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Impact of different benthic animals on phosphorus dynamics across the sediment-water interface

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Abstract

As a diagenetic progress, bioturbation influences solute exchange across the sediment-water interface (SWI). Different benthic animals have various mechanical activities in sediment, thereby they may have different effects on solute exchange across the SWI. This laboratory study examined the impacts of different benthic animals on phosphorus dynamics across the SWI. Tubificid worms and Chironomidae larvae were introduced as model organisms which, based on their mechanical activities, belong to upward-conveyors and gallery-diffusers, respectively. The microcosm simulation study was carried out with a continuous flow culture system, and all sediment, water, and worms and larvae specimens were sampled from Taihu Lake, China. To compare their bioturbation effects, the same biomass (17.1 g wet weight (ww)/m^2) was adopted for worms and larvae. Worms altered no oxygen penetration depth in sediment, while larvae increased the O_2 penetration depth, compared to the control treatment. Their emergence also enhanced sediment O_2 uptake. The oxidation of ferrous iron in pore water produced ferric iron oxyhydroxides that adsorbed soluble reactive phosphorus (SRP) from the overlying water and pore water. Larvae built obviously oxidized tubes with about 2 mm diameter and the maximum length of 6 cm in sediment, and significantly decreased ferrous iron and SRP in the pore water compared to the control and worms treatments. Worms constructed no visually-oxidized galleries in the sediment in contrast to larvae, and they did not significantly alter SRP in the pore water relative to the control treatment. The adsorption of ferric iron oxyhydroxides to SRP caused by worms and larvae inhibited SRP release from sediment. Comparatively, worms inhibited more SRP release than larvae based on the same biomass, as they successively renewed the ferric iron oxyhydroxides rich oxidation layer through their deposition.

Key words: bioturbation; oxygen; pore water; ferrous iron; Tubificid worms; Chironomidae larvae
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Introduction

In biogeochemistry, bioturbation refers to the process of sediment mixing that results from the burrowing, feeding, and ventilation of benthic animals at the sediment-water interface (SWI) (Aller, 2001; Gerino et al., 2007). Bioturbation is a diagenetic progress, and its biogeochemical implications include modification of sediment texture (e.g., changing sediment porosity, permeability, and spatial heterogeneity), bioirrigation (e.g., increasing the oxygen supply and removing metabolites), and the dispersal of solid particles (e.g., putting anoxic particles to the SWI) (Meysman et al., 2006). Many studies concerning bioturbation have been carried out both in the sea and in lakes, and the influences of bioturbation on solute transport in surface sediments and across the SWI are of concern (Jørgensen and Boudreau, 2001; Aller, 2001). Diverse benthic animals influence solute transport in different ways, as they have different activity manners.

Based on their sediment mixing modes, benthic animals are classified into five functional groups: biodiffusers, upward-conveyors, downward-conveyors, regenerators, and gallery-diffusers (François et al., 2002; Gerino et al., 2003). Biodiffusers move sediment in a random manner over a short distance, which results in diffusive sediment transport. Upward-conveyors burrow down into sediment vertically and ingest sediment there, then defecate it on the sediment surface. Downward-conveyors burrow upward and ingest sediment from the SWI, then defecate down to their egestion depth. Regenerators include gallery-digging species, which transfer sediment from deep to the surface, where it is washed away and replaced by sediment of surficial signature. Gallery-diffusers include species whose main activities are to dig systems of galleries, tubes, or burrows in sediment and to practice bioirrigation. Activities of gallery-diffusers lead to the non-local transport of matter from the surface to the deep part of the tubes due to the egestion of feces and to solute diffusion through the burrow

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walls. Biodiffuser (e.g., the marine bivalve *Mya arenaria*) and gallery-diffuser (e.g., the marine worm *Nereis virens*) have been shown to create different O_2 uptakes and nutrient and dissolved organic carbon fluxes across the SWI, based on the same biovolumes, as they alter sediment properties differently (Michaud et al., 2005; Michaud et al., 2006).

Chironomidae larvae and Tubificid worms, which are gallery-diffusers and upward-conveyors, respectively, are common species in eutrophic lake sediments. Their effects on element cycling in aquatic ecology have received much attention (Davis, 1974; Granéli, 1979; Andersson et al., 1988; Svensson and Leonardson, 1996; Lewandowski and Hupfer, 2005; Biswas et al., 2009). However, it is difficult to compare the results from the two organisms, as diverse environmental conditions and methods have been adopted in different studies. It is meaningful to compare the results from diverse benthic animals from the perspective of functional groups, as this makes it possible to reveal the differences hidden in different mechanical activities. This study investigated phosphorus dynamics across the SWI in sediment bioturbated by worms and larvae, respectively.

The present study was carried out with sediment, lake water, and larvae and worms specimens from Lake Taihu, China. To compare their impacts on P dynamics across the SWI, an equal biomass of worms and larvae was used. We hypothesized that the two benthic animals would produce distinct effects on P dynamics across the SWI. The changes of P flux across the SWI and pore water profiles of P and ferrous iron (Fe(II)) were measured over time. Due to the importance of oxygen in biogeochemical processes in sediment diagenesis (Kristensen, 2000; Glud, 2008), the influences of invertebrates on sediment O_2 uptake and O_2 penetration depth were also examined.

