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Phylogenetic diversity of dimethylsulfoniopropionate-dependent demethylase gene *dmdA* in distantly related bacteria isolated from Arctic and Antarctic marine environments

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Abstract

Dimethylsulfoniopropionate (DMSP) is mainly produced by marine phytoplankton as an osmolyte, antioxidant, predator deterrent, or cryoprotectant. DMSP is also an important carbon and sulfur source for marine bacteria. Bacteria may metabolize DMSP via the demethylation pathway involving the DMSP demethylase gene (*dmdA*) or the cleavage pathway involving several different DMSP lyase genes. Most DMSP released into seawater is degraded by bacteria via demethylation. To test a hypothesis that the high gene frequency of *dmdA* among major marine taxa results in part from horizontal gene transfer (HGT) events, a total of thirty-one bacterial strains were isolated from Arctic Kongsfjorden seawater in this study. Analysis of 16S rRNA gene sequences showed that, except for strains BSw22118, BSw22131 and BSw22132 belonging to the genera *Colwellia*, *Pseudomonas* and *Glaciecola*, respectively, all bacteria fell into the genus *Pseudoalteromonas*. *DmdA* genes were detected in five distantly related bacterial strains, including four Arctic strains (*Pseudoalteromonas* sp. BSw22112, *Colwellia* sp. BSw22118, *Pseudomonas* sp. BSw22131 and *Glaciecola* sp. BSw22132) and one Antarctic strain (*Roseicitreum antarcticum* ZS2–28). Their *dmdA* genes showed significant similarities (97.7%–98.3%) to that of *Ruegeria pomeroyi* DSS–3, which was originally isolated from temperate coastal seawater. In addition, the sequence of the gene transfer agent (GTA) capsid protein gene (*g5*) detected in Antarctic strain ZS2–28 exhibited a genetically closely related to that of *Ruegeria pomeroyi* DSS–3. Among the five tested strains, only *Pseudomonas* sp. BSw22131 could grow using DMSP as the sole carbon source. The results of this study support the hypothesis of HGT for *dmdA* among taxonomically heterogeneous bacterioplankton, and suggest a wide distribution of functional gene (i.e., *dmdA*) in global marine environments.

Key words: dimethylsulfoniopropionate-dependent demethylase gene (*dmdA*), horizontal gene transfer, marine bacteria, Arctic, Antarctic

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1 Introduction

Dimethylsulfoniopropionate (DMSP) is an organic sulfur compound produced in massive amounts worldwide (~10^9 t per annum; Johnston et al., 2008), mainly by marine phytoplankton (Keller, 1989; Bürgermeister et al., 1990; Turner et al., 1995). DMSP may function as an osmolyte, antioxidant, predator deterrent, and cryoprotectant (Kirst et al., 1990; Karsten et al., 1996; Wolfe et al., 1997; Sunda et al., 2002). DMSP is perhaps best known as the major precursor of gaseous dimethyl sulfide (DMS), which is the major sulfur compound emitted into the atmosphere from the ocean (Andreae, 1990). Dimethyl sulfide emissions have the potential to influence the Earth's climatic system through formation of aerosols that scatter solar radiation and affect cloud radiative properties (Shaw, 1983; Charlson et al., 1987; Schwartz and Andreae, 1996).

DMSP in marine algae can be released into seawater due to algal senescence, viral lysis and zooplankton grazing, and forms a dissolved pool (DMSPd) for marine bacteria (Kiene, 1990; Visscher et al., 1992). DMSP can be utilized by marine bacteria via the cleavage or the demethylation pathway (Kiene et al., 2000). The cleavage pathway is mediated by various DMSP lyases and results in the formation of DMS. To date, seven DMSP lyase genes (*dddD*, *dddK*, *dddL*, *dddP*, *dddQ*, *dddY* and *dddW*) have been identified from bacterial isolates (Curson et al., 2011; Sun et al., 2016). *DmdA*, the only gene found to encode the first step in the DMSP demethylation pathway (Johnston et al., 2016), is the most widely distributed DMSP degradation genes in the oceans. Approximately 60% of marine bacteria in the open ocean and coastal waters contain the *dmdA* gene (Howard et al., 2008; Cui et al., 2015). Compared with that only a minor proportion (2%–21%) of DMSPd in the marine water column is cleaved into DMS (Kiene et al., 2000; Kiene and Linn, 2000), the demethylation pathway converts a large fraction (50%–90%) of DMSPd to 3-methylmercaptopropionate (MMPA), which can serve as a re-

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duced carbon and sulfur source for microbial cells (Kiene et al., 1999; Howard et al., 2008; Reisch et al., 2011; Sun et al., 2016).

