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TITLE: Interactions between microbial activity and bioturbation modes of benthic invertebrates determine nutrient releases from reservoir sediments

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Abstract

1. Bioturbating invertebrates play key roles in nutrient recycling from sediments to the water column in most lentic ecosystems. Nevertheless, the role of bioturbating fauna on nutrient cycling depends on complex interactions between their bioturbation modes and both the sedimentary conditions and the microbial activity occurring inside sediments.
2. This study aims to evaluate the effect of different bioturbation modes by two invertebrate species (tubificid worm *Tubifex tubifex* and chironomid larvae of *Chironomus plumosus*), on the release of nutrients (NH_4^+ , NO_3^- and PO_4^{3-}) from three different types of sediments characterized by distinct microbial activities and nutrient (N and P) contents. We expected that the influence of a bioturbation mode on nutrient fluxes was dependent on the microbial activity and organic matter processes occurring in sediments.
3. Aquatic mesocosms were setup in the laboratory with three fauna treatments (i.e. without fauna, with tubificid worms, and with chironomid larvae) and three sediment types (collected in three reservoirs).
4. The presence of bioturbating invertebrates increased PO_4^{3-} concentrations into the water column (from 1.3 to 17-fold higher concentrations) depending on the sediments tested. PO_4^{3-} releases in the water column were positively linked to total P concentration and microbial activity in sediments. The influences of tubificid worms and chironomid larvae on PO_4^{3-} releases into the water were not only due to their bioturbation modes but also depended on the interactions with P dynamics (e.g. adsorption of PO_4^{3-} by iron oxides) at the water-sediment interface.
5. The influence of fauna on the release of dissolved inorganic nitrogen (DIN) varied strongly among sediments due to the control of N cycling by microbial processes. In sediments characterized by the lowest microbial activity, DIN release from sediments to the water column was significantly stimulated by invertebrates (from 1.3 to 3.7-fold higher). In contrast, no fauna effect was detected compared to controls in sediments characterized by the highest microbial activity.
6. This study demonstrated that the influence of the bioturbation mode on nutrient (i.e. PO_4^{3-} and DIN) dynamics at the water sediment interface was largely modulated by the intensity of microbial activity and biogeochemical processes occurring in sediments.

Keywords: chironomid, tubificid, water-sediment interface, microbial respiration, bioturbation functional groups

1. INTRODUCTION

Reservoirs contribute to more than 50% of sediment retention in drainage basins around the world (4–5 Gt year⁻¹, Vörösmarty et al. 2003), resulting in a massive accumulation of sediment-associated nutrients (nitrogen N and phosphorus P). Then, reservoir sediments act as sinks of nutrients but they may also act as temporary nutrient sources to the water column (Penn et al. 2000; Qin et al. 2016). Indeed, during the warm season, nutrient release from sediment to the water column has been recognized as a main mechanism (called internal loading) explaining eutrophication problems such as the presence of algal blooms in surface waters (Søndergaard, Jensen & Jeppesen, 2003; Jeppesen et al., 2005). These releases of nutrients from sediment to the water column are known to be influenced by physical (molecular diffusion, water currents, winds, etc.) and biogeochemical (temperature, aerobic-anaerobic conditions, pH) factors but they can be also modulated by the activities of benthic organisms (Kristensen et al. 2000). Bioturbation by benthic fauna (i.e. sediment reworking and bio-irrigation activities) can increase sediment hydraulic conductivity as well as water and solute exchanges across the sediment-water interface (SWI) (Nogaro et al., 2006; Kristensen et al., 2012). Such increased exchanges could stimulate microbial processes (aerobic mineralization of organic matter, nitrification, denitrification) in sediments (Stief, 2013; Cariou et al., 2021) and increase the releases of nutrients such as N and P from the sediments to the water column (Granéli, 1979). For example, Cariou et al. (2021) showed that the presence of tubificid worms (e.g., 20,000 individuals.m⁻²) could stimulate both dissolved inorganic nitrogen (NO₃⁻ + NH₄⁺) and phosphate (PO₄³⁻) releases, by up to 3- and 5-fold, respectively, compared to nutrient fluxes measured in the absence of fauna. These increased nutrient fluxes were associated with a bioturbation-driven stimulation of microbial communities involved in organic matter processing (CO₂ effluxes were stimulated by up to 5-fold). Comparable results were reported with the larvae of *Chironomus plumosus* (at densities close to 2,000 larvae.m⁻²), which could stimulate the release of NH₄⁺ by 5.8-fold (Pelegri & Blackburn, 1994) and the sediment respiration by 2.5-fold (Baranov et al., 2016) due to their burrow irrigation activity (Reitzel et al., 2013).

The extent of fauna influence on nutrient and water exchanges across the SWI depends on their specific mode of bioturbation (Mermillod-Blondin et al., 2004; Kristensen et al., 2012). For example, the sediment reworking by tubificid worms which are upward conveyors ingesting sediment at depth and egest fecal pellets at the SWI can release NH₄⁺ in the water column

(Matisoff, Fisher & Matis, 1985; Anschultz et al., 2012) whereas chironomid larvae which are U-shaped burrow builders produce a non-local transport of surface sediment into burrows that is not expected to influence NH_4^+ fluxes at the SWI (Matisoff & Wang, 2000). In contrast, bio-irrigation by chironomid larvae strongly influences nutrient and dissolved oxygen fluxes at the SWI (e.g., Lewandowski & Hupfer, 2005; Samuiloviene et al., 2019) in comparison with tubificid worms which build a dense network of galleries that are not actively ventilated (McCall & Fisher, 1980). Based on these differences in burrow construction and bio-irrigation, Gautreau et al. (2020) showed that chironomid larvae significantly increased concentrations of N ($\text{NH}_4^+ + \text{NO}_3^-$) and PO_4^{3-} released from reservoir sediments by 3.7-fold and by 17-fold, whereas tubificid worms had a lesser effect (2-fold for N and 3-fold for PO_4^{3-}).

However, bioturbation functional traits (burrow construction, bio-irrigation) do not necessarily predetermine the way in which species mediate biogeochemical processes because the species' effects can be modulated by environmental conditions (Needham et al., 2011; Wohlgemuth, Solan & Godbold, 2017; Cassidy et al., 2020). Recently, Bernard et al. (2019) showed that the same dominant species might have contrasting effects on bioturbation metrics depending on organic matter content in sediments. In the same way, Godbold & Solan (2009) demonstrated that the quantity of total organic carbon in sediments reduced the burrowing depth of benthic species. However, Michaud, Aller & Stora (2010) observed the opposite result in the marine polychaete *Nephtys incisa* with an increased density and depth of biogenic structures along with the organic matter content in sediments.

Contrasting influences of sediment organic matter on bioturbation have been also observed in freshwater environments. According to a positive link between OM content in sediments and bioturbation effect on biogeochemical processes, it has been reported that the presence of tubificid worms stimulated NH_4^+ and PO_4^{3-} fluxes by more than 2-fold from sediments containing 7% of organic carbon (Mermillod-Blondin et al., 2005) while the same density of worms had a very slight effect on nutrient fluxes in sediment containing only 2% of organic carbon (Mermillod-Blondin et al., 2008a). However, Pigneret et al. (2016) showed that tubificid worms produced comparable stimulation of nutrient fluxes in three sediments characterized by an organic carbon content varying from 1.9 to 14.3% of sediment dry mass. These studies highlighted large disparities and demonstrated that the influence of bioturbation on nutrient fluxes in sedimentary environments cannot be solely predicted from the bulk of OM in sediments. In this context, nutrient fluxes generated by bioturbation might more likely depend

on OM mineralization rates associated with microbial activity in sediments (Berner, 1980; D'Angelo & Reddy, 1994; Michaud et al., 2010). Thus, understanding the influence of bioturbation in water and solute exchanges across the SWI needs to consider the combined effects of bioturbation mode, OM mineralization, microbial activity, and nutrient recycling in sediments.