1 Materials and methods

1.1 Study site and sampling

Taihu Lake is located in the delta of the Yangtze River and has an area of 2338 km^2 and a mean depth of about 1.9 m (Qin, 2008). A preliminary investigation before the experiment indicated that the largest biomass of Tubificid worms (10,624 ind./m^2, 17.1 g wet weight (ww)/m^2) appeared at the estuary of the Dapu River (31°18′42.7″N, 119°56′52.2″E), while the highest density of Chironomidae larvae (737 ind./m^2, 3.6 g ww/m^2) occurred at Wuli Bay (31°30′48.4″N, 120°15′7.4″E), in Taihu Lake. *Tanypus chinensis* and *Limnodrilus hoffmeisteri* were respectively the dominant species of Chironomidae larvae and Tubificid worms in Taihu Lake (Cai et al., 2010). The sediment in Wuli Bay was shallow as it was dredged. A previous study on the effects of hydrodynamic processes on phosphorus fluxes across the SWI was also conducted at the estuary of the Dapu River (You, 2007). Thus, the estuary of the Dapu River was selected for the collection of sediment cores and lake water. The sediment cores were collected with Plexiglass tubes (11 cm i.d., 50 cm long) using a gravity corer (11 cm × 50 cm, Rigo Co., Japan) on November 13, 2008. At the same time, overlying water was collected with plastic barrels for incubation experiments in the laboratory. The specimens of worms and larvae used in the research were collected with a Peterson Grab at the estuary of the Dapu River, and Wuli Bay, respectively. The sampled sediment cores, lake water, and organism specimens were brought to the laboratory at *in situ* temperature (15 ± 1)°C. The sediment properties during field sampling were measured (Table 1).

Table 1 Main features of the sediment measured during the field work

Sediment properties	Sediment depth (cm)		
	0–4	4–8	8–12
Clay fraction of particle size 0.02–4 μm (%)	16.4	14.8	13.3
Silt fraction of particle size 4–63 μm (%)	75.9	76.5	79.6
Sand particles of particle size 63–500 μm (%)	7.69	8.64	7.00
Water content (%)	48.2	38.7	37.4
LOI (%)	5.64	4.75	4.35
Phosphorus (μmol/g dw)	25.5	23.7	21.9
Iron (μmol/g dw)	531	496	491
Manganese (μmol/g dw)	17.2	15.4	15.9
Aluminum (μmol/g dw)	2202	2119	2116
Calcium (μmol/g dw)	166	166	167

LOI: loss on ignition.

1.2 Experimental design

On day 0 of the experiment, the top 12 cm of the sediment cores were sliced into 2 cm intervals, and the same intervals were pooled together (Table 2). These were then sieved with 0.6 mm mesh to remove macrofauna and large particles. The sieved sediment samples were then fully homogenized and put into Plexiglass tubes (11 cm I.D., 16 cm long) in 2 cm intervals according to their original sequences (Fig. 1). Holes for inserting Rhizon soil moisture samplers (Rhizosphere Research Products, the Netherlands) in the Plexiglass tube walls were sealed with hydrophobic tape in advance. Filtered *in situ* lake water was added to the sediment top of these microcosms using intravenous needles. Thus, 9 microcosms with 12 cm of sediment and 4 cm of water were made. The microcosms were put in a dark Plexiglass tank with cover plate and

Table 2 Time table of the experimental procedure

Date	Defined day	Preparations and measurements
November 13		Collection of sediment, water, larvae, and worms
November 14	Day 0	Preparations of microcosms
November 28	Day 14	Installations of Rhizon samplers
November 29	Day 15	O_2 uptake (1st)*
November 30	Day 16	SRP flux (1st)
December 1	Day 17	Introduction of larvae and worms
December 4	Day 20	O_2 uptake (2nd)
December 5	Day 21	SRP flux (2nd)
December 6	Day 22	Pore water (1st)
December 11	Day 27	O_2 uptake (3rd)
December 12	Day 28	SRP flux (3rd)
December 13	Day 29	Pore water (2nd)
December 18	Day 34	O_2 uptake (4th)
December 19	Day 35	SRP flux (4th)
December 20	Day 36	Pore water (3rd)
December 21	Day 37	Sediment cores slicing

* The numbers indicate times of O_2 uptake, SRP flux, and pore water measurements. SRP: Soluble reactive phosphorus.

submerged in filtered lake water. The overlying water was aerated to keep O_2 saturation and the microcosms were pre-incubated for 16 days before the introduction of organisms (Table 2).

