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Spatial Patterns of Organic Sulfur and Its Limited Association With Bacterial Communities in the Bohai and Yellow Seas

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Key Points:

- We estimated the inventory of organic sulfur in the Bohai and Yellow Seas
- The concentration of organic sulfur in the Bohai and Yellow Seas is higher than previously reported data for the open ocean
- Organic sulfur showed no significant association with the composition and abundance of bacterial communities in the Bohai and Yellow Seas

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract While the importance of organic sulfur for marine bacteria is widely recognized, how it relates to bacterial community composition, particularly in coastal environments, remains poorly understood. In this study, we quantified dissolved organic sulfur (DOS) and particulate organic sulfur (POS) in the Bohai and Yellow Seas. DOS ranged from 1.7 to 6.8 μM in surface waters and 0.9–5.4 μM in bottom waters, while POS ranged from 0.3 to 1.7 μM in surface waters and 0.2–1.6 μM in bottom waters. In the Bohai Sea, particulate and dissolved C:S ratios averaged 57 ± 38 and 41.4 ± 7.5, respectively, with minimum sulfur inventories of 0.039 ± 0.025 (POS) and 0.300 ± 0.058 Tg S (DOS). In contrast, the Yellow Sea had a lower particulate C:S ratio (25 ± 17) but a comparable dissolved ratio (46.5 ± 12.5), alongside minimum inventories of 1.14 ± 0.69 (POS) and 1.91 ± 0.52 Tg S (DOS). In contrast to previously reported data from the open ocean, the Bohai and Yellow Seas are characterized by distinctly higher organic sulfur concentrations and lower molar C:S ratios. Bacterial communities differed significantly between surface and bottom waters in terms of diversity and network complexity. However, path analysis showed no significant association of organic sulfur with bacterial community composition in either layer. These findings suggest that despite high total organic sulfur concentrations in these coastal waters, its low concentration of bioavailable fractions and taxon-specific utilization may explain its limited association with bacterial community.

Plain Language Summary The extent to which organic sulfur relates to bacterial community composition and abundance in the Bohai and Yellow Seas remains unclear. This study investigated the spatial distribution and inventories of organic sulfur in the Bohai Sea and Yellow Seas, and assessed their association with marine bacterial community composition and abundance. Compared to previously reported data from the open ocean, the coastal waters in this study demonstrated higher concentrations of organic sulfur. The analysis establishes no significant association between organic sulfur and the bacterial community composition. These findings suggest that organic sulfur may have a limited role in shaping bacterial communities in the coastal systems of the Bohai and Yellow Seas.

1. Introduction

Organic sulfur, as a participant in marine biogeochemical cycles, influences the energy metabolism and ecological functions of marine bacteria (Moran & Durham, 2019). Despite high sulfate concentrations (~28 mM) in seawater, there is a substantial energy cost for phytoplankton sulfate assimilation to reduced sulfur (1,815 kJ mol^{-1}) compared to carbon dioxide assimilation to fully reduced carbon (605 kJ mol^{-1}) (Giordano & Raven, 2014; Moran & Durham, 2019). For every 95 carbon atoms absorbed by phytoplankton, 1 sulfur atom is assimilated into biomass (Ho et al., 2003). Approximately 45% of phytoplankton-fixed sulfur enters the DOS pool through active exudation and viral lysis (annual flux: 600 Tg sulfur (S)), providing crucial metabolic substrates for heterotrophic bacterioplankton (Ksionzek et al., 2016). Over 92% of DOS in the ocean is biologically derived (Phillips et al., 2022). A representative component, dimethylsulfoniopropionate (DMSP), contributes approximately 2.0 Pg S annually to the marine organic sulfur pool (Galí et al., 2015), serving as an abundant sulfur source for heterotrophic bacteria (Tripp et al., 2008). Coastal environments, characterized by high primary productivity, exhibit elevated concentrations of DMSP (Jian et al., 2019), typically exceeding that in open ocean (Yang et al., 2011; Zhai et al., 2020). This may result in highly active bacterial metabolism of organic sulfur in coastal regions. While existing studies elucidate the indispensable role of organic sulfur for marine bacterial metabolism,

its broader association with overall community composition and abundance in coastal environments remains largely underexplored.

