Bioturbation has a limited effect on phosphorus burial in salt marsh sediments

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Abstract. It has been hypothesised that the evolution of animals during the Ediacaran-Cambrian transition stimulated the burial of phosphorus in marine sediments. This assumption is centrally based on data compilations from marine sediments deposited under oxic and anoxic bottom waters. Since anoxia excludes the presence of infauna and sediment reworking, the observed differences in P burial are assumed to be driven by the presence of bioturbators. This reasoning however ignores the potentially confounding impact of bottom water oxygenation on phosphorus burial. Here, our goal is to test the idea that bioturbation increases the burial of organic and inorganic phosphorus (P_{org} and P_{inorg}, respectively), while accounting for bottom water oxygenation. We present solid-phase phosphorus speciation data from salt marsh ponds with and without bioturbation (Blakeney salt marsh, Norfolk, UK). In both cases, the pond sediments are exposed to oxygenated bottom waters and so the only difference is the presence/absence of bioturbating macrofauna. Our data reveal that the rate of P_{org} and P_{inorg} burial are indistinguishable between bioturbated and non-bioturbated sediments. A large terrestrial fraction of organic matter and higher sedimentation velocity than generally found in marine sediments (0.3 ± 0.1 cm yr^{-1}) may partially impact these results. However, the absence of a clear effect of bioturbation on total P burial puts into question the presumed importance of bioturbation for phosphorus burial.

1 Introduction

The evolution of animals near the Ediacaran-Cambrian transition ($\sim$542 million years ago - Ma) was a major evolutionary event in Earth's history (Mangano and Buatois, 2017; Meysman et al., 2006; Wood et al., 2019). Early benthic animals developed the ability to burrow (the so-called 'burrowing revolution'; Meysman et al., 2006), which profoundly changed the geochemical cycling and burial of elements in the seafloor (Aller, 1977; McIlroy and Logan, 1999; Meysman et al., 2006). Benthic fauna

affect the seafloor in two separate ways; by reworking of solid-phase particles (bio-mixing) and by flushing of burrows (bio-irrigation), lumped together under the term 'bioturbation' (Kristensen et al., 2012). Bio-mixing and bio-irrigation can have distinct effects on organic carbon mineralisation and early diagenesis (Kostka et al., 2002; van de Velde and Meysman, 2016). For instance, bio-irrigation can promote aerobic respiration by flushing oxygenated bottom waters into deeper anoxic horizons (Archer and Devol, 1992; van de Velde and Meysman, 2016), whereas bio-mixing transports fresh organic from the sediment-water interface into the anoxic zone, thus stimulating anaerobic mineralisation pathways (Berner and Westrich, 1985; van de Velde and Meysman, 2016).

Bioturbation has been proposed to play a key role in the sedimentary phosphorus (P) cycle. Via bio-mixing, bioturbating organisms transport P that is adsorbed on iron oxides from the oxic zone at the sediment surface into deeper sedimentary layers (Slomp et al., 1996). In the anoxic zone of the sediment, these iron oxides are reduced, and P is released further away from the sediment-water interface (SWI). Accordingly, P is retained longer in the sediment, which could stimulate the precipitation and eventual burial of inorganic P (P_{inorg}) minerals, such as apatite (Slomp et al., 1996). Via bio-irrigation, benthic fauna can increase the availability of oxygen in the sediment (Volkenborn et al., 2019), which could stimulate the production of microbial polyphosphate compounds within the sediment column (Dale et al., 2016). Microbial polyphosphates are generated during the breakdown of organic matter under oxic conditions (Diaz et al., 2008), and can be converted into more refractory organic P (P_{org}; as for example phosphate esters or phosphonates) or inorganic P minerals during diagenesis, which would then constitute a permanent P_{org} burial sink (Berner et al., 1993; Van Cappellen and Ingall, 1994; Diaz et al., 2008; Goldhammer et al., 2010; Ingall and Jahnke, 1997). Overall, bioturbation could increase the burial of organic and inorganic P in the sediment. Accordingly, it has been hypothesised that the rise of bioturbation at the Ediacaran-Cambrian boundary increased the burial of P in marine sediments (Boyle et al., 2014; Dale et al., 2016; van de Velde et al., 2018). Marine P burial plays a key role in the long-term functioning of the Earth system, because P is considered the long-term limiting nutrient for marine primary productivity (Van Cappellen and Ingall, 1996). If more P becomes buried, photosynthesis would decrease, thereby limiting the overall burial of C_{org} in the seafloor, subsequently increasing atmospheric CO_2 and lowering atmospheric O_2 (Bergman et al., 2004; Berner, 1982). Hence, the rise of bioturbation may have increased atmospheric CO_2 concentrations and decreased atmospheric O_2 concentrations, thus inducing warmer climatic conditions and more widespread ocean anoxia (Boyle et al., 2014; van de Velde et al., 2018).

