

Nutrient dynamics in river bed sediments: effects of hydrological disturbances using experimental flow manipulations

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Abstract

Purpose River sediments play a crucial role in the storage and transformation of organic matter (OM). Nutrient dynamics are controlled by the interaction of several key parameters, i.e. river discharge, channel geometry and vertical exchanges of water (upwelling vs. downwelling zones). The main aim of this study was to evaluate the effect of channel forms and discharge variation on nutrient spiralling in the hyporheic zone (HZ) of streams.

Materials and methods Four experimental flow manipulations (EFM) were carried out at two reaches with different channel forms (straight vs. sinuous) in an oligotrophic subtropical river in Australia. Flow manipulation consisted of reducing the river width with a temporary dam, diverting and concentrating the main water flux on two different geomorphological units (riffle vs. gravel bar), in order to simulate flooding conditions. Hyporheic waters were analysed for their physicochemical characteristics and nutrient (nitrates+nitrites= NO_x and soluble reactive phosphorus [SRP]) and OM contents at two depths (10 and 50 cm)

within the bed sediments, both upstream and downstream of the geomorphological units.

Results and discussion The physicochemical parameters clearly demonstrated the existence of hyporheic flow paths, characterized by the alternation of downwelling and upwelling areas, with more consistent gradients in gravel bars than in riffles. The HZ acted as source for NO_x and SRP, but this role varied between geomorphological units and reaches. The effect of EFM differed between sampling points, irrespective of the type of geomorphological unit. In gravel bars, a flush out during high discharge was observed for NO_x , SRP and particulate organic matter (POM) at the sinuous channel, whereas storage and removal were recorded at the straight channel for SRP and NO_x , respectively. At the riffle of the sinuous channel, very fine POM accumulated, while removal was noticed for POM. In contrast, at the riffle of the straight channel, SRP accumulated in the HZ and NO_x was removed out of the HZ.

Conclusions Nutrient dynamics in the HZ and the response to flow increases were not governed by the geomorphological unit type. Other parameters that determine water residence time in the sediments, such as local heterogeneity in sediment characteristics (grain size, porosity and hydraulic conductivity), channel sinuosity, reach slope and the size and form of the gravel bar, may be more significant explanatory variables for understanding OM and nutrient dynamics in the HZ. This study emphasizes the need for caution in making generalisations about the role of river sediment in nutrient storage and the impact of floods on nutrient dynamics.

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1 Introduction

Riverbed sediments play a crucial role in stream ecosystem functioning (Jones and Holmes 1996; Fisher et al. 2004). Lying underneath the riverbed, the hyporheic zone (HZ; Orghidan 1959) is recognised as an important location for biogeochemical processes such as organic matter (OM) storage and degradation (Marmonier et al. 1995; Rulik et al. 2001), phosphorus (P) adsorption and transformation (Butturini and Sabater 1999; Vervier et al. 2009) and nitrification or denitrification (Dahm et al. 1998; Lefebvre et al. 2005). Depending upon the dominant processes and the exchange rate with the surface water, the HZ may act either as a nutrient source or sink for the river system (Jones and Holmes 1996; Dahm et al. 1998). Thus, the HZ contributes to river productivity when it is a source of nutrients (Opdyke et al. 2006; Mouw et al. 2009) or to inorganic nutrient limitation when it is a sink of nutrients (Baker and Vervier 2004; Kasahara and Hill 2006). The source/sink equilibrium is partly controlled by vertical exchanges of water between the river and the HZ, thus by sediment characteristics, local geomorphology, alluvium depth, as well as the hydrology of the river (Tonina and Buffington 2007, 2011).

First, channel geomorphology influences the vertical exchanges of water between the river and the HZ (Cardenas et al. 2004; Kasahara and Hill 2006; Hester and Doyle 2008). Obstacles, such as transverse riffles and gravel or sand bars, can increase upstream surface water levels, which enhances downwelling or infiltration into the streambed when its porosity allows (White 1993). Downstream of these obstacles, the hyporheic water (a mix of surface water infiltrated in downwelling zones with deep groundwater) exfiltrates toward the river, resulting in upwelling zones (Valett et al. 1994; Jones et al. 1995). Alternating downwelling and upwelling zones substantially influence river productivity and function by supporting processes that consume or deliver inorganic nutrients (Dent et al. 2001).

Second, flow variability is a key factor in determining most ecological patterns and processes in running water ecosystems (Richter et al. 2003; Datry and Larned 2008; Poff and Zimmerman 2010). A river's flow regime is of paramount importance for sustaining biodiversity and ecological integrity (Bunn and Arthington 2002), which may support the development of regional environmental flow standards (e.g. Ecological Limits of Hydrologic Alteration; Poff et al. 2010). Poff et al. (1997) have characterised flow variations into five major components: magnitude, frequency, duration, timing and rate of change. In this context, flood and drought events correspond to extreme forms of flow variation and have significant consequences on ecological processes.

High discharge variations contribute to river morphodynamics (Creuzé des Châtelliers et al. 1994) and, conversely,

channel geomorphology influences surface water movements during medium to low discharges (Bates 2004). These interactions between geomorphology and hydrology modify the rate of exchanges (Poole et al. 2006) and ultimately affect the biogeochemical processes. These interactions between river discharge and processes along hyporheic flow paths are complex (Poole 2010) and dynamic (Wondzell and Swanson 1999) since changes in river discharge can restructure hydrologic flow networks (including preferential hyporheic flow paths) and thus influence the redox environment and anaerobic metabolism in the HZ. Fisher et al. (2007) plead for a better integration of geomorphology and ecological processes at a variety of scales. With this in mind, it is of great interest to understand how HZ functioning and nutrient cycling are affected by geomorphic structures and their local heterogeneities, as well as by the intensity and duration of discharge variations. Studies that consider geomorphology, flow regime and nutrient dynamics simultaneously are uncommon.

The aim of this work is to determine how geomorphology and hydrology affect biogeochemical processing (i.e. nutrient cycling) in the HZ. To examine the complexity of the interactions between these factors, we studied the effect of experimental flow manipulations (EFM) on the dynamics of dissolved oxygen (DO) and nutrients (nitrate+nitrite= NO_x and soluble reactive phosphorus [SRP]) in an oligotrophic subtropical river in two types of geomorphological units (i.e. riffle and gravel bar). The sink or source role of the HZ was determined for each nutrient by comparing paired changes in concentrations along assumed flow paths (i.e. downwelling to upwelling) over experiments of similar intensities and durations. For generalisation purposes and in order to take into account local heterogeneity, these two experiments (riffle and gravel bar) were repeated in another reach with different form. We hypothesised that local heterogeneity, such as channel form, reach slope and hydraulic conductivity, would affect the exchanges between surface and hyporheic waters during flow experiments. We aimed to identify:

1. The spatial patterns of hyporheic flow paths in the two geomorphological units, with the hypothesis of a stronger gradient for water chemistry in bars owing to longer flow paths;
2. Whether the HZ acts as a source or a sink of nutrients and OM, with the hypothesis that its potential role as a source is more important in gravel bars than in riffles owing to shorter residence time in riffles; and
3. Whether the EFM affect nutrient (nitrogen (N) and P) and OM storage in riffles and in gravel bars and how this effect is influenced by local heterogeneity, with the hypothesis of a flush out in riffles and a minor removal in gravel bars.

