> SECTION IV. PROCESSES
> CHAPTER 9. MICROBES AND MAJOR ELEMENTAL CYCLES

The Sulfur Cycle

BY STEFAN M. SIEVERT, RONALD P. KIENE, AND HEIDE N. SCHULZ-VOGT

The ocean represents a major reservoir of sulfur on Earth, with large quantities in the form of dissolved sulfate and sedimentary minerals (e.g., gypsum and pyrite). Sulfur occurs in a variety of valence states, ranging from –2 (as in sulfide and reduced organic sulfur) to +6 (as in sulfate). Sulfate is the most stable form of sulfur on today's oxic Earth; weathering and leaching of rocks and sediments are its main sources to the ocean. In addition, the reduced inorganic forms of sulfur, with oxidation

fur emissions have currently been overtaken by anthropogenic emissions, primarily from the burning of fossil fuels.

Sulfur is an essential element for life. However, at any given time, only a small fraction is bound in biomass. Sulfur makes up about 1% of the dry weight of organisms, where it occurs mainly as constituents of protein (primarily the S-containing amino acids, cysteine and methionine), but also in coenzymes (e.g., coenzyme A, biotin, thiamine) in the form of iron-sulfur clusters in

reactions, called dissimilatory sulfur metabolism. These latter processes are essential for the cycling of sulfur on our planet, and will be the primary subject of this article.

Sulfur compounds can be used as electron acceptors or electron donors in processes known as sulfate/sulfur reduction and sulfur oxidation, respectively. Whereas the former are strictly anaerobic processes, the latter can occur aerobically as well as anaerobically, with either oxygen or nitrate acting as electron acceptors, or in anoxygenic, anaerobic photosynthesis. The latter process can play an important role in microbial mats or euxinic (anoxic and sulfidic) water columns, such as the Black Sea (e.g., Koblizek et al., 2006), but they will not be further discussed here. In addition, the metabolism of organic sulfur compounds is a key component of the global sulfur cycle.

Although the microorganisms carrying out different reactions of the sul-

> The global sulfur cycle depends on the activities of metabolically and phylogenetically diverse microorganisms, most of which reside in the ocean.

states of –2 and 0 (as in elemental sulfur) are quite common in anoxic environments, with sulfur compounds of mixed valence states (e.g., thiosulfate and polythionates) produced transiently. The natural release of volatile organic sulfur compounds from the ocean, mainly as dimethyl sulfide (DMS), transports sulfur from the ocean to terrestrial regions, and it also affects atmospheric chemistry and the climate system (Figure 1). While they remain very important, natural sul-

metalloproteins, and in bridging ligands (molecules that bind to proteins, for example, in cytochrome c oxidase). Microorganisms can use inorganic sulfur, mainly sulfate, to form these organic compounds in an energy-dependent process referred to as assimilation. However, animals are dependent on preformed organic sulfur compounds to satisfy their sulfur needs. In addition to assimilation, many bacteria and archaea can use sulfur in energy-yielding

