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# Abundance and Diversity of Dimethylsulfoniopropionate Degradation Genes of *Roseobacter* Group in the Northern South China Sea

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Bacterial degradation of dimethylsulfoniopropionate (DMSP) plays a significant role in ecosystem productivity and global climate. In this study, the abundance and diversity of *Roseobacter* group DMSP degradation genes were explored in spatial scale of the South China Sea (SCS). Quantitative PCR showed that a higher abundance of *dmdA* (DMSP demethylase) and *dddP* (DMSP lyase) genes was detected above 75 m than deep water, especially in surface water. A high ratio of *dmdA*/*dddP* existed in all sites and increased with water depth, indicating that demethylation was the main degradation pathway in the *Roseobacter* group. High-throughput sequencing analysis showed that distribution of *dmdA* gene had a significant layering structure in the northern SCS, and high taxonomic diversity of *dmdA* gene was observed in near-surface waters (25 and 50 m). *DmdA* gene in the *Roseobacter* group, such as *Leisingera*, *Nioella*, *Roseobacter*, *Roseovarius*, *Donghicola*, *Phaeobacter*, and *Tateyamaria*, had remarkable specificity due to the effect of different sites and water depths. Different ecological strategies of DMSP degradation may be used by members of the bacterial community harboring demethylation genes. In addition, many *dmdA* sequences were affiliated with unidentified bacteria, indicating that the SCS reserved high diversity of DMSP-degrading bacteria. Canonical correspondence analysis (CCA) suggested that temperature and depth were the most important factors to determine the taxonomic distribution of DMSP degradation genes in the *Roseobacter* group, as well as their abundance. This study highlighted the understanding of the role of *Roseobacter* group in DMSP degradation in the tropical ocean.

**Keywords: *Roseobacter* group, dimethylsulfoniopropionate degradation genes, diversity, abundance, South China Sea**

## INTRODUCTION

Dimethylsulfoniopropionate (DMSP), an important sulfur compound, is mainly produced by marine phytoplankton in marine water (Howard et al., 2006; Michaud et al., 2007; Levine et al., 2012; Moran and Durham, 2019). Association with phytoplankton aggregates may provide many ecophysiological advantages to the marine *Roseobacter* group, including easy access to DMSP and other algal products (González et al., 1999; Amin et al., 2015). When released from phytoplankton, DMSP is mainly assimilated and degraded by members of bacteria *via* a demethylation or cleavage pathway (Malmstrom et al., 2004; Curson et al., 2011; Burkhardt et al., 2017; Raina et al., 2017). The demethylation pathway transforms the majority of DMSP to 3-methiolpropionate, which is then incorporated into the cell biomass (Kiene et al., 1999; Reisch C. R. et al., 2011). By contrast, the cleavage pathway converts DMSP to produce dimethylsulfide (DMS) through various DMSP lyases (Johnston et al., 2016). DMS represents the largest volatile sulfide in the ocean, and its oxidation production can form cloud nucleation and affect global climate (Andreae and Crutzen, 1997; Simó, 2001).

The *Roseobacter* group is affiliated with Alphaproteobacteria, and the majority is of marine origin, constituting a large proportion of the total bacterial community (Brinkhoff et al., 2008; Simon et al., 2017). Members of the *Roseobacter* group can establish symbiotic relationships with phytoplankton, partly through the exchange of DMSP (Liu et al., 2018; Nowinski et al., 2019; O'Brien et al., 2022). *Roseobacter* are often dominant with functional genes, which can encode the capabilities of oxidation sulfur compounds and methylated amines, and catabolism of various carbohydrates (Zhang et al., 2016). The *Roseobacter* group is considered to be a key participant in DMSP metabolism, and nearly 1/3 of DMSP assimilation process is performed through the *Roseobacter* group in the coastal area (Malmstrom et al., 2004). At least 80% of *Roseobacter* group cells contain *dmdA* in the Sargasso Sea (Howard et al., 2006; Howard et al., 2008). Of the seven *ddd* genes identified (*dddD*, *dddK*, *dddL*, *dddP*, *dddQ*, *dddY*, and *dddW*), *dddP* and *dddQ* genes are the most frequently detected in marine bacteria and mainly found in the *Roseobacter* group (Howard et al., 2008; Todd et al., 2009; Todd et al., 2011; Sun et al., 2016). To date, more and more the whole genomes of marine *Roseobacter* strains have been sequenced (Newton et al., 2010; Luo et al., 2012; Voget et al., 2015; Billerbeck et al., 2016; Bakenhus et al., 2018). According to the above studies, *dmdA* and *dddP* genes are the most important genes for DMSP degradation in the *Roseobacter* group.