2 Material and methods

2.1 Study site

The study site is located in the Never Never River (30°21' S, 152°54' E), a subtropical third-order gravel-bed river in northern New South Wales, Australia (Fig. 1). The river catchment (94.6 km²) lies in Dorrigo National Park and World Heritage Area (970 m a.s.l.). Mean annual rainfall in the area is 1,497 mm, with the majority of this falling in austral summer (January to March). In addition, air temperature ranges from 6 to 29 °C. For details on the catchment characteristics, see Boulton and Foster (1998).

The experiments were conducted along one channel in two reaches (1 and 2), located 250 m from each other. At each reach, a riffle (R1 and R2) and its adjacent gravel bar (GB1 and GB2) were selected. At reach 1, width ranged from 3 to 5 m at the riffle and from 8 to 10 m alongside the gravel bar. At reach 2, width was from 3 to 4 m at the riffle and from 5 to 8 m alongside the gravel bar. The median particle diameter (D_{50}) based on the measurement of 50 randomly selected particles (Kellerhals and Bray 1971; Claret et al. 1998) was finer in GB1 (37.5 mm) than in GB2 (55 mm), but coarser in R1 (61 mm) than in R2 (47 mm). Gravel bar shapes differed; GB1 was narrow and

stuck to the riverbank, while GB2 had a strongly convex apex resulting in a hump inside the channel (see Fig. 1).

2.2 Experimental design

EFM were conducted in December 2000, when discharge was approximately 1.2 m³s⁻¹, after a period of around 5 months without significant flooding. The flow manipulation consisted of reducing the river width with a temporary dam and concentrating the water flow on a riffle or on a bar (see Fig. 1), raising the water level upstream of the dam by 30–50 cm and increasing the water velocity by threefold to fivefold. The four EFM were carried out successively, starting with the downstream bar (GB2), then the upstream bar (GB1), the downstream riffle (R2) and finally the upstream riffle (R1); each EFM lasted 12 h. In riffles, hyporheic water was sampled before and during the EFM; in gravel bars, hyporheic water was sampled before and during the EFM and after the dam removal (Fig. 2). Samples were collected 10 and 2 h before the dam installation (T1 and T2, respectively). Once the dam was set up, sampling took place 2 and 10 h later (T3 and T4, respectively). After the dam was removed and the natural water elevation was restored, sampling was carried out 48 h later (T5) in gravel bars only. Since a natural flood of similar amplitude occurred 2 days

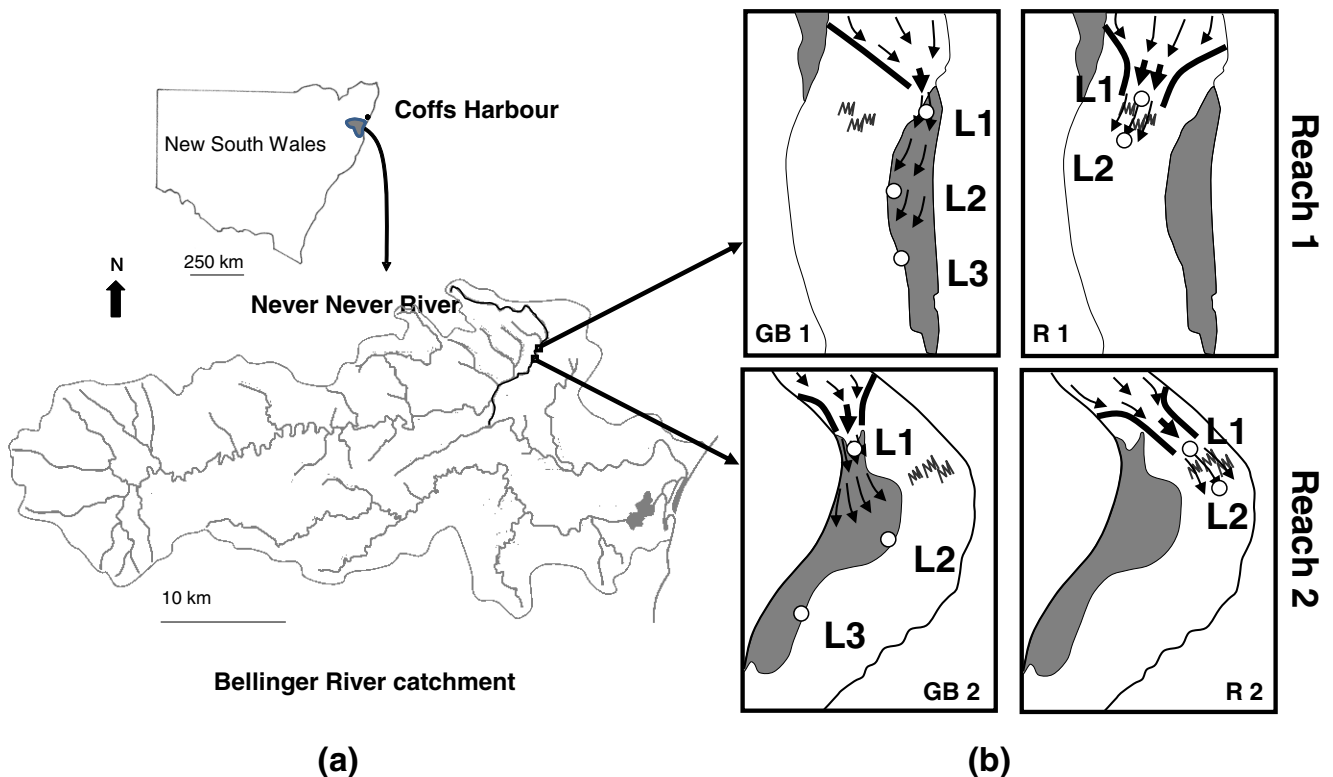
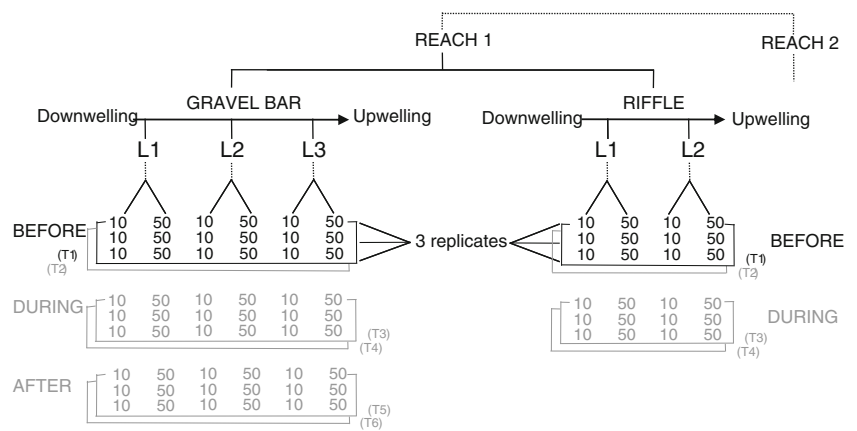


Fig. 1 Map of the study site (in New South Wales, Australia) at **a** catchment and **b** reach scales. The sampling points (L1, L2 and L3) for interstitial water and sediments are represented by white circles. GB gravel bar, R riffle

Fig. 2 Experimental design adopted for flow manipulation experiments in the two reaches. For clarity, details are provided only for reach 1. Two (*L1* and *L2*) and three (*L1*, *L2* and *L3*) sampling points were selected for riffles and gravel bars, respectively. Samples were taken at two depths (10 and 50 cm) below the sediment surface



after the EFM, further samples were collected in gravel bars 48 h after this natural event (T6).

