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Ideas and perspectives: The benthic iron flux from sandy advective bioturbated sediments

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Abstract. Multiple investigators have suggested that the benthic flux of dissolved iron (Fe_d) from continental shelf sediments represents an important source of this micronutrient to ocean waters. The magnitude, biogeochemical controls, and seasonal dynamics of Fe_d fluxes to date, however, have mostly been studied for muddy cohesive sediments dominated by molecular diffusion. Data from these studies have been included in global biogeochemical models to determine the contribution of this Fe source to the ocean. Fe_d fluxes from sandy advective sediments have received little consideration, although these sediments cover 50-60 % of the continental shelves. Sandy permeable deposits function as dynamic catalytic filters characterized by the rapid exchange of solutes and infiltration of particles —including labile C_{org} and reactive metal oxides— and high biogeochemical reaction rates. In this article, we discuss how the fundamentally different modes of solute and particle transport in sands affect the sedimentary Fe cycle and Fe_d flux. We present a case study in which we simulate bioirrigation in sands in summer and winter. In our experiments, Fe_d fluxes from non-irrigated sediments under diffusive conditions did not exceed 6 and 13 µmol Fe m^{-2} d^{-1} in winter and summer, respectively. Fluxes from irrigated cores reached values of 150 µmol Fe m^{-2} d^{-1} (winter) and 115 µmol Fe m^{-2} d^{-1} (summer). The results indicate that the pumping activity of the benthic macrofauna plays a key role in controlling the extent of the benthic Fe_d flux from permeable sediments, and that both biogenic and physical advection enhance fluxes. We argue that bioturbated sandy advective sediments constitute an important benthic Fe source to coastal waters and advocate for a more differentiated treatment of sediment type (muddy diffusive vs. sandy advective) and macrofaunal activity -reflecting different functional groups of the macrobenthos- in global biogeochemical Fe models. A better understanding of the benthic Fe cycle in sandy advective sediments is particularly important to help predict how anthropogenic effects such as changes in the deposition patterns of C_{org} and metals, the expansion of oxygen minimum zones, and changes in benthic biodiversity will affect the tightly coupled benthic-pelagic ecosystem along continental shelves.

1 Introduction

Continental margin sediments are suggested to represent an important source of dissolved iron (Fe_d; here defined as <0.2 µm, which includes aqueous inorganic species, ligand-bound Fe, and other nanoparticulate and some colloidal phases (Raiswell and Canfield, 2012)) to coastal waters and potentially to the open ocean (Conway and John, 2014; Elrod et al., 2004; Lohan and Bruland, 2008; Severmann et al., 2010). In regions with moderate to high organic carbon (C_{org}) input to the sediment, Fe_d

is released predominately during dissimilatory iron reduction (DIR) coupled to organic carbon oxidation and during the reaction of sulfide with Fe oxides in the anoxic zone (Aller, 1980b; Canfield, 1989; Canfield et al., 1993b; Lovley, 1987, 1991). Some of the Fe_d is transported into the overlying water column driven by mechanisms specific to the sediment type. In *muddy diffusive* sediments, transport is constrained by diffusion, and a large fraction of the released Fe_d is quickly reoxidized when encountering oxygen (O_2), nitrate (NO_3^-) or manganese (Mn) oxides and reprecipitates within the sediment surface layer or along macrofaunal burrow walls (Burdige, 1993; McManus et al., 1997; Pakhomova et al., 2007). In permeable *sandy advective* deposits, pore-water advection is oftentimes the dominant mode of solute and particle transport. Bioturbation by benthic macrofauna plays a key role for the benthic Fe cycle in both sediment types by enhancing the transport of particulate labile C_{org}, reactive Fe and Mn oxides, and reduced solid-phase Fe species during particle reworking and by promoting exchange of oxygen, nutrients and dissolved metals between the water column and sediment pore-water by bioirrigation.

Previous studies have integrated benthic flux data from muddy sediment sites into global biogeochemical models to determine the global benthic Fe_d flux from sediments (e.g., Tagliabue et al., 2014; Dale et al., 2015; Nickelsen et al., 2015). These approaches used empirical relationships scaled to organic carbon oxidation rates (Elrod et al., 2004) and bottom water oxygen concentrations (Dale et al., 2015; Nickelsen et al., 2015). Estimates for the flux from shelves range from 27 to 89 Gmol yr^{-1} (shelf area: 3×10^{13} m^2) while the flux from the entire margin was estimated at 109 ± 55 Gmol yr^{-1} (margin area: 7×10^{13} m^2; Elrod et al., 2004; Tagilabue et al., 2014; Dale et al., 2015), which corresponds to an average daily flux value of ~2.5 – 8 $\mu mol\ m^{-2}\ d^{-1}$ for the shelf and ~4.3 $\mu mol\ m^{-2}\ d^{-1}$ for the margin. Data for benthic Fe fluxes that were included in these models were based on a very limited number of studies predominantly from the Oregon-California shelf and Peru Margin (Dale et al., 2015). Thus, they mostly included upwelling areas or regions with enhanced riverine inputs, while areas away from these settings remain little-investigated (Homoky et al., 2016; Eitel et al., 2020). The models relied on generalized bioturbation and bioirrigation coefficients that were scaled to water depth and bottom-water oxygen concentrations. Sediment lithology (muds to sands) and variations in the functional traits of the macrobenthic organisms inhabiting these sediment types were not considered. These estimates therefore fail to take into consideration that 50-60 % of the continental shelf are composed of permeable sand or gravel (Hall, 2002; Huettel et al., 2014).

