Environmental Science and Ecotechnology 20 (2024) 100371

Contents lists available at ScienceDirect

Environmental Science and Ecotechnology

journal homepage: www.journals.elsevier.com/environmental-science-and-ecotechnology/

Review

Electrogenic sulfur oxidation mediated by cable bacteria and its ecological effects

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ARTICLE INFO

Article history:
Received 27 June 2023
Received in revised form
11 December 2023
Accepted 12 December 2023

Keywords:
Cable bacteria
Electrogenic sulfur oxidation
Long-distance electron transfer
Aquatic ecology

ABSTRACT

At the sediment-water interfaces, filamentous cable bacteria transport electrons from sulfide oxidation along their filaments towards oxygen or nitrate as electron acceptors. These multicellular bacteria belonging to the family Desulfobulbaceae thus form a biogeobattery that mediates redox processes between multiple elements. Cable bacteria were first reported in 2012. In the past years, cable bacteria have been found to be widely distributed across the globe. Their potential in shaping the surface water environments has been extensively studied but is not fully elucidated. In this review, the biogeochemical characteristics, conduction mechanisms, and geographical distribution of cable bacteria, as well as their ecological effects, are systematically reviewed and discussed. Novel insights for understanding and applying the role of cable bacteria in aquatic ecology are summarized.

1. Introduction

Microorganisms are key ecosystem agents for biogeochemical elemental cycling, greenhouse gas generation, environmental pollutants degradation, and human health protection [1,2]. These functions are ultimately linked to microbial redox processes [3–5]. In water-sediment systems, the diffusion of dissolved oxygen (DO) results in a redox potential gradient with an oxidizing environment at the surface of the sediment and a reducing anoxic environment below. A low electrical current can be detected by connecting the deep sediment and the overlaying water using metal wires [6]. Notably, recent advancements have confirmed the occurrence of long-distance electrical currents (LDET) involving the coupling of sulfide oxidation with oxygen reduction at the surface of marine sediments (i.e., electrogenic sulfide oxidation (e-SO*x*)) [7,8]. Subsequent research has established that these currents were microbially mediated by a new type of multicellular filamentous bacteria, cable bacteria. These unique organisms form networks of bacterial filaments, connecting thousands of single cells end to end and spanning centimeters from the oxic surface to the anoxic subsurface of the sediment (Fig. 1) [8,9].

The electron transfer capability of cable bacteria, extending over centimeter ranges, surpasses any observed in organisms to date [10]. This remarkable phenomenon involves the guided current along cells via fibers in a common periplasm of the entire cable bacterium [11]. Although the molecular composition remains unclear [8,10,12,13], such long-range electron transfer adds a new dimension to our understanding of biogeochemistry and microbial ecology in aquatic sediments [7,8]. A growing number of findings suggest that cable bacteria are widely distributed in sedimentary environments, such as offshore oceans, mangrove wetlands, freshwater bodies, and underground aquifers [14–17]. Notably, cable bacteria actively influence the redox conditions of the aqueous phase covering the sediment [18,19]. For example, cable

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https://doi.org/10.1016/j.ese.2023.100371

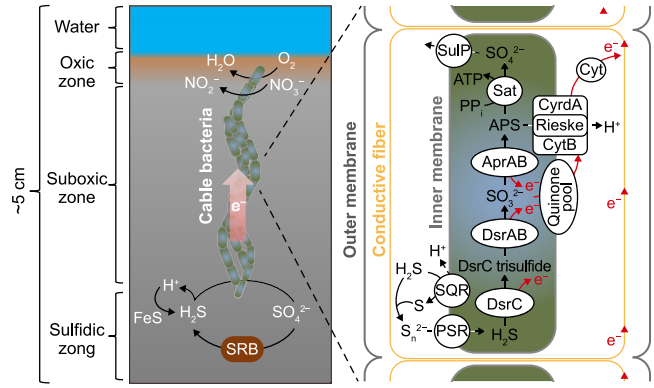

Fig. 1. The e-SO_x process of cable bacteria. Cable bacteria oxidize sulfide to sulfate, channeling electrons upward to oxygen (or nitrate) via conductive fibers connecting each single cell. The illustrated depiction on the right side expounds upon the proposed mechanisms of sulfide oxidation and electron transfer within a singular cell. SRB, sulfate-reducing bacteria; SQR, sulfide-quinone oxidoreductase; PSR, polysulfide reductase; Dsr, dissimilatory bisulfite reductase; Apr, adenosine phosphosulfate reductase; APS, adenosine-5-phosphosulfate; Sat, sulfate adenylyltransferase.

bacteria regulate the cycling of sulfur, phosphorus [20], manganese [21], and iron in seasonal hypoxic environments [18]. Furthermore, cable bacteria can also suppress methane release and serve as an electrical connection to oxygen for other bacteria flocking around them [22–24]. Moreover, filamentous microorganisms, putatively cable bacteria, have been seen to cover the deap sea sulfide chimneys [25]. Therefore, speculation arises regarding the potential of cable bacteria and many other electroactive microorganisms to support biogeochemical cycles in aquatic environments by forming a widespread redox network, especially for cable bacteria through LDET processes from the sediment's depths to its surface [22].

This review summarizes the current knowledge about the niches and functions of cable bacteria in aquatic ecosystems. Additionally, we delve into the key metabolism and LDET mechanisms of cable bacteria. Conclusively, we outline the research gaps and questions that need to be addressed to better understand or apply cable bacteria in aquatic environments.

2. Biological characteristics

2.1. e-SO_x and oxygen/nitrate reduction

Phylogenetically, cable bacteria are categorized within the Desulfobulbaceae family, exhibiting notable diversity [8,26]. Sulfide oxidation occurs in the anodic cells in the anoxic zone, sustaining LDET through continuous conductive fibers in the periplasmic space and feeding oxygen reduction in the cathodic cells in the oxic zone [13]. Cable bacteria lack characteristic marker genes of typical sulfur-oxidizing bacteria [13]. Instead, all key genes of the dissimilatory sulfate reduction (DSR) pathway [13,27,28] were found, and many genes of this pathway were highly expressed in *Candidatus* Electronema sp. GS. The metabolic reconstruction based on the first genome of freshwater cable bacteria suggests that cable bacteria reverse the canonical sulfate reduction pathway for sulfide oxidation to sulfate [29]. This is consistent with the features of DSR found in Desulfobulbaceae bacteria, such as *Desulfurivibrio alkaliphilus* [13]. *D. alkaliphilus* can also grow by sulfur disproportionation and nitrate-dependent sulfide oxidation [29,30] and oxidize sulfides to elemental sulfur and, eventually, sulfate [31]. A similar two-step process is hypothesized to occur in cable bacteria [13]. A periplasmic type III sulfide-quinone oxidoreductase (SQR) is expressed in cable bacteria and, therefore, a reasonable candidate for the initial sulfide oxidation step [15], while a type I SQR oxidizes sulfide in *D. alkaliphilus* [31]. The formed sulfur reacts chemically with sulfide to dissolve polysulfides, which can be translocated from the periplasm into the cytoplasm [32]. Currently, type III SQRs are poorly characterized [32,33]. In the second step, sulfate is produced from polysulfide in the cytoplasm via the reverse DSR pathway [13]. Although the mechanism of elemental sulfur or polysulfide transport across the cytoplasmic membrane in cable bacteria remains unclear, genomic information suggests potential involvements of a membrane protein YeeE mediating thiosulfate uptake, the cytoplasmic enzyme rhodanese, and the sulfur transferases TusA and the subunit-EFH in dissimilatory sulfite reductase complex DsrEFH in the transport process [13,34,35]. Hypotheses propose the formation of the subunit-C in dissimilatory sulfite reductase complex DsrC-trisulfide (DCT) through the reaction of reduced sulfur from TusA or sulfide with DsrC, which is subsequently oxidized by the subunit-AB in dissimilatory sulfite reductase complex DsrAB to form sulfite and DsrC [13]. Finally, sulfate is generated by adenosine 5-phosphate reductase (AprAB) or sulfate adenylyltransferase (Sat), representing an adenosine triphosphate (ATP)-generating process. Sulfate can then be released from the cell via the sulfate permease SulP (Fig. 1) [13,28,36]. Fig. 1 summarizes how cable bacteria oxidize sulfide to sulfate, transferring electrons upward to oxygen (or nitrate) via conductive fibers connecting each single cell.

