27 Genetics and Molecular Features of Bacterial Dimethylsulfoniopropionate (DMSP) and Dimethylsulfide (DMS) Transformations

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Abstract: The transformations of dimethylsulfoniopropionate (DMSP; $(CH_3)_2S^+CH_2CH_2COO^-$) by bacterioplankton play important roles in the global sulfur cycle. This compound is produced in large quantities primarily for use as an osmolyte by marine algae. DMSP is a labile compound although the complete mineralization of DMSP is only a minor fate in the ocean. DMSP is the main precursor of dimethylsulfide (DMS; CH_3-S-CH_3), a radiatively active trace gas that contributes to global climate regulation. However, it is believed that the main pathway for the transformation of DMSP involves an assimilation step in which DMSP sulfur is incorporated efficiently into cell biomass, leaving relatively little sulfur available for release as DMS. DMSP is rapidly turned over in the environment and the diversity of pathways for its transformation are likely not yet fully realized. This chapter covers recent findings on the genetics of DMSP catabolism; their discoveries are changing our view of the role of this compound in the World's oceans. Although even less is known about bacterially-mediated transformations of DMS, the handful of genes that have been described in a limited number of bacteria is also reviewed in this chapter.

1 Introduction

Dimethylsulfoniopropionate (DMSP) is a hugely abundant molecule in nature. It is produced mostly in the oceans, by ubiquitous phytoplankton, seaweeds and some species of terrestrial and aquatic vascular plants. DMSP acts primarily as an osmoprotectant for the organisms that make it, although it may also serve as an antioxidant, a cryoprotectant or a predator deterrent. Intracellular DMSP concentrations vary among organisms, and in some marine algae (e.g., dinoflagellates and prymnesiophytes) they can be as high as 0.2–0.5 M. DMSP is also an important substrate for bacteria that decompose the fraction that leaks from aged algal cells or which is liberated following viral lysis or zooplankton grazing. Once DMSP is released, it is taken up and transformed relatively quickly (Kiene and Linn, 2000) serving as both a sulfur and carbon source to bacterioplankton (Kiene et al., 2000). DMSP can support 1–15% of the marine bacterial carbon demand and all the sulfur demand (Kiene and Linn, 2000; Simó et al., 2002), which represent massive contributions for a single compound.

Many different marine bacteria can degrade DMSP. These include strains from the alpha-, beta- and gammaproteobacteria (e.g., *Roseobacter, Alcaligenes* and *Vibrio* respectively) and several such strains can grow on DMSP as a sole carbon source. It was known early on that bacteria possess at least two different ways to catabolize DMSP. One of these involves a demethylation step, and is the predominant pathway in natural environments (Kiene et al., 1999; Simó and Pedrós-Alió, 1999).

The other general mechanism for DMSP catabolism liberates the highly volatile dimethyl sulfide (DMS), a product that is of major environmental importance in its own right. Most of the DMS is recycled in the marine food web (Simó, 2001) but ~20 Tg escapes into the atmosphere each year (Kettle and Andreae, 2000) making it an important link in sulfur exchange between the oceans and the atmosphere. Furthermore, once released in the air, it is abiologically oxidized to hygroscopic compounds such as sulfuric acid and methanesulfonic acid (MSA). These attract water droplets, and act as cloud condensation nuclei to increase the albedo, regulating the radiation balance of the Earth. It was even suggested that this forms a self-regulated feedback between DMS release and the plankton communities that produce DMSP and DMS (*Fig. 1*; Charlson et al., 1987).

