drift, stranding and established benthic community remain poorly understood, and field studies are rare (but see for example Miller & Judson, 2014; Tanno et al., 2021; Timusk et al., 2016). Such a comprehensive evaluation is yet of importance for an exhaustive understanding of HP-related impacts on MIV and finally for implementation of associated mitigation measures and sustainable operation of HP power plants (Bruder et al., 2016; Moreira et al., 2019; Tonolla, Bruder, & Schweizer, 2017).

The main goal of our field experimental study – conducted in three HP-regulated Swiss rivers – was therefore to quantify the short-term effects of three HP scenarios with different intensity (simulated through an increase in flow amplitude and up-ramping rate) on MIV drift and stranding in addition to the long-term HP effects on the established community composition. As comparison, MIV drift and community composition was quantified in HP-unaffected RF reaches upstream. We hypothesize that: (i) drift increases during the HP scenarios compared to base flow and to drift in the RF reaches as well as a positive relationship between drift

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and stranding; (ii) HP-intensity and associated hydraulic forces, as summarized by pre-selected environmental variables, can explain any observed differences in drift and stranding propensity; (iii) compared to the RF reaches with almost constant hydrological conditions, flow fluctuations due to HP operation lead to lower benthic densities and a different MIV community composition, linked to drift and stranding. Finally, we expected taxa-, trait- and river-specific patterns.

Material and methods

Study sites and hydropower facilities

The study was conducted in three HP impacted river-reaches at the rivers Sitter (hydropower plant Kubel, KUB; canton of St. Gallen), Hasliaare (hydropower plant Innertkirchen, KWO; canton of Bern) and Linth (hydropower plant Linth-Limmern, KLL; canton of Glarus; Figure 1). Additionally, RF reaches located closely upstream of the hydropower plants were used as hydrological comparisons with relatively constant base-flow conditions.

All HP and RF reaches are of comparable size (Strahler order $5 - 6$; natural mean annual discharge $11 - 32$ m^3/s) and located at similar elevations ($590 - 680$ m a.s.l.). Dominant grain size (cover $> 50\%$) in all HP reaches is micro- to mesolithal (grain size $2 - 20$ cm), whereas it is coarser (> 20 cm) in the RF reaches of the Sitter and Linth.

The KUB hydropower plant has the lowest maximum turbinable peak flow (18 m^3/s), flow amplitude (16 m^3/s) and ramping rates (0.1 and 0.05 m^3/s min). The investigated HP reach was located < 0.5 km downstream of the plant release and is characterized by the highest bankfull width (45 m), a near-natural morphology with a right-sided gravel bar and comparably fine substrate ($D_m = 28.1$ mm). Since 2016, the hydropower facilities KWO and KLL both include a HP retention volume of $80,000$ m^3 and $220,000$ m^3, respectively. The maximum turbinable peak flow, amplitude and ramping rates of the corresponding hydropower plant are higher than at KUB. The investigated HP and RF reaches of the Hasliaare and Linth are characterized by a strongly constrained morphology. The HP reach of the Linth has the lowest bankfull width (15 m), no extended gravel bars, and the coarser sediment size ($D_m = 59.9$ mm). Moreover, four small run-off power plants are situated between the water release and the HP reach. The riverbed of all HP reaches showed no or insignificant clogging, whereas it was moderate in the RF reaches of the Sitter and Linth. The HP and RF reaches of these two rivers were also characterized by higher cover of algae and mosses than the Hasliaare. Possible relevance of these aspects on drift, stranding and the benthic community composition, will be picked up in the discussion. Key characteristics of the hydropower plants, as well as associated catchments, HP and RF reaches are available in Data S1 (Appendix A).

Experimental setup

To investigate the short- and long-term effects of HP on MIV, we defined three HP scenarios for each HP reach and requested respective experimental flow releases from the hydropower plant operators. We sampled benthic, drifted and stranded MIV and recorded several environmental variables (see below) over a four-week period between March 15th and April 8th 2018. In each HP and RF reach we defined three sampling sites spaced by $10 - 50$ m (Figure 2a).

HP scenarios

The HP scenarios consisted of the combined increase of flow amplitude and up-ramping rate (Figure 2c and Table 1). To reduce impacts on hydropower flexibility and production, in each river all field experiments were carried out over two consecutive days. The first day, we targeted a combination of three flow amplitudes and three up-ramping rates. The same three scenarios were repeated the next day but the drift nets were placed further towards the river center to achieve higher peak flow velocities as at day one (Figure 2a and Table 1). The selection of the targeted up-ramping rates ($1, 2$ and 3 cm/min) and peak flow velocities (0.4 and 0.8 m/s) was based on the results of previous flume experiments, which showed distinct drift responses in these

ranges (Schülting et al., 2018b). In terms to achieve the targeted HP scenarios and to define appropriate sampling sites, for each HP reach we set up and calibrated 2D unsteady hydrodynamic-numerical models to pre-define the operation mode of each hydropower plant (KUB) or retention basin (KWO, KLL).

In contrast to KUB and KWO, at KLL the maximum turbinable peak flow had to be kept constant to avoid flow velocities > 1 m/s and thus ensure wadable conditions. With this limited discharge setting, for the Linth, it was also necessary to define an alternative HP scenario with a reduced up-ramping rate (0.5 cm/min) as for the Sitter and Hasliaare. Moreover, due to different hydrological conditions (e.g., melting snow, rain) and operational characteristics of the hydropower plants and/or retention basins (e.g., turbine type, concessional limitations), base flow and down-ramping rates varied between the HP reaches. These constraints resulted in some differences between the targeted (modeled) and the measured flow amplitudes, peak flow velocities and up-ramping rates (Appendix B in Data S1). Nevertheless, measured flow amplitudes in the Sitter and Hasliaare increased approximately twofold respectively threefold from HP scenario 1 (SC1) to SC2 and ca. fourfold respectively five-sixfold from SC1 to SC3, whereas it remained almost constant in the Linth (Figure 2c and Table 1). An increase in mean and maximum up-ramping rate from SC1 to SC2 and to SC3 in addition to a higher peak flow velocity at day two was also achieved but varied between HP reaches. Mean up-ramping rate between SC1 and SC3 increased 2.5 times in the Sitter, 1.5 to 4 times in the Hasliaare and 1.5 to 2 times in the Linth. From day one to day two, peak flow velocity over all scenarios increased in average 4 times in the Sitter, 0.25 times in the Hasliaare and 0.15 times in the Linth (Table 1).