The present study aims to determine the interactions between benthic fauna and sediment characteristics and their effects on the release of nutrients from reservoir sediments to the water column. A factorial experimental approach using mesocosms was developed to combine bioturbation mode and sediment characteristics and determine the role of their interactions on nutrient release from sediments to the water column. Sediments were selected and collected from three reservoirs to obtain three sediment types characterized by contrasting microbial activities and aerobic mineralization rates. Bioturbation influence was investigated by manipulating the presence of chironomid larvae and tubificid worms, two invertebrate groups commonly found in reservoir sediments and having distinct bioturbation modes (U-shaped tube building and ventilation for chironomids and gallery building for tubificid worms, Gautreau et al., 2020). We hypothesized that effect of fauna on nutrient release will depend on organic matter mineralization and microbial activities (i.e. respiration rates, microbial activity associated with OM degradation). More precisely, our first hypothesis (Hypothesis 1) was that the presence of fauna would stimulate nutrient fluxes and that the highest stimulation would be observed in sediments characterized by the highest microbial activity and associated organic mineralization rates. In addition, our second hypothesis (Hypothesis 2) was that chironomid larvae and tubificid worms would produce different nutrient fluxes because their contrasting ventilation activities were expected to generate contrasting water and solute fluxes (Mermillod-Blondin et al., 2004; Kristensen et al., 2012). More precisely, the ventilation of tubes by chironomid larvae would produce a higher stimulation of nutrient release rates from sediments than the production of low-ventilated burrows by tubificid worms.

2. METHODS

2.1 Sediments collection and preparation

Three French reservoirs were sampled to collect sediment characterized by contrasting levels of microbial activity (hydrolytic activity associated with organic matter degradation and

aerobic respiration rate). The reservoirs of Puyvalador (42°38'47.4"N, 2°07'28.9"E), Villerest (45°59'07.1"N, 4°02'44.3"E) and Grangent (45°27'58.2"N, 4°14'56.5"E) were selected to obtain an increasing gradient of microbial activity among them. More precisely, mean hydrolytic activity increased from 0.05 $\mu\text{mol.g}^{-1}$ dry sediment.hour⁻¹ in Puyvalador sediments to 0.3 and 1.1 $\mu\text{mol.g}^{-1}$ dry sediment.hour⁻¹ in Villerest and Grangent sediments, respectively. Aerobic respiration rates followed the same gradient with mean O₂ uptake rates of around 1200, 1450 and 2100 μmol of O₂ consumed.hour⁻¹. m⁻² of SWI for Puyvalador, Villerest and Grangent reservoirs, respectively.

Sediments were collected in 2018 during the summer season with an Ekman grab and stored at -18°C for several weeks to kill fauna. As this procedure of sediment freezing could alter microbial communities (Tolhurst et al., 2012), a subsample of fresh sediment was kept at 15°C (temperature at the SWI) to preserve the microbial activity and to be used as an inoculum for the experiments. This subsample was sieved at 80 μm to remove the ambient fauna and thoroughly mixed to defrosted sediments for microbial colonization during 15 days before mesocosm preparation. It has been shown from a previous experiment that this incubation time of 15 days followed by stabilization period of 14 days in mesocosms (see below) was long enough to recover and stabilize sediment oxygen uptake rates (see Figure 4 in Gautreau et al., 2020).

2.2 Mesocosms and experimental set up

The experiment was performed using laboratory mesocosms consisting in Plexiglas cylinders with an internal diameter of 10 cm and a height of 20 cm (Figure 1). Mesocosms were placed in a 15°C temperature-controlled room and filled with a layer of inoculated sediments (10 cm) overlaid with synthetic water (10 cm) (composition of synthetic water: 96 mg.L⁻¹ NaHCO₃; 39.4 mg.L⁻¹ CaSO₄·2H₂O; 60 mg.L⁻¹ MgSO₄·7H₂O; 4 mg.L⁻¹ KCl; pH = 7.5; (US EPA, 1991)). Oxic conditions (i.e. around 8 mg.L⁻¹ of dissolved oxygen) were maintained in the water column by bubbling water with atmospheric air. Mesocosms were equipped with peristaltic pumps for a continuous recirculation of the water column at a flow rate of 6 mL.min⁻¹ to avoid dissolved oxygen (DO) stratification. A gentle water flow rate was applied to avoid sediment resuspension in the water column. The recirculation system of each mesocosm was equipped with oxygen probes (circulation cells equipped with an optical oxygen sensor,

PyroScience GmbH, Aachen, Germany) to evaluate aerobic consumption in mesocosms during incubations of 4 hours at the start and at the end of the experiment (see details in “2.4.3 oxygen uptake rates”). After their setup, mesocosms were allowed to stabilize for a 14-day period. At the end of this stabilization period (day 0), the water column of each mesocosm was gently removed and replaced, with minimum disturbance of sediment, by synthetic water to eliminate the initial flush of nutrients due to sediment manipulation. A detailed description of mesocosms is provided in Gautreau et al. (2020).

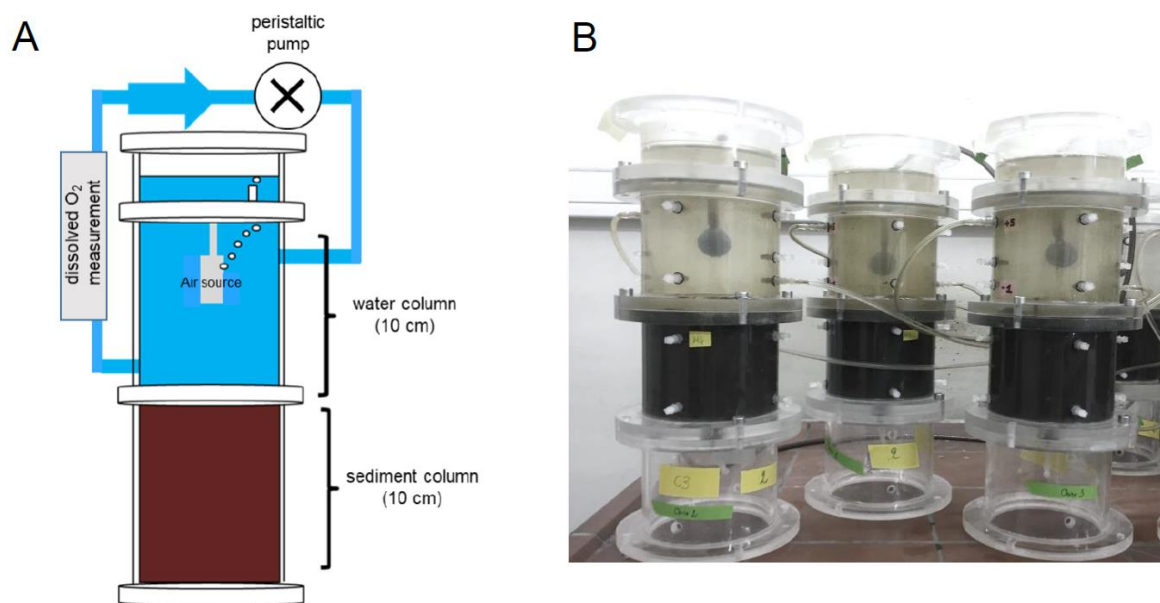


FIGURE 1 Schema of a mesocosm with peristaltic pump, oxygen sensor and air source (A) and photograph of three mesocosms during the experiment (B)

2.3 Experimental design

A total of 36 mesocosms was set up for the experiment. We used 9 mesocosms to determine initial sediment characteristics on day 0 (3 tested sediments * 3 replicates per sediment). The other 27 mesocosms were used to measure nutrient enrichment in the water column, hydrolytic activity and oxygen uptake rate in sediments after 15 days of experiment depending on tested sediment and added fauna (3 sediment treatments * 3 fauna treatments * 3 replicated mesocosms).

For the 9 mesocosms dedicated to the determination of initial conditions before invertebrate introduction (day 0), incubations were performed to evaluate initial oxygen uptake rates. Afterwards, the central area of the 9 microcosms were cored with cut-off syringes (i.e. 1 cm diameter, 9 cm height) and analyzed for measurements of microbial hydrolytic activity and total organic carbon (TOC), total nitrogen (TN) and total phosphorus (TP). As P binding in ferric (oxi)hydroxides play a key role in PO_4^{3-} dynamics in sediments (Boers, Raaphorst & Van der Molen, 1998), iron (Fe) content was also measured for each reservoir sediment. In addition, particle size distributions were determined, and chemical analyses in interstitial water (i.e. concentrations of N-NH_4^+ , N-NO_3^- and P-PO_4^{3-}) linked with OM mineralization were performed after centrifugation of fresh sediments at 2,400 rpm during 20 min at 4°C to collect interstitial water. From TOC and TN analyses, TOC/TN ratio was calculated for each sediment and was used as an indicator of the biodegradability of the OM: lower is the TOC/TN ratio of OM, higher is its biodegradability (Meyers & Teranes, 2001; Sampei & Matsumoto, 2001). All physical, chemical and biological analyses done were described below.

