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1 *Title*

2 Influences of bioturbation and water column oxygenation on nutrient recycling from reservoir sediments

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12 *Abstract*

13 Sediments act as sinks of nutrients in aquatic ecosystems but may also act as nutrient sources, leading to
14 eutrophication of lakes and reservoirs during the warm season of the year. In this context, internal recycling of
15 nutrients from sediments can be largely modulated by abiotic (e.g., redox conditions) and biotic (e.g., activity of
16 benthic organisms) factors occurring at the water-sediment interface. The present study aimed at quantifying the
17 effects of these factors (water column oxygenation and bioturbation by two bioturbating species - the tubificid
18 worm *Tubifex tubifex* and insect larvae of *Chironomus plumosus*) on benthic fluxes of nitrogen (N), phosphorus
19 (P) and silicon (Si) from reservoir water-sediment interface. An experimental approach based on the reconstitution
20 of the water-sediment interface in mesocosms has been developed in the laboratory to test three fauna conditions
21 (no fauna, presence of worms, and presence of chironomids) and three conditions of water column oxygenation
22 (constant aerobic conditions, fluctuations of oxygen concentrations and constant anaerobic conditions). The larvae
23 of chironomids significantly increased by 3.7-fold and by 17-fold the concentrations of N ($\text{NH}_4^+ + \text{NO}_3^-$) and PO_4^{3-}
24 released from sediments, respectively. In comparison, tubificid worms had lower influences on these released
25 nutrients (x2 for N and x3 for PO_4^{3-} in comparison with the control treatment without fauna). These contrasted
26 effects of chironomids and tubificid worms on nutrient fluxes were related to their different bioturbation activities
27 in sediments. Chironomid larvae increased water-sediment exchanges by actively ventilating their U-shaped

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

35

36 *Key words*

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

39 *Acknowledgments*

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45 and advices during field and laboratory works.

46 *Introduction*

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

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

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

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

75 For instance, the solubility of phosphate (PO_4^{3-}) ions is determined by oxygen availability due to their affinity with
76 iron oxides. The PO_4^{3-} ion can be adsorbed on the precipitated $\text{Fe}(\text{OH})_3\text{-PO}_4$ complexes in presence of oxygen
77 (Mortimer, 1941; Boström et al., 1988; Wetzel, 2001a). Phosphates can also precipitate with calcite (CaCO_3) in
78 alkaline condition (as seen by House & Denison, 2002). Bioturbation by benthic animals (i.e. sediment reworking
79 and irrigation of biogenic structures such as tubes and burrows) also influences N and P dynamics at the water
80 sediment interface. By modifying redox potentials and increasing water exchanges at the water-sediment interface,
81 burrowing animals can stimulate the release of N (ammonium and/or nitrate) from interstitial water to the water
82 column (e.g. Krantzberg, 1985). For example, Pelegri & Blackburn, (1996) reported a 5.8-fold stimulation of
83 ammonium (NH_4^+) release rates from lake sediments due to the bioturbation activities of *Chironomus plumosus*
84 (2,000 larvae.m⁻²) in microcosms. Using a comparable experimental approach, Mermillod-Blondin et al. (2005)
85 showed that tubificid worms (20,000 individuals.m⁻²) increased the releases of NH_4^+ , and PO_4^{3-} from sediments by
86 2- and 4-fold, respectively. The influence of benthic fauna on nutrient fluxes at the water-sediment interface
87 depends on their functional traits (building of biogenic structures, ventilation rate, depth of biogenic structures,
88 sediment reworking rate) (Kristensen et al., 2012). For example, Nogaro et al. (2016) showed that chironomid
89 larvae that build and ventilate U-shaped tubes stimulated P release from the sediment to the overlying water,
90 whereas tubificids that produce gallery and egest fecal pellets at the water sediment interface increased P retention
91 in sediment from eutrophic wetlands. Although the presence of *Chironomus plumosus* can contribute to release of
92 nutrients into water column, they also bring oxygen into sediment and create oxic conditions nearby their burrow
93 walls. These oxic conditions lead to trap phosphates in $\text{Fe}(\text{OH})_3\text{-PO}_4$ complexes inside sediments (Hupfer et al.,
94 2019).

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

105 ventilation of biogenic structures, the larvae of *Chironomus plumosus* would generate higher release rates of
106 nutrients and oxygen uptake than tubificid worms (Nogaro et al., 2016). Concerning DO conditions, anaerobic
107 conditions would enhance the release of nutrients, especially N-NH₄⁺ and P-PO₄³⁻, compared with aerobic
108 conditions. For the oxygen fluctuation treatment, we reproduced the daily variations of DO concentrations in the
109 water column of eutrophic reservoirs (e.g. Balangoda, 2017; Wetzel, 2001b) by using the natural oxygen uptake
110 of the sediment column without oxygen supply. Thus, oxygen fluctuations were expected to increase nutrient
111 releases from sediments in comparison with aerobic conditions if oxygen uptake was high enough to produce
112 aerobic-anaerobic fluctuations in the water column.

113 *Materials and methods*

114 *Study site presentation, sediment collection and preparation*

115 The study site is Puyvalador reservoir, which is regularly impacted by blooms of cyanobacteria (e.g.,
116 *Synechococcus sp.* and *Anabaena spiroides*) during the summer. This reservoir is located in the French Pyrenees
117 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
118 of 10.1 hm³. The maximum depth is 21 m and the mean water residence time is 40 days. This reservoir is part of
119 a hydroelectric complex operated by Electricité de France (EDF) and has two mains tributaries: Aude river and
120 Galbe river. Puyvalador reservoir is eutrophic according to EU Water Framework Directive criteria (Agence de
121 l'eau Rhône Méditerranée Corse, 2015). The central area of the reservoir of Puyvalador, where the depth is
122 maximal, is the main sedimentation zone containing a high percentage (80 %) of fine particles (<63µm) compared
123 to areas influenced by the tributaries (Gautreau et al. in prep). Sediments from the central area are characterized
124 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
125 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
126 of benthic fauna densities during summer period indicated that 4th stage larvae of *Chironomus plumosus* and
127 tubificid worms were the most abundant taxa with average densities of 2,095 individuals.m⁻² and 18,190
128 individuals.m⁻², respectively.