Mini-piezometers (1.7 cm diameter) were driven into the bed sediments at 10 and 50 cm deep (D1 and D2, respectively), upstream and downstream of the slope break of riffles (L1 and L2, respectively) and at the head, the apex and the tail of gravel bars (L1, L2 and L3, respectively). At each date and for each sampling point along the gravel bars and the riffles, three independent piezometers were inserted randomly at 10 cm depth and three other independent piezometers at 50 cm depth. At each sampling occasion, the location of the sampling point was moved in a way to avoid any influence of the previous samples.

Hyporheic water samples at –10 and –50 cm were pumped out of the piezometers using a vacuum pump and flexible plastic tubing. Three samples (corresponding to the three independent piezometers) were collected per site, per depth and per sampling time (total number of samples=312). A total water volume of 6 L was pumped from each piezometer for physicochemical characterisation, nutrient analysis and sediment sampling. A hand-driven bilge pump was used for sampling of interstitial water, which is widely recommended (Boulton et al. 1992; Valett 1993; Wood et al. 2010) and allowed pumping intensity to be controlled so as to avoid contamination with surface water. The low pumping intensity within the mini-piezometer minimized the disturbance of the surrounding substratum and avoided actively sucking surface water or a preferential vertical flow at the vicinity of the piezometer (of surface water). When pumping, the hyporheic origin of the sampled water was confirmed by its changing turbidity. In addition, results from an early study (Creuzé des Châtelliers and Dole-Olivier 1991) showed that, when contamination by surface water did occur (i.e. in that study), it was not important and never occurred before the tenth litre.

The vertical hydraulic gradient (VHG) was evaluated at each sampling point by measuring the difference between the water level in the stream and the water level in the piezometers. For comparison, measurements were transformed into percentages of the corresponding depth. The

VHG estimates the direction and potential strength of hydrological exchanges between surface water and hyporheic water: the VHG is negative under downwelling conditions and positive under upwelling conditions (Boulton et al. 1998; Baxter et al. 2003). In situ DO (YSI Model 58 DO Meter, Yellow Springs Instruments, Yellow Springs, OH, USA) and specific conductance (YSI Specific Conductance Meter, Model 30/10 FT, Yellow Springs Instruments, Yellow Springs, OH, USA) were measured on the first 2 L, whereas water samples for nutrient analysis were conducted on the last 2 L (of the 6 L extracted) so that the water was as silt-free as possible. Water subsamples were filtered through glass microfibre filters (GF/C type, Whatman) and brought back to the laboratory for the analysis of NO_x and SRP using standard colorimetric methods (Grashoff et al. 1983).

The sampled water and sediments were filtered through a 125- μm mesh net to retain particulate organic matter (POM). The resulting filtered water was kept in a bucket for 0.5 h to allow for the sedimentation of very fine POM (VFPOM) and fine mineral particles. POM and VFPOM were dried for 24 h at 105 °C before being weighed.

2.3 Data analysis

Principal component analysis (PCA) was used to identify the dominant factors and to interpret relationships between these variables, reducing the dimensionality of data tables. These analyses were performed using R (R Development Core Team 2007).

A mixed-model analysis of variance (ANOVA) was used to determine the significance of discharge variation effects at each geomorphological unit, with ‘flow paths’ as the independent factor ($n=2$ for riffles and $n=3$ for gravel bars) and ‘depth’ nested within ‘flow paths’. To assess the EFM effect, two cumulated sampling periods in riffles ($n=2$: before (T1+T2) and during (T3+T4) the EFM) and three in gravel bars ($n=3$: before (T1+T2), during (T3+T4) and after the EFM and the natural flood (T5+T6)) were processed as repeated measures. Tukey’s honestly significant

difference (HSD) tests were used for pairwise comparisons. Data were analysed by the General Linear Model module of Statistica 7.1 (StatsoftTM, Tulsa, OK, USA). $p < 0.05$ was considered significant.

3 Results

Surface water showed similar physicochemical characteristics and nutrient contents at the two reaches. We recorded a specific conductance of 36.8 ± 2.2 and $38.7 \pm 1.7 \mu\text{Scm}^{-1}$ at reach 1 and reach 2, respectively. DO concentrations were $8.3 \pm 0.8 \text{ mgL}^{-1}$ at reach 1 and $8.2 \pm 0.9 \text{ mgL}^{-1}$ at reach 2. Reach 1 had $3 \pm 1.5 \times 10^{-2}$ and $4.9 \pm 1.1 \times 10^{-3} \text{ mgL}^{-1}$ of NO_x and SRP, respectively. Similar values were recorded at reach 2 with $2.3 \pm 0.7 \times 10^{-2} \text{ mgL}^{-1}$ of NO_x and $4.5 \pm 0.1 \times 10^{-3} \text{ mgL}^{-1}$ of SRP.

The first two axes of the PCA applied to data for interstitial water accounted for 54.6 % of the total variance (Fig. 3). The PC1 axis (31.8 %) highlights the difference between well-oxygenated water at downwelling points (negative VHG) and highly conductive water with higher mineral nutrient concentrations at upwelling points (positive VHG). The PC2 axis (22.8 %) is essentially defined by POM and VFPOM concentrations, highlighting sampling points with higher amounts of OM within sediments. The projection of the samples onto the factorial plane PC1 vs. PC2 gives an insight into the changes induced by the EFM. The PCA showed that gravel bars were more affected by flow variations than riffles. However, a common feature was observed overall, namely, the homogenisation of water during the EFM as illustrated by a clustering of samples. Nevertheless, at GB2, the deepest sampling point located at the tail of the bar (L3D2) remained less affected.

