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Chironomid larvae stimulate biogeochemical and microbial processes in a riverbed covered with fine sediment

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Abstract. We determined if the influence of chironomid larvae on biogeochemical and microbial processes in fine surface sediments of a riverbed depended on the characteristics of the sedimentary habitat. The influence of chironomids was measured on sediment reworking, biogeochemical processes and bacterial characteristics in infiltration sediment columns having three different surface sediments (with different organic matter characteristics). The results showed that chironomids exhibited similar bioturbation activities (construction and irrigation of U-shaped tubes in the upper layers of sediments) and significantly stimulated O₂ uptake and percentage of active bacteria in all sediment treatments. In contrast, the release of NH₄⁺ in anoxic sediment layers was strongly

increased by chironomids in the presence of organic-rich sediments, whereas they had no effect on this process with organic-poor sediments. Our results indicated that the influence of chironomids on biogeochemical processes in river bed sediments are linked to the redox conditions of the system. Moreover, when the effects of chironomid larvae are compared to those measured with tubificid worms in the same experimental conditions, we conclude that the mode of bioturbation (sediment reworking, biogenic structure building, burrowing depth, bioirrigation) can also determine the impact of benthic animals on microbial activities and biogeochemical processes in the sediment.

Key words. Sediment reworking; organic matter; microbial activities; biogeochemical processes; slow infiltration columns.

Introduction

Sedimentation of fine sediments on riverbeds is a natural process occurring in freshwater environments. However, anthropogenic activities such as agriculture, mining, forestry operations, road construction and urbanization have dramatically increased the amount

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of fine sediments transported into streams and rivers (Wood and Armitage, 1997). Deposits of fine sediments may have variable characteristics (granulometry, organic matter, and pollutant contents) depending on their different origins (soil type, drainage area, ground cover, human activities), and so have different effects on biogeochemical processes occurring at the water-sediment interface. For instance, using slow infiltration columns to simulate hyporheic systems, Nogaro et al. (2007a) demonstrated that organic matter (OM) characteristics of sediment deposits significantly affected microbial processes in sediments. Organic-rich sediments produced higher stimulation of biogeochemical processes (O_2 uptake, nitrate consumption, and releases of ammonium and DOC from sediments) and microbial characteristics (bacterial biomass and activities) than organic-poor sediments.

Although anthropogenic sediment inputs can have adverse effects on aquatic fauna (Wood and Armitage, 1997; Yamada and Nakamura, 2002), some benthic invertebrates like oligochaeta are tolerant to such perturbations (Matthaei et al., 2006). Moreover, these invertebrates, by their bioturbation activities, can significantly influence organic matter processing and nutrient cycling in sediments (Fukuhara and Sakamoto, 1987; Pelegri and Blackburn, 1995; Mermillod-Blondin et al., 2000). It has been shown in a previous study (Nogaro et al., 2007b) that bioturbation activities of tubificid worms depended on OM quantity of fine sediments deposited at the surface of infiltration systems: sediment reworking by worms was higher in OM-rich sediments than in OM-poor sediments. Moreover, despite similar bioturbation activities in two different sediments highly loaded with OM, stimulation of microbial activities by worms was more efficient in the presence of a more refractory organic matter than with a labile one. Thus, Nogaro et al. (2007b) concluded that the effects of bioturbation on microbial processes were linked not only to the quantity but also to the quality of organic matter.

Sediment-impacted habitats are commonly colonized by tubificid worms but also by chironomid larvae (Kreutzweiser et al., 2005; Matthaei et al., 2006), another bioturbating taxon. Several studies showed that chironomid larvae could have significant influences on microbial processes in lake or river sediments (Fukuhara and Sakamoto, 1987; Andersson et al., 1988; Svensson and Leonardson, 1996; Svensson, 1997, 1998; Mermillod-Blondin et al., 2002). However, in contrast with tubificid worms, the influence of chironomid larvae on biogeochemical processes in river sediments impacted with fine sediment is poorly understood. Thus, the aim of the present work was to determine if the bioturbation effects due to oligo-

chaetes in impacted systems were also observed with chironomids. Three sediment deposits (with different POM quality and quantity) were added in the surface of infiltration sediment columns. The effects of chironomid larvae were measured on sediment reworking, aerobic respiration (vertical profiles of O_2 in sediments), solute fluxes (fluxes of NO_3^- , NO_2^- , NH_4^+ , and DOC), and microbial characteristics (biomass and activities). Our first hypothesis was that sediment reworking by chironomids was positively linked to the quantity of OM in fine sediment deposits. In freshwater sediments, several studies (Stief and de Beer, 2002; Altmann et al., 2004) showed that chironomid larvae differently affected microbial processes (O_2 uptake, nitrification, and denitrification) in organic-poor and organic-rich sediments. We therefore also hypothesized that the chironomid effects on biogeochemical and microbial processes were linked to the organic matter characteristics of surface sediments in our infiltration sediment systems.

Materials and methods

Sediment columns

Experiments were carried out in slow infiltration columns (Mermillod-Blondin et al., 2000). Each column (height = 45 cm and inside diameter = 10 cm) was constituted by association of four experimental modules (10 cm high) topped by a fifth module 5 cm high (Nogaro et al., 2007a). We used 18 columns that were filled with a mixture of gravel and sand to constitute a deep layer of heterogeneous substrate. Three different types of sediment deposits were added at the surface: (1) a stormwater (STORM) sediment deposit highly loaded with particulate organic matter and pollutants, which originated from the stormwater runoff on urban impervious surfaces, and two deposits from natural aquatic sediments: (2) a particulate organic matter-rich (POM-rich) sediment deposit, and (3) a particulate organic matter-low (POM-low) sediment deposit.

Preparation of gravel/sand substrate and fine sediments

Gravel and sand were collected from the Rhône River. Gravel was sieved manually to select particle sizes ranging from 5–8 mm and then was cleaned with deionized water before being dried at 60 °C. Before filling the columns, 18 kg of dry sand (grain size 100–1000 μm) were manually mixed with 90 g of fibrous cellulose powder (0.5% of the sediment weight) to stimulate microbial growth. A volume of 10 L 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, 19 mg L⁻¹ Ca(NO₃)₂ · 4H₂O, and 1.6 mg L⁻¹ (CH₃CO₂)₂CaH₂O; pH = 7.5) was added to the sand that was inoculated with an extract of natural bacteria as described by Mermillod-Blondin et al. (2000).

