Does hydrological connectivity control functional characteristics of artificial wetland communities? Evidence from the Rhône River

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Abstract

The importance of artificial wetlands for the biodiversity of the Rhône River floodplain was assessed at twelve stations along two sections of the river. The relative roles of the local characteristics of the wetlands (e.g. available nutrients, dissolved oxygen, sediment quality) and of their connectivity with the main channel were considered for three different groups of organisms (benthic microbes, benthic invertebrates and phytoplankton communities). The functional characteristics of these organisms were determined through their enzymatic activities (for microbes) and biological traits (for invertebrates and phytoplankton). The predicted major role of connections between the wetlands and the river channel was confirmed for environmental characteristics (water and sediment) and benthic invertebrates. Connectivity appeared to be less of a driver of benthic microbial communities and phytoplankton, which were partly or mainly controlled by wetland geometry (water depth, light penetration, and resulting organic matter production). We conclude that connectivity with the river channel needs to be considered jointly with the geometry of wetlands to provide functional solutions when defining management and restoration plans.

Keywords: Casier Girardon,·Microbial activities, Benthic invertebrates, Phytoplankton, Novel ecosystems

Introduction

Biodiversity has proved its benefits for man, contributing to the security, resiliency, and welfare of human populations all over the world (Millenium Ecosystem Assessment 2005). However, the increasingly rapid erosion of biodiversity over the last 50 years (e.g. Stuart et al. 2004) highlights the need for its protection and restoration (James et al. 2001; Brooks et al. 2006; Pollock et al. 2017). Nor is the current concern for biodiversity limited to charismatic megafauna or threatened species (Pimm and Raven 2000; Rodrigues et al. 2004). Attention is turning to the everyday, ordinary organisms whose dynamics are also being affected (Hallmann et al. 2017; Sanchez-Bayo and Wyckhuys 2019; van Klink et al. 2020).

Biodiversity must be considered at several levels of complexity, from genes to ecosystems (Mace et al. 2012). At the genetic level, biodiversity is essential to document population variability and stability (e.g. Nelville et al. 2006). At species level, it is a crucial indicator to evaluate local environmental quality or large-scale biogeographic trends (e.g. Eme et al. 2015). Finally, documenting biodiversity at the functional level is a way to describe habitat properties, ecosystem dynamics (Fischer et al. 2010) and productivity. This latter level of integration is, however, complex to consider (Villeger et al. 2008). One strategy consists in quantifying functional groups in each ecosystem compartment using the biological and ecological traits of organisms (e.g. for aquatic invertebrates see Usseglio-Polatera et al. 2000, Doledec and Statzner 2008, or for phytoplankton see Cellamare et al. 2013). For example, in large rivers, considering functional traits provides crucial strategies for biodiversity management and restoration (Doledec et al. 2015).

Large rivers and their floodplains are among the most species-rich environments in the temperate area (Ward et al. 1999), at least when they are not regulated (Grill et al. 2019). Several factors control biodiversity in large rivers. The spatio-temporal heterogeneity makes large rivers and their floodplains highly species-rich, due to extensive hydrological connectivity (Ward and Stanford

1995). But the quantity of nutrients available (i.e. trophic status, Parr and Mason 2003) and the overall pollution level (e.g. Inostroza et al. 2016) may significantly reduce community diversities.

River hydrological connectivity extends in 4 dimensions, longitudinally (up- and downstream in the river channel), vertically (between groundwater and the river), temporally (seasonality of flow), and laterally between the main channel and the floodplain (Ward 1989; Petts and Amoros 1996; Grill et al. 2019). Lateral hydrological connectivity ensures that the heterogeneity of tributaries (Pracheil et al. 2013) and alluvial wetlands (Obrdlik et al. 1996; Ward et al. 1999) plays a major role in biodiversity control at the scale of the entire ecosystem. Large rivers are surrounded by a strip of wetlands arising from their lateral mobility and that generate a series of abandoned channels (Petts and Amoros 1996). The biodiversity in these abandoned channels is controlled and maintained by hydrological exchanges with the main channel (Bornette et al. 1996; Paillex et al. 2009) and the overall diversity of river-wetland system may sharply decrease if these connections are closed (e.g. after embankment construction, see for the Danube River Ward et al. 1999). In regulated sections of large rivers, some constructed ponds may act as abandoned channels now isolated (Thorel et al. 2018). They should be considered as an important compartment of the ecosystem for their contribution to the biodiversity and productivity of embanked rivers (Espanol et al. 2015).

The objective of this work is to document the contribution of constructed ecosystems to aquatic biodiversity conservation (Harper et al 2021). We focus on the role of artificial wetlands in conserving the biodiversity of the Rhône River floodplain. Twelve artificial wetlands connected in varying ways with the main channel were selected from two regulated sections of the river. We examined the local characteristics of the artificial wetlands (i.e. available nutrients, dissolved oxygen, sediment quality) and their connectivity with the main channel. Three different groups of organisms (benthic microbes, benthic invertebrates, and phytoplankton communities) were studied, with a focus on their functional properties, based on functional activities and biological traits. First, we hypothesized that hydrological connectivity controls the environmental characteristics of the wetlands, through the exchange of particulate and dissolved matter with the main channel (Guillon et al. 2019, **H1**). Second, we hypothesized that connection and disconnection between wetland and main channel is the major factor driving the community composition of the three types of organisms, with some functional traits linked to connected wetlands and others limited to isolated pools (Heiler et al. 1995, Amoros and Bornette 2002, **H2**). In return, we predicted that dominant organisms and the dominant functional traits of the benthic and planktonic communities would modify the environmental characteristics and the resulting ecological processes in the wetlands (Jones et al. 1994, **H3**).

Site description

The Rhone River is a regulated large river, 812 km long, that springs in the Swiss Alps and flows to the Mediterranean Sea (Olivier et al. 2009). Its catchment area is approximately 98,500 km^2 and the mean annual discharge main channel was isolated from its alluvial floodplain by constructing engineering structures composed of groynes connected longitudinally with a submersible dike. These infrastructures called "Casiers Girardon" (hereafter wetlands) were built at the end of the 19th and beginning of the twentieth century (Thorel et al. 2018). Similar artificial wetlands were built at the same period on the Elbe (Bormann et al. 2011; Henning and Hentschel 2013), Rhine (Frings et al. 2014), Danube (Savic et al. 2013), Mississippi, and Missouri Rivers (Poulton and Allert 2012). These systems have concentrated the flow in a single channel by disconnecting it from secondary channels and strongly modified the river's hydraulic, ecological, and functional characteristics. Margins increased and the riverbed narrowed, the water level rose during floods, habitat diversity decreased, and there was a disconnection from the floodplain. Currently, most of these artificial wetlands are

terrestrial systems colonized by riparian forest, with only 10% still aquatic (Thorel et al. 2018).

Twelve aquatic wetlands in two sections of the Rhone River were studied. Sampling was performed at six stations in the Péage-de-Roussillon section (hereafter PDR, stations 1 to 6; Fig. 1), a by-passed channel due to a dam. The PDR wetlands are relatively small and shallow (mean depth of 1.1 m, 0.4 to 1.8 m, see below). They differ in degree of connection to the river. Guillon et al. (2019) used the physical characteristics of the embankment (height, permeability, size of opening, and movement of water) to distinguish isolated and connected wetlands. Outside of flood periods, wetland 3 is totally isolated by a hermetic embankment, while the five others are connected to the flowing channel, through slightly permeable dikes (wetland 1, 2, and 5), with a narrow opening (wetland 4) or a large embankment opening (wetland 6).

The six other wetlands were selected in the Arles section (hereafter ARL, stations 7 to 12) located along the main channel of the Rhone River (Fig. 1). These wetlands are larger and deeper than in PDR (mean depth 2.5 m, 0.15 to 4.3 m, see below). Wetlands 8, 9, 10, and 11 are permanently connected to the main channel via a large opening, an impermeable dike permanently isolates wetland 7 and wetland 12 is seasonally isolated (it was clearly connected in June and isolated during summer).

