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1 Past hydraulics influence microhabitat 2 selection by invertebrates and fish in 3 hydropeaking rivers

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9

10 Abstract

11 Hydropeaking hydropower plants are the major source of renewable energy meeting sub-daily
12 peaks in electricity demand. They induce rapid artificial flow variations, highly variable
13 velocities, drift and stranding risks for aquatic organisms. In hydropeaking reaches,
14 microhabitat selection likely depends on both present and past hydraulics (flow velocity and
15 water depth); this study aims to assess their relative impact. For this purpose, we used
16 observations of fish abundance in 1,180 microhabitats (507 sampled by electrofishing, 673 by
17 snorkeling) and of invertebrate abundance in 36 microhabitats (hyporheic and benthic) in a
18 medium-sized hydropeaking river. We described past hydraulics of microhabitats over the 15
19 days preceding sampling, using a 2D hydrodynamic model, by identifying microhabitats
20 dewatering (drying during > 10h) or with high-velocity conditions (>1.3 m s⁻¹ during > 10h).
21 Invertebrates guilds (defined based on their selection of present hydraulics in rivers without
22 hydropeaking) responded significantly to past hydraulics, with abundances 3.5-15.3 times
23 lower in dewatering habitats. Selection for present hydraulics by invertebrates was different
24 from that observed in rivers without hydropeaking. For more mobile fish, responses were
25 weaker and different, with a "bank" guild selecting dewatering microhabitats and, secondarily,
26 a "midstream" guild avoiding them. Selection of present hydraulics by fish was similar to that
27 observed in rivers without hydropeaking. Overall, past hydraulics influenced microhabitat

28 selection, with stronger effects on invertebrates and stronger effects of dewatering than of
29 high past velocities. However, high past velocities force fish to move and invertebrates to
30 experience a large range of velocity.

31 **Keywords**

32 Habitat preferences, Flow variations, 2D hydrodynamic model, Behavior, Dewatering
33 responses, Hydropower

34 **Introduction**

35 Hydropeaking hydropower plants are the major source of renewable energy that meets
36 sub-daily peaks in electricity demand. By producing electricity on demand, they create frequent
37 rapid flow variations known as hydropeaking. Hydropeaking influences the habitats of aquatic
38 organisms, with strong spatial and temporal variations in point flow velocity, water depth and
39 shear stress (hydraulic conditions). In particular, near-shore areas may be subject to
40 dewatering during base flow (i.e., become temporarily dry when turbines are shut down),
41 which may result in stranding of individuals using shallow and slow-flowing habitats (Halleraker
42 et al., 2003; Saltveit et al., 2001). Midstream habitats may be subject to high flow velocity
43 during peak flow (when turbines are on), which may cause forced drift of individuals with low
44 swimming ability (Bruno et al., 2013).

45 Hydropeaking often results in a decrease in abundance, biomass and species diversity in
46 both fish and invertebrate communities (Kjaerstad et al., 2018; Schmutz et al., 2015; Vila-
47 Martínez et al., 2019). However, these negative effects are not systematic and may depend on
48 hydropeaking hydraulic characteristics. For example, Judes et al. (2021) showed, in rivers with
49 moderate hydraulic variations, that hydropeaking could have weaker effects than floods on fish
50 community dynamics and did not greatly modify the organization of fish communities along
51 longitudinal gradients. To improve our mechanistic understanding of hydropeaking influences
52 on biota, we need to better understand individual responses to changes in the spatial and
53 temporal variations of point hydraulic conditions (i.e. microhabitat scale). The microhabitat
54 scale (here corresponding to fixed patches of $\sim 7\text{m}^2$ for fish, 0.05 m^2 for benthic invertebrates

55 and 6 L of hyporheic water for hyporheic invertebrates following Stubbington et al., 2016) is
56 particularly suited for identifying the key hydraulic drivers of biological response to
57 hydropeaking. Several studies quantified key hydraulic conditions in microhabitats for fish and
58 invertebrates drifting and stranding processes (Auer et al., 2017; Halleraker et al., 2003; Saltveit
59 et al., 2001). For example, Halleraker et al., (2003) showed that stranding of juvenile brown
60 trout (*Salmo trutta*) occurs with dewatering vertical water level gradients higher than 0.10 cm
61 h⁻¹. By contrast, little is known concerning how microhabitat selection of fish and invertebrates
62 is influenced by variations in point hydraulic conditions.

63 In rivers without hydropeaking and associated sub-daily variations, microhabitat
64 selection by fish and invertebrates is usually predicted from present hydraulic conditions and
65 substrate size (Forcellini et al., in press.; Lamouroux et al., 1999; Plichard et al., 2020). In
66 hydropeaking rivers, past hydraulic variability during the weeks preceding sampling is expected
67 to influence microhabitat selection by aquatic organisms. Indeed, experiments on fish
68 individual behavior (Green, 1971; Roy & Bhat, 2018) indicated that fish can memorize
69 environmental conditions over durations up to two weeks. Individuals perceive temporal
70 variations in hydraulic conditions (Patton & Braithwaite, 2015) and may avoid habitats that are
71 frequently dewatered or have major variations in flow velocity. For example, using telemetry in
72 the Rhône River (France) to monitor 18 individual fish, Capra et al. (2017) suggested that fish
73 memorize spatial and temporal environmental variations during the two weeks preceding
74 sampling so as to use the “least constraining” microhabitats. Organisms may also have strong
75 habitat fidelity even after their habitats become unsuitable (Kemp et al., 2003). Several studies
76 showed that some fish species are reluctant to move across the river during sudden flow
77 increases and consequently use habitats with higher flow velocity and/or deeper habitats
78 (Kemp et al., 2003; Pert & Erman, 1994; Shirvell, 1994). This behavior may be explained by the
79 energy cost associated with displacement and/or a higher risk of predation. Less mobile taxa,
80 which include many invertebrates, may be unable to respond instantaneously to a rapid shift in
81 habitat conditions (Blinn et al., 1995). Some invertebrate taxa may also be removed from
82 hydropeaking reaches by passive or active drift during periods of low or high flow, altering the
83 taxonomic and functional composition of benthic assemblages in hydropeaking reaches (Bruno
84 et al., 2013). However, in adapting to naturally variable microhabitat conditions, some taxa
85 have developed morphological and behavioral adaptations to maximize colonization of

86 available habitat and can withstand extreme habitat conditions. For example, due to behavior
87 or/and morphological adaptation to high current velocity Simuliidae and Hydropsychidae are
88 less likely to passive drift due to hydropeaking and can be better able to use microhabitat
89 undergoing variable current velocity (Bruno et al. 2010, 2016; Mochizuki et al. 2006, Sidler et
90 al. 2018). Other invertebrate taxa may also colonize subsurface hyporheic habitats to escape
91 from variable benthic hydraulic conditions (Dole-Olivier et al., 1997; Vadher et al., 2017).

92 Studying the effects of past hydraulics on microhabitat selection by aquatic organisms
93 from field data is challenging. A first challenge is to describe past hydraulic conditions in
94 microhabitats. Spatially explicit hydrodynamic models, such as two-dimensional (2D) models
95 that map vertically averaged flow velocities at various discharge rates, are useful for this
96 purpose. However, calibrating and testing 2D models is time-consuming, expensive, and
97 requires an appropriate amount of quality field measurements. A second challenge is to sample
98 organisms at several discharge rates in order to have a sufficient number of microhabitat
99 samples with various combinations of past and present hydraulic conditions. Addressing this
100 challenge requires extensive fieldwork.

101 In this study, we combined extensive biological sampling in microhabitats at various
102 discharge rate with results of a calibrated 2D hydrodynamic model in a hydropeaking reach to
103 weight the relative effects of past and present hydraulic conditions on microhabitat selection.
104 Specifically, we recorded fish taxa abundance in 1,187 microhabitats and the abundance of
105 benthic and hyporheic invertebrate taxa in 36 microhabitats along a 6 km reach of a
106 hydropeaking reach of a medium-sized French river (the Ain River). Due to a limited statistical
107 power, we studied the responses of selected taxonomic guilds that had significant and
108 contrasting microhabitat selection in rivers without hydropeaking, according to the literature.
109 The 2D hydrodynamic model was used to estimate past hydraulics at each microhabitat during
110 the 15 days preceding sampling (Capra et al., 2017).

111 For fish, we expected that fish using shallow and slow-flowing habitats along the banks
112 would be forced to use dewatering habitats at high flows. We expected “midstream” fish taxa,
113 using fast-flowing and deep habitats, to be less forced to use risky dewatering areas at high
114 flows because they should sustain higher flow velocity variations.

