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Release the iron: does the infection of magnetotactic bacteria by phages play a role in making iron available in aquatic environments?

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Abstract Magnetotactic bacteria (MTB) are ubiquitous prokaryotes that orient along magnetic field lines due to magnetosomes' biomineralization within the cell. These structures are ferrimagnetic organelles that impart a magnetic moment to the cell. To succeed in producing magnetosomes, MTB accumulate iron in (i) cytoplasm; (ii) magnetosomes; and (iii) nearby the organelle. It has already been estimated that a single MTB has an iron content of 10 to 100-fold higher than *Escherichia coli*. Phages are the most abundant entity in oceans and are known for controlling nutrient flow such as carbon and nitrogen by viral shunt and pump. The current work addresses the putative role of phages that infect MTB on the iron biogeochemical cycle. Can phage infection in MTB hosts cause a biogenic iron fertilization-like event in localized microenvironments? Are phages critical players in driving magnetosome biomineralization genes (BGs) horizontal transfer? Further investigation of those events, including frequency of occurrence, is necessary to fully comprehend MTB's effect on iron cycling in aqueous environments.

Keyword: horizontal gene transfer; iron biogeochemical cycle; magnetotactic bacteria; magnetosome biomineralization genes; phages

1 INTRODUCTION

1.1 Magnetotactic bacteria and iron flux in aquatic environments

Magnetotactic bacteria (MTB) are ubiquitous aquatic Gram-negative prokaryotes that swim through stratified water columns or sediment exhibiting magnetotaxis (Bazylinski and Frankel, 2004). This behavior is known as a guided dislocation by the active flagellar propulsion along Earth's magnetic field (EMF) lines to find or maintain the bacterial position in optimal conditions for survival and growth in environmental gradients (Frankel and Blakemore, 1980). Cell alignment along magnetic field lines occurs because MTB biomineralize ferrimagnetic nanocrystals surrounded by a lipid bilayer, known as magnetosomes. These structures are organized in chain(s), imparting the cell a magnetic moment (Frankel, 1984). The mineral core of magnetosomes is composed of magnetite (Fe_3O_4) or greigite (Fe_3S_4) (Bazylinski and Frankel, 2004). It is estimated that a single magnetotactic bacterium contains an iron mass of about 0.5×10^{-6} ng (Amor et al., 2020a). This corresponds to a mass 10 to 100 folds higher than that in *Escherichia coli* (Amor et al., 2020a). Some magnetotactic Nitrospirae bacteria biomineralize hundreds of magnetite anisotropic magnetosomes (Amor et al., 2020b). Thus, iron content estimations for these MTB indicate that they can accumulate up to 1 000-fold higher than other microorganisms (Amor et al., 2020b). Although most of the iron content in MTB is located in the mineral core of magnetosomes, iron is also accumulated nearby magnetosomes enmeshed in a magnetosomal matrix as shown in a few recent studies using highly accurate techniques (Werckmann