3.1 Spatial patterns of hyporheic flow

VHG showed similar patterns in riffles and gravel bars, with negative values upstream and positive values downstream of geomorphological units (Tables 1, 2, 3 and 4). ANOVA and resulting post hoc tests (see Tables 1 and 2) before EFM demonstrated differences between upstream and downstream sites, depending on the parameters of water quality and gravel bar evaluated. In GB1, hyporheic water showed similar characteristics and nutrient concentrations, with the exception of DO which decreased from the head to the tail of the bar. This spatial gradient was stronger in GB2 and was reflected by the majority of measured parameters (specific conductance, DO and nutrient concentration), excluding OM content (POM and VFPOM)

In riffles (see Tables 3 and 4) before EFM, post hoc tests indicated a clear trend of water quality between upstream and downstream positions. This can be illustrated by DO at

R2 with decreasing oxygen concentration from L1 to L2. In R1, this spatial gradient was stronger and reflected by most measured parameters, with the exception of SRP concentrations and OM content.

Generally, the EFM affected these gradients since all parameters showed similar values during EFM at all sampling points within each geomorphological unit. Exceptions were observed for GB2 (DO and nutrients), R1 (specific conductance and DO) and R2 (DO). Despite a general decrease during the EFM, the spatial patterns of VHG remained stable at all geomorphological units.

3.2 Spatio-temporal patterns of nutrient concentrations and OM contents

Before the EFM, NO_x concentrations were higher in the HZ than in surface water at both gravel bars and riffles. SRP concentrations were similar in interstitial and surface waters in riffles. In contrast, SRP concentrations in gravel bar in the HZ were higher than in surface water in GB1 and lower in GB2 (see Tables 1 and 2). NO_x concentrations increased along flow paths in GB2 and R1, but remained similar along GB1 and R2 (Tukey HSD test; see Tables 1, 2, 3 and 4). Generally, the EFM resulted in a spatial homogenisation of NO_x concentrations. The EFM did not affect NO_x concentration at R1, while it led to a decrease in NO_x concentrations at the other geomorphological units (ANOVA; see Tables 1, 2, 3 and 4). In the gravel bars, NO_x concentrations increased after the EFM but no spatial gradient was observed (Tukey HSD test).

Before the EFM, no longitudinal gradient was observed for SRP concentrations, except for GB2. The ANOVA showed that the EFM affected SRP concentrations at GB1, GB2 and R1 but not at R2 (see Tables 1, 2, 3 and 4). During the EFM, SRP concentrations increased in the HZ at R1 and GB1, while it decreased at GB2; however, no spatial gradient was observed. After the EFM, SRP concentrations strongly decreased at GB2 but the spatial pattern remained unchanged.

Before the EFM, OM content did not vary significantly along flow paths whatever the geomorphological unit. Variation of OM content resulting from the EFM was dependent on the OM fraction considered as well as on the geomorphological unit. The EFM did not affect OM content at GB1 (ANOVA, $p > 0.25$; see Table 1), whereas it modified POM content at GB2 ($p = 0.02$) and R1 ($p = 0.03$) and VFPOM content at R2 ($p = 0.01$).

4 Discussion

4.1 Spatial patterns of hyporheic flow paths

As widely illustrated in the literature, physicochemical parameters clearly describe hyporheic flow paths,

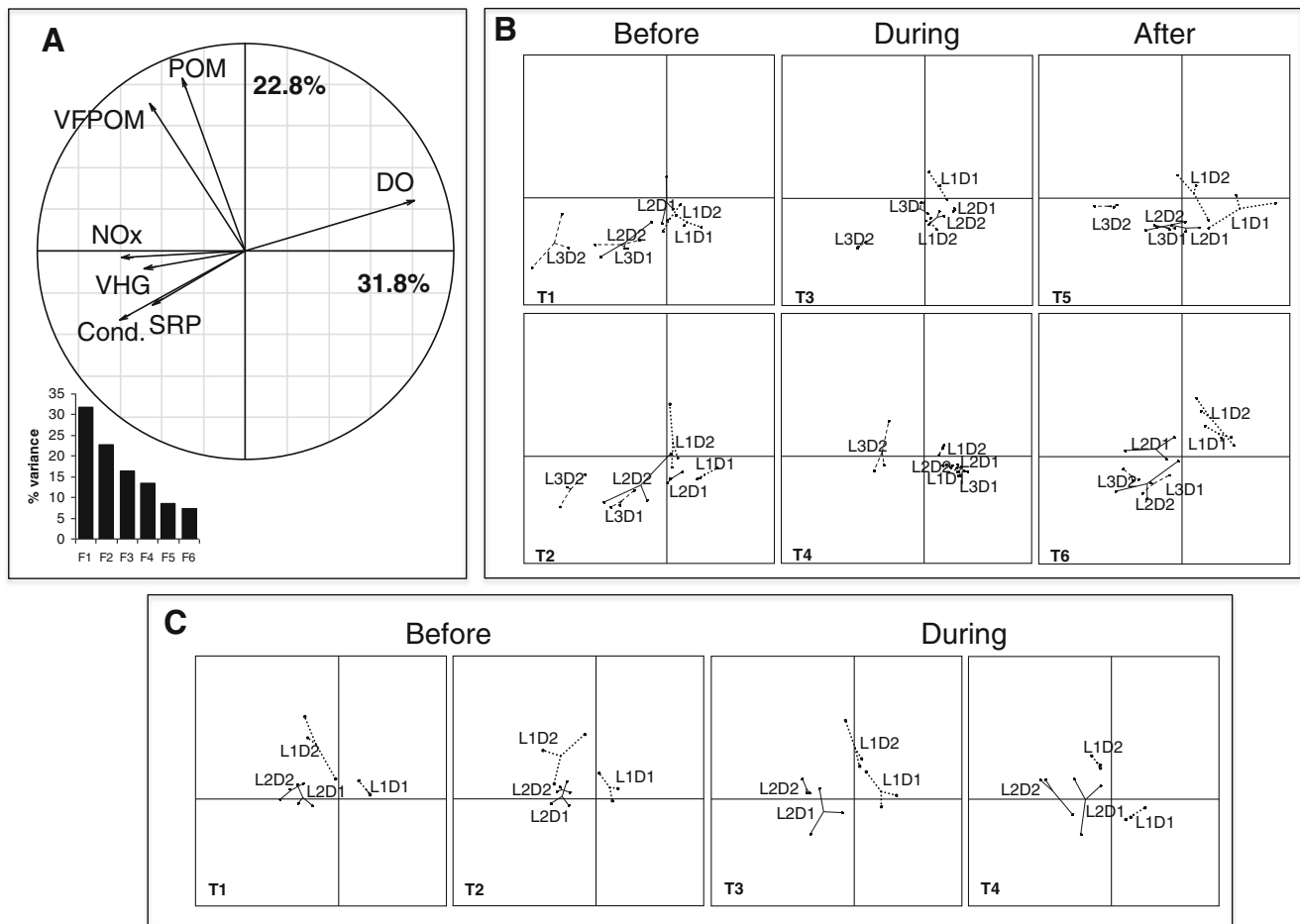


Fig. 3 **a** Correlation circle and the corresponding variance histogram of PCA on physicochemical parameters and OM content data. **b** Distribution of convex gravel bar (GB2) samples from *T1* to *T6* on the F1–F2 factorial plane. **c** Distribution of elongated riffle (R1)

