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Drivers of functional diversity in the hyporheic zone of a large river

Marie-José Dole-Olivier[a], Michel Creuzé des Châtelliers[a], Diana M. P. Galassi[b], Michel Lafont[a], Florian Mermillod-Blondin[a], Frederic Paran[c], Didier Graillot[c], Shishir Gaur[d] and Pierre Marmonier[a] (🖂)

a - Univ. Lyon, University Claude Bernard Lyon 1, CNRS, ENTPE, UMR5023 LEHNA, 43 Boulevard du 11 Novembre 1918, F-69622, Villeurbanne, France

b - University of L'Aquila, Department of Life, Health and Environmental Sciences, Via Vetoio, Coppito, 67100 L'Aquila, Italy.

c – Ecole Nationale des Mines de Saint Etienne, CNRS, UMR5600 PEG, F-42023 Saint Etienne, France

d – Department of Civil Engineering, Indian Institute of Technology (BHU), 221005 Varanasi, India.

(🖂) Corresponding author:
e-mail: pierre.marmonier@univ-lyon1.fr

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Highlights: (3 to 5 point with 85 characters max)

-Hydrogeology, current and past fluvial forms control large-scale distribution of the hyporheos

-Hydrology controls hyporheos composition at the station scale

-Visible characteristics of surface sediment had poor influence

-Upwelling zones are hotspot of groundwater biodiversity

-Downwelling zones harboured high abundances of temporary hyporheos

Abstract

The effects of regional (hydrogeology and geomorphology) and local (sediment and hydrology) characteristics on hyporheic assemblages were studied along a 40-km reach of a large gravel-bed river. Hyporheic water and fauna were sampled at the upstream and downstream positions of 15 large gravel bars. The resulting 30 stations varied in their sediment grain size, stability and direction of river-aquifer exchanges. The study concludes that at the 40-km (sector) scale, the longitudinal distribution of hyporheic fauna was controlled by 1) the hydrogeology of the valley (i.e. gaining vs loosing sectors) that modifies abundance and taxonomic richness of stygobites 2) current channel morphometry of the river (i.e. shape and location of meanders), and 3) historical changes (i.e. river incision) which modify abundance and richness of assemblages. At the local scale, we found that surface grain size and stability of the sediment evaluated by visual observation were poor predictors of hyporheos composition. In contrast, the local hydrology (i.e. downwellings, upwellings, low vertical exchanges) explained a large part of the abundance, taxonomic richness and composition of the hyporheic assemblages. Stations with low vertical exchanges were found poorly colonized, while the upwelling zones were rich in stygobites and downwelling areas harbor abundant and species-rich temporary hyporheos. It was also observed that functional diversity was controlled by the same parameters, with high relative abundances of stygobites in upwelling zones and POM feeders in downwelling zones. The heterogeneity of hydrological patterns, with alternation of upwellings and downwellings may represent the optimal spatial structure for hyporheic biodiversity conservation and resilience in rivers.

Key words: Hyporheos, stygobites, hydrogeology, geomorphology, river incision, dams
(Six max)

1. Introduction

Porous sediment deposits in rivers constitute the hyporheic habitat (Orghidan, 1959), where river-aquifer exchanges occur together with a large number of ecological processes important for stream metabolism (Findlay, 1995; Boulton et al., 1998). Hyporheic processes contribute to the recycling of nutrients (e.g., nitrification / denitrification, Triska et al., 1993; Jones et al., 1995, Storey et al., 2004) and of organic matter (e.g. biodegradation of leaf litter, Cornut et al., 2010). Additionally, the hyporheic habitat contributes to the biodiversity of the river by combining colonization of both obligate groundwater fauna (i.e. stygobites) and benthic organisms (Dole-Olivier and Marmonier 1992; Dole-Olivier et al., 1997; Brunke and Gonzer, 1999). Hyporheic organisms can that modify the structure of the sediment (through bioturbation, Mermillod-Blondin and Rosenberg, 2006; Shrivastava et al., 2021a, 2021b), the dynamics of organic matter (through subsurface biodegradation, Crenshaw et al., 2002; Marmonier et al., 2010) and the concentration of dissolved nutrients (Mermillod-Blondin et al., 2000; Nogaro and Burgin, 2014). Thus, their biodiversity is of crucial importance for river integrity and functioning.

The hydrological, geomorphological, physicochemical, and/or biological processes control major ecological features of streams (Petts & Amoros, 1996). The local hydrology, with the occurrence of water exchanges between the river and the adjacent groundwater is the major driver for the control of hyporheic processes and biodiversity (Dole-Olivier and Marmonier 1992; Valett et al., 1993; Brunke and Gonzer, 1999). Many studies have demonstrated the influence of river-aquifer exchanges on the physicochemical characteristics, nutrient recycling and invertebrate biodiversity of streams (e.g., Olsen and Townsend, 2003; Navel et al., 2011; Mathers et al., 2017). The intensity and direction of these exchanges are crucial; in downwelling zones, the river water infiltrates into the riverbed sediments carrying fresh organic matter and dissolved oxygen, while in upwelling zones, the flow of groundwater towards the surface stabilizes stream temperature and water level (Claret et al., 1998; Franken et al., 2001; Peralta-Maraver et al., 2018). Additionally, the direction and magnitude of hydrological exchanges through the hyporheic zone also control hyporheic biodiversity (Dole-Olivier & Marmonier, 1992; Lin et al., 2020).

These river-aquifer interactions are generally controlled by the geology of the valley and the geomorphology of the streambed at different scales (Williams, 1993; Poole, 2002, 2010; Capderrey et al., 2013). The geology of the valley controls the characteristics of the aquifer (e.g. volume, general slope) and the relative elevation of the piezometric level compared to the river level (Graillot et al., 2014; Marmonier et al., 2019). Similarly, the geomorphology of the streambed controls the water exchanges between the river and the hyporheic zone (Buffington and Tonina, 2009): at a regional scale, the shape of the channel influences the direction of water exchanges (Cardenas et al., 2004). For example, large gravel bars induce infiltration of surface water at their heads and exfiltration of groundwater at their tails (Dole-Olivier and Marmonier, 1992). Furthermore, the geomorphology controls the local characteristics of sediments like their grain sizes and their stability (e.g. Singer, 2008; Snelder et al., 2011). For example, the occurrence of fine sediment patches may modify the nature and intensity of most hyporheic microbial processes, due to reductions in vertical water exchanges, availability of dissolved oxygen and organic matter (Lefebvre et al., 2005; Nelson et al., 2019). Likewise, sediment grain size may control hyporheic assemblages, for both taxonomic richness and species composition (Descloux et al., 2013; O'Sullivan et al., 2019) and sediment mobility maintain hyporheic permeability and vertical migration of the hyporheic fauna (Dole-Olivier et al., 1997). The effects of these large-scale characteristics (i.e. hydrogeology and geomorphology) are not limited to hyporheic processes, but also control the global functioning of the river and the dynamics of most organisms that live inside and in close relation to the river, supporting the importance to consider the river in its valley (Hynes, 1975) as a global hydrosystem (Petts & Amoros, 1996).

Hyporheic assemblages (hyporheos) are characterized by a variety of taxa with very different ecological requirements. Some species use the hyporheic zone for only part of their life cycle (i.e. temporary hyporheos), while other species can spend their entire life cycle within the sediment (i.e. permanent hyporheos). In addition, taxa such as stygobites are obligated to live in groundwater habitats (Williams, 1984; Marmonier et al., 1993). The relative composition of these three groups of species may determine zones of high diversity (hyporheic hotspots, Marmonier et al., 2020; Hutchins et al., 2020). Furthermore, the hyporheic fauna is very diverse in food preferences ranging from fine sediment feeders, to particulate organic matter-feeders (detritivores) and predators (Williams et al., 2010). While taxonomic composition of river assemblages may be strongly influenced by biogeography, evolutionary processes and dispersal (Eme et al., 2015), the functional diversity based on ecological groups (Usseglio-Polatera et al., 2000) can help to elucidate the dynamics of hyporheic assemblages.

Functional diversity relates to the range and value of those species and organismal traits that influence how an ecosystem functions (Lawton, 1994; Tilman et al., 1997). It may also be affected by large-scale gradients in habitat characteristics (Poff, 1997; Brown et al., 2018) or by local disturbances (Schmera et al., 2017; Graco-Rosa et al., 2021). For example, Parker et al. (2018) used a functional index based on fish habitats and foraging traits to evaluate the effect of long-term improvements in water quality in four reaches of the Illinois River. In the same way, Paillex et al. (2013) used the functional diversity of macroinvertebrate assemblages based on 11 biological traits to estimate the effect of the restoration of the connectivity across the Rhône River floodplain. Also, functional diversity of invertebrates may be of interest to evaluate the effects of disturbances in the hyporheic zone (Magliozzi et al., 2019; Di Lorenzo et al., 2021). Changes in direction and/or intensity of river-groundwater exchanges can lead to shifts in hyporheic biodiversity, whether they are natural (e.g. floods) or human-induced (e.g. dewatering, groundwater abstraction; Dole-Olivier et al., 1997; Datry, 2012). Similarly, changes in the local characteristics of the bottom sediment (e.g. erosion, sediment clogging) can also modify the composition of hyporheic assemblages (Strayer et al., 1997; Marmonier et al., 2010b), but with poor changes in taxonomic richness due to species replacement (Descloux et al., 2013). Functional diversity -that include ecological requirements of species-may be efficient to evaluate the effect of changes in river-groundwater exchanges or in sediment characteristics on hyporheic species composition (Marmonier et al., 2012; Descloux et al., 2014; Lewandowski et al., 2019).

The present work aims to determine the combined effects of regional patterns (i.e. hydrogeological and geomorphological characteristics of a 40-km long reach) and local characteristics (i.e. sediment grain size, sediment stability and river-hyporheic water exchanges) on the composition and the functional diversity of hyporheic assemblages. The local hydrology was described using water chemistry, while the sediment characteristics was assessed by image analyses. The functional diversity was characterized using two functional traits based on the affinity of the species for groundwater habitats and their food-type preferences. For this purpose, 30 stations were selected along 15 gravel bars of a large gravel-bed river (the Ain River, France), with varying river-groundwater exchanges, sediment grain size and stability. Specifically, the following three hypotheses were proposed.

- First, hydrogeology and geomorphology control hyporheic assemblages at the scale of the 40-km reach (**H1**, Poole, 2010). More precisely, both river-groundwater exchanges (obtained from hydrogeology modelling) and channel morphology (e.g., location of incision zones, meanders) explain the longitudinal variations of hyporheic abundance, its taxonomic richness, and the variation of ecological groups along the studied reach.
- Second, surface sediment characteristics (visual estimation of the grain size composition and stability) have an effect on the composition of the hyporheic assemblages at the local scale (**H2**, Descloux et al., 2013). Taxonomic richness and abundances are high in coarse and mobile sediment, which favor the vertical migration of benthic organisms (temporary hyporheos) and organisms that feed on POM infiltrating from the surface. Whereas organisms that feed on fine sediment and algae are more abundant in sandy and stable areas covered by abundant biofilms. Finally, the stygobites that live in deep groundwater and are sensible to environmental instability are more abundant in stable shallow sediments.

- Third, the vertical hydrological exchanges at a local scale (i.e. upwelling, downwelling, low exchange zones) would control the abundance, taxonomic richness and functional diversity (**H3**, Dole-Olivier & Marmonier, 1992). Unfavorable conditions for the hyporheic fauna exist in low exchange zones (for both benthic and groundwater fauna); upwelling conditions lead to enhanced taxonomic richness of obligate groundwater-dwellers (stygobites), while downwelling conditions lead to increase the abundance and species richness of both temporary (benthic) and permanent hyporheos.

2. Study area

The study was conducted in the lowest 40-km reach of the Ain River, a tributary of the Rhône River, France (Dole-Olivier et al., 2019, Fig. 1). In this sector, the Ain River flows in a large alluvial plain composed of recent alluvia covering 5 to 30 m thick fluvio-glacial deposits, overlying Miocene molasses that represent the impermeable substratum. The alluvial plain width is reduced in its central part by two morainic hills between which the river flows (dotted lines in Fig. 1). In this sector, the mean annual discharge is 120 $m^3 s^{-1}$, with low flow conditions during the summer period (mean July-August, discharge: 54 $m^3 s^{-1}$). The river hydrology is also strongly influenced by five dams located upstream of the studied reach that produce daily discharge fluctuations and a significant sediment deficit (Rollet et al., 2014).

The lower Ain River is relatively wide with a wetted channel width of 51.5 m (± 15.9 m) and an active strip of 89.5 m wide (± 31.2 m, Dole-Olivier et al., 2019). The sediment deficit due to the dams induced a degradation of the riverbed of 2 to 4 cm per year from 1976 to 1999 (Rollet et al., 2014) on the first 10 km of the upstream part of the studied sector, around the four upstream gravel bars (noted by a pointed dark line on the Fig. 1). This riverbed degradation resulted in the erosion of fine particles and the local pavement of the riverbed (Rollet et al., 2014; Słowik et al., 2021). From 2005 on, a restoration program progressively took place in this sector of the Ain River, with injection of medium-to-fine sediment, just upstream of gravel bar 5, to reduce the riverbed degradation (Lejot, 2008). A total of 89,000 m^3 were injected in 6 years (Syndicat de la Rivière d'Ain Aval et de ses Affluents). Presently, the introduced fine sediment covers the river bottom and hides the local pavement (except at gravel bar 7).

3. Material and methods

3.1. Sampling design

Distribution of the hyporheic biodiversity along the Ain River was analysed in 2015 from June 29th to July 3rd when the stream was at its lowest discharge (i.e. between 12.5 and 16 m^3 s^{-1}) for at least 10 days. The sampling stations were located on gravel bars as they are relevant geomorphological units to predict local downwellings and upwellings (at upstream and downstream positions along the bar respectively, Dole-Olivier and Marmonier, 1992). Of the 40 gravel bars studied in 2014, a total of 15 gravel bars were selected from Pont d'Ain to Saint Maurice de Gourdans (coded from 5 to 33, similarly to Dole-Olivier et al., 2019; Fig. 1). The gravel bars were sampled at two stations (upstream and downstream of the bar), in three repeated points per position (hereafter called triplicates) randomly chosen 1.5 m apart from one another (Boulton et al., 2003) and at three depths for each point, i.e. -20, -40 and -60 cm below the sediment surface (i.e. 15 x 2 x 3 x 3 = 270 samples). The codes used for stations were labelled by a number for the gravel bar (from 5 to 33) and a letter for the position (U for upstream and D for downstream). These stations were selected to cover most of the studied sector and to include all types of hydrological characteristics: 26 with downwelling or upwelling conditions and 4 with low hyporheic exchanges, in a similar proportion to those selected in the study conducted in 2014 by Dole-Olivier et al. (2019) (i.e. 84% of stations with vertical exchanges and 16% with low or no exchanges).

3.2. Hydrological characteristics of the study sector

The hydrogeological characteristics of the Ain alluvial plain and resulting river-aquifer interactions were studied using geomatics analysis (Graillot et al., 2014; Paran and Augeard, 2017; Marmonier et al., 2019). The direction of groundwater/river hydraulic exchanges was inferred from point observations of water levels (or piezometric maps) for both the aquifer and the river. In unconfined alluvial aquifers, where the hydraulic connection with the river is proven, the water flow between the groundwater and the river is proportional to the slope of the free surface of the groundwater near the bank and the permeability of the alluvium following Darcy's law). We consider that the exchanges are made through a vertical plane whose area is defined by the bank length and the water height.