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et al., 2017), or in ferrosomes (Grant and Komeili, 2020), besides its accumulation in cytoplasm (Bazylinski and Frankel, 2004; Amor et al., 2020a). Uncultured and cultured MTB accumulate iron ions close to magnetosomes as an event before crystal nucleation (Werckmann et al., 2017). Recently, Cypriano et al. (2020) demonstrated that the mineral core of magnetosomes as well as the lipid membrane of the crystal could resist up to 300 °C heating. Magnetosomes can endure this condition without loss of crystallographic morphology or exhibiting oxidation in the magnetite mineral core. This is a first indication that magnetosomes can endure high temperatures, which naturally occur during sediments diagenesis. In the iron biogeochemical flux context, Lin et al. (2014) showed that lacustrine MTB could provide an annual yield of 2×10^6 kg of magnetite. Following these estimates, Amor et al. (2020a) proposed that the ranges of MTB concentration in sediments were 10^5–10^7 cells/cm^3 in freshwater, 10^3–10^5 cells/cm^3 in seawater and 10^4–10^7 cells/cm^3 in estuaries. Amor et al. (2020a) presented calculations of the global mass of iron in environmental MTB populations (M_{MTB}). The ranges of total flux of iron processed by M_{MTB} were 1.5×10^5–4×10^7 kg/a for freshwater, 1×10^5–3×10^7 kg/a for the ocean, and 0.3×10^5–5×10^8 kg/a for estuaries. The most conservative estimations show that MTB are capable of incorporating ≈1%–500% of the mass of dissolved iron transported by the rivers to the oceans, affecting the biogeochemical iron cycle (Amor et al., 2020a). Thus MTB contribution to the iron flux is significant compared to the contribution of atmospheric dust and hydrothermalism (Fantle and DePaolo, 2004), which is 5×10^8 kg iron/a and 3×10^8 kg iron/a, respectively. It is possible that MTB can act as a sink of iron in aquatic environments, avoiding the accumulation of dissolved iron (Chen et al., 2014), and possibly affecting other microbial community members. Recently, Yuan et al. (2020) presented the first proof of magnetosome magnetite fossils in found in Fe-Mn crusts from the Pacific Ocean and South China Sea. This finding brought up a previously unappreciated source of iron removal in the deep sea (Yuan et al., 2020). Dependent on environmental conditions, magnetofossils can persist in the environment for over billions of years (Chang et al., 1989; Akai et al., 1997). To confirm the actual contribution of magnetofossils in the iron biogeochemical cycle, the specific MTB flux of Fe-Mn needs quantification.

1.2 Iron availability in aquatic environments

Iron is an essential micronutrient for microbial organisms and communities to thrive in any environment. Bioavailability of iron is used as a bottom-up control on primary productivity in much of the modern surface ocean, making characterization of iron speciation of vital importance to understanding the carbon cycle and global climate (Martin et al., 1989). Marine bacteria are known to thrive in an oligotrophic environment, and to survive, natural selection enforced those capable of acquiring iron due to specialized mechanisms. Many are known to produce siderophores, high-affinity iron-chelating compounds (Butler, 2005). This organic complexation of iron prevents it from precipitating and integrates it again on the water column (Kuma et al., 1996). Although the biosynthesis and uptake of siderophores are species-specific, some bacteria evolved to hijack other's siderophores and scavenge the available iron. This competition behavior is possible due to xenosiderophores (Matzanke et al., 1997).

1.3 Phage in oceans

Phages are the most abundant entity on Earth, and their major reservoir is the oceans. In freshwater habitats, it has been estimated that viruses can overcome eukaryotic and bacterial populations up to 10^6 and 10^3 times, respectively (Wetzel, 2001; Kavagutti et al., 2019). Metagenomic analysis of oceans samples around the globe showed the presence of 195 728 viral populations and 90% of them could not be taxonomically annotated (Gregory et al., 2019); see Dion et al. (2020) for detailed information regarding virus diversity in environments. Ocean waters comprise an average of 10^7–10^8 phage particles per milliliter (Suttle, 2007). This abundance can decrease with depth and distance from shore. Marine sediments near the coast have the highest phage abundance, where 10^8–10^9 phage particles per cubic centimeter can be found (Suttle, 2007). There are estimated to be 10^{31} phage particles around the globe (Brüssow and Hendrix, 2002). Regarding phage distribution, viral abundance decreases further offshore and deeper in the water column (Suttle and Chan, 1994). These trends are also reflected in the virus-bacteria ratio (VBR). Within any environment, the total viral abundance generally varies with the prokaryotic quantity and productivity (e.g., the concentration of chlorophyll *a*) (Cochlan et al., 1993). Many factors are responsible for interfering with viral