Long regarded as unimportant for global element cycles due to their low C_{org} content (cf., Webb and Theodor, 1968; Aller, 2014; Boudreau et al., 2001), sandy deposits are now considered highly active “bioreactors” due to their prolific and efficient mineralization of C_{org} driven by oxic respiration and denitrification (e.g., Cook et al., 2007; Janssen et al., 2005; Marchant et al., 2016; Rao et al., 2007; Huettel et al., 2014). Few studies have investigated the biogeochemical cycling of Fe in sands, presumably due to a similar notion that reactive Fe (oxyhydr)oxides, which are commonly found in smaller grain size classes (Poulton and Canfield, 2005; Poulton and Raiswell, 2005), are of minor importance in these deposits, potentially minimizing DIR. However, as Poulton and Raiswell (2005) point out, reactive Fe phases can also occur —in close association with aluminosilicate mineral surfaces— in coarser materials. For example, Huettel et al. (1998) determined Fe(III) oxide contents (0.5 N HCl, 1 h extraction) of 15-18 $\mu mol\ cm^{-3}$ in sandy advective sediments close to Giglio Island. Cook et al. (2007) and Jensen et al. (2003) measured lower HCl-extractable Fe(III) oxide contents of up to 9 $\mu mol\ cm^{-3}$ in sandy sediments at the

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island of Sylt (German Wadden Sea) and the southern and western Kattegat, and of less than 2 µmol cm^{-3} at the Hel Peninsula (Baltic Sea). In comparison, Jensen et al. (2003) observed HCl-extractable Fe(III) oxide concentrations exceeding 20 µmol cm^{-3} in fine-grained sediments of the northeastern Kattegat, where DIR dominated anaerobic carbon mineralization. These studies highlight that reactive Fe oxide contents determined for sandy sediments to date are quite variable. They may, however, support a significant role for DIR in total organic carbon mineralization —especially at the higher end of the observed values (Thamdrup, 2000). The produced Fe_d can enter the overlying water column if subjected to advective transport. This mechanism has, for example, been postulated by Jahnke et al. (2005) who observed elevated pore-water concentrations of Fe_d in permeable sediments in the South Atlantic Bight and suggested the presence of a significant pool of readily reducible Fe oxides. Their data also indicate that during the summer, a benthic Fe^{2+} flux of ~100 µmol m^{-2} d^{-1} is possible, a magnitude quite comparable to reported fluxes from muds (estimated from their reported pore-water inventory production rates at 0-16 cm). The reduced Fe_d that is lost is presumably replenished continuously by extraction of particulate reactants from the water column.

Here, we present a case study in which we simulate bioirrigation in a sandy advective sediment, and argue that permeable sediments provide an important benthic Fe flux to coastal waters. We highlight that the activities of the benthic macrofauna play a key role in controlling the extent of this flux and advocate for a more differentiated treatment of sediment type (muddy diffusive vs. sandy advective) and macrofaunal activity in global biogeochemical Fe models.

1.1 Particle and solute transport in sandy advective sediments

We define sandy advective sediments as those characterized by a permeability exceeding 10^{-12} m^2, following common definition (e.g., Glud et al., 1996; Huettel et al., 2014; Huettel et al., 2003; Huettel et al., 1998). At this permeability, fluid movement is no longer dominated by diffusive but rather advective transport (Huettel et al., 2001). In high permeability sands pore-water exchange is driven by pressure gradients caused, for example, by physical effects such as wave-topography interactions, bottom currents, density gradients (Reimers et al., 2004; Huettel et al., 1998; Precht et al., 2004; Thibodeaux and Boyle, 1987; Santos et al., 2012; Ahmerkamp et al., 2017) and the bioirrigation activity of the benthic macrofauna (Volkenborn et al., 2010; Woodin et al., 2010; Neumann et al., 2021). In near-shore permeable tidal flat systems, solute transport also occurs via tidally driven pressure gradients that can pump deep (metal-rich) pore-water to tidal flat margins (e.g., Billerbeck et al., 2006; Beck et al., 2008). Sandy sediments are open systems characterized by high —and oftentimes both temporally and spatially dynamic— exchange rates of dissolved and particulate reactants and products. They act as biocatalytic filters that continuously extract reactive particles, including C_{org} and reactive Fe and Mn oxides, and dissolved nutrients from the water column into surface and subsurface sediment layers (Huettel et al., 1996; Huettel and Rusch, 2000; Rusch and Huettel, 2000). It has been shown that labile C_{org} can readily be transported into sediment depths of at least several centimeters during infiltration (Huettel and Rusch, 2000; Rusch and Huettel, 2000; Huettel et al., 2007). At the same time, the products of remineralization reactions within the sand matrix are advected into overlying water. The flow-through properties of permeable sands can thus, despite low C_{org} standing stocks, sustain high rates of C_{org} remineralization while at the same time preventing the build-up of reaction products, including Fe_d, ammonium, and dissolved inorganic carbon (DIC) (de Beer et al., 2005;

Volkenborn et al. 2007a; Huettel and Rusch, 2000; Huettel et al., 2014). These properties are fundamentally different from muddy cohesive sediment. Here, solute transport is driven by diffusion along concentration gradients, and solid-phase electron acceptors and C_{org} are deposited to the sediment surface. In contrast, vertical particle transport in muds only occurs by macrofaunal activity or by strong physical forcing, for example in mobile deltaic muds (Aller, 1998; Song, et al., 2022).

1.2 Bioturbation and bioirrigation in sands

There is a diverse community of macro-invertebrates living in marine surface sediments, for example numerous species of polychaetes, bivalves, crustaceans, and echinoderms, with a range of life histories and behaviors (feeding modes, burrow types, etc.; Kristensen and Kostka, 2005). These infaunal organisms represent an important modulator of the benthic-pelagic coupling in continental margin environments and affect the functional properties and biogeochemical processes in sandy sediments in a number of ways. The biological reworking of sediments, referred to as bioturbation, encompasses both *biomixing*, i.e., the physical re-working of sediment particles, and *bioirrigation*, i.e., the enhanced transport of pore-water and seawater associated with ventilation of burrows/tubes by animals (Kristensen et al., 2012). Biomixing is caused by feeding and burrowing activities (e.g., Meysman et al., 2005, 2008). It leads to the enhanced dispersal of particulate sedimentary components, including the simultaneous transport of labile C_{org} (reductant) and Fe and Mn oxides (oxidant) into deeper sediment layers (Aller, 1994; Thamdrup et al., 1994), and to the transport of reduced compounds, such as iron sulfides, and recalcitrant C_{org} into the oxic surface zone (e.g., Aller and Rude, 1988; Berner and Westrich, 1985; Van de Velde and Meysman, 2016).