From the 27 mesocosms used to evaluate the influence of fauna in the three sediments, bioturbating invertebrates were introduced in 18 mesocosms on day 0 to obtain three fauna conditions per tested sediment: 1) three control mesocosms without fauna, 2) three mesocosms with addition of 150 tubificid worms *Tubifex tubifex* (Müller, 1774), (Michel Lafond, pers. com), and 3) three mesocosms with addition of 15 larvae of 4th stage *Chironomus plumosus* (Linnaeus, 1758). All tested animals were obtained from professional breeders. Tested densities (19,230 individuals per m² for tubificid worms and 1,923 individuals per m² for *Chironomus plumosus*) fitted with natural densities (Svensson & Leonardson, 1996; Svensson, 1997 for chironomids ; Nogaro et al., 2007; Mermillod-Blondin et al., 2008b for tubificid worms). After 14 days of invertebrate incubation (on day 14), oxygen uptake was measured in each mesocosm to quantify the role of the two bioturbating invertebrates on microbial respiration in the three sediments. For a logistic reason, nutrient concentrations were measured one day later (i.e. day 15 of the experiment) in the water column of each mesocosm to quantify nutrients released from sediment depending on invertebrate activities and tested sediment. Then, sediment cores were collected in each mesocosm with cut-off syringes (i.e. 1 cm diameter; 9 cm height) to measure microbial hydrolytic activity in sediments. The aim of these analyses was to determine the influence of bioturbating fauna on microbial activity in the three sediment treatments.

2.4 Methods of analyses

2.4.1 Physico-chemical analyses on sediment

Grain size distribution was determined by laser diffractometry (Malvern Mastersizer 2000G, Malvern Products, Palaiseau, France) on fresh sediments obtained by coring. The percentage of fine particles (i.e. silt and clay, $< 63\mu\text{m}$) was calculated by using package `rysgran` v2.1.0 (Ronael Gilbert, Garcia de Camargo & Sandrini-Neto, 2014) on R software v3.3.2. Sediment samples were dried (60°C for 72 h), grinded in a mortar, and analyzed to determine their content (% per sediment dry mass) of TOC, TN and TP. TOC and TN were measured according to the method described by Nieuwenhuize, Maas & Middelburg (1994). The method of Murphy & Riley (1962) was used to determine TP. For each reservoir sediment, Fe content was measured per sediment dry mass by optic Inductively Coupled Plasma (ICP) after sediment mineralization with nitric acid and hydrochloric acid.

2.4.2 Chemical analyses on water

The water samples collected in the water column and in sediments (interstitial water) were filtered through a GF/F filter ($0.7\mu\text{m}$, Whatman) and stored at 4°C before inorganic nutrient analyses. N-NH_4^+ , N-NO_3^- , P-PO_4^{3-} concentrations were then determined by colorimetric methods with a sequential analyzer (SmartChem200, AMS Alliance, Frépillon, France).

2.4.3 Oxygen uptake

Oxygen uptake measurements made on day 0 and on day 14 were performed according to Gautreau et al. (2020). Briefly, aeration of water column of mesocosms was stopped and each mesocosm was sealed to avoid contact with the atmosphere. Using the water recirculation system equipped with an oxygen probe connected to a Pocket Oxygen Meter FireStingGO₂ (Pyroscience GmbH, Aachen, Germany), decrease in DO concentration was measured every hour during an incubation time of 4 h in each mesocosm. DO uptake rates in the mesocosms were calculated from the linear decrease of DO over time and expressed as μmol of O_2 consumed per hour and m^2 of sediment surface.

2.4.4 Microbial hydrolytic activity

Microbial hydrolytic activity was measured on fresh sediment samples collected on day 0 and day 15 of the experiment by the fluorescein diacetate (FDA) hydrolysis method (Battin,

1997; Mermillod-Blondin et al., 2005). Fresh sediment samples (0.5 g) 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 for 30 min in the dark at 15°C until the fluorescein turned green. Then, the reaction was stopped by freezing the samples at -20°C after the addition of 3 ml of acetone. 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 hydrolysed per hour and per gram of dry sediment.

2.5 Data analysis

For measurements performed at day 0 of the experiment (i.e. concentrations of nutrients in interstitial water, microbial hydrolytic activity, oxygen uptake rates, grain size distribution, TOC, TN, TP, Fe concentrations and TOC/TN ratio), initial conditions among sediment treatments (i.e. Puyvalador, Villerest and Grangent) were compared using one-way analyses of variance (1-way ANOVA) with sediment as the fixed factor. When 1-way ANOVA were significant (i.e. $p < 0.05$), Tukey's post hoc tests were performed to evaluate which sediment treatment differed.

For nutrient concentrations, oxygen uptakes and microbial hydrolytic activity measured at the end of the experiment (day 14 and 15), the effects of fauna treatments (i.e. controls without fauna, tubificid worms, chironomid larvae), sediment treatments (i.e. Puyvalador, Villerest and Grangent) and their interactions were tested using two-way analyses of variance (2-ways ANOVA) with fauna and sediment as the fixed factors. When 2-ways ANOVA were significant (i.e., $p < 0.05$), Tukey's post hoc tests were performed to evaluate which treatments differed. For all variables and before statistical analyses, the normality and the homoscedasticity of the residues were verified using the Shapiro-Wilk's test and the Bartlett's test, respectively.

In addition, we used linear models to evaluate the influence of sediment and fauna factors on N-NH_4^+ , N-NO_3^- and P-PO_4^{3-} released from sediment to the water column. Each model (one per released nutrient) focused on three factors that represented (1) the loading of the studied nutrients in sediments (TN for evaluating NH_4^+ and NO_3^- released to the water column, or TP for evaluating PO_4^{3-} released to the water column), (2) the microbial activity in sediments (oxygen uptake rate) and (3) the bioturbation activity (fauna). We checked for multicollinearity among the three variables (TN or TP, oxygen uptake rate, and fauna) using variance

inflation factors (VIF, Zuur, Ieno & Elphick, 2010) and found them to be in acceptable range (all VIF < 10; Hair et al., 1995). As the three factors and their interactions could influence release rates of nutrients, we performed a procedure of model selection based on information theory (Burnham & Anderson, 2002) and the ranking of models according to Akaike's Information Criterion corrected for small sample size (AICc, “car” R package), starting from the most comprehensive model (including all interactions). The adjusted McFadden's pseudo- R^2 (McFadden 1974) was computed for all tested models to provide for a comparable estimation of the amount of explained variance among models with different number of parameters. All statistical analyses were done with the R v.3.3.2 software.

3. RESULTS

3.1 Initial characteristics of the studied sediments

Following our experimental design, significant differences in hydrolytic activity and O_2 uptake rates were detected among sediment treatments (1-way ANOVAs, $p < 0.001$ for hydrolytic activity, $p < 0.005$ for O_2 uptake rates). Microbial activity and respiration rates were the highest for Grangent sediments and the lowest for Puyvalador sediments (Table 1). The same gradient was observed for total phosphorus (TP) and $P-PO_4^{3-}$ concentrations measured in interstitial water with concentrations significantly decreasing from Grangent to Villerest and Puyvalador sediments (1-way ANOVAs, $**p < 0.05$ for TP, $**p < 0.001$ for $P-PO_4$, Table 1). For example, $P-PO_4^{3-}$ concentrations measured in interstitial water of Grangent sediments were around 3-fold higher than in Puyvalador sediments and 1.8-fold higher than in Villerest sediments which had intermediate $P-PO_4^{3-}$ concentrations (Table 1).

TABLE 1 Initial characteristics of Puyvalador, Villerest and Grangent sediments before fauna addition on Day 0 (mean \pm standard error, N = 3). Different exponent symbols (#, § and @) indicate significant differences among sediments (Tukey post hoc tests, $p < 0.05$).