The northern South China Sea (nSCS) is a marginal sea characterized by tropical and subtropical climates and representing typical oligotrophic characteristics with significant environmental gradients. High concentrations of DMSP and DMS are detected in surface water, especially between 20 and 75 m (Yang, 2000; Yang et al., 2008). Previous studies reported that the abundance of DMSP degradation genes had spatial variability in the seawater (Howard et al., 2011; Levine et al., 2012; Varaljay et al., 2012; Choi et al., 2015; Cui et al., 2015), indicating that DMSP degradation genes are strongly impacted by primary production, UV radiation, DMSP and DMS concentrations, and *Chl a* concentration. To date, DMSP degradation genes have been little reported in the SCS, and biogeography of DMSP degradation genes in spatial-vertical distribution of marine water needs further study. In this study, *dmdA* and *dddP* genes were targeted and collected from the surface to 200 m depth during a cruise across the SCS. The aims of this study were to describe the spatial–vertical distribution and abundance of *Roseobacter*-like DMSP degradation genes, and to explore the diversity shift of DMSP degradation genes related to water environment in the SCS.

## MATERIALS AND METHODS

### Sample Collection

The cruise was carried out in the South China Sea with the *Shiyan 3* from August to September 2011 (**Figure 1**). A conductivity-temperature-depth (CTD) system (SeaBird SBE-911 Plus, US) was deployed to acquire hydrographic parameters. Seawater samples were collected at different depths (0, 25, 50, 75, 100, 150, and 200 m) with CTD 12-L Niskin bottles (General Oceanics, Inc., Miami, FL). Once collected, the samples were immediately filtered using polycarbonate membranes (EMD Millipore, US) with a pore size of 0.22 μm. The filter was immediately placed in a 1.5-ml sterile centrifuge tube and stored in liquid nitrogen for further DNA extraction. Sample DNA were extracted using the DNA Extraction Kit (OMEGA, US) according to the protocol instructions. Nitrate ($NO_3$), phosphate ($PO_4$), silicate ($SiO_3$), and chlorophyll (*Chl* a) concentrations were measured according to the protocols of "the specialties for oceanography survey" (GB17378.4-2007, China).

### Quantitative PCR of *dmdA* and *dddP* Genes Abundance in the *Roseobacter* Group

Two *dmdA* primers were used to amplify the different *Roseobacter* subclades (A/1 and A/2) (Varaljay et al., 2010) for the DMSP demethylase gene, and *dddP* primers targeting the *Roseobacter* group were used to detect the DMSP lyase genes (Levine et al., 2012). The reactions were performed in the iQ5 Real-Time PCR Detection System (Bio-Rad, US). Quantification was based on the increasing fluorescence intensity of the SYBR green dye during amplification. QPCR standards were made from PCR products amplified from environmental samples using the pMD19-T cloning kit (TaKaRa, Japan). The real-time PCR assay was performed in a 20-μL reaction volume with SYBR Premix Ex Taq II (TaKaRa, Japan). All qPCRs were run in triplicate for each sample. QPCR conditions were as follows: predenaturation at 95°C for 30 s, 35 cycles at 95°C for 5 s, and annealing at 60°C for 30 s. Tenfold serially diluted standard and no-template controls were run in triplicate for each reaction.

### Illumina MiSeq Sequencing of *dmdA* Genes in the *Roseobacter* Group

The primer pairs, dmdA282F (5′-TGCTSTSAACGAYCCSGT-3′) and dmdA591R (5′-ACRTAGAYYTCRAAVCCBCCYT-3′) (Zeng et al., 2016), were used for *Roseobacter*-like *dmdA* gene amplification. PCR conditions were as follows: 94°C for 3 min, 35 cycles at 94°C for 1 min, 54°C for 30 s, extension at 72°C for 30 s,

