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Interactions Between Sulphur-Oxidizing Bacteria and Sediment Chemistry in Brackish Water Ecosystems

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Abstract: Brackish water ecosystems like estuaries and lagoons are subject to high organic matter loads and the sulphide produced by microbial sulphate reduction in the sediments can build up to toxic levels, diffuse to the overlying waters and exacerbate hypoxia. Biological barrier to this sulphide consists primarily of sulphur-oxidizing bacteria (SOB), but their relationship with the sediment chemistry along the salinity gradient is not well quantified. A one-dimensional reaction–transport model (1 D RTM) of an 8 cm nonbiological column of brackish sediment was used to investigate the distribution of oxygen, sulphide, and sulphate for three functional configurations (abiotic – only oxidation, canonical aerobic SOB, and SOB with filamentous cable bacteria) at 3, 8, 15 and 25 under normoxic (250 μmol L^{-1}) and hypoxic (60 μmol L^{-1}) bottom water. The salinity increases from 3 to 25 led to an increase in sulphate reduction from 3.5 to 6.6 mmol m^{-2} d^{-1}, and in maximum porewater sulphide from 350 to 702 μmol L^{-1}. If not for biological oxidation, there would have been overlap in the presence of oxygen and sulphide for 13.5 mm and approximately 71% of sulphide would have been lost to the water column. Aerobic SOB oxidized 82% of the sulphide, reduced the oxic layer to 4.4 mm and reduced the sulphide efflux by approximately 800-fold. Cable bacteria accounted for up to 83% of sulphide oxidation and achieved 82% reduction of peak sulphide. Hypoxia caused a significant decrease in buffering capacity in canonical SOB while the electrogenic pathway also reduced sulphide efflux by 84%. The findings suggest that the composition of sulphur-oxidising community – not salinity per se – determines whether brackish sediments are sulphide sinks or sources.

Keywords: Sulphur-Oxidizing Bacteria; Cable Bacteria; Sulphate Reduction; Porewater Sulphide; Brackish Sediments; Estuarine Biogeochemistry; Reaction–Transport Modelling; Hypoxia.

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I. Introduction

The brackish water ecosystems are in the transitional zone between the river and the sea and are represented by estuaries, coastal lagoon, tidal creek, mangrove channel and semi enclosed basin. They are among the most productive aquatic systems on earth, providing fisheries, aquaculture, bird habitat and enabling the livelihoods of large coastal populations. However, their productivity is accompanied by a significant input of organic matter to the sea bed as a result of in situ primary production as well as riverine and anthropogenic sources. A large fraction of this organic matter is decomposed in the top few centimetres of the sediment; oxygen is used up within millimetres of the sediment surface, so anaerobic processes control carbon turnover. In coastal sediments, dissimilatory sulphate reduction is the most important of these pathways and can contribute up to 50% of the mineralisation of organic carbon (Jørgensen, 1982). The final result of this process is hydrogen sulphide, which is very toxic for benthic fauna, seagrass roots and fish, and when re-oxidized consumes oxygen, and can cause euxinia when it escapes from the sediment. The fate of sulphide is, therefore, a major issue in the wellbeing of brackish water ecosystems. The majority of the sulphide formed in coastal sediments is re-oxidized, either chemically or biologically, within the sediment (Jørgensen, 1982; Wasmund et al., 2017) with only a small proportion permanently buried as iron sulphide and pyrite. Oxygen-driven chemical oxidation is relatively slow at the low concentrations in porewater, whereas oxidation by Fe and Mn oxides relies on the availability of Fe and Mn oxides and bioturbation. Biologically catalysed oxidation by sulphur-oxidizing bacteria (SOB) is therefore the critical sink which removes sulphide from the water column. SOB is an extremely heterogeneous group, physiologically and phylogenetically.