Sediment characteristics	Puyvalador	Villerest	Grangent
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Microbial hydrolytic activity ($\mu\text{mol.g}^{-1}$ dry sediment.hour ⁻¹)	0.05 ± 0.005 #	0.35 ± 0.07 §	1.13 ± 0.02 @
Oxygen uptake (μmol of O ₂ .hour ⁻¹ m ⁻² of sediment surface)	1196 ± 34 #	1437 ± 143 §	2090 ± 255 @
P-PO ₄ ³⁻ ($\mu\text{g.L}^{-1}$) in interstitial water	210 ± 25.5 #	355 ± 43.6 #	627 ± 52.4 §
N-NH ₄ ⁺ (mg.L^{-1}) in interstitial water	30.9 ± 5.24 #	25.7 ± 2.62 #§	21.0 ± 2.29 §
N-NO ₃ ⁻ (mg.L^{-1}) in interstitial water	0.5 ± 0.03 #	0.1 ± 0.04 §	0.4 ± 0.03 #
TOC (% in mass of dry sediment)	5.65 ± 0.02 #	5.90 ± 0.01 §	4.47 ± 0.07 @
TN (% in mass of dry sediment)	0.66 ± 0.008 #	0.76 ± 0.007 §	0.61 ± 0.007 @
TOC/TN (molar ratio)	10.02 ± 0.03 #	9.10 ± 0.03 §	8.48 ± 0.01 @
TP (mg.g^{-1} dry sediment)	0.896 ± 0.090 #	0.957 ± 0.138 #§	1.260 ± 0.149 §
Fe (mg.g^{-1} dry sediment)	30.9 ± 0.7 #	29.8 ± 0.2 §	36.6 ± 0.6 @
Grain size (<63 μm) (% in volume)	82.4 ± 0.41 #	75.7 ± 0.58 §	79.5 ± 0.86 @

TOC = total organic carbon, TN = total nitrogen, TP = total phosphorus

TOC and TN concentrations in the sediment did not follow the gradient observed for microbial activity, O₂ uptake rates and P concentrations as the lowest concentrations were measured in Grangent sediments and the lowest in Villerest sediments (1-way ANOVA, * $p < 0.05$, Table 1). TOC/TN ratios varied significantly among reservoir sediments (1-way ANOVA, * $p < 0.05$) with increasing values from Grangent (8.5) to Villerest (9.1) and Puyvalador (10.0) sediments (Table 1). As the main dissolved inorganic form of nitrogen in interstitial waters (Table 1), N-NH₄⁺ concentrations were not linked to TN concentrations in sediments. Indeed, N-NH₄⁺ concentrations were more than 20% higher in Puyvalador sediments than in Villerest sediments (1-way ANOVA, * $p < 0.05$, Table 1), the reservoir sediment characterized by the highest TN concentrations. Fe concentrations were comparable among the three reservoir sediments with values ranging from 29.8 (Villerest) to 36.6 (Grangent) mg per g of dry sediment. Concerning grain size analyses, the volumetric percentages of fine particles (i.e. silt and clay < 63 μm) in

the three reservoir sediments were comparable with values comprised between 75 and 83% despite significant statistical differences among the three sediments (Table 1).

3.2 Influence of bioturbating fauna on the release of nutrients in the water column

Bioturbating fauna significantly increased the P-PO_4^{3-} concentration in the water column for the three reservoir sediments (2-ways ANOVA, “fauna” effect, $**p < 0.001$, Figure 2-A) but this effect depended on the tested sediment treatment (2-ways ANOVA, “sediment * fauna” effect, $**p < 0.001$). The effect of fauna was the most significant in mesocosms filled with Grangent sediments (Figure 2-A) characterized by the highest P contents and the highest microbial activity (Table 1). P-PO_4^{3-} concentrations with tubificid worms and chironomids were respectively 3- and 4-fold higher than in the control treatment with Grangent sediments (Tukey’s tests, $**p < 0.001$) while the effects of the two bioturbating species was less marked in Villerest sediments (Figure 2-A). In addition, tubificid worms and chironomid larvae had comparable effects on P-PO_4^{3-} concentrations released to the water column (Tukey’s tests, $p > 0.05$, see Figure 2-A). The procedure of model selection started from the most comprehensive model (including TP, oxygen uptake rate and fauna) and all interactions as predictors of P-PO_4^{3-} released from sediments (Table S1). This procedure resulted in the selection of a model with the interaction of oxygen uptake rate and fauna as the main predictors (linear model; $p < 0.0001$, $R^2 = 0.759$). These results confirmed that the stimulating effect of chironomids and tubificid worms on P-PO_4^{3-} released from sediment to the water column was mediated by microbial activity in sediments.

The N-NH_4^+ concentrations measured in the water column at the end of the experiment differed among sediment and fauna treatments (2-ways ANOVA, “sediment * fauna” effect, $***p < 0.0001$). A positive effect of bioturbation on the N-NH_4^+ concentrations in the water column was detected in mesocosms with Villerest and Grangent sediments compared to mesocosms with Puyvalador sediments (Figure 2-B), leading to a significant difference in N-NH_4^+ concentrations in the water column among sediments (2-ways ANOVA, sediment effect, $***p < 0.05$). Moreover, tubificid worms had a significant effect on N-NH_4^+ concentrations whereas chironomid larvae did not increase N-NH_4^+ concentrations in the water column compared with the control treatment (Tukey’s tests, $p > 0.05$, Figure 2-B). For example, N-NH_4^+ concentrations in the water column of mesocosms with Grangent sediments were at least 3-fold higher in presence of tubificid worms (almost 1 mg.L^{-1}) compared to the controls

(without fauna) or in the presence of chironomids (Tukey's tests, $*p < 0.05$ for pairwise comparisons). Related to these results, the model selection procedure resulted in fauna (and the presence of tubificid worms) as the main predictor of N-NH₄⁺ concentrations released to the water column (linear model; $p < 0.05$, Table S2), but the variance explained by the selected model was low ($R^2 = 0.154$).

N-NO₃⁻ concentrations measured in the water column at the end of the experiment were significantly increased by tubificid worms and chironomid larvae depending on the sediment treatment (2-ways ANOVA, “sediment * fauna” effect, $**p < 0.01$, Figure 2-C). Tubificid worms only had a significant effect on N-NO₃⁻ concentration in comparison with the controls in mesocosms filled with Villerest sediments characterized by the highest TN concentrations (Tukey's post-hoc test, $*p < 0.05$). Chironomids increased N-NO₃⁻ concentrations in mesocosms with Puyvalador and Villerest sediments compared to control treatment (Tukey's post-hoc tests, $*p < 0.05$) whereas they had no effect on this variable in mesocosms with Grangent sediments (Tukey's post-hoc tests, $p > 0.05$, Figure 2-C). Related to these different effects of bioturbating species depending on sediments, an additive model including the three predictors (TN, oxygen uptake rate and fauna) was selected to predict N-NO₃⁻ released from sediments (linear model; $p < 0.0001$, $R^2 = 0.839$, TableS3). In addition, N-NO₃⁻ concentrations measured in the water column at the end of the experiment were significantly higher in mesocosms with Villerest sediments than in mesocosms filled with the two other sediments (2-ways ANOVA, “sediment” effect $**p < 0.001$, Figure 2-B).