The stormwater (STORM) deposit was collected from a stormwater infiltration basin located on the campus of the University Claude Bernard (Lyon-France). The particulate organic matter-rich (POM-rich) and particulate organic matter-low (POM-low) deposits were collected from braided channels of the Rhône River at about 80 km east of Lyon. These three types of surface deposits were sieved (<1000 µm) and homogenized in the laboratory before use. The particle size distributions of the different deposits were determined by a laser diffraction granulometer (Mastersizer 2000, Malvern Instrument, UK). The STORM, the POM-rich, and the POM-low deposits were characterized by a high proportion of fine sediment particles with respectively 42–48, 45–52, and 47–54 % of volume of particles smaller than 100 µm. Chemical characteristics of the gravel/sand substrate and fine sediment deposits are described below.

Experimental design

Each column was filled with the gravel and incubated sand to a height of 28 cm on day -11 (11 days before chironomid addition). Constant masses of gravel (600 g) and incubated sand (215 g) were alternately added (five times) and finally 150 g of sand were added at the sediment surface to obtain a heterogeneous interface corresponding as much as possible to river natural sediments. On day -9, the columns were supplied from above with synthetic water using a peristaltic pump controlling a constant infiltration flow rate (1.5 mL min⁻¹). Supplied water was aerated to maintain a high dissolved oxygen (O₂) concentration. On day -6, a further 100 g of incubated sand were added to each column before the surface sediment to minimize penetration of the surface sediment into the sand/gravel substrate. Then, we added 250 g of each sediment deposit (STORM, POM-rich and POM-low deposits) to each treatment (6 columns per sediment treatment). The total height of substrate in each column was 30 cm (28 cm of heterogeneous sand/gravel mix and 2 cm of fine sediment deposit). The use of a 2 cm layer of fine sediment was similar to the depth of fine sediments that can occur on the bed of impacted rivers (Wood and Armitage, 1997). About 10 cm of water was left above the sediment surface. Experiments were performed at constant temperature (15 ± 0.5 °C) and the light was controlled on a 12 h light, 12 h dark cycle in the overlying water. In contrast, the sediment of the column was kept in the dark to suppress photoautotrophic growth.

On day 0, chironomid larvae were introduced in columns (in free water). These chironomids were collected in a braided channel of the Rhône River and kept 2 weeks in laboratory before introduction in columns. They were identified and assigned to *Chironomus riparius* agg. (larval stage IV, mean body length 1 cm) according to Vallenduuk and Moller Pillot (2002). For each surface deposit treatment (STORM, POM-rich, and POM-low deposits), two treatments were performed with three replicates per treatment: (1) without chironomid (controls) and (2) with 80 chironomid larvae per experimental unit (density = 10 200 individuals m⁻²). The chironomid densities used in our experiment were close to highest densities observed in area impacted by deposits of fine POM-rich sediments (Bishop et al., 2000) and were in the range of *Chironomus riparius* densities (10,000 individuals m⁻²) used by Stief and de Beer (2002) and Altmann et al. (2004) in their laboratory experiments.

Methods of analysis

Chemical composition of the sediment deposits and the sand/gravel substrate

Concentrations of particulate organic matter (POM), particulate organic carbon (POC), particulate nitrogen (PN), and particulate phosphorus (PP) were determined in the three sediment deposits and in the sand of the sand/gravel substrate. The measurements were performed in fresh material before use in experimental columns to characterize the chemical properties of the different deposits. POM content was determined as loss upon ignition at 550 °C for 5 h. POC, PN, and PP analyses were performed by the Central Service of Analysis of the French National Centre for Scientific Research (CNRS) in Lyon (France) following standard methods (Buchanan, 1984). POC was determined by high-temperature combustion and subsequent measurement of CO₂ by infrared detectors (Org CHN-analyzer, Central Service of Analysis of CNRS). PN was analyzed by high-temperature combustion and subsequent measurement of N₂ by thermal conductometry (Org CHN-analyzer, Central Service of Analysis of CNRS). PP was measured with the ascorbic acid method after microwave-assisted digestion with HNO₃ and HClO₄ and analyzed by inductively coupled plasma-atomic emission spectrometry (ICP-AES, Thermo Electron Maxim).

Sediment reworking analyses

Luminophores (natural sediment particles covered with a luminescent paint) were used to estimate sedimentary reworking by invertebrates in the col-

umns. The day after introduction of invertebrates (on day 1), one g of yellow luminophores (160 – 315 μm) was deposited at the sediment surface of each column. At the end of the experiment (on day 22), the water layer was carefully pumped out and the substrate of each column was cut into slices. The top 3 cm were sliced at 0.5 cm thickness, while the next 7 cm were sliced in 1 cm layers. Each slice was sieved to remove gravel (with a 2 mm mesh sieve) and recover living organisms (with a 500 μm mesh sieve). Five grams of sediment were taken from each slice and dried at 40 °C for 48 hours before being mixed delicately to homogenize the sediment without breaking the luminophores.

Luminophores were counted with a UV light microscope and expressed as number of luminophore per gram of dry sediment. Sediment transport at the interface due to the invertebrate activities was estimated by analyzing the vertical profiles of luminophores in each treatment (i.e. control and chironomid). The number of luminophores found at a given depth was expressed as percentage of the total luminophore content found in the whole column. So, the vertical profiles of luminophores were expressed as percentages.

Physico-chemical analyses

Physico-chemical analyses were performed in water samples of slow infiltration columns to study the biogeochemical processes in sedimentary columns. We measured dissolved oxygen (O_2), nitrate, nitrite, ammonium, and dissolved organic carbon (DOC) in water samples taken from different depths (5 cm above and 1, 5, 15, and 25 cm below the water-sediment interface) of slow filtration columns at days 0 (before the chironomid introduction), 2, 6, 10, 14, and 20 (after the chironomid introduction). The water samples were taken using openings integrated at different depths of the experimental columns. To avoid a hydraulic disturbance of the system, water samples were collected at the constant flow rate determined by the peristaltic pump supplying the columns with water (1.5 mL min^{-1}). Measurements of solutes were also performed in the tank containing the supplied synthetic water and at -25 cm below the water-sediment interface of each column every second day during the course of the experiment (from days 1 to 20). The average release rate of each solute for each column and then, the average release rate per fauna treatment (control vs. chironomid) for each deposit treatment were calculated.