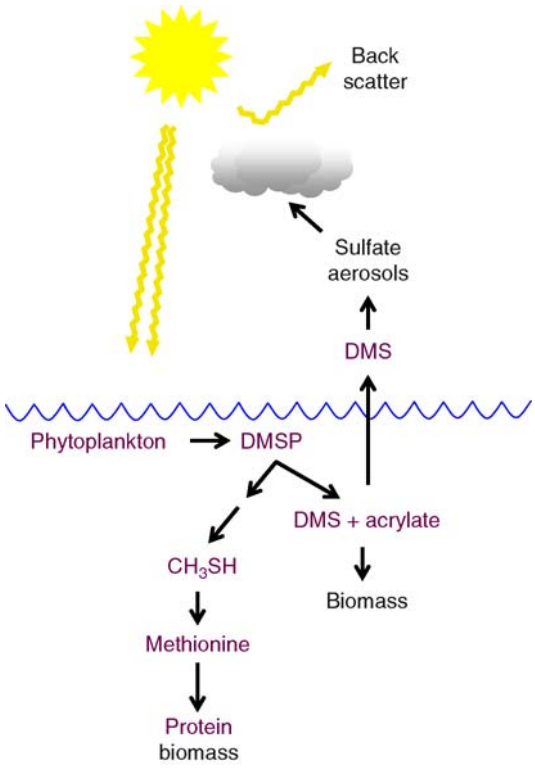

Figure 1

Proposed main pathways for DMSP cycling in seawater and atmosphere.

Despite the importance of bacterial DMSP catabolism and DMS production, studies of the molecular genetics and detailed enzymology of these processes are in their infancy.

2 Demethylation of DMSP: Assimilation of DMSP Sulfur into Protein

The utilization of DMSP is a clear example of how bacterioplankton are adapted to optimize growth by utilizing reduced forms of a substrate (Vallino et al., 1996). Sulfate is one of the most abundant ions in natural waters, especially seawater, and its concentration is far from growth-limiting. However, the sulfate S atom is in its most oxidized state (+VI) and must be reduced to its most reduced (−II; sulfide) form during bacterial S assimilation. This major energetic cost may explain why bacteria prefer DMSP as a sulfur source, even though it is 2–3 orders of magnitude less abundant than sulfate in seawater. Not surprisingly, other sulfur substrates have been previously found to substitute for sulfate as a sulfur source, such as amino acids, which can inhibit the assimilation of sulfate (Kiene et al., 1999).

Bacteria also assimilate DMSP in laboratory cultures, indicating that model organisms can be isolated as pure cultures for physiological studies. For example, *Silicibacter pomeroyi*

obtained all its sulfur from DMSP in medium with a relatively high concentration of glucose (5 mM). Only when the concentrations of DMSP were high enough did a different pattern take place: *S. pomeroyi* released DMS into the medium (González et al., 1999). The widely distributed oligotrophic marine bacterium *Pelagibacter ubique* (a member of the SAR11 group) obtains its sulfur exclusively from DMSP or other forms of organic sulfur, since it lacks the genes necessary to assimilate S-sulfate (Tripp et al., 2008).

The utilization of DMSP sulfur in *S. pomeroyi* and *P. ubique* involves the demethylation pathway, with the formation of methanethiol (MeSH), some of which is incorporated subsequently into bacterial amino acids (Fig. 2). The enzyme cystathionine γ-synthetase can incorporate either sulfide or MeSH directly into O-acyl homoserine and, in the latter case, the result is the direct formation of methionine (Kiene et al., 1999).

A DMSP methyltransferase in the glycine cleavage T-family, encoded by the *dmdA* gene, was first identified in the *Roseobacter* and SAR11 clades (Howard et al., 2006). The DmdA enzyme generates methylmercaptopropionate (MMPA) plus a methyl group that enters the C_1 pool via the coenzyme tetrahydrofolate (Fig. 2). Subsequently, sulfur derived from MMPA can be incorporated into methionine via MeSH and from here to higher trophic levels.

