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Ecological characterization of natural and impacted meander cut-offs of the River Allier using benthic macroinvertebrates

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Keywords: habitats, physical and chemical monitoring, between-class Correspondence Analysis (bCA), Canonical Correspondence Analysis (CCA), Monte Carlo permutation test, communities, distribution, biodiversity.

Today, the hydrological function and biodiversity of riverine secondary channels are generally recognized and managers tend to protect and restore them. In this study we focused on different parapotamal meander cut-offs. Six sites were examined, two of them being impacted by gravel extraction or deepened for halieutic activity. In order to test whether systematic differences in communities occurred upstream and downstream of the different sites, temperature and dissolved oxygen concentration were continuously monitored, other physical and chemical data were monthly measured and benthic macroinvertebrates were sampled in two seasons. Related to the abiotic data, in each site, water exchanges occurred between the river and / or the groundwater. In the unmodified sites, those few silted up displayed the greatest biodiversity with numerous EPT (Ephemeroptera, Plecoptera and Trichoptera) while in those largely silted, the habitat homogeneity induced a low biodiversity. In the two impacted sites, the upstream modification enhanced natural silting and few EPT were present while in the site largely open to the river, water quality, diversity and EPT richness remained high.

Caractérisation écologique de bras morts naturels et impactés de la rivière Allier en utilisant les macroinvertébrés benthiques.

Mots-clés : habitats, suivi des paramètres physiques et chimiques, Analyse des Correspondances intergroupes, Analyse Canonique des Correspondances, test de permutation de Monte Carlo, communautés, distribution, biodiversité.

Aujourd'hui, les services écosystémiques (rôles hydrologiques, réservoir de biodiversité, etc.) rendus par les bras morts sont généralement reconnus et les actions de gestion tendent à se multiplier afin de les protéger et de les restaurer. Dans cette étude, nous nous sommes concentrés sur des bras morts parapotamiques qui diffèrent par leur degré d'envasement ou par des interventions humaines. Six sites ont été examinés, deux d'entre eux ayant été affectés par l'extraction de gravier ou par un curage ayant pour but de maintenir l'activité halieutique. Afin de tester si des différences systématiques apparaissent dans les communautés entre l'amont et l'aval des différents sites : 1) la température et l'oxygène dissous ont été enregistrés en continu, 2) d'autres variables physico-chimiques ont été mesurées tous les mois et 3) les macroinvertébrés benthiques ont été prélevés durant deux saisons. Dans chaque site, des échanges ont eu lieu entre l'eau de la rivière et / ou les eaux souterraines au regard des variables physico-chimiques. Dans les sites non modifiés, les moins envasés présentent la plus grande biodiversité avec de nombreux EPT (Éphéméroptères, Plécoptères et Trichoptères), tandis que dans ceux fortement envasés, l'homogénéité des habitats induit une faible biodiversité. Dans les deux sites impactés, la modification amont augmente l'envasement naturel, et peu d'EPT ont été collectés, alors que dans le site largement connecté avec la rivière, la qualité de l'eau, la diversité et le nombre d'EPT restent élevés.

1. Introduction

In earlier decades, meander cut-offs were considered unhealthy areas, and most of them were drained and filled. Today their hydrological functions and their importance for biodiversity as other ecosystem services are recognised, and there is consensus considering their protection and restoration. Recently, a number of studies have focused on the diversity of their form, size and dynamics, highlighting the function of these meander cut-offs in relation to hydrological exchanges (AMOROS & BORNETTE 2002; LE COZ 2007). Indeed, they can provide attenuation of flood peaks, regulation of water-level, recharge of groundwater and retention of sediment and nutrients (ADAMUS & STOCKWELL 1983; JOHNSTON et al. 1997), while riverine habitats sustain wildlife diversity (SHEAFFER & NICKUM 1986a; CASTELLA et al. 1991; BORNETTE et al. 1996; DÉCAMPS & NAIMAN 1989). Many studies have underlined the importance of environmental factors for aquatic plant diversity (BORNETTE et al. 1998, 2001), planktonic organisms (ROSSETI et al. 2008), macroinvertebrate distribution (CASTELLA 1987; FOECKLER et al. 1994; WEILHOEFFER & PAN 2006; CASTELLA et al. 2007; PAILLEX et al. 2007), refuges for fish communities during flood events, or dry periods, and favourable areas for nurseries (WELCOMME 1985; SHEAFFER & NICKUM 1986 b; SCOTT & NIELSEN 1989; BENGEN et al. 1992). Focusing on parapotamal (i.e. connected to the main channel only at their downstream ends) and plesiopotamal (i.e. disconnected) meander cut-offs, the importance of their connexion with the main river has been related to the recruitment of young fish (NUNN et al. 2007). Such studies reveal an interest in ecological diagnosis leading to the restoration of such areas (CASTELLA et al. 2007; PAILLEX et al. 2007).

We extended approaches introduced above, focusing on a series of parapotamal meander cut-offs of the Allier River in the French "Massif Central" mountains. So, to evaluate the functionalities of such secondary channels, we analysed up and downstream changes of six meander cut-offs situated in two longitudinal reaches, related to abiotic variables and macroinvertebrate biodiversity. Four sites, ranging from recently to formerly cut-off from the main stream, were unmodified. The two others had been impacted by gravel extraction or deepened for halieutic activity. To determine the criteria that influence the organisms, the water quality and biodiversity differences were analysed by comparing reaches, sites, up and downstream zones, in relation to the main physical and chemical characteristics. To evaluate the changes in the colonisation (diversity / density) of benthic invertebrates, we focused on the position of these meander cut-offs along the main channel, related to different degrees of disturbance: (a) low degree of siltation, (b) high degree of siltation (c) disturbance by dredging (d) groundwater input and (e) agricultural pressure.

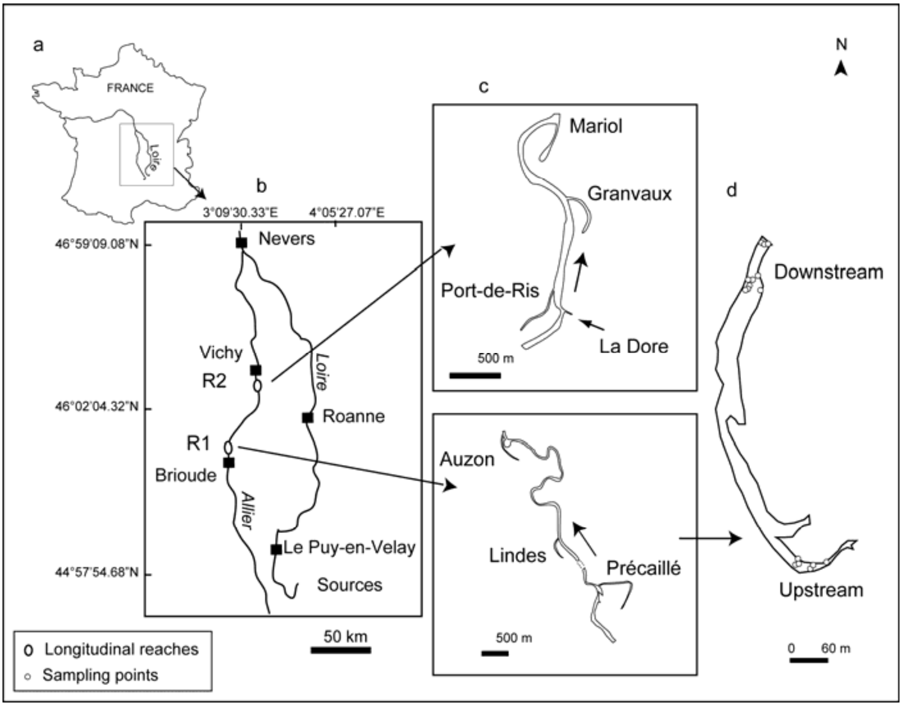

Figure 1. Map of France (a) with insert of the Massif Central, (b) showing the Brioude reach (R1) and Vichy reach (R2) in the Allier River, with three metamorphic and three sedimentary basin cut-off meander sites, respectively (c). An example of the sampling design for each cut-off meander is presented (d).

Figure 1. Carte de la France (a) des linéaires étudiés, (b) avec le tronçon de Brioude (R1) et celui de Vichy (R2) sur la rivière Allier, et des trois bras morts situés dans le bassin métamorphique et des trois autres dans le bassin sédimentaire (c). Exemple de stratégie d'échantillonnage utilisée dans chaque bras mort (d).

