



Burrowing macroinvertebrates alter phosphorus dynamics in drainage ditch sediments

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Abstract

Consumptive and nonconsumptive interactions of benthic organisms play important roles in regulating rates of ecosystem services such as nutrient cycling in freshwater ecosystems. Studies of macroinvertebrate communities in drainage ditches have focused on documenting the biodiversity supported by these human-altered environments, but none have explored the ecosystem functions provided by those biological communities in ditches. Bioturbation by burrowing benthic invertebrates in ditch sediments may change rates of biogeochemical processes controlling fluxes of nutrients across the sediment–water interface. We used microcosms to test the effect of four species of burrowing invertebrates (Naididae: *Ilyodrilus templetoni*, Naididae: *Limnodrilus hoffmeisteri*, Gammaridae: *Crangonyx* sp., Chironomidae: *Chironomus decorus* S.G.) on exchanges of phosphorus between sediment and water from a drainage ditch. These effects were measured across a range of sediment and water characteristics, representing variability within ditches. All species reduced concentrations of P (as molybdenum-reactive phosphorus) in the surface water relative to controls under conditions where sediment porewater was not likely to contain higher concentrations of P than surface water. Decreases in P concentration were linked to changes in the sediment redox potential and water pH. Two species (*L. hoffmeisteri* and *C. decorus*) increased P concentrations under conditions where sediment porewater likely had higher concentrations of P than surface water. Increases in P concentrations were likely due to physical changes to the sediment from burrowing, and increased transport of dissolved P from sediment porewater to surface waters. Management of ditches should consider effects of burrowing benthic invertebrates on physical and biogeochemical processes at the sediment–water interface. Habitat manipulation in ditches could lead to unpredicted changes in nutrient dynamics mediated by changes to the burrowing benthic invertebrate community.

Keywords Agriculture · Pollution · Nutrient cycling · Eutrophication · Invertebrates

Introduction

Reducing the delivery of phosphorus (P) from agricultural lands to aquatic habitats is a primary concern for reducing eutrophication of inland and coastal waters (Boesch et al. 2001; Hagy et al. 2004; Russell et al. 2008). In many areas with intensive agricultural land-use, networks of drainage ditches function as headwaters where excess nutrients can enter the watershed (Sims et al. 1998; Blann et al. 2009; Smith et al. 2015). Drainage ditch networks are typically a combination of straightened, channelized streams and man-made channels that increase water conveyance from

naturally poorly drained soils. Biological, chemical, and physical processes occurring at the sediment–water interface of these ditches have been studied for their ability to immobilize P in water draining from farms (Nguyen and Sukias 2002; Needelman et al. 2007a; Kröger et al. 2008). Drainage ditches also support communities of benthic invertebrates, many of which burrow within the sediment–water interface (Hill et al. 2016; Leslie and Lamp 2017). Current drainage ditch research and management practices do not take into account any effects that aquatic invertebrates have on P uptake and release by ditch sediments. In this study, we investigate the effect that bioturbation by benthic invertebrates has on P dynamics over a range of environmental conditions in drainage ditch sediments.

A history of constant manure application can produce high background concentrations of P in agricultural soils, which increases the mobility of P in subsurface water

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draining from these lands (Kleinman et al. 2007). Chemical, physical, and biological processes occurring along the flow-path of water draining from agricultural lands into ditches determine whether excess nutrients are delivered to downstream waters. Gradients of oxidation–reduction potential that develop across the sediment–water interface provide a highly reactive site for chemical transformations in water that discharges into drainage ditches (Needelman et al. 2007b). P can be adsorbed to surfaces such as iron and aluminum oxides where it can be easily exchanged with P in solution (Mackie 2001). Sharp redox gradients often exist at the surface of drainage ditch sediments, and anaerobic conditions may exist close to the surface where iron oxide coatings can be reduced, releasing adsorbed P (Venterink et al. 2002; Leslie et al. 2012). Reduced iron may become oxidized at the surface, forming poorly crystalline ferrihydrite, which may adsorb some of the released P (Axt and Walbridge 1999). Phosphorus can form complexes with iron, aluminum, or calcium and precipitate as secondary minerals (Dunne and Reddy 2005). Microbial biofilms and plant roots can take up some forms of reactive P directly from solution where it can be stored as microbial and plant biomass (Kern-Jespersen and Henze 1993; Huett et al. 2005; Huang et al. 2011).

As a part of agricultural infrastructure, some ditches are exempt from regulation as natural bodies of water by the United States Environmental Protection Agency (Grumbles 1991, EPA 2015). Nevertheless, ditches do provide aquatic habitat to many different species of plants and animals, and ditches may also function as significant sources of biodiversity as the only non-cropped areas within intensely agricultural landscapes (Herzon and Helenius 2008; Verdonshot et al. 2011). Ditches can also function as mitigation wetlands, where biogeochemical processes occurring primarily within ditch sediment improve the quality of water draining from agricultural fields (Hill and Robinson 2012; Kröger et al. 2013; Osborne et al. 2013). Few studies to date have recognized the potential for the macroscopic biological communities within ditches to have an effect on beneficial biogeochemical processes occurring within sediments (but see Needelman et al. 2007b; Vaughan et al. 2008). Physical disturbance of sediments by aquatic organisms, or bioturbation, may play an important role in regulating exchanges of P between the sediment and surface water in drainage ditches.

Bioturbation by benthic invertebrates alters rates of nutrient cycling in streams and other bodies of water (Meysman et al. 2006; Michaud et al. 2006; Chaffin and Kane 2010). The effects of bioturbation on ecosystem processes can be complex, with strong effects of environmental context and variability between species of the same functional group (Mermillod-Blondin et al. 2001; Mermillod-Blondin and Rosenberg 2006; Michaud et al. 2006; Roskosch et al. 2012). Bioturbation by benthic invertebrates can increase

(Mermillod-Blondin et al. 2005; Chaffin and Kane 2010), decrease (Lewandowski et al. 2007), or have no effect (Mermillod-Blondin et al. 2005) on P movement from sediment to water, depending on the type of burrowing and environmental conditions. The exact effect that bioturbation has on P movement likely depends on the sediment, porewater, and surface water chemistry, as well as the nature of mineral particle redistribution caused by the burrowing organisms.