DmdA genes have been detected in members of the *Alphaproteobacteria*, including SAR11 (e.g., *Pelagibacter ubique*), SAR116 (e.g., Candidatus *Puniceispirillum marium*), the *Rhodospirillales* and *Roseobacter* clade, and *Gammaproteobacteria* (e.g., the OM60 clade; Curson et al., 2011; Howard et al., 2011; Johnston et al., 2016), with most being found in the *Roseobacter* and SAR11 clades (Howard et al., 2006, 2008). These genes are also detected in members of *Actinobacteria* and *Planctomycetes* and even in the animal *Amphimedon queenslandica* (https://www.ncbi.nlm.nih.gov/nuccore). This distribution may reflect at least one horizontal gene transfer (HGT) event, contributing to the homogenization of biogeochemical roles of *dmdA* among heterotrophic marine bacterioplankton (Howard et al., 2008).

HGT through transformation, transduction, and conjugation is important in prokaryotic evolution. Recently, a novel genetic exchange process mediated by phage-like gene transfer agents (GTAs) has been reported to be active in marine environments and to have the potential to catalyze high levels of gene transfer (McDaniel et al., 2010). GTAs are found in phylogenetically diverse prokaryotes (Lang et al., 2012). A capsid protein-encoding gene (*g5*) from the GTA gene cluster has been used as a marker to characterize the *Rhodobacterales* community structure because GTA genes are well conserved in the *Rhodobacterales* (Zhao et al., 2008; Fu et al., 2010).

To test the hypothesis that the high gene frequency of *dmdA* among major marine taxa results in part from HGT events (Howard et al., 2008), marine bacteria belonging to different genera were isolated from Arctic seawater and Antarctic intertidal sediment and then analyzed for the *dmdA* gene using a PCR method. Phylogenetic analyses of the *dmdA* gene sequences and DmdA amino acid sequences were then conducted. In addition, GTA capsid protein gene (*g5*) was examined and analyzed in the investigated isolates.

2 Materials and methods

2.1 *Sample collection and bacterial isolation*

Arctic seawater samples K3, K4 and K5 were collected from Kongsfjorden, Spitsbergen, in July of 2016. Bacteria were isolated by direct plating serial dilutions of seawater onto three different agar plates. These included low-nutrient seawater medium agar plate as described by González et al. (2003), 1.5% agar plate supplemented with f/2 media (Guillard and Ryther, 1962) and 1 mmol/L DMSP, and seawater medium agar plate as described by Fuhrman et al. (1994). After 30 d of incubation in the dark at 8°C, colonies were selected for further testing after purification. Strain *Roseicitreum antarcticum* ZS2-28 was isolated from intertidal sediment on the coast of the Larsemann Hills of Princess Elizabeth Land, East Antarctica (Yu et al., 2011). The reference strain *Ruegeria pomeroyi* DSS-3 was obtained from the German Collection of Microorganisms and Cell Cultures (DSMZ).

2.2 *DNA extraction and PCR amplification of 16S rRNA, dmdA and g5 genes*

Bacterial DNA preparation and PCR amplification and sequencing of 16S rRNA gene were performed as described by Zeng et al. (2007). One of bacterial strains within the same genus was randomly selected as a representative of distantly related bacteria for further analysis. Using primer pair dmdA282F (5′-TGCTSTSAACGAYCCSGT-3′) and dmdA591R (5′-ACRTAGAYYTCRAAVCCBCCYT-3′), bacterial *dmdA* genes were cloned and sequenced as described earlier (Zeng et al., 2016). PCR amplification and sequencing of gene transfer agent *g5* gene were performed as described by Zhao et al. (2008). The PCR reaction mixture for the *g5* gene consisted of 1 μL of template DNA, 12.5 μL of DreamTaq Green PCR Master Mix (2×; Thermo Scientific, Germany), 2 μg bovine serum albumin (BSA), and 0.4 μmol/L of each primer. Genomic DNA from one reference strain *Ruegeria pomeroyi* DSS-3, which possesses a *dmdA* gene of 1 095 bp and a *g5* gene of 1 179 bp (CP000031), was used as a template for standards. Both distilled water and genomic DNA from *Escherichia coli* DH5α were used as a template for negative controls.

