

Does spatial heterogeneity of hyporheic fauna vary similarly with natural and artificial changes in braided river width?

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22 Abstract

23 Heterogeneity of hyporheic fauna is associated with geomorphological features and related vertical 24 water exchanges. Constrictions on river floodplain is known to induce groundwater inputs and increase stygobite fauna. Two floodplain constrictions were studied in a large braided river (the Drôme River): 25 26 one linked to a natural process (valley narrowing), another to an artificial river regulation (early 20th 27 embankment). Spatial distribution of hyporheic organisms were sampled upstream and downstream 28 of the two constrained sections, at 9 stations, 3 positions (left and right sides, centre of the braided 29 strip), 3 replication points and at a depth of 50 cm in the river sediment. The spatial heterogeneity in 30 community composition was higher near the banks than at the centre of the braided strip, no matter 31 the width of the strip. The artificial constriction induced a decrease in spatial heterogeneity of the 32 benthic fraction of the hyporheic fauna, but no changes were detected for the stygofauna. The natural 33 valley narrowing reduced width and thickness of the alluvium and induced an inflow of groundwater 34 resulting in an increase in stygofauna abundance. Natural floodplain narrowing linked to geology thus 35 control the distribution of stygobite species, while artificial constrictions only modify the spatial 36 distribution of the benthic fraction of the hyporheic fauna. 37 38 39 Key words: invertebrates, groundwater, stygofauna, geomorphology, floodplain, embankment.

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43 **1.** Introduction.

River geomorphology is a major driver of aquatic habitats heterogeneity (Kasahara and Wondzell 2003; 44 45 Tonina and Buffington, 2009) and therefore of biodiversity reported in rivers and streams (Ward and Tockner, 2001; Tockner et al., 2003; Chessman & al., 2006). A significant portion of these aquatic 46 47 organisms live within the sediment, at the interface of surface water and groundwater, where they constitute the hyporheic fauna (Orghidan, 1959). Benthic invertebrates colonise the hyporheic zone as 48 49 they find protection from changes in river flow and from biotic pressures present at the stream surface 50 (e.g. Robertson et al., 1995). The distribution of the hyporheic fauna is highly heterogeneous and 51 mainly linked to geomorphology, alluvial forms and their related hydrological exchanges (Marmonier 52 and Dole 1986; Dole-Olivier and Marmonier, 1992; Brunke and Gonser, 1997). At a local scale, geomorphological units such as gravel bars and riffles induce surface water infiltration at their 53 54 upstream end. This surface-water infiltration produces an inflow of dissolved oxygen and fresh organic matter, creating large inputs of available resources strongly attractive for the benthic fauna 55 56 (Marmonier and Dole-Olivier, 1986), but it also generates thermic variability within the sediments 57 (Boulton et al., 1998). On the contrary, groundwater generally upwells at the downstream part of these 58 geomorphological units (Dole-Olivier et al., 1993; Harvey and Bencala, 1993). Upwellings of 59 groundwater reduce temperature variability in the hyporheic zone, but also reduce dissolved oxygen 60 concentration and the quality of organic matter (Claret et al., 1998; Dahm et al., 1998). In such 61 environmental conditions, the stygofauna are potentially abundant and diversified (Dole-Olivier and 62 Marmonier, 1992; Mermillod-Blondin et al., 2000) and some deep groundwater organisms (i.e. phreatobites, Gibert et al., 1994) can reach shallow hyporheic habitats. 63

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65 At a kilometre scale, variations in floodplain width are known to induce changes in river-aquifer 66 exchanges. When the river reaches a confined floodplain section, the volume of alluvial deposits 67 decreases along with the progressive reduction of substratum depth (Clarke et al., 1999; Gibling, 2006; White et al., 2010). Such geological conditions force groundwater to upwell into the surface stream 68 69 (Doering et al., 2007), modifying the hyporheic assemblages (Malard et al., 2003). This large-scale pattern of distribution of the hyporheic fauna was predicted by the "hyporheic corridor concept" 70 71 (Stanford and Ward, 1993) and verified by some field studies (Creuzé des Châtelliers and Reygrobellet, 72 1990; Stanley et al., 1997; Malard et al., 2001). These two scales are interdependent and their effect 73 may be combined (Thot, 1963; Dole-Olivier, 2011). For example, Capderrey et al. (2013) observed an increased abundance of taxa closely linked to sediments (e.g. Clitellata, stygofauna) downstream of 74 75 gravel bars, with greater intensity at the downstream end of floodplains, where valley width is reduced 76 and groundwater drainage is highest.

78 The effect of changes in floodplain width is particularly marked in braided rivers that are characterized 79 by multiple mobile channels separated by large bare gravel bars. The high discharge variability of 80 braided rivers and their strong sediment instability explain the frequent modification of channel 81 locations (Petts and Amoros, 1996; Piégay et al., 1999; Gurnell et al., 2012). This geomorphological 82 dynamic generates a great transversal heterogeneity in habitat characteristics (Arscott et al., 2002; Ward *et al.*, 2002) linked to the concomitance of different channel-types with distinct connection-types 83 to surface water or groundwater (Stanley et al., 1997; Arscott et al., 2000; Malard et al., 2001, 2006). 84 85 Heterogeneity in connexion controls water chemistry (Malard et al., 1999) and thermic variability of 86 surface waterbodies (Tonolla et al., 2010). In the same way, a large variety of flow velocities can be 87 observed in the various channels (Prevot and Prevot, 1986; Ward et al., 2002) favouring colonization 88 of slow-flowing patches by lentic species (Legier and Talin, 1975; Karaus, 2004) and community 89 resilience (Sedell et al., 1990). Similarly, the diversity of local characteristics induces various hyporheic 90 assemblages (Malard et al., 2003), especially in upwelling areas associated with narrowing of the 91 floodplain (Ward et al., 2002; Capderrey et al., 2013). On the contrary, constrained sections show 92 reduced channel diversity, geomorphological complexity and thus surface habitat heterogeneity 93 (Latterell et al., 2006) with potential consequences on the benthic assemblages. Yet Peeters and Tachet 94 (1989) observed weak changes in benthic faunal composition certainly due to the high mobility of 95 species colonizing unstable rivers. This may also explain the intense migration of the fauna to the 96 hyporheic zone (Dole-Olivier, 2011; Vander Vorste et al., 2016a) and the outstanding resilience of 97 benthic assemblages in braided rivers after disturbance (Vander Vorste et al., 2016b).

