B

BACTERIA IN SEDIMENTS

Epibenthic bacteria forming biofilms and microbial mats

Bacteria live in an extremely wide range of habitats, and their occurrence is only restricted by the requirement for water and the physico-chemical stability limits of biomolecules (Knoll and Bauld, 1989). In sediments, epibenthic bacteria attach firmly to the surfaces of mineral particles by their adhesive and mucous, 'extracellular polymeric substances (EPS)' often more abundant than the cell material itself (Decho, 1990 for overview and introduction; Decho, 2000). The mucilaginous substances aid the microbes to sequester nutrients, to protect themselves against osmotic pressure caused by changing salinities, and to maintain an optimal chemical microenvironment for activities of extracellular enzymes (Decho, 1990). These coatings, composed of single cells and their mucilages enveloping mineral particles are known as biofilms (Marshall, 1984; Charaklis and Wilderer, 1989; compare also Stolz, 2000). Further biomass enrichment leads to the formation of discrete, tissue-like organic layers, microbial mats, that cover extensive areas of the seafloor (definition of term see Krumbein, 1983; Cohen and Rosenberg, 1989; Stal and Caumette, 1994; Stolz, 2000; brief historic outline included in Stal 2000). Microbial mats are biologically stratified communities. Different bacterial populations organize in horizontal layers in dependence to intrasedimentary, chemical gradients (Stolz, 2000, and references therein). Their highly active metabolic cycles are in steady interaction with chemical parameters with their surroundings, and thus the microbes powerfully influence their environment (Stal, 2000). This bacterially-mediated element transfer causes diverse intrasedimentary mineral deposits and structures of high preservation potential (Krumbein, 1986). In consolidated rocks, occurrences of the minerals permit conclusions on the biology of ancient microbiota, and on the environmental conditions of the past.

Epibenthic bacterial populations as 'bioreactors'

Epibenthic microorganisms and their slimy secretions contribute to a high porosity of the surface sediments, and their intensive metabolic and catalysatory activities rise the amount of chemical reactions substantially. The transfer capicity of a multi-layered microbial mat is even greater, because the different metabolic cycles interlock with each other. Therefore a microbial mat was compared with an intrasedimentary 'bioreactor' (Hanselmann, 1989; compare also model of 'bioid' by Krumbein, 1986). Within the stratified community of a microbial mat (Figure B1), each population depends on the metabolic products of the other below or above (Cohen and Rosenberg, 1989; Hanselmann, 1989; Stal and Caumette, 1994; Ehrlich, 1996; Nealson, 1997; Stal, 2000; Stolz, 2000; Nisbeth and Sleep, 2001). In the photic zone, primary producers, mainly cyanobacteria (and diatoms), build up biomass by oxygenic or anoxygenic photosynthesis. Below the cyanobacteria, a layer of purple sulfur bacteria may establish (depending on the relative depth gradients of light and oxygen). Their purely anaerobic photosynthesis makes use of lower light intensities than cyanobacteria. Sulfur bacteria require sulfide, which is provided by sulfate-reducing bacteria colonizing deeper parts of the sediments. Here, a great variety of heterotrophic bacteria decompose the primary organic material. With the aid of their highly effective enzymes, they degrade polysaccharides, lipids, or proteins, of the primary biomass, and release monomers. These are further decomposed by sulfate reducing and methanogenic bacteria to carbon dioxide, hydrogen sulfide, methane, and inorganic nutrients. These microbial communities in turn provide the substances required for methanogenic bacteria to build their own biomass.

Chemical processes as a consequence of decomposition and mineralization of organic material lead to precipitation of sulfides, carbonates, silicates, and many other minerals (Krumbein, 1986). This will be outlined in the following.

