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

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Abstract

Few studies have addressed how the diversity of basal resources change with stream regulation and the potential consequences on river biota. We sampled invertebrates above and below a series of dams, over two years, at both downwelling and upwelling zones. In each zone, we recorded the daily temperature and flow variations, estimated the algal development, measured the available resources, and analysed carbon and nitrogen stable isotope compositions of the invertebrate community. The number of hydrological pulses were typically higher below the dams than above the dams especially during high-flow periods whereas the groundwater outlets had minor effects on invertebrate assemblages. Invertebrate abundance, richness and diversity tended to decrease below the dams. Co-inertia analysis showed that flow and temperature variations, and eutrophication explained most of the variance in the invertebrate assemblages, which comprised a higher number of resilient taxa below than above the dams. The proportions of pesticide-sensitive invertebrates were lower below the dams and ovoviviparous and more generalist taxa were prominent. We did not observe the expected CPOM decrease and FPOM increase downstream. Accordingly, the proportions of each functional feeding group were remarkably similar above and below the dams despite the long distance between the sectors (>100 kms). The diversity of basal resources used within assemblages progressively increased downstream above dams. In contrast, the diversity of resources used by organisms below the dams decreased from upstream to downstream suggesting a significant influence of flow regulation on aquatic food webs. Finally, the shorter trophic chains for the invertebrate assemblages below the dams suggests that the effects of stream regulation and eutrophication induced a simplification of food webs. To our knowledge, this study is the first to connect taxonomic and functional trait changes in response to multiple stressors with the associated modifications in isotopic niches within aquatic invertebrate assemblages.

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

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

Methods: We used univariate and multivariate analyses to compare the invertebrate assemblages above and below the dams and to assess the contributions of hydrology (including groundwater supplies to the river), temperature and eutrophication to the variability in the composition of invertebrate assemblages. We also considered the relative utilization of a selected set of traits describing invertebrate resilience, resistance and specialization to address the potential functional effects of stream regulation on invertebrate assemblages. Finally, carbon and nitrogen isotope analyses allowed us to characterize the length and width of invertebrate assemblage food webs as related to the availability and diversity of basal resources.

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

Conclusion: This study provides insights about the impacts of flow regime alteration and eutrophication on food webs that may have been caused by regulation of permanent streams. To our knowledge, this is the first to connect taxonomic and functional trait changes in response to multiple stressors with the associated modifications in energy fluxes in aquatic invertebrate assemblages. This study suggests that bed stability, which is associated with a reduction in channel mobility below the dams and with moderate eutrophication, may provide the shelter and resources that can locally favour invertebrate assemblage dynamics and lessen the effects of flow regulation. In addition, the study suggests that the biological trait-based approach and isotope analysis are complementary approaches for addressing ecosystem functioning. The relative utilization of traits indicates the functional potential of aquatic invertebrate assemblages to face multiple stressors whereas isotope analysis is an expression of the actual effect of the stressors on the trophic structure of aquatic invertebrate assemblages.

Key words

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

1. Introduction

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

The abiotic effects of damming and more generally the effects of anthropogenic disruption of the river continuum have been studied for many years (e.g. Baxter, 1977; Ward and Stanford, 1983a; Ligon *et al.*, 1995; Rosenberg *et al.*, 2000). Apart from changes in the flow regime, they include pronounced changes in the temperature, dissolved oxygen concentrations, and chemical composition of water. In addition, the fragmentation of the rivers by dams prevents the transport of sediment downstream, which may deeply modify the channel structure and dynamics by causing river incision and bed armouring (Brenna *et al.*, 2019). These changes generally result in a loss of aquatic diversity and in river homogenization (e.g. Poff *et al.*, 2007; Rolls *et al.*, 2012; Mbaka and Mwaniki, 2015; Mellado-Diaz *et al.*, 2019). The alteration of the channel dynamics may also modify the exchanges between the hyporheic zone and surface flow (Caschetto *et al.*, 2014) whereas local hydrological exchanges greatly contribute to stream functioning (Boulton *et al.*, 1998, 2010). For example, groundwater outlets provide a supply of cooler water (White *et al*., 1987) that is rich in nutrients (Valett *et al*., 1994). In addition, in natural situations benthic invertebrates may migrate within the sediment to escape flow disturbances (Dole-Olivier and Marmonier, 1992; Maazouzi *et al.*, 2017; Vander Vorste *et al.*, 2017). However, less is known about the direct effect of groundwater supply and the associated water quality on the benthos. Damming has also been shown to affect leaf litter decomposition and the distribution of functional feeding groups (Martinez *et al.*, 2013) as well as functional richness (Laini *et al.*, 2019) and to cause profound changes in food webs (Power *et al.*, 1996; Mor *et al.*, 2018). For example, damming in Mediterranean streams can increase hydrological and sedimentological stability downstream dams, leading to a modification of available resources and a change from a detritus-based to an algae-based food web (Mor et al., 2018). Finally, apart from the direct effects of low flows or changes in flow timing associated with stream regulation, nutrient effluents from the catchment combined with low flows (damming and water abstraction for agriculture) and the higher transparency associated with a lack of fine sediment transport may exacerbate primary production, ultimately leading to eutrophication (Biggs, 2000). Moreover, chemical releases associated with agricultural or industrial activities or with contaminants accumulated in the reservoir may interact with flow alteration (Colas *et al.*, 2013).

As a result, stream regulation involves multiple stressors that constrain the resilience and resistance capabilities of aquatic invertebrate assemblages, which can potentially be assessed through a multiple trait-based approach (Statzner *et al.*, 2010). According to the literature, the disturbances associated with frequent flow fluctuations may favour small size invertebrates (higher resilience capability; Townsend *et al.*, 1997), and/or invertebrates with short development periods (life duration <1 y.) and/or with more than one generation per year (multivoltine). Apart from the specific hydraulic effects of stream regulation, the eutrophication that frequently occurs below dams results in selection for organisms with traits that allow them to resist the potential degradation of the water quality (e.g. offspring protection by ovoviviparity, less sensitivity to oxygen depletion). As a consequence, by modifying the composition of assemblages, stream regulation may lead to simplified food webs. Food webs can be also affected by dams and associated reservoirs which act as powerful retention structures in river networks by burying particulate organic matter in sediments (Vörösmarty et al., 2003). This retention process decreases the availability of particulate organic matter to downstream benthic food webs, affecting the secondary production of consumers (Ward and Stanford, 1983b; Power et al., 1996; Kominoski and Rosemond, 2012). Moreover, reduction of POM below dams would lead to dominant algae-based food webs characterized by a lower complexity than food webs based on both algae and detritus (Power et al., 1996). Indeed, Layman et al. (2007) showed that a reduction of food diversity (as expected below dams) would strongly reduce the trophic niche width of primary consumers and predators, reflecting a homogenization of energy flow pathways to top predators. This reduction of trophic niche width could be critical for ecosystem structure and functioning as it destabilizes food webs and increases the extinction risk of top predators. With this objective, stable isotopes appear as very pertinent tools to evaluate the consequences of environmental stressors affecting food sources for benthic communities (Pingram et al., 2012; Burdon et al. 2019). Understanding the combined effect of different stressors and the contribution of the different environmental parameters in the structure and function of aquatic communities remains a key question for managers to address restoration goals and mitigation measures (Azzellino *et al.*, 2015). Therefore, integrated approaches that consider various physical and chemical compartments and biological processes in a single study are required. The Ain River, which rises in the Jura Mountains from a karstic emergence at approximately 680 metres above sea level, is a major tributary of the Upper Rhône. It is 190 km long and has 3765 km^2 drainage area. Five hydroelectric power plants were built on its main course between 1928 and 1968. Among them, the Vouglans dam, built in 1968, forms a 35-km long reservoir of more than 600 million m^3 of water. This large reservoir is followed by a series of four other dams in succession along the river course that strongly influence water flow and generate a significant sediment deficit (Rollet *et al.*, 2013; Dole-Olivier *et al.*, 2019). This river thus represents a good experimental situation for addressing the complex effects of stream regulation and its associated stressors on the taxonomic composition, functional responses and potential changes in food web complexity.

In this study, we hypothesize that the combination of thermal, hydraulic and land use disturbances below the dams is likely to (i) decrease the abundance and richness of invertebrate assemblages, (ii) modify their taxonomic composition, by favouring organisms with resilience and resistance traits as well as generalists, and (iii) alter the balance among functional feeding groups, and (iv) modify the resource use by invertebrates and in turn the complexity of the invertebrate food web by reducing the niche width of primary consumers and predators. At the same time, we evaluate the potential of upwelling zones, which are characterized by thermally buffered groundwater supplies and are rich in nutrients to modulate the impacts of dams on benthic invertebrates. More precisely, we hypothesize that the groundwater upwellings below the dams may (i) locally limit the negative thermal impacts of stream regulation on invertebrate assemblages and (ii) stimulate primary production with potential consequences on food webs.