115 For invertebrates, given their reduced mobility, we expected that past hydraulic
116 conditions would have a stronger influence on their microhabitat than for fish. They should be
117 disfavored by past dewatering and high flow velocity periods. Consequently, we also expected
118 invertebrate selection for present hydraulics to be different in hydropeaking rivers than those
119 without hydropeaking. Finally, we expected different responses in benthic and in hyporheic
120 invertebrates, with a weaker effect of dewatering and high flow velocities on hyporheic
121 invertebrates, the hyporheic area acting as shelter.

122 **Materials and methods**

123 **Study reach**

124 The Ain River in eastern France flows from the Jura mountains to the Rhône River, with a
125 catchment area of 3,630 km². The study reach is 6 km long and 110 m wide, with a mean
126 discharge of 103 m³ s⁻¹, an altitude of 230 m and a Strahler order of 5. It includes a diversity of
127 morphological units (runs, riffles and pools), secondary channels and tributaries. Substrate is
128 dominated by cobbles and the reach contains a few woody debris but little macrophyte cover.
129 The reach is located 20 km downstream from the Allement hydropower plant (46° 06' 44" N, 5°
130 25' 20" E), the last of a series of five hydropeaking hydropower plants along the river between
131 Vouglans and the Rhône confluence. According to data measured by DREAL Rhône-Alpes
132 (between 1960 and 2019) at Pont-d'Ain (7.5 km upstream of the study reach), mean daily
133 discharge is generally between 13.5 m³ s⁻¹ (exceeded 95% of the time) and 278 m³ s⁻¹ (exceeded
134 5% of the time). The study reach is subject to frequent sub-daily discharge variations, with base
135 flow generally between 14 m³ s⁻¹ and (occasionally) 150 m³ s⁻¹ and peak flow generally between
136 40 m³ s⁻¹ and 200 m³ s⁻¹ (Figure 1). Discharge is more stable during weekends and low-flow
137 periods (June-September).

138 **Reach hydraulics: the 2D model**

139 A 2D unsteady hydrodynamic model (mapping flow velocities averaged over the vertical; Rubar
140 2D; Bazin et al. 2017) was built, based on a digital elevation model obtained from topographic
141 and bathymetric LiDAR surveys carried out in 2015 and 2016. Model calibrations used water
142 surface levels derived from the LiDAR surveys at 16 m³ s⁻¹ and from field surveys at 90 m³ s⁻¹.

143 Calibrations were made so that the absolute difference between the water level simulated by
144 the model and that measured in the field was less than 10 cm at any measuring point. We used
145 the model to translate the hourly flow time-series given by the gauging station of Pont d'Ain,
146 seven kilometers upstream of the study site (from <http://hydro.eaufrance.fr>), into maps of
147 hourly hydraulic time-series (flow velocity, water level and water depth) over the 403,591
148 nodes of the 2 m-edge rectangular mesh of the model.

149 **Sampling**

150 **Fish sampling**

151 Fish species abundance was estimated by electrofishing in 507 microhabitats and by snorkeling
152 in 673 microhabitats. With both protocols, the sampled surface area of microhabitats was
153 approximately 7 m², fish being attracted (electrofishing) or observable (snorkeling) within a
154 radius of about 1.5 m (although this distance can depend on fish size; Regis et al., 1981)

155 Electrofishing was conducted by a team of three or four operators from a motorboat in
156 deep areas and by wading in shallow areas, approaching the microhabitat as discreetly as
157 possible to minimize fish escape. An anode was immersed and held steady, and all fish around
158 the anode were captured with a landing net, identified, measured and released. Microhabitat
159 positions were recorded by GPS with a precision of 5 m. Electrofishing surveys covered
160 different flow conditions (Figure 2) and microhabitat locations were chosen to cover diverse
161 combinations of past and present hydraulic conditions. In practice, the 2D model was used to
162 draw maps of simulated past hydraulic conditions corresponding to a typical hydropeaking
163 week, to help finding these different combinations of past and present hydraulics in the field.
164 Sampling at different flows also reduced the correlation between present and past hydraulic
165 conditions (e.g., the expected negative correlation between dewatering frequency and water
166 depth).

167 Snorkeling observations targeted only large individuals of species that are difficult to
168 sample by electrofishing (estimated length > 25 cm) (Plichard et al., 2017). Observations were
169 made along six longitudinal transects, regularly spaced laterally across the reach, in the
170 direction of flow over the entire study reach, during base flow only to ensure fish identification
171 (~16 m³ s⁻¹). Two persons drifted along the transect in a downstream direction: (1) an

172 experienced snorkeler detecting and identifying fish, followed by (2) an hydrospeeder
173 recording the observations and GPS positions with a waterproof recorder. As reported by
174 others (Chamberland et al., 2014), we did not frequently observed strong escape behavior
175 while snorkeling and judged that most fish were observed by snorkelers. Underwater visibility,
176 estimated as the distance at which snorkelers could see their bright swimming fins, was 5 m.
177 Fish were observed and identified when in a 1.5 m radius around the snorkeler, and several fish
178 individuals were associated to the same GPS position when observed simultaneously.
179 Therefore, each GPS position in the dataset was considered as a microhabitat of $\sim 7\text{m}^2$,
180 containing one or several fish. When drifting, snorkelers observed large fish (estimated length $>$
181 25 cm) of eight species (*Barbus barbus*, *Squalius cephalus*, *Chondrostoma nasus*, *Thymallus*
182 *thymallus*, *Perca fluviatilis*, *Esox lucius*, *Cyprinus carpio*, *Salmo trutta fario*) and smaller
183 individuals of *Thymallus thymallus* only (estimated length $<$ 25 cm).

184 All snorkeling microhabitats were presence-only (microhabitats with fish presence),
185 unlike the electrofishing and invertebrate microhabitats. To enable common statistical
186 processing of all data, we created fictive snorkeling microhabitats with fish absence (“pseudo-
187 absence microhabitats”; Manly et al. 2002). In practice, for each taxon \times microhabitat
188 combination, we randomly picked $n = 10$ pseudo-absence microhabitats among the nodes of
189 the 2D model network. At this step, we considered only nodes with water depth > 30 cm, as
190 snorkeling was not conducted in shallower habitats. The choice of $n = 10$ pseudo-absence
191 microhabitats was intended to provide a global prevalence comparable with that of the
192 electrofishing data. We tested the sensitivity of results to this choice by repeating the analysis
193 for $n=20$.

194 **Invertebrate sampling**

195 We sampled benthic and hyporheic invertebrates in 36 microhabitats, under different flow
196 conditions (Figure 2). Similarly to the procedure used for fish, we used the 2D model to draw
197 maps of simulated past hydraulic conditions corresponding to a typical hydropeaking week, to
198 help finding different combinations of past and present hydraulics in the field. We chose
199 microhabitats in six cross-sections with low and six with high velocity, distributed along the
200 reach to have different present and past flow velocity. Within each cross-section, we selected

201 three points with low ($0 \leq \text{depth} < 0.2$ m), medium ($0.2 \leq \text{depth} < 0.5$ m) and high water depth
202 ($0.5 \leq \text{depth} < 0.8$ m) (and thus different dewatering frequencies).

203 We sampled benthic invertebrates with a Hess sampler (surface area 0.05 m^2 , $250 \mu\text{m}$
204 mesh size) and recorded their positions by GPS. Then, within a radius of one meter around the
205 Hess sampler, hyporheic invertebrates were sampled with a Bou-Rouch pump (Bou & Rouch,
206 1967; Dole-Olivier et al., 2014), which extracted 6L of water from 30 cm below the stream bed
207 (using a planted steel pipe) to catch organisms living in the interstices of substrate particles.
208 Benthic samples were filtered through a sieve with $250 \mu\text{m}$ mesh size to be consistent with the
209 benthic sampling. Invertebrates were preserved in 96% ethanol and were sorted, counted and
210 identified to the lowest practical taxonomic level using a microscope in the laboratory (list of
211 references used for invertebrate identification in Supporting Information, list S1).

212 **Classification in species guilds**

213 We grouped fish and invertebrate individuals into a few habitat guilds with comparable habitat
214 selection according to Plichard et al. (2020) and Forcellini et al. (in press), who synthesized a
215 large part of the available information on fish and invertebrate microhabitat selection in a wide
216 range of mostly non-hydropeaking European rivers. This grouping by guilds was used to
217 increase the statistical power of our analyses and the potential transferability of our results in
218 rivers with other species composition.