Organisms that inhabit permeable burrows in sandy sediments drive advective transport of solutes (bioirrigation) during e.g., burrow ventilation, feeding, siphon movement, defecation or clearing of pseudofeces (Wethey and Woodin, 2005; Woodin et al., 2010). Bioirrigators can be divided into those forming open-ended (U- or Y- shaped) burrows and those with blind-ended (I- or J-shaped) burrows (Kristensen et al., 2012). The pumping activities of bioirrigators can result in different directions of flow, as animals oftentimes pump inward during burrow ventilation but flow can reverse during burrow excavation or defecation. Fluctuating pore-water pressure signals and thus porewater advection can be detected in the sediment at distances exceeding 50 cm from burrows (Volkenborn et al., 2010; Wethey et al., 2008). The downward pumping of water into burrows results in the injection of water into the surrounding sediment, especially at the depth of the feeding pocket for animals living in I- or J-shaped burrows (Meysman et al., 2006). This drives the advective transport of pore-water upward along the path of least resistance, often along the feeding funnel, out of the sediment (Banta et al., 1999; Rijken, 1979). Macrobenthic organisms that portray this type of behavior in sandy advective sediment often represent important species in coastal and estuary environments, such as the lugworm *Arenicola marina*, common along the European coast, and the bamboo worm *Clymenella torquata*, mainly found in the Northwest Atlantic. Studies on oxygen dynamics in sediments inhabited by these species show that the injection of overlying water into the feeding pockets results in the intermittent oxygenation of this subsurface zone while the upward movement of anoxic pore-water is expressed in a narrowing of the surface oxygenated zone and sometimes in plumes of anoxic exiting the sediment surface. In contrast, during under-pressurization, the surface oxygenated zone expands

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as oxygenated seawater is drawn in (Volkenborn et al., 2010). This highlights that intermittent pumping activity results in rapid redox oscillations in surficial sediment and adjacent to burrows on the scale of minutes to hours (e.g., Kristensen, 2000; Aller, 1994; Wenzhöfer and Glud, 2004; Volkenborn et al., 2010, 2012) leading to geochemically complex and dynamic microenvironments within otherwise geochemically stable deposits (see Aller, 2014 for review). Aside from pumping rates and the shape of macrofaunal burrows, the chemical composition and permeability of the burrow lining are important factors controlling the exchange of solutes in permeable sediments. Burrow linings can be made up of various materials ranging from almost unaltered sediment particles to organic mucopolysaccharides and proteins to fibrous tube linings consisting of cerianthin and parchment-type walls (Aller and Yingst, 1978; Aller and Aller, 1986; Lalonde et al., 2010; Konhauser et al., 2020). Consequently, burrow walls are characterized by varying microbial degradability, permeability and oxygen diffusivity (Aller, 1983; Zorn et al., 2006) and ability to directly adsorb metal cations (Konhauser and Gingras, 2011; Over, 1990).

Sediment-dwelling macrofauna also directly affect the overall sediment permeability through the preferential ingestion (followed by surface defecation) or excavation of fine particles (Ziebis et al., 1996; Volkenborn et al., 2007b, Wendelboe et al. 2013). Furthermore, particle transport during biomixing helps prevent sediment deposits from “clogging” which can result from the efficient infiltration and trapping of fine particles, including algal cells (Huettel et al., 2014). This renewal mechanism is critical to maintaining advective properties and thus the characteristic functioning of sandy sediments as low standing stock – high turnover flow-through systems that constantly exchange solutes and particulates with the overlying water column (Volkenborn et al., 2007a, b).

1.3 The effect of macrofaunal activity on the benthic Fe_d cycle and fluxes

Boundary conditions such as C_{org} supply, temperature, and overlying water oxygen concentration affect the sedimentary Fe cycle by regulating benthic community composition, metabolic activities/rates and interactions of the microbial and macrofaunal communities (Dauer et al., 1992; Herman et al., 1999; Nilsson and Rosenberg, 2000; Berelson et al., 2003; Bertics and Ziebis, 2009; Beam et al., 2020). The net effects of bioturbation on the sedimentary Fe cycle and the flux of Fe_d into the overlying water column in sandy advective sediments are complex. They depend amongst other things on the type and lifestyle of the organisms, i.e., functional traits, the spatial scaling of burrows and/or active organisms (population density; size distributions), and activity patterns of the organisms (Aller ,2001, Kristensen and Kostka, 2005; Michaud et al., 2021).

When biomixing results in the upward transport of recalcitrant C_{org} into the oxygenated surface layer, re-exposure to oxygen enhances overall organic carbon mineralization rates in surface deposits (see Aller, 1994; Kristensen, 2001; for review). The downward transport of both labile C_{org} and reactive Fe and Mn oxides into the anoxic zone promotes the occurrence of sulfate reduction and metal oxide reduction pathways in the anoxic zone of the sediment (Berner and Westrich, 1985; Canfield et al., 1993; Thamdrup et al., 1994; Van de Velde and Meysman, 2016), potentially allowing for a sustained supply of Fe_d to pore-waters that can be transported into the water column. Bioirrigation by infaunal organisms introduces oxygen into burrows and surrounding anoxic sediment, while at the same time enhancing the transport of nutrient- and metal-rich pore-water solutes into the overlying water across a range of sediment types (e.g., Aller, 1982, 2001; Kristensen and

Kostka, 2005). Enhanced Fe_d fluxes due to bioirrigation have been demonstrated using in situ incubation chamber measurements across several shelf sites dominated by muddy diffusive sediment (Berelson et al., 2003; Homoky et al., 2012; Severmann et al., 2010; Elrod et al., 2004). A modelling study by Van de Velde and Meysman (2016) supported the hypothesis that the transport of Fe_d to the water column is enhanced when bioirrigators are present. In contrast, Berg et al. (2003) and Dale et al. (2013) set their bioirrigation parameter to zero, and Dale et al. (2015) scaled theirs to 20% of the flux determined for other solutes, because these authors assumed (almost) quantitative oxidation of Fe^{2+} in burrows. We suggest that a more differentiated view based on the sediment mixing or bioirrigation modes of different macrobenthic functional groups and sediment types is warranted to more accurately evaluate Fe mobilization and transport by bioturbation. In our case study, we focus on bioirrigation impacts on Fe_d fluxes from permeable sands. We do so by experimentally simulating the bioirrigation behavior of the bamboo worm *Clymenella torquata* and its effects on advective flow, and by directly quantifying Fe_d fluxes.