STEFAN M. SIEVERT (*ssievert@whoi.edu*) *is Associate Scientist, Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA, USA.* RONALD P. KIENE *is Professor, Department of Marine Sciences, University of South Alabama, Mobile, AL, USA.* HEIDE N. SCHULZ-VOGT *is Juniorprofessor, Institute for Microbiology, Leibniz University, Hannover, Germany.*
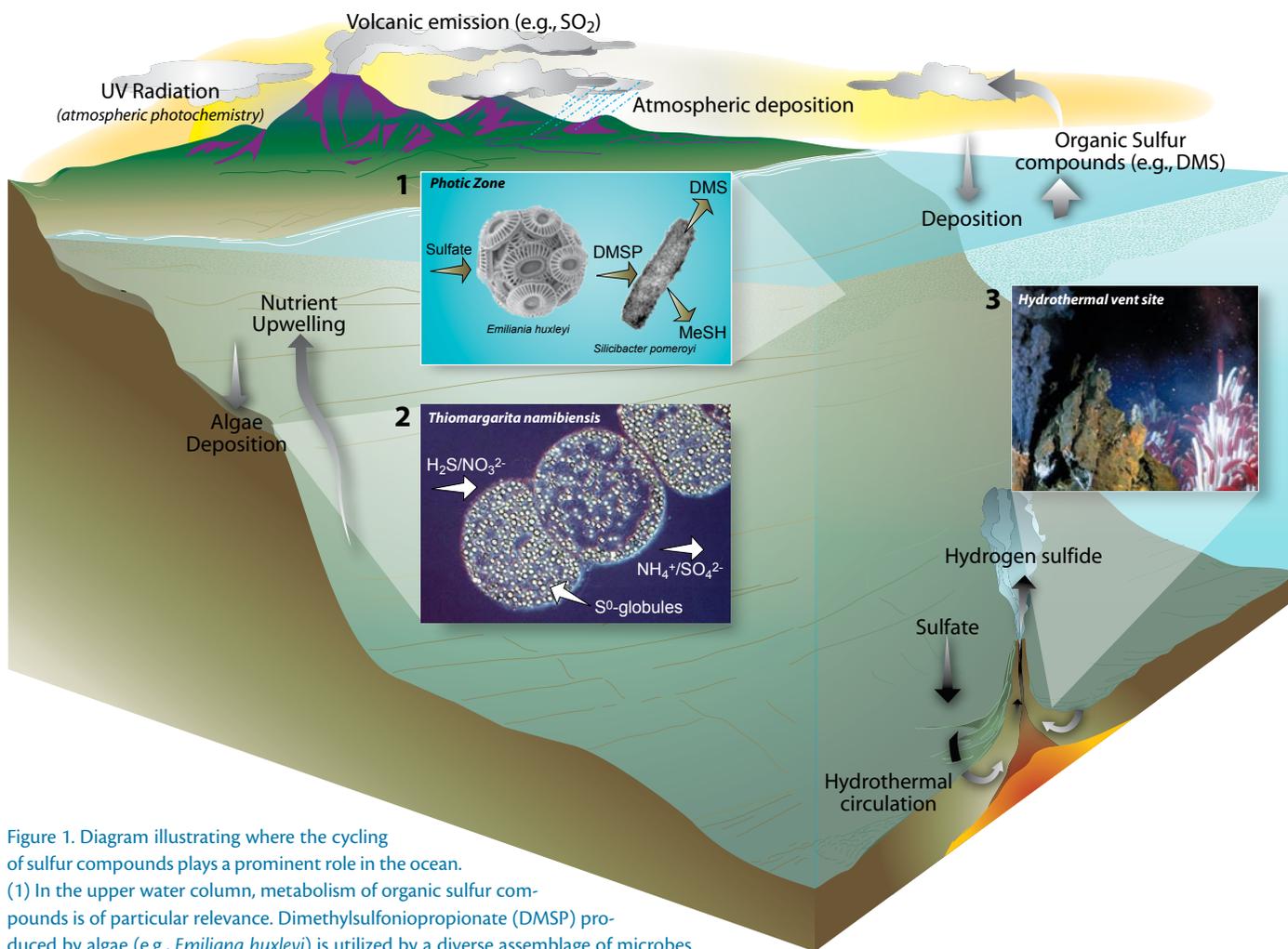
Figure 1. Diagram illustrating where the cycling of sulfur compounds plays a prominent role in the ocean. (1) In the upper water column, metabolism of organic sulfur compounds is of particular relevance. Dimethylsulfoniopropionate (DMSP) produced by algae (e.g., *Emiliana huxleyi*) is utilized by a diverse assemblage of microbes (e.g., *Silicibacter pomeroyi*), leading either to the production of methanethiol (MeSH) or dimethylsulfide (DMS), both of which are highly reactive volatile compounds that can escape to the atmosphere. (2) On the continental shelf, sulfate reduction contributes significantly to organic-matter degradation. The hydrogen sulfide produced can be re-oxidized by so-called colorless sulfur-oxidizing bacteria (e.g., *Thiomargarita namibiensis*). These processes are of particular importance in coastal upwelling regions, such as off the coast of Namibia, where *Thiomargarita namibiensis* becomes abundant. It is also in these regions that large sedimentary deposits of phosporites are found. (3) At deep-sea hydrothermal vents, sulfate precipitates out of seawater as anhydrite ($CaSO_4$) at temperatures above 150°C. However, hydrogen sulfide is produced by leaching sulfur from basalt at high temperatures (~ 400°C) in the oceanic crust. The hydrogen sulfide contained in the ensuing reduced hydrothermal fluids is utilized in energy-yielding reactions by free-living and symbiotic sulfur-oxidizing microbes, providing the basis for the lush animal communities found at deep-sea vents. On land, volcanic emissions are the main natural sources of sulfur to the atmosphere. Photochemical processes in the atmosphere oxidize various sulfur species.

fur cycle are extremely diverse, most of them belong to the bacterial domain (Figure 2). Sulfur-metabolizing archaea are mainly restricted to high-temperature environments, such as deep-sea hydrothermal vents. Sulfur cycling in the biosphere is very rapid, and microorganisms in the ocean play an essential role. As a result of the activities of these microbes,

the sulfur cycle has multiple ties to the cycles of other elements, most notably those of carbon, nitrogen, phosphorous, and iron. Below, we highlight three marine habitats where sulfur cycling is particularly important, namely, the photic zone of the coastal and open ocean, continental margin sediments, and deep-sea hydrothermal systems.