The electrons released from the sulfide oxidization process can be transferred to the membrane quinone pools in dissimilatory sulfite reductase complex DsrMK and the quinone-interacting membrane-bound oxidoreductase QmoABC complexes. Subsequently, a membrane-anchored complex, i.e., CydA (subunit-A in cytochrome bd oxidase) -CytB (subunit-B in cytochrome *bc* complex) -Rieske protein, may oxidize the quinols and transfer electrons to periplasmic conductive fibers via soluble cytochromes. Meanwhile, the CydA-CytB-Rieske complex is predicted to play a key role in forming *trans*-membrane proton gradient and generating energy in cable bacteria [13].

The mechanism of the oxygen reduction step during e-SO_x is yet unclear. Despite extensive investigations, classical terminal membrane-bound oxidases within the genomes of cable bacteria have not been conclusively identified, with a potential exception being the membrane-bound cytochrome *c* oxidase. However, the presence of periplasmic cytochromes suggests an oxygen reduction process without energy conservation [13]. Two independent studies concluded that the cathodic oxygen-reducing cells within the filament are solely responsible for efficient electron transport to oxygen without energy conservation or carbon fixation [37,38]. The ability to oxidize inorganic sulfur compounds using oxygen as electron acceptors has also been demonstrated in single-cell sulfate reducers. *Desulfovibrio desulfuricans* and *Desulfobacterium autotrophicum* can perform oxygen reduction that is not associated with growth or energy generation [39]. Moreover, it has been demonstrated that *Desulfovibrio vulgaris* Hildenborough exhibits adaptive responses to increased oxygen concentrations facilitating energy conservation after 114 generations [39].

Cable bacteria can also use nitrate and nitrite as electron acceptors for oxidation of inorganic sulfur compounds via LDET, forming ammonium as the end product via dissimilatory nitrate reduction to ammonium (DNRA) [40]. A model for the DNRA of *Ca.* Electronema sp. GS has been proposed: nitrate is reduced by a periplasmatic nitrate reductase (NapAB), and the formed nitrite is reduced to ammonium by a putative nitrite reductase (pOCC) in the periplasm [38]. The reduction of nitrate and nitrite is likely not connected to energy generation in *Ca.* Electronema sp. GS during LDET, similar to oxygen reduction [38]. Notably, cable bacteria can favor other DNRA bacteria as they stimulate Fe^{2+} dissolution (e.g., either by oxidizing Fe–S-containing minerals or decreasing the

ambient pH), which can serve as an exclusive electron donor for DNRA [9]. Nitrate reduction by cable bacteria using LDET to get privileged access to distant electron donors is a hitherto unknown mechanism in nitrogen transformations, and the quantitative importance in elements cycling remains to be addressed [40].

2.2. Long-distance electron transport mechanism

In contrast to the extracellular electron transfer (EET) of other electroactive microorganisms, electrons in cable bacteria travel along the periplasmic conductive fibers, extending from anodic to cathodic cells [41,42]. A gradient in cytochrome redox potential along individual cable bacteria was detected by Raman spectroscopy, and was immediately disrupted upon oxygen removal or laser-cutting of the filaments [10]. These results provide direct evidence for LEDT in living cable bacteria. Studies using conductive atomic force microscopy showed that the parallel conductive fibers of cable bacteria have a conductivity of 10 S cm^{-1}, comparable to some artificial polymer nanowires [43]. Moreover, these fibers are electrically interconnected between adjacent cells and thus form a fail-safe electrical network [44]. This unique biological electrical circuit can maintain the LDET of cable bacteria even when partial fibers or cells are impaired.

In addition to their electrical conductivity, the periplasmic fibers also have an important function in maintaining the integrity of individual cable bacteria cells as a united filament [45]. Moreover, it was recently demonstrated that these fibers also provide a community-serving electrical conduit that can deliver electrons from diverse microorganisms flocking around cable bacteria to oxygen. When the conductive fibers of cable bacteria actively mediate e-SO_x, their associated bacteria flock around the anoxic part of cable bacteria with oxidized cytochromes [23,46]. Upon a cut between the anoxic and oxic parts of cable bacteria, the flocking cells spread out, and their cytochromes are reduced, indicating the flocking cells (mostly aerobes) donate electrons to the conductive fibers of cable bacteria and eventually to oxygen (Fig. 2) [46]. Although the mechanisms of the interspecies electron transfer between cable bacteria and the flocking microorganisms are unclear, this function renders an even broader role of cable bacteria in microbial ecology with electrons derived from multiple donors. These results indicate a crucial role played by the conductive fibers in facilitating connections not only among cable bacteria cells but also in establishing links between cable bacteria and other microorganisms.

Although the periplasmic fibers of cable bacteria have been extensively studied, the molecular structure and mechanism of electron conduction remain unclear [11,44,47,48]. Cytochromes are common electron carriers in bacterial cells [49]. *C*-type cytochromes were identified in cable bacteria and gradually changed from a reducing state to an oxidation state from the anoxic end to the oxic end, but there is no direct evidence that *c*-type cytochromes are the main electron carrier for cable bacteria's LDET [10,13]. The mechanism of electron conduction in cable bacteria has not been elucidated yet, but was found to be thermally activated [48].

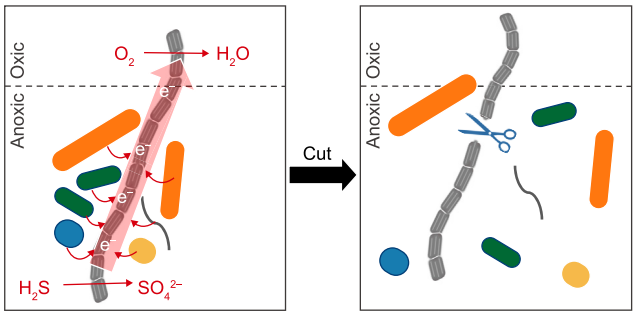

Fig. 2. The role of cable bacteria as an electronic conduit delivering electrons from the flocking bacteria to oxygen. Left: oxygen-respiring cable bacteria with flocking bacteria; Right: bacteria spread out after a cut of cable bacteria.

High-resolution observation on the fiber structure of cable bacteria is the key to understanding their LDET mechanism. High-resolution microscopy, spectroscopy, and chemical imaging of individual cable bacterium filaments showed that the periplasmic wires of cable bacteria encompass a conductive protein core surrounded by an insulating protein shell layer [50]. The core proteins contain a sulfur-ligated nickel cofactor, essential for electron conduction; this importance is underscored by observations of decreased conductivity when nickel undergoes oxidation or selective removal [50]. Recent studies have further demonstrated the formation of a fiber network in cable bacteria, showcasing electrical interconnectivity between adjacent cells [11,44]. Such structural organization provides a fail-safe electrical network for LDET in these filamentous microorganisms [44]. Moreover, the electron conduction within this network does not exhibit apparent directionality. Remarkably, when anodic cells were exposed to oxygen, electric currents were rapidly restored, indicating a seamless transition from oxidation to reduction in the anodic cells [37].