2 Case study

2.1 Set-up of benthic chamber incubation experiments

We used cylindrical incubation chambers (polycarbonate, 14.6 cm ID, 27 cm height) filled with 15 cm of sediment and 12 cm of seawater to carry out a winter and a summer microcosm incubation experiment. For each experiment, sediment was collected at an intertidal flat at Old Ponqougue Bridge Marine Park (Shinnecock Bay), Hampton Bays, NY, USA. Sediment at this site is comprised of medium to fine grained sand (220 ± 15 µm; mean ± SD; Hildebrandt, 2017), with a typical porosity of 0.44 and a permeability of 1.6×10^{-11} m^2 (Dwyer et al., in prep.). The lower portions of the intertidal sand flat and the shallow subtidal are inhabited by high densities (up to ~2500 individuals m^{-2}) of the tube-building maldanid polychaete *C. torquata* which is a head-down deposit feeder that is widespread along the eastern coast of North America (Sanders et al., 1962). Seawater for the experiments was collected from the same site (with a salinity of 31 for summer and 34 for winter) and filtered (1 µm pore size).

The sediment retrieved from cores were sliced into three intervals (0-1 cm, 1-6 cm, 6-15 cm), sieved through 2 mm mesh to remove large fauna and shells and homogenized using large plastic spoons. For summer and winter experiments, six incubation chambers were constructed with the sediment following the original depth layering. Three of the chambers, hereafter called “irrigated cores”, were equipped with irrigation mimics (Na et al., 2008; Matsui et al., 2011) consisting of a mesh-covered inlet tube (0.5 cm ID) protruding upward from the radial center of the core base at 12 cm sediment depth and 3 cm above the bottom of the chambers. The mimics were used for injecting water from a reservoir tank into the sediment in pre-programmed irrigation patterns using a peristaltic pump. Season-specific pumping patterns were chosen to be representative of temporal bioirrigation behavior of *C. torquata* (Dwyer et al., in prep.). Specifically, an irrigation pattern of 3.75 minutes of pumping followed by 3.75 minutes of resting and 10 minutes of pumping followed by 10 minutes of resting was established in summer and winter, respectively, in both cases with a pumping rate of 0.39 ml min^{-1}. The respective total volume of solute injection per day of 281 mL falls in the typical range of the total volume of solute pumped by ~5 individuals of *C. torquata* over the same time period (Mangum, 1964). Cores were allowed to settle with recirculated overlying water for two to four days before irrigation was started. In addition, two "control" chambers were filled with seawater only (equivalent in volume to the overlying water in the experimental cores) to assess any presence of iron in our experimental setup that was not related to sediments.

The incubation chambers were connected to individual seawater reservoirs fitted with air stones for aeration to allow for continuous circulation and reoxygenation of the overlying water. At the outflow, the chambers were equipped with glass wool Fe extractors which allow for the quantification of the amount of Fe_d leaving the chamber water over a given period of time (Aller et al., in revision). Flow through the chambers was maintained at a flow rate of 32 mL min^{-1} for the winter experiment resulting in an overlying water turnover time of approximately 1 hour. For the summer experiment, the flow rate ranged from 32-64 mL min^{-1} as it was adjusted to maintain less than 10% in O_2 concentration change (between the inflow and outflow). To minimize pore-water advection by overlying water stirring, the chambers were stirred bidirectionally with magnetic stirring bars at ~100 rpm with a pattern of 15 sec clockwise, 15 sec paused, 15 sec counter clockwise, 15 sec paused. The experiments were carried out for 7 days (summer experiment, 21.4°C ± 0.2°C) and 13 days (winter experiment, 7.2°C ± 0.3°C) in a temperature-controlled room. Dissolved oxygen concentrations in water entering and exiting the chambers were monitored using Pyroscience or Presens fiber optic probes in one control core, one non-irrigated and two irrigated cores for each experiment. Iron extractor traps, consisting of 50 mL centrifuge tubes cut open at the bottom and loosely filled with 2 g of glass wool (Pyrex C3950, 8 µm diameter), were exchanged every ~24 hours (exact times were recorded) and frozen until analyses. Iron bound to the glass wool was extracted with 0.5 N trace metal grade HCl for 7.5 hours (Aller et al., in revision) and the leachate Fe concentration was analyzed using the Ferrozine method (Stookey, 1970). The Fe traps from the first days prior to the onset of irrigation were not included in flux calculations. Benthic Fe fluxes were calculated based on chamber dimensions and Fe extractor concentration values. Iron values for traps from the control cores without sediment were always below detection limit. After the completion of the experiments, pore-water samples were collected through pre-drilled ports on the sides of the experimental cores using Rhizons (Rhizosphere Inc.) at a spacing of 1-2 cm (Seeberg-Elverfeldt et al., 2005). Pore-water samples were stored cooled and concentrations of ammonium, a product of organic carbon mineralization, were determined within a few days by spectrophotometric analysis following Solórzano (1969). Ratios of ammonium inventories for the top 8.5 cm of summer and 9 cm of winter non-irrigated to irrigated cores were calculated from ammonium concentration profiles, using a porosity of 0.44.