Burrowing by different species of macroinvertebrates creates different types of disturbance within sediments, which may have different effects on specific sediment-phosphorus processes. Burrows may create preferential flow paths that keep pore water from interacting with some reactive surfaces within the sediment (Nogaro et al. 2006). Irrigation of burrows may alter redox potentials near the surface by bringing water carrying dissolved oxygen into subsurface sediment layers (Hunting et al. 2012). Altered sediment redox potentials could oxidize reduced iron, which can chemically bind available P. Deposit-feeding organisms may redistribute clay-sized particles through selective feeding, and may directly alter microbial biomass through grazing (McCall and Fisher 1980). Differences in the physical effects that different species have on the sediment have been used to classify burrowers into functional groups based on the nature of the mechanical disruption they create (Gerino et al. 2003). *Conveyors* are deposit-feeding organisms that ingest sediment particles at depth and deposit egested sediment at the surface, creating a net-upward movement of sediment. *Gallery-diffusers* occupy burrows that are kept aerated by moving currents of water through the tunnels. *Biodiffusers* are organisms that do not necessarily construct defined burrows, but live or forage within surface sediments, causing surface sediments to be randomly scattered and mixed. Burrowing groups such as gallery diffusers and biodiffusers that transport oxygenated surface waters below the sediment surface are generally expected to increase the redox potential of those sediment layers. Alternatively, burrowing groups that transport sediment porewater to the surface are expected to increase surface P concentrations as P released in anaerobic sediment layers is transported to the surface. Species belonging to each of these functional groups are common and highly abundant in drainage ditch habitats (Leslie and Lamp 2017).

Agricultural drainage ditches are dynamic habitats that show a range of environmental conditions across sites and within sites over time (Herzon and Helenius 2008; Leslie et al. 2012; Leslie and Lamp 2017). Ditches can range from small, hand-dug trenches that may only hold water during storm events to large perennial conveyances that receive water from many smaller ditches. Differences in sediment structure can develop between perennial and intermittent ditches. Granular sediment structure develops in intermittent ditches from cycles of wetting and drying forming

aggregates of sediment particles while sediment in perennial ditches tends to remain as unconsolidated, single-grained mineral particles (Vaughan et al. 2008). Flow velocities may vary between relatively high flows in ditches constructed from existing stream channels to alternating periods of stagnation and flow in created channels. Differences in sediment physical characteristics and hydrology may mediate the effect that benthic invertebrates have on sediment chemistry through bioturbation.

The goal of this study was to determine the effects that different types of macroinvertebrate-caused bioturbation have on P exchange between ditch sediment and water across a range of environmental conditions. Our hypothesis was that burrowing invertebrates alter the exchange of P between the sediment and surface water. Burrowers likely alter P exchange by altering the physical structure of the sediment, disrupting chemical gradients between anaerobic sediment and aerobic surface water, and having direct effects on the microbial biomass through grazing. Microcosms were used to test the effect of different functional groups of burrowers on P exchange between sediment and surface water, using different species of macroinvertebrates to produce different types of bioturbation. We also hypothesized that physical and chemical changes made to the sediment by burrowing invertebrates would have different effects on P dynamics under different environmental conditions. Therefore, sediment was manipulated to simulate physical differences that exist between intermittent and perennial ditches and water was manipulated to simulate different hydrologic conditions that occur in drainage ditches.

Methods

Four species of burrowing invertebrates were used in four separate experiments, representing different modes of burrowing. Species were chosen to reflect the most common and abundant burrowers found from surveys of drainage ditches in MD (Leslie and Lamp 2017). Experiments 1 and 2 used the two aquatic worm species (Tubificida: Naididae) *Ilyodrilus templetoni* and *Limnodrilus hoffmeisteri*, respectively. Both species feed on silt and clay-size particles at depth and egest feces at the sediment's surface and represent the *conveyor* bioturbation functional group. Experiment 3 used the freshwater crustacean *Crangonyx* sp. (Amphipoda: Crangonyctidae). Amphipods such as *Crangonyx* do not build defined burrows, and instead randomly scatter surface sediments as a result of feeding on detritus within the surface of the sediment–water interface. They represent the *biodiffuser* bioturbation functional group. Experiment 4 used the aquatic larvae of the midge *Chironomus decorus* S.G. (Diptera: Chironomidae). Larvae of midges like *C. decorus* build U-shaped

burrows within aquatic sediments, and keep those burrows aerated as they feed on small detritus and suspended microbes. They represent the *gallery-diffuser* bioturbation functional group. Each species was tested in a microcosm, constructed to allow aquatic macroinvertebrates to burrow within a layer of anaerobic, aquatic sediments with a layer of oxygenated water above and water moving through the sediment layer to be discharged at the surface, resembling conditions in Maryland drainage ditches. The four experiments were each completely randomized designs with a crossed factorial treatment structure. Each experiment had two factors under investigation (sediment size and burrowing invertebrates) and each factor had two levels (coarse/fine, present/absent, respectively) for a total of four treatment combinations per experiment and five replicates of each. Samples for water/sediment measurements (P and redox) were collected at five times during each experiment, corresponding to key events in the microcosms as described below.

Sediments

Sediment was collected from a single perennial ditch located in Caroline County, on Maryland's Eastern Shore. This ditch is a tributary of Mason Branch, within the Choptank River watershed, and was bordered by maize (*Zea mays*) on one side and soybean (*Glycine max*) on the other. For each experiment, approximately 20 L of surface sediments (approximately 15 cm deep) were randomly collected on separate occasions between 14 Oct 2013 and 4 Feb 2014 prior to each microcosm experiment. Sediments were homogenized, removing large pieces of organic matter, and dried in an oven at 60 °C for 72 h to defaunate sediments. Dry sediment was crushed and sieved to two different sizes. Sediments were first passed through a 4 mm sieve, which gave a product with coarse aggregates of soil material approximating the structure found in small, intermittent ditches that have actively developing soil structure. A subset of those coarse sediments were then crushed with a mortar and pestle, and passed through a 500 µm sieve. This fine sediment approximates the loose, unconsolidated sediments found in larger perennial ditches that do not often dry or develop soil structure.

For each experiment, a subset of sediment was analyzed for pH, organic matter (percent mass lost on ignition), ammonium-oxalate extractable P, Al, and Fe, and mineral particle size composition by the University of Delaware Soils Testing Laboratory (Table 1). Linear mixed models were used to determine whether there were consistent differences in physical and chemical qualities of the two sediment size classes while accounting for differences between experiments as a random factor.