Interestingly, the most abundant protein in *Ca.* Electronema sp. GS is subunit-A in pilin (PilA), a type IV pili-forming protein [13]. However, no pili-like structures have been observed on the surface of cable bacteria. Although it has been demonstrated that PilA can facilitate the construction of conductive nanowires (or even build conductive e-pili directly) in some electroactive microorganisms such as *Geobacter* species [51], the role of the highly expressed PilA in cable bacteria remains unclear, and the existence of e-pili is still debatable [52].

3. Geochemical and geographical distribution characteristics

3.1. Geochemical characteristics

e-SO_x significantly affects the cycles of sulfur, iron, manganese, nitrogen, phosphorus, and other redox-active elements, resulting in a distinct geochemical fingerprint detectable by microsensor profiling [7,8,20,21]. Noteworthy characteristics include the presence of a wide suboxic zone with no detectable oxygen and sulfide in the porewater ($[O_2] < 1$ μmol L^{-1}, $[H_2S] < 1$ μmol L^{-1}). The depth of the suboxic zone serves as a reliable indicator of the extent to which the cable bacteria network is prevalent [8]. Another feature is a distinct pH signature in the sediment porewater caused by the spatial segregation of the two redox half-reactions [53]. Cathodic reduction of oxygen generates alkalinity in the top sediment while protons are produced (acidification) by the anodic sulfide oxidation in the bottom [40,54,55]. The acidification caused by the e-SO_x of cable bacteria in deep sediment increases the dissolution of many solid minerals, such as calcium carbonates and iron sulfides [56]. On the other hand, the alkaline sediment-water interface can buffer the diffusion of the dissolved carbonate, Fe^{2+}, and Mn^{2+} from the deep sediment to the overlying water by accelerating the rate of carbonate accumulation and the process of mineral diagenesis [57,58].

3.2. Geographic distribution

By combining microsensor profiling [7,8,15,59], microscopic techniques [8,24,25,55], and 16S rRNA gene sequencing [22,54], cable bacteria have been observed in over sixty locations

worldwide. Predominantly, these occurrences are situated in marine environments, encompassing 42 sites, with subsequent instances identified in freshwater and other environments. A map of the global distribution of cable bacteria based on recent reports is provided in Fig. S1.

3.2.1. Coastal sediments

Cable bacteria exhibit growth across diverse coastal sediment environments, encompassing salt marshes, seasonally hypoxic basins, and subtidal coastal mud plains [55]. Within marine sediments, these cable bacteria are classified under the taxon *Ca.* Electrothrix, featuring four species: *Ca.* Electrothrix marina, *Ca.* Electrothrix aarhusiensis, *Ca.* Electrothrix japonica, and *Ca.* Electrothrix communis [13]. Complementary laboratory experiments with intertidal sands demonstrated that mechanical disturbance destroyed the e-SO_x signal, showing that bioturbation may control the natural distribution of cable bacteria [55]. In New England salt marsh sediments, the activity of cable bacteria appeared to be more persistent compared to that of coastal sediments, as the sulfide was constantly provided by sulfate reduction rather than accumulated iron sulfide [17]. Microsensor profiling combined with fluorescence in situ hybridization (FISH) recorded filament densities of 77 m cm^{-2} and the signature of e-SO_x in laboratory incubations of sediments from grey mangroves near Melbourne, Australia, which shows that cable bacteria are present and active in mangrove sediments [60]. Furthermore, cable bacteria were found in the salt pans (sabkhas) in Tunisia, characterized by a highly variable salinity [14]. Salinity is a controlling factor for cable bacteria diversity and species composition. Recent evidence showed that cable bacteria living in freshwater or marine environments have different ion translocation channels to maintain the osmotic balance [26].

3.2.2. Freshwater sediments

In freshwater sediment, cable bacteria were first observed in the freshwater stream Giber Å, Denmark [15]. This finding hinted at the broader prevalence and biogeochemical significance of cable bacteria, surpassing initial expectations tied to the lower sulfide/sulfate content in freshwater compared to marine environments [15,16,26]. The density of cable bacteria in freshwater sediments was shown to be less than 100 m cm^{-2}, while the density of cable bacteria in marine sediments can be up to 2000 m cm^{-2} [14,15]. River sediments host a diverse array of cable bacteria, featuring both generalists and many specialists [15,61]. Despite this diversity, the contribution of cable bacteria in the freshwater ecosystem and other influencing factors remain unclear due to sulfide limitations. Dong and colleagues (2022) evaluated cable bacteria assemblages from ten river sediments in the Pearl River Delta, China. The results revealed that the communities of cable bacteria were deterministically assembled through water quality-driven selection; sulfide-lacking or highly contaminated water environment could reduce the cell width and diversity of cable bacteria [59]. However, cable bacteria were found in contaminated freshwater sediments, and the density of cable bacteria after enrichment reached a maximum of 95.48 m cm^{-2}. This revelation contributes fundamental data that supports further exploration of the role of cable bacteria in the bioremediation of freshwater sediment [16,22].

3.2.3. Other habitats

Aquatic plants can release oxygen into the rhizosphere, rendering it an ideal habitat for cable bacteria. Direct observations revealed the presence of cable bacteria at seagrass roots (Fig. 3), with the oxygen-leaking roots contributing to a higher abundance of cable bacteria [62]. Cable bacteria are also associated with the rhizosphere of freshwater aquatic plants, including the important crop *Oryza sativa* (rice), *Lobelia cardinalis*, and *Salicornia europaea* [63]. Large filamentous bacteria (LFB) have also been found in deep seafloor environments, playing a considerable role in the biogeochemical cycling of elements in such environments [25]. Analyses of a 16S rRNA gene clone library showed that these LFB belongs to the Desulfobulbaceae. Notably, compared to cable bacteria through phylogenetic, morphological, and environmental considerations, they exhibit high similarity [25]. Additionally, the discovery of cable bacteria in hydrocarbon-contaminated aquifers and black-odorous sediments suggests that cable bacteria may tolerate a certain degree of pollutant stress and survive in contaminated habitats [64–67]. Yet, a survey of published geochemical data and 16S rRNA gene sequences identified that the global distribution of cable bacteria is strongly underestimated [14].

4. Cable bacteria for environmental protection

4.1. Promoting degradation of organic pollutants in sediments

The detection of Desulfobulbaceae at the oxic–anoxic interface of fresh sediment cores taken at a hydrocarbon-contaminated aquifer suggests that cable bacteria are active and mediate the sulfur cycle of polluted aquifers [64,65]. In a BMFC operating in a temperate estuarine environment for over a year, cable bacteria attached to the fibers of a carbon brush anode might use the anode as an electron acceptor to motivate toluene degradation in sediments [68]. Furthermore, it was demonstrated that cable bacteria and other Desulfobulbaceae members could be enriched in bioelectrochemical snorkels deployed for the remediation of hydrocarbon-contaminated marine sediment, concomitant with sulfur metabolism and toluene degradation. SRBs have been known to participate in the degradation of hydrocarbons [69–71], and the accelerated degradation of some hydrocarbons, such as toluene or petroleum hydrocarbons, has been related to the sulfate generation from the e-SO_x of cable bacteria [22,67,72]. Meanwhile, the sulfide-scavenging capability of cable bacteria also plays an important role in accelerated degradation, as sulfide is toxic to sulfate-reducers [68,74]. Cable bacteria can also behave like bioelectrochemical snorkels and stimulate sulfate regeneration in the anoxic sediment, accelerating alkane degradation by 24% [73]. Phylogenetic ecological network analyses further revealed that elevated DO concentrations in the overlying water reinforced interspecific interactions between cable bacteria and functional microorganisms, such as SRB, contaminant degraders, and electroactive microorganisms in anoxic sediment. This suggests enhanced microbial syntrophies using cable bacteria LDET and metabolism to regenerate SO_4^{2-} [22].