For O_2 measurements, water sampling was first performed in a 30 mL plastic bottle previously saturated with nitrogen to avoid the contact of the sample with atmospheric oxygen. The water was then

circulated using a peristaltic pump in a measuring chamber containing a Clark type electrode connected to a 3600 Orbisphere model oxygen meter to determine the O_2 content of the water sample. Nitrate, nitrite and ammonium contents were measured using colorimetric HACH methods and DOC measurements were performed using a Dohrman DC 80 “Total carbon analyser” according to Mermillod-Blondin et al. (2000, 2005a).

Microbial characteristics

Microbial characteristics were measured in sediment at different depths to study the influence of chironomid larvae on microbial communities (bacterial abundance and percentages of active eubacteria) and activities (hydrolytic, respiration and denitrification activities) in the presence of different sediment deposits. The sediment layers (from the surface to 10 cm depth) sampled for luminophore analyses (see above) were pooled to obtain sediment layers of 0–3 and 3–6 cm depth. Then, for each column, the sediment from four depth layers (0–3, 3–6, 13–16, and 23–26 cm) was collected for microbial analyses. Each layer was sieved to remove gravel (sieve = 2 mm) and recover living organisms (sieve = 500 μm).

The DNA intercalating dye (DAPI) and a Cy3-probe (EUB 338, eubacteria, Amann et al., 1995) were used on sediment samples to determine the total numbers of bacteria stained with DAPI and the percentages of active eubacteria (% EUB/DAPI). Two grams of wet sediment were taken from each layer and prepared according to Mermillod-Blondin et al. (2005b). Sediment samples were fixed in 4% paraformaldehyde in phosphate-buffered saline (PBS) for 10 h. Fixed samples were subsequently washed twice in PBS and were stored in ethanol and PBS (50:50) at -20 °C. Fixed samples of 0.5 g of sediment were mixed with 20 mL of 0.1% pyrophosphate in PBS (Phosphate Buffer Saline) and homogenized by sonication. Aliquots (10 μL) of homogenized samples were spotted onto gelatine-coated slides and hybridized with the Cy3-labelled oligonucleotide probe (EUB 338) and concomitantly stained with the DNA intercalating dye DAPI (200 ng μL^{-1} , Sigma, Buchs, Switzerland) according to Schönholzer et al. (2002). Slides were mounted with Citifluor solution (Citifluor Ltd, London, U.K.) and the preparations were each examined at 1000 \times magnification with a BH2-RFCA Olympus microscope fitted for epifluorescence with a high-pressure mercury bulb (50 W) and filter sets BP 405 (for DAPI) and BP 545 (for Cy3). Bacteria from each sample were analyzed in 20 fields per sample with up to 30 cells per field. Numbers of DAPI and Cy3-bacteria were counted separately from the same microscope field in order to calculate the

Table 1. Chemical composition of the sediment deposits before introduction in the columns (mean \pm 1 SD, n = 3). Abbreviations used: POM – Particulate Organic Matter; POC – Particulate Organic Carbon; PN – Particulate Nitrogen; PP – Particulate Phosphorus.

Chemical composition	STORM deposit	POM-rich deposit	POM-low deposit
POM (g kg ⁻¹ sed. DW)	70.0 \pm 5.3	85.0 \pm 2.6	20.3 \pm 5.1
POC (g kg ⁻¹ sed. DW)	55.6 \pm 1.6	37.8 \pm 6.1	14.9 \pm 6.1
PN (g kg ⁻¹ sed. DW)	2.93 \pm 0.47	1.1 \pm 0.2	0.7 \pm 0.2
PP (g kg ⁻¹ sed. DW)	1.11 \pm 0.15	0.41 \pm 0.01	0.35 \pm 0.02
Atomic C/N	22.4 \pm 3.35	40.1 \pm 7.55	24.9 \pm 6.04
Atomic C/P	126.3 \pm 14.8	230 \pm 34.3	114.0 \pm 37.5

percentage of active bacteria (EUB/DAPI) and the total number of bacteria stained with DAPI g⁻¹ of sediment dry weight (DW) from each analyzed field.

Aerobic respiration and denitrification measurements were performed following the slurry technique (Furutani et al., 1984). About 10 g of wet sieved substrate of each sediment layer were prepared according to Nogaro et al. (2007a). Results were expressed as μ g of C or N h⁻¹g⁻¹ sediment DW. Hydrolytic activity was measured using fluorescein diacetate (FDA) as substrate for hydrolases (Fontvieille et al., 1992). Results were expressed as micromoles of hydrolyzed FDA h⁻¹g⁻¹ of sediment DW.

Vertical distribution of invertebrates at the end of experiment

The living invertebrates were recovered at the end of the experiment to estimate mortality and vertical migration in each column. At the end of the 22-day experiment, the top 15 cm of sediments were sliced (the top 3 cm in slices of 0.5 cm thickness and the lower 12 cm in slices of 1 cm thickness) and sieved through a 500 μ m mesh. For each column, chironomids recovered were preserved in alcohol (96%) before counting within the different slices under a dissecting microscope. At the end of the experiment, we recovered 62.03 \pm 9.84% (mean \pm 1 SD, n = 9) of the animals added initially. Chironomid distributions in the sediment at the end of the experiment were expressed as percentages of organisms found in the column at each sampled depth.

Data treatment

For luminophore analysis, we tested the effects of fauna treatment (control and chironomid) and surface deposit treatment (STORM, POM-rich, and POM-low deposits) for each depth of sediment using a two-way analysis of variance (ANOVA). If significant differences were detected (p < 0.05), Scheffé post hoc tests were performed to determine which treatment differed.