2. Material and Methods

2.1. Study locations

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

2.2. Environmental characterization

2.2.1. Water level and temperature

Two Mini-Diver sensors (Schlumberger, Water Services, Waterloo, Canada) were installed per site to monitor pressure (corresponding to the water level after correction for atmospheric pressure) and temperature dynamics during the experiment (from August 10, 2014 to July 08, 2016). One sensor was installed in the streambed sediments in a zone influenced by groundwater outlets (upwelling) and the other in a downwelling zone (no influence of groundwater) in order to assess the relative importance of these zones for the epigean benthic invertebrates (Fig. 1B). Water levels (cm) were further transformed into hourly discharge ($m^3.s^{-1}$) by using the relationship between the measured discharges and the water levels at each site. We used the water level series to compute, at each site and each date, four metrics related to the prevailing hydrological conditions for the 15 days preceding the invertebrate sampling: (i) the number of extreme ecological events, which was measured by the number instances of an increase of >50% in less than 1 day, (ii) the average discharge ($m^3.s^{-1}$), (iii) the standard deviation of the discharge, and (iv) the coefficient of variation of the discharge. Similarly, we used the water temperature series to compute for each site, each zone and each date, three metrics considering the prevailing water temperature conditions for the 15 days preceding the invertebrate sampling: (i) the average temperature (°C), (ii) the standard deviation of the temperature, and (iii) the temperature range (°C).

2.2.2. Chemical parameters

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

2.3. Basal resources and stable isotope analyses

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

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

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

2.4. Primary production

To cover a maximum range of environmental conditions over the width of each zone (up and downwelling), 2 transects, separated by a few metres and parallel to each other, were defined per site. Three points corresponding to different substrates (sand, gravel, pebbles) were selected at random on each of the transects over an area of approximately 0.025 m^2. Six samples were thus taken in each zone on each sampling occasion. In each sample, the biofilm was scraped with a brush, and the substrate was rinsed several times to obtain a complete collection of the biofilm. The sample was transferred into a propylene bottle, after removing any macroinvertebrates, leaves and stones. The sample was then homogenized and divided into two equal subsamples. The first subsample was used for chlorophyll-*a* measurement. The second subsample was fixed with Lugol solution for further identification of the different groups of algae. On the same day, the chlorophyll-*a* was quantified in the laboratory by filtering each biofilm sample on a glass fibre membrane GF/C (pore diameter 1.2 µm). Pigment extraction was carried out with 90% acetone. After centrifugation, the absorbance of the supernatant was measured at 630, 645, 663 and 750 nm wavelengths, using a spectrophotometer. The concentrations in chlorophyll-*a* were obtained by applying the Lorenzen formula (according to the NF T90-117 French standard) and used as a proxy for algal biomass. For each benthic biofilm subsample, the individuals were classified into the main functional groups, i.e. cyanobacteria, chlorophytes and diatoms, and counted under a microscope as the number of cells per m^2 (Bourrely, 1968, Prescott *et al.*, 1978). Given the high densities observed, we used a Nageotte chamber to count the cells in small volumes.

2.5. Benthic invertebrates

2.5.1. Sampling

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

2.5.2. Biological traits metrics

The biological traits used in this study were extracted from a European database constructed from the literature that contains information on life history, resilience and resistance potential, morphology, physiology and feeding behaviour for European freshwater invertebrate genera (Tachet *et al.*, 2010). In this public database, available on the web (see Schmidt-Kloiber and Hering, 2015), traits are usually divided into categories and are quantified using affinity scores between 0 and 3 (maximal size, voltinism, reproduction types, locomotion and relation to substrate) or 0 and 5 (food and feeding habits) (Chevenet *et al.*, 1994). This quantification, which enables the compilation of information from various sources, also (i) captures the variability in traits that often occurs in an organism at different life stages and (ii) accounts for within-taxon variations in responses. We computed metrics describing (i) the relative utilization of fuzzy-coded traits such as multi-voltinism, small size, short life span, ovoviviparity, and oligotrophy (Table 2; see Mondy and Usseglio-Polatera, 2013) to address the response of organisms in terms of resilience and resistance abilities, (ii) food Rao diversity and community specialization (Table 2; Mondy and Usseglio-Polatera, 2014) in terms of food and trophic status, and (iii) the 'Species at Risk' index to consider a potential additional stress associated to agricultural activities (SPEAR pesticide relative abundance index; Liess and von der Ohe, 2005). Selected metrics are available in Appendix 3.

2.6. Data analyses

To assess temporal and spatial effects on the above selected abiotic parameters and biological metrics, we used mixed ANOVAs with zones (upwelling and downwelling), sectors (above and below dams) and sampling dates as fixed effects, and the sampling sites as random effects. When the normality assumption was not met, we used the Box-Cox transformation (Box and Cox, 1964). We used co-inertia analysis (CoiA) to assess the contributions of parameters describing hydrology, temperature and eutrophication, for explaining the variance in invertebrate assemblage composition. Since algal variables (eutrophication) were taken on transects whereas benthic invertebrate samples were taken at sampling point, we summed samples by zones (upwelling vs. downwelling) within each site at each season, thus ending up with 72 sampling units. CoiA provides factorial axes from each dataset that are the most covariant, i.e., they simultaneously depict the highest possible variance of each dataset and optimize their correlation (Dolédec and Chessel, 1994; Dray *et al.*, 2003), and we considered the loadings of variables to assess the relative contribution of each of them to the covariance between benthic invertebrates and environmental variables. The strength of the relationship was measured by means of the *Rv* coefficient, a multidimensional equivalent for two tables of the regression coefficient for two variables (Robert and Escoufier, 1976). We tested the statistical significance of the *Rv* coefficient by a Monte Carlo permutation test and by comparing the distribution of 999 replicated matches of the two datasets (after random permutations of their rows) with the observed *Rv* coefficient.

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

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

3. Results

3.1. Environmental characterization

3.1.1. Water level and temperature

According to the flow variation, 2015 was the driest year, 2016 was the wettest year, and 2014 fell in between (Fig. 2). On average, the number of pulses was lower above the dams than below the dams (Table 3A). Despite stream regulation, the discharge was obviously higher below the dams than above the dams (Table 3A) but the significant interaction with the sampling date was associated with the very low difference in discharge in summer 2015, i.e., the driest period. Finally, coefficient of variation of the discharge values were significantly lower below the dams than above the dams in summer and fall 2015, and the opposite trend was observed for the 4 other sampling dates (Table 3A). Similarly, the water temperature varied across the years. The highest temperatures occurred in the summer of 2015, and the lowest occurred in the winter of 2014, and 2016 was slightly cooler (Fig. 3). Apart from the obvious effect of the sampling date (Table 3A), the average temperature preceding each sampling occasion below the dams was significantly higher than that above the dams (Table 3A). In contrast, the temperature range did not significantly change between sectors located below and above the dams (Table 3A). There was a statistical interaction between the presence of groundwater outlets and the sampling date (Table 3A), i.e., water temperature was significantly lower in the upwelling zone (20.3±2.2°C) than in the downwelling zone (23.0±1.6°C) in summer 2015. The variations in water temperature were buffered in the upwelling zones in comparison with the more pronounced variations in the downwelling zones (1.6°C more on average; Fig. 3).

3.1.2. Water chemistry

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

3.1.3. Primary production

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

3.2. Invertebrate assemblage responses

3.2.1. Spatial and temporal patterns

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

3.2.2. Main drivers of invertebrate assemblage responses

The co-inertia analysis between the invertebrate assemblage composition and environmental metrics showed a significant correlation (*Rv*=0.318, simulated-*P*<0.001, *n*=72). The first-three axes depicted 83% of the co-variability between the invertebrate assemblage composition and the environmental metrics (46%, 20.9% and 16.1% for the first, second and third co-inertia axes, respectively; Fig. 4). The first two co-inertia axes depicted 96% and 72.6% of the environmental and faunal variance, respectively. The first co-inertia axis clearly separated the two sectors suggesting that invertebrate composition responded significantly to the environmental context above and below the dams (Fig. 4A). This separation was associated with the higher temperature range (Tr in Fig. 4B) and standard deviation (Ts) above the dams, and with the higher discharge (Qm), flow pulse (Qp) and algal development below the dams

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

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

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

3.2.3. Assemblage resilience and resistance

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

These changes in resilience traits mirrored in the proportions of individuals sensitive to pollution, which decreased from upstream to downstream. The sites below the dams exhibited slightly lower proportions of organisms that are sensitive to eutrophication (Fig. 5C) and sensitive to pesticide as measured by the SPEAR index (Fig. 5D), though overall differences below and above dams were marginally statistically significant (Table 5A). Likewise, the proportion of ovoviviparous organisms was higher below the dams than above the dams (Table 5A; Fig. 5B) and was higher in the upwelling in comparison to the downwelling (0.154±0.09 vs. 0.132±0.06).