Rhizon samplers were used to successively acquire pore water samples at sediment depths of 0.5, 1.5, 2.5, 3.5, 5.0, 7.0, and 9.0 cm. The key part of a Rhizon sampler is a 10 cm long filter section made of a hydrophilic porous polymer tube with a typical pore diameter of 0.1 μm, and extracted pore water flows out through the connected polyvinyl chloride tube (Seeberg-Elverfeldt et al., 2005). On day 14, Rhizon samplers, with the oxygen removed in de-ionized water by high-purity nitrogen for 4 hr, were gently inserted into the sediment cores through holes and sealed with silicone glass cement outside the core (Fig. 1).

Nine microcosms were divided into three treatments with three replicates each: treatment A, control without organisms; treatment B, 101 worms in each microcosm (10,624 ind./m^2, 17.1 g ww/m^2); and treatment C, 33 larvae in each microcosm (3500 ind./m^2, 17.1 g ww/m^2). To compare their effects on sediment reworking with that of worms, the larvae biomass in our experiments was set equal to the biomass of worms. The increased larvae density was also reported in eutrophic lakes (Gong et al., 2001). On day 17, active worms (35–45 mm body length, average weight 1.6 mg ww/ind.) and larvae (fourth instar, 6–8 mm body length, average weight 4.9 mg ww/ind.) specimens were selected, counted, and introduced into the corresponding microcosms as described above. Most worms and larvae dug into the sediment within an hour. The remaining specimens were picked out and replaced with active ones after an hour. Then, all of the microcosms were covered with sealing lids and connected to a continuous-flow culture system, which used to renew the overlying water with 2 mL/min O_2 saturation water from tank (Fig. 1). The continuous-flow culture was powered by a peristaltic pump and lasted for 21 days (Table 2). Throughout the whole experiment, the incubation system

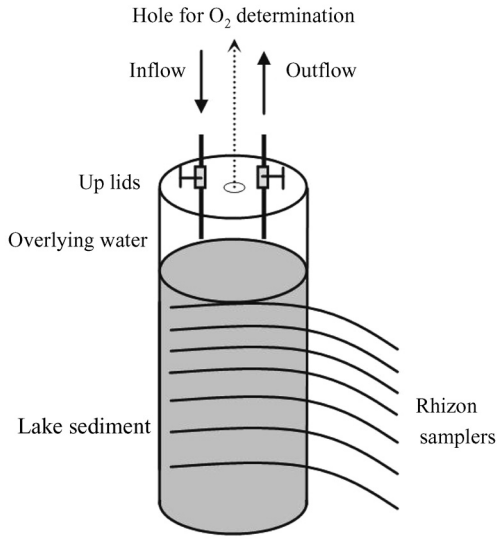

Fig. 1 Experimental microcosm set-up for O_2 uptake and SRP flux measurements and successive measurements of pore water.

was kept 12 hr intervals of dark and light by controlling the cover plate of the tank and light in room, and a temperature of (15 ± 1)°C was maintained. The continuous-flow culture was interrupted when measuring O_2 uptake and P flux across the SWI. All measurements of O_2 uptake and P flux were carried out in the dark to eliminate the influence of photosynthesis (Michaud et al., 2006).

1.3 Sampling and analyses

Oxygen uptake measurements were based on O_2 depletion in the enclosed overlying water. Oxygen concentration was determined by an optical fiber O_2 microoptode with tip diameter less than 0.1 mm (Presens, Germany). In the center of each lid, a 12 mm hole was drilled through which the O_2 microoptode could be inserted. Oxygen concentrations were recorded every hour until they decreased to 80% of the saturation concentration. For each measurement, the O_2 microoptode tip was gently set at 2.0, 1.5, 1.0, and 0.5 cm above the SWI, and at each site 3 values were taken; thus, 12 values were collected each time. The mean of these 12 values represented the O_2 concentration in the core at the measurement time. During the intervals between measurements, the holes were sealed with rubber stoppers. Oxygen uptake was measured once before the introduction of larvae and worms and three times after (Table 2). Oxygen profiles were determined by the same O_2 microoptode, and the insertion of the O_2 microoptode was controlled by a 3-dimensional motorized micromanipulator (Presens, Germany).

Phosphorus flux across the SWI was calculated from the change of soluble reactive phosphorus (SRP) concentration over time in the overlying water. The SRP flux measurements were carried out on the day after the O_2 uptake measurements (Table 2). In each core, 10 mL water was withdrawn by a syringe and replaced with water from the tank. Samples were immediately filtered through 0.45 μm cellulose acetate membranes and frozen until analysis. Samples were collected at 1 hr intervals for 4 hr. The SRP concentrations were corrected for the replacement of water from the tank, which was determined simultaneously.

No pore water was sampled before the introduction of larvae and worms, and it was extracted 3 times after the introduction of organisms (Table 2). At each time, 1 mL of pore water was extracted using a 5-mL medical syringe through each Rhizon sampler. All samples were acidified using hydrochloric acid with pH < 2, then frozen for analysis. At the end of this experiment (Table 2), one sediment core in each treatment was sliced into 3-cm intervals to quantify the distribution of worms and larvae in sediment.