They oxidise sulphide, elemental sulphur, thiosulphate and sulphite to oxygen and/or nitrate through enzymatic systems like the periplasmic Sox multienzyme complex, sulphide:quinone oxidoreductase and the reverse dissimilatory sulphite reductase pathway (Friedrich et al., 2001; Ghosh & Dam, 2009). Many are fixers of carbon dioxide chemolithoautotrophically, and thus are in the position of linking the sulphur cycle with dark primary production in sediments. Molecular surveys of coastal and intertidal sediments have revealed that uncultured members of the Gammaproteobacteria, along with *Epsilonproteobacteria* (now *Campylobacterota*) and *Alphaproteobacteria* are the predominate group of sulphur oxidizers, and contribute to a significant fraction of sulphur oxidation and inorganic carbon fixation (Lenk et al., 2011). A survey of coastal sediments further indicated that a handful of ubiquitous gammaproteobacterial clades make up the vast majority of dark carbon fixation with sulphur compounds as primary energy source (Dyksma et al., 2016). The organisms are usually found in the narrow region where downward diffusion of oxygen and upward diffusion of sulphide overlap and where the organisms are also usually competing with abiotic reactions for both oxygen and sulphide.

Their activity affects the redox boundary, consumes much of the flux of oxygen into the sediments, and controls the oxic surface layer of sediments that supports aerobic fauna. The traditional view of the sediment redox zonation has been altered by a second group of sulphur oxidizers that has recently been discovered. In 2010, electric currents were demonstrated to tie up sulphide oxidation in deeper, anoxic sediment with oxygen reduction at the surface of the sediment, over distances greater than 1 cm (Nielsen et al., 2010). Later, the agents of this long-distance electron transport were determined to be filamentous bacteria of the family *Desulfobulbaceae*, commonly known as cable bacteria, which carry electrons along long, multi-cellular filaments extending up to a centimetre in length (Pfeffer et al., 2012). Since then, cable bacteria have been discovered in many different marine and brackish habitats, such as seasonally hypoxic basins, salt marshes and mangrove sediments (Malkin et al., 2014). They leave behind a geochemical signature: an anoxic suboxic zone several millimetres to centimetres deep with neither oxygen nor free sulphide, acidification of the anodic zone, and dissolution of FeS and FeCO3, and alkalinization of the surface oxic layer (Malkin et al., 2014). Cable bacteria activity in a seasonally hypoxic coastal basin created a reservoir of iron oxides on the surface of the sediment that subsequently trapped sulphide, and delayed the onset of euxinia which was termed a sulphide firewall (Seitaj et al., 2015).

Brackish systems are especially difficult to study these interactions because the sediment chemistry is greatly varying along the salinity gradient. The concentration of sulphate in the bottom water increases with salinity from < 1 mmol L^{-1} in the oligohaline to ~ 28 mmol L^{-1} in fully marine water, and the availability of sulphate determines the extent and depth distribution of sulphate reduction. Riverine inputs provide iron in the form of a reactive species that can bind sulphide as FeS, and seasonal stratification and eutrophication often lead to hypoxic conditions at the bottom. All of these variables influence the availability of sulphide and oxygen to the sulphur-oxidizing community and the community affects the chemistry of the pore water. Field studies usually only record a single site or a single season and do not separate out the role of the microbial community from the physical and chemical. There are models that allow for the separation of these effects, called process-based reaction–transport models. A model can help determine the relative contribution of the microbial community to the observed chemical zonation if transport and the supply of organic matter are kept constant and the oxidation pathways are changed.

The present study was thus designed to quantify the interaction between SOB and sediment chemistry in brackish water ecosystem using one-dimensional diagenetic model. The study aimed to answer the following questions: (i) how sulphate availability changes with salinity affect sulphide production and porewater chemistry; (ii) how canonical aerobic SOB and electrogenic cable bacteria control oxygen penetration, sulphide accumulation and sulphide efflux; and (iii) how bottom-water hypoxia changes the buffering capacity of each functional configuration. The findings are discussed in relation to the health of the ecosystem, monitoring and management of estuaries, lagoons and brackish aquaculture areas.