Additionally, motile microorganisms in sediments can potentially transport organic pollutants into deeper sediments through microbial gliding or twitching motility [74]. Gliding motility is particularly common in sulfur bacteria and Cytophaga-Flavobacterium groups [75,76]. Cable bacteria use gliding or twitching motility to access sulfide [72,77]. Recent studies have evidenced that cable bacteria can accelerate the migration of pyrene from the sediment surface to deeper layers, where they collaboratively enhance pyrene degradation alongside SRB and other contaminant degraders [72]. Furthermore, e-SO_x can influence the redox potential and pH of sediments, consequently impacting the physical and chemical properties of minerals. This, in turn, leads to changes in the bioavailability of organic pollutants adsorbed on the surface of the mineral particles (Fig. 3) [19,22]. Therefore, cable bacteria may play important roles in the self-healing capacity of contaminated sediments and inspire novel remediation treatments upon persistent organic pollutants (POPs) spillage.

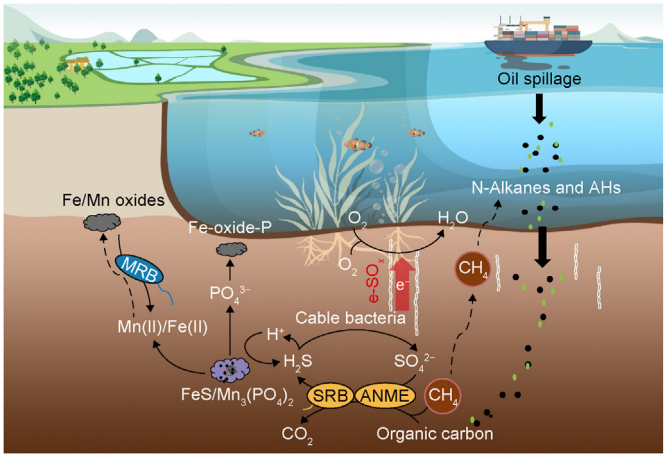

Fig. 3. The effects of cable bacteria e-SO_x on water ecosystems. MRB, mineral-reducing bacteria; ANME, anaerobic methanotrophic archaea; SRB, sulfate-reducing bacteria; AHs, aromatic hydrocarbons.

4.2. Regulating the migration and cycling of metal elements

Furthermore, beyond their crucial involvement in the cycles of C, N, S, and O elements, cable bacteria affect the ecosystem by regulating the cycles of pivotal metal elements, such as Fe, Mn, and As, as summarized in Fig. 3 [14,19–21,53].

The metabolic activity of cable bacteria was found to induce an electrical field of 12–17 mV m^{-1} in the upper centimeters of freshwater sediment, which affected the depth profiles and fluxes of major cations (e.g., Ca^{2+}, Fe^{2+}, and Mn^{2+}) and anions (SO_4^{2-}) in the pore water through an ionic drift [78,79]. The strong acidification of the pore water at greater depths increased the dissolution of calcium carbonates and iron sulfides, thus elevating the concentrations of Ca^{2+} and Fe^{2+} in the pore water [56,78,79]. Subsequently, the mobilized iron diffused to the oxic zone, oxidizing it as FeOOH, while calcium precipitated in the oxic zone as magnesium-calcite [79]. The development of e-SO_x also increased the release of dissolved manganese at the sediment–water interface and inhibited phosphate efflux [21,56]. Trace elements arsenic and cobalt can be adsorbed on the sulfide precipitation, and when e-SO_x acidifies the pore water, the dissolution of iron sulfide may release the trace elements again to the overlying water [79]. Molybdenum in sediments was mainly enriched on the surface of iron oxides and hydroxide particles. The metabolism of cable bacteria causes the dissolution of manganese carbonate and FeS, indirectly affecting molybdenum kinetics and expanding the seasonal variation of molybdenum change [80]. Based on these reports, it can be assumed that cable bacteria also play an important role in affecting the redox and distribution of many other heavy metals (e.g., Cr, U) in sediments, indicating possible applications of cable bacteria in remediating metal-contaminated environments and recovering noble metals.

4.3. Relieving sulfide toxicity

Seasonal oxygen depletion (hypoxia) is very common in coastal bottom waters, leading to the release and persistence of free sulfide (euxinia), which is highly toxic to ecosystems [81,82]. A recent report showed that cable bacteria can delay the onset of euxinia in coastal waters [18]. Cable bacteria generate a large buffer of sedimentary iron oxides before the onset of summer hypoxia, capturing free sulfide in the surface sediment, thus likely preventing the development of bottomwater euxinia and protecting aquatic life [18]. For example, bivalves rely on external microbial sulfide oxidation to prevent diffusive uptake of sulfide across the gill surface [83,84]. This protective mechanism, however, is not observed in other organisms like blue mussels and Pacific oysters [85]. High cable bacteria densities may be critical in sediment detoxification for bivalve reef sustainability [85]. A symbiosis between cable bacteria and seagrass was recently proposed [62]. Aquatic plants release oxygen into the rhizosphere of marine and freshwater sediments, influencing the balance between sulfide-oxidizing bacteria (SOB, sulfide consumption) and SRB (sulfide production) within the rhizosphere. It was demonstrated that cable bacteria were enriched at the oxic–anoxic transition zone next to roots compared to the bulk sediment in the same depth [63]. There is a possibility that radial oxygen loss (ROL), by influencing the abundance, activity, and spatial distribution of SOB, such as cable bacteria and SRB that colonize these younger roots, acts as a 'barrier' to sulfide intrusion [62]. Given the presence of cable bacteria in many seasonally hypoxic systems, the euxinia-preventing firewall mechanism, characterized by a substantial buffer of sedimentary iron oxides, may be widely active. This could elucidate why euxinia is relatively infrequently observed in the coastal ocean [18].

4.4. Mitigation of greenhouse gas emissions

Methane, mainly generated by methanogens, is the second most important greenhouse gas on Earth, superseded only by CO_2. It has more than 80-fold greater global warming potential than CO_2 over the first 20 years after it enters the atmosphere. Cable bacteria have a competitive effect on methanogens due to their ability to induce a surge in sulfate concentrations in the surface layer, thereby stimulating SRB. This stimulation competes with methanogenic archaea for substrates like acetate [22,86]. Scholz and colleagues (2020) found that inoculating rice-vegetated soil pots with cable bacteria led to a fivefold increase in sulfate inventory, resulting in a remarkable 93% reduction in methane emissions compared to control pots lacking cable bacteria [86]. Liu and colleagues (2021) also showed increased activity of cable bacteria promoting the accumulation of sulfate and depletion of organic carbon (Fig. 3) [22]. There is a possibility that the acidification by cable bacteria hinders the production of organic carbon from root exudations and sloughed root material, thus further limiting the fermentation and methane production of sediments [86,87]. Therefore, promoting cable bacteria in different habitats by enrichment or sensible management may contribute to climate change mitigation by reducing methane emissions [86].

