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1 **Multiple stressors shape invertebrate assemblages and reduce their trophic niche: a case**
2 **study in a regulated stream**

3

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14

15 **Abstract**

16 Few studies have addressed how the diversity of basal resources change with stream regulation
17 and the potential consequences on river biota. We sampled invertebrates above and below a
18 series of dams, over two years, at both downwelling and upwelling zones. In each zone, we
19 recorded the daily temperature and flow variations, estimated the algal development, measured
20 the available resources, and analysed carbon and nitrogen stable isotope compositions of the
21 invertebrate community. The number of hydrological pulses were typically higher below the
22 dams than above the dams especially during high-flow periods whereas the groundwater outlets
23 had minor effects on invertebrate assemblages. Invertebrate abundance, richness and diversity
24 tended to decrease below the dams. Co-inertia analysis showed that flow and temperature
25 variations, and eutrophication explained most of the variance in the invertebrate assemblages,

26 which comprised a higher number of resilient taxa below than above the dams. The proportions
27 of pesticide-sensitive invertebrates were lower below the dams and ovoviviparous and more
28 generalist taxa were prominent. We did not observe the expected CPOM decrease and FPOM
29 increase downstream. Accordingly, the proportions of each functional feeding group were
30 remarkably similar above and below the dams despite the long distance between the sectors
31 (>100 kms). The diversity of basal resources used within assemblages progressively increased
32 downstream above dams. In contrast, the diversity of resources used by organisms below the
33 dams decreased from upstream to downstream suggesting a significant influence of flow
34 regulation on aquatic food webs. Finally, the shorter trophic chains for the invertebrate
35 assemblages below the dams suggests that the effects of stream regulation and eutrophication
36 induced a simplification of food webs. To our knowledge, this study is the first to connect
37 taxonomic and functional trait changes in response to multiple stressors with the associated
38 modifications in isotopic niches within aquatic invertebrate assemblages.

39
40 **Context:** Understanding how stream regulation and associated anthropogenic pressures act on
41 aquatic assemblages and trophic niches is necessary to guide management actions.

42
43 **Goal:** We aimed to investigate the functional responses (traits and trophic niches) of aquatic
44 invertebrate assemblages to stream regulation and eutrophication.

45
46 **Methods:** We used univariate and multivariate analyses to compare the invertebrate
47 assemblages above and below the dams and to assess the contributions of hydrology (including
48 groundwater supplies to the river), temperature and eutrophication to the variability in the
49 composition of invertebrate assemblages. We also considered the relative utilization of a
50 selected set of traits describing invertebrate resilience, resistance and specialization to address

51 the potential functional effects of stream regulation on invertebrate assemblages. Finally,
52 carbon and nitrogen isotope analyses allowed us to characterize the length and width of
53 invertebrate assemblage food webs as related to the availability and diversity of basal
54 resources.

55

56 **Results:** Invertebrate abundance and richness generally decreased below the dams, with the
57 highest impacts on insect taxa. Co-inertia analysis showed that stream regulation and
58 eutrophication were main drivers of the aquatic invertebrate assemblages. The analysis
59 separated the sites above and below the dams according to flow and temperature variation,
60 whereas eutrophication appeared as a secondary stressor that separated the sites within each
61 sector. Furthermore, the series of dams resulted in (i) a higher proportion of resilient (e.g.,
62 multivoltine) and resistant (ovoviviparous) taxa and a majority of generalists in assemblages
63 below dams, (ii) an impact on the classical dynamics of CPOM (decrease) and FPOM
64 (increase) sources from upstream to downstream, and (iii) a reduction in the diversity of
65 resource use and in the trophic chain length of invertebrate assemblages below dams. The
66 cooler and less oxygenated upwelling zones had lower invertebrate abundance; however,
67 contrary to our expectation, the variation in the groundwater supply did not affect the
68 composition of epigeal invertebrate assemblages.

69

70 **Conclusion:** This study provides insights about the impacts of flow regime alteration and
71 eutrophication on food webs that may have been caused by regulation of permanent streams.
72 To our knowledge, this is the first to connect taxonomic and functional trait changes in response
73 to multiple stressors with the associated modifications in energy fluxes in aquatic invertebrate
74 assemblages. This study suggests that bed stability, which is associated with a reduction in
75 channel mobility below the dams and with moderate eutrophication, may provide the shelter

76 and resources that can locally favour invertebrate assemblage dynamics and lessen the effects
77 of flow regulation. In addition, the study suggests that the biological trait-based approach and
78 isotope analysis are complementary approaches for addressing ecosystem functioning. The
79 relative utilization of traits indicates the functional potential of aquatic invertebrate
80 assemblages to face multiple stressors whereas isotope analysis is an expression of the actual
81 effect of the stressors on the trophic structure of aquatic invertebrate assemblages.

82

83 **Key words**

84 benthic invertebrates – biological traits – aquatic food web – stream regulation

85

86 **1. Introduction**

87 Flowing waters are dynamic ecosystems whose functioning depends closely on the continuity
88 of energy and material flows through longitudinal, transversal, vertical and temporal
89 dimensions (Amoros and Petts, 1993). However, most of the flowing water worldwide has been
90 massively modified by impoundments to meet different objectives such as flood protection,
91 river navigation, recreation, and water supplies; these modifications represent an important
92 threat to aquatic communities in the context of climate change (Nilsson *et al.*, 2005). In
93 addition, in response to the rapid development of human populations, the demand for energy
94 has greatly increased in recent decades and has resulted in the construction of many
95 hydropower dams, making the threat even more prevalent (Zarfl *et al.*, 2014).

96

97 The abiotic effects of damming and more generally the effects of anthropogenic disruption of
98 the river continuum have been studied for many years (e.g. Baxter, 1977; Ward and Stanford,
99 1983a; Ligon *et al.*, 1995; Rosenberg *et al.*, 2000). Apart from changes in the flow regime, they
100 include pronounced changes in the temperature, dissolved oxygen concentrations, and

101 chemical composition of water. In addition, the fragmentation of the rivers by dams prevents
102 the transport of sediment downstream, which may deeply modify the channel structure and
103 dynamics by causing river incision and bed armouring (Brenna *et al.*, 2019). These changes
104 generally result in a loss of aquatic diversity and in river homogenization (e.g. Poff *et al.*, 2007;
105 Rolls *et al.*, 2012; Mbaka and Mwaniki, 2015; Mellado-Diaz *et al.*, 2019). The alteration of the
106 channel dynamics may also modify the exchanges between the hyporheic zone and surface
107 flow (Caschetto *et al.*, 2014) whereas local hydrological exchanges greatly contribute to stream
108 functioning (Boulton *et al.*, 1998, 2010). For example, groundwater outlets provide a supply
109 of cooler water (White *et al.*, 1987) that is rich in nutrients (Valett *et al.*, 1994). In addition, in
110 natural situations benthic invertebrates may migrate within the sediment to escape flow
111 disturbances (Dole-Olivier and Marmonier, 1992; Maazouzi *et al.*, 2017; Vander Vorste *et al.*,
112 2017). However, less is known about the direct effect of groundwater supply and the associated
113 water quality on the benthos. Damming has also been shown to affect leaf litter decomposition
114 and the distribution of functional feeding groups (Martinez *et al.*, 2013) as well as functional
115 richness (Laini *et al.*, 2019) and to cause profound changes in food webs (Power *et al.*, 1996;
116 Mor *et al.*, 2018). For example, damming in Mediterranean streams can increase hydrological
117 and sedimentological stability downstream dams, leading to a modification of available
118 resources and a change from a detritus-based to an algae-based food web (Mor *et al.*, 2018).
119 Finally, apart from the direct effects of low flows or changes in flow timing associated with
120 stream regulation, nutrient effluents from the catchment combined with low flows (damming
121 and water abstraction for agriculture) and the higher transparency associated with a lack of fine
122 sediment transport may exacerbate primary production, ultimately leading to eutrophication
123 (Biggs, 2000). Moreover, chemical releases associated with agricultural or industrial activities
124 or with contaminants accumulated in the reservoir may interact with flow alteration (Colas *et*
125 *al.*, 2013).

126

127 As a result, stream regulation involves multiple stressors that constrain the resilience and
128 resistance capabilities of aquatic invertebrate assemblages, which can potentially be assessed
129 through a multiple trait-based approach (Statzner *et al.*, 2010). According to the literature, the
130 disturbances associated with frequent flow fluctuations may favour small size invertebrates
131 (higher resilience capability; Townsend *et al.*, 1997), and/or invertebrates with short
132 development periods (life duration <1 y.) and/or with more than one generation per year
133 (multivoltine). Apart from the specific hydraulic effects of stream regulation, the
134 eutrophication that frequently occurs below dams results in selection for organisms with traits
135 that allow them to resist the potential degradation of the water quality (e.g. offspring protection
136 by ovoviviparity, less sensitivity to oxygen depletion). As a consequence, by modifying the
137 composition of assemblages, stream regulation may lead to simplified food webs. Food webs
138 can be also affected by dams and associated reservoirs which act as powerful retention
139 structures in river networks by burying particulate organic matter in sediments (Vörösmarty *et*
140 *al.*, 2003). This retention process decreases the availability of particulate organic matter to
141 downstream benthic food webs, affecting the secondary production of consumers (Ward and
142 Stanford, 1983b; Power *et al.*, 1996; Kominoski and Rosemond, 2012). Moreover, reduction
143 of POM below dams would lead to dominant algae-based food webs characterized by a lower
144 complexity than food webs based on both algae and detritus (Power *et al.*, 1996). Indeed,
145 Layman *et al.* (2007) showed that a reduction of food diversity (as expected below dams) would
146 strongly reduce the trophic niche width of primary consumers and predators, reflecting a
147 homogenization of energy flow pathways to top predators. This reduction of trophic niche
148 width could be critical for ecosystem structure and functioning as it destabilizes food webs and
149 increases the extinction risk of top predators. With this objective, stable isotopes appear as very
150 pertinent tools to evaluate the consequences of environmental stressors affecting food sources

151 for benthic communities (Pingram et al., 2012; Burdon et al. 2019). Understanding the
152 combined effect of different stressors and the contribution of the different environmental
153 parameters in the structure and function of aquatic communities remains a key question for
154 managers to address restoration goals and mitigation measures (Azzellino *et al.*, 2015).
155 Therefore, integrated approaches that consider various physical and chemical compartments
156 and biological processes in a single study are required. The Ain River, which rises in the Jura
157 Mountains from a karstic emergence at approximately 680 metres above sea level, is a major
158 tributary of the Upper Rhône. It is 190 km long and has 3765 km² drainage area. Five
159 hydroelectric power plants were built on its main course between 1928 and 1968. Among them,
160 the Vouglans dam, built in 1968, forms a 35-km long reservoir of more than 600 million m³ of
161 water. This large reservoir is followed by a series of four other dams in succession along the
162 river course that strongly influence water flow and generate a significant sediment deficit
163 (Rollet *et al.*, 2013; Dole-Olivier *et al.*, 2019). This river thus represents a good experimental
164 situation for addressing the complex effects of stream regulation and its associated stressors on
165 the taxonomic composition, functional responses and potential changes in food web
166 complexity.

167

168 In this study, we hypothesize that the combination of thermal, hydraulic and land use
169 disturbances below the dams is likely to (i) decrease the abundance and richness of invertebrate
170 assemblages, (ii) modify their taxonomic composition, by favouring organisms with resilience
171 and resistance traits as well as generalists, and (iii) alter the balance among functional feeding
172 groups, and (iv) modify the resource use by invertebrates and in turn the complexity of the
173 invertebrate food web by reducing the niche width of primary consumers and predators. At the
174 same time, we evaluate the potential of upwelling zones, which are characterized by thermally
175 buffered groundwater supplies and are rich in nutrients to modulate the impacts of dams on

176 benthic invertebrates. More precisely, we hypothesize that the groundwater upwellings below
177 the dams may (i) locally limit the negative thermal impacts of stream regulation on invertebrate
178 assemblages and (ii) stimulate primary production with potential consequences on food webs.

179

180 **2. Material and Methods**

181 *2.1. Study locations*

182 We selected three sites (A1 to A3; Fig. 1A) above the series of dams to represent environmental
183 situations that are not or moderately subjected (by passed section in A3) to hydrological
184 alterations and three sites below the series of dams (A4 to A6; Fig. 1A). According to a
185 preliminary study, the six sites were assumed to be influenced by various alterations in land
186 use, and the differences in temperature and trophic status among the three sites within each
187 sector allowed us to consider the possible confounding effects of these factors (Table 1). In
188 addition, at each of the six sites, groundwater supply zones were mapped using the method of
189 Dole-Olivier *et al.* (2019). This mapping permitted the identification of one zone that was
190 supplied with groundwater (upwelling; Fig. 1B) and one zone that was supplied with surface
191 water only (downwelling; Fig. 1B) for each site.

192

193 *2.2. Environmental characterization*

194 *2.2.1. Water level and temperature*

195 Two Mini-Diver sensors (Schlumberger, Water Services, Waterloo, Canada) were installed per
196 site to monitor pressure (corresponding to the water level after correction for atmospheric
197 pressure) and temperature dynamics during the experiment (from August 10, 2014 to July 08,
198 2016). One sensor was installed in the streambed sediments in a zone influenced by
199 groundwater outlets (upwelling) and the other in a downwelling zone (no influence of
200 groundwater) in order to assess the relative importance of these zones for the epigean benthic

201 invertebrates (Fig. 1B). Water levels (cm) were further transformed into hourly discharge ($\text{m}^3 \cdot \text{s}^{-1}$)
202 ¹) by using the relationship between the measured discharges and the water levels at each site.
203 We used the water level series to compute, at each site and each date, four metrics related to
204 the prevailing hydrological conditions for the 15 days preceding the invertebrate sampling: (i)
205 the number of extreme ecological events, which was measured by the number instances of an
206 increase of >50% in less than 1 day, (ii) the average discharge ($\text{m}^3 \cdot \text{s}^{-1}$), (iii) the standard
207 deviation of the discharge, and (iv) the coefficient of variation of the discharge. Similarly, we
208 used the water temperature series to compute for each site, each zone and each date, three
209 metrics considering the prevailing water temperature conditions for the 15 days preceding the
210 invertebrate sampling: (i) the average temperature ($^{\circ}\text{C}$), (ii) the standard deviation of the
211 temperature, and (iii) the temperature range ($^{\circ}\text{C}$).

212

213 2.2.2. *Chemical parameters*

214 Sampling was performed at six times (August 2014, October 2014, April 2015, July 2015,
215 October 2015, and June 2016; arrows on Fig. 2) to cover all environmental conditions
216 (hydrology and temperature) in three seasons (spring, summer and fall) twice. To assess the
217 influence of ground waters on water quality, we considered 3 sampling points under the direct
218 influence of upwelling and 3 sampling points in the downwelling zone. Chemical parameters
219 were measured at these sampling points sampling time, with the exception of October 2014
220 due to a device malfunction. The dissolved oxygen concentration ($\text{mg} \cdot \text{L}^{-1}$) and electrical
221 conductivity ($\mu\text{S} \cdot \text{cm}^{-1}$) were measured directly in the field using portable EC (electric
222 conductivity) and DO-meter (HQ20, HACH, Dusseldorf, Germany) probes. Inorganic nutrients
223 (NH_4^+ , NO_3^- , and PO_4^{3-}) were measured in previously filtered (glass fibre membrane GF/F,
224 porosity: $0.7 \mu\text{m}$) water samples by standard colorimetric methods (Grasshoff *et al.*, 1999)
225 using an automatic analyser (SmartChem200, AMS, Frepillon, France).

226

227 *2.3. Basal resources and stable isotope analyses*

228 To allow a temporal and spatial comparison of the availability of nutrient resources and their
229 ability to provide energy (in the form of carbon) to organisms, we collected and quantified the
230 basal nutrient resources available for the invertebrates at each site and in the upwelling and
231 downwelling zones for the three sampling occasions in 2015. Following the approach of
232 François *et al.* (2020), this sampling consisted of collecting all available resources occurring
233 within a standardized area (256 cm²) at a depth of 1 cm at the six points selected in the
234 upwelling and downwelling zones of each site. The nutritional resources sampled were sorted
235 in the laboratory, dried, and weighed, and the quantity of organic carbon in each resource (g.
236 of C. m⁻²) was assessed by elemental analysis (Thermo FlashEA 1112; Thermo Electron). The
237 seven quantified nutrient sources found were: (i) sedimentary biofilm (biofilm), (ii) algal
238 biofilm developing on stones (perilithon), (iii) coarse particulate organic matter (CPOM,
239 organic matter particles > 1 mm), (iv) fine particulate organic matter (FPOM, organic matter
240 particles < 1 mm), (v) aquatic mosses (moss), (vi) filamentous algae (algae) and (vii) aquatic
241 macrophytes (macrophyte).