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99 Despite this research, the consequences of braided network simplification on aquatic invertebrates 100 are not fully understood. Alluvial plain narrowing may have different effects according to the habitat 101 considered (benthic versus hyporheic). Moreover, hydrological and ecological consequences may also 102 vary according to the origin of the braided strip constriction. Some have a natural origin such as 103 knickpoint, which are linked to a decrease in the distance between hillslopes or to changes in bedrock 104 depth (Clarke et al., 1999; Gibling, 2006; White et al., 2010). Others have an artificial origin, due to 105 river regulation, embankment or channelization (Gilvear, 1993; Piegay et al., 2009) that transform 106 multiple-channel rivers into straight sections with a low diversity of surface habitats (Hauer and Lorang, 107 2004; Jahnig et al., 2009). Furthermore, the artificial channelization may act as a physical constraint to 108 surface flow but not as an obstacle to aquifer flow (Maazouzi et al., 2018). The respective effects of 109 artificial vs natural constrictions on hyporheic hydrology and fauna are still understudied.

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111 In the present work, the spatial patterns of hyporheic assemblages were studied in relation with 112 alluvial plain width and river-aquifer exchanges in a large braided sector of the Drôme River (the

"Ramières du Val de Drôme", Piégay et al., 1999). In this area, the river has a large braided channel 113 network, which is subjected to two major constrictions. The first one is natural and linked to a 114 115 geological knickpoint (i.e. a narrowing of the alluvial plain associated with a potential change in fluvial deposit thickness). The second one has an artificial origin (embankment), due to early 20th century 116 117 railway construction. Embankments generally induce bottom sediment erosion and groundwater drainage (Surian and Rinaldi, 2003; Marmonier et al., 2010). In the present case, the erosion is limited 118 119 by an artificial weir that prevents river incision. The study of the relationship between river-aquifer 120 water exchanges and hyporheic assemblages at large scale is complex, we thus applied a truly 121 multidisciplinary methodology using four types of data concomitantly: geophysical, hydrogeological, 122 physico-chemical and faunal. Hyporheic fauna was sampled at 9 stations along a 13 km sector 123 according to changes in alluvial plain width and related hydrogeological constraints, at 3 positions in 124 the braided strip (centre and both margins) and at 3 repeated points (hereafter called 'replicates'). This design is drawn to evaluate the spatial heterogeneity of a braided river hyporheic fauna at 125 126 microhabitat (replicates), habitat (positions), and section scales (here alluvial plain width).

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128 We thoroughly describe our studied section for the alluvial plain width, the alluvium thickness and the 129 groundwater dynamics in relation to the artificial and the natural narrowings in order to assess two 130 main hypotheses. Firstly, we hypothesized (H1) that the braided strip constriction reduces the spatial 131 heterogeneity of hyporheic assemblages by reducing the geomorphological complexity of the river 132 (Ascott et al. 2000; Malard et al. 2006) in both natural and artificial constrictions. Secondly, we hypothesized (H2) contrasted effects in natural vs artificial constrictions on stygobite species (i.e. 133 obligate groundwater fauna). Little or no change in stygofauna assemblages was expected at the 134 135 artificial constriction section, because the embankment and the limited incision modifies river-136 groundwater exchange minimally (Maazouzi et al. 2018). In contrast, the natural narrowing of the 137 valley due to a geological knickpoint may force groundwater to upwell into the channel and modify the abundance and composition of the stygofauna (Creuzé des Châtelliers and Reygrobellet 1990; 138 139 Capderrey et al. 2013).

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141 **2. Studied area**

The Drôme River is 106 km long for a 1640 km² catchment ranging from alpine (1262 m a.s.l.) to Mediterranean (90 m a.s.l.) climates at its confluence with the Rhône River. The studied sector was located between Crest (5°00′66″E, 44°73′97″N) and Loriol (4°84′38″E, 44°76′38″N) and consists in a large alluvial plain (13 km length, 3.2 km width). When distances along the river were expressed from the confluence with the Rhône River (noted as kilometric points, kp, in Fig. 1a), the studied sector was located between kp 5 and kp 18, with a maximal width at kp 14. In the upstream part of the studied 148 section (from kp 18 to kp 15.9), the river flows in a large floodplain with a high slope (6‰) and a braided 149 fluvial style with several parallel channels separated by poorly or un-vegetated gravel bars on a strip 150 of 180 to 360 m width. In the central part (from pk 15.9 to pk 11.1), a 4.8 km section was embanked during the early 20th century for a railway setting opened in 1906 (Fig. 1a). There, the floodplain was 151 152 removed and the Drôme River is reduced to a single channel bordered by alternating gravel bars with 153 a total width varying between 90 and 115 m. An artificial weir was built at the downstream end of this 154 embanked section to prevent river incision. Just downstream of this weir (from kp 11.1 to kp 7.5), another wide floodplain occurred with a large braided strip, varying between 125 and 265 m width. 155 156 There, the channel is bordered on both sides by abandoned channels (called 'Freydière d'Allex' and 157 'Freydières brook', Fig. 1a) fed by alluvial plain groundwater. In the downstream part of the alluvial 158 plain, the river crosses a narrowing of the valley where the two Hauterivien calcareous hills of Loriol 159 and Livron-sur-Rhône get closer (around kp 7; Fig. 1a). Here again, the braided strip is reduced to a 160 single channel of 50 to 100 m width. Finally, downstream of kp 6, the river enters its last alluvial plain 161 before its confluence with the Rhône River and turns back to its braided fluvial style, with several gravel 162 bars and a width varying between 150 and 190 m.



163

164 Fig. 1. Drôme River studied area with the location of the alluvial plain, the floodplain and the braided165 channels (a). Along the river the hyporheic sampling stations (noted from St1 to St9, white bars), the

artificial weir (red bar) and the abandoned channels (noted "Freydières") were located together with
 the kilometric points (from 5 to 19, yellow triangles). Maps modified from the National Geographic

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Institute. Location of the drill logs (b, with the alluvium thickness in m) and simplified geological map (c) with locations of the five GPR profiles (satellite images from Google Earth 2015).

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1713. Material and methods

172 **3.1. Geological characteristics of the area**

The studied zone is the south end of tertiary lower Dauphine Basin (La Vassière, 2006; Cave, 2011). Its geological context is characterized on the East side by Pliocene (marl and sand) and Miocene (molasses) deposits bordered on the West side by Mesozoic (Hauterivian) limestone and marl (BRGM, 1977). In the quaternary period loess deposits covered the hillsides of the Rhône and the Drôme rivers, until the present time (Toone, 2014). The aquifer is located in a layer of fluvial deposits (coarse sand, gravel and rolled pebbles) that covers a lowly permeable substratum.