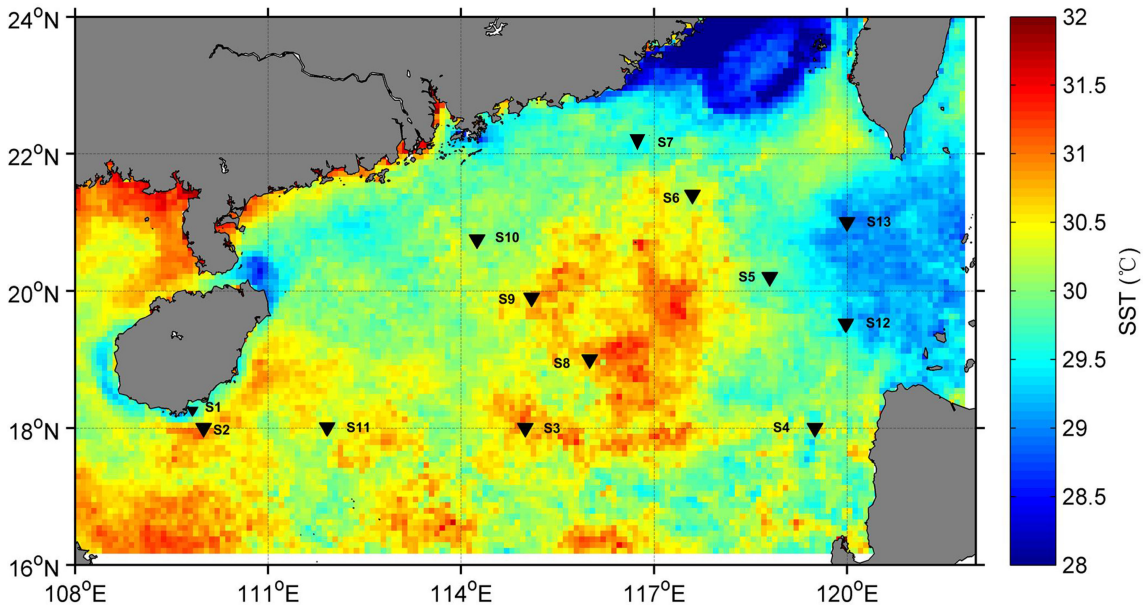


**FIGURE 1** | Map of sampling stations in the South China Sea. Sea surface temperature (SST) during investigation time was shown in the base map that was obtained from NOAA.

and a final extension at 72°C for 10 min. The PCR comprised a 20-μL reaction volume containing 4 μL of 5× FastPfu Buffer, 2 μL of 2.5 mM dNTPs, 0.5 μL of FastPfu polymerase, 1.0 μL of primers (5 μM), and 10 ng of template DNA. A positive control and non-template control samples were run to validate PCR. PCR products were purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, US), and quantified using QuantiFluor™-ST (Promega, US). An Illumina MiSeq platform (Illumina, US) was used for paired-end sequencing (2 × 300) according to the standard protocols.

For pair-ended reads obtained by Illumina sequencing, barcodes and primers were trimmed and then assembled using FLASH (V1.2.7). Reads that contained Ns were shorter than 50 bp or had primer mismatches which were also excluded. Sequences were compared with RDP reference database using VSEARCH (1.9.6) to detect chimeric sequences. Then sequences were grouped into OTUs (operational taxonomic units) using UPARSE (v7.0.1001), and pre-clustered at 97% sequence identity. The highest OTU frequencies were selected as representative OTU sequences. The taxonomy of each *dmd*A gene sequence was analyzed by RDP classifier algorithm against the NCBI non-redundant (nr) database using a confidence threshold of 70%.

## RESULTS AND DISCUSSION

### Characteristics of the Abundance of *dmdA* and *dddP* Gene in the South China Sea

Two subclades (A/1 and A/2) of *dmdA* genes and *dddP* genes were quantified using qPCR (**Figure 2**). The copy numbers of *dmdA* and *dddP* genes and their distribution in the northwestern SCS varied greatly among sampling sites and depths. This result was similar with the study in the Pacific Ocean (Cui et al., 2015), indicating that the abundance of DMSP degradation genes had great variability of abundance in the ocean. Overall, the abundance of *dmdA* and *dddP* genes located in the northwest SCS was higher than that located in the northeastern SCS. As seen from a spatial scale, sites (S1, S2, S3, S8, and S9) showed higher copy numbers of *dmdA* and *dddP* genes than other sites (S5, S6, S12, and S13). In these five stations, two sites (S1 and S2) are close to the shore, and the remaining three (S3, S8, S9) are in the middle of the survey area. Similar to previous studies in the SCS (Ling et al., 2012; Sun et al., 2015), bacterial community in the northwestern SCS had higher diversity than that in the northeastern SCS. The abundance difference is likely due to water temperature. As seen in **Figure 1**, the SST of the sites to the left of longitude 117°E is higher than that of the sites to the right. This result was similar to other reports that temperature is an important factor in determining the abundance of *dmdA* and *dddP* in surface water (Levine et al., 2012; Varaljay et al., 2012; Cui et al., 2015).