MIV sampling

The benthic community was sampled during base flow with Hess samplers (sampling area 0.045 m^2, mesh size 500 μm,) $2 - 5$ m upstream of each drift net. At each sampling site, three benthic samples were collected transect-wise (from the bank margin to the in-stream area) along a flow velocity gradient to include taxa of different current preferences (Figure 2a). Benthic samples in the HP reaches were collected four times a day (before each HP scenario and at the end of the day; Figure 2b), whereas they were taken twice a day (beginning and end of the day) in the RF reaches.

Drifting MIV were collected at each sampling site with drift nets (frame size 53 x 27 cm, mesh size 500 μm) fixed with thick rebars on both sides. The long side of each net was placed on the riverbed. Samples in the HP reaches were taken separately (nets exchanged) during base flow (exposure time 60 min) and during each HP phase: up-ramping (UR), first and second part of the peak (P1, P2; each 30 min) and down-ramping (DR; Figure 2b). In the RF reaches, MIV drift was sampled for approximately 60 min, simultaneously with the induced peak flows in the HP reaches.

Stranding MIV were collected according to Tanno et al. (2016). Four flat nets (net size 50 x 50 cm, mesh size 500 μm) were installed at each sampling site nearby the drift nets on the dewatering area (temporally wetted area, dry at base flow and wetted during peak flow; Figure 2a): two nets directly at the waterline and two nets 1 m away from the waterline and 0.5 m offset from the other nets. Ten stones of the dominant grain size were placed on each flat net to increase roughness and thus better mimic the substrate condition of the dewatering area. Stranded MIV on the nets and on the stones were collected after each HP scenario (Figure 2b). In the RF reaches, stranding was not assessed, due to stable flow conditions.

MIV samples treatment and identification of taxa

In total, 864 samples were collected, fixed with 90% ethanol in the field and then transported to the laboratory. MIV were separated from other organic and inorganic material. The individuals were sorted and identified to family or, in some cases, to lower taxonomic levels (i.e., Oligochaeta, Hydracarina, Lepidoptera) following the identification key of Tachet, Richoux, Bournaud and Usseglio-Polatera (2000) and were then counted (Appendix C in Data S1). Pupae, adult individuals in a non-aquatic life stage and terrestrial invertebrates were excluded.

Sampling of environmental variables

At each drift net, flow velocity and water depth were measured three times during base flow and three times

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each during the P1 and P2 phase. The values of the three measurements were then averaged. Flow velocity was recorded using a micro propeller (Flowatch Flowmeter) 2 cm above the substrate surface (v_0), at the net-center approximately 13 cm from the substrate surface (v_{net}) and 6 cm below the water surface (v_{100}). Water depth was measured in front of each net with a rigid meter. Concurrently, turbidity as NTU (Nephelometric Turbidity Unit) was measured at the drift net of the central sampling site using a portable turbidity meter (Hach Lange 2100Q). Additionally, the extension of the dewatering area (DA_{ex}) as distance between the waterline at base flow (Q_{base}) and at peak flow (Q_{peak}; i.e., flow magnitude) was measured nearby the stranding nets.

Water temperature (T) and water level were continuously recorded (1 min interval) using one logger (Vemco Minilog II-T, AMIRIX Systems Inc.) and one pressure probe (DCX-22 SG/VG CTD, Keller), respectively, placed at the upstream sampling site of each HP reach. Based on the water level measurements, the mean and maximum up- (UR_{mean}, UR_{max}) and down-ramping rates (DR_{mean}, DR_{max}) were determined. Discharge data were obtained from federal and cantonal gauging stations as well as from the operators of the hydropower plants and were used to determine Q_{base}, Q_{peak}, flow amplitude (Q_{peak} - Q_{base}) and ratio (Q_{peak}/Q_{base}). The grain size distribution (GSD) along gravel bars of each HP reach was determined by a representative number of line-by-number analyses (n = 1 – 3) using a gravelometer. GSD curves were determined and analyzed, taking particle values as 'percent finer'. Froude number (Fr) and bed shear stress (τ_β) according to Whiting and Dietrich (1990) were calculated for each HP sampling site.

Data analysis

Data analysis were either based on the total community or at taxa-level. To ensure consistency and to down-weight the influence of rare taxa, only taxa with a relative abundance > 1% over all drift, stranding or benthic samples, were selected to express taxa-specific responses (Appendix C in Data S1). Additionally, to assess trait-specific responses, we classified taxa found in the benthic samples based on two relevant ecological trait categories related to HP sensitivity (RHEOPHYLAX, 2021; Schülting et al., 2021): 'hydraulic habitat preference' (classes: lentic/lotic; indicating taxa adaptation to low or high current) and 'vertical habitat preference' (classes: interstitial/surface; indicating taxa flow exposure; Appendix C in Data S1).

Benthic community composition and stranding were analyzed in terms of density, expressed as the number of individuals standardized by the sampled area (ind./m^2). Single samples were pooled per sampling site (Figure 2a) and chronological sampling (Figure 2b), resulting in 24 and 18 composite samples respectively for each HP reach as well as 12 benthic composite samples for each RF reach.

MIV drift intensity was calculated following Pegel (1980) as the number of individuals in the drift standardized by the drift-net area and the exposure time (ind./m^{2}min). To consider the effect of an entire HP scenario, drift samples collected during the UR, P1, P2 and DR phase were pooled per sampling site and HP scenario. For each HP and RF reach this resulted in 18 composite samples each for base flow and HP scenario. Further, since MIV drift patterns, and probably also stranding patterns, are strongly related to the benthic source population, we calculated the drift and stranding propensity (e.g., Bruno et al., 2013; Timusk et al., 2016) as the drift intensity and stranding density, respectively, standardized by the benthic density. All benthic samples were pooled per HP reach to generate a single estimate of benthic density at the reach scale.