samples from *T1* to *T4* on the F1–F2 factorial plane. *DO* dissolved oxygen, *NO_x* nitrites+nitrates, *SRP* soluble reactive phosphorus, *POM* particulate organic matter, *VFPOM* very fine POM, *VHG* vertical hydraulic gradient

characterised by the alternation of downwelling and upwelling areas (Hendricks 1993). The VHG measurements suggest that the areas situated upstream of riffles and bars correspond to downwelling zones, where surface water infiltrates into the sediment, and the areas situated downstream correspond to upwelling zones, where hyporheic water and/or groundwater reach the surface stream (Boulton et al. 1998; Baxter et al. 2003). Longitudinal and vertical patterns of physicochemical characteristics (i.e. specific conductance and DO) fit with these pathways of hydrological exchange (Hendricks 1993). Similar observations have already been widely reported in other rivers having both different mean size of river and catchment area (e.g. Marmonier and Dole 1986; Boulton et al. 1998; Claret et al. 1998; Lefebvre et al. 2006). Generally, from downwelling zones to upwelling zones, specific conductance increases due to solute dissolution from the substratum and/or inputs of deep groundwater, while DO concentrations decrease. DO in hyporheic water results from the balance between supply

(inputs from surface water) and consumption by community respiration (microbes and invertebrates), all modulated by the residence time of the water within the sediments.

We proposed as a first hypothesis that spatial patterns of hyporheic flow paths are observed along gravel bars and riffles, with a probable stronger gradient in gravel bars compared to riffles, as suggested by longer flow paths and longer residence time in gravel bars. The measures of VHG demonstrated downwelling conditions at the upstream parts of geomorphological units and upwelling conditions at the downstream parts of both gravel bars and riffles. Nevertheless this spatial pattern was not corroborated by all parameters and in all individual geomorphological units. The strongest gradients were observed at both GB2 (for specific conductance, oxygen, NO_x and SRP) and R1 (for specific conductance, oxygen, NO_x and VHG), indicating that there was no simple relation between the type of geomorphological unit and hyporheic water transformations along flow paths. In the same way, hyporheic water quality

Table 1 Mean±SD (*n*=6) of measured parameters at the elongated gravel bar (GB1) before (T1+T2), during (T3+T4) and after (T5+T6) the EFM

Parameters	Position depths	L1		L2		L3		ANOVA (EFM effect)
		D1	D2	D1	D2	D1	D2	
VHG (%)	Before	-24.3±31.4a	-15.2±1.7ab	0.2±0.4b	-0.8±0.7b	1.2±0.9b	2.4±1.0b	<i>F</i> =14.67; <i>p</i> <0.001
	During	-40.2±14.8a	-31.1±3.0a	-6.3±7.7b	-5.8±3.4b	-4.7±6.7b	1.0±1.9b	
	After	-9.8±4.5a	-11.3±3.1a	0.5±6.2a	-2.5±6.1a	1.7±1.0a	1.9±0.3a	
Specific conductance (µScm ⁻¹)	Before	37.8±2.0a	38.1±1.3a	38.5±2.4a	38.5±1.8a	39.3±2.7a	39.0±2.6a	<i>F</i> =1.41; <i>p</i> =0.26
	During	37.3±0.7a	37.5±0.9a	37.4±0.9a	37.8±0.8a	37.2±0.9a	37.5±1.1a	
	After	36.3±3.9a	36.9±3.7ab	36.6±3.2ab	37.1±3.2ab	39.8±3.7b	39.2±3.6ab	
DO (mgL ⁻¹)	Before	7.9±0.3a	6.9±0.5ab	7.1±0.6ab	6.4±0.4b	6.0±1.1b	6.9±0.3ab	<i>F</i> =1.55; <i>p</i> =0.22
	During	7.4±0.2a	6.9±0.4a	7.4±0.3a	6.7±0.1a	7.4±0.6a	7.0±0.2a	
	After	8.1±0.6a	7.4±1.1ac	7.3±0.7ac	6.9±1.0ac	5.0±1.2bc	6.3±1.5c	
NO _x (×10 ⁻²) (mgL ⁻¹)	Before	3.0±1.1a	4.3±1.5a	5.2±1.1a	5.2±1.7a	5.3±2.6a	5.3±2.1a	<i>F</i> =16.77; <i>p</i> <0.001
	During	3.1±0.5a	4.1±0.6a	3.3±0.7a	2.7±1.2a	2.7±1.0a	2.9±1.3a	
	After	4.1±2.2a	6.2±2.9ab	6.3±3.3ab	7.7±2.3b	5.2±2.0ab	5.0±1.8ab	
SRP (×10 ⁻³) (mgL ⁻¹)	Before	3.1±0.7a	3.2±0.7a	4.1±0.9a	3.5±0.7a	3.6±0.8a	4.1±1.7a	<i>F</i> =10.34; <i>p</i> <0.001
	During	5.0±0.8a	4.1±1.2a	3.8±0.6a	4.4±0.6a	4.4±0.7a	4.7±0.8a	
	After	4.2±0.8a	4.2±0.3a	4.9±1.5a	4.7±0.9a	4.1±0.2a	4.6±1.0a	
POM (mg6 L ⁻¹)	Before	1.9±0.3a	0.7±0.7a	1.0±0.3a	1.5±1.2a	0.7±0.5a	0.6±0.3a	<i>F</i> =0.43; <i>p</i> =0.65
	During	1.0±0.7a	0.8±0.9a	1.2±0.2a	0.9±0.6a	1.4±0.9a	1.3±0.4a	
	After	1.4±1.2a	1.3±1.0a	1.5±0.4a	1.5±0.7a	0.8±0.6a	0.6±0.2a	
VFPOM (mg6 L ⁻¹)	Before	2.9±1.3a	0.7±0.6a	3.9±0.7a	3.4±4.7a	0.9±0.6a	2.4±2.8a	<i>F</i> =1.40; <i>p</i> =0.25
	During	2.6±1.9a	0.7±1.2a	2.8±1.1a	1.3±1.3a	0.5±0.7a	3.6±3.1a	
	After	2.2±1.5ab	3.1±2.0ab	1.6±0.7a	2.6±0.9ab	0.9±0.5a	6.8±5.9b	

For each line, significant differences between sampling positions and depths are indicated by different letters (Tukey HSD, *p*<0.05). For positions and depths, see Fig. 2

NO_x nitrites+nitrates, SRP soluble reactive phosphorus, POM particulate organic matter, VFPOM very fine POM, VHG vertical hydraulic gradient

remained relatively homogeneous along both GB1 and R2 (especially for specific conductance, NO_x and SRP). Considering the fact that hyporheic flow paths are longer in gravel bars than in riffles, the most important factor may be water residence time (probably longer in GB2 than in GB1 and shorter in R2 than in R1). Several parameters may explain these variations in water residence time, such as local variations in sediment characteristics (e.g. grain size, porosity and permeability), river slope and channel sinuosity, and the small-scale morphology of units (Cardenas et al. 2004). Poole et al. (2006) used a physical model to show that complex geomorphology enhances the dynamics of hyporheic flow paths. In this study, GB1 is narrow and elongated, while GB2 is broader with a strongly convex apex (see Fig. 1). The sediments at the two gravel bars also have distinctly different grain sizes, at least at the surface, demonstrating possible heterogeneities and dissimilarities in sediment deposition at the two gravel bars. Finally, local heterogeneity may also be related to inputs from lateral groundwater at GB2, as reflected by the higher specific conductance of interstitial water and the positive VHG values at L3. Thus, the present data do not support our first hypothesis, since different geomorphological units (i.e.

gravel bar and riffle) may show similar changes along flow paths. However, our results verify the expectations of Poole et al. (2006), with the strongest interaction between hydrology and geomorphology at the spatial scale where the highest level of geomorphic diversity is expressed (here GB2). These results highlight the importance of the residence time and local heterogeneities, rather than the type of geomorphological unit, for understanding hyporheic processes.

