The influence of bioturbation and water column oxygenation on nutrient recycling in reservoir sediments

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Title

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Abstract

Sediments act as sinks of nutrients in aquatic ecosystems but may also act as nutrient sources, leading to eutrophication of lakes and reservoirs during the warm season of the year. In this context, internal recycling of nutrients from sediments can be largely modulated by abiotic (e.g., redox conditions) and biotic (e.g., activity of benthic organisms) factors occurring at the water-sediment interface. The present study aimed at quantifying the effects of these factors (water column oxygenation and bioturbation by two bioturbating species - the tubificid worm *Tubifex tubifex* and insect larvae of *Chironomus plumosus*) on benthic fluxes of nitrogen (N), phosphorus (P) and silicon (Si) from reservoir water-sediment interface. An experimental approach based on the reconstitution of the water-sediment interface in mesocosms has been developed in the laboratory to test three fauna conditions (no fauna, presence of worms, and presence of chironomids) and three conditions of water column oxygenation (constant aerobic conditions, fluctuations of oxygen concentrations and constant anaerobic conditions). The larvae of chironomids significantly increased by 3.7-fold and by 17-fold the concentrations of N (NH_4^+ + NO_3^-) and PO_4^{3-} released from sediments, respectively. In comparison, tubificid worms had lower influences on these released nutrients (x2 for N and x3 for PO_4^{3-} in comparison with the control treatment without fauna). These contrasted effects of chironomids and tubificid worms on nutrient fluxes were related to their different bioturbation activities in sediments. Chironomid larvae increased water-sediment exchanges by actively ventilating their U-shaped

burrows whereas tubificid worms produced deep galleries but they did not ventilate them to the same extent as chironomid burrows. Anaerobic conditions increased by 56-fold N fluxes and by 102-fold PO_4^{3-} fluxes in comparison with the aerobic treatment. While anaerobic conditions could produce higher stimulation of N fluxes than bioturbation process, oxic-anoxic shift was also a stronger regulator of P fluxes than benthic fauna. Overall, bioturbating fauna and occurrence of anoxic conditions at the water-sediment interface should not be neglected in model assessing the role of sediments on nutrient dynamics in lakes and reservoirs during the season favorable to algal blooms.

Key words

water-sediment interface, aerobic/anaerobic conditions, chironomid larvae, tubificid worms, fauna activity, nitrogen, phosphorus

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Introduction

The increasing anthropogenic discharge of nutrients is the primary cause of eutrophication in aquatic ecosystems. This phenomenon is predominantly observed in aquatic systems such as lakes and reservoirs (Vitousek et al., 1997; Smith, 2003; Galloway et al., 2004). Indeed, reservoirs participate to more than 50% of the sediment retention in drainage basins around the world (4-5 gigatons/year, Vörösmarty et al., 2003), leading to a massive accumulation of sediment-associated nutrients (nitrogen N and phosphorus P).

During the warm season of the year, the eutrophication of aquatic ecosystems leads to algal blooms, especially cyanobacteria blooms resulting from oxygen depletion in ecosystems (Schindler, 1974; Findlay & Kasian, 1987), which can lead to effects on fishes and macroinvertebrates (i.e. reduction of populations, Breitburg et al., 2009). For example, Foley et al. (2012) reported decreasing dissolved oxygen (DO) concentration with eutrophication in a lake monitored during more than 40 years. Consequently, eutrophication significantly impacts the human activities linked to reservoirs (e.g. drinking purposes, fishing) and eutrophic aquatic ecosystems have difficulties to meet EU Water Framework Directive (WFD 2000/60/EC ; European Council, 2000) requirements, which have to reach the good ecological status by 2027 for all surface waters.

In reservoirs, excessive nutrient loadings leading to the eutrophication of the water column have 2 origins: external (tributaries, atmospheric deposition, surface run-off, groundwater (Meinikmann et al., 2015)) and internal sources from the sediment compartment. In multiple cases, a reduction of external inputs did not efficiently reduce eutrophication because of internal sources associated with the massive amounts of nutrients accumulated in the sediments, as shown for phosphorus (P) by Søndergaard et al. (2003) or for nitrogen (N) by Jeppesen et al. (2005). For example, the modelling approach developed by Wu et al. (2017) on the eutrophic lake Dianchi (China) showed that internal loading contributed to 77% for total P and 72% for total N of the total inputs to the water column compared to external loading. Moreover, the contribution of internal sources of nutrients from sediments to water column eutrophication was the highest during the warm season of the year. Indeed, the release rate of P from lake sediments to the water column can be more than 12-fold higher in late spring and summer than during other seasons (Penn et al., 2000; Qin et al., 2016).

For internal inputs, molecular diffusion is classically considered as the main mechanism influencing nutrient fluxes from the sediments to the water column (Berner, 1980 *in* Anschutz *et al*., 2012). Nevertheless, these fluxes are also known to be influenced by chemical (temperature, redox conditions, pH), physical (hydrodynamics like water currents or wind) and biological (bioturbation) factors (Kristensen, 2000; Lavery et al., 2001; Ni & Wang, 2015).

For instance, the solubility of phosphate (PO_4^{3-}) ions is determined by oxygen availability due to their affinity with iron oxides. The PO_4^{3-} ion can be adsorbed on the precipitated $Fe(OH)_3$-PO_4 complexes in presence of oxygen (Mortimer, 1941; Boström et al., 1988; Wetzel, 2001a). Phosphates can also precipitate with calcite ($CaCO_3$) in alkaline condition (as seen by House & Denison, 2002). Bioturbation by benthic animals (i.e. sediment reworking and irrigation of biogenic structures such as tubes and burrows) also influences N and P dynamics at the water sediment interface. By modifying redox potentials and increasing water exchanges at the water-sediment interface, burrowing animals can stimulate the release of N (ammonium and/or nitrate) from interstitial water to the water column (e.g. Krantzberg, 1985). For example, Pelegri & Blackburn, (1996) reported a 5.8-fold stimulation of ammonium (NH_4^+) release rates from lake sediments due to the bioturbation activities of *Chironomus plumosus* (2,000 larvae.m^{-2}) in microcosms. Using a comparable experimental approach, Mermillod-Blondin et al. (2005) showed that tubificid worms (20,000 individuals.m^{-2}) increased the releases of NH_4^+, and PO_4^{3-} from sediments by 2- and 4-fold, respectively. The influence of benthic fauna on nutrient fluxes at the water-sediment interface depends on their functional traits (building of biogenic structures, ventilation rate, depth of biogenic structures, sediment reworking rate) (Kristensen et al., 2012). For example, Nogaro et al. (2016) showed that chironomid larvae that build and ventilate U-shaped tubes stimulated P release from the sediment to the overlying water, whereas tubificids that produce gallery and egest fecal pellets at the water sediment interface increased P retention in sediment from eutrophic wetlands. Although the presence of *Chironomus plumosus* can contribute to release of nutrients into water column, they also bring oxygen into sediment and create oxic conditions nearby their burrow walls. These oxic conditions lead to trap phosphates in $Fe(OH)_3$-PO_4 complexes inside sediments (Hupfer et al., 2019).