For physico-chemical variables (O₂, N-NO₃⁻, N-NO₂⁻, N-NH₄⁺ and DOC), we tested the homogeneity among the columns before the chironomid addition using a two-way ANOVA for each sediment deposit

with fauna treatment and depth (5 cm above and 1, 5, 15, 25 cm below the water-sediment interface) as main effects. After chironomid addition, a two-way repeated-measure ANOVA (RM ANOVA) was used on physico-chemical variables to detect differences among fauna treatments and depths using time as the repeated factor (days 2, 6, 10, 14, and 20). If significant differences were detected among fauna treatments, Scheffé post hoc tests were performed to determine the differences among fauna treatments for each depth and time. For the average release rates of solutes (N-NH₄⁺ and DOC) from days 1 to 20, we tested the effects of fauna treatment and surface deposit treatment using a two way ANOVA and Scheffé post hoc tests.

For bacterial measurements, we tested the fauna treatment and depth effects using a two-way ANOVA and Scheffé post hoc tests for each type of surface deposit.

When necessary, data were log-transformed, and data expressed as percentages (% of luminophores and active bacteria) were arcsine-transformed before statistical analysis, to fit the assumption of homoscedasticity. Statistical analyses were performed using Statistica 6TM (Statsoft, Tulsa, OK, USA).

Results

Composition of the surface sediments and sand/gravel substrate

POM and POC contents of the STORM and the POM-rich deposits were higher compared to the POM-low deposit (Table 1). STORM and POM-low deposits had similar atomic ratios of C/N and C/P which were lower than those of POM-rich deposit. At the start of the experiment, the sand of the heterogeneous sediment was characterized by 17.3 (\pm 1.2), 7.7 (\pm 0.6), 0.3 (\pm 0.06), and 0.16 (\pm 0.01) g kg⁻¹ sed. DW of POM, POC, PN, and PP, respectively (mean \pm 1 SD, n = 3).

Sediment reworking analyses

In control columns, most of luminophores (>97%) deposited at the sediment surface at the beginning of

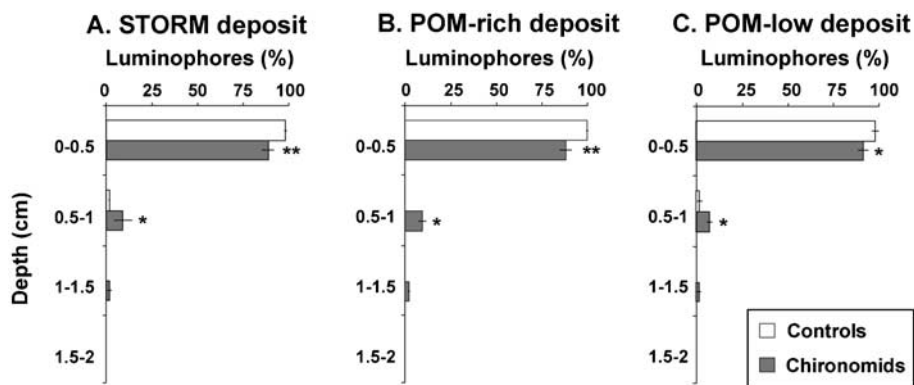


Figure 1. Depth profiles of luminophores for (A) the STORM, (B) the POM-rich and (C) the POM-low sediment deposits at the end of the experiment (mean \pm 1 SD, $n = 3$). Scheffé post hoc tests between control and chironomid treatments revealed significant differences at $p < 0.05$ (*) and $p < 0.01$ (**).

the experiment were recovered in the upper sediment layer (0–0.5 cm) on day 22 in all deposit treatments (Fig. 1). In contrast, the chironomids buried luminophores to depths of 1.5 cm in all deposit treatments (two-way ANOVAs, fauna effect, $p < 0.001$, see Scheffé post hoc tests in Fig. 1). The influence of chironomids on luminophore profiles did not depend on the type of the surface deposit tested (two-way ANOVA, deposit effect, interaction “fauna x deposit” effect, $p > 0.05$).

Physico-chemical analyses

Before chironomid addition (day 0), concentrations of dissolved O_2 , $N-NO_3^-$, $N-NO_2^-$, $N-NH_4^+$, and DOC were not significantly different between the groups of columns assigned to each treatment (control vs. chironomid) in all deposit treatments (two-way ANOVAs, fauna effect, $p > 0.05$). Oxygen and nitrate concentrations decreased significantly with depth during the experiment in all columns (two-way RM ANOVAs, depth effect, $p < 0.001$, see Fig. 2 for day 14). The presence of chironomids induced significant decreases of O_2 concentrations compared to the controls in all deposit treatments (two-way RM ANOVAs, fauna effect, $p < 0.001$, see Scheffé post hoc tests in Fig. 2 for day 14). In contrast, no effect of chironomid was detected on nitrate values during the experiment (two-way RM ANOVAs, fauna effect, $p > 0.05$, see Fig. 2 for day 14).

A low production of $N-NO_2^-$ ($< 0.2 \text{ mg L}^{-1}$) was measured in depth in the three experimental treatments with no significant differences among fauna treatments (two-way RM ANOVAs, fauna effect, $p > 0.05$, data not shown). Concentrations of ammonium increased with depth and with the occurrence of invertebrates in the presence of STORM and POM-rich deposits (two-way RM ANOVAs, depth effect, $p < 0.001$, fauna effect, $p < 0.05$). In these two deposit

treatments, the presence of chironomids significantly increased NH_4^+ concentrations in interstitial water (Scheffé post hoc tests, Figs. 2A and 2B for day 14). Occurrence of chironomids also produced higher values of DOC in interstitial water for the STORM and the POM-rich deposits (two-way RM ANOVAs, depth effect, $p < 0.001$, fauna effect, $p < 0.05$) than controls despite no significant influence of chironomids at any specific depth (Scheffé post hoc tests, $p > 0.05$, see Figs. 2A and 2B for day 14). In POM-low deposit treatment, ammonium and DOC concentrations were very low with no significant differences among fauna treatments (two-way RM ANOVAs, fauna effect, $p > 0.05$).