Table 1 Characteristics of sediment used for each experiment

Experiment	Sediment	Texture	pH	O.M. (%)	P (g/kg)	Al (g/kg)	Fe (g/kg)
1. <i>I. templetoni</i>	Coarse	Loam	4.6	22.6	0.52	0.91	6.12
	Fine	Loam	4.6	22.6	0.56	0.97	6.46
2. <i>L. hoffmeisteri</i>	Coarse	Loam	4.5	23.1	0.48	0.84	5.28
	Fine	Loam	4.4	22.9	0.62	1.09	7.08
3. <i>Crangonyx</i> sp	Coarse	Loam	4.5	22.9	0.54	0.69	5.88
	Fine	Loam	4.5	22.2	0.69	0.97	7.41
4. <i>C. decorus</i>	Coarse	Sandy loam	4.4	23.5	0.43	0.68	4.98
	Fine	Loam	4.5	23.1	0.52	0.88	6.00

Microcosms

Microcosms were constructed of 600 mL glass beakers filled with 150 g of acid-washed pea gravel (diameter 0.5–1 cm) and 100 g of either fine or coarse prepared sediments. For the first experiment, microcosms were filled with dechlorinated tap water and subsequent experiments used standard, synthetic, moderately hard freshwater (EPA 2002). Microcosms had a hydraulic connection to a 200 mL reservoir beaker through aquarium tubing embedded within the gravel layer. Tubing was housed within a section of 9.5 mm diameter PVC tubing, attached to the side of the 600 mL beaker with a metal clip. By raising the reservoir so that its water level was above that of the microcosm, the difference in hydraulic head allowed water to move through the aquarium tubing and through the sediments, to be discharged at the surface of the microcosm.

For each experiment, 20 microcosms were housed in an environmental chamber (20 °C, and a 14:10 h day/night cycle). Surface water was kept oxygenated by bubbling air through a Pasteur pipette inserted just below the surface of the water. Each pipette was connected via a section of aquarium tubing to a central manifold, pressurized by an electric air pump. Valves located at each connection point controlled air flow to ensure that turbulence from bubbling did not disturb sediments within the microcosms. Water levels in the microcosms were examined daily and topped off with deionized water to replace water lost to evaporation. Microcosms were wrapped in aluminum foil to block light from reaching the sediments and stimulating photosynthesis below the sediment surface. After the first experiment, each microcosm was enclosed in a clear plastic cylinder with the top covered in insect netting to prevent unwanted insects from colonizing the microcosms over the course of the experiment.

Invertebrates

Four species of burrowing invertebrates were used in four separate experiments, representing different modes of burrowing. *I. templetoni* were introduced to microcosms in experiment 1 at a density of 100 individuals per microcosm.

L. hoffmeisteri were introduced to microcosms in experiment 2 at a density of 50 individuals per microcosm. *Crangonyx* sp. were introduced to microcosms in experiment 3 at a density of 8 per microcosm. *C. decorus* were introduced to microcosms in experiment 4 at a density of 10 per microcosm. Densities of macroinvertebrates were chosen to reflect maximum densities observed from surveys of burrowing ditch macroinvertebrates (8,436 *I. templetoni*/m², 10,361 *L. hoffmeisteri*/m², 1,310 *Crangonyx*/m², 34,005 *Chironomus*/m²; Leslie and Lamp 2017). An exception was *C. decorus*, which had a maximum observed density that was an order of magnitude higher than the other three species, which was very rarely measured in the field and therefore the mean observed density was used for experiments (1203 *Chironomus*/m²).

Invertebrates were collected at different dates from the same ditch where sediments were collected, as well as some nearby ditches. On each sampling date, organisms were collected using a D-frame net (500 µm mesh, 0.05 m² opening) to sweep through the ditches. All material was returned to the laboratory, where it was stored at 20 °C and kept aerated to allow organisms to acclimate to temperature conditions of the environmental chamber. Just prior to adding organisms to microcosms, samples were rinsed in a 500 µm sieve and organisms were collected without magnification.

Water and redox measurements

Samples of surface water (~ 100 mL) were taken from microcosms using a 60 mL syringe fitted with a short length (~ 15 cm) of aquarium tubing. Water was carefully siphoned from just below the surface of the water level within the microcosm to avoid disturbing the sediments below. The volume of water removed was replaced with dechlorinated tap water or synthetic freshwater directly to the microcosm, and not through the reservoir. Water samples were vacuum-filtered through Whatmann #1 filter paper and stored in 125 mL polyethylene bottles at – 20 °C prior to analysis. Concentration of molybdenum-reactive phosphorus (P) was determined from a 50 mL aliquot of

the total sample using the ascorbic acid method and a spectrophotometer (Spectronic 20D; Eaton et al. 1995).

Water samples were taken at five points during the course of each experiment (denoted as A–E) corresponding to different environmental conditions within the microcosms. The first two samples were taken to characterize microcosm conditions prior to addition of burrowing invertebrates. The first water sample (measurement A) was taken within a day of the construction of the microcosms (0–1 days after start) as a measure of the concentration of P extracted by the water moving through the sediment layer. The second sample (measurement B) was taken about a week after the construction of the microcosms (6–10 days after start) to measure the change in concentration of P related to development of anaerobic conditions, and was also the time at which burrowing invertebrates were added to half of the microcosms. The last three samples were taken to characterize the effect of burrowing invertebrates on surface water P concentrations, and the interaction of that effect with sediment size. The third sample (measurement C) was taken about 2 weeks after the introduction of the burrowing invertebrates (19–22 days after start, 10–15 days after introduction of burrowers) to measure the new phosphorus concentration that resulted from bioturbation. The fourth water sample (measurement D) was taken shortly after the third (21–27 days after start, 2–5 days after measurement C), and was preceded by a complete water change in the microcosms with water containing 1.0 mg/L PO_4^{3-} . This concentration was chosen to reflect an above-average concentration that is still commonly observed in drainage ditches during baseflow (Leslie et al. 2012). This water change simulated the subsurface flow and discharge of high-nutrient water that occurs in drainage ditches and was a measure of the capacity of the sediment to rapidly take-up dissolved phosphate through processes such as adsorption. The fifth and final water sample (measurement E) was taken about a week after the water replacement (29–36 days after start, 8–10 days after water replacement) to measure the differential uptake of phosphate from the water as a result of processes that are slower than rapid adsorption.

Redox potential and pH were measured using electrodes inserted into the microcosms. Redox potential was measured from three Pt-tipped microelectrodes embedded into each microcosm just below the sediment surface. Potentials were measured using a hand-held multimeter (Radio Shack model 22–810), modified according to Rabenhorst (2009) with a TL082 dual JFET operational amplifier (Texas Instrument model TL082ACP) and a calomel reference electrode (Accumet model 13-620-259) that was inserted into the surface water of the microcosm. A temperature-specific correction factor of +243 mV was added to each measured potential to convert measures to

be relative to a standard hydrogen electrode (Vepraskas and Faulkner 2001).

Statistical analyses

To determine the effects of sediment size and anaerobic reduction of iron on P release, we compared P concentrations between measurements A and B using linear mixed models with sediment size and time as fixed factors while accounting for differences between experiments and repeated measure of individual microcosms as a random factor.