2.2 Results benthic chamber incubation experiments

Overlying water O_2 concentrations in all experiments remained close to saturation with values at the chamber outflow lines of 228.8 ± 3.5 µM (mean and sd of control core without sediment), 217.5 ± 17.9 µM (non-irrigated core) and 199.4 ± 12.7 µM (irrigated cores) in the summer experiment and 292.4 ± 8.3 µM (control core), 290.7 ± 7.7 µM (non-irrigated core) and 294.6 ± 9.2 µM (irrigated cores) in the winter experiment. In all experiments, the highest Fe_d flux values were observed for the first two days after the experiment onset, likely due to higher carbon turnover rates following disturbance and the initial transient phase of the experiments (Banta et al., 1999). These initial values are not considered in the following discussion as

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this study focuses on the effect of bioirrigation on Fe_d. Iron fluxes from irrigated cores during summer (starting at Day 3) ranged from 67 to 115 µmol Fe m^{-2} d^{-1} while average values from the non-irrigated cores were between 9 and 13 µmol Fe m^{-2} d^{-1} (Fig. 1). Winter experiment irrigated cores showed similar fluxes to the summer experiment with values of 36 to 150 µmol Fe m^{-2} d^{-1} while average Fe fluxes from non-irrigated cores were very low with values of 0 to 6 µmol Fe m^{-2} d^{-1} (Fig. 1). Ratios of ammonium inventories of non-irrigated to irrigated cores at the end of the experiment were 9 for the summer experiment and 4 for the winter experiment.

3 Discussion

The role of sandy advective sediments in providing Fe to overlying waters by diffusive or advective transport is poorly constrained. In our experiments Fe_d fluxes from sandy Shinnecock Bay sediments in the absence of any macrofauna or simulated bioirrigation, i.e., when diffusion dominated, were relatively low, although intriguingly in the range of the average diffusive flux reported for continental shelf muds (Dale, et al., 2015). Values above detection were mostly determined for the summer experiment (Fig. 2). Similarly, undetectable or very low pore-water maximum diffusive fluxes were determined for sandy shelf sediments near Cape Lookout, North Carolina, using microelectrodes (and thus not accounting for bioturbation or organic-Fe(III)) (Eitel et al., 2020) and settings characterized by medium sands along the North Sea continental margin based on pore-water profiles (Slomp et al., 1997). The low diffusive fluxes at these sites were attributed to very low pore-water Fe_d concentrations reflecting low reactive Fe(III) contents of the sediments and a minor role of DIR in organic carbon mineralization. In the investigated sandy settings, including our non-irrigated cores, the oxygen supply to the surface sediment under diffusive conditions thus appears to be high enough to result in the almost quantitative precipitation of upward diffusing Fe_d (Huettel et al., 2014). The detection of the low Fe_d fluxes from our summer experiment can likely be attributed to the lower oxygen solubility at higher temperatures and potentially seasonal differences in labile C_{org} supply and Fe oxide inventories (Jensen et al., 2003; Cook et al., 2007; Herbert et al., 2021; Slomp et al., 1997; Neumann et al., 2021), as well as bioturbation by very small infauna that passed our sieves. Nonetheless, even summer fluxes from non-irrigated cores were relatively low with values not exceeding 13 µmol Fe m^{-2} d^{-1} (Fig. 1). These flux values can be regarded as a minimum estimate of Fe_d fluxes from the investigated sandy sediments under diffusive conditions only.

However, in sandy permeable sediments advective solute transport typically dominates over diffusive exchange (see Huettel et al., 2014, for review), and these deposits act as open systems governed by rapid oscillations in flow direction and rate (e.g., Volkenborn et al., 2010; Wethey et al., 2008). Concomitantly, reactive Fe oxides and pore-water Fe_d are often distributed heterogeneously in the sediment as a result of the complex three-dimensional geochemical zonation that is created by physical processes, e.g., associated with pressure gradients created by ripples and mounds (Huettel et al., 1998, 2014) or bioirrigation by benthic macrofauna (Aller, 1978). In our case study, average Fe_d fluxes from the irrigated compared to the non-irrigated cores during each sampling interval were 6-9 fold higher in summer and 5-50 fold higher in the winter experiments (in the cases where fluxes from the non-irrigated cores were detected). The elevated fluxes under irrigated

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conditions are the result of the additional advective transport of Fe_d across the sediment-water interface (Aller, 1978; Banta et al., 1999; Meysman et al., 2006). This Fe is produced during DIR throughout the anoxic zone of the sediment. Importantly, the intermittent irrigation of the subseafloor sediment associated with macrofaunal burrows (in our experiment irrigation mimics) enhances this Fe mobilization as it facilitates the re-oxidation of previously formed iron sulfides to iron (oxyhydr)oxides which can subsequently be reduced by DIR again (Fig. 2). The Fe_d leaves the sediment when the injected water percolates upward and pushes overlying pore-water containing Fe_d across the sediment-water interface into the water column (Fig. 2). Further, since this mechanism also results in a narrowing of the oxygenated surface zone, a large amount of Fe_d is not oxidized here but instead remains in solution. This is an important distinction from muddy diffusive sediments, where pore-water Fe_d concentrations are typically higher, but Fe_d is quantitatively oxidized when slowly diffusing upward and therefore does not escape the sediment. Lower NH_4^+ inventories of the irrigated compared to non-irrigated cores —assuming similar NH_4^+ production rates in both core types— reflect the additional, advective transport of solutes out of the sediment when the irrigation mimics are present. The ratio of NH_4^+ inventories at the end of the experiment of the non-irrigated to irrigated cores are remarkably close to the ratios of Fe fluxes from the two treatments during these seasons, further strengthening the assumption that when advective Fe_d transport occurs, Fe^{2+} escapes the sediment with little precipitation occurring. The observed values for benthic Fe_d fluxes from the irrigated cores in summer (67 to 115 μmol Fe m^{-2} d^{-1}) and winter (36 to 150 μmol Fe m^{-2} d^{-1}) are higher than would be predicted based on bottom water oxygen concentrations (Dale et al., 2015; Homoky et al., 2015) supporting the hypothesis that the additional transport of solutes by bioirrigation and advection strongly increases benthic Fe fluxes in sandy advective sediments.

