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Electrogenic sulfur oxidation by cable bacteria in two seasonally hypoxic coastal systems

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ABSTRACT

Cable bacteria can reach high densities in coastal sediments, and as a result of their unusual electrogenic lifestyle and intense metabolic activity, exert a major and distinct impact on biogeochemical cycling, both locally in sediments and at the ecosystem level. This appears to be particularly true for seasonally hypoxic systems, but the driving force behind the proliferation of cable bacteria in these systems is not well understood. Moreover, the metabolism of cable bacteria induces strong acid production, which can be buffered through carbonate dissolution in sediments. A strong depletion of alkalinity in the pore water is therefore expected in carbonate-poor sediments. To evaluate the impact of cable bacteria metabolism on sediment geochemistry, we performed field sampling and laboratory sediment incubations in two seasonally hypoxic sites: one carbonate-poor site with low levels of free sulfide in pore water (Yarra Estuary, Australia) and one carbonate-rich site with high free sulfide (Lake Grevelingen, The Netherlands). Active cable bacteria populations were found in both field locations, with higher abundance and activity observed in spring compared to autumn. The sediment incubations tracked the metabolic activity of cable bacteria over time (maximum 84 days), and confirmed the fast development of an electric network (cell doubling time: ~19 h). These results suggest that cable bacteria are widespread in seasonally hypoxic systems, supporting previous findings. Cable bacteria acidified the sediment by > 1.5 pH units in 6–13 days (differing per site) and their activity accounted for >70% of the oxygen uptake. A clear subsurface accumulation of Fe^{2+} was observed after 8 days of Yarra sediment incubations, indicative of increased FeS dissolution as e-SOx developed. The increased availability of sulfide from FeS dissolution promotes a positive-feedback loop that we infer allowed for a faster development of cable bacteria in the carbonate-poor sediments. A depletion of total alkalinity was observed in the deeper Yarra sediment, whereas, a higher alkalinity efflux was previously observed in the carbonate-rich sediments from Lake Grevelingen. These results suggest a differential pH and alkalinity dynamic due to the interaction between the local carbonate content of the sediment and cable bacteria activity.

1. Introduction

In coastal sediments, oxygen is transported by diffusion from the overlying water across the sediment-water interface, while free sulfide is produced in deeper sediment layers through sulfate reduction. Although the oxidation of sulfide with oxygen or nitrate is highly energetically favorable, sedimentary microorganisms performing oxygen or nitrate-coupled sulfide oxidation are faced with an important challenge: the

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electron donor (free sulfide) and the electron acceptor (oxygen or nitrate) are typically available in spatially separated locations (Canfield and Thamdrup, 2009; Wasmund et al., 2017). To resolve this problem, many sulfur oxidizing microorganisms have evolved unique adaptations. Filamentous members of the Beggiatoaceae family utilize a combination of internal storage of nitrate in vacuoles and gliding motility. These gliding microbes take nitrate from the surface and move it to deeper sediment which is rich in sulfide (Sayama et al., 2005; Seitaj et al., 2015). By contrast, cable bacteria employ an entirely different strategy to bridge the gap between oxygen or nitrate and sulfide by conveying electrons directly via a long distance electron transport mechanism (Nielsen et al., 2010; Pfeffer et al., 2012; Nielsen and Risgaard-Petersen, 2015; Meysman, 2018). Cable bacteria are filamentous and orient themselves vertically in the sediment. The bottom cells of a filament reside in deeper anoxic sediment layers and harvest electrons from free sulfide through "anodic" sulfide oxidation. The electrons are subsequently conducted from cell-to-cell to the surface of the sediment, where they are used in "cathodic" oxygen reduction by the top cells of each filament. The electrons are internally conducted along the axis of the filament via an elaborate conductive fiber network that is embedded in the periplasm of the cell envelope (Meysman et al., 2019; Boschker et al., 2021). Because this particular form of aerobic sulfide oxidation relies on electrical currents across centimeter distances, it is called electrogenic sulfur oxidation (e-SOx; Malkin et al., 2014).

The spatial segregation of redox half-reactions imposed by e-SOx has a strong impact on the local geochemical cycling in aquatic sediments (Risgaard-Petersen et al., 2012, Meysman et al., 2015, van de Velde et al., 2016, Rao et al., 2016; Sulu-Gambari et al. 2016a, 2016b; Hermans et al., 2020). Primarily, it leads to amplified excursions in pH depth profiles, due to enhanced proton production in deeper sediment layers (where sulfide oxidation takes place) and intensified proton consumption within the oxic zone (where oxygen reduction takes place). This leads to a pH depth profile that is distinctive for e-SOx, which shows a pH maximum in the oxic zone followed by a strong pH decrease below the oxic zone (Pfeffer et al., 2012; Meysman et al., 2015). The induced pH excursions are large compared to sediments without e-SOx activity. An active cable bacteria population can impose an alkalinization of >0.5 pH units in the oxic zone and an acidification of >3 pH units below the oxic zone (e.g. Vasquez-Cardenas et al., 2015; Burdorf et al., 2017; Liau et al., 2022). Nevertheless, pore water pH gradients are not exclusively determined by the production and consumption of protons by cable bacteria, but also by the buffering capacity of the environment. The proton production by cable bacteria below the oxic zone may be counteracted by the dissolution of carbonates ($CaCO_3 + H^+ \rightarrow Ca^{2+} + HCO_3^-$) and metal sulfides $FeS + H^+ \rightarrow Fe^{2+} + HS^-$ (Rao et al., 2014, 2016). However the relationship between the pH excursion and the buffering capacity in sediments with e-SOx activity is presently not well-documented.

Cable bacteria are active in a variety of freshwater and marine sediments across a wide salinity range (salinity 0–40) (Malkin et al., 2014; Burdorf et al., 2017; Hermans et al., 2019; Dam et al., 2021). The common denominator between these environments is i) a high production of sulphide via sulfate reduction in the sediment, ii) availability of oxygen in the overlying water and iii) limited sediment disturbance. These criteria also include systems with transient low-oxygen conditions such as those occurring in seasonally hypoxic basins (Hermans et al.,

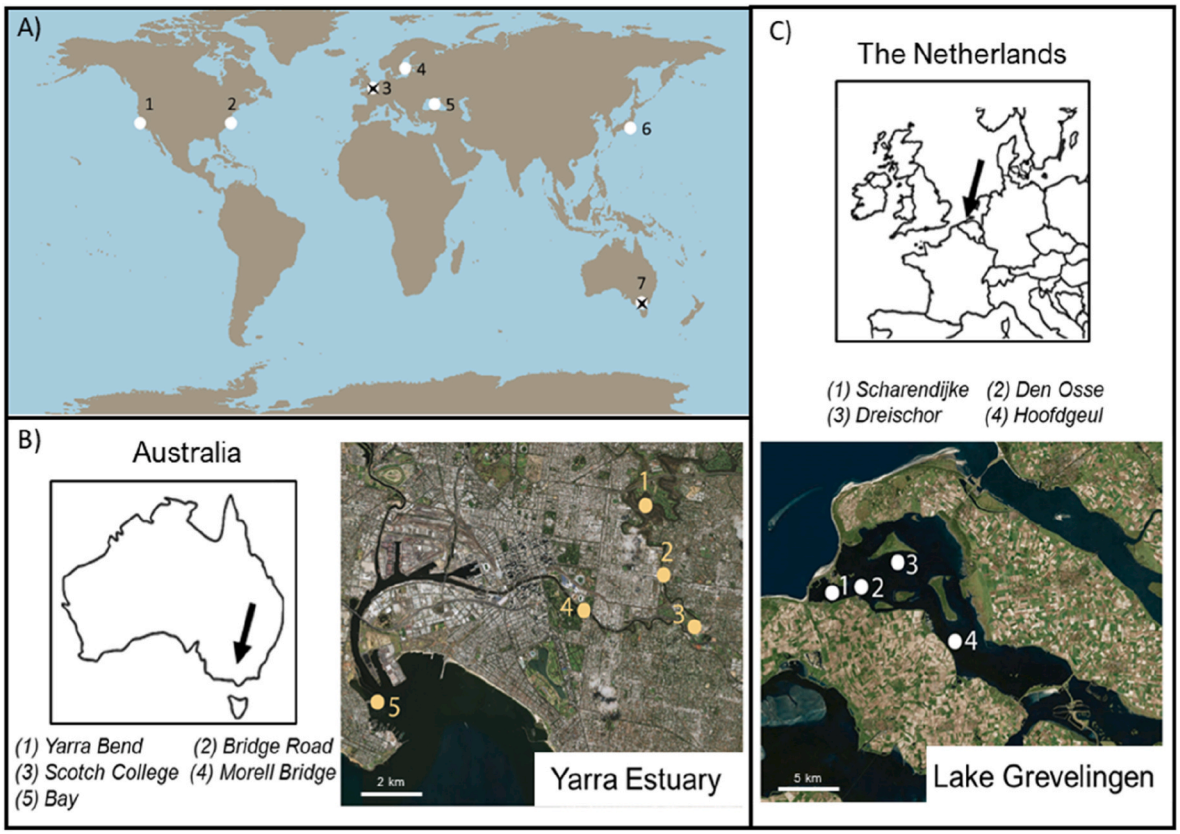

Fig. 1. A) World map of hypoxic systems where geochemical evidence of e-SOx activity has been found in the field or enriched in laboratory incubations, sites are as follows: 1) Santa Monica Bay (Reimers et al., 1996; Figueroa et al., 2023), 2) Chesapeake Bay (Malkin et al., 2022), 3) Lake Grevelingen (Malkin et al., 2014; Seitaj et al., 2015), 4) Baltic Sea (Marzocchi et al., 2018; Hermans et al., 2019), 5) Black sea (Hermans et al., 2020), 6) Tokyo Bay (Sayama, 2011), 7) Yarra Estuary (Burdorf et al., 2017). B) Locations of the five sampling sites within the Yarra Estuary, Melbourne, Australia (site 7 in panel A). All sites were sampled during summer (January–March) with varying oxygen concentrations. C) Locations of the four sampling sites within Lake Grevelingen, The Netherlands (site 3 in panel A). All sites are impacted by summer hypoxia. Scharendijke and Den Osse were sampled in spring and autumn, whereas Dreischor and Hoofdgul were sampled only in autumn.