*DmdA* and *dddP* genes from the *Roseobacter* group were particularly enriched in surface waters with an order of magnitude difference in their abundance relative to deep waters (**Figure 2**), which indicated that the abundance of *dmdA* and *dddP* genes was strongly separated by water depth. Copy numbers of *dmdA* and *dddP* genes were higher above 75 m water than those below 100 m water, and the highest abundance of these genes was observed in the surface layer. Variation of gene abundance of *dmdA* and *dddP* may be closely related to the DMSP concentration in vertical depth. Previous studies reported that DMSP and DMS concentrations in SCS were markedly high

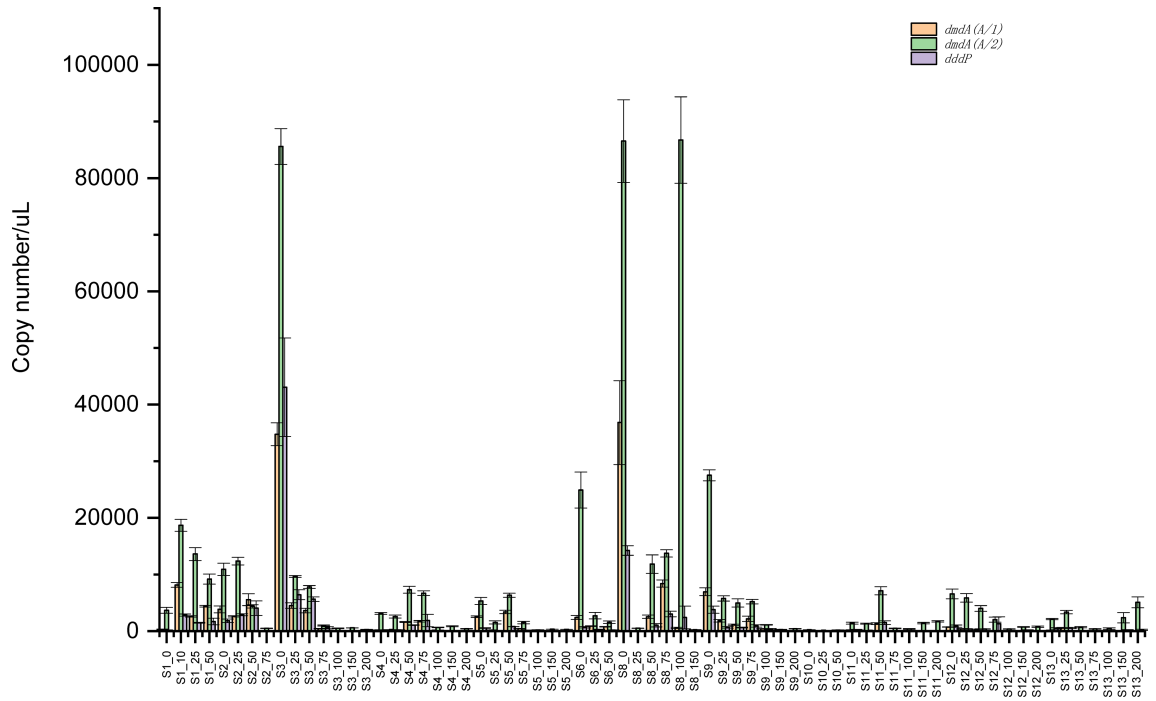


**FIGURE 2** | Abundance of dmdA and dddP in the SCS from surface water to 200 m depth based on quantitative PCR.

in the surface seawater, and decreased gradually with increasing depth (Yang, 2000; Zhai et al., 2020). Other studies also reported that distribution patterns of *dmdA* and *dddP* were roughly consistent with the distribution characteristics of DMSP concentration, and were mainly influenced by the *Chl* a concentrations, depth, salinity, and temperature (Howard et al., 2011; Varaljay et al., 2012; Cui et al., 2015).