As typical shelf marginal sea system in the Northwest Pacific, the Bohai and Yellow Seas feature dynamic material circulation influenced by monsoons and ocean currents, with their connectivity mediated by the Bohai Strait. This region experiences widespread eutrophication fueled by nutrient inputs from rivers and anthropogenic emissions from coastal cities, causing frequent algal blooms events (Wang et al., 2021). Such high primary productivity intensifies the dynamics and regulatory mechanisms governing bacteria processes (Han et al., 2022). While previous studies have extensively examined the relationship between bacterial communities and organic carbon, two critical factors influencing community structure in this region are the sources of organic carbon (Wang et al., 2018) and the dynamic compositional and concentration changes in organic matter during algal blooms (Chen et al., 2020). Notably, the intracellular substances released during the decline of algal blooms contain abundant organic sulfur components (such as DMSP), which are known to enhance microbial metabolism and transformation of organic sulfur (Xu et al., 2019). Furthermore, metatranscriptomic evidence indicates that heterotrophic bacteria in these seas perform active sulfur metabolism, supported by abundant algal-derived organic sulfur substrates such as sulfoquinovose (SQ) (Liu et al., 2023). These studies reveal that heterotrophic bacteria actively degrade organic sulfur. For heterotrophic bacteria, directly acquiring sulfur from organic molecules is an energy-saving strategy (Moran & Durham, 2019). However, given the millimolar concentration of seawater sulfate, a concentration that is orders of magnitude greater than the nanomolar to micromolar organic sulfur pool (Ksionzek et al., 2016), and the ubiquitous presence of sulfate assimilation pathways in marine bacteria (Moran & Durham, 2019), the sulfur obtained from organic matter is unlikely to be a key factor limiting coastal bacterial community composition. Nevertheless, this premise has not been directly evaluated in previous research. This study has three main objectives: (a) to characterize the spatial distribution patterns of organic sulfur compounds and quantify their standing stocks in the Bohai and Yellow Seas; (b) to investigate the potential environmental factors affecting organic sulfur concentrations in the Bohai and Yellow Seas; (c) to evaluate the relationship organic sulfur on bacterial community and its abundance. These findings will provide novel insights into organic sulfur-microbial interactions in coastal ecosystems.

2. Materials and Methods

2.1. Study Sites and Sample Collection

All samples were collected in July 2022 from 31 sampling stations across the Bohai and Yellow Seas (Figure 1a), encompassing both surface (approximately 3 m below the sea surface) and bottom water (approximately 3 m above the sea floor) (Figure S1 in Supporting Information S1). Water samples were obtained using a conductivity-temperature-depth (CTD) rosette sampler and then transferred from Niskin bottles through a hose fitted with a 200 μm mesh filter (to remove larger zooplankton) into pre-acid-washed polycarbonate (PC) bottles for further processing. A 1 L water sample was filtered through a pre-combusted (at 450°C for 6 hr) 0.7 μm GF/F filter membrane (Whatman, UK) for particulate organic carbon (POC) and POS analysis. The remaining 1 L of filtered seawater was acidified to pH 2.0 and then subjected to solid-phase extraction (SPE) to concentrate DOS (Pohlabeln et al., 2017). Extraction was performed using 200 mg PPL cartridges (Agilent Technologies, USA), based on validation experiments showing no significant difference in efficiency for 1 L coastal seawater compared to 1 g cartridges ($p = 0.053$, Student's t-test; Figure S2a in Supporting Information S1). The 200 mg PPL cartridges are routinely used for the extraction of coastal organic carbon (Zheng et al., 2022). We chose to desalt the enriched samples using three column volumes of 0.1% formic acid (aq.), as validation experiments confirmed its extraction efficiency was not significantly different from the more commonly used 0.01 M hydrochloric acid ($p = 0.099$, Student's t-test; Figure S2b in Supporting Information S1). The desalted samples were then dried under negative pressure. For DOC, the filtrate from the 0.7 μm GF/F filtration was collected into a pre-combusted 30 mL brown glass bottle. For chlorophyll a, a 0.5 L aliquot was filtered onto a separate GF/F filter. For 16S rRNA gene sequencing (bacterial community analysis), 1 L of seawater was filtered through a 0.22 μm polycarbonate membrane (Millipore, USA). The resulting filtrate from this 0.22 μm filtration was collected into 15 mL acid-washed centrifuge tubes for nutrient analysis. For total heterotrophic bacteria abundance, 1,980 μL of seawater was fixed with 20 μL of glutaraldehyde. We collected triplicate samples for the analysis of heterotrophic bacterial abundance, DOC/DOS, and POC/POS. All collected filter membrane samples, along with those for heterotrophic bacteria abundance, were stored at −80°C, while water samples (including DOC, DOS, and nutrient samples) were preserved at −20°C until laboratory analysis.