II. Materials and Methods

Conceptual Framework and Study Design

The study is representative of a typical fine-grained, organic-rich, brackish sediment of the sheltered embayments, lagoon basins and mangrove creeks. These sediments are usually muddy, highly porous and poorly bioturbated, and molecular diffusion is the most important transport process for solutes in the top centimetres. The design was based on a 3-factor factorial modelling experiment. First, salinity was varied to cover the Venice classification: Oligohaline at 3, Mesohaline at 8, Polyhaline at 15 and Lower Euhaline at 25. The second factor was the functional configuration of the sulphur-oxidizing community: (a) abiotic oxidation only, in which sulphide is oxidized at the oxic–anoxic interface at the slow chemical rate; (b) canonical aerobic SOB in which sulphide is oxidized at the oxic–anoxic interface at the slow chemical rate and is microbially catalysed; (c) SOB combined with cable bacteria in which a second electrogenic pathway consumes sulphide in the suboxic zone and prodigiously releases oxygen at the surface. The third factor was bottom-water oxygen, which was kept at 250 μmol L^{-1} for normoxic conditions and reduced to 60 μmol L^{-1} for a hypoxia test at salinity 15. This resulted in 12 normoxic and 3 hypoxic scenarios.

Model Domain and Transport

The model domain spanned from the sediment–water interface up to 8 cm depths and has been subdivided into 320 layers, each 0.25 mm thick, which is suitable to resolve the millimetre-scale oxic zone. The porosity was assumed as 0.85 which is the typical value for brackish mud and kept constant as the depth increases. The three solutes modelled were dissolved oxygen, total dissolved sulphide ($H_2S + HS^-$) (sulphide) and sulphate. The transport of oxygen, sulphide and sulphate was described by Fick's second law and the effective diffusion coefficients were corrected for tortuosity, taking the value of the porosity (φ) as 0.4 for oxygen and 0.35 for sulphide and sulphate. Burial and bioirrigation were not counted, so their interactions with diffusion and reaction have been eliminated. Concentrations were maintained at values at the bottom at the upper boundary, and a zero gradient condition was used at the lower boundary. The salinity of the bottom-water sulphate was increased conservatively by dividing the salinity by 35, resulting in 2.4, 6.4, 12.0 and 20.0 mmol L^{-1} for the four bottom-water salinity levels, and the bottom-water sulphide was considered to be zero.

Reaction Network

The mineralization of organic matter was prescribed to be an exponentially decreasing function of depth, $R(z) = R_0 \exp(-z/L)$, where R_0 = 1000 μmol C L^{-1} d^{-1} and L is the attenuation length, which was prescribed to be 2 cm. This integrates to about 17 mmol C m^{-2} d^{-1}, which is within the range reported for eutrophic estuarine and lagoon sediments. Because mineralization can take place either in the presence of oxygen by aerobic respiration or below the oxic zone by sulphate reduction, the mineralization was divided into these two pathways and a half-saturation constant for oxygen (8 μmol L^{-1}) was used to ensure aerobic respiration was the predominant pathway when oxygen was present and sulphate reduction was the predominant pathway below the oxic zone. Sulphate reduction was found to be according to Monod kinetics, with a half-saturation constant of 1.6 mmol L^{-1}, and thus sulphate limitation was observed at low salinity. One mole of sulphide was produced for every 2 moles of organic carbon oxidized. Four processes were used to remove sulphide. Abiotic oxidation was of oxygen and was second order with a rate constant of 0.002 μmol-1 L^{-1}. The second-order expression in oxygen and sulphide with a rate constant of 10 μmol^{-1} L d^{-1} for the reaction corresponded to biologically catalysed oxidation (BCO) by the canonical SOB reaction and was ~4 orders of magnitude faster than the abiotic reaction, indicating the dominance of microbial catalysis at the oxic–anoxic interface (Wasmund et al., 2017; Lenk et al., 2011). Iron sulphide precipitation was found to be a first order sink with rate constant of 0.03 d-1, which corresponds to a moderate supply of reactive iron. The spatial separation of the anodic and cathodic half-reactions (Nielsen et al., 2010; Malkin et al., 2014) is assumed to represent a first-order anodic reaction in sulphide (rate constant 20 d^{-1}) only in the top 4 cm and where oxygen is below 1 μmol L^{-1}. It was balanced by a cathodic sink of oxygen