179 To evaluate the changes in the volume of the aquifer, together with the alluvial valley width, the 180 thickness of the fluvial layer was investigated using two different sources of information. Firstly, the alluvium thickness data from 16 drill logs were extracted from the French subsurface databank 181 182 (http://infoterre.brgm.fr/page/banque-sol-bss; drill locations are noted by crosses on Fig. 1b) of which 11 located close to the river were retained to estimate the changes in alluvium thickness. Secondly, 183 184 five transects were performed using Geological Penetrating Radar (GPR) (Fig. 1c). GPR is a non-invasive 185 geophysical technique that detects electrical discontinuities in the shallow subsurface. This technique 186 is based on the generation, transmission, propagation, reflection, and reception of discrete pulses of 187 high-frequency (MHz) electromagnetic energy. It assesses the spatial structure of sediments to a depth 188 of 10–20 m over extended areas (Huggenberger et al., 1994; Beres et al., 1995; Bridge and Lunt, 2006, 189 Mermillod-Blondin et al., 2015, Paz et al., 2017). Sediment geologists widely used this technique to 190 reconstruct depositional environments and document historic sediment processes (Schrott and Sass, 191 2008). The GPR measurements were carried out with the GSSI SIR 3000 system (Geophysical Survey 192 System Inc., Salem, USA), operated with a shielded antenna at a central frequency of 100 MHz, running 193 in monostatic mode. The data processing was performed using the GSSI Radan 7 software. This 194 processing consisted in distance normalization, static time shift (to align direct ground wave arrival to 195 0 ns), background removal (to eliminate the high-amplitude direct ground wave), and Kirchhoff 196 migration. The velocity of the electromagnetic waves was determined by common midpoint (CMP) with two antennas. This velocity ranged from 0.12 m.ns⁻¹ in the unsaturated zone to 0.06m.ns⁻¹ in the 197 198 saturated zone. Accordingly, a velocity of 0.06 m.ns⁻¹ was selected to convert two-way travel time into 199 actual depth, a velocity that is comparable with those measured in the saturated zone of analogous 200 alluvial deposits using the common midpoint method (Woodward et al., 2003; Neal, 2004; Mumphy et 201 al., 2007; Lindhorst et al., 2008). In addition, a topographic survey using a GPS Trimble station was 202 performed to localize the acquisition and corrections were applied to the data using transect elevation.

204 3.2. Hydrogeological characteristics

205 The local hydrogeological characteristics of the alluvial plain and resulting river-aquifer exchanges 206 were studied using geomatic analysis (Paran and Augeard, 2017; Graillot et al., 2014). This method 207 consists in using point observations of water levels both in the aquifer and in the river (or piezometric 208 maps) to infer the direction of groundwater/river hydraulic exchanges. In unconfined alluvial aquifers, 209 the water flow between the groundwater and the river is proportional to the slope of the free surface 210 of the groundwater near the bank and the permeability of the alluvium (application of Darcy's law). 211 We consider that the exchanges are made through an exchange surface on a vertical plane whose area 212 is evaluated with the bank length and the water height. Two river-groundwater exchange maps were 213 built during two low water periods. Firstly, calculations were based on a reference piezometric map of 214 the sector built with measures of water levels in 74 piezometers during 1996 low water period (Artelia, 215 2012). Secondly, calculations were based on the 2014 studied period using piezometric measurements 216 (21 piezometers) and a longitudinal profile of the river, performed from a canoe with an on-board GPS 217 (using an average river depth of 0.3m, Artelia, 2012). These field data thus take into account all 218 disturbances of the groundwater level (extraction for irrigation and drinking water supply).

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220 A TIN mesh (Triangulated Irregular Network) was used to build the 3D model of the groundwater 221 surface, using the slope (in %) and the direction of the flow (in degrees). The permeability of the aquifer (K) was estimated using generic values from the literature (here from 10⁻² to 3.10⁻³ m/sec, Artelia, 222 223 2012). The calculation of flow exchanges between the alluvial groundwater and the Drôme River was 224 carried out using the ArcGIS 10.4 software. Data were available only between kp 20 to 7, thus the 225 calculation was restricted to this section of the Drôme River. The resulting exchange diagnosis was 226 established by aggregating the flows calculated at two scales: (1) a kilometric aggregation on the linear 227 banks of the river (left and right) and (2) an aggregation of 250 m on either side of each invertebrate 228 sampling stations (see hereafter). Because of the difficulty of precisely evaluating the permeability of 229 the aquifer (high spatial heterogeneity) only the direction of exchanges was considered here.

230

231 3.3. Hyporheic water and fauna

Hyporheic fauna and water were sampled at 9 stations from kp 17.5 to kp 5. Three stations (St1, St2, St3) were situated in the first wide floodplain, two stations (St4, St5) were located in the embankment section, two other stations (St6, St7) were positioned in the second large floodplain, the St8 was located just upstream of the natural narrowing and finally the last St9 was located downstream of the calcareous hills (Fig. 1a). At each station, 3 positions were investigated, on the left (L), the right (R) and the centre (C) of the braided strip. At each position, water and fauna were sampled in 3 replicates,
the sampling design resulting in a total of 9 stations × 3 positions × 3 replicates = 81 samples.

239

The hyporheic zone was sampled between the 28th and 30th of April 2014, a period of medium to low 240 241 discharge (18 to 20 m³/sec). For comparison, the mean water discharge for the last century is 28.8 242 m³/sec in April and 26.3 m³/sec in May (data Agence de l'Eau RM&C). River water was directly sampled 243 at the surface while hyporheic water and fauna were sampled at the 81 points at a depth of -50 cm 244 under sediment surface using the Bou-Rouch technique (Bou and Rouch, 1967; Bou, 1974). A 245 perforated metal pipe of 23 mm-internal diameter (9 rows of 5-mm-diameter holes in a 13-cm band, 246 4 cm from the distal end of the pipe) was driven into the sediment at each point (Stubbington et al., 247 2016).

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Water temperature (in °C), electric conductivity (in µS/cm), and dissolved oxygen (mg/L; Hach HQ-40d Multiparameter) were measured directly in the surface water and in the hyporheic water pumped inside the Bou-Rouch pipe using a peristaltic hand pump (Willy A. Bachofen type). Vertical Hydraulic Gradient (VHG in %) was measured between surface and hyporheic layers and additional water samples were taken, filtered on GF/F Whatman filters, stored in 40 mL plastic bottles, and kept in insulated containers for the return to the laboratory to measure Na, K, Ca, Mg and Nitrate concentrations (± 0.1 %) with an ionic chromatography (Dionex 1100, conductivity detector).