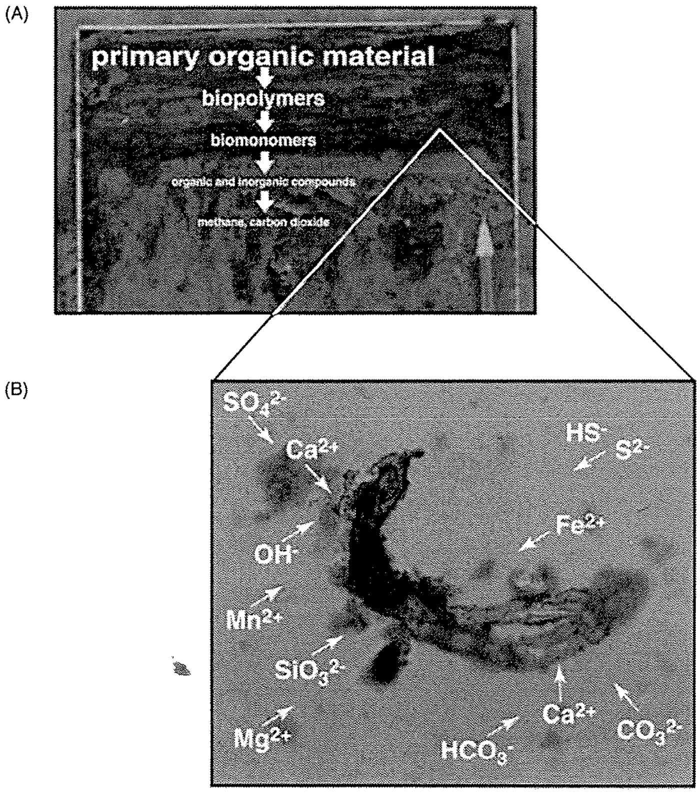

Figure B1 Bacterial decomposition of organic material leads to precipitation of sulfides, carbonates, silicates, and other minerals. (A) Within microbial mats, primary organic material is decomposed in several steps until inorganic nutrients are formed. (B) In microscale, ions dissolved in the surroundings react with reactive chemical groups along the outer cell wall. This might induce mineral precipitation. Photo shows initial precipitates (? pyrite) along cyanobacterial filament.

Decomposition of organic material causing precipitation of minerals

In microscopic scale, the cell walls of bacteria are composed of macromolecules that give an overall electro-negative charge to the outer cell walls (Beveridge, 1989; Beveridge and Doyle, 1989; Schulze-Lam *et al.*, 1996). The reactive chemical groups of the cell wall project into the surrounding environment, but protons released through the cell membrane in course of ATP-generation of the living cell occupy the negatively charged sites. Additionally, the heterogeneously charged microsites of the cell wall adsorb water molecules (that have bipolar chemical structure), and as a consequence a film of water permanently envelopes and buffers the cells (Schulze-Lam *et al.*, 1996). It is assumed that after bacterial cells die, the increasingly electro-negative charge of the cell surfaces react with electro-positive metal ions dissolved in the seawater. In laboratory experiments, the first metal ions serve as nucleus for further metal enrichment, and counter-ions are attracted (Beveridge, 1989; Beveridge and Doyle, 1989; Schulze-Lam *et al.*, 1996; Douglas and Beveridge, 1998; Ferris, 2000). Because of the water molecules enveloping bacterial cells, initial precipitates are hydrated and amorphous (Beveridge, 1989; early steps of aragonite formation on cell envelopes are documented by Krumbein, 1979a; see also Schulze-Lam *et al.*, 1996). Over time, dehydratation of the precipitates leads to a crystalline mineral phase, and during this diagenetic alteration e.g., aragonite changes to calcite (Beveridge, 1989). Depending on microenvironmental geochemistry induced by decomposing heterotroph bacteria, counter ions like sulfate, carbonate, or sulfide ions determine formation of specific minerals, (Figure B1). For example, pyrite is formed in presence of Fe^{2+} and HS^- or S^{2-} ions, and often can be found intimately related to carbonate layers in subrecent, decaying microbial mats (Gerdes *et al.*, 2000).

Microbial ecosystems are ancient and nearly as old as the earliest geological record, so knowledge of bacterially induced chemical processes provides important clues on the biological and environmental evolution of Earth and other planets.

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Cross-references

Oceanic Sediments
Algal/Microbial Sediments
Sulfide Minerals in Sediments