The exchange evaluation was based on a groundwater model by Burgeap (an environmental engineering group, Costaz, 2005-2006) with the modular three-dimensional finite-difference groundwater flow model Modflow (USGS, Harbaugh et al., 2000). In a second step, the model was improved by D. Mimoun, S. Gaur and F. Paran (Bornette et al., 2014) using river and groundwater levels, volume of water extraction, and hydraulic conductivity obtained from the Syndicat de la Basse Vallée de l’Ain (SBVA), the Centre d’Étude Technique de l’Équipement (CETE Lyon), the Diren Rhône-Alpes and the French geological survey (BRGM). The resulting regional groundwater flow model (grid size 60 m; 249,000 grid cells) for the Ain basin area (360 km²) was constructed and calibrated for transient-state conditions. The regional piezometric surface was based mainly on water hydrographs for 280 wells in the alluvial plain, while the mean thickness of the surface soil layer and vadose zone is about 3 m. The median values of hydraulic conductivity range from 0.0018 m s^{-1} (for the old fluvio-glacial deposits) to 0.003 m s^{-1} (for the recent layers). The horizontal hydraulic conductivity has been estimated from well tests and published data (Costaz, 2005, 2006) and found to vary between 3.10-5 to 4.10-2 m.s-1, with a strong decrease in the central part of the studied sector (between the two morainic hills, downstream of the gravel bars 10 to 12). Specific yield (Ss) values for alluvial deposits ranged from 1 to 17% (mean 5%).

The geomatic analysis was based on the model calibration expressed as a water table contour maps of the alluvial aquifer during a dry period (July 2006). A TIN mesh (Triangulated Irregular Network) was used to build the 3D model of the groundwater surface, using the slope of the water table (in %) and the direction of the flow (in degrees). The permeability of the aquifer (K) was estimated using model calibrated values. The calculation of flow exchanges between the alluvial groundwater and the Ain River was carried out using the ArcGIS Desktop 10.6 software. Because of uncertainties inherent in the geomatic analysis only the direction of exchanges was considered for this study.

3.3. Local scale hydrological patterns

A mobile standpipe was pushed inside the sediment at 20, 40 and 60 cm depth, and 1 L of hyporheic water was pumped using a peristaltic pump. A HACH thermo-conducti-oxymeter was used to measure temperature (° C), electric conductivity (µS cm^{-1}) and dissolved oxygen (mg L^{-1}). Similar measurements were collected concomitantly in the surface water. The vertical hydraulic gradient (VGH) was obtained by measuring the difference between the groundwater level in the mobile piezometer and the surface water level reported for the sampling depth (Baxter et al., 2003).

Using conductivity-temperature biplots (Dole-Olivier et al., 2019; Fig. 2A to 2C), the stations were separated into three groups according to the direction of the hydrological exchanges: (i) stations located in an upwelling zone with a positive VHG, a low hyporheic temperature (generally below 17°C) and high electric conductivity (generally above 400 µS cm^{-1}, Fig. 2A); (ii) stations located in a downwelling zone with negative VHG, low electric conductivity (generally below 400 µS cm^{-1}) and high temperature (generally above 17°C, Fig. 2C) and (iii) stations with weak or no exchange between river and aquifer with null values of VHG combined with low oxygen concentration (average O_2 concentration < 2.5 mg L^{-1}, Fig. 2B). Accordingly, 9 stations were located in "upwelling zones" (Fig. 2A), 4 stations in "low exchange sites" (Fig. 2B) and 17 stations in "downwelling zones" (Fig. 2C, full data in supplementary material Fig. S1). No upstream-downstream segregation along the study reach was observed in these 3 groups, but a segregation of the stations was found with river geomorphology:

most of the downwelling stations (10 out of 17) were located upstream of gravel bars (noted U), whereas most of the upwelling stations (6 out of 9) were located downstream of gravel bars (noted D in the Fig. 2). The low-exchange stations were evenly distributed at the upstream and downstream ends of three different gravel bars.

3.4. Sediment characteristics

Several methods were proposed to estimate the sediment characteristics (Descloux et al., 2010). Yet, most of them only consider the surface layer, despite potential vertical heterogeneity of the river sediment due to variability in fine particle penetration (e.g. Brunke 1999, Gayraud & Philippe, 2001). To evaluate the relevance of these methods based on surficial sediment assessment for hyporheic biodiversity, we used a visual estimation of sediment characteristics based photograph analysis. At each station, thee images of 0.25 m^2 of the surface sediments were randomly taken with a digital camera to define 3 types of substrate, scored as follows (Fig. 2D to 2E): substrate type dominated by sand, gravel and small pebbles (score 1), substrate type defined by a mixture of gravel and large pebbles (score 2), substrate type dominated by large pebbles (score 3). The mean score values (calculated with the three replicate photographs) identified three groups of station (Fig. 2D to 2E): 13 stations were characterized by fine sediments, 10 by mixed sediments and 7 by coarse sediments, without upstream-downstream segregation or any relation with the last century eroded zone (stations 5 to 9).

The sediment stability was estimated using the same images considering biofilm cover (Fig. 2G and 2H). We used differences in biofilm development to evaluate sediment stability because the river discharge was low for only 10 days. The mobile and instable areas were devoid of biofilm (score 0), while the stable sediment was covered by a filamentous biofilm (score 1). The mean score values identified two homogeneous groups: 13 stations were devoid of biofilm, while 17 were covered by filamentous algae. This stability index did not show any upstream-downstream segregation or relation with the last century eroded zone.

Coarse Particulate Organic Matter (CPOM) content per mass of dried sediment was measured by loss on ignition (550°C for 4.5 hours) in the laboratory for each 5L faunal sample (see below) after all invertebrate removal (CPOM expressed in mg L^{-1}).

3.5. Hyporheic invertebrates

The hyporheic fauna was collected using Bou-Rouch sampling equipment (Bou & Rouch, 1967, Stubbington et al., 2016) including a steel standpipe and a piston pump. Each sample consisted of 5 L mixture of water, sediment, particulate organic matter, and organisms. This procedure was applied at each point and depth (-20, -40 and -60 cm). Samples were sieved through a 200 µm mesh after elutriation to retain invertebrates and CPOM, and preserved with 96% alcohol. In the laboratory sorting and identification of invertebrates were performed with the aid of a stereomicroscope Olympus ZSX16 and a light microscope Olympus BX40, when needed. Clitellata, Copepoda, Ostracoda, Cladocera, Amphipoda, and Isopoda were identified to the species level. Flatworms, leeches, molluscs and most insect instars were identified to the genus or species levels (when possible). Diptera were identified to the family or the tribe levels. Finally, Acari Hydrachnidia Hydrachnidae and Nematoda were not identified further.

To study spatial patterns of functional diversity, the invertebrates were separated into two functional groups:

-Affinity to the groundwater habitat: (i) temporary hyporheos: organisms found inside the sediment that have an obligate aerial stage (i.e. benthic insects, excluding some Coleoptera that have aquatic adults); (ii) permanent hyporheos: organisms without specialization to groundwater life but that can complete their biological cycle without aerial stages (mainly flatworms, leeches, some oligochaetes, molluscs, some micro and macro-crustaceans, and Coleoptera with aquatic adults); and (iii) stygobites: obligate groundwater species that cannot survive in surface water (some oligochaetes, molluscs, and micro and macro-crustaceans in the Ain River).

-Food types used: (i) organisms feeding on biofilm covering fine sediments, hereafter sediment-feeders; (ii) feeding on particulate organic matter, hereafter POM-feeders; (iii) feeding on algae; and (iv) predators. Abundances in each group correspond to the sum of the abundances of all taxa of this group, corrected by a percentage of affinity when a species is known to belong to more than one trophic group. Food type uses were assessed using Tachet et al. (2000) for most benthic organisms, Juget and Lafont (1994) for Clitellata, and Marmonier et al. (1994) and Dole-Olivier et al. (2000) for micro-crustaceans.

The functional group diversity was calculated separately on the two types of grouping using the Simpson Index ($D = 1 / \Sigma p_i^2$) calculated on abundance-weighted functional groups (Gallardo et al., 2009; Schmera et al., 2017).

3.6. Data analysis

The spatial variation in physicochemical characteristics of the hyporheic water (n = 270 samples) was analysed using Principal Component Analysis (PCA) for the 5 parameters (i.e. VHG, electric conductivity, dissolved oxygen (concentration and saturation), and temperature). Concentrations of dissolved oxygen and CPOM were compared among groups of stations defined by sediment grain sizes (fine sediment, mixed, coarse), sediment stability (stable, unstable) or hydrology (upwellings, low exchanges, downwellings) using one-way ANOVAs after log-transformation, with mean value per station as replicates.

At the scale of the study reach, spatial autocorrelation among stations has been estimated for each variable using the acf function in R 4.1.2 software (R Core Team, 2021). As these preliminary analyses did not reveal any significant spatial autocorrelation, the longitudinal distribution of the hyporheic fauna was analysed using linear correlation, with the distance downstream of the last dam (expressed in km) as independent variable, while dependent variables were taxonomic richness and abundances of the total assemblages, of the 3 ecological groups and the 4 trophic groups. Taxonomic richness of trophic groups was not used because most taxa belongs to more than one trophic group. The composition of hyporheic assemblages was studied using a Correspondence Analysis (CA, Benzécri, 1973) to highlight spatial trends along the study reach and for different groups of stations based on sediment grain size, sediment stability and hydrology. PCA and CA were both performed using ExcelStat 2014. Total taxonomic richness was compared among the three groups based on hydrology. Due to the uneven distribution of samples among downwelling, upwelling and no-exchange stations (153, 81, and 36 samples each), rarefaction curves were generated based on sample-based incidence data to allow comparison of taxa richness at the same level of sampling effort using EstimateS, Version 9 (R. K. Colwell, http://purl.oclc.org/estimates).

At the local scale, statistical differences among taxonomic richness and abundances of all functional groups were investigated for groups of stations based on grain size categories (fine, mixed and coarse), sediment stability categories (stable vs unstable) or hydrology (upwelling, downwelling and low exchange) by one-way ANOVAs with stations as replicates (mean values for all depths and replicates and at the -20cm depth alone). In a last step, abundances and taxonomic richness of the total assemblages, of the ecological groups, and the abundances of the functional groups were compared among depths (-20, -40 and -60 cm depths) and hydrological patterns (downwelling, upwelling, no exchange) using two-way ANOVAs with stations as replicates, after log (x+1) transformation when necessary, followed by a Tukey’s test. For all variables, the normality and the homoscedasticity of the residues were verified using the Shapiro-Wilk's test and the Levene's test, respectively. Significance level for statistical tests was set at $\alpha < 0.05$. All ANOVAs were performed using Statistica (Statsoft Inc., USA).

4. Results

4.1. Hyporheic water chemistry and hydrogeology of the sector

The dissolved oxygen concentrations in the hyporheic water increased from upstream to downstream (r^2=0.21, p = 0.006; Supplementary material Fig. S3), with low oxygen values upstream (stations 5 to 9) and higher values downstream (stations 22 to 33). In contrast, no longitudinal trends for temperature, electric conductivity, VGH and CPOM were detected (Supplementary material Fig. S3). Any longitudinal variability for these parameters was better explained by river-groundwater exchanges evaluated by geomatic modelling (Fig. 3A). On one hand, the groundwater flow in the Ain alluvial plain was north-east to south-west directed, which resulted in local groundwater inflow along the river (e.g. near the stations 7, 22, 31-33 for the left bank). On the other hand, when the geomatic model was combined with the river forms (here meanders), the hyporheic water chemistry showed repeated inversions of the river-aquifer exchanges between upstream and downstream ends of the meanders (e.g. at gravel bars 12, 15 and at the large meander surrounded by the morainic hills from gravel bars 25 to 29). The geomatic analysis thus supported the majority of the diagnostics based on hyporheic water chemistry (20 of 30 stations, Fig. 3A and B). The stations classified "low exchange" type were poorly predicted by the geomatic analysis (3 of 4 stations were incorrected classified as "groundwater inflow" type by the geomatic model). In contrast, most stations classified in the "upwelling zone" type by the hyporheic water chemistry (8 out of 9) were consistent with the geomatic analysis. The only exception was the upwelling observed at station 31U, which occurred in a section where low exchange was predicted by the geomatic analysis (Fig. 3B). In the same way, most of the stations classified as "downwelling zones" by the hyporheic water chemistry (11 of 17) concurred with the geomatic model. The six cases of discrepancy between the geomatic model and the water chemistry were linked to narrow gravel bars located in straight sections of the river (i.e. not associated to meanders). In all cases, the downwelling zones observed at the upstream end of these small gravel bars (i.e. in stations 22U and 29U) or at both ends (i.e. stations 9U-9D and 17U-17D) were not predicted by the geomatic model. In contrast, when the gravel bars were associated with meanders, the prediction based on the geomatic analysis and the hyporheic water chemistry agreed quite well, with a reversion of exchange direction between upstream and downstream positions (i.e. for stations 12U-12D and 15U-15D) or a massive groundwater influence all along the downstream part of the large central meander (i.e. stations 26D, 28U-28D, 29D).

4.2. Hyporheic water chemistry and sediment characteristics at the local scale.

The hyporheic water characteristics also varied at the station scale, with variations according to the position, the sediment characteristics and the sampling depth. The PCA on the 270 samples (i.e. 15

stations, 2 positions, 3 depths and 3 replicates, Fig. 4) showed a gradient of high electric conductivity and positive VHG to warmer and well oxygenated water on the 1st axis.

The consistence of the three groups of stations based on the hydrology (using the biplots of temperature and electric conductivity) could be verified with their location in the PCA (Fig. 4B). The stations classified in upwelling zones (blue dots) had negative coordinates on the 1st axis, stations classified as downwelling zones (red dots) had mostly positive coordinates on the same axis, and stations classified as low exchange (black dots) were all closely grouped on the negative side on the two principal components (Fig. 4B). The distribution of these groups along the 2nd axis was due to a significant gradient in dissolved oxygen concentration that decreased from downwelling to upwelling zones and to low exchange areas (Fig. 4E; $F_{(2,\ 27)}$ = 11.45, p-value = 0.0002). Nevertheless, the three groups of stations were not strictly separated by the PCA: some sampling points pertaining to upwelling and downwelling zones were close to or overlapped with low exchange stations (Fig. 4B). This mixing was due to varying hydrological exchange intensities. For example, the station 12D (fed by groundwater, 16.8°C and 481 $\mu S\ cm^{-1}$ at -60 cm depth) and the stations 25U (fed by surface water, 20.3°C and 385 $\mu S\ cm^{-1}$ at -60 cm depth) were mixed with “low exchange” stations because of zero VGH. More than three clearly separated groups, the PCA highlighted a gradient of stations with different exchange intensities.

In contrast, stations characterized by contrasting sediment grain sizes (Fig. 4C) or sediment stability (Fig. 4D) were poorly or not separated at all by the two first axes of the PCA. The only chemical parameter that significantly changed with grain size was the dissolved oxygen concentration (Fig. 4F; $F_{(2,\ 27)}$=5.21, p-value = 0.012), with higher mean values below “mixed sediments” than under sediments visually estimated as fine or coarse. Finally, the CPOM concentrations were not significantly different between the groups of stations, regardless of the criteria used (hydrology, grain size or stability) because of high intragroup variability (p-value > 0.05).

4.3. The hyporheic fauna distribution at the sector scale

A total of 110,106 individuals belonging to 156 taxa were collected in the 270 samples (see dominant species in the frequency histograms, Supplementary material, Fig. S3). At the scale of the study reach (Fig. 5), both abundances and taxonomic richness of hyporheic fauna increased from upstream to downstream, with very low values measured from gravel bars 5 to 9 and higher values obtained downstream (e.g. gravel bars 30 and 33), resulting in significant correlations with the distance from the last dam located upstream of the studied reach (p-values < 0.01; Fig. 5).

One of the ecological groups, the permanent hyporheos, followed a similar increase with distance downstream of the dams (p-values < 0.01; Fig. 5), with very low abundances measured from gravel bars 5 to 9. In contrast, the temporary hyporheos (aquatic insect instars with flying adults) did not show any significant longitudinal trend (p-value > 0.05). High abundances were measured in all stations along the studied sector. The stygobites showed a heterogeneous longitudinal distribution, with high abundances measured in stations located downstream of meanders (i.e. stations 12D and 15D), or close to the morainic hills (i.e. gravel bars from 26 to 29) and in two gravel bars downstream of the sector (i.e. 30 and 33). The link between stygobite abundance and the presence of the meanders and morainic hills was associated with stygobite crustaceans, such as the amphipods *Niphargus* spp. that reached their highest abundances in the stations 12D, 15D, 26D and 28U-D (Fig. 5), four stations located in areas where the hydrological model predicted groundwater inflows (Fig. 3).