256

257 Hyporheic invertebrates were collected at the same 81 sampling points using the Bou-Rouch sampler; 258 10 L of water and sediment were pumped and filtered through a 160 µm mesh net. Samples were 259 preserved in the field in 96° alcohol and stained with Bengal Pink. Invertebrates were sorted in the 260 laboratory under a stereomicroscope (x20) after sieving. Clitellata and most crustaceans (Ostracoda, 261 Cladocera, Isopoda, and Amphipoda) were identified to species level. Planaria, Acheta, Mollusca and 262 most Insects (Ephemeroptera, Plecoptera, Trichoptera, and Coleoptera) were identified to genus level 263 or to the group of species, while Diptera remained at the Family or sub-Familly levels. Finally, 264 Nematoda, Hydracarina, Cyclopids and Harpacticids were not further identified. For Clitellata, Isopoda 265 and the stygobite Amphipoda of the genus *Niphargus*, the morphological identification was completed by mitochondrial DNA barcoding to ensure tricky morphological identifications and to identify 266 267 damaged/young individuals. DNA was extracted from all individuals (for Isopoda) or from several 268 individuals of each morphological species (for Clitellata and Niphargus) using the Chelex protocol (Bio-269 Rad, Richmond, CA, USA; Casquet et al., 2012). Mitochondrial cytochrome oxidase subunit I (COI) for 270 Clitellata, COI gene and 28S nuclear rDNA gene for Niphargus and 16S mitochondrial rDNA gene for

Isopoda were used for this barcoding approach. Detailed method and primers are given insupplementary material (Table S1).

273

274 **3.4. Statistical analyses**

Principal Component Analysis (PCA) was used to assess the spatial variation in physicochemical characteristics of hyporheic water with 8 parameters (i.e. VHG, electric conductivity, Mg, Ca, K, Na, NO₃ and dissolved oxygen) excluding temperature that changed during the day. All replicate samples of hyporheic water were included in the PCA (n=81) together with the mean value of surface water sampled at the centre position of each station (n=9) and groundwater sampled in two wells and two abandoned channels (noted Freydières d'Allex and Freydières brook on Fig. 1a, n= 4).

281

282 The structure of hyporheic assemblages was studied using two analyses. Firstly, a Non-Metric 283 Multidimensional Scaling based on Bray-Curtis similarity index (nMDS, Legendre and Legendre, 1998) 284 was used to describe the underlying gradients with a large number of rare taxa. Because replicates 285 were grouped within positions (R, C, L), samples were nested by position in the model as "strata" 286 (results presented in supplementary material). Secondly, a Correspondence Analysis (CA, Benzécri, 287 1973) was used to highlight spatial trends linked to the abundant species. The PCA and the nMDS were 288 performed using the R statistical software (R core Development Team, 2013), with the ade4 R package 289 for PCA and the vegan R package for nMDS (Oksanen *et al.*, 2012), while the CA was performed using 290 ExcelStat 2014.

291

292 Differences between the 9 stations in taxonomic richness, total hyporheic fauna abundance, stygobite 293 abundance and abundances of the most frequent stygobite species were tested using Analyses of 294 Variance (ANOVA). Because of non-independence of repeated measurements per position, nested-295 ANOVAs (with positions R, C, L nested into stations) were performed, after log(x+1) transformation 296 when necessary. Similarities between hyporheic assemblages were measured using the Bray-Curtis 297 index. To study the variability between positions (R, C, L), Bray-Curtis indices were calculated between 298 the 3 replicates at each position and then compared using Nested-ANOVA after Arc Sinus 299 transformation. While to compare the variability between the 9 stations, the Bray-Curtis indices were 300 calculated between the 3 positions at each station and then tested using one-way ANOVA after Arc 301 Sinus transformation. All tests were performed using Statistica (Statsoft, Tulsa, OK, USA) or Excel 2016, 302 the limit of significance was a *p*-value of 0.05.

303

304 **4. Results**

305 **4.1. Changes in the fluvial deposit thickness**





Fig. 2. (a) profile of the thickness of alluvium deposit form the GPR profile and BRGM Core databank
 selected. (b) Representative ground-penetrating radar (GPR1, GPR4 and GPR5) profiles and
 interpretative sketches of the radar facies and major GPR reflection patterns. Location, length, and
 direction of GPR profile sections are illustrated on the figure 1.

The width of the Drôme alluvial plain increased from Crest to the Allex hill (kp 20 to kp 13, Fig. 1a) and 312 deceased downstream Allex until the Livron hill (kp 7). Together with this change in alluvial plain width, 313 314 the thickness of the alluvium varied. Three of the five radar profiles (noted GPR1, GPR4 and GPR5) and 315 the 11 drill logs of the 16 available logs in the subsurface databank documented together the changes 316 in the alluvium thickness along the studied sector (Fig. 2). In the upstream braided section (Fig. 2a), 317 the thickness of substratum ranged from 7.6 to 8.5 m between the station St1 and St2 and increases 318 in the embanked section to 11 - 11.5 m deep between the stations St 4 and St 5. The maximum alluvium thickness was observed in the entrance of the downstream braided section, where the substratum 319 320 depth reached 14.8 m close to the station St6. This maximum was followed by a slight reduction near 321 the station St7 (from 9.5 m to 11 m). The three radar profiles clearly documented this reduction of alluvium thickness close to the narrowing of the valley (Fig. 3b). With this technique, small-scale 322 323 (centimeter-scale) internal cross stratifications could not be detected with the resolution of the 100-324 MHz antennae (~0.50 m), but the radar facies reflection observed represented macroform bounding 325 surfaces of ancient channels (yellow lines) and the limestone substratum (in orange in Fig. 2b) located at a depth of 6-7 m below the surface. The limestone substratum was detected in all radar profiles 326 327 with two opposed apparent dips. The apparent 6° dip measured on the north side of the GPR1 and 328 GPR4 profiles was consistent with the 20° dip measured on the Hauterivien rock outcrop (N20-20E, 329 Fig. 1). These two opposed dips on the two sides of the valley, suggested the presence of an

undescribed fault below the river channel (dotted line in Fig. 2b) or a discordance between thePliocene-Miocene deposits and the Hauterivien layer.

332

333 4.2. Groundwater dynamic and exchanges with the river

334 There was a relatively good consistency between the geomatic analyses performed with a kilometric aggregation (along the banks) and a 250m aggregation around the 8 invertebrate sampling stations 335 336 (Fig. 3) and between the 1996 piezometric map (noted with continuous blue lines on Fig. 3a) and the 337 2014 field measures (66% of similarity, Fig. 3b). The patterns of groundwater-surface water 338 interactions on the right side of the braided strip were roughly similar in 1996 and 2014. The river fed the aquifer in most of the embanked sector (St4-R and St5-R) and drain the aquifer upstream (St2-R in 339 1996 and from St1R to St3-R in 2014) and downstream (St6-R to St8-R). Hydrological patterns changed 340 341 more consistently on the left side of the braided strip where the drainage of the groundwater increased in 2014 around St5-L and St8-L compared to 1996. No calculation of river-groundwater exchange was 342 343 possible at St9.