HABITATS

Photic Zone

The sulfur cycle of the surface ocean begins with the assimilatory uptake of sulfate by phytoplankton (both eukaryotic algae and prokaryotic cyanobacteria) (Figure 1). Some sulfate is incorporated, in oxidized form, into sulfated polysaccharides (e.g., mucus), but most

Archaea

Crenarchaeota
Thermoproteales
Desulfurococcales
Sulfolobales

Euryarchaeota
Archaeoglobales
Thermococcales
Thermoplasmatales
Some methanogens, e.g., *Methanosarcina*

Bacteria

Nitrospiraceae
Thermodesulfovibrio

α-Proteobacteria
Roseobacter-clade, SAR-11
Paracoccus
Various genera, e.g., *Rhodobacter*,
Rhodospirillum, *Rhodomicrobium*

β-Proteobacteria
Thiobacillus, *Thiomonas*
Alcaligenes
Rubrivivax, *Rhodocyclus*, *Rhodoferax*

γ-Proteobacteria
Various genera, e.g., *Thiomicrospira*, *Beggiatoa*,
Thioploca, *Thiomargarita*
Symbionts of invertebrates (e.g., *Riftia*, *Calyptogena*)
Methylophaga, *Pseudomonas*,
Unidentified Gammaproteobacteria
Chromatiaceae, *Ectothiorhodospiraceae*

δ-Proteobacteria
Various genera, e.g., *Desulfovibrio*, *Desulfotalea*
Desulfonema, *Desulfosarcina*, *Desulfobacter*
Desulfuromonas, *Desulfurella*, *Desulfuromusa*,
Geobacter
Some sulfate reducers, e.g., *Desulfovibrio*

ε-Proteobacteria
Arcobacter, *Thiovulum*, *Sulfurimonas*,
Sulfurovum
Various genera, e.g., *Sulfurospirillum*,
Nautilia, *Caminibacter*

Aquificae
Aquifex, *Persephonella*,
Sulfurihydrogenibium
Desulfurobacterium, *Thermovibrio*,
Balnearum

Thermodesulfobacteriaceae
Thermodesulfatator,
Thermodesulfobacterium

Chloroflexaceae
Chloroflexus

Firmicutes
Desulfotomaculum,
Desulfosporosinus
Ammonifex

Chlorobiaceae

Legend:
☐ Phototrophic sulfur-oxidizers ☐ Chemolithotrophic sulfur-oxidizers ☐ Sulfur reducers ☐ Sulfate reducers ☐ Organic sulfur utilizers
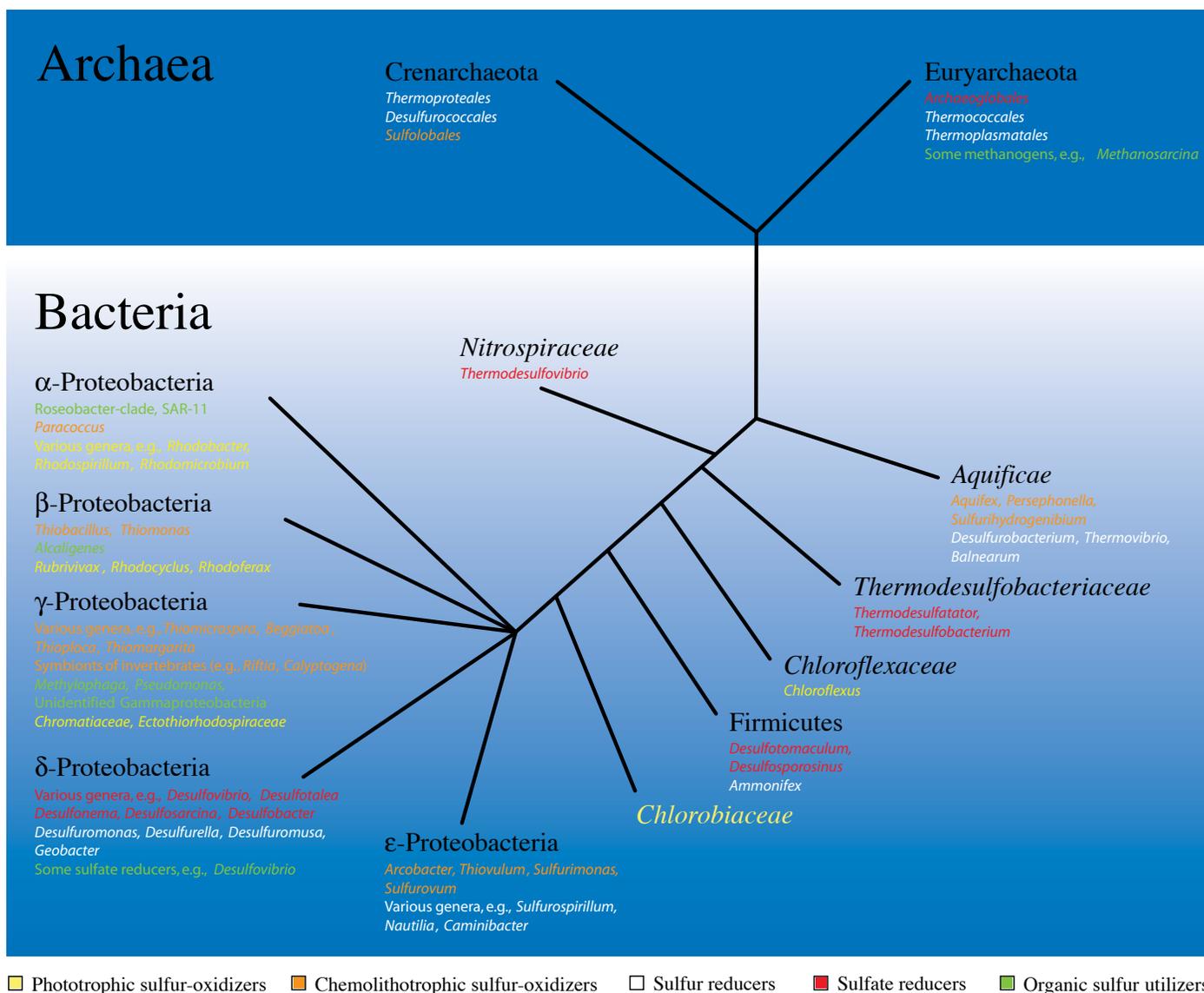
Figure 2. Schematic phylogenetic tree depicting the distribution of different types of sulfur-metabolizing microorganisms among major phylogenetic lineages. All forms of sulfur metabolism can be found within the *proteobacteria*, whereas as other lineages are more restricted in their physiological repertoire. Note that the capability to convert DMSP into DMS is widespread among bacteria, and that not all of the lineages with members capable of this conversion are shown in the tree. *Adapted from Giovannoni and Stingl (2005)*