In addition, the copy numbers of the *dddP* gene were far lower than those of the *dmdA* gene at almost all sites and depths (**Figure 2**), even if only the *dmdA* A/2 clade was considered. The copy number ratios (*dmdA*/*dddP*) of these genes ranged from 2 to 156 times. The copy numbers of the *dmdA* A/2 gene were higher than those of the *dmdA* A/1 gene at almost all sites and depths, which suggested that subclade A2 was the main group of *Roseobacter* group in the demethylation pathway. The other study reported that two *Roseobacter* group *dmdA* gene subclades (A/1 and A/2) showed opposite depth distributions in the summer (Levine et al., 2012). Interestingly, high ratios of *dmdA*/*dddP* and *dmdA2*/*dmdA1* were mainly observed in deep waters (below 75 m), even if these three genes had relatively low abundance, indicating that demethylation is the main pathway of DMSP degradation in the water. Previous studies suggested that 80% of DMSP degradation is processed through the demethylation pathway, and only 20% is cleaved to DMS (Kiene et al., 1999). Marine bacteria keep the ability of DMSP demethylation to a suitable evolutionary pressure, which can explain the consistently stable and high *dmdA* gene frequencies in the ocean (Varaljay et al., 2012). In marine waters, nutrients and organic sulfur such as DMSP are important because cells need increased sulfur demand for growth, causing more sulfur to be incorporated into cell protein (Kiene et al., 1999).

## Diversity Distribution of *dmdA* Gene in the *Roseobacter* Group

A total of 231,246 valid reads and 688 OTUs were obtained from the 19 samples through Illumina MiSeq sequencing analysis. Each of the samples contained 9155 to 17,955 reads, with OTUs ranging from 12 to 55. The coverage was more than 0.999, which suggested that sequencing data had favorable coverage for *dmdA* diversity. Diversity indices, including Shannon, Chao, Ace, and Simpson, are demonstrated in **Supplementary Table S1**. The result indicated that the *dmdA* gene had higher community diversity above 50 m than in deep waters (100 and 200 m).

The study revealed that the composition of the *dmdA* gene varied significantly among the sites and depths (ANOVA, $p < 0.01$). Overall, the *dmdA* gene was mainly affiliated with Alphaproteobacteria and Gammaproteobacteria (**Figure 3**). In most sites, the *dmdA* gene was dominated by Alphaproteobacteria, whereas a few of the samples (S2_0, S6_0, S6_50, and S9_25) were dominated by Gammaproteobacteria. In addition, low abundance of Acidithiobacillia-like *dmdA* gene was detected (1.37%). High abundance of *dmdA* (2.64%–87.95%), which had very low similarity with the amino acid identity of uncultured bacteria, was found in some samples. Moreover, 21.78% of all sequences had 73%–79% amino acid similarity with Gammaproteobacteria. This result provided further

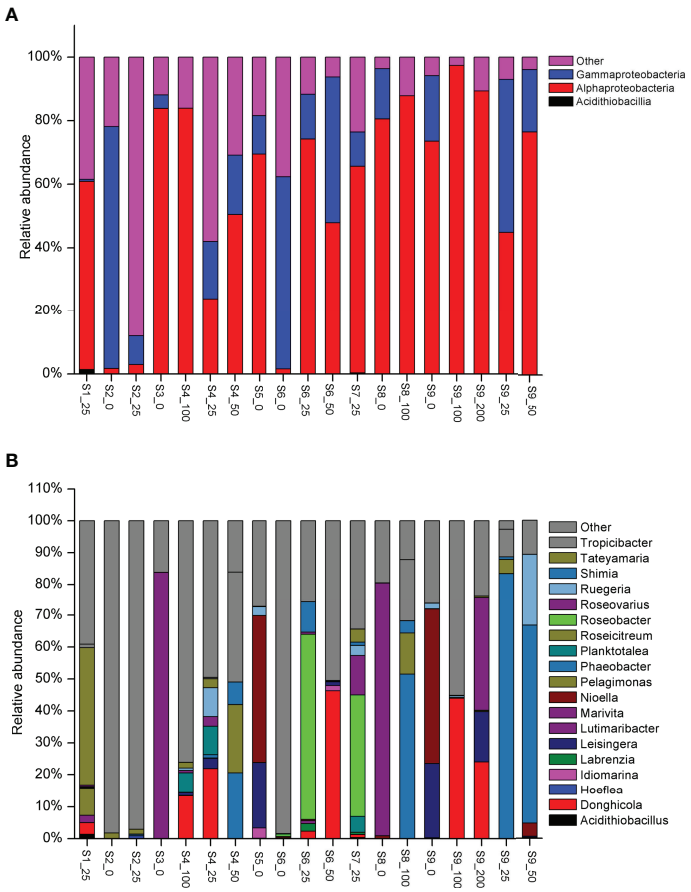


**FIGURE 3** | Taxonomic distribution of samples through High-throughput sequencing analysis in class level **(A)** and genus level **(B)**.

evidence that ocean water contains a high diversity of *dmdA* genes, which has not yet been unearthed in the tropical ocean.