Statistical analyses

Canonical Correspondence Analyses (CCA) were used to explore differences in drift and stranding propensity, respectively, among the three HP reaches and to assess their correlation with a pre-selection of explanatory environmental variables (based on the state of knowledge, see introduction). Drift: $X_{\pi\epsilon\alpha\kappa}$, $X_{\pi\epsilon\alpha\kappa}$ - $X_{\beta\alpha\sigma\epsilon}$, $\Upsilon P_{\mu\epsilon\alpha\nu}$, $\Upsilon P_{\mu\alpha\xi,\ 0,\ \nu\epsilon\tau,\ 100}$, τ_β, $\Phi\rho$, T, $NT\Upsilon$. Stranding: Q_{peak}, Q_{peak}/Q_{base}, DR_{mean}, DR_{max}, v_0, v_{net}, v_{100}, DA_{ex}, T, NTU. Drift and stranding propensity, respectively, were used as response variable. Environmental variables were log-transformed (x + 1) and then sequentially checked for variance inflation factor (vif), while variables exceeding a vif of five were removed prior to the CCA modeling. The final selection of vif validated variables was based on a stepwise model selection (permutational forward and backward) based on the Akaike

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information criterion (AIC). Environmental variables that were selected in both approaches were used for the final CCA model construction. The CCA model was then tested for total significance, significant axes and significant terms via PERMANOVAs. An additional factor fitting was performed to assess statistical differences in drift and stranding propensity, respectively, between HP reaches (Sitter *vs* Hasliaare *vs*Linth), sampling day (day 1 *vs* day 2; corresponding to higher peak flow velocities at day 2, see Table 1) and HP scenario (SC 1*vs* SC2 *vs* SC3).

Non-metric multidimensional scaling (NMDS) was used to explore differences in the benthic community compositions among the different HP and RF reaches. Benthic densities were used to create a resemblance matrix based on the Bray-Curtis similarity index. Permutational multivariate analysis of variance (PERMANOVA) with a similarity percentage (SIMPER) analysis were performed to assess for significant differences in the benthic community composition among reaches and to identify the taxa that most contributed to dissimilarity.

In addition to CCA and NMDS, non-parametric Mann-Whitney or Kruskal-Wallis tests followed by pairwise post hoc tests, and linear regression models were applied for specific analyses. CCA and NMDS analyses were performed using the software R version 4.1.1 (R Core Team, 2021) with the package 'vegan' (Oksanen et al., 2019). Non-parametric tests and linear regressions were performed using the software SPSS Statistics version 27.0 and SigmaPlot version 12.5.

Results

Short-term response of macroinvertebrate (drift, stranding) to hydropeaking

Across all reaches, drift intensity was 2.5 times higher during HP (12.5 ± 0.9 ind./m^{2}min) compared to base flow (4.9 ± 0.8 ind./m^{2}min, p< 0.001) and approximately 1.5 times higher than in the RF reaches (7.4 ± 0.8 ind./m^{2}min, $p < 0.001$, 'ALL' in Figure 3). Drift intensity in the RF reaches was also significantly higher than at base flow in the HP reaches ($p < 0.05$). At the river level, significantly higher drift intensities were found during HP compared to base flow of the Sitter ($p < 0.01$), Hasliaare ($p < 0.001$) and Linth ($p < 0.01$) as well as compared to the RF reaches of the Sitter ($p < 0.001$) and Hasliaare ($p < 0.01$). The Linth showed a different pattern with higher drift intensity in the RF reach compared to HP ($p = 0.06$) and to base flow ($p < 0.001$).

Across all HP reaches, drift intensities during all HP phases (UR, P1, P2, DR) were significantly higher than during base flow (p [?] 0.001, Appendix D in Data S1). Moreover, drift intensity in the UR phase was significantly higher compared to the DR phase ($p < 0.01$). The highest average drift intensity was found for the UR phase (17.1 +- 1.7 ind./m^{2}min) and the first part of the peak phase (P1; 13.7 +- 1.3 ind./m^{2}min) which showed drift intensities 3.5 times and approximately three times higher, respectively, than during base flow (4.9 +- 0.8 ind./m^{2}min).

Across all HP reaches, and considering the entire HP scenario (i.e., UR, P1, P2 and DR phase), stranding density was not significantly related to drift intensity ('ALL' in Figure 4a). However, if considering only the UR phase, a positive significant relationship was found ($R = 0.368$, $p < 0.01$, 'ALL' in Figure 4b). At the reach level, a positive significant relationship was found in the Hasliaare and in the Sitter (but only for the UR phase) but not in Linth. In general, stranding was much less pronounced than drift and many stranding samples contained only few individuals (Appendix C in Data S1).

The CCA analyses revealed that taxa drift and stranding composition significantly differed between the three rivers (drift: $r^2 = 0.23$, $p < 0.01$; stranding: $r^2 = 0.32$, $p < 0.01$; Figure 5). Additionally, but to a lesser extent, the lateral sampling location (day 1 *vs* day 2: higher peak flow velocities at day 2, see Table 1; drift: $r^2 = 0.16$, $p < 0.01$; stranding: $r^2 = 0.27$, $p < 0.01$) significantly contributed to the differences. Drift composition in the Sitter and Linth were more similar than in the Hasliaare (Figure 5a, confidence ellipses). The HP scenario also significantly contributed to the drift ($r^2 = 0.16$, $p = 0.05$) but not to the stranding

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differences. 43.5% and 40.8% of the total variation of drift and stranding taxa distributions, respectively, can be explained by the selected environmental variables. The main environmental variables that could affect the taxa drift propensity to the greatest extent were the flow velocity near the surface (v_{100} ; F = 12.5, p < 0.001), mean up-ramping rate (UR_{mean}; F = 10.4, p < 0.001), turbidity (NTU ; F = 6.4, p < 0.001), and water temperature (T ; F = 6.0, p < 0.001) which explained 8.0, 9.8, 9.0, and 8.5% of the variation, respectively (Figure 5a). Froude number (Fr) also contributed to the explained variation (8.2%) but not significantly (F = 1.7, p = 0.119). The main environmental variables that could affect the taxa stranding propensity to the greatest extent were the flow ratio (Q_{peak}/Q_{base} ; F = 9.7, p < 0.001), max. down-ramping rate (DR_{max} ; F = 8.8, p < 0.001), water temperature (T ; F = 5.5, p < 0.001), turbidity (NTU ; F = 4.1, p < 0.001) and flow velocity near the surface (v_{100} ; F = 3.7, p < 0.01), which explained 7.3, 8.8, 8.2, 8.1, and 8.3 % of the variation, respectively (Figure 5b).