However, other factors play an important role for the burial of P in marine sediments. High sedimentation velocities stimulate the preservation of organic matter (Canfield, 1994), causing less mineralisation of organic matter, and consequently more burial of P_{org} associated with organic matter. Additionally, bottom water redox conditions are important for P burial; sediments underlying oxic bottom waters generally show higher burial rates of P_{org} than sediments underlying anoxic bottom waters (Ingall and Jahnke, 1997; Ruttenberg, 2014; Slomp and Van Cappellen, 2007), as sediments underlying oxic bottom waters likely receive an extra source of P_{org} in the form of microbial polyphosphates (Diaz et al., 2008). It is difficult to disentangle the confounding effect or sediment accumulation, redox conditions and bioturbation, because within the present-day seafloor, most sediments deposited under oxic conditions generally also experience bioturbation (Levin et al., 1991). As a result, the proposed effect of bioturbation on P burial has not been extensively verified under field or laboratory conditions.

To be able to adequately tease apart the impact of bioturbation from other confounding factors, one requires sites that have oxygenated waters and a similar input of organic matter, but no bioturbation. While these conditions are extremely rare in the modern seafloor, they are found in salt marsh ponds along the North Sea coast of Norfolk (UK), which contain sediments with overlying oxygenated water that are either bioturbated or non-bioturbated (Antler et al., 2019; Hutchings et al., 2019). These two different sediment types can be found in neighbouring ponds, less than five meters apart, and no systematic difference in local sediment input, organic matter supply or other boundary conditions has been found between the two pond types (Antler et al., 2019; Hutchings et al., 2019; van de Velde et al., 2020). This remarkable biogeochemical dichotomy between the pond sediments has recently been attributed to alternative stable states, in which small initial differences between ponds are amplified through non-linear positive feedbacks in the sedimentary iron-sulphur cycle (van de Velde et al., 2020).

Whatever the cause of the biogeochemical dichotomy, the important aspect here is that by comparing the geochemistry of the two oxygenated pond types, we can single out the effect of burrowing fauna on sediment biogeochemistry. These ponds within the Norfolk salt marsh complex, hence, provide a unique environment to study the impact of bioturbation on the burial of organic and inorganic phosphorus, without the confounding effect of bottom water oxygenation. To this end, we collected solid-phase phosphorus data during three separate visits and quantified the burial rates of P in the bioturbated and non-bioturbated ponds.

2 Materials and Methods

2.1 Field site

Blakeney salt marsh (Fig. 1) is part of a larger salt marsh complex along the North Sea coast of East Anglia (UK). The higher, vegetated, marsh hosts several shallow, water-filled ponds with a surface area of $\sim$50 - 500 m^2 and a water depth of $10 - 20$ cm (Fig. 1; van de Velde et al., 2020). These ponds show a conspicuous dichotomy in terms of their sediment geochemistry, and belong to either one of two end-member types. Pond sediments are either heavily bioturbated and the solid phase is rich in iron oxides, or sediments are non-bioturbated and the pore water is rich in hydrogen sulphide (Antler et al., 2019; Hutchings et al., 2019; van de Velde et al., 2020). The bioturbated ponds are colonised by large macrofauna, mostly Nereis and Arenicola, at high densities ($\sim$1000 organisms m^{-2}; Antler et al., 2019), while the non-bioturbated sediments do not show signs of macrofauna or burrows. Water column concentrations of oxygen, DIC and nutrients are not statistically different between pond types, and both types of ponds have the same sedimentation flux (0.9 ± 0.1 $kg m^{-2} yr^{-1}$), indicating they receive a similar input of detrital minerals. Furthermore, all ponds display similar inputs of organic matter, thus suggesting that the only important difference between the ponds is the presence of burrowing fauna (van de Velde et al., 2020). Depth profiles of ^{137}Cs show a well-defined peak in the non-bioturbated ponds, suggesting they have been undisturbed by fauna for at least 60 years (van de Velde et al., 2020).
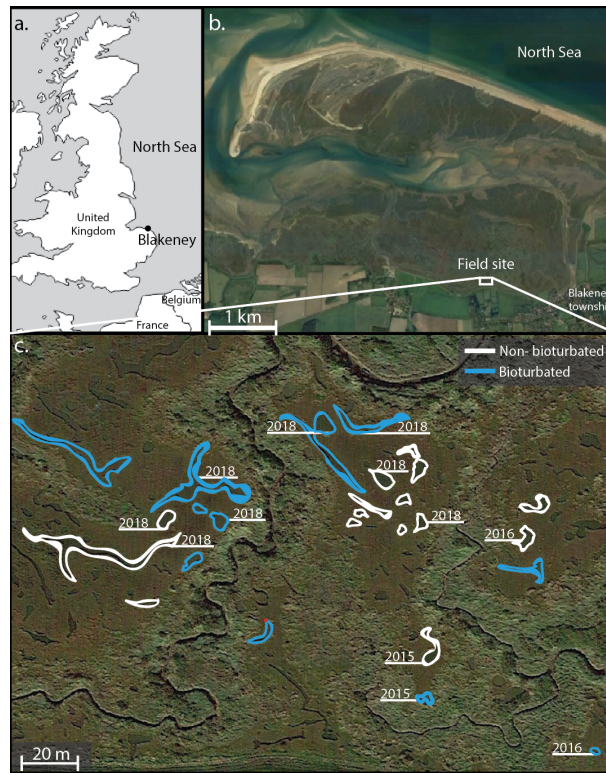
Figure 1. Overview of the field site in the Blakeney saltmarsh system, UK. Sampled ponds are outlined in white (non-bioturbated) and blue (bioturbated), with ponds where sediment cores taken denoted with the sampling year. Coordinates of the sampled ponds are given in Table A1. (b,c) Map data ©2020 Google.