4.2 Sink or source

The movement of stream water towards the subsurface and, conversely, of interstitial water to the stream is a vector for OM and dissolved elements (e.g. nutrients and DO). The storage of OM in the HZ has been observed in many studies (Pusch 1996; Naegeli and Uehlinger 1997; Minshall et al. 2000; Sobczak and Findlay 2002). Smock (1990) reported a sixfold higher POM content in the subsurface than in the surface sediment in a first-order stream in south-eastern USA. Stored OM in the HZ may account for up to 82 % of the total OM retained in streams (Smock 1990; Jones 1997). In the present study, OM content (POM and VFPOM) increased with depth in

Table 2 Mean±SD ($n=6$) of measured parameters at the convex gravel bar (GB2) before (T1+T2), during (T3+T4) and after (T5+T6) the EFM

Parameters	Position depths	L1		L2		L3		ANOVA (EFM effect)
		D1	D2	D1	D2	D1	D2	
VHG (%)	Before	-19.5±22.4a	-12.5±4.0a	0a	1.9±1.7a	6.7±1.9a	1.7±0.5a	$F=4.51; p=0.01$
	During	-1.5±1.9a	-8.70±2.2a	2.7±3.2a	4.8±1.9a	7.2±4.4a	3.5±1.4a	
	After	-47.8±63.1a	-16.8±11.2a	1.0±1.2b	2.6±1.3a	2.3±1.6a	1.4±0.5a	
Specific conductance (μScm^{-1})	Before	39.7±0.9a	39.5±1.6a	40.2±1.4a	45.0±3.9ab	42.8±1.7ab	49.0±1.7b	$F=136.55; p<0.001$
	During	36.5±0.7a	36.9±1.1a	36.4±0.8a	37.2±0.8a	35.9±0.9a	41.8±2.9a	
	After	38.5±2.9a	39.1±3.3a	43.3±2.0ab	46.4±3.4b	42.4±2.0ab	48.0±1.0b	
DO (mgL^{-1})	Before	7.7±0.2a	7.1±0.5a	7.0±0.4a	6.1±0.7ab	4.5±1.0bc	3.5±0.4c	$F=26.12; p<0.001$
	During	7.7±0.3a	7.4±0.4a	7.6±0.1a	7.1±0.2a	7.3±0.6a	4.7±0.9b	
	After	8.4±1.0a	7.8±1.3ab	6.8±0.5ab	6.0±0.8bc	4.7±0.8c	4.3±0.6c	
NO_x ($\times 10^{-2}$) (mgL^{-1})	Before	2.3±0.6a	3.0±0.9ab	3.6±0.5ab	5.2±1.4bc	5.4±0.4bc	7.5±0.3c	$F=11.77; p<0.001$
	During	2.6±0.7a	3.0±0.6a	2.6±0.6a	3.4±0.5a	3.7±0.7ab	6.3±1.1b	
	After	4.1±1.7a	3.9±2.2a	5.2±2.2a	5.76±1.4a	4.7±1.5a	5.5±1.3a	
SRP ($\times 10^{-3}$) (mgL^{-1})	Before	8.3±1.7a	9.5±1.7ab	7.4±1.3a	9.9±2.5ab	10.6±1.2ab	14.0±4.9b	$F=104.82; p<0.001$
	During	7.2±1.6a	11.4±3.2b	5.5±0.7a	6.4±1.5a	7.7±1.9ab	10.2±1.0ab	
	After	4.4±0.9a	3.8±0.6a	4.0±0.7a	3.8±1.4a	4.1±0.7a	5.0±1.2a	
POM (mg6 L^{-1})	Before	0.4±0.2a	1.2±1.0a	0.9±0.7a	0.6±0.4a	0.3±0.2a	0.9±0.6a	$F=4.17; p=0.02$
	During	0.2±0.1a	1.0±0.4a	0.4±0.2a	0.5±0.2a	0.3±0.2a	0.9±0.5a	
	After	0.6±0.5a	1.6±1.1a	0.7±0.5a	0.6±0.2a	0.6±0.2a	1.1±0.2a	
VFPOM (mg6 L^{-1})	Before	0.5±0.6a	2.3±1.7ab	1.4±0.9a	1.3±0.9a	1.1±1.2a	4.8±1.0b	$F=1.44; p=0.25$
	During	4.1±4.3a	1.6±1.1a	0.9±0.4a	0.9±0.3a	1.9±2.1a	3.3±3.3a	
	After	2.5±2.6ab	3.3±2.5ab	2.8±2.9ab	1.7±1.0a	1.1±0.3a	5.1±2.2b	

For each line, significant differences between sampling positions and depths are indicated by different letters (Tukey HSD, $p<0.05$)

NO_x nitrites+nitrates, SRP soluble reactive phosphorus, POM particulate organic matter, VFPOM very fine POM, VHG vertical hydraulic gradient

both riffles (see Tables 3 and 4), indicating an accumulation in the HZ. However, such accumulation was not observed in gravel bars, contrary to plausible expectations

(see Tables 1 and 2). Thus, in the reaches studied in the Never Never River, the HZ may act as a temporary reservoir for OM only at the riffles.

Table 3 Mean±SD ($n=6$) of measured parameters at the elongated riffle (R1) before (T1+T2) and during (T3+T4) the EFM