Across all HP reaches, Rhyacophilidae and Limnephilidae showed high propensity to drift and strand, whereas Oligochaeta and Heptageniidae showed the lowest propensity ('ALL' in Table 2). Simulidae also showed high propensity to drift and Perlodidae to strand. However, drift and stranding propensity varied considerably between reaches. Limnephilidae and Simuliidae showed considerable propensity to drift in all three HP reaches, whereas Rhyacophilidae only in the Hasliaare. Limnephilidae, Rhyacophilidae and Nemouridae showed considerable propensity to strand only in the Hasliaare, whereas Empididae and Perlodidae in the Linth. Almost all taxa showed highest propensity to drift and strand in the Hasliaare and lowest propensity to drift and strand in the Sitter.

Long-term response of macroinvertebrate (density and community composition) to hydropeaking

Average benthic density was five times higher in the Hasliaare RF reach (1146 +- 229 ind./m^2) compared to the HP reach (227 +- 23 ind./m^2, p < 0.001), whereas in the Sitter a contrasting trend was observed with average density approximately 3.5 times higher in the HP reach (1838 +- 357 ind./m^2) than in the RF reach (493 +- 97 ind./m^2, p < 0.001, Figure 6). The density variability of the Sitter HP samples was the largest of all reaches. No significant differences were found for the Linth and considering all reaches together ('ALL' in Figure 6).

The NMDS analysis showed that benthic community composition was significantly different between the six reaches (p = 0.001), whereby it was more similar in the three RF reaches than in the three HP reaches (Figure 7, overlap vs no overlap of the confidence ellipses; lower R^2 and F values in Appendix E in Data S1). The Hasliaare showed the largest dissimilarity between RF and HP reaches, whereas the other two rivers grouped more together, indicating more considerable consistency in benthic community composition.

Four taxa (Heptageniidae, Chironomidae, Baetidae and Leuctridae) remarkably contributed to differences in community composition among RF and HP reaches of all three rivers (Table 3). Among these taxa, Heptageniidae, Chironomidae and Baetidae in the Sitter, and Chironomidae, Baetidae and Leuctridae in the Linth cumulatively contributed for approximately 70% of the dissimilarities. In the Hasliaare two other taxa, Limnephilidae and Nemouridae, accounted for 41% of the differences among RF and HP reaches, and Chironomidae additionally contributed for approximately 15%.

Across all reaches, Leuctridae, Nemouridae and Limnephilidae showed significantly higher benthic densities in the RF than in the HP reaches (p < 0.001, Appendix E in Data S1). In contrast, Simuliidae showed significantly higher benthic densities in the HP reaches (p < 0.05). However, differences between HP and RF reaches varied widely among taxa and river (Appendix E in Data S1).

On average, lentic taxa were 5.5 times more abundant in the benthic samples of the RF reaches (191.2 +- 47.7 ind./m^2) compared to the HP reaches (35.0 +- 6.1 ind./m^2; p < 0.001), whereas lotic taxa were two times more abundant in the HP reaches (437.8 +- 105.3 ind./m^2) than in the RF reaches (222.2 +- 35.1 ind./m^2), but the difference was not significant ('ALL' in Figure 8). Differences between RF and HP reaches for taxa classified as surface dwelling or interstitial were also not statistically different.

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Discussion

Considering expected future developments of the energy demand and the concurrent progression of the implementation of climate change goals, the need for energy storage capabilities such as hydropower reservoirs will become more and more important in the near future (Boes et al., 2021). As a result, an increase in HP operation thus poses a further threat to physical habitats and biodiversity within riverine ecosystems, highlighting the need for a prudent approach. Even though the mitigation of HP impacts is a legal requirement in many countries (e.g., Swiss Water Protection Act, European Water Framework Directive), the complex interplay of HP-related impacts on MIV still remains poorly understood, which complicates the implementation of efficient mitigation strategies.

Several studies suggest that river reaches affected by HP are characterized by reduced benthic abundance, biomass and altered community composition (Cereghino et al., 2002; Cereghino & Lavandier, 1998;; Elgueta et al., 2021; Leitner et al., 2017; Moog, 1993), which in consequence may have negative effects on metacommunity-wide functional diversity (Kjaerstad et al., 2018; Ruhi et al., 2018). Within this field experimental study – conducted in three HP-regulated Swiss rivers – we could prove short-term (drift and stranding) and long-term (benthic density, established community composition) effects of HP operation within the investigated river reaches. Further, we could identify some HP-related parameters most likely responsible for triggering active and/or passive drift and stranding, as well as show that MIV response to HP is highly taxa-, trait- and river-context dependent. In conclusion, our study adds knowledge about effective implementation of mitigation measures and more sustainable operation of HP power plants (Bruder et al., 2016; Moreira et al., 2019; Smokorowski, 2021).

General response of macroinvertebrate to hydropeaking

Consistent with our hypotheses and in accordance to other published literature (Aksamit, Carolli, Vanzo, Weber, & Schmid, 2021; Bruno et al., 2010, 2016; Imbert & Perry, 2000; Miller & Judson, 2014; Schulting et al., 2018a, 2021; Timusk et al., 2016), HP generally led to increased MIV drift intensities compared to base flow and to the upstream-located RF reaches with highest drift during the up-ramping phase and the first part of the peak flow. Furthermore, the analyzed data partially supports the result of Tanno et al. (2021) that an increased drift of MIV also increases their risk of stranding (especially considering the UR phase). Comparison could be biased by the low number of individuals found in our stranding samples as well as the different equations used for drift intensity (our study) and drift density (Tanno et al., 2021). The use of drift density as response variable artificially decreases the effects of HP scenarios with higher flow magnitude and corresponding flow velocities because MIV drift mostly does not increase proportionally to the increase in water volume, leading to a dilution effect (Naman, Rosenfeld, Richardson, & Way, 2017; Pegel, 1980). This effect was already highlighted in the study of Naman et al. (2017) who showed that the parameter 'drift density' negatively correlates with the investigated water volume, whereas 'drift flux' (i.e., total number of drifting invertebrates) showed opposite patterns. We therefore decided to use the 'drift intensity' (because not affected by dilution effects) as a parameter for analyzing the effect of field HP experiments with non-comparable flow conditions.