242

243 In addition, during these three sampling occasions in 2015, additional benthic invertebrate
244 samples (Surber net mesh size: 500 µm) were collected to estimate the size of the trophic niche
245 of organisms and assemblages at each site and each zone (upwelling and downwelling).
246 Invertebrates were sorted and identified at the lowest possible taxonomic level (see Appendix
247 1 and 2 for identification level used) and 5 individuals of each taxon were used for isotopic
248 analyses for each date, site and zone. When possible, we avoided using parts of the animals
249 that contained the digestive tracts, as gut contents may affect the isotope ratio of the sample
250 (Mateo *et al.*, 2008). Invertebrates were weighed individually (dry mass between 0.1 and

251 0.5mg) in tin capsules. The basal resources were acidified using 1 M HCl to remove carbonates
252 before carbon isotope analysis, and an amount of 2 to 20 mg of basal resources, depending on
253 the carbon and nitrogen content, was encapsulated in tin capsules. The isotopic compositions
254 of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) of the different invertebrates selected and of the
255 basal resources described above were measured using an isotope ratio mass spectrometer
256 (Isoprime 100, Elementar) coupled to an elementary analyser (Vario PyroCube, Elementar).
257 In-house standards calibrated against IAEA-N1, IAEA-N2, IAEA-CH6 and IAEA-C3
258 reference materials were analysed with the samples, and the standard deviations of the replicate
259 analyses were lower than 0.20‰. The carbon and nitrogen stable isotope compositions were
260 expressed as δ in ‰ with V-PDB ($\delta^{13}\text{C}$) and air ($\delta^{15}\text{N}$) as standards.

261

262 *2.4. Primary production*

263 To cover a maximum range of environmental conditions over the width of each zone (up and
264 downwelling), 2 transects, separated by a few metres and parallel to each other, were defined
265 per site. Three points corresponding to different substrates (sand, gravel, pebbles) were selected
266 at random on each of the transects over an area of approximately 0.025 m². Six samples were
267 thus taken in each zone on each sampling occasion. In each sample, the biofilm was scraped
268 with a brush, and the substrate was rinsed several times to obtain a complete collection of the
269 biofilm. The sample was transferred into a propylene bottle, after removing any
270 macroinvertebrates, leaves and stones. The sample was then homogenized and divided into two
271 equal subsamples. The first subsample was used for chlorophyll-*a* measurement. The second
272 subsample was fixed with Lugol solution for further identification of the different groups of
273 algae. On the same day, the chlorophyll-*a* was quantified in the laboratory by filtering each
274 biofilm sample on a glass fibre membrane GF/C (pore diameter 1.2 μm). Pigment extraction
275 was carried out with 90% acetone. After centrifugation, the absorbance of the supernatant was

276 measured at 630, 645, 663 and 750 nm wavelengths, using a spectrophotometer. The
277 concentrations in chlorophyll-*a* were obtained by applying the Lorenzen formula (according to
278 the NF T90-117 French standard) and used as a proxy for algal biomass. For each benthic
279 biofilm subsample, the individuals were classified into the main functional groups, i.e.
280 cyanobacteria, chlorophytes and diatoms, and counted under a microscope as the number of
281 cells per m² (Bourrely, 1968, Prescott *et al.*, 1978). Given the high densities observed, we used
282 a Nageotte chamber to count the cells in small volumes.

283

284 2.5. *Benthic invertebrates*

285 2.5.1. *Sampling*

286 Three Surber samples (area 0.05 m², mesh size 500 µm) were taken from each zone (upwelling
287 and downwelling), at each site on each sampling occasion. In addition, at each site and each
288 sampling occasion, we collected three additional Surber samples in the vicinity of the
289 upwelling and the downwelling zones to cover the different hydraulic and substrate conditions.
290 Individuals were identified at the genus level using Tachet *et al.* (2010), with the exception of
291 Diptera, which were identified at the family level. The community matrix data are available in
292 Appendix 1 and 2.

293

294 2.5.2. *Biological traits metrics*

295 The biological traits used in this study were extracted from a European database constructed
296 from the literature that contains information on life history, resilience and resistance potential,
297 morphology, physiology and feeding behaviour for European freshwater invertebrate genera
298 (Tachet *et al.*, 2010). In this public database, available on the web (see Schmidt-Kloiber and
299 Hering, 2015), traits are usually divided into categories and are quantified using affinity scores
300 between 0 and 3 (maximal size, voltinism, reproduction types, locomotion and relation to

301 substrate) or 0 and 5 (food and feeding habits) (Chevenet *et al.*, 1994). This quantification,
302 which enables the compilation of information from various sources, also (i) captures the
303 variability in traits that often occurs in an organism at different life stages and (ii) accounts for
304 within-taxon variations in responses. We computed metrics describing (i) the relative
305 utilization of fuzzy-coded traits such as multi-voltinism, small size, short life span,
306 ovoviviparity, and oligotrophy (Table 2; see Mondy and Usseglio-Polatera, 2013) to address
307 the response of organisms in terms of resilience and resistance abilities, (ii) food Rao diversity
308 and community specialization (Table 2; Mondy and Usseglio-Polatera, 2014) in terms of food
309 and trophic status, and (iii) the ‘Species at Risk’ index to consider a potential additional stress
310 associated to agricultural activities (SPEAR pesticide relative abundance index; Liess and von
311 der Ohe, 2005). Selected metrics are available in Appendix 3.

312

313 2.6. Data analyses

314 To assess temporal and spatial effects on the above selected abiotic parameters and biological
315 metrics, we used mixed ANOVAs with zones (upwelling and downwelling), sectors (above
316 and below dams) and sampling dates as fixed effects, and the sampling sites as random effects.
317 When the normality assumption was not met, we used the Box-Cox transformation (Box and
318 Cox, 1964). We used co-inertia analysis (CoiA) to assess the contributions of parameters
319 describing hydrology, temperature and eutrophication, for explaining the variance in
320 invertebrate assemblage composition. Since algal variables (eutrophication) were taken on
321 transects whereas benthic invertebrate samples were taken at sampling point, we summed
322 samples by zones (upwelling vs. downwelling) within each site at each season, thus ending up
323 with 72 sampling units. CoiA provides factorial axes from each dataset that are the most
324 covariant, i.e., they simultaneously depict the highest possible variance of each dataset and
325 optimize their correlation (Dolédec and Chessel, 1994; Dray *et al.*, 2003), and we considered

326 the loadings of variables to assess the relative contribution of each of them to the covariance
327 between benthic invertebrates and environmental variables. The strength of the relationship
328 was measured by means of the Rv coefficient, a multidimensional equivalent for two tables of
329 the regression coefficient for two variables (Robert and Escoufier, 1976). We tested the
330 statistical significance of the Rv coefficient by a Monte Carlo permutation test and by
331 comparing the distribution of 999 replicated matches of the two datasets (after random
332 permutations of their rows) with the observed Rv coefficient.

333

334 To evaluate the changes in the trophic diversity of the benthic invertebrate assemblages, we
335 used community-wide metrics based on the carbon and nitrogen isotope compositions. The
336 isotopic space area was used to quantify the trophic diversity (Newsome *et al.*, 2007; Jackson
337 *et al.*, 2011). The $\delta^{13}\text{C}$ (CR) and $\delta^{15}\text{N}$ (NR) ranges in the $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ biplot space were calculated
338 using the mean isotope composition of each taxon following the approach developed by
339 Laymann *et al.* (2007). These ranges provide, respectively, an integrative measure of the
340 diversity of the basal resources that are exploited by the assemblage (noted CR) and of the
341 trophic level diversity (NR). Because the convex hull approach emphasizes the weight of
342 species with extreme positions in the $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ biplot space, we used the standard ellipse
343 approach (SEAnr), which was calculated using a Bayesian framework with 2×10^4 iterations,
344 10^3 burning-in and 10% of thinning (Jackson *et al.*, 2011). Since the variability in the isotope
345 composition of the basal resources among sampling sites and dates explained a part of the
346 variation in the isotope space area, we normalized values by the standard ellipse area of the
347 resources (knowing that all resources were recovered from all sites, zones and dates).

348

349 Statistics and graphical outputs were performed and generated with R freeware (R
350 Development Core Team, 2020) including the *ade4* and *adegraphics* (Thioulouse *et al.*, 2018),
351 *lme4* (Bates *et al.*, 2015), and *siber* (Jackson *et al.*, 2011) packages.

352

353 **3. Results**

354 *3.1. Environmental characterization*

355 *3.1.1. Water level and temperature*

356 According to the flow variation, 2015 was the driest year, 2016 was the wettest year, and 2014
357 fell in between (Fig. 2). On average, the number of pulses was lower above the dams than
358 below the dams (Table 3A). Despite stream regulation, the discharge was obviously higher
359 below the dams than above the dams (Table 3A) but the significant interaction with the
360 sampling date was associated with the very low difference in discharge in summer 2015, i.e.,
361 the driest period. Finally, coefficient of variation of the discharge values were significantly
362 lower below the dams than above the dams in summer and fall 2015, and the opposite trend
363 was observed for the 4 other sampling dates (Table 3A). Similarly, the water temperature varied
364 across the years. The highest temperatures occurred in the summer of 2015, and the lowest
365 occurred in the winter of 2014, and 2016 was slightly cooler (Fig. 3). Apart from the obvious
366 effect of the sampling date (Table 3A), the average temperature preceding each sampling
367 occasion below the dams was significantly higher than that above the dams (Table 3A). In
368 contrast, the temperature range did not significantly change between sectors located below and
369 above the dams (Table 3A). There was a statistical interaction between the presence of
370 groundwater outlets and the sampling date (Table 3A), i.e., water temperature was significantly
371 lower in the upwelling zone ($20.3\pm 2.2^{\circ}\text{C}$) than in the downwelling zone ($23.0\pm 1.6^{\circ}\text{C}$) in
372 summer 2015. The variations in water temperature were buffered in the upwelling zones in

373 comparison with the more pronounced variations in the downwelling zones (1.6°C more on
374 average; Fig. 3).

375

376 *3.1.2. Water chemistry*

377 Apart from interaction between sector and sampling date and site effect, the dissolved oxygen
378 concentration and nitrate concentrations varied significantly among zones (Table 3B). On
379 average, the concentrations of dissolved oxygen and nitrate measured in upwelling zones were
380 respectively lower (-0.5 mg.L⁻¹ of oxygen) and higher (+0.056 mg.L⁻¹ of nitrogen) than
381 concentrations measured in the downwelling zones. Electrical conductivity was on average 20
382 µS.cm⁻¹ lower below the dams than above the dams, but the magnitude of the difference
383 changed with the sampling date (Table 3B). Ammonium concentrations ranged from 4.0 to
384 65.2 µg.L⁻¹ and from 0.7 to 57.0 µg.L⁻¹ above and below the dams, respectively (Table 3B).
385 Similarly, orthophosphate concentrations ranged from 0.8 to 25.1 µg.L⁻¹ and from 1 to 17.3
386 µg.L⁻¹ above and below the dams, respectively (Table 3B). Most measured concentrations were
387 very low (<20 µg.L⁻¹) and significant differences between sectors or zones would be of low
388 biological relevance. Thus, the ammonium and orthophosphate concentrations did not allow us
389 to make any further inferences.

390

391 *3.1.3. Primary production*

392 The chlorophyll-*a* concentration and the densities of cyanobacteria, chlorophytes and diatoms
393 showed similar spatial patterns including a high variability among sites in each sector and with
394 the highest values reported at site A4 below dams (Table 4A). Cyanobacteria had the greatest
395 development with densities generally higher on both sides of the dams (especially at sites A3
396 and A4; Table 5A). As expected, seasonal changes in algal development also explained the
397 variability in the algal dataset for all algal metrics (Table 4A).

398

399 3.2. Invertebrate assemblage responses

400 3.2.1. Spatial and temporal patterns

401 With the exception of spring 2015, the total abundance of benthic invertebrates was generally
402 lower below the dams than above the dams (497 ± 460 vs. 415 ± 582 individuals; Table 4B) and
403 lower in the upwelling zones than in downwelling zones (401 ± 436 vs. 511 ± 598 individuals).
404 The total richness was not significantly lower below the dams than above the dams (Table 4B).
405 Nevertheless, as for the total abundance, the richness values below the dams at the last two
406 sites were significantly lower than those at the other sites (Table 4B). No significant difference
407 in richness was observed between the upwelling and downwelling zones. Shannon diversity
408 was significantly lower below the dams than above the dams (1.8 ± 0.1 vs. 2.1 ± 0.4 ; Table 4B)
409 and highlighted significantly lower values in upwelling than in downwelling zones at three
410 sampling dates (fall 2014, spring and summer 2015).

411

412 3.2.2. Main drivers of invertebrate assemblage responses

413 The co-inertia analysis between the invertebrate assemblage composition and environmental
414 metrics showed a significant correlation ($R_v=0.318$, simulated- $P<0.001$, $n=72$). The first-three
415 axes depicted 83% of the co-variability between the invertebrate assemblage composition and
416 the environmental metrics (46%, 20.9% and 16.1% for the first, second and third co-inertia
417 axes, respectively; Fig. 4). The first two co-inertia axes depicted 96% and 72.6% of the
418 environmental and faunal variance, respectively. The first co-inertia axis clearly separated the
419 two sectors suggesting that invertebrate composition responded significantly to the
420 environmental context above and below the dams (Fig. 4A). This separation was associated
421 with the higher temperature range (T_r in Fig. 4B) and standard deviation (T_s) above the dams,
422 and with the higher discharge (Q_m), flow pulse (Q_p) and algal development below the dams

423 (E1-E4; Fig. 4B). The second co-inertia axis separated sites within sectors according to the
424 higher flow variation (Q_c in Fig. 4B) above the dams and the higher temperature (T_m) and
425 algal development (E1) at the moderately regulated above-dam site (A3; Fig. 4A) and the
426 regulated below-dam site (A4; Fig. 4A). The apparent proximity of sites A5 and A6 with A1
427 and A2 (Fig. 4A) was a consequence of the multivariate analysis projection, and the third co-
428 inertia axes clearly separated them according to their discharge values (Q_c , Q_m ; Fig. 4D).
429 Noticeably, algal development appeared again as a driver at the moderately regulated above-
430 dam site (A3; Fig. 4C) and the regulated below-dam site (A4; Fig. 4C).

431

432 Accordingly, taxa responsible for these differences above and below the dams included
433 Ephemeroptera such as *Torleya* sp. (expressed in average % of individuals collected in sites:
434 $1.18\% \pm 1.75$ vs. $0.003\% \pm 0.015$ above and below dams respectively; supplementary
435 information, Fig. S1E), *Serratella* sp. ($4.65\% \pm 6.20$ vs. $2.86\% \pm 3.39$), *Rhithrogena* sp.
436 ($0.85\% \pm 1.56$ vs. $0.10\% \pm 0.21$) and *Ecdyonurus* sp. ($0.75\% \pm 0.58$ vs. $0.20\% \pm 0.45$); various
437 Plecoptera including *Leuctra* sp. ($2.45\% \pm 2.65$ vs. $1.31\% \pm 2.34$; Fig. S1G), Perlodidae
438 ($0.13\% \pm 0.26$ vs. $0.01\% \pm 0.05$), *Nemoura* sp. ($0.04\% \pm 0.08$ vs. $0.00\% \pm 0.00$), *Protonemura* sp.
439 ($0.07\% \pm 0.20$ vs. $0.00\% \pm 0.00$), *Dinocras* sp. ($0.01\% \pm 0.03$ vs. $0.00\% \pm 0.00$) and *Perla*
440 ($0.07\% \pm 0.11$ vs. $0.00\% \pm 0.00$); Coleoptera such as *Stenelmis* sp. ($0.08\% \pm 0.22$ vs. $0.03\% \pm 0.05$;
441 Fig. S1C); and Trichoptera such as *Hydropsyche* sp. ($6.09\% \pm 7.19$ vs. $3.85\% \pm 4.47$), *Micrasema*
442 sp. ($0.21\% \pm 0.39$ vs. $0.00\% \pm 0.00$) and *Odontocerum* sp. ($0.22\% \pm 0.7$ vs. $0.00\% \pm 0.00$) (Fig.
443 S1H). The taxa having higher proportions below the dams included the Ephemeroptera
444 *Heptagenia* sp. ($0.00\% \pm 0.02$ vs. $0.69\% \pm 1.04$ above and below dams respectively; Fig. S1E)
445 and *Potamanthus* sp. ($0.00\% \pm 0.00$ vs. $0.22\% \pm 0.53$), *Dreissena* sp. ($0.00\% \pm 0.00$ vs.
446 $0.02\% \pm 0.04$; Fig. S1A), triclads such as *Dugesia* sp. ($0.15\% \pm 0.39$ vs. $0.67\% \pm 1.31$; Fig. S1A),
447 various taxa belonging to the Trichoptera Leptoceridae family (*Athripsodes* sp. ($0.18\% \pm 0.27$

448 vs. $0.76\% \pm 1.00$), *Setodes* sp. ($0.18\% \pm 0.27$ vs. $0.76\% \pm 1.00$), *Mystacides* sp. ($0.00\% \pm 0.01$ vs.
449 $0.07\% \pm 0.20$); Fig. S1H); Crustacea such as *Gammarus* sp. ($13.1\% \pm 10.9$ vs. $29.9\% \pm 18.8$; Fig.
450 S1A) and Asellidae sp. ($0.58\% \pm 1.49$ vs. $2.34\% \pm 3.82$; Fig. S1A); Hirudinea such as *Piscicola*
451 sp. ($0.00\% \pm 0.00$ vs. $0.04\% \pm 0.09$; Fig. S1A); and lentic Coleoptera such as *Dryops* sp.
452 ($0.00\% \pm 0.00$ vs. $0.03\% \pm 0.12$) and *Haliphus* sp. ($0.00\% \pm 0.01$ vs. $0.02\% \pm 0.05$; Fig. S1C).