is assimilated into methionine and cysteine. Methionine is converted by some phytoplankton into dimethylsulfoniopropionate (DMSP) (Gage et al., 1997), a highly stable and soluble form of reduced sulfur. Because of its high cytoplasmic concentrations, DMSP functions as an osmolyte, but it also has other functions, such as an antioxidant and grazing deterrent (Stefels, 2000; Sunda et al., 2002). Diatoms produce relatively low amounts of DMSP (1–50 mM intracellular concentrations), but dinoflagellates, prymnesiophytes, and some chrysophytes produce very large amounts (100–300 mM intracellular concentrations). On the whole, DMSP synthesis by marine photoautotrophs accounts for about 50 x 10^{12} moles of sulfur per year. Because each molecule of DMSP contains five atoms of carbon, DMSP synthesis is also important in the carbon cycle; its production is estimated to account for 3–10% of the global marine primary production of carbon (Kiene et al., 2000), and its degradation supplies about 3–10% of the carbon

requirements of heterotrophic bacteria in surface waters (Simó et al., 2002).

The importance of DMSP in biogeochemical cycling is magnified by its role as the main precursor of volatile DMS. DMS emissions from the surface ocean to the atmosphere range from 0.5 to 1.0 x 10^{12} moles per year (Kettle and Andreae, 2000). In the atmosphere, DMS is oxidized to acidic aerosol particles that affect cloud properties and the amount of solar radiation reflected back to space (Charlson et al., 1987). Thus, DMS production by the plankton community can influence climate, and the potential exists for DMS-linked climate feedbacks to the plankton (Charlson et al., 1987).

Some phytoplankton that produce DMSP have enzymes that cleave DMSP into DMS and acrylic acid. Bacteria from diverse lineages also can convert dissolved DMSP into DMS (Yoch, 2002), but the amount of DMS produced by bacteria is limited by the fact that they metabolize most (e.g., 80–90%) of the DMSP by a demethylation pathway that does not produce DMS (Kiene et al., 2000). Instead, this alternative pathway results in formation of methiolpropionate and, subsequently, methanethiol (CH$_3$SH; MeSH). The gene that encodes for the key DMSP demethylating enzyme, *dmdA*, was only recently discovered in the genomes of *Silicibacter pomeroyi* and *Candidatus Pelagibacter ubique*, and it appears to be prevalent in members of the numerically important Roseobacter and SAR11 clades (Howard et al., 2006).

Because MeSH is so reactive, very little escapes to the atmosphere. Most of the MeSH produced is oxidized, and some is assimilated into sulfur amino acids by microorganisms. The assimilation of MeSH occurs by an elegant reaction whereby the entire CH$_3$S group is incorporated directly into methionine (Kiene et al., 2000). A large fraction of the active bacteria in surface seawater assimilates sulfur from DMSP, with members of the α- and γ-proteobacteria being particularly important (Malmstrom et al., 2004). Even photoautotrophs such as cyanobacteria and diatoms assimilate sulfur from dissolved DMSP (Vila-Costa et al., 2006a), although it remains unclear whether they assimilate DMSP directly or whether they obtain the sulfur from MeSH produced by other organisms. Interestingly, DMSP contributes 50–100% of the sulfur required for heterotrophic bacterial biomass production (Kiene et al., 2000). This is remarkable considering seawater contains 1–10 million times more sulfate than DMSP.