Microbial, phytoplanktonic, and zoobenthic communities were obtained for study through two sampling campaigns, at the start and at the end of summer 2014 (between June 18 and July 1, and between August 27 and September 16, respectively). During both periods, 44 sampling points were examined in the 12 wetlands (i.e. 3 points for the smaller and 5 points for the larger wetlands).
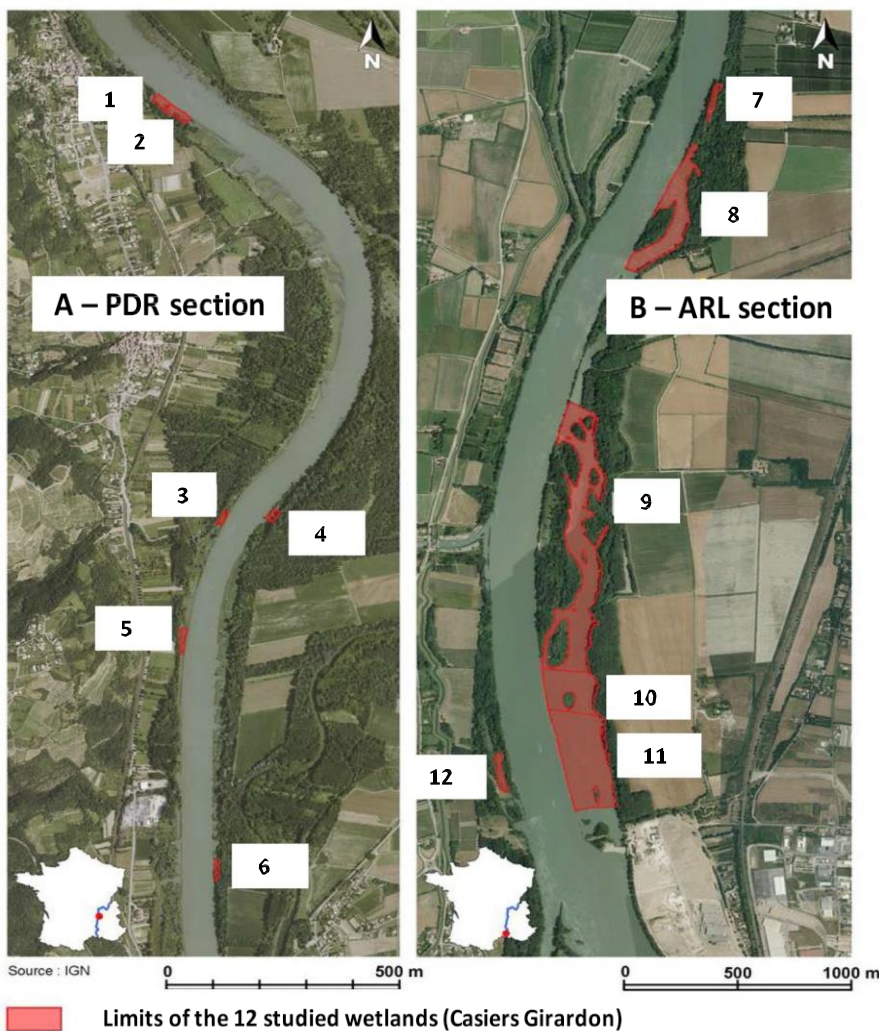
Fig. 1. Location of the wetlands in PDR section (Péage-de-Roussillon, **A**) and ARL section (Arles, **B**) with wetland codes (Casiers Girardon). Wetlands are numbered from 1 to 6 for PDR section and from 7 to 12 for ARL section

Material and methods

Environmental characteristics

Water temperature (T°C, °C), electrical conductivity (Cond, $\mu S\ cm^{-1}$), dissolved oxygen (O_2, mg l^{-1}) were measured in situ using portable IDS numeric probes (Multi 3430, WTW, Germany). Water transparency (Trans, m) was measured with a Secchi disc. Dissolved anions and cations (Na^+, K^+, $Ca2^+$, Mg^{2+}, Cl^-, NH_4^+, NO_2^-, NO_3^{2-}, PO_4^{3-}, SO_4^{2-}) and dissolved silicate (SiO_2) were analyzed in the laboratory by ionic chromatography (METROHM, 930 Compact IC Flex). The instrument was calibrated using multi-elementary standard solutions (Analab, France) and analyses were validated using certified reference material (Rain-12). Chlorophyll a (chloro a) concentrations were estimated from triplicate samples and calculated via the Lorenzen (1967) method. Suspended Particulate Matter (SPM) was quantified in the laboratory after filtration on a GF/F Whatman filter. Quantity of Total Organic Matter (TOM, in %) in sediment was measured by loss on ignition (4 h at 550 °C), sediment total Carbon (TC, mg g^{-1}) and total Nitrogen (TN, mg g^{-1}) were measured using an elemental analyzer (EA) (ThermoScientifique, FlashEA 1112) and C/N ratios were calculated. All these measurements were performed at the greatest depth (Depth) point in each wetland.

Functional characteristics of benthic microbes

The global esterase activity of the benthic biofilm was estimated with Fluorescein Diacetate (FDA) hydrolysis (Claret and Fontvieille 1997; Mermillod-Blondin et al. 2004), a measure that covers the activity of a wide range of organisms (including algae and bacteria, Battin 1997). Sediment samples (0.5 g fresh weight) were placed in 3 mL of a pH 7.6 phosphate buffer solution with 0.15 mL of 4.8 mM FDA solution. Incubation was maintained until the fluorescein turned green, ensuring that FDA concentration did not limit enzymatic activity. The reaction was stopped by freezing the samples at − 20 °C after adding 3 mL of mercuric chloride solution (400 mg L^{-1}). Fluorescein concentration was estimated from the absorbance of the filtered supernatant (0.45 µm, Millipore) measured at 490 nm. Hydrolytic activity was expressed as µmol of FDA hydrolyzed per hour and per gram of dry matter.

Functional diversity of microbial communities was evaluated using specific substrate activities via the BIOLOG EcoPlate™ method (Biolog Inc., Hayward, CA), with simultaneous measurement of the degradation of 31 organic compounds belonging to 6 biogeochemical groups (carboxylic acids, carbohydrates, amino acids, amines, phenols, and polymeric compounds). This method determines the physiological profiles of the microbial assemblages from their heterotrophic metabolic activities (Handelsman et al. 1998) and roughly describes the diversity of microbial functional groups (e.g. Stefanowicz 2006; Foulquier et al. 2013).

Benthic invertebrates

Benthic invertebrates were sampled using an Ekman grab, rinsed with a 500 µm-mesh riddle, fixed with ethanol 96% and stored at + 4 °C until analysis. They were counted and identified to the finest taxonomic resolution possible using a binocular magnifier or an optic microscope (only for Ostracoda and Cladocerans). Invertebrate densities were expressed as ind. m^{-2} and calculated as an average per wetland and per period based on 3 or 5 samples. Functional characteristics of benthic invertebrate assemblages were estimated using 61 categories distributed in 3 Grinnellian fuzzy-coded traits (Food, substrate, and transversal location) and 5 Eltonian fuzzy-coded traits (locomotion mode, feeding group, reproduction technique, resistance stages, and respiration mode, Table 1), as proposed by Tachet et al. (2010) or Mondy and Usseglio-Polatera (2014). The association between a taxon and a trait

category was described using an affinity score based on a fuzzy-coding technique (Chevenet et al. 1994).

Phytoplankton

Phytoplankton was sampled using the Laplace-Treyture method (Laplace-Treyture et al. 2009); water samples were collected at each point with a 1 L Niskin bottle in the euphotic zone at a depth of 1.5 Secchi distance (or 1 m above the bottom sediment when there was light penetration of the whole water column). Samples were preserved in formaldehyde solution and stored in the dark at 4 °C until analysis.

Phytoplankton was counted according to the Utermöhl (1958) method at 40-fold magnification under an inverted microscope (Olympus IX 70; AFNOR 2006). Phytoplankton abundances were calculated in algae units (unicell, colony or filament) per unit of volume (L). Phytoplankton taxa were identified using appropriate taxonomic guides. Specific biovolume was estimated, obtained by geometrical approximations from measuring 30–40 individuals per species (Hillebrand et al. 1999).

Four functional traits of phytoplanktonic organisms were documented following Cellamare et al. (2013) and Kruk et al. (2010) (Table 1): the organism dimension estimated firstly through biovolume (BV 1 to 4, Litchman & Klausmeier 2008) and secondly through greatest axial linear dimension (GALD 1 to 4), thirdly the Life forms (LF) considering unicellular and multicellular forms and finally the Morphological-Based Functional Groups (MBFG 1 to 7, Kruk et al. 2010).

Statistical analyses

Differences in water and sediment characteristics between the two sections (i.e. PDR versus ARL) were described by performing one-way ANOVA using wetlands as replicates ($n = 12$, after log-transformation if necessary) and a Principal Component Analysis (PCA) with 24 samples (12 wetlands × 2 sampling periods) and 22 variables, using reduced-centered data without other transformations. To evaluate the effect of a connection between each wetland and the main channel (for either section), a within-class PCA was performed on the same set of environmental characteristics, with transformed data to quantify the hydrological connectivity gradient without any "section" effect.

Differences in microbial activity (FDA activity), chlorophyll *a* content, and benthic invertebrate taxonomic richness between wetlands were tested for each section (PDR and ARL) and each period using one-way ANOVAs ($n = 3$ or 5, after logarithmic transformation when necessary). Post-hoc analyses were performed to compare connected and isolated wetlands (station 3 on both dates in PDR, 7 on both dates and 12 in September in ARL). For microbial activities, the FDA hydrolysis was correlated to organic matter quantity and quality and the diversity of microbial activities (estimated by BIOLOG method) were analyzed via two separate PCAs (for June and September).