453

454 3.2.3. Assemblage resilience and resistance

455 The relative utilization of some life history traits demonstrated significant changes between
456 sectors (i.e. above vs. below the dams). For example, the proportion of multivoltine individuals
457 was significantly higher below dams than above dams (Table 5A; Fig. 5A). This proportion
458 was significantly and positively correlated with the proportion of short-lived organisms
459 ($n=432$, $r=0.165$, $P<0.0001$, not shown) but not with small-sized organisms. The proportion of
460 multivoltine organisms was also negatively related to the proportion of individuals with aerial
461 dispersal ($n=432$, $r=-0.694$, $P<10^{-16}$, not shown) and positively related to the proportion of
462 drifting organisms ($n=432$, $r=0.300$, $P<10^{-10}$, not shown). In addition, the proportion of small
463 and short life duration organisms were slightly lower in the upwelling than in downwelling
464 zones (0.64 ± 0.07 vs. 0.66 ± 0.09 and 0.69 ± 0.09 vs. 0.71 ± 0.08 respectively), especially below
465 dams (Table 5, Se:UD interaction). The reverse occurred for the proportion of drifting
466 organisms (0.38 ± 0.04 vs. 0.37 ± 0.04).

467

468 These changes in resilience traits mirrored in the proportions of individuals sensitive to
469 pollution, which decreased from upstream to downstream. The sites below the dams exhibited
470 slightly lower proportions of organisms that are sensitive to eutrophication (Fig. 5C) and
471 sensitive to pesticide as measured by the SPEAR index (Fig. 5D), though overall differences
472 below and above dams were marginally statistically significant (Table 5A). Likewise, the

473 proportion of ovoviviparous organisms was higher below the dams than above the dams (Table
474 5A; Fig. 5B) and was higher in the upwelling in comparison to the downwelling (0.154 ± 0.09
475 vs. 0.132 ± 0.06).

476

477 *3.3. Assemblage trophic responses*

478 *3.3.1. Functional feeding groups*

479 The proportions of each functional group generally differed across sites (Fig. 5E-H). A within-
480 sector decreasing trend from upstream to downstream was observed for shredders (Fig. 5F),
481 scrapers (Fig. 5G), and predators (Fig. 5H), whereas the opposite trend was observed for
482 filtering feeders (Fig. 5E). As this trend occurred in both sectors, there were no significant
483 differences above and below the dams in the average proportion of each functional feeding
484 group (Table 5B). In addition, the proportions of filter feeders and scrapers were slightly lower
485 in the upwelling than in downwelling zones (0.10 ± 0.05 vs. 0.11 ± 0.06 and 0.34 ± 0.06 vs.
486 0.36 ± 0.06 respectively). The reverse occurred for the proportion of shredders (0.29 ± 0.06 vs.
487 0.26 ± 0.07). Even statistically significant, these differences in proportions were too low to be
488 further interpreted.

489

490 Finally, food specialization showed no statistically significant difference above and below
491 dams (Table 5B). Nevertheless, sites A5 and A6 located below the dams tended to have fewer
492 food-specialized taxa (Fig. 6A). Trophic status specialization also differed significantly across
493 sites (Fig. 6B) with a trend towards more generalists below the dams but again the difference
494 between above and below dams was hardly statistically significant (Table 5C). Finally, food or
495 trophic status specialization did not differ between the upwelling and downwelling zones
496 located at each site (Table 5C).

497

498 3.3.2. *Isotope analysis*

499 3.3.2.1. *Basal resources*

500 The resource diversity available to benthic invertebrates did not significantly differ above and
501 below the dams (Table 6A). Neither, the amount of FPOM (Table 6A; supplementary
502 information Fig. S2), sedimentary biofilm (Table 6A; Fig. S2), mosses (Table 6A; Fig. S2) and
503 more generally the total amount of carbon (Table 6A; Fig. S2). A within-sector decreasing
504 trend from up to downstream occurred for sedimentary biofilm, whereas FPOM and mosses
505 peaked at site A4 (Fig. S2), below the dams. Finally, the total organic carbon content decreased
506 from upstream sites to downstream sites within each sector and peaked at site A4 (Fig. S2).

507

508 3.3.2.2. *Isotopic niche*

509 The isotope space area determined as the standard ellipse area normalized to the isotope
510 composition of the basal resource (SEAnr) differed significantly among sampling dates (Table
511 6B) and between sectors (Table 6B) (supplementary information, Fig. S3). SEAnr generally
512 increased from upstream to downstream in the sites above the dams, reaching its highest value
513 at A3 (Fig. 7A); however, this tendency was weaker during summer. Below the dams, SEAnr
514 decreased from sites A4 to A6, except in fall, when the maximum value was measured at site
515 A5. The diversity in the basal resource use, quantified by the $\delta^{13}\text{C}$ range (CR in Fig. 7C),
516 showed an increase from sites A1 to A3 but no difference between above and below dams
517 could be detected (Table 6B). Finally, the diversity of trophic levels quantified by the $\delta^{15}\text{N}$
518 range again showed an increase from upstream to downstream above the dams and a decrease
519 below the dams (Table 6B). At all sampling occasions, the most downstream site, A6, displayed
520 the lowest trophic diversity (SEAnr), with a low diversity in the exploitation of the basal
521 resources (CR) and a low diversity in trophic levels (NR). Regardless of the index used, no
522 significant influence of surface water-groundwater exchanges on the invertebrate food web

523 was detected (e.g. average values of SEAnr were 41.9 ± 16.2 vs. 39.6 ± 19.1 for the upwelling
524 and downwelling zones, respectively).

525

526 The calculation of linear correlations allowed the detection of the potential influences of
527 environmental conditions (hydrology, temperature, basal resources) on invertebrate food web
528 indexes (SEAnr, CR, and NR values). Interestingly, there was a positive linear relationship
529 between the organic carbon quantity in food sources and the isotope space area in summer (Fig.
530 8), when the hydrological conditions (cf. Fig. 2) were not disturbed by dramatic flood events.
531 No correlation was found in summer between SEAnr and hydrological parameters, whereas
532 SEAnr displayed a negative correlation with the variation in the discharge in spring ($r = -0.70$,
533 $P < 0.015$) and fall ($r = -0.70$, $P < 0.012$ and $r = -0.65$, $P < 0.025$, respectively).

534

535 **4. Discussion**

536 To our knowledge, this study is the first to simultaneously compare the taxonomic and
537 functional spatial and temporal responses of aquatic invertebrate assemblages and the
538 associated modifications in the isotopic metrics describing food webs in a regulated river. On
539 the one hand, our hypotheses about the effects of the alteration of the hydrological regime and
540 temperature and the potential eutrophication associated with stream regulation on the
541 invertebrate assemblages are generally supported by the results of the study. The overall
542 abundance and richness, resilience and resistance potential, sensitivity to pollution and food
543 specialization in invertebrate assemblages were found to be lower below the dams than above
544 the dams. The aquatic invertebrate assemblages above and below the dams significantly
545 responded to the combined effects of hydrology, temperature, and algal development. Even
546 moderate stream regulation seemed to promote eutrophication locally above the dams (site A3).
547 The reduction in basal resource use that occurred in the downstream sites (A5 and A6) below

548 the dams was found to narrow the isotopic niche (i.e. isotopic space that describes food web)
549 of invertebrates but local eutrophication (algal development) sometimes modified this scheme
550 (A4). Finally, the balance among functional feeding groups was unexpectedly found to be
551 similar below and above the dams. On the other hand, our hypotheses concerning groundwater
552 supplies are not supported because groundwater outlets only marginally influenced benthic
553 invertebrate assemblages and food web complexity despite their buffering effect on
554 temperature during summer and the stimulation of primary production by nutrient (especially
555 nitrate) supplies.

556

557 *4.1. Main drivers of benthic invertebrate assemblages between sectors and among sites*

558 The co-inertia analysis suggested that hydrological (flow pulses) and thermal (temperature
559 variations) conditions were the main drivers explaining changes in the invertebrate assemblage
560 structure between sectors. The damming conditions generated a global reduction in invertebrate
561 density and diversity at the sites below the dams. This reduction, which is expected in theory
562 for rivers of the same stream order as the Ain River (Ward and Stanford, 1983a), has generally
563 been observed elsewhere (e.g. Fleituch, 2003; Kjærstad *et al.*, 2017; Mellado-Diaz *et al.*, 2019).
564 As observed in other studies (Krajenbrink *et al.*, 2019), the number of Ephemeroptera and
565 Plecoptera taxa was especially affected due to their sensitivity to habitat alteration. However,
566 this reduction was especially observed at the two downstream sites (A5 and A6). Even if the
567 dams similarly affected discharge dynamics and thermal changes, eutrophication (dense algal
568 development) and high quantities of basal food sources (e.g., CPOM) seemed to buffer the
569 effects of stream regulation at site A4. This interpretation was supported by the wider isotopic
570 niche of invertebrate food web measured in site A4 than in sites A5 and A6. Indeed, this result
571 highlighted that food webs were mainly fuelled by algal sources in A5 and A6 sites whereas
572 food webs were based on more diversified food sources (algae and detritus) in site A4. In

573 addition, the fact that sites A3 and A4, characterized by the highest algal growth, had the
574 highest density and diversity of invertebrates suggests that algal development on cobbles and
575 stones was an important local condition favouring benthic invertebrates. Indeed, it has been
576 demonstrated in the literature that biofilms (including bryophytes) that develop on hard
577 substrates act as both a preferential habitat (Linhart *et al.*, 2002) and a food source (Suren,
578 1992) for a wide range of benthic invertebrates (Wulf and Pearson, 2017). Local nutrient
579 enrichment and eutrophication could thus have a positive influence on the biological
580 compartment of the Ain River. Nevertheless, this interpretation cannot be extended to all lotic
581 systems because the water flow dynamics in the Ain River facilitate the oxygenation of water
582 and prevent the occurrence of low-oxygen conditions associated with eutrophication in the
583 water column (Table 2). Indeed, eutrophication may generate water column anoxia that can
584 markedly damage the benthic life when hydrological conditions are not strong enough to
585 efficiently reoxygenate the water column (see Parr and Mason, 2004 and Pardo and Garcia,
586 2016 for examples in lowland streams).

587

588 *4.2. Biological traits of the invertebrates above and below the dams*

589 The invertebrate taxa found below the dams were generally more resilient and resistant than
590 the taxa found above the dams. These results fit well with observations from the literature
591 showing that hydrological disturbances such as those generated by dam functioning can select
592 for small, multivoltine species with short life spans (Wallace, 1990). A higher number of
593 generations per year is expected to occur under unstable conditions, as it allows rapid
594 population growth and an increase in resilience capacity in invertebrates (Townsend and
595 Hildrew, 1994) as observed elsewhere (e.g. Usseglio-Polatera and Beisel, 2002; Statzner *et al.*,
596 2010; Feio and Dolédec, 2012). The biological trait approach thus appears as highly relevant
597 for highlighting the hydrological impacts on benthic invertebrate assemblages; resilience traits

598 were apparently not affected by trophic resources or eutrophication at each site, which suggests
599 some specificity in their responses (see e.g. Mondy *et al.*, 2016). We did not find significant
600 differences in traits associated with tolerance to eutrophication between the two sectors. This
601 result is coherent with the analyses performed on algae, which did not indicate any differences
602 in eutrophication status between the two sectors. In contrast, we observed a higher proportion
603 of biological traits associated with tolerance to pesticides at sites below the dams than at sites
604 above the dams suggesting a difference in pesticide exposure. In addition, ovoviviparity, a
605 parental care strategy that may prevent high egg mortality in harsh environmental conditions,
606 was prominent below the dams. This egg protection trait has been shown to increase in the
607 presence of pesticides (Kuzmanovic *et al.*, 2017). The higher pesticide resistance of
608 invertebrates sampled below the dams is consistent with the surrounding land use patterns
609 because crop production occurred predominantly in sites below the dams (see Table 1), and
610 this agricultural practice is often associated with pesticide use (e.g., Papadakis *et al.*, 2018).
611 Under these conditions, it is thus not surprising that the eutrophication response traits of species
612 were not tightly linked with algal development at the sites because herbicides might have
613 impaired algae growth at sites below the dams (especially in sites A5 and A6, which had low
614 algal development). An additional explanation for the biological trait distribution among the
615 sites could be linked to the physical disturbances that change channel morphodynamics below
616 the dams (e.g., Brenna *et al.*, 2020). Indeed, Rollet *et al.* (2013) showed that changes in
617 sediment transport in the Lower Ain River resulted in bed coarsening and sediment instability,
618 and their pavement index, measuring river bed alteration, was high in one reach (corresponding
619 to our site A4) and low in another reach (corresponding to our two last sites, A5 and A6). Such
620 sediment instability may also favour resilient traits (e.g. multivoltine taxa see Fig. 5B;
621 Townsend and Hildrew, 1994). Thus, the responses of invertebrate biological traits below the
622 dams may result from both physical disturbances and chemical stresses. To evaluate whether

623 the chemical impacts of pesticides on algae and invertebrates are a relevant explanation of the
624 benthic invertebrate assemblages' structure and functioning, the content of pesticides and
625 herbicides in the sediment are needed to assess the contamination levels at the six studied sites.

626

627 Another set of traits addresses invertebrate functional feeding groups of invertebrates (FFGs).
628 According to the river continuum concept (RCC; Vannote *et al.*, 1980), FFGs along a stream
629 should shift from a dominance of shredders upstream associated with high CPOM availability
630 (due to dense riparian vegetation) to a dominance of grazers, scrapers and collectors
631 downstream, where the riparian vegetation is no longer the main food source for stream
632 invertebrates. In line with several studies and reviews highlighting the limits on the application
633 of the RCC (e.g. Statzner and Higler, 1985), dams seem to modify the natural stream zonation
634 of food sources and their associated FFGs from the upstream sector to the downstream sector
635 in the Ain River. Indeed, the balance in functional feeding groups was unexpectedly similar
636 below and above the dams; for example, site A4, below the dams presented the same proportion
637 of shredders as site A1 above the dams. Relatedly, in terms of organic matter resources, site
638 A4 was characterized by a CPOM content (6.03 mg/m² of organic carbon) comparable to that
639 observed at site A1 (7.83 mg/m² of organic carbon). As suggested by Sanchis-Ibor *et al.*
640 (2018), the changes in channel morphodynamics caused by dams can favour the presence of a
641 riparian vegetation made up of pioneering tree species (e.g. *Salix*, which are prominent trees
642 on the Lower Ain, see Rollet *et al.*, 2013). Tree installation on gravel bars may in turn both
643 reduce sediment mobility and feed the river with leaf litter and woody debris. Thus, the bed
644 artificialization associated with dams can also affect the availability of resources at each site
645 and the FFG distribution along the river course.