2. Methods

2.1. Description of sites

Two longitudinal reaches of the River Allier, a tributary of the River Loire situated in the Massif Central (France), were studied (Figure 1a and b). In this area, the channel width varies between 40 m and 50 m and the unit stream power at bankfull discharge is 120 $W.m^{-2}$. The upstream reach (R1) is located near Brioude in a metamorphic and basaltic catchment at about 400 m above sea level and is 153-161 km from the source. The downstream reach (R2) is located near Vichy in a sedimentary catchment at about 270 m above sea level and is 270-274 km from the source. Upstream (reach R1), agricultural activities (cattle farming and cereal crops) form the main anthropogenic pressure. The downstream reach (R2) is much less impacted. For the two reaches, the physical and chemical variables measured by the Loire-Bretagne Water Agency (WFD standard), showed that the Allier River was of good water quality. However, the macroinvertebrate quality index, previously calculated, remained good upstream, but was medium downstream (BEAUGER 2008b; Loire-Bretagne Water Agency data).

Basin	Site	Right bank	Left bank	Maximum depth (m)	Connection width (m)	Cut-off period*
Metamorphic	Précaillé upstream	forest	crops	0.5	7	ca. 1950
	Précaillé downstream	forest	crops	0.5		
	Lindes upstream	forest	crops	0.9	12	after 1980
	Lindes downstream	forest	pastures	2		
	Auzon upstream	forest	crops	1.3	25	after 1980
	Auzon downstream	forest	crops	1.2		
Sedimentary	Mariol upstream	forest	forest	4	4	after 1980
	Mariol downstream	herbaceous	forest	0.8		
	Granvaux upstream	forest	forest	0.5	6	ca. 1950
	Granvaux downstream	forest	pastures	0.5		
	Port-de-Ris upstream	forest	forest	0.8	7	after 1980
	Port-de-Ris downstream	forest	pastures	1.1		

Table 1. Characteristics of the upstream and downstream zones of the six cut-off meander sites of the metamorphic and sedimentary basins.

Tableau 1. Caractéristiques des zones amont et aval des six bras morts étudiés et situés dans des bassins, l'un métamorphique et l'autre sédimentaire.

Cut-offs from upstream and downstream reaches were selected for the following characteristics (Table 1):

-high degree of silting (Précaillé and Granvaux), with > 1m of mud in some areas;

-low silt accumulation with cobbles on the surface in Auzon and Port-de-Ris;

-artificially deepened (Lindes and Mariol). All cut-off meanders were parapotamal, i.e., permanently connected at downstream end and disconnected upstream (AMOROS et al. 1982). The sites of Précaillé and Granvaux were characterized by mud and organic matter (OM). At the sites of Auzon and Port-de-Ris, habitats were highly diverse, including sand, coarse mineral substrates, mud and macrophytes. Upstream in Auzon (maximum depth ≈ 1.20 m), macrophyte cover was extensive. Between the upstream and downstream ends, the area corresponded to a geomorphologic riffle and the downstream end remained well connected to the main channel, even though an alluvial plug was beginning to form. The Lindes site was deepened in its downstream zone with a maximum depth of 2 m, whereas Mariol's upstream zone suffered from gravel extraction creating a deeper hole of 4 m. The main anthropogenic pressure in the first longitudinal reach came from agricultural activities (cereal production and cattle farming), whereas the downstream reach was less impacted.

2.2. Physical and chemical measurements

They were made every month during a hydrological cycle (May 2009 - May 2010). Dissolved oxygen (%), pH (pH units) and conductivity ($\mu S.cm^{-1}$) were measured in situ 30 cm beneath the water surface with a WTW Multiline P4 (Figure 1d). In the upstream reach the water temperature (°C) was monitored since 2007 and in the other from 2008 to the summer of 2010. All data were recorded at the upper and lower end of each site and in the main channel (several meters before the confluence). The degree of siltation was obtained by measuring the thickness with a handled graduated perch (except in the deeper zone of Mariol). In the laboratory, water samples were filtered using Whatman GF/F filters before ionic chromatography analysis (Dionex ICS 1500) of the concentrations ($mg.L^{-1}$) of calcium, magnesium (indirect hardness), ammonium, nitrite, nitrate and phosphates were retained. In addition, to observe dial ranges, dissolved oxygen data-loggers were successively placed: one upstream Lindes and one downstream Lindes from 15 to 22 September and for Auzon (up and downstream) from 22 September to 1st October.

In the absence of water level monitoring continuously in the cut-off channels, as in PAILLEX et al. (2007), we used surrogate variables to describe the lateral connectivity gradient (in the studied area, the simple distance between a site and the river does not reflect connectivity due to local embankments). To integrate the level of connectivity of the sites with the main river channel, we retained four variables, of which three were expected to decrease with increasing hydrological connectivity: water conductivity (CARREL 1986; CELLOT et al. 1994), organic content of the sediment upper layer (ROSTAN et al. 1987) and average cover by aquatic vegetation (CHAMBERS et al. 1991; AMOROS et al. 2005). The fourth was expected to increase: NH_3-N concentration (CELLOT et al. 1994; AMOROS & BORNETTE 2002). Moreover we estimated the substrate composition (%).

2.3. Macroinvertebrate sampling

To obtain summer and autumn situations, organisms were sampled (from R1 to R2) from the end of June to the start of July 2009 and from the end of September to the start of October 2009. A transect procedure was used to sample all habitats, except in the upstream zone of Mariol, where samples were all taken around the deep zone (maximum depth sampled ≈ 1.30 m, as in the other sites). Three transects were done in the up- and downstream zones of each site, in which three samples, located with a DGPS (Differential Global Positional System), were taken (Figure 1d). At each sampling point, depth was measured and the substrates {coarse mineral substrates (CMS), sand, macrophytes, algae, mud, organic matter, silt and litter} were characterised. Macroinvertebrates were collected with a Surber net (mesh size: 500 µm) in shallow areas, or with a hand-net when the depth exceeded 0.70 m (sampling surfaces 0.05 m²), giving 107 field samples in the summer and 94 in the autumn. Living invertebrates were sorted in situ and preserved in 10 % formalin.

In the laboratory, in accordance with the recommendations of CASTELLA (1987), all the systematic groups were examined. Insecta such as Odonata, Heteroptera, Megaloptera and Coleoptera were identified to genus, and Diptera to tribe or family (GUIGNOT 1947; PERRIER 1961; DETHIER 1985, 1986; ELLIOTT et al. 1988; TACHET et al. 2000; HEIDEMANN & SEIDENBUSCH 2002; ELLIOTT 2009). According to TACHET et al. (2000), Turbellaria, Hirudinea, Mollusca and Crustacea were identified to genus (and species when there was only one species) or to family, and Oligochaeta to family. As usually in the literature (ELLIOTT 1988; STUDEMANN et al. 1992;

WARINGER & GRAF 1997; TACHET et al. 2000), particular attention was paid to the most pollution-sensitive taxa: Ephemeroptera, Plecoptera and Trichoptera (EPT) which were identified to their species {or to genus when species determination was not possible (first instars, damaged individuals) but, as the other insects, they were few numerous whatever the season}. The systematic richness of each sample was calculated as the number of invertebrate taxa in the genus, tribe or family levels. The percentage of EPT per site and per season and the total density in each sample were also calculated.

2.4. Statistical analysis

To define the best explanation of water quality differences, a between-class Principal Correspondence analysis (bPCA) was carried out on the physical and chemical characteristics of the meander cut-offs (DOLÉDEC & CHESSEL 1989; CHESSEL & DOLÉDEC 1993). Comparisons were successively made between seasons (two categories: Summer and Autumn), reaches (two categories: R1 = upstream near Brioude and R2 = downstream near Vichy) and sites (six categories corresponding to the six sites studied), (cf. Table I). Finally, a last bPCA was performed on the six sites divided into up and downstream zones (12 categories). The bPCA is an ordination technique in which the variables of interest (in our case, the table containing physical and chemical data per sample) are linked to a categorical variable grouping the observations into classes (*i.e.* the six cut-off meanders or the 12 zones). Between-class ordinations are a special case of constrained ordination methods in which the constraining variable is categorical, not continuous. Therefore, bPCA ordinates sites under the constraint that the ordination maximally separates sites in the various classes of the constraining variable (CHESSEL et al. 2004; BATY et al. 2006). The significance of the between-season, between-reach, between-site or between-zone separation was tested in a Monte Carlo procedure against simulated values of the between-class inertia obtained after 1,000 random permutations (significance level $p < 0.05$) of the rows of the water quality table (ROMESBURG 1985).