Based on these findings, our study aimed to quantify the relative contribution of bioturbation and oxygen concentration conditions on nutrient fluxes at the water-sediment interface of a eutrophic reservoir during the warm season of the year when low oxygen conditions were expected to occur at the water-sediment interface. Laboratory experimentations in mesocosms mimicking the water-sediment interface of the studied reservoir were developed for evaluating the influences of bioturbating fauna (chironomid larvae, tubificid worms) and oxygen conditions in the water column (aerobic, anaerobic and fluctuating conditions) on nutrient ($N\text{-}NH_4^+$, $N\text{-}NO_3^-$, $P\text{-}PO_4^{3-}$ and SiO_2) released from sediments. For bioturbating fauna, oxygen uptake was also measured in the experiment as animals can stimulate nutrient released from sediment by stimulating organic matter mineralization in sediments (Baranov et al., 2016; Murniati et al., 2017; Saaltink et al., 2018). We expected that bioturbating fauna would significantly increase the release of nutrients from sediments (Mermillod-Blondin et al., 2004). Moreover, due to higher

ventilation of biogenic structures, the larvae of *Chironomus plumosus* would generate higher release rates of nutrients and oxygen uptake than tubificid worms (Nogaro et al., 2016). Concerning DO conditions, anaerobic conditions would enhance the release of nutrients, especially $N\text{-}NH_4^+$ and $P\text{-}PO_4^{3-}$, compared with aerobic conditions. For the oxygen fluctuation treatment, we reproduced the daily variations of DO concentrations in the water column of eutrophic reservoirs (e.g. Balangoda, 2017; Wetzel, 2001b) by using the natural oxygen uptake of the sediment column without oxygen supply. Thus, oxygen fluctuations were expected to increase nutrient releases from sediments in comparison with aerobic conditions if oxygen uptake was high enough to produce aerobic-anaerobic fluctuations in the water column.

Materials and methods

Study site presentation, sediment collection and preparation

The study site is Puyvalador reservoir, which is regularly impacted by blooms of cyanobacteria (e.g., *Synechococcus sp.* and *Anabaena spiroides*) during the summer. This reservoir is located in the French Pyrenees Mountains (42°38'N, 2°07'E) at altitude of 1421 m. At its maximum storage level, its surface is 90 ha for a volume of 10.1 hm^3. The maximum depth is 21 m and the mean water residence time is 40 days. This reservoir is part of a hydroelectric complex operated by Electricité de France (EDF) and has two mains tributaries: Aude river and Galbe river. Puyvalador reservoir is eutrophic according to EU Water Framework Directive criteria (Agence de l'eau Rhône Méditerranée Corse, 2015). The central area of the reservoir of Puyvalador, where the depth is maximal, is the main sedimentation zone containing a high percentage (80 %) of fine particles (<63µm) compared to areas influenced by the tributaries (Gautreau et al. in prep). Sediments from the central area are characterized by concentrations of 45 g. kg^{-1} DW (dry weight) of total organic carbon, 6 g kg^{-1} DW of total N and 0.5 g kg^{-1} DW of total P, 33 g.kg^{-1} DW of Fe, 342 mg.kg^{-1} DW of Mn, 4 g.kg^{-1} DW of Ca, and 34 g.kg^{-1} DW of Al. Measurements of benthic fauna densities during summer period indicated that 4th stage larvae of *Chironomus plumosus* and tubificid worms were the most abundant taxa with average densities of 2,095 individuals.m^{-2} and 18,190 individuals.m^{-2}, respectively.

For the present experiment, sediments from the central area were collected with an Eckman grab in September 2017. After sampling, they were frozen at -18°C for several weeks to kill the ambient fauna (Biles et al., 2002). In parallel, a subsample of unfrozen sediment was kept at 15°C (corresponding to the reservoir temperature at the water-sediment interface during sediment collection) to preserve the microbial activities of the collected sediments and to be used as an inoculum for the experiment. Fifteen days before mesocosm preparation, this subsample was

sieved at 80 µm to remove the ambient fauna and added to unfrozen sediments. This incubation time of 15 days was long enough as Mermillod-Blondin *et al.* (2001) showed a bacterial recolonization of previously sterilized sediments in less than 1 week**.**

Mesocosms and experimental set up

Experiments were performed in 15 mesocosms made of 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 for mimicking summer temperature at the water-sediment interface of the reservoir and filled with a layer of incubated sediments (10 cm) overlaid with synthetic water (10 cm) (composition of synthetic water: 96 $mg.L^{-1}$ $NaHCO_3$; 39.4 $mg.L^{-1}$ $CaSO_4 \cdot 2H_2O$; 60 $mg.L^{-1}$ $MgSO_4 \cdot 7H_2O$; 4 $mg.L^{-1}$ KCl; pH = 7.5; (US EPA, 1991)). Oxic conditions were maintained in the mesocosms by bubbling water column with atmospheric air (Figure 1). Mesocosms were equipped with peristaltic pumps for a continuous recirculation of the water column to avoid DO stratification but water flow was adjusted to limit sediment resuspension (6 $mL.min^{-1}$). Oxygen probes were placed on the recirculation system of peristatic pumps to measure DO concentrations.

Mesocosms were run over a period of 14 days to homogenize the experimental conditions among systems. After this period, we measured oxygen uptake in all mesocosms to make sure that similar aerobic microbial activities were occurring in the sediment of all mesocosms. Afterwards, the water column of all mesocosms was renewed with synthetic water to eliminate the initial flush of nutrients during the filling of mesocosms with sediments and water.

Fig. 1 Schema of mesocosm installation with peristaltic pump, oxygen sensor and air source. Sediment and water column compartments were 10 cm in height, corresponding to a volume of 0.785 L for each compartment.

Experimental design

A total of 15 mesocosms was set up to quantify the influence of fauna and DO on nutrient fluxes. For testing the influence of fauna, the water column of the mesocosms was saturated in DO. Three conditions were tested with three mesocosms per condition: 1) control mesocosms without fauna, 2) mesocosms with addition of 150 tubificid worms (more than 90% belonging to the species *Tubifex tubifex*, Michel Lafond, pers. com) and 3) mesocosms with addition of 15 4^{th} stage larvae of *Chironomus plumosus*. Tested animals were from professional breeders. Densities (19,230 individuals per m^2 for tubificid worms and 1,923 individuals per m^2 for *Chironomus plumosus*) fitted with natural densities measured in the field in summer (see Study site presentation). Three conditions with

three replicated mesocosms per condition were used to test the influence of DO concentrations on nutrient fluxes: 1) mesocosms with a water column saturated in DO (same systems than those used as control mesocosms without fauna), 2) mesocosms without fauna and experiencing DO decrease every 12 hours (aeration turn on and off every 12 hours), 3) mesocosms without fauna experiencing anaerobic conditions in the water column.

Measurements

Nutrient dynamics and aerobic microbial respiration were measured during the 15 days of experiment to study the effects of oxygen conditions and bioturbation on biogeochemical processes. Nutrient dynamics were measured by collecting water samples from the water column at 7 times: on Day 0 just before the treatment application and on days 3, 6, 8, 10, 13 and 15 after the treatment application. At each sampling date, a volume of 30 mL of overlying water was sampled from the top of the water column and filtered through a GF/F filters (0.7 µm, Whatman) and conserved at 4°C before chemical analyses. $N\text{-}NH_4^+$, $N\text{-}NO_3^-$, $P\text{-}PO_4^{3-}$ and SiO_2 concentrations of all samples were determined by colorimetric methods with a sequential analyzer (SmartChem200, AMS Alliance). During the experiment, the sampled volume of water for analyses (30 mL) was replaced with 30 mL of artificial water for keeping a constant volume of overlying water. Moreover, to prevent oxygenation of anoxic mesocosms during sampling, collected water was replaced by synthetic water at the top of the mesocosms without air entrance.

DO fluxes were measured to evaluate the influence of bioturbating fauna on aerobic microbial respiration. These measurements were performed a day before fauna introduction (day -1) and on days 2, 7 and 14 after the addition of fauna. At each sampling date, mesocosms were sealed for avoiding contact with the atmosphere and the incubation time was limited to 4 hours to avoid the decrease of DO concentrations below 5 $mg.L^{-1}$. DO was measured with a Pocket Oxygen Meter FireStingGO_2 (Pyroscience) every hour during the incubations. DO fluxes 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.