646

647 *4.3. Food web responses to environmental factors*

648 Above the dams, we observed an increase in the isotope space area from upstream to
649 downstream that was mainly driven by an increase in the basal resource diversity used by the
650 invertebrate assemblages. Such an increase has been observed in unregulated rivers and
651 generally suggests a structural change in the food web along the longitudinal gradient
652 (Winemiller *et al.*, 2011; Hette-Tronquart *et al.*, 2016). Indeed, the increase of food web
653 diversity from site A1 to site A3 above dams highlighted modifications of food sources used
654 by invertebrate communities: a detritus-based food web dominated in site A1 whereas a food
655 web based on both algae and detritus occurred in site A3. The decrease in the isotope space
656 area below the dams (from site A4 to site A6) indicates a decrease in the diversity of resource
657 use and in the number of trophic levels. This decrease could be explained by the wide diversity
658 of resources (algae and detritus) fuelling invertebrate food web in site A4 whereas food web in
659 site A6 was uniquely based on algae. Thus, changes in food sources may have caused the
660 reduction in the prey diversity, which is potentially corroborated by the trend of decrease in
661 taxonomic diversity and invertebrate abundance at the last two sites (Table 4A). This resource
662 use decrease appeared to be negatively correlated with the discharge values and their rates of
663 variation. Marty *et al.* (2009) showed comparable results in boreal rivers where high ramping
664 rates during hydropeaking were responsible for a one-trophic-level decrease in the length of
665 the food chain between macroinvertebrates and fish. Stream hydrodynamics thus appear to be
666 the dominant factor in structuring the invertebrate assemblages, as positive correlations
667 between food resources and their use by benthic invertebrates were only detected during low
668 flow conditions (summer 2015). At this time, a positive relationship was observed between the
669 quantity of energy (organic carbon) in the benthic environment and the area of the food web of
670 the benthic invertebrates. According to the literature (Wright, 1983; Smith, 2007), this
671 relationship could be due to the positive species-energy relationship encountered in many
672 ecosystems. More precisely, an increase in energy (available resources) increases the ability of

673 trophic specialists to develop persistent populations (Evans *et al.*, 2005). Consequently, these
674 specialist species increase the isotopic area of the food web by feeding on one or two resources
675 without mixing isotopic signatures from several sources as generalist species would do
676 (Layman *et al.*, 2007; Hette-Tronquart *et al.*, 2016). Increases in basal energy resources would
677 allow the development of predatory levels (Oksanen *et al.*, 1981; Mermillod-Blondin *et al.*,
678 2020). This pattern was observed in summer with the linear relationship between the organic
679 carbon content and the $\delta^{15}\text{N}$ range. Therefore, the trophic structure of benthic fauna was
680 dominated by resources (bottom-up control) in summer. However, the same connections
681 between the total organic carbon content and the isotopic indexes were not observed on the two
682 other sampling dates when hydrological conditions were less stable than in summer. Indeed,
683 significant correlations between hydrological variables and isotopic areas were observed in
684 spring and fall, while this kind of result has not been detected in summer. We can thus conclude
685 that hydrological disturbance appeared to be the main stressor on trophic food webs in the Ain
686 River and that it disrupted the observed connection between food webs and basal resources
687 (e.g. Menge *et al.*, 2002).

688

689 *4.4. Upwelling zones as refuges for benthic invertebrates during harsh thermal conditions*

690 According to the literature (White *et al.*, 1987; Capderrey *et al.*, 2013), upwelling zones are
691 cooler than downwelling zones during the summer, when water temperatures are the highest
692 and potentially harshest for benthic invertebrates. This difference in temperature is also
693 associated with a reduction in dissolved oxygen concentrations in upwelling zones compared
694 with those in downwelling zones. This pattern of dissolved oxygen concentrations is due to the
695 contrast between the highly oxygenated water of the Ain River downwelling in sediments and
696 the moderately oxygenated groundwater upwelling from hyporheic and/or riparian zones. As
697 aerobic microbial processes reduce the dissolved oxygen concentration in water during its

698 transfer through sediments (Jones Jr *et al.*, 1995; Boulton *et al.*, 1998), upwelling water, which
699 is characterized by a higher retention time in sediments than downwelling water, is more
700 depleted in dissolved oxygen. In line with the literature (Valett *et al.*, 1994; Dahm *et al.*, 1998),
701 the groundwater supply was also richer in nitrate than the surface waters. Despite these
702 differences in benthic conditions between the upwelling and downwelling zones, the variation
703 in groundwater supply moderately affected the composition of benthic invertebrate
704 assemblages and their life history traits (e.g., reduction in small and short-lived organisms).
705 Even in summer, when the thermal conditions were the harshest for benthic fauna, the
706 upwelling zones did not act as efficient refugia for invertebrates. This lack of an effect may be
707 associated with the fact that (i) the thermal conditions were not very stressful for invertebrates
708 as most taxa found in the sites below dams are generally resistant to higher temperatures and
709 oxygen depletion, as is typical for generalists, and (ii) most epigeal invertebrates are quite
710 mobile and may not use cool upwelling zones permanently (taxa can move from one patch to
711 another for foraging activities and can recover from damage induced by thermal stress during
712 foraging periods by resting periods in cool habitats; see e.g. Colinet *et al.*, 2015). As observed
713 by Capderrey *et al.* (2013), who demonstrated significant effects of surface-groundwater
714 exchanges on hyporheic invertebrates but no effects on benthic fauna, the upwelling flow of
715 groundwater directly into the main channel might not be sufficient to affect habitat conditions
716 in the benthic zones of the Ain River. Supporting this interpretation, we did not find a positive
717 influence of the nutrient enrichment associated with upwelling zones on benthic algae, whereas
718 this influence has been observed in many streams (e.g. Grimm and Fisher, 1989; Pepin and
719 Hauer, 2002; Hunt *et al.*, 2006). Therefore, the selected upwelling zones in the Ain River were
720 probably too spatially restrained to allow the development and maintenance of specific benthic
721 invertebrate assemblages.

722

723 4.5. Concluding remarks

724 Understanding the combined effects of different stressors and the contribution of each stressor
725 to the structure and function of aquatic communities remains crucial for managers in addressing
726 restoration goals and mitigation measures. We observed that stream hydrology is a key driver
727 aquatic invertebrate assemblage and that the modification of the interplay between water and
728 sediment transport may inhibit biological processes in some areas while favouring these
729 processes in other areas. In addition, the temporal variation in the hydrological regime may
730 have a different effect on the biological processes since, for example, the responses of the food
731 web structure to the available resources were visible only during a certain season. These
732 spatiotemporal changes must be considered in the design of future studies. As a second
733 outcome of our study, combining approaches based on biological traits and stable isotope
734 analyses provides better insights into the biological process patterns since these approaches are
735 complementary in evaluating invertebrate assemblage changes and modifications in species
736 feeding behaviours. On the one hand, the biological trait-based approach provides information
737 about the substantial impacts of environmental stressors on benthic fauna and contributes to
738 understanding the potential of an assemblage in terms of resistance and/or resilience to
739 disturbance and in terms of trophic specialization. On the other hand, isotopic food web metrics
740 can highlight “short” temporal changes in the structuring of benthic invertebrates, since food
741 web characterization using isotopic analyses may reveal changes in the feeding behaviour of
742 invertebrates due to short-term stressors. Nevertheless, repeated measurements of the isotopic
743 niche at the downstream site (A6) demonstrated a long-term pattern. At this site, the lower
744 diversity of the resources supporting the food web ($\delta^{13}\text{C}$ range) and the reduced length of the
745 trophic chains ($\delta^{15}\text{N}$ range) in comparison with those at the other sites indicated a reduction in
746 the trophic linkages and a simplification of the food web, which are characteristics of low-
747 stability food webs (Post *et al.*, 2000; Rooney *et al.*, 2006). Finally, we recommend the use of

748 both biological trait-based and stable isotope-based approaches to clarify the complex impacts
749 of multiple stressors on stream communities at different spatial and temporal scales.

750

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763

764 **Figure legends**

765 **Figure 1.** (A) Map showing the 6 study sites (noted A1 to A6) along the Ain river. Reservoirs
766 are identified by light blue colour. Insert indicates the position of the catchment on the right
767 side of the Rhône river. (B) Diagram showing the hydrological exchanges between surface
768 flow and groundwaters (downwelling) and between groundwaters and surface flow (upwelling)
769 within a gravel bar.

770

771 **Figure 2.** Average daily discharge variations in (A) site A3 (above the dams) and (B) site A4
772 (below the dams). Invertebrate sampling occasions are indicated by arrows.

773

774 **Figure 3.** Average daily temperature variations in (A) site A3 (above the dams) and (B) site
775 A4 (below the dams) and showing downwelling (black) and upwelling (dashed grey) values
776 over the study period.

777

778 **Figure 4.** Result of a co-inertia analysis between the invertebrate assemblage composition and
779 environmental factors depicting hydrology, temperature and eutrophication. (A) First-two co-
780 inertia axes position of samples from the faunistic (squares) and environmental dataset (dots),
781 respectively and green (faunistic dataset). Samples made above and below dams are coloured
782 in blue and green respectively. Labels are positioned at the center of gravity of the samples
783 belonging to a site (faunistic dataset). (B) Environmental factor loadings along the first-two
784 co-inertia axis (E1: cyanobacteria density; E2: chlorophyte density; E3: diatom density; E4:
785 Chlorophyll-a concentration; Tm: average temperature; Ts: standard deviation of the
786 temperature; Tr: temperature range; Qp: number of extreme ecological events; Qm: average
787 discharge; Qs: standard deviation of the discharge; Qc: coefficient of variation of the
788 discharge). (C) Same as (A) for the second and third co-inertia axes. D. Same as B for the
789 second and third co-inertia axes.

790

791 **Figure 5.** Violin plot showing the probability density curves of changes in the proportion of
792 individuals being (A) multivoltine, (B) ovoviviparous, (C) sensitive to pollution (oligotrophic)
793 and (D) to pesticides and functional feeding groups with (E) filtering feeders, (F) shredders,
794 (G) scrapers and (D) predators in each site along the river course. Sites above dams are in grey
795 and those below dams are in white. The dotted vertical line marks the dam separation. Large
796 dots stand for median and small dots represent the data ($n=72$ per site).

797

798 **Figure 6.** Violin plot showing the probability density curves of changes in (A) food and (B)
799 trophic status specialization at each site along the river course. Sites above dams are in grey
800 and those below dams are in white. The dotted vertical line marks the dam separation. Large
801 dots stand for the median value and small dots represent the data ($n=72$ per site).

802

803 **Figure 7.** Violin plot showing the probability density curves of changes in (A) the normalized
804 isotopic areas (SEAnr), (B) the diversity of the exploited basal resources (range of $\delta^{13}\text{C}$, CR),
805 and (C) the diversity of trophic levels (range of $\delta^{15}\text{N}$, NR) along the river course at each site.
806 Sites above dams are in grey and those below dams are in white. The dotted vertical line marks
807 the dam separation. Large dots stand for the median value and small dots represent the data
808 ($n=6$ per site).

809

810 **Figure 8.** Relationship between the amount of total organic carbon and the normalized isotopic
811 area (SEAnr) at each sampling date.

812

813 **Table Captions**

814 **Table 1.** General characteristics of the study sites.

815

816 **Table 2.** A priori hypotheses and rationale of expected changes in invertebrate trait metrics
817 selected in this study.

818

819 **Table 3.** (A) Flow ($n=36$) and temperature ($n=72$) characteristics in each study site
820 (mean \pm standard deviation). (B) Chemical parameters in each study site (mean \pm standard
821 deviation, $n=432$ for oxygen and $n=360$ for other parameters) Significance of mixed ANOVAs

822 are given for fixed (UD: zone; Se: sector, Da: sampling date) interactions, and random effects
823 (**P<0.001; *P<0.01; . P<0.1; ns: non-significant).

824

825 **Table 4.** Algal (A) and invertebrate (B) metrics in each study site (mean±standard deviation;
826 $n=72$ and $n=432$ for algal and invertebrate metrics respectively). Significance of mixed
827 ANOVAs are given for fixed (UD: zone; Se: sector, Da: sampling date) interactions, and
828 random effects (**P<0.001; *P<0.01; . P<0.1; ns: non-significant).

829

830 **Table 5.** Invertebrate trait metrics in each study site (mean±standard deviation, $n=432$)
831 separated into resilience and resistance trait (A), functional feeding groups (B) and trophic
832 specialization (C). Significance of mixed ANOVAs are given for fixed (UD: zone; Se: sector,
833 Da: sampling date) interactions, and random effects (**P<0.001; *P<0.01; . P<0.1;
834 ns: non-significant).

835

836 **Table 6.** Resource (A) and niche metrics (B) in each study site (mean±standard deviation,
837 $n=36$). Significance of mixed ANOVAs are given for fixed (UD: zone; Se: sector, Da: sampling
838 date) interactions, and random effects (SEAnr: normalized isotopic area; CR: index of basal
839 resource exploitation; NR: index of trophic level diversity) (**P<0.001; *P<0.01; . P<0.1;
840 ns: non-significant).

841

842

843 **Appendices**

844 **Appendix 1.** Community matrix showing the abundance of taxa summed by sampling zone
845 ($n=6$) and collected above the dams with the indication of sampling date (“1408” to “1606”),
846 sampling site (“A1” to “A6”), and sampling zone (“u” for upwelling, “d” for downwelling).
847 Taxa are listed in alphabetical order.

848

849 **Appendix 2.** Community matrix showing the abundance of taxa summed by sampling zone
850 ($n=6$) and collected below the dams with the indication of sampling date (“1408” to “1606”),
851 sampling site (“A1” to “A6”), and sampling zone (“u” for upwelling, “d” for downwelling).
852 Taxa are listed in alphabetical order.

853

854 **Appendix 3.** Trait matrix showing values for (a) maximum size, (b) life duration, (c) number
855 of generations per year, (d) reproduction type, (e) dispersal, (f) food types, (g) feeding habits,
856 (h) trophic status, and (i) SPEAR pesticide sensitivity. Values in (a-h) represent affinity scores
857 (fuzzy coding). Values in (i) equal "1" if the taxon is sensitive to pesticide, "0" otherwise (NA:
858 not available) (extracted from Tachet *et al.* (2010) and Schmidt-Kloiber and Hering (2015)).

859

860 **Supplementary information**

861 **Figure S1.** First-two axes taxon scores yielded by the co-inertia analysis between the
862 invertebrate assemblage composition and the environmental variables depicting hydrology,
863 temperature and eutrophication. Scores are separated by taxonomic groups with (A) Mollusca,
864 Hirudinea and Tricladida; (B) Crustacea, Hydracarina and Heteroptera; (C) Coleoptera; (D)
865 Diptera; (E) Ephemeroptera; (F) Odonata; (G) Plecoptera; (H) Trichoptera.

866

867 **Figure S2.** Changes in the amount of total carbon and five main basal resources along the river
868 course. Sites above dams are in grey and those below dams are in white. The dotted vertical
869 line marks the dam separation.

870

871 **Figure S3.** Carbon and Nitrogen isotope compositions of invertebrate taxa (open dots) and
872 resources (see legend) in spring (A), summer (B) and fall (C). The ellipse corresponds to the
873 SIBER ellipse without normalisation by the composition of the resources.

874

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Table 1. General characteristics of the study sites.

	A1	A2	A3	A4	A5	A6
Latitude	46°44'28.5"N	46°41'09.9"N	46°36'00.0"N	46°02'42.9"N	45°57'28.6"N	45°48'31.4"N
Longitude	5°47'39.9"E	5°45'57.0"E	5°41'52.3"E	5°19'56.1"E	5°14'58.6"E	5°11'33.3"E
Elevation (m)	469	458	436	234	216	188
Source distance (km)	47	53	67	151	170	186
Flow	Natural	Natural	Moderately regulated	Regulated	Regulated	Regulated
Land use	Mixed forest, extensive pasture	Mixed forest, extensive pasture	Mixed forest, extensive pasture	Alluvial forest, crops	Alluvial forest, crops	Alluvial forest, crops

Table 2. A priori hypotheses and rationale of expected changes in invertebrate trait metrics selected in this study.

Metric	Trait category	Rationale
Maximum size	≤10 mm	Should increase below dams due to better resilience ability in response to hydropeaking
Life cycle duration	≤1 yr	<i>idem</i>
Nb of generations per year	Multivoltine	<i>idem</i>
Dispersal	Aquatic passive	<i>idem</i>
Reproduction	Ovoviviparity	Should provide a better resistance to human disturbance though egg protection
Trophic status	Oligotrophic	Eutrophication should decrease the proportion of oligotrophic taxa below dams
Shredder	Shredders	Should decrease below dams due to the retention of CPOM in reservoirs
Scraper	Scrapers	Eutrophication and POM reduction below dams should increase proportions of algae-food scrapers
Filtering-feeder	Filtering-feeders	Should decrease below dams due to the reduction of POM below dams
Predator	Predators	Should decrease below dams due to a reduction of detritus-based food web
Food diversity (Rao)	all food types	<i>idem</i>
Food community specialization	all food types	<i>idem</i>
Trophic status community specialization	all trophic status types	<i>idem</i>
SPEAR pesticide (% abundance)	-	Should decrease in sites located in areas with high crop production

Table 3. (A) Flow ($n=36$) and temperature ($n=72$) characteristics in each study site (mean±standard deviation). (B) Water chemistry in each study site (mean±standard deviation, $n=432$ for oxygen and $n=360$ for other parameters) Significance of mixed ANOVAs are given for fixed (UD: zone; Se: sector, Da: sampling date) interactions, and random effects (*** $P<0.001$; ** $P<0.01$; * $P<0.05$; . $P<0.1$; ns: non-significant).

