

# Microbial mats: a bioreactor of lithification



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Microbial mats: a bioreactor of lithification and an indicator of Earth's evolution

## 1. Introduction

Microbial mat is a general term that is used to describe a variety of microbial communities that are found at interfaces between different types of material, mostly on submerged or moist surfaces such as estuarine environment and salt marshes (Krumbein et al., 1977; Nicholson et al., 1987). Bacteria and archaea are two main microbes forming the layers. Microbial mats contain a variety of different but essential trophic groups including primary producers, consumers, and decomposers. This is why even though microbial mats are, to an extreme extent, geographically small, they are ecosystems from an ecological perspective.

Microbial mats are dynamic ecosystems in which a wide range of metabolic processes take place. Inside this tiny ecosystem, different physical and chemical environments are distinguished by a variety of gradients, include but not limited to light, oxygen and sulfide (Visscher and van den Ende, 1994). The gradients may not be always constant. For example, oxygen concentration may have varied from diurnally to seasonally. In some aquatic systems, it will drop from supersaturated to undetectable within a few centimeters. The light penetration depth is fluctuated because of change of seasons or just with cloud covering. All these temporal environmental oscillations mentioned above, will result in coupled reactions, that are critical to the biogeochemical cycle, like reduction and oxidation of elements such as carbon and sulfur. Therefore, heterogeneity of microbe habitat is a common character that exhibits among all microbial mats.

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Microbial mat ecosystems can be viewed as a semiclosed system which require little more than sunlight to function, as such it is efficient in all kinds of reactions and element cycling. The relatively simple but functional structures make it, to a certain extent, easy to reach equilibrium and mass balances. Generally, microbial mats tend to have high rates of oxygenic photosynthesis, aerobic respiration, sulfate reduction, and sulfide oxidation (Canfield and Des Marais, 1993; Revsbech et al., 1986), when compared to other benthic ecosystems.

A classical view of a microbial mat (Figure 1)(Visscher et al., 2000) is that a fixed sequence of microbial groups exists: starting with oxygenic cyanobacteria as a surface community, underlain by oxygenic phototropic bacteria and sulfate-reducing bacteria as subsequent layer (Krumbein, 1983). This view, however, was later questioned and revised. Structure and the layers are not a result of different metabolic reaction types, on the contrary, they might be found in association with the cyanobacterial layer. Some research showed that the sulfur reducing bacteria was also found in the surface layer (Fründ and Cohen, 1992; Visscher et al., 1992).

## 2. Microbial mats and mineral interaction

In microbial ecosystems, when the precipitation rate of minerals is faster than that of dissolution, lithification will occur. Precipitations mediated by microbial mats is not limited to carbonates but also constituted by other minerals, such as gypsum and anhydrite (Ehrlich, 1998). Among all these precipitation types, carbonate precipitation is perhaps the most important process as it is directly related to the global carbon cycling. Therefore, in this

section, a main focus will be put on sedimentary biofilms in hypersaline environments to help with the interpretation of the rock record.

## 2. 1 Stromatolites and carbonate precipitation

Stromatolites are lithifying organic sedimentary structures formed by microorganisms (Figure 2). Carbonate precipitation activities of microbial mats are trapped and recorded in stromatolites layered structures. As such, microbial mats can be viewed as bioreactors (Dupraz et al., 2004a). The stromatolites structure is characterized as an alternating soft and hard layers whose heights ranges from a few centimeters to two meters. The evolutionary processes of stromatolites remain largely uncharacterized (Zavarzin, 2002). There are two major hypotheses. Des Marais (1997) speculated that microbial lithification is a result of by-product of microbial metabolism. On the other hand, McConnaughey and Whelen (1997) suggested that this could be directly related to the consequence of microbes harvesting energy from protons released during calcium carbonate precipitation. However, regardless of origin, stromatolites have thrived for a long history that could be seen as a major evolutionary advance for us to study the Earth's early history and global biogeochemical cycles.

Cyanobacteria have played a crucial role in carbonate precipitation as shown in Figure 3. Two microbially as well as physicochemically controlled factors determine carbonate precipitation: the saturation index (SI) and exopolymeric substances (Lozano-García et al.).  $SI = \log(IAP/K_{sp})$ , where IAP denotes the ion activity product (i. e.  $[Ca^{2+}][CO_3^{2-}]$ ) and  $K_{sp}$ , the solubility product of the corresponding mineral ( $10^{-6.37}$  for calcite at 25°C,

1bar atmospheric pressure and 35 PSU salinity (Zeebe and Wolf-Gladrow, 2001)). If  $IAP > K_{sp}$ , the solution is supersaturated, and when  $SI > 0.8$ , calcite carbonate tends to precipitates (Kempe and Kazmierczak, 1994). Or else, calcite carbonate will dissolve. The  $[CO_3^{2-}]$  depends on the carbonate equilibrium, which comprises three species as followed:  $H_2CO_3$ ,  $HCO_3^-$  and  $CO_3^{2-}$ . In another word, pH is influencing the precipitation. Therefore, before investigating how microbial metabolism affect the  $CaCO_3$  precipitation, understanding production and consumption of inorganic carbon and the environmental pH change is a prerequisite. EPS act as a chelator for cations and the template for crystal nucleation (Costerton et al., 1995; Decho, 2000). It is constantly modified by including but not limited to UV radiation, pH and microbial degradation (e. g. through hydrolysis, decarboxylation).