To determine the effect of bioturbation by burrowing invertebrates and sediment grain size on phosphorus dynamics, we ran separate two-way analysis of variance (ANOVA) for each sampling date using sediment size, burrower presence, and their interaction as explanatory variables. Statistical comparisons were not made between different experiments because of slight differences in experimental set-up (e.g. water source) and sampling schedule. Where there was a significant interaction between burrower presence and sediment size, we used contrasts to test the significance of the burrower effect within each level of sediment size, and sediment size effect within each level of burrower (i.e., we did not test for significant differences between treatment combinations that differed in both factor levels). We used a Bonferroni correction to account for experiment-wide error rate. To determine whether bioturbation by burrowing invertebrates and sediment size had effects on sediment and water chemistry, we ran two-way ANOVAs with the same explanatory variables and pH and mean redox potential as response variables. When significant differences were found in P concentrations between treatments, linear regressions were used to determine whether pH or mean redox potential were significantly related to P concentrations across microcosms.

All analyses were performed using R v 3.4.3 (R Core Team 2016). Linear mixed-effects models were built using the package *nlme* (Pinheiro et al. 2014). ANOVAs were performed using the *car* package (Fox and Weisberg 2011). Matrices for orthogonal contrasts were coded using the package *contrast* (Kuhn et al. 2013). Pairwise means comparisons were performed using the package *multcomp* (Hothorn et al. 2008). Graphics were produced using the package *ggplot2* (Wickham 2009).

Results

Sediments

Most sediment fell into the loam textural class, except for coarse sediment used for the experiment with *C. decorus*, which was sandy loam. Grinding and sieving resulted in fine sediment having fractions of silt 11.8% higher and fractions

of sand 11.8% lower than coarse sediment. Fine sediment contained 0.3% less organic matter than coarse sediment. Fine sediment had higher concentrations of P, Al, and Fe than coarse sediment, though there was no difference in the P saturation ratio (Table 1). There were no significant differences in pH of the two sediment size classes.

Initial P measurements

Across all experiments, there was a significant increase in surface water P concentration between A and B sampling points (Wald- $\chi^2=79.8$; $df=1$; $P<0.001$). The mean P concentration was 0.04 mg/L at measurement A at the onset of the experiment and 0.65 mg/L at measurement B, just prior to addition of burrowing invertebrates. Sediment size had no effect on P concentration at measurements A and B (Wald- $\chi^2<0.01$; $df=1$; $P=0.98$).

P and redox measurements at C-E

Experiment 1 *I. templetoni*. At measurement C (19 days, and 13 days after burrower introduction), there was no effect of sediment size on the mean P concentration, and the effect of burrowers was not significant at an alpha of 0.05 (i.e. $P=0.06$; Fig. 1a). There were no significant differences in P concentration between treatments following P spike at measurement D (21 days). At measurement E (29 days), P concentration was 0.364 mg/L higher in microcosms with coarse sediment than fine sediment ($F_{1,15} = 30.15$; $P<0.001$) and P concentrations were 0.27 mg/L lower in microcosms receiving *I. templetoni* than controls ($F_{1,15} = 18.06$; $P<0.001$) with no significant interaction between factors. There was not a significant linear regression between P concentrations and pH or mean redox potential for sample dates where burrowers had a significant effect on P concentrations.

Burrower and sediment treatments had significant effects on pH and redox potential on different sampling dates (Fig. 4b,c). At 5 days, coarse sediment treatments had lower mean redox potentials than fine sediment ($F_{1,17} = 4.10$; $P=0.059$). At 15 days, there were significant effects of sediment ($F_{1,15} = 5.79$; $P=0.029$), burrowers ($F_{1,15} = 6.93$; $P=0.02$), and their interaction ($F_{1,15} = 5.95$; $P=0.03$) on mean redox potential. Microcosms with *I. templetoni* had lower redox potentials ($t=3.60$; $P=0.005$), but only for the fine sediment treatment. Coarse sediment treatments had lower redox potentials than fine sediment ($t=3.42$; $P=0.01$), but only among no-burrower controls. At 19 d there was a significant effect of *I. templetoni* on redox potential ($F_{1,15} = 8.06$; $P=0.01$), and the interaction between *I. templetoni* and sediment size is almost significant ($F_{1,15} = 3.84$; $P=0.07$). Microcosms with *I. templetoni* have lower redox potentials only in the fine sediment treatments ($t=3.41$; $P=0.01$). There was a significant effect of *I. templetoni* on pH at 29 d,

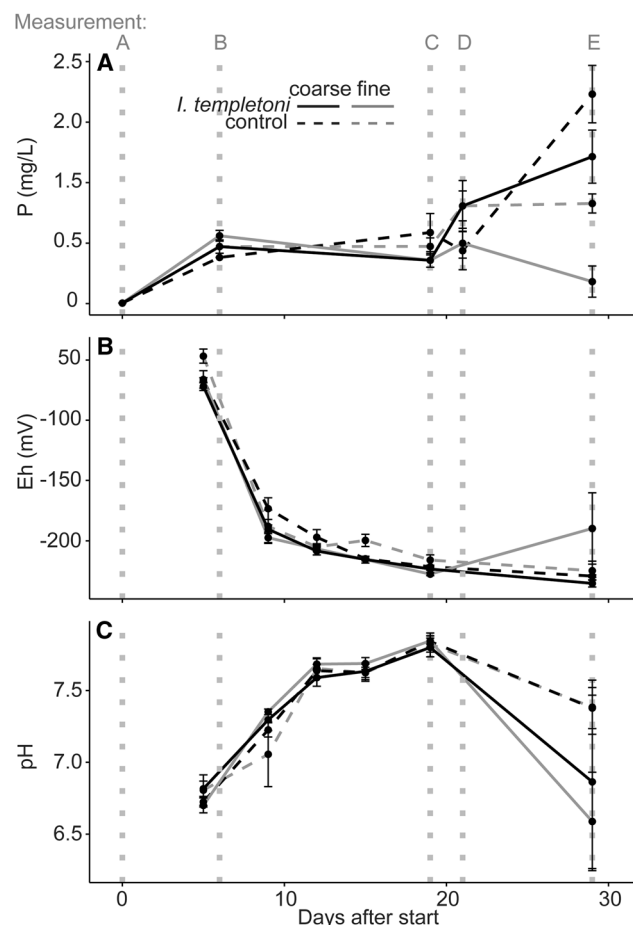


Fig. 1 Response variables measured from experiment 1 (*I. templetoni*—conveyor): **a** P concentration, **b** pH, **c** redox potential. Burrowers were introduced at measurement B

with burrower treatments having a lower pH than controls ($F_{1,15} = 4.36$; $P=0.054$; Fig. 1c).