2.3 *Phylogenetic analysis*

The obtained 16S rRNA gene, *dmdA* gene, and *g5* gene sequences were checked for chimeras using the Bellerophon program (Huber et al., 2004), then subjected to a BLAST sequence similarity search in GenBank (http://blast.ncbi.nlm.nih.gov/Blast.cgi). Bacterial 16S rRNA gene sequence was subsequently aligned against those of type strains within the same genus or family obtained from the GenBank database via Clustal W (Thompson et al., 1994), while the *dmdA* gene and *g5* gene sequences of the bacterial isolates were aligned against those reported for organisms belonging to different taxa in GenBank, respectively. The DNA sequences of *dmdA* gene were subsequently translated into amino acid sequences. The resulting DmdA sequences were aligned and compared with reference sequences from different taxa in the GenBank database. Maximum-likelihood phylogenetic trees were constructed using the MEGA5.1 software (Tamura et al., 2011). For DNA sequences of the 16S rRNA gene, the *dmdA* gene and the *g5* gene, the evolutionary distances were calculated under the Kimura two-parameter model. For DmdA amino-acid sequences, the evolution distances were calculated under the Jones-Taylor-Thornton model. Neighbor-joining bootstrap tests of phylogeny were performed using 1000 replicates.

2.4 *Bacterial growth*

To check the ability to use DMSP as the sole carbon source for cell growth, five selected isolates, BSw22112, BSw22118, BSw22131, BSw22132 and *Roseicitreum antarcticum* ZS2-28, were cultured in two media: basal carbon utilization medium (0.5 g $(NH_4)_2HPO_4$, 1.3 g KH_2PO_4, 3.2 g Na_2HPO_4, 0.8 g Na_2SO_4, 1.0 g $NaNO_3$, 2.0 g DMSP, 30.0 g Sigma sea salts per liter distilled water) and modified M9 medium (3.0 g KH_2PO_4, 12.8 g Na_2HPO_4, 0.5 g NaCl, 1.0 g NH_4Cl, 240 mg $MgSO_4$, 111 mg $CaCl_2$, 1.7 g DMSP, 24.0 g Sigma sea salts per liter distilled water; Sambrook and Russell, 2001). Bacterial growth was observed after incubation at 15°C in dark for 8 d.

2.5 *Nucleotide sequence accession numbers*

Sequences have been deposited in the GenBank database under accession numbers MF630588–630618 (16S rRNA genes), MF621769–621772 (*dmdA* genes), MG569947 (*dmdA* gene), and MG569950 (*g5* gene).

3 Results

3.1 *Diversity of bacterial isolates from Arctic Kongsfjorden*

A total of thirty-one bacterial strains were isolated from seawaters in Kongsfjorden. Among them, thirteen strains were isolated from low-nutrient seawater medium plates containing DMSP. Moreover, these all fell into the genus *Pseudoalteromonas* except for strains BSw22131 and BSw22132, which belonged to the

Pseudomonas and *Glaciecola*, respectively. Eight strains isolated on seawater medium plate were members of the genus *Pseudoalteromonas*. The rest of the bacterial strains were isolated on 1.5% agar plate supplemented with f/2 media and DMSP. All of these were also in the genus *Pseudoalteromonas*, except for strain BSw22118 which belonged to the genus *Colwellia*. Among the twenty-eight *Pseudoalteromonas* isolates, strain BSw22112 was randomly selected as a representative of the genus *Pseudoalteromonas* for further analysis.

The 16S rRNA gene phylogenetic tree (**Fig. 1**) revealed that strains BSw22112, 22118, 22131 and 22132 fell into the cluster composed of *Pseudoalteromonas* species, *Colwellia* species, *Pseudomonas* species and *Glaciecola* species, respectively. In addition, the four gammaproteobacterial strains formed a large cluster separate from the cluster consisting of the *Alphaproteobacteria* (e.g., *Roseicitreum* and *Ruegeria*).