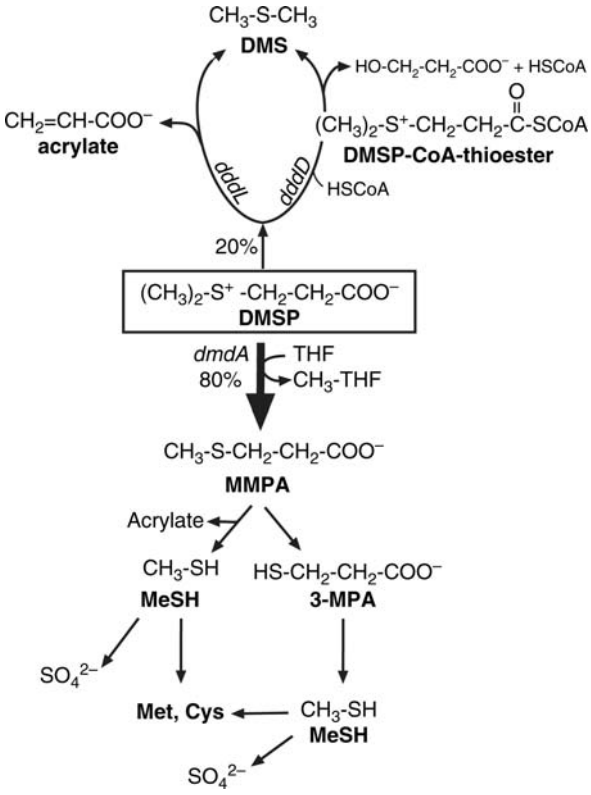

Figure 2

Pathways for the transformation of DMSP in seawater and genes involved. Percentages indicate the amount of carbon that goes through each pathway based on environmental data.

No gene or enzyme that releases MeSH has been identified thus far. Alternatively, MMPA can be degraded to mercaptopropionate (3-MPA) in a second demethylation reaction and thence to acrylate and sulfide (Visscher and Taylor, 1994).

In the natural environment, DMSP sulfur demethylation is a competing route for the transformation of DMSP into the climate active gas DMS (Fig. 1). Incorporation of DMSP dominates the microbial transformation of this compound in the environment, based on bulk activity measurements (Kiene et al., 2000). Consistent with this, gene stoichiometry in metagenomic libraries shows that the *dmdA* homologs occur in ~30% of the cells in bacterial cells in the oceans (Howard et al., 2008), whereas the *ddd* genes involved in pathways that generate DMS are less abundant (Curson et al., 2008; Todd et al., 2007).

DMSP functions as a labile substrate that many different bacteria can exploit in the natural environment. Using microautoradiography combined with in situ oligonucleotide hybridization, the contribution of bacteria that assimilated DMSP sulfur in environmental samples was found to be similar or only slightly smaller than the fraction of bacteria that took up the amino acid leucine (Malmstrom et al., 2004; Vila et al., 2004). The seasonal pattern of uptake of both leucine and DMSP was also shown to be similar (Vila et al., 2004; Vila-Costa et al., 2007). These studies showed that taxa that are known to dominate the marine bacterioplankton communities take up DMSP. However, recent results suggest that the fate of DMSP sulfur is controlled by changes in the carbon reservoir and less by the phylogenetic composition of the bacterioplankton (Vila-Costa et al., 2007). Therefore, one would expect that enzymes and pathways for the transformation of DMSP would be widespread across different phylogenetic groups.

3 Genes for the Release of DMS from DMSP

For decades, the widely accepted route for DMSP dependent DMS production was that DMSP was cleaved by a "DMSP lyase," releasing DMS, acrylate and a proton. A gene, *dddL,* was recently found in several marine Rhodobacterales (alphaproteobacteria) whose product has the characteristics of such a DMSP lyase (Curson et al., 2008). The DddL protein was previously in a DUF (domain of unknown function) and did not contain the N-terminal sequence that was reported for a DMSP lyase from *Pseudomonas doudoroffii* and of *Alcaligenes* (De Souza and Yoch, 1996).

A second, completely different mechanism for DMS emission, and encoded by the *dddD* gene was found in several other bacteria (Todd et al., 2007). The *dddD* polypeptide is not a lyase, but may add acyl-CoA to DMSP (Fig. 2), the resulting DMSP-CoA being predicted to liberate DMS non-enzymatically before further catabolism of the C_3 compound acryloyl-CoA to 3-hydroxy propionate. The fact that the very different genes *dddD* and *dddL* are involved in the initial release of DMS may explain earlier findings that "DMSP lyase" was very different in different bacteria (Yoch, 2002).

The DddL-type of DMSP lyase is confined to the Order Rhodobacterales, although not all strains, even of a single species (e.g., *Rhodobacter sphaeroides*) contain it (Curson et al., 2008). In contrast, the DddD acyl CoA transferase is very widespread, being found in strains of alpha- and gammaproteobacteria (e.g., *Sagittula* and *Marinomonas*, respectively), and also in terrestrial bacteria that interact with roots of land plants. These include strains of the N_2-fixing symbiont *Rhizobium* and the rhizosphere bacterium *Burkholderia* (Todd et al., 2007). Thus *dddD* may be prone to horizontal gene transfer among bacteria.