In addition to funneling most of the DMSP away from DMS production, bacteria control the emissions of DMS by consuming a large fraction of the DMS produced and converting it into the nonvolatile products dimethyl sulfoxide (DMSO) and sulfate (del Valle et al., 2007). We are only beginning to learn which organisms might be involved in DMS consumption. A recent experimental study shows that *Methylophaga* spp., a genus known to metabolize DMS, is a prominent group that developed in seawater enriched with DMS (Vila-Costa et al., 2006b). Ultimately, only 1–2% of the synthesized DMSP sulfur is released to the atmosphere as DMS, yet this small leak from the DMSP/DMS biogeochemical system is responsible for the massive transfer of sulfur from the oceans to the atmosphere and ultimately to land.

Marine Sediments

As soon as organic material settles on the seafloor, oxygen is rapidly exhausted and sulfate is used as an electron acceptor by sulfate-reducing prokaryotes (SRP) to oxidize organic material (Figure 1). As a result of this anaerobic respiration, which accounts for up to 50% of organic carbon mineralization in ocean margin sediments (Jørgensen, 1982), large amounts of foul-smelling sulfide are produced. Some of the energy in the original organic matter is conserved in the sulfide, and it can be released by a special group of bacteria, the large, vacuolated sulfur bacteria of the genera *Beggiatoa*, *Thioploca,* and *Thiomargarita*. They occur as dense mats in sediments of coastal upwelling areas (e.g., Chile, Peru, Namibia, Arabian Sea), at whale carcasses, at hydrothermal vents and seeps, at methane hydrates, but also in quite ordinary eutrophic coastal environments such as fjords or salt marshes (Teske and Nelson, 2006).

These three closely related genera are adapted to oxidize sulfide, even when oxygen is absent, by using nitrate as the electron acceptor. To be able to compete with other sulfide oxidizers, they monopolize this metabolism, storing nitrate from the bottom water internally in a vacuole and transporting the nitrate into the sediment, where sulfide is produced (Fossing et al., 1995). To store as much nitrate as possible, they have to enlarge their vacuoles, and, as a result, this group of bacteria contains many giant forms easily visible to the naked eye, with cell diameters of 0.1–0.75 mm (Schulz et al., 1999). The large sulfur bacteria respire nitrate, but

in contrast to denitrifying bacteria, they seem to reduce the nitrate to ammonia and not to N_2. This has important consequences for the nitrogen budget of their habitats, as ammonia can be re-oxidized to nitrate and stay within the system. Additionally, these bacteria store polyphosphate, which they release periodically as phosphate, leading to rapid precipitation of phosphorous-containing minerals. Thus, they can also play an important role in phosphorous cycling in the sediment by removing phosphorous from the biosphere (Schulz and Schulz, 2005). The metabolism of organic sulfur compounds is also important in sedimentary habitats. For example, DMS is used by aerobes like *Methylophaga* spp. and *Hyphomicrobium* spp. as well as strict anaerobes such as the methylotrophic methanogens in the domain Archaea. DMS can also be formed in anoxic habitats from the methylation of sulfide and methanethiol, a process that may support some of the anaerobic methylotrophs.

In areas where small amounts of organic material settle on the seafloor, sulfate is only used up slowly and may still be present several hundred meters down into the sediment (D'Hondt et al., 2004). At some sites on the Peruvian shelf, sulfate is depleted in surface sediments but becomes available again at greater depths from an underlying ancient brine. Thus, sulfate can be an important electron acceptor for bacteria populating the deep biosphere. Here, as well as in other anaerobic environments, it may be used as an electron acceptor by a microbial consortium oxidizing the greenhouse gas methane (Widdel et al., 2004).

Deep-Sea Hydrothermal Vents

Deep-sea hydrothermal vents are highly productive ecosystems, where chemolithoautotrophic microorganisms mediate the transfer of energy from the geothermal source to the higher trophic levels (Jannasch and Mottl, 1985). Dissimilatory sulfur metabolism is a key component driving these systems, with sulfur oxidation being of particular importance. At deep-sea vents, H_2S is produced geothermally within the oceanic crust as a result of rock-seawater interactions at high temperatures rather than as a result of dissimilatory sulfate reduction (Figure 1). The ensuing hot hydrothermal fluids contain high concentrations of H_2S (usually around 3–10 mM), but no sulfate, which precipitates as anhydrite at temperatures > 150°C. Currently, not much is known about the metabolism of organic sulfur compounds at deep-sea vents, although this might potentially be an important process (e.g., Schulte and Rogers, 2004).

In the future, it will be important to improve quantitative estimates of these processes and to learn more about their interdependencies.