After entering the overlying water column, the dissolved Fe^{2+} released from sandy advective sediments is likely rapidly reoxidized to nanoparticulate, colloidal and particulate Fe (oxyhydr)oxides (Raiswell and Canfield, 2012; Aller et al., in revision) or adsorbed onto suspended particulate Fe and Mn phases (Homoky et al., 2012; Richard et al., 2013). A fraction of the forming Fe(III) may also be stabilized by complexation with organic Fe(III)-binding ligands (Millero, 1998; Rue and Bruland, 1997; Taillefert et al., 2000; Jones et al., 2011), which have been previously detected in sandy coastal sediments (Eitel et al., 2020). The different Fe phases can be picked up by bottom currents and vertically mixed into surface waters as previously described for continental margin sites (e.g., Johnson et al., 1999; Elrod et al., 2004; Severmann et al., 2010). A large fraction of the particulate Fe phases, however, are likely rapidly re-deposited to the sediment. Complexed Fe(III) and reactive colloidal, nanoparticulate and particulate Fe oxides (along with fresh C_{org}) can be moved deeper into the sediment by biomixing as well as during rapid particle infiltration induced by advective transport associated with biogenic surface structures, e.g., mounds, and abiotic topographic features such as ripples (Huettel and Rusch, 2000; Rusch and Huettel, 2000; Huettel and Webster, 2001). These processes are of high importance in sandy advective sediments for re-supplying reactive Fe to the microbial Fe-reducing community and for reaction with H_2S and thus to replace the Fe_d lost by advective transport.

Our experiment tested the effect of *C. torquata* irrigation on benthic Fe_d transport at an approximate spatial scale of 300 individuals m^{-2} which is in the typical range of densities reported for this species (250-675 individuals m^{-2}; Mangum, 1964),

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although the distribution of this animal is often very patchy (Hildebrandt, 2018). Importantly, the influence of the benthic macrofaunal community on biogeochemical processes and metal fluxes is dependent on spatial scaling, i.e., the size and spacing of individual burrows or feeding pockets (Wethey et al., 2008; Aller, 2001; Michaud et al., 2009). One can envision that, given a particular labile C_{org} and reactive Fe oxide availability, there is an optimal size-density relation that maximizes and one that minimizes net fluxes of Fe_d. For example, if C_{org} availability is low and bioirrigation rates are high (i.e., pore-water residence times are short), the sediment remains oxygenated and/or remineralization controlled by denitrification occurs and little Fe_d will be produced. The apparent nonlinear dependence of net reaction rates and fluxes on transport scaling suggests that reaction balances are highly sensitive to small changes in burrow spacing and geometry (Braeckman et al., 2010; Aller, 2001). Additionally, interactions between different functional groups of infauna can promote or suppress diagenetic reactions depending on the specific species and processes (e.g., Teal et al., 2013; Levin et al., 2001; Waldbusser and Marinelli, 2006; Waldbusser et al., 2004).

Our experiment only simulates the bioirrigation activity of a typical head-down deposit feeder in sandy sediment while its particle reworking via feeding, defecation and burrowing is not represented (Na et al., 2008). Given that *C. torquata* tends to stay at a specific location/burrow for several days-weeks, however, bioirrigation likely represents the main mode of fluid transport in the sediments they inhabit. Particle movement during burrowing results in the concomitant movement of associated pore-water in the same direction as the sediment is transported. It is suggested that the amount of fluid moved in this way is an order of magnitude lower than what is transported by irrigation (Aller 1982, Kristensen, 2001, 2012). We expect that the vertical movement of particles by upward conveyors, such as *C. torquata*, during burrowing transports iron sulfides to the sediment surface which undergo reoxidation. This process, along with the passive movement of Fe oxides and labile C_{org} from the surface and surrounding sediment downward along the sides of the burrows, fuel the described Fe oxidation-reduction cycles in bioturbated sediments (Aller, 1980a; Canfield et al., 1993a). In addition, maldanids are well known to rapidly subduct surface sediment (Levin et al 1997), thereby replenishing the labile Fe oxide pool at depth. The high Fe_d fluxes we observe during the first two days of the experiments immediately following core constructions give an indication that vertical particle reworking and labile C_{org} burial, as occurring during biomixing, likely increase benthic Fe fluxes as these processes enhance carbon turnover rates in surface sediments.

A map of sediment type in the New York-New Jersey Continental Shelf Region (Fig. 3; Williams et al., 2017), including our study site, highlights that the sediment we examined is very common in this ocean region. Particularly the inner shelf is dominated by sand and gravel, while muddy deposits are found in specific locations on the slope (and dominate in Long Island Sound; Williams et al., 2017). Given that ocean waters along this shelf region are highly productive, as reflected in relatively high chlorophyll concentrations (Ma and Smith, 2022; Xu et al., 2011; Yoder et al., 2002), we expect macrofauna here to be important for biogeochemical processes in the sediment across the different continental margin habitats. Detailed studies of the macrobenthos in sediments of the Middle Atlantic Bight showed that polychaetes and crustaceans dominate the macrobenthic invertebrate community in this area (Boesch, 1979). Differences in macrofauna abundances (ranging in total densities from 250 individuals m^{-2} to 18,000 individuals m^{-2}) and species composition were observed between different sediment types and topographic habitats (e.g., ridges, shallow swale, upper shelf break), with the highest biomass distribution of annelids and molluscs on the outer shelf and in topographic lows and highest echinoderm biomass on the central shelf (Boesch, 1979; Gaston, 1987). Thus, we expect that advective Fe$_d$ transport and elevated fluxes driven by bioturbation is common over a large area in the New York-New Jersey Continental Shelf Region and therefore permeable sediments constitute a significant source of Fe to the productive surface waters. Given that sandy advective sediments are common on continental shelves (covering ~50-60 % of the shelf area; Hall, 2002), we suggest that bioturbation-driven Fe$_d$ supply from sandy advective sediments to continental shelf waters is a globally important mechanism.