We found taxa- and river-specific long-term effects on the benthic community under HP (discussed below). However, in contrast to our hypothesis, considering all taxa and all study reaches together, we did not detect a significant reduction in benthic density between RF and HP reaches, even though drift and/or stranding were increased in all HP reaches. We conclude that drift and stranding can contribute to a reduction in benthic density of some taxa, as reported in several studies (e.g., Cereghino & Lavandier, 1998; Leitner et al., 2017; Moog, 1993), but most likely HP further induces organism stress and hampers important processes such as feeding and reproduction. The combination of the HP-induced effects on biota may in consequence lead to a thinning of the benthic community and to a long-term change in species composition.

Effect of HP intensity and associated hydraulic forces on drift and stranding

Flow velocity near the surface (v_{100}) and mean up-ramping rate (UR_{mean}) were identified as major deter-

minants for macroinvertebrate drift propensity, indicating that the flow magnitude and amplitude (leading to different flow velocities) as well as the up-ramping rate are important HP-related parameters. A strong relationship between drift and flow-related hydraulic forces such as flow velocity is widely known (e.g., Gibbins, 2016). Recently, Schulting et al. (2021) found that discharge-related parameters, such as mean-column flow velocity at peak flow, primarily affect MIV drift and the importance of the up-ramping rate increases only once certain discharge-related thresholds are exceeded. Following, a reduction of the up-ramping rate may lead to a lower drift since the MIV have more time to seek shelter in the interstices during flow increase (Imbert & Perry, 2000; Schulting et al., 2021; Timusk et al., 2016).

We also found a positive link between down-ramping rate (DR_{max}) and stranding propensity, corresponding to findings by Kroger (1973) and Perry & Perry (1986). In line with Tanno et al. (2016), a larger flow ratio (Q_{peak}/Q_{base}) also led to higher stranding, possibly due to increased drift and a larger wetted area. Additionally, we showed that turbidity (NTU) and water temperature (T) most likely influence drift and stranding risk. However, this could also be an indirect effect as variations in water temperature and turbidity are influenced by HP operation (e.g., flow ratio). We conclude that the magnitude of drift and stranding propensity is most likely affected by a combination of hydrological and hydraulic factors as well as by their interaction (v_{100}, UR_{mean}, Q_{peak}/Q_{base}, DR_{max}) and possibly by behavioral (NTU, T) responses. Indeed, thermopeaking has been shown to induce behavioral MIV drift of many taxa and often has a synergic magnifying effect with the HP wave (e.g., Bruno et al., 2013). Similarly, water temperature has been shown to influence stranding risk of fish, with greatest effect in winter due to low temperatures (e.g., Halleraker et al., 2003). HP-induced changes of turbidity and their effects on MIV are poorly understood. Though, re-mobilized and re-suspended fine sediments during peak flows are mainly responsible for an increase in the river's turbidity and can induce fine sediment infiltration and potential clogging (Hauer et al., 2019), thereby exposing MIV to increased abrasion and reduced potential interstitial habitats (Bo et al., 2007; Crosa et al., 2010; Jones et al., 2012).

Taxa- and traits-specific responses to hydropeaking

Long-term HP effects were found only for a few taxa such as Limnephilidae, Nemouridae and Leuctridae, which were abundant in the RF reaches yet strongly reduced in the HP reaches. Limnephilidae further showed short-term response reflected in their high propensity to drift and strand. In contrast, Heptageniidae seemed to be more resistant in respect to short and long-term HP effects.

Limnephilidae are adapted to slow flowing lentic habitats on the substrate surface and, due to their size and shape, they experience high drag (Rader, 1997). Moreover, for case-building Limnephilidae it has been shown that an increased flow velocity decreases their ability to return to the stream bottom from the drift (de Brouwer, Besse-Lototskaya, ter Braak, Kraak, & Verdonschot, 2017). Therefore, this taxon is easily detached passively from its habitat and has poor settling efficiency which might explain its particularly high sensitivity towards short- and long-term HP effects. In line with these observations, other studies suggest that HP often contributes to a decrease in the density of limnophilic taxa associated to lentic habitats and to strong drift (Graf et al., 2013; Leitner et al., 2017; Schulting et al., 2021). Correspondingly, in our study, lentic taxa were more abundant in the RF reaches compared to the HP reaches, confirming the sensitivity of this trait to HP (Schulting et al., 2021).

Heptageniidae showed higher abundances in the benthic samples of the HP reaches compared to the RF reaches (Appendix F in Data S1) and lowest propensity to drift and strand. This emphasized the tolerance towards HP of this family. Similar observations were reported by other authors (e.g., Bruno et al., 2013; Graf et al., 2013; Moog, 1993, Schulting et al., 2018a, 2021). Although different taxa within this family may show varying responses towards HP, they generally prefer lotic habitats on the substrate surface and are characterized by high agility and active settling efficiency (Elliott, 1971) as well as by various morphological adaptations that enhance attachment (streamlined body shape, sharp tarsal crawls, sucker-like ventral gills) and reduce drag (Rader, 1997). Nemouridae and Leuctridae did not show distinctively high drift and stranding following HP, possibly due to relatively thin source populations. Schulting et al. (2021) reported high drift induced by HP for Nemouridae (*Nemoura/Nemurella* sp.), whereas Leuctridae (*Leuctra* sp., a

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taxon associated with the interstices) showed comparably low response, and this family is often not affected by HP (e.g., Graf et al., 2013; Moog, 1993).

Simuliidae and Rhyacophilidae also showed high propensity to drift – Rhyacophilidae also to strand – but both families were more abundant in the benthic samples of the HP reaches compared to the RF reaches. Both taxa are known to prefer lotic habitats and they own adaptations (claws and silk) to prevent passive drift (Rader, 1997). Nevertheless, Simuliidae have been reported to often drift (Bruno et al., 2013, 2016; Imbert & Perry, 2000) and strand (Perry & Perry, 1986; Tanno et al., 2021) following HP. As surface-dwelling taxon, they are naturally exposed to high flow, which can likely explain their high drift propensity, even under natural conditions (Elliot, 1967). Rhyacophilidae are generally associated to the interstices, but as predators, they may also actively move on the surface seeking prey and are thus exposed to abruptly increased hydraulic forces. The cold thermopeaking in the Hasliaare (Figure 2c) might also explain the high (probably behavioral) drift and stranding of Rhyacophilidae (Bruno et al., 2013) in this reach. However, our experimental setup does not allow a separation of active and passive drift. In conclusion, our data suggests that high drift and/or stranding induced by HP flow fluctuations do not lead to distinct density reductions of Simuliidae and Rhyacophilidae. Thus, these taxa are less sensitive towards HP compared to Limnephilidae.