2019; Marzocchi et al., 2018). Indeed, the e-SOx fingerprint and cable bacteria filaments are found in natural sediments and in laboratory incubations originated from seasonally hypoxic systems around the globe (Fig. 1A): Tokyo Bay (Japan), Lake Grevelingen (Netherlands), Yarra Estuary (Australia), Chesapeake Bay (USA), Baltic Sea (EU) and the Black Sea (Sayama, 2011; Malkin et al. 2014, 2022; Seitaj et al., 2015; Lipsewers et al., 2017; Burdorf et al., 2017; Marzocchi et al., 2018; Hermans et al., 2019, 2020). An additional hypoxic system, Santa Monica Basin, shows geochemical evidence of e-SOx actvity (Reimers et al., 1996; Figueroa et al., 2023) however direct evidence of cable bacteria filaments remains to be reported. Cable bacteria can also use nitrate as an alternative electron acceptor though overall rates of e-SOx are lower under oxygen-depleted conditions (threshold of 5 μM O_2, Marzocchi et al., 2014, 2018; Burdorf et al., 2018). The widespread presence of e-SOx in seasonal hypoxic coastal sites opens up a number of ecological questions such as: is the activity of e-SOx activity patchy or evenly distributed in seasonally hypoxic basins? Which factors determine the development of cable bacteria in hypoxic systems?

The specific seasonal "rhythm" that is imposed on coastal hypoxic systems is suggested to create favorable conditions for a prolific, albeit seasonal, development of cable bacteria (Seitaj et al., 2015; Malkin et al., 2022). In winter and spring, the large pool of FeS serves as a proficient stock of electron donors, which can be tapped into by means of the positive feedback mechanism of FeS dissolution induced by the acidification of deeper sediments by cable bacteria activity (Nielsen and Risgaard-Petersen, 2015; Meysman et al., 2015). Simultaneously, the increase in alkalinity in surface sediments by e-SOx enhances the formation of metal oxides creating an "iron firewall" that regulates the development of euxinia in these systems (Seitaj et al., 2015; Sulu--Gambari et al., 2016a). During summer time, when the bottom water becomes oxygen depleted over sufficiently long time, sulfide can accumulate to toxic levels in the bottom water, e.g. euxinia, which negatively affects the ambient fauna (Diaz and Rosenberg, 1995). However in sediments with previous cable bacteria activity, the surface "iron firewall" (formed in spring) scavenges the sulfide that diffuses from below during summer. This stops the release of sulfide to the water column, and hence prevents or delays the development of euxinia (Seitaj et al., 2015). During the hypoxic/anoxic summer period, anoxic processes again restock the top sediment with iron sulfide by transforming FeOOH into FeS (Sulu-Gambari et al., 2016a).

The main objectives of this study were to i) provide insights into the factors controlling the proliferation of cable bacteria in seasonally hypoxic systems, ii) investigate the influence of the buffering capacity of the sediment on the development of cable bacteria in hypoxic systems, and iii) investigate the combined impact of cable bacteria activity and sediment buffering capacity on the pH and alkalinity dynamics of the pore water. For this, we studied two seasonally hypoxic systems with known cable bacteria activity and contrasting carbonate and sulfide content: Yarra Estuary (Australia) and Lake Grevelingen (The Netherlands). The sediment in the Yarra Estuary has a low carbonate content and lower free sulphide in the pore water, while the sediments of Lake Grevelingen has a high carbonate content and high free sulphide in the pore water. To investigate the geochemical impact by the cable bacteria in these two systems, we conducted field sampling, complemented by a detailed laboratory sediment incubation study.

2. Material and methods

2.1. Site description and field sampling

The presence of cable bacteria and the resulting e-SOx activity were tracked in the sediments of two seasonally hypoxic systems: (1) carbonate-poor sediments of the Yarra Estuary (Melbourne, Australia) and (2) carbonate-rich sediments of Lake Grevelingen (The Netherlands). These two systems are known to harbor cable bacteria activity (Malkin et al., 2014; Burdorf et al., 2017), but differ greatly in terms of their sediment composition and buffering capacity towards pH excursions (Table 1).

Table 1
Sediment properties of Yarra Estuary in Australia and Lake Grevelingen in the Netherlands.

	Yarra Estuary	Lake Grevelingen	unit	
	Scotch College	Den Osse		
Coordinates	37°50′00.1"S 145°00′53.7"E	51°44′50.0"N 3°53′24.0"E		
Water depth	3.5	23	m	*this study*
Salinity	27	28	–	*this study*
Porosity	0.92	0.89	–	*this study*
Median Grain size	<20	16	μm	Rao et al., (2016)/ Ellaway et al., 1982
Organic Carbon content	3.7	3.4	weight %	Rao et al., (2016)/*unpublished data*
$CaCO_3$ content	0.1	22	weight %	Smith and Milne (1979)/*unpublished data*

The Yarra Estuary cuts through the highly urbanized area of Melbourne, Australia. The tidal estuary is 22 km long and generally shallow (1–12 m water depth), and experiences strong stratification when the river discharge is low (Beckett et al., 1982; Roberts et al., 2012; Bruce et al., 2014). Salinity-driven stratification occurs over dry periods in summer that lead to hypoxic events, which can be periodically overturned by rainfall (Roberts et al., 2012; Bruce et al., 2014). The sediments are cohesive and organic-rich, but have a low $CaCO_3$ content (Table 1; Smith and Milne, 1979; Ellaway et al., 1982). Sediment cores and bottom water samples were collected at five sites along the Yarra estuary during summer (January–March 2014) when oxygen saturation in bottom water was depleted in parts of the estuary (Fig. 1). Bottom water oxygen concentration at the time of sampling was ~100% O_2 saturation at Yarra Bay and Yarra Bend (>280 μM), 60% at Bridge Road, 30% at Scotch college and a minimum of 10% O_2 saturation at Morell Bridge (Robertson et al., 2016). Sites were selected to cover the salinity gradient along the estuary spanning persistently fresh to marine sections (Yarra Bend S = 0.01, Bridge Road S = 4, Scotch College S = 27, Morell Bridge and Yarra Bay S = 31. Sediment was collected using a hand-corer (Aquatic Research Instruments) deployed from a zodiac and plastic core liners (inner diameter: 6.6 cm). Cores were capped and immediately transferred to a nearby laboratory (Monash University) where high resolution depth profiles of pH, O_2 and H_2S were recorded in at least two cores per site.

Lake Grevelingen is a former estuary located in the southwest delta of The Netherlands, which is enclosed by dams on both the seaward and landward sides (Fig. 1). The basin is generally shallow (average depth 5.3 m) with the exception of the former tidal gullies that extend down to 50 m water depth (Bannink et al., 1984). The water in the basin is kept permanently saline (salinity 28–31) through exchange with the North Sea via an opening in the seaward dam (Westeijn, 2011). Every summer, the water column of Lake Grevelingen stratifies, which leads to seasonal oxygen depletion in the deeper parts of the water column (>15 m). The sediments of these deeper sub-basins are characterized by fine-grained, organic rich sediments (Table 1) that have a particularly high concentration of solid carbonates (22.0 ± 0.4 wt % $CaCO_3$; (Rao et al., 2016). The source of the high $CaCO_3$ input to the sediment is currently unknown, but there is likely a substantial contribution from high shellfish production (mussels, oysters) in shallower waters in combination with import of carbonate-rich fine sediment from the North Sea. The bioturbation intensity is low due to the seasonal oxygen depletion, as every summer the benthic fauna below 15 m of water depth dies off (Seitaj et al., 2015). Four deep water (>15 m) sites in Lake Grevelingen were sampled in 2015 over two seasons: in spring (March) only two sites were sampled (Scharendijke and Den Osse) whereas in autumn (November)

the spatial extent of the survey was enlarged and sediment cores were retrieved at two additional sites (Dreischor and Hoofdgeul, Fig. 1). Sediment samples were retrieved shipboard using a UWITEC gravity corer (cores: 60 cm length, diameter: 6 cm). Sediment cores were stored at *in situ* temperature until further analysis. Within 6 h of sampling in a ship-board laboratory, depth profiles of pH, O_2 and H_2S were recorded using micro-electrodes, a minimum of two cores were microprofiled per site.