The total estimated richness of each meander cut-off at each sampling period, was calculated with the Chao2 estimator (CHAO 1987), using EstimateS 8.2 software (COLWELL 2009). We selected this non-parametric technique that requires presence-absence data, to obtain robust estimates, even if a large portion of species are missing from the sample (COLWELL & CODDINGTON 1994). It is also robust to large sample sizes and patchiness (CHAZDON et al. 1998). For the macroinvertebrate distribution differences, a between-class Correspondence Analysis (bCA) (between-seasons, between-reaches, between-sites, between zones and between-grouped sites, according to their particularities, cf. Table I) was carried out on taxa with relative abundance ≥1% to avoid any undue effect of rare species (DOLÉDEC & CHESSEL 1989; CHESSEL & DOLÉDEC 1993; ROSSY & BLANCHART 2005; PAILLEX et al. 2007). Their densities were log-transformed, prior to analyses, to normalize and homogenize the variance. The bCA is also an ordination technique in which the variables of interest (in our case, the table containing the abundance of each taxon per sample) are linked to a categorical variable (i.e. the cut-off meanders or the zones). The significance of the comparisons was tested using the same Monte Carlo random re-sampling tests.

Moreover, a Canonical Correspondence Analysis (CCA), followed by a Monte Carlo random re-sampling test, was carried out to link environmental variables measured in the field {conductivity, dissolved oxygen concentration (%), temperature, dominant substrate and depth may affect the taxa distribution}, with the previous dominant taxa. Results of the CCA were plotted on the first two canonical axes. ADE4 in R 2.10.1 (R development Core Ream 2009) provided the software for all the calculations.

3. Results

3.1. Connectivity gradient and physical and chemical characteristics

Previously, sites were chosen according to the degree of siltation, related to their age, and measures of the mud thickness illustrate the main difference between sites with low and high siltation. The Auzon-Port-de-Ris sites, little silted up, contrasted with the high degree of silting up of Précaillé and Granvaux. Lindes was close to Auzon-Port-de-Ris, while Mariol was essentially silted upstream (Table 2). The level of connectivity with the main river channel that occurred downstream was more important for Lindes, Auzon and Port-de-Ris, than for Précaillé and Mariol. As shown with the conductivity value, Mariol had the lowest connectivity (Table 2).

	Conductivity µS/cm in summer	NH_3-N (mg.L^{-1}) in summer	Average cover by aquatic vegetation %	Substrate composition (%)	
				Benthic particulate organic matter	Pebble & gravel
Précaillé UP	771	1.6	30	40	50
Précaillé DO	647	5.9	30	95	3
Lindes UP	849	1.8	40	30	60
Lindes DO	555	1.9	30	40	50
Allier Lindes	99	2.0	/	/	/
Auzon UP	332	1.5	90	90	10
Auzon DO	323	1.7	40	40	50
Allier Auzon	100	1.9	/	/	/
PdR UP	330	1.0	40	20	70
PdR DO	259	1.1	10	30	70
Allier PdR	289	1.6	/	/	/
Granvaux UP	232	1.0	10	40	10
Granvaux DO	216	0.9	50	80	8
Mariol UP	238	1.4	90	90	3
Mariol DO	258	1.5	20	40	10
Allier Mariol	275	1.3	/	/	/

Table 2. Main characteristics of the six meander cut-offs studied on the River Allier related to the connectivity gradient. PdR = Port-de-Ris; UP= upstream; DO= downstream.

Tableau 2. Principales caractéristiques des six bras morts étudiés sur la rivière Allier en relation avec leur gradient de connectivité. PdR = Port-de-Ris ; UP= amont ; DO= aval.

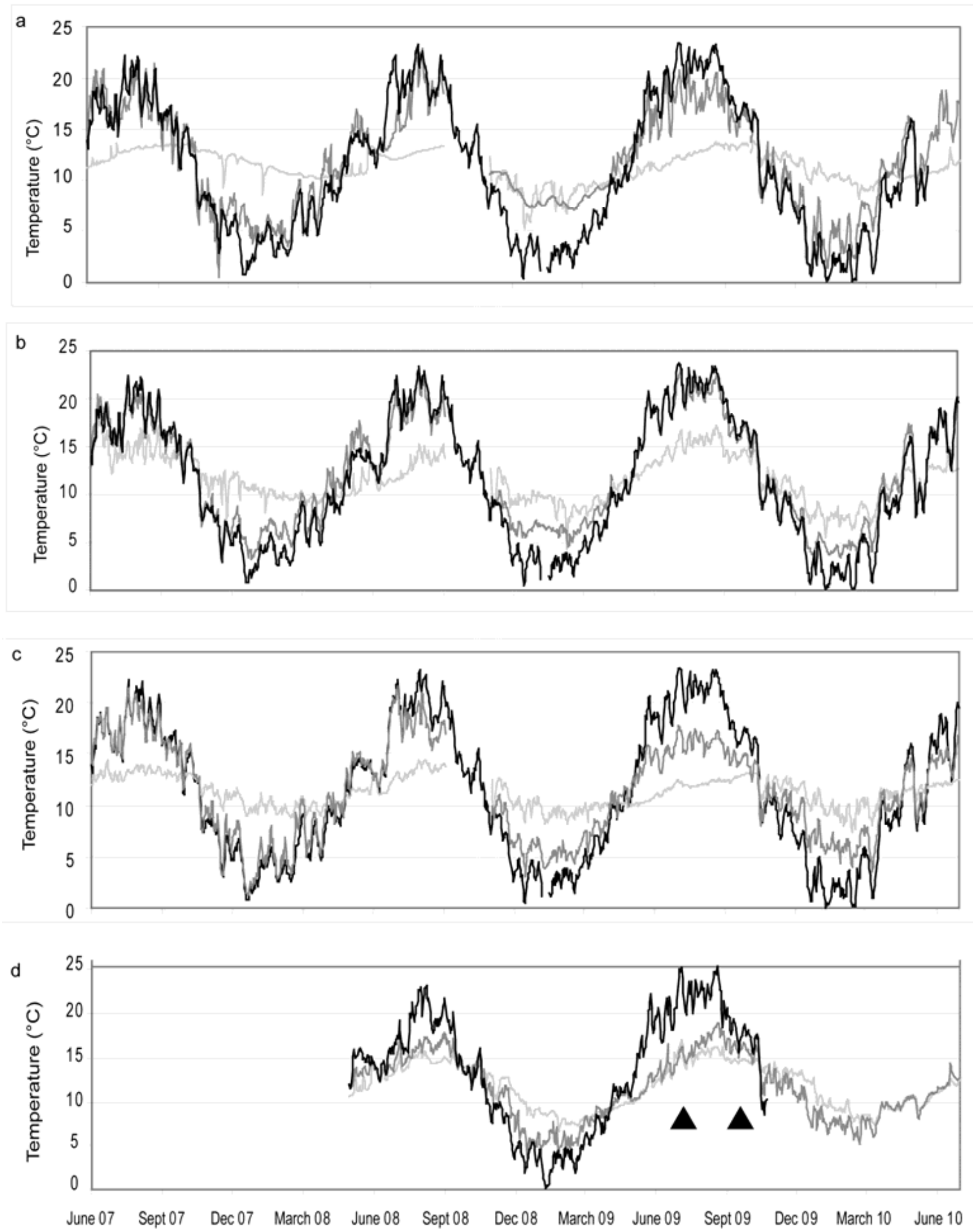

Figure 2. Variations in water temperature at upstream (pale grey) and downstream sites (dark grey) recorded at (a) Précaillé, (b) Lindes, (c) Auzon and (d) Mariol, and the Allier River (black) from June 2007 to June 2010. ▲: sampling periods.

Figure 2. Variations de la température de l'eau en amont (en gris clair) et en aval (en gris foncé) des sites, enregistrées à (a) Précaillé, (b) Lindes, (c) Auzon et (d) Mariol, et dans la rivière Allier (en noir) de juin 2007 à juin 2010. ▲ : périodes d'échantillonnage.