2.2 Sediment sampling and analysis

Sediment cores were collected on three separate visits (October 2015, August 2016 and August 2018). Twelve ponds were examined in total (sampling sites are indicated in Fig. 1). During each sampling campaign, two replicate sediment cores were collected from each sampled pond. Core sectioning was done at 0.5 cm resolution from 0 to 3 cm depth, at 1 cm resolution

5 between 3 and 8 cm depth, and in 2 cm slices from 8 to 22 cm depth. Sediment sections were collected in 50 mL centrifuge tubes (polypropylene; TPP, Switzerland). In 2015 and 2016, sediment cores were processed under anaerobic conditions in a glove bag with N_2, freeze-dried and stored in a sealed aluminium bag under N_2 atmosphere for later solid-phase analysis. In 2018, cores were immediately sliced in open air in the field, and subsequently freeze-dried and stored under room conditions in 50 mL centrifuge tubes. This difference in sampling procedure reflects the subsequent analyses. In 2015 and 2016, solid

10 phase was analysed for different phosphorus fractions following the SEDEX phosphorus extraction (Ruttenberg, 1992; Slomp et al., 1996). In 2018, due to the higher amount of samples, we decided to use a simpler and faster extraction method that only differentiates between inorganic and organic phosphorus fractions (Bowman, 1989; Olsen and Sommers, 1982).

Sediment samples from all three campaigns were analysed for carbon and nitrogen content. To this end, freeze-dried solid phase samples were ground to a fine powder and analysed by an Interscience Flash 2000 organic element analyser (precision <5%) for determination of particulate organic carbon (POC) and total nitrogen (TN). Before analysis, samples for POC were first acidified with 0.1M HCl to remove the inorganic carbon (Nieuwenhuize et al., 1994). Concentrations of POC and TN are

5 expressed as mass % of dry sediment. Organic matter $C_{org} : N_{tot}$ was calculated as the molar ratio of POC over TN. The POC and TN results have been presented previously in van de Velde et al. (2020).

The SEDEX procedure used in 2015 and 2016 separates total sedimentary P in 5 fractions; exchangeable P (P_{exch}), P associated with iron (P_{Fe}), authigenic P (P_{auth}), detrital P (P_{det}) and P associated with organic matter (P_{org}). All extractions were performed on a subsample of 300 mg, under room temperature and under constantly agitated conditions (the extraction

10 procedure is detailed in Table A2). Inorganic phosphorus (P_{inorg}) is calculated as

$$P_{inorg} = P_{exch} + P_{Fe} + P_{auth} + P_{det} \tag{1}$$

and expressed as μmol g^{-1} dry sediment. The extraction procedure used in 2018 separates the sediment phosphorus content in 2 fractions; total phosphorus (P_{tot}) and inorganic phosphorus (P_{inorg}), organic phosphorus is then calculated as the difference between P_{tot} and P_{inorg} (Bowman, 1989; Olsen and Sommers, 1982). Extractions were performed on a subsample of 1 g,

15 under room temperature and under constantly agitated conditions (extraction procedure detailed in Table A2).

2.3 Burial fluxes and solid phase inventories

Burial fluxes of solid phase species were calculated based on the sedimentation flux (J_{sed}) and the concentration of the solid component at the bottom of the sediment column (C_{solid}):

$$J_{burial} = J_{sed} C_{solid} \tag{2}$$

20 The sedimentation flux was previously determined based on ^{210}Pb and ^{137}Cs dating, and was statistically indistinguishable between pond types (0.9 ± 0.1 kg m^{-2} yr^{-1}; van de Velde et al., 2020).

Solid phase inventories were calculated by integrating measured concentrations over the first 20 cm of the sediment cores:

$$INV = \rho_{solidphase} \int_{x_{down}}^{x_{up}} (1 - \phi_x) C_{solid} dx \tag{3}$$

Where ϕ_x is the porosity at depth x and $\rho_{solidphase}$ the solid phase density (previously determined to be 2.2 g cm^{-3}; van de

25 Velde et al., 2020). The porosity depth profile was determined from the water content and solid-phase density, considering the salt content of the pore water. The water content of the sediment was determined as the difference in sediment weight before and after freeze-drying. Porosity profiles have been presented previously in van de Velde et al. (2020).