2.2. Laboratory sediment incubations

Within both seasonal hypoxic systems, one site was selected (Scotch College in the Yarra Estuary, and Den Osse in Lake Grevelingen; Table 1) to target the development of electrogenic sulfur oxidation under laboratory conditions. To this end, the sediment incubation procedure from Nielsen et al. (2010) as described in more detail in Burdorf et al. (2017) was employed. In brief, sediments were sieved (0.5–1 mm mesh) upon collection, homogenized and kept anoxic in sealed containers to ensure that no macrofauna could develop. Subsequently the sieved sediment was transferred into plastic core liners (inner core diameter Yarra Estuary: 6.6 cm and Lake Grevelingen: 3.0 cm) and submerged in a water bath at *in situ* temperature and salinity (Yarra Estuary: 20–24 °C, S = 27; Lake Grevelingen: 16 °C, S = 30) in the dark.

During laboratory sediment incubations, the overlying water of the aquarium was continuously bubbled with ambient air to retain a fully oxygenated water column. The sediment incubations for the Yarra Estuary lasted for two weeks, with O_2, H_2S and pH depth profiles at 0, 2, 4, 6, 8, 11 and 15 days, with profiles in 2 replicate sediment cores per time point. At each time point, two sediment cores were sectioned for the analysis of alkalinity and ferrous iron in the pore water. Additionally, the sediment was sliced for microbial analysis at the start and end of the sediment incubations (t = 0 and t = 15 days). The incubations for Lake Grevelingen lasted 3 months, and high resolution depth profiles of O_2, H_2S and pH were recorded at 1, 5, 8, 13, 16, 21, 29, 42, 57 and 89 days after the start of the incubation (profiles in >2 replicate sediment cores per time point). Sediments were examined under a stereoscope to qualitatively determine the presence of filamentous bacteria during each time points.

2.3. Microsensor profiling

Microsensor profiles were recorded as described in Malkin et al. (2014) and Burdorf et al. (2017) using commercial micro-electrodes (Unisense A.S. Denmark, tip sizes pH: 200 μm, H_2S: 100 μm, O_2: 50 μm) operated with a motorized micromanipulator (Unisense A.S., Denmark). pH and H_2S depth profiles were recorded simultaneously with a 200 μm resolution in the oxic zone of the sediment, and increasing resolution (up to 400 μm) in the deeper part of the sediments. Oxygen profiles were measured separately at 50 μm or 100 μm depth resolution. Sensors were calibrated following the standard calibration procedures as described previously (Malkin et al., 2014) (H_2S: 3 to 5 point standard curve using Na_2S standards; O_2: 2 point calibration using 100% in air bubbled seawater and the anoxic zone of the sediment; pH: 3 NBS standards (4, 7, 10) and TRIS buffer). The pH data are reported on the total pH scale and ΣH_2S was calculated from H_2S based on the pH values measured at the same depth.

Three indicators of cable bacteria activity were calculated from the micro-sensor data. Foremost, the metabolism of cable bacteria induces pH excursions within the sediment, and the amplitude of these pH excursions can be used as an indicator of the intensity of cable bacteria activity (Burdorf et al., 2016). The pH excursion amplitude, ΔpH is defined as the difference between the highest pH in the oxic zone and the lowest pH in the suboxic zone. A second indicator of cable bacteria activity relates to the depletion of sulfide in the top of the sediment. As cable bacteria grow downwards into the sediment, a suboxic zone is established where neither O_2 or H_2S are freely present (Schauer et al., 2014). The width of this suboxic zone ΔL is operationally defined as the sediment zone where $[O_2] < 1$ μmol L^{-1} and $[H_2S] < 1$ μmol L^{-1}. Previous studies have demonstrated that the width of the suboxic zone is a good indicator for the depth distribution of the cable bacteria (Schauer et al., 2014; Vasquez-Cardenas et al., 2015). Finally, diffusive oxygen fluxes (DOU) were calculated according the Fick's first law from the O_2 depth profiles just underneath the sediment-water interface. The diffusive oxygen flux $(J_{O2}) = \Phi * (D_{O2}/(1–2 \ln(\Phi)) * (d[O_2]/dx)$ was calculated using the slope of the oxygen concentration depth profile ($d[O_2]/dx$), the porosity (Φ) and the molecular diffusion coefficient (D_{O2}) corrected for tortuosity ($1–2 \ln(\Phi)$). The molecular diffusion coefficient was calculated in R using the *marelac* package (Soetaert et al., 2010) taking into account the temperature and salinity of the incubations.

2.4. Chemical analysis of pore water

In the sediment incubations of the Yarra Estuary, one sediment core was sectioned at each time point (0.5 cm intervals over the first 5 cm; 1 cm intervals up to 10 cm). Sediment was centrifuged in 50 mL polypropylene centrifuge tubes (2000 rpm for 5 min) and the pore water was filtered (0.2 μm) and preserved for iron and alkalinity analysis. Total alkalinity was analyzed via Gran titration using 100 μL aliquots of HCl (0.01 mol L^{-1}) standardized with 1 mmol L^{-1} Na_2CO_3. The ferrous iron in the pore water was determined via the ferrozine method (Stookey, 1970; Viollier et al., 2000). Samples were measured using absorbance readings at 632 nm (GBC UV Visible Spectrophotometer).

Seasonal *in situ* porewater chemistry of Lake Grevelingen was thoroughly studied in previous years, including iron and alkalinity measurements (e.g Seitaj et al., 2015, Sulu-Gambari et al., 2016a,b) and in laboratory incubations where e-SOx developed (71 days) with sediments collected from Den Osse site (Rao et al., 2016). The previously published data will be used for comparison with the results from the Yarra estuary obtained here.

2.5. Microbial analysis

Fluorescence *in situ* Hybridization (FISH) was chosen to study the presence of cable bacteria in sediments as it selectively identifies microbial taxa by targeting specific regions of the ribosomal RNA with molecular stains. In previous studies, the probe DSB706 (Loy et al., 2002) was used to successfully hybridize with cable bacteria (e.g. Pfeffer et al., 2012; Schauer et al., 2014; Trojan et al., 2016). Here, we performed standard FISH analysis with the DSB706 probe, following the protocol described in Schauer et al. (2014). For this, 0.5 mL of sediment was preserved in 96% ethanol at a 1:1 ratio and stored at −20 °C. Subsamples of 100 μl were transferred in 500 μl of a 1:1 mixture of PBS/ethanol, and subsequently, 10 μl of this mixture was filtered through a polycarbonate membrane filter (type GTTP, pore size 0.2 μm, Millipore, USA). Probe hybridization was performed according to previously published protocols (Pernthaler et al., 2002). The samples were quantified using an epifluorescence microscope at 100× magnification (Zeiss Axioplan, Germany). The length of all observed cable bacterium filaments were counted within 200 fields-of-view (dimensions: 105 × 141 μm). Using the appropriate dilution factors, we report cable bacteria abundance as filament length per volumetric unit (i.e. m of cable bacteria per cm^3 of sediment).

3. Results

3.1. Yarra estuary: field survey

The metabolic activity of cable bacteria can be identified and quantified by the analysis of high-resolution depth profiles of pH, H_2S and O_2 in sediment cores (Pfeffer et al., 2012; Meysman et al., 2015). Five sites in the Yarra River Estuary were investigated by microsensor depth profiling in February 2014 (Fig. 1), and at four sites, we were able

to successfully retrieve microsensor depth profiles. No depth profiles could be obtained for the Bay station as the sediment contained a lot of bivalve shells and plant material, which inhibited the deployment of micro-electrodes. The oxygen penetration depth (OPD – depth where $[O_2] < 1$ μmol L^{-1}) varied slightly from the marine site, Morell Bridge (2.5 ± 0.3 mm (±SD); 31 salinity) to the freshwater site, Yarra Bend (2.3 ± 0.1 mm; 0.01 salinity).

Sulfide concentrations in the pore water increased with increasing salinity (and hence SO_4 availability for sulfate reduction), but generally remained low at all sites (Fig. 2). At the freshwater site (Yarra Bend; S = 0.01) almost no free sulfide was detected. At Bridge Road (S = 4) sulfide increased above the detection limit below 12 mm deep and reached a maximum of 7 μmol L^{-1} at 21 mm deep. At Scotch College (S = 27) a suboxic zone of ΔL = 5 mm was present in the sediment and sulfide increased to ~20 μmol L^{-1} at 21 mm depth. At the most saline site (Morell Bridge, S = 31), ΣH_2S increased to >20 μmol L^{-1} directly below the oxygen penetration depth.