Parameters	Position depths	L1		L2		ANOVA (EFM effect)
		D1	D2	D1	D2	
VHG (%)	Before	-5.7±2.6a	-6.7±1.9a	9.2±4.2b	3.6±1.0c	$F=53.82; p<0.001$
	During	-15.5±6.6a	-23.0±2.4b	4.7±1.7c	3.9±1.3c	
Specific conductance (μScm^{-1})	Before	39.2±1.0a	39.7±1.1a	40.4±0.3ab	40.9±0.6b	$F=14.2; p=0.001$
	During	38.3±0.5a	38.3±0.5a	39.7±0.9b	40.3±0.8b	
DO (mgL^{-1})	Before	7.9±0.2a	6.6±0.5b	4.7±0.3c	4.4±0.2c	$F=0.88; p=0.36$
	During	8.2±0.7a	7.1±0.8b	5.2±0.7c	3.7±0.4d	
NO_x ($\times 10^{-2}$) (mgL^{-1})	Before	3.0±0.4a	5.1±1.2ab	5.8±1.4b	5.7±1.2b	$F=0.99; p=0.33$
	During	3.8±0.8a	4.7±0.0a	5.1±0.9a	5.0±0.8a	
SRP ($\times 10^{-3}$) (mgL^{-1})	Before	5.8±2.3a	7.0±4.3a	4.5±1.7a	4.4±1.9a	$F=7.85; p=0.01$
	During	8.2±3.3a	7.4±0.8a	7.3±2.8a	7.9±2.7a	
POM (mg6 L^{-1})	Before	1.7±0.6a	2.8±0.9a	2.0±0.4a	2.1±0.4a	$F=5.52; p=0.03$
	During	1.2±0.9a	2.7±0.7b	1.2±0.4a	2.3±0.4ab	
VFPOM (mg6 L^{-1})	Before	1.5±1.0a	7.2±2.2b	1.7±0.8a	2.9±1.0a	$F=0.03; p=0.87$
	During	0.8±0.8a	5.5±1.4b	2.9±2.8ab	3.9±2.3ab	

For each line, significant differences between sampling positions and depths are indicated by different letters (Tukey HSD, $p<0.05$)

NO_x nitrites+nitrates, SRP soluble reactive phosphorus, POM particulate organic matter, VFPOM very fine POM, VHG vertical hydraulic gradient

Table 4 Mean±SD ($n=6$) of measured parameters at the convex riffle (R2) before (T1+T2) and during (T3+T4) the EFM

Parameters	Position	L1		L2		ANOVA (EFM effect)
		D1	D2	D1	D2	
VHG (%)	Before	-18.3±6.6a	-10.5±1.6ac	13.2±10.2b	4.6±2.9bc	$F=5.16; p=0.03$
	During	-32.5±19.3a	-24.3±3.9a	21.2±8.0b	5.2±1.6b	
Specific conductance (μScm^{-1})	Before	39.8±1.8a	40.3±1.4a	40.2±1.8a	41.0±2.7a	$F=0.10; p=0.76$
	During	40.0±0.8a	40.0±0.6a	40.0±0.5a	41.9±1.9a	
DO (mgL^{-1})	Before	8.5±0.4a	7.9±0.5ab	7.6±0.6ab	7.1±0.4b	$F=44.31; p<0.001$
	During	7.4±0.6a	6.9±0.5ab	6.9±0.4ab	6.3±0.5b	
NO_x ($\times 10^{-2}$) (mgL^{-1})	Before	3.0±1.5a	4.6±1.3a	4.1±2.0a	3.6±1.6a	$F=8.30; p<0.01$
	During	2.8±0.4a	2.9±0.7a	2.5±0.9a	3.0±1.4a	
SRP ($\times 10^{-3}$) (mgL^{-1})	Before	4.2±1.4a	4.5±2.3a	3.7±1.0a	4.0±1.4a	$F=1.42; p=0.25$
	During	4.3±1.1a	4.2±1.3a	4.0±0.7a	6.3±1.9a	
POM (mg6 L^{-1})	Before	0.4±0.2a	1.0±0.6a	0.7±0.2a	3.6±1.7b	$F=3.97; p=0.06$
	During	0.3±0.2a	0.7±0.3a	0.8±0.3a	3.3±1.4b	
VFPOM (mg6 L^{-1})	Before	1.2±1.2ab	0.4±0.2a	0.4±0.2ab	6.1±4.3b	$F=7.79; p=0.01$
	During	0.7±0.7a	0.4±0.3a	0.9±0.4a	10.9±4.8b	

For each line, significant differences between sampling positions and depths are indicated by different letters (Tukey HSD, $p<0.05$)

NO_x nitrites+nitrates, SRP soluble reactive phosphorus, POM particulate organic matter, VFPOM very fine POM, VHG vertical hydraulic gradient

Our second line of study investigated the role of the HZ as acting as a source or a sink of nutrients, with our hypothesis being that gravel bars have a higher potential as a source than riffles due to the shorter water residence time in riffles. In streams, most biological processes in the HZ concern buried material (Webster et al. 1999; Lamberti and Gregory 2006). Hyporheic respiration may reach up to 70 % and, in some cases, 90 % of whole ecosystem respiration (Battin et al. 2003 and references therein). After OM decomposition and mineralisation by hyporheic microbe assemblages, the resulting NO_x and SRP may be released to the surface water, enhancing primary production in the river (Mulholland et al. 1997; Fisher et al. 1998; Mouw et al. 2009). In the Never Never River, the potential role of HZ as a source of nutrients is supported by the higher NO_x and SRP concentrations measured at the end of the hyporheic flow paths, where the interstitial water upwells toward the surface stream. This function is especially enhanced at GB2 for both nutrients and at R1 for NO_x (Table 5). Such results have been reported previously in other streams (Wondzell and Swanson 1996; Mulholland et al. 1997; Dent et al. 2001). Nevertheless, this process was not observed at all locations and may be modulated by local characteristics of the HZ. Indeed, the role of the HZ as a source of N and P for the surface system was not observed in GB1 and R2. Such dissimilarities may suggest a patchy distribution defining ‘hot spots’ of biogeochemical and microbial activity (Fisher et al. 1998; Claret and Boulton 2009), which depend on the interactions between hydrology and geomorphology. Another source of heterogeneity in the pattern of N and P may be the distribution of fine sediments and OM, since low

nutrient contents (NO_x and SRP) were observed in areas with high OM content (mainly VFPOM). Similarly, Claret et al. (1997) reported that some hyporheic processes (i.e. nitrification and denitrification) are influenced by the distribution of fine sediments and OM.

4.3 Effect of flow manipulation

This work addresses the hypothesis of a flush out of OM and nutrients in riffles and a minor removal in gravel bars. The results demonstrate that different geomorphological units from different sites, and thus with different local heterogeneities, do not respond in a similar way to increasing flow discharge. Comparable results were found by Tonina and Buffington (2007) in flume experiments, especially for gravel bars. The transport of both dissolved and colloidal matter is mainly controlled by the advective exchange between the stream and HZ (Packman et al. 2000).

In the two gravel bars, the flow manipulation generally had no effect on the distribution of OM (weak effect at GB2 for POM). The intensity of flow variation was probably too low to induce a flushing effect of the hyporheic OM out of gravel bars (high local stability). In contrast, in one riffle (R2), the flow manipulation induced changes in OM concentrations, with an increase in VFPOM at -10 and -50 cm in the upwelling zone. This suggests an input of OM into the HZ during the EFM. Minshall et al. (2000) found that the retention of fine POM was correlated with hydrologic exchange. Based on differences in specific conductance, DO and NO_x contents between the downwelling and upwelling zones, the residence time seemed to be longer in R1 than in

Table 5 Potential role of the HZ as a source (positive percentage) or a sink (negative percentage) of nutrients (N and P) and POM and the effect of the EFM on the HZ

Site	Before EFM		During EFM			
	Sink/source role		Washout/storage effect			
	N	P	N	P	POM	VFPOM
R1	+55.2 % ($p=0.33$)	n.s.	n.s.	+47.6 % ($p=0.01$)	-17.4 % ($p=0.03$)	n.s.
R2	n.s.	n.s.	-25 % ($p<0.01$)	n.s.	n.s.	+37.4 % ($p=0.01$)
GB1	n.s.	n.s.	-44.6 % ($p<0.001$)	+14.0 % ($p<0.001$)	n.s.	n.s.
GB2	+49.0 % ($p<0.001$)	+46.1 % ($p<0.001$)	-27.7 % ($p<0.001$)	-28.9 % ($p<0.001$)	-17.2 % ($p=0.02$)	n.s.