2.4 Statistics

The measured values of $C_{org} : N_{tot}$ and $C_{org} : P_{org}$, calculated burial fluxes of P_{org} and P_{inorg} and solid-phase inventories

30 were averaged over the duplicate cores from each pond and one-way ANOVA's were used to test for significant differences

between bioturbated and non-bioturbated ponds. Due to the different methods used for P extraction in 2015 and 2016 relative to 2018, the inclusion of the sampling year as a random effect was tested through model evaluation using AIC (Akaike information criterion). Sampling year was not significant for all dependent factors, and so it was excluded from subsequent analyses. Residuals were tested for normality and homoscedasticity, and all but $C_{org} : P_{org}$ fulfilled these assumptions. The values of

5 $C_{org} : P_{org}$ were log transformed before analysis.

3 Results

3.1 Bioturbation and organic phosphorus burial

Individual depth profiles of solid-phase variables (POC, TN, TP, POP, PIP) show variation within the sediments of a given pond type, indicating spatial heterogeneity (Fig. 2). Still, averaged depth profiles of the six non-bioturbated and the six bioturbated

10 ponds reveal that non-bioturbated sediments have generally a stronger down-core gradient (Fig. 2A-J), which is expected as sediment bio-mixing by bioturbating fauna acts to erase solid phase gradients (van de Velde and Meysman, 2016). Differences in POC, TN and POP inventories in the top 20 cm between bioturbated and non-bioturbated cores are insignificant (Fig. 2A,D,G,H; Table A4). Consistently, $C_{org} : N_{tot}$ and $C_{org} : P_{org}$ values are not significantly different between bioturbated and non-bioturbated pond types ($p > 0.1$; Table A4). Values of $C_{org} : N_{tot}$ range from 9 to 15, with an average value of 12 (Fig. 2K).

15 These values are slightly higher than expected for sediments from fully marine settings ($C_{org} : N_{tot} < 10$; Burdige, 2006), but are consistent with sediments from temperate salt marshes, which generally have $C_{org} : N_{tot}$ values of 10 or higher (Spivak et al., 2018). Similarly, $C_{org} : P_{org}$ values averaged around 500 in both the non-bioturbated and bioturbated sediment cores (2G). These $C_{org} : P_{org}$ values are higher than expected for marine sediments with similar sedimentation rates underlying oxygenated waters ($C_{org} : P_{org} \sim 200$; Slomp and Van Cappellen, 2007), and are more representative of low-oxygen and anoxic marine

20 environments ($C_{org} : P_{org}$ = 300-700; Slomp and Van Cappellen, 2007). However, since the pond waters were oxygenated at the time of sampling (van de Velde et al., 2020), the elevated $C_{org} : P_{org}$ values most likely reflect the contribution of plant material from the surrounding marsh ($C_{org} : P_{org} > 500$; Table A3), which is substantially elevated above the $C_{org} : P_{org}$ of marine plankton ($\sim$106; Redfield, 1934).

Overall, our organic P data show two main findings: (i) bioturbated sediments have similar amounts of P_{org} (P_{inv} = 0.067 $\pm$

25 0.005 mmol cm^{-2}; Fig. 3A) compared with non-bioturbated sediments (P_{inv} = 0.072 $\pm$ 0.004 mmol cm^{-2}; Fig. 2,3a), and (ii) differences in P_{org} burial in bioturbated sediments (17 $\pm$ 4 μmol m^{-2} d^{-1}) are not statistically significant from non-bioturbated sediments (19 $\pm$ 2 μmol m^{-2} d^{-1}) (Fig. 3B; $p > 0.1$; Suppl. Table A4).

3.2 Bioturbation and inorganic phosphorus burial

Our solid phase analyses show that bioturbated sediments (203 $\pm$ 70 μmol cm^{-2}) contain significantly more particulate inor-