Four Arctic isolates, *Pseudoalteromonas* sp. BSw22112, *Colwellia* sp. BSw22118, *Pseudomonas* sp. BSw22131 and *Glaciecola* sp. BSw22132 belonging to different genera within the *Gammaproteobacteria*, were selected for further study. In addition, since *dmdA* genes appeared to be most prevalent among members of the *Alphaproteobacteria* (Moran et al., 2012; Reisch et al., 2008), one Antarctic marine bacterium *Roseicitreum antarcticum* ZS2-28 isolated from sediment was also used for further study.

3.2 *Phylogenetic relationships of dmdA genes between bacterial isolates and reported organisms*

Using primer pair dmdA282F and dmdA591R, a major PCR product band of approximately 308 bp was obtained from each of the investigated isolates (BSw22112, BSw22118, BSw22131, BSw22132 and ZS2-28), showing significant similarity (97.7%–98.3%) to the *dmdA* gene of *Ruegeria pomeroyi* DSS-3. A maximum-likelihood tree (**Fig. 2**) revealed that the *dmdA* genes of the five isolates formed a coherent cluster with each other as well as *Ruegeria pomeroyi* DSS-3 and *Leisingera methylohalidivorans* DSM 14336, but distinctly separate from those of other organisms. Both *Ruegeria pomeroyi* DSS-3 and *Leisingera methylohalidivorans* DSM 14336 are within the family *Rhodobacteraceae*, and were isolated from seawater in the United States (data from GenBank).

The *dmdA* gene sequences of the five isolates were subsequently translated into amino acid sequences. Phylogenetic analysis of *dmdA* amino-acid sequences placed the five isolates in a cluster consisting of *Ruegeria pomeroyi* DSS-3 and *Leisingera methylohalidivorans* DSM 14336 (**Fig. 3**), showing an essentially

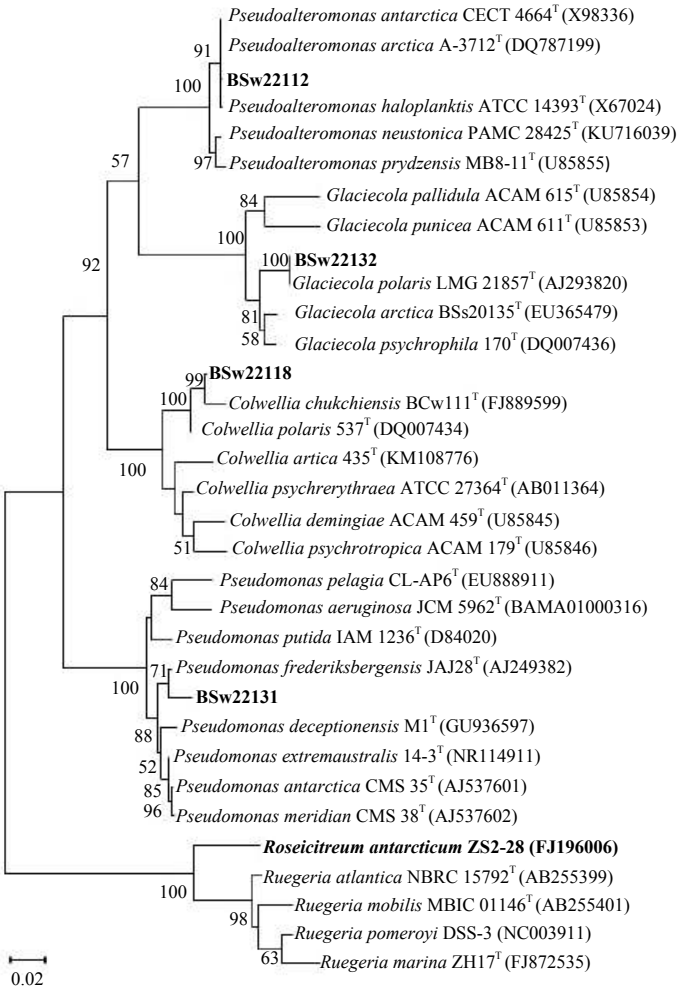

Fig. 1. Maximum-likelihood tree based on 16S rRNA gene sequences showing the phylogenetic position of five bacterial isolates from Arctic and Antarctic marine environments. Bootstrap numbers are shown as percentages based on 1 000 replicates, and values less than 50% are omitted. The scale bar indicates evolutionary distance.