The mean release rate of $N-NH_4^+$ measured from days 1 to 20 was significantly different among fauna and deposit treatments (two-way ANOVAs, fauna effect, deposit effect, $p < 0.001$, Fig. 3A). The chironomid influences on $N-NH_4^+$ releases depended on the surface deposit tested (two-way ANOVA, interaction “fauna x deposit” effect, $p < 0.05$) because chironomids induced the highest increases of ammonium releases in presence of STORM and POM-rich deposits (Scheffé post hoc tests, $p < 0.001$, Fig. 3A). The mean release rates of DOC were also significantly different among fauna and deposit treatments (two-way ANOVAs, fauna effect, deposit effect, $p < 0.05$), despite no particular effect of fauna for each type of deposit (Scheffé post hoc tests, $p > 0.05$, Fig. 3B).

Microbial characteristics

At the end of the experiment, the total number of bacteria (stained with DAPI) decreased significantly with depth and no significant differences were detected among control and chironomid treatments for the 3 types of deposit (two-way ANOVA, depth effect, $p < 0.001$, fauna effect, $p > 0.05$, Fig. 4). The

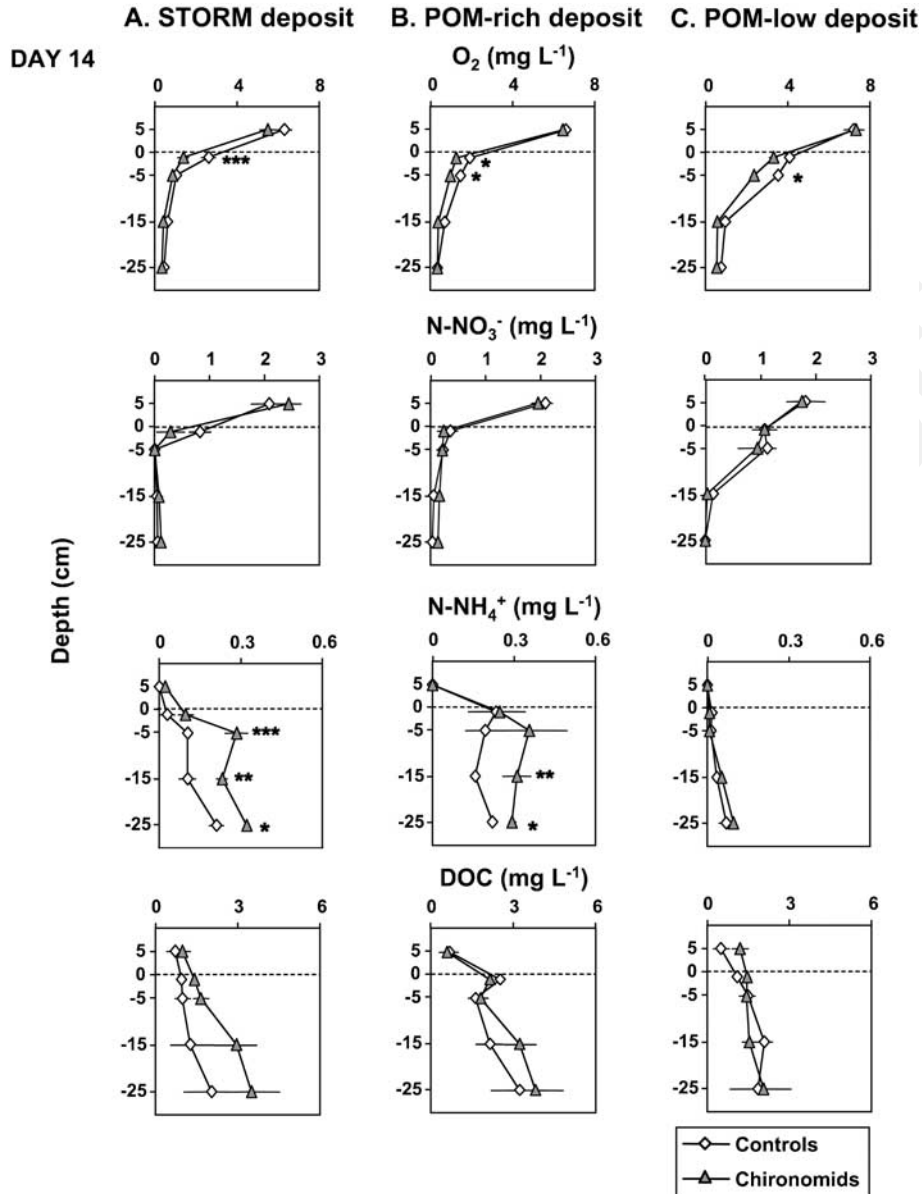


Figure 2. Examples of depth profiles of oxygen (O_2), nitrate ($N-NO_3^-$), ammonium ($N-NH_4^+$), and dissolved organic carbon (DOC) concentrations obtained on day 14 for (A) the STORM, (B) the POM-rich, and (C) the POM-low deposits (mean \pm 1 SD, $n = 3$). Scheffé post hoc tests between control and chironomid treatments revealed significant differences at $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***)

percentage of active bacteria (EUB/DAPI) also decreased significantly with depth and was significantly affected by the occurrence of invertebrates (two-way ANOVA, depth effect, fauna effect, $p < 0.01$). In the first sediment layer (0–3 cm), the percentages of active bacteria were increased by more than 20% in the chironomid treatment for the 3 surface deposits compared to the controls (Scheffé post hoc tests, Fig. 4). Chironomid larvae also increased the percentage of active bacteria at 13–16 cm with the POM-rich deposit and at 3–6 cm in the presence of the POM-low deposit (Scheffé post hoc tests, Fig. 4).