344

Fig. 3. River –groundwater exchange maps based on 74 piezometric measures made during the 1996 low water period (a, modified from from Artelia 2012) and on 21 piezometric measures made in 2014 (b). Section of the bank (1km aggregation) where river fed the groundwater are noted with red dotted lines, while the bank where the groundwater fed the river are noted with continuous green lines. Exchanges around the invertebrate sampling stations (aggregation of 250m on both sides of the station) were noted by red circles when the river fed the groundwater and by green squares when the groundwater fed the river.

353 **4.3. Hyporheic water chemistry**

354 The two first axes of the PCA explained 64% of the total variance (Fig. 4). A decreasing gradient of 355 electric conductivity and concentrations in Mg, Ca, K, Na was observed along the C1 axis of the PCA, 356 with the surface water (noted SW) located on the positive side of the axis and the groundwater (noted 357 GW) on the negative side. The C2 axis of the PCA (18% of the total variance) represents a decreasing 358 gradient of dissolved oxygen and nitrate concentrations with increasing positive VHG. This second axis 359 separates waters with enough oxygen to maintain nitrate contents at a medium to high level on the 360 negative side of C2 axis from hyporheic waters in which oxygen and nitrate were removed by microbial 361 activities (respiration and denitrification) on the positive side.

362

363 Samples from the 9 stations were differently distributed on the C1 x C2 plan (Fig. 4). In the upstream 364 braided section, all samples from St1 were located on the positive side of the C1 and C2 axes, close to 365 the surface water reference because of similar electric conductivity and solute contents, whereas some 366 samples from the St2 and St3 shifted towards the positive side of the C2 axis. This is especially true for 367 the right bank position at St2 and the two banks and one central point at St3. An increase in electric 368 conductivity, low changes in Na, K, Mg concentrations, but a decrease in oxygen and nitrate contents 369 were measured here (Supplementary material, Table S2) suggesting dissolved oxygen respiration and 370 denitrification here.

371

In the central embanked section (St4, St5) and just downstream (St6, Fig. 4) all samples were located on the positive side of C1, close to the mean surface water and the hyporheic water of St1 (regardless of the position sampled in the channel). The water sampled in these stations and positions was characterized by low electric conductivity, low solutes, intermediate nitrate and high oxygen concentrations (Table S2), suggesting close connections between the river and the hyporheic zone.





Fig. 4. Principal Component Analysis on chemical characteristics of the water. The two first axes were kept for illustration. Parameters included were Vertical Hydraulic Gradient (VGH), electric conductivity (cond.), Magnesium (Mg), Calcium (Ca), Potassium (K), Sodium (Na), Nitrate (NO₃) and Oxygen (O₂) concentrations. Reference for surface water (SW) is the mean value of water collected in the centre of the Drôme river; reference for groundwater (GW) is the mean value of water collected in two floodplain channels and two wells. Three replicates of interstitial water sampled in the channel (green triangles), on the left bank (blue squares), and on the right bank (black dots).

385

In the downstream braided section (St7) and close to the valley narrowing (St8, Fig. 4), the electric conductivity and the concentrations of Mg, Ca, K, Na increased strongly, while dissolved oxygen and nitrate remained high (Table S2). These high values occurred especially on the right bank and at the centre of the channel in St7 and on both banks at St8. All these samples were located on the negative side of the C1 axis close to the groundwater reference sample, suggesting inflows of floodplain groundwater.

392

Finally, downstream of the valley narrowing at St9, samples were located on the positive side of C1 (Fig. 4), close to the surface water reference and to the hyporheic samples made at St1, St4, St5, and St6, thus with low conductivity, low solute concentrations, intermediate nitrate and high oxygen contents (Table S2), suggesting high vertical exchanges between the river and the hyporheic zone.

397

398 4.4. General characteristics of the hyporheic assemblages

A total of 36,980 individuals and 76 taxa were collected during the study, of which 25 species were stygobites. The dominant organisms were the Nematoda (not identified further), the Clitellata (with *Trichodrilus* sp. and *Chaetogaster* sp. as most abundant taxa), the Hydracarina, the Cyclopoida and Harpacticoida (not identified further), the Ostracods (*Marmocandona zschokkei*), the Amphipoda (*Niphargus* cf. *fontanus*, *Niphargus* cf. *kochianus* and *Niphargus casparyi*), the Isopoda (*Proasellus walteri*), the Plecoptera (*Leuctra* gr. *nigra*), the Ephemeroptera (*Caenis* gr. *robusta*) and the Diptera (Chironomidae, Orthocladiinae and Tanytarsini).

406

407

7 4.5. Variability of the hyporheic fauna at the microhabitat and habitat scales

408 Changes in the composition of the hyporheic assemblages according to the microhabitats (replicates) 409 or to the habitat scale (positions in the floodplain, L, R or C) were similar using an nMDS 410 (supplementary material, Fig. S1) or a CA (F1xF2 plan, Fig. 5). The most significant source of 411 heterogeneity concerned habitats: the samples from the centre were located on the negative side of 412 the F1 axis of the CA (at least for 23 of the 27 samples), while the samples from the margins of the 413 braided strip were scattered along the F1 axis (Fig. 5A). The organisms sampled in the central part of 414 the floodplain (with negative coordinates on the F1 axis; supplementary material Fig. S2) were mostly 415 benthic organisms. Most were benthic rheophilous species (e.g. the Diptera Simulidae and 416 Ceratopogonidae, the Trichoptera Polycentropus sp., the Ephemeroptera Ecdyonurus sp. and Baetis 417 sp., the Plecoptera Leuctra cf. nigra and Leuctra major, and the Coleoptera Esolus sp. and Dryops sp.), 418 while others live in gently flowing channels (e.g. the Diptera Stratiomyidae, Orthocladiinae and 419 Tanypodinae, the Clitellata Chaetogaster sp., the Mollusca Potamopyrgus antipodarum and the 420 Ostracoda Candona neglecta). Finally, the unidentified taxa (i.e. Cyclopoida, Harpacticioda, Nematoda) 421 were also abundant in the central part of the braided strip.

422

423 The assemblages sampled close to the margins (i.e. taxa with positive coordinates on the F1 Axis, 424 supplementary material Fig. S2) were characterized by slow flowing benthic species frequent in 425 wetlands (e.g. the Tibificidae, the Ostracoda Ilyocypris sp. and Prionocypris zenkeri, the Trichoptera 426 *Holocentropus* sp.) or in springs (e.g. the flatworm *Dugesia* sp., the Ostracoda *Pseudocandona albicans*) 427 together with several the stygobite taxa. Among stygobites the most abundant taxa were close to the origin of the axis (e.g. the Amphipoda Niphargus cf. fontanus, N. cf. kochianus, N. casparyi, the 428 429 Cladocera Phreatalona phreatica, the Ostracoda Marmocandona zschokkei, and the Isopoda Proasellus walteri), whereas the species with low densities had higher positive coordinates on the F1 axis and 430 431 were scattered along the F2 axis (supplementary material Fig. S2): the taxa living in shallow sediment 432 (e.g. the Mollusca B. cf diaphanum, the Ostracoda Fabaeformiscandona wegelini) on the positive side 433 and with deep groundwater dwellers (e.g. the Amphipods Salentinella juberthiae, and Niphargus

- 434 gallicus, the Ostracoda Schellencandona triquetra or the Coleoptera Siettitia avenionensis) on the
- 435 negative side.