The SRP in overlying water and the SRP and Fe(II) in pore water were measured with a UV-Vis spectrophotometer (Shimadu UV-2445, Japan). The molybdenum blue method was used for SRP (Murphy and Riley, 1962) and the ferrozine method was used for Fe(II) (Stookey, 1970). Sediment particle size was measured using a Mastersizer 2000 Laser Size Analyzer (Malvern Co., UK). Sediment water content was calculated based on the weight loss after drying fresh sediment to a constant weight at 60°C. The

loss on ignition (LOI) was determined by calculating the weight loss after heating sediment samples to 550°C for 5 hr. The determination of phosphorus, iron, calcium, manganese, and aluminum in sediment were completed using inductively coupled plasma-atomic emission spectrometry (ICP-AES, Perkin-Elmer DV4300, USA) after microwave-assisted acid digestion (Yin et al., 2008). All analyses were completed within ten days.

1.4 Calculation and statistical analysis

The concentration of SRP was corrected based on the following Eq. (1):

$$C_i' = C_i + (C_{i-1}' - C_0) \times V_0/V \quad (1)$$

where, C_i' (μmol/L) is the corrected value of SRP concentration at i ($\geqslant 2$) time, C_i (μmol/L) is the determined SRP concentration at i ($\geqslant 1$) time, C_0 (μmol/L) is SRP concentration of water from tank for replacement, V (L) and V_0 (L) are the volumes of overlying water in the microcosm and the sampled water for determination, respectively.

$$F = k \times V/A \quad (2)$$

where, F (μmol/(m^2·hr)) indicates O_2 uptake rate or SRP flux, k (μmol/(L·hr)) is the slope of the linear regression fit to the gathered O_2 (SRP) data against time, V (L) is the volume of overlying water, and A (m^2) is the area of sediment surface.

The mean and standard deviation of three replicate data were carried out by descriptive statistics. Before the introduction of larvae and worms, the differences of O_2 uptake (day 15) and SRP flux (day 16) among three treatments were tested using one-way analyses of variance (ANOVA). After day 17, the effects of treatment on O_2 uptake and SRP flux in each group were tested using one-way repeated measures ANOVA (RM-ANOVA) with time as the repeated factor. If significant difference was determined, Tukey's post-hoc test was used to detect which treatments differed. For the variables of Fe(II) and SRP in pore water, we used a two-way RM-ANOVA to detect differences among treatments and depths, with time as the repeated factor (day 22, 29, and 36). If differences were determined, Tukey's post-hoc test was also used to define which treatments differed. All statistical analyses were conducted using SPSS 13.0 software (SPSS, USA).

2 Results

2.1 General observation

Larvae dug into sediment then built galleries for their living. The diameter of galleries was about 2 mm. Once they finished digging their holes, larvae occasionally moved part of their bodies out of the galleries and then went back. These movements increased the influx of overlying oxygenated water into the sediment and oxidation of the dug galleries (shown in brown, and verified by O_2 profiles in Fig. 2). Larvae also pumped water out of the tubes to irrigate fresh overlying water. Red-brown secretion was observed on sediment surface in larvae treatment,

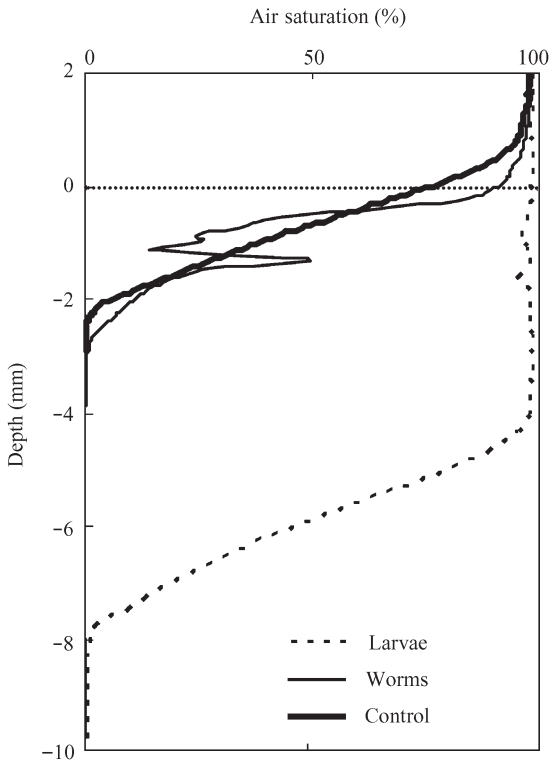

Fig. 2 Oxygen profiles in different sediments. The profiles of invertebrates were detected in the holes or at fecal pellet deposition sites caused by larvae and worms. The horizontal dashed line at 0 mm depth indicates the SWI.

and it increased with time. No fecal pellet of larvae was examined on sediment surface. Worms burrowed into the sediment and deposited fecal pellets onto the sediment surface, but the activities of worms caused no visually-oxidized galleries. More and more fecal pellets of worms gathered on sediment surface during the course of the experiment. No signs of burrowing were observed in the control microcosms. At the end of this experiment, 24 larvae and 94 worms were recovered from the sliced sediment cores. The gallery holes of larvae were observed in the top 6 cm sediment, and all recovered larvae also inhabited the top 6 cm of the sediment, with 90% in the first 3 cm. Of the worms, 94% lived in the upper 6 cm of the sediment.