219 Fish at electrofishing points were first grouped by size class, using the taxa definitions of
220 Plichard et al. (2020). These taxa combined a specific code and one or several size classes (1: < 8
221 cm; 2: 8–18 cm, 3: 18–30 cm; 4: > 30 cm; Table 1). For example, taxon Lel_cl123 corresponds to
222 *Leuciscus Leuciscus* (Lel) fish with sizes < 30 cm. We defined two fish guilds for which we
223 expected different influence of past hydraulics on microhabitat selection. The ‘bank’ guild
224 grouped together taxa selecting shallow and slow-flowing habitats, thus incurring high
225 dewatering risk. Conversely, the ‘midstream’ guild grouped together species selecting deep and
226 fast-flowing habitats, typically found in the center channel, which should better sustain high
227 flow velocity variations. Observed graylings (*Thymallus thymallus*) were also assigned to the
228 midstream guild (Mallet et al. 2000). Plichard et al. (2020) summarized the microhabitat
229 selection by fish taxa for microhabitat velocity V using the statistic AGV_V, which in short

230 corresponds to the average microhabitat velocity that would be used by the taxa if velocities
231 between 0 and 0.94 m s⁻¹ were uniformly available in the river. Similarly, AVG_D summarizes
232 selection for depth D over the depth range 0-3 m. Our midstream guild comprised the nine taxa
233 with the highest value for the product AVG_V*AVG_D, and our bank guild the eight taxa with
234 the lowest value. The number of taxa per guild was a compromise between guild abundance
235 and magnitude of habitat selection.

236 For invertebrates, we defined two guilds according to selection for bottom shear stress
237 reported in Forcellini et al. (in press), where shear stress was measured using hemispheres
238 (FST, Statzner & Müller, 1989) numbered from 0 to 19 (low to high shear stress). As done by
239 Plichard et al. (2020) for fish, Forcellini et al. (in press) summarized microhabitat selection by
240 invertebrates, using AVG_V and AVG_FST, which is the equivalent of AVG_V but over the FST
241 range 0-19. The AVG_FST given by Forcellini et al. (in press) were calculated by species or
242 higher levels, without accounting for variations in habitat use with individual size. Therefore,
243 we used the same guild definitions for both benthic and hyporheic taxa, although individuals in
244 hyporheic samples were generally smaller. The 'limnophilic' guild grouped together taxa
245 selecting low shear stress (AVG_FST < 5), and thus expected to be negatively affected by high
246 flow velocity variations. Conversely, the 'rheophilic' guild corresponded to taxa selecting high
247 shear stress (AVG_FST > 8).

248 **Present and past microhabitat hydraulics**

249 In each electrofishing and invertebrates sampling microhabitat (i.e. a couple
250 benthic/hyporheic), we measured the present water depth (D in m), and present flow velocity
251 (V_{40} in m s⁻¹; measured at 40% of water depth from the bottom with an electromagnetic 30 Hz
252 current meter and averaged over 10 seconds, using a Marsh McBirney FLO MATE 2000).

253 We described past hydraulic conditions using the 2D hydraulic model simulations for
254 flows observed during the 15 days preceding sampling. The duration of 15 days was consistent
255 with previous experiments on fish individual learning (Green, 1971; Roy & Bhat, 2018) and
256 previous field studies on fish in hydropeaking reaches (Capra et al., 2017). This 15 days duration
257 also allowed to account for typical discharge variations observed in the Ain River (Figure 2).

258 Nevertheless, we tested the sensitivity of results to our choice of a duration of 15 days, by
259 repeating our analyses for durations of 5 and 10 days before sampling.

260 For estimating past hydraulics at a given microhabitat (electrofishing point or
261 invertebrate sample), we associated the sampled microhabitat to a node of the 2D model that
262 (1) had comparable water depth, and (2) was as close as possible from the sampled
263 microhabitat. We judged the primary use of a “depth similarity criteria” as essential for an
264 optimum estimation of the dewatering frequency of the microhabitat. Indeed, for a given
265 measurement discharge, water depth and past dewatering frequency are expected to be
266 strongly correlated. In addition, even if the morphology of the river had changed locally
267 between the 2D model calibration and the biological survey, we expected that velocity
268 variations for a given water depth was well represented by the 2D model. In the Ain River,
269 mesohabitats (e.g., riffles, run, pools) have surface areas of several hundred m², and the 2D
270 model is expected to well reflect hydraulic behavior of these mesohabitats, event it can be
271 locally imprecise (Guay et al., 2000). In practice, we selected the closest 2D node that had a
272 modeled depth differing from the measured depth at the microhabitat by less than 10 cm. For
273 snorkeling observations, depth measurement was not available and we assigned snorkeling
274 microhabitats to the closest 2D node.

275 The past hydraulic conditions during the 15 days preceding sampling were described
276 with two variables coded as boolean categories:

277 (1) Duration of dewatering: we considered the microhabitat as “dewatering” if the dewatering
278 time (depth = 0 cm) over the 15-days period before sampling was >10 hours, and as “non-
279 dewatering” if ≤10 hours. We tested the sensitivity of results to our choice of a duration of 10
280 hours, by repeating our analyses for a duration of 1 hour.

281 (2) Duration of high flow velocity conditions (>1.3 m s⁻¹): We considered that microhabitats had
282 “high past velocities” if the total duration with velocity >1.3 m s⁻¹ was >10 hours, and “low past-
283 velocities” if ≤10 hours. We chose a threshold of 1.3 m.s⁻¹ because this value is above the velocity
284 used by most aquatic organisms (Plichard et al., 2020; Forcellini et al., in press), and is also
285 frequently reached in many microhabitats of the Ain River. Here again, we tested the sensitivity

286 of results to our choice of a threshold of 1.3 m.s⁻¹, by repeating our analyses for a threshold of
287 0.7 m.s⁻¹.

288 **Microhabitat selection models by guild**

289 For the two fish (electrofishing, snorkeling) datasets and the benthic invertebrates dataset, we
290 related guild abundance to past and present microhabitat characteristics (measured when
291 available, modeled otherwise). We derived similar microhabitat selection models based on the
292 hyporheic dataset, for testing if the influence of past hydraulics observed on benthic
293 invertebrates was still observed in hyporheic samples, or if the hyporheic area played a
294 particular role for these guilds. For each dataset, following Plichard et al. (2020) and Forcellini
295 et al. (in press), we used GLMs with B-spline transformations of the present hydraulic variable
296 (enabling non-linear responses) and assuming a negative binomial distribution of abundance
297 (accounting for abundance overdispersion). We used splines with two degrees of freedom, with
298 a single knot positioned at the median value (Plichard et al., 2020). To avoid
299 overparameterization and due to limited statistical power, we had to consider models involving
300 combinations of a single present hydraulic variable (*PresHyd* = V_{40} or D) and a single past
301 hydraulic variable (*PastHyd*= Dew or HV). Consistently, we looked at the inter-correlations
302 between present and past hydraulic variables to interpret the results.

303 For each *PresHyd* × *PastHyd* combination, the abundance Y_i of a guild in microhabitat i was
304 assumed to follow a negative binomial distribution of mean μ_i and dispersion parameter Θ :

$$305 Y_i \sim NB(\mu_i, \Theta)$$

306 Three GLMs of increasing complexity were compared to explain μ_i as a function of hydraulics:

$$307 \mathbf{M0 (no microhabitat selection):} \log(\mu_i) = \beta_0$$

$$308 \mathbf{M1 (habitat selection with present hydraulic conditions only):} \log(\mu_i) = \beta_0 + f(\text{PresHyd}_i)$$

$$309 \mathbf{M2 (habitat selection with present and past hydraulic conditions):} \log(\mu_i) = \beta_0 + f(\text{PresHyd}_i) + \beta_1$$

310 *PastHyd* _{i}

311 where β_0 is the intercept, $f()$ is a spline transformation of the present hydraulic variable
312 *PresHyd* _{i} , and β_1 the coefficient of the past hydraulics effect. In M0, microhabitat variables have

313 no influence on abundance, in M1 present hydraulic conditions have an influence, and in M2
314 there is an additive effect of past hydraulics.

315 We fitted all models using the R software (R Development Core Team 2018) and the
316 `glm.nb` function of the 'MASS' package (Venables & Ripley, 2002), combined with spline
317 functions of the 'splines' package. We used likelihood ratio tests comparing M0 vs. M1 to test
318 the influence of present hydraulics on microhabitat selection, and tests comparing M1 vs. M2
319 to assess for an additive effect of past hydraulics. Following Plichard et al. (2020), we used non-
320 parametric Spearman Rho rank correlation (Spearman, 1904) to assess fits; this is an
321 appropriate statistic for overdispersed data such as our abundance data, based on the
322 correlation between the ranks of predicted and observed abundance.