5. Outlook

The study on cable bacteria is still in its infancy. To further discover the functions and underlying mechanisms of cable bacteria, numerous questions and challenges must be tackled.

The primary consideration revolves around cultivating cable bacteria in a pure form. The development of reliable genetic engineering protocols, the investigation of specific syntrophic interactions, and an assessment of the ecological safety of cable bacteria for potential biomaterial production or environmental remediation necessitate their cultivation in pure culture. To this end, further genomic and metabolic information on cable bacteria in different environments becomes imperative for optimizing cultivation strategies. Moreover, a simplified sediment-like cultivation environment and isolation of cable bacteria-associated microorganisms are also important in cultivating cable bacteria, whether in pure culture or co-culture. Secondly, the interaction or cross-feeding networks of cable bacteria and their microbial partners need to be comprehensively elucidated. Unraveling the nature

of the interaction between cable and flocking bacteria and discerning whether the latter can contribute nutrients to the former holds the key to securing a purified culture of cable bacteria. These insights are paramount for comprehending and regulating the ecological role of cable bacteria within ecosystems. Thirdly, the mechanism underlying the LDET of cable bacteria remains unknown. Clarifying elements such as the molecular structure of conductive fibers and the process by which these fibers accept electrons from the redox chain of cable bacteria is indispensable for unraveling the distinctive lifestyle of cable bacteria. Furthermore, this knowledge serves as a catalyst for advancements in green electronic materials. Finally, the application and regulation of cable bacteria in diverse environments warrant scrutiny. The potential of cable bacteria in fields such as the bioremediation of contaminated environments, mitigation of global warming, and design of green conductive materials is promising. The global distribution of cable bacteria and numerous laboratory-scale studies affirm their impact and environmental application potential. Therefore, shifting focus towards large-scale and in situ investigations is imperative to further ascertain the practical implications and real-world viability of cable bacteria in various contexts.

Cable bacteria represent a lifeform characterized by a unique cellular organization dependent on a highly efficient yet unidentified electron conduction mechanism and serves an important environmental function. To answer these inquiries, future research should apply various interdisciplinary theories and techniques, including but not limited to microbiology, structural biology, geochemistry, environmental engineering, and material chemistry. Uncovering the solutions to these queries will undoubtedly contribute to advancing knowledge within these respective disciplines.

CRediT authorship contribution statement

Zhenyu Wang: Investigation, Visualization, Writing - Original Draft, Writing -Review & Editing. **Leonid Digel:** Investigation, Writing - Original Draft, Writing-Review & Editing. **Yongqiang Yuan:** Investigation, Writing - Review & Editing. **Hui Lu:** Writing - Review. **Yonggang Yang:** Conceptualization, Writing - Review & Editing, Supervision, Funding Acquisition. **Carsten Vogt:** Conceptualization, Writing - Review & Editing, Supervision, Funding Acquisition. **Hans-Hermann Richnow:** Conceptualization, Revising - Original Draft. **Lars Peter Nielsen:** Conceptualization, Revising - Original Draft, Project Administration, Funding Acquisition.

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.

Acknowledgements

This study was supported by the Key-Area Research and Development Program of Guangdong Province (2020B1111380003), Guangdong Provincial Programs for Science and Technology Development (2022A0505030006), National Natural Science Foundation of China (31970110, 32370111), GDAS' Special Project of Science and Technology Development (2021GDASYL-20210103022), State Key Laboratory of Applied Microbiology Southern China (Grant SKLAM005-2020) and Danish National Research Foundation (DNRF136). Zhenyu Wang (File No. 202208080044) is financially supported by the China Scholarship Council. Leonid Digel was supported by FEMS Research and Training Grant (1725) and EMBO Scientific Exchange grant (9720) for a visit to the UFZ in Leipzig, Germany.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ese.2023.100371.

References

[1] N. Gruber, J.N. Galloway, An Earth-system perspective of the global nitrogen cycle, Nature 451 (7176) (2008) 293–296.
[2] A.L. Heathwaite, Multiple stressors on water availability at global to catchment scales: understanding human impact on nutrient cycles to protect water quality and water availability in the long term, Freshw. Biol. 55 (2010) 241–257.
[3] S. Peiffer, A. Kappler, S.B. Haderlein, C. Schmidt, J.M. Byrne, S. Kleindienst, C. Vogt, H.H. Richnow, M. Obst, L.T. Angenent, C. Bryce, C. McCammon, B. Planer-Friedrich, A biogeochemical-hydrological framework for the role of redox-active compounds in aquatic systems, Nat. Geosci. 14 (5) (2021) 264–272.
[4] T. Borch, R. Kretzschmar, A. Kappler, P. Van Cappellen, M. Ginder-Vogel, A. Voegelin, K. Campbell, Biogeochemical redox processes and their impact on contaminant dynamics, Environ. Sci. Technol. 44 (1) (2010) 15–23.
[5] N. Karimian, S.G. Johnston, E.D. Burton, Iron and sulfur cycling in acid sulfate soil wetlands under dynamic redox conditions: a review, Chemosphere 197 (2018) 803–816.
[6] C.E. Reimers, L.M. Tender, S. Fertig, W. Wang, Harvesting energy from the marine sediment-water interface, Environ. Sci. Technol. 35 (1) (2001) 192–195.
[7] L.P. Nielsen, N. Risgaard-Petersen, H. Fossing, P.B. Christensen, M. Sayama, Electric currents couple spatially separated biogeochemical processes in marine sediment, Nature 463 (7284) (2010) 1071–1074.
[8] C. Pfeffer, S. Larsen, J. Song, M.D. Dong, F. Besenbacher, R.L. Meyer, K.U. Kjeldsen, L. Schreiber, Y.A. Gorby, M.Y. El-Naggar, K.M. Leung, A. Schramm, N. Risgaard-Petersen, L.P. Nielsen, Filamentous bacteria transport electrons over centimetre distances, Nature 491 (7423) (2012) 218–221.
[9] A.J. Kessler, M. Wawryk, U. Marzocchi, K.L. Roberts, W.W. Wong, N. Risgaard-Petersen, F.J.R. Meysman, R.N. Glud, P.L.M. Cook, Cable bacteria promote DNRA through iron sulfide dissolution, Limnol. Oceanogr. 64 (3) (2019) 1228–1238.
[10] J.T. Bjerg, H.T.S. Boschker, S. Larsen, D. Berry, M. Schmid, D. Millo, P. Tataru, F.J.R. Meysman, M. Wagner, L.P. Nielsen, A. Schramm, Long-distance electron transport in individual, living cable bacteria, Proc. Natl. Acad. Sci. U.S.A. 115 (22) (2018) 5786–5791.
[11] F.J.R. Meysman, R. Cornelissen, S. Trashin, R. Bonne, S.H. Martinez, J. van der Veen, C.J. Blom, C. Karman, J.L. Hou, R.T. Eachambadi, J.S. Geelhoed, K. De Wael, H.J.E. Beaumont, B. Cleuren, R. Valcke, H.S.J. van der Zant, H.T.S. Boschker, J.V. Manca, A highly conductive fibre network enables centimetre-scale electron transport in multicellular cable bacteria, Nat. Commun. 10 (2019) 4120.
[12] A. Teske, Cable bacteria, living electrical conduits in the microbial world, Proc. Natl. Acad. Sci. U.S.A. 116 (38) (2019) 18759–18761.
[13] K.U. Kjeldsen, L. Schreiber, C.A. Thorup, T. Boesen, J.T. Bjerg, T.T. Yang, M.S. Dueholm, S. Larsen, N. Risgaard-Petersen, M. Nierychlo, M. Schmid, A. Boggild, J. van de Vossenberg, J.S. Geelhoed, F.J.R. Meysman, M. Wagner, P.H. Nielsen, L.P. Nielsen, A. Schramm, On the evolution and physiology of cable bacteria, Proc. Natl. Acad. Sci. U.S.A. 116 (38) (2019) 19116–19125.
[14] L.D.W. Burdorf, A. Tramper, D. Seitaj, L. Meire, S. Hidalgo-Martinez, E.M. Zetsche, H.T.S. Boschker, F.J.R. Meysman, Long-distance electron transport occurs globally in marine sediments, Biogeosciences 14 (3) (2017) 683–701.
[15] N. Risgaard-Petersen, M. Kristiansen, R.B. Frederiksen, A.L. Dittmer, J.T. Bjerg, D. Trojan, L. Schreiber, L.R. Damgaard, A. Schramm, L.P. Nielsen, Cable bacteria in freshwater sediments, Appl. Environ. Microbiol. 81 (17) (2015) 6003–6011.
[16] X. Xu, S. Huo, H. Zhang, X. Li, F. Wu, Identification of cable bacteria and its biogeochemical impact on sulfur in freshwater sediments from the Wenyu River, Sci. Total Environ. 769 (2021) 144541.
[17] S. Larsen, L.P. Nielsen, A. Schramm, Cable bacteria associated with long-distance electron transport in New England salt marsh sediment, Environmental Microbiology Reports 7 (2) (2015) 175–179.
[18] D. Seitaj, R. Schauer, F. Sulu-Gambari, S. Hidalgo-Martinez, S.Y. Malkin, L.D.W. Burdorf, C.P. Slomp, F.J.R. Meysman, Cable bacteria generate a firewall against euxinia in seasonally hypoxic basins, Proc. Natl. Acad. Sci. U.S.A. 112 (43) (2015) 13278–13283.
[19] S. van de Velde, L. Lesven, L.D.W. Burdorf, S. Hidalgo-Martinez, J.S. Geelhoed, P. Van Rijswijk, Y. Gao, F.J.R. Meysman, The impact of electrogenic sulfur oxidation on the biogeochemistry of coastal sediments: a field study, Geochem. Cosmochim. Acta 194 (2016) 211–232.
[20] F. Sulu-Gambari, D. Seitaj, F.J.R. Meysman, R. Schauer, L. Polerecky, C.P. Slomp, Cable bacteria control iron-phosphorus dynamics in sediments of a coastal hypoxic basin, Environ. Sci. Technol. 50 (3) (2016) 1227–1233.
[21] F. Sulu-Gambari, D. Seitaj, T. Behrends, D. Banerjee, F.J.R. Meysman, C.P. Slomp, Impact of cable bacteria on sedimentary iron and manganese dynamics in a seasonally-hypoxic marine basin, Geochem. Cosmochim. Acta 192 (2016) 49–69.
[22] F.F. Liu, Z.Y. Wang, B. Wu, J.T. Bjerg, W.Z. Hu, X. Guo, J. Guo, L.P. Nielsen,