2.2 Oxygen uptake rates and penetration

Typical O_2 profiles indicated that oxygen penetration in the control treatment was merely 2.5 mm (Fig. 2). The activity of worms changed O_2 distribution pattern but did not dramatically increase O_2 penetration depth compared to the control treatment. However, larvae led to deeper O_2 penetration than that in worms and control treatments. Before the introduction of worms and larvae, O_2 uptake rates of the different treatment microcosms ranged from (579 ± 45) to (588 ± 70) μmol/(m^2·hr), while no difference was detected (one-way ANOVA, treatment effect, $p = 0.97$) (Fig. 3a). The appearance of larvae and worms enhanced sediment O_2 uptake (one-way RM-ANOVA, treatment effect, $p = 0.042$) (Fig. 3b). For specific benthic animals, larvae significantly increased O_2 uptake compared to the

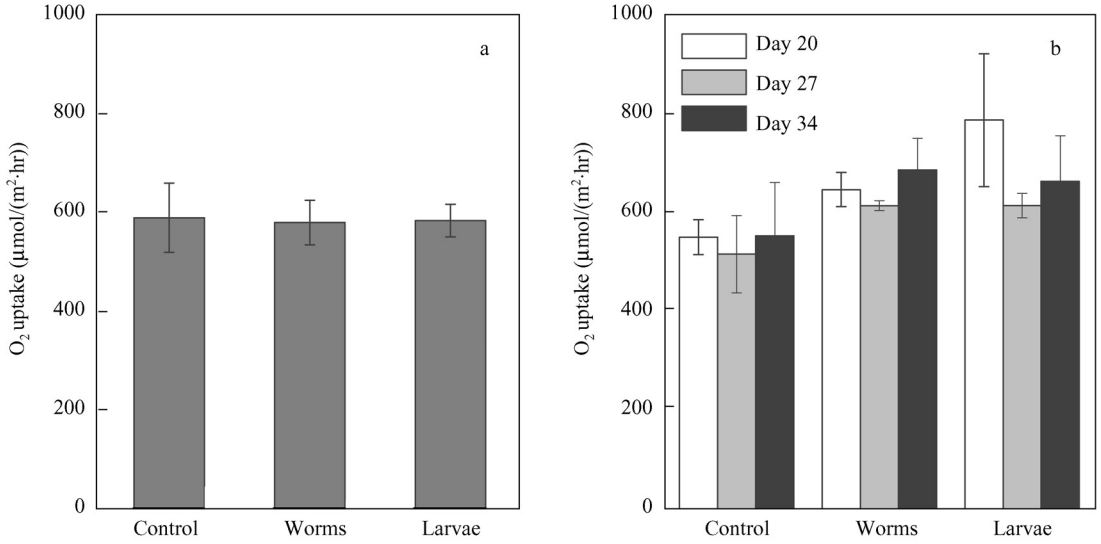

Fig. 3 Oxygen uptake measured before (a, day 15) and after (b, day 20, 27, and 34) the introduction of worms and larvae. All results are expressed as means +/- SD (n = 3).

control treatment (Tukey's HSD test, p = 0.025), while worms created no significant difference relative to the control (Tukey's HSD test, p = 0.080), and larvae treatment (Tukey's HSD test, p = 0.62). Oxygen uptake remained virtually constant during the whole experiment (one-way RM-ANOVA, time effect, p = 0.085).

2.3 SRP fluxes

On day 16, no difference in SRP flux from sediment was detected among the different treatments (one-way ANOVA, treatment effect, p = 0.88) (Fig. 4a). The emergence of worms and larvae decreased SRP release from sediment (one-way RM-ANOVA, treatment effect, p = 0.0070) (Fig. 4b). More specifically, larvae did not significantly affect SRP release (Tukey's HSD test, p = 0.24), while worms significantly inhibited SRP release compared to the control treatment (Tukey's HSD test, p = 0.0060) and larvae treatment (Tukey's HSD test, p = 0.045). SRP release rates fluctuated significantly over time (one-way RM-ANOVA, time effect, $p < 0.001$).