323 **Influence of hydropeaking on taxa selection for present hydraulics**

324 For the fish electrofishing dataset and benthic invertebrates, we computed an average
325 preferred velocity `AGV_V` and depth `AVG_D` as defined by Plichard et al. (2020), but
326 corresponding to the fits of our M1 model by taxa. We then compared our values with those of
327 Plichard (2020) for fish and Forcellini et al. (in press) for invertebrates, to estimate how
328 hydropeaking modifies the selection of present microhabitat hydraulics generally observed in
329 rivers without hydropeaking. We used only electrofishing data for the fish comparison, because
330 fish size was not available in snorkeling data, preventing comparison with the size classes of
331 Plichard et al. (2020). We used only the benthic invertebrate data, to be consistent with
332 Forcellini et al. (in press).

333 **Results**

334 **Biological assemblages**

335 We sampled 3,642 fish of 23 species by electrofishing. The bank guild contained 2,344
336 individuals and was composed mainly of *Phoxinus phoxinus* cl12 ($N=1,785$). The midstream
337 guild contained 73 individuals, mainly *Barbus barbus* cl34 ($N=27$) (Table 1). We sampled 1,610
338 fish of 12 species by snorkeling (mainly *Thymallus thymallus*, $N=444$; *Barbus barbus*, $N=437$ and
339 *Chondrostoma nasus*, $N=238$). In the snorkeling dataset, large *Barbus barbus*, large

340 *Chondrostoma nasus* and all *Thymallus thymallus* belonged to the midstream guild, with many
341 more individuals sampled than with electrofishing (N =356) (Table 1).

342 We sampled 48,275 invertebrates: 38,196 in benthic samples and 10,079 in hyporheic
343 samples. The full list of taxa of both datasets are available as Supporting Information (Table S1).
344 For the benthic dataset, the limnophilic guild contained 687 individuals (principally composed
345 of *Chironomini*, N=612) and the rheophilic guild contained 2988 individuals (principally
346 composed of *Esolus*, N=2,021) (Table 2). For the hyporheic dataset, the limnophilic guild
347 contained 170 individuals (principally composed of *Chironomini*, N=140) and the rheophilic
348 guild contained 961 individuals (principally composed of *Esolus*, N=754) (Table S2). Note that
349 only 10% of all benthic individuals and 11% of all hyporheic individuals belong to a habitat guild
350 (i.e. documented and significant habitat selection).

351 Present and past hydraulic variables and their intercorrelation (Figure 3)

352 Present depth and velocity typically ranged between 0-4 m and 0-2 m s⁻¹ in the fish
353 datasets (Figure 3A). By contrast, depth was generally shallower than 0.8 m and velocity lower
354 than 1 m s⁻¹ in the invertebrate dataset, due to sampling limits. Water depth and flow velocity
355 were poorly correlated (and with different directions) for the fish data (electrofishing: r=0.13,
356 P<0.05; snorkeling: r=-0.48, P<0.05) (Figure 3A). The correlation was greater in the invertebrate
357 dataset (r=0.57; P<0.05).

358 When calculating past hydraulics using the 2D hydrodynamic model, 76% of the
359 electrofishing microhabitats and 75% of the invertebrate microhabitats were associated with a
360 model node within a radius of 5.5 m around the sampled microhabitat. In the electrofishing
361 dataset, 102/507 microhabitats were dewatering habitats and 255/507 had high past velocities
362 (Figure 3B). The snorkeling dataset contained no dewatering microhabitats and 342/673
363 microhabitats with high past velocities. A little less than half of the invertebrate samples
364 (32/72) were dewatering and a higher proportion (44/72) had past low velocities. For fish
365 (electrofishing) and invertebrates, all combinations of dewatering × high past velocity habitats
366 were sampled (Figure 3B). Nevertheless, dewatering habitats were generally those with low
367 past velocity for both fish and invertebrates (Xhi2 test, P<0.05).

368 Correlations between present and past hydraulics were limited ($r^2 < 0.30$ in all cases).
369 The strongest correlation was between flow velocity and high past velocities (Figure 3C),
370 especially for the electrofishing and the invertebrate datasets. Dewatering habitats also often
371 had lower flow velocities and depths (Figure 3D).

372 **Microhabitat selection models by guilds**

373 As expected from the fish guild definitions, the midstream guild used higher present velocities
374 and depths than the bank guild, according to both electrofishing and snorkeling data. The bank
375 guild significantly avoided fast-flowing and deep microhabitats (Table 3, Figure 4). Differences
376 in response to flow velocity between guilds, however, were less clear for benthic invertebrates
377 than for fish (Table 3, Figure 4A). The rheophilic benthic invertebrate guild significantly avoided
378 shallow microhabitats (Table 3, Figure 4A). Similar patterns were observed for hyporheic
379 invertebrates (Table S3, Figure S1).

380 Several significant additive effects of past hydraulics were observed (indicated by
381 asterisks in Figure 4). Benthic and hyporheic invertebrates responded more significantly to past
382 hydraulics, all invertebrate guilds being 3.5-15.3 times less abundant in dewatering habitats
383 (Figure 4A, Figure S1). Consistently, Spearman Rho values for benthic invertebrate M2 models
384 involving dewatering (between 0.27 and 0.61, Table 3) were much higher than the
385 corresponding values for M1 models (between 0.04 and 0.35, Table 3). Again, similar patterns
386 were observed for hyporheic invertebrates (Table S3). Secondarily, benthic rheophilic
387 invertebrates selected microhabitats with high past velocities (3.9 times more abundant in high
388 past velocity microhabitats in average) and hyporheic limnophilic invertebrates tend to avoid
389 them (0.4 times less abundant, only significant with the model including water depth as
390 present hydraulic variable) (Figure 4A, Figure S1). The influence of high past velocities was not
391 significant for hyporheic rheophilic invertebrates and benthic limnophilic invertebrates. For fish
392 (electrofishing), responses were weaker and clearly different, with the bank guild selecting
393 dewatering microhabitats (Figure 4A) and, less evidently, the midstream guild avoiding
394 dewatering microhabitats. Midstream fish of the snorkeling dataset selected microhabitats
395 with high past velocities.

396 The sensitivity tests concerning the choice of a 15 days duration for calculating past
397 hydraulics and a 10 hours duration for defining dewatering microhabitats did not modify any of
398 our results (significance tests in Table 3 and Figure 4).

399 By contrast, a threshold of 0.7 m.s⁻¹ instead of 1.3 m.s⁻¹ for defining microhabitats with
400 high past velocities and, a number of 20 instead of 10 pseudo-absence when building model on
401 the snorkeling dataset modified some of our (secondary) results on the effects of high past
402 velocities. With a lower 0.7 m.s⁻¹ threshold, the bank fish guild and hyporheic rheophilic
403 invertebrates significantly selected high past velocities (M2 models) and the midstream fish
404 (electrofishing) guild avoided them (M2 model with velocity). In addition, the selection of high
405 past velocities by midstream fish (snorkeling) was no longer significant. The selection of high
406 past velocities by midstream fish (snorkeling) was also no longer significant with a number of
407 20 instead of 10 pseudo-absence when building models.

408 **Influence of hydropeaking on taxa selection for present hydraulics**

409 Microhabitat selection for present hydraulics could be compared between the present study
410 and the literature for nine fish taxa and thirteen benthic invertebrate taxa. Present velocity and
411 water depth selection by fish taxa corresponded to those reported in the literature (Figure 5A)
412 and had comparable Spearman Rho values (Figure 5B). By contrast, present velocity and water
413 depth selection by benthic invertebrate taxa did not match values reported in the literature
414 (Figure 5C) and had lower Spearman Rho values here (Figure 5D).

415 **Discussion**

416 By studying the combined influence of present and past hydraulics on microhabitat selection,
417 we improved our mechanistic understanding of the impact of hydropeaking on fish and
418 invertebrate guilds. We found that both benthic limnophilic and rheophilic invertebrates were
419 less abundant in dewatering microhabitats. This confirms findings such as those of Blinn et al.
420 (1995), who reported a four-fold lower invertebrate biomass in dewatering habitats of the
421 Colorado River. Consistently with this result, we also showed that the average velocity and
422 water depth preferences of some invertebrate taxa differed from those previously established
423 in mainly non-hydropeaking rivers (Figure 5). This suggests that invertebrates are not able to

424 maintain habitat preferences when flow changes too rapidly or frequently: they likely stay at
425 the same location, undergoing different hydraulic conditions according to flow conditions.