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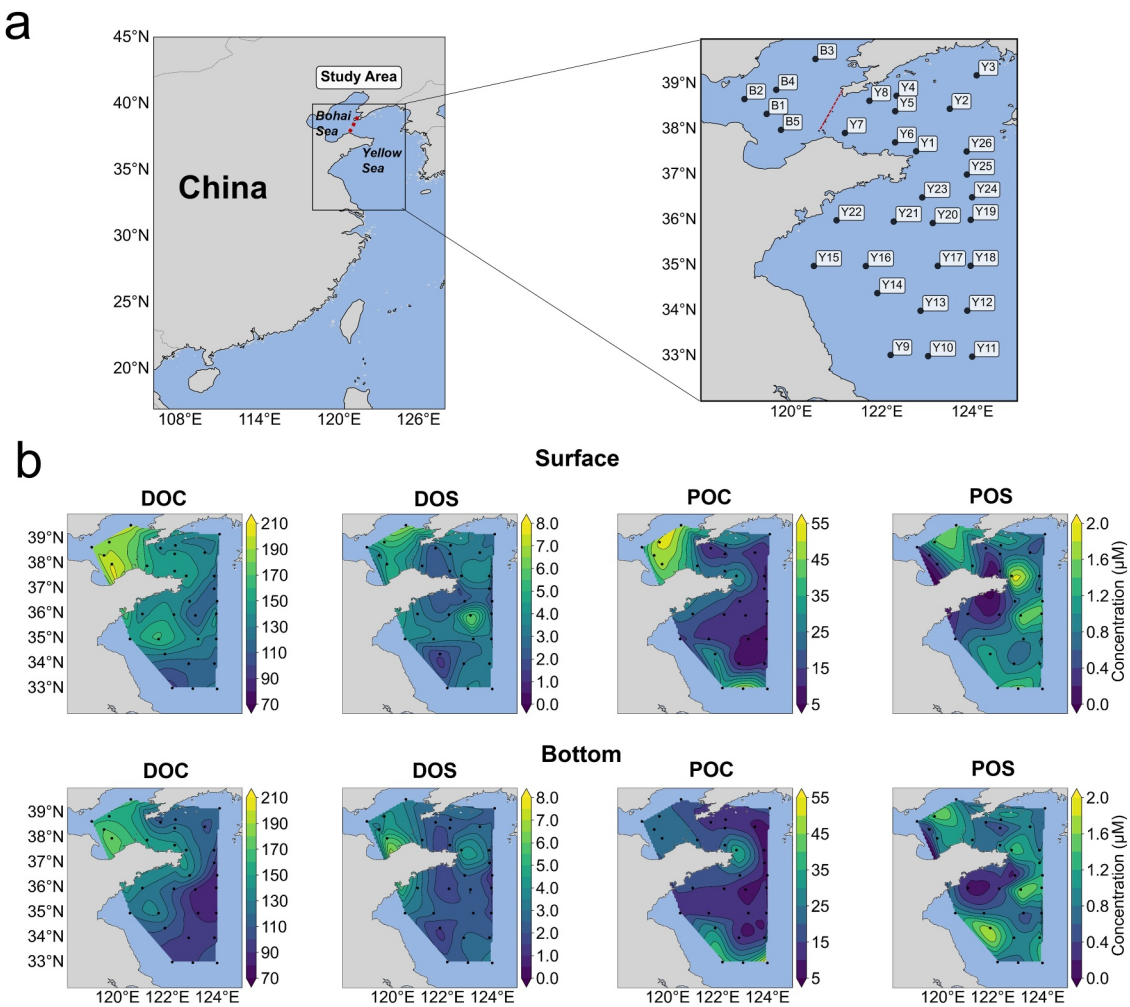


Figure 1. Spatial distributions of dissolved and particulate organic carbon and sulfur in the Bohai and Yellow Seas. (a) Study area and sampling stations. (b) Surface (upper) and bottom (lower) distributions of DOC, DOS, POC, and POS.