All trophic functional groups followed a significant increase with the distance downstream of dams (p-values < 0.01; Fig. 5). The upstream area harbored low abundances of all feeding groups, which increased downstream. When the proportions (in %) were calculated, the sediment feeders were dominant in the upstream part of the sector (more than 50% of the individuals) and decreased downstream (negative correlation with distance $r^2 = 0.270$, p-value = 0.0016), while the POM feeders were poorly represented in upstream areas (around 5% of the assemblage) and increased with the distance downstream ($r^2 = 0.274$, p-value = 0.0015). No significant trend was observed in the percentages of algae feeders and predators at the scale of the study reach.

4.4. Effect of sediment characteristics and local hydrology on hyporheic fauna at the station scale

The Correspondance Analysis (Fig. 6) highlighted a gradient in the composition of the assemblages, but with a rather low percentage of variance explained by the two first axes (11.3%). The 1st axis represented a gradient of taxa with different affinities to groundwater. Most stygobite species were located on the negative side of this axis: oligochaetes *Haber turquini*, *Trichodrilus* spp., *Rhyacodrilus balmensis*, *Spiridion phreaticola*, the mollusc *Spiralix* sp., *Bythiospeum* cf *diaphanum*, *Islamia* cf *minuta*, the Crustacea *Microcharon reginae*, *Parabathynella* cf *stygia*, *Salentinella angelieri*, *Niphargus* spp., *Proasellus* sp., *Parastenocaris* cf *glareola*, *Phreatalona phreatica*, *Cryptocandona kieferi* and *Marmocandona zschokkei*. On the positive side of this axis, most species were burrowers in fine sediments (e.g. the Clitellata *Lophochaeta ignota*, *Tubifex tubifex, Tubife*x spp., *Potamothrix moldaviensis*, the Epheremoptera *Ephemera* sp., the Diptera Chironomini and Tanytarsini) together with species living at the surface in moderate to slow flowing zones of rivers (e.g. *Erpobdella* *octoculata, Glossiphonia* sp., *Asellus aquaticus, Cypria ophtalmica*). Finally, a group of taxa were located close to the origin of the 1st axis, but with negative values on the 2nd axis, largely consisting of insects (e.g. *Potamanthus luteus*, *Micronecta* sp., *Stenelmis* sp., *Leuctra* cf *nigra*, *Corinoneura* sp.) or epigean crustaceans (e.g. *Alona rectangula, Chydorus sphaericus, Cypridopsis vidua*) that mostly live in the benthic layer of rivers. As some stygobite species have positive coordinates on the 2nd axis (e.g. *Spiralix* sp., *Microcharon* cf *reginae* or *Parabathynella* cf *stygia*) there is a light redundancy between the 1st and the 2nd axis that induced an arc distribution of the samples (Fig. 6D to F).

Considering the distribution of samples along the two first axes (Fig. 6D to F), sediment characteristics (grain size (Fig. 6E) and stability (Fig. 6F)) had poor influences on the hyporheic fauna: samples of the different groups strongly overlapped. Similarly, no differences were observed for the abundance and taxonomic richness of the whole assemblage, for the ecological groups and for the trophic functional groups under coarse, mixed, and fine sediment or under stable or unstable sediment patches (Table 1, Supplementary material Fig. S4, in all cases p-values < 0.05). This lack of difference was also observed when the -20 cm depth was analysed alone (p-values < 0.05 for abundances and richness of all taxa groups).

In contrast, the local hydrology influenced the composition of the hyporheic assemblages (Fig. 6D). The samples from upwelling zones were all located on the negative side of the 1st axis, closely associated with the stygobite fauna. A part of the samples from the downwelling and most of those from low exchange zones were mixed together on the positive side of the 1st axis, closely associated with species living in slow flowing water and fine sediment. Finally, a large set of samples from downwelling zones was located close to the origin of the 1st axis and on the negative side of the 2nd axis, closely associated to benthic species. These differences in assemblage composition among hydrology groups were also linked to higher abundances and taxonomic richness in areas with vertical exchanges (i.e. upwelling and downwelling zones) than in low exchange areas. The total abundance, the abundance of the temporary hyporheos and the abundances of organisms feeding on fine sediment, POM and algae were significantly higher in the stations located in downwelling zones than in the two other contexts (Table 1, Supplementary material Fig. S4). The stygobites followed a rather different trend with higher abundance and richness found in stations located in upwelling zones (but only significant for taxonomic richness, Table 1, see stygobite abundance in the Supplementary material Fig. S4).

4.5. Local hydrology, taxonomic richness and functional groups.

The local hydrology (downwelling, upwelling and low exchange) had a strong effect on the taxonomic richness of the hyporheic assemblages. The taxonomic richness estimated by rarefaction curves (i.e.

for a similar sampling effort of 36 samples, Fig. 7) was consistently higher in stations located in the downwelling and upwelling zones than in stations from low exchange zones.

In addition to local hydrology, the sampling depths had major effects on the hyporheic assemblages (Fig. 8): the abundances and the taxonomic richness of 1) all fauna, 2) the temporary and permanent hyporheos and 3) the abundances of all food type groups decreased from the downwelling zones to the low exchange areas and with depths (from -20 to -60 cm depths). These changes linked to hydrology were similar at all depths (no significant interaction between hydrology and depth was detected, see Supplementary material Table S2). A very different pattern was observed for stygobites (Fig. 8). These organisms adapted to groundwater habitats reached their highest species richness and abundances in the upwelling zones and did not show any significant change with depth.

In addition, the total taxonomic richness and total abundances did not uniquely differ with the direction of water exchanges, but also changed with the intensity of these exchanges. This was particularly clear at -60 cm depth in the downwelling zones, where the taxonomic richness and the abundance increased with the water temperature (r^2=0.159** and 0.155** for taxonomic richness and total abundance, respectively) and with the concentration in dissolved oxygen (r^2=0.257*** and 0.158** for taxonomic richness and total abundance, respectively, Supplementary material, Fig. S5) is highlighting a more abundant and diversified hyporheic fauna in areas where the infiltration of surface water was most intense.

4.6. Functional diversity

Different trends were observed for the two types of functional groups (Fig. 9). The functional diversity based on food type groups significantly increased with the distance downstream of the last dam (r^2=0.31, p-value = 0.0006). In contrast, the functional diversity based on the ecological groups (i.e. affinities with groundwater) did not increase as predicted from upstream to downstream. Functional diversity reached maximum values in the central part of the studied sector (resulting in a correlation with a bell-shaped trend, r^2=0.21, p-value = 0.0052), but with high values in two downstream stations (29D and 31U), located in upwelling zones.

The functional diversity based on ecological groups was higher in the upwelling zones compared to low exchange areas (without vertical trend; Fig. 9), while the functional diversity based on food type groups changed with the combination of local hydrology and depth. The later was slightly higher in the two groups of stations with vertical exchanges compared to low exchange zones, and decreased significantly with depth (at least in downwelling and upwelling zones).

The diversity based on affinity to groundwater was mainly controlled by the relative abundance of stygobites in the assemblage. The diversity index was significantly correlated to the percentage of stygobites for the longitudinal trend (r^2=0.13, p-value = 0.022) and for the local hydrology (r^2= 0.59, p-value = 0.03). The diversity based on food type groups increased with the decreasing relative abundance of sediment feeders (negative correlation r^2=0.95, p-value = 4.10^{-20}), the increasing relative abundances of predators (r^2=0.45, p-value = 2.10^{-5}) and POM feeders (r^2=0.37, p-value = 0.0002), two groups that followed the same upstream-downstream increase in the hyporheos. A similar relationship with the relative abundances of sediment feeders (negative correlation r^2=0.86, p-value = 0.003) was observed when the depth and the hydrology were combined.

5. Discussion

5.1. Distribution of the hyporheic fauna at the scale of the study reach.

The hypothesis of a combined control of hyporheic fauna distribution by hydrogeology of the valley and geomorphology of the river channel (**H1**) was clearly verified when considering the distribution of the hyporheic fauna along the studied 40-km reach. Several studies highlight the role of large scale hydrogeological heterogeneity and local scale geomorphology in the spatial patterns of river-groundwater exchanges (e.g. Faulkner et al., 2012, Gomez-Velez et al., 2017), especially the location of large-scale draining sectors (i.e. sections of several kilometers where local upwelling zones are fed by deep groundwater, Marmonier et al., 2020).

In the Ain River, these large-scale groundwater inflows were mostly located in the central part of the studied sector, controlled by the dominant direction of the groundwater flow (illustrated by the geomatic model) and by the presence of the two morainic hills. At this regional scale, the groundwater inflows had a weak influence on the richness and abundances of the hyporheic assemblages, of the permanent and the temporary hyporheos and on the abundance of the trophic functional groups. However, we found a significant effect on the stygobite abundance and taxonomic richness. The stygobites can establish permanent and sometime abundant populations at shallow depths, in areas where the environmental characteristics (e.g. temperature, solute contents, flow velocity) exhibit low temporal variability (Dole-Olivier and Marmonier, 1992; Malard et al., 2003). For example, several *Niphargus* species (here *N. casparyi*, *N. rhenorhodanensis* and *N. fontanus*) are known to live in the hyporheic zone of other tributaries of the Rhône River, especially in upwelling areas of gaining sectors (Marmonier et al., 2019, 2020). In the Ain River, they were mostly sampled downstream of meanders located in the central part of the sector (station 12D and 15D) or close to the morainic hills (stations 26D, 28U-D). In addition to these very abundant amphipods, some other rare stygobite crustaceans (e.g. *Parabathynella* cf *stygia* and *Microcharon reginae* according to Dole and Chessel, 1986; Dole-Olivier et al., 2009) were sampled here, representing shallow populations of species living deeper in the sediments. These species are rare (in abundance and distribution) and represent a high heritage value for the region. Thus, they must be considered in the management plan for the protection of river-groundwater exchanges and global river biodiversity (Michel et al, 2009; Boulton, 2020). The proportion of stygobites in the assemblages control the level of functional diversity (based on the ecological groups). In addition to their importance in the total taxonomic richness (e.g. Dole-Olivier et al., 2015; Marmonier et al., 2020), their role in ecological functions must be considered with attention (Ercoli et al., 2019; Fattorini et al., 2020; Di Lorenzo et al., 2021).

This study also highlights the importance of the geomorphology of the Ain River. The shape and location of the channel within its floodplain, and the occurrence of meanders are essential for river-groundwater exchanges (Magliozzi et al., 2018), because these channel forms induce intra-meander hyporheic flows (Boano et al., 2006). The hydrological role of meanders has been documented by several authors, both for water exchanges between the river and the hyporheic zone (Stonedahl et al., 2013; Nelson et al., 2019) and for biogeochemical processes (e.g. for nitrogen dynamics, Dwivedi et al., 2018). In the present study, all gravel bars located along meanders showed clear downwelling-upwelling successions (e.g. stations 12U-D, 15U-D, 25U to 28D). In contrast, gravel bars in straight sections were generally narrow and did not follow the expectation of the geomatic modelling. For example, stations 22U and 29U, predicted to be in two upwelling zones by the geomatic model, were found in downwelling conditions (based on water chemistry). These narrow and straight lateral bars were not taken into account by the large-scale geomatic model, even if they were large enough to support downwelling conditions at their head and upwelling at their tail (Dole-Olivier & Marmonier, 1992). Thus large-scale hydrogeological modelling has some limits for integrating small gravel bars and local heterogeneities in the prediction of hydrological exchanges (Stonedahl et al., 2013).

Finally, the history of river incision was surprisingly important for most of the characteristics of the hyporheic fauna at the 40-km scale. Abundances and taxonomic richness of the total assemblages, and of the permanent hyporheos and the abundances of all food type groups increased with the distance downstream, because of very low values in the four upstream gravel bars (from 5 to 9). These stations were located in an area where an intense incision occurred during the XXth century, after the construction of dams and the reduction of sediment transit (Rollet et al., 2014). This was particularly surprising because the riverbed erosion is not yet visible. The recent restoration program with sediment reinjection in the main channel (Lejot, 2008) resulted in fine sediment deposits at the surface (e.g. at gravel bars 5, 8 and 9). Nevertheless, the historical erosion, while completely hidden, is still detectable in the composition of the hyporheic fauna. During river incision, the erosion of sand and gravel generated a re-arrangement of coarse pebbles resulting in a pavement of the river bottom and an accumulation of fine sediment between these large particles (Gomez, 1984; Jain, 1990). In these conditions, the habitability of the interstices progressively decreased and apparently still persisted 10 years after the beginning of the injection of gravel and sand in the main channel. The effect of the historical pavement of the upstream sector was also visible in the low concentrations of dissolved oxygen (i.e. positive correlation with distance to the dams), generally associated with low vertical exchanges (Lefebvre et al., 2005) and the reduction of the abundances and richness of the hyporheic fauna (Strayer et al., 1997). None of the ecological groups were affected in a similar way: the very mobile temporary hyporheos (i.e. the aquatic insect instars with flying adults) did not exhibit its lowest richness and abundances in the upstream stations. While the less mobile permanent hyporheos (i.e. Clitellata, Mollusca and Crustacea) showed lower abundance and lower richness in the four upstream gravel bars than downstream. In addition, the hyporheic assemblages sampled in these stations showed specific feeding traits, with a dominance of the fine sediment feeders, certainly favored here by the storage of fine particles. This dominance resulted in lower functional diversity, which increased downstream together with the proportion of other trophic groups, such as POM feeders. Some of these POM feeders, being attracted by porous and mobile sediment (e.g. the *Gammarus* species, Vadher et al., 2015; Navel et al., 2010), were more abundant downstream. The functional diversity based on trophic traits appeared thus to be sensitive to the physical characteristics of the hyporheic zone, even if differences are not visually obvious.

5.2. Weak influence of surface grain size and sediment stability

Surprisingly, our results did not support the influence of heterogeneity in surface sediment grain size and sediment stability on the hyporheic fauna (**H2** rejected). The importance of sediment grain size and heterogeneity on hyporheic processes has been widely documented (Richards and Bacon, 1994; Wood and Armitage, 1997; Tonina et al., 2016; Nelson et al., 2019). For example, decreases in dissolved oxygen concentrations and nitrification processes were generally observed in fine sediment, while ammonium concentrations and denitrification process increased (Dahm et al., 1987; Lefebvre et al., 2005). This shift from oxic to hypoxic or anoxic processes was related to fine sediment being the substrate of the biofilm, which stimulated its growth and respiration (Claret and Fontvieille, 1997) and decreased vertical hydrologic exchanges and oxygen supply in the hyporheic zone (Tonina and Buffington, 2009; Cook et al., 2020). A relationship between surface sediment grain size and hyporheic processes was not always detected (Descloux et al., 2010; Nogaro et al., 2010), but appeared strong enough to justify methods of visual assessment of surface sediment characteristics for river bed clogging (Peck et al., 2000; Sennatt et al., 2006). In the present study, very few changes were observed in the habitat characteristics and in the fauna composition between areas differing in surface sediment grain size. First, the hyporheic water chemistry was poorly controlled by the surface sediment grain size. Most chemical parameters did not change at all, and only a minor increase in dissolved oxygen concentrations was measured at stations with mixed sediment size and lower values in the fine and coarse sediment contexts. This increase in oxygen content in mixed sediment was probably a side effect of the local hydrology: stations 22U, 30D and 33D were all located in strong downwelling zones, with more than 11 mg L^{-1} of dissolved oxygen at 60 cm depth inside sediments. Second, the expected decrease in the hyporheos abundance and taxonomic richness with decreasing sediment size was not observed in this study: the surface characteristics of the bed sediment did not explain the composition and the functional diversity of the hyporheic assemblages. This was likely due to a strong vertical stratification of bed sediment (as observed with a geological radar by Mermillod-Blondin et al., 2015 or with field measures and modelling by Cardenas and Zlotnik, 2003) that generally controls hyporheic water fluxes. The vertical stratification of river sediment is linked to the history of the sediment origin, transit and deposition (Marion et al., 2008). The visual estimate of surface sediment grain size may be efficient for small streams with a thin layer of bottom sediment, but it is less informative for a consistent diagnostic of hyporheic habitat quality in large gravel-bed rivers (Nogaro et al., 2010; Descloux et al., 2010).