of 2 mol O_2/moles sulphide, and this was distributed where it was needed, according to the concentration of oxygen in the oxic zone. Sulphur mass was conserved in the domain in both aerobic oxidation pathways, with the oxidized sulphur being returned to the sulphate pool, apart from the burial of FeS and efflux to the water column.

Numerical Solution and Output Variables

The coupled system of partial differential equations was approximated numerically using a finite-volume method and solved using an implicit backward-differentiation solver in Python (NumPy and SciPy) over a simulated time period of 3000 days, which represents the end of the simulations. All the simulations were performed to steady state over a simulated time period of 3000 days using the finite-volume method and an implicit backward-differentiation solver, both implemented in Python (NumPy and SciPy). Eight indicators were used to summarise model output that could be directly compared with field measurements: oxygen penetration depth (OPD, depth at which oxygen dropped below 1 μmol L^{-1}); sulphide onset depth (depth at which sulphide first exceeded 5 μmol L^{-1}); peak porewater sulphide; depth-integrated sulphate reduction rate; diffusive oxygen uptake (DOU) at the sediment–water interface; diffusive sulphide efflux to the water column; and the proportions of sulphide produced removed by SOB, by cable bacteria and by iron sulphide formation. These indicators relate to microsensor profiles of oxygen and sulphide, to colorimetric analysis of porewater sulphide (Cline, 1969) and to the determination of acid-volatile sulphur and chromium-reducible sulphur in the sediment solid phase Canfield et al., (1986) in field programmes, so that field data can be directly compared with model output.

III. Results

Porewater Zonation Under the Three Functional Configurations

Under the three functional configurations, porewater zonation has been modeled for the following characteristics: At the same salinity and organic matter supply, the sulphur-oxidizing community in the functional configuration resulted in significantly different porewater profiles (Figure 1a). Only by abiotic oxidation could oxygen reach 13.9 mm at salinity 15 and sulphide appeared at 0.4 mm, thus forming a zone of coexistence between oxygen and sulphide that is 13.5 mm thick. Chemical oxidation was not effective enough in the zone to remove sulphide, and sulphide diffused across the zone at 3.19 mmol m^{-2} $d^{-}1$, a rate of approximately 71% of the sulphide generated (Table 1; figure 1b). Only 25% of the sulphide was retained as iron sulphide and about 3% was chemically oxidized.

The zonation was completely altered after activation of canonical SOB. Nearly 800-fold more sulphide was lost by SOB oxidation (82%) than through iron sulphide formation (18%), and the overlap between the sites of sulphide oxidation and iron sulphide formation was reduced to approximately 2 mm. The rate of sulphide efflux was reduced by nearly 800-fold from 6.7 to 4.1 mmol m^{-2} d^{-1}. However, the sulphide concentration in pore water that exceeded the oxic–anoxic boundary (oxic–anoxic boundary), remained high at 658 μmol L^{-1} since aerobic SOB do not function at the deeper layers where the sulphide reservoir is located.

In the presence of cable bacteria, sulphide was mostly depleted from the top 3 cm and maximum sulphide concentration reached 116 μmol L^{-1}, which is 82% lower than in the SOB-only case. Cable bacteria oxidized 83% of the sulphide while canonical SOB was responsible for only 15%. Despite the increase in oxygen uptake to 15.0 mmol m^{-2} d^{-1}, which was achieved via cathodic oxygen consumption, the zone of direct oxygen–sulphide contact remained around 1 mm and the depth of penetration of oxygen increased to 7.1 mm owing to the removal of sulphide by the cable bacteria. The concentration of iron sulphide was reduced below 2% of sulphide production because there was not much free sulphide left to react with Fe in the upper sediment layer.