129 For the present experiment, sediments from the central area were collected with an Eckman grab in September
130 2017. After sampling, they were frozen at -18°C for several weeks to kill the ambient fauna (Biles et al., 2002). In
131 parallel, a subsample of unfrozen sediment was kept at 15°C (corresponding to the reservoir temperature at the
132 water-sediment interface during sediment collection) to preserve the microbial activities of the collected sediments
133 and to be used as an inoculum for the experiment. Fifteen days before mesocosm preparation, this subsample was

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

137 *Mesocosms and experimental set up*

138 Experiments were performed in 15 mesocosms made of Plexiglas cylinders with an internal diameter of 10 cm and
139 a height of 20 cm (Figure 1). Mesocosms were placed in a 15°C temperature-controlled room for mimicking
140 summer temperature at the water-sediment interface of the reservoir and filled with a layer of incubated sediments
141 (10 cm) overlaid with synthetic water (10 cm) (composition of synthetic water: 96 mg.L^{-1} NaHCO_3 ; 39.4 mg.L^{-1}
142 $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$; 60 mg.L^{-1} $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$; 4 mg.L^{-1} KCl ; $\text{pH} = 7.5$; (US EPA, 1991)). Oxic conditions were
143 maintained in the mesocosms by bubbling water column with atmospheric air (Figure 1). Mesocosms were
144 equipped with peristaltic pumps for a continuous recirculation of the water column to avoid DO stratification but
145 water flow was adjusted to limit sediment resuspension (6 mL.min^{-1}). Oxygen probes were placed on the
146 recirculation system of peristaltic pumps to measure DO concentrations.

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

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

154 *Experimental design*

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

162 three replicated mesocosms per condition were used to test the influence of DO concentrations on nutrient fluxes:
163 1) mesocosms with a water column saturated in DO (same systems than those used as control mesocosms without
164 fauna), 2) mesocosms without fauna and experiencing DO decrease every 12 hours (aeration turn on and off every
165 12 hours), 3) mesocosms without fauna experiencing anaerobic conditions in the water column.

166 *Measurements*

167 Nutrient dynamics and aerobic microbial respiration were measured during the 15 days of experiment to study the
168 effects of oxygen conditions and bioturbation on biogeochemical processes. Nutrient dynamics were measured by
169 collecting water samples from the water column at 7 times: on Day 0 just before the treatment application and on
170 days 3, 6, 8, 10, 13 and 15 after the treatment application. At each sampling date, a volume of 30 mL of overlying
171 water was sampled from the top of the water column and filtered through a GF/F filters (0.7 μm , Whatman) and
172 conserved at 4°C before chemical analyses. N-NH₄⁺, N-NO₃⁻, P-PO₄³⁻ and SiO₂ concentrations of all samples were
173 determined by colorimetric methods with a sequential analyzer (SmartChem200, AMS Alliance). During the
174 experiment, the sampled volume of water for analyses (30 mL) was replaced with 30 mL of artificial water for
175 keeping a constant volume of overlying water. Moreover, to prevent oxygenation of anoxic mesocosms during
176 sampling, collected water was replaced by synthetic water at the top of the mesocosms without air entrance.

177 DO fluxes were measured to evaluate the influence of bioturbating fauna on aerobic microbial respiration. These
178 measurements were performed a day before fauna introduction (day -1) and on days 2, 7 and 14 after the addition
179 of fauna. At each sampling date, mesocosms were sealed for avoiding contact with the atmosphere and the
180 incubation time was limited to 4 hours to avoid the decrease of DO concentrations below 5 mg.L⁻¹. DO was
181 measured with a Pocket Oxygen Meter FireStingGO₂ (Pyroscience) every hour during the incubations. DO fluxes
182 in the mesocosms were calculated from the linear decrease of DO over time and expressed as μmol of O₂ consumed
183 per hour and m² of sediment surface.

184 *Data analysis*

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

190 fluctuation, and anoxia treatments) as the main effect. When one-way RM-ANOVAs were significant (i.e.,
191 $p < 0.05$), Tukey's post hoc tests were performed for the last day of the experiment to evaluate which treatments
192 differed after 15 days of mesocosm stabilization. For all variables and before statistical analyses, the normality
193 and the homoscedasticity of the residues were verified using the Shapiro-Wilk's test and the Bartlett's test,
194 respectively. All statistical analyses were done with the R v.3.3.2 software.

195 *Results*

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

197 *Visual observations during the experiment*

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

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

207 *Nutrient concentration dynamics and release rates*

208 N-NH_4^+ concentrations measured in the water column of all treatments significantly increased during the first 6 to
209 8 days of the experiment and decreased thereafter (Figure 3A, one-way RM-ANOVA, time effect, $***p < 0.0001$).
210 This initial N-NH_4^+ increase was significantly higher in the chironomid treatment compared to the control and
211 tubificid treatments (one-way RM-ANOVA, fauna treatment, $*p < 0.01$). Nevertheless, after 15 days of mesocosm
212 stabilization with fauna, N-NH_4^+ concentrations were comparable in control, tubificid worm and chironomid
213 treatments (Tukey's test, $p\text{-value} > 0.05$).

214 N-NO_3^- concentrations measured in the water column significantly increased during the course of the experiment
215 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
216 the chironomid treatments, respectively (Figure 3B, one-way RM-ANOVA, time effect, $***p < 0.0001$). These N-

217 NO_3^- increases differed over time depending on the treatment (one-way RM-ANOVA, “fauna treatment * time”
218 effect, *** $p < 0.0001$). Significant N-NO_3^- increases occurred on the first days for the controls and in presence of
219 tubificids whereas N-NO_3^- concentrations increased between day 6 and day 13 in presence of chironomids (Figure
220 3B). Such N-NO_3^- increase in the chironomid treatment was concomitant with the N-NH_4^+ decrease of
221 concentration in the water column (Figure 3A). At the end of the experiment, N-NO_3^- concentrations were
222 significantly higher in the chironomid treatment compared to the control and tubificid treatments (Tukey’s tests,
223 p -value < 0.05). Considering both inorganic N-NH_4^+ and N-NO_3^- concentrations, inorganic N concentrations
224 measured on day 15 in chironomid and tubificid treatments were 3.7-fold and 2-fold higher than in control
225 treatment, respectively (Tukey’s tests, p -value < 0.05).