The large supply of H_2S fuels sulfur-oxidizing bacteria that exist either as free-living forms in the mixing zone between oxygenated seawater and the highly reduced hydrothermal fluids, above or below the seafloor, or in a symbiotic relationship with various invertebrates (Jannasch and Mottl, 1985).

Besides the well-known γ-proteobacterial sulfur-oxidizers like *Beggiatoa* spp., *Thiomicrospira* spp.*,* and endosymbionts of invertebrates (e.g., *Riftia pachyptila*), bacteria belonging to ε-proteobacteria have only recently been recognized as important members of the microbial communities at deep-sea vents (Campbell et al., 2006). Novel sulfur-oxidizing ε-proteobacteria belonging to the genus *Arcobacter* produce sulfur in filamentous form that is morphologically and chemically similar to material observed after deep-sea volcanic eruptions (Taylor and Wirsen, 1997; Sievert et al., 2007). These microbes might also be part of a subseafloor biosphere, which is, at present, a poorly defined, yet critically important component of deep-sea hydrothermal systems (Wilcock et al., 2004). Interestingly, these and many other autotrophic microorganisms present at deep-sea vents use the reductive tricarboxylic acid cycle for autotrophic carbon fixation, questioning the para-digm that the well-known Calvin cycle is at the base of deep-sea hydrothermal ecosystems (Campbell et al., 2006 and references therein; Hügler et al., 2007; Markert et al., 2007). Recently, the genomes of a number of either free-living or symbiotic sulfur-oxidizing bacteria have become available, greatly

facilitating progress in our understanding of this important process and the development of functional gene assays to assess the diversity and activity of these organisms in situ (Scott et al., 2006; Markert et al., 2007; Newton et al., 2007; Sievert et al., in press). Interestingly, the presence of a gene cluster predicted to encode proteins involved in phosphonate utilization in the genome of the free-living, sulfur-oxidizing bacterium *Thiomicrospira crunogena* XCL-2 suggests that phosphate could potentially be a limiting nutrient at deep-sea hydrothermal vents, similar to what has been described for the marine cyanobacterium *Trichodesmium erythraeum*, which thrives in phosphate-depleted surface waters (Dyhrman et al., 2006; Scott et al., 2006).

Elemental sulfur (S^0) is a key substrate at hydrothermal vents, particularly at higher temperatures, as a number of thermophilic and hyperthermophilic bacteria and archaea can use S^0 as an electron donor in either autotrophic or heterotrophic metabolism (e.g., Stetter, 2006). Some of these organisms can also use nitrate as an alternative electron acceptor (e.g., Vetriani et al., 2004). In addition, many hyperthermophiles use S^0 as an electron sink during fermentation. At Guaymas Basin, a sediment-covered deep-sea vent site, microbial sulfate reduction occurs at temperatures up to 110°C, which exceeds the maximum growth temperature for cultivated hyperthermophilic sulfate reducers of the genus *Archaeoglobus* (Jørgensen et al., 1992). In addition, liquid and gaseous aliphatic and aromatic hydrocarbons generated by hydrothermal heating of immature sedimentary organic matter serve as carbon sources for sulfate-reducing prokaryotes at this vent site (Widdel et al., 2004). Studies based on the detection of a gene coding for a key enzyme of sulfate reduction (i.e., dissimilatory sulfite reductase) further reveal that many SRP exist in these environments that are currently not represented in culture collections (e.g., Dhillon et al., 2003), indicating that we might yet have to characterize the real "players."

CONCLUSIONS AND FUTURE PROSPECTS

The global sulfur cycle depends on the activities of metabolically and phylogenetically diverse microorganisms, most of which reside in the ocean. Although sulfur rarely becomes a limiting nutrient, its turnover is critical for ecosystem function. Organic sulfur compounds fuel microbial metabolism in the upper water column and their turnover has important consequences, for example, for the climate system. Changes in phyto- and bacterioplankton composition due to global change could thus have dramatic, but as yet poorly understood, ramifications. Sulfur-metabolizing microorganisms also fulfill essential functions in their habitats by either degrading or forming biomass (organic carbon), as exemplified by the degrading activities of sulfate-reducing bacteria in marine sediments and the formation activities of sulfur-oxidizing bacteria at deep-sea hydrothermal vents. Some sulfur-oxidizing bacteria further increase ecosystem productivity by retaining nitrogen and phosphorous compounds. In the future, it will be important to improve quantitative estimates of these processes and to learn more about their interdependencies. Such knowledge will enable us to better assess their environmental impact and their possible responses to environmental changes. At present, we have only limited ability to identify the actual microbial "players" and to couple the identity of the organisms with their functions and activities in situ. New developments in sensor technology to measure rates in situ and the availability of genomes, in combination with metagenomic and microbiological approaches, will facilitate progress along these lines.