Overall, *dmdA* genes in the nSCS showed greater variation near surface water than in deep waters, which is related to the vertical structure of water (**Figure 3**). At the genus level, high abundance of *dmdA* genes below 100 m belonged to *Phaeobacter*, *Roseicitreum*, *Ruegeria*, *Tropicibacter*, and *Shimia*. The upwelling site (S1-25) was characterized by *Tateyamaria* (43.11%) and *Pelagimonas* (8.40%). These findings indicated that coastal upwelling had different *dmdA* taxonomy of the *Roseobacter* group with open water. S5_0 and S9_0 sites were dominated by *Leisingera* (>20%) and *Nioella* (>46%). S3_0 and S8_0 sites were characterized by highly abundant *Roseovarius* (>80%). Site S6_25 was mainly composed of *Roseobacter* (58%) and *Shimia* (9.56%). Site S7_25 was mainly composed of *Roseobacter* (38%), *Roseovarius* (12.32%), and *Planktotalea* (4.97%). The *dmdA* gene of *Donghicola* mainly dominated in the 25- and 50-m water layer. Moreover, *dmdA* genes of *Leisingera*, *Planktotalea*, *Roseovarius*, and *Ruegeria* were dominant in the 25- or 50-m water layer.

Principal component analysis (PCA) illustrated that the *dmdA* gene of the bacterial community had distinct differences among different sites and depths (**Figure 4**). The results indicated that the *dmdA* gene of the *Roseobacter* group in shallow water (0 m, 25 m, and 50 m) and deep layer (100 and 200 m) had clustered together separately. The *dmdA* gene of the deep water was separated by a large distance from the shallow layer. Overall, the results indicated the clearly distinct structure among sampling sites and depths (ANOVA, $p < 0.01$). Veen analysis showed that *dmdA* gene diversity had 14 and 11 common OTUs between the surface water and 25-m depth of the horizontal scale. Considering the vertical depths, no common OTU was found from the surface to 200 m water depths (**Figure 5**).

## Environmental Factors Affected the Distribution of the *dmdA* Gene

The CCA analysis constructed a correlation between environmental factors and *dmdA* gene diversity (**Figure 6A**). The first ordination axis accounted for 32.1% of the cumulative percentage variance in the matrix, while the second axis accounted for 31.2%. *DmdA* gene in the upwelling (S1-25) was mainly positively related to *Chl* a and silicate concentration ($p<0.05$). *DmdA* gene below 100-m depth was negatively defined by water depth ($p<0.01$), while shallow water samples (0 m and 25 m) were strongly determined by water temperature ($p<0.01$). Other environmental factors, such as salinity, nitrate,