226 P-PO_4^{3-} concentrations measured in the water column in presence of chironomids significantly increased from 1
227 $\mu\text{g.L}^{-1}$ at day 0 to 60 $\mu\text{g.L}^{-1}$ at day 6 and then decreased to reach 21 $\mu\text{g.L}^{-1}$ at day 15 (Figure 3C). In comparison,
228 P-PO_4^{3-} concentration in the water column of control and tubificid treatments remained below 10 $\mu\text{g.L}^{-1}$ during the
229 whole course of the experiment. Then, after 15 days of experiment, P-PO_4^{3-} concentrations in chironomid treatment
230 was 17-fold higher than those measured in control treatment. Despite low P-PO_4^{3-} concentrations, the occurrence
231 of tubificid worms also increased by 3-fold P-PO_4^{3-} concentrations in water column in comparison with control
232 treatment (Tukey test, p -value < 0.05).

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

239 *Oxygen uptake*

240 DO uptake rates were comparable in all mesocosms before the fauna addition (around 1500 $\mu\text{mol.h}^{-1}.\text{m}^{-2}$) and
241 significantly varied during the course of the experiment with the highest rates measured on day 7 (Figure 4, one-
242 way RM-ANOVA, time effect, *** $p < 0.0001$). After the fauna addition, the presence of chironomid larvae
243 significantly increased oxygen uptake rates in comparison with the other treatments (one-way RM-ANOVA,
244 treatment effect, *** $p < 0.0001$; Tukey’s tests, $p < 0.01$). For example, mean DO uptake rate measured on day
245 14 was 2-fold higher in the chironomid treatment (i.e. 2665 $\mu\text{mol.hour}^{-1}.\text{m}^{-2}$) than in the control treatment (i.e.

246 1196 $\mu\text{mol}\cdot\text{hour}^{-1}\cdot\text{m}^{-2}$). Mean DO uptake rates measured in tubificid treatment were slightly higher than in
247 control treatment but this effect was not statistically significant at all dates (see post-hoc Tukey's tests in Figure
248 4).

249 **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
250 mesocosms during the course of the experiment for the three fauna treatments (mean \pm standard error, $n=3$).

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

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

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

260 N-NH_4^+ concentration measured in the water column significantly increased from 0.5 $\text{mg}\cdot\text{L}^{-1}$ to 6.4 $\text{mg}\cdot\text{L}^{-1}$
261 during the course of the experiment in the anoxia treatment whereas only small variations in N-NH_4^+
262 concentrations were measured in the DO-saturated control and the DO fluctuation treatments (Figure 5A, one-way
263 RM-ANOVA, "treatment * time" effect, $***p < 0.0001$). Indeed, at the end of the experiment, concentration of N-
264 NH_4^+ was 102-fold time higher in anoxia treatment than in DO-saturated control treatment (Tukey's tests, $*p <$
265 0.01).

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

271 Similarly to N-NH_4^+ dynamics, P-PO_4^{3-} concentrations in the water column significantly increased from 0 to 1034
272 $\mu\text{g}\cdot\text{L}^{-1}$ during the course of the experiment in the anoxia treatment whereas P-PO_4^{3-} concentrations remained low
273 (around 3 $\mu\text{g}\cdot\text{L}^{-1}$) 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-PO₄³⁻ in the water column was 56-fold time higher in
275 anoxia treatment than in control treatment (Tukey's tests, *p < 0.01).

276 SiO₂ 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-NH₄⁺ (A), N-NO₃⁻ (B), P-PO₄³⁻ (C), and SiO₂ (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-PO₄³⁻ 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-NH₄⁺ and P-PO₄³⁻
287 in the water column during the first 8 days of experiment. These releases of reduced compounds (N-NH₄⁺ and P-
288 PO₄³⁻) 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-NH₄⁺ concentrations decreased concomitantly with an increase of N-NO₃⁻
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

302 was illustrated on Figure 2B with oxidized sediment nearby U-shaped tubes. Therefore, after 15 days of
303 stabilization, the influence of chironomid larvae bioturbation on N fluxes was predominantly associated with a
304 release of N-NO_3^- from oxidized sediments (Figure 6B) than a release of N-NH_4^+ from poorly-oxygenized
305 sediments (as observed during chironomid installation, Figure 6A). Concerning P dynamics, the presence of
306 chironomids induced an initial flush of P-PO_4^{3-} from the sediment to the water column (i.e, up to 60 mg.L^{-1})
307 during the first week of the experiment followed by a small decrease of P-PO_4^{3-} concentrations in the water
308 column the second week of the experimentation, which remained around $30\text{-}40 \text{ }\mu\text{g.L}^{-1}$ until the end of the
309 experiment. Then, the stimulating effect of chironomid ventilation on P-PO_4^{3-} concentrations compared to the
310 control treatment without fauna was detected until the end of the experiment. According to Lewandowski and
311 Hupfer (2005) and Hupfer et al. (2019), the supply of DO in chironomid burrows could have produced an
312 adsorption of the P-PO_4^{3-} initially flushed in the water column into $\text{Fe(OH)}_3\text{-PO}_4$ complexes in Fe-rich sediments
313 (ie. 33 g.kg^{-1} DW of total Fe, see materials and methods). Such mechanism probably occurred during our
314 experiment inducing the small decrease of P-PO_4^{3-} in the water column after day 6 but did not lead to a complete
315 adsorption of P-PO_4^{3-} flushed from the sediment. We suppose that P-PO_4^{3-} adsorption occurring in aerobic
316 conditions and enhanced by chironomid ventilation was compensated by a constant flush of P-PO_4^{3-} from the
317 anoxic sediments due to chironomid bioturbation (Figure 6). As the dynamics of nutrients during the course of
318 the experiment in chironomid treatment were largely associated with the installation of benthic chironomid
319 larvae in sediments, we compared the effects of three fauna treatments on nutrients in water column by
320 considering the last day of the experiment after 15 days of stabilization of biogeochemical processes in the
321 mesocosms.