REFERENCES

Campbell B.J., A.S. Engel, M.L. Porter, and K. Takai. 2006. The versatile ε-proteobacteria: Key players in sulphidic habitats. *Nature Reviews Microbiology* 4:458–468.

Charlson, R.J., J.E. Lovelock, M.O. Andreae, and S.G. Warren. 1987. Oceanic phytoplankton, atmospheric sulfur, cloud albedo and climate. *Nature* 326:655–661.

D'Hondt S., B.B. Jørgensen, D.J. Miller, A. Batzke, R. Blake, B.A. Cragg, H. Cypionka, G.R.

Dickens, T. Ferdelman, K.-U. Hinrichs, and others. 2004. Distributions of microbial activities in deep subseafloor sediments. *Science* 306:2,216–2,221.

del Valle, D.A., D.J. Kieber , and R.P. Kiene. 2007. Depth-dependent fate of biologically-consumed dimethylsulfide in the Sargasso Sea. *Marine Chemistry* 103:197–208.

Dhillon, A, A. Teske, J. Dillon, D.A. Stahl, and M.L. Sogin. 2003. Molecular characterization of sulfate-reducing bacteria in the Guaymas Basin. *Applied and Environmental Microbiology* 69:2,765–2,772.

Dyhrman, S.T., P.D. Chappell, S.T. Haley, J.W. Moffett, E.D. Orchard, J.B. Waterbury, and E.A. Webb. 2006. Phosphonate utilization by the globally important marine diazotroph *Trichodesmium*. *Nature* 439:68–71.

Fossing H., V.A. Gallardo, B.B. Jørgensen, M. Huttel, L.P. Nielsen, H. Schulz, D.E. Canfield, S. Forster, R.N. Glud, J.K. Gundersen, J. Kuver, N.B. Ramsing, A. Teske, B. Thamdrup, and O. Ulloa. 1995. Concentration and transport of nitrate by the mat-forming sulphur bacterium Thioploca. *Nature* 374:713–715.

Gage, D., D. Rhodes, K.D. Nolte, W.A. Hicks, T. Leustek, A.J.L. Cooper, and A.D. Hanson. 1997. A new route for the synthesis of dimethyl-sulfoniopropionate in marine algae. *Nature* 387:891–894.

Giovannoni, S.J. and U. Stingl. 2005. Molecular diversity and ecology of microbial plankton. *Nature* 437:343–348.

Howard, E., J.R. Henriksen, A. Buchan, C.R. Reisch, H. Bürgmann, R. Welsh, W. Ye, J.M. González, K. Mace, S.B. Joye, and others. 2006. Bacterial taxa that limit sulfur flux from the ocean. *Science* 314:649–652.

Hügler M., H. Huber, S.J. Molyneaux, C. Vetriani, and S.M. Sievert. 2007. Autotrophic CO_2 fixation via the reductive tricarboxylic acid cycle in different lineages within the phylum *Aquificae*: Evidence for two ways of citrate cleavage. *Environmental Microbiology* 9:81–92.

Jannasch, H.W., and M.J. Mottl. 1985. Geomicrobiology of deep-sea hydrothermal vents. *Science* 229:717–725.

Jørgensen, B.B. 1982. Mineralization of organic matter in the sea bed—The role of sulfate reduction. *Nature* 296:643–645.

Jørgensen, B.B., M.F. Isaksen, and H.W. Jannasch. 1992. Bacterial sulfate reduction above 100°C in deep sea hydrothermal vent sediments. *Science* 258:1,756–1,757.

Kettle, A.J., and M.O. Andreae. 2000. Flux of dimethylsulfide from the oceans: A comparison of updated data sets and flux models. *Journal of Geophysical Research* 105:26,793–26,808.

Kiene, R.P., L.J. Linn, and J.A. Bruton. 2000. New

and important roles for DMSP in marine microbial communities. *Journal of Sea Research* 43:209–224.

Koblizek, M., P.G. Falkowski, and Z.S. Kolber. 2006. Diversity and distribution of photosynthetic bacteria in the Black Sea. *Deep-Sea Research Part II* 53:1,934–1,944.

Malmstrom, R., R.P. Kiene, and D.L. Kirchman. 2004. Identification and enumeration of bacteria assimilating dimethylsulfoniopropionate (DMSP) in the North Atlantic and Gulf of Mexico. *Limnology and Oceanography* 49(2):597–606.

Markert, S., C. Arndt, H. Felbeck, R.A. Feldman, D. Becher, S.M. Sievert, M. Hügler, D. Albrecht, J. Robidart, S. Bench, and others. 2007. Approaching the uncultivable endosymbiont of *Riftia pachyptila* by physiological proteomics. *Science* 315:247–250.

Newton I.L.G., T. Woyke, T.A. Auchtung, G.F. Dilly, R.J. Dutton, M.C. Fisher, K.M. Fontanez, E. Lau, F.J. Stewart, P.M. Richardson, and others. 2007. The *Calyptogena magnifica* chemoautotrophic symbiont genome. *Science* 315:998–1,000.