Functional traits of benthic invertebrates and phytoplankton were analyzed by fuzzy correspondence analysis (fuzzy COA, Chevenet et al. 1994). These analyses were performed on the species-trait matrix, which yielded species scores accounting for the trait dissimilarity among species. All PCAs and COAs were performed using the ade4 R package of the R statistical software (R Development Core Team 2013) and all ANOVAs and linear correlations using ExcelStat 2014.

Table 1. Biological and ecological traits considered for benthic macroinvertebrates and phytoplankton. For benthic macroinvertebrates, 8 traits fuzzy-coded in 61 categories were considered (abbreviations used in Fig. 4c). For phytoplankton, 4 traits coded in 20 categories were considered (abbreviations used in the Fig. 5b).

Traits	Categories	Abbreviation
Benthic invertebrates		
Food	Microorganisms	Sedim
	Detritus (< 1 mm)	Detritic
	Dead plants	Pldetr
	Living microphytes	Microphyt
	Living macrophytes	Macrophyt
	Dead animal	Deadan
	Living microinvert	Microinv
	Living macroinvert	Macroinv
	Vertebrates	Vert
Locomotion or substratum relation	Surface swimmer	Surfswim
	Full water swimmer	Swim
	Crawler	Crawl
	Burrower	Burrow
	Interstitial	Interstit
	Temporarily attached	Tempattach
	Permanently attached	Attached
Feeding habits	Absorber	Abs
	Deposit feeder	Deposit
	Shredder	Shred
	Scraper	Scrap
	Filter feeder	Filtr
	Piercer,	Pierce
	Predator	Predate
	Parasite	Parasite
Reproduction technique	Ovoviviparity	Ovoviv
	Isolated eggs, free	Eggfree Eggcem
	Isolated eggs, cemented	
	Clutches, cemented or fixed	Stick
	Clutches, free Clutches, in vegetation	Free
	Clutches, terrestrial Asexual reproduction	Veget terrestr
		Asex
Resistance form	Eggs, statoblasts ()	Eggs
	Cocoon Housings against desiccation	Cell
	Diapause or dormancy	Torpid
	None	None
Respiration mode	Tegument	Teg
	Gill	Gill
	Plastron	Plast
	Spiracle	Spi
	Hydrostatic vesicle	Vesicle
Substratum preferences	Flags- boulders- cobbles- pebbles	Coarse
	Gravel, Sand, Silt	Fine
	Macrophytes	Macrophyt
	Microphytes	Microphyt
	Twigs- roots	Roots
	Organic detritus- litter	Litter
	Mud	Mud

Table 1. (continued)

| Traits	Categories	Abbreviation
Lateral distribution	Outside river	Out
	River channel	Chanel
	Banks or connected side arms	Sidearm
	Ponds or pools or disconnected side arms	Pond
	Marshes or peat bogs	Marsh
	Temporary waters	Temporary
	Lake	Lake
	Groundwaters	gw
Biovolume (BV)	$\leq 100\ \mu m3$	BV1
	From 100 to 1000 $\mu m3$	BV2
	From 1001 to 10,000 $\mu m3$	BV3
	> 10,000 $\mu m3$	BV4
Greatest axial linear dimension (GALD)	$\leq 10\ \mu m$	GALD1
	From 10 to 20 μm	GALD2
	From 20 to 50 μm	GALD3
	> 50 μm	GALD4
Life form (LF)	Unicellular flagellated	UF
	Unicellular non-flagellated	UNF
	Colonial-flagellated	CF
	Colonial non-flagellated	CNF
	Filaments	FI
Morphological-based functional groups	Small organisms with high S/V	MBFG I
	Small flagellated organisms with siliceous exoskeletal	MBFG II
	Large, high S/V filaments with aerotopes	MBFG III
	Organisms of medium size lacking specialized traits	MBFG IV
	Unicellular flagellates of medium to large size	MBFG V
	Non-flagellated organisms with siliceous exoskeletons	MBFG VI
	Large mucilaginous colonies with low S/V	MBFG VII

Results

Environmental characteristics

Differences between the two sections (i.e. ARL *versus* PDR) were weak (Fig. 2): the wetlands were grouped by section, but the two resulting groups were poorly separated on the 1st axis (31.1% of the inertia) and on the 2nd axis (17.9% of the inertia, Fig. 2b). Some differences were linked to the morphometric characteristics of the wetland, especially depth (on the negative side of the 1st axis), greater in ARL than in PDR. In contrast, few chemical and biological characteristics differed between sections, while there was generally strong within-section variability (Table 2). Some dissolved nutrient concentrations (i.e. Nitrate and Sulfate, on the negative side of the 1st axis, and Silica, on the negative side of the 2nd axis, Fig. 2a) were higher in ARL than in PDR, but with strong within-section variability for Nitrate and Sulfate. Conversely, Chlorophyll *a* was slightly higher in PDR than in ARL (positive side of the 1st axis, although the difference was not significant, Table 2), as were total sediment organic matter content (TOM) and its quality (i.e. low C/N ratio). Finally, the electrical conductivity was located near the origin of the 1st and the 2nd axes; this measure of total dissolved solutes was seasonally more stable in ARL than in PDR, resulting in significantly higher values in ARL in June and lower values in September (Table 2).

When these weak differences between sections were removed, using a within-class PCA, the isolation effect between the wetlands and the river channel was clearly visible on the first two components (i.e. 46.4% of total inertia, Fig. 2c, d). The 1st component is explained by chlorophyll *a* concentration, organic matter (both TC and TN) on the negative side, and nitrate, sulfate, dissolved Oxygen and water transparency on the positive side, while the 2nd component is explained by a gradient of ammonium, phosphate, and silica (Fig. 2c). Wetlands were scattered along these two axes, but the connection to the river was clearly associated with the 1st axis (36.9% of total inertia, Fig. 2d) where wetlands 3 (in PDR), 12, and 7 (in ARL) are located on the negative side, due to high concentrations of Chlorophyll *a* (reaching 24 $\mu g\,L^{-1}$ in wetland 3 and 9.5 $\mu g\,L^{-1}$ in wetland 7), of sediment TC (reaching 58 $mg\,g^{-1}$ in 3 and 60 $mg\,L^{-1}$ in wetland 7), and of TOM (between 5 and 6 $mg\,g^{-1}$ in wetland 3 for example, Table S1 in supplementary material). In contrast, there were very low concentrations of dissolved Oxygen (between 2 and 4 $mg\,L^{-1}$ in wetlands 12 and 7 in June), strong nitrate depletion (reaching 0 $mg\,L^{-1}$ in 3 and 12), and low sulfate values (ranging from 1.6 to 5.1 $mg\,L^{-1}$ in wetland 3 for example).

The wetlands more connected to the river (i.e. wetlands 1, 2, 4, 5, 6 in PDR and most wetlands in ARL) were located on the positive side of the 1st axis (Fig. 2d) because of high nitrate concentrations (reaching 2.4 $mg\,L^{-1}$ in wetland 6 or 4.8 $mg\,L^{-1}$ in 11), high sulfate values (mainly around 30 $mg\,L^{-1}$ in PDR and around 50 in ARL) and high oxygenation of the water (between 7 and 12 $mg\,L^{-1}$ in PDR and around 8 $mg\,L^{-1}$ in ARL).