abundance in the water column. One particular abiotic factor that plays a crucial role in viral abundance is salinity. For example, VBR in the surface waters of the Pacific and Arctic Oceans are ≈40 and ≈10, respectively, while in freshwater lakes, the average VBR is less than 5 (Clasen et al., 2008). An interesting fact is that deep-sea waters from the Northern Atlantic Ocean are natural viral hotspots where VBR often exceeds 100 (Parada et al., 2007). In that way, viral abundance does not decrease in sediments and does not exhibit homogenous distribution patterns. Instead, its abundance is influenced by environmental factors, bacterial populations occurring at microbial hotspots, and the variation of host individual cells' spatial scales (Danovaro et al., 2001). Phages are also catalysts for biogeochemical cycling, as they constitute a significant reservoir of genetic diversity. One example is the viral shunt, which controls the carbon, nitrogen, and other nutrients flow from phytoplankton and bacteria, preventing those nutrients to migrate to higher trophic levels, thus accumulating in the primary production, which is majorly composed of digested or particulate organic matter (D-P-OM). The immediate result is an increase in carbon respiration, which leads to a decrease in the trophic transfer efficiency of nutrients and energy through the marine food web (Suttle, 2005). Finally, they are known for their capacity to transduce genetic information as a modality of horizontal gene transfer (HGT), which is one of the most relevant events that drive microbial diversity (Clokie et al., 2011). Several examples were discovered in the last years with the advance of viral metagenomics. Phages encode auxiliary metabolic genes (AMGs) which in oceans are responsible for a broad range of metabolic pathways such as: (i) antioxidation; (ii) carbon metabolism; (iii) cell defense; (iv) nutrient cycling (e.g. nitrogen, phosphorus and sulfur); (v) fatty acid metabolism; (vi) iron-sulfur clusters; (vii) photosynthesis; (viii) purine and pyrimidine metabolism; and (ix) protein synthesis (Breitbart et al., 2018).

Bartual et al. (2010) demonstrated the presence of seven iron ions in the crystal structure of the bacteriophage T4 tail. The presence of iron ions in the gp37 tail fiber proteins stabilizes the tail conformation and serves as a strategy to infect bacterial cells that intend to capture the iron. The gp37 tail fiber protein competes to the binding site of the siderophore-bound iron receptor (Bartual et al., 2010). This process is a well-characterized protein-protein interaction for non-marine phage-bacteria relations (Braun, 2009). Another hijacking mechanism is the bacterial membrane piercing by a phage using an iron-loaded spike (Browning et al., 2012). This membrane-attacking apex was described for P2 and phi2 phages. Based on these findings, Bonnain et al. (2016) hypothesized the "Ferrojan Horse Hypothesis", which states that iron content in the phage tail could be used as a hijacked system promoting a new pathway that leads to a viral infection. Considering the limitation of bioavailable iron in oceans and phage's ocean abundance, the authors hypothesize that the phage hijack mechanisms could be of significant importance in marine microbial ecology. Bonnain et al. (2016) estimate that phages could contain up to 7×10^{-13} mol/L of iron, which is equivalent to as much as 70% of the colloidal fraction of organically complexed dissolved iron in the surface ocean.

Therefore, tailed phages that have iron-loaded spikes in their tail structure have high affinity for bacterial siderophore receptors on the cell membrane. This hypothesis suggests that this could be another mechanism for hijacking bacterial receptors thus initiating a new phage infection. Whether the infection outcome results in lytic or lysogenic cycle depends on intrinsic bacterial or extrinsic environmental factors (e.g. quorum sensing) (Erez et al., 2017). The mechanism then proposed by Bonnain et al. (2016) suggests that this mechanism is already well stablished for horizontal gene transfer in soils, but is not proven in oceans yet. Considering that MTB presents high demand and affinity for iron, as well as accumulate huge amount of this element, this process could possibly be relevant in oceans. However, the role of these phages in magnetotaxis evolution in the Bacteria domain needs further investigation.