The stability or mobility of surface sediment has also been evaluated as an explanation for changes in hyporheic processes (e.g. Peterson et al., 2008; Zheng et al., 2019; Dudunake et al., 2020). Sediment mobility may have different effect on hyporheic biodiversity because of direct (invertebrate migration) and indirect consequences (sediment modifications). At a small time-scale sediment mobility may induce an increase in invertebrate drift (Gibbins et al., 2007) and in the vertical migration of the hyporheic fauna (Dole-Olivier et al., 1997, Schmid-Araya, 2000). At a long time-scale, a low mobility of bed sediment may reduce the resuspension of fine particles, resulting in local clogging of the interstices, and the formation of anoxic microzones with local denitrification (Roy Chowdhury et al., 2020).In the studied sector, the development of a filamentous biofilm at the surface of the particles was not a consistent predictor of the hyporheic habitat suitability and hyporheos composition. Even the expected increase in algae-feeder densities below the thick biofilm was not supported, probably because of very different porosity under similar level of biofilm development. Hence, the use of surface biofilm development to evaluate sediment stability seems poorly informative. In the future studies, the sediment stability must be considered using combined methods , such as hydraulic modelling (e.g. Buffington and Montgomery, 1997) or direct measures of sediment movement (e.g. spray-painted or magnetically tagged stones, Mao and Surian, 2010) to evaluate gravel mobility.

5.3. Local hydrology, the major driver for hyporheic biodiversity

The present study clearly demonstrated that local hydrology (i.e. downwelling, upwelling *versus* low exchange areas) had a major role in the distribution and composition of hyporheic fauna (**H3** verified). Several significant differences were observed in the abundance, the taxonomic richness and the functional diversity according to the hydrological connections, with a similar trend at all depths.

First, specific environmental and faunal characteristics were observed in low exchange areas. Here the zero VHG suggested nearly immobile hyporheic water with poor exchanges with both surface water and groundwater. These hydrological conditions resulted in very low oxygen concentrations (i.e. less than 2 mg.L^{-1} at -60 cm depth). Similar low values in dissolved oxygen were measured in poorly connected riverbeds and were generally associated with denitrification and ammonium accumulation (Dahm et al., 1987; Lefebvre et al., 2005; Marzadri et al., 2012; Harvey et al., 2013). In this study, the low water exchanges induced low hyporheic abundances and low taxonomic richness (for total hyporheos, most ecological groups and the food type groups) compared to the well-connected stations located in downwelling or upwelling zones. The negative impact of a reduction in the water exchange on the hyporheic fauna has been well documented (Brunke and Gonser, 1999; Hunt and Stanley, 2003; O'Sullivan et al., 2019). The hyporheos abundance was generally correlated positively with dissolved oxygen concentrations (Strayer et al., 1997; Boon et al., 2016) and negatively with the accumulation of potentially toxic ammonia inside sediment (Dahm et al., 1987; Dehedin et al., 2013; Caschetto et al., 2014, 2017; Di Lorenzo et al., 2021). In contrast, the consequence of a reduced hydrological vertical exchange on the functional diversity is less understood. In this study, the functional diversity evaluated by the ecological groups (i.e. the affinity of organisms with groundwater) followed a similar pattern as taxonomic richness with lower values in the low exchange area than in the other hydrological contexts. While the low taxonomic richness was due to the reduction in the number of temporary hyporheic species (i.e. the benthic insects), the low values in functional diversity were linked to a lower proportion of stygobites. The limitation of vertical exchanges reduced the hyporheic assemblages to a set of permanent hyporheic species (mostly oligochaetes and micro-crustaceans) as already observed in sandy and lowland rivers (e.g. Palmer et al., 1992).

In areas fed by groundwater (i.e. upwelling zones), the environmental conditions were less stressful for the hyporheic fauna because of rather large interstices (fine sediment washout) and regular water renewal. These conditions resulted in intermediate dissolved oxygen concentrations (at least in the studied sector where groundwater-fed springs contains between 5.2 and 8.7 mg.L^{-1} of oxygen, Dehédin, 2012). Here, the total hyporheic abundance was intermediate between the low exchange zones and the downwelling zones. In contrast, the taxonomic richness was high in upwelling zones, because of the large number of stygobite species. Such increases in stygobite richness and abundance in upwellings were frequently observed in a wide range of rivers (Dole-Olivier and Marmonier, 1992; Malard et al., 2003; Di Lorenzo et al., 2013). The upwellings did not represent a real storage zone for river biomass (Dole-Olivier, 2011), but they appeared to be hotspots for biodiversity, especially for rare stygobite species. The high relative abundance of stygobites in the upwelling zones induced an increase in functional diversity based on ecological groups, which did not decrease with increasing depth, because of the ability of most of the ambient stygobites to live in deep river sediment (Dole and Chessel, 1986). In contrast, the functional diversity based on food types (that poorly changed with the local hydrology) decreased with depth in the upwelling zones. This vertical pattern was probably due to a reduction of food diversity with depth, selecting preferentially sediment feeders, which was the trophic group feeding on the most available resource: fine sediments and associated biofilm.

Finally, in the downwelling zones, the abundance and taxonomic richness were the highest, especially for the temporary hyporheos (i.e. benthic insects with flying adults). This high density may be explained by the inflow of surface water into the sediment, which brings dissolved oxygen and organic matter (Brunke & Gonser, 1999; Franken et al., 2001). This study demonstrates that downwelling zones represent essential storage zones for the benthic fauna, contributing to river resilience through recolonization process of the benthic layer (Dole-Olivier, 2011, Vander Vorste et al., 2016). Although not all downwelling zones were similarly populated: the highest densities of the temporary hyporheos were measured in strong downwellings. This influence of infiltration intensity was illustrated by the positive correlation between the abundance and taxonomic richness with temperature and dissolved oxygen at -60 cm depth. Intense downwellings represented attractive areas for faunal vertical migration (Dole-Olivier, 2011). This richness in benthic species was probably due to the higher diversity of food types in the downwelling zones than in other zones (upwelling and no exchange zones). These downwelling areas had high dissolved oxygen concentration and fresh organic matter, which was reflected in a higher proportion of POM feeders, algae feeders and predators in comparison with other zones with no direct supply of fresh organic matter from surface waters. Therefore, the downwellings were hotspots for biomass and taxonomic richness in the hyporheic zone, but with a different assemblage of species compared to upwelling zones. The importance of upwelling zones is often emphasized by river managers, particularly because of their role in fish reproduction and survival during low water periods (e.g. Curry and Noakes, 1995; Malcolm et al., 2005). In contrast, the importance of downwelling zones is rarely considered. This study supports the idea that the heterogeneity of hydrological patterns, with alternation of upwellings and downwellings, may represent the optimal spatial structure for biodiversity conservation in rivers, with both contributing to the diversity and resilience of the river (Leigh et al., 2016).

6. Conclusions

At the local scale, the composition of the hyporheos was controlled by vertical exchanges of water between the river, the hyporheic zone and the deep groundwater (i.e. downwelling, upwelling or low exchange areas). The upwellings were hotspot of taxonomic richness, but also for functional diversity based on ecological groups. Here, the functional diversity was mostly related to the relative abundance of stygobites and the reduction of dominance of the permanent hyporheos. In contrast, the downwelling zones were hotspots of abundances, especially for the temporary hyporheos (mostly benthic insects). These organisms, living temporarily inside sediment, contribute to the river biomass and resilience. In downwellings, the food-type diversity was mostly controlled by the proportion of POM feeders and the reduction in dominance of sediment feeders. Low exchange zones appeared to be less populated areas with low functional diversity.

Compared to hydrology, the surface characteristics of the riverbed sediment (i.e. visual estimation of the grain size and the stability) was not informative for the hyporheos composition of this large gravel-bed river. The visual estimation of surface sediment characteristics neglected the vertical stratification of the sediment, which is a consequence of the history of sediment transit and deposition.

These links between vertical water exchanges and hyporheic assemblages must be combined with large-scale patterns of hyporheic distribution. In the 40-km long reach assessed in this study, the hyporheic fauna was controlled by a combination of two factors: the hydrogeology of the alluvial plain (i.e. large-scale groundwater movement) and the geomorphology of the river channel (i.e. location of meanders and history of the river incision). In consequence, river managers must carefully consider the ongoing activities that modify the dynamics of the river-groundwater exchanges (e.g. river regulation or groundwater extraction), but also the long-term history of sediment fluxes due to past regulations.

CRediT authorship contribution statement.
M.J. Dole-Olivier: Conceptualization, Investigation, Writing – original draft. M. Creuzé des Châtelliers: Conceptualization, Investigation. D. Galassi: Investigation. M. Lafont: Investigation. F. Mermillod-Blondin: Investigation. F. Paran: Investigation. D. Graillot: Investigation. S. Gaur: Investigation. P. Marmonier: Conceptualization, Investigation, Writing – original draft.

Declaration of competing interest

The authors declare the following financial interests, which may be considered as potential competing interests: Electricité de France (EDF) who built and manage the upstream dams funded the research program, however the LTSER Rhône River Basin and the Rhône River Water Agency were included in the following committee and guaranty the objectivity of our conclusions.

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Table 1: Comparison of the effects of local hydrology, sediment grain size and sediment stability on the functional traits of the hyporheic assemblages. One way ANOVAs were performed with stations as replicates (mean values for all depths and replicates, after log transformation; n.s. above the significant level, - no test possible for food type groups because a species may belong to more than one trophic group, see histogram in Supplementary material Fig. S4).

	Local hydrology(1)				Grain size(2)		Stability(3)	
	Abundances		Richness		Abd	Rich	Abd	Rich
	$F_{(2,27)}$	p	$F_{(2,27)}$	p	$F_{(2,27)}$	$F_{(2,27)}$	$F_{(1,28)}$	$F_{(1,28)}$
Total fauna	4.97	0.014	4.96	0.014	n.s.	n.s.	n.s.	n.s.
Ecological groups								
Temp. hyporheos	12.05	0.0002	8.94	0.001	n.s.	n.s.	n.s.	n.s.
Perm. hyporheos		n.s.	3.51	0.04	n.s.	n.s.	n.s.	n.s.
Stygobites		n.s.	6.83	0.004	n.s.	n.s.	n.s.	n.s.
Food type groups								
Sediment feeders	5.40	0.011	-	-	n.s.	-	n.s.	-
POM feeders	4.69	0.017	-	-	n.s.	-	n.s.	-
Algae feeders	3.47	0.04	-	-	n.s.	-	n.s.	-
Preadators		n.s.	-	-	n.s.	-	n.s.	-

(1) Local hydrology are downwelling (n=16), low exchange (n=4) and upwelling contexts (n=10).

(2) Sediment grain size classes are fine (n=13), mixed (n=10) and coarse surface sediment (n=7).

(3) Sediment stability are with (n=17) or without biofilm development (n=13).

Figure legends:

Figure 1: Study area (A), the Lower Ain River from Pont d'Ain to the confluence with the Rhône River (background elevation map from Geographic National Institute, Géoportail). Blue lines: Ain and Rhône river channels; pointed dark line: upstream eroded sector before 2005; dotted lines: limits of the morainic hills. Location of the 15 sampled gravel bars (A), upstream and downstream stations at each gravel bar (B) and sampling design at each station (C).

Figure 2. Chemical characteristics of hyporheic water, sediment grain size and sediment stability. Examples showing the classification of the stations into the three groups of stream-groundwater exchanges according to electric conductivity and temperature of the surface and hyporheic waters: A- Upwellings (UPW), B- Low exchanges (LOW EX), C- Downwelling (DNW). Examples of sediment characteristics: D- fine sediment, E- mixed, F- coarse. Example of biofilm development on unstable (G) or stable (H) benthic layer. List of the stations in each group with U for upstream and D for downstream positions along the gravel bars (see Fig. 1).

Figure 3: Hydrogeological characteristics of the studied sector based on geomatic analysis of the study reach (A) and details of the eight stations with upwelling zones as derived by the hyporheic water chemistry (B).

Figure 4. Principal Component Analysis on hyporheic water characteristics. Correlation circle of physico-chemical parameters (A) Cond-Electric conductivity, VGH-Vertical Hydraulic Gradient, O_2-Dissolved oxygen, T°C-Temperature. Location of the sampling points on the Axis 1 x Axis 2 biplots, according to the local hydrology (B), the grain size (C) and the sediment stability (D). Oxygen concentrations by groups and depths (means and standard errors) for local hydrology groups (E), grain size groups (F) and stability groups (G) with results of ANOVA tests between groups.

Figure 5: Longitudinal distribution of hyporheic assemblages. Means (and standard errors) for the 15 gravel bars and positions (i.e. 30 stations) for total abundance and taxonomic richness (left panels), for ecological groups based on affinities to groundwater (center panels) and for trophic functional groups (right panels).

Figure 6. Correspondance analysis on hyporheic assemblages (the 1st axis represented 6% and the 2nd axis 5.3% of the total inertia). Location of the taxa in the 1st and 2nd axes is separated in three major taxonomic groups: (A) oligochaetes, molluscs, leeches, (B) crustaceans and (C) insects, with stygobite species in blue and other hyporheic species in black. The location of all samples between the 1st and

2nd axes also separated by hydrological exchange groups (D), sediment grain size groups (E) and sediment stability groups (F).

Figure 7: Rarefaction curves of the taxonomic richness in different hydrological contexts (Dwn: downwelling zones, Upw: upwelling zones and LowEX: low exchange zones). Shaded areas represented confidence intervals.

Figure 8: Taxonomic richness (left panels), abundances of the total fauna and of the 3 functional groups based on affinities with groundwater (center panels), and abundances of the food type groups (right panels) in different hydrological contexts and depths (means and standard errors). Differences between hydrological contexts (H) and depths (D) tested by a two-ways ANOVA with *<5%, **<1%, ***<0.1%, n.s. non significant.

Figure 9. Functional diversity for ecological groups (A) and food type groups (B) for the longitudinal trend (left) and the combination of depth and hydrological contexts (right, means and standard errors). The ecological group diversity significantly correlated with the distance (in km) with a polynomial regression curve ($y = 0.0021 x^2 + 0.075 x + 1.3$), while the food type group diversity significantly fitted with a linear regression curve ($y = 0.023 x + 2.396$). Differences between hydrological contexts (H) and depths (D) tested by a two-ways ANOVA with *<5%, **<1%, ***<0.1%, n.s. not significant.