A distinct feature of the geochemical fingerprint for e-SOx is the pH maximum in the oxic zone, linked to the consumption of protons by the cathodic oxygen reduction half reaction (Nielsen et al., 2010; Meysman et al., 2015). Yet, none of the *in situ* cores in the Yarra estuary had the surface pH peak, and the shape of the pH depth profile varied between sites. The pH profile at Scotch College decreased to the lowest pH values (~6.5) at the sulfide appearance depth in pore water (Fig. 2). Although no pH maximum was present, Scotch College site showed geochemical indications of e-SOx activity by cable bacteria (presence of a suboxic zone, acidification of the suboxic zone). FISH analysis confirmed the presence of cable bacteria (Fig. 3). Cable bacteria presented length densities of 295 m cm^{-2}, mostly confined to the upper 2 cm of the sediment core as expected from the length of the suboxic zone (i.e. 2.1 cm). The other sites did not indicate active e-SOx (Fig. 2). In Yarra Bend (S = 0) the pH reached a minimum at the base of the oxic zone and subsequently increased again to reach a stable level between pH 6.5–7, this pH profile is likely indicative of active metal reoxidation (Seitaj et al., 2015). The pore water pH profiles at Bridge Road (S = 4) and Morell Bridge (S = 31) showed a similar pattern, although at both sites the pH decreased to reach a minimum around 25 mm.

3.2. Lake Grevelingen: field survey

Sampling campaigns were conducted in Lake Grevelingen before and after the summer hypoxia (Fig. 1). In March, >90% of the sediment cores (n = 16) inspected by microsensor profiling showed the geochemical fingerprint of e-SOx, indicating that the process was widespread in spring (Fig. 2). In November, the geochemical fingerprint of e-SOx was active in 45% of the cores (n = 17), and so the activity of the cable bacteria appeared more patchy during autumn. Spatial variability occurred both within and between sites. In each of the four basins, at least one sediment core showed the e-SOx signature, except for Hoofdgeul, where all cores exhibited characteristic e-SOx profiles. For Hoofdgeul basin in November, cable bacteria filaments were mostly constrained to the top sediment up to the sulfide appearance depth (25 mm) in accordance with the e-SOx fingerprint corresponding to a cable bacteria density of 358 m cm^{-2} (Figs. 2 and 3).

The pH excursion was largest in November in the Dreischor basin (ΔpH = 1.3), followed by Hoofdgeul (ΔpH = 1.0), Den Osse (ΔpH = 0.7) and Scharendijke (ΔpH = 0.5, Fig. 2). A suboxic zone was always present in cores when the pH signature of e-SOx was present, although the magnitude of ΔL varied between the basins (Fig. 2). In autumn 2015, the suboxic zone range was ΔL = 10–13 mm, while in spring the suboxic zone was deeper with ΔL = 20–35 mm. Regardless of the station, sulfide concentration increased sharply below the suboxic zone (Fig. 2). Oxygen penetration was shallow at all sites and at all times, ranging from 0.8 mm (Dreischor in November) to 3 mm (Den Osse in March).

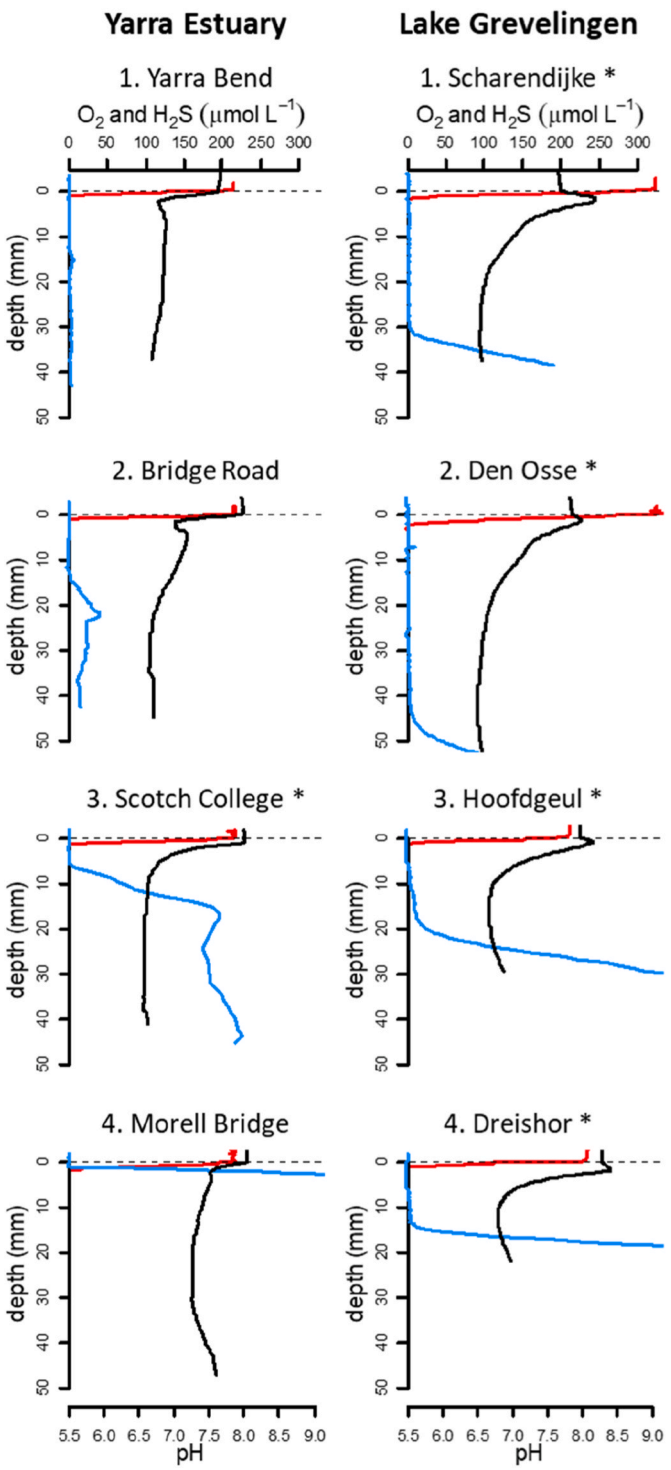

Fig. 2. Characteristic *in situ* high resolution depth profiles of pH (black), ΣH_2S (blue) and O_2 (red) for Yarra Estuary (left) and Lake Grevelingen (right). The four sites of the Yarra Estuary represent a salinity gradient: Yarra Bend (salinity = 0.01), Bridge Road (salinity = 4), Scotch college (salinity = 27), Morell Bridge (salinity = 31). No depth profiles could be obtained for the Bay station. The four sites of Lake Grevelingen are representative of different gullies affected by yearly occurring seasonal hypoxia (salinity = 28–31). Profiles for Scharendijke and Den Osse were collected in spring while profiles for Hoofdgeul and Dreishor were collected in autumn. Profiles that show geochemical indications of e-SOx activity by cable bacteria are indicated by a (*).

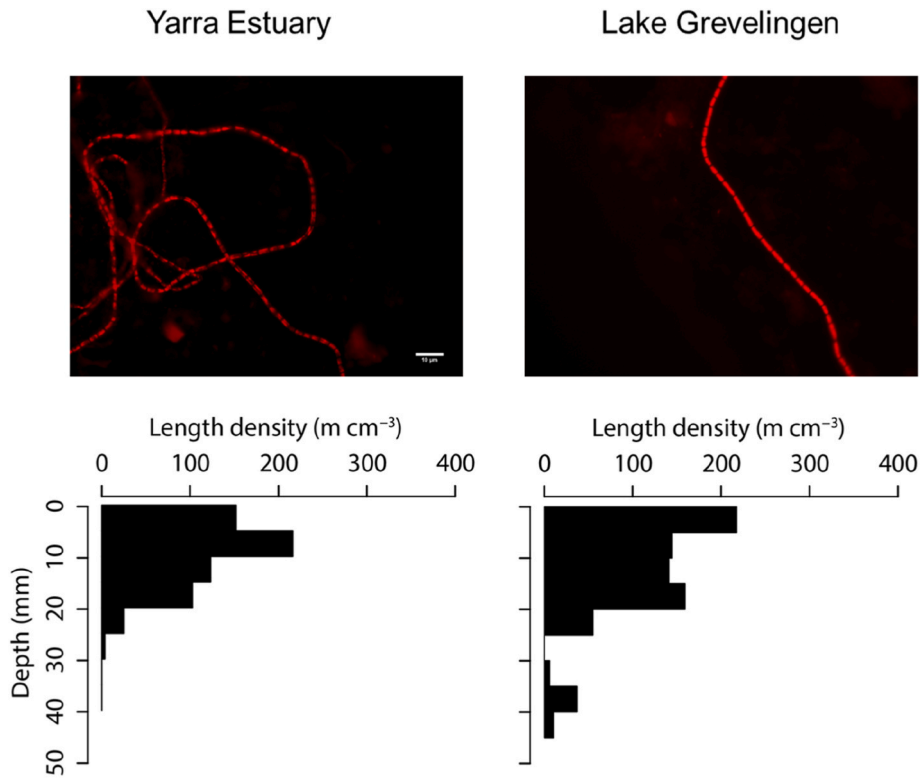

Fig. 3. Identification and quantification of cable bacteria in the field survey. (top) Representative FISH images of cable bacteria present in the Scotch College (Yarra Estuary) and Hoofdegul (Lake Grevelingen), November sampling. (bottom) Depth distribution of cable bacteria using fluorescence *in situ* hybridization (FISH) confirms their presence at both sites down to the sulfide appearance depth.