2 DISCUSSION

Considering all aspects hence, we propose that the role of MTB in the iron cycle is broader than just capturing iron to form magnetosomes. In the light of the "Ferrojan Horse Hypothesis", MTB infection by phages in the environment might be a frequent event, possibly playing a significant role in making iron available for the local microbial community. Figure 1 explores the possible routes that the phage course of infection might undergo in MTB. Once the phage adsorbed into the cell surface, it starts infection and hijacks cell's enzymatic machinery to make copies of itself (Fig.1, 2nd step). One crucial point might be the nucleic acid packaging into the phage capsid (Fig.1, 3rd step). During this stage of infection, three situations

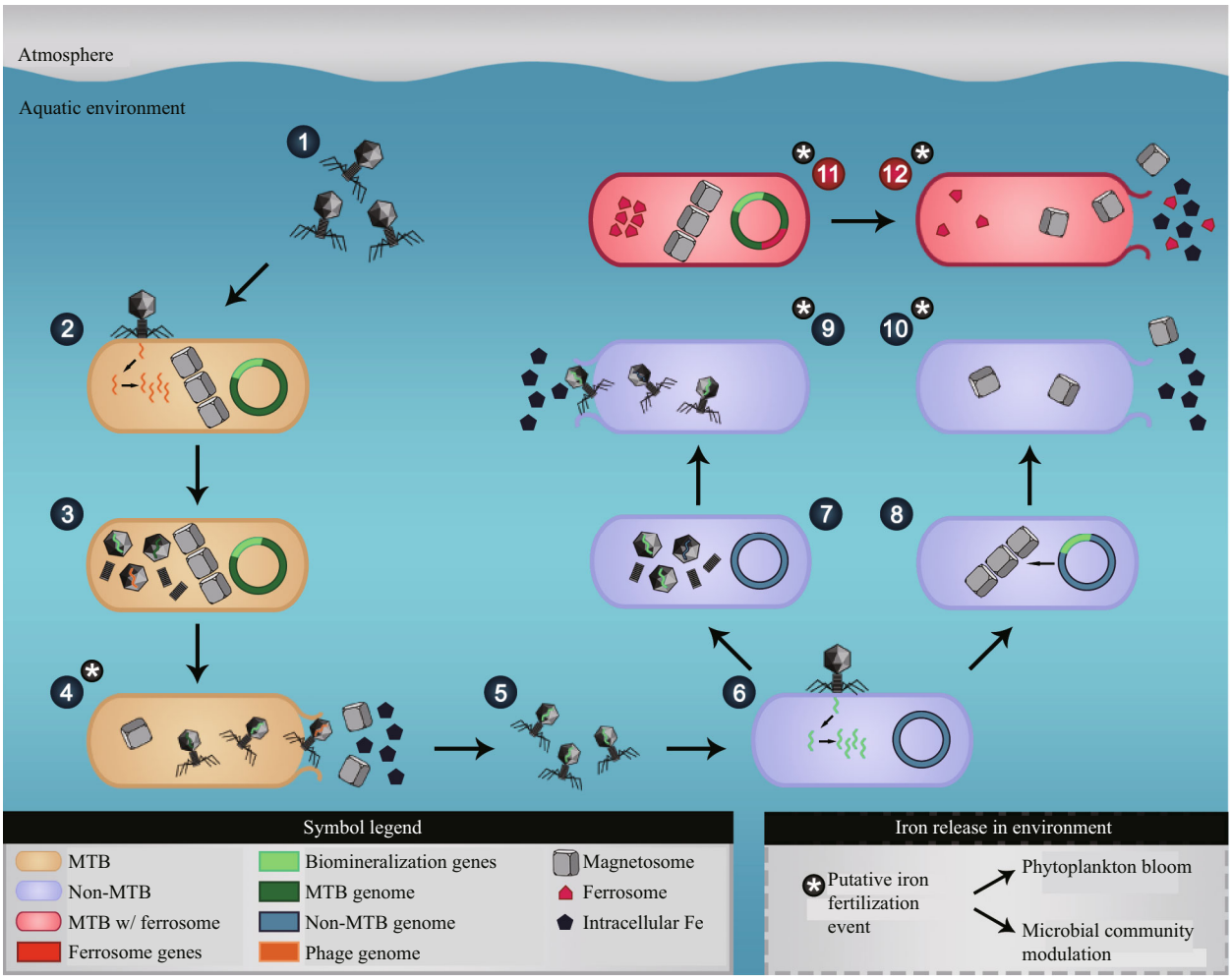

Fig.1 Role of MTB and phages in aquatic environments

1: phage pool in the water column containing viable viral particles; **2**: phage infecting a susceptible and permissive MTB (gold rod-shaped). During the course of infection bacteria will synthesize phage's nucleic acid (orange), metabolic, and structure; **3**: phage's components ready for self-assembly in cytoplasm. During phage infection the nucleic acid packing is extremely important. Three possible routes are demonstrated: (i) phage genome correctly packed into capsid (orange); (ii) piece of bacterial DNA carried into capsid (dark green); and (iii) piece of biomineralization genes (BGs) carried into phage capsid (light green); **4**: phage exit from cell can occur by: (i) lysis liberating a large pool of phages into the environment; and/or (ii) constitutively release by the exocytic route liberating constant amounts of phage over time. In both situations magnetosomes and intracellular Fe can be released into the water column; **5**: phages exit the cell and may proceed to search another host; **6**: phage containing BGs infect a non magnetotactic bacteria (lilac). Copies of genetic material are replicated in cytoplasm using host enzymatic machinery. If phages lose an