Taxa associated to lentic areas showed reduced benthic density compared to lotic taxa. However, on the long-term, HP did not considerably reduce benthic densities of most taxa, especially of Chironomidae and Baetidae. Even though these taxa showed comparably high drift and stranding responses (Appendix E and F in Data S1), they were also dominant in the respective benthic samples. Matching our results, these two families are often reported as dominant components of the benthic assemblages and drift following HP (Bruno et al., 2010, 2013, 2016; Gibbins et al., 2016; Imbert & Perry, 2000; Moog, 1993; Schulting et al., 2018a, 2021; Tanno et al., 2016, 2021; Timusk et al., 2016) as well to frequently strand (Perry & Perry, 1986; Tanno et al., 2016, 2021). Chironomidae and Baetidae are likely to be represented strongly in the drift and stranding due to the high density and density dependence of drift (Waters, 1972). Accordingly, they showed comparably low propensity to drift and strand and did not show reduced benthic densities under HP, probably due to their morphological and behavioral adaptations to high currents (Chironomidae: rapid colonizers with rapid growth rates and short life cycles; Baetidae: good swimmers with a streamlined body, rapid settling capabilities, frequent intentional drift; Elliott, 1971; Milner, 1994; Naman et al., 2016; Rader, 1997; Wilzbach, Cummins, & Knapp, 1988). Even though, results regarding Chironimidae cannot be generalized since this family consists of many different taxa with different adaptations. Our study suggests that some Chironomid species and Baetidae are resistant and resilient to long-term HP effects and most likely have flexible habitat needs. We therefore conclude that high passive drift and/or stranding, especially of individual-rich taxa, does not necessarily indicate strong HP sensitivity. Yet it must be stated that the benthic community composition in all investigated river reaches has already been significantly affected by the long history and huge variety of anthropogenic impacts on river ecosystems. The presented results should therefore only be interpreted in consideration of the limitations related to the altered source populations.

Some studies suggest that functional descriptions are maintained, even with coarser taxonomic resolution, and it barely influences the discrimination of impact levels (e.g., Doledec, Olivier, & Statzner, 2000; Gayraud et al., 2003). However, since organisms in our study were identified only to family-level, taxa-specific results should not be over-interpreted. This level of taxonomic resolution inevitably leads to a loss of information, especially for families that have heterogeneous adaptations among the constituent genera, such as Chironomidae. Thus, diverse species/genera within a family can react quite differently to HP or other flow modifications (e.g., RF). Lastly, some taxa were found only in low numbers (e.g., Limnephilidae), limiting the statistical power of some of our results. Moreover, the comparably low number of drifting and stranding individuals can probably be explained by the peak magnitude of our experimental setup, which were lower as normally found in Swiss HP rivers (e.g., Tanno et al. 2016, 2021).

River- and reach-specific responses

MIV responses to HP were not only taxa- and trait-specific but varied widely among the investigated rivers and reaches. Disparities in the direction and magnitude of responses among rivers likely resulted from

differences in community composition but also from variability in the HP intensity and river morphological characteristics. Indeed, it is likely that the lower peak flow in the Sitter in combination with its higher morphological heterogeneity compared to the Hasliaare and the Linth lead to lower hydraulic forces acting on the MIVs favoring benthic abundance in concert with a reduced drift and stranding risk. The high drift in the RF reach of the Linth can be explained by the hydraulic forces measured, such as flow velocities and Froude number, which were similar to the ones measured in the HP reach during peak flow. In contrast, in the RF reaches of the Sitter and Hasliaare, they were comparable to the ones measured during base flow (Appendix B in Data S1). This finding underlines that discharge-related hydraulic forces (e.g., flow velocity) acting on the riverbed are most probably the major determinant for MIV drift. Further, the HP-induced removal and mobilization of organic matter from the substrate, which is often associated to passive drift of MIV (Aksamit et al, 2021; Bruno et al., 2016; Miller & Judson, 2014; Timusk et al., 2016), is a another determining factor. The RF reach of the Linth was characterized by high algal cover on the substrate (>50%; Appendix A in Data S1) and showed the highest drifting biomass (ash free dry mass) of FPOM and CPOM compared to the other two rivers (Tonolla, Kastenhofer, Vogeli Kummert, & Gufler, 2020).

In general, these river- and reach-specific responses confirm the importance of structural complexity (such as in the Sitter) for providing lentic habitats and hydraulic refugia at the locale scale as well as the retention of organic matter during high flow disturbance (e.g., Bruno et al., 2016; Hauer et al., 2017; Lancaster, 2000). In structurally complex rivers with moderately sloping bank, velocity and bottom shear stress remain relatively constant (Naman et al., 2017), thereby reducing passive drift. In contrast, fluctuation of the dewatering area is enhanced if the river-bank slope is low, forcing organisms to shift habitats which subsequently increase their risk of stranding.

In addition to river widening and a general increase in structural complexity, morphological measures should aim to reduce substrate-deficit and clogging due to fine substrate infiltration in the dewatering area (often occurring in combination; Hauer et al., 2019), thereby increasing interstitial space as potential hyporheic refugial habitat during HP (Bruno et al., 2010). Further, the reconnection of tributaries with a natural flow and sediment regime, as well as improving the morphology upstream of HP impacted reaches (e.g., in the RF reach), may provide refugial habitats and a connection with benthic source populations for faster recolonization downstream of HP power plants (Aksamit et al., 2021; Bruno et al., 2016; Hauer et al., 2017; Kennedy et al., 2016; Milner, Yarnell, & Peek, 2019).

Overall, our results highlight that different MIV taxa (and traits) vary in their vulnerability and response to flow alteration (HP and RF) and that the river-specific physical context (HP intensity, morphology, distance to potential, source populations) mediate the magnitude and direction of this response. Therefore, next to structural and/or operational measures to reduce HP discharge (and related hydraulic forces) and the ramping-rates, morphological measures should be considered as an essential component of HP mitigation.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author, [D.T.], upon reasonable request.

Tables

Table 1. Measured hydrological/hydraulic variables in the HP reaches, separated in the three HP scenarios SC1, SC2, SC3. Values for day one (D1) are indicated in black and values for day two (D2) in light grey.