Fig. 5. F1xF2 axes plan of the Factorial Correspondence Analysis (F1 represents 10.1% and F2 represents 6.1% of the total variance) with location of all sampling points divided in three maps according to their location in the river (Left side, central, right side, A). F1xF2 plan divided into 9 maps according to the sampling stations with the replicates from the left side (blue squares), the centre (green triangles) and the right side (black dots, B).

442

Samples collected in St1 to St3 and St7 to St9 were scattered along the F1 and F2 axes (Fig. 5B),
especially for the margins (L or R), three of them being on the negative side of F2 axis (St1-R and St2R, St8-L) and a last one on the positive side of the F2 axis (St3-R and one replicate in St3-L). In contrast,
the samples collected at St4, St5 and St6 were grouped close to the origin of both axes (or slightly
negative on the F1 axis, Fig. 5B), whatever the habitat sampled (L, R, or C).

448

449 **4.6.** Variability of the hyporheic fauna between positions

450 The abundance of the hyporheic fauna was significantly higher in the centre of the braided strip and 451 lower along the two margins (Nested-ANOVA F(18.54) = 3.573, p-value = 0.00014, supplementary material Fig. S3). This difference was observed in all the 9 stations, whatever the alluvial plain width and the 452 abundance was significantly correlated to oxygen concentrations ($r^2 = 0.35$, p-value = 0.0006). The 453 454 taxonomic richness varied significantly with the position (Nested-ANOVA $F_{(18,54)}$ = 2.086, *p*-value = 455 0.019, supplementary material Fig. S3), but with very slight differences (from 19.5 + 5.9 to 17.4 + 8.9) 456 and no clear spatial pattern (supplementary material Fig. S3). Finally, the assemblages displayed a 457 patchy distribution: the centre of the floodplain appeared more homogeneous than the two margins when all taxa were considered (Nested-ANOVA $F_{(18.54)}$ =3.3266, *p*-value = 0.00032) or when only benthic 458 organisms were included (Nested-ANOVA F(18,54)=1.9213, p-value = 0.0335). This difference between 459 460 the centre and the margins occurred in 8 of the 9 stations whatever the alluvial plain width 461 (supplementary material Fig. S3).

463 **4.7. Variability of the hyporheic fauna between stations**

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Fig. 6. Longitudinal distribution of the total abundances (a), taxonomic richness (b), stygobite abundances (c) and similitude Bray-Curtis Index for the benthic fauna noted EPTC (Ephemeroptera, Plecoptera, Trichoptera and Coleoptera, d). Means ± Standard error, differences between stations: n.s. nonsignificant, * significant difference with p-value < 0.05, ** with p-value < 0.01, *** with p-value < 0.001 for Nested ANOVA after log(x+1) transformation for abundances and richness, or ANOVA after for one-way ArcSin(x)transformation for Bray-Curtis indices.

465 The total abundances of hyporheic invertebrates changed significantly between the 9 stations (Nested-466 ANOVA F_(8,54)=4.473, *p-value*=0.00033; Fig. 6a) with high values from St5 to St7 where the alluvial plain 467 width progressively decreased. Similar observations were made for total taxonomic richness (Nested-ANOVA $F_{(8,54)}$ =3.534, *p*-value = 0.0023; Fig. 6b), but with less marked spatial pattern. The spatial 468 variability of the hyporheic fauna between positions (estimated using the Bray-Curtis Index between 469 470 the centre and the two margins) did not vary significantly between stations when all taxa were 471 considered (*p*-value > 0.05), but significantly changes when the benthic fraction of the hyporheic fauna 472 was considered alone (i.e. EPTC, one-way ANOVA $F_{(8,18)}$ =3.296, *p*-value = 0.016; Fig. 6d). In this case, 473 the assemblages were significantly less variable at St4, St5 and St6 (i.e. 3 stations concerned by 474 embankment). In contrast, the downstream valley narrowing (at St7 and St8) did not induce noticeable 475 decrease in variability.

476

477 **4.8. Distribution of the stygofauna at the section scale**

The stygofauna species richness did not significantly vary along the studied section (nested-ANOVA F_(8,54) = 1.078, n.s.,), with a relatively low mean value (i.e. 5.7 ± 1.1 species per sample) and low variations (from 4.4 ± 2.0 at St2 to 7.0 ± 3.6 taxa at St8). In contrast, the total abundance varied significantly at the sector scale with a significant trend between stations (Nested-ANOVA F_(8,54) = 4.1106, *p*-value = 0.0007, Fig. 6c) with high values from St5 to St7 where the alluvial plain width progressively decreased. Significant differences were also observed between positions (NestedANOVA F_(18,54) = 3.8113, *p-value* = 0.00007, qsupplementary material Fig. S4), but with contrasting
spatial trends. The mean abundance of stygofauna was low in the upstream area (from St1 to St4),
with few restricted abundant patches on both margins: in St1-R with a large number of Amphipoda
like *N.* cf *fontanus*, *N.* cf *kochianus*, *N. casparyi* or in St2-L with numerous *P. walteri* and *M. zschokkei*.

489 The abundance of stygofauna significantly increased in the downstream part of the sector with an 490 increase in the abundances of the three stygobite Amphipoda (N. cf fontanus, N. cf kochianus or N. 491 casparyi in all cases Nested-ANOVA test with p-values < 0.05, supplementary material Fig. S4), the 492 Isopoda P. walteri, the Ostracoda M. zschokkei and the Clitellata Trichodrilus sp., which reached their highest values from St5 to St8, where the alluvial plain width progressively decreased. The highest 493 494 abundances occurred on the right margin (at St5) or in the centre (St6 and St7) or on the left margin 495 (St8). Finally, downstream of the natural narrowing (at St9), the abundance of stygofauna was 496 extremely low or even null on the right margin (for 2 of the 3 replicates at St9R).