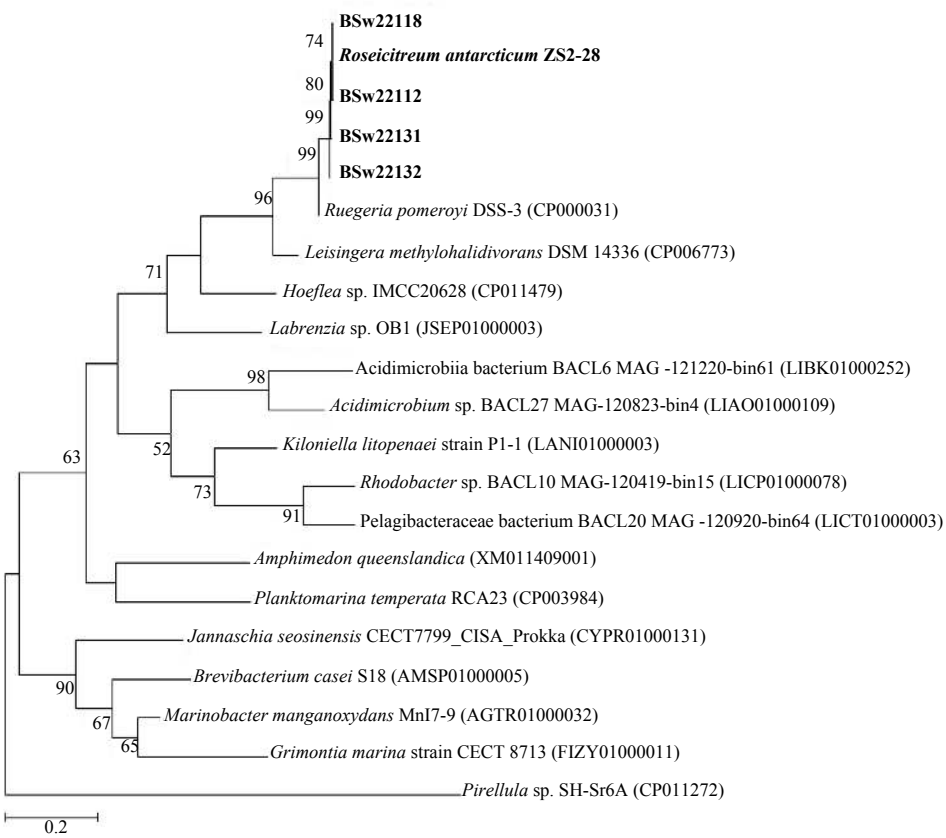

Fig. 2. Maximum-likelihood tree based on *dmdA* gene sequences showing the phylogenetic relationships of five bacterial isolates from Arctic and Antarctic marine environments with known organisms available in the NCBI database. Bootstrap numbers are shown as percentages based on 1 000 replicates, and values less than 50% are omitted. The scale bar indicates evolutionary distance.

similar topology with that of the maximum-likelihood *dmdA* gene tree. The results revealed close phylogenetic relationships of *dmdA* genes among the five bacteria isolated from polar regions and *Ruegeria pomeroyi* DSS-3, which is a well-known roseobacterium possessing both pathways for metabolism of DMSP (González et al., 1999).

3.3 *Phylogenetic relationships of g5 genes between bacterial isolates and reported organisms*

Using primer pair MCP-109F and MCP-368R, no PCR product band was obtained from bacterial isolates BSw22112, BSw22118, or BSw22132 within the *Gammaproteobacteria*. Although three PCR product bands were detected in strain *Pseudomonas* sp. BSw22131, sequence analysis based on BLASTX revealed that none of these PCR bands were related to the gene transfer agent. A single PCR product band of 782 bp was obtained from strain ZS2-28 within the *Rhodobacterales*, showing significant similarity (99.6%) to the gene transfer agent major capsid protein gene (*g5*) of *Ruegeria pomeroyi* DSS-3. A maximum-likelihood tree (**Fig. 4**) showed that the *g5* gene of strain ZS2-28 formed a coherent cluster with *Ruegeria pomeroyi* DSS-3 that was distinctly separate from those of other organisms.