Monitoring data from 2007 to 2010 showed that summer temperature were lower in the upstream than the downstream zone and the opposite was true in winter (Fig. 2). Moreover, the downstream zones had temperature changes mimicking those of the Allier River, except during flood periods (as in spring 2009, underlined the superimposing of the curves) with the exception of Mariol. In this last site, up- and downstream temperatures were similar and varied independently of the main channel.

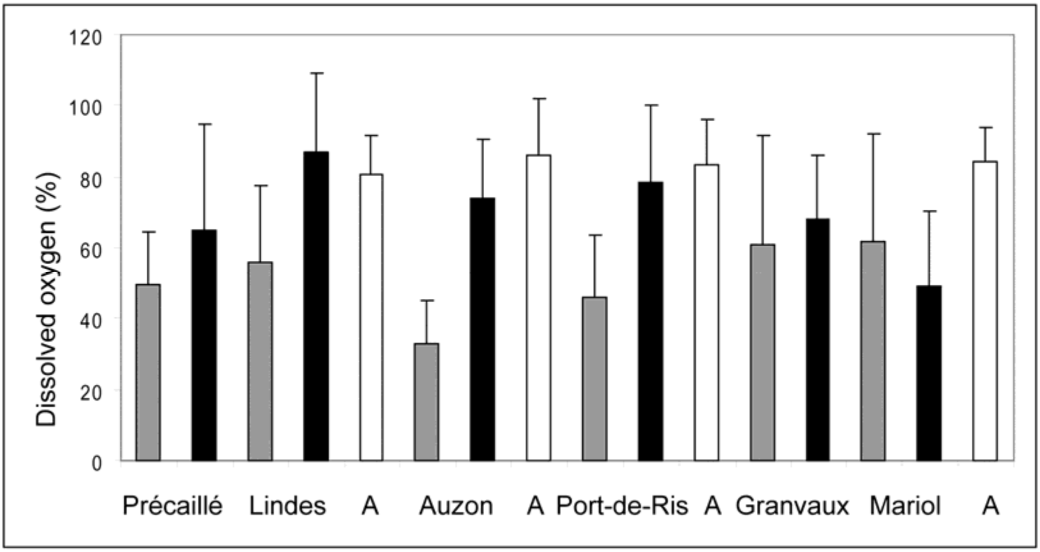

Figure 3. Dissolved oxygen measured (mg.L^{-1}) in the six meander cut-offs and in the Allier River (A). Grey: upstream; black: downstream.

Figure 3. Oxygène dissous mesuré (mg.L^{-1}) dans les six bras morts et dans la rivière Allier (A). Gris : amont ; noir : aval.

The oxygen saturation in the Allier River varied (Fig. 3). Moreover, both monthly dissolved oxygen measurements and monitoring in Lindes and Auzon indicated important differences between the up and downstream zones, with higher concentrations downstream. Using the dissolved oxygen data-loggers that were placed up- and downstream of Lindes and Auzon, the dissolved oxygen concentration in upstream zones registered 0 mg.L^{-1} at times between the end of the night and mid-morning, whereas at the end of the day (3–4 hours before sunset), concentrations varied between 3 and 6 mg.L^{-1}. At night, downstream dissolved oxygen concentrations were always > 4 mg.L^{-1}, but were > 10 mg.L^{-1} during the day.

The bPCA analysis performed with physical and chemical variables (except nitrite and phosphate concentrations found below the detection limits), revealed that the highest physical and chemical differences observed between the 12 zones had a total variability of 59 % (Table 3). The water samples taken in the Allier River were all situated in the positive right part of the factorial plane, illustrating good oxygenation and water quality. In the river, lower conductivity (around 100 µS.cm^{-1}) was measured in the upstream reach and increased downstream (270 <

µS.cm^{-1} < 300), a large increase in conductivity related to the Dore tributary. The differences between zones were linked to their proximity to the main channel, except again in Mariol (Figure 4). In the left part of the factorial plane, the highest conductivity (750 to 926 µS.cm^{-1} upstream), calcium, magnesium (90 to 130 mg.L^{-1} upstream) and nitrate (40 to 130 mg.L^{-1} upstream) concentrations occurred in the up- and downstream zones of Précaillé and the upstream zone of Lindes, the highest ammonium concentration (1.2 < mg.L^{-1} < 7.1) being observed in Précaillé. The lowest conductivity (139 to 555 µS.cm^{-1}) and calcium, magnesium (10 to 97 mg.L^{-1}) and nitrate concentrations (4 to 19 mg.L^{-1}), were observed in the downstream zone of Lindes and were closer to those of the Allier River. In the right part of the factorial plane, the lowest conductivity (155 and 350 µS.cm^{-1}) and calcium concentration (16 to 55 mg.L^{-1}) corresponded to the downstream reach sites, with a chemical composition close to that of the Allier. In Granvaux, the concentrations in nitrates were higher downstream (5.1 ± 3.3 mg.L^{-1}) than upstream (3.9 ± 3.7 mg.L^{-1}).

Between-class	**Variability (%)**	**Significance $p < 0.05$**
Seasons	18	< 0.0001
Reaches	10	< 0.0001
Sites	48	< 0.0001
Zones	59	< 0.0001

Table 3. Results of between-class Principal Correspondence Analysis done on physico-chemical variables and the six meander cut-offs.

Tableau 3. Résultats des analyses inter-groupes réalisées sur les variables physico-chimiques et les six bras morts.

	Sites	**Upstream zone**	**Downstream zone**
Low degree of silting up	A Chao2 mean (95% CI)	79 (59-140)	89 (72-136)
	PdR Chao2 mean (95% CI)	72 (60-110)	63 (55-88)
High degree of silting up	P Chao2 mean (95% CI)	64 (50-112)	33 (32-42)
	G Chao2 mean (95% CI)	69 (47-138)	57 (49-86)
Human impact	L Chao2 mean (95% CI)	81 (58-150)	70 (59-98)
	M Chao2 mean (95% CI)	74 (63-106)	56 (52-71)

Table 4. Total estimated richness on the six meander cut-offs at both seasons (CI = Confidence Interval).

Tableau 4. Richesse estimée pour les six bras morts aux deux saisons (CI = intervalle de confiance).

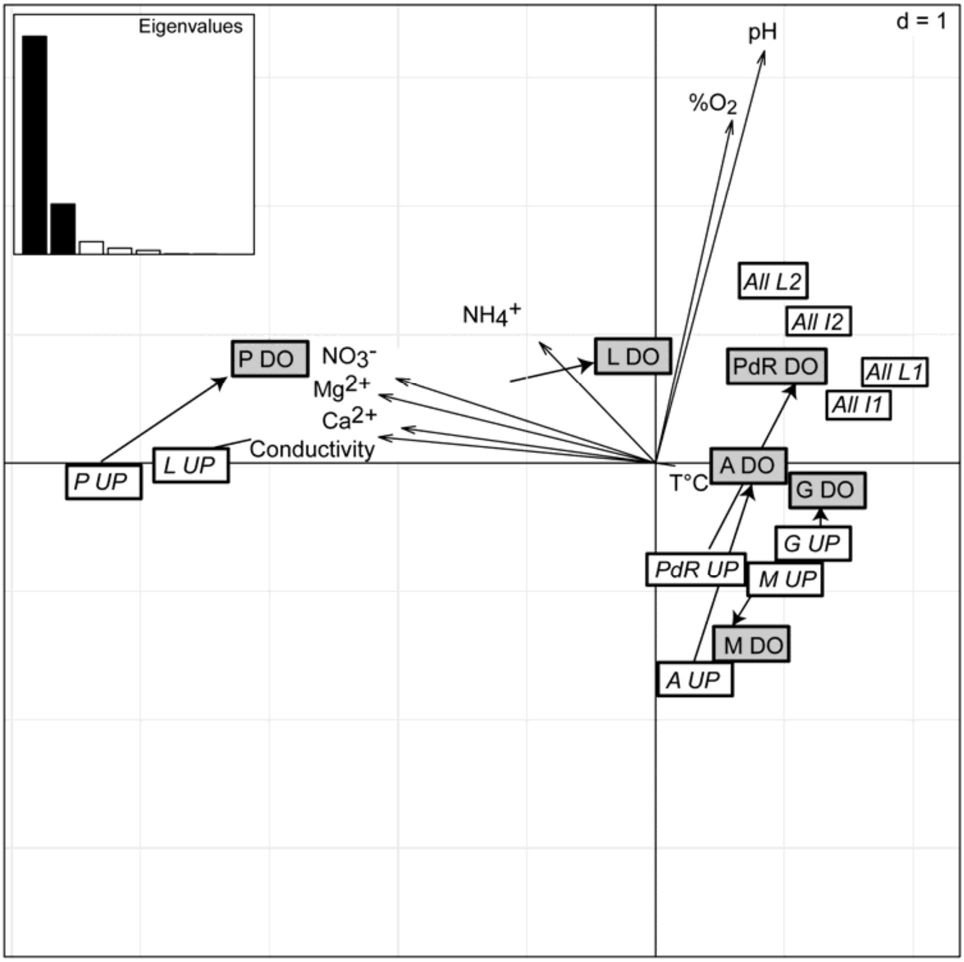

Figure 4. Ordination plots (F1 X F2) of a between-zone Principal Correspondence Analysis of the samples based on the physico-chemical variables. The rectangles identify the center of gravity of each zone. P = Précaillé; L = Lindes; A = Auzon; PdR = Port-de-Ris; G = Granvaux; M = Mariol; UP = upstream zone; DO = Downstream zone; All = River Allier.