3.3. Yarra Estuary: laboratory incubation

At the start of the incubation (Day 0), the pore water pH decreased in the top 5 mm, but stabilized at pH ~7.8 in deeper layers. The free sulfide concentration (ΣH_2S) increased just below the oxygen penetration depth, but remained low and constant (~5 μmol L^{-1}) deeper in the sediment (Fig. 4). No ferrous iron (Fe^{2+}) was detectable in the pore water, and the alkalinity (A_T) steadily increased from 2 mmol L^{-1} to 15 mmol L^{-1} over the 4 first centimeters (Fig. 4). FISH analysis confirmed that negligible densities of cable bacteria were present following the sediment pre-treatment prior to the start of the incubation (Fig. 4; filament length density <5 m cm^{-2}, only 6 cable bacteria filament fragments were detected in 1200 microscopic fields-of-view). The first signs of e-SOx activity were seen after 4 days of incubation, when a small suboxic zone appeared (ΔL = 1 mm). Two days later, all characteristic features of the e-SOx fingerprint were present: a small increase in pH was visible in the oxic zone, alongside a notable decrease of pH in the suboxic zone (ΔpH = 2.0). The suboxic zone had expanded to ΔL = 4 mm. The curvature in the depth profile suggested alkalinity consumption around 5 mm depth, in accordance with proton production by the anodic sulfide oxidation half-reaction. On Day 8, the subsurface sediment further acidified, while the pH maximum in the oxic layer remained (ΔpH = 2.3). The acidification caused the dissolution of FeS in the suboxic zone, and as a consequence, Fe^{2+} started to accumulate in the top of the sediment. Three days later, the alkalinity reached values close to zero (~0.2 mmol L^{-1}) within the suboxic zone, while ferrous iron showed strong accumulation (0.95 mmol L^{-1}), thus suggesting strong FeS dissolution in tandem with high rates of proton production through anodic sulfide oxidation. On day 15, alkalinity consumption decreased and ΣH_2S increased to 39 μmol L^{-1} (8 μmol L^{-1} on Day 11), giving rise to a conspicuous subsurface maximum just below the suboxic zone. However, no corresponding Fe enrichment in the pore water was observed (Fig. 4). This excludes FeS dissolution as the source, and so the actual cause of the ΣH_2S increase remains unclear. After Day 8 pH excursion decreased slightly on Day 11 (ΔpH = 1.9) and then increased to ΔpH = 2.3 on Day 15 (Fig. 5). At the end of the experiment (Day 15), FISH analysis revealed a depth-integrated filament density of 549 m cm^{-2}. The filament density was highest in the first sediment layer (416 m cm^{-3}), but also all subsequent depth layers (down to 40 mm) had at least 90 m cm^{-3} of cable bacteria present (Fig. 4). Over the same period, diffusive oxygen uptake rates increased steeply from Day 2 (19 ± 6 mmol m^{-2} d^{-1}) to reach a maximum on Day 6 (61 ± 16 mmol m^{-2} d^{-1}) and then decreased to Day 15 (46 ± 18 mmol m^{-2} d^{-1}), suggesting a decrease in the e-SOx activity (less cathodic O_2 reduction) (Fig. 5).

3.4. Lake Grevelingen: laboratory incubation

The temporal development of e-SOx was recorded by microsensor profiling (pH, H_2S and O_2, Fig. 6) at ten consecutive time points. During the first three time points (Day 1, 5 and 8) no suboxic zone was detected: pore water ΣH_2S increased right at the interface where the oxygen disappeared. The oxygen penetration depth was less than 1 mm and the diffusive oxygen uptake varied from 46 mmol m^{-2} d^{-1} on Day 1 and 5, to 19 mmol m^{-2} d^{-1} on Day 8 (Fig. 5). The initial high oxygen uptake can be explained by the reoxygenation of the previously anoxic sediment (reducing oxidized compounds) right after homogenization. After 13 days of incubation however, the geochemical fingerprint of e-SOx was observed (Fig. 6). A pH maximum was detected in the pore-water just underneath the sediment-water interface (pH 8.4), accompanied by a pH minimum at 1.0 cm (ΔpH = 1.4). Up to Day 29, the ΔpH increased to 1.8 (Day 21 ΔpH = 1.9), the DOU remained high (>40 mmol m^{-2} d^{-1}), the oxygen penetration depth remained shallow (<1.5 mm) and the suboxic zone expanded with the ΔL increasing from 7 mm to 22 mm (Figs. 5 and 6). Between 42 and 84 days, oxygen uptake rate decreased from 31 to 14 mmol m^{-2} d^{-1} and oxygen penetration increased to 2.7 mm (Fig. 5). The pH excursion decreased steadily to 1.21 pH units and the suboxic zone

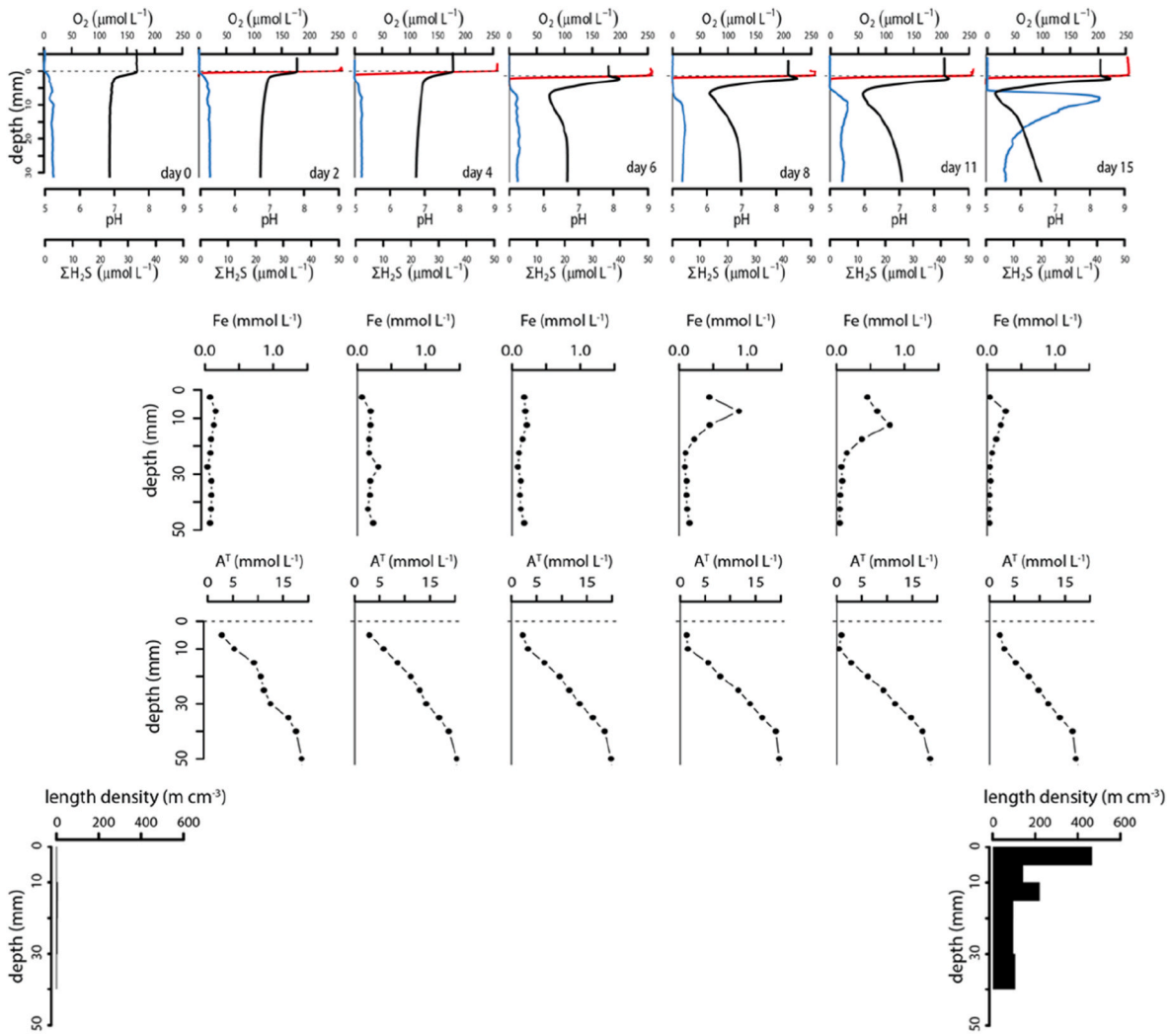

Fig. 4. Detailed laboratory sediment timeseries of the Yarra Estuary over the span of 15 days. From top to bottom row: Representative, high resolution depth profiles of pH, ΣH_2S and O_2 at 7 timepoints. Pore water profiles of Fe^{2+} and total alkalinity, 6 timepoints. Length density of cable bacteria filaments at Day 0 and Day 15 of incubation.

width decreased to 7 mm indicating a decrease in cable bacteria activity by the final time point (Figs. 5 and 6).