322 *Influence of bioturbation on nutrient concentrations and oxygen uptake*

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

332 sediment interface was burrow ventilation which increased the release rates of nutrients (inorganic nitrogen N-
333 NH_4^+ + N-NO_3^- and P-PO_4^{3-}) accumulated in pore water (Lewandowski & Hupfer, 2005; Lewandowski et al.,
334 2007). The increase (+ 50%) of SiO_2 concentration in water column with *Chironomus plumosus* was in accordance
335 with this mechanism of burrow ventilation as silicate fluxes were found to depend on irrigation of biogenic
336 structures by benthic fauna (e.g., Mermillod-Blondin et al., 2004).

337 In contrast with chironomid larvae, tubificid worms had lower influences on N (x2 in comparison with the control
338 treatment) and P (x3 in comparison with the control treatment) concentrations in the water column in our
339 experimental conditions. Such contrasted effects of *Chironomus plumosus* and tubificid worms on nutrient
340 concentrations were related to their different bioturbation activities in the sediment. Tubificid worms produce deep
341 biogenic structures in the sediment column but they do not ventilate their galleries to the same extent as
342 chironomids (Leuchs, 1986; Wood, 1975 in Svensson et al., 2001). In presence of tubificid worms, SiO_2
343 concentrations were not significantly different compared to the controls without fauna, indicating that tubificids
344 did not strongly enhance water exchanges, oxygen uptake and release of reduced compounds (N-NH_4^+ and P-PO_4^{3-}
345) at the water-sediment interface (Figure 7). Our results contrasted with several studies showing a significant
346 stimulating effect of tubificid worms on oxygen uptake at the water sediment interface (Fukuhara & Sakamoto,
347 1987; Mermillod-Blondin & Rosenberg, 2006; Saaltink et al., 2018). For example, Mermillod-Blondin et al. (2008)
348 showed that tubificid worms at a density (21,000 individuals.m⁻²) close to those used in our experiment (19,230
349 individuals.m⁻²) stimulated by around 2-fold oxygen uptake from sediments rich in organic matter. Such
350 contrasting results were more likely due to differences in sediment characteristics, which could largely modulate
351 the functional significance of bioturbation at the water-sediment interface (e.g. Nogaro et al., 2016). In the present
352 study, total organic carbon concentrations in sediments were indeed 4-fold lower than concentrations in sediments
353 tested by Mermillod-Blondin et al. (2008) (i.e. about 4.5% vs. 20% DW, respectively). Sediment organic content
354 could have a significant influence on nutrient dynamics because the microbial mineralization of organic matter in
355 the sediment determines (1) the production of inorganic nutrients (N-NH_4^+ and P-PO_4^{3-}) and (2) the redox
356 conditions in the sediment column (Forsberg, 1989; Kristensen, 2000). Lower sediment organic content in our
357 study might have induced lower microbial activity and associated redox conditions (eg, more oxygen, less
358 anaerobic sediment processes) compared to Mermillod-Blondin et al. (2008). This could explain why N-NO_3^-
359 released from sediments was higher in the present study than N-NH_4^+ released in presence of tubificids compared
360 to control treatment (Figure 3) whereas N-NH_4^+ concentrations dominated inorganic N fluxes in Mermillod-
361 Blondin et al. (2008). Therefore, we hypothesize that the role of bioturbation in nutrient dynamics is tightly linked

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

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

368 *Influence of the oxygenation treatment on nutrient fluxes*

369 According to our prediction, the anoxia treatment increased by 102-fold N-NH₄⁺ concentrations and by 56-fold P-
370 PO₄³⁻ concentrations in comparison with the well-oxygenated control treatment. In contrast, the treatment with
371 DO-fluctuations did not affect nutrient fluxes in comparison with the control treatment because sediment DO
372 uptake was not high enough to produce anoxic conditions in the water column (DO concentrations never
373 dropped below 5 mg.L⁻¹ during the experiment). In consequence, DO fluctuations had no significant effect on P
374 released from sediment as desorption of P from Fe, Mn, Al or Ca only occurs under anoxic conditions (Dahm *et*
375 *al.*, 1987 in Boulton *et al.*, 1998). Moreover, the Fe:P ratio (by weight) in Puyvalador sediments is around 66 (so
376 above 15) and can control internal P loading in presence of oxygen (Jensen *et al.*, 1992). Moreover, DO fluctuations
377 did not stimulate organic matter mineralization in sediments, a mechanism reported by Aller (2001) in marine
378 sediments.

379 Several studies highlighted that anaerobic condition in the water column was a major factor for the release rates
380 of N-NH₄⁺ and P-PO₄³⁻ from sediments (Boström *et al.*, 1988; Hedin *et al.*, 1998; Wetzel, 2001b, 2001c; Beutel,
381 2006; Ekeröth *et al.*, 2016; Rapin *et al.*, 2019). Indeed, N-NH₄⁺ produced by organic matter mineralization was
382 nitrified into N-NO₃⁻ when DO was available for microorganism (in the control and fluctuation treatments) whereas
383 N-NH₄⁺ accumulated in anoxic conditions (in the anoxic treatment). Therefore, fluxes of inorganic N
384 from the sediment to the water column were dominated by N-NO₃⁻ fluxes in the control and fluctuation treatments
385 and by N-NH₄⁺ in the anoxic treatment (Figure 7). P fluxes were linked with adsorption mechanisms modulated
386 by DO concentrations: P-PO₄³⁻ was adsorbed with Fe(OH)₃ and Mn(OH)₂ in aerobic conditions and released when
387 oxygen was limited (Figure 7). Surprisingly, SiO₂ fluxes from sediment to water column were also stimulated by
388 anoxic conditions whereas the SiO₂ dynamics was not dependent on redox conditions like P or Fe which
389 precipitated in oxic conditions (Tessenow, 1972 in Granéli, 1979). We can suppose that this increase of SiO₂ fluxes
390 under anoxic conditions was associated with the production and ebullition of CH₄ bubbles produced in sediments

391 during the experiment. Indeed, production of gas has been observed in the anoxic treatment during the course of
392 the experiment and it has been shown that the ebullition of CH₄ could be as a significant driver of water fluxes and
393 associated dissolved solutes from pore water to water column (Klein, 2006; Cheng et al., 2014). Consequently,
394 such process might have contributed to the releases of SiO₂ but also reduced nutrients (N-NH₄⁺ and P-PO₄³⁻) from
395 pore water to water column.