essential gene that promotes infection, they can become defective, thus BGs will remain in phage genome; **7**: phages can be packed with BGs (light green) or a piece of bacterial genome (blue); **8**: infection may undergo lysogenesis and BGs might be integrated in the non-MTB genome. During transcription and translation BGs might be able or not to code a complete magnetosome. The presence of the magnetosome into cell's cytoplasm does not make it necessarily magnetotactic; **9**: cell's rupture releases newly assembled phages and intracellular Fe. Intracellular Fe thus become available for other microorganisms; **10**: cell's death leads to the release of magnetosomes and intracellular Fe; **11**: MTB (light red) with ferrosomes (red polygon) and magnetosomes. MTB contains ferrosome genes (red); **12**: upon cell's death the cytoplasmatic content is release such as cytoplastic iron, magnetosomes, and ferrosomes. Asterisk: situations where putative iron fertilization-like events can be performed by MTB and non-MTB. MTB can release iron in the environment by cell natural death or due to lysis during a phage infection (4^{th} step). Non-MTB could release iron in the environment due to cell lysis (10^{th} step) or due to lysis during a phage infection (9^{th} step). MTB with ferrosomes contains this additional organelle, which could be an addition of iron release in environment upon cell's death (12^{th} step). These events could release a large pool of cytoplasmic iron or magnetite/greigite, thus promoting the iron fertilization-like phenomenon, which could lead to a local microbial community modulation.

can be foreseen: (i) phage genome can be correctly packed into the capsid; (ii) a piece of the bacterial genome can be mispackaged into the capsid; or (iii) biomineralization genes (BGs) can be mispackaged into the capsid. In all these scenarios, cell death would cause the release of magnetosomes (magnetite or greigite) and intracellular iron from the cell's cytoplasm to the water column (Fig.1, 4^{th} step).