R.L. Qiu, M.Y. Xu, Cable bacteria extend the impacts of elevated dissolved oxygen into anoxic sediments, ISME J. 15 (5) (2021) 1551–1563.
[23] J.J. Bjerg, J.J. Lustermans, I.P. Marshall, A.J. Mueller, S. Brokjær, C.A. Thorup, P. Tataru, M. Schmid, M. Wagner, L.P. Nielsen, Cable bacteria with electric connection to oxygen attract flocks of diverse bacteria, Nat. Commun. 14 (1) (2023) 1614.
[24] D. Vasquez-Cardenas, J. van de Vossenberg, L. Polerecky, S.Y. Malkin, R. Schauer, S. Hidalgo-Martinez, V. Confurius, J.J. Middelburg, F.J.R. Meysman, H.T.S. Boschker, Microbial carbon metabolism associated with electrogenic sulphur oxidation in coastal sediments, ISME J. 9 (9) (2015) 1966–1978.
[25] S. Kato, A. Yamagishi, A novel large filamentous deltaproteobacterium on hydrothermally inactive sulfide chimneys of the Southern Mariana Trough, Deep Sea Res. Oceanogr. Res. Pap. 110 (2016) 99–105.
[26] M. Sereika, F. Petriglieri, T.B.N. Jensen, A. Sannikov, M. Hoppe, P.H. Nielsen, I.P. Marshall, A. Schramm, M. Albertsen, Closed genomes uncover a saltwater species of Candidatus Electronema and shed new light on the boundary between marine and freshwater cable bacteria, ISME J. 17 (4) (2023) 561–569.
[27] I.A.C. Pereira, A.R. Ramos, F. Grein, M.C. Marques, S.M. da Silva, S.S. Venceslau, A comparative genomic analysis of energy metabolism in sulfate reducing bacteria and archaea, Front. Microbiol. 2 (2011) 69.
[28] A.A. Santos, S.S. Venceslau, F. Grein, W.D. Leavitt, C. Dahl, D.T. Johnston, I.A.C. Pereira, A protein trisulfide couples dissimilatory sulfate reduction to energy conservation, Science 350 (6267) (2015) 1541–1545.
[29] H. Muller, S. Marozava, A.J. Probst, R.U. Meckenstock, Groundwater cable bacteria conserve energy by sulfur disproportionation, ISME J. 14 (2) (2020) 623–634.
[30] C. Thorup, A. Schramm, A.J. Findlay, K.W. Finster, L. Schreiber, Disguised as a sulfate reducer: growth of the deltaproteobacterium Desulfurivibrio alkaliphilus by sulfide oxidation with nitrate, mBio 8 (4) (2017) e00671, 17.
[31] A. Pellerin, G. Antler, S.A. Holm, A.J. Findlay, P.W. Crockford, A.V. Turchyn, B.B. Jorgensen, K. Finster, Large sulfur isotope fractionation by bacterial sulfide oxidation, Sci. Adv. 5 (7) (2019) eaaw1480.
[32] M. Marcia, U. Ermler, G. Peng, H. Michel, Function, and Bioinformatics. A new structure-based classification of sulfide: quinone oxidoreductases, Proteins 78 (5) (2010) 1073–1083.
[33] A.M. Lencina, Z. Ding, L.A. Schurig-Briccio, R.B.J. Gennis, Characterization of the type III sulfide: quinone oxidoreductase from Caldivirga maquilingensis and its membrane binding, Biochim. Biophys. Acta Bioenerg. 1827 (3) (2013) 266–275.
[34] T. Koch, C. Dahl, A novel bacterial sulfur oxidation pathway provides a new link between the cycles of organic and inorganic sulfur compounds, ISME J. 12 (10) (2018) 2479–2491.
[35] S.S. Venceslau, Y. Stockdreher, C. Dahl, I.A.C. Pereira, The "bacterial heterodisulfide" DsrC is a key protein in dissimilatory sulfur metabolism, Biochim. Biophys. Acta Bioenerg. 1837 (7) (2014) 1148–1164.
[36] A. Marietou, H. Roy, B.B. Jorgensen, K.U. Kjeldsen, Sulfate transporters in dissimilatory sulfate reducing microorganisms: a comparative genomics analysis, Front. Microbiol. 9 (2018) 309.
[37] N.M.J. Geerlings, C. Karman, S. Trashin, K.S. As, M.V.M. Kienhuis, S. Hidalgo-Martinez, D. Vasquez-Cardenas, H.T.S. Boschker, K. De Wael, J.J. Middelburg, L. Polerecky, F.J.R. Meysman, Division of labor and growth during electrical cooperation in multicellular cable bacteria, Proc. Natl. Acad. Sci. U.S.A. 117 (10) (2020) 5478–5485.
[38] S. Scilipoti, K. Koren, N. Risgaard-Petersen, A. Schramm, L.P. Nielsen, Oxygen consumption of individual cable bacteria, Sci. Adv. 7 (7) (2021) eabe1870.
[39] M. Schoeffler, A.L. Gaudin, F. Ramel, O. Valette, Y. Denis, W.B. Hania, A. Hirschler-Réa, A.J. E.m. Dolla, Growth of an anaerobic sulfate-reducing bacterium sustained by oxygen respiratory energy conservation after O2-driven experimental evolution, Environ. Microbiol. 21 (1) (2019) 360–373.
[40] U. Marzocchi, D. Trojan, S. Larsen, R.L. Meyer, N.P. Revsbech, A. Schramm, L.P. Nielsen, N. Risgaard-Petersen, Electric coupling between distant nitrate reduction and sulfide oxidation in marine sediment, ISME J. 8 (8) (2014) 1682–1690.
[41] Y.G. Yang, Z.G. Wang, C.F. Gan, L.H. Klausen, R. Bonne, G.N. Kong, D.Z. Luo, M. Meert, C.J. Zhu, G.P. Sun, J. Guo, Y.X. Ma, J.T. Bjerg, J. Manca, M.Y. Xu, L.P. Nielsen, M.D. Dong, Long-distance electron transfer in a filamentous Gram-positive bacterium, Nat. Commun. 12 (1) (2021) 1709.
[42] D.R. Lovley, D.E. Holmes, Electromicrobiology: the ecophysiology of phylogenetically diverse electroactive microorganisms, Nat. Rev. Microbiol. 20 (1) (2022) 5–19.
[43] R. Bonné, K. Wouters, J.J. Lustermans, J.V.J.F. Manca, Biomaterials and electroactive bacteria for biodegradable electronics, Front. Microbiol. 13 (2022) 906363.
[44] R.T. Eachambadi, R. Bonne, R. Cornelissen, S. Hidalgo-Martinez, J. Vangronsveld, F.J.R. Meysman, R. Valcke, B. Cleuren, J.V. Manca, An ordered and fail-safe electrical network in cable bacteria, Advanced Biosystems 4 (7) (2020) 2000006.
[45] Z.X. Jiang, S. Zhang, L.H. Klausen, J. Song, Q. Li, Z. Wang, B.T. Stokke, Y.D. Huang, F. Besenbacher, L.P. Nielsen, M.D. Dong, In vitro single-cell dissection revealing the interior structure of cable bacteria, Proc. Natl. Acad. Sci. U.S.A. 115 (34) (2018) 8517–8522.
[46] J.J. Lustermans, J.J. Bjerg, L.D. Burdorf, L.P. Nielsen, A. Schramm, I.P.J. Marshall, Persistent flocks of diverse motile bacteria in long-term incubations of electron-conducting cable bacteria, Candidatus Electronema aureum, Front. Microbiol. 14 (2023) 1008293.