4 Conclusions and outlook

Iron plays an important role in controlling primary production and nitrogen fixation in the ocean (Boyd and Ellwood, 2010; Martin and Fitzwater, 1988; Moore et al., 2002; Morel and Price, 2003; Tagliabue et al., 2017) and in regulating the ocean carbon cycle and ultimately atmospheric CO_2 concentrations (Martin, 1990; Martínez-García et al., 2014; Watson et al., 2000). A detailed understanding of the sources and cycling of Fe to the ocean are needed to decipher and predict changes to the ocean carbon cycle at present, in the past and with future climate change. Sedimentary release represents an important, yet poorly constrained, sources of this micronutrient to the ocean (e.g., Elrod et al., 2004; Johnson et al., 1999; Moore and Braucher, 2008; Tagliabue et al., 2014). The distinct biogeochemical function of permeable sandy sediments as dynamic flow-through bioreactors has not been explicitly considered in global Fe models. For muddy cohesive sediments, it has been shown that the contribution of DIR to C$_{org}$ oxidation is dependent on the poorly crystalline Fe(III) content of the sediment (Thamdrup, 2000; Jensen et al., 2003). Dissolved Fe fluxes appear to primarily scale to C$_{org}$ content and bottom water oxygen concentrations (Elrod et al., 2004; Homoky et al., 2016). To our knowledge no systematic studies have determined Fe$_d$ fluxes from sands or attempted to link benthic Fe$_d$ fluxes to C$_{org}$ and/or reactive Fe oxide availability in these deposits. Given that sandy advective sediments cover a large part of the continental shelves, this reveals a glaring gap in our understanding of the benthic Fe source to the ocean and the potential for a large error in global benthic Fe$_d$ flux estimates.

In this article, we describe the mechanisms underpinning the bioturbation-driven advective transport of Fe$_d$ from permeable sandy sediments and emphasize that this mode of transport is distinctly different from the diffusive Fe$_d$ release common for muddy cohesive sediments. We highlight that bioturbated sandy sediments can sustain a large benthic Fe$_d$ flux that exceeds the flux expected from bottom water oxygen concentrations. The determined flux values are similar to, for example, fluxes from muddy sediments of Fe-rich Arctic fjords (Wehrmann et al., 2014; Herbert et al., 2021) and other embayments (e.g., Galveston Bay, Warnken et al., 2001). We suggest that —given the ubiquitous presence of sandy advective sediments along continental shelves— bioirrigation and bioturbation coefficients specific to the different sediment types need to be considered and will likely provide a more realistic representation of the Fe$_d$ release from these deposits. To comprehensively parameterize sandy advective sediments in biogeochemical models, physical solute exchange at the sediment-water interface need to be included as well (see Huettel et al. (2014); Rühl et al. (2020), for review). Imposing diffusive conditions on sand deposits, as we have done in our chamber experiments, results in minimum estimates of Fe_d fluxes that likely severely underestimate fluxes from biologically active permeable sediments.

Furthermore, the functional groups that characterize the macrobenthic community are very diverse with various sediment mixing modes, bioirrigation depth and frequencies, etc., which likely drive different overall effects on biogeochemical Fe cycling and Fe_d fluxes. Previous studies have classified macrobenthos based on sediment type and topographic habitat reflecting the preference of species belonging to specific functional groups to distinct environmental parameters due to, for example, their feeding behavior and motility (e.g., Boesch, 1979; Gaston 1987; Jumars et al., 2015). Ecosystem-scale multi-parameter studies that link seafloor morphology to macrobenthos functional traits and key biogeochemical processes may represent valuable approaches that provide the key to deciphering the underlying patterns of interactions between bioturbation and biogeochemical processes and allow upscaling of predictive parameters to wider ocean areas (e.g., Fang et al., 2019; Gogina et al., 2018; Mestdagh et al., 2020; Norling et al., 2007; Thoms et al., 2018).

We advocate for a concerted multidisciplinary effort to better understand the rates, controlling factors, and seasonal dynamics of the benthic Fe cycle and Fe_d fluxes in sandy advective sediments across the ocean. Results from these studies will provide a quantitative basis for constraining and predicting dissolved Fe fluxes for different sedimentary facies, boundary conditions, and benthic community activity. An improved understanding of sedimentary Fe cycling and concomitant revision of global biogeochemical Fe models will enhance prediction of future responses of primary production to rapidly changing environmental conditions and to optimally infer past conditions from authigenic Fe minerals preserved in the sedimentary record. The benthic-pelagic Fe cycle is closely connected to the cycling of the macronutrient phosphorus and of trace metals, including Co, Ni, and Cu, which function as micronutrients but are toxic at high concentrations (Morel et al., 1991; Crompton, 1997; Whitfield, 2001; Sunda 2012). In the light of the observed and predicted vulnerability of continental shelf environments to anthropogenic effects, for example, increasing bottom water hypoxia, bottom trawling, loss of benthic biodiversity and species density, enhanced deposition of C_{org} from eutrophication, and global climate-driven changes such as future expansion of oxygen minimum zones, these efforts are of immediate importance for our understanding of biogeochemical feedbacks linked to carbon cycling, as well as the progressive changes of these ecosystems in the centuries to come.

Data availability

The data presented in this manuscript will be available on BCO-DMO following manuscript acceptance.

Author contribution

LMW, NV, and RCA conceptualized and acquired funding for this research. IPD and DASP collected field samples. All authors carried out the laboratory experiments. IPD acquired and processed the O_2 data and DASP and CH carried out the laboratory geochemical analyses. LMW prepared the original draft of the manuscript and all authors reviewed and edited the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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Figures