The 2nd axis of the PCA was also related to wetland connectivity in both sections, but for different reasons (Fig. 2d). In PDR, the 2nd axis separated isolated wetland 3, with high phytoplankton biomass (11 to 24 $\mu g\,L^{-1}$ of Chloro *a*) and resulting low nutrient concentrations, from the highly connected wetland 6, where nutrient content remained high (i.e. 0.17 $mg\,L^{-1}$ of NH_4 and 0.24 $mg\,L^{-1}$ of PO_4), certainly because of exchanges with the main channel. In ARL, the 2nd axis separated poorly oxygenated isolated wetlands 7 and 12 (4.3 and 2.9 $mg\,L^{-1}$ in September) from all the other connected stations fed by the main channel oxygen-rich water (all above 8 $mg\,L^{-1}$).
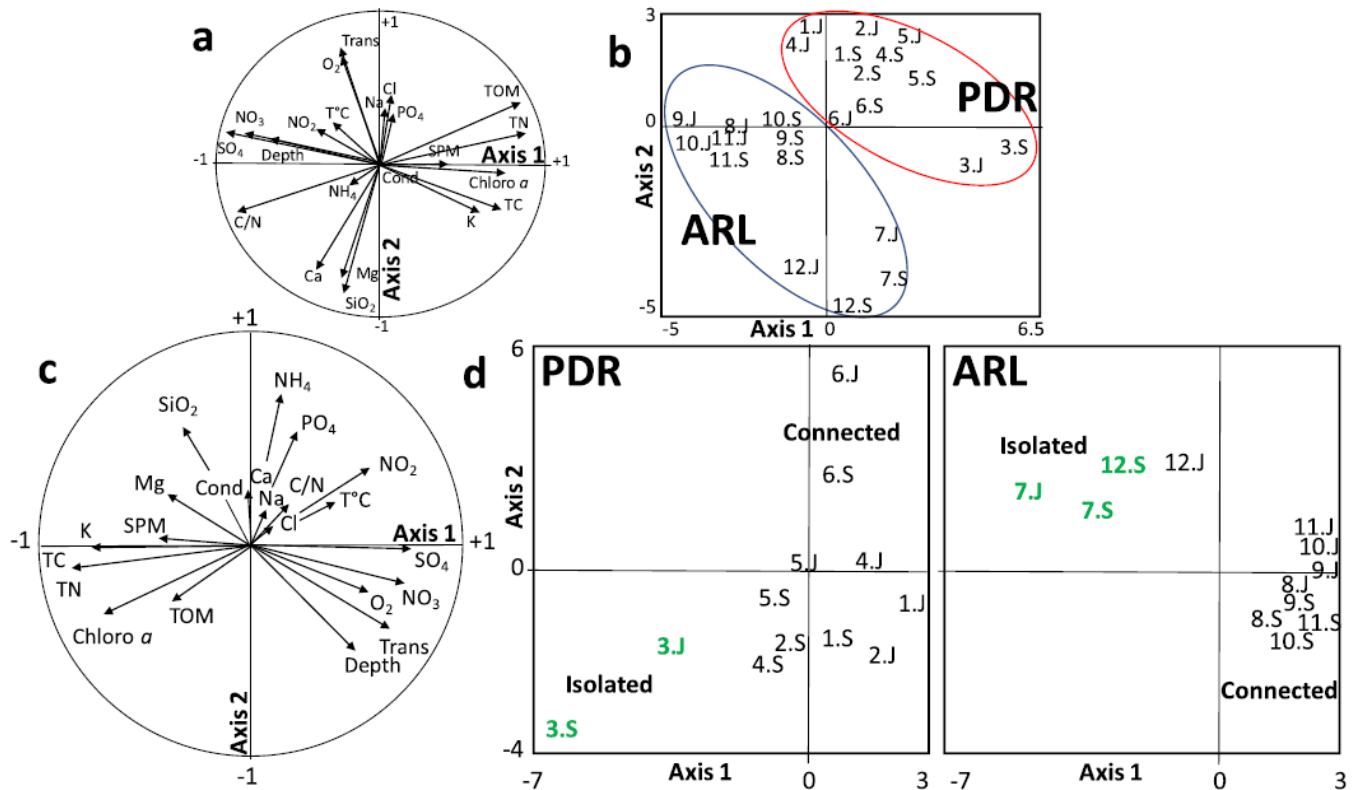
Fig. 2. Two Principal Component Analyses performed on 22 environmental characteristics (**a** and **c**) and 12 wetlands (6 in PDR and 6 in ARL, **b** and **c**) for June and September sampling. **a**, **b** Results of a PCA on reduced-centered data, without other transformations (Axis 1 = 31.1% and Axis 2 = 17.9% of the total inertia), **c**, **d** results of a within-class PCA removing between-section differences (Axis 1 = 36.9% and Axis 2 = 9.5% of total inertia). Isolated wetlands are noted in green and connected ones in black.

Table 2. Differences in physical and chemical characteristics between the two studied sections (PDR and ARL) at the two sampling periods (June and September) with wetlands used as replicates ($n = 6$ for each section, with one-way ANOVAs)

	Depth m	Conductivity µS cm^{-1}	Nitrate mg L^{-1}	Sulfate mg L^{-1}	Silica mg L^{-1}	Chloro a µg L^{-1}	TOM %	C :N
PDR								
June	1.18 ± 0.47	347 ± 24	1.6 ± 1.2	30 ± 14	1.5 ± 0.4	4.1 ± 4.1	4.6 ± 1.1	33 ± 8
September	0.99 ± 0.46	552 ± 44	1.5 ± 1.4	26 ± 11	1.3 ± 0.5	7.9 ± 8.4	4.7 ± 1.1	34 ± 6
ARL								
June	2.28 ± 1.65	428 ± 7	3.6 ± 1.9	48 ± 15	2.7 ± 0.8	0.8 ± 0.8	2.4 ± 0.8	63 ± 14
September	2.58 ± 1.61	449 ± 39	3.1 ± 2.4	39 ± 14	2.3 ± 0.8	2.3 ± 3.6	3.0 ± 0.4	51 ± 14
ANOVA								
June $F_{(1,10)}$		60.51			10.7		19.3	15.5
p value	n.s	0.00001	n.s	n.s	0.008	n.s	0.0013	0.0027
September	5.61	15.8			8.2		6.8	12.2
p value	0.039	0.0026	n.s	n.s	0.016	n.s	0.026	0.0057

Benthic microbial communities

The overall activity of biofilm estimated by the hydrolysis of the FDA (Fig. 3a, b) varied only slightly between sections, with wetland isolation, but greatly with organic matter characteristics (Fig. 3). This pattern was clear in June when FDA activity significantly increased with the quantity of organic matter (% of TOM in the sediment) and decreased with decreasing organic matter quality (C:N, Fig. 3). The relationships between FDA activity and organic matter characteristics disappeared in September, suggesting a homogenization of the esterase activity in the different wetlands.
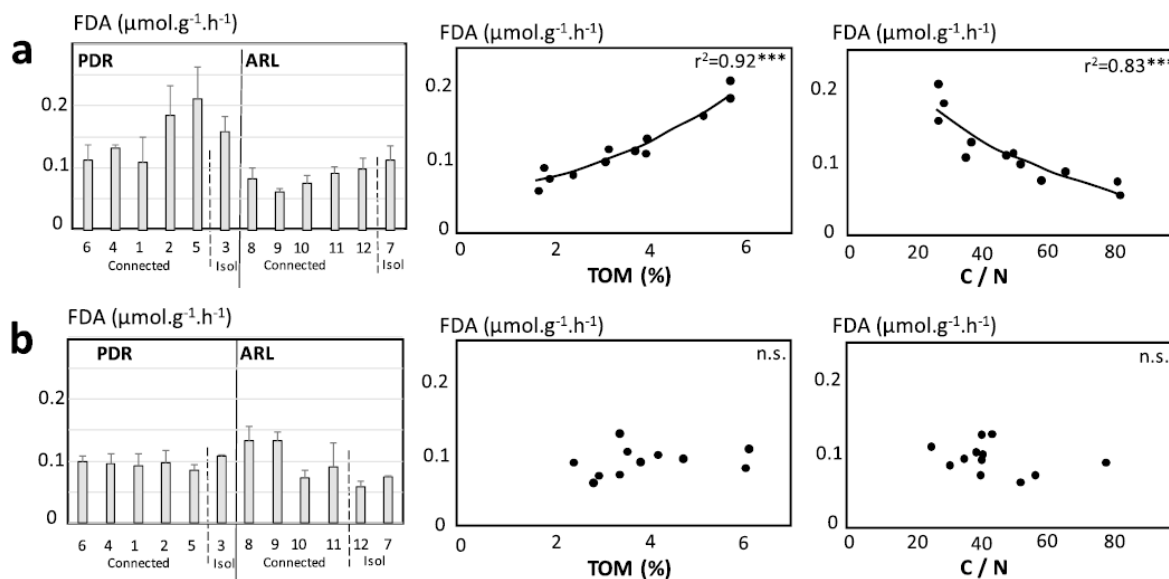

Fig. 3. FDA hydrolysis activity in the different wetlands of PDR and ARL (left) ranked by their connection level to the main channel. Relation between FDA hydrolysis and percentage of TOM in the sediment (center), and with C/N ratio (right), for June (**a**) and for September (**b**)

The functional profiles of microbial communities associated with wetland sediment measured using the BIOLOG method clearly separated the isolated ponds (especially wetlands 3 and 7, and, to a lesser extent, wetland 12) from the connected wetlands, but with clear differences between sampling periods (Fig. 4a, b).

In June, the wetlands were scattered along the 1st axis, with a clear separation between the two studied sections (ARL versus PDR, Fig. 4a): the ARL wetlands were located on the positive side of the 1st axis (32.4% of total inertia), characterized by high carbohydrate hydrolysis, while the PDR wetlands had negative coordinates, as microbial communities hydrolyzed a wide diversity of substrates (i.e. ranging from labile organic matter, such as carboxylic acid, amine and mainly amino acid, to poorly biodegradable substrates, such as phenols). Isolated wetlands 3 and 7 were separated from the other wetlands on the negative side of the 2nd axis (12.6% of total inertia), due to the very low activities for most substrates hydrolyzed by aerobic processes. During this first sampling period, the discharge of the Rhône River was rather high, and isolated pond 12 did not differ from the other connected wetlands.