[47] C. Li, C.E. Reimers, Y. Alleau, Inducing the attachment of cable bacteria on oxidizing electrodes, Biogeosciences 17 (3) (2020) 597–607.
[48] R. Bonne, J.L. Hou, J. Hustings, K. Wouters, M. Meert, S. Hidalgo-Martinez, R. Cornelissen, F. Morini, S. Thijs, J. Vangronsveld, R. Valcke, B. Cleuren, F.J.R. Meysman, J.V. Manca, Intrinsic electrical properties of cable bacteria reveal an Arrhenius temperature dependence, Sci. Rep. 10 (1) (2020) 19798.
[49] G.W. Chong, S. Pirbadian, Y. Zhao, L.A. Zacharoff, F. Pinaud, M.Y.J. El-Naggar, Single molecule tracking of bacterial cell surface cytochromes reveals dynamics that impact long-distance electron transport, Proc. Natl. Acad. Sci. U.S.A. 119 (19) (2022) e2119964119.
[50] H.T.S. Boschker, P.L.M. Cook, L. Polerecky, R.T. Eachambadi, H. Lozano, S. Hidalgo-Martinez, D. Khalenkow, V. Spampinato, N. Claes, P. Kundu, D. Wang, S. Bals, K.K. Sand, F. Cavezza, T. Hauffman, J.T. Bjerg, A.G. Skirtach, K. Kochan, M. McKee, B. Wood, D. Bedolla, A. Gianoncelli, N.M.J. Geerlings, N. Van Gerven, H. Remaut, J.S. Geelhoed, R. Millan-Solsona, L. Fumagalli, L.P. Nielsen, A. Franquet, J.V. Manca, G. Gomila, F.J.R. Meysman, Efficient long-range conduction in cable bacteria through nickel protein wires, Nat. Commun. 12 (1) (2021) 3996.
[51] D.J.F. Walker, R.Y. Adhikari, D.E. Holmes, J.E. Ward, T.L. Woodard, K.P. Nevin, D.R. Lovley, Electrically conductive pili from pilin genes of phylogenetically diverse microorganisms, ISME J. 12 (1) (2018) 48–58.
[52] T. Boesen, L.P. Nielsen, A. Schramm, Pili for nanowires, Nature Microbiology 6 (11) (2021) 1347–1348.
[53] F.J.R. Meysman, N. Risgaard-Petersen, S.Y. Malkin, L.P. Nielsen, The geochemical fingerprint of microbial long-distance electron transport in the seafloor, Geochem. Cosmochim. Acta 152 (2015) 122–142.
[54] R. Schauer, N. Risgaard-Petersen, K.U. Kjeldsen, J.J.T. Bjerg, B.B. Jorgensen, A. Schramm, L.P. Nielsen, Succession of cable bacteria and electric currents in marine sediment, ISME J. 8 (6) (2014) 1314–1322.
[55] S.Y. Malkin, A.M.F. Rao, D. Seitaj, D. Vasquez-Cardenas, E.M. Zetsche, S. Hidalgo-Martinez, H.T.S. Boschker, F.J.R. Meysman, Natural occurrence of microbial sulphur oxidation by long-range electron transport in the seafloor, ISME J. 8 (9) (2014) 1843–1854.
[56] A.M.F. Rao, S.Y. Malkin, S. Hidalgo-Martinez, F.J.R. Meysman, The impact of electrogenic sulfide oxidation on elemental cycling and solute fluxes in coastal sediment, Geochem. Cosmochim. Acta 172 (2016) 265–286.
[57] E. Remoudaki, A. Hatzikioseyian, P. Kousi, M. Tsezos, The mechanism of metals precipitation by biologically generated alkalinity in biofilm reactors, Water Res. 37 (16) (2003) 3843–3854.
[58] H. Maraghechi, F. Rajabipour, C.G. Pantano, W.D. Burgos, Effect of calcium on dissolution and precipitation reactions of amorphous silica at high alkalinity, Cement Concr. Res. 87 (2016) 1–13.
[59] M.J. Dong, S. Yang, X.A. Yang, M.Y. Xu, W.Z. Hu, B. Wang, Y.D. Huang, J.R. Xu, H.B. Lu, Y.G. Yang, X.J. Chen, H.B. Huang, G.P. Sun, Water quality drives the distribution of freshwater cable bacteria, Sci. Total Environ. 841 (2022) 156468.
[60] L.D.W. Burdorf, S. Hidalgo-Martinez, P.L.M. Cook, F.J.R. Meysman, Long-distance electron transport by cable bacteria in mangrove sediments, Mar. Ecol. Prog. Ser. 545 (2016) 1–8.
[61] W. Hu, J. Pan, B. Wang, J. Guo, M. Li, M.J.E.M. Xu, Metagenomic insights into the metabolism and evolution of a new Thermoplasmata order (Candidatus Gimiplasmatales), Environ. Microbiol. 23 (7) (2021) 3695–3709.
[62] B.C. Martin, J. Bougoure, M.H. Ryan, W.W. Bennett, T.D. Colmer, N.K. Joyce, Y.S. Olsen, G.A. Kendrick, Oxygen loss from seagrass roots coincides with colonisation of sulphide-oxidising cable bacteria and reduces sulphide stress, ISME J. 13 (3) (2019) 707–719.
[63] V.V. Scholz, H. Muller, K. Koren, L.P. Nielsen, R.U. Meckenstock, The rhizosphere of aquatic plants is a habitat for cable bacteria, FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol. 95 (6) (2019) fiz062.
[64] M. Daghio, E. Vaiopoulou, S.A. Patil, A. Suarez-Suarez, I.M. Head, A. Franzetti, K. Rabaey, Anodes stimulate anaerobic toluene degradation via sulfur cycling in marine sediments, Appl. Environ. Microbiol. 82 (1) (2016) 297–307.
[65] H. Muller, J. Bosch, C. Griebler, L.R. Damgaard, L.P. Nielsen, T. Lueders, R.U. Meckenstock, Long-distance electron transfer by cable bacteria in aquifer sediments, ISME J. 10 (8) (2016) 2010–2019.
[66] Z. Wong, F. Liu, E. Li, Y. Yuan, Y. Yang, R. Qiu, M.J. F.i.M. Xu, Network analysis reveals microbe-mediated impacts of aeration on deep sediment layer microbial communities, Front. Microbiol. 13 (2022) 3814.
[67] Y. Huang, W. Hu, M. Dong, Y. Yang, X. Yang, H. Huang, S. Yang, W. Jia, B. Wang, M.J.J. Xu, Cable bacteria accelerate the anaerobic removal of pyrene in black odorous river sediments, J. Hazard Mater. 443 (2023) 130305.
[68] C.E. Reimers, C. Li, M.F. Graw, P.S. Schrader, M.J. F.i. m. Wolf, The identification of cable bacteria attached to the anode of a benthic microbial fuel cell: evidence of long distance extracellular electron transport to electrodes, Front. Microbiol. 8 (2017) 2055.
[69] J.D. Coates, R.T. Anderson, D.R. Lovley, Oxidation of polycyclic aromatic hydrocarbons under sulfate-reducing conditions, Appl. Environ. Microbiol. 62 (3) (1996) 1099–1101.
[70] O.N. Pavlova, O.N. Izosimova, S.M. Chernitsyna, V.G. Ivanov, T.V. Pogodaeva, A.V. Khabuev, A.G. Gorshkov, T.I. Zemskaya, Anaerobic oxidation of petroleum hydrocarbons in enrichment cultures from sediments of the Gorevoy Utes natural oil seep under methanogenic and sulfate-reducing conditions, Microb. Ecol. 83 (4) (2022) 899–915.
[71] J.D. Coates, R. Chakraborty, M.J. McInerney, Anaerobic benzene biodegradation - a new era, Res. Microbiol. 153 (10) (2002) 621–628.