426 Similarly, to benthic invertebrates, we found that hyporheic invertebrates are also less
427 abundant in dewatering microhabitat. Yet, we expected the opposite since we suggested that
428 hyporheic area provide shelter under dewatering conditions in the Ain River (Williams & Hynes,
429 1974). Others studies find some comparable results suggested that benthic macroinvertebrates
430 may not always use the hyporheic area as shelter in response to a discharge reduction (del
431 Rosario and Resh 2000; James et al. 2008). In our case, since some microhabitats could have
432 been dewatered for several days before sampling, we cannot exclude that in some case the
433 hyporheic area undergone dewatering or low oxygen levels resulting in death of some
434 individuals. Furthermore, invertebrates may have migrate rapidly through the benthic area just
435 after flow increases and before sampling (Bruno et al., 2020). Sampling during the dry period
436 could allow to test if the hyporheic area plays the role of shelter.

437 In contrast to invertebrates, fish followed their preferred habitat preferences observed
438 in other rivers and were less influenced by past hydraulics. Nevertheless, fish from the “bank”
439 guild probably stayed along the bank and moved to dewatering microhabitats when flow
440 increased, in order to remain within their strict range of preferred hydraulic conditions. This
441 result contrasts with many studies concerning salmonid juveniles, also living near the banks,
442 and indicating that only a fraction of individuals relocate when flow changes (Kemp et al., 2003;
443 Korman & Campana, 2009; Shirvell, 1994). High velocities in the Ain River and the different
444 species considered here (mostly cyprinids) may explain these differences. In the Ain River, fish
445 from the bank guild are probably exposed to a high risk of stranding, particularly because
446 cobble bars have very low slopes (Tuhtan et al., 2012). It would be interesting to quantify the
447 influence of horizontal down-ramping rate (water surface retreat rate) on fish stranding near
448 these cobble bars. The fish “midstream” guild also followed their preferred range of habitat,
449 and tended to avoid dewatering and stressful microhabitats (Capra et al., 2017; Reeb, 1996).
450 Although it concerned other species (large barbel, catfish and chub), the telemetry experiment
451 by Capra et al. (2017) also reported that fish could avoid dewatering microhabitats. However,
452 due to the small number (N=73) of fish involved in this present result, it is not possible to
453 generalize.

454 Observed microhabitat selection by fish and invertebrates was not negatively affected
455 by high past velocities, suggesting a weaker influence of high past velocities compared to
456 dewatering. In addition, the statistical significance of the weak responses to high past
457 velocities depended on the threshold chosen for defining high past velocities, indicating
458 unstable results. However, considering that hydropeaking has occurred since the 1930s in the
459 Ain River, environmental filtering may have selected only species that can cope with rapid and
460 frequent variations in hydraulic conditions. Furthermore, our results suggest that high
461 velocities force fish to move (sticking to their general hydraulic preference) and invertebrates
462 to find flow-shelter or attach to the substrate (e.g. with silk draglines, tarsal claws, or a
463 muscular foot; Holomuzki et al. 2000). Moving (fish) or staying in sub-optimal habitat
464 conditions (invertebrates) may create energetic costs that influence community structure on
465 the long term and explain reach-scale effects of hydropeaking (Judes et al., 2021). More
466 detailed observations of behavior at high flows (e.g. by snorkeling or with cameras),
467 experimental/physiologic experiments in flumes, or additional comparisons between reaches
468 subjected to different degrees of hydropeaking (Schmutz et al., 2015; Judes et al., 2021) will be
469 useful to confirm this interpretation.

470 We identify five major limits and ways of improvement in our study. First, we pooled
471 microhabitat samples under low and high flow conditions due to a limited statistical power.
472 However, habitat availability strongly changes according to flow conditions. For example, in the
473 Ain, 77% of the wetted surface is less than 1 m deep at $14 \text{ m}^3 \text{ s}^{-1}$ versus 33% at $214 \text{ m}^3 \text{ s}^{-1}$. Such
474 differences in habitat availability could influence species microhabitat selection (Arthur et al.,
475 1996; Schooley, 1994). Further sampling could target a more detailed analysis of the effects of
476 habitat availability. Similarly, improved analyses should also consider the effects of woody
477 debris, macrophyte cover, tributary proximity and/or thermal refugia. Secondly, here, guilds
478 are composed only of taxa with significant habitat selection documented in the literature. In
479 the future, it would be interesting to be more representative of the community in place. In
480 particular, it would be interesting to study ubiquitous taxa, to account for size distributions
481 within taxa, or to analyze responses of functional traits. Thirdly, discharge before and during
482 our sampling period combined hydropeaks and artificial releases of intermediate flows (around
483 $100 \text{ m}^3 \text{ s}^{-1}$, Figure 2) to compensate for low discharge in the Rhône River. The duration of
484 intermediate flow may influence observed fish and invertebrates microhabitat selection. Future

485 sampling will need to be implemented during different hydropeaking regimes, especially for
486 invertebrates sampling, which was conducted at only three flow conditions here. Fourthly,
487 because our results were little sensitive to a number of our methodological choices (duration
488 considered for past hydraulics, threshold used for defining dewatering habitats and high past
489 velocities), additional experiments/data would be useful to specify the key quantitative drivers
490 of biological responses. Finally, although the 2D hydrodynamic model allowed us to estimate
491 past hydraulics at each microhabitat, its accuracy and the methods used for associating field
492 observations with model nodes would deserve further investigation (see Guay et al., 2000).

493 In conclusion, our microhabitat-scale study shows a stronger effect of dewatering than
494 high past velocities on invertebrates, and secondarily on fish. Although this study failed to
495 identify critical past velocity thresholds for hydropeaking management, the results suggests
496 that fish are forced to move and invertebrate to hide due to these high past velocities.
497 Comparing our results with data collected in other rivers and at a larger variety of flows,
498 combined with experimental studies, should help further identifying the key hydropeaking
499 characteristics to consider in mitigation policies.

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631

632 Figure legends

633 Figure 1. Location of the Ain River study reach and maps of its flow velocity and water depth for the
634 maximum and the minimum flow discharge encountered over the study period.

635 Figure 2. Hourly discharge at Pont d'Ain (7.5 km upstream the study reach) during the 15 days preceding
636 sampling and during sampling (2018). The vertical lines represent indicate sampling days at noon.

637 Figure 3. Relationship (A) among present hydraulic variables, (B) among past hydraulic variables and
638 (C,D) between present and past hydraulic variables for invertebrates (\Rightarrow), one value for a
639 benthic/hyporheic pair), fish sampled by electrofishing (\bullet), and fish sampled by snorkeling (\circ). Points
640 represent microhabitats.

641 Figure 4. Fits of M2 models relating guild abundance to present hydraulics and including an additive
642 effect of dewatering (A) or past velocity (B). Red and green curves reflect the effect of past hydraulic
643 variables, when significant. Graphs are shown for the electrofishing (\bullet) snorkeling (\circ) and benthic
644 invertebrate (\Rightarrow) datasets. Stars show the significance of the past hydraulics effect (**) $P < 0.01$; (*)
645 $P < 0.05$.

646 Figure 5. Comparison of the average preferred velocity (AVG_V, corresponding to model M3) obtained
647 in this study with data from Plichard et al. (2020) for fish and from Forcellini et al. (in press) for benthic
648 invertebrates. Axis regressions (full lines) are shown as well as the $y = x$ lines (dotted lines). For Plichard
649 et al. (2020), AVG_V: $y = -0.76x - 0.09$, $R^2 = 0.76$, $P < 0.01$; Spearman Rho: $-0.48x + 0.33$, $R^2 = 0.13$, $P = 0.34$.
650 AVG_D: $y = 0.54x + 0.08$, $R^2 = 0.21$, $P = 0.22$; Spearman Rho: $-0.13x + 0.26$, $R^2 = 0.03$, $P = 0.66$. For Forcellini et
651 al. (in press), AVG_V: $y = 0.02x + 0.68$, $R^2 = 0.01$, $p\text{-value} = 0.92$; Spearman Rho: $0.56x + 0.091$, $R^2 = 0.03$,
652 $P = 0.63$, AVG_D: $y = -0.09x + 0.52$, $R^2 = 0.01$, $P = 0.84$; Spearman Rho: $0.05x + 0.20$, $R^2 = 0.00$, $P = 0.79$. GPUL:

653 *Gammarus pulex*; HYDROP: *Hydropsyche contubernalis*; TANYT: *Tanytarsini* (tribe); LIMN: *Limnomysis*
654 *benedeni*; OVIL: *Orectochilus villosus*; VCRI: *Valvata cristata*; PISI: *Pisidium* (genus); TIPUL: *Tipula*
655 (genus). See table 1 and 2 for other taxa names.