Data analysis

For chemical variables and DO fluxes measured at different times (after the treatment application), the effect of fauna was tested using one-way repeated measures analyses of variance (RM-ANOVAs) on days 3, 6, 8, 10, 13 and 15 for nutrients concentrations and 2, 7 and 14 for DO fluxes with fauna treatment (i.e. control without fauna, chironomids, and tubificids treatments) as the main effect. The effect of DO was also tested by one-way RM-ANOVAs on days 3, 6, 10, 13 and 15 for nutrients with oxygenation treatment (i.e. control with saturated DO, DO

fluctuation, and anoxia treatments) as the main effect. When one-way RM-ANOVAs were significant (i.e., $p<0.05$), Tukey's post hoc tests were performed for the last day of the experiment to evaluate which treatments differed after 15 days of mesocosm stabilization. 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. All statistical analyses were done with the R v.3.3.2 software.

Results

Influence of bioturbation on nutrient dynamics, nutrient release rates and DO fluxes

Visual observations during the experiment

During the experiment, sediments of control mesocoms presented a dark color characteristics of anoxic conditions (Fig. 2A). Chironomid larvae produced U-shaped tubes in the top 5 cm of the sediment (Fig. 2B). The ventilation of these structures by the chironomids produced a brown colored oxic zone on the tube walls surrounded by dark colored anoxic sediments in the non-bioturbated zones (Fig 2B). Tubificid worms dug galleries in the whole sediment column (10 cm deep, Fig 2C) and deposited fecal pellets at the sediment surface. Nevertheless, we did not observe any brown oxidized zone on the gallery walls produced by the tubificid worms.

Fig. 2 Pictures from the mesocosms: (A) control treatment without fauna, (B) U-shaped tubes produced by chironomid larvae on the inner wall of a mesocosm and (C) galleries produced by tubificid worms on the inner wall of a mesocosm.

Nutrient concentration dynamics and release rates

$N\text{-}NH_4^+$ concentrations measured in the water column of all treatments significantly increased during the first 6 to 8 days of the experiment and decreased thereafter (Figure 3A, one-way RM-ANOVA, time effect, $***p < 0.0001$). This initial $N\text{-}NH_4^+$ increase was significantly higher in the chironomid treatment compared to the control and tubificid treatments (one-way RM-ANOVA, fauna treatment, $*p < 0.01$). Nevertheless, after 15 days of mesocosm stabilization with fauna, $N\text{-}NH_4^+$ concentrations were comparable in control, tubificid worm and chironomid treatments (Tukey's test, p-value > 0.05).

$N\text{-}NO_3^-$ concentrations measured in the water column significantly increased during the course of the experiment from 0.1 $mg.L^{-1}$ at day 0 to 1.1, 2.2 and 3.4 $mg.L^{-1}$ at the end of the experiment for the control, the tubificid and the chironomid treatments, respectively (Figure 3B, one-way RM-ANOVA, time effect, $***p <0.0001$). These N-

NO_3^- increases differed over time depending on the treatment (one-way RM-ANOVA, "fauna treatment * time" effect, ***p <0.0001). Significant $N\text{-}NO_3^-$ increases occurred on the first days for the controls and in presence of tubificids whereas $N\text{-}NO_3^-$ concentrations increased between day 6 and day 13 in presence of chironomids (Figure 3B). Such $N\text{-}NO_3^-$ increase in the chironomid treatment was concomitant with the $N\text{-}NH_4^+$ decrease of concentration in the water column (Figure 3A). At the end of the experiment, $N\text{-}NO_3^-$ concentrations were significantly higher in the chironomid treatment compared to the control and tubificid treatments (Tukey's tests, p-value < 0.05). Considering both inorganic $N\text{-}NH_4^+$ and $N\text{-}NO_3^-$, concentrations, inorganic N concentrations measured on day 15 in chironomid and tubificid treatments were 3.7-fold and 2-fold higher than in control treatment, respectively (Tukey's tests, p-value < 0.05).

$P\text{-}PO_4^{3-}$ concentrations measured in the water column in presence of chironomids significantly increased from 1 $\mu g.L^{-1}$ at day 0 to 60 $\mu g.L^{-1}$ at day 6 and then decreased to reach 21 $\mu g.L^{-1}$ at day 15 (Figure 3C). In comparison, $P\text{-}PO_4^{3-}$ concentration in the water column of control and tubificid treatments remained below 10 $\mu g.L^{-1}$ during the whole course of the experiment. Then, after 15 days of experiment, $P\text{-}PO_4^{3-}$ concentrations in chironomid treatment was 17-fold higher than those measured in control treatment. Despite low $P\text{-}PO_4^{3-}$ concentrations, the occurrence of tubificid worms also increased by 3-fold $P\text{-}PO_4^{3-}$ concentrations in water column in comparison with control treatment (Tukey test, p-value < 0.05).

SiO_2 concentrations measured in the water column significantly increased in all treatments during the course of the experiment (Figure 3D, one-way RM-ANOVA, time effect, ***p < 0.0001) and reached 20 $mg.L^{-1}$ for the chironomid treatment and 13 $mg.L^{-1}$ for the control and tubificid treatments at day 15 (one-way RM-ANOVA, treatment effect, *p < 0.01). Such SiO_2 increase was significantly higher in the chironomid treatment than in other treatments (Tukey's tests, *p < 0.01). At day 15, concentration of SiO2 was 1.4-fold higher in chironomid treatment than in control treatment.

Oxygen uptake

DO uptake rates were comparable in all mesocosms before the fauna addition (around 1500 $\mu mol.h^{-1}.m^{-2}$) and significantly varied during the course of the experiment with the highest rates measured on day 7 (Figure 4, one-way RM-ANOVA, time effect, ***p < 0.0001). After the fauna addition, the presence of chironomid larvae significantly increased oxygen uptake rates in comparison with the other treatments (one-way RM-ANOVA, treatment effect, ***p < 0.0001; Tukey's tests, p *< 0.01). For example, mean DO uptake rate measured on day 14 was 2-fold higher in the chironomid treatment (i.e. 2665 $\mu mol.hour^{-1}.m^{-2}$) than in the control treatment (i.e.

1196 µmol.hour^{-1}.m^{-2}). Mean DO uptake rates measured in tubificid treatment were slightly higher than in control treatment but this effect was not statistically significant at all dates (see post-hoc Tukey's tests in Figure 4).

Fig. 3 Concentrations of N-NH_4^+ (A), N-NO_3^- (B), P-PO_4^{3-} (C), and SiO_2 (D) measured in the water column of mesocosms during the course of the experiment for the three fauna treatments (mean ± standard error, n=3).

Fig. 4 Oxygen uptake rates (fluxes from water column to sediment) measured for the three fauna treatments (mean ± standard error, n=3 mesocosms). For each panel, different letters (A, B and C) show significant differences among treatments (see axis label, Tukey post hoc test, $p<0.05$).

Influence of oxygen conditions in the water column on nutrient dynamics and release rates

Our experimental approach allowed generating contrasted oxic/anoxic conditions in the water column for the three treatments. DO concentrations were maintained above 9 mg/L in the water column for the DO-saturated control treatment whereas they were below 0.05 mg/L in the anoxic treatment during the whole experiment. In the DO fluctuation treatment, DO concentrations varied daily from 9 mg/L during the water column aeration to 5 mg/L about 12 h after the shutdown of the water column aeration (Supplementary Material 1).

N-NH_4^+ concentration measured in the water column significantly increased from 0.5 mg.L^{-1} to 6.4 mg.L^{-1} during the course of the experiment in the anoxia treatment whereas only small variations in N-NH_4^+ concentrations were measured in the DO-saturated control and the DO fluctuation treatments (Figure 5A, one-way RM-ANOVA, 'treatment * time" effect, ***$p < 0.0001$). Indeed, at the end of the experiment, concentration of N-NH_4^+ was 102-fold time higher in anoxia treatment than in DO-saturated control treatment (Tukey's tests,*$p < 0.01$).

In contrast, N-NO_3^- concentrations in the water column significantly increased in the DO-saturated control and DO-fluctuation treatments from 0 mg.L^{-1} on day 0 to about 1 mg.L^{-1} from day 3 to day 15 whereas N-NO_3^- concentrations in the anoxia treatment remained low (around 0.04 mg.L^{-1}) throughout the experiment (Figure 5B, one-way RM-ANOVA, "treatment * time" effect, ***$p < 0.0001$). Then, N-NO_3^- concentration was 27-fold time higher in control treatment than in anoxia treatment at the end of the experiment (Tukey's tests, *$p < 0.01$).