Consistent with this, the *ddd* gene clusters of different bacteria that contain *dddD* posses other genes involved in DMSP transport (see below), catabolism or gene regulation. Strikingly, the gene products for a given function may be in wholly different gene families; thus the DMSP transporter in *Marinomonas* is an integral membrane-bound BCCT (betaine, choline, carnitine transport) type but *Rhizobium* transports DMSP by an ABC (ATP-binding cassette) system (Todd et al., 2007). In addition to these specialized DMSP transporters, most bacteria, including several known DMSP-catabolizing ones, have other versions of the BCCT-type and betaine ABC transporters that may serve for the general import of structurally similar molecules. Indeed, it was shown directly that *E. coli* has transporters that can import both betaine and DMSP (Cosquer et al., 1999) while Kiene et al. (1998) used bioassays with natural samples, to show that DMSP and glycine betaine share the same transporters. Also, *S. pomeroyi* has genes for BCCT-type and ABC-type transporters that were induced by exposure of the cells to DMSP (Bürgmann et al., 2007) and a likely DMSP uptake gene, similar to *opuD* was noted by Moran et al. (2004).

4 Why Make DMS in the First Place?

On the face of it, the DMS-releasing pathway(s) of DMSP catabolism seem inherently wasteful, since all the sulfur and 40% of the carbon is lost as the DMS escapes. Indeed, insignificant amounts of carbon and sulfur are incorporated into cell biomass from DMS by natural assemblages (del Valle et al., 2007; Kiene et al., 1999; Vila-Costa et al., 2006). Given that bacteria can recoup *all* of the S and the C from DMSP via demethylation, and that some strains, such as *S. pomeroyi* can express both the DmdA demethylase and the DddD acyl-CoA transferase, the apparently wasteful release of DMS seems odd. Interestingly, experimental observations on *S. pomeroyi* grown on media with sufficient carbon (5 mM glucose) plus DMSP that served as the sole sulfur source, only liberated DMS when the concentration of DMSP was higher than 0.01 mM (González et al., 1999). Another *Roseobacter* strain, *Dinoroseobacter shibae* DFL 12, not only contains homologs of *dmdA*, and both *dddA* and *dddL*, but also has genes involved in the transformation of the products of DMSP degradation. These are a putative homolog of the DMS monooxygenase (see below) and inorganic sulfur oxidation enzymes, making it quite a versatile sulfur-transforming organism. Bacteria in the *Roseobacter* cluster, such as *S. pomeroyi* and *D. shibae*, make good candidates to study the physiological roles of the different types of DMSP catabolism that can be accomplished by a single strain.

Additionally, it may be relevant that DMS can act as a signal molecule and that maybe at least some bacteria make DMS to either attract other organisms or in defense, perhaps together with the acrylate that is formed by the bacteria that use the DMSP lyase. Certainly, bacteria that can make DMS from DMSP do not necessarily grow on DMSP as sole carbon source, or degrade DMS any further, at least under laboratory conditions, suggesting that this process may not be wholly involved in nutrition.

5 Degradation of DMS

DMS could potentially be a source of sulfur for marine bacterioplankton since its degradation products include MeSH and sulfide (*Fig. 3*). However, the DMS that is catabolized in marine

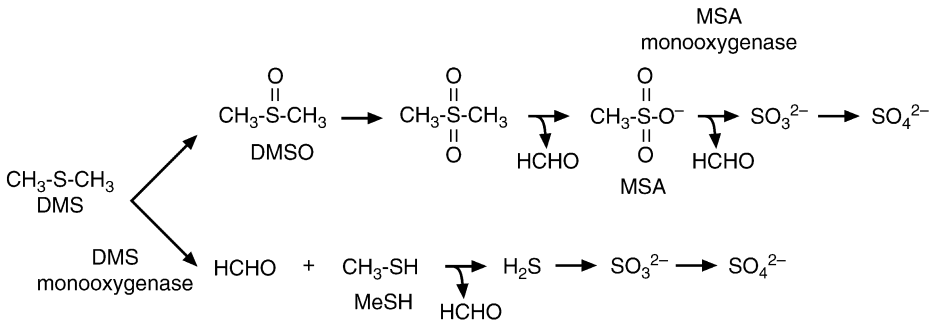

Figure 3

Known routes for the aerobic transformation of DMS for which key genes have been identified.

systems mostly ends up as DMSO and sulfate (del Valle et al., 2007; Kiene et al., 1999; Vila-Costa et al., 2006). DMS turnover rate is also lower when compared to that of DMSP (Kiene et al., 1999).