	A1	A2	A3	A4	A5	A6	UD	Se	Da	Se:UD	Se:Da	UD:Da	random
A													
Flow ($m^3.s^{-1}$)	35±26	37±27	38±27	124±81	138±92	133±104	-	***	***	-	***	-	ns
Pulse	1-4	1-4	1-4	1-10	1-10	1-10	-	***	ns	-	-	-	ns
Flow CV	0.67	0.66	0.58	0.58	0.65	0.60	-	ns	***	-	***	-	ns
Temperature (°C)	12.1±4.6	12.4±3.7	13.8±5.2	13.8±3.9	14.2±4.3	14.2±4.1	ns	*	***	ns	***	**	**
Temperature range (°C)	5.5±3.6	5.0±1.0	7.7±3.4	3.1±3.7	4.9±3.3	4.8±3.0	**	ns	***	**	ns	ns	ns
B													
Dissolved oxygen ($mg. L^{-1}$)	10.8±1.2	11.1±2.3	11.4±1.0	10.0±1.8	9.5±1.9	10.9±1.7	**	.	***	ns	***	ns	***
Electric conductivity ($\mu S.cm^{-1}$)	400±24	408±19	383±38	364±27	389±13	376±9	ns	.	***	ns	***	ns	***
N-NO ₃ ($mg. L^{-1}$)	0.87±0.09	0.85±0.14	0.69±23	0.63±0.17	0.84±0.16	0.92±0.13	***	ns	***	.	***	.	***
N-NH ₄ ($\mu g. L^{-1}$)	20.3±9.5	21.3±13.6	26.0±15.3	26.3±13.4	19.5±13.7	16.0±11.1	-	-	-	-	-	-	-
P-PO ₄ ($\mu g. L^{-1}$)	10.0±7.9	11.3±9.0	6.3±6.5	8.3±3.8	7.7±2.8	7.4±4.1	-	-	-	-	-	-	-

Table 4. Algal (A) and invertebrate (B) metrics in each study site (mean±standard deviation; $n=72$ and $n=432$ for algal and invertebrate metrics, respectively). Significance of mixed ANOVAs are given for fixed (UD: zone; Se: sector, Da: sampling date) interactions, and random effects (*** $P<0.001$; ** $P<0.01$; * $P<0.05$; . $P<0.1$; ns: non-significant).

Station	A1	A2	A3	A4	A5	A6	UD	Se	Da	Se:UD	Se:Da	UD:Da	random
A													
Cyanobacteria (10^6cells.m^{-2})	1.8±2.4	1.8±21.9	2.4±3.0	5.1±4.6	0.3±0.6	1.6±2.6	ns	ns	***	ns	**	ns	***
Chlorophytes (10^6cells.m^{-2})	0.3±0.4	0.5±0.6	0.4±0.3	0.7±0.8	0.2±0.1	0.3±0.3	ns	ns	***	ns	***	ns	***
Diatoms (10^6cells.m^{-2})	0.6±0.8	0.8±0.7	0.7±0.6	1.2±0.7	0.2±0.3	0.8±0.9	ns	ns	***	ns	**	ns	***
Chlorophyll- <i>a</i> (mg.cm^{-2})	1.9±92.3	2.6±2.6	2.6±2.6	4.1±2.7	0.5±0.4	1.2±1.2	ns	ns	***	ns	***	ns	***
B													
Total abundance	522±410	432±351	533±586	834±774	225±318	186±240	*	ns	***	ns	***	ns	***
Richness	23±6	22±9	24±7	23±5	16±6	14±6	ns	ns	***	ns	***	ns	***
Shannon diversity	2.1±0.3	2.0±0.4	2.1±0.4	1.9±0.3	1.9±0.5	1.7±0.5	ns	**	***	ns	***	*	***

Table 5. Invertebrate trait metrics in each study site (mean±standard deviation, $n=432$) separated into resilience and resistance trait (A), functional feeding groups (B) and trophic specialization (C). Significance of mixed ANOVAs are given for fixed (UD: zone; Se: sector, Da: sampling date) interactions, and random effects (*** $P<0.001$; ** $P<0.01$; * $P<0.05$; . $P<0.1$; ns: non-significant).

	A1	A2	A3	A4	A5	A6	UD	Se	Da	Se:UD	Se:Da	UD:Da	random
A													
Maximal size <10 mm	0.63±0.09	0.67±0.09	0.68±0.05	0.63±0.06	0.64±0.09	0.64±0.10	**	ns	***	***	***	ns	**
Life duration <1 y.	0.69±0.06	0.75±0.06	0.71±0.06	0.67±0.08	0.68±0.11	0.71±0.12	**	ns	***	**	***	ns	***
Multivoltine	0.33±0.05	0.36±0.05	0.39±0.06	0.42±0.05	0.43±0.09	0.47±0.07	ns	*	***	ns	*	.	***
Aquatic passive dispersal	0.37±0.02	0.34±0.03	0.37±0.03	0.39±0.03	0.40±0.05	0.38±0.05	**	.	***	ns	**	ns	***
Ovoviviparity	0.11±0.04	0.08±0.04	0.13±0.05	0.19±0.05	0.19±0.09	0.17±0.10	**	*	***	***	***	ns	***
Oligotrophic	0.47±0.04	0.45±0.04	0.40±0.03	0.36±0.03	0.40±0.05	0.39±0.06	.	.	***	*	ns	ns	***
Pesticide sensitivity	10.5±3.8	9.3±4.7	8.3±3.2	7.8±2.7	5.4±2.8	4.7±3.1	ns	*	***	ns	***	ns	***
B													
Shredders	0.29±0.04	0.23±0.05	0.25±0.05	0.30±0.05	0.31±0.07	0.25±0.09	***	ns	***	***	***	ns	***
Scrapers	0.38±0.05	0.38±0.06	0.35±0.04	0.29±0.05	0.37±0.07	0.35±0.06	*	ns	***	ns	***	ns	***
Filter feeders	0.06±0.03	0.12±0.05	0.12±0.05	0.10±0.04	0.08±0.05	0.13±0.07	**	ns	***	*	***	ns	***
Predators	0.15±0.04	0.13±0.04	0.13±0.04	0.18±0.04	0.13±0.05	0.15±0.06	ns	ns	***	ns	***	ns	***
C													
Food Rao diversity	0.12±0.03	0.13±0.05	0.13±0.04	0.13±0.04	0.13±0.04	0.12±0.05	*	ns	***	***	ns	ns	*
Food specialization	0.31±0.04	0.32±0.04	0.32±0.04	0.32±0.04	0.29±0.06	0.29±0.04	ns	ns	***	ns	ns	ns	***
Trophic status specialization	0.26±0.02	0.24±0.02	0.22±0.010	0.21±0.01	0.22±0.02	0.21±0.02	ns	ns	***	**	***	ns	***

Table 6. Resource (A) and niche metrics (B) in each study site (mean±standard deviation, $n=36$). Significance of mixed ANOVAs are given for fixed (UD: zone; Se: sector, Da: sampling date) interactions, and random effects (SEAnr: normalized isotopic area; CR: index of basal resource exploitation; NR: index of trophic level diversity) (*** $P<0.001$; ** $P<0.01$; * $P<0.05$; . $P<0.1$; ns: non-significant).

	A1	A2	A3	A4	A5	A6	UD	Se	Da	Se:UD	Se:Da	UD:Da	random
A													
Shannon diversity	1.06±0.26	0.96±0.20	1.09±0.26	0.99±0.54	1.05±0.19	0.96±0.24	ns	ns	.	.	ns	ns	ns
CPOM	0.56±0.76	0.06±0.08	0.09±0.08	0.43±0.61	0.31±0.33	0.07±0.07	.	ns	ns	ns	ns	.	ns
FPOM	0.08±0.02	0.11±0.09	0.30±0.41	0.65±0.74	0.12±0.06	0.04±0.06	ns	ns	ns	ns	ns	ns	**
Sedimentary biofilm	0.23±0.28	0.01±0.00	0.00±0.00	0.06±0.06	0.04±0.04	0.02±0.02	ns	ns	ns	ns	ns	ns	***
Perilithon	0.23±0.16	0.25±0.18	0.16±0.14	0.52±0.40	0.18±0.12	0.17±0.19	ns	ns	*	*	ns	ns	ns
mosses	0.16±0.36	0.43±0.51	0.16±0.18	1.89±1.56	0.42±0.85	0.14±0.25	ns	ns	ns	ns	ns	ns	.
Total C	17.7±10.8	16.1±11.5	15.7±18.2	52.9±21.9	14.9±11.8	6.0±5.2	ns	ns	ns	ns	ns	ns	**
B													
SEAnr	40.2±14.1	39.5±12.8	59.4±22.4	44.1±18.6	37.7±7.4	23.6±8.9	ns	*	**	ns	*	ns	*
CR	7.7±1.0	8.2±0.9	10.0±2.1	9.6±3.0	10.4±3.4	6.7±0.9	ns	ns	.	ns	ns	ns	.
NR	7.6±1.4	6.2±1.2	6.7±1.1	9.2±2.8	7.0±0.9	5.3±1.6	ns	ns	ns	ns	ns	ns	*

Appendix 1. Community matrix showing the abundance of taxa summed by sampling zone (n=6) and collected above the dams with the indication of sampling date (“1408” to “1606”), sampling site (“A1” to “A6”), and sampling zone (“u” for upwelling, “d” for downwelling). Taxa are listed in alphabetical order.

	1408		1410		1504		1407		1410		1606		1408		1410		1504		1407		1410		1606		1408		1410		1504		1407		1410		1606				
	A1d	A1u	A1d	A1u	A1d	A1u	A1d	A1u	A1d	A1u	A1d	A1u	A2d	A2u	A2d	A2u	A2d	A2u	A2d	A2u	A2d	A2u	A2d	A2u	A3d	A3u	A3d	A3u	A3d	A3u	A3d	A3u	A3d	A3u	A3d	A3u			
<i>Amphinemura</i> sp.	0	0	3	5	0	2	0	0	2	1	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0		
<i>Ancylus</i> sp.	1	0	0	1	0	0	0	0	0	0	1	0	0	0	11	7	0	2	2	4	9	9	0	0	1	1	8	0	0	1	1	1	0	0	0	0	0		
Anthomyidae	4	0	0	1	0	0	1	4	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0		
<i>Asellus</i> sp.	0	0	0	2	0	1	0	0	1	3	0	0	0	0	5	2	0	0	0	0	2	5	0	0	13	191	81	86	1	14	38	1	260	5	1	2	2		
<i>Atherix</i> sp.	3	3	1	2	1	2	20	3	4	3	1	2	10	44	14	13	0	0	35	43	8	12	0	0	1	1	3	4	0	0	53	25	18	14	0	0	0		
<i>Athripsodes</i> sp.	0	0	0	1	0	0	0	0	3	7	10	15	0	0	0	0	0	0	0	0	28	25	5	10	0	1	1	4	3	0	0	0	38	5	24	10	10		
<i>Baetis</i> sp.	154	273	150	96	32	112	129	252	72	19	43	155	559	533	143	157	92	62	48	141	21	38	14	14	196	158	33	57	199	50	50	51	16	18	40	34			
<i>Bithynia</i> sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	23	2	0	0	0	0		
<i>Brychius</i> sp.	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Caenis</i> sp.	0	0	1	4	6	4	0	0	2	8	9	11	0	0	0	0	0	0	0	6	4	0	0	0	8	5	2	2	5	25	107	66	24	7	20	20			
<i>Calopteryx</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	7	1	0	0	0		
<i>Centroptilum</i> sp.	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	4	8	0	0	0	0	
<i>Ceraclea</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	2	1	1	0	0	24	4	2	0	0	0		
Ceratopogonidae	6	4	38	22	8	26	1	2	37	0	9	6	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	3	2	2		
<i>Cheumatopsyche</i> sp.	0	0	0	0	0	0	0	0	16	1	2	1	0	0	0	0	7	49	0	322	54	2	4	19	2	124	61	27	27	301	162	411	1901	7	14	14	14		
Chironomini	29	23	2	0	4	24	267	150	4	7	2	6	82	314	1	0	17	71	60	52	28	7	0	0	131	171	25	11	199	71	183	47	28	14	5	2			
<i>Dendrocoelum</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	
<i>Dinocras</i> sp.	0	1	0	1	0	0	5	1	3	0	0	0	2	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Dreissena</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dryops</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dugesia</i> sp.	0	0	2	2	1	0	2	3	68	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	8	3	0	4	13	2	30	108	0	0	0	0	
<i>Ecdyonurus</i> sp.	1	6	28	37	4	16	35	10	19	7	7	13	20	26	52	44	10	6	20	39	58	80	7	8	5	7	12	15	29	2	13	21	0	0	37	22	22		
<i>Elmis</i> sp.	40	43	70	100	14	95	454	69	981	66	11	10	64	165	159	127	28	20	89	66	595	751	0	3	126	65	321	380	59	22	583	94	645	522	12	7	7		
Empididae	21	24	22	27	5	73	22	9	21	7	2	8	8	13	25	11	4	3	1	2	10	14	0	0	4	3	2	5	4	2	1	1	3	2	0	0	0	0	
<i>Epeorus</i> sp.	0	0	9	5	1	2	0	0	0	2	0	0	1	0	14	6	8	25	0	0	1	0	0	0	0	7	3	3	1	0	0	0	0	0	0	0	0	1	1
<i>Ephemera</i> sp.	3	1	5	2	0	3	0	2	1	1	0	0	0	0	3	0	1	7	2	6	0	0	0	0	0	2	3	1	1	1	7	12	0	0	0	0	0	0	
<i>Erbobdella</i> sp.	6	1	7	3	1	3	5	3	8	18	2	0	0	3	5	6	0	1	2	13	5	11	0	0	1	0	0	2	3	14	26	20	9	1	4	4	4		

Appendix 1. Continued.

<i>Esolus</i> sp.	108	224	240	212	90	168	978	601	346	363	232	204	67	75	82	59	58	29	79	41	189	146	32	66	57	160	263	277	44	54	215	117	310	187	55	115		
<i>Gammarus</i> sp.	1065	549	439	896	336	584	1020	949	864	206	100	116	140	519	489	632	81	16	28	30	112	199	5	16	357	289	730	899	427	122	765	42	297	35	230	66		
<i>Glossiphonia</i> sp.	1	0	1	0	1	0	0	3	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	3	1	1	6	0	6	0	0	0	0		
<i>Habroleptoides</i> sp.	0	1	1	2	1	0	0	1	0	1	0	0	0	0	3	3	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	
<i>Habrophlebia</i> sp.	0	0	0	0	0	0	0	1	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Halipus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	
<i>Helobdella</i> sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	6	0	0	0	
<i>Hemiclepsis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	
<i>Heptagenia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	6	0	0	
Hydracarina	1	5	3	2	12	30	124	162	171	41	29	83	0	3	12	18	11	6	115	246	120	247	9	12	3	18	41	13	17	64	61	30	117	11	17	14		
<i>Hydraena</i> sp.	1	4	1	7	1	1	2	0	6	2	0	1	1	4	2	9	1	0	3	0	1	3	0	0	0	6	2	5	0	0	1	1	15	0	0	0	0	
Hydroporinae	0	0	0	0	0	0	5	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	4	1	0	0	0	0	
<i>Hydropsyche</i> sp.	37	39	30	154	1	18	49	19	694	32	4	4	73	370	380	217	31	52	226	45	276	972	2	4	93	11	317	507	44	28	1848	256	465	1144	13	3		
<i>Hydroptila</i> sp.	0	2	22	29	0	26	16	18	14	55	7	57	1	11	29	13	0	0	81	99	244	319	6	2	6	5	48	22	4	1	8	19	689	148	42	2		
<i>Ithytrichia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	45	17	0	0	0	
<i>Lepidostoma</i> sp.	0	0	0	3	0	0	9	5	2	2	1	1	2	28	21	5	0	1	60	140	76	217	1	0	3	1	3	6	0	8	1	0	19	7	11	0	0	
<i>Leuctra</i> sp.	78	133	13	22	43	62	400	185	17	28	176	269	113	151	5	5	13	7	26	43	21	25	32	67	25	39	0	2	3	5	61	74	12	10	114	109		
Limnephilinae	1	0	1	9	10	6	1	1	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Limnius</i> sp.	68	132	98	159	13	105	515	389	123	156	186	217	12	29	41	19	1	6	12	12	24	13	0	6	4	5	14	12	3	1	65	17	157	60	22	13		
Limoniidae	140	118	80	51	44	363	13	17	42	17	0	1	48	84	39	31	1	5	35	19	64	27	0	1	92	28	7	36	15	19	9	22	30	17	0	0		
<i>Metalype</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Micrasema</i> sp.	2	0	0	0	0	0	0	0	1	0	0	0	4	14	8	13	0	0	1	1	21	23	0	0	0	3	43	36	6	1	3	0	66	32	0	0	0	
<i>Micronecta</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mystacides</i> sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	4	0	2	1	0	0	0	
<i>Nemoura</i> sp.	0	0	3	3	0	0	0	0	3	6	0	0	0	6	6	0	0	0	0	0	3	3	0	0	0	0	4	0	1	1	0	0	1	1	0	0	0	
<i>Odontocerum</i> sp.	9	5	17	23	24	15	19	16	68	10	5	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Onychogomphus</i> sp.	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Orectochilus</i> sp.	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	1	10	14	0	1	0	0	5	7	1	0	8	2	11	54	0	0	0	
Orthoclaadiinae	618	825	269	291	145	1155	167	56	1135	1083	381	1165	1894	2160	631	450	93	77	182	259	1486	1154	313	292	1287	1196	169	373	287	186	586	162	801	486	1246	632		
<i>Oulimnius</i> sp.	0	0	1	0	0	5	3	1	7	9	1	0	0	3	7	6	0	0	3	5	98	81	0	0	7	122	122	63	4	8	31	55	238	59	2	5	0	
<i>Perla</i> sp.	1	4	4	1	0	0	5	0	5	1	0	0	3	3	5	2	2	5	1	1	2	2	0	2	0	1	1	1	0	1	1	1	1	1	1	2	0	0

Appendix 1. Continued.