Fig. 1

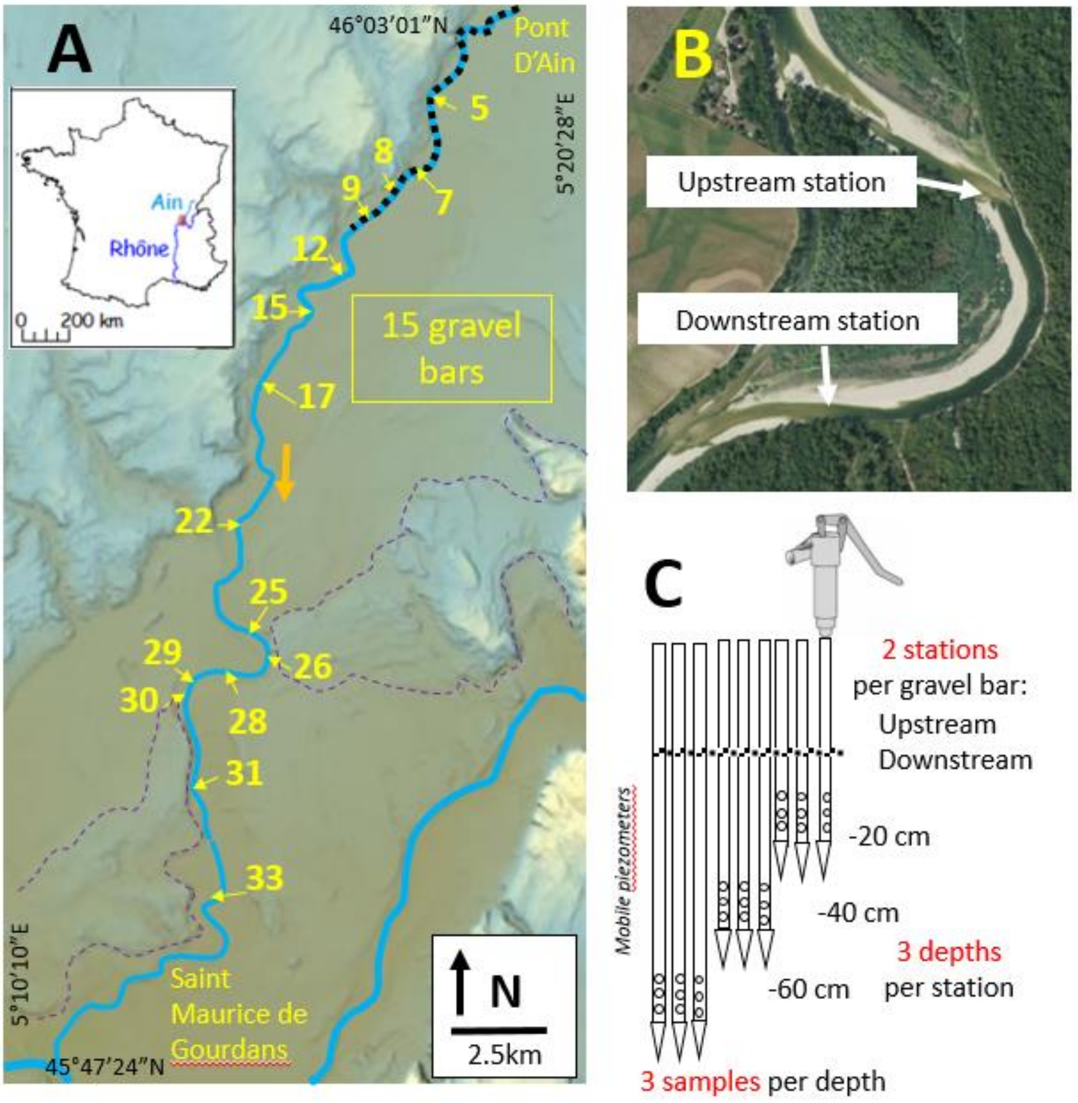

A
46°03'01"N
Pont D'Ain
5°20'28"E
Ain
Rhône
0 200 km
5
8
9
7
12
15
15 gravel bars
17
22
25
29
26
30
28
31
33
Saint Maurice de Gourdans
5°10'10"E
45°47'24"N
N
2.5km
B
Upstream station
Downstream station
C
2 stations per gravel bar:
Upstream
Downstream
Mobile piezometers
-20 cm
-40 cm
-60 cm
3 depths per station
3 samples per depth

Fig. 2

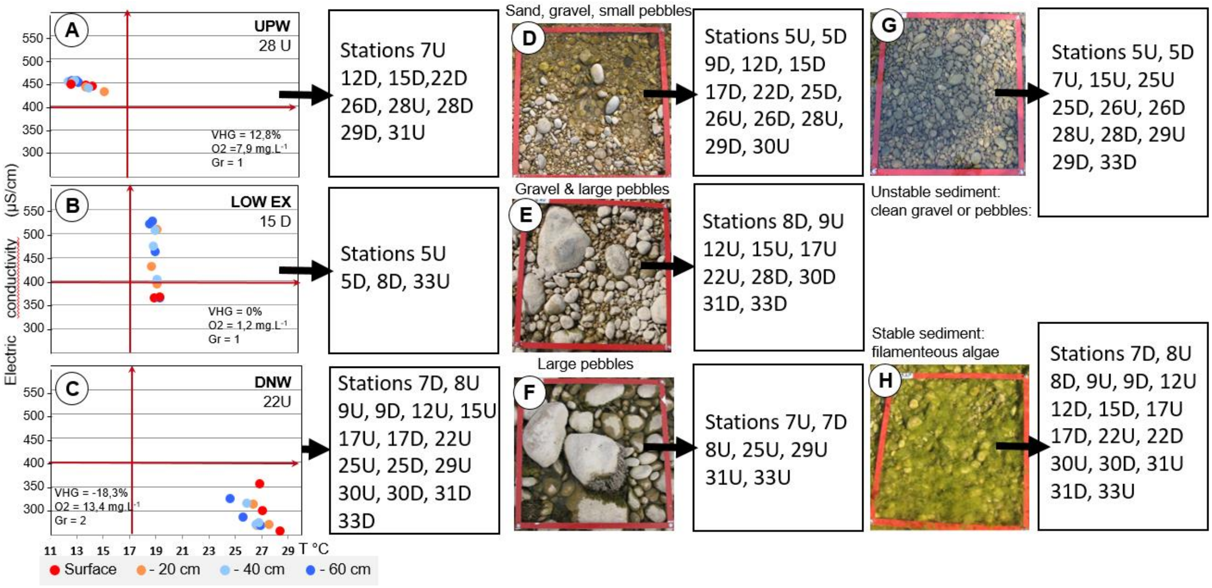
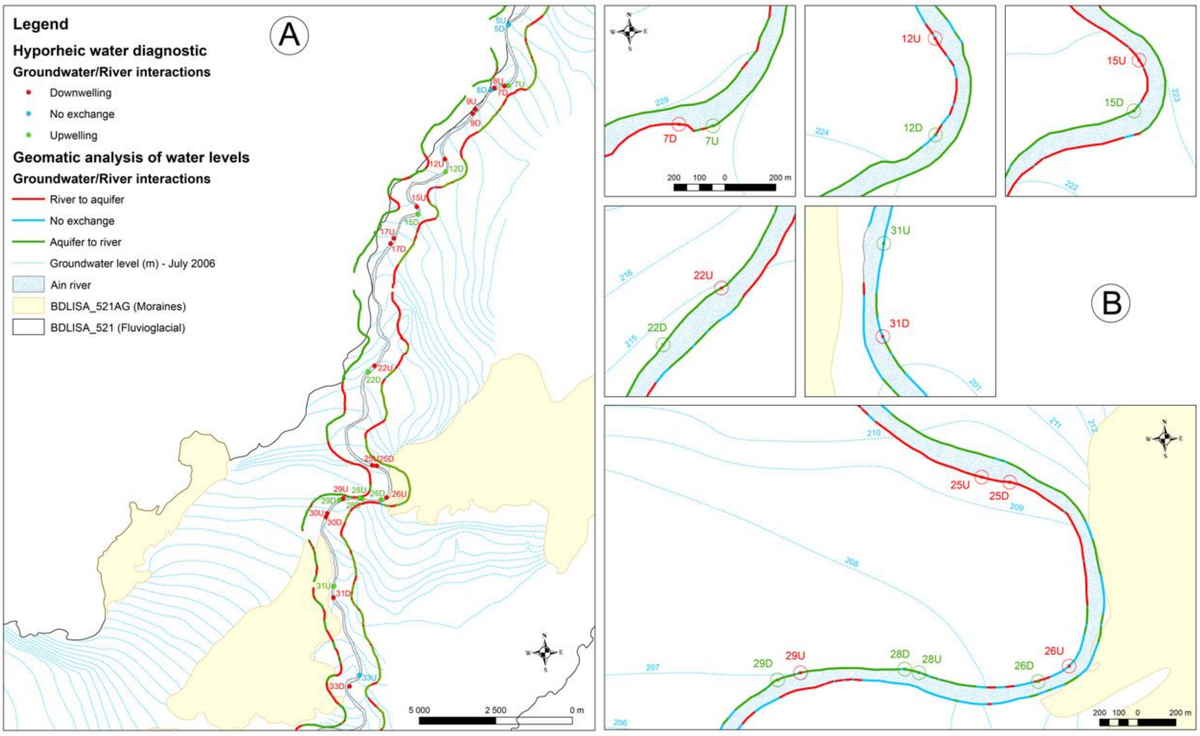

A
UPW
28 U
550
500
450
400
350
300
VHG = 12,8%
O2 =7,9 mg.L-1
Gr = 1
Stations 7U, 12D, 15D,22D, 26D, 28U, 28D, 29D, 31U
B
LOW EX
15 D
VHG = 0%
O2 = 1,2 mg.L-1
Gr = 1
Stations 5U, 5D, 8D, 33U
C
DNW
22U
VHG = -18,3%
O2 = 13,4 mg.L-1
Gr = 2
Stations 7D, 8U, 9U, 9D, 12U, 15U, 17U, 17D, 22U, 25U, 25D, 29U, 30U, 30D, 31D, 33D
Electric conductivity (µS/cm)
11 13 15 17 19 21 23 25 27 29 T °C
● Surface ● - 20 cm ● - 40 cm ● - 60 cm
Sand, gravel, small pebbles
D
Stations 5U, 5D, 9D, 12D, 15D, 17D, 22D, 25D, 26U, 26D, 28U, 29D, 30U
Gravel & large pebbles
E
Stations 8D, 9U, 12U, 15U, 17U, 22U, 28D, 30D, 31D, 33D
Large pebbles
F
Stations 7U, 7D, 8U, 25U, 29U, 31U, 33U
G
Unstable sediment: clean gravel or pebbles:
Stations 5U, 5D, 7U, 15U, 25U, 25D, 26U, 26D, 28U, 28D, 29U, 29D, 33D
Stable sediment: filamenteous algae
H
Stations 7D, 8U, 8D, 9U, 9D, 12U, 12D, 15D, 17U, 17D, 22U, 22D, 30U, 30D, 31U, 31D, 33U

Fig. 3


Legend
Hyporheic water diagnostic
Groundwater/River interactions
● Downwelling
● No exchange
● Upwelling
Geomatic analysis of water levels
Groundwater/River interactions
River to aquifer
No exchange
Aquifer to river
Groundwater level (m) - July 2006
Ain river
BDLISA_521AG (Moraines)
BDLISA_521 (Fluvioglacial)
A
B
5U
5D
7U
7D
8U
8D
9U
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12D
15U
15D
17U
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Fig. 4

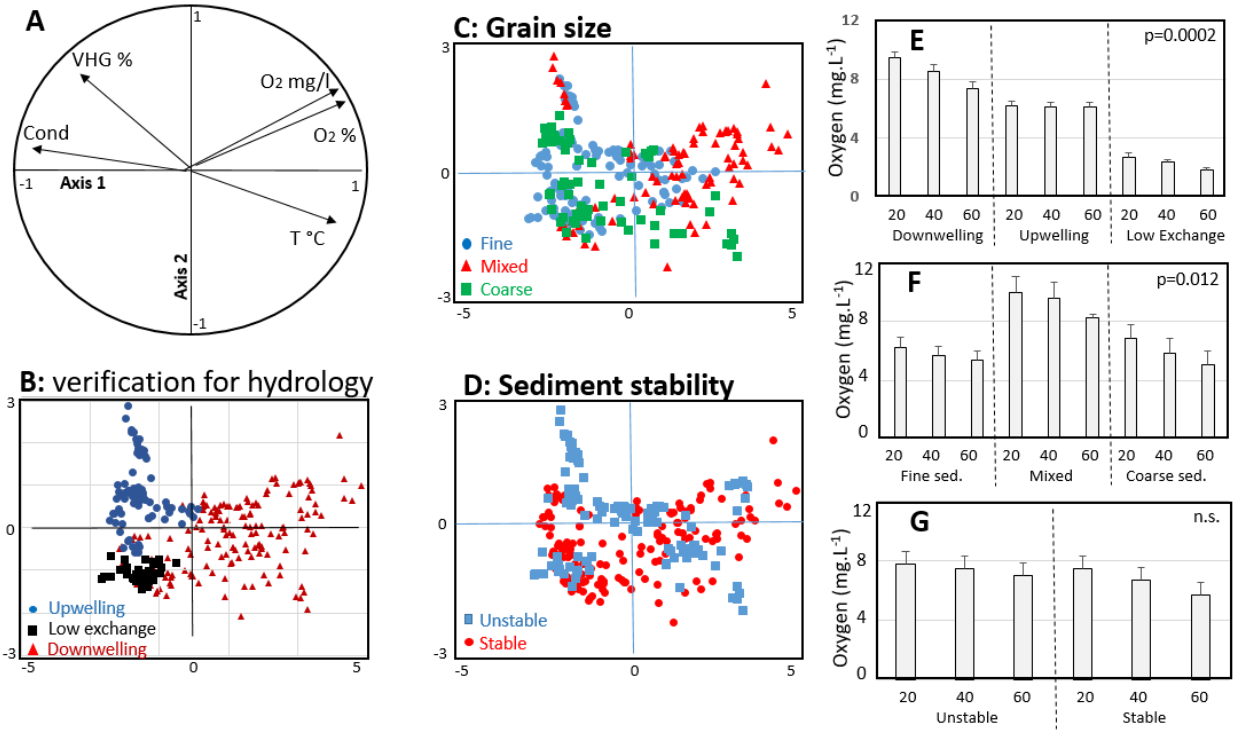
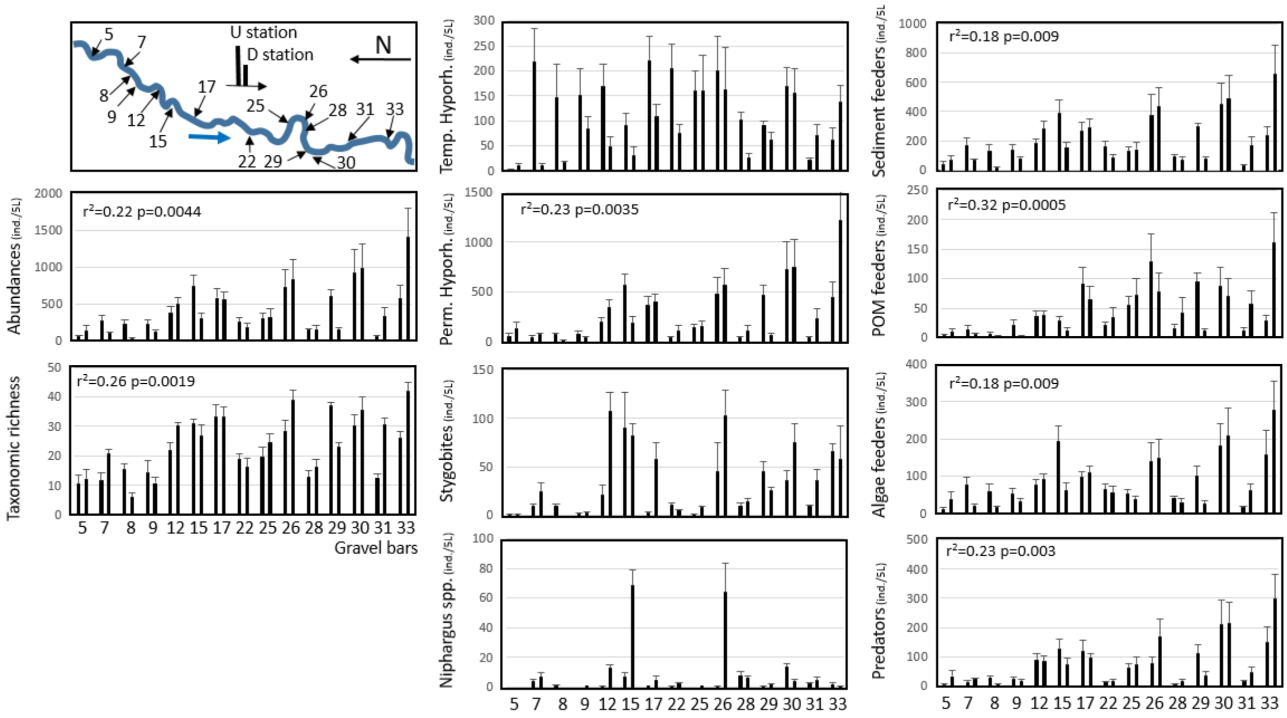
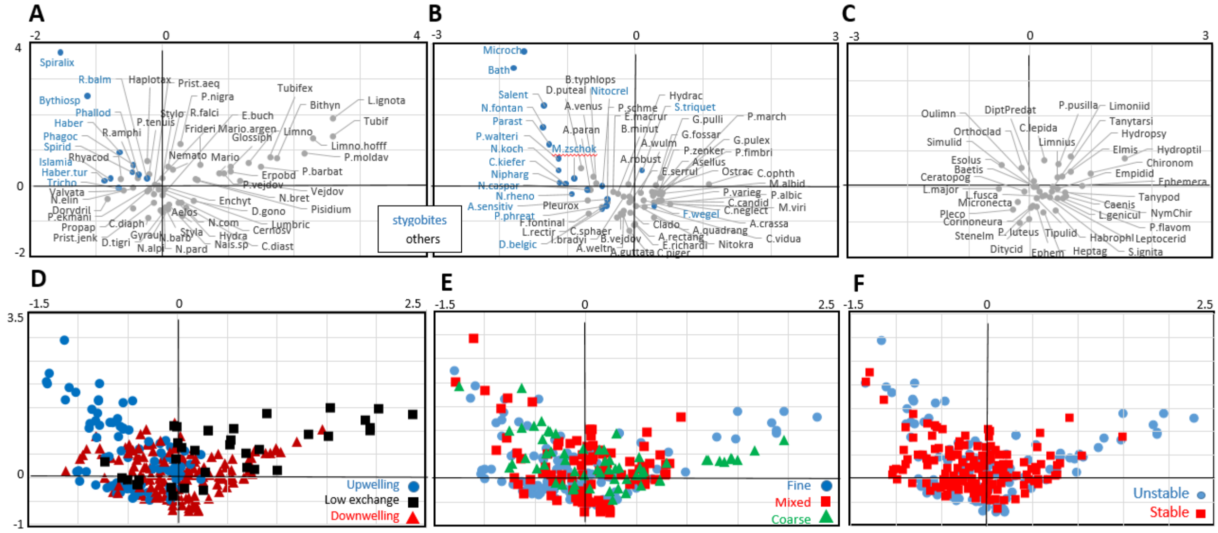