2.4 Fe(II) in pore water

In the control treatment, Fe(II) in the pore water increased with depth in the top 2 cm and then decreased at greater depths (Fig. 5, upper panel). Ferrous iron profiles revealed significant differences among depths (two-way RM-ANOVA, $p < 0.001$). The emergence of worms and larvae significantly decreased Fe(II) in sediment pore water (two-way RM-ANOVA, $p < 0.001$, treatment effect). Compared with the control treatment, both larvae and worms significantly decreased Fe(II) concentration (Tukey's HSD test, $p < 0.001$ for larvae and p = 0.0027

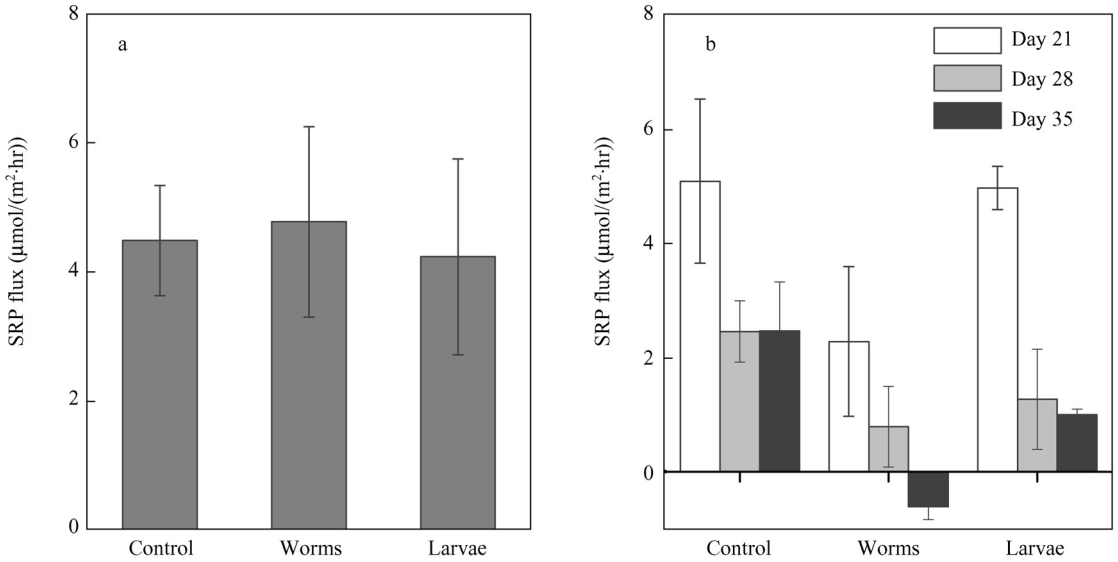

Fig. 4 SRP flux across the SWI measured before (a, day 16) and after (b, day 21, 28, and 35) the introduction of worms and larvae. All results are expressed as means ± SD (n = 3). Positive values indicate SRP release from the sediment to the overlying water, and negative values indicate SRP movement from the overlying water to the sediment.