2.2. Analysis of Environmental Parameters

An SBE43 CTD sensor to measure the temperature, salinity, dissolved oxygen and sampling depth of surface and bottom waters. A WET Labs ECO turbidity sensor was used to measure turbidity. A fluorometer (Turner Designs, TD-700) was used to analyze chlorophyll *a*. A SKALAR San++ continuous flow analyzer (SA3000/5000 chemistry unit) determined the concentrations of five key nutrients (NO_3^-, PO_4^{3-}, NO_2^-, NH_4^+, and SiO_3^{2-}). For DOC analysis, samples were run on a Shimadzu TOC-VCPH analyzer. Prior to analysis, 40 μL of phosphoric acid was added to remove inorganic carbon, followed by thorough mixing. Quantification used potassium hydrogen phthalate as standards for DOC, with deep seawater serving as a quality control (Álvarez-Salgado & Miller, 1998). The seawater solid-phase extract was eluted with LC-MS grade methanol (Thermo Fisher Scientific, USA) into pre-combusted amber glass vials. The eluted extract was split into two aliquots for the analysis of Solid-phase extractable DOC(DOCSPE) and Solid-phase extractable DOS (DOSSPE). The extract was completely dried under a nitrogen stream. For DOSSPE, the residue was then re-dissolved in a 5% nitric acid solution and subjected to ultrasonication to ensure complete re-solubilization. Quantification of DOS was performed using an Inductively Coupled Plasma Optical Emission Spectrometer (Agilent 5110VDV, USA). For DOCSPE, the dried extract was re-dissolved in 30 mL of ultrapure water, ultrasonicated to ensure complete dissolution and dilution, and then quantified following the previously described analytical procedure and instrumentation for DOC. The extraction efficiency of SPE was calculated as the concentration ratio of DOCSPE to DOC. It is important to note that the direct extraction efficiency of SPE for marine DOS has not been

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systematically established. Therefore, DOS concentrations in this study were estimated based on the DOC extraction efficiency following previous methodology (Ksionzek et al., 2016; Pohlabeln et al., 2017). Prior work implies that the SPE recovery of polar organic sulfur compounds is likely lower than that of DOC (Ksionzek et al., 2016). Consequently, the DOS concentrations derived here using DOC-based extraction efficiency should be interpreted as conservative estimates, representing minimum estimates of in situ marine DOS concentrations. For POC analysis, inorganic carbon was removed by hydrochloric acid fumes treatment (Pavia et al., 2019). For POS analysis, sulfate was removed by rinsing with 3.2% ammonium formate (Chen et al., 1996), with verification details provided in the Supplementary Methods and Figure S3 in Supporting Information S1. After drying, both POC and POS were quantified using a vario EL cube CHNS elemental analyzer (Elementar, Germany). Total bacterial abundance samples were thawed at a constant temperature, thoroughly stained with SYBR GREEN nucleic acid dye, and counted using a BD C6 flow cytometer (Chen et al., 2022).

2.3. 16S rRNA Sequencing

Total DNA from environmental samples was extracted by DNeasy Powersoil Kit (MoBio, USA) following the manufacturer's protocol. The V4 region of the 16S rRNA gene was amplified using the primer pair 515F (5′-GTGYCAGCMGCCGCGGTAA-3′) and 806R (5′-GGACTACNVGGGTWTCTAAT-3′) (Walters et al., 2016). Paired-end sequencing (2 × 250 bp) was then performed on the Illumina NovaSeq platform (Illumina, USA). Raw sequencing data underwent quality control using FASTQC and adapter sequences from Fastq sequences using Trimmomatic, which also trimmed sequences based on base quality scores. Subsequently, the DADA2 pipeline was employed for sequence denoising, amplicon sequence variant (ASV) identification, and generation of representative sequences and feature tables. This process infers biological sequences precisely by modeling and correcting Illumina-sequencing errors, thereby defining ASVs without the need for a clustering threshold based on sequence similarity. Consequently, each ASV represents a group of 100% identical sequences. The representative sequences were classified by comparison with the SILVA v138 database (Yilmaz et al., 2014).

2.4. Data Processing and Analysis

The study visualized the spatial distributions of factors (POC, POS, DOC, DOS) across different water layers in the Bohai Sea and Yellow Sea using the Cartopy and Matplotlib libraries in Python. Subsequently, the Mann-Whitney U test from the scipy.stats module analyzed significant differences in these factors between sea regions and water layers, with results also visualized in Python. The relative abundance of bacterial families, calculated as the percentage of sequences from constituent ASVs against the total sequences per sample, was visualized in a heatmap using OriginPro 2024 (v10.1.0.178). The analysis calculated alpha-diversity indices (Shannon, Simpson, Chao1, Richness) using the vegan package in R (version 2024.12.0). For beta-diversity, the study computed Bray-Curtis dissimilarities and performed ordination (e.g., PCoA) with the vegan package, then visualized the results using OriginPro (version 10.1.0.178). Microbial co-occurrence network construction employed the Hmisc and igraph packages in R. This process filtered ASVs by retaining only those with a total abundance greater than 0.01% and a presence in over 20% of samples. The analysis determined pairwise correlations between ASVs using Spearman's rank correlation, defining robust connections as those with an absolute $|r| > 0.7$ and a Benjamini-Hochberg adjusted p-value <0.001. Finally, Gephi (version 0.10) visualized the resulting network. The study performed and visualized Mantel tests in R using the linkET, ggplot2, and dplyr packages. To determine the potential causal relationships, we performed partial least squares path modeling (PLS-PM) with the plspm package in R. Principal coordinate analysis (PCoA) reduced the bacteria community structure at the ASV level, and the PC1 axis, which captures the primary variation, served as the variable for model fitting (Winterfeldt et al., 2024). A goodness-of-fit goodness (GOF) index greater than 0.6 indicate an acceptable model fit.