In September, limited differences were observed between sections on the two axes (Fig. 4b), for both isolated and connected wetlands. The connected wetlands of both sections were strongly grouped on the 1st axis (27.5% of the total inertia), supporting a homogenization of microbial activities as suggested by the measures of esterase activity. The connected wetlands in ARL were slightly more negative on the 2nd axis (14.5% of total inertia) because of higher carbohydrate hydrolysis, while the PDR wetlands were located close to the origin, again due to homogenization of the substrates used by

microbial communities. In contrast, the isolated ponds were all located on the positive side of the 2nd axis (high carboxylic acid hydrolysis and low values for most other activities) but scattered on the 1st one (Fig. 4b): wetlands 3 and 7 were isolated on the positive side of the 1st axis because of low hydrolysis activities, while wetland 12 was located on the negative side of the 1st axis because of very high activities for most substrates.
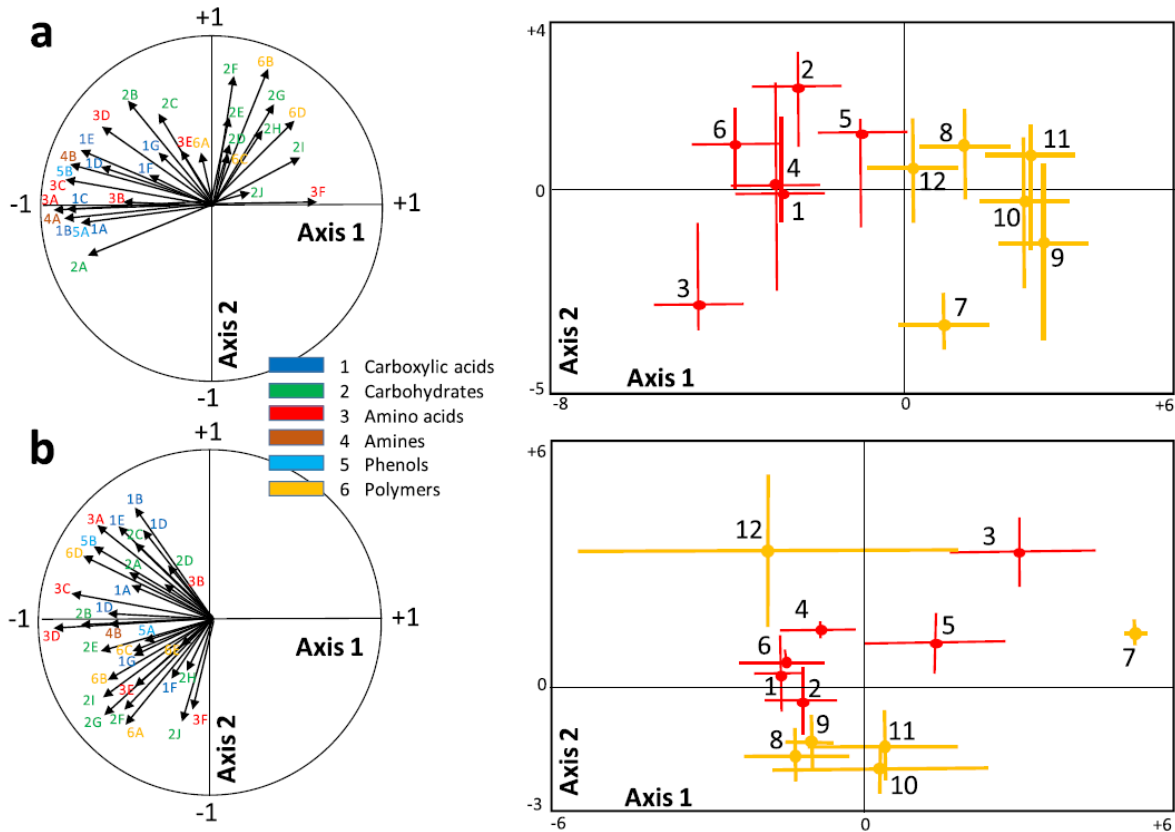

Fig. 4. PCA on microbial activities for June (**a**) and September (**b**). Axes 1 and 2 represent 32.4% and 12.6% of the total inertia in June and 27.5% and 14.5% in September, respectively. For each sampling period, the correlation circle (left) represents the relationships between the six types of hydrolyzed substrate and the Axis 1 × Axis 2 maps give the mean positions of the 12 wetlands and the intra-wetland variability (indicated by standard errors on both axes).

Benthic invertebrates

Few between-section differences were observed in the abundances and taxonomic richness of the benthic communities. In June, a total of 26,122 individuals and 8000 individuals were sampled in ARL and PDR, respectively, whereas the September abundances were quite similar, with a total 5692 individuals in ARL and 5553 individuals in PDR. Total taxonomic richness was lower in ARL than in PDR during both sampling periods: 32 and 21 taxa were sampled in ARL in June and September respectively, while 47 and 45 were sampled in PDR. Differences linked to the connectivity of the wetlands with the river channel were generally high: mean taxonomic richness was always lower in isolated wetlands (i.e. wetland 3 in PDR, 7 and 12 in September in ARL) than in the other connected wetlands (Fig. 5a). This is particularly true in PDR at both dates ($F_{(5,12)} = 7.64$, $p = 0.002$ in June, and $F_{(5,12)} = 4.38$, $p = 0.016$ in September) where the invertebrates sampled in the wetland 3 had lower taxonomic richness than all

other connected wetlands (post-hoc test, $p < 0.05$, except for station 4 in June and station 1 in September that were similarly poorly diversified). In ARL, the differences between wetlands were less marked and only significant in June ($F_{(5,20)} = 2.69$, $p = 0.050$) where the taxonomic richness of the assemblages sampled in the isolated station 7 was significantly lower than in the connected stations 10, 11 and 12 (post-hoc test, $p < 0.05$).

The composition of the benthic macroinvertebrate communities varied between wetlands more than between sections (fuzzy COA using ecological and biological traits, Fig. 5b, c). The analysis clearly grouped the isolated ponds of both ARL and PDR (3, 7 and 12 in September) on the negative side of the 1st axis (35.8% of the inertia) and on the positive side of the 2nd axis (16.4% of the inertia). These wetlands have similar invertebrate communities dominated by organisms with differing mobility traits: several organisms move by swimming (e.g. *Chaoborus* sp., Copepod Calanoida) and a few endobenthic organisms move slowly inside the bottom sediment (e.g. Clitellata). The communities of the isolated ponds are dominated by organisms feeding on sediment and detritus or predators hunting in bottom sediment (e.g. Ceratopogonidae).
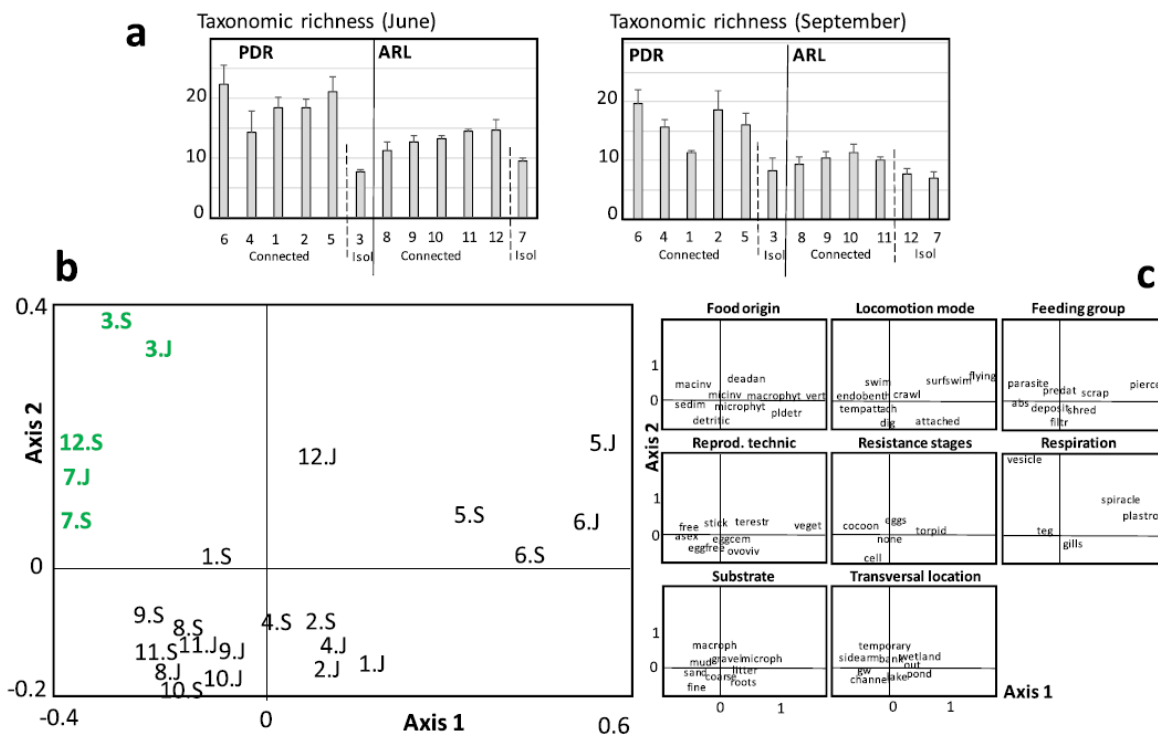
Fig. 5. Taxonomic richness in the 12 wetlands at each sampling period (mean values and standard errors, **a**). Fuzzy-coding correspondence analysis on benthic macroinvertebrates' functional traits showing location of samples on the Axis 1 × Axis 2 map (**b**) and location of biological and ecological traits (**c**, see codes in Table 1). Axes 1 and 2 represent, respectively, 35.82% and 16.38% of total inertia. Isolated wetlands are noted in green and connected ones in black (color figure online)