4. Discussion

4.1. Distribution and development of cable bacteria in hypoxic systems

Electrogenic sulfur oxidation by cable bacteria are observed frequently in coastal sediments (Malkin et al., 2014; Burdorf et al., 2017), and are widespread in coastal systems that experience seasonal hypoxia, Fig. 1). The most extensive targeted spatial survey so far was performed in the Baltic Sea by Hermans et al. (2019) included 12 sites spread across oxic, hypoxic, anoxic and reoxygenated basins. In the Baltic Sea survey, although cable bacteria filaments were collected at all sites, only sites with seasonal variation in oxygen concentrations showed an e-SOx geochemical fingerprint accompanied by highest cable bacteria abundances. Our results here reinforce this observation as cable bacteria activity was found *in situ* in the sediments of two seasonally hypoxic systems: Scotch College located in the Yarra Estuary (Australia) and Lake Grevelingen (The Netherlands, Fig. 1).

However, cable bacteria activity is not persistently detected in seasonally oxygen depleted systems, as it is strongly impacted by the depletion of oxygen (the electron acceptor of e-SOx) in summer. Previous studies of Lake Grevelingen have indicated that cable bacteria are not active year-round, but show a strong seasonality, with low abundances and e-SOx activity in summer and early autumn, and high abundances and activity from late autumn to spring (Seitaj et al., 2015; Lipsewers et al., 2017). Our field surveys in March and November of 2015 in Lake Grevelingen affirm this model. e-SOx activity was widespread in spring (>90% of all investigated cores), and far more heterogenous in autumn (45% of all investigated cores), which could indicate that cable bacteria populations were still in recovery and/or outcompeted by other sulfur oxidizers (Seitaj et al., 2015) after the summer hypoxia. This seasonal pattern remains to be studied in the Yarra estuary but *in situ* cable bacteria densities at Scotch College (with 30% O_2 saturation in overlying water) were comparable to those found in Lake Grevelingen in autumn after hypoxia (295 m cm^{-2} and 358 m cm^{-2} respectively, Fig. 4), but nearly double the abundances reported for the Baltic sea at reoxygenated sites (max 160 m cm^{-2}, Hermans et al., 2019) Cable bacteria communities hence appear well-adapted to the seasonal availability of oxygen in overlying water. When the oxygen becomes depleted in summer, e-SOx activity halts and the cable bacteria population crashes, but when the oxygen levels climb in early autumn (after the seasonal overturning and mixing of the water column), the presence and activity of cable bacteria quickly returns.

Laboratory incubations of sediment from Yarra and Grevelingen

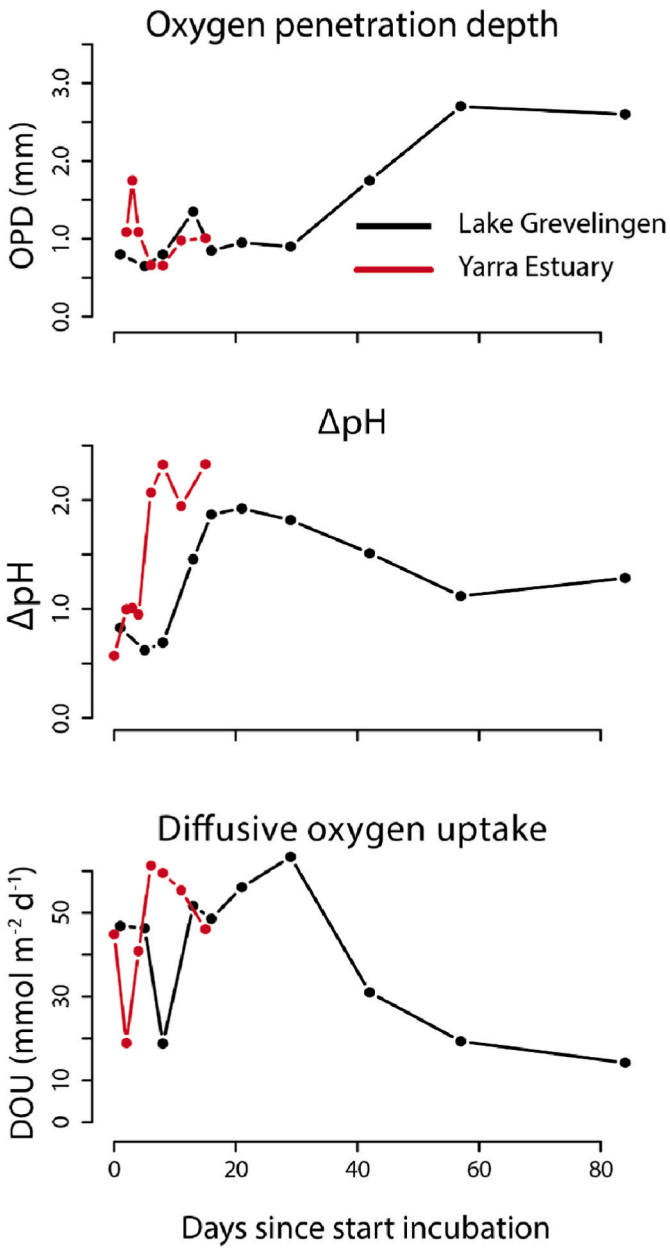

Fig. 5. Microprofile characteristics for the Yarra Estuary and Lake Grevelingen timeseries. From top to bottom: Oxygen penetration depth (OPD) defined as the depth in the sediment where $[O_2] < 1$ μmol L^{-1} over time. ΔpH defined as the pH_{max} in the oxic zone – pH_{min} in the suboxic zone) over time. The diffusive oxygen uptake (DOU) calculated as a first derivative from the O_2 depth profile over time.

confirm that the development of e-SOx can initiate within a few days of incubation (4 days in Yarra; 13 days in Grevelingen; Fig. 5). The initial drop in DOU indicates a clear change in geochemistry brought about by the rapid growth of cable bacteria (Fig. 5). Establishment of a suboxic zone in the sediment was concurrent with the emergence of the characteristic pH excursions induced by e-SOx. Cable bacteria promptly and strongly modify the pH of the pore water: an acidification of the suboxic zone of >1.5 pH units occurs within 6 days in the Yarra estuary and 13 days in Lake Grevelingen (Figs. 4 and 6). This acidification is linked to an increased mobilization of Ca^{2+}, Fe^{2+}, Mn^{2+} and trace metals (e.g. Zn, As, Co) due to dissolution of FeS and $CaCO_3$ minerals (Risgaard-Petersen et al., 2012; Rao et al., 2016; van de Velde et al., 2016, 2017). Concurrent with the fast pH changes, the initial rapid growth stage shows an increase in the oxygen consumption of the sediment (DOU increased by 40 mmol m^{-2} d^{-1} from Day 2 to Day 8 in the Yarra Estuary time series and by 30 mmol m^{-2} d^{-1} from Day 8 to Day 16 in Lake Grevelingen, Fig. 5). If we assume that the increase in DOU during the initial developmental phase of cable bacteria is solely due to an increase in metabolic activity by the cable bacteria, e-SOx would be the major pathway consuming O_2 in the sediment. In both the Yarra Estuary and Lake Grevelingen cable bacteria account for >70% of the total sedimentary O_2 consumption in accordance with previous observations (Schauer et al., 2014; Malkin et al., 2014; Vasquez-Cardenas et al., 2015). We acknowledge that some unknown proportion of O_2 consumption could be due to re-oxidation of compounds mixed in the sediment during sediment core preparation. However, we infer this to be a small proportion by the end of the rapid growth period of cable bacteria (8 days in the Yarra Estuary timeseries and 21 days in the Lake Grevelingen experiment) given that the measured O_2 consumption rates at this time point indicates that the maximal rate of e-SOx is similar in both time series experiments (~230 mA m^{-2}, assuming 4 mol of electrons per mole O_2 reduced). The initial rapid growth ends and gives way to the stabilization of the oxygen penetration, ΔpH, and ΔL, with minor changes in DOU (Fig. 5). The apparent stable phase lasted up to Day 40 in Lake Grevelingen, while the Yarra estuary incubations ended during the stabilization stage. Previous studies have related the decline in cable bacteria activity to the depletion of FeS in the sediment (Rao et al., 2016) but this hypothesis remains to be proven.

Our dataset also allows a preliminary assessment of the growth kinetics of cable bacteria in contrasting settings. Assuming that cable bacteria filaments completely span the suboxic zone (7 mm at Day 8 for Yarra Estuary and 20 mm at Day 13 for Lake Grevelingen), and cell length is 3 μm, the estimated doubling time of cable bacteria is ~18 h during the exponential growth phase, integrated over the length of their filaments, 12 in the Yarra Estuary and 19 h in Lake Grevelingen. These estimates are very close to the doubling time of 20 h as previously estimated from other sediment incubations (Schauer et al., 2014; Vasquez-Cardenas et al., 2015). In the environmental context of seasonal hypoxic basins, the rapid growth of cable bacteria after a period of anoxia is an important asset. Our results, combined with previous laboratory enrichment of cable bacteria (Schauer et al., 2014; Vasquez--Cardenas et al., 2015, 2022; Burdorf et al., 2017; Hermans et al., 2020; Aller et al., 2019; Yin et al., 2022; Liau et al., 2022), demonstrate the ability of cable bacteria to rapidly colonize the sediment (within 2 weeks) and dominate the geochemistry of the sediment via the large metabolic effects of e-SOx on pH and O_2 (Figs. 4 and 6).