30 ganic phosphorus than non-bioturbated sediments (113 $\pm$ 17 μmol cm^{-2}) ($p < 0.1$; Fig. 2I,J; Fig. 3A; Table A4).
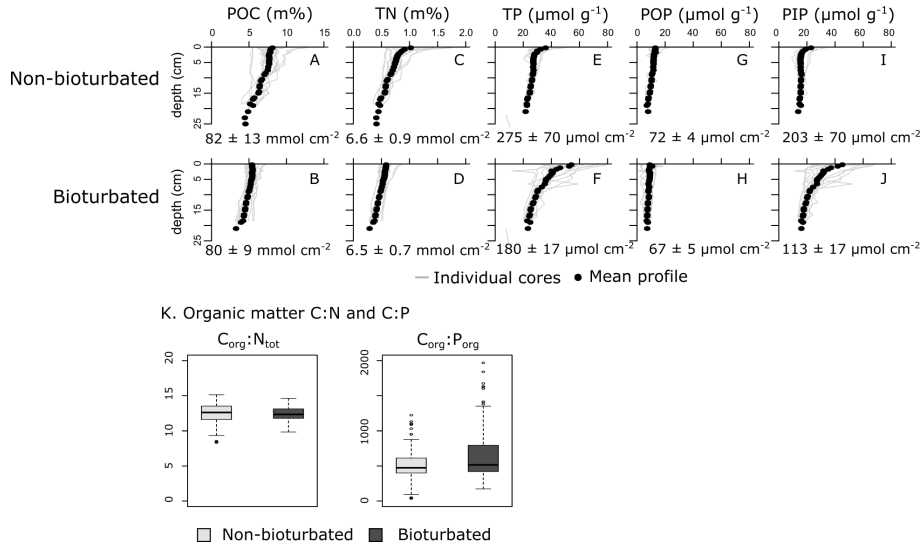
Figure 2. Vertical solid phase profiles of (A,B) particulate organic carbon (POC), (C,D) total nitrogen (TN), (E,F) total phosphorus (TP), (G,H) particulate organic phosphorus (POP) and (I,J) particulate inorganic phosphorus (PIP). Individual cores are plotted as a light gray lines, and the average vertical profile over all cores is plotted as black dots. Values are averaged inventories and errors are 1 standard deviation. (K) Boxplots of the $C_{org} : N_{tot}$ and $C_{org} : P_{org}$ of the particulate organic matter fraction.

SEDEX extractions, performed on sediment cores collected in 2015 and 2016, show that the large difference in P_{inorg} is caused by the much higher P_{exch} and P_{Fe} contents in the bioturbated sediments (Fig. 4; $P_{exch} + P_{Fe}$ is up to 90 mmol P cm^{-2} higher in the bioturbated sediments; Table A5). Phosphorus adsorbed onto iron oxide minerals, is transported from the sediment-water interface to the deeper sedimentary layers by the downward mixing of benthic fauna (Slomp et al., 1996).
5   Indeed, $\sim 50\%$ of the Fe minerals in the bioturbated sediments at Blakeney salt marsh are in oxidised form, whereas $< 10\%$ are in the non-bioturbated sediments (see van de Velde et al. (2020) for an extended discussion of the Fe-S cycle at the field site).

    The increased inventory of P_{exch} and P_{Fe} at depth seemingly does not lead to more precipitation of P_{auth} (Table A5), since we do not find detectable formation of authigenic apatite, the concentrations of which are negligible throughout all sediment
10   cores in both ponds (< 1 μmol g^{-1}). While P_{inorg} concentrations are high in the top layers, they strongly decrease with depth, thus P_{inorg} is not efficiently buried. Overall, we find that the burial rate of P_{inorg} is 38 ± 3 μmol m^{-2} d^{-1} in bioturbated sediments, and 36 ± 3 μmol m^{-2} d^{-1} in the non-bioturbated sediment, and this difference is not significant ($p > 0.1$; Table A4).
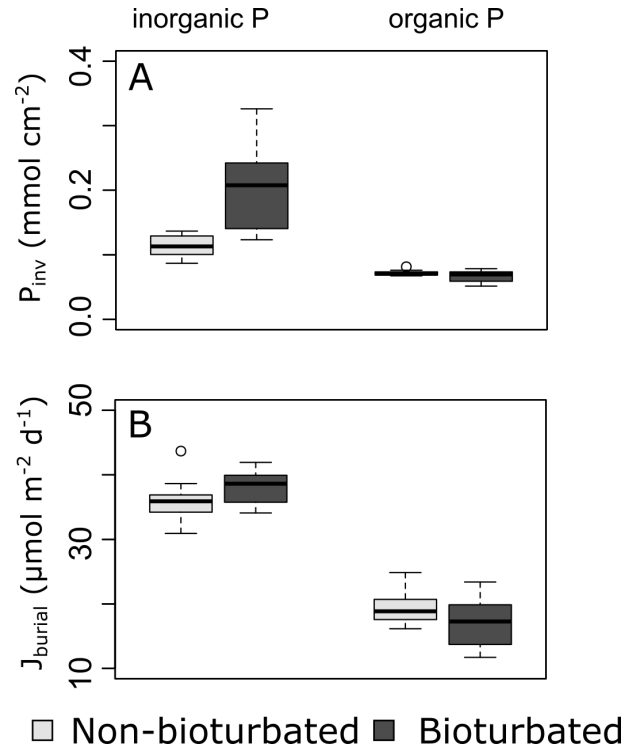
Figure 3. Boxplots of (A) inventories and (B) burial rates of inorganic and organic P fractions. The data of 2015 are not included in panel A, since some depth samples were not analysed for P fractionation.
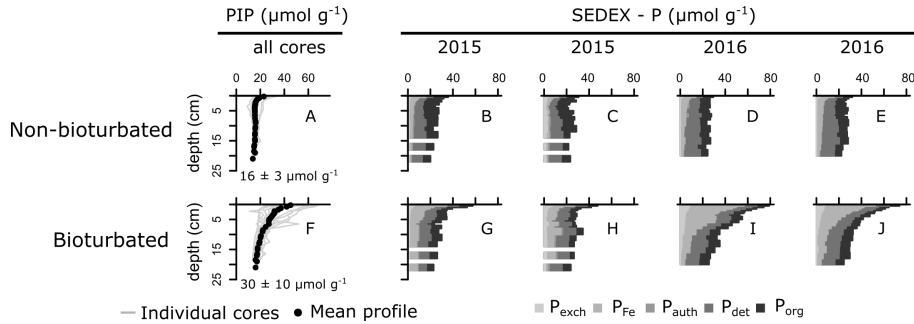
Figure 4. Vertical solid phase profiles of (A,F) particulate inorganic phosphorus (PIP). Values are depth-averaged concentrations. (B)-(E), (G)-(J) Solid phase phosphorus speciation (SEDEX) of cores collected in 2015 and 2016. P_{exch}=exchangeable phosphorus, P_{Fe}=iron-bound phosphorus, P_{auth}=authigenic phosphorus, P_{det}=detrital phosphorus, P_{org}= organic phosphorus. Note that the P_{auth} fraction is too small to be visible on the figure.