Q_{base}: base flow; Q_{peak}; peak flow; Q_{peak}/Q_{base}: flow ratio; Q_{peak} - Q_{base}: flow amplitude; UR_{mean} and UR_{max}: Mean and maximum up-ramping rate; v_{net}: peak flow velocity at net; dh: difference between water depth at Q_{peak} and Q_{base} . v_{net} is indicated as mean +- standard deviation of the HP phases P1 and P2 at the three sampling sites (n = 6 for each HP scenario). dh is indicated as mean +- standard deviation at the three sampling sites (n = 3 for each HP scenario).

	KUB – Sitter	KUB – Sitter	KUB – Sitter	KWO – Hasli-aare	KWO – Hasli-aare	KWO – Hasli-aare	KLL – Linth	KLL – Linth	KLL – Li
Sampling date	March 15th & 16th	March 15th & 16th	March 15th & 16th	March 30th & 31st	March 30th & 31st	March 30th & 31st	April 7th & 8th	April 7th & 8th	April 7th & 8th
Hydropeaking scenario	SC1	SC2	SC3	SC1	SC2	SC3	SC1	SC2	SC
Characteristics									
Q_{base} [m³/s]; D1 | D2	1.97 | 1.96	1.97 | 1.97	1.99 | 1.99	2.72 | 3.53	2.65 | 3.57	2.73 | 3.82	5.16 | 6.32	5.13 | 6.08	5.2 | 6.2
Q_{peak} [m³/s]; D1 | D2	5.99 | 5.92	10.04 | 10.75	17.50 | 17.55	5.02 | 5.53	8.74 | 9.59	14.36 | 15.84	11.52 | 13.62	11.53 | 13.22	11. | 14.
Q_{peak}/Q_{base} [-]; D1 | D2	3.04 | 3.02	5.10 | 5.46	8.79 | 8.82	1.85 | 1.57	3.30 | 2.69	5.26 | 4.15	2.23 | 2.16	2.25 | 2.17	2.2 | 2.3
Q_{peak} - Q_{base} (m³/s); D1 | D2	4.02 | 3.96	8.07 | 8.78	15.51 | 15.56	2.30 | 2.00	6.09 | 6.02	11.63 | 12.02	6.36 | 7.30	6.40 | 7.14	6.7 | 8.4
UR_{mean} [cm/min]; D1 | D2	0.75 | 0.80	1.65 | 1.60	2.00 | 2.00	0.40 | 0.50	0.70 | 0.60	1.60 | 0.75	0.95 | 1.00	1.55 | 1.80	1.9 | 1.6
UR_{max} [cm/min]; D1 | D2	1.60 | 1.70	2.80 | 3.40	4.70 | 4.80	0.80 | 1.10	1.80 | 1.20	3.00 | 3.00	3.30 | 2.20	5.60 | 5.10	7.1 | 5.2
v_{net} [m/s]; D1 v_{net} [m/s]; D2	0.12 ± 0.07	0.21 ± 0.09	0.33 ± 0.07	0.24 ± 0.04	0.44 ± 0.14	0.24 ± 0.11	0.34 ± 0.22	0.41 ± 0.25	0.3 ± 0.2
	0.77 ± 0.29	0.59 ± 0.17	0.55 ± 0.12	0.58 ± 0.10	0.54 ± 0.08	0.57 ± 0.10	0.42 ± 0.14	0.55 ± 0.08	0.5 ± 0.0
dh [m]; D1 dh [m]; D2	0.13 ± 0.02	0.26 ± 0.01	0.43 ± 0.04	0.09 ± 0.00	0.21 ± 0.17	-0.03 ± 0.01	0.16 ± 0.02	0.16 ± 0.00	0.1 ± 0.0
	0.21 ± 0.04	0.33 ± 0.02	0.44 ± 0.02	0.09 ± 0.02	0.27 ± 0.03	0.37 ± 0.06	0.18 ± 0.03	0.14 ± 0.01	0.1 ± 0.0

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Table 2. Propensity to drift/strand based on drift intensity respectively stranding density to benthic density of the most common taxa across all HP reaches ('ALL') and separated by reach. Larger numbers (mean ± standard error) suggest higher propensity to drift/strand (the three largest numbers of each reach and for 'ALL' are indicated in bold). Asterisks indicate taxa with relative abundances > 1% in the drift/stranding but not in the benthic samples (Appendix C in Data S1).

Taxa Drift[+]	ALL (n = 54)	Sitter (n = 18)	Hasliaare (n = 18)	Linth (n = 18)
Oligochaeta	0.005 ± 0.002	0.011 ± 0.005	0.003 ± 0.001	0.003 ± 0.001
Baetidae	0.079 ± 0.013	0.007 ± 0.001	0.197 ± 0.020	0.032 ± 0.003
Heptageniidae	0.004 ± 0.001	0.002 ± 0.000	0.004 ± 0.001	0.005 ± 0.001
Leuctridae	0.068 ± 0.013	0.003 ± 0.001	0.176 ± 0.021	0.026 ± 0.004
Nemouridae	0.046 ± 0.007	0.009 ± 0.002	0.086 ± 0.015	0.043 ± 0.007
Elimidae	0.040 ± 0.012	0.011 ± 0.001	0.063 ± 0.031	**0.045 ± 0.015**
Chironomidae	0.041 ± 0.007	0.009 ± 0.001	0.095 ± 0.012	0.017 ± 0.001
Simuliidae	**0.125 ± 0.024**	**0.021 ± 0.003**	**0.311 ± 0.046**	**0.044 ± 0.012**
Taeniopterygidae*	0.035 ± 0.005	**0.024 ± 0.008**	0.042 ± 0.008	0.040 ± 0.010
Limnephilidae*	**0.299 ± 0.085**	**0.084 ± 0.053**	**0.683 ± 0.224**	**0.128 ± 0.036**
Rhyacophilidae*	**0.691 ± 0.194**	0.008 ± 0.003	**2.057 ± 0.432**	0.007 ± 0.002
Taxa Stranding[++]	**ALL (n = 54)**	**Sitter (n = 18)**	**Hasliaare (n = 18)**	**Linth (n = 18)**
Oligochaeta	0.041 ± 0.018	**0.022 ± 0.009**	0.013 ± 0.008	**0.086 ± 0.052**
Baetidae	0.042 ± 0.011	0.001 ± 0.000	0.104 ± 0.028	0.021 ± 0.004
Heptageniidae	0.006 ± 0.003	0.001 ± 0.000	0.003 ± 0.001	0.014 ± 0.007
Nemouridae	0.232 ± 0.068	0.002 ± 0.002	**0.617 ± 0.171**	0.078 ± 0.030
Chironomidae	0.075 ± 0.015	**0.005 ± 0.001**	0.167 ± 0.035	0.054 ± 0.007
Simuliidae	0.079 ± 0.034	**0.006 ± 0.003**	0.231 ± 0.000	0.000 ± 0.000
Empididae*	0.049 ± 0.022	0.000 ± 0.000	0.000 ± 0.000	**0.148 ± 0.059**
Perlodidae*	**0.550 ± 0.295**	0.000 ± 0.000	0.090 ± 0.000	**1.560 ± 0.847**
Limnephilidae*	**0.270 ± 0.103**	0.000 ± 0.000	**0.810 ± 0.270**	0.000 ± 0.000
Rhyacophilidae*	**0.322 ± 0.130**	0.000 ± 0.000	**0.960 ± 0.348**	0.006 ± 0.006