The numbers of bacterial isolates that can utilize DMS as a source of carbon, sulfur or energy are not as great as those that grow on DMSP. In most cases, isolates that transform DMS have been enriched or isolated from environments, such as biofilters, with high concentrations of DMS and related compounds (Pol et al., 1994). However, bacteria that break down DMS belong to a wide range of phylogenetic groups. *Hyphomicrobium* spp. have been isolated after DMS enrichment (de Bont et al., 1981; Pol et al., 1994; Suylen and Kuenen, 1986). *Rhodovulum sulfidophilum* SH1 utilizes DMS as an electron donor during photoautotrophic growth (Hanlon et al., 1994). The Gram positive *Rhodococcus* sp. SY1 (Omori et al., 1995) and *Arthrobacter* (Borodina et al., 2000) have been demonstrated to utilize DMS. *Acinetobacter* sp. 20B (Horinouchi et al., 1997) grows on DMS as the sole source of sulfur, whilst *Marinobacterium* sp. DMS-S1 does it only in the presence of light (Fuse et al., 2000). Methanogens (Kiene et al., 1986) and sulfate-reducing bacteria (Tanimoto and Bak, 1994) also grow on DMS as sole carbon and energy sources. *Roseobacter* strains break down DMS into MeSH (González et al., 1999), although in only one case has it been demonstrated that DMS sustains growth (Schaefer et al., 2002).

Some of these bacterial isolates are obligate methylotrophs and others can use compounds other than C_1; in other cases, they are both methylotrophs and inorganic sulfur oxidizers. Nevertheless, the role that the transformation of DMS by bacterioplankton plays in the ocean is not known. Enrichment with DMS selectively stimulated the growth of *Methylophaga* (Schäfer, 2007; Vila-Costa et al., 2006). Vila-Costa et al. (2006) enriched for *Methylophaga* in sea water samples to which a small amount of DMS had been added and followed its degradation pathway in the presence and absence of additional carbon sources. Even though the communities did not change significantly between the different treatments, the transformation followed a different pathway when an additional readily utilizable carbon source was present in the medium. S-DMS was completely mineralized to sulfate in DMS enrichments, whilst it was oxidized to DMSO and was not further degraded when glucose was present in the medium. *Methylophaga* is known to be an obligate methylotroph, such is the case of *Methylophaga sulfidovorans*, which grows on DMS (deZwart et al., 1996). Although to a lesser extent *Thiomicrospira*, a sulfur oxidizer, also dominated the communities in these enrichments. Neither *Methylophaga* nor *Thiomicrospora* are known to dominate the bacterial communities

of the ocean and only five *Thiomicrospira* 16S rRNA sequences were found in the GOS metagenome (Rusch et al., 2007), whereas *Methylophaga*-related sequences were not detected. Therefore, it is likely that additional, currently unrecognized, groups of bacteria are involved in the degradation of DMS in the natural environment. The role of facultative autotrophic sulfur oxidizers in the degradation of DMS remains also unknown.

6 Genes for the Transformation of DMS

Hyphomicrobium and *Thiobacillus* both possess an NADH dependent DMS monooxygenase, whose products are MeSH and formaldehyde respectively (de Bont et al., 1981; Kanagawa and Kelly, 1986; Suylen and Kuenen, 1986). A MeSH oxidase participates in the breakdown of MeSH into formaldehyde, sulfide and H_2O_2 as first reported in *Hyphomicrobium* (Suylen et al., 1987). No gene that encodes these enzymes has been fully characterized. However, the large subunit of a methanol monooxygenase was induced during growth on DMS by a *Methylophaga* strain that can grow on DMS as sole carbon source, suggesting that it has DMS monooxygenase activity (Schäfer, 2007). Homologs of the gene for this enzyme are found in seven *Roseobacter* genomes, including that of *Sagittula stellata*, which is known to metabolize DMS (González et al., 1999), as well as in several strains of *Rhodobacter sphaeroides*. None of the available SAR11 genomes contain homologs of this putative DMS monooxygenase gene.