4.2. What environmental characteristics favor cable bacteria in coastal seasonal hypoxic sediments?

Cable bacteria are prevalent in coastal hypoxic sediments around the world (Fig. 1A), which raises the question as to why cable bacteria particularly thrive in these environments. We suggest there are likely two main reasons favoring e-SOx in coastal environments with seasonal hypoxia.

Firstly, periodic oxygen depletion leads to a hostile environment for benthic macrofauna (Diaz and Rosenberg, 1995). A yearlong monthly survey of Lake Grevelingen has shown the loss of the macrofauna community during the summer hypoxia, the subsequent absence of macrofauna over the cold autumn and winter, and the reappearance of juveniles at the end of the spring of the year thereafter (Seitaj et al., 2015). Although a similarly extensive study of the macrofauna in the Yarra Estuary is absent, it is generally accepted that there is an absence of macrofauna in the part of the Yarra Estuary affected by seasonal hypoxia (Santos et al., 2012). Likewise, during sediment preparation and sieving, no macrofauna was observed in the sediment of the sites from this area. However, burrowing macrofauna are thought to exert an important physical control on the natural distribution of cable bacteria, as the filamentous network at the sediment surface can be disrupted during intense sediment biomixing (Malkin et al., 2014; Rao et al.,

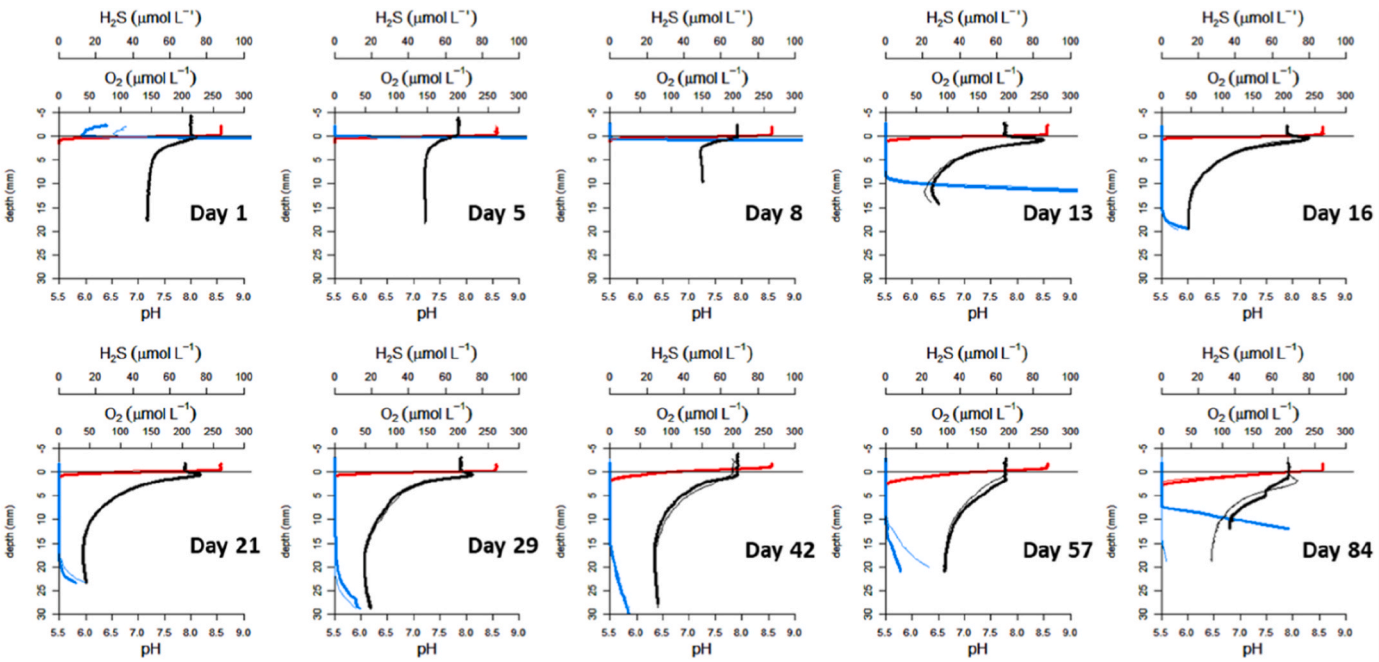

Fig. 6. Lake Grevelingen: representative, high resolution depth profiles of pH, ΣH_2S and O_2 over the span of 84 days. Two sets of pH, ΣH_2S and O_2 microprofiles are given at each timepoints.

2014). Moreover, reworking of sediment strongly modifies the cycling of iron and sulfur (Aller, 1982), which could indirectly hamper cable bacteria metabolism at the sediment surface. Particle mixing favors metal reduction over sulfate reduction, thus reducing the production of free sulfide (van de Velde and Meysman, 2016). At the same time, oxygen can be actively introduced by macrofaunal bio-irrigation into anoxic sediment layers, leading to a rapid oxidation of the available H_2S. In Chesapeake Bay, seasonal observations demonstrated that cable bacteria density was highest in channel sediments that experience severe seasonal oxygen depletion and negligible macrofauna bioturbation, while shallower shoal sediments with milder oxygen depletion and greater bioturbation favored Beggiatoaceae, highlighting that the outcomes of microbial competition may be affected by bioturbation intensity (Malkin et al., 2022). Still, other recent investigations show that cable bacteria can be present in bioturbated sediments, and the occurrence of cable bacteria associated with oxic biogenic structures such the rhizosphere and irrigated worm burrows that are physically stable for longer time is noteworthy (Scholz et al., 2019; Li et al., 2020; Aller et al., 2019; Yin et al., 2021). Evidence presented in Bonaglia et al. (2020) from a laboratory experiment further suggest that the proliferation of benthic meiofauna may shorten the lag time before exponential growth of cable bacteria is observed. The specific mechanisms underlying this observation and its generality remain uncertain. The interactions between meiofauna, cable bacteria, and seasonal hypoxia is of interest in seasonally hypoxic systems as meiofauna may be the last to be extinguished by oxygen depletion, and the first to recolonize following re-oxygenation. As observed by Yin et al. (2021) the time scale and intensity of the disturbance, rather than occurrence of a disturbance, are determinant factors for the success of cable bacteria networks in sediments.

A second potential reason for the prevalence of cable bacteria in coastal hypoxic systems is that oxygen depletion imposes a seasonal "reset" of the geochemistry. The term 'reset' implies that hypoxia promotes seasonal iron sulfide accumulation in surface sediments, which could benefit the development of cable bacteria once the bottom water is re-oxygenated in autumn. The key factor in this appears to be the magnitude of the iron sulfide (FeS) pool in the sediment (Risgaard-Petersen et al., 2012; Seitaj et al., 2015; Sulu-Gambari et al., 2016a), which increases the access of cable bacteria to electron donors. This is because upon dissolution (i.e. $FeS + H^+ \rightarrow Fe^{2+} + HS^-$), FeS provides a source of free sulfide in addition to the sulfide that is produced by sulfate reduction (Risgaard-Petersen et al., 2012). At the same time, FeS dissolution is stimulated in acidic pore waters, and in this way, the metabolism of cable bacteria is capable of inducing a positive feedback cycle or "FeS-turboboost" (Meysman et al., 2015, Fig. 7). This feedback implies that more e-SOx activity leads to more proton production, increased FeS dissolution and an increased availability of H_2S, which in turn leads to more e-SOx activity. Positive feedback cycles inherently have a "runaway character", in the sense that they can lead to very rapid changes. This also applies to sediment geochemistry, as clearly illustrated by the Yarra Estuary time series. Over the course of only 6 days (from Day 6 to Day 11 Fig. 4), a strong acidification of the suboxic zone was observed together with a depletion of A_T (from 2.5 to 0.2 mmol L^{-1}) and intense FeS dissolution (Fe^{2+} accumulation up to 1 mmol L^{-1} in pore water). Such large and rapid changes in the geochemical composition of the pore water are generally uncommon in aquatic sediments, thus our results illustrate once more the specific importance of cable bacteria activity in sediment geochemistry.

4.3. *Sediment buffering capacity impacts the geochemical fingerprint of e-SOx*

Along with sulfide removal, the most prominent impact of cable bacteria affects sediment pH and thus potentially alkalinity dynamics. This study therefore aimed to investigate the potential effects of differing sedimentary buffering capacity on the geochemical fingerprint of e-SOx. Carbonate dissolution and precipitation are the main pH buffering mechanisms in marine sediments (Zeebe and Wolf-Gladrow, 2001; Stumm and Morgan, 2012). Therefore two sites, with contrasting $CaCO_3$ content were selected: $CaCO_3$-poor Scotch College in the Yara Estuary and $CaCO_3$-rich Lake Grevelingen. (Table 1). In the context of e-SOx, and the associated proton production in the suboxic zone and proton consumption in the oxic zone, larger pH excursions are expected in carbonate-poor environments (as modelled in Meysman et al., 2015).