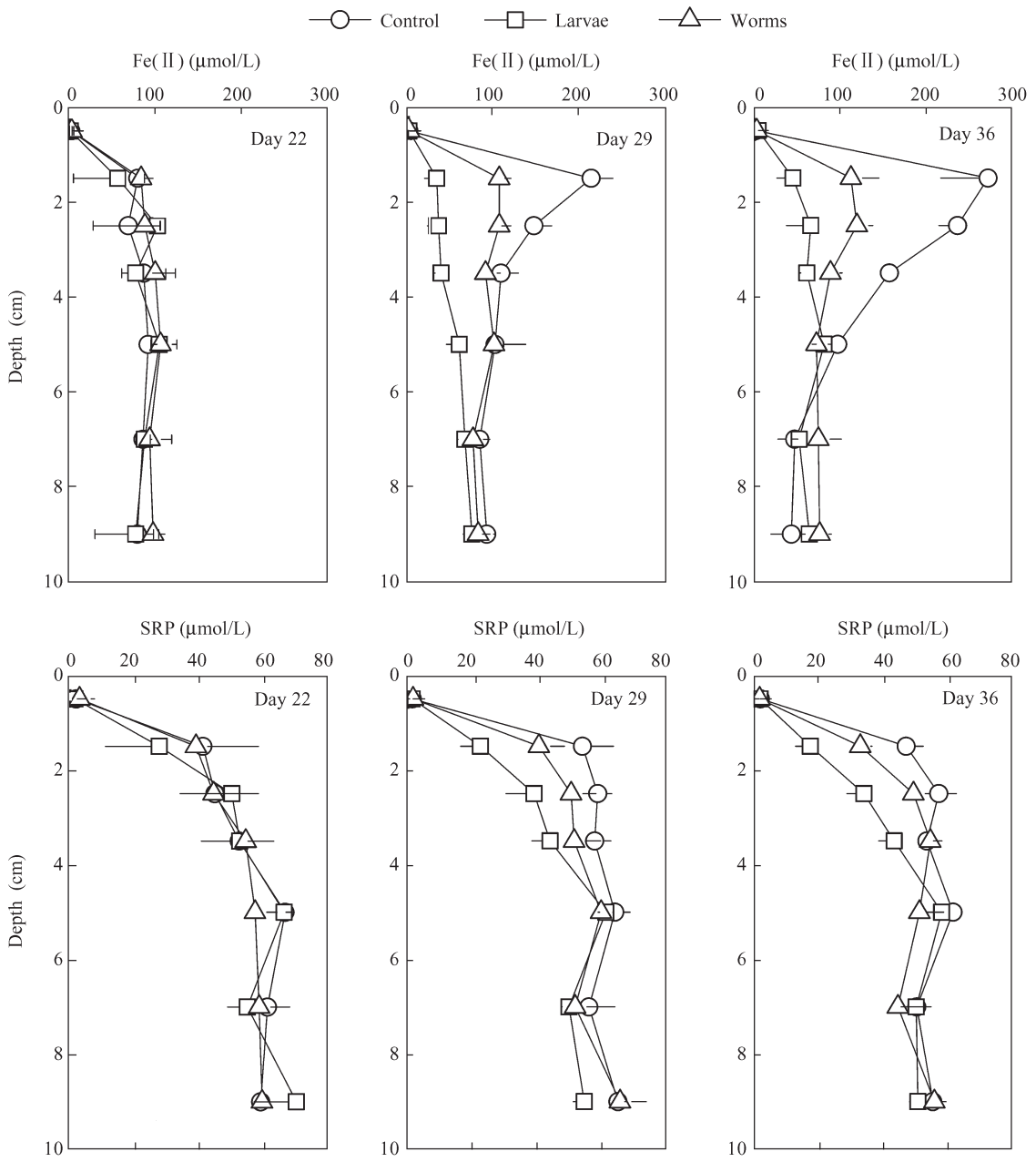

Fig. 5 Ferrous iron (upper panel) and SRP (lower panel) profiles in pore water sampled on day 22, day 29, and day 36 in different treatments. The results are expressed as means ± SD (n = 3) to keep the chart concise.

for worms). The effect of worms in decreasing pore water Fe(II) concentration was notably smaller than larvae (Tukey's HSD test, $p < 0.001$). Successive measurements on the three days also indicated that pore water Fe(II) changed over time (two-way RM-ANOVA, time effect, $p = 0.035$).

2.5 SRP in pore water

Pore water SRP of the control treatment increased with depth to 5 cm, and then remained constant (Fig. 5, lower panel). The pore water SRP profiles revealed significant differences among depths (two-way RM-ANOVA, depth effect, $p < 0.001$). Organisms greatly altered SRP profiles (two-way RM-ANOVA, treatment effect, $p = 0.014$). Larvae significantly decreased the SRP concentration (Tukey's HSD test, $p < 0.001$) while the effects of worms were not significant (Tukey's HSD test, $p = 0.21$). There was also no detectable difference between larvae and worms treatments (Tukey's HSD test, $p = 0.082$). The pore water measurements in the three days showed that SRP also significantly fluctuated over time (two-way RM-ANOVA, time effect, $p < 0.001$).

3 Discussion

Some species of Chironomidae larvae (e.g., *Chironomidae plumosus*) have been reported as gallery-diffusers that build U or J shaped tubes from the sediment surface into deep anoxic sediment (McLachlan and McLachlan, 1976; McLachlan, 1977). The activities and habits of *Tanypus chinesis* were less known. The result in our experiment indicates they dug galleries up to 6 cm in sediment

depth. Larvae ingest sediment bacteria and phytoplankton (Walshe, 1947). The undulations of larvae irrigate fresh water through the tubes, replenishing oxygen and flushing out metabolites and carbon dioxide (Pinder, 1995). Larvae increased O_2 penetration in sediment compared to the control and worms treatments (Fig. 2). The O_2 profiles may not reflect the whole situation in the galleries, as the galleries were not as vertical as the insertion of the O_2 microoptode. However, it indeed identified that the larvae galleries were rich in O_2. Imported O_2 diffuses through the burrow walls into the surrounding sediment, resulting in oxidized zones around the tubes. The oxidation of burrow walls increased the oxic-anoxic interface and the volume of oxic sediment, and changed the redox-sensitive Fe(II) profiles in the pore water (Matisoff et al., 1985). The oxidation of Fe(II) produced Fe(III) oxyhydroxides that adsorbed SRP from pore water, thus decreasing SRP in pore water (Fig. 5). The alteration of pore water SRP and Fe(II) was accordant to the location of larvae that were located in the top 6 cm of sediment, with most in the first 3 cm of sediment.

As upward-conveyors, worms burrow into the deep sediment, ingest anoxic sediment, and defecate onto the sediment surface (Davis, 1974; Kaster et al., 1984). Their respiratory irrigation is mediated through the undulating movement of the posterior end (Andersson et al., 1988). The undulation of worms generates advective movement of oxic sediment particles around them from the sediment surface to the bottom of their feeding zone (François et al., 1997; Gerino et al., 2003). The activities of worms increased sediment water content and sediment mixing (Davis, 1974; Fukuhara, 1987), which provided a large quantity of electron acceptors and decreased Fe(II) and SRP concentrations in the sediment (Fig. 5). The alteration of Fe(II) and SRP profiles indicated that worms were active in the upper 4 cm in the present study (Fig. 5), which was accordant to most of them lived in the top 6 cm sediment in the present experiment and their greatest feeding occurred at a sediment depth of 3 to 4 cm (Davis, 1974).