Experiment 2 *L. hoffmeisteri*. At measurement C (20 d and 10 d after burrower introduction), there was no effect of the burrower treatment on P concentration of surface water, while coarse sediment treatments had P levels 0.473 mg/L higher than fine sediment ($F_{1,16} = 6.03$; $P=0.03$; Fig. 2a). At measurement D (P spike, 22 days), coarse sediment treatments had P concentrations 0.758 mg/L higher than fine sediment ($F_{1,16} = 33.38$; $P<0.001$), and *L. hoffmeisteri* treatments had P concentrations 0.276 mg/L higher than controls ($F_{1,16} = 4.41$; $P=0.052$). Linear regression showed no significant relationship between P concentration and redox potential or pH. At measurement E (29 days), coarse sediment treatments had P concentrations 0.487 mg/L higher than fine sediment ($F_{1,16} = 33.80$; $P<0.001$). The effect of burrowers was reversed with *L. hoffmeisteri* treatments having P concentrations 0.412 mg/L lower than controls ($F_{1,16} = 22.40$; $P<0.001$). Again, there was not a significant relationship between P concentration and redox potential.

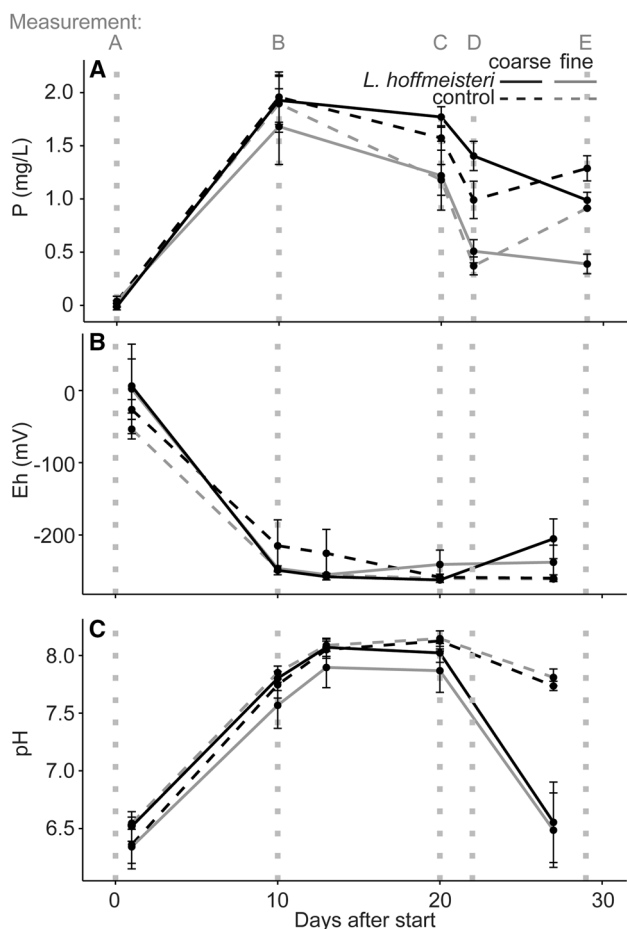


Fig. 2 Response variables measured from experiment 2 (*L. hoffmeisteri*—conveyor): **a** P concentration, **b** pH, **c** redox potential. Burrowers were introduced at measurement B

There was a significant linear relationship between pH and P concentration at 29 days, with higher P concentrations measured in microcosms with higher pH values ($r^2=0.35$; $P=0.01$; Fig. 3). Redox potential was higher in *L. hoffmeisteri* treatments ($F_{1,16} = 4.51$; $P=0.05$) only at the last redox measurement (27 days; Fig. 2b). At 27 days there was a significant effect of *L. hoffmeisteri* on pH, with burrower treatments having lower pH than controls ($F_{1,16} = 27.00$; $P<0.001$; Fig. 2c).

Experiment 3 *Crangonyx sp.* At measurement C (22 days and 15 days after burrower introduction), there was no effect of burrower treatment on P concentrations, but coarse sediment treatments had P concentrations 0.291 mg/L higher than fine sediment ($F_{1,16} = 6.07$; $P=0.03$; Fig. 4a). At measurement D (P spike, 27 days), coarse sediment treatments had P concentrations 0.337 mg/L higher than fine sediment ($F_{1,16} = 16.41$; $P<0.001$), and *Crangonyx* treatments had P 0.169 mg/L than controls ($F_{1,16} = 4.15$; $P=0.059$). P concentrations had a significant relationship with measured redox potentials ($r^2=0.27$; $P=0.02$), with lower P

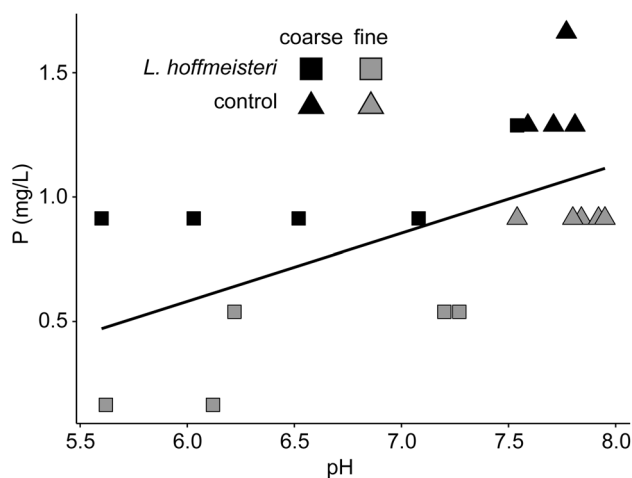


Fig. 3 Experiment 2: Linear relationship between pH and P measured at measurement E (29 d after start); line represents least-squares regression ($r^2=0.35$, $P=0.006$)

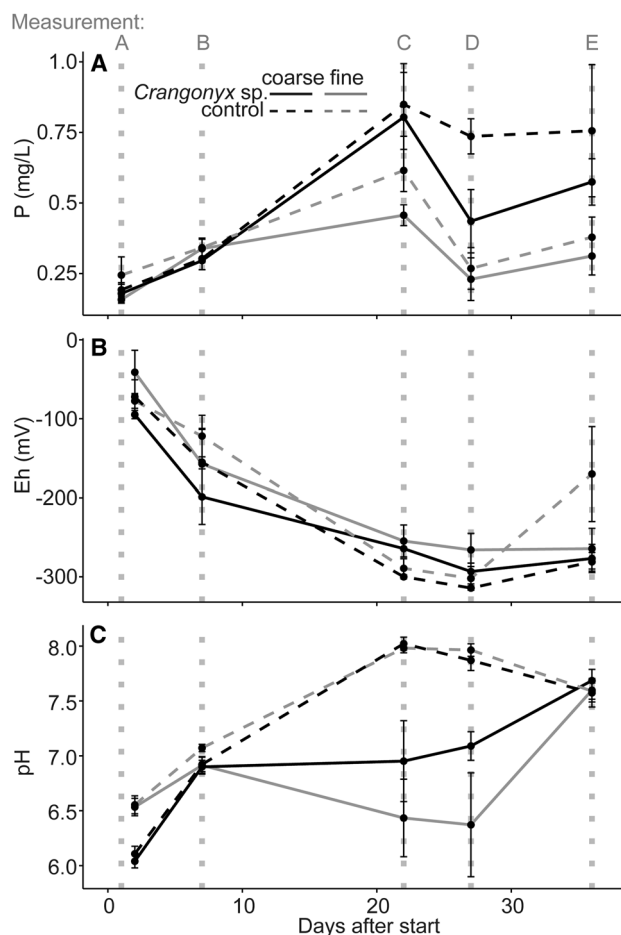


Fig. 4 Response variables measured from experiment 3 (*Crangonyx sp.*—biodiffusor): **a** P concentrations, **b** pH, **c** redox potential. Burrowers were introduced at measurement B