In the presence of STORM deposit, respiratory, denitrification, and hydrolytic activities measured at the end of the experiment decreased significantly with depth with no significant difference among fauna treatments (two-way ANOVA, depth effect, $p < 0.001$, fauna effect, $p > 0.05$, Fig. 5A). These microbial activities also decreased significantly with depth in the POM-rich deposit treatment (two-way ANOVA, depth effect, $p < 0.001$, Fig. 5B). However, in contrast with results observed with the STORM deposit, CO_2 and N_2O productions (respiration and denitrification, respectively) were significantly increased by chironomids in the upper sediment layer in the presence of the

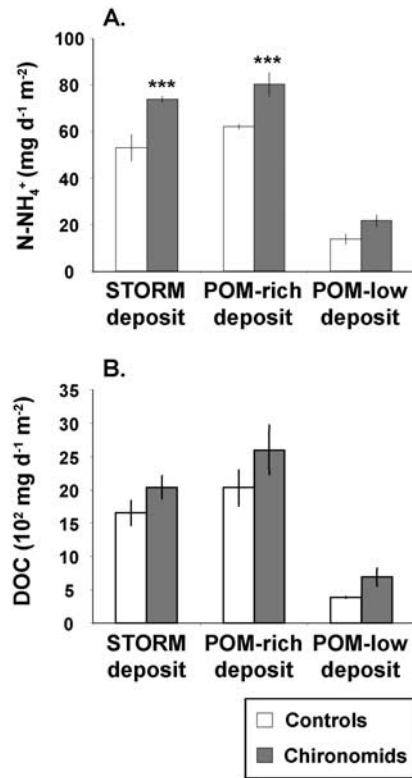


Figure 3. Mean release rates of (A) ammonium (N-NH_4^+) and (B) dissolved organic carbon (DOC) from days 1 to 20 (mean \pm 1 SD, $n = 3$). Scheffé post hoc tests between control and chironomid treatments revealed significant differences at $p < 0.001$ (***).

POM-rich deposit (two-way ANOVA, depth effect, $p < 0.001$, fauna effect, $p < 0.05$, Fig. 5B). The POM-low deposit treatment showed low microbial activities in all sediment layers with no significant differences among fauna treatments and depths (two-way ANOVA, depth effect, fauna effect, $p > 0.05$, Fig. 5C).

Vertical distribution of invertebrates at the end of experiment

At the end of the experiment, all living chironomid larvae were recovered in the top 2 cm of the sediment in all sediment treatments (Table 2). Most chirono-

Table 2. Vertical distributions of chironomids in the sediment at the end of experiment for the STORM, the POM-rich, and the POM-low sediment treatments (mean \pm 1 SD, $n = 3$).

Depth layers (cm)	STORM deposit	POM-rich deposit	POM-low deposit
0 -0.5	77.8 \pm 18.9	84.7 \pm 13.7	94.7 \pm 5.0
0.5-1	16.4 \pm 15.2	10.7 \pm 7.3	5.3 \pm 5.1
1 -1.5	5.2 \pm 4.6	3.4 \pm 4.8	-
1.5-2	0.6 \pm 0.1	1.1 \pm 1.6	-
2 -2.5	-	-	-
2.5-3	-	-	-
3 -4	-	-	-

mids (between 78 and 95%) were found in the top 0.5 cm layer of the sediment for all sediment treatments.

Discussion

Biogeochemical processes in systems with the three deposited sediments

According to a previous study (Mermillod-Blondin et al., 2005a), our experimental system well reproduced the biogeochemical processes naturally occurring in river sediments. A clear vertical gradient from aerobic to anaerobic processes was measured at a centimetre scale. The strong microbial activity at the water-sediment interface led to a rapid decrease of O_2 (aerobic respiration) and NO_3^- (denitrification) with depth in the sediment. High releases of NH_4^+ and DOC were measured in the deepest sediment layers mainly due to the anaerobic mineralization of OM. Indeed, as measured in a previous study using infiltration sediment columns (Mermillod-Blondin et al., 2000), the production of DOC in the sediment was probably linked to production of volatile fatty acids resulting from the anaerobic degradation of the particulate organic matter (Hvitved-Jacobsen et al., 1995). Our results also indicated the occurrence of anaerobic processes such as denitrification and anaerobic mineralization of OM, whereas O_2 contents could be above 0.5 mg l^{-1} . This occurrence is probably due the physical heterogeneity of sediments resulting in anaerobic micro-environments (Triska et al., 1993).

In these systems, the three fine sediment deposits had different influences on biogeochemical processes (Nogaro et al., 2007a): O_2 uptake, nitrate consumption and releases of ammonium and DOC were higher with the sediment deposits highly loaded with OM (STORM and POM-rich deposits) than with the POM-low deposit. As shown by Crenshaw et al. (2002), addition of sediments that had a low C/N ratio (STORM deposit) induced a more intense microbial metabolism than addition of sediments with less available OM (POM-rich deposit, Nogaro et al., 2007a). Considering these links between OM characteristics of the deposits and system functioning, the present study aimed to determine if chironomid effects on microbial processes were highly dependent on these OM characteristics.

Chironomid bioturbation and OM quantity of surface sediments

Our first hypothesis that chironomid bioturbation was positively linked to the quantity of OM in surface sediments was not supported by our results. Although POM content was more than 3-fold higher in STORM