Figure 4. Premier plan factoriel (F1 X F2) de l'Analyse en Composantes Principales réalisée sur les variables physico-chimiques dans l'analyse inter-zones. Les rectangles représentent les centres d'inertie des prélèvements réalisés dans chaque zone. P = Précaillé ; L = Lindes ; A = Auzon ; PdR = Port-de-Ris ; G = Granvaux ; M = Mariol ; UP = zone amont ; DO = zone aval ; All = rivière Allier.

3.2. Characteristics of the macroinvertebrate communities

The highest estimated total richness of the benthic macroinvertebrates was observed on the sites with the lowest silt accumulation (Table 4). On the impacted sites the situation was inversed, as in Mariol (deepened upstream), the estimated richness was lower downstream.

	Upstream reach			Downstream reach		
	Sites	Season	Dominant taxa	Sites	Season	Dominant taxa
Little silting up	Auzon	S	*Asellus aquaticus*	Port-de-Ris	S	Chironomini Tanypodinae
		A	*Asellus aquaticus* *Cloeon dipterum* Oligochètes		A	Oligochètes *Asellus aquaticus*
High degree of silting up	Précaillé	S	Oligochètes *Asellus aquaticus*	Granvaux	S	Oligochètes Chironomini
		A	*Asellus aquaticus* Oligochètes Ceratopogoninae		A	Chironomini Tanypodinae
Human impact	Lindes	S	Oligochètes *Asellus aquaticus* *Cloeon dipterum*	Mariol	S	Oligochètes *Asellus aquaticus*
		A	Oligochètes *Asellus aquaticus* *Cloeon dipterum*		A	Oligochètes *Bithynia*

Table 5. Dominant taxa (>10%) observed on the six meander cut-offs for the two seasons (S = summer, A = autumn).

Tableau 5. Taxons dominants (> 10%) observés pour les six bras morts et pour chaque saison (S = été, A = automne).

Between-class	**Variability (%)**	**Significance $p < 0.05$**
Seasons	-	NS
Reaches	8	< 0.0001
Sites	27	< 0.0001
Zones	43	< 0.0001

Table 6. Results of between-class correspondence analysis done the macroinvertebrates observed on the six meander cut-offs.

Tableau 6. Résultats des analyses inter-groupes réalisées sur les macroinvertébrés observés sur les six bras morts.

The highest densities of macroinvertebrates were observed in the downstream zones of Précaillé, Granvaux and Mariol. They were largely populated, with on average 15,000 ind.m^{-2}, (Figure 5a). In contrast, the sites with lower densities (Auzon, Port-de-Ris and Lindes), harboured the largest numbers of EPT which are practically absent in Granvaux (0.62 %) and Mariol (0.09 %) (Figure 5b). Generally, Oligochaeta were among the dominant taxa, with more than 50 % of the community in Mariol. In the three sites of R1, the dominant taxa (relative abundance > 10 %) were mainly *Asellus aquaticus* (Table 5), Diptera Chironomidae and Ceratopogoninae, being particularly abundant in this areas largely silted. Related to the bCA, no significant difference appeared between the two seasons, allowing all the data to be mixed in the following analysis (Table 6). The highest variability (43 %) was obtained for the between-zones analysis, indicating, such as the physical and chemical data, large differences between the 12 zones (Figure 6).

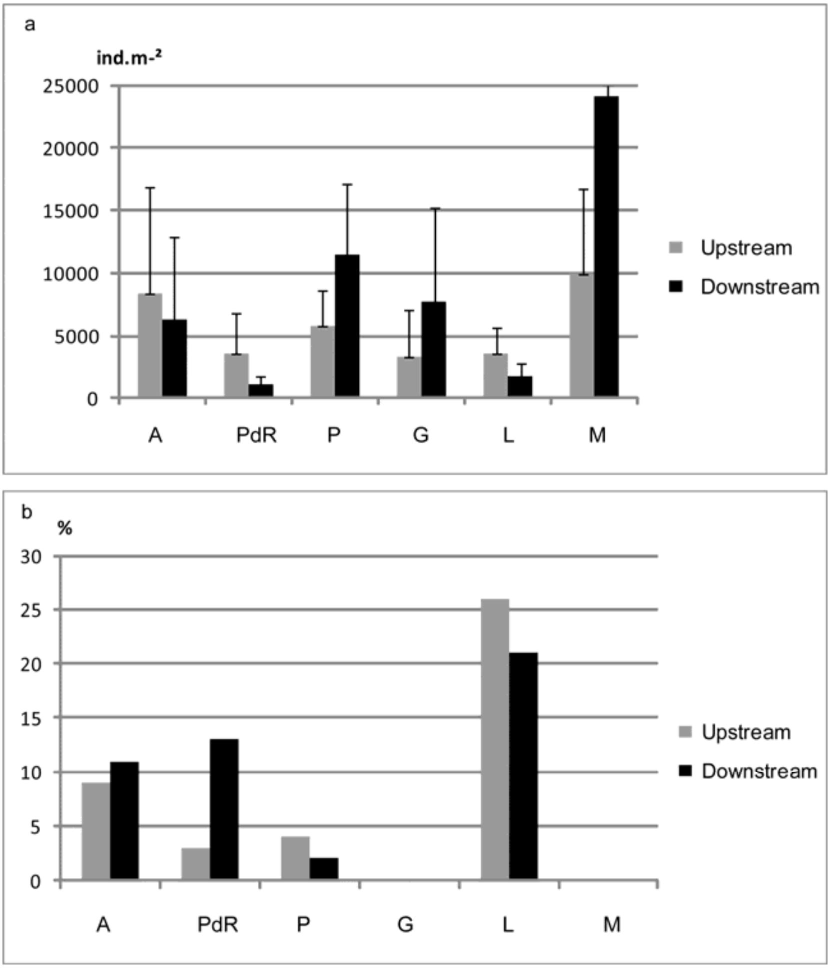

Figure 5. a – Community densities observed on each meander cut-off at the two seasons. b - Percentage of EPT on each meander cut-off at the two seasons. P = Précaillé; L = Lindes; A = Auzon; PdR = Port-de-Ris; G = Granvaux; M = Mariol.

Figure 5. a – Densités des communautés observées pour chacun des bras morts aux deux saisons. b – Pourcentage d'EPT observés pour chacun des bras morts aux deux saisons. P = Précaillé ; L = Lindes ; A = Auzon ; PdR = Port-de-Ris ; G = Granvaux ; M = Mariol.