3.3. Assemblage trophic responses

3.3.1. Functional feeding groups

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

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

3.3.2. Isotope analysis

3.3.2.1. Basal resources

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

3.3.2.2. Isotopic niche

The isotope space area determined as the standard ellipse area normalized to the isotope composition of the basal resource (SEAnr) differed significantly among sampling dates (Table 6B) and between sectors (Table 6B) (supplementary information, Fig. S3). SEAnr generally increased from upstream to downstream in the sites above the dams, reaching its highest value at A3 (Fig. 7A); however, this tendency was weaker during summer. Below the dams, SEAnr decreased from sites A4 to A6, except in fall, when the maximum value was measured at site A5. The diversity in the basal resource use, quantified by the δ^{13}C range (CR in Fig. 7C), showed an increase from sites A1 to A3 but no difference between above and below dams could be detected (Table 6B). Finally, the diversity of trophic levels quantified by the δ^{15}N range again showed an increase from upstream to downstream above the dams and a decrease below the dams (Table 6B). At all sampling occasions, the most downstream site, A6, displayed the lowest trophic diversity (SEAnr), with a low diversity in the exploitation of the basal resources (CR) and a low diversity in trophic levels (NR). Regardless of the index used, no significant influence of surface water-groundwater exchanges on the invertebrate food web was detected (e.g. average values of SEAnr were 41.9±16.2 vs. 39.6±19.1 for the upwelling and downwelling zones, respectively).

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

4. Discussion

To our knowledge, this study is the first to simultaneously compare the taxonomic and functional spatial and temporal responses of aquatic invertebrate assemblages and the associated modifications in the isotopic metrics describing food webs in a regulated river. On the one hand, our hypotheses about the effects of the alteration of the hydrological regime and temperature and the potential eutrophication associated with stream regulation on the invertebrate assemblages are generally supported by the results of the study. The overall abundance and richness, resilience and resistance potential, sensitivity to pollution and food specialization in invertebrate assemblages were found to be lower below the dams than above the dams. The aquatic invertebrate assemblages above and below the dams significantly responded to the combined effects of hydrology, temperature, and algal development. Even moderate stream regulation seemed to promote eutrophication locally above the dams (site A3). The reduction in basal resource use that occurred in the downstream sites (A5 and A6) below the dams was found to narrow the isotopic niche (i.e. isotopic space that describes food web) of invertebrates but local eutrophication (algal development) sometimes modified this scheme (A4). Finally, the balance among functional feeding groups was unexpectedly found to be similar below and above the dams. On the other hand, our hypotheses concerning groundwater supplies are not supported because groundwater outlets only marginally influenced benthic invertebrate assemblages and food web complexity despite their buffering effect on temperature during summer and the stimulation of primary production by nutrient (especially nitrate) supplies.

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

The co-inertia analysis suggested that hydrological (flow pulses) and thermal (temperature variations) conditions were the main drivers explaining changes in the invertebrate assemblage structure between sectors. The damming conditions generated a global reduction in invertebrate density and diversity at the sites below the dams. This reduction, which is expected in theory for rivers of the same stream order as the Ain River (Ward and Stanford, 1983a), has generally been observed elsewhere (e.g. Fleituch, 2003; Kjærstad *et al.*, 2017; Mellado-Diaz *et al.*, 2019). As observed in other studies (Krajenbrink *et al.*, 2019), the number of Ephemeroptera and Plecoptera taxa was especially affected due to their sensitivity to habitat alteration. However, this reduction was especially observed at the two downstream sites (A5 and A6). Even if the dams similarly affected discharge dynamics and thermal changes, eutrophication (dense algal development) and high quantities of basal food sources (e.g., CPOM) seemed to buffer the effects of stream regulation at site A4. This interpretation was supported by the wider isotopic niche of invertebrate food web measured in site A4 than in sites A5 and A6. Indeed, this result highlighted that food webs were mainly fuelled by algal sources in A5 and A6 sites whereas food webs were based on more diversified food sources (algae and detritus) in site A4. In addition, the fact that sites A3 and A4, characterized by the highest algal growth, had the highest density and diversity of invertebrates suggests that algal development on cobbles and stones was an important local condition favouring benthic invertebrates. Indeed, it has been demonstrated in the literature that biofilms (including bryophytes) that develop on hard substrates act as both a preferential habitat (Linhart *et al.*, 2002) and a food source (Suren, 1992) for a wide range of benthic invertebrates (Wulf and Pearson, 2017). Local nutrient enrichment and eutrophication could thus have a positive influence on the biological compartment of the Ain River. Nevertheless, this interpretation cannot be extended to all lotic systems because the water flow dynamics in the Ain River facilitate the oxygenation of water and prevent the occurrence of low-oxygen conditions associated with eutrophication in the water column (Table 2). Indeed, eutrophication may generate water column anoxia that can markedly damage the benthic life when hydrological conditions are not strong enough to efficiently reoxygenate the water column (see Parr and Mason, 2004 and Pardo and Garcia, 2016 for examples in lowland streams).

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

The invertebrate taxa found below the dams were generally more resilient and resistant than the taxa found above the dams. These results fit well with observations from the literature showing that hydrological disturbances such as those generated by dam functioning can select for small, multivoltine species with short life spans (Wallace, 1990). A higher number of generations per year is expected to occur under unstable conditions, as it allows rapid population growth and an increase in resilience capacity in invertebrates (Townsend and Hildrew, 1994) as observed elsewhere (e.g. Usseglio-Polatera and Beisel, 2002; Statzner *et al.*, 2010; Feio and Dolédec, 2012). The biological trait approach thus appears as highly relevant for highlighting the hydrological impacts on benthic invertebrate assemblages; resilience traits were apparently not affected by trophic resources or eutrophication at each site, which suggests some specificity in their responses (see e.g. Mondy *et al.*, 2016). We did not find significant differences in traits associated with tolerance to eutrophication between the two sectors. This result is coherent with the analyses performed on algae, which did not indicate any differences in eutrophication status between the two sectors. In contrast, we observed a higher proportion of biological traits associated with tolerance to pesticides at sites below the dams than at sites above the dams suggesting a difference in pesticide exposure. In addition, ovoviviparity, a parental care strategy that may prevent high egg mortality in harsh environmental conditions, was prominent below the dams. This egg protection trait has been shown to increase in the presence of pesticides (Kuzmanovic *et al.*, 2017). The higher pesticide resistance of invertebrates sampled below the dams is consistent with the surrounding land use patterns because crop production occurred predominantly in sites below the dams (see Table 1), and this agricultural practice is often associated with pesticide use (e.g., Papadakis *et al.*, 2018). Under these conditions, it is thus not surprising that the eutrophication response traits of species were not tightly linked with algal development at the sites because herbicides might have impaired algae growth at sites below the dams (especially in sites A5 and A6, which had low algal development). An additional explanation for the biological trait distribution among the sites could be linked to the physical disturbances that change channel morphodynamics below the dams (e.g., Brenna et al., 2020). Indeed, Rollet *et al.* (2013) showed that changes in sediment transport in the Lower Ain River resulted in bed coarsening and sediment instability, and their pavement index, measuring river bed alteration, was high in one reach (corresponding to our site A4) and low in another reach (corresponding to our two last sites, A5 and A6). Such sediment instability may also favour resilient traits (e.g. multivoltine taxa see Fig. 5B; Townsend and Hildrew, 1994). Thus, the responses of invertebrate biological traits below the dams may result from both physical disturbances and chemical stresses. To evaluate whether the chemical impacts of pesticides on algae and invertebrates are a relevant explanation of the benthic invertebrate assemblages' structure and functioning, the content of pesticides and herbicides in the sediment are needed to assess the contamination levels at the six studied sites.