[+] *Hydracarina was excluded because drift propensity was not computable in one or more of the three reaches; also for the drift CCA (Figure 5a).* [++]

Chloroperlidae, Lepidostomatidae and Gammaridae were excluded because stranding propensity was not computable in one or more of the three reaches; also for the stranding CCA (Figure 5b).

Table 3. Simper statistic showing the taxa that most contributed to dissimilarity among RF and HP reaches of the three rivers. Taxa that cumulatively contribute (cum sum) to ca. 90 % of the differences between each pair of groups (RF vs HP) are shown.

River reach	Taxa (cum sum)	Taxa (cum sum)	Taxa (cum sum)	Taxa (cum sum)	Taxa (cum sum)	Taxa (cum sum)
Sitter RF *vs* HP	Heptageniidae 0.292	Chironomidae 0.551	Baetidae 0.731	Simuliidae 0.791	Leuctridae 0.848	Oligochaeta 0.889
Hasliaare RF *vs* HP	Limnephilidae 0.228	Nemouridae 0.410	Chironomidae 0.562	Baetidae 0.702	Heptageniidae 0.822	Leuctridae 0.918
Linth RF *vs* HP	Chironomidae 0.352	Baetidae 0.535	Leuctridae 0.678	Nemouridae 0.814	Heptageniidae 0.921	

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Figure legends

Figure 1. Overview map of the three study sites. White dots show the water releases of the hydropower plant (KUB) and of the retention basins (KWO and KLL). HP and RF reaches are identified with white and yellow rectangles, respectively. White arrows show the flow direction. Source background Orthophotos: Swissimage © Swisstopo.

Figure 2. Experimental setup. (a) Schematic sampling design for HP (top panel) and RF reaches (bottom panel). (b) Chronological sampling illustrated as example of the three HP scenarios (SC1, SC2, SC3) at day one in the HP reach of the Sitter. Drift samples were collected separately at base flow (B) and during each HP phase: up-ramping (UR), first and second peak (P1, P2), down-ramping (DR). (c) HP scenarios. Water level (blue solid line) and water temperature (red solid line) measured in the HP reaches as well as water temperature measured in the RF reaches (red dotted line). Grey squares indicate sampling period at day one and two. Please note different scales on y-axes.

Figure 3. Drift intensity (ind./m^2min) across all reaches ('ALL') and separated by reach. RF: residual flow reach; B: base flow; HP: during hydropeaking (i.e., entire HP scenario: UR, P1, P2 and DR phase). Boxplots show the 25th and 75th percentiles, median (solid line in the box), mean (dashed line in the box), whiskers (10th and 90th percentiles) and outliers (white dots). Numbers indicate the sample size, whereas letters show group affiliation according to post hoc tests with Bonferroni correction.

Figure 4. Relationship between drift intensity (ind./m^2min) and stranding density (ind./m^2) based on linear regression models across all three HP reaches ('ALL') and separated by reach (Sitter: black square; Hasliaare: dark grey circle; Linth: light grey triangle). (a) Drift data of an entire HP scenario: UR, P1, P2 and DR phase. (b) Only drift data of the UR phase. Solid lines: linear regressions; dashed black lines in the left plots: 95% confidence intervals. To better meet assumptions of normality and homogeneity of variances, all data were log transformed (X+1) prior to computing regressions. Although, in (b) the data for 'ALL' and Hasliaare are not normally distributed. R: coefficient of multiple correlation.

Figure 5. Biplot of Canonical Correspondence Analysis (CCA) based on (a) drift propensity and (b) stranding propensity ofthe most common taxa in the three HP reaches. Left panels: confidence ellipses (95% confidence limit, standard deviation) are fitted on the CCA plots to depict differences between river reaches. Right panels: distribution of the species scores of the most common taxa (the larger the circle the higher the propensity). Asterisks indicate taxa with abundances > 1% in the drift/stranding but not in the benthic samples (Appendix C in Data S1). Factor fitting shows the statistical differences in drift/stranding propensity between HP reaches (Sitter vs Hasliaare vs Linth), sampling day (day 1 vs day 2) and HP scenario (SC 1 vs SC2 vs SC3). Significance levels: *0.05, **0.01, ***0.001.

Figure 6. Benthic density (ind./m^2) across all three RF respectively all three HP reaches('ALL_RF', 'ALL_HP') and separated by reach. Numbers indicate the sample size, whereas letters show group affiliation according to Mann-Whitney tests.

Figure 7. NMDS ordination of the three RF and three HP reaches based on benthic densities (ind./m^2) of the most common taxa (relative abundance > 1%, Appendix C in Data S1). 95% confidence ellipses of the standard deviations of site scores of the three rivers (Sitter, Hasliaare, Linth) within the two respective reaches (RF: solid ellipses; HP: dashed ellipses) are depicted. Taxa that most contributed to dissimilarity (p < 0.05) are fitted on the NMDS plot and indicated with black dots and taxon name.

Figure 8. Benthic density (ind./m^2) across all three RF respectively all three HP reaches separated by the two traits 'interstitial/surface' and 'lentic/lotic'. Numbers indicate the sample size, whereas letters show group affiliation according to Mann-Whitney tests.

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