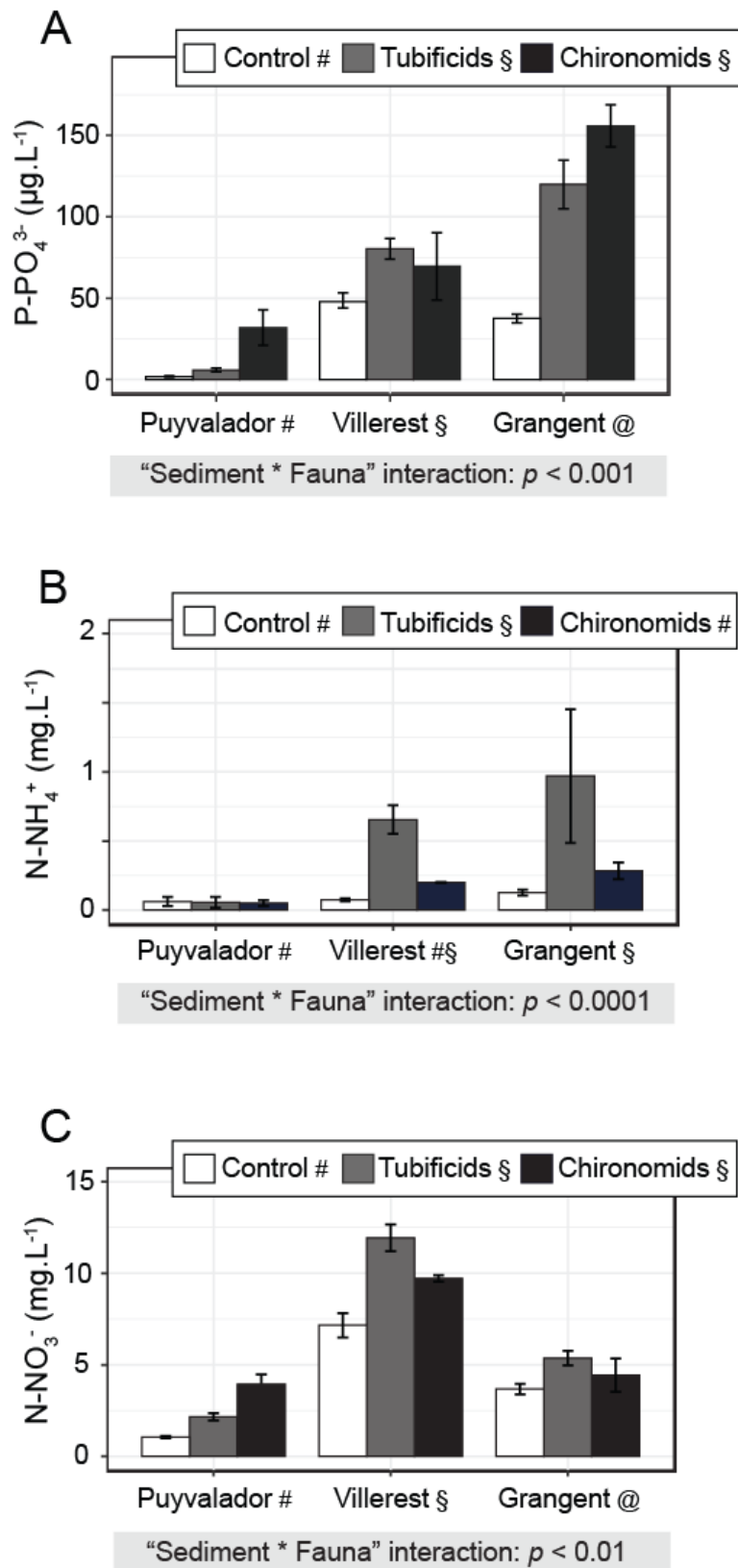


FIGURE 2 Concentrations of P-PO₄³⁻ in µg.L⁻¹ (A), N-NH₄⁺ in mg.L⁻¹ (B), and N-NO₃⁻ in mg.L⁻¹ (C) measured in the water column of mesocosms at the end of the experiment (Day 15) for the three treatments and the three sediments (mean ± standard error, $N=3$). Different

symbols (#, § and @) indicate significant differences among sediments or among fauna treatments (Tukey post hoc tests, $p < 0.05$). Caution, scales and units are not the same for the three panels. Statistical results (2-ways ANOVA) for interactions between sediment and fauna are indicated below panels for each nutrient.

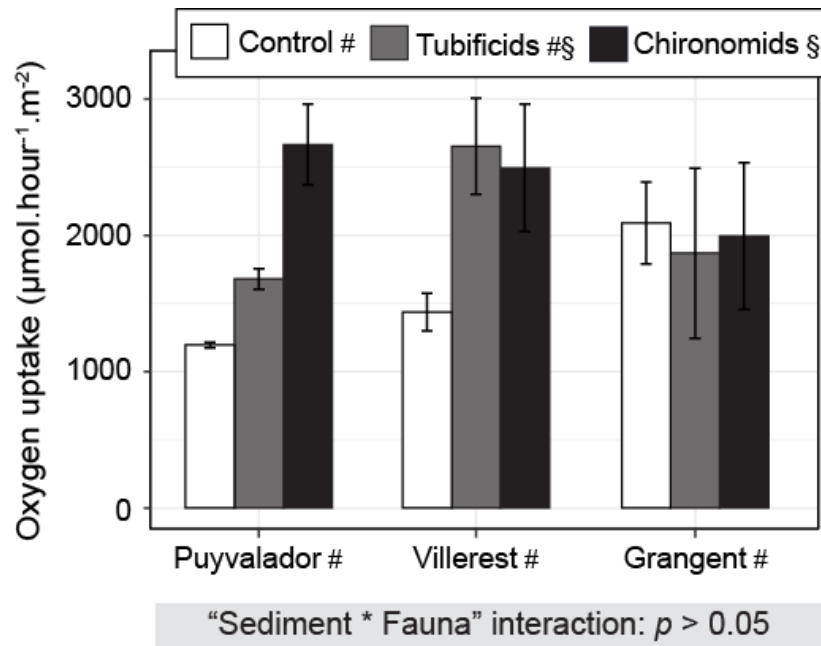


FIGURE 3 Oxygen uptake rates (fluxes from water column to sediment in $\mu\text{mol}\cdot\text{hour}^{-1}\cdot\text{m}^{-2}$) measured on Day 14 of the experiment for the fauna treatments and the three sediments (mean \pm standard error, $N=3$). Different symbols (#, § and @) indicate significant differences among sediments or among fauna treatments (Tukey post hoc tests, $p < 0.05$). Statistical results (2-ways ANOVA) for interactions between sediment and fauna are indicated below panels for each nutrient.

3.3 Influence of bioturbating fauna on DO uptake rates

Bioturbating fauna had a significant positive influence on DO uptake rates (2-ways ANOVA, “fauna” effect, $*p < 0.05$) that was not dependent on sediment treatments (2-ways ANOVA, “sediment * fauna” effect, $p > 0.05$) (Figure 3). However, tubificid worms tended to increase mean oxygen uptakes in mesocosms filled with Puyvalador (+40% compared with the control

treatment) and Villerest (+80% compared with the control treatment) sediments whereas they had no effect in Grangent sediments. Similarly, chironomids tended to stimulate oxygen uptake in mesocosms with Puyvalador (+120% compared with the control treatment) and Villerest (+75% compared with the control treatment) sediments and had no influence in Grangent sediments (Figure 3) characterized by the highest microbial activity (Table 1).

3.4 Influence of bioturbating fauna on hydrolytic activity in sediments

As observed at the start of the experiment (Table 1), microbial hydrolytic activity remained significantly different among sediments on day 15 (Figure 4) (2-ways ANOVA, “sediment” effect, $**p < 0.001$). We did not detect a significant influence of bioturbating species on microbial hydrolytic activity (2-ways ANOVA, “fauna” effect, $p > 0.05$). Nevertheless, in Grangent sediments, mean hydrolytic activity was more than 60% higher in tubificid worm treatment than in control and chironomid treatments (Figure 4).

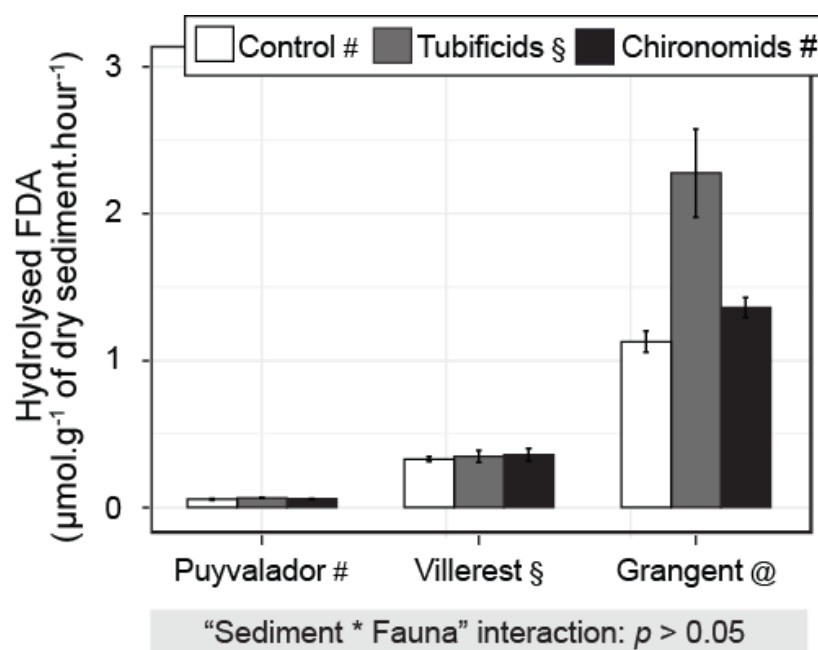


FIGURE 4 Hydrolytic activity (μmol of hydrolyzed FDA. g^{-1} of dry sediment. hour^{-1}) measured at the end of the experiment for the three fauna treatments for Puyvalador sediment, Villerest sediment and Grangent sediment (mean \pm standard error, $N=3$). Different symbols (#, § and @) indicate significant differences among sediments or among fauna treatments (Tukey post hoc tests, $p < 0.05$). Statistical results (2-ways ANOVA) for interactions between sediment and fauna are indicated below panels for each nutrient.