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

4.3. Food web responses to environmental factors

Above the dams, we observed an increase in the isotope space area from upstream to downstream that was mainly driven by an increase in the basal resource diversity used by the invertebrate assemblages. Such an increase has been observed in unregulated rivers and generally suggests a structural change in the food web along the longitudinal gradient (Winemiller *et al.*, 2011; Hette-Tronquart *et al.*, 2016). Indeed, the increase of food web diversity from site A1 to site A3 above dams highlighted modifications of food sources used by invertebrate communities: a detritus-based food web dominated in site A1 whereas a food web based on both algae and detritus occurred in site A3. The decrease in the isotope space area below the dams (from site A4 to site A6) indicates a decrease in the diversity of resource use and in the number of trophic levels. This decrease could be explained by the wide diversity of resources (algae and detritus) fuelling invertebrate food web in site A4 whereas food web in site A6 was uniquely based on algae. Thus, changes in food sources may have caused the reduction in the prey diversity, which is potentially corroborated by the trend of decrease in taxonomic diversity and invertebrate abundance at the last two sites (Table 4A). This resource use decrease appeared to be negatively correlated with the discharge values and their rates of variation. Marty *et al.* (2009) showed comparable results in boreal rivers where high ramping rates during hydropeaking were responsible for a one-trophic-level decrease in the length of the food chain between macroinvertebrates and fish. Stream hydrodynamics thus appear to be the dominant factor in structuring the invertebrate assemblages, as positive correlations between food resources and their use by benthic invertebrates were only detected during low flow conditions (summer 2015). At this time, a positive relationship was observed between the quantity of energy (organic carbon) in the benthic environment and the area of the food web of the benthic invertebrates. According to the literature (Wright, 1983; Smith, 2007), this relationship could be due to the positive species-energy relationship encountered in many ecosystems. More precisely, an increase in energy (available resources) increases the ability of trophic specialists to develop persistent populations (Evans *et al.*, 2005). Consequently, these specialist species increase the isotopic area of the food web by feeding on one or two resources without mixing isotopic signatures from several sources as generalist species would do (Layman *et al.*, 2007; Hette-Tronquart *et al.*, 2016). Increases in basal energy resources would allow the development of predatory levels (Oksanen *et al.*, 1981; Mermillod-Blondin *et al.*, 2020). This pattern was observed in summer with the linear relationship between the organic carbon content and the $\delta^{15}N$ range. Therefore, the trophic structure of benthic fauna was dominated by resources (bottom-up control) in summer. However, the same connections between the total organic carbon content and the isotopic indexes were not observed on the two other sampling dates when hydrological conditions were less stable than in summer. Indeed, significant correlations between hydrological variables and isotopic areas were observed in spring and fall, while this kind of result has not been detected in summer. We can thus conclude that hydrological disturbance appeared to be the main stressor on trophic food webs in the Ain River and that it disrupted the observed connection between food webs and basal resources (e.g. Menge *et al.*, 2002).

4.4. Upwelling zones as refugees for benthic invertebrates during harsh thermal conditions

According to the literature (White *et al.*, 1987; Capderrey *et al.*, 2013), upwelling zones are cooler than downwelling zones during the summer, when water temperatures are the highest and potentially harshest for benthic invertebrates. This difference in temperature is also associated with a reduction in dissolved oxygen concentrations in upwelling zones compared with those in downwelling zones. This pattern of dissolved oxygen concentrations is due to the contrast between the highly oxygenated water of the Ain River downwelling in sediments and the moderately oxygenated groundwater upwelling from hyporheic and/or riparian zones. As aerobic microbial processes reduce the dissolved oxygen concentration in water during its transfer through sediments (Jones Jr *et al*., 1995; Boulton *et al*., 1998), upwelling water, which is characterized by a higher retention time in sediments than downwelling water, is more depleted in dissolved oxygen. In line with the literature (Valett *et al*., 1994; Dahm *et al*., 1998), the groundwater supply was also richer in nitrate than the surface waters. Despite these differences in benthic conditions between the upwelling and downwelling zones, the variation in groundwater supply moderately affected the composition of benthic invertebrate assemblages and their life history traits (e.g., reduction in small and short-lived organisms). Even in summer, when the thermal conditions were the harshest for benthic fauna, the upwelling zones did not act as efficient refugia for invertebrates. This lack of an effect may be associated with the fact that (i) the thermal conditions were not very stressful for invertebrates as most taxa found in the sites below dams are generally resistant to higher temperatures and oxygen depletion, as is typical for generalists, and (ii) most epigean invertebrates are quite mobile and may not use cool upwelling zones permanently (taxa can move from one patch to another for foraging activities and can recover from damage induced by thermal stress during foraging periods by resting periods in cool habitats; see e.g. Colinet *et al.*, 2015). As observed by Capderrey *et al*. (2013), who demonstrated significant effects of surface-groundwater exchanges on hyporheic invertebrates but no effects on benthic fauna, the upwelling flow of groundwater directly into the main channel might not be sufficient to affect habitat conditions in the benthic zones of the Ain River. Supporting this interpretation, we did not find a positive influence of the nutrient enrichment associated with upwelling zones on benthic algae, whereas this influence has been observed in many streams (e.g. Grimm and Fisher, 1989; Pepin and Hauer, 2002; Hunt *et al*., 2006). Therefore, the selected upwelling zones in the Ain River were probably too spatially restrained to allow the development and maintenance of specific benthic invertebrate assemblages.

4.5. Concluding remarks

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

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Figure legends

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

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

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

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

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

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

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

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

Table Captions

Table 1. General characteristics of the study sites.

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

Table 3. (A) Flow (*n*=36) and temperature (*n*=72) characteristics in each study site (mean±standard deviation). (B) Chemical parameters 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).

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).

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).

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).

Appendices

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.

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.

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 affinity scores (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)).

Supplementary information

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

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

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

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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	*idem*
Nb of generations per year	Multivoltine	*idem*
Dispersal	Aquatic passive	*idem*
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	*idem*
Food community specialization	all food types	*idem*
Trophic status community specialization	all trophic status types	*idem*
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 (µS.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$_4$ (µg. 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$_4$ (µg. 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^{6}cells.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^{6}cells.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^{6}cells.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	***
Chlorophylle-*a* (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	013±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
Amphinemura 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	0	1	1	0	0	0	0	0	0	0
Ancylus 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	0	1	1	8	0	0	1	1	1	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	0	0	7	0	0	0	0	0	0	0	0
Asellus 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
Atherix 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
Athripsodes 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
Baetis 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
Bithynia 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	0	1	0	0	0	1	0	23	2	0	0
Brychius sp.	0	0	0	1	0	0	1	0	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
Caenis sp.	0	0	1	4	6	4	0	0	2	8	9	11	0	0	0	0	0	0	0	0	6	4	0	0	0	8	5	2	2	5	25	107	66	24	7	20
Calopteryx 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
Centroptilum 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
Ceraclea 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	1	2	1	1	0	0	24	4	2	0
Ceratopogonidae	6	4	38	22	8	26	1	2	37	0	9	6	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	3	2
Cheumatopsyche sp.	0	0	0	0	0	0	0	0	16	1	2	1	0	0	0	0	0	7	49	0	322	54	2	4	19	2	124	61	27	27	301	162	411	1901	7	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
Dendrocoelum 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
Dinocras 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	0	1	0	0	0	0	0
Dreissena 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
Dryops 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
Dugesia 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
Ecdyonurus 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
Elmis 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
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
Epeorus 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	0	7	3	3	1	0	0	0	0	0	1
Ephemera sp.	3	1	5	2	0	3	0	2	1	1	0	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
Erpobdella 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	0	1	0	0	2	3	14	26	20	9	1	4

Appendix 1. Continued.

Esolus 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
Gammarus 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
Glossiphonia 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	0	3	1	1	6	0	6	0	0	0
Habroleptoides 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
Habrophlebia 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
Haliplus 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	4	0	0	0
Helobdella 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	1	1	0	0	0	1	6	0	0	0
Hemiclepsis 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
Heptagenia 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	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
Hydraena 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
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
Hydropsyche 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
Hydroptila 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
Ithytrichia 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
Lepidostoma 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
Leuctra 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
Limnius 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
Metalype 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
Micrasema 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
Micronecta 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
Mystacides sp.	0	0	0	1	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	4	0	2	1	0	0
Nemoura sp.	0	0	3	3	0	0	0	0	3	6	0	0	0	0	6	6	0	0	0	0	3	3	0	0	0	0	4	0	1	1	0	0	1	1	0	0
Odontocerum 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
Onychogomphus 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
Orectochilus 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
Orthocladiinae	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
Oulimnius 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
Perla 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	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
Piscicola 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	1	0	0	0
Pisidium 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
Planorbidae 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	1	0	0	0	3	1	11	4	2	0
Polycelis 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
Polycentropus 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
Potamanthus 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	1	0
Protonemura 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	1	8	4
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	1	0	0	0
Psychomyia 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
Radix 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
Rhithrogena 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	2	1	2
Rhyacophila 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
Riolus 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
Sericostoma 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	4	0
Serratella 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
Setodes 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	2
Silo 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
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
Siphonoperla 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
Stenelmis sp.	0	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
Tabanidae	0	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
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
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
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
Torleya 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

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
Amphinemura 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
Ancylus 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
Anthomyidae	1	16	0	9	0	0	0	0	6	0	1	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
Asellus 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
Atherix sp.	0	1	0	1	0	0	0	0	0	0	2	0	4	0	0	0	0	0	14	3	0	0	0	0	0	0	0	0	0	0	3	2	2	0	0	0
Athripsodes 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
Baetis 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
Bithynia 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
Brychius 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
Caenis 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
Calopteryx 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
Centroptilum 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
Ceraclea 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	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
Cheumatopsyche 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
Dendrocoelum 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
Dinocras 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
Dreissena 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
Dryops 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	11	0	0	0
Dugesia 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
Ecdyonurus 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
Elmis 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
Epeorus 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
Ephemera 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
Erpobdella 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
Esolus 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 2. Continued.