Similarly to N-NH_4^+ dynamics, P-PO_4^{3-} concentrations in the water column significantly increased from 0 to 1034 µg.L^{-1} during the course of the experiment in the anoxia treatment whereas P-PO_4^{3-} concentrations remained low (around 3 µg.L^{-1}) in the two other treatments (Figure 5C, one-way RM-ANOVA, "treatment * time" effect, ***p

274 < 0.0001). At the end of the experiment, concentration of $P\text{-}PO_4^{3-}$ in the water column was 56-fold time higher in
275 anoxia treatment than in control treatment (Tukey's tests, *p < 0.01).

276 SiO_2 concentration measured in the water column significantly increased in all treatments during the course of the
277 experiment (Figure 5D, one-way RM-ANOVA, time effect, ***p < 0.0001) with higher increases detected in the
278 anoxia treatment (e.g., 19.2 $mg.L^{-1}$ at day 15) compared to the other treatments (e.g., about 13-14 $mg.L^{-1}$ at day15)
279 (one-way RM-ANOVA, treatment effect, *p < 0.01).

280 **Fig. 5** Dynamics of $N\text{-}NH_4^+$ (A), $N\text{-}NO_3^-$ (B), $P\text{-}PO_4^{3-}$ (C), and SiO_2 (D) measured in the water column during the
281 course of the experiment for the three DO treatments (mean ± standard error, n=3).

282 * Concentrations of $P\text{-}PO_4^{3-}$ in the anoxia treatment at day 15 are lacking due to an analytical problem.

283 *Discussion*

284 *Influence of fauna on the dynamics of nutrients in water column*

285 Nutrient concentrations in water column were highly variable during the course of the experiment in fauna
286 treatments. More precisely, the occurrence of chironomids in mesocosms produced peaks of $N\text{-}NH_4^+$ and $P\text{-}PO_4^{3-}$
287 in the water column during the first 8 days of experiment. These releases of reduced compounds ($N\text{-}NH_4^+$ and $P\text{-}PO_4^{3-}$) from the pore water of sediments were more probably due to the initial installation (building and
289 ventilation of U-shaped tubes) of chironomids in poorly-oxygenated sediments (as illustrated in Figure 6). This
290 effect of chironomid larvae on the flush of reduced compounds from sediments to the water column has been
291 commonly observed in experimental studies with organic-rich lake sediments (Pelegri & Blackburn, 1996;
292 Hansen et al., 1998; Stief & De Beer, 2006). Nevertheless, this effect was temporary in the present experiment
293 and, after an initial flush, $N\text{-}NH_4^+$ concentrations decreased concomitantly with an increase of $N\text{-}NO_3^-$
294 concentrations in the water column. This evolution of inorganic N compounds in the water column corresponds to
295 a classic sequence of nitrification (Bowen et al., 2014; Pigneret et al., 2016), which was more likely performed by
296 aerobic microorganisms present in the oxygen-saturated water column and the top oxidized sediment layer.
297 Since this process was mainly detected in presence of chironomids, we also expect that the burrow walls acted as
298 a very active zone for nitrification. Several authors demonstrated that burrow construction and ventilation by
299 *Chironomus plumosus* could increase the aerobic surface of the water-sediment interface, and then the favorable
300 zones for nitrification and coupled nitrification-denitrification (Pelegri & Blackburn, 1996; Svensson &
301 Leonardson, 1996; Lewandowski & Hupfer, 2005; Lewandowski et al., 2007; Moraes et al., 2018). This effect

was illustrated on Figure 2B with oxidized sediment nearby U-shaped tubes. Therefore, after 15 days of stabilization, the influence of chironomid larvae bioturbation on N fluxes was predominantly associated with a release of $N\text{-}NO_3^-$ from oxidized sediments (Figure 6B) than a release of $N\text{-}NH_4^+$ from poorly-oxygenized sediments (as observed during chironomid installation, Figure 6A). Concerning P dynamics, the presence of chironomids induced an initial flush of $P\text{-}PO_4^{3-}$ from the sediment to the water column (i.e, up to 60 $mg.L^{-1}$) during the first week of the experiment followed by a small decrease of $P\text{-}PO_4^{3-}$ concentrations in the water column the second week of the experimentation, which remained around 30-40 $\mu g.L^{-1}$ until the end of the experiment. Then, the stimulating effect of chironomid ventilation on $P\text{-}PO_4^{3-}$ concentrations compared to the control treatment without fauna was detected until the end of the experiment. According to Lewandowski and Hupfer (2005) and Hupfer et al. (2019), the supply of DO in chironomid burrows could have produced an adsorption of the $P\text{-}PO_4^{3-}$ initially flushed in the water column into $Fe(OH)_3\text{-}PO_4$ complexes in Fe-rich sediments (ie. 33 $g.kg^{-1}$ DW of total Fe, see materials and methods). Such mechanism probably occurred during our experiment inducing the small decrease of $P\text{-}PO_4^{3-}$ in the water column after day 6 but did not lead to a complete adsorption of $P\text{-}PO_4^{3-}$ flushed from the sediment. We suppose that $P\text{-}PO_4^{3-}$ adsorption occurring in aerobic conditions and enhanced by chironomid ventilation was compensated by a constant flush of $P\text{-}PO_4^{3-}$ from the anoxic sediments due to chironomid bioturbation (Figure 6). As the dynamics of nutrients during the course of the experiment in chironomid treatment were largely associated with the installation of benthic chironomid larvae in sediments, we compared the effects of three fauna treatments on nutrients in water column by considering the last day of the experiment after 15 days of stabilization of biogeochemical processes in the mesocosms.

Influence of bioturbation on nutrient concentrations and oxygen uptake

According to our prediction, the ventilation of U-shaped burrows by *Chironomus plumosus* highly increased inorganic N (x 3.7) and $P\text{-}PO_4^{3-}$ (x 17) concentration in water column after 15 days of experiment by creating water exchanges at the water sediment interface. Indeed, the presence of oxic brown sediments observed on the burrow walls of chironomids demonstrated a transport of oxygen-saturated water from the water column in the biogenic structures built by animals in anoxic sediments. This ventilation of U-shaped burrows produced a significant stimulation of oxygen uptake (2-fold increase on day 7 compared to control treatment without fauna) by increasing the supply of DO in sediments. This stimulation of oxygen uptake by chironomids probably contributed to nutrient dynamics by stimulating microbial activities and organic matter mineralization in sediments (Aller, 2001). Nevertheless, the major mechanism explaining the influence of chironomid larvae on nutrient fluxes at the water-

sediment interface was burrow ventilation which increased the release rates of nutrients (inorganic nitrogen N-NH_4^+ + N-NO_3^-- and P-PO_4^{3-}) accumulated in pore water (Lewandowski & Hupfer, 2005; Lewandowski et al., 2007). The increase (+ 50%) of SiO_2 concentration in water column with *Chironomus plumosus* was in accordance with this mechanism of burrow ventilation as silicate fluxes were found to depend on irrigation of biogenic structures by benthic fauna (e.g., Mermillod-Blondin et al., 2004).