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

398 *Conclusions*

399 The present study showed that natural densities of *Chironomus plumosus* larvae could increase N (N-NH₄⁺ + N-
400 NO₃⁻) and P-PO₄³⁻ release rates by 3.7- and 17-fold, respectively. Anoxic conditions in the water column had
401 higher influences on N (x102 in comparison with the control) and P (x56 in comparison with the control)
402 concentrations in the water column than the most efficient bioturbator - chironomid larvae - (x3.7 for N and x17
403 for P). These results confirmed the main conclusion of Ekeroth et al. (2016) in marine sediments which stated that
404 oxygen condition was a stronger regulator of P fluxes than benthic fauna. The higher influence of anoxia on N
405 release from sediments in comparison with bioturbation was more surprising and can be due to a lack of
406 denitrification in anoxic conditions. Indeed, the stimulating influence of ventilated U-shaped tubes on nitrification-
407 denitrification coupling reported in several studies (Svensson & Leonardson, 1996; Moraes et al., 2018) might
408 have led to N loss from chironomid mesocosms (NH₄ → NO₃ → N₂) and then a limitation of inorganic dissolved
409 N accumulated in the water column during the course of the experiment. In contrast, the lack of nitrification in
410 anoxic conditions might have suppressed N-NO₃⁻ denitrification and produced a high accumulation of N-NH₄⁺ in
411 the water column during the course of the experiment. Nevertheless, this explanation needs to be verified by
412 measuring the denitrification potential in each experimental treatment.

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

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

423 *Supplementary material*

424

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

428 *Author's contributions*

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

433

434 *Ethical approval*

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

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440

441 *Conflict of Interest*

442 The authors declare that they have no conflict of interest.

443

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617 **Fig. 3** Concentrations of N-NH₄⁺ (A), N-NO₃⁻ (B), P-PO₄³⁻ (C), and SiO₂ (D) measured in the water column of
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622 **Fig. 5** Dynamics of N-NH₄⁺ (A), N-NO₃⁻ (B), P-PO₄³⁻ (C), and SiO₂ (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-PO₄³⁻ in the anoxia treatment at day 15 are lacking due to an analytical problem.