Table 1: Steady-State Model Indicators for The Three Functional Configurations Across Salinity and Bottom-Water Oxygen Conditions

Salinity (SO_4^{2-}, mmol L^{-1})	Configuration	OPD (mm)	H_2S onset (mm)	Peak H_2S (µmol L^{-1})	SR (mmol m^{-2} d^{-1})	DOU (mmol m^{-2} d^{-1})	H_2S efflux (µmol m^{-2} d^{-1})	SOB (%)	CB (%)
3 (2.4)	Abiotic	14.1	0.4	371	2.56	6.65	1,847	0.0	0.0
3 (2.4)	SOB	5.9	4.1	350	3.50	9.27	1.8	83.4	0.0
3 (2.4)	SOB + cable bacteria	8.9	8.6	77	3.63	11.61	1.8	16.5	81.6
8 (6.4)	Abiotic	13.9	0.4	582	3.92	6.70	2,802	0.0	0.0
8 (6.4)	SOB	4.6	2.9	567	5.39	11.62	2.9	82.4	0.0
8 (6.4)	SOB + cable bacteria	7.6	6.6	105	5.08	13.93	2.5	15.2	82.9
15 (12.0)	Abiotic	13.9	0.4	667	4.46	6.71	3,187	0.0	0.0
15 (12.0)	SOB	4.4	2.4	658	6.17	12.67	4.1	82.1	0.0
15 (12.0)	SOB + cable bacteria	7.1	6.1	116	5.69	14.95	2.8	14.8	83.4
25 (20.0)	Abiotic	13.9	0.4	708	4.73	6.72	3,377	0.0	0.0
25 (20.0)	SOB	4.1	2.4	702	6.57	13.21	5.1	82.0	0.0
25 (20.0)	SOB + cable bacteria	7.1	5.9	122	6.02	15.50	3.0	14.6	83.6
15 (12.0), hypoxic	SOB	2.1	0.4	728	6.87	8.54	1,802	55.4	0.0
15 (12.0), hypoxic	SOB + cable bacteria	2.1	1.4	116	6.96	14.03	295	6.7	87.6
15 (12.0), hypoxic	Abiotic	7.4	0.1	730	5.96	3.02	4,678	0.0	0.0

Note. SO_4^{2-} = bottom-water sulphate; OPD = oxygen penetration depth; H_2S onset = depth at which sulphide exceeds 5 µmol L^{-1}; SR = depth-integrated sulphate reduction; DOU = diffusive oxygen uptake; efflux = diffusive sulphide flux to the water column; SOB and CB = percentage of produced sulphide oxidized by sulphur-oxidizing bacteria and cable bacteria; Abiotic = chemical oxidation only. Hypoxic scenarios were run at salinity 15 with 60 µmol L^{-1} bottom-water oxygen; all others at 250 µmol L^{-1}.

Effect of Salinity on Sulphate Reduction and Sediment Chemistry

The production of sulphide was controlled by saltiness and by the availability of sulphate (Table 1). Under SOB configuration, the depth-integrated SR (DISR) was increased from 3.50 mmol m-2 d-1 for salinity 3 to 5.39, 6.17, and 6.57 mmol m-2 d-1 for salinity 8, 15 and 25, respectively. Sulphate (2.4 to 6.4 mmol L-1) was close to the half-saturation range and depth-related depletion of sulphate occurred in the bottom-water between salinity of 3 and 8, while above salinity 15 the response leveled off when sulphate reduction approached saturation. Peak porewater sulphide increased from 350 to 702 µmol L^{-1}, whereas diffusive oxygen uptake increased from 9.3 to 13.2 mmol m^{-2} d^{-1}, as it was necessary to reoxidize more sulphide at the interface. Consequently, the oxic layer became thinner (5.9-4.1 mm) across the salinity range. Within each salinity configuration the relative fate of sulphide remained quite consistent despite production changes. In all four SOB-only scenarios, SOB removed 82–83% of the sulphide, while the cable bacteria took out 82–84% of the sulphide in all four electrogenic scenarios. However, in absolute terms, sulphide efflux increased with salinity (from 1.8 to 5.1 µmol m-2 d-1 in the presence of SOB, but remained low compared to the abiotic case (from 1.85 to 3.38 mmol m-2 d-1). So, the sulphide produced was a function of salinity, and the sulphur-oxidizing community was responsible for the fate of the sulphide.