In contrast with chironomid larvae, tubificid worms had lower influences on N (x2 in comparison with the control treatment) and P (x3 in comparison with the control treatment) concentrations in the water column in our experimental conditions. Such contrasted effects of *Chironomus plumosus* and tubificid worms on nutrient concentrations were related to their different bioturbation activities in the sediment. Tubificid worms produce deep biogenic structures in the sediment column but they do not ventilate their galleries to the same extent as chironomids (Leuchs, 1986; Wood, 1975 *in* Svensson *et al.*, 2001). In presence of tubificid worms, SiO_2 concentrations were not significantly different compared to the controls without fauna, indicating that tubificids did not strongly enhance water exchanges, oxygen uptake and release of reduced compounds (N-NH_4^+ and P-PO_4^{3-}) at the water-sediment interface (Figure 7). Our results contrasted with several studies showing a significant stimulating effect of tubificid worms on oxygen uptake at the water sediment interface (Fukuhara & Sakamoto, 1987; Mermillod-Blondin & Rosenberg, 2006; Saaltink et al., 2018). For example, Mermillod-Blondin et al. (2008) showed that tubificid worms at a density (21,000 individuals.m^{-2}) close to those used in our experiment (19,230 individuals.m^{-2}) stimulated by around 2-fold oxygen uptake from sediments rich in organic matter. Such contrasting results were more likely due to differences in sediment characteristics, which could largely modulate the functional significance of bioturbation at the water-sediment interface (e.g. Nogaro et al., 2016). In the present study, total organic carbon concentrations in sediments were indeed 4-fold lower than concentrations in sediments tested by Mermillod-Blondin et al. (2008) (i.e. about 4.5% vs. 20% DW, respectively). Sediment organic content could have a significant influence on nutrient dynamics because the microbial mineralization of organic matter in the sediment determines (1) the production of inorganic nutrients (N-NH_4^+ and P-PO_4^{3-}) and (2) the redox conditions in the sediment column (Forsberg, 1989; Kristensen, 2000). Lower sediment organic content in our study might have induced lower microbial activity and associated redox conditions (eg, more oxygen, less anaerobic sediment processes) compared to Mermillod-Blondin *et al*. (2008). This could explain why N-NO_3^- released from sediments was higher in the present study than N-NH_4^+ released in presence of tubificids compared to control treatment (Figure 3) whereas N-NH_4^+ concentrations dominated inorganic N fluxes in Mermillod-Blondin et al. (2008). Therefore, we hypothesize that the role of bioturbation in nutrient dynamics is tightly linked

to the sediment organic content (and associated redox conditions) but further experiments using a wide variety of sediments are needed to clarify this link.

Fig. 6 Summary of the main influence of fauna bioturbation processes on water fluxes and associated nutrient fluxes: (A) burrow construction and ventilation by *Chironomus plumosus* during the first week and (B) during the second week. The arrows from the water to the sediment compartment represent the fluxes of water and DO (larger arrow means larger fluxes). Arrows from the sediment to the water compartment show the release of nutrients.

Influence of the oxygenation treatment on nutrient fluxes

According to our prediction, the anoxia treatment increased by 102-fold $N\text{-}NH_4^+$ concentrations and by 56-fold $P\text{-}PO_4^{3-}$ concentrations in comparison with the well-oxygenated control treatment. In contrast, the treatment with DO-fluctuations did not affect nutrient fluxes in comparison with the control treatment because sediment DO uptake was not high enough to produce anoxic conditions in the water column (DO concentrations never dropped below 5 $mg.L^{-1}$ during the experiment). In consequence, DO fluctuations had no significant effect on P released from sediment as desorption of P from Fe, Mn, Al or Ca only occurs under anoxic conditions (Dahm *et al.*, 1987 *in* Boulton *et al.*, 1998). Moreover, the Fe:P ratio (by weight) in Puyvalador sediments is around 66 (so above 15) and can control internal P loading in presence of oxygen (Jensen et al., 1992). Moreover, DO fluctuations did not stimulate organic matter mineralization in sediments, a mechanism reported by Aller (2001) in marine sediments.

Several studies highlighted that anaerobic condition in the water column was a major factor for the release rates of $N\text{-}NH_4^+$ and $P\text{-}PO_4^{3-}$ from sediments (Boström et al., 1988; Hedin et al., 1998; Wetzel, 2001b, 2001c; Beutel, 2006; Ekeroth et al., 2016; Rapin et al., 2019). Indeed, $N\text{-}NH_4^+$ produced by organic matter mineralization was nitrified into $N\text{-}NO_3^-$ when DO was available for microorganism (in the control and fluctuation treatments) whereas $N\text{-}NH_4^+$ accumulated in anoxic conditions (in the anoxic treatment). Therefore, fluxes of inorganic N from the sediment to the water column were dominated by $N\text{-}NO_3^-$ fluxes in the control and fluctuation treatments and by $N\text{-}NH_4^+$ in the anoxic treatment (Figure 7). P fluxes were linked with adsorption mechanisms modulated by DO concentrations: $P\text{-}PO_4^{3-}$ was adsorbed with $Fe(OH)_3$ and $Mn(OH)_2$ in aerobic conditions and released when oxygen was limited (Figure 7). Surprisingly, SiO_2 fluxes from sediment to water column were also stimulated by anoxic conditions whereas the SiO_2 dynamics was not dependent on redox conditions like P or Fe which precipitated in oxic conditions (Tessenow, 1972 *in* Granéli, 1979). We can suppose that this increase of SiO_2 fluxes under anoxic conditions was associated with the production and ebullition of CH_4 bubbles produced in sediments

during the experiment. Indeed, production of gas has been observed in the anoxic treatment during the course of the experiment and it has been shown that the ebullition of CH_4 could be as a significant driver of water fluxes and associated dissolved solutes from pore water to water column (Klein, 2006; Cheng et al., 2014). Consequently, such process might have contributed to the releases of SiO_2 but also reduced nutrients ($N\text{-}NH_4^+$ and $P\text{-}PO_4^{3-}$) from pore water to water column.

Fig. 7 Summary of the main influence of DO conditions in the water column on nutrient fluxes (A) oxic conditions and (B) anoxic conditions.

Conclusions

The present study showed that natural densities of *Chironomus plumosus* larvae could increase N ($N\text{-}NH_4^+$ + $N\text{-}NO_3^-$) and $P\text{-}PO_4^{3-}$ release rates by 3.7- and 17-fold, respectively. Anoxic conditions in the water column had higher influences on N (x102 in comparison with the control) and P (x56 in comparison with the control) concentrations in the water column than the most efficient bioturbator - chironomid larvae - (x3.7 for N and x17 for P). These results confirmed the main conclusion of Ekeroth et al. (2016) in marine sediments which stated that oxygen condition was a stronger regulator of P fluxes than benthic fauna. The higher influence of anoxia on N release from sediments in comparison with bioturbation was more surprising and can be due to a lack of denitrification in anoxic conditions. Indeed, the stimulating influence of ventilated U-shaped tubes on nitrification-denitrification coupling reported in several studies (Svensson & Leonardson, 1996; Moraes et al., 2018) might have led to N loss from chironomid mesocosms (NH4 → NO3 → N2) and then a limitation of inorganic dissolved N accumulated in the water column during the course of the experiment. In contrast, the lack of nitrification in anoxic conditions might have suppressed $N\text{-}NO_3^-$ denitrification and produced a high accumulation of $N\text{-}NH_4^+$ in the water column during the course of the experiment. Nevertheless, this explanation needs to be verified by measuring the denitrification potential in each experimental treatment.

Overall, we can conclude that the presence of efficient bioturbating fauna and anoxia at the sediment-water interface should not be neglected in the evaluation of nutrient dynamics in lake sediments during the warmer season of the year. This demonstrates the need to integrate environmental biogeochemistry with the dynamics of benthic invertebrates to provide reliable and ecologically relevant assessments of nutrient cycling in reservoirs. Nevertheless, nutrient dynamics in sediments can be largely dependent on several factors linked to sediment characteristics such as organic matter concentration and Fe content (e.g., Forsberg, 1989; Jensen et al., 1992). Extending our experimental approach to several reservoir sediments is greatly needed to evaluate how the role of

bioturbation and anoxia on nutrient dynamics depends on sedimentary characteristics. This is a necessary step to develop a more generalized framework on the contribution of environmental factors on nutrient dynamics in reservoirs during the warm season that may be subject to algal blooms.