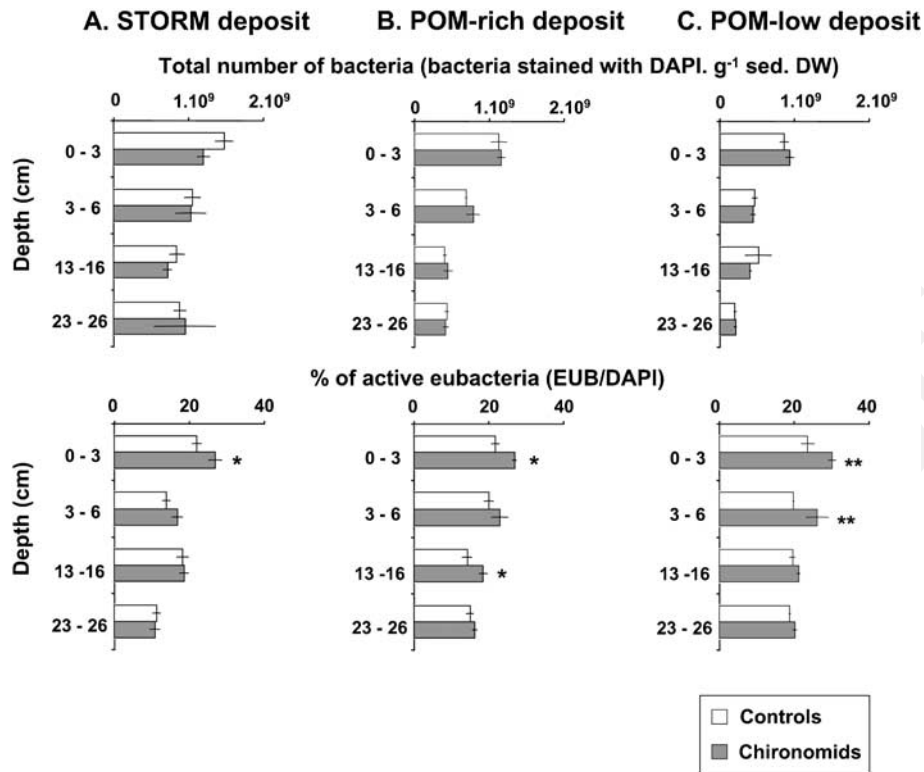


Figure 4. Depth profiles of total number of bacteria and percentage of active bacteria at the end of the experiment for (A) the STORM, (B) the POM-rich, and (C) the POM-low deposits (mean \pm 1 SD, n = 3). Scheffé post hoc tests between control and chironomid treatments revealed significant differences at $p < 0.05$ (*) and $p < 0.01$ (**).

and POM-rich sediment deposits than in the POM-low deposit, bioturbation activities of chironomids were similar in all deposit treatments. Such lack of differences among sediment deposits showed that the specific life mode of chironomids was not affected by fine sediment characteristics. Chironomid larvae dig U-shaped tubes using a mixture between their own salivary secretions and detritus particles to consolidate the walls of the tubes (Brennan and McLachlan, 1979). In our experimental conditions, sediment reworking by chironomids was due to this burrow construction and the transport of surface particles in tubes through ventilation and non-selective feeding of surface sediments (Brennan and McLachlan, 1979; Fukuhara, 1987). Because the sediment reworking process was due to the occurrence of tubes, the same number of chironomid larvae introduced in all deposit treatments probably produced a similar number of tubes, similarly affecting sediment transport.

In a previous study, we showed that bioturbation activities of tubificids were higher in presence of STORM and POM-rich sediments than with POM-low sediment deposit (Nogaro et al., 2007b). Such difference in sediment reworking between chironomids and tubificids was probably due to the different burrowing and feeding activities of these two taxa.

While chironomid larvae did not increase vertical sediment transport because they lived in their tubes and fed at the sediment surface, tubificid worms fed on the whole sedimentary column and actively mixed sediment through conveyor-belt activities and creation of dense networks of galleries (McCall and Fisher, 1980). As a consequence, tubificid worm activities were the most sensitive to OM characteristics of the sediment.

Chironomid effects on biogeochemical and microbial processes depending on organic matter characteristics of surface sediments

Our second hypothesis stated that the chironomid effects on biogeochemical and microbial processes depended on the organic matter characteristics of surface sediments. This hypothesis was only supported by data concerning NH_4^+ release in interstitial water because chironomids significantly increased NH_4^+ production with sediments highly loaded with OM (STORM and POM-rich deposits) whereas they had no effect on this process with the POM-low sediment deposit. Because ammonium releases were due to OM degradation under anaerobic conditions, presence of surface sediments with high OM content were more favourable to NH_4^+ release processes (for instance, by

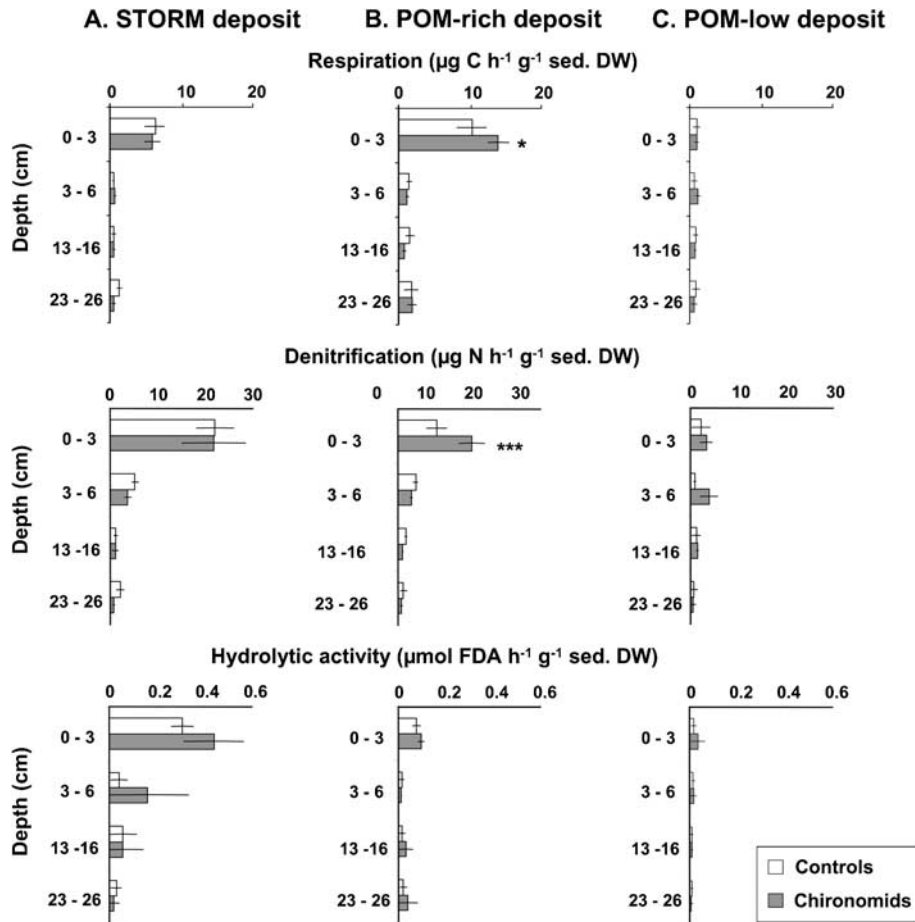


Figure 5. Depth profiles of respiration, denitrification and hydrolytic activities at the end of the experiment for (A) the STORM, (B) the POM-rich, and (C) the POM-low deposits (mean \pm 1 SD, $n = 3$). Scheffé post hoc tests between control and chironomid treatments revealed significant differences at $p < 0.05$ (*) and $p < 0.001$ (***)

creation of anaerobic conditions) than POM-poor sediments. Stimulations of OM processing by chironomid larvae in STORM and POM-rich sediment deposits appeared to create conditions favouring microbial N mineralization and release of NH_4^+ .