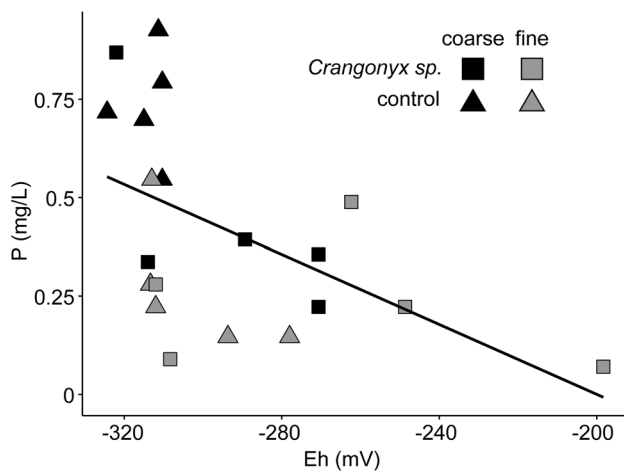


Fig. 5 Experiment 3: Relationship between mean redox potential and P concentration at measurement D (27 days after start); line represents least-squares regression ($r^2=0.27$, $P=0.02$)

concentrations in microcosms with higher redox potentials (Fig. 5). There was no significant linear relationship between pH and P concentration at measurement D. At measurement E (36 days), coarse sediment treatments had P concentrations 0.320 mg/L higher than fine sediment ($F_{1,16} = 5.75$; $P=0.03$) and there was no effect of burrowers on P concentrations. *Crangonyx* had a significant effect on redox potential at 22 d ($F_{1,16} = 7.28$; $P=0.016$) and 27 days ($F_{1,16} = 5.31$; $P=0.04$; Fig. 4b). *Crangonyx* treatments had higher redox potentials than controls on both sampling dates. *Crangonyx* also had a significant effect on pH at 22 days ($F_{1,16} = 25.78$; $P<0.001$) and 27 days ($F_{1,16} = 22.26$; $P<0.001$). At both sampling dates, pH was lower in microcosms with *Crangonyx* than controls (Fig. 4c).

Experiment 4 *C. decorus*. At measurement C (21 days, and 14 days after burrower introduction), there was no effect of sediment size on P concentrations, but a significant effect of burrowers ($F_{1,16} = 13.40$; $P=0.002$) and a significant interaction between the two factors ($F_{1,16} = 6.50$; $P=0.02$; Fig. 6a). Comparisons between burrower treatments within the two types of sediment show that *C. decorus* treatments had P concentrations 2.049 mg/L higher than controls in fine sediment treatments only ($t=4.39$; $P<0.001$). There was no difference in P concentration between coarse sediment treatments with and without *C. decorus*. There was not a significant relationship between P concentration and pH or redox potential. At measurement D (P spike, 23 days), coarse sediment treatments had P concentrations 0.127 mg/L higher than fine sediment ($F_{1,16} = 4.97$; $P=0.041$) and there was no effect of *C. decorus*. At measurement E (33 days), there were significant effects of sediment size ($F_{1,16} = 9.28$; $P=0.01$), *C. decorus* ($F_{1,16} = 16.51$; $P<0.001$), and their

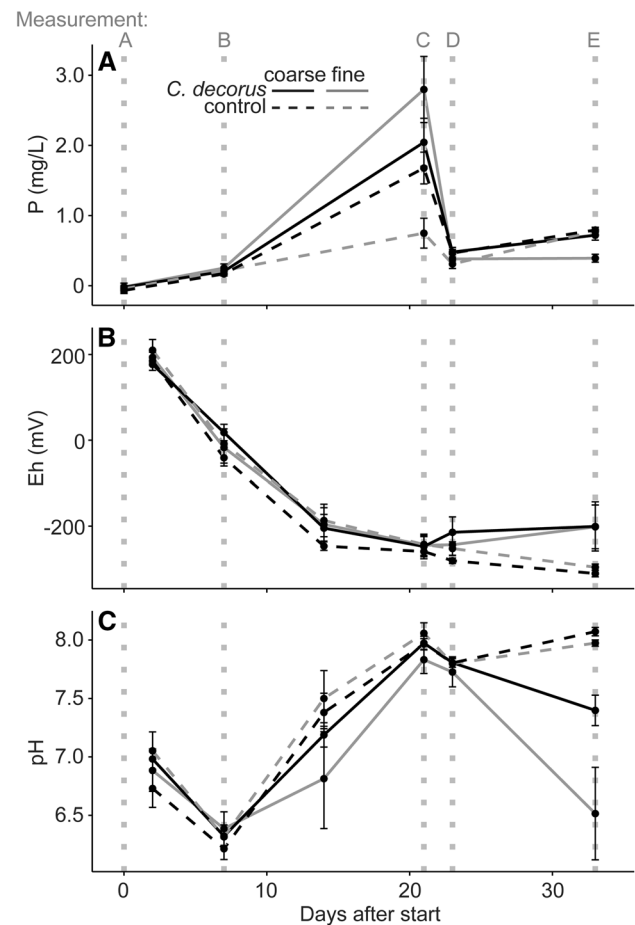


Fig. 6 Response variables measured from experiment 4 (*C. decorus*—gallery-diffuser): **a** P concentrations, **b** pH, **c** redox potential. Burrowers were introduced at measurement B

interaction ($F_{1,16} = 7.60$; $P=0.01$). Within fine sediment treatments, those with *C. decorus* larvae had P concentrations 0.386 mg/L lower than controls ($t=4.82$; $P<0.001$), and within microcosms receiving *C. decorus* larvae, coarse sediment treatments had P concentrations 0.329 mg/L higher than fine sediment ($t=4.10$; $P=0.002$). There was not a significant relationship between P and redox potential, but there was a significant linear relationship between pH and P concentration at the final sample date. Microcosms with lower pH values had lower P concentrations ($r^2=0.40$; $P=0.004$) (Fig. 7). At 33 d, *C. decorus* treatments had higher redox potentials than controls ($F_{1,16} = 6.93$; $P=0.02$). There were also significant effects of burrowers ($F_{1,16} = 34.10$; $P<0.001$), sediment ($F_{1,16} = 6.84$; $P=0.02$), and their interaction ($F_{1,16} = 4.81$; $P=0.05$) on pH at 33 d after start. For both sediment treatments, microcosms with *C. decorus* have lower pH than controls, and for burrower treatments only, microcosms with fine sediment have lower pH than coarse sediment (Fig. 6c).