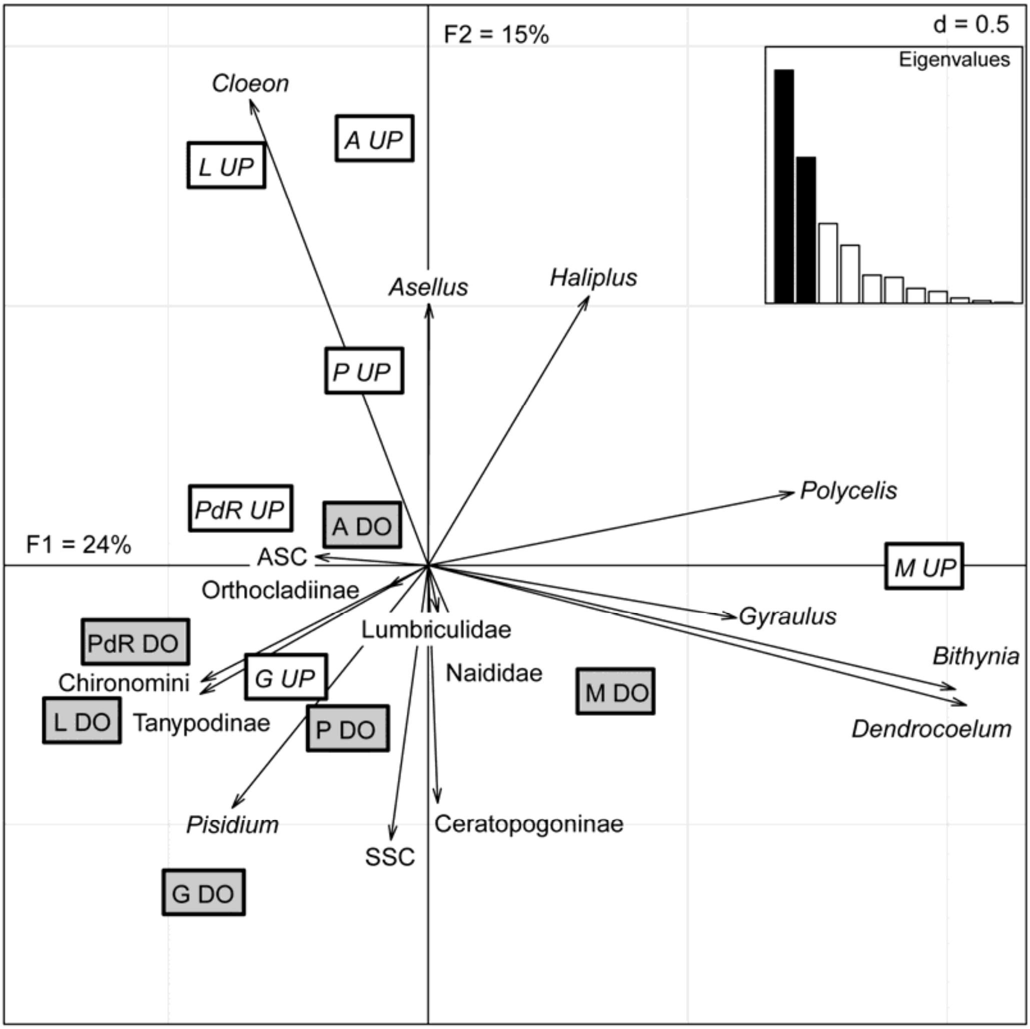

Figure 6. Ordination plots of the first factorial plane (F1 X F2) of a between-zone Correspondence Analysis based on the taxa with a relative abundance ≥ 1% of the community, grouped according to the zones. The rectangles identify the center of gravity of each zone. P = Précaillé; L = Lindes; A = Auzon; PdR = Port-de-Ris; G = Granvaux; M = Mariol; ASC = Tubificidae with hair setae; SSC = Tubificidae without hair setae.

Figure 6. Premier plan factoriel (F1 X F2) de l'Analyse factorielle des Correspondances réalisée sur les taxons dont l'abondance relative est ≥ 1% des communautés dans l'analyse inter-zones. Les rectangles représentent les centres d'inertie des prélèvements réalisés dans chaque zone. P = Précaillé ; L = Lindes ; A = Auzon ; PdR = Port-de-Ris ; G = Granvaux ; M = Mariol ; ASC = Tubificidae with hair setae ; SSC = Tubificidae without hair setae.

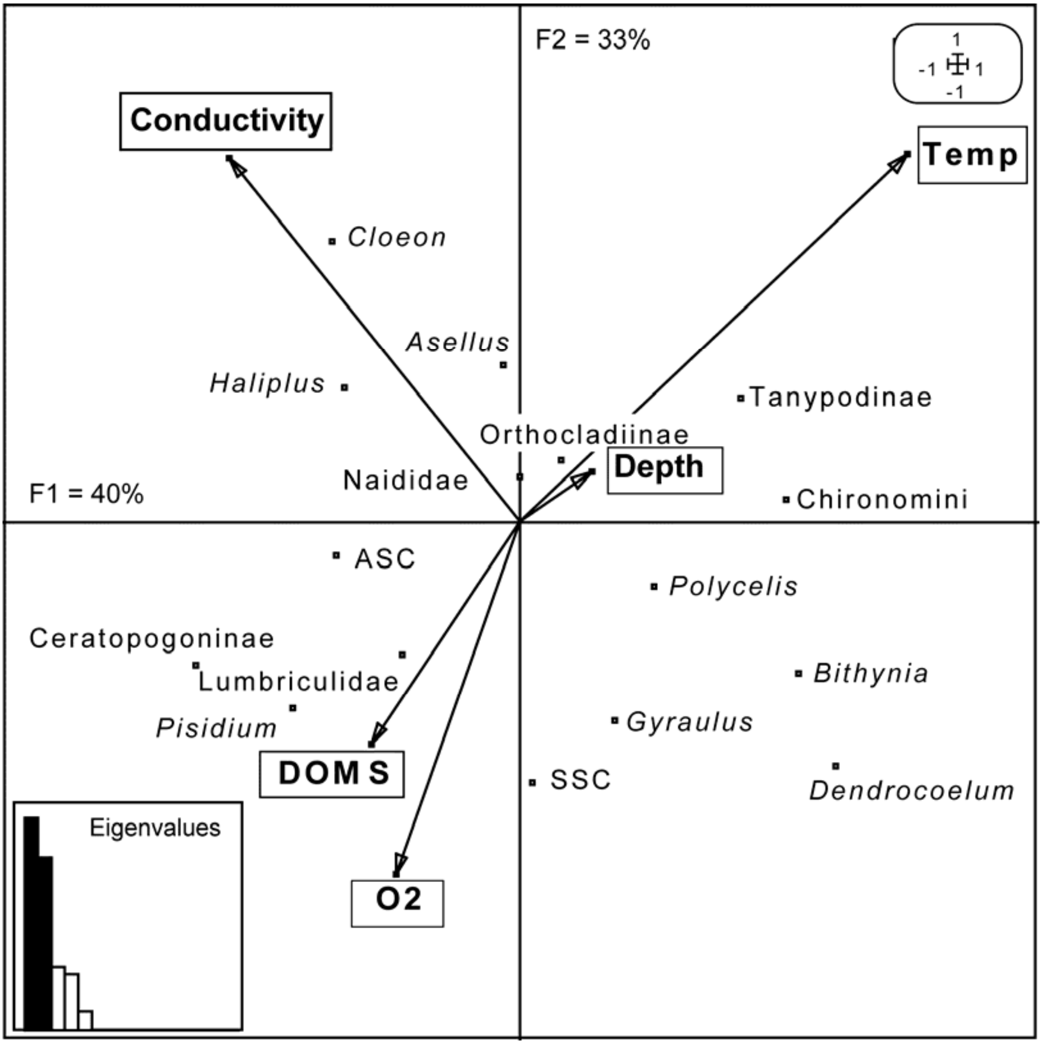

Figure 7. First factorial plane of the Canonical Correspondence Analysis (CCA) done on environmental variables and the taxa with a relative abundance ≥ 1% of the community.
DOM S = dominant organic matter substrate.

Figure 7. Premier plan factoriel de l'Analyse Canonique des Correspondances effectuée sur les variables environnementales et les taxons dont l'abondance relative est ≥ 1% des communautés.
DOM S = matière organique.

This analysis underlined again that, with taxa such as the Turbellaria *Dendrocoelum lacteum, Polycelis*, and the Gastropoda *Bithynia* and *Gyraulus*, Mariol differed from the other sites. Moreover, systematic differences between the up- and downstream zones of each site appeared.

On one hand, the upstream zones of Auzon, Port-de-Ris, Lindes and Précaillé were grouped and characterized by the following taxa: the mayfly *Cloeon dipterum*, the Isopod *Asellus aquaticus* and the beetle *Haliplus*. On the other hand, the downstream zones of Auzon, Port-de-Ris, Précaillé, Granvaux and Lindes, as well as the upstream zone of the site Granvaux, were associated with the bivalve *Pisidium*, Diptera Chironomini, Ceratopogoninae and Oligochaeta.