4 Discussion

By comparing non-bioturbated and bioturbated sediment cores collected from an East Anglian salt marsh, this study provides a field verification for the hypothesis that bioturbation stimulates the burial of inorganic and organic P minerals. Our field data show that a bioturbated sediment contains more inorganic P, which exists mainly in the form of iron-associated P. Nevertheless, the accumulation of inorganic P occurs principally in the top layers of the sediment. At 20 cm, the P_{inorg} levels in bioturbated sediments decrease to similar levels as in non-bioturbated sediments (Fig. 4). We find no evidence for the formation of authigenic P (Fig. 4), which is at odds with previous hypotheses (Slomp et al., 1996; Zhao et al., 2020). Potentially, the high concentrations of Fe^{2+} in the pore water of the bioturbated sediments (up to 300 μM; van de Velde et al., 2020) promoted the formation of vivianite over apatite (Ruttenberg, 2014). Because vivianite is extracted in the P_{Fe} fraction (Nembrini et al., 1983), we cannot separate between P associated with iron oxides, and P in the form of vivianite. The precipitation of vivianite in the bioturbated sediments could potentially stimulate the burial of P_{inorg}, but this effect is not readily seen in our data. As a consequence, we find that the burial of P_{inorg} was not significantly different between bioturbated and unbioturbated ponds, which does not support the idea that bioturbation stimulates the burial of inorganic P minerals. Our data are hence not congruent with previous modelling and field studies that have suggested that bioturbating fauna stimulates the burial of authigenic apatite (Slomp et al., 1996; Zhao et al., 2020). These studies argued that bioturbators mix iron oxides, on which phosphate is adsorbed, further away from the sediment-water interface (SWI), increasing the retention time of phosphate in the sediment, and subsequently stimulating the precipitation and eventual burial of inorganic phosphorus minerals (Slomp et al., 1996; Dale et al., 2016). Bioturbators also flush their burrows however, which removes phosphate from the pore water (Dale et al., 2016). Consequently, depending on the animal community (irrigation versus mixing), the pore water can become undersaturated with respect to apatite, leading to lower precipitation rates and burial of apatite. The difference between oxic, bioturbated and oxic, non-bioturbated sediments inferred from the model study of Dale et al. (2016) is only a few μmol m^{-2} d^{-1}, which is likely undetectable in a field study like ours (Fig. 3). Consequently, our results suggest that the effect of bioturbation on P_{inorg} minerals is small, consistent with diagenetic modelling results (Dale et al., 2016).

We find that the burial of P_{org} is indistinguishable between bioturbated and non-bioturbated sediments (Fig. 2G). Accordingly, our field data do not support the idea that bioturbation increases the burial of organic phosphorus. It should be noted however that the C:N:P ratios of the organic matter in the salt marsh pond sediments suggests a large contribution of plant material from the surrounding marsh (Fig. 2), which has elevated C:N:P ratios compared to marine organic matter (Suppl. Table A3). Because terrestrial material is less easily degraded, the addition of plant material to the sediment organic matter pool dilutes the signal of the marine organic matter (Ruttenberg, 2014), which could explain why we see no effect of bioturbation. Another possible reason is that the sedimentation velocity in Norfolk salt marsh ponds is relatively high (0.3 cm yr^{-1}, compared to a mean value of 0.1 cm yr^{-1} for shelf sediments; Burwicz et al., 2011). High sedimentation velocities stimulate the preservation of organic matter (Canfield, 1994), and would potentially further dilute the effect of bioturbation on P_{org} burial. Nevertheless, the POC profiles suggest an appreciable amount of organic matter is being degraded in the salt marsh pond sediments (Fig. 2). Indeed, organic matter mineralisation rates based on POC and nutrient profiles range from 6-38 mmol C m^{-2} d^{-1}, which is

comparable to rates observed in shallow marine sediments (Burdige, 2007) and thus indicates that the Blakeney salt marsh site shows a comparable metabolic activity to marine sediments. The observation then still remains; bioturbation seems to have no significant impact on P_{org} burial.