497

498 **5. Discussion**

499 5.1. Geological characteristics, river-groundwater exchanges and hyporheic water chemistry

500 At the 13 km scale, the use of drill logs and GPR profiles highlighted significant changes in alluvium 501 thickness with the highest value, at the downstream end of the embanked section (close to St6), and 502 the lowest value closer to the natural valley narrowing (St8). This decrease in alluvium thickness was 503 concomitant with the decrease of the alluvial plain width resulting in a reduction of the aquifer volume 504 and a groundwater inflow into the river. The aquifer size variation was confirmed by the 505 hydrogeological modelling of the sector: in the upstream part the embanked section, the river 506 recharged the aquifer, while the groundwater fed the river in the downstream stations close to the 507 alluvial plain narrowing (from St5 to St8). This pattern was partially confirmed by the hyporheic water 508 chemistry, which was very similar to the surface water along the embanked section, and became 509 different at St7 and St8 (especially at St8L) with high electrical conductivity, high Na, K, Mg and nitrate 510 concentrations (and intermediate dissolved oxygen contents). These characteristics indicate a 511 groundwater origin of this hyporheic water (Williams, 1989; Boissier et al., 1996; Fraser and Williams, 1998; Boulton et al., 2010). Altogether, geological reconstruction of alluvium thickness, 512 513 hydrogeological modelling and hyporheic water chemistry support the existence of a large-scale 514 upwelling (Ward et al., 2002; Dole-Olivier, 2011) just upstream of the natural alluvial plain constriction 515 (Malard et al., 1999; Capderrey et al., 2013).

516

517 Rather divergent results were obtained with the three methods in the upstream portion of the sector (especially at St2 and St3). Alluvium thickness reconstructed from drill logs showed slight and regular 518 519 deepening of the substratum suggesting homogeneous water infiltration from the river to the aquifer. 520 This dominant downwelling trend was verified at St1-L by the hydrogeological modelling and hyporheic 521 water chemistry, but groundwater outflow was predicted by hydrogeological modelling on the right 522 bank in 2014 and nearby in 1996. These inputs were not supported by the hyporheic water chemistry 523 (however, see stygofauna distribution). Similarly, the hydrogeological modelling suggested changes in 524 hydrological patterns at St2 and St3 (e.g. groundwater inputs to the river at St3-L were observed in 525 1996 but not in 2014) where hyporheic water chemistry gave a different image: the hyporheic water 526 of the right bank was characterized by high electric conductivity, but without enrichment in solute, 527 which is generally high in deep groundwater (i.e. K, Na and Mg), and a strong decrease in dissolved 528 oxygen and nitrate. These chemical characteristics differed from reference groundwater, but were 529 rather similar to the shallow hyporheic water traveling along gravel bars, characterized by high 530 conductivity and denitrification due to intense oxygen respiration (Holmes et al., 1994; Boissier et al., 531 1996; Claret et al., 1997; Dahm et al., 1998; Lefebvre et al., 2004). The existence of such long flow 532 paths of hyporheic water inside gravel bars at St2 and St3 may potentially hide true groundwater inputs 533 suggested by the hydrogeological modelling.

534

535

5.2. Faunal heterogeneity in constrained and unconstrained sections (H1)

536 The hyporheic assemblages were more abundant and more homogeneous (between replicates) at the 537 centre than at the margins of the braided strip whatever its width. These patterns could be related to 538 the relative homogenization of water characteristics in the central part of the river due to intense 539 exchanges with the surface water (highlighted by the PCA, Fig. 4). These intense vertical water 540 exchanges may support faunal connectivity between benthic and hyporheic layers, resulting in the high 541 abundances and low spatial variability of the hyporheic fauna (Brunke and Gonser, 1997; Olsen and 542 Townsend, 2003). For example, Descloux et al. (2013) observed that abundances and local 543 heterogeneity decreased together with vertical connectivity in three alpine rivers. In the centre of the 544 braided strip, the assemblages were characterized by insects frequent in the benthos (e.g. L. cf nigra, 545 Baetis sp., Esolus sp., Polycentropus sp., Empididae or Ceratopogonidae). These organisms colonize the 546 hyporheic zone when interstices are well connected to the surface water resulting in favourable 547 conditions within the sediment (Dole-Olivier and Marmonier, 1992; Boulton et al., 1998; Storey and Williams, 2004). 548

549

550 In contrast, the samples collected near the margins were sometimes very dissimilar for the hyporheic 551 fauna, together with variable solute concentrations (e.g. at St2-R and St8-L) or dissolved oxygen

552 availability (e.g. at St3-R). This heterogeneity in the hyporheic fauna at the margins may also reflect 553 the heterogeneity of benthic assemblages linked to variability in surface water velocities and habitat 554 characteristics (Beisel et al., 1998, 2000; Brunke et al., 2001; Strayer et al., 2003; Demars et al., 2012; 555 Verdonschot et al., 2016). This heterogeneity in the benthos distribution may directly influence the 556 heterogeneity in the hyporheic fauna, due to the close connections between benthic and hyporheic 557 layers at least at a depth of 50 cm (Bretschko, 1991). The occurrence at a same hyporheic station of 558 rheophilous taxa (e.g. G. fossarum or L. cf nigra) together with slow flowing species (e.g. Limnius sp. or 559 Holocentropus sp.) and phytophilous organisms (e.g. P. zenkeri or H. reptans) on the margins of the 560 station 3) reflect this heterogeneity of benthic habitats and fauna.

561

562 The environmental characteristics in the hyporheic microhabitats may also directly control the 563 distribution of the hyporheic fauna. The most evoked factors of variability were the direction of water exchanges (upwelling vs downwelling) in relation to fluvial forms (e.g. Dole-Olivier and Marmonier, 564 565 1992; Brunke and Gonser, 1999; Mermillod-Blondin et al., 2000), the patchy distribution of fine 566 particles inside the sediments (Descloux et al., 2013; Mathers et al., 2014), or the available resources, 567 such as organic matter or dissolved oxygen (Strayer et al., 1997). For example, in the studied area, the 568 abundance of hyporheic fauna was significantly correlated to oxygen concentration, and replicate 569 samples at the same station and position (e.g. at St7-L and St8-L) could harbour high or very low 570 abundance of stygobionts.

571

572 The first hypothesis (H1) predicted changes in spatial variability of hyporheic assemblages according 573 to floodplain width. The geomorphological complexity of braided rivers controls benthic and terrestrial 574 biodiversity and spatial patterns (Peeters and Tachet, 1989; Vander Vorste et al., 2016b; Datry et al., 575 2014). For the hyporheic fauna, we predicted that transversal heterogeneity (centre vs the two margins 576 of the braided strip) would be high in unconstrained sections because of marked differences in 577 environmental conditions between the positions. Conversely, reduced differences would prevail in 578 narrow sections, due to channel network simplification and habitat diversity reduction. We did not 579 observe any significant change in the variability of hyporheic assemblages when all hyporheic taxa 580 were considered, but a significant decrease in the variability when considering benthic organisms only (EPTC, H1 partly verified). For this benthic part of the hyporheic assemblage, the Bray-Curtis Index 581 582 between the centre and the margin decreased 25 to 50% in the constrained sections.