[72] Y.D. Huang, B. Wang, Y.G. Yang, S. Yang, M.J. Dong, M.Y. Xu, Microbial carriers promote and guide pyrene migration in sediments, J. Hazard Mater. 424 (2022) 127188.
[73] U. Marzocchi, E. Palma, S. Rossetti, F. Aulenta, A. Scoma, Parallel artificial and biological electric circuits power petroleum decontamination: the case of snorkel and cable bacteria, Water Res. 173 (2020) 115520.
[74] M.J. McBride, Bacterial gliding motility: multiple mechanisms for cell movement over surfaces, Annu. Rev. Microbiol. 55 (2001) 49–75.
[75] D.L. Kirchman, The ecology of Cytophaga-Flavobacteria in aquatic environments, FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol. 39 (2) (2002) 91–100.
[76] C.G. Friedrich, F. Bardischewsky, D. Rother, A. Quentmeier, J. Fischer, Prokaryotic sulfur oxidation, Curr. Opin. Microbiol. 8 (3) (2005) 253–259.
[77] J.T. Bjerg, L.R. Damgaard, S.A. Holm, A. Schramm, L.P. Nielsen, Motility of electric cable bacteria, Appl. Environ. Microbiol. 82 (13) (2016) 3816–3821.
[78] N. Risgaard-Petersen, A. Revil, P. Meister, L.P. Nielsen, Sulfur, iron-, and calcium cycling associated with natural electric currents running through marine sediment, Geochem. Cosmochim. Acta 92 (2012) 1–13.
[79] S. van de Velde, I. Callebaut, Y. Gao, F.J.R. Meysman, Impact of electrogenic sulfur oxidation on trace metal cycling in a coastal sediment, Chem. Geol. 452 (2017) 9–23.
[80] F. Sulu-Gambari, A. Roepert, T. Jilbert, M. Hagens, F.J.R. Meysman, C.P. Slomp, Molybdenum dynamics in sediments of a seasonally-hypoxic coastal marine basin, Chem. Geol. 466 (2017) 627–640.
[81] R. Vaquer-Sunyer, C.M.J.P. Duarte, Thresholds of hypoxia for marine biodiversity, Proc. Natl. Acad. Sci. U.S.A. 105 (40) (2008) 15452–15457.
[82] L. Levin, W. Ekau, A. Gooday, F. Jorissen, J. Middelburg, S. Naqvi, C. Neira, N. Rabalais, J.J.B. Zhang, Effects of natural and human-induced hypoxia on coastal benthos, Biogeosciences 6 (10) (2009) 2063–2098.
[83] J.E. Doeller, M.K. Grieshaber, D.W. Kraus, Chemolithoheterotrophy in a metazoan tissue: thiosulfate production matches ATP demand in ciliated mussel gills, J. Exp. Biol. 204 (21) (2001) 3755–3764.
[84] S. Duperron, S. Gaudron, C. Rodrigues, M. Cunha, C. Decker, K.J.B. Olu, An overview of chemosynthetic symbioses in bivalves from the North Atlantic and Mediterranean Sea, Biogeosciences 10 (5) (2013) 3241–3267.
[85] S.Y. Malkin, D. Seitaj, L.D.W. Burdorf, S. Nieuwhof, S. Hidalgo-Martinez, A. Tramper, N. Geeraert, H. De Stigter, F.J.R. Meysman, Electrogenic sulfur oxidation by cable bacteria in bivalve reef sediments, Front. Mar. Sci. 4 (2017) 28.
[86] V.V. Scholz, R.U. Meckenstock, L.P. Nielsen, N. Risgaard-Petersen, Cable bacteria reduce methane emissions from rice-vegetated soils, Nat. Commun. 11 (1) (2020) 1–5.
[87] P. Schonheit, J.K. Kristjansson, R.K. Thauer, Kinetic mechanism for the ability of sulfate reducers to out-compete methanogens for acetate, Arch. Microbiol. 132 (3) (1982) 285–288.