Supplementary material

Online Resource 1 (A) Concentration of dissolved oxygen ($mg.L^{-1}$) in control treatment from day 2 to day 14, (B) concentration of dissolved oxygen ($mg.L^{-1}$) in anoxia treatment from day 2 to day 14 and (C) concentration of dissolved oxygen ($mg.L^{-1}$) monitored in fluctuation treatment from day 12 to day 15.

Author's contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Edwige Gautreau, Florian Mermillod-Blondin and Laurence Volatier. The first draft of the manuscript was written by Edwige Gautreau, Florian Mermillod-Blondin and Laurence Volatier. All authors contributed critically to the drafts and gave final approval for publication.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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610

611 *List of figures*

612 **Fig. 1** Schema of mesocosm installation with peristaltic pump, oxygen sensor and air source. Sediment and water
613 column compartments were 10 cm in height, corresponding to a volume of 0.785 L for each compartment.

614 **Fig. 2** Pictures from the mesocosms: (A) control treatment without fauna, (B) U-shaped tubes produced by
615 chironomid larvae on the inner wall of a mesocosm and (C) galleries produced by tubificid worms on the inner
616 wall of a mesocosm.

617 **Fig. 3** Concentrations of $N\text{-}NH_4^+$ (A), $N\text{-}NO_3^-$ (B), $P\text{-}PO_4^{3-}$ (C), and SiO_2 (D) measured in the water column of
618 mesocosms during the course of the experiment for the three fauna treatments (mean ± standard error, n=3).

619 **Fig. 4** Oxygen uptake rates (fluxes from water column to sediment) measured for the three fauna treatments (mean
620 ± standard error, n=3 mesocosms). For each panel, different letters (a, b and c) show significant differences among
621 treatments (see axis label, Tukey post hoc test, $p<0.05$).

622 **Fig. 5** Dynamics of $N\text{-}NH_4^+$ (A), $N\text{-}NO_3^-$ (B), $P\text{-}PO_4^{3-}$ (C), and SiO_2 (D) measured in the water column during the
623 course of the experiment for the three DO treatments (mean ± standard error, n=3).

624 * Concentrations of $P\text{-}PO_4^{3-}$ in the anoxia treatment at day 15 are lacking due to an analytical problem.

625 **Fig. 6** Summary of the main influence of fauna bioturbation processes on water fluxes and associated nutrient
626 fluxes: (A) burrow construction and ventilation by *Chironomus plumosus* during the first week and (B) during the
627 second week. The arrows from the water to the sediment compartment represent the fluxes of water and DO (larger
628 arrow means larger fluxes). Arrows from the sediment to the water compartment show the release of nutrients.

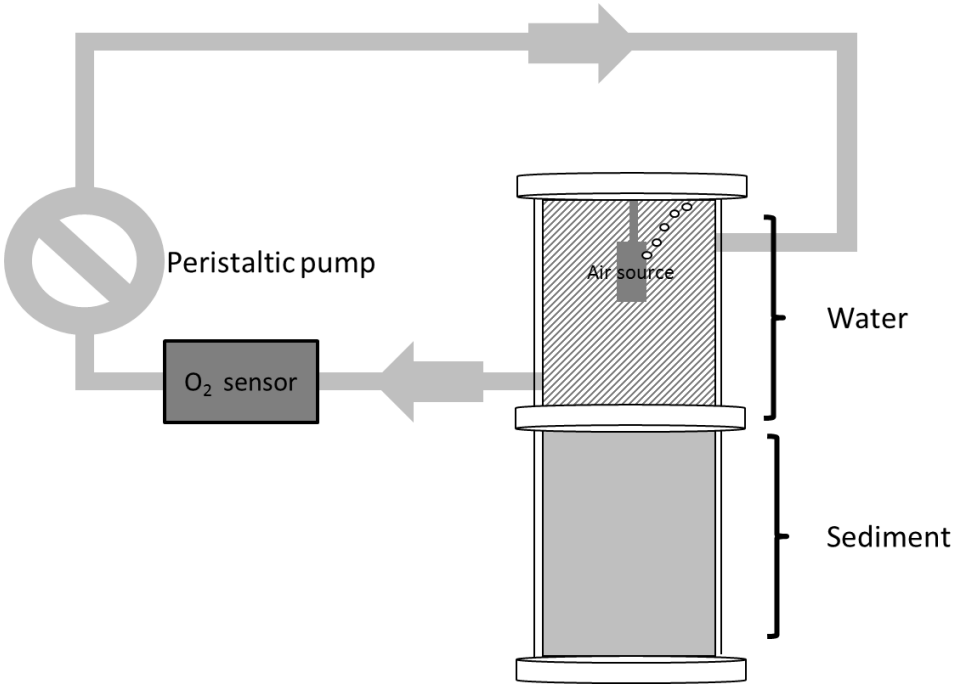
629 **Fig. 7** Summary of the main influence of DO conditions in the water column on nutrient fluxes (A) oxic
630 conditions and (B) anoxic conditions.

631

632 **Fig. 1** Schema of mesocosm installation with peristaltic pump, oxygen sensor and air source. Sediment and water

633 column compartments were 10 cm in height, corresponding to a volume of 0.785 L for each compartment

634



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637 **Fig. 2** Pictures from the mesocosms: (A) control treatment without fauna, (B) U-shaped tubes produced by
638 chironomid larvae on the inner wall of a mesocosm and (C) galleries produced by tubificid worms on the inner
639 wall of a mesocosm