The more connected ponds were separated into two groups. Firstly, PDR wetlands 5 and 6 on the positive side of the 1st axis had a fauna that was diversified but dominated by organisms living and reproducing on vegetation (e.g. Molluscs and Zygoptera), those with respiration via a plastron or a spiracle (e.g. Planorbidae, *Radix* sp.), scrapers (e.g. *Physella acuta*, *Potamopyrgus antipodarum*) or predators hunting in the open water (e.g. *Coenagrion* sp., *Platycnemis* sp., Micronectinae). Secondly, all the other wetlands from both sections (4, 1, 2 in PDR and 8 to 11 in ARL), were located on the negative side of the 2nd axis and characterized by species with a wide range of traits. Some organisms live in the

flowing water of the main channel (e.g. Amphipoda *Gammarus*, Trichoptera *Ecnomus* sp., Ephemeroptera *Caenis* sp.), fixed to or closely associated with the coarse substratum (e.g. *Hydra* sp., Amphipoda *Echinogammarus* sp., and *Chelicorophium* sp.). Others occur frequently in slow-flowing secondary channels, associated with sand and fine sediment (e.g. Diptera Chironominae or Ephemeroptera *Ephemera* sp.), filtering surface water (e. g. Molluscs *Corbicula* sp. and *Sphaerium* sp. or Cladocera) or feeding on detritus and fine sediment (e.g. Chironominae, Polychaeta *Hypagna invalida*).
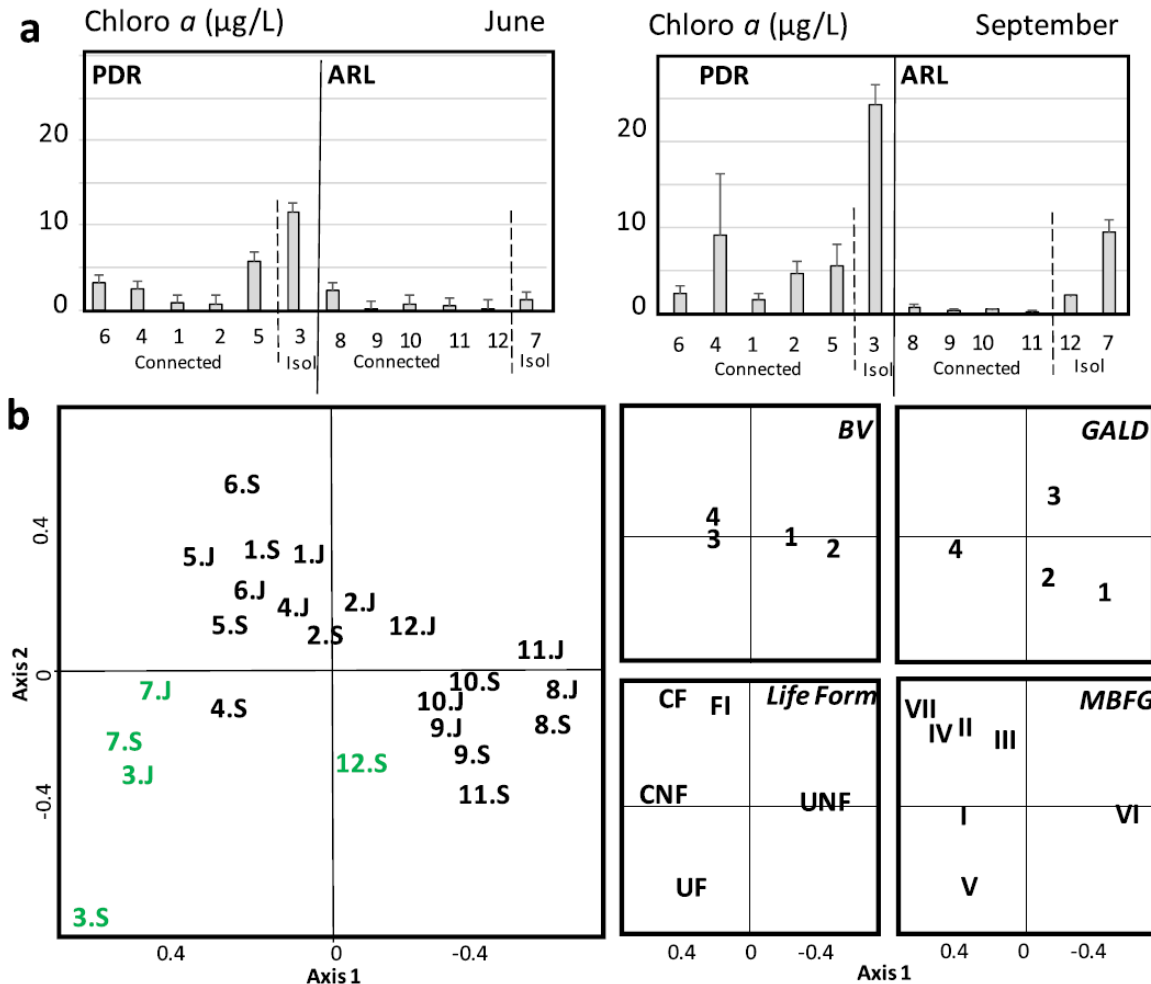
Phytoplancton

Regarding phytoplankton quantity, the active chlorophyll *a* content (Fig. 6a) was lower in ARL (from 0.13 to 9 µg L^{-1}) than in PDR (0.70 and 24 µg L^{-1}, respectively), but with significant differences between wetlands of the same section. In the PDR sector, the chlorophyll *a* content measured in the isolated wetland 3 was significantly higher than in most of the connected wetlands in June ($F_{(5,12)} = 4.05$, $p = 0.022$), especially with stations 1 and 2 (post-hoc test $p < 0.05$). In September, the wetland 3 had higher chlorophyll *a* content than all other wetlands ($F_{(5,12)} = 4.48$, $p = 0.015$), except station 4 where phytoplankton was well developed at the end of the summer. In the ARL sector, low and homoge-neous chlorophyll *a* values were measured in June, while significant differences appeared for wetlands 7 and 12 in September ($F(5,20) = 87.3$, $p = 7.10–13$), where chlorophyll *a* contents were higher than in all other wetlands (post-hoc test, $p < 0.05$). In a similar way, the highest concentration of phytoplanktonic cells was observed in wetlands 3 (3400 to 5300 cells mL^{-1}) and 7 (4700 to 13,000 cells mL^{-1}). In contrast, no significant differences were observed for phytoplanktonic species richness, neither between the two sections (from 9 to 36 in PDR and from 11 to 29 in ARL) nor between the isolated and the connected wetlands.

For community composition, the dominant taxa sampled differed between the two sections: Chrysophytes, Chlorophytes, Euglenophytes and Dinoflagellates were more abundant in PDR, while Cryptophytes and Diatoms were more abundant in ARL. Cyanobacteria were present in both sections. The two sections also differed in the dominant functional traits of their communities (Fig. 6b). Most of the ARL wetlands (except 7) were located on the positive side of the 1st axis (representing 41.6% of the inertia), with rather similar communities dominated by non-flagellated unicellular species (UNF) of small size (BV1-2, GALD1-3) and belonging to the MBFG VI group (non-flagellated organisms with siliceous exoskeletons, i.e. Diatoms). On the negative side of this 1st axis, the PDR wetlands were characterized by large species (BV3-4 and GALD 4) with a wide range of functional traits: flagellate unicellular species (UF: Euglenophytes, Dinoflagellates MBFG V), colonial species with flagellate cells (CF: Chrysophyte *Dinobryon divergens* -MBFG II- and Chlorophyte *Pandorina morum* -MBFG VII) or with non-flagellate cells (CNF: *Scenedesmus* sp.) and some filamentous species (FI: *Spirogyra varians* -MBFG IV).

Examining differences between wetlands of the same section, connection to the channel was found to play a major role. The two wetlands isolated from the Rhône channel (i.e. 7 in ARL and 3 in PDR) were located close together on the negative side of the 1st and 2nd axes (Fig. 6b), having communities very poor in Diatoms (consistently less than 1% of the community) but rich in large species (BV3-4 and GALD4) and unicellular mobile species (UF). The dominant species of these isolated wetlands differed: Dinoflagellate *Ceratium hirundinella* in wetland 3 and Cyanobacteria *Planktothrix aghardii* in 7.