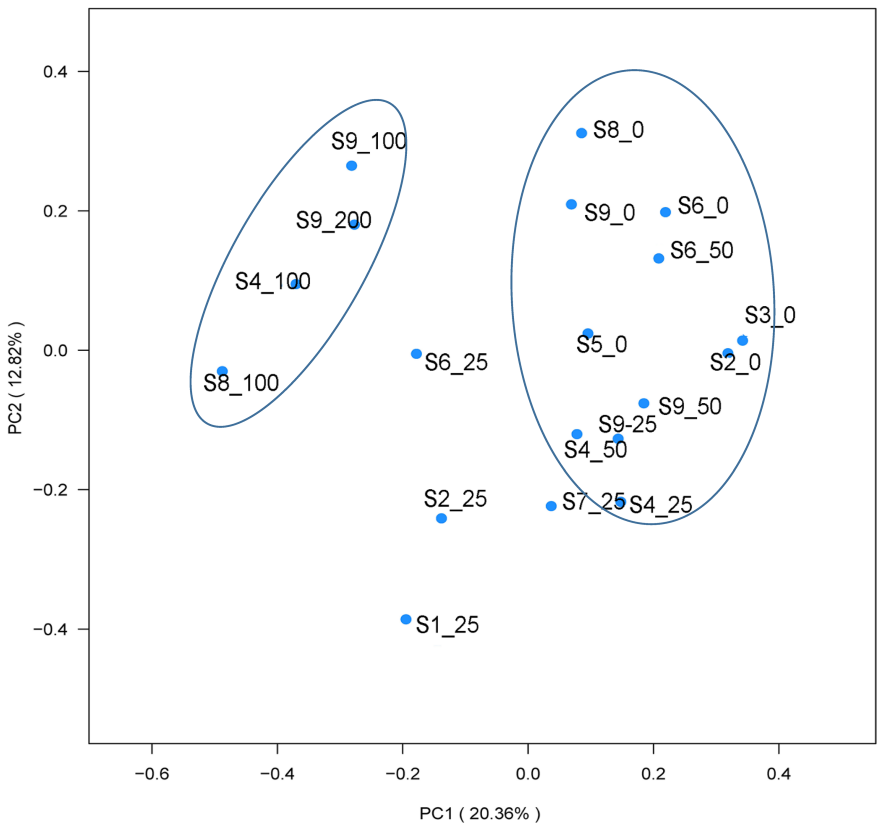


**FIGURE 4** | Principal components analysis (PCA) based on phylogenetic UniFrac distance metrics.

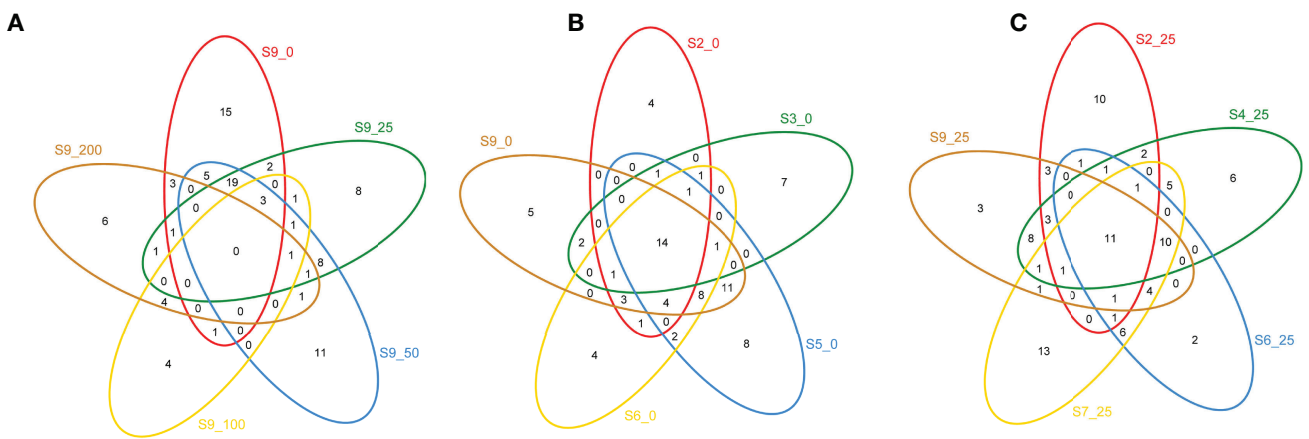


**FIGURE 5** | Veen map analysis of *dmdA* gene diversity in spatial and vertical scale. **(A)** common OTUs in the vertical layers; **(B)** common OTUs in the surface water; **(C)** common OTUs in the 25-m water layers.

and phosphate, had no obvious effects on the diversity of *dmdA* genes.

In the CCA map (**Figure 6B**), cluster A, mainly composed by *Tateyamaria*, *Pelagimonas*, and *Marivita*, had significant correlation ($p < 0.05$) with *Chl* a and silicate concentration, which was influenced by the upwelling. High abundance OTUs of cluster B, which was afflicted with *Leisingera*, *Nioella*, *Roseovarius*, and *Roseobacter*, were mainly positively related to temperature. High abundance of OTUs (cluster C), which was afflicted with *Roseobacter*, *Shimia*, *Planktotalea*, and