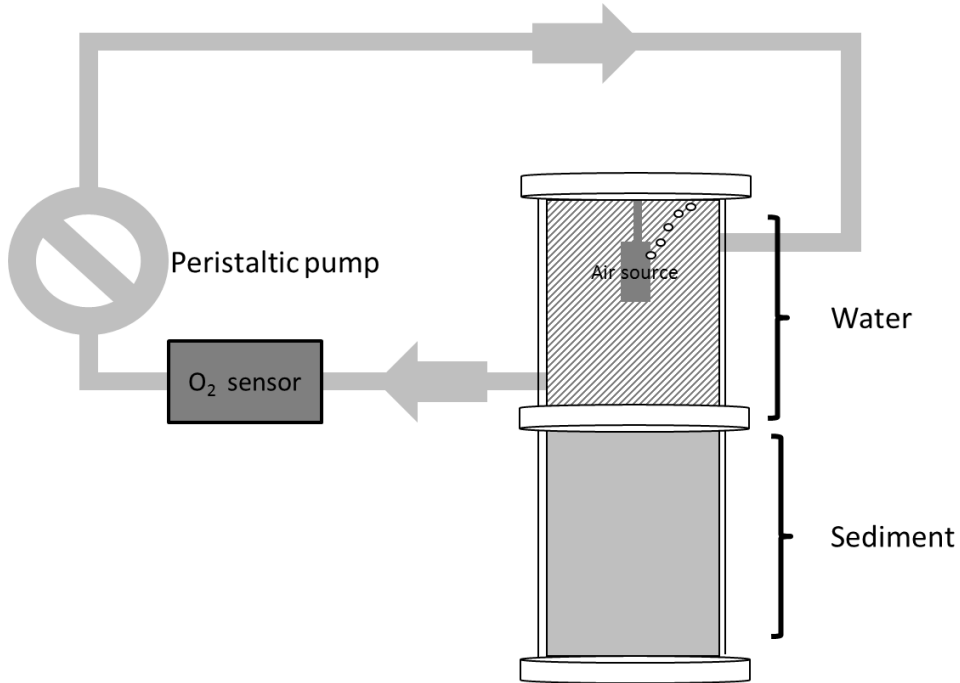
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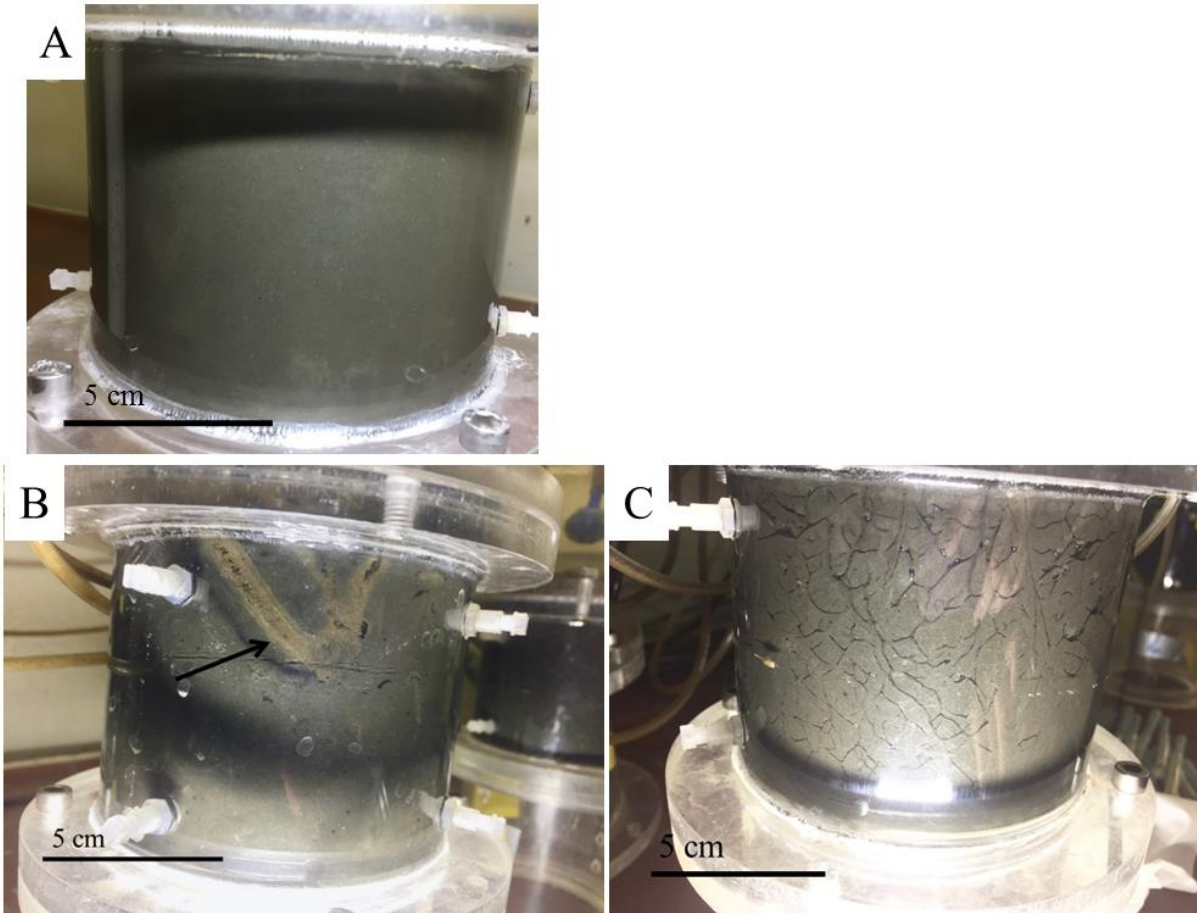
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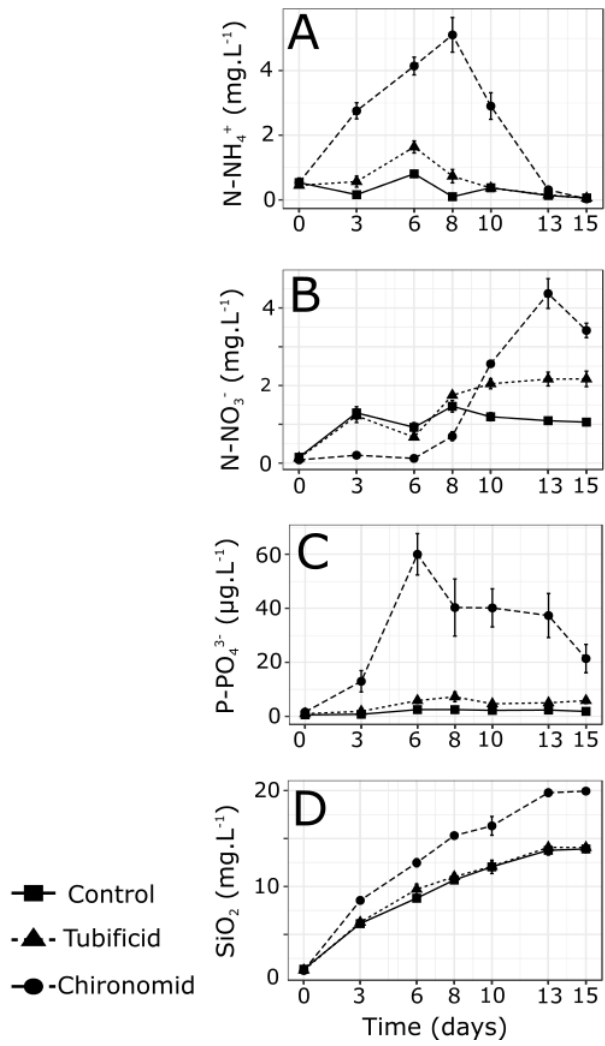
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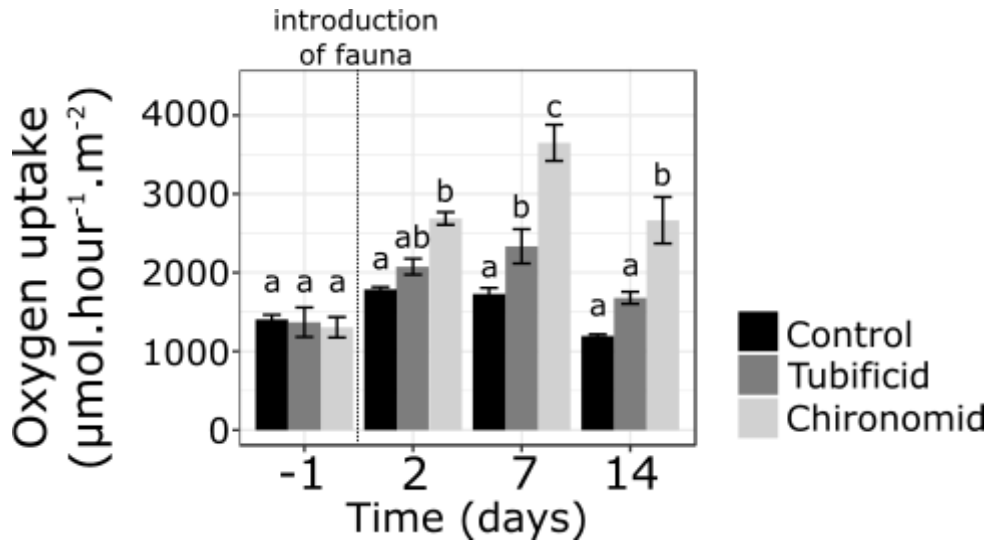