Gammarus sp.	1922	462	1842	1368	2558	2393	3420	820	487	88	4330	1942	1269	175	570	175	539	92	206	679	189	617	1046	143	35	146	135	2121	120	51	38	158	28	183	48	201
Glossiphonia sp.	3	3	0	0	1	2	0	0	1	0	0	1	0	1	0	0	0	2	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Habroleptoide sp.s	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	4	1	0	0	0	0	1	0	0	0	0	7	0	0	1	0	0	2	1	0	0
Habrophlebia 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
Haliplus sp.	0	2	0	0	0	0	0	0	2	3	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Helobdella sp.	0	0	1	0	0	0	0	5	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
Hemiclepsis sp.	0	2	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	0	0	0	0	0	0	0	0
Heptagenia sp.	0	0	0	0	1	1	16	15	3	3	3	4	2	0	2	8	6	7	36	20	0	2	0	1	0	12	18	11	5	5	18	9	13	42	0	7
Hydracarina	11	38	102	16	261	176	212	295	17	13	85	158	10	28	32	18	135	20	27	25	16	18	51	47	5	19	2	5	24	8	7	208	11	29	11	18
Hydraena sp.	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0
Hydroporinae	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	2	0	0	1	0	0
Hydropsyche sp.	240	16	395	287	198	45	683	553	114	27	28	8	81	5	22	15	43	4	75	12	6	1	14	3	55	19	31	6	6	2	275	191	180	83	6	4
Hydroptila sp.	12	6	44	46	173	115	12	80	55	293	16	7	1	1	7	2	23	3	20	0	8	14	4	0	10	2	0	1	0	1	10	28	52	24	1	0
Ithytrichia 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
Lepidostoma sp.	0	4	1	11	13	64	2	4	0	2	0	4	0	0	2	0	2	1	7	1	0	2	0	0	0	1	1	4	0	0	0	8	0	14	0	0
Leuctra sp.	1	7	0	0	7	1	101	36	1	3	41	26	9	23	0	0	5	1	167	131	3	7	8	29	51	2	0	1	4	0	5	3	0	0	25	19
Limnephilinae	1	0	0	0	0	12	0	0	0	1	0	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnius sp.	49	36	25	32	106	31	79	45	37	36	23	18	9	1	15	3	7	6	8	2	9	3	2	3	1	0	0	0	1	0	0	0	2	1	0	1
Limoniidae	33	35	59	69	162	182	45	11	2	3	6	7	46	1	9	1	98	4	5	0	0	0	21	0	21	1	16	0	1	0	12	24	5	1	0	0
Metalype sp.	0	0	1	5	5	10	1	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	0	0	0
Micrasema 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
Micronecta sp.	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Mystacides sp.	0	0	0	7	0	1	0	0	2	18	0	12	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	2	0	0
Nemoura 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
Odontocerum 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
Onychogomphus sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	2	1	0	0	0	0	0	0	0	0	0	2	1	1	0
Orectochilus sp.	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	19	0	0	0
Orthocladiinae	2655	840	201	218	1569	292	184	169	835	366	3819	1962	799	147	156	9	678	22	468	157	139	22	593	25	421	880	388	29	159	5	55	273	527	239	105	45
Oulimnius sp.	9	14	6	34	7	4	7	8	11	21	0	5	7	7	12	0	7	1	4	1	17	15	2	1	0	0	0	2	0	0	0	8	5	29	0	1
Perla 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
Perlodidae	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	0	0	0	0	0	0	0	0
Piscicola sp.	0	0	1	0	3	2	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0

Appendix 2. Continued.

Pisidium sp.	0	0	0	0	0	0	5	17	1	16	4	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
Planorbidae	1	1	1	6	1	1	2	2	0	3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Polycelis sp.	27	88	29	34	9	129	12	23	0	1	10	17	4	1	2	1	4	1	0	1	0	11	0	0	0	0	0	10	0	1	0	0	0	1	1	0
Polycentropus sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	4	2	0	0
Potamanthus sp.	0	0	0	0	0	0	0	0	0	0	3	29	1	2	0	1	1	2	1	9	0	14	2	14	0	0	1	0	0	0	0	0	3	5	1	1
Protonemura sp.	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	0	0	0	0	0	0	0	0	0	0
Psychodidae	2	3	4	27	0	0	7	1	1	3	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Psychomyia sp.	9	5	8	5	131	171	20	35	4	1	1	0	33	5	25	5	148	6	24	13	1	0	5	0	23	9	41	1	10	2	24	97	22	1	0	0
Radix sp.	1	4	2	2	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhithrogena sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0	2	7	0	0	2	0	2	0	2	0	0	0	3	4	0	1
Rhyacophila sp.	28	3	19	16	49	15	18	59	2	1	101	26	10	0	2	2	7	3	2	1	0	0	19	1	20	0	25	4	12	0	23	0	11	0	3	2
Riolus sp.	2	4	12	4	12	4	6	3	30	11	0	1	2	0	7	0	3	0	3	1	1	0	0	1	25	1	9	0	0	0	8	9	2	2	1	0
Sericostoma sp.	2	39	2	7	11	13	3	2	0	0	1	0	0	3	1	2	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Serratella sp.	203	58	35	6	160	180	1199	287	3	1	1025	425	29	3	9	3	41	16	199	48	0	0	102	22	13	8	1	0	3	0	57	84	0	0	15	30
Setodes sp.	0	0	0	0	1	0	0	0	0	0	3	1	0	0	0	0	0	0	0	1	0	4	1	4	0	0	0	0	0	0	0	0	3	2	1	1
Silo 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	0	0	0	0	0	0	0	0	0	0
Simuliidae	15	27	0	0	72	2	0	19	3	2	406	9	13	1	1	0	65	2	8	1	0	0	30	4	22	0	4	1	69	8	206	23	5	2	107	36
Siphonoperla sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	5	0	0	0	0	0	0	2	0	0	0	2	2	0	0
Stenelmis sp.	0	1	2	0	0	0	1	0	3	0	0	0	1	0	0	0	0	0	2	1	0	1	0	1	0	0	0	0	0	0	0	0	1	2	0	0
Tabanidae	1	1	0	1	0	0	0	0	0	0	4	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Tanypodinae	0	7	3	4	13	16	170	70	1	5	17	7	1	3	0	0	4	9	110	67	0	0	4	2	5	12	1	2	0	0	18	79	2	1	1	0
Tanytarsini	39	102	4	20	429	417	263	294	16	27	6	13	54	6	3	0	101	4	170	142	1	1	4	0	15	20	4	0	7	1	16	297	6	6	1	0
Tipulidae	0	2	1	13	0	0	1	0	9	23	0	1	0	0	2	1	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0
Torleya 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	0	0	0	0	0	0	0	0	0	0

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)).

	(a)	(b)	(c)	(d)	(e)	(f)							(g)				(h)			(i)
Taxa	< 10	< 1	>1	ovoviviparity	aquatic passive	micro organisms, detritus < 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
Amphinemura 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
Ancylus 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
Atherix 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
Athripsodes 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
Baetis 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
Bithynia 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
Brychius 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
Caenis 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
Calopteryx 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
Centroptilum 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
Ceraclea 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
Cheumatopsyche 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
Dendrocoelum 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
Dinocras 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
Dreissena 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
Dryops 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
Dugesia 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
Ecdyonurus 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
Elmis 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
Epeorus 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

Ephemera 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
Erpobdella 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
Esolus 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
Gammarus 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
Glossiphonia 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
Habroleptoides 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
Habrophlebia 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
Haliplus 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
Helobdella 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
Hemiclepsis 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
Heptagenia 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
Hydraena 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
Hydropsyche 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
Hydroptila 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
Ithytrichia 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
Lepidostoma 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
Leuctra 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
Limnius 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
Metalype 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
Micrasema 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
Micronecta 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
Mystacides 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
Nemoura 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
Odontocerum 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
Onychogomphus 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
Orectochilus 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
Orthocladiinae	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
Oulimnius 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

Perla 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
Piscicola 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
Pisidium 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
Polycelis 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
Polycentropus 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
Potamanthus 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
Protonemura 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
Psychomyia 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
Radix 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
Rhithrogena 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
Rhyacophila 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
Riolus 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
Sericostoma 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
Serratella 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
Setodes 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
Silo 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
Siphonoperla 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
Stenelmis 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
Torleya 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