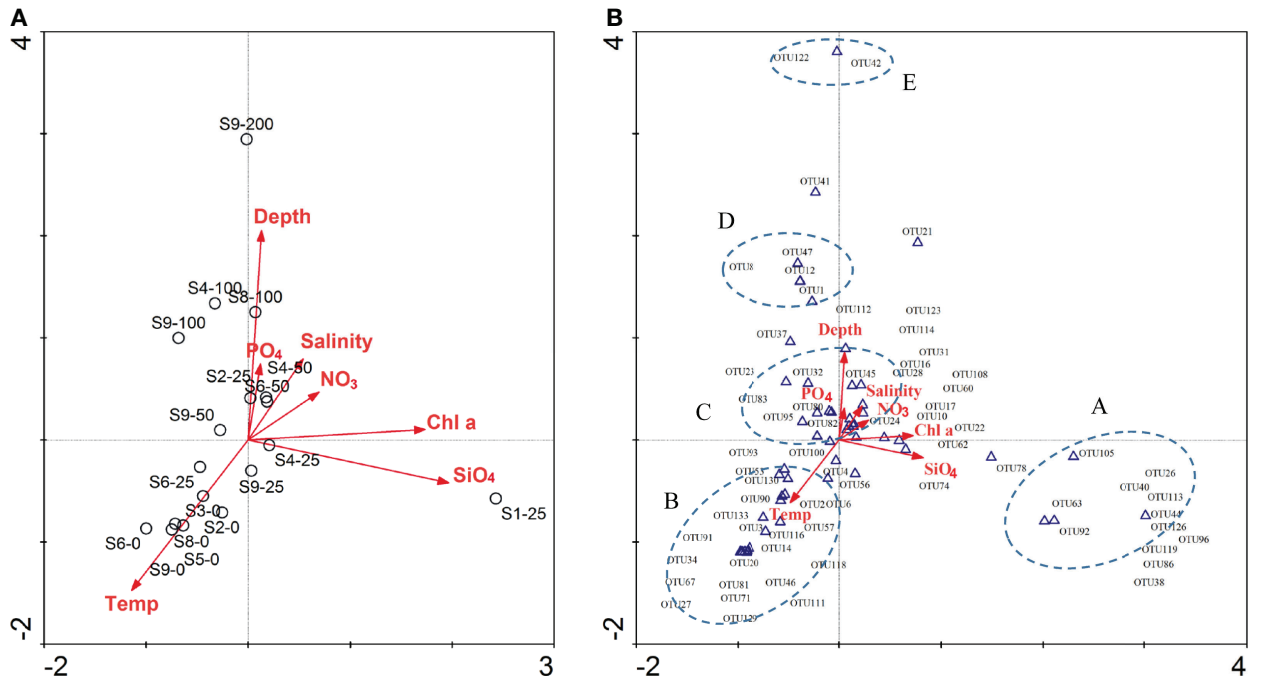


**FIGURE 6** | Canonical correspondence analysis (CCA) of the relationship of *dmdA* gene diversity **(A)** and OTU level **(B)** in the *Roseobacter* group, with environmental factors. Areas surrounded by the blue dashed lines represented the dominant OTUs of different genera.

*Donghicola*, were mainly related to depth, phosphate, and salinity. Cluster D and E, mainly composed by *Phaeobacter*, *Roseicitreum*, *Ruegeria*, and *Tropicibacter*, were mainly positively related to depth, indicating that these *Roseobacter* OTUs were suitable to environment change with deep water. As described above, a high ratio of *dmdA*/*dddP* was found in deep water, which indicated that the *Roseobacter* group had more nutrition demand and greater degree of demethylation than DMSP cleavage. Different ecological strategies of DMSP degradation may be used by members of the bacterial community harboring demethylation and/or cleavage genes (Reisch C. et al., 2011). In previous studies, the *Roseobacter* group is the dominant microbial taxa in the offshore, upwelling, and mesoscale eddy of the South China Sea (Zhang et al., 2016; Sun et al., 2020; Sun et al., 2022), and diversity of DMSP degradation potential has obvious significance for sulfur material cycling and transformation.

## CONCLUSION

This study showed that DMSP degradation genes varied significantly in spatial scale of the South China Sea. The current study found that temperature and water depth mainly induced variations in taxonomic affiliations of *Roseobacter* group DMSP degradation genes over space. These findings further implied that additional factors including light, salinity, and temperature, which are caused by an increase in depth, may play important roles in regulating the DMSP degradation genes. These factors play an important role in regulating the switch process between bacterial DMSP demethylation and DMSP cleavage. This study highlighted the understanding of the role of *Roseobacter* group in sulfur cycling and transformation conversion in the tropical ocean.

## DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: NCBI [accession: SRP133746].

## AUTHOR CONTRIBUTIONS

All authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.895613/full#supplementary-material

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