4. DISCUSSION

4.1 Hypothesis 1: The effect of bioturbation on nutrients released to the water column is positively linked with microbial activities in sediments

We expected nutrient fluxes to be stimulated in the presence of fauna and to be highest in sediments characterized by the highest microbial activity involved in OM mineralization. It was thus expected that released PO_4^{3-} and dissolved inorganic nitrogen (DIN) associated with bioturbating fauna would be highest in mesocosms with Grangent sediments characterized by the highest microbial respiration and hydrolytic activity. This hypothesis was validated for PO_4^{3-} concentrations because both chironomids larvae and tubificid worms produced the highest PO_4^{3-} release from sediments to the water column in mesocosms with Grangent sediments compared to the other sediments. Moreover, the selected linear model supported this hypothesis by showing that the interaction of oxygen uptake rate (i.e. microbial respiration) and fauna explained more than 75% of the variability of PO_4^{3-} concentrations released into the water column.

The effect of microbial activity on PO_4^{3-} released from sediments to the water column could have resulted from two mechanisms: (1) microbial hydrolytic activity was involved in mineralization of organic matter and the release of inorganic P and (2) microbial respiration determined aerobic-anaerobic conditions and P mobility in sediments (Rapin et al., 2019). The first mechanism was not supported by the whole dataset because we did not detect a link between PO_4^{3-} released from sediments and microbial hydrolytic activity involved in organic matter mineralization by ubiquitous free and membrane-bound digestion enzymes such as lipase, protease, and esterase enzymes (Adam & Duncan, 2001; Li et al., 2009). For example, although tubificid worms significantly increased hydrolytic activity in Grangent sediments in comparison with chironomid larvae, they did not create a higher stimulation of PO_4^{3-} release from Grangent sediments than chironomid larvae. The second mechanism based on aerobic-anaerobic conditions was more probable because O_2 uptake rate was significantly higher in control mesocosms with Grangent than in mesocosms with Villerest and Puyvalador sediments. Without bioturbating fauna, it has been largely shown that aerobic-anaerobic conditions in sediments mainly depend on microbial oxygen uptake (Glud et al., 1994). Moreover, Van Dael et al. (2020) showed that increased sediment respiration favored phosphate release to surface

waters. Thus, Grangent sediments which presented the highest oxygen uptake rates would be more depleted in dissolved oxygen and would be more under anaerobic conditions than the two other sediments. Therefore, aerobic-anaerobic conditions at the SWI could be considered as a main determinant of PO_4^{3-} release rates from sediments to the water column in the present experiment.

P adsorption mechanisms are known to be modulated by DO concentrations (Boström et al., 1988; Wetzel, 2001; Ekeröth, Blomqvist & Hall, 2016; Rapin et al., 2019): PO_4^{3-} is adsorbed with $\text{Fe}(\text{OH})_3$ and $\text{Mn}(\text{OH})_2$ under aerobic conditions and released under anaerobic conditions. Søndergaard, Windolf & Jeppesen (1996) showed from 32 lakes that total Fe concentration of 20-30 $\text{mg}\cdot\text{g}^{-1}$ in sediments could retain high TP concentrations (i.e. 3 $\text{mg}\cdot\text{g}^{-1}$ of dry sediment). The total Fe concentrations measured in the three reservoir sediments tested (29-37 $\text{mg}\cdot\text{kg}^{-1}$ of dry sediment) were sufficiently high to retain TP contained in sediments (from 0.90 to 1.26 $\text{mg}\cdot\text{g}^{-1}$ of dry sediment) on iron oxides under aerobic conditions. Thus, microbial respiration in sediments that modulated aerobic-anaerobic conditions in sediments could significantly influence the adsorption-desorption mechanisms of P in the three tested sediments (as illustrated on Figure 5 by a decreasing thickness of the aerobic zone at the SWI with increasing microbial respiration in the three sediments). Nevertheless, it is important to mention that the P adsorption mechanism was dependent on Fe concentrations in sediments and P releases induced by bioturbation would be significantly higher in sediments characterized by low Fe concentrations (Hölker et al., 2015).

It is also worth noting that the higher concentrations of TP in Grangent sediment than in the other two sediments could also partly explain the differences in PO_4^{3-} enrichment of the water column among mesocosms. As TP contained in sediment was the main source of P in the mesocosms, bioturbation was more prone to stimulate the release of P from sediments characterized by the highest concentrations of TP. Supporting this assumption, a relationship has been clearly demonstrated between the release rate of P and TP in anoxic lake sediments (see Nümborg, 1988 for an example). However, the selected model did not include TP as the main predictor of PO_4^{3-} release from sediments to the water column in the present study. Thus, microbial respiration activity seemed to be the main determinant of P release rates from bioturbated mesocosms.

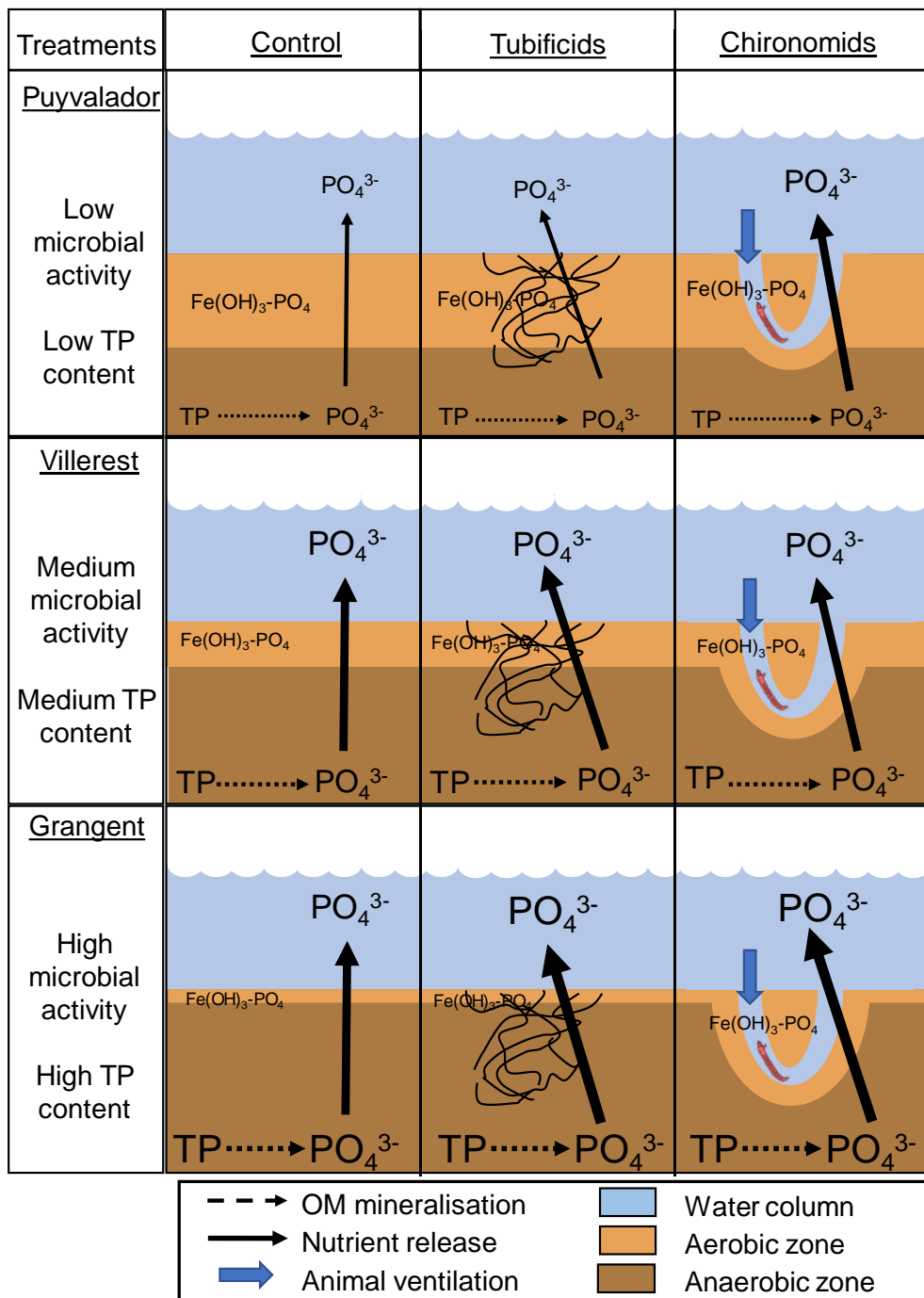


FIGURE 5 Schematic diagrams illustrating the expected PO_4^{3-} fluxes in mesocosms depending on sediment and fauna treatments.