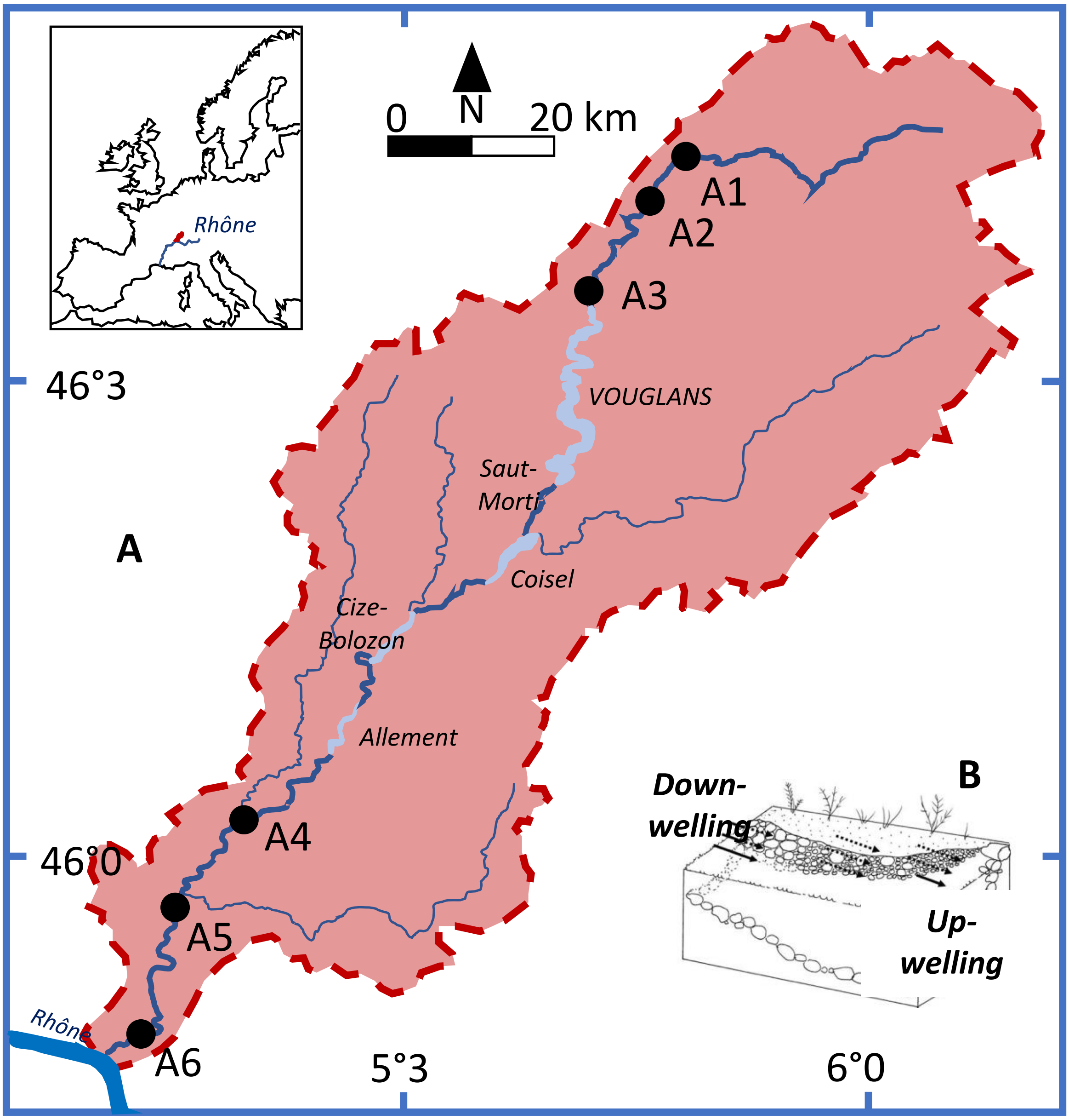
Rhône
0
N
20 km
A1
A2
A3
46°3
VOUGLANS
Saut-
Morti
A
Coisel
Cize-
Bolozon
Allement
Down-
welling
B
A4
46°0
Up-
welling
A5
Rhône
A6
5°3
6°0

Figure 1.

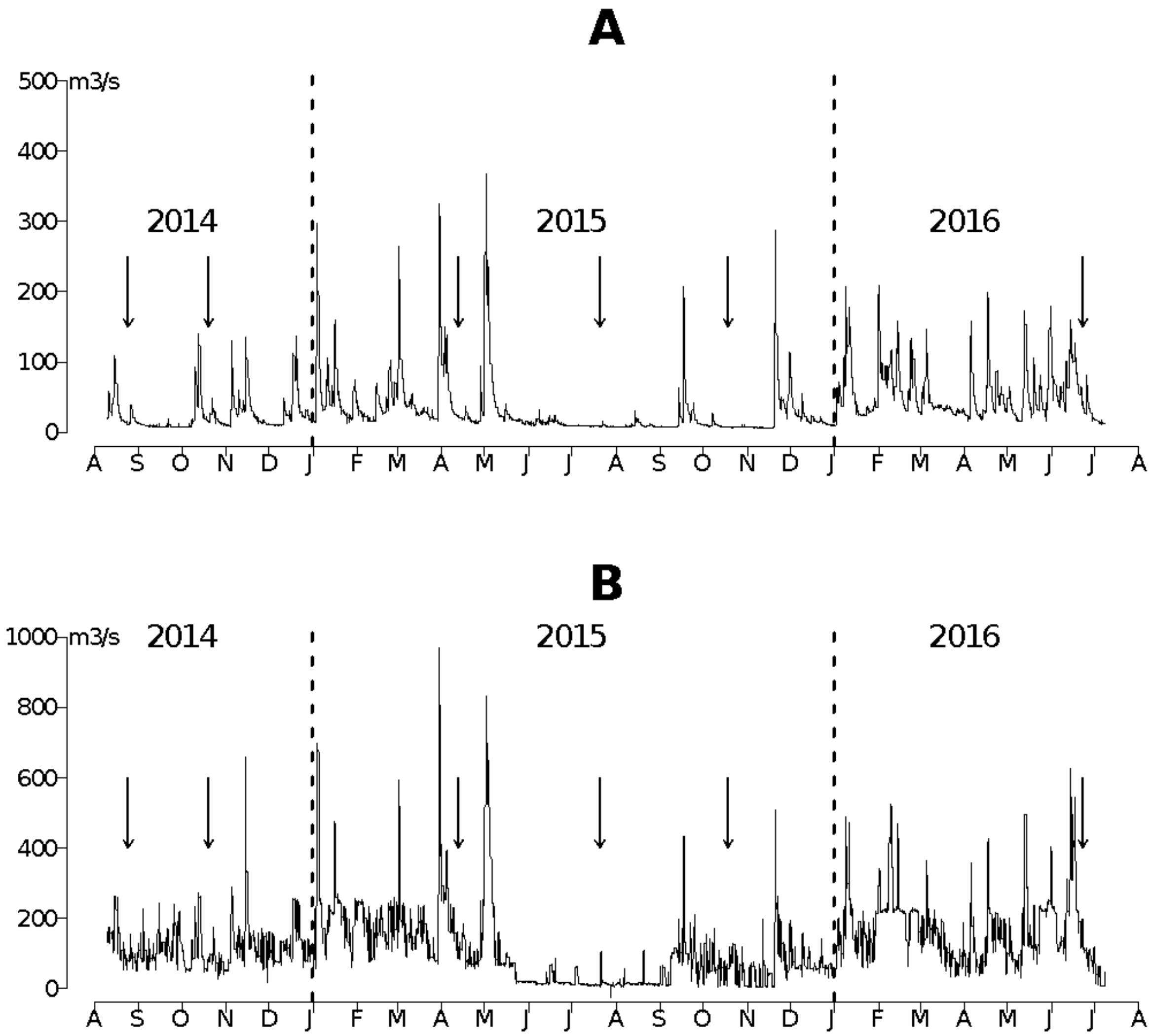
A
500
400
300
200
100
0
m3/s
2014
2015
2016
A S O N D J F M A M J J A S O N D J F M A M J J A
B
1000
800
600
400
200
0
m3/s
2014
2015
2016
A S O N D J F M A M J J A S O N D J F M A M J J A

Figure 2.