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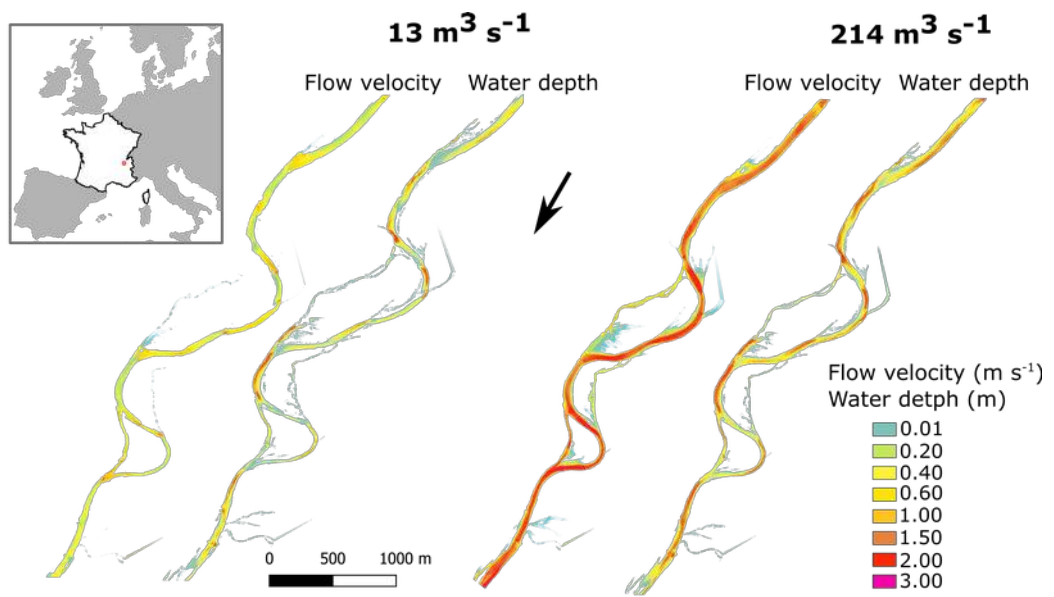


Figure 1.

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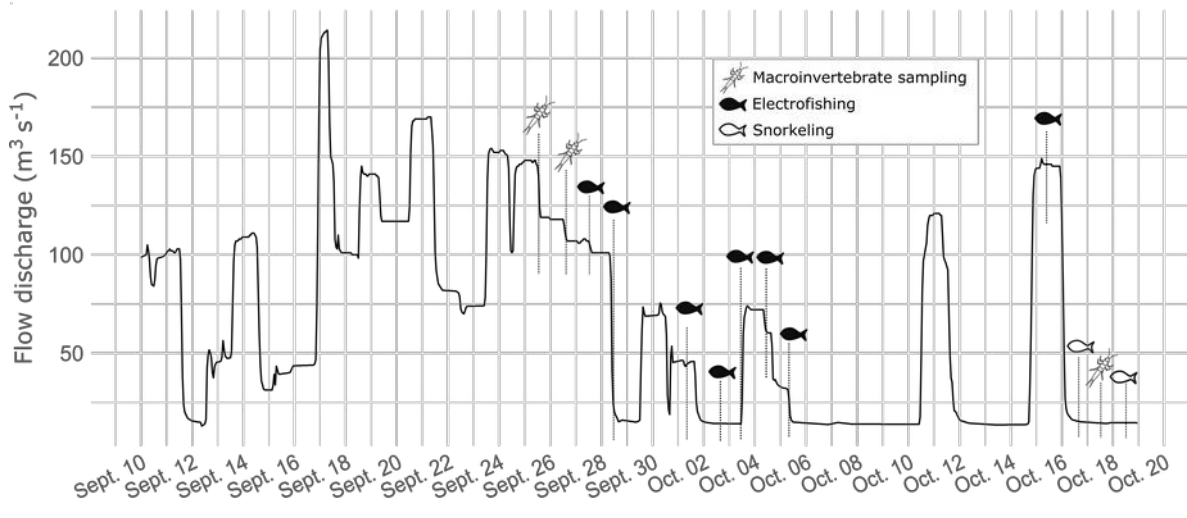
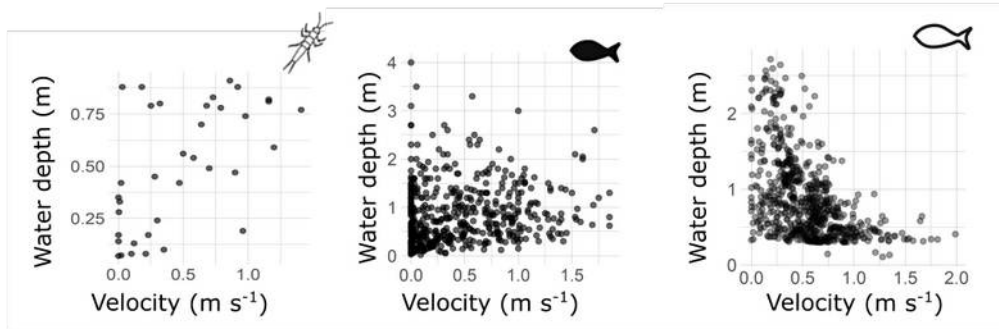
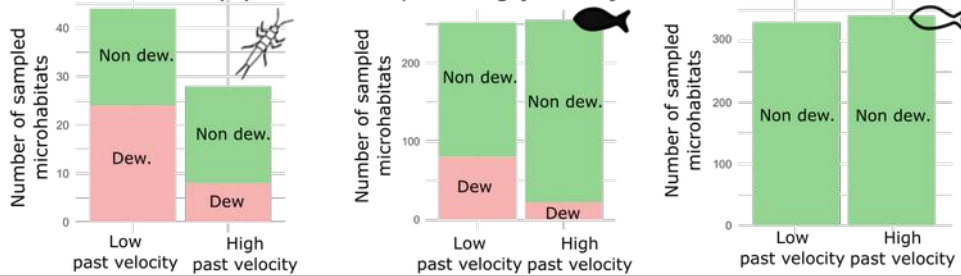


Figure 2.

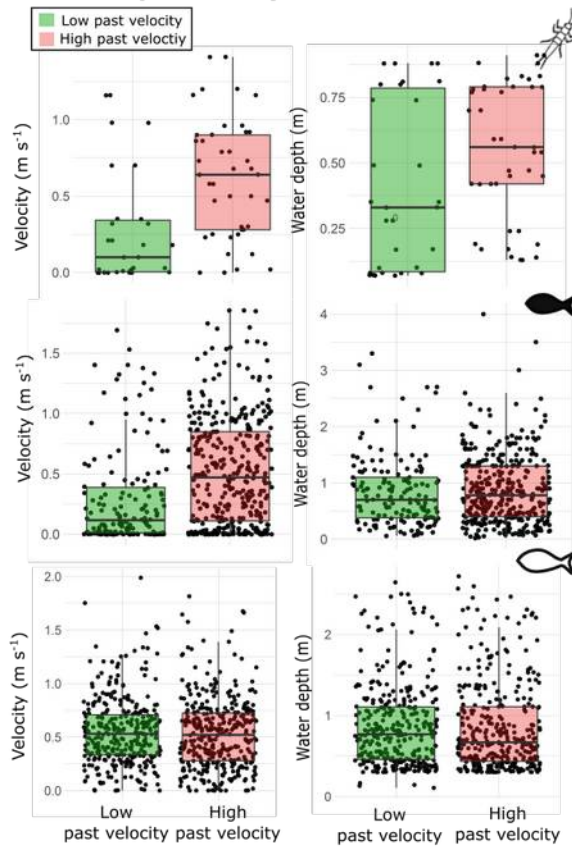
(A) Relationship among **present hydraulic variables**