The other wetlands connected to the Rhône River showed a different set of phytoplankton species, but again with high between-section differences. The connected PDR wetlands (i.e. 6, 4, 1, 5) were located on the positive side of the 2nd axis (representing 21.8% of the inertia, Fig. 6b) rich in large (BV4), colonial (CF and MBFG VII, II) or filamentous species (FI and MBFG III or IV) sometimes associated

with macrophytes (e.g. *Ulothrix* sp.). In contrast, the connected ARL wetlands (i.e. 8, 10, 11) were located on the positive side of the 1st axis, with small (BV1-2) non-flagellated unicellular species (UNF) such as Diatoms (MBFG VI e.g. small centric species like *Cyclotella* sp.).

Fig. 6. Phytoplankton characteristics. **a** Chlorophyll *a* content in the 12 wetlands ranked according to their connection level with the main channel, in June (left) and September (right). **b** Fuzzy COA on phytoplankton functional traits (based on Cellamare et al. 2013 and Kruk et al. 2010). Axis 1 × Axis 2 map for wetlands (left) and for functional traits (right). Axes 1 and 2 represent, respectively, 41.6% and 21.8% of total inertia. Isolated wetlands are noted in green and connected ones in black (color figure online).

Discussion

Environmental characteristics and connectivity

Few differences in water and sediment characteristics were observed between the two river sections studied (PDR and ARL). Silica concentrations (and to a lesser extent, nitrate and sulfate concentrations) were higher in the downstream section (ARL), no doubt due to the longitudinal enrichment in solutes observed in most river basins (e.g. Lefebvre et al. 2007; Hensley et al. 2020). In contrast, the quantity and quality of the organic matter found in the bottom sediment were higher in the upstream section (PDR), clearly because of the morphometric characteristics of the wetlands there. Firstly, these wetlands are shallow compared to those of ARL and therefore more conducive to macrophyte development due to better light penetration. Secondly, they are located along a by-passed channel of the Rhône and less frequently connected to the river than the ARL wetlands, which means their sediments are less frequently eroded and washed out (Räpple 2018).

In comparison, the within-section differences between wetlands were very consistent and directly linked to their degree of connection to the river, as suggested by Guillon et al. (2019; H1 confirmed). The isolated wetlands (3 in PDR, 7 and 12 for September in ARL) were characterized by sediment with high TOM, TC, and TN, together with very high Chlorophyll *a* concentrations and very low transparency of the surface water. All these characteristics suggest very high primary production which, after deposition, results in sediments with high organic matter quality (C:N was generally low in the isolated wetlands). The conditions also lead to limited light-exposure in the bottom sediment and lower macrophyte development compared to phytoplankton (Santonja et al. 2018), as observed in many stagnant ponds (i.e. the "marsh type" suggested by Guillon et al. 2019). Additionally, these isolated wetlands are characterized by low dissolved oxygen, nitrate, and sulfate concentrations, suggesting anoxic microbial processes (see 5.2 below). Conversely, the wetlands well-connected to the river channel or the by-passed channel harbored weaker primary production, with lower Chlorophyll *a* concentrations in the water, lower quantity and quality of the organic matter stored in the sediment, high available dissolved oxygen, together with high nitrate and sulfate concentrations in the water column (suggesting low or no anoxic microbial processes).

Similar trends in primary production, OM sediment content, and water chemistry were previously observed in natural or artificial wetlands (e.g. Chen and Twilley 1999; Espanol et al. 2015), especially in wetlands located in alluvial plains, where connections to the river channel are crucial (Buijse et al. 2002; Jungwirth et al. 2002; Paillex et al. 2009, 2013). For example, Tockner et al. (1999) showed close relationships between the Danube River discharge, the connectivity between the main channel and wetlands, and Chlorophyll *a* and organic matter concentrations in the floodplain backwaters. In our two river sections, as in a natural floodplain, the hydrological connectivity between the main channel and wetland controlled the physical and chemical characteristics of these artificial wetlands.

Connectivity and diversity of microbial activities

Fairly consistent differences in microbial activities were found between the two sections: higher functional diversity (i.e. number of substrates used by biofilms) in PDR than in ARL, at least in June. As described above, in upstream PDR, the wetlands are shallow (allowing light to reach the bottom sediment) and less connected to the channel (reducing sediment erosion). These conditions likely enhance the diversity of available organic substrates used by microbial assemblages in PDR, explaining the higher functional diversity of microbes, as already observed in marine sediment (Fagervold et al. 2014) and streams (Zeglin 2015).

Wetland connectivity with the main channel had a noticeable effect on within-section heterogeneity of microbial processes, associated with the 2nd PCA axis at both sampling periods. In the isolated wetlands (3, 7, and 12 in September), the high primary production and quantity of organic matter stored in the sediment explain the specific range of substrate used. There was also a decrease in dissolved oxygen that resulted in a decrease in nitrate (certainly through denitrification) and sulfate (certainly through sulfato-reduction) in the isolated wetlands. Similar links between connectivity and anaerobic processes such as denitrification have frequently been documented in floodplains (e.g. Argiroff et al. 2017).

In contrast, the connected wetlands were characterized by high concentrations of dissolved oxygen, even close to the bottom sediment in PDR section (Guillon et al. 2019), resulting in the dominance of aerobic processes and high concentrations of nitrate and sulfate. The microbes degraded a wide range of substrates, especially in June. Similar seasonal change was observed in esterase activity, with a significant correlation of the rate of FDA hydrolysis with organic matter quantity (%TOM) and quality (C:N) in June, which disappeared in September. Such seasonal changes in microbial activities in wetlands have been documented in side channels, floodplains of rivers or artificial wetlands. While generally linked to changes in water level or drying (Hefting et al. 2004; Foulquier et al. 2013), they have also been attributed to temperature increases modifying oxygen availability and organic matter consumption (e.g. Stein and Hook 2005, for artificial wetlands). Despite this homogenization of microbial activities in the connected wetlands in September, the differences between connected and isolated wetlands remained fairly consistent in both periods, although generally less pronounced than the differences between sections. The expected relationship between connectivity and functional diversity (2nd hypothesis) is thus partially confirmed for benthic microbes.

Connectivity and benthic invertebrate functional diversity

Despite the lower taxonomic richness in ARL than in PDR, the two sections showed minor differences in assemblage composition: some species were more abun dant in PDR (e.g. Molluscs *Physella acuta, Potamopyrgus antipodarum, Valvata* sp., or Ephemeroptera *Baetis* sp. and *Caenis* sp.), while others were more abundant in ARL (e.g. *Corbicula* spp., *Ephemera* sp., Tanytarsini and *Chironomus thummi* group). This illustrates the differences in physical characteristics between the shallower and more isolated PDR wetlands and those in ARL. Nevertheless, the functional characteristics and diversity of the benthic assemblages were fairly similar in the two sections (see Fig. 5b).

In contrast, there was strong within-section wetland heterogeneity, according to the wetlands' degree of connectivity with the river channel. In the isolated wetlands (3, 7, and 12 in September), several organisms were swimmers or lived inside the bottom soft sediment; most fed on this fine sediment, rich in organic matter (e.g. Clitellata) resulting from algal production, sedimentation and protection from erosion. In these isolated wetlands, the functional diversity of the benthic assemblages was weak. The connected wetlands' assemblages, on the other hand, differed according to the degree of vegetation development. In the vegetation-rich wetlands ("aquarium type" in Guillon et al. 2019), assemblages were dominated by organisms living on the vegetation (e.g. Zygoptera), scrapers (e.g. *Physella acuta*) or swimming predators (e.g. Micronectidae). In the other wetlands, widely open to the channel and poorly vegetated, assemblages were dominated by species living in the main channel of the river (e.g. *Gammarus* sp., *Ecnomus* sp., *Caenis* sp.) with affinities to a wide range of sediment grain size (e.g. *Gammarus* sp. and *Echinogammarus* sp.). In both cases, benthos functional diversity was higher in the connected than in the isolated wetlands.

The importance of connectivity for floodplain biodiversity was pointed out by Ward et al. (1999) for the Danube River, by Paillex et al. (2009) for natural wetlands along the Rhône River, or by Gallardo

et al. (2008 and 2014) for several river floodplains under different climates. Artificial wetlands may play a similar role to natural ones, at least when nutrients and organic matter are available and of good quality (Espanol et al. 2015). Our results support the hypothesis of a strong link between connection to the main channel and the functional diversity of benthic invertebrates at the floodplain scale (2nd hypothesis confirmed for aquatic invertebrates), with some weak differences between sections due to morphometric characteristics and vegetation development.