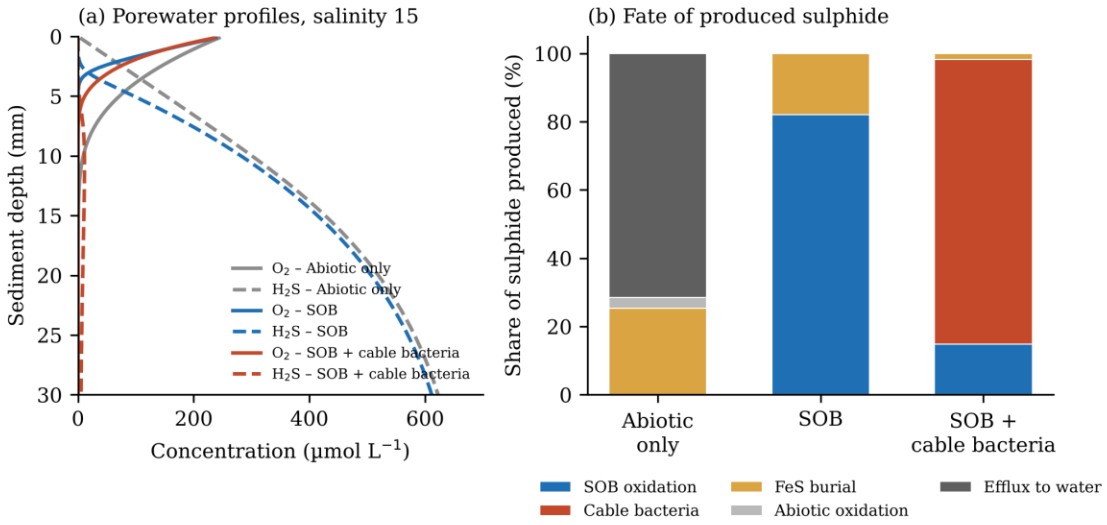


Figure 1: (a) Modelled Steady-State Porewater Profiles of Oxygen (Solid Lines) And Sulphide (Dashed Lines) At Salinity 15 For the Three Functional Configurations; (B) Fate of The Sulphide Produced by Sulphate Reduction Under the Same Conditions

Response to Bottom-Water Hypoxia

At salinity 15, there was a clear difference between the two biological pathways when the oxygen concentration in the bottom water was lowered to 60 µmol L-1 (Table 1). In the case of SOB alone, the penetration of oxygen reached 2.1 mm, sulphides appeared at the top layer of the sediment and the contribution of sulphide oxidation by SOB dropped from 82% to 55%. The sulphide efflux increased from 4.1 to 1.80 mmol m-2 d-1 which is 26% of the sulphide production. Where cable bacteria were present, they also inhibited the cathodic reaction, but the anodic oxidation of sulphide in the suboxic zone proceeded and most of the sulphide was removed by the action of the cable bacteria (88%). Peak sulphide levels were 116 µmol L^{-1}, and the rate of sulphide efflux was 0.29 mmol m^{-2} d^{-1}, which is 84% less than in the case of the SOB alone, and 94% less than in the abiotic hypoxic case (4.68 mmol m^{-2} d^{-1}).