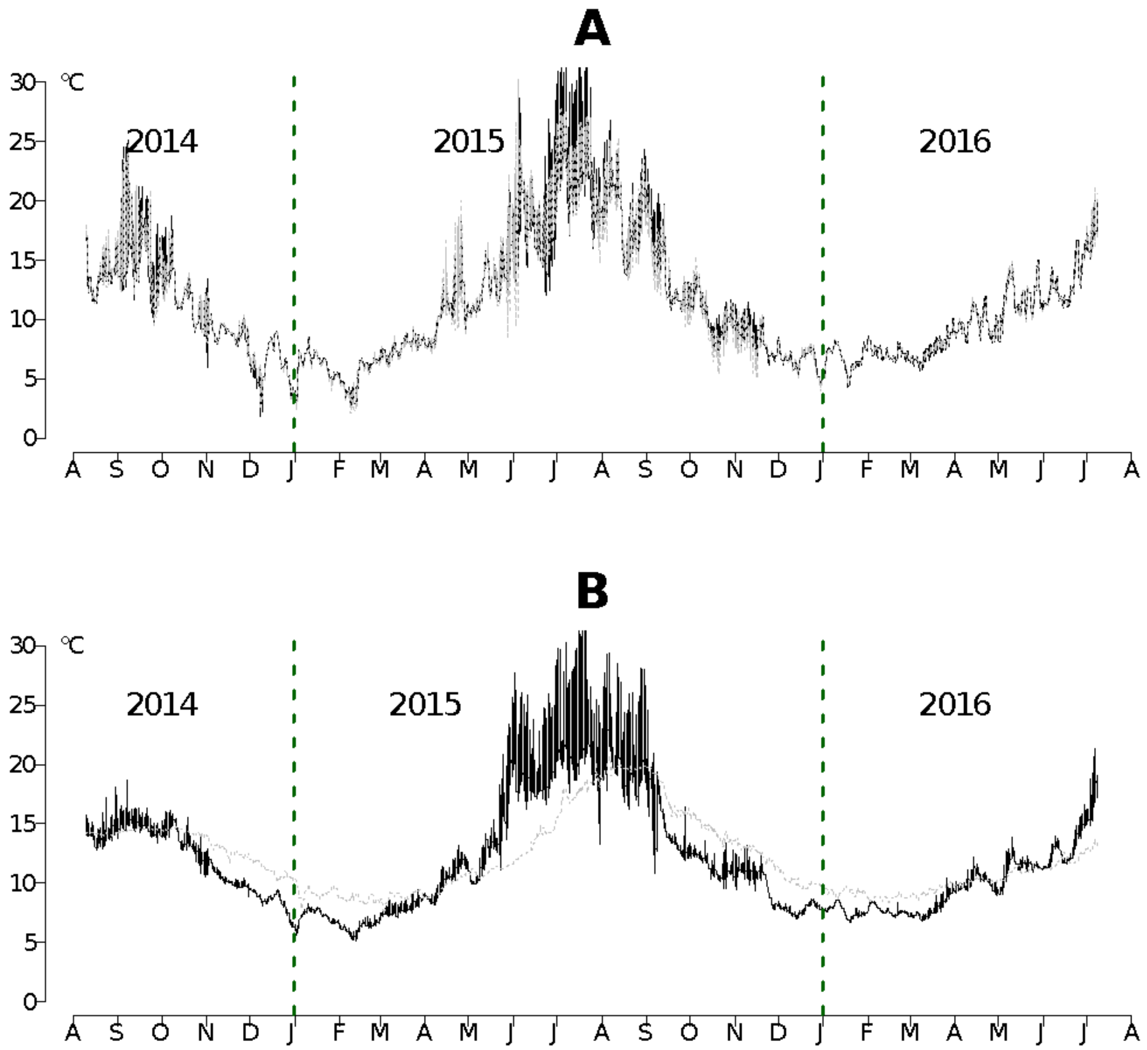
A
30
25
20
15
10
5
0
°C
2014
2015
2016
A S O N D J F M A M J J A S O N D J F M A M J J A
B
30
25
20
15
10
5
0
°C
2014
2015
2016
A S O N D J F M A M J J A S O N D J F M A M J J A

Figure 3.

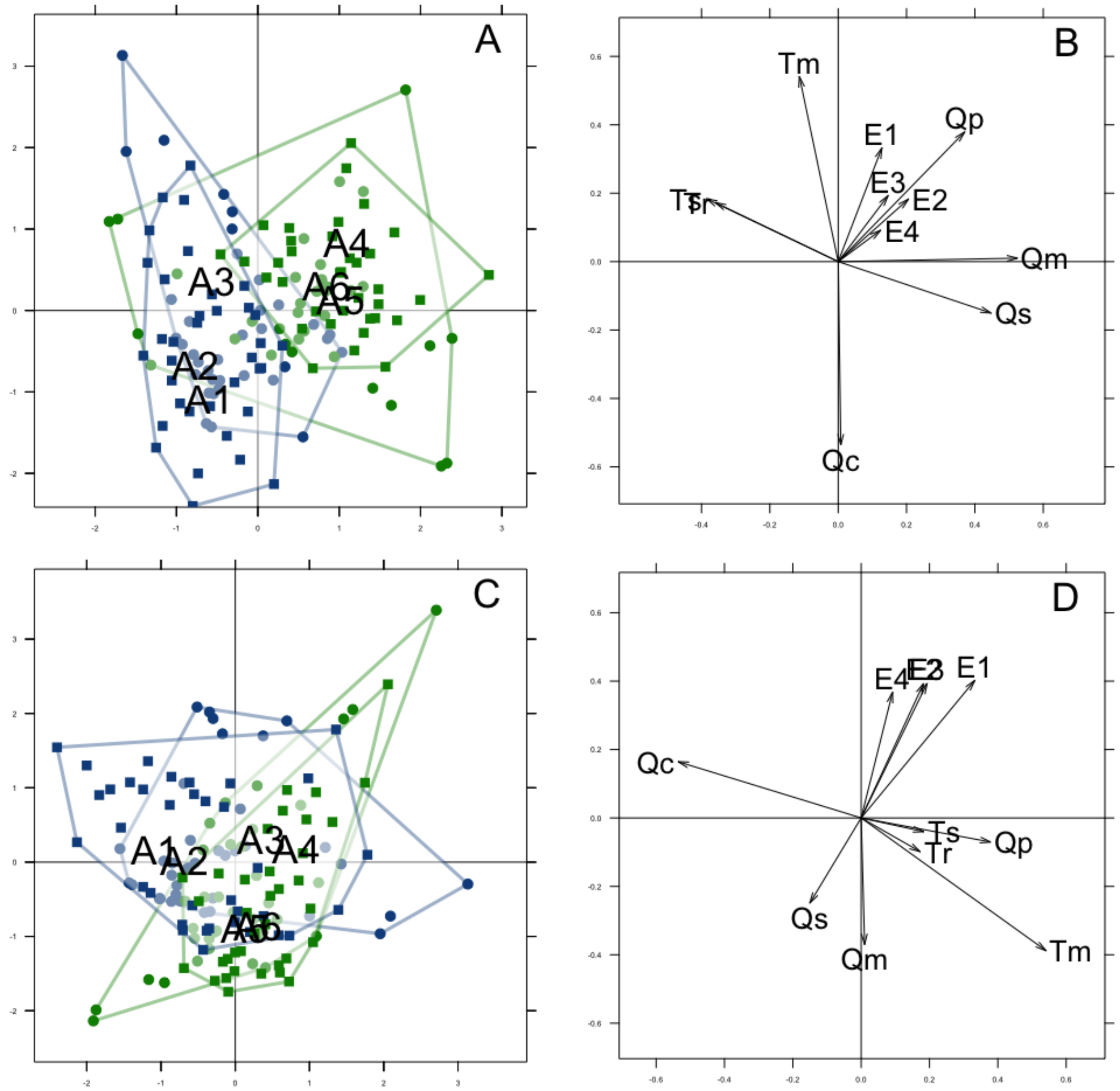
A
A3
A4
A6
A5
A2
A1
B
Tm
E1
Qp
E3
E2
E4
Ts
Tr
Qm
Qs
Qc
C
A1
A2
A3
A4
A5
A6
D
E4
E2
E3
E1
Qc
Ts
Qp
Tr
Qs
Qm
Tm

Figure 4.