Despite this effect of sediment characteristics on chironomid-mediated release of NH_4^+ , aerobic processes (decrease of O_2 concentrations with depth) did not validate our hypothesis. Whatever the deposit treatment, chironomids induced a similar stimulation of aerobic respiration that was linked to a stimulation of the bacterial activities in the top sediment layer. An increase of 20% of EUB-hybridized bacteria was indeed measured in presence of chironomids compared to the controls in the three deposit treatments. Using hybridization with EUB 338, some starved and dormant bacteria may be detected as active bacteria if their rRNA contents were sufficiently high (Christensen et al., 1999). However, in our experimental conditions, 20% increase of EUB-hybridized bacteria was likely due to a stimulation of micro-organisms by

chironomids. As observed in lake sediments (Svensson and Leonardson, 1996; Goedkoop et al., 1997; Svensson, 1997; Hansen et al., 1998), the stimulation of the microbial community measured in our system mainly resulted from the animal bioturbation in the sediment. *Chironomus sp.* have intermittent water pumping activities (ventilation) through their burrows that enhance the accessibility of oxygen and nutrients to the microbial community (Van de Bund et al., 1994). Chironomid larvae could also stimulate the activity of sediment bacteria by their feeding activity (Johnson et al., 1989) acting as surface deposit-feeder scraping the sediment surface for detritus and bacteria attached to fine sediment particles (McCall and Tevesz, 1982). Due to these several activities, the surface sediment and the chironomid tubes are very active zones with enhanced aerobic and anaerobic microbial activities (Svensson, 1998). In our infiltration conditions, ventilation of U-shaped tubes present in the top 1 cm of fine sediments stimulated O_2 exchanges between flowing water and sediment,

enhancing aerobic microbial activities. We can also expect that ventilation processes produced O₂ oscillations in the fine sediment layer, such oscillations potentially stimulating OM degradation in sediment as observed in marine systems (Aller, 1994; Kristensen and Holmer, 2001).

In comparison with chironomids, effects of tubificid worms on O₂ respiration were highly affected by the characteristics of the deposits (Nogaro et al., 2007b). They had no significant effect with the STORM deposit, whereas they stimulated respiration with the other deposits. Such differences were associated with the high availability of OM in the STORM sediment deposit that supported strong microbial activities. These microbial activity rates were therefore not easily increased by tubificid worm activity. The fact that chironomids stimulated aerobic respiration with the STORM deposit may be due to the ability of chironomids to increase O₂ exchanges at higher rates than tubificid worms. Even if oligochaetes dig complex networks of burrows and transport particles from depth to the sediment surface (Mc Call and Tevesz, 1982), they do not ventilate their burrows in contrast with chironomid larvae. These differences of life mode between invertebrates could explain that *Chironomus sp.* induced the highest stimulation of the biogeochemical processes in the sedimentary columns. Similarly to our results, Van de Bund et al. (1994) showed with the same invertebrate densities (about 10,000 chironomids per m² and 20,000 tubificids per m²) that the stimulation of bacterial activity (bacterial production) was more effective (more than 2-fold) in the presence of chironomids than with tubificid worms. As a consequence, the biogeochemical processes occurring in sediments were the results of complex interactions between the bioturbation mode of invertebrates and organic matter characteristics of the sediment.

Although chironomid larvae similarly affected the biogeochemical processes occurring in slow infiltration columns with the STORM and the POM-rich deposits, they did not affect similarly the potential microbial activities (respiration and denitrification measured in slurries). They enhanced the potential respiratory and denitrification activities by more than 90% and 36%, respectively, in the POM-rich deposit columns, whereas they had no effects in the presence of the STORM deposit. These differences could be due to the higher availability of OM in the STORM deposit (indicated by its low C/N and C/P ratios) than in the POM-rich deposit. Although the modification of water transport at the water-sediment interface due to chironomids influenced processes measured in the whole system (water-sediment columns) with the STORM deposit, microbial communities were not

affected enough by chironomids to modify their potentials measured in slurries under optimal conditions. This result was probably linked to the high content of labile POM in the STORM sediment deposit allowing the microbial communities to work at high metabolic rates that could not be easily affected by chironomids. In contrast, chironomids were able to affect the potential of microbial communities developed on more refractory sediments (POM-rich deposit).

Conclusion

The present experiment demonstrated that bioturbation activities of *Chironomus sp.* stimulated the aerobic microbial activity whatever the sediment deposit. However, chironomids increased the release of reduced compounds such as NH₄⁺ with deposits highly loaded with OM, whereas they had no effect with POM-low deposit. This effect of OM quantity indicates that influences of chironomids on biogeochemical processes in the porous media may be modulated by redox conditions in the sediments (organic-rich deposits favouring anaerobic conditions in sediments and acting as a source of C and N for the system). It is also interesting to note that the occurrence of a fine sediment layer at the sediment surface induced a stimulating effect of chironomid larvae on aerobic processes, whereas Mermillod-Blondin et al. (2002) showed the opposite effect (decrease of microbial activity in the presence of chironomids) in the first 5 cm of hyporheic sediment not influenced by fine sediment deposits. We therefore need to develop experiments in a wide range of environmental conditions in order to better understand the interactions between habitat characteristics (granulometry, OM contents, hydrodynamics) and bioturbation influences. Moreover, the comparison between the effects of chironomid larvae and those of tubificid worms under the same experimental conditions demonstrated that the mode of bioturbation (sediment reworking, biogenic structures building, burrowing depth, bioirrigation) strongly influenced the impact of benthic animals on microbial activities and biogeochemical processes in the sediment. Thus, according to Mermillod-Blondin and Rosenberg (2006), further experiments are needed to consider both the diversity of the benthic habitats and the diversity of the bioturbation process to make a qualitative model of the role of bioturbation on sediment biogeochemistry.

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