N nitrogen, P phosphorus, POM particulate organic matter, n.s. not significant

R2. Hence, R2 appears more permeable and thus more sensitive to hydrological disturbances than R1, at least for particulate material.

Contrasting patterns were found for mineral nutrients (N and P). A significant decrease in NO_x concentrations was observed during the EFM in gravel bars and in R2 (see Table 5). This flush out effect of N during the EFM has been observed in other studies during high water periods (Dent et al. 2001; Hancock and Boulton 2005). For example, Wondzell and Swanson (1996) found that, during summer months, a gravel bar could be an important site for the transformation of dissolved organic N into ammonium and ultimately into nitrate, but did not serve as a source of nitrate for the stream due to a disconnection related to water table lowering. However, during fall storms, the gravel bar acted as a strong source of inorganic N for the stream, since the nitrate and ammonium were flushed out of the gravel bar.

After the EFM, the concentration in NO_x increased in the gravel bars, suggesting a rapid recovery of biological processes producing NO_x . The N cycle is predominantly a microbiologically mediated redox-based process and the HZ is a region of intense N cycling (Triska et al. 1993; Duff and Triska 2000). In GB1 and GB2, the post-disturbance recovery of NO_x may be enhanced by a re-oxygenation of the HZ induced by the intensification of surface water infiltration during the EFM. Thus, our results suggest that the regeneration of N in the HZ of the Never Never River is provided by the oxygen-consuming nitrification process.

In contrast, the SRP concentrations followed reverse trends in the two reaches. In GB2, SRP concentrations decreased during the EFM, suggesting a flush out of this dissolved form of P by strong infiltrations of surface water (Dent et al. 2001). However, SRP concentrations increased at GB1 and R1, suggesting a stimulation of biological production of SRP by the biodegradation of in situ OM (Mulholland et al. 1997; Deforet et al. 2009). The long water residence time in the subsurface at reach 1 (as described above) may explain the accumulation of SRP released via

decomposition of the hyporheic organic detritus, but not at GB2 where the EFM seemed to enhance vertical connectivity. Regarding P, the cycle is more complex than that of N and its dynamics in the HZ zone is submitted to complex processes controlling speciation, sorption and fate (Hendricks and White 2000). Under potentially oxygenated and high redox conditions, P tends to be adsorbed onto metal oxides. By contrast, P complexes break down under anoxic reducing conditions and SRP is released into solution (Hendricks and White 2000; Carlyle and Hill 2001). In view of our results, it seems that observed SRP patterns and the difference in P dynamics between the two reaches were the result of the interaction of two processes: (1) the renewal of oxygen in the HZ zone during the EFM which may result in an increase in the sorption capacity of sediments for P and hence a decrease in SRP (physical process), and (2) OM mineralisation and SRP production which may increase in the HZ (biological process).

4.4 Importance of local heterogeneity

Local heterogeneity, such as channel form, reach slope and hydraulic conductivity, can affect the direction and the intensity of exchanges between surface and hyporheic waters during flow variations (Poole et al. 2006). In this study, during the EFM, POM content decreased at R1 and GB2, while VFPOM increased at R2. Differences in OM storage can be explained by VHG and sediment grain size. The combination of coarser sediments ($D_{50}=61$ mm) and intermediate VHG (mean absolute values of 15.5 and 23 % at D1 and D2, respectively) in the downwelling zone of R1 may induce the infiltration of the drifting OM. However, the relatively low VHG in the upwelling zone (mean absolute values of 4.67 and 3.87 % at D1 and D2, respectively), even with coarser sediment, seemed to be insufficient with regards to flushing the hyporheic OM to the surface. In contrast, despite a small sediment size at R2 ($D_{50}=47$ mm), the negative VHG (mean absolute values of 32.5 and 24.30 % at the downwelling zone at D1 and D2,

respectively) promoted the infiltration of surface water and its associated VFPOM.

The difference in storage of dissolved N and P may be due to local heterogeneities, including the shape and size of geomorphological units. For instance, the difference in nutrient concentration along GB1 and GB2 could be attributed to the channel sinuosity and to the gravel bar shape (Cardenas et al. 2004). GB1 is narrow and confined to the bank with rather fine sediments and GB2 is strongly convex while also occupying a large part of the channel with medium to coarse sediments. Such morphological characteristics may reduce surface water infiltration and heterogeneities along the flow path in GB1, while GB2 may be crossed by an intense hyporheic flow producing a gradient of nutrient concentrations along the hyporheic flow path. The influence of gravel bar shape has been observed in several studies regarding hydrological processes (Kasahara and Hill 2007; Tonina and Buffington 2007) but not for nutrient dynamics.

5 Conclusions

During the last three decades, a significant effort has been made to determine the effect of surface–subsurface exchanges on nutrient dynamics. It is now recognised that, generally, in oligotrophic streams, the HZ acts as a source of OM and nutrients via upwelling patches, whereas it acts as a sink in nutrient-rich rivers via hydrological and physical or chemical processes (i.e. adsorption, denitrification). Nevertheless, only a few studies have examined the spatial patterns of OM and nutrient dynamics in the HZ at the scale of geomorphological units (e.g. Sterba et al. 1992; Pusch 1996; Claret et al. 1998; Rulik 2000; Anbutsu et al. 2006; Pretty et al. 2006).

To our knowledge, there are no comparative data regarding the functioning of riffles and gravel bars. Our study leads to the several conclusions which collectively may be of great interest for river restoration and management:

1. This study demonstrated the alternation of upstream downwelling and downstream upwelling zones at both riffles and gravel bars. Nevertheless, the processing of nutrients along the hyporheic flow path and the response to discharge increase are not governed by the type of geomorphological unit.
2. At the reach scale, differences in surface–subsurface exchanges in response to flow variation and their consequences on nutrient dynamics are mostly regulated by other geomorphological features, such as channel form (e.g. slope, sinuosity) and sediment characteristics (e.g. grain size, porosity), influencing the hydraulic conductivity and the hyporheic residence time.
3. Since the interactions between geomorphology and discharge are nonlinear, their effects on hyporheic

processes are not additive. In order to understand hyporheic processes and for future generalisations regarding the effect of floods on nutrient dynamics, knowledge of local characteristics is required and the use of an eco-morphologic view (Fisher et al. 2007) of functional processes is a necessity.

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