Bioturbation is believed to impact P_{org} burial by stimulating the formation of polyphosphates, which can act as an intermediate for the formation of apatite or more refractory organic P compounds (Berner et al., 1993; Goldhammer et al., 2010). Polyphosphates are formed during aerobic respiration of organic matter (Diaz et al., 2008), and because bio-irrigation stimulates aerobic respiration in the sediments (Archer and Devol, 1992; van de Velde and Meysman, 2016), it has been hypothesised that more polyphosphates could be formed in bioturbated sediments (Dale et al., 2016). However, other studies have shown that polyphosphates and the subsequent conversion to apatite also occurs under anoxic conditions (Goldhammer et al., 2010), so it is questionable whether periodic influshing of oxygenated water would have a large impact on polyphosphate formation. Unfortunately, our analysis method does not allow us to differentiate between bulk organic P and microbial polyphosphates to investigate whether polyphosphate formation plays a role in both bioturbated and non-bioturbated sediments. This would be an interesting avenue for future research.

A number of caveats need to be taken into account when interpreting our results, as observations made in the surface sediments of the Norfolk salt marsh ponds are not necessarily representative of burial signals made at several metres deep in coastal and shelf sediments. As noted above, the $C_{org} : P_{org}$ ratio of buried organic matter is high, as it is influenced by the deposition of the salt marsh vegetation with high C:P ratios, and therefore, caution is required when extrapolating our results to other coastal and shelf sediments. A difference in time scale is another caveat to take into account. Based on an average sedimentation velocity of 0.3 cm yr^{-1} measured via radionuclide dating (van de Velde et al., 2020), our samples represent only 60 years of sediment accumulation and they hence indicate that, after ~ 60 years of early diagenesis, there is no discernible difference in burial of P minerals. Diagenesis later in the burial history could still affect long-term P burial. Data reported in the literature are collected from geological formations (see, e.g., Ingall et al., 1993) or deep drill cores (see, e.g., Slomp et al., 2004). These samples have undergone several hundreds to thousands years of diagenesis before being sampled and analysed. However, we cannot see a mechanism via which bioturbation could have an imprint on the sediment that eventually leads to differential diagenesis of P minerals later in their burial history. If bioturbation does not already create a difference in P burial in the early phase of diagenesis, it is highly unlikely that will happen afterwards. So the difference in time scale cannot easily explain why P burial rates are similar in bioturbated and non-bioturbated sediments.

Overall, more field studies and laboratory experiments are required to verify our results. Nevertheless, the absence of a clear impact of bioturbation on P burial questions whether the modelled effects of the evolution of bioturbation in the early Cambrian, if they are solely based on inferred effects of bioturbation on P burial, do not overestimate the true impact of the 'burrowing revolution'. Our study highlights that assumptions made in Earth System models should be firmly grounded in field observations, before accurate inferences about large-scale questions can be made, such as the impact of the burrowing revolution on the composition of the atmosphere and climate.

Data availability. All data presented in this manuscript is available from the VLIZ data repository (doi:10.14284/419)

Table A1. Coordinates and type of the ponds sampled in the 2015, 2016 and 2018 field campaigns in the Blakeney salt marsh. See Fig. 1c in the main text for relative geographical location of the ponds.

	Coordinates	Type	Year sampled
1	52° 57' 22.7"N 01° 00' 14.0"E	Bioturbated	2015
2	52° 57' 23.0"N 01° 00' 14.0"E	Unbioturbated	2015
3	52° 57' 22.2"N 01° 00' 16.6"E	Bioturbated	2016
4	52° 57' 24.0"N 01° 00' 16.0"E	Unbioturbated	2016
5	52° 57' 25.2"N 01° 00' 13.2"E	Bioturbated	2018
6	52° 57' 25.3"N 01° 00' 12.5"E	Bioturbated	2018
7	52° 57' 24.6"N 01° 00' 10.6"E	Bioturbated	2018
8	52° 57' 24.3"N 01° 00' 10.9"E	Bioturbated	2018
9	52° 57' 24.7"N 01° 00' 13.4"E	Unbioturbated	2018
10	52° 57' 24.4"N 01° 00' 14.1"E	Unbioturbated	2018
11	52° 57' 24.3"N 01° 00' 9.9"E	Unbioturbated	2018
12	52° 57' 24.1"N 01° 00' 10.1"E	Unbioturbated	2018

Table A2. Specifics for the sequential extractions of phosphorus. After the extraction, the sample was centrifuged (2500g for 10 min) and the supernatant was filtered (0.45 μm cellulose acetate).