Bioturbation also increased the release of NH_4^+ in the water column in relation to the sediment tested. Whatever the TN content in the sediment, Grangent sediment produced very

high NH_4^+ release in the water column compared to Puyvalador sediment, which showed 20-fold lower microbial activities and negligible enrichment in NH_4^+ in the water column. However, we could not validate the main hypothesis that NH_4^+ release from sediments associated with bioturbation was largely dependent on microbial activity and OM mineralization in sediments. The selected model only considered fauna treatment as a significant predictor of NH_4^+ release from sediments to the water column. However, the variance explained by fauna was lower than 20% and this observation could have resulted from the rapid nitrification of NH_4^+ into NO_3^- in the mesocosms. A classical nitrogen remineralization sequence would have occurred in mesocosms with a rapid flux of NH_4^+ resulting from OM decomposition followed by a nitrification of NH_4^+ into NO_3^- (Bowen et al., 2014). Gautreau et al. (2020) already demonstrated the occurrence of this remineralization sequence during an experiment of 15 days with mesocosms filled with Puyvalador sediments. In the present experiment, it was clear that a nitrification process occurred as NH_4^+ was the dominant DIN form in the interstitial water and NO_3^- the dominant DIN form in the water column.

Theoretically, a link between NH_4^+ and NO_3^- enrichments of the water column was expected because NH_4^+ produced in sediments and released to the water column was nitrified into NO_3^- (Pignoret et al. 2016). However, the enrichment of water column with NO_3^- did not follow the same pattern than NH_4^+ concentrations measured in water column. Although fauna treatment had a significant influence on both NH_4^+ and NO_3^- concentrations released to the water column, the highest NH_4^+ concentration measured in the water column of Grangent mesocosms with tubificid worms did not result in the highest concentration of NO_3^- in the water column suggesting that nitrification of the NH_4^+ released from the sediment did not accumulate as NO_3^- in the water column of this treatment. Therefore, we can hypothesize that NO_3^- present in the water column might have been subsequently transformed into gaseous nitrogen (N_2) through denitrification in Grangent mesocosms, reducing the concentrations of NO_3^- in the water column (as observed by Svensson & Leonardson, 1996). Related to this explanation, the model selection showed that oxygen uptake rate in addition with fauna treatment and TN were selected to predict N- NO_3^- released from sediments. Thus, the highest DO uptake rates and microbial activities measured in mesocosms with Grangent sediments could explain the lower NO_3^- concentrations measured in the water column with Grangent sediments than with Villerest sediments because anaerobic processes were probably favored in Grangent sediments in

comparison with Villerest sediments (as discussed above for P dynamics). In these conditions, the higher denitrification rates in Grangent sediments compared to Villerest sediments might explain the lower NO_3^- concentrations measured in control mesocosms with Grangent sediments than in mesocosms with Villerest sediments.

Finally, the NO_3^- concentrations measured in the water column after 15 days of experiment probably resulted from a series of processes: NH_4^+ production (OM mineralization and ammonification, Blackburn & Henriksen, 1983), NH_4^+ fluxes to the water column, NH_4^+ nitrification and subsequent NO_3^- denitrification (Jenkins & Kemp, 1984). With DO uptake and fauna treatment, TN concentration, which was the highest in Villerest sediments, was also selected in the best model to explain NO_3^- release to the water column. Based on these results, we can suggest that the highest stimulation of NO_3^- fluxes by bioturbation was reported from Villerest sediments because these sediments were characterized by the highest TN content but also by a medium microbial activity that did not lead to high denitrification rates (as expected in Grangent sediments as illustrated in Figure 6). Although specific experimental works aiming at quantifying ammonification, nitrification and denitrification processes (following protocols developed in Gilbert et al., 2016 for example) are needed to support these interpretations, the present study clearly highlighted that the influence of bioturbating fauna on nutrient dynamics at the SWI was largely dependent on TN that can be mineralized in sediments and microbial processes involved in the mineralization of organic matter, the creation of aerobic-anaerobic gradients and the transformation of DIN.

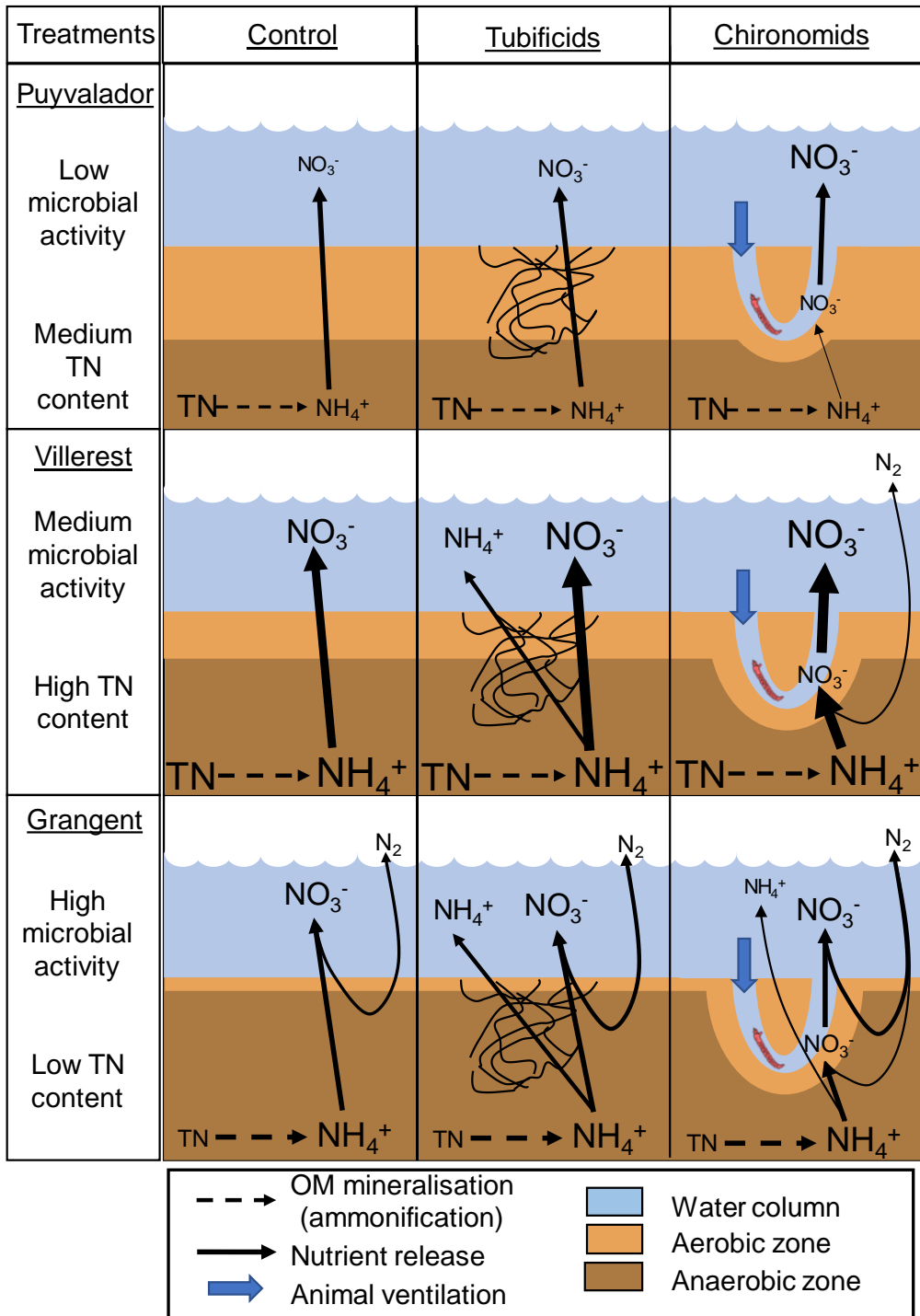


FIGURE 6 Schematic diagrams illustrating the expected DIN fluxes in mesocosms depending on sediment and fauna treatments.

4.2 Hypothesis 2: Chironomid larvae produced higher nutrient release rates from sediments to the water column than tubificid worms.