583

This influence of alluvial plain narrowing on the benthic component was not predicted by Peeters and
 Tachet (1989) who did not see any change in the transversal heterogeneity of benthic fauna and found
 poor variation between unconstrained and constrained sections of the Drôme river. They explain this

587 lack of differences by the biological traits of the most abundant benthic species adapted to the high 588 mobility of the sediments. In the case of the hyporheic zone, the changes in the characteristics of the 589 hyporheic environment may be crucial. For example, Capderrey et al. (2013) reported that the 590 colonization of the hyporheic zone by insects and EPT changed significantly with position in 12 braided 591 rivers of the South-Est basin of the Rhône River (France). In the present case, the homogenization of 592 environmental characteristics in the hyporheic zone was evident in the embanked section (St4 and St5, 593 Fig. 4) where the three positions were very close on the C1xC2 plan of the PCA reflecting similar water 594 characteristics for solute contents and dissolved oxygen availability. On the contrary, such similarity 595 was not observed at St8 submitted to a natural valley narrowing, because of high heterogeneity in the 596 hyporheic water characteristics.

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598

5.3. Floodplain width and stygofauna distribution (H2)

599 Regarding the large-scale river-aquifer exchanges, we predicted that narrowing of the Drôme alluvial 600 plain would induce changes in stygofauna distribution (H2). The studied sector was composed of two 601 main constrictions of the braided strip: one is natural and linked to a geomorphological nickpoint and the other is artificial and due to an early 20th century embankment, with a sharp reduction in channel 602 603 width (just downstream of St3) and a long constrained section (St4 to St5). No significant increase in 604 the abundance or richness of stygofauna assemblages was observed in this section (Fig. 6c). 605 Embankments are known to enhance incision of the river bottom (Surian & Rinaldi, 2003) and generally 606 resulted in an increase in groundwater drainage (Bravard et al., 1997; Sophocleous, 2002; Marmonier 607 et al., 2010). For example, in a Swiss river the embankment of the channel induced an inflow of 608 groundwater on one bank stimulating the occurrence of stygofauna in the hyporheic zone (Brunke and 609 Gonser, 1999). In the same way, in an embanked channel of the Rhône River (Miribel channel), a 610 longitudinal study of the hyporheic fauna demonstrated a significant input of groundwater and an 611 increase in stygobite abundance and richness at the upstream portion of the channel, where incision 612 was maximal (just downstream of the dam, Creuzé des Châtelliers and Reygrobellet, 1990). In the 613 present study, the high mobility of the bed sediments induces a downstream drift of large mineral 614 particles in the embanked section (Lisle et al., 2000; Mao and Surian, 2010) and the downstream weir 615 increases sediment retention, thus reducing the incision process and the subsequent drainage of the 616 aquifer (at least at the upstream end of the embanked sector, Landon et al., 1998). Together with this 617 stability of the sediment level, the regular deepening of the substratum below this section of the river 618 enhanced the recharge of the aquifer by surface water at least before the beginning of the alluvial 619 plain constriction (I.e. downstream of the kp 14).

621 In contrast, the natural constriction of the alluvial plain had a major effect on the stygofauna: a 622 significant increase in stygobite abundance was observed at the corresponding stations (from kp 13 -623 St5 to kp9 - St8), from the left margin to the centre and to the right margin (H2 verified). The 624 geomorphological knickpoint located just downstream of St8 was associated with a reduction of the 625 aquifer volume (see GPR profiles), producing an input of groundwater to the river from St5 and St8 reflected by piezometric level measures and a change in the hyporheic water chemistry at St7 and St8 626 627 (see variations in solute concentrations). Groundwater upwelling zones are known to support rich and 628 abundant stygofauna assemblages in the hyporheic zone at both small scale (i.e. few meters, Dole-629 Olivier & Marmonier, 1992; Brunke and Gonser, 1997; Mermillod-Blondin et al., 2000) and large scale 630 (i.e. kilometres, Creuzé des Châtelliers and Reygrobellet, 1990; Capderrey et al., 2013). In the studied sector, this increase concerned only the abundance of stygobites and more precisely the abundance 631 632 of three of the five dominant species (all amphipods). Contrasting with previous results on the Rhône River, such changes in alluvial plain width did not enhance the richness of the stygobite assemblage 633 634 (Dole-Olivier et al. 1993), likely in relation with the instability characteristic braided strip (Bravard et 635 al., 1997).

636

637 The results also highlighted a mismatch concerning the length of the river concerned by groundwater 638 upwelling and the increase in the abundance of stygofauna. On one hand, the hyporheic water 639 chemistry detected groundwater inflow on a short section of the river (from St7 to St8, and especially 640 in St8-L; Fig. 4). On the other hand, the hydrogeological modelling and the stygofauna abundances 641 indicated a rather large groundwater inflow area, between kp13 and kp9 (from St5 to St8, Fig. 3 and 642 Fig. 6c). This difference in the size of area concerned by groundwater upwelling may be explained by 643 the local characteristics of groundwater drainage. On both sides of the braided strip (in the floodplain), 644 abandoned channels represent major drains collecting and driving groundwater downstream. These 645 channels may stop the direct discharge of groundwater to the main channel, reducing the changes in 646 water chemistry. In the same way, an abundant stygofauna was observed in two isolated spots at the 647 upstream end of the studied section, (St1-R and St2-L, supplementary material Fig. S4). These spots 648 were not linked to changes in the narrowing of the valley. Although, they were both located in a large 649 braided section of the floodplain, they were found to drain groundwater in 2014 (St1-R) or in 1996 650 (St2-L, Fig. 3) suggesting the occurrence of local groundwater inputs with subsequent patches of 651 abundant stygofauna (e.g. Brunke and Gonzer, 1999, Marmonier et al., 2010). In this study, the 652 stygobite assemblages represented a more integrative indicator of groundwater upwelling than hyporheic water chemistry. 653

654

655 6. Conclusions

656 This study highlighted the crucial role of river-aquifer exchanges at the sector-scale controlled by large-657 scale patterns in geology and geomorphology on the composition and the heritage value of benthic 658 and hyporheic biodiversity (e.g., Sophocleous, 2002; Boulton et al., 1998). The most original result 659 brought by this study is the contrasted responses of hyporheic fauna to artificial and natural floodplain 660 constrictions. Contrasting with general findings (Amoros et al., 1997), the artificial constriction of the 661 Drôme River does not induce channel incision nor alter river-aquifer exchanges and only modifies the 662 spatial distribution of benthic fauna in the hyporheic zone. On the contrary, the natural constriction 663 reduces the aquifer thickness and enhances groundwater drainage and stygobite abundance in the 664 hyporheic zone. Distinguishing natural and anthropogenic constrictions of river channel is thus crucial 665 to understand large-scale distribution patterns of biodiversity (Dole-Olivier et al., 2009) and 666 groundwater management plans at the river sector scale (Graillot et al., 2014).

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668

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