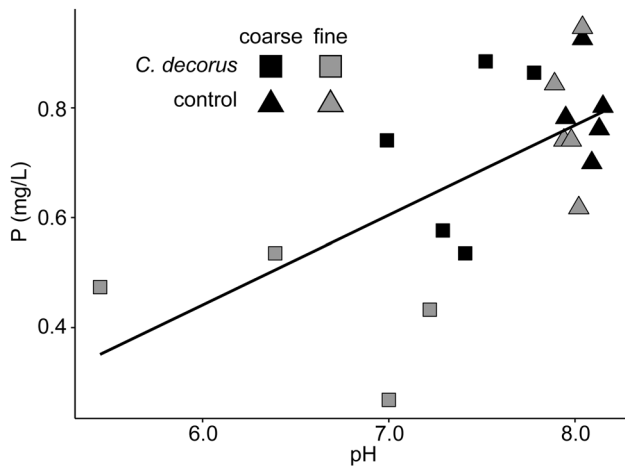


Fig. 7 Experiment 4: Linear relationship between pH and P concentration at measurement E (33 d after start); line represents least-squares regression ($r^2=0.40$, $P=0.004$)

Discussion

Bioturbation is an important ecological function of macroinvertebrates in aquatic ecosystems (Meysman et al. 2006). Understanding how different burrowing species alter rates of exchanges between subsurface sediments and surface water is important for understanding how aquatic ecosystems store and transport nutrients. The objective

of this study was to determine how four common species of burrowing macroinvertebrates in Maryland drainage ditches affect the exchange of P between sediment and surface water using microcosms. These experiments show that burrowing macroinvertebrates can alter dynamics of P storage and release in ditches. The magnitude and direction of these effects depend on the type of bioturbation produced by the burrower and conditions within the sediment and water (Table 2). This could result in different amounts of P available to be transported to local watersheds under different conditions.

In flooded, anaerobic soils and sediments such as drainage ditches, the availability of orthophosphates in solution is determined primarily by adsorption and desorption to oxidized iron and aluminum (Richardson 1985). The stability of iron oxides and oxyhydroxides is determined by the redox potential of the system, with reduction of ferric iron to soluble ferrous iron occurring at low redox potentials, coupled with the release of any adsorbed phosphates (Ponnamperuma 1972). In the microcosm experiments, iron was apparently reduced from sediments and translocated to the surface water where it was then oxidized. This was evident in microcosms as a rusty, orange coating of the sediment surface and sides of the beakers (Vaughan et al. 2008). The strength of adsorption of orthophosphate to iron and aluminum oxide surfaces is determined by the pH of the system, with adsorption being favored at lower pH (Holford and Patrick 1979). The precipitation of iron and aluminum phosphates is also

Table 2 Mean surface water P concentration of bioturbation and sediment treatment combinations and effect sizes of main treatment effects across four experiments at three sampling periods

Experiment	Meas. ^a	Means ± standard error				Effect size	
		Fine sediment		Coarse sediment		Bioturbation	Sediment
		Control	Burrowers	Control	Burrowers		
<i>I. templetoni</i> (conveyor)	C	0.19 ± 0.03	0.14 ± 0.02	0.24 ± 0.06	0.12 ± 0.00	-0.97	0.20
	D	0.32 ± 0.08	0.20 ± 0.05	0.18 ± 0.06	0.31 ± 0.06	0.00	-0.17
	E	0.33 ± 0.03	0.07 ± 0.05	0.69 ± 0.09	0.41 ± 0.05	-1.29*	1.89*
<i>L. hoffmeisteri</i> (conveyor)	C	1.18 ± 0.14	1.22 ± 0.32	1.57 ± 0.11	1.77 ± 0.10	0.25	1.15*
	D	0.37 ± 0.08	0.51 ± 0.11	0.99 ± 0.18	1.40 ± 0.14	0.56*	2.36*
	E	0.91 ± 0.00	0.39 ± 0.09	1.29 ± 0.12	0.99 ± 0.07	-1.30*	1.70*
<i>Cranonyx</i> sp. (biodiffusor)	C	0.62 ± 0.07	0.46 ± 0.04	0.85 ± 0.11	0.80 ± 0.19	-0.35	1.13*
	D	0.27 ± 0.07	0.23 ± 0.08	0.74 ± 0.06	0.44 ± 0.11	-0.65*	1.62*
	E	0.38 ± 0.07	0.31 ± 0.07	0.76 ± 0.23	0.57 ± 0.08	-0.38	1.10*
<i>C. decorus</i> (gallery diffusor)	C	0.75 ± 0.21	2.80 ± 0.47	1.68 ± 0.23	2.04 ± 0.34	2.34* ^b	0.08
	D	0.31 ± 0.06	0.38 ± 0.03	0.46 ± 0.08	0.48 ± 0.04	0.32	1.03*
	E	0.78 ± 0.06	0.39 ± 0.06	0.79 ± 0.04	0.72 ± 0.07	-1.09* ^b	0.87* ^c

*Differences are statistically significant ($P < 0.05$) based on ANOVA

^aMeasurements represent the effect of: C addition of burrowers, D rapid uptake of P following spike with 1.0 mg/L PO_4^{3-} , E uptake of P after a week of incubation

^bSimple-effects comparison of bioturbation effect between fine sediment treatments only

^cSimple-effects comparison of sediment effect between burrower treatments only

avored at lower pH. In measurements where burrowers significantly reduced P concentrations, there was also a significant effect of burrowers on pH and/or redox potential. For all four species, measurements where burrowers produced lower P concentrations relative to controls were coupled with significantly lower pH values measured in burrower treatments. For three of those measurements, there were also significantly higher redox potentials measured in burrower treatments. Burrowing species can alter redox potentials in the sediment by constructing burrows that allow oxygen-rich surface water to move deeper into sediment layers. Higher redox potentials would also be measured in microcosms as a result of increased proton concentration with lower pH measures. Burrowing may have lowered the pH in the system by exposing iron monosulfides (FeS) to the surface (Fig. 8b). FeS species are common in ditches on Maryland's Eastern Shore and produce acidity upon oxidation (Needelman et al. 2007b). FeS was apparent in microcosms at the completion of the experiment as black coatings on redox electrodes and surfaces of the beaker below the sediment surface. These black coatings reacted with hydrogen peroxide to produce the rotten-egg smell of hydrogen sulfide gas and turned a rusty, orange color, which identified them as FeS (Vaughan et al. 2008).