The hypothesis stating that the bioirrigation activity by chironomid larvae produced higher nutrient release rates to the water column than gallery building by tubificid worms was not verified for the three sediments tested. Although chironomid larvae more strongly influenced nutrient release to the water column than tubificid worms in mesocosms with Puyvalador sediments, the two bioturbating species had comparable effects on PO_4^{3-} and NO_3^- releases in the water column for the two other sediments. In addition, tubificid worm activity produced a higher NH_4^+ release to the water column of Villerest and Grangent mesocosms than the bioturbation activity of chironomid larvae. Upward conveyance and deposition of fecal pellets at the sediment surface by tubificid worms could explain this difference as direct excretion of NH_4^+ by animals in the water column was more probable with tubificid worms than with chironomid larvae (Matisoff et al., 1985). Nevertheless, such an explanation was not validated by PO_4^{3-} measurement as upward conveyance by tubificid worms would have also releases more PO_4^{3-} into the water column than chironomid activity (as observed by Fukuhara & Sakamoto, 1987). Thus, the dynamics of DIN and PO_4^{3-} observed in the present experiment were more likely due to differences between the two species in bioirrigation behavior that modifies water and solute fluxes at the sediment-water interface.

Following our initial hypothesis, the production and irrigation of biogenic structures by chironomid larvae were expected to generate more exchanges of water and solutes at the SWI than the deep gallery network of tubificid worms that were poorly ventilated. However, bioirrigation by chironomid larvae had also the potential to favored the adsorption of PO_4^{3-} by iron oxides as $\text{Fe}(\text{OH})_3\text{-PO}_4$ (Lewandowski, Laskov & Hupfer, 2007) and the nitrification of NH_4^+ in sediments (Pelegri & Blackburn, 1996) by creating a deeper oxygen penetration into sediments (e.g. Søndergaard et al., 2003; Lewandowski et al., 2007; Hupfer et al., 2019). Consequently, bioirrigation activity of chironomids larvae generated water and solute fluxes that could increase but also decrease the releases of PO_4^{3-} and NH_4^+ from sediments (Figures 5 and 6).

In the present experiment, the influence of chironomids on nutrient fluxes was probably modulated by microbial activity determining biogeochemical processes and aerobic-anaerobic conditions in sediments. U-shaped tubes of chironomids are known to be active nitrification-denitrification zones in sediment (Svensson, 1997; Stief & De Beer, 2006; Samuiloviene et al.,

2019) but the effects of these bio-irrigated structures on denitrification (NO_3^- uptake) were reported to increase with anaerobic conditions in sediments (Pelegri & Blackburn, 1996). Following these results, we can thus hypothesize that high microbial activity leading to highly anaerobic conditions in Villerest and Grangent sediments might have favored the stimulation of denitrification process by bioirrigation activities of chironomids (illustrated in Figure 6). In contrast, this stimulation of denitrification by chironomids was not expected in Puyvalador sediments characterized by the lowest levels of microbial activity. These expected differences in chironomid-mediated denitrification among sediments could explain the comparable effects of tubificid worms and chironomid larvae on DIN release to the water column for Villerest and Grangent sediments while chironomids had more influence on NO_3^- release to the water column than tubificid worms in Puyvalador sediments. Indeed, the stronger stimulation of denitrification process by chironomids than by tubificid worms in Villerest and Grangent sediments probably limited the accumulation of NO_3^- in mesocosms with chironomids (gaseous N_2 produced from NO_3^- being exported out of the mesocosms), leading to results distinct from those observed in Puyvalador sediments.

For P dynamics, the lack of contrasting effects of tubificid worms and chironomid larvae on PO_4^{3-} release in the water column in Villerest and Grangent sediments could be also due to the complex interactions between the sedimentary environment and the bioirrigation activity of chironomid larvae. While chironomids had a stronger effect than tubificid worms in Puyvalador sediments by pumping water and increasing exchanges between the aerobic and anaerobic zones of the sediment, chironomid larvae might have a more mitigated effect in more anaerobic sediments by increasing the oxidized layer of sediments and PO_4^{3-} adsorption (Hupfer et al., 2019, Figure 5).

In summary, the influence of chironomid larvae on DIN and PO_4^{3-} was modulated among sediments depending on the aerobic-anaerobic conditions and biogeochemical processes affected by ventilated U-shaped burrows (Figures 5 and 6). Tubificid worms, which did not actively ventilate their dense and deep network of galleries (Lagauzère et al., 2009), had a moderate effect on aerobic-anaerobic conditions and did not stimulate nitrification-denitrification processes or PO_4^{3-} adsorption to the same extent than chironomid larvae. This difference was also observed on NH_4^+ dynamics. In addition with excretion mechanisms associated with fecal pellet deposition at the sediment surface by worms, deep worm galleries increased the release rate of NH_4^+ accumulated in the interstitial water whereas ventilated U-

shaped tubes of chironomids increased the aerobic zone at the SWI, stimulating the nitrification process and the release of NO_3^- rather than the release of NH_4^+ from sediments (as illustrated in Figure 6). The dynamics of nutrient releases at the SWI was largely modulated by the burrow ventilation of bioturbating species that could generate multiple fluxes of DIN and P between sediments and the water column depending on aerobic-anaerobic conditions.

4.4 Main conclusions

The present study clearly highlighted that the effect of bioturbating fauna on nutrient release to the water column depended on the sedimentary context and more especially on the rates of microbial processes occurring in sediments. The modelling approach highlighted that the influence of bioturbation on P dynamics was mainly controlled by microbial activity in sediments that determined aerobic-anaerobic conditions at the SWI. For N dynamics, the role of bioturbation played by benthic organisms such as chironomid larvae was more complex and depended on total N and microbial activity in sediments involved in the N cycle. For example, biogeochemical processes like nitrification and denitrification can be strongly modulated by bioturbating fauna, inducing contrasting dynamics of DIN at the SWI. These results support the conclusions of several authors (e.g., Bernard et al., 2019; Cassidy et al., 2020) stating that bioturbation functional traits (burrow construction, bio-irrigation) of benthic organisms do not necessarily predetermine the way in which species mediate biogeochemical processes because of interactions with the environment. Consequently, it is necessary to bear in mind that the results of the present experiment could be modulated by environmental factors not considered in the experimental design like temperature, dissolved oxygen in water column, phytoplankton density or the presence of a microphytobenthos that were reported to affect the burrowing activity of bioturbators (Roskosch et al., 2012) and the microbial processes occurring in sediments (Deng et al., 2020). Therefore, including these factors in future experiments is necessary to expand our understanding of the role of the complex interactions between benthic organisms and environmental conditions on nutrient dynamics at the SWI of reservoirs.

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AUTHOR CONTRIBUTION STATEMENT

Conceptualisation: EGa, LV, GN, EGo, FMB. Developing methods: EGa, GN, FMB. Data analysis: EGa, GN, FMB. Data interpretation: EGa, LV, GN, PM, FMB. Preparation figures & tables: EGa, FMB. Writing: EGa, LV, GN, EGo, PM, FMB.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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Figure legends:

Figure 1: Schema of a mesocosm with peristaltic pump, oxygen sensor and air source (A) and photograph of three mesocosms during the experiment (B)

Figure 2: Concentrations of P- PO_4^{3-} in $\mu\text{g.L}^{-1}$ (A), N- NH_4^+ in mg.L^{-1} (B), and N- NO_3^- in mg.L^{-1} (C) measured in the water column of mesocosms at the end of the experiment (Day 15) for the three treatments and the three sediments (mean \pm standard error, $N=3$). Different symbols (#, § and @) indicate significant differences among sediments or among fauna treatments (Tukey post hoc tests, $p < 0.05$). Caution, scales and units are not the same for the three panels. Statistical results (2-ways ANOVA) for interactions between sediment and fauna are indicated below panels for each nutrient.

Figure 3: Oxygen uptake rates (fluxes from water column to sediment in $\mu\text{mol.hour}^{-1}.\text{m}^{-2}$) measured on Day 14 of the experiment for the fauna treatments and the three sediments (mean \pm standard error, $N=3$). Different symbols (#, § and @) indicate significant differences among sediments or among fauna treatments (Tukey post hoc tests, $p < 0.05$). Statistical results (2-ways ANOVA) for interactions between sediment and fauna are indicated below panels for each nutrient.

Figure 4: Hydrolytic activity (μmol of hydrolyzed FDA. g^{-1} of dry sediment. hour^{-1}) measured at the end of the experiment for the three fauna treatments for Puyvalador sediment, Villerest sediment and Grangent sediment (mean \pm standard error, $N=3$). Different symbols (#, § and @) indicate significant differences among sediments or among fauna treatments (Tukey post hoc tests, $p < 0.05$). Statistical results (2-ways ANOVA) for interactions between sediment and fauna are indicated below panels for each nutrient.

Figure 5: Schematic diagrams illustrating the expected PO_4^{3-} fluxes in mesocosms depending on sediment and fauna treatments.

Figure 6: Schematic diagrams illustrating the expected DIN fluxes in mesocosms depending on sediment and fauna treatments.