3.4 *Bacterial growth with DMSP as the sole carbon source*

No cell growth was observed for strains BSw22112, BSw22118, BSw22132 or ZS2-28 in either basal carbon utilization medium or M9 medium when DMSP was used as the sole carbon source. However, strain *Pseudomonas* sp. BSw22131 was found to be able to grow in M9 medium supplemented with DMSP, but unable to grow in basal carbon utilization medium supplemented with DMSP.

4 Discussion

The DMSP demethylase, DmdA, is primarily found in the *Roseobacter* and SAR11 clades of marine *Alphaproteobacteria* (Howard et al., 2006, 2008), both of which are very populous in oceans. However, besides Antarctic *Roseicitreum antarcticum* ZS2-28 within the *Roseobacter*, Arctic strains *Pseudoalteromonas* sp. BSw22112, *Colwellia* sp. BSw22118, *Pseudomonas* sp. BSw22131 and *Glaciecola* sp. BSw22132 belonging to the *Gammaproteobacteria* were all found to harbor *dmdA* genes in the present study. In addition, significant relationships were observed between the *dmdA* genes from the five bacterial isolates and *Ruegeria pomeroyi* DSS-3, a model microorganism for DMSP degradation studies (Salgado et al., 2014), suggesting that horizontal gene transfer (HGT) is likely responsible for the wide distribution of *dmdA* among diverse bacterial taxa (Howard et al., 2008). HGT activity in the ocean is thought to contribute to the homogenization of biogeochemical roles among planktonic heterotrophic bacteria (Howard et al., 2008).

It has been suggested that high gene frequency results in part from horizontal transfer events of the *dmdA* gene among major marine taxa (Howard et al., 2008). One genetic exchange process of HGT is mediated by phage-like gene transfer agents (GTAs; Zhao et al., 2008) that contain a random piece of the genome of the producing cell (Solioz and Marrs, 1977). GTA activity may fa-