Schulte, M.D., and K.L. Rogers. 2004. Thiols in hydrothermal solution: Standard partial molal properties and their role in the organic geochemistry of hydrothermal environments. *Geochimica et Cosmochimica Acta* 68:1,087–1,097.

Schulz, H.N., T. Brinkhoff , T.G. Ferdelman, M. Hernández Mariné, A. Teske, and B.B. Jørgensen. 1999. Dense populations of a giant sulfur bacterium in Namibian shelf sediments. *Science* 284:493–495.

Schulz, H.N., and H.D. Schulz. 2005. Large sulfur bacteria and the formation of phosphorite. *Science* 307:416–418.

Scott K.M., S.M. Sievert, F.N. Abril, L.A. Ball, C.J. Barrett, R.A. Blake, A.J. Boller, P.S.G. Chain, J.A. Clark, C.R. Davis, and others. 2006. The genome of deep-sea vent chemolithoautotroph *Thiomicrospira crunogena* XCL-2. *PLoS Biology* 4:e383 doi:10.1371/ journal.pbio.0040383.

Sievert, S.M., M. Hügler, C.D. Taylor, and C.O. Wirsen. In press. Sulfur oxidation at deep-sea hydrothermal vents. In: *Microbial Sulfur Metabolism*, C. Dahl and C. Friedrich, eds, Springer, New York.

Sievert, S.M., E.B.A. Wieringa, C.O. Wirsen, and C.D. Taylor. 2007. Growth and mechanism of filamentous-sulfur formation by *Candidatus Arcobacter sulfidicus* in opposing oxygen-sulfide gradients. *Environmental Microbiology* 9:271–276.

Simó, R., S.D. Archer, C. Pedros-Alio, L. Gilpin, and C.E. Stelfox-Widdicombe. 2002. Coupled dynamics of dimethylsulfoniopropionate and dimethylsulfide cycling and the microbial food

web in surface waters of the North Atlantic. *Limnology and Oceanography* 47:53–61.

Stefels, J. 2000. Physiological aspects of the production and conversion of DMSP in marine algae and higher plants. *Journal of Sea Research* 43:183–197.

Stetter, K.O. 2006. History of discovery of the first hyperthermophiles. *Extremophiles* 10:357–362.

Sunda, W., D. J. Kieber, R.P. Kiene, and S. Huntsman. 2002. An antioxidant function for DMSP and DMS in marine algae. *Nature* 418:317–320.

Taylor, C.D., and C.O. Wirsen. 1997. Microbiology and ecology of filamentous sulfur formation. *Science* 277:1,483–1,485

Teske, A., and D. Nelson. 2006. The genera *Beggiatoa* and *Thioploca*. Pp. 784–810 in *The Prokaryotes: A Handbook on the Biology of Bacteria,* vol. 6, 3rd ed., *Proteobacteria: Gamma Subclass.* M. Dworkin, S. Falkow, E. Rosenberg, K.-H. Schleifer, and E. Stackebrandt, eds, Springer, New York.

Vetriani, C, M.D. Speck, S.V. Ellor, R.A. Lutz, and V. Starovoytov. 2004. Thermovibrio ammonificans sp. nov., a thermophilic, chemolithotrophic, nitrate-ammonifying bacterium from deep-sea hydrothermal vents. *International Journal of Systematic and Evolutionary Microbiology* 54:175–181.

Vila-Costa, M., R. Simó, H. Harada, J.M. Gasol, D. Slezak, and R.P. Kiene. 2006a. Dimethylsulfonio propionate uptake by marine phytoplankton. *Science* 314:652–654.

Vila-Costa, M., D.A. del Valle, J.M. González, D. Slezak, R.P. Kiene, O. Sánchez, and R. Simó. 2006b. Phylogenetic identification and metabolism of marine dimethylsulfide-consuming bacteria. *Environmental Microbiology* 8:2,189–2,200.

Widdel, F., A. Boetius, and R. Rabus. 2004. Anaerobic biodegradation of hydrocarbons including methane. Pp. 1,028–1,049 in *The Prokaryotes. Third Edition. A Handbook on the Biology of Bacteria. Ecophysiology and Biochemistry: Volume 2*. M. Dworkin, S. Falkow, E. Rosenberg, K.-H. Schleifer, and E. Stackebrandt, eds, Springer, New York.

Wilcock, W.S.D., E.F. DeLong, D.S. Kelley, J.A. Baross, and S.C. Cary, eds. 2004. *The Subseafloor Biosphere at Mid-Ocean Ridges.* Geophysical Monograph 144, American Geological Union, Washington, D.C.

Yoch, D.C., 2002. Dimethylsulfoniopropionate: Its sources, role in the marine food web, and biological degradation to dimethylsulfide. *Applied and Environmental Microbiology* 68(12):5,804–5,815.