Perlodidae	0	0	14	15	4	4	0	0	2	0	0	0	0	2	14	28	2	0	0	0	3	4	0	1	0	0	2	0	4	1	0	0	0	0	0	0	0	0	
<i>Piscicola</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
<i>Pisidium</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	89	2	0	4	0	0	
Planorbidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	3	1	11	4	2	0	0	0		
<i>Polycelis</i> sp.	0	0	0	1	1	3	0	0	0	0	0	1	0	0	1	2	0	0	0	0	4	3	0	0	0	14	9	13	2	2	4	0	25	0	1	0	0	0	
<i>Polycentropus</i> sp.	0	0	0	1	0	0	0	0	0	0	2	0	0	1	4	8	0	0	1	4	45	12	1	0	2	1	6	2	1	0	10	13	11	4	1	3	0	0	
<i>Potamanthus</i> sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
<i>Protonemura</i> sp.	0	0	0	8	0	0	2	0	64	0	1	0	1	0	4	1	0	0	0	0	1	6	0	0	0	0	0	2	0	0	0	0	0	0	0	1	8	4	0
Psychodidae	205	170	132	150	0	12	5	8	12	1	1	0	0	0	1	30	0	0	1	3	10	4	0	0	54	0	0	95	0	0	0	0	0	1	0	0	0	0	
<i>Psychomyia</i> sp.	0	3	6	8	4	22	0	0	14	23	2	9	0	0	8	16	0	1	5	0	91	48	2	4	4	4	12	9	13	5	9	17	19	41	3	1	0	0	
<i>Radix</i> sp.	9	11	7	13	12	5	1	0	22	43	1	1	0	0	1	1	0	0	0	2	47	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rhithrogena</i> sp.	0	1	96	19	18	8	0	1	38	48	6	3	1	0	8	16	41	33	0	0	35	36	4	4	0	0	10	2	20	49	0	0	0	0	2	1	2	0	
<i>Rhyacophila</i> sp.	21	23	30	35	14	22	0	2	30	8	0	2	57	67	64	59	4	8	5	18	38	56	0	0	26	8	16	42	9	5	9	12	1	7	5	5	0	0	
<i>Riolus</i> sp.	0	0	11	27	0	39	49	38	28	8	1	2	0	0	7	7	1	0	9	8	14	22	1	0	17	0	19	57	34	5	83	26	134	24	1	1	0	0	
<i>Sericostoma</i> sp.	26	26	32	81	21	39	7	12	45	77	16	51	0	10	5	15	0	3	0	4	9	6	0	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0	
<i>Serratella</i> sp.	23	66	68	155	6	2	532	239	0	0	251	750	59	79	93	64	5	0	198	209	0	0	230	184	79	40	7	13	4	4	434	144	1	0	211	113	0	0	
<i>Setodes</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0
<i>Silo</i> sp.	0	0	4	3	1	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simuliidae	0	5	12	31	109	2	0	4	67	8	35	17	2	27	4	2	41	439	28	195	9	57	355	369	9	9	3	4	158	280	95	4	498	207	1010	713	0	0	
<i>Siphonoperla</i> sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Stenelmis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	2	6	0	0	18	1	74	13	3	8	0	0		
Tabanidae	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanypodinae	19	17	1	12	4	13	147	86	23	6	11	32	5	15	1	0	0	0	79	84	14	10	1	2	9	18	6	5	3	2	29	33	28	7	24	3	0	0	
Tanytarsini	81	379	4	7	15	195	617	395	485	62	23	62	22	145	8	9	23	28	636	871	69	285	0	5	76	78	17	12	55	48	658	142	141	85	36	22	0	0	
Tipulidae	4	5	7	10	0	0	0	0	1	4	0	0	0	0	4	2	0	0	0	0	0	0	0	0	0	0	2	10	0	0	0	0	3	0	0	0	0	0	0
<i>Torleya</i> sp.	11	8	119	95	4	19	0	0	51	80	0	3	1	3	100	105	3	5	0	2	245	221	0	0	11	6	26	22	63	16	2	0	25	12	1	1	0	0	

Appendix 2. Community matrix showing the abundance of taxa summed by sampling zone (n=6) and collected below the dams with the indication of sampling date (“1408” to “1606”), sampling site (“A1” to “A6”), and sampling zone (“u” for upwelling, “d” for downwelling). Taxa are listed in alphabetical order.

	1408		1410		1504		1407		1410		1606		1408		1410		1504		1407		1410		1606		1408		1410		1504		1407		1410		1606			
	A4d	A4u	A4d	A4u	A4d	A4u	A4d	A4u	A4d	A4u	A4d	A4u	A5d	A5u	A5d	A5u	A5d	A5u	A5d	A5u	A5d	A5u	A5d	A5u	A6d	A6u	A6d	A6u	A6d	A6u	A6d	A6u	A6d	A6u	A6d	A6u		
<i>Amphinemura</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Ancylus</i> sp.	1	1	8	2	2	6	2	7	0	3	0	3	0	0	8	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthomyidae	1	16	0	9	0	0	0	0	6	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Asellus</i> sp.	188	417	183	206	43	282	1	74	52	119	106	285	1	2	3	7	4	1	0	13	19	180	0	2	2	0	1	4	0	0	0	0	4	84	0	3		
<i>Atherix</i> sp.	0	1	0	1	0	0	0	0	0	0	2	0	4	0	0	0	0	14	3	0	0	0	0	0	0	0	0	0	0	0	3	2	2	0	0	0		
<i>Athripsodes</i> sp.	2	0	6	21	49	81	16	6	5	5	40	82	0	0	2	2	20	6	1	2	6	47	24	15	0	0	0	2	7	1	0	1	6	22	3	22		
<i>Baetis</i> sp.	43	43	8	2	32	5	33	163	21	5	310	46	25	36	0	0	92	8	195	155	2	1	38	34	124	80	96	5	19	0	488	83	161	10	14	19		
<i>Bithynia</i> sp.	0	0	0	3	0	1	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
<i>Brychius</i> sp.	0	2	0	0	0	0	0	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Caenis</i> sp.	0	2	0	1	0	0	0	2	0	12	46	102	0	0	0	1	2	0	7	4	3	5	6	15	0	0	1	0	0	0	1	1	4	39	19	0		
<i>Calopteryx</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Centroptilum</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ceraclea</i> sp.	0	0	0	0	0	0	0	0	0	0	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
Ceratopogonidae	0	1	0	0	4	5	0	1	0	3	1	0	2	1	0	0	2	1	6	4	0	0	1	2	0	0	1	1	0	0	0	0	0	0	0	0	0	
<i>Cheumatopsyche</i> sp.	19	1	29	35	33	3	752	713	62	11	15	2	75	0	9	2	71	5	68	23	3	1	8	7	70	6	9	0	13	2	92	136	153	89	1	19		
Chironomini	170	66	1	254	270	69	198	206	1	32	20	7	253	4	0	0	229	8	48	39	0	0	19	3	25	39	0	2	25	0	8	59	1	0	1	0		
<i>Dendrocoelum</i> sp.	0	0	0	0	0	1	0	0	0	0	1	4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dinocras</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dreissena</i> sp.	1	2	1	0	0	2	5	0	4	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dryops</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	
<i>Dugesia</i> sp.	14	36	18	21	17	44	38	21	29	19	12	7	18	1	5	0	1	0	0	1	0	46	0	0	3	15	2	17	0	1	1	146	3	11	0	0	0	
<i>Ecdyonurus</i> sp.	0	0	0	0	0	0	1	0	0	0	1	1	0	0	4	8	0	4	0	3	2	1	0	2	0	1	0	0	0	0	1	0	16	6	0	4	0	
<i>Elmis</i> sp.	505	210	346	474	116	176	948	221	598	328	106	38	128	33	111	14	59	4	32	6	55	19	19	1	18	11	6	15	4	1	8	51	9	36	0	0		
Empididae	7	2	11	30	57	31	8	15	4	1	7	5	1	1	1	1	10	0	4	0	0	0	7	0	2	1	8	1	2	0	19	4	3	0	0	0		
<i>Epeorus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	1	0	0	0	0	0	0	
<i>Ephemera</i> sp.	0	1	0	1	5	7	0	8	0	2	2	6	0	0	0	0	0	3	5	0	0	6	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	
<i>Erpobdella</i> sp.	7	12	1	4	2	7	2	2	7	0	3	3	0	1	0	2	1	0	2	2	2	2	0	2	0	0	0	1	0	0	1	1	0	3	1	0	0	
<i>Esolus</i> sp.	5	12	10	21	9	48	8	24	32	40	12	32	50	142	84	81	150	54	66	222	91	272	42	80	55	9	152	61	79	32	42	18	246	101	32	166		

Appendix 3. Trait matrix showing values for (a) maximum size, (b) life duration, (c) number of generations per year, (d) reproduction type, (e) dispersal, (f) food types, (g) feeding habits, (h) trophic status, and (i) SPEAR pesticide sensitivity. Values in (a-h) represent affinities (fuzzy coding). Values in (i) equal "1" if the taxon is sensitive to pesticide, "0" otherwise (NA: not available) (extracted from Tachet *et al.* (2010) and Schmidt-Kloiber and Hering (2015)).

Taxa	(a)	(b)	(c)	(d)	(e)	(f)						(g)				(h)			(i)	
	< 10	< 1	>1	ovoviviparity	aquatic passive	micro organisms, < 1mm	dead plant ≥ 1mm	living micro phytes	living macro phytes	dead animal ≥ 1mm	living micro inver-tebrates	large animals	shredder	scraper	filter feeder	predator	oligotrophic	mesotrophic	eutrophic	pesticides
<i>Amphinemura</i> sp.	1.00	1.00	0.00	0.00	0.40	0.25	0.50	0.25	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.00	1.00	0.00	0.00	1
<i>Ancylus</i> sp.	0.50	1.00	0.00	0.00	0.50	0.00	0.22	0.56	0.22	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.67	0.33	0.00	0
Anthomyidae	0.75	1.00	0.75	0.17	0.00	0.13	0.00	0.13	0.13	0.00	0.00	0.63	0.25	0.00	0.00	0.75	0.00	0.25	0.75	1
Asellidae	0.49	0.51	0.71	1.00	1.00	0.17	0.50	0.17	0.17	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.18	0.55	0.27	NA
<i>Atherix</i> sp.	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.60	0.40	0.00	1
<i>Athripsodes</i> sp.	0.50	1.00	0.00	0.00	0.29	0.00	0.00	0.20	0.80	0.00	0.00	0.00	0.75	0.25	0.00	0.00	0.25	0.75	0.00	1
<i>Baetis</i> sp.	0.75	1.00	0.60	0.00	0.33	0.18	0.18	0.45	0.09	0.09	0.00	0.00	0.00	0.75	0.00	0.00	0.33	0.33	0.33	0
<i>Bithynia</i> sp.	0.75	0.50	0.00	0.00	0.67	0.08	0.15	0.38	0.08	0.08	0.15	0.08	0.00	0.33	0.67	0.00	0.00	0.60	0.40	0
<i>Brychius</i> sp.	1.00	0.25	0.75	0.00	0.33	0.00	0.00	0.50	0.50	0.00	0.00	0.00	0.50	0.00	0.00	0.50	0.50	0.50	0.00	0
<i>Caenis</i> sp.	1.00	1.00	0.75	0.00	0.40	0.50	0.20	0.10	0.10	0.10	0.00	0.00	0.25	0.00	0.00	0.00	0.17	0.50	0.33	1
<i>Calopteryx</i> sp.	0.00	0.50	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.33	0.50	0.17	1
<i>Centroptilum</i> sp.	1.00	1.00	1.00	0.00	0.29	0.40	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.60	0.00	0.00	0.40	0.60	0.00	0
<i>Ceraclea</i> sp.	0.40	0.75	0.25	0.00	0.29	0.40	0.10	0.10	0.20	0.00	0.00	0.20	0.43	0.14	0.00	0.29	0.25	0.25	0.50	1
Ceratopogonidae	0.49	1.00	0.45	0.00	0.34	0.07	0.05	0.35	0.05	0.07	0.27	0.14	0.14	0.08	0.00	0.41	0.31	0.39	0.31	0
<i>Cheumatopsyche</i> sp.	0.75	1.00	0.40	0.00	0.38	0.33	0.00	0.33	0.00	0.00	0.33	0.00	0.00	0.00	0.75	0.25	0.00	0.60	0.40	0
Chironomini	0.17	1.00	0.75	0.20	0.29	0.45	0.00	0.18	0.18	0.00	0.09	0.09	0.20	0.10	0.20	0.20	0.00	0.40	0.60	0
<i>Dendrocoelum</i> sp.	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.40	0.60	0
<i>Dinocras</i> sp.	0.00	0.00	0.00	0.00	0.25	0.20	0.00	0.00	0.00	0.00	0.00	0.80	0.75	0.00	0.00	0.25	1.00	0.00	0.00	NA
<i>Dreissena</i> sp.	0.00	0.00	0.00	1.00	0.75	0.38	0.00	0.25	0.00	0.00	0.38	0.00	0.00	0.00	1.00	0.00	0.00	0.67	0.33	0
<i>Dryops</i> sp.	1.00	0.25	0.00	0.00	0.00	0.00	0.50	0.50	0.00	0.00	0.00	0.00	0.50	0.50	0.00	0.00	0.00	0.40	0.60	0
<i>Dugesia</i> sp.	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.20	0.40	0.40	0
<i>Ecdyonurus</i> sp.	0.00	0.75	0.00	0.00	0.38	0.38	0.38	0.25	0.00	0.00	0.00	0.00	0.40	0.60	0.00	0.00	0.40	0.60	0.00	1
<i>Elmis</i> sp.	1.00	0.25	0.00	0.00	0.40	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.60	0.40	0.00	0
Empididae	1.00	1.00	0.35	0.00	0.28	0.00	0.00	0.11	0.00	0.00	0.00	0.89	0.00	0.00	0.00	1.00	0.20	0.60	0.20	1
<i>Epeorus</i> sp.	0.00	1.00	0.00	0.00	0.29	0.20	0.00	0.60	0.20	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.75	0.25	0.00	1