The influence of the environmental variables on the taxa, analyzed with the CCA ordination and the Monte Carlo permutation test, indicated that significant relationships occurred ($p = 0.001$). *Cloeon dipterum*, *Asellus aquaticus, Haliplus* sp. were associated with coarse mineral substrates and high water conductivity, whereas Diptera Tanypodinae and Chironomini were linked with warmer waters (Figure 7). All these taxa were associated with low dissolved oxygen levels. *Pisidium*, Ceratopogoninae and Oligochaeta were associated with mud, high oxygenation, and low temperature and conductivity. Finally, *Dendrocoelum lacteum, Polycelis, Bithynia* and *Gyraulus* were found in relatively well oxygenated waters and in the macrophytes.

3.3. Characterization of the meander cut-offs related to EPT

Cloeon dipterum was present up- and downstream at both seasons in the six sites except in Granvaux. The representativeness of the EPT was the highest in Lindes (Figure 5b), and only a few differences appeared throughout the length of the meander cut-off, these being linked to the species lifespan. In the summer many Ephemeroptera such as *Caenis luctuosa*, *Ephemera lineata*, *Thraulus bellus* and *Potamanthus luteus* were collected from the upstream zone, as well as three individuals of *Leuctra* sp. (first instars). In autumn, *Caenis luctuosa*, *Ephemera lineata* were observed only downstream, and were associated with many Trichoptera such as *Ecnomus deceptor, Goera pilosa, Athripsodes aterrimus, Mystacides azureus* and *Cyrnus trimaculatus*. In Mariol in the summer, a few Ephemeroptera such as *Potamanthus luteus* were sampled only downstream and some individuals of the caddis *Leptocerus tineiformis* were collected upstream.

Considering the little silted sites, in Auzon, where the EPT were largely represented, upstream only an individual of *Anabolia nervosa* was found in summer. Downstream, *Athripsodes aterrimus*, *Caenis luctuosa*, *Serratella ignita* and *Potamanthus luteus* were collected in summer, while in autumn, *Cyrnus trimaculatus, Baetis* sp. and *Baetis rhodani* were present. In Port-de-Ris, *Potamanthus luteus* was collected in the summer all along the site. Downstream, different Trichoptera were observed at both seasons as *Ceraclea annulicornis*, *Setodes punctatus* and *Mystacides azureus*.

Considering the sites with a high degree of silting, few individuals of EPT were observed. These taxa were: *Baetis rhodani, Habrophlebia fusca, Potamanthus luteus, Serratella ignita*, *Athripsodes aterrimus* and *Leptocerus tineiformis*,.

4. Discussion

In these two reaches, the main aim of this study was to evaluate the changes in the colonisation of benthic invertebrates in six meander cut-offs related to: different degrees of siltation and disturbance (dredging), groundwater input and agricultural pressure. Our results underlined that statistical biotic differences occurred between and within our studied sites. Related to different theoretical concepts about river functioning as “The flood pulse concept”, and “The hydrosystem concept”, (WARD 1989; PIÉGAY & SCHUMM 2003; JUNK & WANTZEN 2004; TOCKNER et al.

2006), the links between all the compartments of the plain are complex. These links, influenced notably by the geology (in our study: metamorphic vs. sedimentary rocks) and the anthropological pressure, induced different degrees of connectivity, hydraulic exchanges, water quality, etc. between and within the six sites (*i.e.* separation of upstream zones and downstream zones on the bPCA ordination plot). On the whole, in the upstream zones of parapotamal meander cut-offs, that are disconnected from the main channel, autogenous processes dominate (AMOROS & PETTS 1993; TOCKNER et al. 1999; AARTS et al. 2004) except during floods. Moreover, the groundwater inputs were observed in our sites as they buffered the upstream temperature. During floods, that could occur in autumn and in spring in the two studied reaches, the upstream connection with the main channel was underlined by the superimposing of temperature curves (up- and downstream meander cut-off and river) (cf. Figure 2) leading to allogenous processes. Downstream, the connection with the main channel allowed allogenous processes and the influence of groundwater was lower (except during low-water level that could lead to disconnection), the physical and chemical conditions being more similar to those of the river (except Mariol). In this part of the sites, the taxonomic diversity was high in all the studied hydraulic annexes.

Between the sites, the connectivity differed related to connection width, alluvial plug, infilling, etc. inducing different lateral exchanges of water and sediments between the main channel and the meander cut-offs. In such areas, the life span and the composition of the benthic macroinvertebrate community depends on their efficiency to live in this ecosystem linked to the upstream characteristics of the basin (sediment supply, flood frequency…) where sediment trapping occurred (PIÉGAY & SCHUMM 2003). Downstream zones of sites Lindes, Auzon and Port-de-Ris, where the connectivity was high, the richness and number of EPT were high (the highest percentage of EPT being observed in Lindes). Moreover, the river inputs can contribute to the attenuation of the effects of agricultural activity by diluting the concentration of ammonium and nitrates improving the water quality.

Considering independently each site, local anthropogenic pressure and differences in abiotic variables led to classically known macroinvertebrate distribution differences (HYNES 1960, 1970; MILLS 1972; WARD 1992; BEAUGER 2008b; STERNET et al. 2008). In the three sites of the upstream reach (low silted Auzon, highly silted Précaillé and impacted site Lindes), the hydraulic exchanges differed. In Précaillé and Lindes, the groundwater drainage from upstream to the river confluence associated with temperature changes, induced a gradient in conductivity and ionic concentrations from up- to downstream. As observed in other countries by BENGEN et al. (1992), FRASER & WILLIAMS (1997) and LEFEBVRE et al. (2006) the highest values were observed upstream (ex. conductivity > 700 $\mu S.cm^{-1}$ in summer: Table 2 & Figure 4). Such processes can also be linked to the up / downwelling movements, something that is typical of groundwater / hyporheic / surface water ecotones (MERMILLOD-BLONDIN et al. 2000; LEFEBVRE et al. 2004; LEFEBVRE et al. 2006). In the low silted Auzon, the water quality variables were lower underlining difference in water inputs both up and downstream (Figure 4). In comparison with the previous sites, Auzon was linked both to groundwater originated from infiltration off the land within the basin, and from groundwater flowing through the river deposits. These water inputs can contribute to the water composition of this site and could explain the lower conductivity and ionic concentrations.

Thus, even if the water composition was similar in Précaillé and Lindes, the degree of silt accumulation induced the presence of different communities. Thus, in the shallow waters of Précaillé, the fine sediment deposit altered the benthic community structure, limiting the organism's colonization as a direct result of the smothering and clogging of interstices (RALEIGH 1982;

RYAN 1991; WOOD & ARMITAGE 1999). The biodiversity was low, with few EPT, and the habitat homogeneity contrasts with a high density of animals. In such areas, the higher levels of organic matter may explain the preponderance of burrowing deposit feeders such as Oligochaeta and Chironomini (MINSHALL & MINSHALL 1977; VOS 2001) and, as observed in the depositional zones of lotic waters (cf. BEAUGER et al. 2010), the increase in predators such as Ceratopogoninae and Tanypodinae (TACHET et al. 2000). These results were also supported by those of STERNET et al. (2008) who underlined that density was positively correlated with the percentage of sedimentary organic matter. In contrast, at Lindes, both downstream extraction and wider connection with the channel enhanced the influence of the river in this zone where the temperature remained similar to that of the river (a scheme which extends in a large part of the meander cut-off). Downstream, the mix of allogenous processes (organic matter coming from the river), coarse mineral substrates and organic matter due to the degradation of the numerous macrophytes, explained the presence of many deposit feeders (Diptera Chironomini and Oligochaeta) and Trichoptera such as *Athripsodes aterrimus*, *Ecnomus decepto*r and *Cyrnus trimaculatus* (CASTELLA 1987; FOECKLER et al. 1994; GRAF et al. 2008). The connection with the main channel induced good oxygenation which, added to the high diversity of habitats, offered a large macroinvertebrate biodiversity. In the little silting up site Auzon, in the absence of lotic input upstream, wide dial variations in dissolved oxygen reached low levels during the night inducing drastic conditions for biota. The presence of numerous macrophytes accentuated this phenomenon and explained the presence of very numerous *Cloeon dipterum*, adapted to low oxygenation (MENETREY et al. 2008). In contrast, downstream, higher dissolved oxygen concentrations favoured the growth of species typical of the River Allier as *Baetis rhodani*, *Caenis luctuosa* and *Potamanthus luteus*. The habitats (including coarse mineral substrates, macrophytes and a little silt accumulation) were diversified, and the biodiversity higher. These results join those of STERNET et al. (2008), who demonstrated that the wetlands richness was positively associated with habitat diversity. Furthermore, even though the densities were not very high, shredders such as *Asellus aquaticus*, which feed on coarse particulate organic matter, were numerous, and associated with grazers such as *Cloeon dipterum*, deposit feeders such as Chironomini and predators such as Tanypodinae (GRAÇA et al. 1994; TACHET et al. 2000). This underlined the positive influence on the river biota, of a good connection with the main channel (BEAUGER et al. 2006).