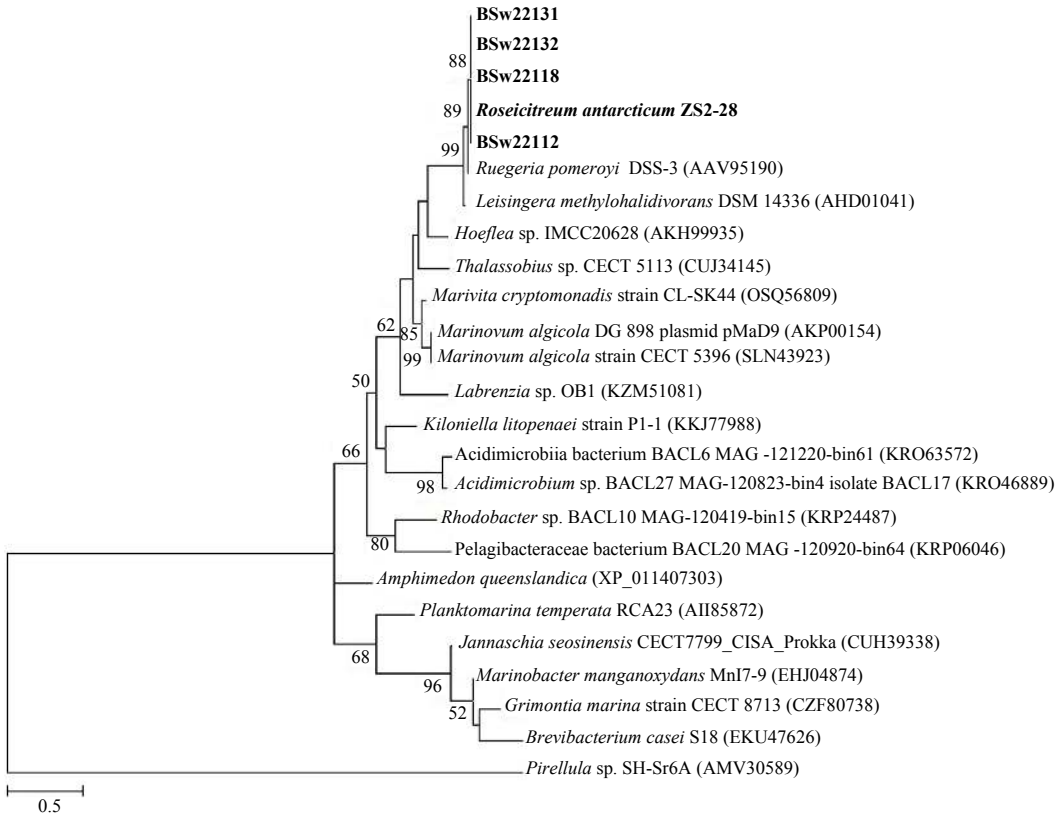

Fig. 3. Maximum-likelihood based on partial *dmdA* amino-acid sequences showing the phylogenetic relationships of five bacterial isolates from Arctic and Antarctic marine environments to known organisms available in the NCBI database. Bootstrap numbers are shown as percentages based on 1 000 replicates, and values less than 50% were omitted. The scale bar indicates evolutionary distance.

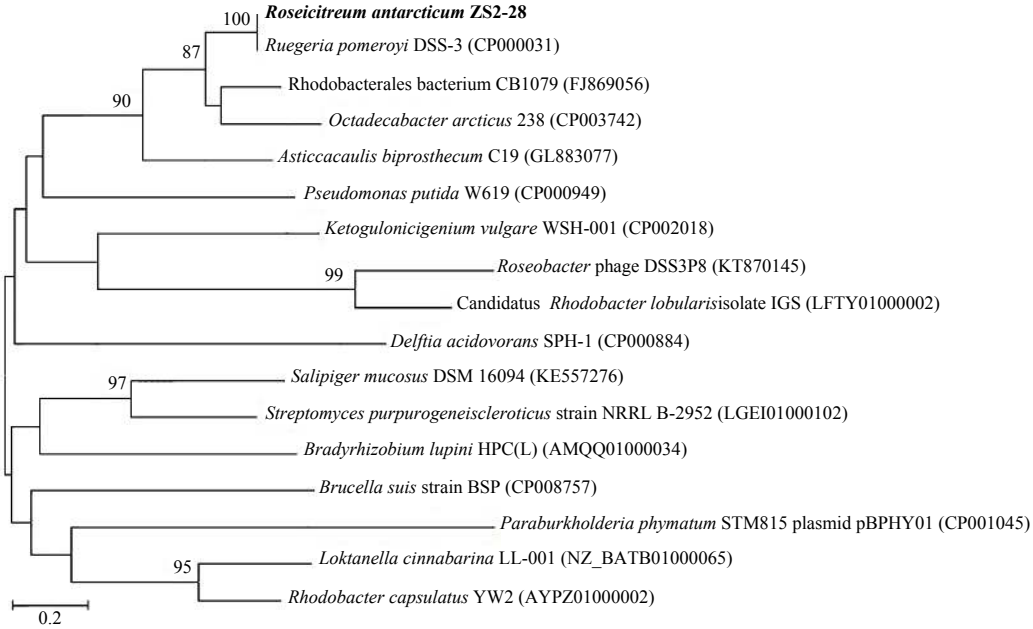

Fig. 4. Maximum-likelihood tree based on *g5* gene sequences showing the phylogenetic relationship of bacterial isolate ZS2-28 from the Antarctic marine environment to that of known organisms available in the NCBI database. Bootstrap numbers are shown as percentages based on 1 000 replicates, and values less than 50% are omitted. The scale bar indicates evolutionary distance.