A
VHG %
O2 mg/l
Cond
O2 %
Axis 1
T °C
Axis 2
1
-1
B: verification for hydrology
Upwelling
Low exchange
Downwelling
C: Grain size
Fine
Mixed
Coarse
D: Sediment stability
Unstable
Stable
3
0
-3
-5
5
E
p=0.0002
Oxygen (mg.L-1)
12
8
4
0
20
40
60
Downwelling
Upwelling
Low Exchange
F
p=0.012
Fine sed.
Mixed
Coarse sed.
G
n.s.
Unstable
Stable

Fig. 5



5
7
8
9
12
15
17
22
25
26
28
29
30
31
33
U station
D station
N
Abundances (ind./SL)
r²=0.22 p=0.0044
Taxonomic richness
r²=0.26 p=0.0019
Gravel bars
Temp. Hyporh. (ind./SL)
Perm. Hyporh. (ind./SL)
r²=0.23 p=0.0035
Stygobites (ind./SL)
Niphargus spp. (ind./SL)
Sediment feeders (ind./SL)
r²=0.18 p=0.009
POM feeders (ind./SL)
r²=0.32 p=0.0005
Algae feeders (ind./SL)
r²=0.18 p=0.009
Predators (ind./SL)
r²=0.23 p=0.003
5 7 8 9 12 15 17 22 25 26 28 29 30 31 33

Fig. 6



A
-2
0
4
4
0
-2
Spiralix
R.balm
Haplotax
Prist.aeq
Bythiosp
P.nigra
Tubifex
Bithyn
L.ignota
Phallod
Stylo
R.falci
P.tenuis
E.buch
Haber
R.amphi
Frideri
Mario.argen
Glossiph
Limno
Tubif
Phagoc
Spirid
Limno.hofff
Rhyacod
Nemato
Mario
P.moldav
Islamia
Haber.tur
Erpobd
P.barbat
Tricho
P.vejdov
Valvata
N.elin
Vejdov
Enchyt
N.bret
Dorydril
P.ekmani
D.gono
Pisidium
Aelos
C.diaph
N.com
Lumbric
Propap
Prist.jenk
Gyrau
N.barb
Styla
Hydra
Cernosv
D.tigri
N.alpi
N.pard
Nais.sp
C.diast
stygobites
others
B
-3
0
3
Microch
Bath
B.typhlops
D.puteal
Nitocrel
Salent
A.venus
Hydrac
N.fontan
P.schme
S.triquet
E.macrur
G.pulli
Parast
A.paran
B.minut
P.march
P.walteri
G.fossar
A.wulm
G.pulex
N.koch
M.zschok
P.zenker
P.fimbri
C.kiefer
A.robust
Asellus
Nipharg
E.serrul
Ostrac
C.ophth
N.caspar
M.albid
P.varieg
P.albic
N.rheno
C.candid
A.sensitiv
Pleurox
C.neglect
M.viri
P.phreat
F.wegel
F.fontinal
Clado
A.crassa
L.rectir
C.sphaer
A.quadrang
I.bradyi
B.vejdov
A.rectang
C.vidua
D.belgic
A.weltn
E.richardi
Nitokra
A.guttata
C.piger
C
-3
0
3
Oulimn
DiptPredat
P.pusilla
Limoniid
C.lepida
Tanytarsi
Orthoclad
Hydropsy
Simulid
Limnius
Elmis
Hydroptil
Chironom
Esolus
Baetis
Empidid
Ceratopog
Ephemera
L.major
L.fusca
Tanypod
Micronecta
Caenis
Pleco
L.genicul
NymChir
Corinoneura
P.flavom
Stenelm
P. luteus
Tipulid
Habrophl
Leptocerid
Ditycid
Ephem
Heptag
S.ignita
D
-1.5
0
2.5
3.5
0
-1
Upwelling ●
Low exchange ■
Downwelling ▲
E
-1.5
0
2.5
Fine ●
Mixed ■
Coarse ▲
F
-1.5
0
2.5
Unstable ●
Stable ■

Fig. 7

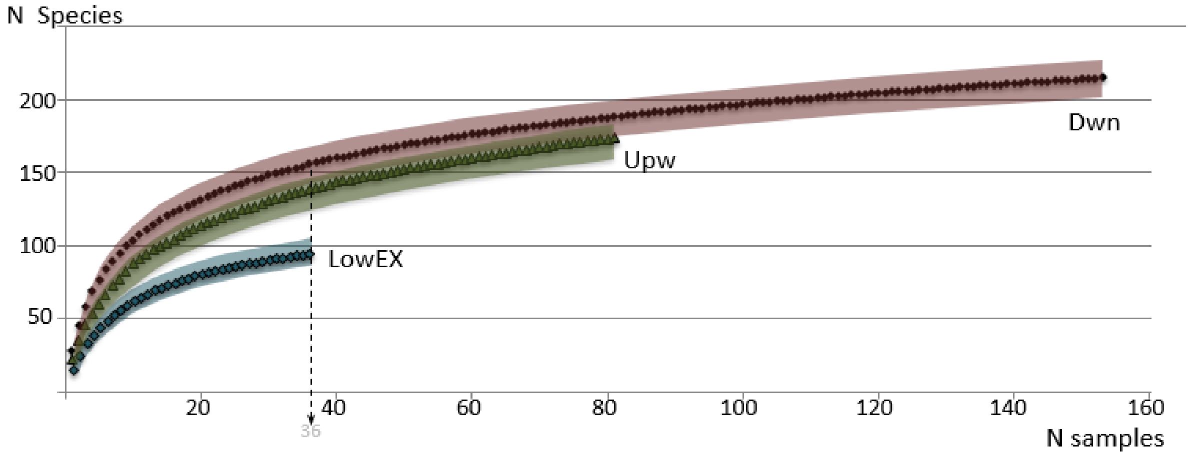

N Species
200
150
100
50
20
40
36
60
80
100
120
140
160
N samples
Dwn
Upw
LowEX

Fig. 8

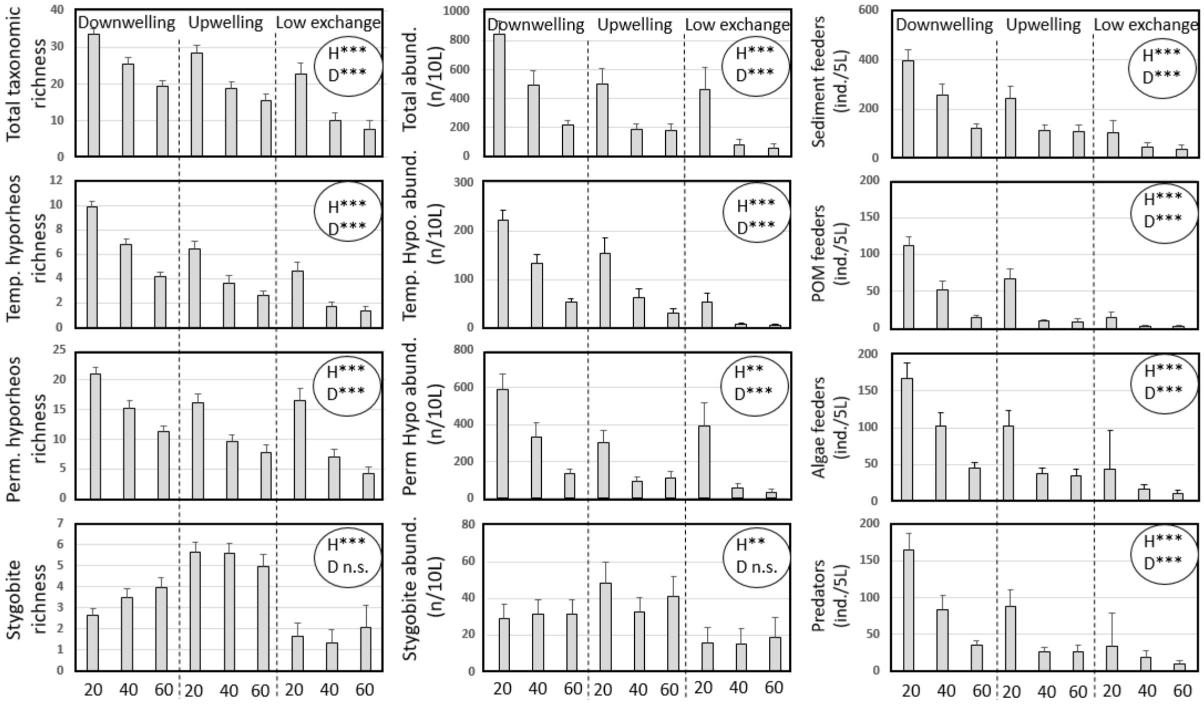
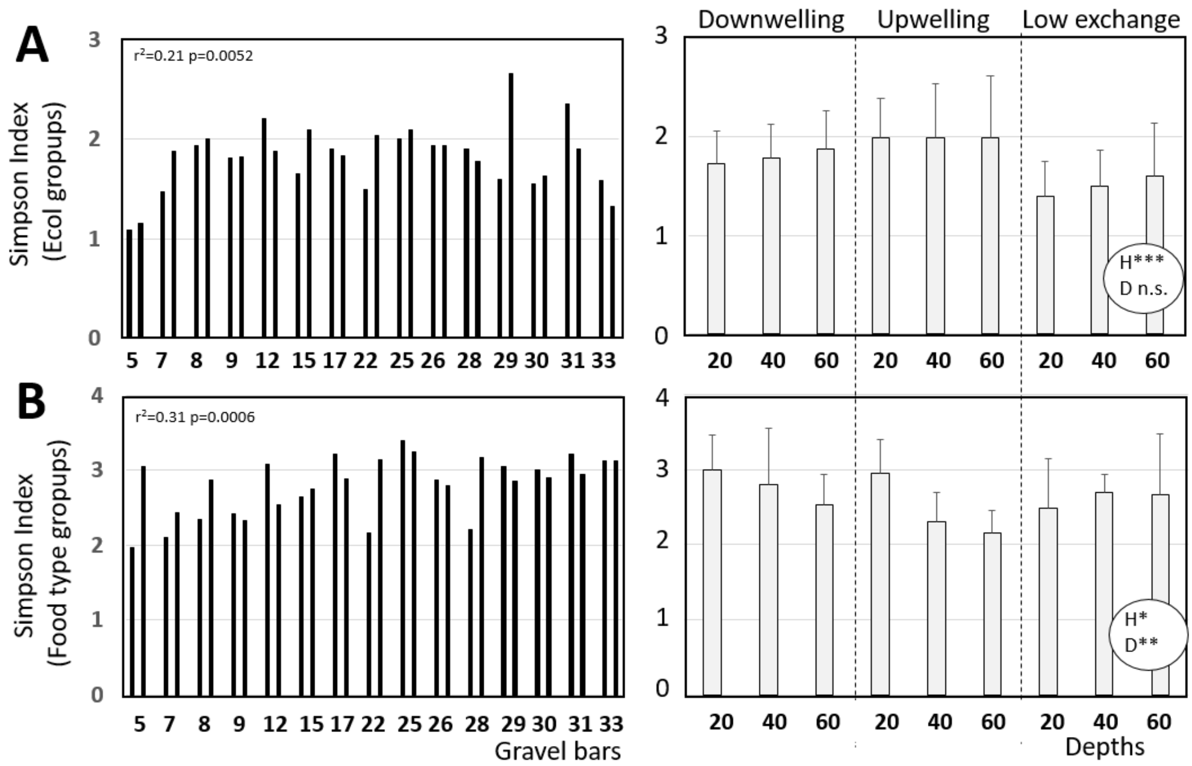

Downwelling
Upwelling
Low exchange
Total taxonomic richness
Total abund. (n/10L)
Sediment feeders (ind./5L)
Temp. hyporheos richness
Temp. Hypo. abund. (n/10L)
POM feeders (ind./5L)
Perm. hyporheos richness
Perm Hypo abund. (n/10L)
Algae feeders (ind./5L)
Stygobite richness
Stygobite abund. (n/10L)
Predators (ind./5L)
H***
D***
H**
D n.s.
20
40
60

Fig. 9


A
3
2
1
0
Simpson Index (Ecol gropups)
r²=0.21 p=0.0052
5 7 8 9 12 15 17 22 25 26 28 29 30 31 33
Downwelling
Upwelling
Low exchange
20 40 60 20 40 60 20 40 60
H***
D n.s.
B
4
3
2
1
0
Simpson Index (Food type gropups)
r²=0.31 p=0.0006
5 7 8 9 12 15 17 22 25 26 28 29 30 31 33
Gravel bars
20 40 60 20 40 60 20 40 60
Depths
H*
D**

Supplementary material: Tables.

Table S1. Codes for the taxa used in the Factorial Analysis (Stygobite species in red).