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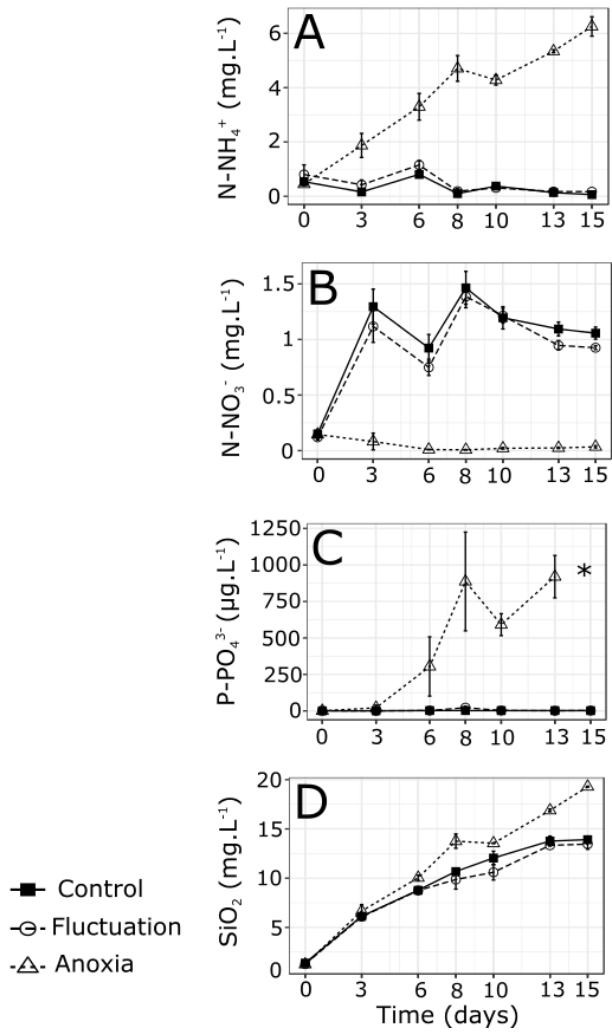
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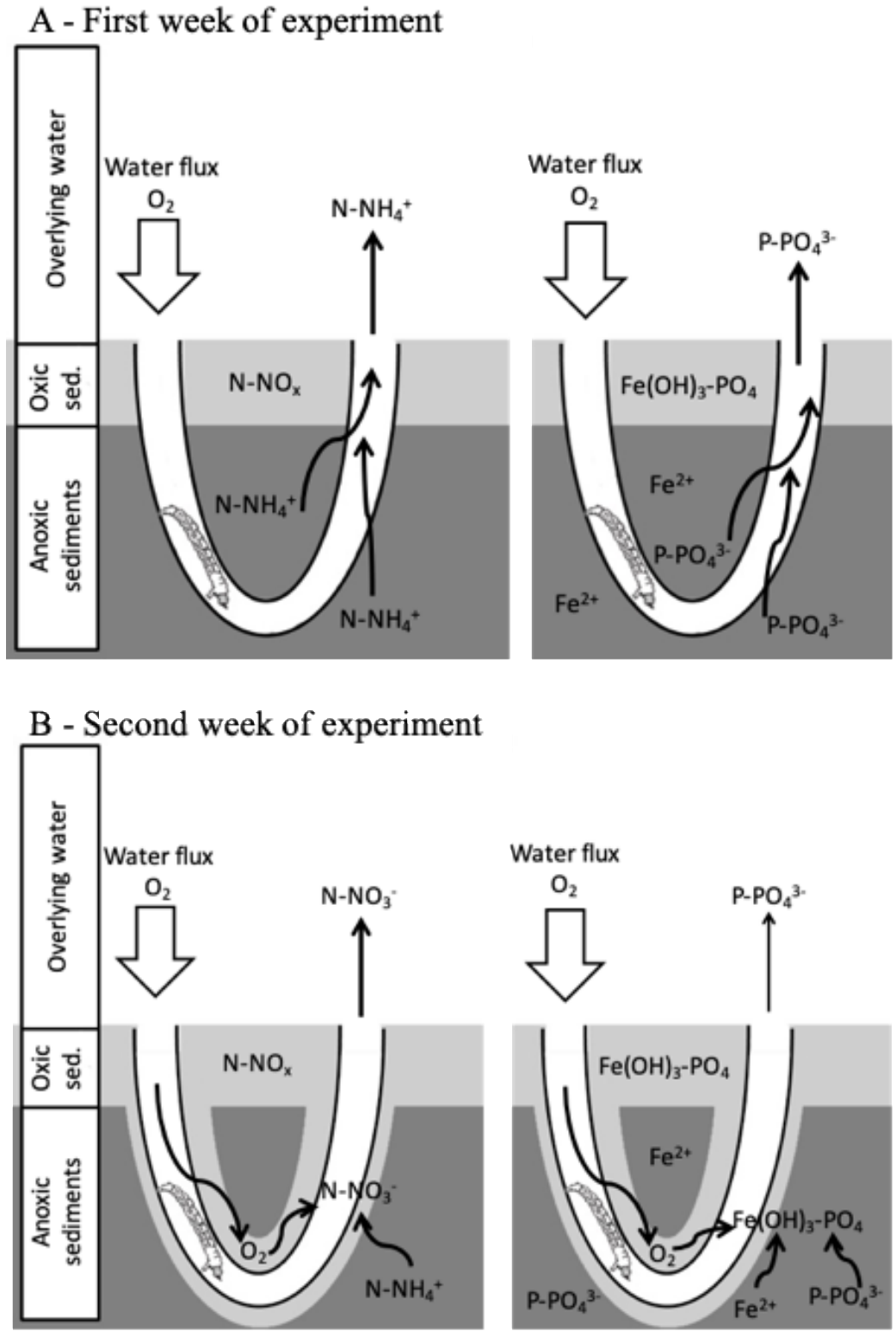
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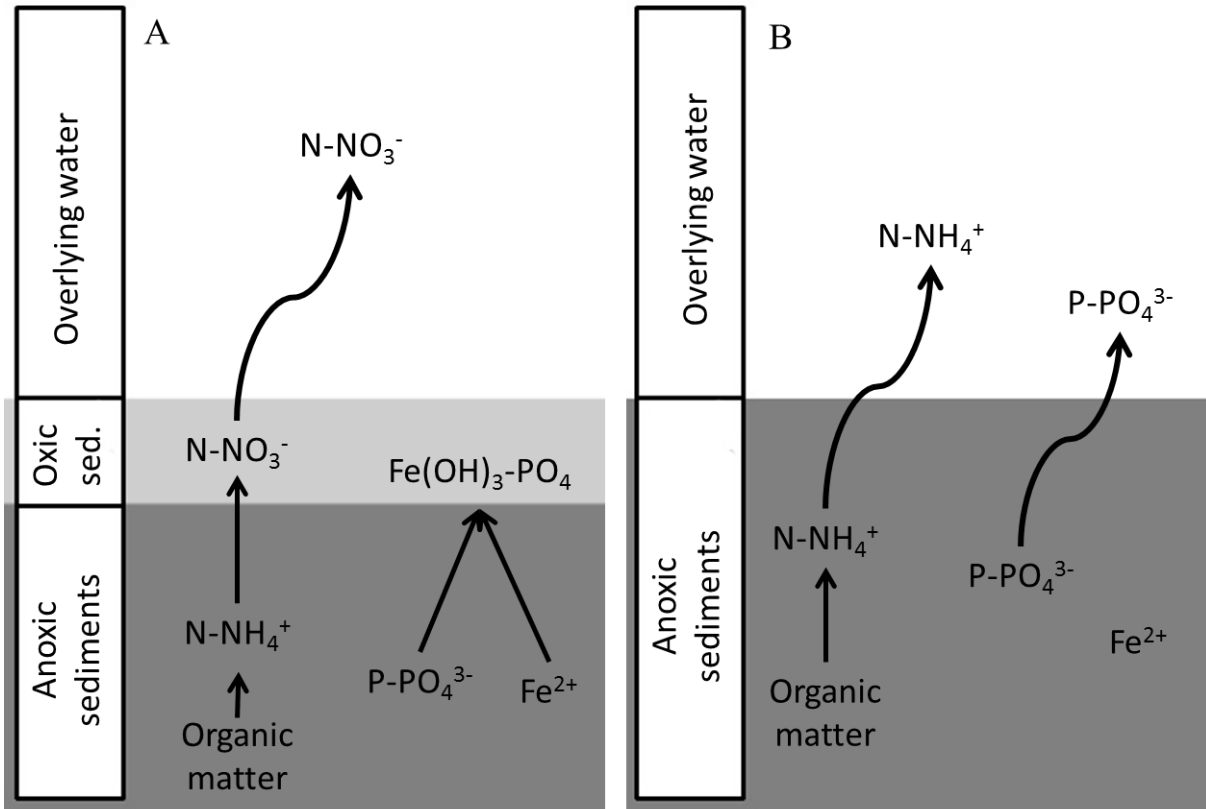