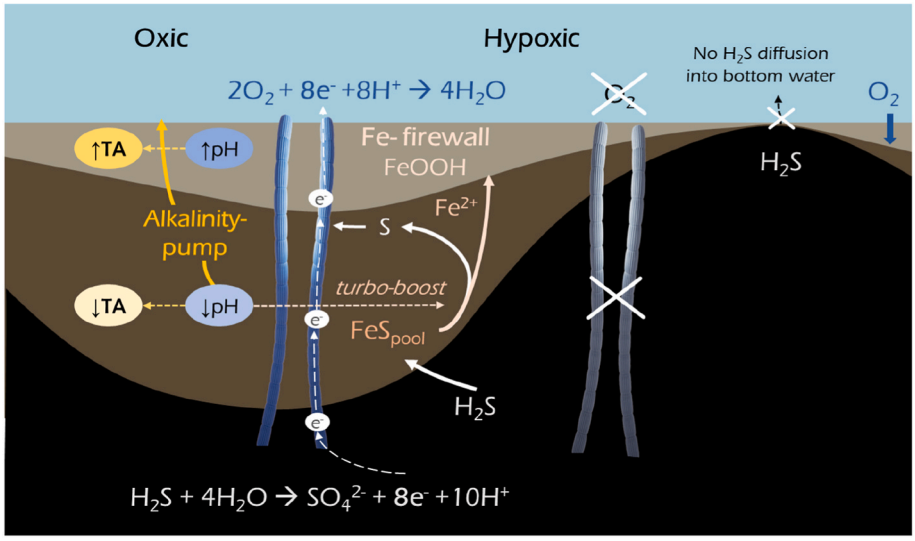

Fig. 7. In oxygenated bottom water conditions increasing cable bacteria activity forms the e-SOx geochemical fingerprint in sediments mainly identified by the decreased pH in subsurface sediment up to the sulfide horizon, and increased pH in oxic surface sediment. In deeper sediment the low pH produces an Fe-turboboost by dissolving the FeS pool, allowing Fe^{++} to diffuse upward to precipitate as Fe-oxides and form an Fe-firewall. With the onset of hypoxia the Fe-firewall prevents the diffusion of H_2S into bottom waters. The large difference in pH over centimeter distances also implies a spatial separation of proton production and consumption that leads to a transfer of alkalinity (TA) from the suboxic to the oxic zone of the sediment, the so-called "alkalinity pump". The intensity of this alkalinity-pump largely depends on the buffering capacity of the local sediments. See text for detailed explanation on these processes.

Cable bacteria were present and active in both Lake Grevelingen and Yarra Estuary (Scotch college) sediments (Figs. 2 and 3). While the maximal rates of e-SOx are comparable in both systems (~230 mA m^{-2}), and hence the proton production during anodic sulfide oxidation must be similar, the lower buffering capacity in the Yarra Estuary means that e-SOx has a far larger acid-base impact on the pore water. The microsensor depth profiles of the time series illustrate the difference in pH response (Fig. 5): the maximal amplitude of the pH excursion is noticeably larger in the Yarra Estuary (max $\Delta pH = 2.3$ units) sediment compared to Lake Grevelingen (max $\Delta pH = 1.9$ pH units). Similarly, in the absence of any compensating alkalinity production by $CaCO_3$ dissolution, the alkalinity consumption by anodic sulfide oxidation decreases the alkalinity to very low values. In our incubation of the carbonate-poor Yarra Estuary sediment we found that e-SOx activity can deplete the alkalinity in the pore water of the suboxic zone (A_T drops to ~0.2 mmol L^{-1} on Day 8; Fig. 4). To our knowledge, such low alkalinity values have not been previously documented in marine surface sediment, thus indicating once more the strong impact e-SOx can have on sediment geochemistry (Meysman et al., 2015). Alkalinity depth profiles were not recorded in this study in Lake Grevelingen. However, Rao et al. (2016) performed a similar time series incubation experiment with Lake Grevelingen sediment in which alkalinity also decreased in suboxic sediment after the development of cable bacteria on Day 7. In that study strong alkalinity excursions as observed in Yarra Estuary (i.e., A_T drops to 2–5 mmol L^{-1}) were not observed. Likewise, development of cable bacteria in carbonate-rich sediments from Florida also showed an absence of alkalinity depletion in deeper sediments, attributed to the high buffering capacity of the sediment (Yin et al., 2022). Accordingly, in the carbonate-rich sediments of Lake Grevelingen, we conclude that the alkalinity consumption by anodic sulfide oxidation is compensated to a great extent by alkalinity production by $CaCO_3$ dissolution thus giving rise to less pronounced alkalinity excursions.

In addition to alkalinity consumption in the suboxic zone, e-SOx also drives strong alkalinity production in the oxic zone, which gives rise to a pH maximum (Day 6, Figs. 4 and 7) but this does not necessarily lead to an observable maximum in alkalinity within the sediment. The likely reason for this discrepancy may be partly due to the extent of the oxic zone (<1.5 mm thick) and partly methodological, as pore water sampling was performed at 5 mm intervals whereas a higher resolution of the pH depth profiling (100 μm) was used. Additionally, part of the cathodic oxygen reduction by cable bacteria could happen directly in the water column (and hence not in the oxic zone of the sediment) masking the alkalinity production in the overlying water. Indeed microscopy observations of the sediment-water interface combined with electron balance calculations suggest that cable bacteria filaments can extend out of the sediment in the water column in order to enhance their access to O_2 (Burdorf et al., 2018).

Overall, these results show that the geochemical response of coastal sediments towards e-SOx is strongly modulated by the carbonate content of the sediment. A direct consequence for cable bacteria is that the so-called "FeS turboboost" operates more efficiently in carbonate-poor sediments, which could increase the speed by which the cable bacteria network can develop downward into the sediment. In a system with a low buffering capacity, proton production by anodic sulfide oxidation will lead to a faster and more pronounced decrease of the pH in the suboxic zone (Scotch College, Yarra estuary Fig. 2). Consequently, acid-sensitive minerals such as FeS are more readily dissolved to form ferrous iron (Fe^{2+}) and H_2S. A subsurface ΣH_2S maximum was encountered on Day 15 of the Yarra incubations potentially suggesting a large release of sulfide from FeS dissolution as cable bacteria activity intensified (Fig. 4). The ΣH_2S subsurface maximum further suggests that cable bacteria may be oxidizing sulfide at a lower rate than the FeS dissolution. Most likely, such an accelerated FeS dissolution could fuel a faster development of the cable bacteria population, and indeed e-SOx developed quicker in $CaCO_3$-poor Yarra sediments (Fig. 5).

The generation of alkalinity by sediments plays a large role in regulating the CO_2 uptake in the coastal ocean (Thomas et al., 2009; Faber et al., 2012). For example, in the North Sea, 25% of the CO_2 uptake capacity is estimated to stem from sedimentary produced alkalinity (Thomas et al., 2009; Brenner et al., 2016). The extent to which e-SOx impacts the alkalinity efflux from the sediment currently remains an open question. In sediments with e-SOx, the spatial separation of the redox half-reactions, and thus the spatial separation of proton production and consumption, leads to a transfer of alkalinity from the suboxic to the oxic zone of the sediment (Fig. 7). This so-called "alkalinity pump" then increases the vertical gradient of total alkalinity at the sediment-water interface and hence the efflux from the sediment (Rao et al., 2014, 2016; Meysman et al., 2015). Additionally, the increased

dissolution in the suboxic zone of $CaCO_3$ generates alkalinity, and hence can strengthen the upward flux of alkalinity. Indeed Rao et al. (2016) observed a large increase in the alkalinity efflux (from 46 to 136 mmol m^{-2} d^{-1}) concurrent with the development of e-SOx in $CaCO_3$-rich Lake Grevelingen. Of the total efflux, 25% was directly ascribed to the alkalinity pump induced by e-SOx, while the remaining 75% was ascribed to alkalinity generation via the increased $CaCO_3$ dissolution in the suboxic zone. A similar observation was made by Seitaj et al. (2017) *in situ* during a yearlong campaign in Lake Grevelingen, where a large efflux of alkalinity was observed in spring in conjunction with an increased rate of e-SOx. In $CaCO_3$-poor sediments (e.g. Yarra estuary), the alkalinity pump may be less efficient and the total alkalinity efflux may be lower as e-SOx develops, but this remains to be confirmed.

Overall, our results confirm the powerful effect cable bacteria activity has on the acid-base dynamics of the pore water, as a direct consequence of the spatial segregation of the two redox half-reactions in e-SOx. The spatial segregation also implies that the proton production and consumption are spatially separated, which hence gives rise to large excursions with depth, in both pH and alkalinity. The extent to which e-SOx impacts pH and alkalinity dynamics inherently varies depending on the buffering capacity of the sediment as observed with the lab incubations (Figs. 4 and 6). Interestingly, cable bacteria appear to develop more rapidly in carbonate-poor sediments (Fig. 5) potentially due to an increase in the rate of FeS dissolution (electron donor) as lower pH values are possible (e.g. low buffering capacity of the sediment). Given the prevalence of cable bacteria in seasonally hypoxic systems around the globe (Fig. 1A), the influence of e-SOx on the biogeochemistry of coastal sediments (e.g sulfur, iron, alkalinity dynamics) is of high importance.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors did not use any AI-assisted technologies. The authors take full responsibility for the content of the publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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