Taxa names	Codes	Taxa names	Codes	Taxa names	Codes
Aeolosomatidae	Aelos	*Valvata* sp.	Valvata	*Cypridopsis vidua*	C.vidua
Lumbricidae	Lumbric	*Bithynia tentaculata*	Bithyn	*Potamocypris variegata*	P.variegata
Dorydrilus michaelseni	Dorydril	*Gyraulus* sp.	Gyraul	*Gammarus* sp. (juveniles)	G.pulli
Stylodrilus sp.	Stylo	*Islamia* cf *minuta*	Islamia	*Gammarus pulex*	G.pulex
Trichodrilus sp.	Tricho	*Bythiospeum* cf *diaphanum*	Bythiosp	*Gammarus fossarum*	G.fossar
Chaetogaster diaphanus	C.diaph	*Spiralix* cf *vitrea*	Spiralix	*Niphargus* sp. (juveniles)	Niphargus
Chaetogaster diastrophus	C.diast	*Pisidium* sp.	Pisidium	*Niphargus rhenorhodanensis*	N.rheno
Nais alpina	N.alpi	Hydracarina	Hydrac	*Niphargus* gr. *kochianus*	N.koch
Nais barbata	N.barb	*Acanthocyclops venustus*	A.venustus	*Niphargus casparyi*	N.caspar
Nais bretscheri	N.bret	*Acanthocyclops robustus*	A.robustus	*Niphargus* gr *fontanus*	N.fontan
Nais gr communis	N.com	*Acanthocyclops sensitivus*	A.sensitivus	*Salentinella* sp	Salentinel
Nais elinguis	N.elin	*Macrocyclops albidus*	M.albidus	*Asellus* sp.	Asellus
Nais pardalis	N.pard	*Megacyclops viridis*	M.viridis	*Proasellus walteri*	P.walteri
Nais div sp	Nais.sp	*Paracyclops fimbriatus*	P.fimbri	*Microcharon* cf *reginae*	Microcharon
Stylaria lacustris	Styla	*Eucyclops serrulatus*	E.serrul	*Parabathynella* cf *stygia*	Bathynel
Vejdovskiella intermedia	Vejdov	*Eucyclops macruroides*	E.macrur	Plecoptera (juveniles)	Pleco
Pristina aequiseta foreli	Prist.aeq	*Diacyclops belgicus*	D.belgicus	*Leuctra major*	L.major
Pristina jenkinae	Prist.jenk	*Diacyclops putealis*	D.putealis	*Leuctra* cf *fusca*	L.fusca
Tubificinae	Tubif	*Bryocamptus minutus*	B.minutus	*Euleuctra geniculata*	L.geniculata
Haber sp.	Haber	*Bryocamptus typhlops*	B.typhlops	Ephemeroptera (juveniles)	Ephem
Haber turquini	Haber.tur	*Bryocamptus vejdovskyi*	B.vejdov	*Serratella ignita*	S.ignita
Limnodrilus sp.	Limnodri	*Attheyella crassa*	A.crassa	*Baetis* sp.	Baetis
Limnodrilus hoffmeisteri	Limno.hof	*Attheyella paranaphtalica*	A.paran	Heptageniidae (juveniles)	Heptagen
Lophochaeta ignota	L.ignota	*Attheyella wulmeri*	A.wulm	*Potamanthus luteus*	P. luteus
Potamothrix moldaviensis	P.moldav	*Pesceus schmeili*	P.schme	*Habroleptoides* sp.	Habrolep
Potamothrix vejdovskyi	P.vejdov	*Nitocrella psammophila*	Nitocrella	*Ephemera* sp	Ephemera
Psammoryctides barbatus	P.barbat	*Nitokra hibernica*	Nitokra	*Caenis* sp.	Caenis
Tubifex sp.	Tubifex	*Epactophanes richardi*	E.richardi	*Hydropsyche* sp.	Hydropsy
Rhyacodrilus sp.	Rhyacod	*Fontinalicaris fontinalis*	F.fontinalis	*Cheumatopsyche lepida*	C.lepida
Rhyacodrilus amphigenus	R.amphi	*Parastenocaris cf. glareola*	Parasteno	*Polycentropus* cf *flavomaculatus*	P.flavom
Rhyacodrilus falciformis	R.falci	Cladocera (juveniles)	Clado	*Psychomyia pusilla*	P.pusilla
Pararhyacodrilus ekmani	P.ekmani	*Alona guttata*	A.guttata	Hydroptilidae	Hydroptil
Phallodrilinae	Phallod	*Alona quadrangularis*	A.quadrang	Leptoceridae	Leptocerid
Rhyacodrilus balmensis	R.balmensis	*Alona rectangula*	A.rectang	*Esolus* sp.	Esolus
Spiridion phreaticola	Spirid	*Alona weltneri*	A.weltn	*Limnius* sp.	Limnius
Enchytraeidae	Enchyt	*Chydorus piger*	C.piger	*Stenelmis* sp.	Stenelm
Cernosvitoviella sp	Cernosv	*Chydorus sphaericus*	C.sphaer	*Elmis* sp.	Elmis
Enchytraeus buchholzi	E.buch	*Lathonura rectirostris*	L.rectir	*Oulimnius* sp.	Oulimn
Fridericia sp.	Frideri	*Phreatalona phreatica*	P.phreatica	Dyticidae div. sp.	Ditycid
Marionina sp.	Marion	*Pleuroxus* sp.	Pleurox	*Micronecta* sp.	Micronecta
Marionina argentea	M.argent	Ostracoda (juveniles)	Ostrac	Ceratopogonidae	Ceratopog
Propappus volki	Propap	*Pseudocandona albicans*	P.albicans	Empididae	Empididae
Haplotaxis gordioides	Haplotax	*Pseudocandona marchica*	P.marchica	Limoniidae	Limoniid
Hydra sp.	Hydra	*Marmocandona zschokkei*	M.zschok	Simulidae	Simulidae
Dugesia gonocephala	D.gono	*Cryptocandona kieferi*	C.kieferi	Tipulidae	Tipulidae
Dugesia tigrina	D.tigri	*Schellencandona triquetra*	S.triquetra	Brachycera predators	DiptPredat
Phagocata sp.	Phagoc	*Fabaeformiscandona wegelini*	F.wegelini	Nymphe of Chironomidae	NymChir
Polycelis nigra	P.nigra	*Candona candida*	C.candida	Orthocladiinae	Orthoclad
Polycelis tenuis	P.tenuis	*Candona neglecta*	C.neglecta	*Corinoneura* sp.	Corinoneura
Nematoda	Nemato	*Cypria ophthalmica*	C.ophth	Tanypodinae	Tanypodinae
Erpobdella cf *octoculata*	Erpobd	*Ilyocypris bradyi*	I.bradyi	Tanytarsini	Tanytarsini
Glossiphonia sp.	Glossiph	*Prionocypris zenkeri*	P.zenkeri	Chironomini	Chironomini

Table S2. Results of two-ways ANOVA between depths (-20, -40 and -60cm) and hydrological patterns (downwelling, upwelling, no exchange) for abundances and richness of the total hyporheic fauna, the temporary and the permanent hyporheos and the stygobites, after log(x+1) transformation.

Total richness of the hyporheos

Effects	DF	F	p
Depths	2	15.61	0.000002
Hydrological patterns	2	12.96	0.000013
Hydro x depths	4	1.11	n.s.

Total abundances of the hyporheos

Effects	DF	F	p
Depths	2	20.88	$< 10^{-5}$
Hydrological patterns	2	15.72	0.000002
Hydro x depths	4	0.79	n.s.

Richness of the temporary hyporheos

Effects	DF	F	p
Depths	2	19.17	$< 10^{-5}$
Hydrological patterns	2	20.19	$< 10^{-5}$
Hydro x depths	4	0.38	n.s.

Abundances of the temporary hyporheos

Effects	DF	F	p
Depths	2	23.17	$< 10^{-5}$
Hydrological patterns	2	30.63	$< 10^{-5}$
Hydro x depths	4	0.61	n.s.

Richness of the permanent hyporheos

Effects	DF	F	p
Depths	2	18.65	$< 10^{-5}$
Hydrological patterns	2	8.61	0.0004
Hydro x depths	4	0.65	n.s.

Abundances of the permanent hyporheos

Effects	DF	F	p
Depths	2	15.41	0.000002
Hydrological patterns	2	7.26	0.001
Hydro x depths	4	0.34	n.s.

Richness of the stygobites

Effects	DF	F	p
Depths	2	0.028	n.s.
Hydrological patterns	2	16.34	0.000001
Hydro x depths	4	0.52	n.s.

Abundances of the stygobites

Effects	DF	F	p
Depths	2	0.056	n.s.

Hydrological patterns	2	6.64	0.002
Hydro x depths	4	0.38	n.s.

Abundances of the sediment feeders

Effects	DF	F	p
Depths	2	18.03	$< 10^{-5}$
Hydrological patterns	2	15.79	0.000002
Hydro x depths	4	0.94	n.s.

Abundances of the POM feeders

Effects	DF	F	p
Depths	2	23.45	$< 10^{-5}$
Hydrological patterns	2	11.07	0.00005
Hydro x depths	4	0.31	n.s.

Abundances of the Algae feeders

Effects	DF	F	p
Depths	2	19.31	$< 10^{-5}$
Hydrological patterns	2	13.04	0.000012
Hydro x depths	4	0.70	n.s.

Abundances of the predators

Effects	DF	F	p
Depths	2	11.34	0.00004
Hydrological patterns	2	9.05	0.0003
Hydro x depths	4	0.11	n.s.

Ecological groups’ diversity

Effects	DF	F	p
Depths	2	0.42	n.s.
Hydrological patterns	2	8.11	0.0006
Hydro x depths	4	0.19	n.s.

Food-type groups’ diversity

Effects	DF	F	p
Depths	2	5.25	0.007
Hydrological patterns	2	4.15	0.019
Hydro x depths	4	1.23	n.s.

Supplementary material: Figures

Fig. S1 : Biplots for hydrological patterns.

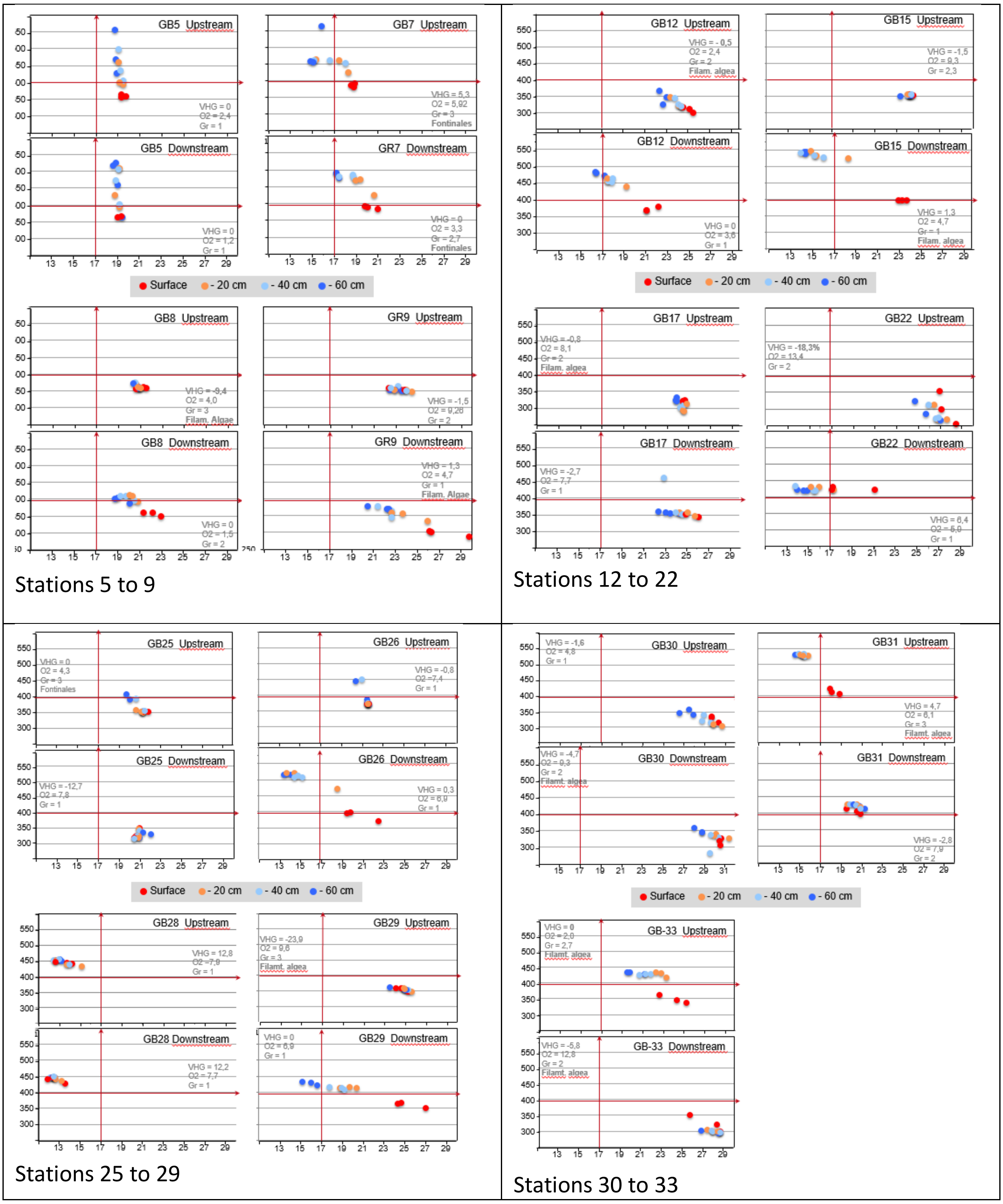


Fig. S2 : Longitudinal profiles of temperature, electric conductivity, dissolved oxygen, vertical hydraulic gradient and POM (mean values per stations, all depths and all replicated cumulated)