Many processes are relevant to SRP flux across the SWI in bioturbated sediment. Bioturbation increases diffusive interface and advection movement of SRP in pore water and overlying water, which is prone to stimulate SRP release. In addition, the metabolisms of benthic animals evacuate phosphorus into the pore water and overlying water. However, the oxidation of anoxic sediment adsorbs SRP from the pore water and overlying water, which decreases SRP release from sediment (Matisoff et al., 1985; Tuominen et al., 1999; Lewandowski and Hupfer, 2005). Therefore, SRP flux across the SWI is a mixing result of the above-mentioned processes. Both worms and larvae decreased SRP release in this microcosm simulation study, which is contrary to the well-accepted opinion that benthic animals increase phosphorus release from sediment (Granéli, 1979; Andersson, 1988; Hansen et al., 1998; Mermillod-Blondin et al., 2005). However, similar decreased phosphorus releases across the SWI have also been reported (Andersen and Jensen, 1991; Mortimer et al., 1999; Lewandowski and Hupfer, 2005). Ferrous iron is believed to play a key role in explaining the different results. In iron-rich sediment, macroinvertebrates inhibited phosphorus release by the high phosphorus coprecipitation capacity of Fe(III) oxyhydroxides (Lewandowski and Hupfer, 2005). The pore water Fe(II) profiles indicated that the sediment in our experiment was also rich in ferrous iron, and the activity of benthic animals indeed reduced Fe(II) concentration. The activities of worms and larvae also release Fe(II) that exits in the form of Fe(II) sulfide by oxidizing sulfide, that released Fe(II) may diffuses into oxic zones where it is oxidized and precipitates as Fe(III) oxyhydroxides, and the other part may precipitate as ferrous phosphates such as $Fe_3(PO_4)_2{\cdot}8H_2O$ (Gächter and Müller, 2003; Lewandowski and Hupfer, 2005). The production of a large quantity of Fe(III) oxyhydroxides adsorbed SRP from the pore water or overlying water, which exceeded the release effects caused by other processes, and thus inhibited SRP release was observed. The sediment from the same site also adsorbed SRP from overlying water under hydrodynamic processes, and freshly produced Fe(III) oxyhydroxides under hydrodynamic processes that adsorbed SRP was also believed as a key factor (You, 2007).

Although worms did not influence sediment pore water as significantly as larvae, they inhibited more SRP release than larvae, even causing the adsorption of SRP from the overlying water to the sediment (Figs. 4 and 5). Their mechanical activities are responsible for the result. The holes of larvae galleries were about 2 mm in diameter, and the surrounding oxidized zone extended to 5–6 mm. However, worms constructed no visually-oxidized galleries in the sediment. In the built galleries, larvae irrigate O_2 saturated overlying water into tubes, and flushed out metabolites and carbon dioxide. The burrow flushing caused the oxidation of burrow walls. Thus, larvae were able to influence the chemical properties of the sediment and pore water more obviously. Larvae seldom dug new galleries when they inhibited in built galleries. However, worms continuously move sediment particles through their ingestion and defecation. More and more fecal pellets of worms were gathered on sediment surface in our experiment, which was accordant to the published papers (Davis, 1974; Lewandowski and Hupfer, 2005; Mermillod-Blondin, 2005). A previous study revealed that the defecation rate of worms (*Limnodrilus hoffmeisteri*) was (0.69 ± 0.058) mg dry feces/(hr·mg dry worms) (Kaster et al., 1984), which indicates the ingestion and defecation of worms are intense compared to their own weight. The fecal pellets were continuously expelled on the sediment surface and oxidized by the overlying water, therefore a thin layer rich in Fe(III) oxyhydroxides could be expected. The freshly precipitated Fe(III) oxyhydroxides in the new thin layer adsorbed SRP from the pore water and overlying water (Gunnars et al., 2002). At the same time, the thin layer was constantly refreshed by worms. This is why worms inhibited SRP release more than larvae. The deposited P by worms and larvae exists in the form of iron bound-P (Lewandowski and Hupfer, 2005), this will enhance the retention of P in lake sediment.

Based on the same biomass, worms deposited more P than larvae due to their different mechanical activities. The result indicates the importance of the mechanical activities of different benthic animals on P dynamics across the SWI. This is just a short time microcosm simulation result, the long time effects of larvae and worms on P dynamics across the SWI need to be carried out in the future.

4 Conclusions

Worms changed O_2 distribution pattern but did not increase O_2 penetration depth in sediment, while larvae dramatically increased O_2 penetration depth in sediment. Both worms and larvae decreased Fe(II) and SRP concentrations in pore water, and increased sediment O_2 uptake. The activity worms and larvae inhibited SRP release from the sediment to the overlying water. Larvae dug obvious tubes across oxic-anoxic sediment, which decreased Fe(II) and SRP concentration in the pore water more than worms. Although worms constructed no visible holes in the sediment, they continuously deposited fecal pellets onto the sediment surface. Based on the same biomass, worms inhibited SRP release more than larvae and even caused the adsorption of SRP from the overlying water to the sediment.

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