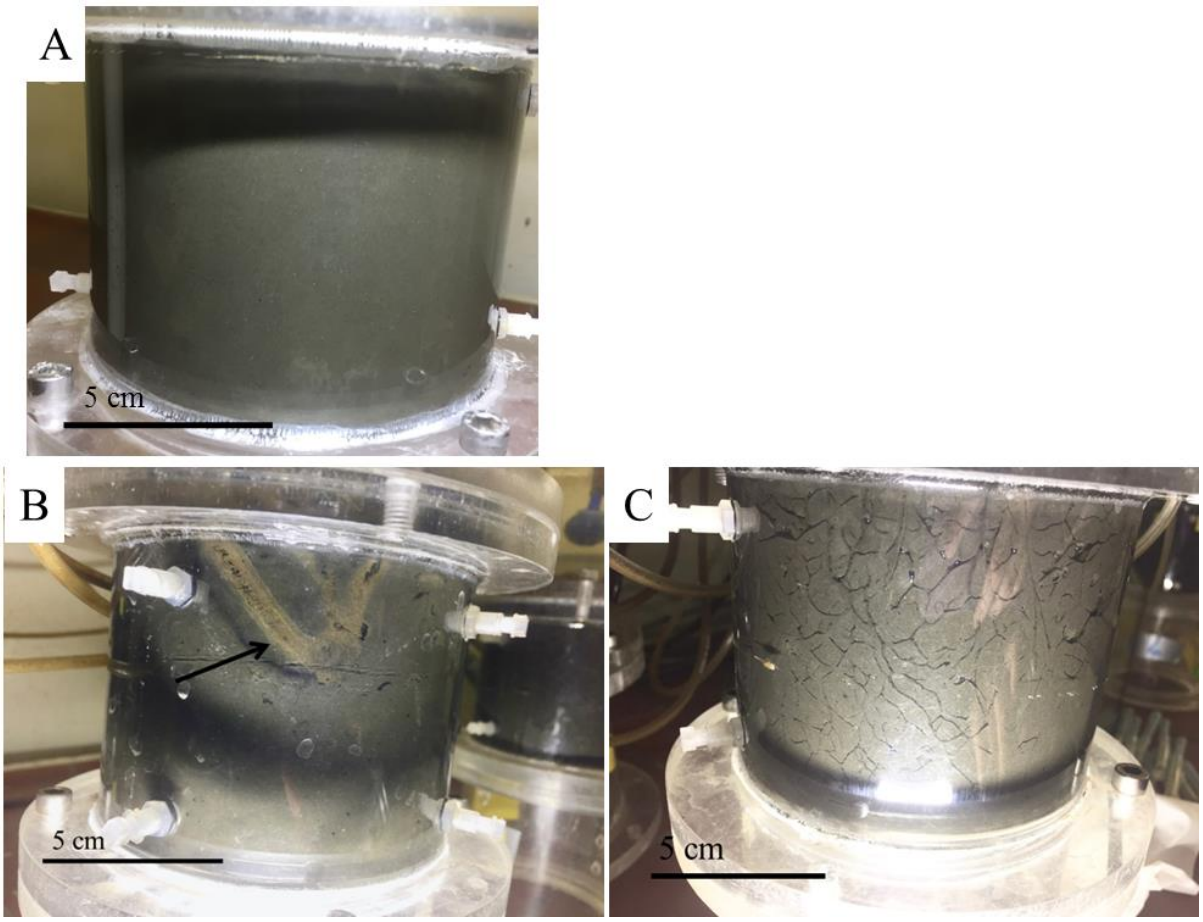

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Fig. 3 Concentrations of $N\text{-}NH_4^+$ (A), $N\text{-}NO_3^-$ (B), $P\text{-}PO_4^{3-}$ (C), and SiO_2 (D) measured in the water column of mesocosms during the course of the experiment for the three fauna treatments (mean ± standard error, n=3).

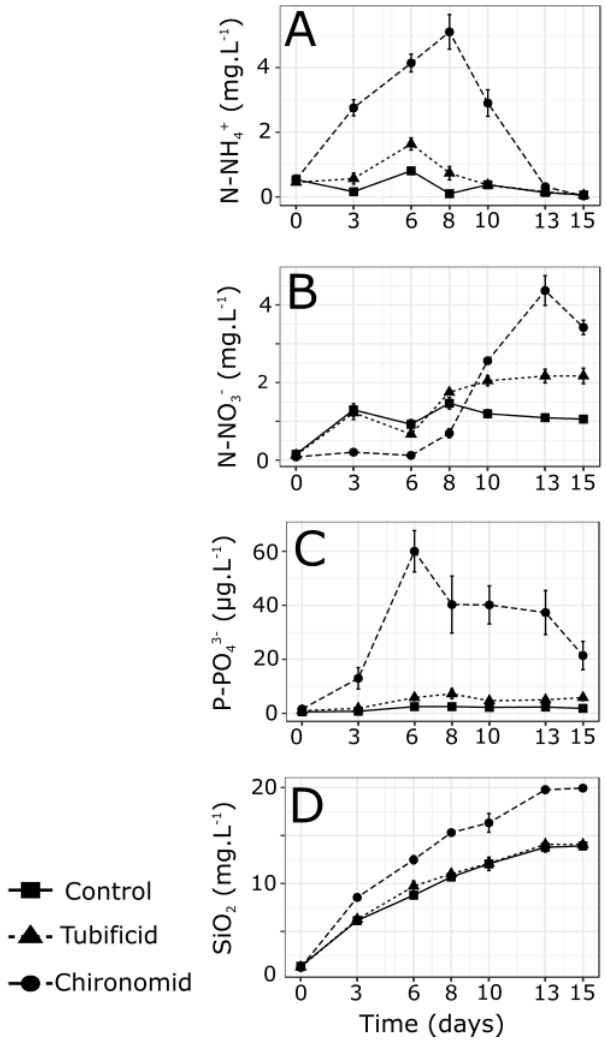
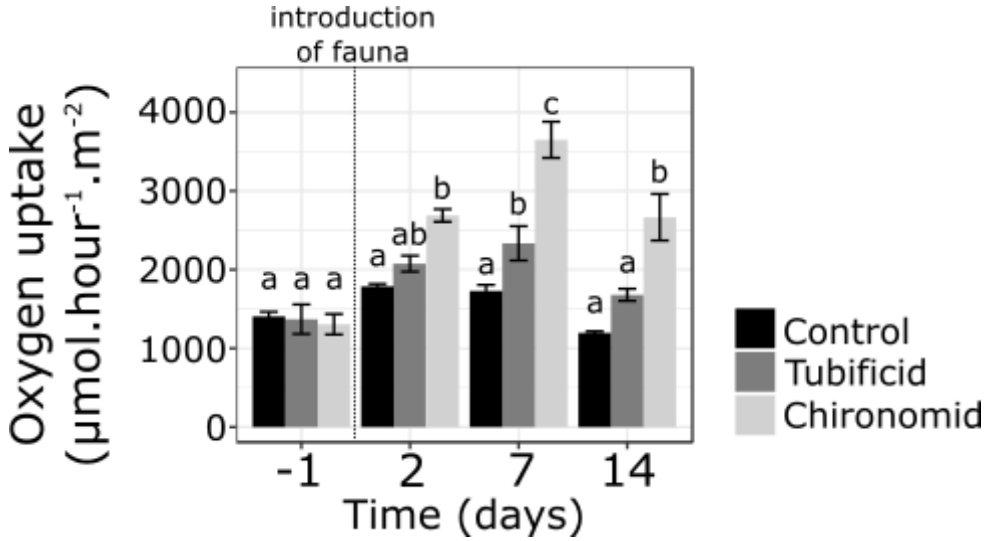


Fig. 4 Oxygen uptake rates (fluxes from water column to sediment) measured for the three fauna treatments (mean ± standard error, n=3 mesocosms). For each panel, different letters (a, b and c) show significant differences among treatments (see axis label, Tukey post hoc test, $p<0.05$).



650 **Fig. 5** Dynamics of N-NH_4^+ (A), N-NO_3^- (B), P-PO_4^{3-} (C), and SiO_2 (D) measured in the water column during the

651 course of the experiment for the three DO treatments (mean ± standard error, n=3).

652 * Concentrations of P-PO_4^{3-} in the anoxia treatment at day 15 are lacking due to an analytical problem.

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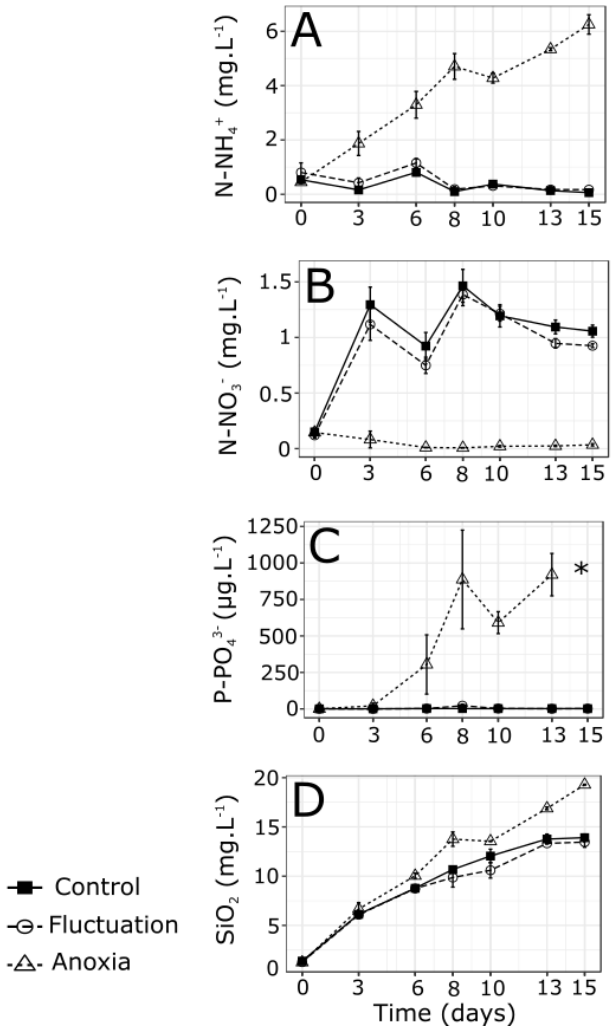

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Fig. 6 Summary of the main influence of fauna bioturbation processes on water fluxes and associated nutrient fluxes: (A) burrow construction and ventilation by *Chironomus plumosus* during the first week and (B) during the second week. The arrows from the water to the sediment compartment represent the fluxes of water and DO (larger arrow means larger fluxes). Arrows from the sediment to the water compartment show the release of nutrients.