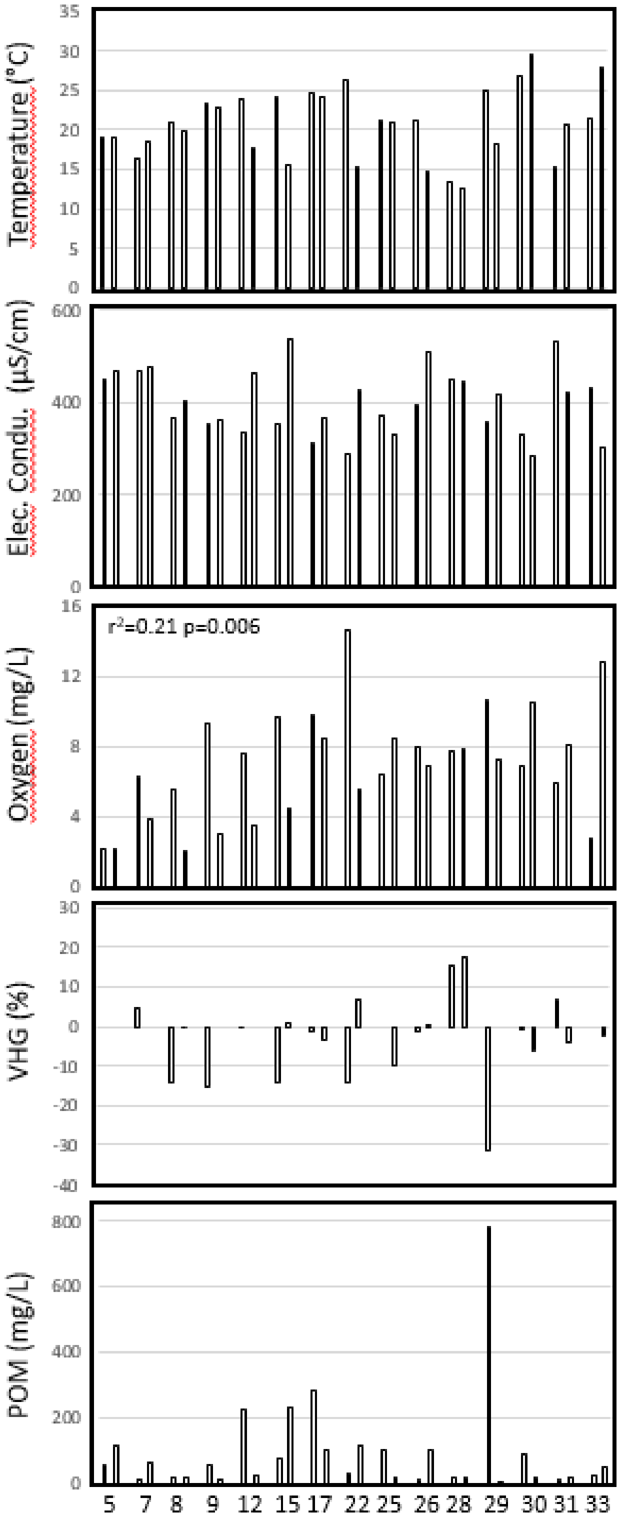


Fig. S3a: Frequences of temporary hyporheic taxa according to local hydrology

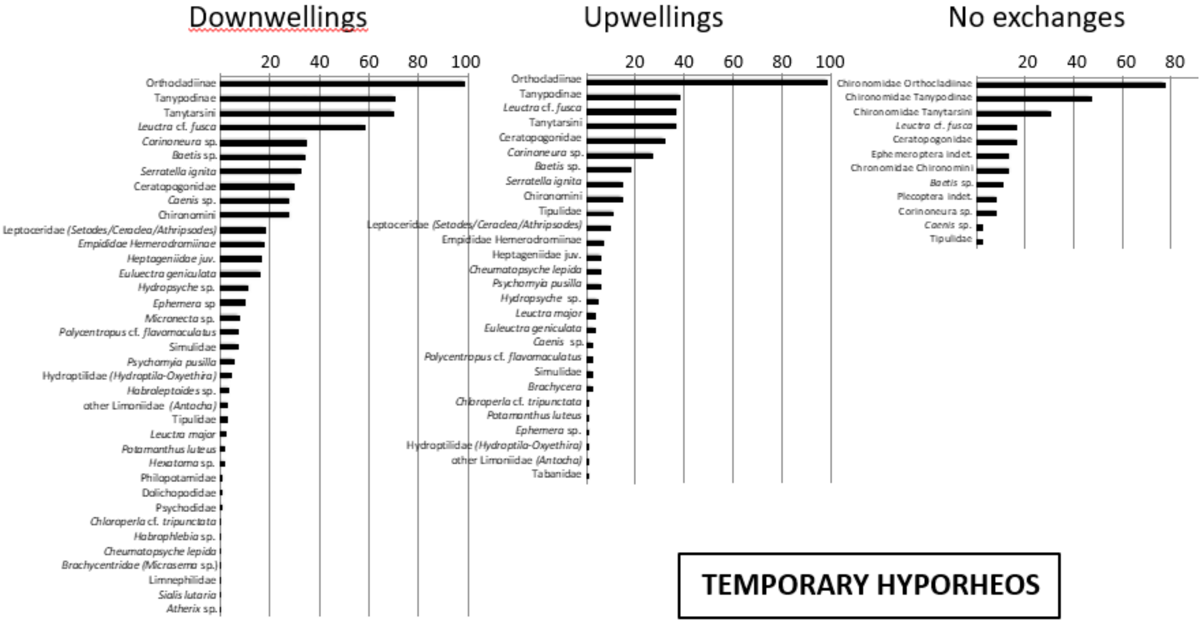


Fig. S3b: Frequences of permanent hyporheic taxa according to local hydrology

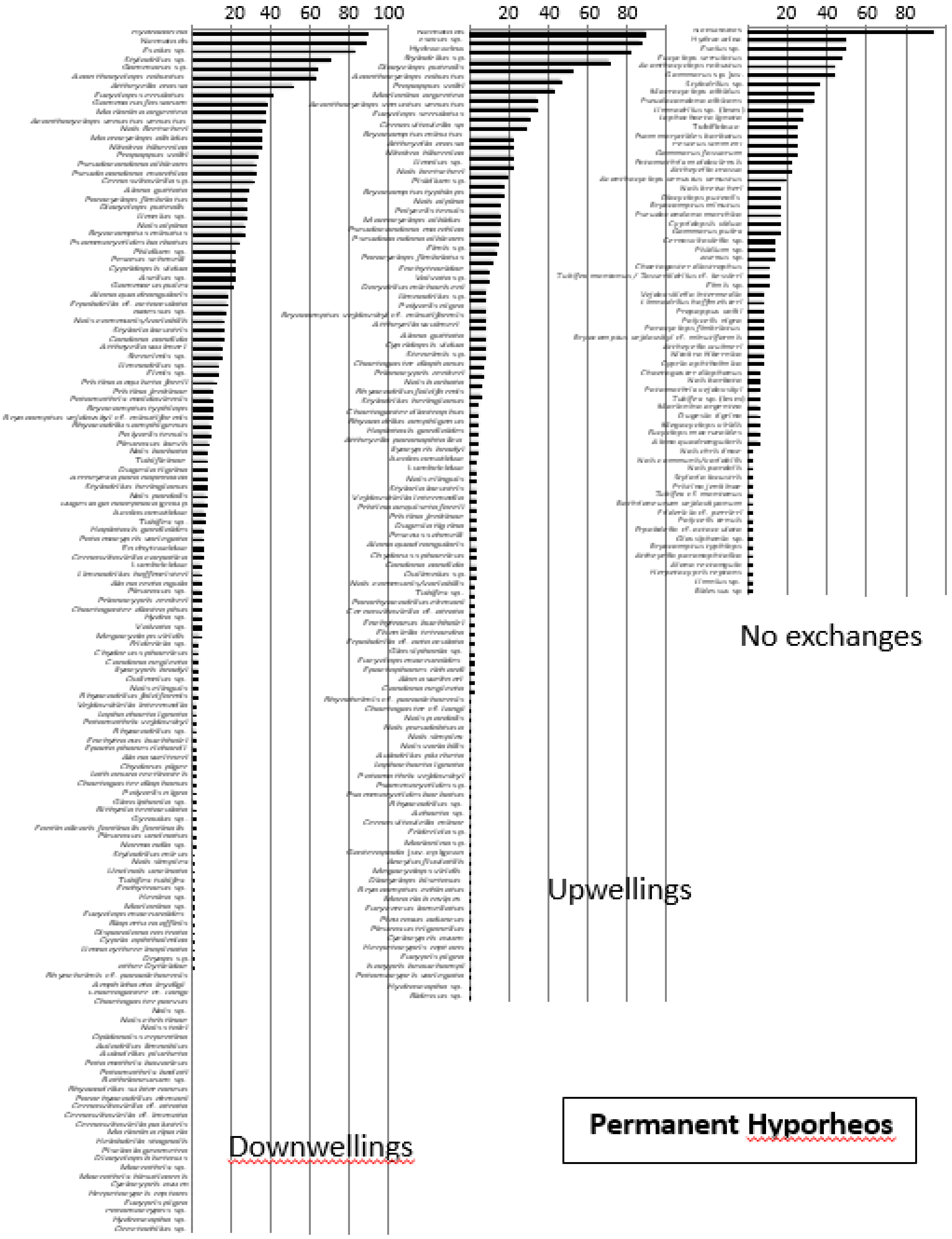


Fig. S3c: Frequences of stygobites according to local hydrology

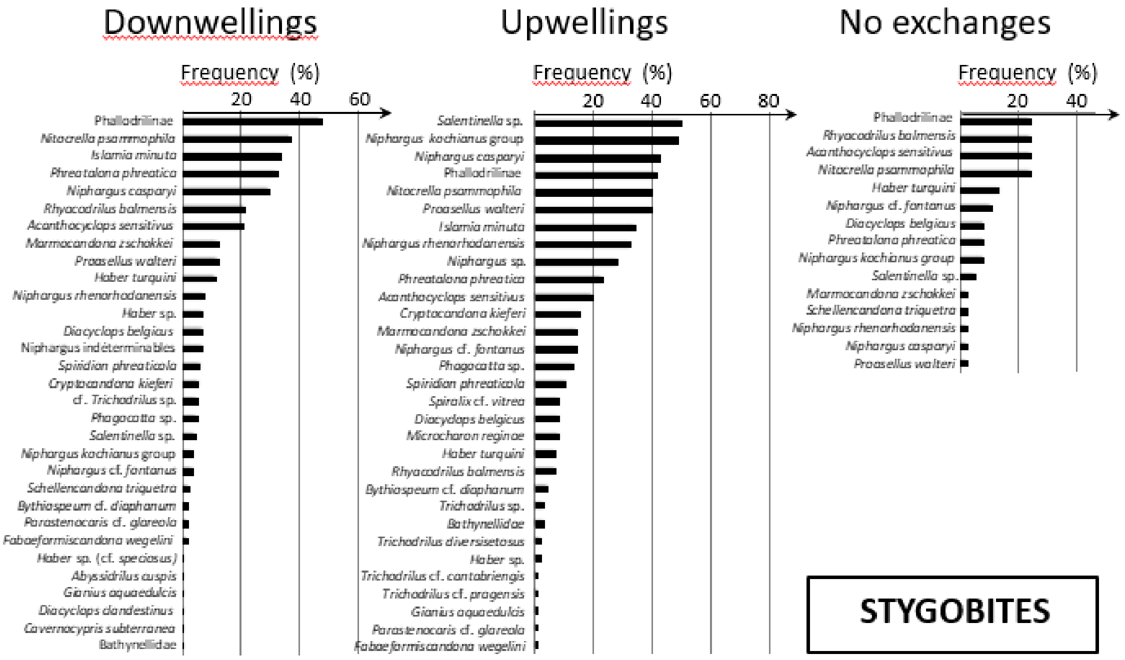


Fig. S4: Effects of sediment grain size (left column), sediment stability (central column) and hydrology (right column) on taxonomic richness, abundances and functional group abundances of the hyporheic assemblages. Results of one-way ANOVAs on classes after log-transformation, using stations as replicates. Mean values and error-types.

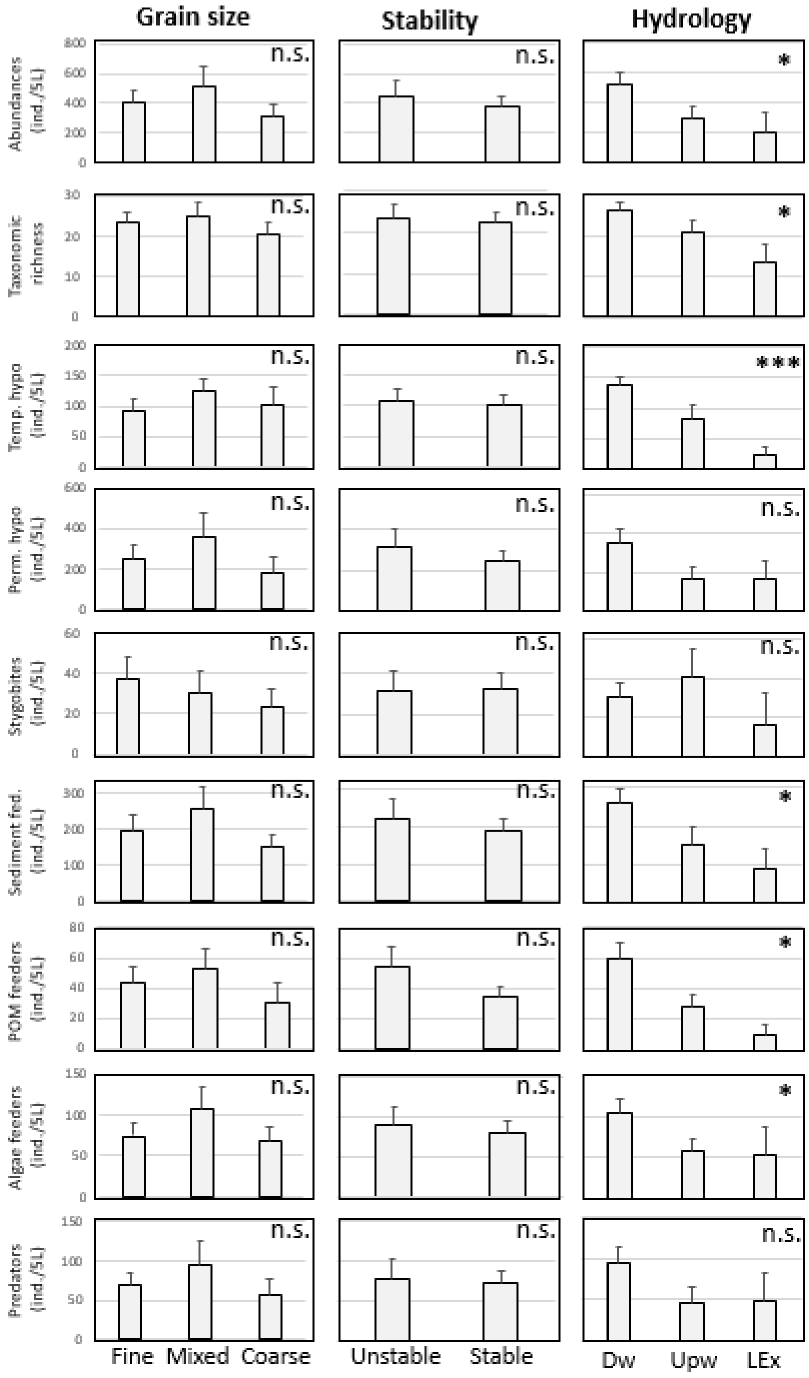
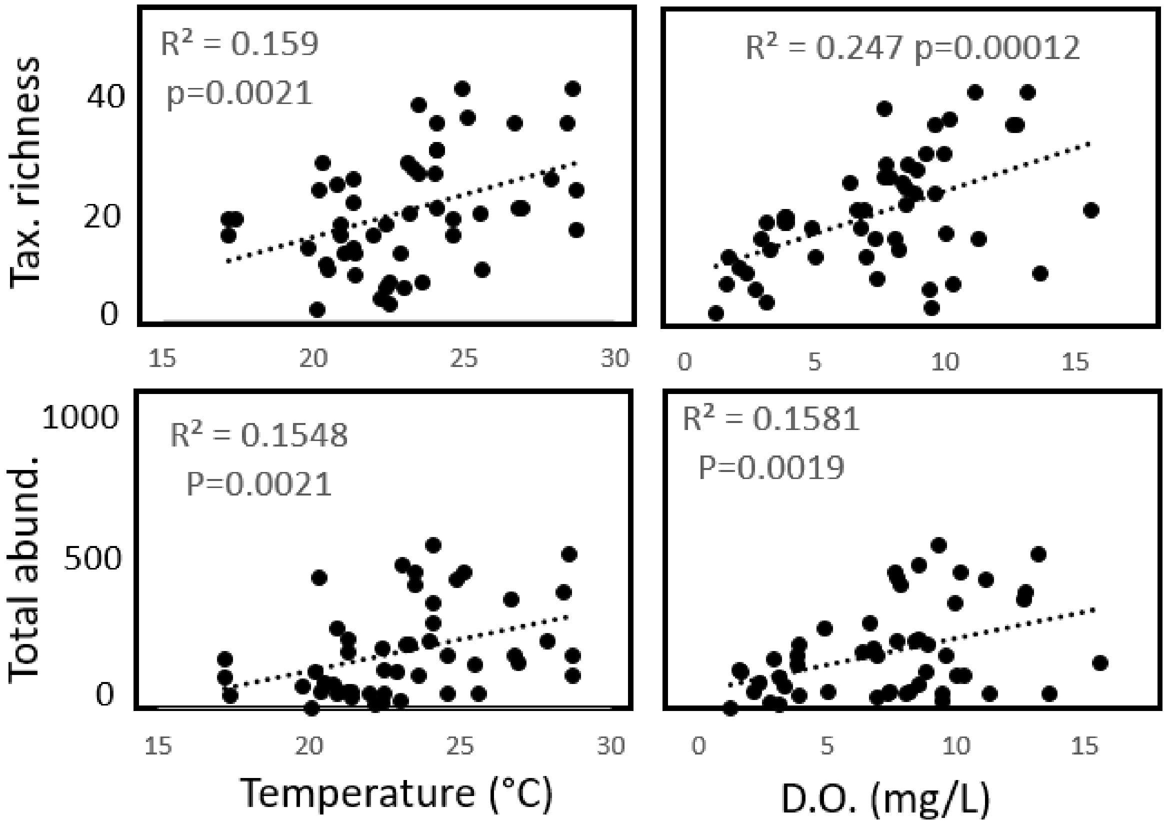


Fig. S5: Correlations between abundances and taxonomic richness and local characteristics (Temperature and Dissolved Oxygen) at 60cm depth in downwelling zones.



When considering the relationship of the abundances (upper pannels) and taxonomic richness (lower pannels) with temperature and Oxygen at -60 cm depth in downwelling zones, we observed similar patterns with increasing number of species and individuals with increasing temperature (with maximum values above 25°C) and with available Oxygen (with maximum values above 7 mg.L^{-1}). The hyporheic fauna developp abundant and diversifies assemblages in strong downwelling zones (with warm and well oxygenated water).