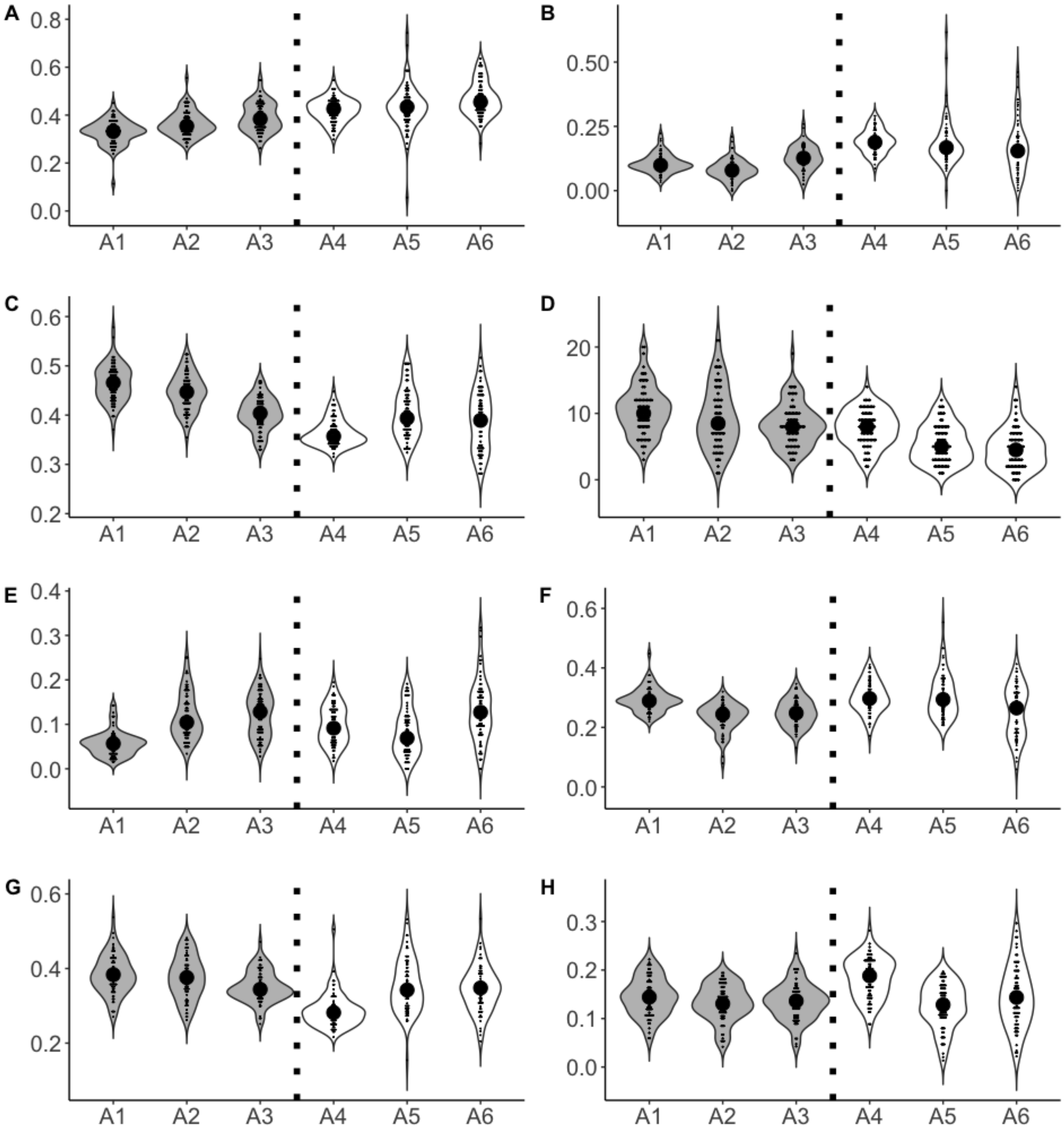
A
0.8
0.6
0.4
0.2
0.0
A1 A2 A3 A4 A5 A6
B
0.50
0.25
0.00
A1 A2 A3 A4 A5 A6
C
0.6
0.5
0.4
0.3
0.2
A1 A2 A3 A4 A5 A6
D
20
10
0
A1 A2 A3 A4 A5 A6
E
0.4
0.3
0.2
0.1
0.0
A1 A2 A3 A4 A5 A6
F
0.6
0.4
0.2
0.0
A1 A2 A3 A4 A5 A6
G
0.6
0.4
0.2
A1 A2 A3 A4 A5 A6
H
0.3
0.2
0.1
0.0
A1 A2 A3 A4 A5 A6

Figure 5.

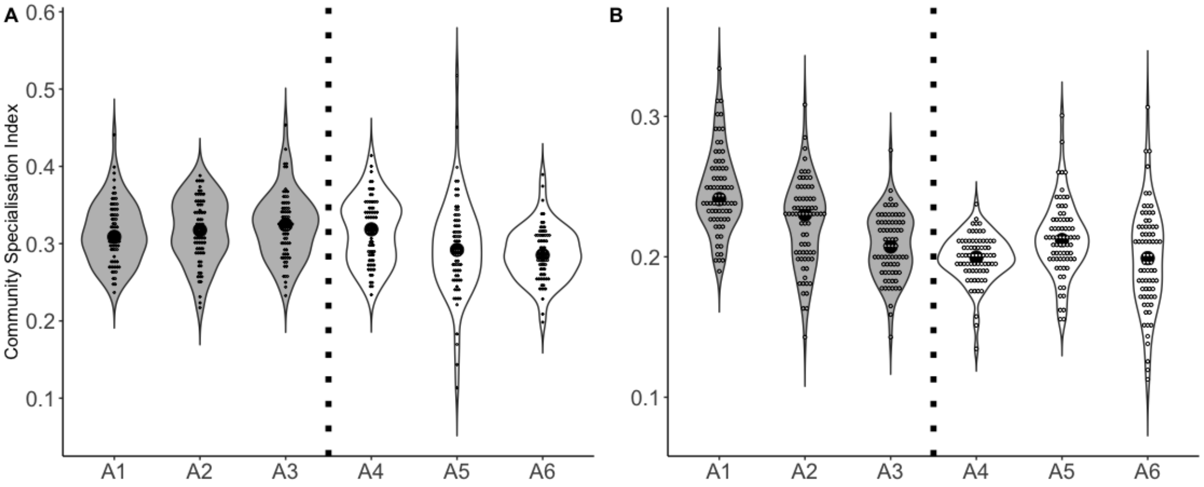
A
B
Community Specialisation Index
0.6
0.5
0.4
0.3
0.2
0.1
0.3
0.2
0.1
A1
A2
A3
A4
A5
A6
A1
A2
A3
A4
A5
A6

Figure 6.

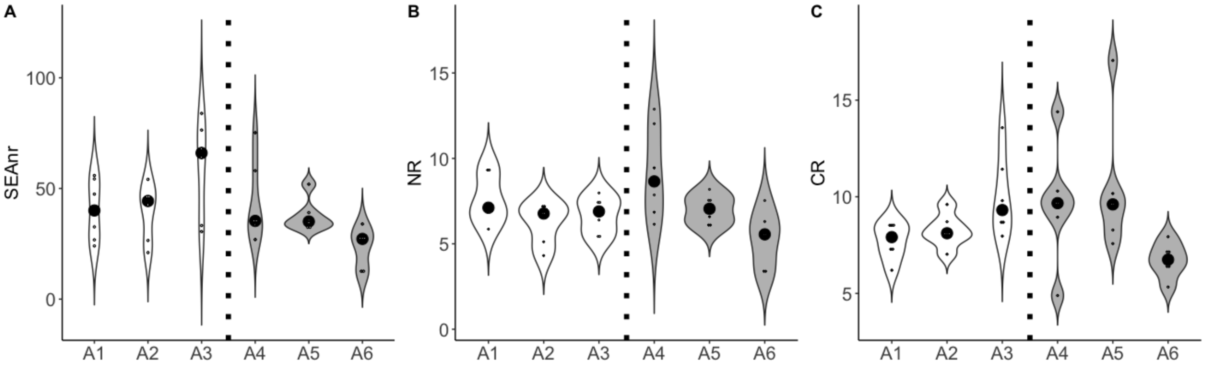
A
SEAnr
0
50
100
A1
A2
A3
A4
A5
A6
B
NR
0
5
10
15
A1
A2
A3
A4
A5
A6
C
CR
5
10
15
A1
A2
A3
A4
A5
A6

Figure 7.

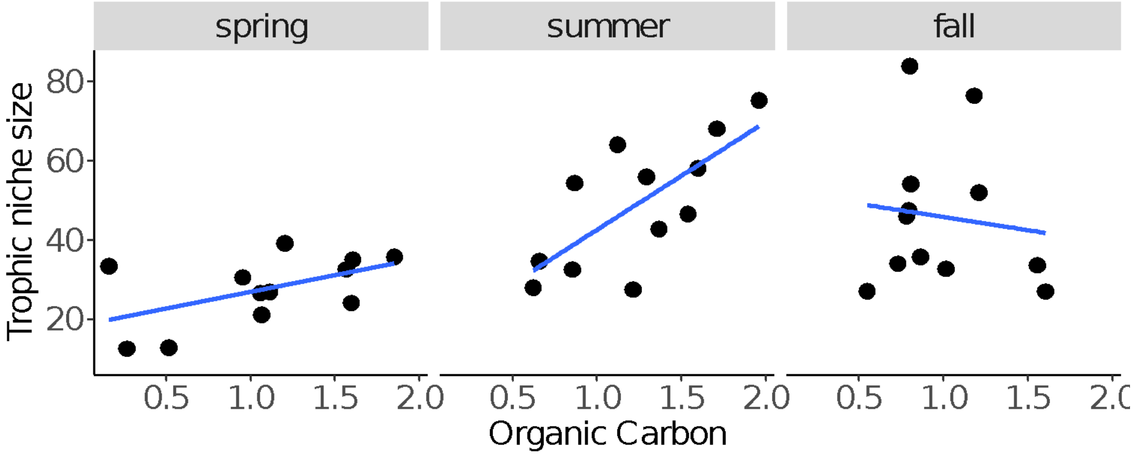
spring
summer
fall
Trophic niche size
80
60
40
20
0.5
1.0
1.5
2.0
0.5
1.0
1.5
2.0
0.5
1.0
1.5
2.
Organic Carbon

Figure 8.