## 2. 2 Microbial mats and lithification

Contemporary microbial mats, vertically laminated ecosystems, resemble the layered sedimentary structures of stromatolites. As such, they have been attracting extensively research interests for being analogues for stromatolites. Shown in Figure 3, there are 6 different functional groups of microbes exist in microbial mats. From top of the figure to the bottom are: Cyanobacteria act as primary producers, which are believed to affect the trapping and biding of sediments; Aerobic heterotrophic bacteria, which gain energy from oxygen respiration and organic carbon; Anoxygenic phototrophs, mainly purple and green bacteria, which using  $HS^-$  for photosynthesis; Sulfate reducing bacteria (SRB), which respiring organic

carbon with  $\text{SO}_4^{2-}$  while producing  $\text{HS}^-$ ; Sulfide oxidizing bacteria (SOB), chemolithoautotrophs that oxidize  $\text{HS}^-$  with oxygen or nitrate while fixing  $\text{CO}_2$ ; fermenters, using organic carbon or sulfur compounds as electron donor and acceptor. However, this view of the mat composition is facing challenge because nucleic acid sequences will undoubtedly reveal more diverse and complex community structures than the simple classified ones.

Cyanobacteria is more like an important mediator of biogeochemical cycle of the mats ecosystem. It produces oxygen for the whole system to be functional (Fenchel, 1998). As mentioned before, the mat ecosystem is very efficient and productive. The relatively high photosynthetic rates, which shows a diurnal fluctuation, will reach its peak in the afternoon. Aerobic heterotrophs respire during the daytime when there is abundant oxygen, thereby creating an anoxia environment at twilight. Fermenters degrade complex organic molecules into smaller ones and benefit the SRB. SOB and anoxyphototrophs have contributed less to carbon fixation comparing with cyanobacteria and the role of fermentation remains ambiguous. All these activities above have resulted in steep vertical geochemical gradients with extreme diel fluctuations (Figure 3).

To understand the role of microbial mats in precipitation and dissolution, it is important to determine both the abundance and metabolic activity of these key functional groups. Because the quality and quantity of EPS are largely determined by the metabolic activity of the community. In the previous researches, several microbial mat systems have been found to produce carbonate phases: travertine in hot springs in Yellowstone (Fouke et al., 2000), dolomite in Lagoa Vermelha, Brazil (Vasconcelos and McKenzie, 1997) <https://assignbuster.com/microbial-mats-a-bioreactor-of-lithification/>

and Salt Pan, Bahamas (Dupraz et al., 2004a). However, there are still mats that will not lithify or fossilize. So here comes the question, what determines the lithification potential?

A previous study, using a combination of geological and microbial techniques, of lithifying microbial mat systems in hypersaline lake system was carried on in Salt Pan in Eleuthera, Bahamas (Dupraz et al., 2004a). The lake is not deep with an average depth less than 60cm. From the shoreline towards the center of the lake, a gradient from lithifying mats to jellylike soft mats exists (Figure 4). The shallow water column was found to contain cyanobacterial pigments that efficiently quench the sunlight. Not surprisingly, the photosynthesis, aerobic respiration, sulfate reduction are generally higher and geochemical gradients are steeper in the shallower lithifying mats. Moreover, EPS is easily destructed by strong UV radiation in shallower mats. This process helps with removing inhibition of precipitation by releasing more  $\text{Ca}^{2+}$  into the environment. The combination of these processes benefits carbonate precipitation.

### 2. 3 Microstructure of precipitation and EPS

UV radiation will cause browning reactions, dehydration and alkalinity. However, EPS production in stromatolite mat can prevent damages such as desiccation of the mat, retains essential nutrients, and provides water channels for transporting metabolites and signaling compounds (Costerton et al., 1995; Decho, 2000). Decho, A. W. et al. (Decho et al., 2005) had shown that EPS production in a stromatolite mat accounted only for 8% of  $^{14}\text{HCO}_3^-$  uptake during the light, and a rapid turnover followed during the dark. They

concluded that despite the fast rate of production, the net EPS production was low. The production and consumption are in equilibrium. Once being hydrolyzed, EPS components were readily consumed by the mat community, particularly anaerobes instead of aerobes. This is somehow surprising that when *Schizothrix* EPS, xanthan, or sugar and amino acid monomers and polymers that comprise EPS were supplied in mats, stimulation of anaerobic heterotrophic activity stimulation was greater than aerobic heterotrophs activity (Decho et al., 2005; Visscher et al., 2000). The combined action of fermentative organisms and SRB could be responsible for this high consumption rate. Oxygen levels are influenced by the rapid and extensive diurnal fluctuations as well as cloud cover and O<sub>2</sub>-consuming cell clusters in the EPS can produce anoxic microenvironments, therefore, the anaerobic pathway plays an important role in microbial EPS degradation.