IV. Discussion

Sulphur-Oxidizing Bacteria as Gatekeepers of The Sediment–Water Interface

The model results are also in quantitative agreement that the biological sulphide oxidation is the principal process to maintain sulphide in brackish sediments. In the absence of chemical oxidation, the majority of sulphide was lost, which is rarely seen in the oxygenated coastal waters and further supports the conclusion that microbial catalysis are the main agents of sulphide reoxidation in nature (Jørgensen, 1982; Wasmund et al., 2017). The presence of SOB pushed the sulphide front closer to the sediment surface and focused oxygen uptake in a very thin layer, which is typical of microsensor profiles in organic rich coastal muds, where the oxic layer is typically less than a few millimetres thick (Malkin et al., 2014). It is also evident from the increased oxygen uptake from SOB activity that a large proportion of sediment oxygen demand in brackish systems is not directly associated with the respiration of organic matter but with re-oxyldation of reduced sulphur. This is of practical importance, because sediment oxygen demand is often used as a measure of organic loading, but in part reflects activity of the sulphur-oxidizing community. This dominance of chemolithoautotrophic SOB at the redox boundary also suggests that significant amounts of energy are recycled to the production of new biomass through dark carbon fixation (Lenk et al., 2011; Dyksma et al., 2016). In brackish food webs this microbial production can lead to higher trophic levels in the sulphur cycle, via the deposit feeders and meiofauna. The buffering modelled here, under oxygen as the

only oxidant, is likely to be conservative for nitrate-rich estuaries because of SOB's physiological versatility, such as its ability to use nitrate as an alternative electron acceptor and to store elemental sulphur (Friedrich et al., 2001; Ghosh & Dam, 2009).

Salinity, Sulphate and The Brackish Gradient

The salinity experiment shows a saturating response of sulphate reduction to sulphate availability. Sulphate was limiting below the upper centimetre at low salinity while at higher salinity organic matter was limiting sulphate reduction. This is consistent with the overall trend that sulphate reduction becomes the main anaerobic pathway in marine and polyhaline sediments while methanogenesis and iron reduction becomes more important in oligohaline and freshwater sediments (Jørgensen, 1982; Wasmund et al., 2017).

No methanogenesis were modeled, so the decrease in sulphate reduction at low salinity is not balanced by another pathway, but in real sediments of low salinity, coupling of anaerobic methane oxidation and sulphate reduction would compensate for this. A key result is that there was no effect of salinity on the relative effectiveness of SOB. This means that the sulphur-oxidizing guild can be kept up with increased sulphide production provided there is sufficient oxygen supplied from the water column. Sea level rise and lower river discharge/abstraction will increase the sulphide production from previously oligohaline sediments due to the increased supply of sulphate. From the above results, it is clear that this would primarily lead to thinner oxic layers and higher pore water sulphide levels, with no direct escape of sulphide unless a functional SOB community does not exist, or if bottom water is depleted of oxygen.

Cable Bacteria, Iron and The Sulphide Firewall

The electrogenic configuration produced the largest change in porewater chemistry. By oxidizing sulphide in the suboxic zone and passing electrons to oxygen at the surface, cable bacteria disconnected sulphide removal from direct contact with oxygen (Nielsen et al., 2010; Pfeffer et al., 2012). In the model, this lowered peak sulphide by more than 80% and almost eliminated iron sulphide formation in the upper sediment. In real sediments, the acidification of the anodic zone dissolves iron sulphides, and the released ferrous iron diffuses upward and is oxidized to iron oxides at the surface (Malkin et al., 2014). This process was not represented explicitly, but the low iron sulphide share in the electrogenic scenarios is consistent with it. The resulting layer of iron oxides can later capture sulphide when oxygen falls, which explains why cable bacteria activity in spring delayed sulphide release in a seasonally hypoxic basin (Seitaj et al., 2015).

The hypoxia experiment adds a further dimension. Canonical SOB depends on simultaneous access to oxygen and sulphide, so their efficiency declines when the oxic zone becomes very thin. Cable bacteria can bridge a larger distance and continue to oxidize sulphide at depth as long as some oxygen is available at the surface. In the model they still prevented 84% of the sulphide efflux that occurred with SOB alone under hypoxia. For brackish systems prone to seasonal oxygen depletion, such as stratified estuaries, lagoon basins and intensively used aquaculture ponds, the presence of an active cable bacteria population may therefore be an important factor delaying the transition from hypoxia to sulphidic bottom water.