Fraction	Extraction solution	Atmosphere	Time	Analysis
SEDEX Phosphorus extraction (Ruttenberg, 1992; Slomp et al., 1996)				
P_{exch}	1 M $MgCl_2$	N_2	30 min.	spectrophotometer
P_{Fe}	12 g sodium dithionite in 480 mL sodium acetate (1M) + 60 mL sodium bicarbonate (1 M)	N_2	8 h	ICP-OES
	+ wash: 1 M $MgCl_2$	N_2	30 min.	spectrophotometer
P_{auth}	300 mL sodium acetate (1M) + 1700 mL acetic acid (1 M)	open air	6h	spectrophotometer
	+ wash: 1 M $MgCl_2$	open air	30 min.	spectrophotometer
P_{det}	1 m HCl	open air	24 h	spectrophotometer
	+ wash: 1 M $MgCl_2$	open air	30 min.	spectrophotometer
P_{org}	Combustion at 550°C	open air	2h	
	1 M HCl	open air	24 h	spectrophotometer
	+ wash: 1 M $MgCl_2$	open air	30 min.	spectrophotometer
One-step Phosphorus extraction (Bowman, 1989; Olsen and Sommers, 1982)				
P_{inorg}	1 M H_2SO_4	open air	overnight	spectrophotometer
P_{tot}	Combustion at 550°C	open air	1h	
	1 M H_2SO_4	open air	overnight	spectrophotometer

Table A3. Summary of salt marsh plant properties. Data was first published in van de Velde et al. (2020)

Salt marsh properties

	Suaeda maritima	Salicornia radicans	Spartina anglica	Ameria maritima	Elytrigia atherica	Halimione portulacoides	Limonium vulgare
$C_{org} : N_{tot}$	18	20	27	20	74	26	25
$C_{org} : P_{org}$	682	492	669	554	1289	802	692

Table A4. Results from One-way ANOVA analysis and calculated 95% confidence intervals. Residuals were tested for normality and heterogeneity, all passed these assumptions except C:P, which was log-transformed.

	One-way ANOVA			
	P_{inorg} burial rate	P_{org} burial rate	$C_{org} : N_{tot}$	$C_{org} : P_{org}$
Pond type Mean square (df)	13.69 (1)	11.826 (1)	0.04417 (1)	0.0001 (1)
Residuals Mean square (df)	6.59 (10)	9.768 (10)	0.22665 (10)	0.07641 (10)
F-value	2.077	1.211	0.195	0.0
p	0.18	0.297	0.668	0.991
Pond type	**95% Confidence Intervals**			
Non-bioturbated	33.65, 38.32	16.38, 22.07	11.52, 12.39	6.04,6.54
Bioturbated	35.79, 40.46	14.40, 20.08	11.40, 12.27	6.04,6.54
	P_{inorg} inventory	P_{org} inventory	POC inventory	TN inventory
Pond type Mean square (df)	20006 (1)	1.05 (1)	28.61 (1)	0.0033 (1)
Residuals Mean square (df)	2847 (10)	75.8 (8)	132.14 (10)	0.6345 (10)
F-value	7.026	0.014	0.217	0.005
p	0.029	0.91	0.652	0.944
Pond type	**95% Confidence Intervals**			
Non-bioturbated	58.26, 168.31	61.85, 79.81	72.40, 93.31	5.86,7.31
Bioturbated	147.71, 257.77	61.20, 79.16	69.31, 90.22	5.82,7.27

Table A5. Inventories of the individual phosphorus fractions. P_{org} and P_{inorg} are reported as mean ± 1 s.d., SEDEX fractions are given as a range (due to the low number of replicates) from the 2016 cores (2015 was omitted because some depth samples were not analysed for P fractionation).

	P_{org}	P_{inorg}	Individual P_{inorg} fractions (only 2016)			
			P_{exch}	P_{Fe}	P_{auth}	P_{det}
	$mmol\,cm^{-2}$	$mmol\,cm^{-2}$	$\mu mol\,cm^{-2}$	$\mu mol\,cm^{-2}$	$\mu mol\,cm^{-2}$	$\mu mol\,cm^{-2}$
Non-bioturbated	0.071 ± 0.004	0.11 ± 0.02	0.13-0.19	30.1-32.2	2.4-3.8	100-103
Bioturbated	0.067 ± 0.009	0.20 ± 0.07	10.1-17.3	86.5-108	2.2-2.8	111-114

Author contributions. SJV conceived the hypothesis. SJV and FJRM organised the field sampling. All authors contributed to the field sampling. SJV and IC performed the SEDEX extractions. SJV analysed the data. RKJ did the statistical analyses. SJV and FJRM wrote the manuscript with input from all co-authors.

Competing interests. The authors declare that they have no conflict of interest.

5 *Acknowledgements.* This research was financially supported by the Research Foundation Flanders (FWO project grant G038819N), a TOP-BOF grant by the University of Antwerp, and the Netherlands Organization for Scientific Research (VICI grant 016.VICI.170.072 to FJRM). SJV is supported by the Belgian Science Policy office (FED-tWIN2019-prf-008 – ReCAP project grant). The authors would like to thank Tom Van der Spriet from the University of Antwerp for the phosphorus extraction on the 2018 sediment samples.

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