EPS can not only release Ca<sup>2+</sup> and HCO<sub>3</sub><sup>-</sup> during microbial alteration, but also influence chemical gradients, which will in turn affect the mineral phases. The EPS matrix preferably slows down the mobility of hydrated Mg<sup>2+</sup>, therefore, temporarily increase relative abundance of Ca<sup>2+</sup> (Figure 5). The delay of Mg diffusion would lead to a decrease of the Mg<sup>2+</sup> : Ca<sup>2+</sup> ratio of mineral products forming inside the EPS (Verrecchia et al., 1995). As mentioned above, changes in the amount or type of EPS could influence the rate of precipitation or types of crystals formed.

## 2. 4 Microbial metabolism and saturation index

Simple redox reactions form the basis of microbial metabolism. These metabolic reactions often involve C and either O, S or N (Figure 3;(Fenchel, <https://assignbuster.com/microbial-mats-a-bioreactor-of-lithification/>



1998)). Daytime and nighttime metabolism of the six key functional groups is typically different, especially when it is influenced by oxygen and sunlight. Chemical alterations of the microenvironment that result from different metabolic reactions might change the alkalinity and thus facilitate carbonate precipitation or dissolution (Visscher and Stolz, 2005). Microbial mats have a high metabolic activities, thus it is not surprising that the rapid SI changes, despite the internal buffering capacity of the carbonate system, would result in a chemical alteration of the microenvironment. High rates of cyanobacterial photosynthesis cause a rapid depletion of  $\text{CO}_2$ , which challenge the resilience or reestablishment of the carbonate equilibrium, and the increasing alkalinity will results in carbonateprecipitation through removal of the  $\text{H}^-$  that is produced in the latter reaction. It should be noted that in these reactions, organic carbon is assumed to be  $\text{CH}_2\text{O}$  and different outcomes are expected with different organic compounds. For example,  $\text{CO}_2$  produced bythe decomposition of carboxylic acids, will potentially increase the carbonate alkalinity by  $\text{CO}_2$  degassing(Visscher et al., 1992). As such, this could probably explain why heterotrophic aerobes have been shown to precipitate carbonate.

### 3. Microbial mats as an indicator of sulfur evolution

The sulfur cycle has evolved over the long history of the Earth, with the concentration and the isotopic fractional abundance much different between Precambrian and contemporaneous environment (Cameron, 1982). The surface environment of the early Earth was basically reducing. Little atmospheric oxygen existed. Even though it is still under debate how the oxygen was produced at first, a majority of researchers believe that the

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history of atmospheric oxygen and seawater sulphate are closely linked (Habicht and Canfield, 1996; Ohmoto et al., 1993; Walker and Brimblecombe, 1985).

Sulphate in Archaean and early Proterozoic sediment was found to be consistent in  $^{34}\text{S}$  depletion, which is similar to meteorites and mantle-derived igneous rocks (Cameron, 1982; Monster et al., 1979). Moreover, sulphate level was found to positively influence the rate of  $^{34}\text{S}$  depletion as lower levels sulphate (<1mM) was observed with less  $^{34}\text{S}$  depletion (Harrison and Thode, 1958). These mean that sulphides may be result from either one of them: bacterial sulphate reduction in low concentrations of seawater sulphate or a mantle origin. On the contrary, in pure cultures experiment, sulphate bacteria slowly, rather than in a high rate, produced most  $^{34}\text{S}$ -depleted sulphides when abundant of sulphate was provided, a phenomenon showing that  $^{34}\text{S}$  depletion will increase as the sulphate reduction rate decrease because of high levels of sulphate (Chambers et al., 1975; Kaplan and Rittenberg, 1964). In 1996, a study of microbial mats of Solar Lake, Sinai had proved that the latter view was not true. Habicht and Canfield reported large  $^{34}\text{S}$  depletion observed during rapid sulphate reduction by sulphate-reducing bacteria in modern photosynthetic cyanobacterial mats (Habicht and Canfield, 1996). Their result supported the view that sedimentary sulphides formed in Archaean and early Proterozoic are likely to be originated from biological or mantle sources. Hence they concluded that high sulphate concentrations give rise to highly  $^{34}\text{S}$ -depleted sulphides and thus that the concentrations of seawater sulphate did not accumulate until the initial accumulation of oxygen into the atmosphere, <https://assignbuster.com/microbial-mats-a-bioreactor-of-lithification/>

which is between 2. 2-2. 3 Gyr when large early Proterozoic burial pulse of organic matter started.

#### 4. Conclusions

\* This part will be written after the peer review. Mainly because I need some advices to see if I should write something more about the Sulphur or not. The problem is that mats and the carbonate lithification is not enough to write a 10 page paper. But if I need to write a Sulphur part, than I would need to do more work and write more about it. It is interesting but I am not sure if I have enough time to do that. \*

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