Each burrowing species caused a decrease in P concentration relative to no burrower controls in at least one of the measurements over the course of the experiments. This suggests that burrowing by different species increases the capacity of P immobilization in the sediment, but that

effect depends on environmental conditions in which the burrowing is occurring. *Crangonyx* caused a short-term reduction in P concentrations following simulated flow condition in the microcosms. Lower P concentrations showed a significant linear relationship with redox potential, indicating that burrowing by *Crangonyx* may have altered the redox chemistry at the sediment–water interface, creating more favorable conditions for rapid P sorption to surfaces of redox-sensitive species such as iron oxyhydroxides. The other three burrowing species (*I. templetoni*, *L. hoffmeisteri*, and *C. decorus*) each caused a reduction in the P concentration after the incubation period following a simulated flow event. Under these conditions, there was no longer a concentration gradient of P between sediment porewater and the surface water, and processes that caused a change in P concentration were likely to be slower-acting than rapid sorption reactions (Fig. 8b). In each case where the burrowers reduced P concentrations, there was also a significant reduction in pH, which may have favored binding and precipitation of P with dissolved Al or Fe in the surface water.

Limnodrilus hoffmeisteri and *Chironomus decorus* each caused an increase in P concentration relative to controls in one measurement. This suggests that in some cases, large deposit-feeding oligochaetes and gallery-diffusing chironomid larvae may contribute significantly to fluxes of P from sediment porewater to surface water (Fig. 8a). These effects were not measured in conjunction with changes to sediment or water chemistry, and therefore are likely due to differences in transport of P from sediment porewater to the surface that resulted from physical changes to the sediment, rather than changes in chemical immobilization or microbial uptake of P. The effect of the conveyor was seen after the simulated flow of water through the system. Burrows created by *L. hoffmeisteri* may have created preferential flow paths through the sediment layer, which allowed more dissolved phosphates to be transported to the surface water without interacting with surfaces within the sediment that could immobilize P. The effect of gallery diffusors seems to be mediated by the relative concentration of P in porewater compared to surface water. Microcosms were allowed to develop anaerobic conditions over a week of flooding prior to disturbance of the sediment by burrowers, and water pumped through U-shaped burrows by *C. decorus* larvae essentially caused a mixing of sediment porewater and surface water. Drainage ditch sediments can contain high amounts of exchangeable P, and are not often in equilibrium with the surface water (Nguyen and Sukias 2002). This can result in sediment porewater having concentrations of P that are up to two orders of magnitude higher than the surface water (Hill and Robinson 2012). Soil P concentrations can also be highly variable within a ditch, which may make it possible for gallery-diffusors like *C. decorus* to enhance and

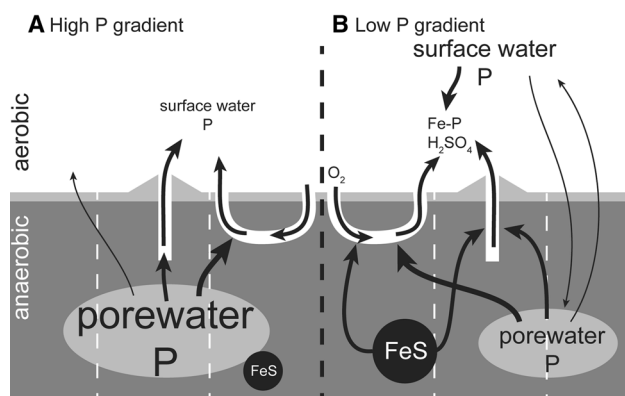


Fig. 8 Conceptual diagram of effects of conveyors and gallery-diffusors compared to no-burrower controls on P movement from sediment to surface water under **a** high and **b** low P concentration gradient. Arrows indicate fluxes of materials across the sediment–water interface, and the width of the arrow indicates the relative magnitude of the flux. Size of text represents relative concentration of pools of different chemical species dissolved in water. **a** Under high gradient conditions, burrowers increase the flux of dissolved P from the sediment porewater to the surface water. **b** Under low gradient conditions, burrowers decrease the surface water P concentration by exposing reduced iron monosulfides, creating a pH environment that favors precipitation of Fe–P complexes

reduce the movement of P within a ditch simultaneously (Vaughan et al. 2007).

This study demonstrates the importance of sediment structure in the dynamics of P movement from sediment to overlying water. With only two exceptions, the measurements of P were higher in microcosms with coarse sediment than fine sediment, despite the higher concentration of ammonium oxalate-extractable P in the fine sediment (Table 1). This suggests that diffusion of P from sediment porewater to the surface occurs faster in drainage ditches that have more aggregated structure in the sediment. The aggregated structure may produce macropores that act as preferential flow paths for water during flow events. This could enable faster rates of diffusion from the sediment to the water, and could result in less interaction between incoming water and sediment surfaces that could adsorb P. The clumped structure of sediment could also decrease the ability of porewater to interact with the inside of aggregates, and effectively reduces the surface area in contact with the porewater. Microbial biofilms occur on surfaces, and a reduction in the effective surface area could reduce the ability of microbes to take up P. This suggests that small, primary ditches that tend to develop granular soil structure from cycles of drying and wetting may release P at higher rates than large collection ditches that tend to have single-grained sediments.

Bioturbation by the different species of burrowers had significant effects on movements of P to the surface water, and these effects differed within and between functional groups. Across all four experiments, bioturbation resulted in lower P concentrations in at least one of the three water measurements. Current management practices for drainage ditches focus on enhancing the ability of ditches to reduce the load of nutrients and sediment delivered to receiving waters as a way of preventing eutrophication of aquatic habitats downstream (Needelman et al. 2007a; Kröger et al. 2013). Studies of macroinvertebrate communities in ditches have generally focused on biological conservation, and not on direct roles that macroinvertebrates play in altering water quality (Verdonschot et al. 2011; Chester and Robson 2013). This study demonstrated that burrowing aquatic invertebrates can significantly increase or decrease the concentration of P in surface waters, depending on the type of bioturbation and the relative availability of P in the ditch habitat. The effect of increasing diversity among burrowers, either by increasing species richness within a functional group or representing different bioturbation functional groups, on P concentrations in surface water is as yet unknown. Furthermore, the mechanisms producing changes in P concentrations involve complex interactions, as burrowers alter the microbial community, advection of solutes, and pH and redox chemistry. Finally, different species within these functional groups

may produce different effects on sediment P, and multiple species within the community may interact to affect P concentrations in unpredictable ways. The contributions of burrowing invertebrate fauna to nutrient dynamics need to be taken into account to understand the movement of nutrients through agricultural drainage networks.

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