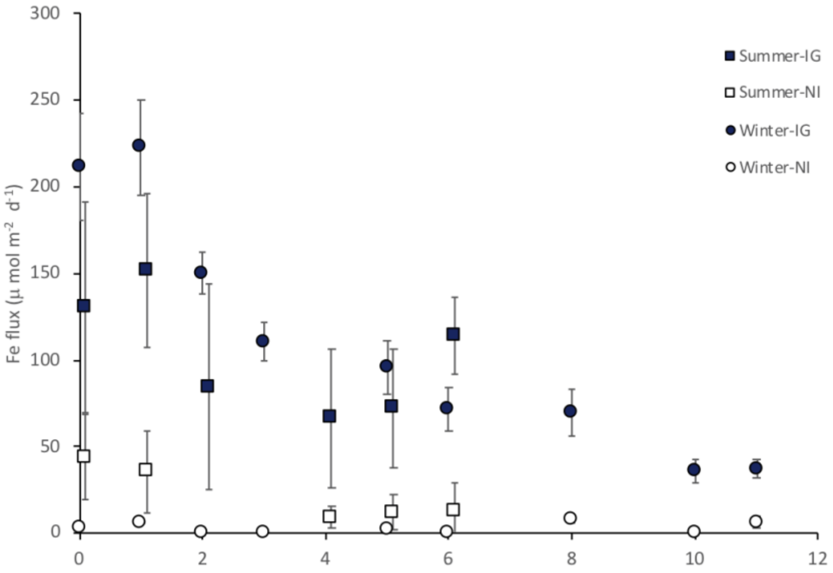

Figure 1: Mean and standard deviation of dissolved iron (Fe_d) fluxes calculated for irrigated (IG) and non-irrigated (NI) cores in the summer (n=3) and winter (n=3 for NI and n=4 for IG) experiments.

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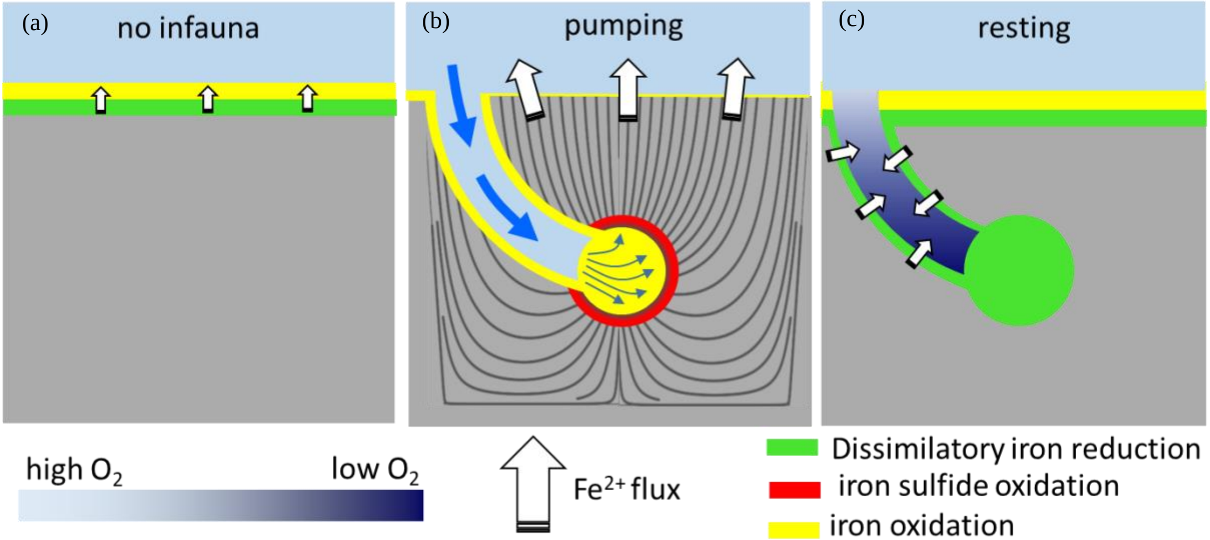

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Figure 2: Conceptual schematic of O_2 distribution, and redox-sensitive iron cycling processes in permeable sediments without infauna (a), and in the presence of infauna with blind-ending burrows during burrow ventilation (b) and resting (c).

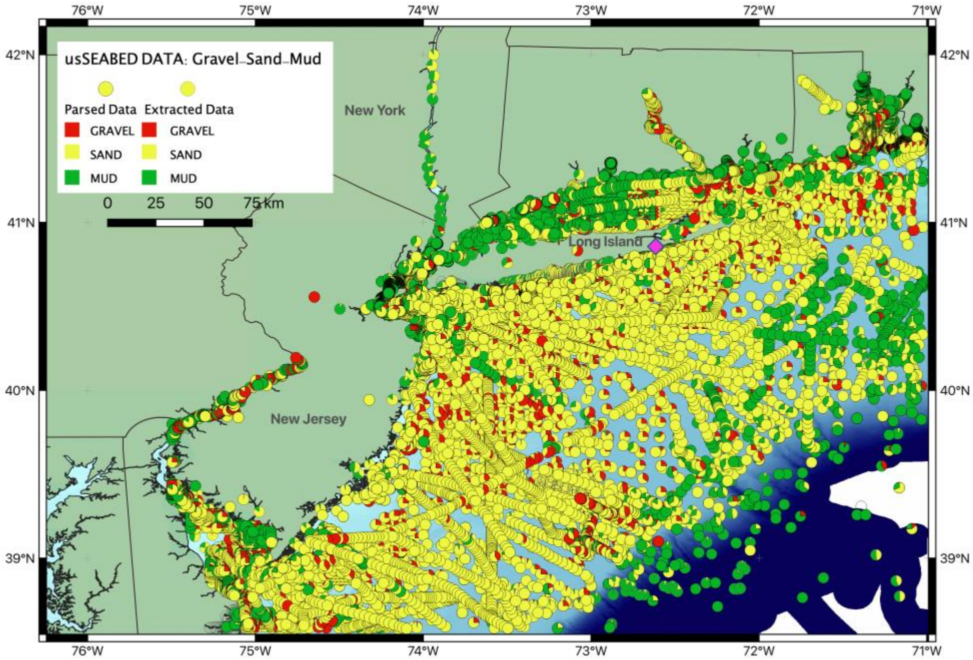

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Figure 3: Map of sediment composition (gravel-sand-mud percentages) of the New York-New Jersey continental shelf based on the integrated usSEABED sea-floor-characterization database (adapted from Williams et al. (2007)). Our study site is shown by a pink star. Map created using the Free and Open Source QGIS.