Implications for Monitoring and Management

The analysis has three implications for management. Combining oxygen penetration depth, porewater sulphide profiles and solid-phase sulphur pools should be done in sediment chemistry monitoring in brackish ecosystems, as these indicators jointly inform on the buffering of sulphide due to biological or chemical processes. The presence of a thin oxic layer with low porewater sulphide suggests electrogenic sulphur oxidation, while a thin oxic layer and high shallow sulphide suggests dependence on canonical SOB and thus vulnerability to hypoxia. Second, the microbial community must be considered a functional part of ecosystem resilience. Physical disturbance from trawling and dredging, strong bioturbation and periodicity of anoxia are known to interrupt the cable bacteria filaments, thereby reducing the capacity of the sediment to store sulphide. Third, the nutrient load reduction is still the most important measure, as it will also reduce the supply of organic matter, and the production of sulphide will then be even more sensitive to the level of organic loading and sulphide supply than to the share oxidized by SOB.

Limitations

The model is a simplified model of a complex system. It applies steady state and constant porosity conditions, neglects bioturbation, bioirrigation, burial, methanogenesis, nitrate reduction, manganese cycling, and assumes that the formation of iron sulphide is a first order sink, with no explicit iron and pH dynamics. The values were not calibrated to a particular site, but rather were set within a realistic range of values for rate constants for biological oxidation and should be considered illustrative of biological oxidation processes rather than as predictions for any specific estuary. The relative differences between the configurations, however, were solid, since the inputs of supplies of organic matter and transport were the same among these configurations. An obvious next step is to validate paired microsensor, porewater and microbial community data from brackish sites, as well as to explicitly model pH, iron and transient hypoxic events.

V. Conclusion

The interaction between sulphur-oxidizing bacteria and sediment chemistry is the most important factor in determining whether the sediments contain or do not contain toxic sulphide, according to this modelling study. The production of sulphide was controlled by salinity, with the increase in sulphate reduction nearly doubling from 3.5 to 6.6 mmol m^{-2} d^{-1} between salinity 3 and 25, and peak porewater sulphide increased with salinity. The fate of this sulphide, however, was determined by the composition of the sulphur-oxidizing community. If there were no biological catalysis, oxygen and sulphide would have been present together for more than a centimetre and about 71% of the sulphide would have been lost to the overlying water. At all salinities, nearly 82% of the sulphide was oxidized by Canonical aerobic SOB, whereas high levels of sulphide remained at depth, and the efflux of sulphide was reduced by almost 3 orders of magnitude and sediment oxygen uptake doubled. When the canonical SOB lost a considerable amount of their buffering capacity, cable bacteria shifted oxidation into the suboxic zone, reduced sulphide peaks by more than 80% and effectively retained sulphide under hypoxic bottom water. In estuaries, lagoons, mangrove creeks and brackish aquaculture systems these results suggest that sediment oxygen demand and sulphide risk is not only dependent on organic loading and salinity, the condition of the microbial sulphur-oxidizing community needs to be taken into account. Therefore, monitoring programmes should integrate oxygen penetration depth, porewater sulphide profiles and solid-phase sulphur pools, and management should minimise nutrient inputs and physical disturbance which could lead to disruption of electrogenic microbial networks. To further support these conclusions, field validation based on porewater chemistry and molecular characterization of SOB and cable bacteria along salinity gradients is recommended.

Declarations

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Conflict of Interest: The author(s) declare no conflict of interest.

Ethics Statement: No human participants, no animals or field sampling were involved in this study so there was no need for ethical approval.

Data Availability: The model code, parameter values and output data supporting the findings of this study are available from the corresponding author on reasonable request.

Use of Generative AI: The text was drafted using Generative AI and the numerical model was implemented using these tools. All content has been reviewed, verified by the author(s), and edited by the author(s) and the author(s) accept responsibility for the manuscript.

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