Appendix 3. Continued

<i>Ephemera</i> sp.	0.00	0.25	0.00	0.00	0.17	0.38	0.25	0.13	0.00	0.00	0.25	0.00	0.38	0.00	0.38	0.13	0.25	0.50	0.25	1
<i>Erpobdella</i> sp.	0.00	0.25	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.33	0.17	0.50	0.00	0.00	0.00	1.00	0.00	0.60	0.40	0
<i>Esolus</i> sp.	1.00	0.25	0.00	0.00	0.40	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.60	0.40	0.00	0
<i>Gammarus</i> sp.	0.00	0.25	1.00	1.00	0.60	0.07	0.36	0.14	0.07	0.14	0.14	0.07	0.75	0.25	0.00	0.00	0.50	0.50	0.00	0
<i>Glossiphonia</i> sp.	0.00	0.25	0.00	0.67	0.50	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.75	0.25	0
<i>Habroleptoides</i> sp.	0.25	1.00	0.00	0.00	0.40	0.50	0.13	0.38	0.00	0.00	0.00	0.00	0.40	0.60	0.00	0.00	0.75	0.25	0.00	1
<i>Habrophlebia</i> sp.	1.00	1.00	0.00	0.00	0.25	0.14	0.43	0.43	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.00	0.25	0.75	0.00	1
<i>Haliphus</i> sp.	1.00	0.25	0.75	0.00	0.20	0.00	0.00	0.50	0.50	0.00	0.00	0.00	0.50	0.00	0.00	0.50	0.14	0.43	0.43	0
<i>Helobdella</i> sp.	0.75	0.75	0.25	0.67	0.50	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.40	0.60	0
<i>Hemiclepsis</i> sp.	0.00	0.00	0.00	0.67	0.75	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.75	0.25	0
<i>Heptagenia</i> sp.	0.00	0.75	0.00	0.00	0.38	0.33	0.22	0.33	0.11	0.00	0.00	0.00	0.33	0.50	0.00	0.00	0.00	0.75	0.25	1
Hydracarina	1.00	1.00	0.75	0.20	0.50	0.17	0.00	0.08	0.17	0.08	0.17	0.33	0.20	0.00	0.00	0.70	0.33	0.33	0.33	NA
<i>Hydraena</i> sp.	1.00	0.25	0.25	0.00	0.33	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.33	0.50	0.17	0
Hydroporinae	1.00	0.25	0.75	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.40	0.60	0.50	0.00	0.00	0.50	0.25	0.47	0.29	0
<i>Hydropsyche</i> sp.	0.20	1.00	0.50	0.00	0.33	0.20	0.10	0.30	0.00	0.00	0.30	0.10	0.00	0.00	0.75	0.25	0.17	0.50	0.33	0
<i>Hydroptila</i> sp.	1.00	1.00	0.60	0.00	0.20	0.29	0.00	0.14	0.57	0.00	0.00	0.00	0.17	0.67	0.00	0.00	0.33	0.50	0.17	1
<i>Ithytrichia</i> sp.	1.00	1.00	0.00	0.00	0.20	0.29	0.00	0.57	0.14	0.00	0.00	0.00	0.20	0.60	0.00	0.00	0.75	0.25	0.00	1
<i>Lepidostoma</i> sp.	0.75	0.75	0.25	0.00	0.20	0.00	0.80	0.20	0.00	0.00	0.00	0.00	0.75	0.25	0.00	0.00	0.60	0.40	0.00	1
<i>Leuctra</i> sp.	0.75	0.75	0.00	0.00	0.40	0.14	0.14	0.29	0.29	0.14	0.00	0.00	0.60	0.20	0.00	0.00	0.75	0.25	0.00	1
Limnephilinae	0.00	0.90	0.01	0.00	0.05	0.02	0.44	0.04	0.33	0.03	0.02	0.12	0.88	0.03	0.00	0.07	0.43	0.37	0.08	1
<i>Limnius</i> sp.	1.00	0.25	0.00	0.00	0.40	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.60	0.40	0.00	0
Limoniidae	0.53	1.00	0.25	0.00	0.12	0.04	0.43	0.04	0.21	0.00	0.00	0.29	0.45	0.07	0.00	0.35	0.34	0.66	0.00	1
<i>Metalype</i> sp.	1.00	1.00	1.00	0.00	0.25	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.60	0.40	0.00	0.00	0.50	0.50	1
<i>Micrasema</i> sp.	1.00	0.67	0.00	0.00	0.00	0.11	0.22	0.22	0.33	0.00	0.11	0.00	0.38	0.25	0.25	0.00	0.75	0.25	0.00	0
<i>Micronecta</i> sp.	1.00	1.00	1.00	0.00	0.75	0.00	0.00	0.29	0.29	0.00	0.43	0.00	0.38	0.25	0.00	0.38	0.50	0.33	0.17	1
<i>Mystacides</i> sp.	0.75	1.00	0.00	0.00	0.20	0.22	0.00	0.22	0.44	0.00	0.00	0.11	0.50	0.33	0.00	0.00	0.14	0.43	0.43	1
<i>Nemoura</i> sp.	1.00	0.50	0.00	0.00	0.33	0.25	0.50	0.25	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.33	0.50	0.17	1
<i>Odontocerum</i> sp.	0.00	0.60	0.00	0.00	0.43	0.00	0.00	0.11	0.33	0.00	0.33	0.22	0.50	0.00	0.00	0.50	1.00	0.00	0.00	1
<i>Onychogomphus</i> sp.	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.40	0.60	0.00	0
<i>Orectochilus</i> sp.	1.00	0.25	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.25	0.75	0.50	0.00	0.00	0.50	0.25	0.75	0.00	0
Orthoclaadiinae	0.80	1.00	0.75	0.00	0.40	0.25	0.00	0.50	0.13	0.00	0.13	0.00	0.00	0.50	0.17	0.17	0.40	0.40	0.20	0
<i>Oulimnius</i> sp.	1.00	0.25	0.00	0.00	0.40	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.60	0.40	0.00	0

Appendix 3. Continued

<i>Perla</i> sp.	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.20	0.80	0.75	0.00	0.00	0.25	1.00	0.00	0.00	NA
Perlodidae	0.17	0.22	0.00	0.00	0.28	0.10	0.01	0.12	0.01	0.00	0.08	0.68	0.39	0.06	0.00	0.54	0.71	0.23	0.06	1
<i>Piscicola</i> sp.	0.00	1.00	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.75	0.25	0
<i>Pisidium</i> sp.	0.83	0.40	0.50	1.00	0.60	0.30	0.00	0.50	0.00	0.00	0.20	0.00	0.00	0.00	1.00	0.00	0.60	0.20	0.20	0
Planorbidae	0.70	0.87	0.03	0.00	0.63	0.09	0.26	0.31	0.18	0.16	0.00	0.01	0.45	0.55	0.00	0.00	0.26	0.44	0.30	0
<i>Polycelis</i> sp.	0.25	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.25	0.00	0.75	0.00	0.00	0.00	1.00	0.25	0.50	0.25	0
<i>Polycentropus</i> sp.	0.25	0.75	0.33	0.00	0.20	0.08	0.08	0.23	0.08	0.00	0.23	0.31	0.20	0.00	0.20	0.60	0.40	0.40	0.20	1
<i>Potamanthus</i> sp.	0.00	1.00	0.00	0.00	0.29	0.33	0.33	0.22	0.11	0.00	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.50	0.50	NA
<i>Protonemura</i> sp.	0.75	1.00	0.00	0.00	0.40	0.25	0.50	0.25	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	1
Psychodidae	1.00	1.00	0.75	0.20	0.60	0.18	0.36	0.18	0.09	0.18	0.00	0.00	0.50	0.17	0.00	0.00	0.14	0.43	0.43	0
<i>Psychomyia</i> sp.	1.00	1.00	0.75	0.00	0.25	0.13	0.00	0.63	0.13	0.00	0.13	0.00	0.00	0.50	0.33	0.00	0.25	0.75	0.00	1
<i>Radix</i> sp.	0.00	0.40	0.00	0.00	0.67	0.00	0.19	0.31	0.19	0.06	0.19	0.06	0.25	0.75	0.00	0.00	0.00	0.75	0.25	0
<i>Rhithrogena</i> sp.	0.25	0.75	0.00	0.00	0.33	0.20	0.00	0.60	0.20	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.75	0.25	0.00	1
<i>Rhyacophila</i> sp.	0.23	0.43	0.11	0.00	0.38	0.05	0.09	0.19	0.00	0.03	0.07	0.57	0.14	0.00	0.00	0.86	0.83	0.17	0.00	1
<i>Riolus</i> sp.	1.00	0.25	0.00	0.00	0.40	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.60	0.40	0.00	0
<i>Sericostoma</i> sp.	0.00	0.75	0.17	0.00	0.40	0.00	0.38	0.13	0.25	0.00	0.13	0.13	0.75	0.25	0.00	0.00	0.60	0.40	0.00	1
<i>Serratella</i> sp.	1.00	1.00	0.25	0.00	0.22	0.08	0.25	0.33	0.25	0.00	0.08	0.00	0.33	0.33	0.00	0.17	0.40	0.60	0.00	1
<i>Setodes</i> sp.	1.00	1.00	0.00	0.00	0.20	0.25	0.00	0.13	0.50	0.00	0.13	0.00	0.75	0.25	0.00	0.00	0.00	0.33	0.67	1
<i>Silo</i> sp.	0.75	1.00	0.00	0.00	0.20	0.17	0.17	0.67	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.50	0.33	0.17	1
Simuliidae	1.00	0.85	0.60	0.00	0.27	0.62	0.00	0.25	0.00	0.00	0.13	0.00	0.00	0.25	0.75	0.00	0.48	0.39	0.13	0
<i>Siphonoperla</i> sp.	0.60	0.67	0.00	0.00	0.40	0.18	0.18	0.09	0.00	0.00	0.09	0.45	0.50	0.17	0.00	0.17	1.00	0.00	0.00	0
<i>Stenelmis</i> sp.	1.00	0.25	0.00	0.00	0.40	0.25	0.00	0.75	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	0.40	0.60	0.00	0
Tabanidae	0.00	1.00	0.00	0.00	0.00	0.14	0.14	0.00	0.00	0.00	0.00	0.71	0.25	0.00	0.00	0.75	0.00	0.50	0.50	1
Tanypodinae	0.67	1.00	0.00	0.00	0.40	0.00	0.09	0.09	0.00	0.09	0.27	0.45	0.00	0.00	0.00	1.00	0.17	0.33	0.50	0
Tanytarsini	1.00	1.00	0.50	0.20	0.17	0.63	0.13	0.25	0.00	0.00	0.00	0.00	0.25	0.25	0.13	0.00	0.33	0.50	0.17	0
Tipulidae	0.00	0.40	0.20	0.00	0.00	0.15	0.31	0.15	0.15	0.00	0.08	0.15	0.43	0.00	0.00	0.29	0.50	0.33	0.17	1
<i>Torleya</i> sp.	1.00	1.00	0.00	0.00	0.33	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.67	0.33	0.00	1

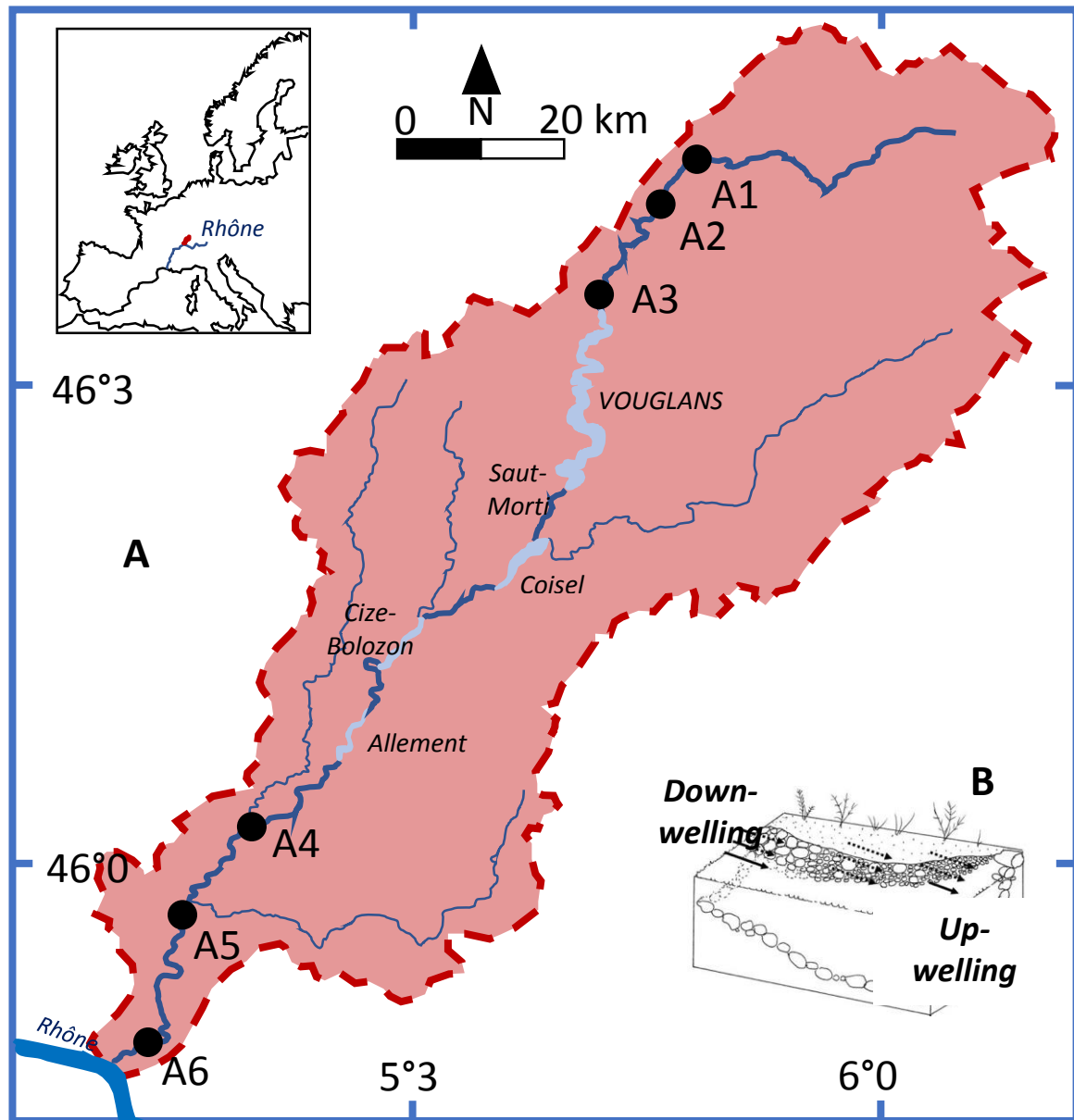


Figure 1.

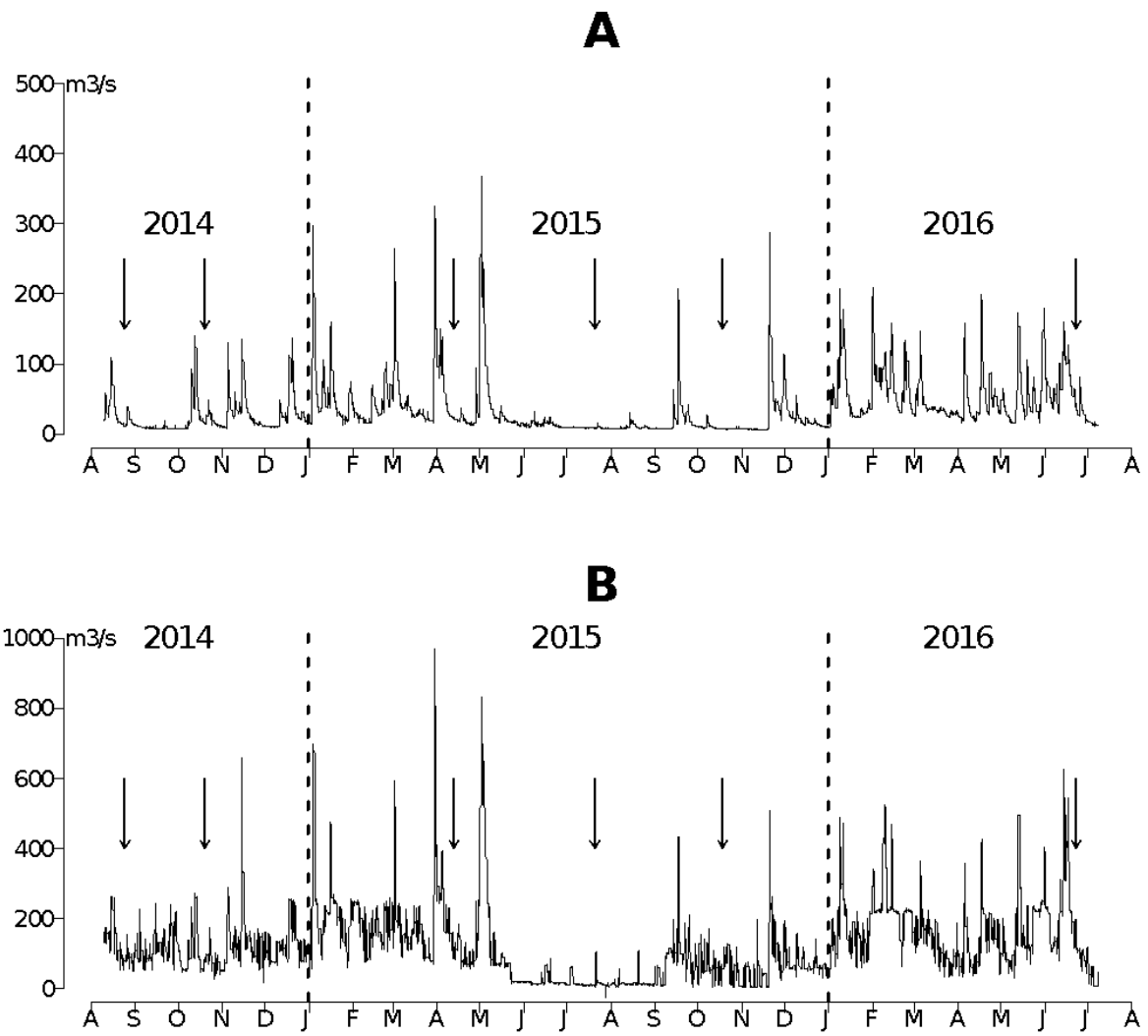


Figure 2.