(B) Relationship among **past hydraulic variables**



(C) Relationship **between past velocity and present hydraulic variables**



(D) Relationship **between past dewatering and present hydraulic variables**

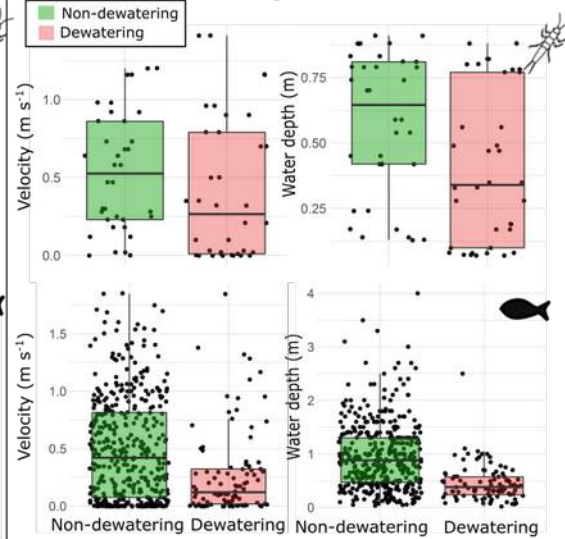
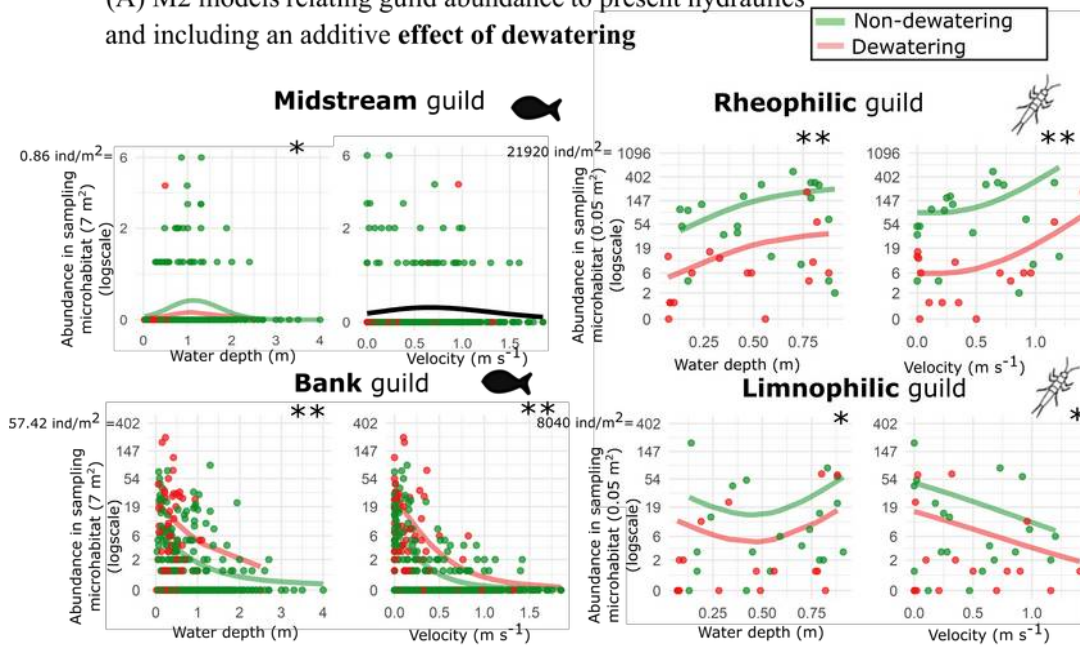


Figure 3.

(A) M2 models relating guild abundance to present hydraulics and including an additive effect of dewatering



(B) M2 models relating guild abundance to present hydraulics and including an additive effect of past velocity

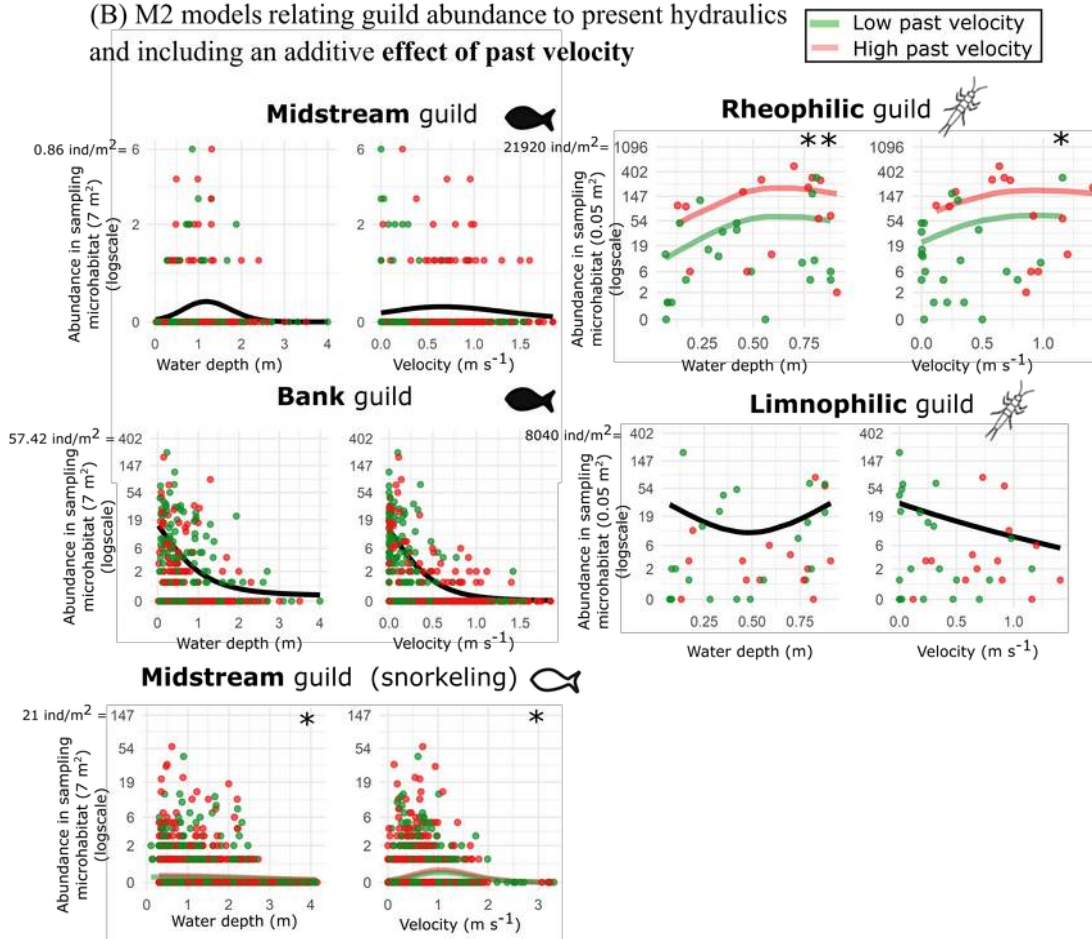
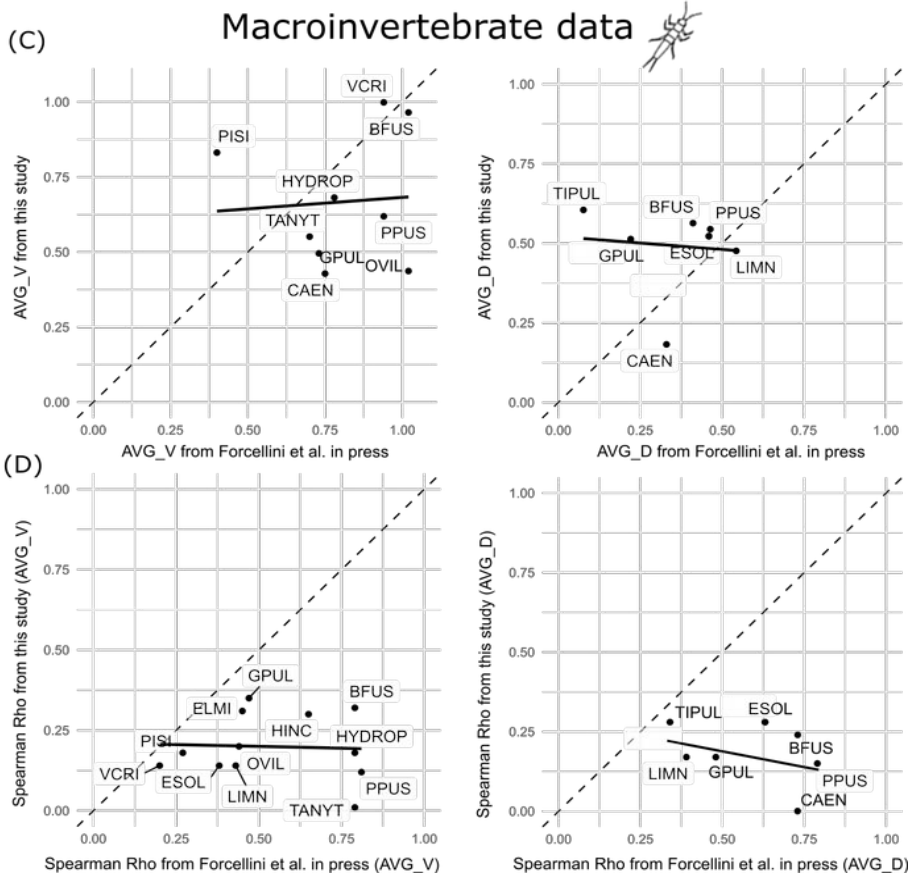
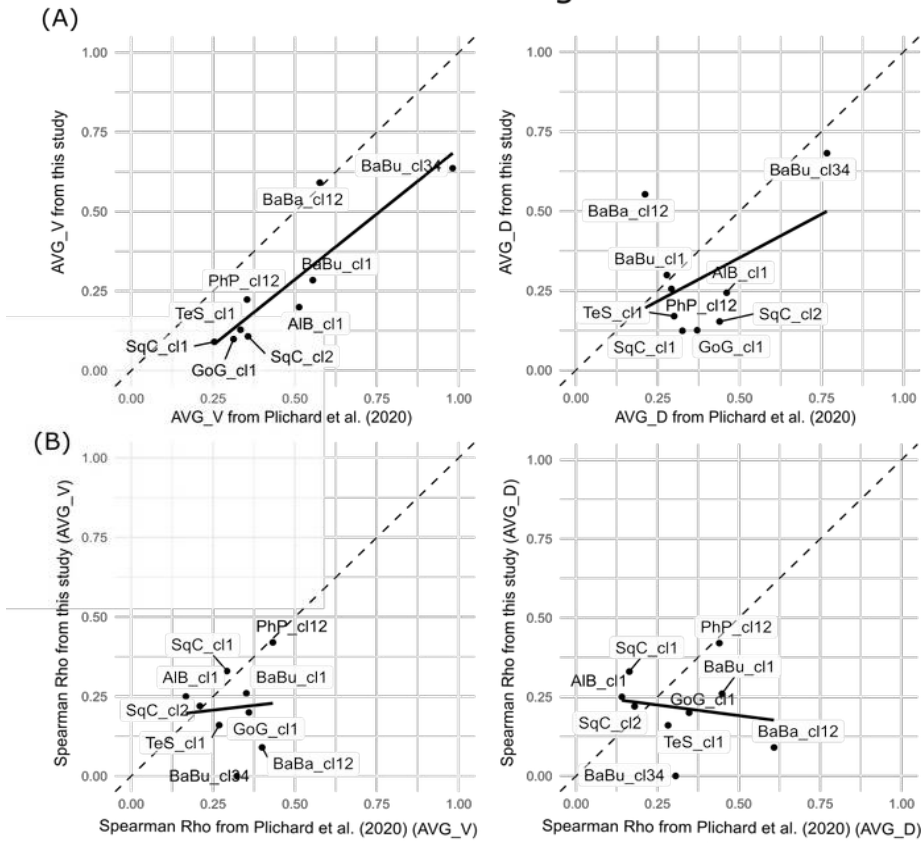