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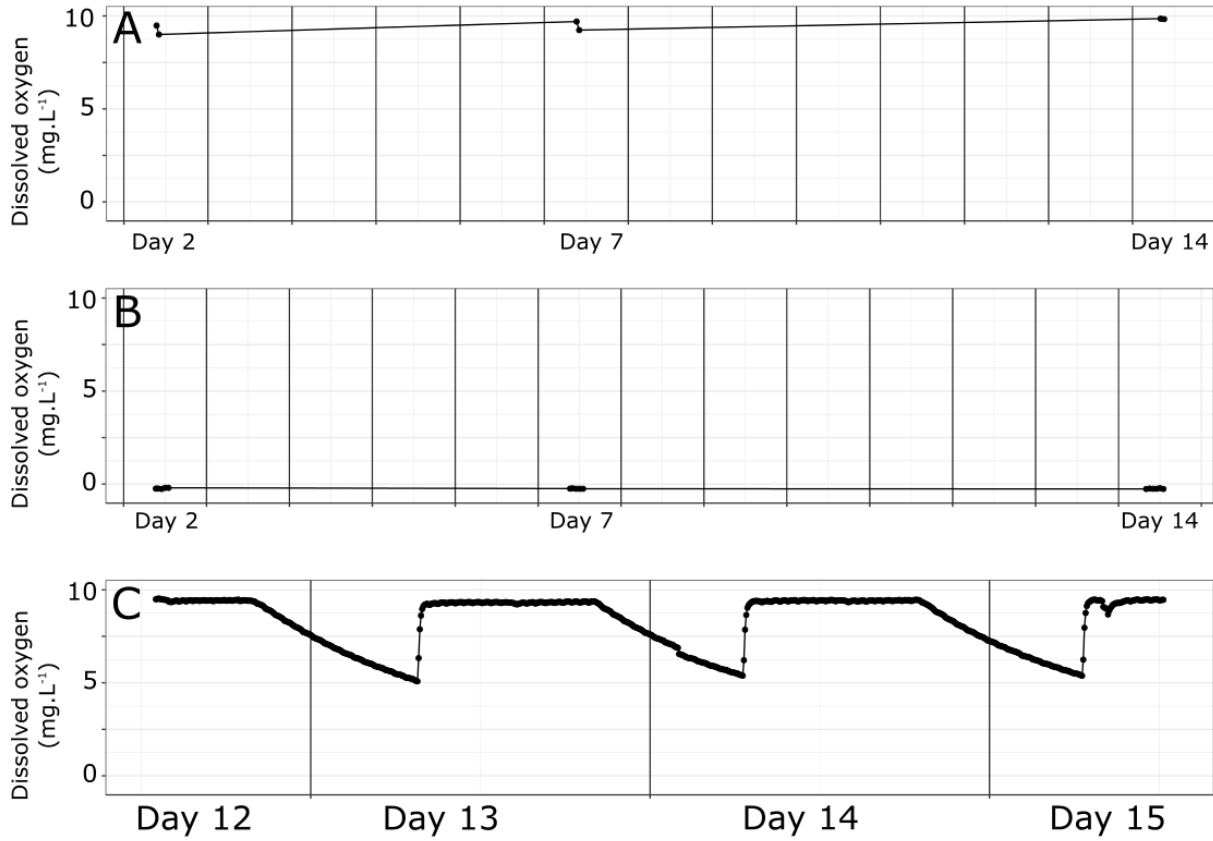
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666 **Online Resource 1** (A) Concentration of dissolved oxygen (mg.L^{-1}) in control treatment from day 2 to day 14, (B)
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668 dissolved oxygen (mg.L^{-1}) monitored in fluctuation treatment from day 12 to day 15.



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