In the downstream reach R2, located in a geological sedimentary catchment, the physical and chemical water composition of the three other sites was more similar to that of the river, groundwater exchanges (underlined by a temperature lower than the main channel) being less accentuated than in R1 (cf. Figure 2 & 4). In this reach (except in the highly silted site Granvaux where cattle trampling occurs), the agricultural pressure was lower and nitrate concentration negligible. However, as R1, large macroinvertebrate differences were linked to the habitats. Thus, in low silted Port-de-Ris, the habitats were well diversified and (as in Auzon), they sustained a high biodiversity, with the presence of numerous EPT.

In the silted-up site Granvaux, the same biotic characteristics as in Précaillé were observed (high community density and few EPT). The dominance of sand and mud in the upstream zone, however, could explain the small differences between the two zones, as underlined in the between-zones analyses.

Finally, at the impacted site Mariol, both the upstream extraction (that turned the site into a pond) and the narrow connection with the river induced a situation opposite to deepened sites such as Lindes. Indeed, as shown by the low downstream oxygen content, few inputs from the main channel occurred and the two zones of the site evolved independently from the river. This has induced autogenous processes and the installation of a particular community, with the presence of the bivalve *Bithynia* and of many Turbellaria. In this site, biodiversity and community density were high, but EPT were few. Upstream, silting was high, macrophytes were numerous, and in the absence of lotic inputs, the wide dial variations in dissolved oxygen induced very drastic conditions for biota, enhanced by a large aquatic vegetal cover. In this zone, filterers, scrapers and shredders such as *Bithynia* sp. and *Leptocerus tineiformis* (GRAF et al. 2008; TACHET et al. 2000) were associated with numerous predators such as *Dencrocoelum lacteum* and *Polycelis* sp. *Planaria torva* was also well represented in this cut-off meander during the two seasons. This taxon known to occur in the lowlands (oceanic) biogeographic region of France (TACHET et al. 2000) was found for the first time in a continental area. The sandy downstream zone, drained by the upstream water (the high organic matter content inducing a superficial infilling), sheltered numerous deposit feeders such as Oligochaeta, which represented 50 % of the community in terms of numbers of individuals. In autumn, filterers such as Diptera Simuliidae were also collected in this zone, confirming the presence of suspended organic matter.

5. Conclusion

In European rivers, human impacts are caused by rip-rap, confinement, dams, etc. inducing a decrease in fluvial dynamic which limits the formation of meander cut-offs that naturally evolve to a progressive alluviation. The present study, which was conducted on a series of six parapotamal meander cut-offs under varying levels of pressure, illustrates the complexity of exchanges with the river and/or the underground, with the level of infilling influencing both the water quality and the settlement of biocenoses.

On the whole, sites silted and cut off since a long time, characterized by low habitats diversity and biodiversity will naturally evolve to the final stage soil formation and land cover. On the contrary, cut-off meander, deepened downstream to maintain the connectivity with the main channel, presented high habitat diversity and biodiversity even if agricultural pressure was high in the catchment. This artificial deepening works had induced the rejuvenation of the meander cut-off as it presented the same characteristics as "young sites" cut off. Our results supported those of MIRANDA (2005) on fish assemblages, which showed that if disconnection increases, communities are negatively affected. It is a process that applies to the benthic macroinvertebrates. Indeed, as long as the downstream alluvial plug does not disconnect the meander cut-off from the main channel {leading to isolation of the water body with increasing autogenous processes and infilling (MORKEN & KONDOLF 2003), and decreasing habitat and macroinvertebrate diversity}, the conditions will allow a high density and diversity of macroinvertebrate and particularly of Ephemeroptera, Plecoptera and Trichoptera.

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Annex (Page 108)

Table 7. Total list of taxa collected in the six cut-off meanders.

Tableau 7. Liste totale des taxons collectés sur l’ensemble des six sites bras morts.

TURBELLARIA
Dendrocoelum sp.
Dugesia sp.
Planaria torva
Polycelis nigra
Polycelis tenuis

OLIGOCHAETA
Enchytraeidae Gen. spp.
Lumbricidae Gen. spp.
Lumbriculidae Gen. spp.
Naididae Gen. spp.
Sparganophilidae Gen. spp.
Tubificidae with hair setae
Tubificidae without hair setae

HIRUDINEA
Boreobdella verrucata
Erpobdella sp.
Glossiphonia sp.
Haementeria costata
Helobdella stagnalis
Piscicola geometra

LAMELLIBRANCHIA
Anodonta sp.
Corbicula sp.
Musculium lacustre
Pisidium sp.
Sphaerium sp.

GASTROPODA
Bithynia sp.
Galba truncatula
Gyraulus sp.
Hippeutis complanata
Physa sp.
Potamopyrgus antipodarum
Radix sp.

MALACOSTRACA
Asellus aquaticus
Gammarus fossarum
Gammarus pulex

INSECTA
Ephemeroptera
Baetis rhodani
Baetis sp./spp.
Caenis horaria
Caenis luctuosa
Caenis sp./spp.
Cloeon dipterum
Ephemera lineata
Habrophlebia fusca
Potamanthus luteus
Serratella ignita
Thraulus bellus

Odonata
Chalcolestes viridis
Coenagrion sp.
Coenagrionidae Gen. spp.
Cordulegaster sp.
Erythromma sp.
Gomphus vulgatissimus
Ischnura sp.
Onychogomphus uncatus
Orthetrum sp.
Platycnemis latipes
Platycnemis pennipes
Sympecma fusca

Plecoptera
Leuctra geniculata
Leuctra sp.

Heteroptera
Corixinae Gen. spp.
Gerris sp.
Hesperocorixa sp.
Hydrometra sp.
Ilyocoris cimicoides
Mesovelia sp.
Micronecta sp.
Nepa cinerea
Notonecta glauca
Sigara sp.

Megaloptera
Sialis lutaria

Planipenna
Osmylus sp.

Lepidoptera
Cataclysta lemnata
Nymphula stagnata

Trichoptera
Anabolia nervosa
Athripsodes aterrimus
Ceraclea annulicornis
Cyrnus trimaculatus
Ecnomus deceptor
Goera pilosa
Leptocerus tineiformis
Leptoceridae Gen. spp.
Limnephilidae Gen. spp.
Mystacides azureus
Polycentropodidae Gen. spp.
Setodes punctatus

Coleoptera
Agabus spp.
Aulonogyrus sp.
Colymbetes fuscus
Colymbetinae Gen. spp.
Dryops sp.
Dytiscidae Gen. spp.
Enochrus sp.
Esolus sp.
Haliplus sp.
Helochares sp.
Hydrobius sp.
Hydrocara sp.
Hydroporinae Gen. spp.
Hydroporus spp.
Hygrobia hermanni
Hyphydrus spp.
Ilybius fuliginosus
Laccobius sp.
Laccophilus spp.
Limnius sp.
Macronychus quadrituberculatus
Oulimnius sp.
Peltodytes sp.
Platambus sp.
Stictotarsus sp.

Diptera Nematocera
Chaoborus sp.
Ceratopogoninae Gen. spp.
Chironomini Gen. spp.
Culicidae Gen. spp.
Dixa sp.
Hexatomini Gen. spp.
Orthocladiinae Gen. spp.
Simuliini Gen. spp.
Tanypodinae Gen. spp.
Tanytarsini Gen. spp.
Tipulidae Gen. spp.

Diptera Brachycera
Atrichops crassipes
Stratiomyidae Gen. spp.
Tabanidae Gen. spp.
Ephydridae Gen. spp
Anthomyidae Gen. spp.