cilitate gene homogenization among diverse bacteria (Biers et al., 2008), since GTA particles contain only host genomes (Marrs, 1974; Yen et al., 1979). To date, four genetically unrelated GTAs have been identified in proteobacteria, archaea and virus (Lang et al., 2012). Among them, RcGTA (*Rhodobacter capsulatus* GTA) are usually observed in the *Rhodobacterales* and some other *Al-*

phaproteobacteria (e.g., marine *Parvularculales*, *Rhizobiales* and *Sphingomonadales*; Lang and Beatty, 2007; Biers et al., 2008). In the present study, the five bacterial isolates were in the *Proteobacteria* and harbored *dmdA* genes showing close relationships with *Ruegeria pomeroyi* DSS-3. Therefore, a highly conserved RcGTA major capsid protein gene (*g5*; Lang and Beatty, 2007) was examined in those isolates. The results revealed the existence of the *g5* gene in strain *Roseicitreum antarcticum* ZS2-28, which agrees with the ubiquitous presence of RcGTA genes in members of the *Rhodobacterales* (Lang et al., 2012). However, GTA-like genes are not harbored by the *Pelagibacterales* (Biers et al., 2008), which is known as the ecologically dominant marine alphaproteobacterial SAR11 clade (Herlemann et al., 2014). GTA transduction is likely to be most efficient for marine roseobacters associated with particle surfaces, biofilms, and other high-cell-density habitats (Ripp and Miller, 1995; Vettori et al., 1999; Weinbauer, 2004; Biers et al., 2008). Expression of GTA genes and extracellular release of GTA particles has been reported for *Ruegeria pomeroyi* DSS-3, and intraspecific gene transfer has been documented (Biers et al., 2008). It has also been suggested that the gene transfer agent (GTA) evolved from a prophage that was present before the divergence of *Proteobacteria* (Lang and Beatty, 2007); however, the *g5* gene was not found in four gammaproteobacterial strains in this study. Therefore, considering that both *dmdA* and *g5* gene sequences of Antarctic *Roseicitreum antarcticum* ZS2-28 exhibited a closely related genetically to those of *Ruegeria pomeroyi* DSS-3 from coastal Georgia seawater, the results of this study indicate in part that GTA can serve as one of the HGT mechanisms leading to the *dmdA* gene distribution among the *Rhodobacterales* bacteria. For the gammaproteobacterial strains, the genetic exchange process of HGT of *dmdA* genes remains unclear, and further study is required to clarify the mechanism of HGT between marine *Alpha-* and *Gammaproteobacteria*.

The close phylogenetic relationships of *dmdA* genes among the bacteria BSw22112, BSw22118, BSw22131, BSw22132 and ZS2-28 isolated from cold marine environments in the Antarctic or Arctic, and strain *Ruegeria pomeroyi* DSS-3 from temperate coastal Georgia (USA) seawater (González et al., 1999), indicate the adaptability of DmdA and its wide distribution in global marine environments. In addition, a significant relationship between *g5* genes from the Antarctic bacterium *Roseicitreum antarcticum* ZS2-28 and bacterium *Ruegeria pomeroyi* DSS-3 from the Northern hemisphere was observed. The results of the present study indicate a cosmopolitan distribution of some functional genes (e.g., *dmdA* genes and GTA major capsid protein *g5* genes) in marine environments, which is in agreement with previous findings pertaining to bipolar gene flow in deep-sea benthic foraminifera (Pawlowski et al., 2007) and marine bacterioplankton (Hollibaugh et al., 2002; Pommier et al., 2005).

Except for strain *Pseudomonas* sp. BSw22131, four bacterial strains harboring *dmdA* genes in this study could not grow when DMSP was used as the sole carbon source. These suggest that marine bacteria containing only *dmdA* gene cannot utilize DMSP as the sole carbon source for cell growth. In addition, no *dddP* gene (the most widely distributed DMSP lyase gene in marine environments; Bullock et al., 2017) was detected in the five investigated strains using a PCR method (data not shown). Therefore, strain *Pseudomonas* sp. BSw22131 may have other DMSP lyase(s) so that it can utilize DMSP as a carbon source for cell growth.

In conclusion, the results of the present study revealed the existence of *dmdA* genes showing significant relationships with each other in various bacteria isolated from bipolar and temperate marine environments, supporting the hypothesis that the same DmdA proteins may be harbored by taxonomically heterogeneous marine bacteria due to HGT of *dmdA* (Howard et al., 2008). Moreover, bipolar, or even global, distribution of functional gene (i.e., *dmdA*) was observed in this study. However, partial *dmdA* gene sequences with only approximately 308 bp were investigated in this study; therefore, complete *dmdA* gene sequences of the five bacterial isolates are required for further analysis to ensure their phylogenetic relationship to the model organism *Ruegeria pomeroyi* DSS-3.

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