An alternative to the degradation of DMS exists in which MeSH is not a degradation product (◉ *Fig. 3*). DMS is instead oxidized first to DMSO and then further to $DMSO_2$. $DMSO_2$ is broken down into formaldehyde and MSA in *Acinetobacter* sp. 20B (Horinouchi et al., 1997) and *Pseudomonas putida* DS1 (Endoh et al., 2003). Genes involved in the oxidation of DMS to $DMSO_2$ have been identified in *Acinetobacter* sp. 20B. The gene cluster had homology with multicomponent phenol and methane monooxygenases (Horinouchi et al., 1997). A gene cluster for the oxidation of MSA has been described in the soil bacterium *Methylosulfonomonas methylovora* (de Marco et al., 1999) and the *Roseobacter* strain *Marinosulfonomonas methylotropha* (Baxter et al., 2002). The cluster *msmABCD* codifies an NADH-dependent MSA monooxygenase in these two organisms as well as other MSA utilizers.

7 Bacteria Make the Most of DMS(P): Oxidation of Inorganic Sulfur

The reduction state of the atom of sulfur in DMSP or DMS should allow for potentially higher growth yields if an organism is also able to oxidize it. This is supported by the fact that bacteria that both degrade DMS and oxidize inorganic sulfur have been isolated with relative ease (deZwart et al., 1996; Schäfer, 2007; Suylen et al., 1986).

The genetics of inorganic sulfur oxidation to sulfate has been studied most extensively in lithoautotrophic bacteria (Friedrich et al., 2001), although little is known about the mechanism of oxidation from sulfur to sulfite. Both lithoautotrophs and phototrophs, as well as heterotrophic sulfur oxidizers, share components. Autotrophic sulfur oxidizers of the genus *Thiomicrospira* were also enriched in DMS-treated mesocosms (Schäfer, 2007; Vila-Costa et al., 2006). These organisms could gain additional energy from the inorganic sulfur moiety of DMS during growth on DMS. Reductants and ATP from the oxidation of inorganic sulfur

can be used to fix formaldehyde released from the degradation of this type of methylated sulfur compounds. Although sulfur oxidizer-related 16S rRNA genes, such as from *Thiomicrospira*, are not typically found in environmental sequences from the oceanic environment (except for symbiotic communities), the *soxB* gene, one of the components of the sulfur oxidation system, was found in proportions that reached as high as 25% of the bacterioplankton from the Sargasso Sea (Moran et al., 2004). DMS(P) transformations might account for the widespread occurrence of sulfur oxidation genes in marine bacteria.

Inorganic sulfur oxidation has not been as deeply studied in heterotrophic bacteria. *sox* gene systems appear widespread in members of the marine *Roseobacter* group (Moran et al., 2007). Analysis of twenty *Roseobacter* genome sequences reveals 13 that contain the *sox* operon for sulfur oxidation. Interestingly, isolates of this clade were the first marine strains found to simultaneously possess two key pathways for the degradation of DMSP (González et al., 1999), suggesting this group of marine bacteria are adept at a variety of sulfur transformations.

8 Research Needs

The biogeochemical significance of DMS(P) transformations has been recognized since the 1970s. However, our understanding of the function and importance of DMSP and related compounds in marine food webs has improved significantly in just the last few years. What seems clear is that DMSP and DMS are remarkably versatile substrates when it comes to biological transformations in seawater. Descriptions of key genes and the enzymology of proteins involved in the assimilation and degradation of DMSP have only just begun; however, the little genetics that is known and the distribution of the few genes that have been found in metagenomic libraries are changing our perspective of the roles of DMS(P) in the ocean. Continued study of DMSP and DMS transformations will undoubtedly reveal some of the strategies employed by marine bacteria to adapt to their natural environment and how these adaptations affect cycling of Earth's major elements.

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