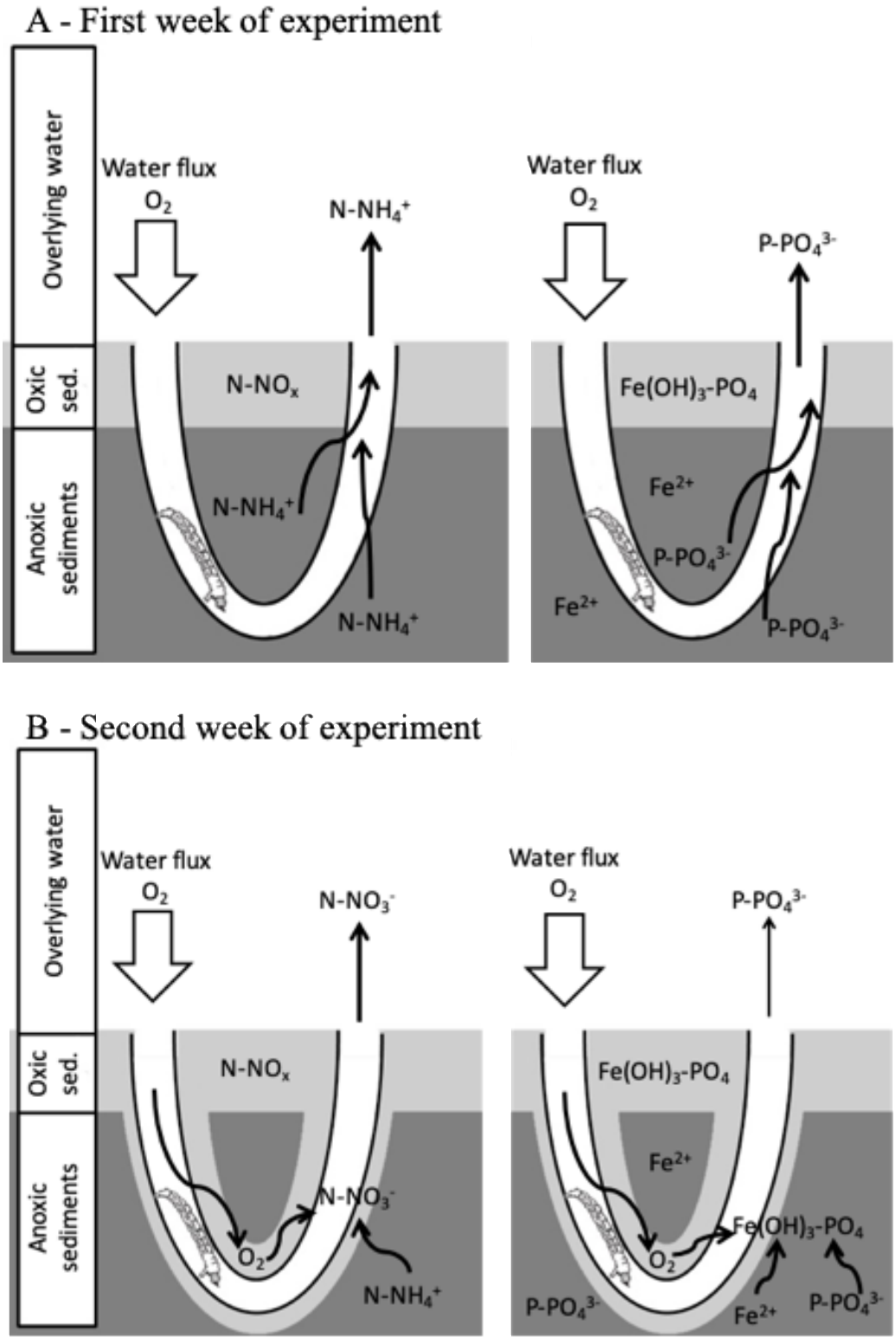
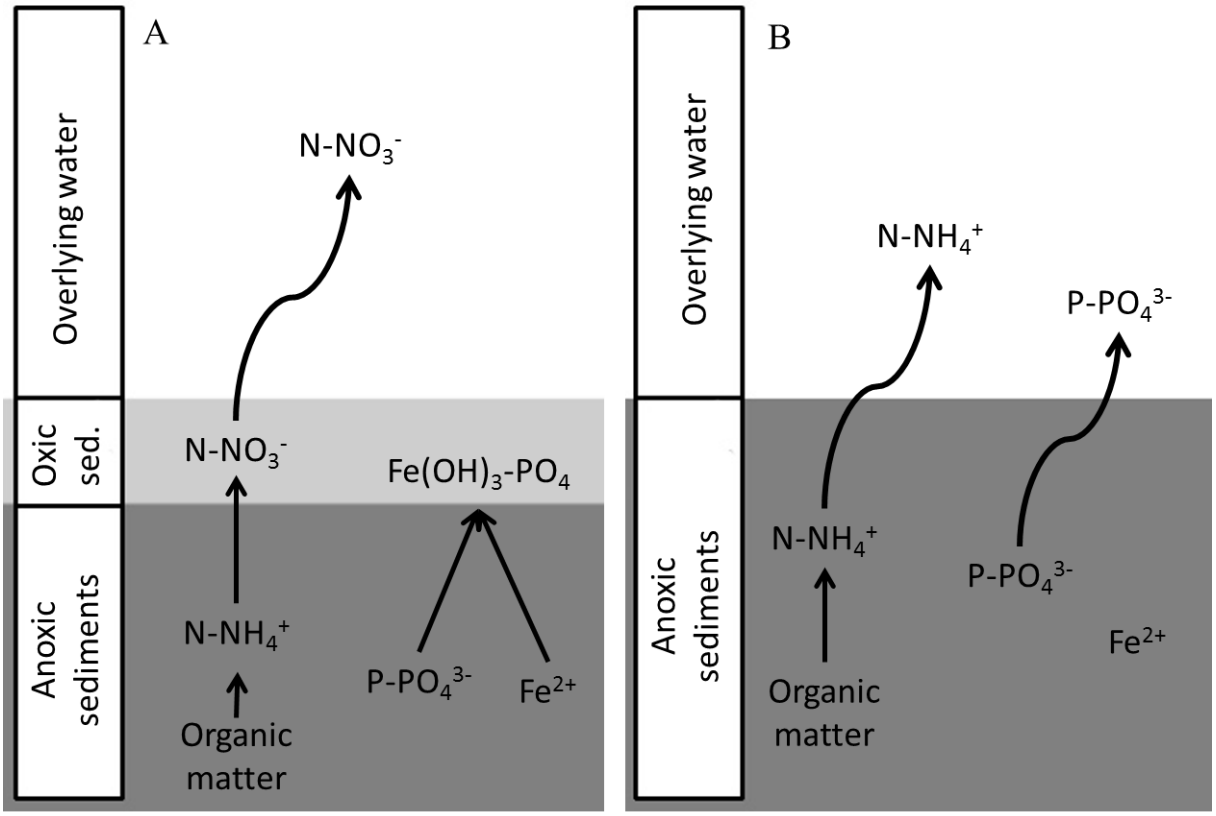


Fig. 7 Summary of the main influence of DO conditions in the water column on nutrient fluxes (A) oxic conditions and (B) anoxic conditions.



Online Resource 1 (A) Concentration of dissolved oxygen ($mg.L^{-1}$) in control treatment from day 2 to day 14, (B) concentration of dissolved oxygen ($mg.L^{-1}$) in anoxia treatment from day 2 to day 14 and (C) concentration of dissolved oxygen ($mg.L^{-1}$) monitored in fluctuation treatment from day 12 to day 15.