Figure 4.

Electrofishing data



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Figure 5

Table 1. Fish guilds, species, taxa codes, with total abundance and occurrence in microhabitats.

Dataset	Guild	Family	Scientific name	Common name	Taxa code	Abundance	Occurrence
Electrofishing	Bank N=2344	Cyprinidae	<i>Phoxinus phoxinus</i>	Minnow	PhP_cl12	1785	134
		Cyprinidae	<i>Squalius cephalus</i>	Chub	SqC_cl1	217	47
		Cyprinidae	<i>Rutilus rutilus</i>	Roach	RuR_cl1	122	15
		Balitoridae	<i>Barbatula barbatula</i>	Stone loach	BaBa_cl12	116	57
		Cyprinidae	<i>Telestes soufia</i>	Blageon	TeS_cl1	57	17
		Cyprinidae	<i>Gobio gobio</i>	Gudgeon	GoG_cl1	30	16
		Percidae	<i>Perca fluviatilis</i>	Perch	PER_cl12	11	11
		Centrarchidae	<i>Lepomis gibbosus</i>	Pumpkinseed	LeG_cl123	6	5
	Midstream N=73	Cyprinidae	<i>Barbus barbus</i>	Barbel	BaBu_cl34	27	17
		Salmonidae	<i>Thymallus thymallus</i>	Grayling	ThT_cl2	15	10
		Cyprinidae	<i>Chondrostoma nasus</i>	Nase	ChN_cl34	12	7
		Cyprinidae	<i>Barbus barbus</i>	Barbel	BaBu_cl2	8	8
		Cyprinidae	<i>Alburnus alburnus</i>	Bleak	AlA_cl23	4	5
Salmonidae		<i>Thymallus thymallus</i>	Grayling	ThT_cl4	3	2	
Salmonidae		<i>Thymallus thymallus</i>	Grayling	ThT_cl3	2	3	
Snorkeling	Midstream N= 1119	Salmonidae	<i>Thymallus thymallus</i>	Grayling	ThT_cl234	444	347
		Cyprinidae	<i>Barbus barbus</i>	Barbel	BaBu_cl34	437	164
		Cyprinidae	<i>Chondrostoma nasus</i>	Common nase	ChN_cl34	238	43

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Table 2. Benthic macroinvertebrate guilds, family, genus, taxa codes, with total abundance and occurrence in microhabitats.

Guild	Family	Tribe	Genus	Taxa	Code taxa	Abundance	Occurrence
Limnophilic c N=687	Chironomidae	Chironomini			CHIR	612	23
	Sphaeriidae		<i>Pisidium spp.</i>		PISI	70	15
	Tabanidae				TABA	3	3
	Baetidae (non Baetis)		<i>Procloeon spp.</i>	<i>Procloeon bifidum</i>	PBIF	2	1
Rheophilic N=2988	Elmidae		<i>Esolus spp.</i>		ESOL	2021	34
	Hydropsychidae		<i>Cheumatopsyche spp.</i>	<i>Cheumatopsyche lepida</i>	CLEP	393	14
	Psychomyiidae		<i>Psychomyia spp.</i>	<i>Psychomyia pusilla</i>	PPUS	214	14
	Elmidae		<i>Elmis spp.</i>		ELMI	192	17
	Baetidae		<i>Baetis spp.</i>	<i>Baetis fuscatus</i>	BFUS	102	14
	Hydropsychidae		<i>Hydropsyche spp.</i>	<i>Hydropsyche incognita</i>	HINC	48	10
	Psychodidae				PSYC	7	4
	Heptageniidae		<i>Heptagenia spp.</i>	<i>Heptagenia sulphurea</i>	HSUL	6	3
	Baetidae		<i>Baetis spp.</i>	<i>Baetis vardarensis</i>	BVAR	3	1
	Hydropsychidae		<i>Hydropsyche spp.</i>	<i>Hydropsyche exocellata</i>	HEXO	1	1
	Baetidae		<i>Baetis spp.</i>	<i>Baetis rhodani</i>	BRHO	1	1

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Table 3. Fitting statistics for models M0 (no microhabitat selection), M1 (effects of present hydraulics) and M2 (additional effect of past hydraulics), including AIC and Spearman Rho values. M2 models correspond to those shown in Figure 4. Asterisks indicate significance of likelihood ratio tests comparing M1 vs. M0 or M2 vs. M1, with (*) for $P < 0.05$ and (**) for $P < 0.01$. In bold: abundance is significantly higher in past high velocity or dewatering habitat; Underlined: abundance is lower.

Model type	Hydraulic variables involved	Dataset									
		Electrofishing data				Snorkeling data		Benthic macroinvertebrate data			
		Bank guild		Midstream guild		Midstream guild		Limnophilic guild		Rheophilic guild	
		AIC	Spea. Rho	AIC	Spea. Rho	AIC	Spea. Rho	AIC	Spea. Rho	AIC	Spea. Rho
M0		1780		392		4108		256		273	
M1	Flow velocity	1670**	0.41	395	0.11	4847*	0.16	258	0.09	370*	0.13
M2	Flow velocity + Dewatering	1650**	0.44	<u>392*</u>	0.14			<u>256*</u>	0.27	<u>353*</u>	0.61
	Flow velocity + Past velocity	1672	0.40	395	0.11	4843*	0.15	259	0.09	369*	0.31
M1	Water depth	1734**	0.43	385**	0.10	4933	0.04	259	0.04	370*	0.35
M2	Water depth + Dewatering	1725**	0.43	386	0.13			<u>258*</u>	0.44	<u>358*</u>	0.53
	Water depth + Past velocity	1734	0.44	384	0.12	4931*	0.03	259	0.15	366*	0.46