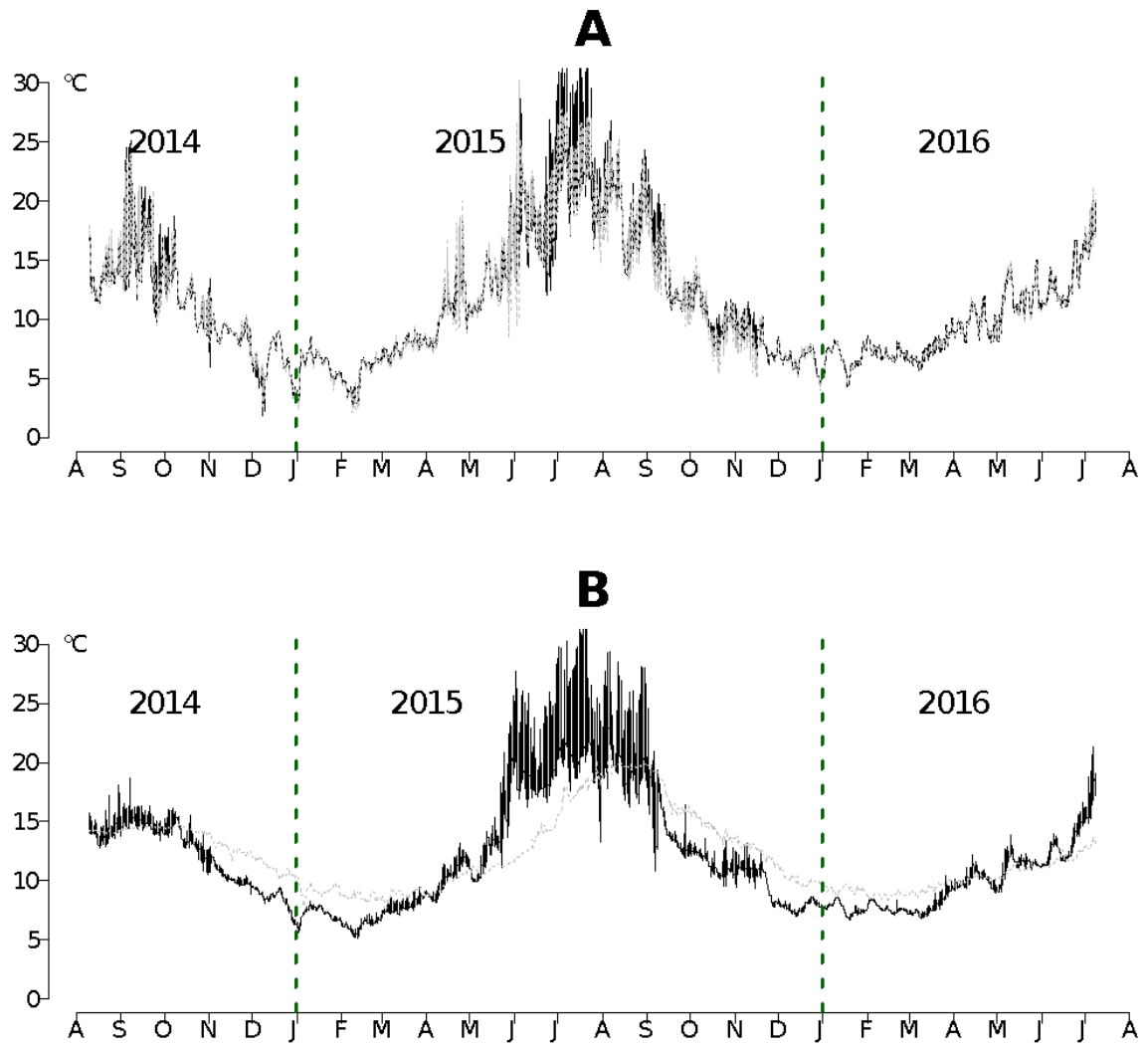


Figure 3.

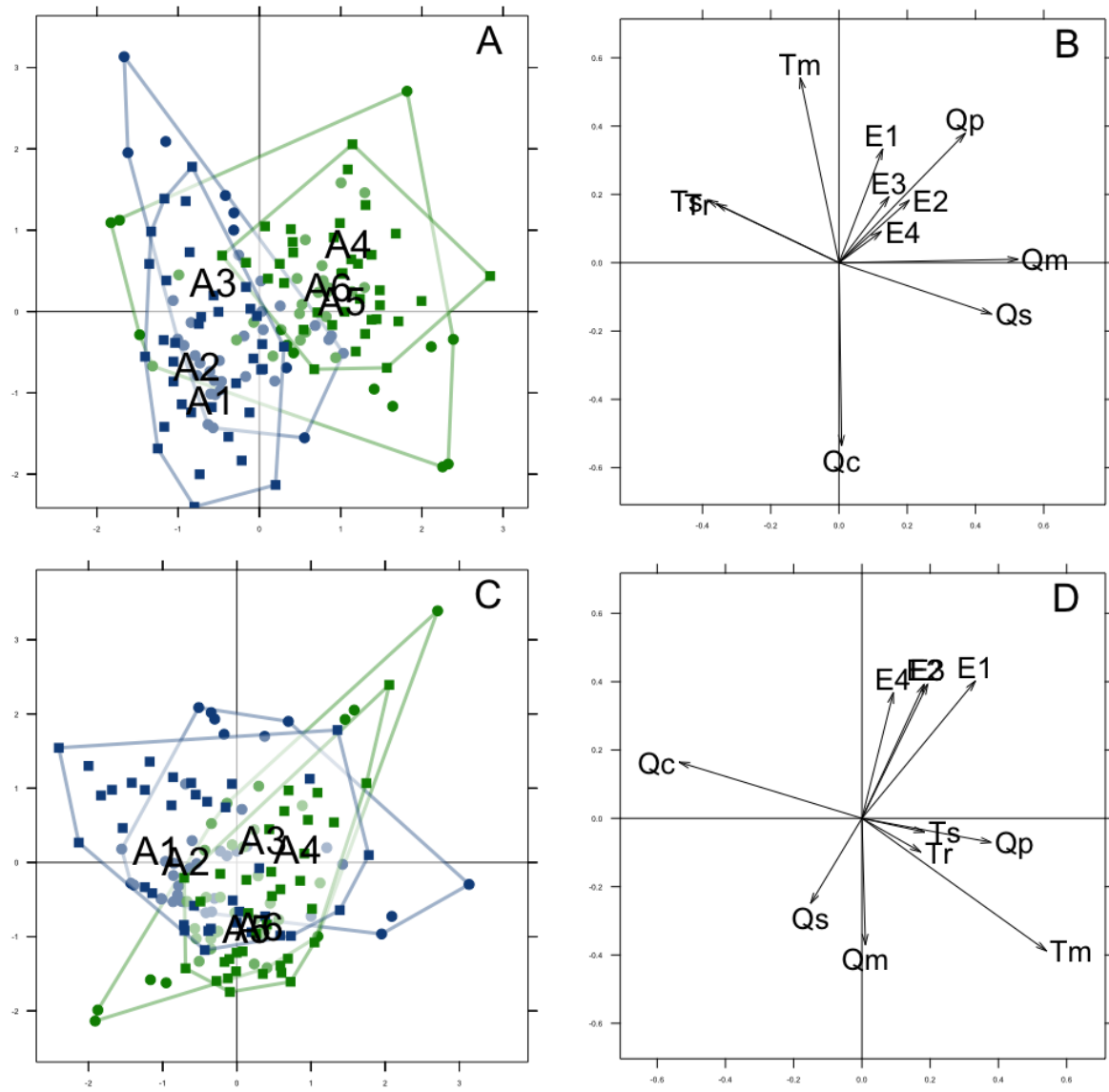


Figure 4.

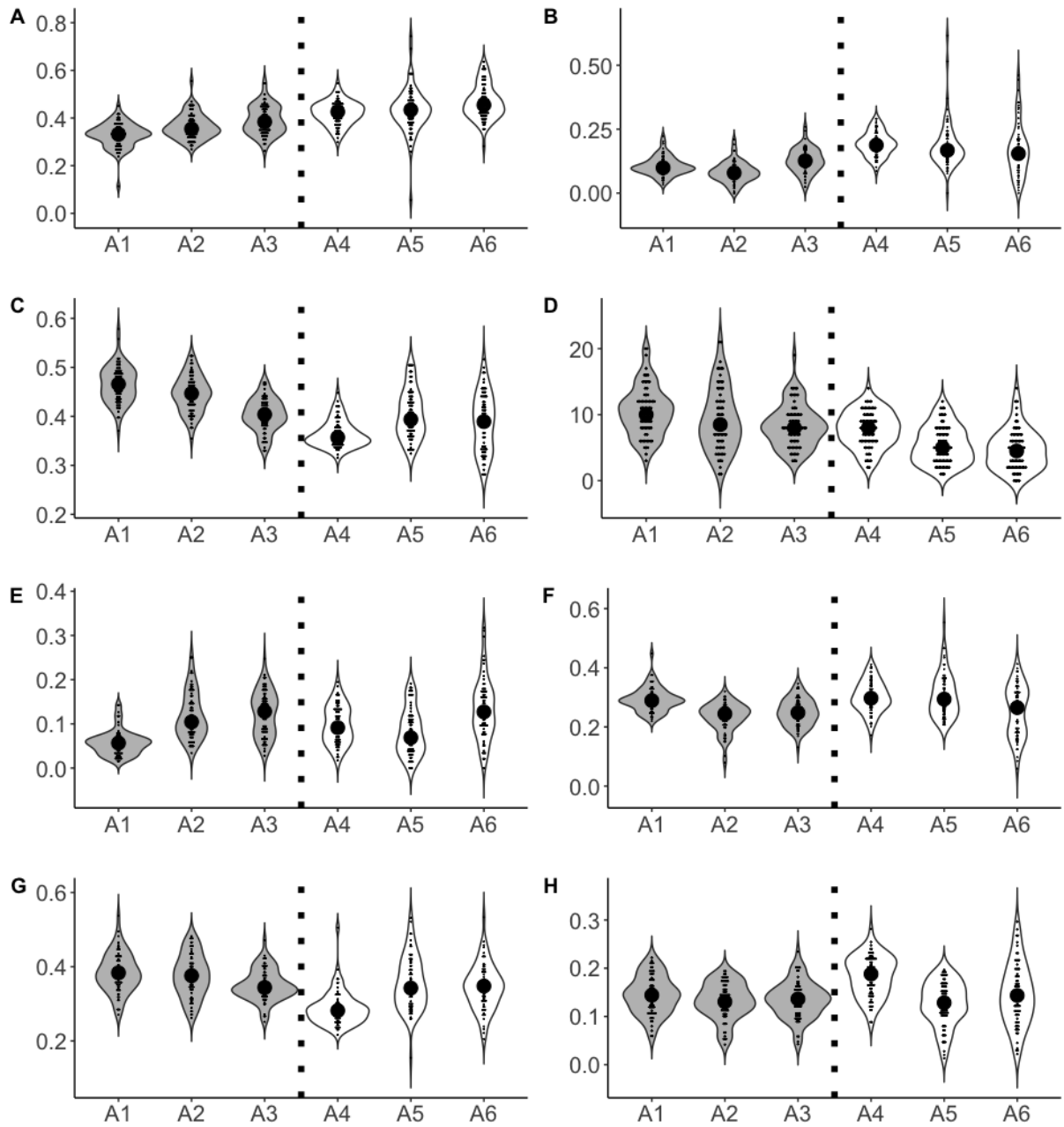


Figure 5.

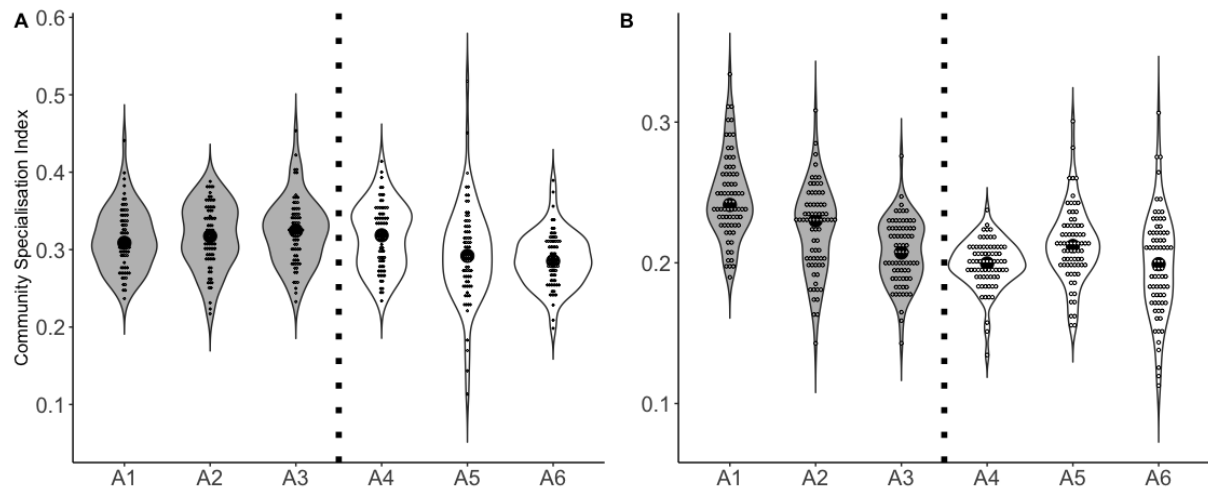


Figure 6.

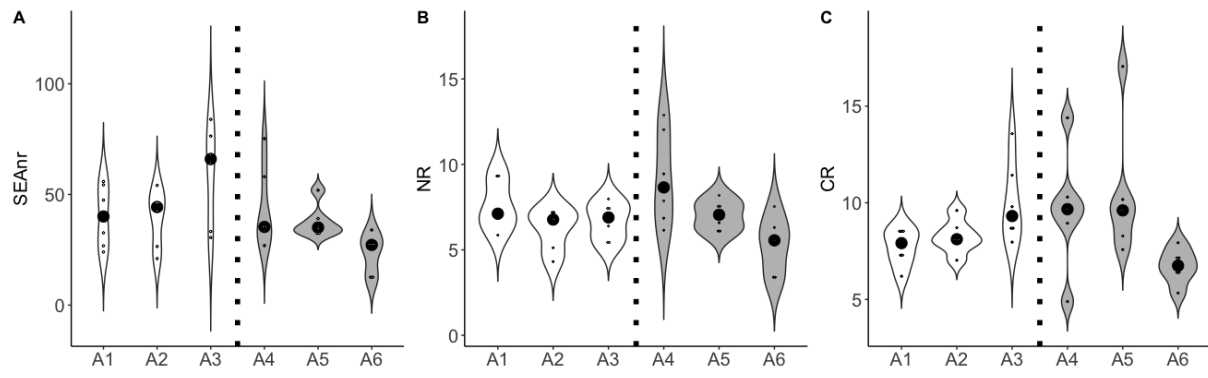


Figure 7.

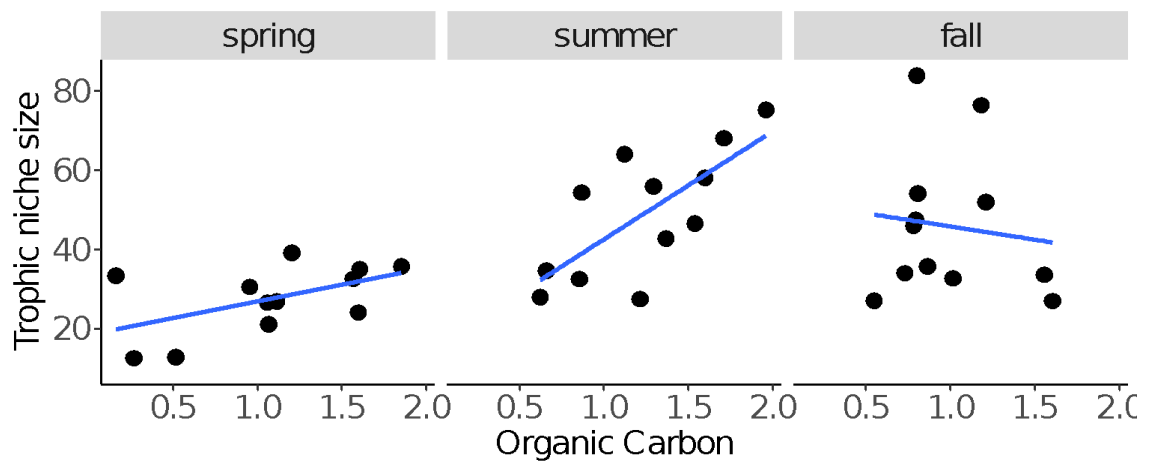


Figure 8.