In general, the relevance of phage's role in the iron cycle has been underestimated in the literature, but new studies are beginning to bring up this issue. To our knowledge, MTB infection by phages has never been detailed analyzed. However, as a single MTB contains $\approx 0.5\times10^{-6}$ ng of iron per cell (Amor et al.,

2020a), cell death or lysis by phage infection can release a considerable amount of unmineralized iron in aquatic microenvironments, supposing a localized population of MTB. The outcome in this situation could represent a biogenic iron fertilization-like event, in which iron accumulated by MTB would be released back to the environment and be available for other bacteria. Iron fertilization is a well-known phenomenon to occur in high-nutrient, low-chlorophyll areas that lead to phytoplankton blooms (Martin et al., 1994). Microbial productivity is enhanced within the fertilized area and a succession like the response of the microbial community upon the algal bloom is averted by highly effective grazing (Thiele et al., 2012). Globally, it was estimated that MTB promote a constant iron flux in aquatic environments (Amor et al., 2020a). Therefore, MTB population might directly regulate local microbial communities because of their exceptional ability to capture iron from the environment, which reduces this element's availability, and indirectly regulates other populations, especially the growth of phototrophs if MTB susceptibility to phages is considered. This event is relevant in microbial community modulation, especially in oceans where iron is a limiting nutrient (Martin et al., 1994).

Another interesting outcome of MTB infection by phages is that it possibly allows the dissemination of BGs through horizontal gene transfers (Fig.1). When phage containing BGs infects a bacterium, two possible routes must be considered. The new phage components are synthesized and assembled (Fig.1, 7th step) and then, through cell death or lysis, can release phage particles; or phage may undergo lysogenesis and have its genome integrated to bacterial chromosome or plasmid (Fig.1, 8th step). During the lysogenic pathway, BGs might be expressed to synthesize magnetosomes or similar structures, which might not be fully functional, contain crystallographic defects and do not necessarily make the cell magnetotactic. Another possibility could be the increment of BGs content and variability in an infected magnetotactic cell. Yet during activation of the phage lytic cycle would lead to cell death and a large pool of iron might be released (Fig.1, 10th step). Other aspect to be considered is the presence of ferrosomes in some MTBs (Grant and Komeili, 2020) (Fig.1, 11th step). MTB with ferrosomes could release an addition iron load in aquatic environments upon cell's death contributing to the iron fertilization-like phenomenon (Fig.1, 12th step). In conclusion, this hypothesis might be one of the forces driving magnetotaxis evolution, yet further investigation is required.

3 PERSPECTIVES IN MTB AND PHAGE INTERACTIONS

To understand phage and MTB interactions, a few questions need addressing. The first and most important is to know if all or which MTB is susceptible to phage infections and what is the outcome of that infection. Following that question, it is mandatory to understand the frequency of the infection events in MTB, and what guides the lysis-lysogeny decisions in this group of organisms. The frequency and the outcomes of those events could help answer the accurate role of phage impact in MTB populations and the magnetotaxis evolution.

Despite all those questions that need addressing, there are technical obstacles in executing them. For example, cultivating MTB is not an easy task, as many of them require specific oxygen, sulfur, and other chemical gradients (Bazylinski and Frankel, 2004). These gradients are intrinsic within the water column, but hard to replicate in laboratory conditions. Specific nutrients for MTB growth are not fully known as all representatives from the phyla Nitrospirae and Omnitrophica have not been isolated yet (Lin et al., 2017). The isolation and decontamination process is also laborious, as MTB have to be sorted from environmental contaminants. The process itself is composed of a magnetic concentration in a capillary known as "racetrack" and is responsible for the loss of many MTB morphotypes during the execution (Wolfe et al., 1987).

Another hindrance is phage isolation by plaque assay, because few MTB (e.g. species affiliated to the genus *Magnetospirillum*) are capable of growing in solid media, which makes the natural process of phage isolation and characterization more difficult. Magnetotactic cocci, the most abundant MTB morphotype in environmental samples, have few representatives isolated until this day and their cultivation is even more laborious (Liu et al., 2021). Thus, a series of complex techniques have to be established and adapted in order to properly study phages impact on MTB ecology and evolutions. These facts make this topic very challenging, yet capable of resolving important issues to fully understand the magnetotactic behavior and what shaped its evolution in Bacteria domain.

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