Connectivity and plankton functional diversity

In contrast to benthic invertebrates, strong between-section differences were observed in phytoplankton assemblages, certainly because of differences in the geometry of the wetlands. The ARL wetlands are deeper and more connected to the channel, resulting in weak functional diversity of the phytoplankton. These were dominated by small non-flagellated algae, such as Diatoms (MBFG VI group), rapid-growing r-strategic species (Reynolds 2006) with low light and high-turbulence tolerance (Kruk et al. 2010; Naselli-Flores et al 2021). In contrast, the PDR wetlands offer a wide range of shallow habitats, relatively protected from the influence of the river (here a by-passed channel), resulting in high functional diversity (MBFG I to V and VII groups present; Kruk and Segura, 2012). They host a combination of small organisms, unicellular (e.g. *Chlorella* sp. nanoplanktic forms, fast-growth-rate strategy and high quality as food) or colonial (e.g. *Dinobryon divergens*, MBFG II, flagellated organisms with low to moderate sinking, low-nutrient tolerance and capacity for mixotrophy in oligotrophic conditions, Saad et al. 2016), large motile unicellular species (e.g. the mixotrophic and phagotrophic species, Dinoflagellates *Peridinium sp., Ceratium hirundinella* or Euglenophyte *Euglena* sp., MBFG V), together with some mucilaginous colonies (e.g. K-strategic Chlorophyte *Pandorina morum*, MBFG VII with a preference for high-temperature, high-trophic and low-mixing conditions), and some filamentous forms (e.g.*Spirogyra varians*, K-strategic species, MBFG IV).

The within-section differences between wetlands were less marked. Wetlands connected to the river harbored a set of species that differed between sections: large, unicellular, colonial or filamentous species (sometime associated with macrophytes like *Ulothrix* sp.) in PDR, small non-flagellated unicellular species, such as Diatoms (e.g. *Cyclotella* sp.), in ARL. Small Diatoms are rapid-growing r-strategic species (Kruk et al. 2010), but they are poorly motile organisms with a siliceous exoskeleton that increases density, sinking rate, and sedimentation (Kruk and Segura 2012). A siliceous wall is a disadvantage in stagnant water (Sommer 1996); mixing favors the negatively buoyant Diatoms (Naselli-Flores et al. 2021). Moreover, the sinking rate is higher in spherical species such as the diatom *Cyclotella sp.* than in elongated organisms of similar size (Durante et al., 2019). The permanent connection of the ARL wetlands with the main channel maintains a high level of water turbulence that may limit this sedimentation and promote the development of a Diatom-rich assemblage. Turbulence, a key driver of biological traits of phytoplankton (Naselli-Flores et al. 2021), appears to be key in these constructed wetlands too.

Contrastingly, the isolated wetlands (3 in PDR, 7 in ARL) showed similar phytoplankton characteristics: a high biomass (high Chlorophyll *a* content), a high proportion of large flagellated mixotrophic and phagotrophic organisms (MBFG V), and very few non-flagellated organisms with siliceous exoskeletons, i.e. Diatoms (MBFG VI less than 1%). Once again, however, the dominant species differed between sections: Dinoflagellate *Ceratium hirundinella* in wetland 3 and Cyanobacteria *Planktothrix aghardii* in 7. *C. hirundinella* is a large motile and mixotrophic organism with low sinking losses, sensitive to mixing and tolerant to low nutrient availability, grazing, K-strategic, frequently sampled in organic-rich ponds, in summer epilimnia in eutrophic conditions (Kruk et al. 2010; Reynolds 2006). *P. aghardii* is a highly competitive Cyanobacteria species with a low sinking rate, also tolerant to limited light conditions, high turbidity, low nutrient availability, grazing, present in highly enriched

shallow waters (Reynolds 2006). The dominance of these species in the isolated wetlands testified to their reduced turbulence and to their light availability and enrichment in organic matter.

In conclusion, the predicted importance of connectivity as a driver of wetland functional diversity is partially supported by our findings on phytoplankton (2nd hypothesis partially confirmed). However, other environmental characteristics such as water depth, transparency, and nutrient loads may also control phytoplankton dynamics at the river section scale, as suggested by Reynolds 2006 and Naselli-Flores et al. 2021.

Effect of the dominant organisms on ecological processes

The composition of benthic and planktonic assemblages is not wholly dependent on the physical and chemical characteristics of the habitat. Some organisms (or groups of organisms) can modify the available resources for the rest of the community (i.e. ecological engineers, Jones et al. 1994). In the wetlands studied here along the Rhône River, phytoplankton primary production certainly controlled the level of microbial activities, especially in the isolated wetlands. The high concentrations of Chlorophyll a measured in wetlands 3 and 7 suggest intense primary production of organic matter enriching the bottom sediment with a range of high-quality substrates that supported high and diversified microbial activities (at least in June). This biological stimulation of biofilms resulted in partial anoxia of the bottom sediment and a reduction of nitrate and sulfate concentrations (denitrification and sulfato-reduction). This succession of processes has frequently been observed in systems with high phytoplankton production (e.g. in upwelling zones, Canfield 2006).

The strong development of the phytoplankton also impacted the benthic invertebrate communities. In the isolated wetlands, organic-matter enrichment of the bottom sediment resulted in an increase in endobenthic invertebrates feeding on fine organic sediment (e.g. Clitellata, Nogaro et al. 2006). However, the associated decrease in available oxygen (Guillon et al. 2019) also induced a decrease in taxonomic richness, significantly weaker in the isolated wetlands (3 and 7) than in the connected ones. Assemblages promote certain traits to avoid these locally anoxic conditions (increased numbers of swimmers, respiration with vesicles, Gallardo et al. 2014) or modify their spatial distribution. For example, Van der Lee et al. (2017) showed that during anoxic periods, invertebrate consumption of benthic detritus decreases, as detritivorous invertebrates move to the pelagic layer to consume particulate organic matter. In contrast, low phytoplankton productivity has been shown to increase light penetration and stimulate macrophyte growth (in some cases, with a reduction of the allelopathic inhibition of this growth, Santonja et al. 2018). As a result, dense aquatic vegetation developed in some of the connected PDR wetlands, supporting a wide range of macroinvertebrate species living and feeding on macrophytes (e.g. some Gastropoda like *Radix* sp. or *Valvata* sp., some Ephemeroptera like *Baetis* sp., Tachet et al. 2010).

Phytoplankton can also constitute a feeding resource for many filtering invertebrates (such as Bivalvia and Cladocera), but the biological characteristics of the phytoplankton species present are crucial to this consumption by invertebrates. Some taxa are known to produce toxins (e.g. some Harmful Cyanobacteria, Burford et al. 2020). The size of the phytoplankton cells also determines their use at higher trophic levels. For example, taxa of GALD $< 35\,\mu m$ include small and edible specimens whereas taxa of GALD $> 35\,\mu m$ include large and inedible organisms (Hulot et al. 2000). The phytoplankton of isolated wetlands 3 and 7 was dominated by large species (GALD 3 and 4) unsuitable as feeding resources for invertebrates.

Benthic invertebrates may also include some species with an active role in ecological processes. Some of the Gastropods sampled in the connected PDR wetlands (e.g. *Physella acuta, Potamopyrgus antipodarum*) feed on algal periphyton (Tachet et al. 2010), potentially limiting its development on macrophyte leaves (do Nascimento Filho and do Nascimento Moura 2021) or at the surface of bottom

sediment (Estragnat et al. 2018). Benthic invertebrates sampled in the wetlands may also play an important role in the bioturbation of the bottom sediment and nutrient production (e.g. Clitellata, Fukuhara and Sakamoto 1987) or in the biodegradation of dead macrophyte leaves (e.g. *Gammarus* or *Echinogammarus*, Boiché et al. 2011).

In regards to the field of the aquatic sciences, the hypothesis that aquatic communities (through their functional traits) contribute to the modification of environmental characteristics and the resulting ecological processes only applied to phytoplankton in the present study (3rd hypothesis verified). However, future research could usefully consider the role of other groups in wetland functioning (Estragnat et al. 2018), especially for the development of innovative restoration plans (Thorel et al. 2018). Indeed, the functional restoration of ecosystems and the maintenance of ecosystem services require the identification of drivers inducing communities with particular functional characteristics. Among these drivers, the hydrological connectivity, allowing water and nutrients exchanges and also organisms displacement appears to be one of the first to be considered (Batzer et al. 2015).

Conclusions

The predicted major role of connectivity with the main channel in the functioning of artificial riverine wetlands was confirmed here for environmental characteristics (water and sediment), for benthic invertebrates and, to a lesser extent, for benthic microbial communities (at least in June). In contrast, the phytoplankton community was driven by connectivity mainly in terms of biomass (an increasing chlorophyll *a* gradient from connected to isolated wetlands), but less than expected in terms of composition. Heterogeneity in dominant species and major biological traits depended more on the river section (PDR versus ARL) than on the degree of connection to the river channel. These between-section differences may be explained by the geometry of the wetlands (depth and resulting light penetration), which also influence water chemistry and microbial activities. It is thus essential to jointly take into account the connectivity with the river channel and the geometry of the wetland, to understand the functional diversity of organisms and the ecological processes that take place in constructed wetlands. This is particularly pertinent to the design of restoration programs, where it is important to define which single species (or group of species with similar traits) can act as efficient engineers for the particular ecosystems being protected or enhanced.

Thorel, M. et al. (2022). Does hydrological connectivity control functional characteristics of artificial wetland communities? Evidence from the Rhône River. **Aquatic Sciences** 84: 66. https://doi.org/10.1007/s00027-022-00889-w

Declarations

Conflict of interest.
Authors declare no conflict of interests.

Data availability statement.
Some Data are in supplementary information, the other data will be made available on reasonable request.

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