Insights into marine microbial communities that couple anaerobic biogeochemical cycles to remote oxidants

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Extracellular electron transfer (EET) is a process whereby microbes shuttle electrons outside the cell, and access solid-phase oxidants as well as spatially remote oxidants. EET has been well-studied in cultivated microbes, e.g., heterotrophic iron-reducing δ-proteobacteria. The relevance of EET in nature, however, and its impact on biogeochemical cycles remains poorly constrained. Anaerobic marine sediments host microbial communities that are involved in numerous biogeochemical cycles, and those capable of EET would have access to solid-phase as well as remote oxidants. Here we present the first comprehensive data on the population structure and functional potential of marine bacteria associated with EET. These communities were recovered from two systems: the anode of a bioelectrochemical system (BES) deployed in marine sediments *in situ*, and a BES deployed in high temperature hydrothermal vents. These communities were dominated by distinct groups of Proteobacteria and Fusobacteria. Metagenomic analyses and geochemical considerations suggest that they are participating in a complex sulfur cycle that includes the recycling of sulfur among oxidizers, reducers and disproportionators. Unexpectedly, these analyses revealed numerous other physiological capacities. These data suggest that microbial EET is likely more widespread than previously considered, and the functional potential of these communities requires us to reconsider the canonical view of anaerobic sediment biogeochemistry. If these microbial metabolisms are coupled to remote oxidants such as oxygen and nitrate via EET, the biogeochemical cycling of these elements will likely be more vigorous than previously recognized (as these reactions become more thermodynamically favorable). The findings presented herein provide a plausible explanation for some previously observed elevated rates of recalcitrant carbon degradation, and underscores the need for further investigation into the relevance of EET to global biogeochemical cycles.

Aerobic hydrogen oxidation by a chemolithotrophic *Beggiatoa* strain

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Hydrogen oxidation in oxic/anoxic gradients

Transition zones between oxic and anoxic environments are primary habitats for aerobic hydrogen oxidizers. In sulfidic sediments, filamentous bacteria of the genus *Beggiatoa* thrive within this narrow horizon and feature fine-tuned chemotactic responses to keep track of the interface. So far, only anaerobic hydrogen oxidation coupled to reduction of stored sulfur has been shown for a heterotrophic *Beggiatoa* strain [1]. Here we demonstrate aerobic hydrogen oxidation by the chemolithoautotrophic strain *Beggiatoa* 35Flor grown in a mineral medium featuring artificial oxygen, sulfide and hydrogen gradients.

Beggiatoa 35Flor uses hydrogen as an accessory electron donor

In the presence of hydrogen, *Beggiatoa* 35Flor mats exhibit higher oxygen consumption once the sulfide flux decreases, as indicated by a shorter distance of the mats to the air/agar interface. Microsensor profiles show that low hydrogen fluxes are continually and fully oxidized within the oxic region of the *Beggiatoa* mat. Higher hydrogen fluxes have initially a more pronounced influence on the mat position, but oxidation ceases after a few days for a yet not determinable reason. A gene encoding for the large subunit of a hydrogen uptake hydrogenase was retrieved from strain 35Flor. Supply with fixed nitrogen compounds does not impair the hydrogen-oxidizing capacity of this nitrogen-fixing strain, suggesting that the hydrogenase is regulated independently of the nitrogenase. This result indicates that hydrogen is used as an electron donor and not merely oxidized for energy recycling. All attempts to grow the strain 35Flor with hydrogen as the only electron donor failed so far.

Our findings show that the strain *Beggiatoa* 35Flor is capable of aerobic hydrogen oxidation when grown in gradient medium imitating its natural habitat. However, hydrogen appears to serve only as an accessory electron donor since growth on hydrogen alone could not be achieved.

[1] Schmidt *et al.* (1987), *J. Bacteriol.* **169**, 5466-5472.