3. Results

3.1. Spatial Distribution of Organic Carbon and Sulfur in the Bohai and Yellow Seas

This study conducted a comprehensive spatial survey of organic carbon and organic sulfur across 31 stations in the Bohai and Yellow Seas (Figure 1). In surface waters, DOC concentrations ranged from 96 to 200 μM, and DOS concentrations varied between 1.7 and 6.8 μM. In bottom waters, DOC and DOS concentrations ranged from 81 to 174 μM and 0.9–5.4 μM, respectively. The concentrations of DOC and DOS were significantly higher

Table 1
Estimation of Organic Sulfur Pool in Bohai Sea and Yellow Sea

	POC μM	POS μM	DOC μM	DOS μM	POC-C:S -	DOC-C:S -	POC[a] Tg	DOC[a] Tg	POS Tg	DOS Tg
Bohai Sea	33.6 ± 12.7	0.82 ± 0.44	178.3 ± 15.4	4.46 ± 1.03	57 ± 38	41.4 ± 7.5	0.52	4.51	0.039 ± 0.025	0.300 ± 0.058
Yellow Sea	18.2 ± 10.8	0.87 ± 0.36	120.3 ± 19.4	2.75 ± 0.76	25 ± 17	46.5 ± 12.5	7.22	31.07	1.14 ± 0 0.69	1.91 ± 0.52

[a]Data from Jiao et al. (2018).

in surface waters than in bottom waters (Mann-Whitney U test, all $p < 0.01$; Figures S4a and S4c in Supporting Information S1). Notably, both DOC and DOS concentrations in the Bohai Sea (surface and bottom waters) were significantly higher than those in the Yellow Sea ($p < 0.001$; Figures S5a, S5b, S5e, and S5f in Supporting Information S1). Concentrations of POC and POS in surface waters (POC: 8.8–51.2 μM; POS: 0.3–1.7 μM) were overall comparable to those in bottom waters (POC: 7.68–59.06 μM; POS: 0.2–1.6 μM), with no statistically significant difference ($p > 0.05$; Figures S4b and S4d in Supporting Information S1). When comparing sea regions, surface water POC concentrations were significantly higher in the Bohai Sea (32–51 μM) than in the Yellow Sea (8.8–50.9 μM) ($p < 0.001$; Figures S5c and S5g in Supporting Information S1), whereas no such difference was observed in bottom waters ($p > 0.05$). In contrast, POS concentrations showed no significant differences, either between water layers (surface vs. bottom) or among sea regions (Bohai Sea vs. Yellow Sea) (all $p > 0.05$; Figures S4d, S5d, and S5h in Supporting Information S1).

3.2. Estimation of Organic Sulfur Pool in the Bohai and Yellow Seas

We calculated the molar C:S ratios of organic matter in the Bohai and Yellow Seas (Table 1). In the Bohai Sea, the particulate C:S ratio averaged 57 ± 38, while the dissolved ratio was 41.4 ± 7.5. The Yellow Sea showed a lower particulate C:S (25 ± 17) but a comparable dissolved C:S ratio (46.5 ± 12.5). Organic sulfur inventories were estimated using these C:S ratios and the atomic masses of carbon and sulfur, based on previous organic carbon stock estimates (0.52 Tg POC and 4.51 Tg DOC for the Bohai Sea; 7.22 Tg POC and 31.07 Tg DOC for the Yellow Sea) (Jiao et al., 2018). Applying the measured C:S ratios, the estimated minimum sulfur inventories were 0.039 ± 0.025 Tg S for POS and 0.300 ± 0.058 Tg S for DOS in the Bohai Sea. The Yellow Sea exhibited minimum inventories with 1.14 ± 0.69 Tg S (POS) and 1.91 ± 0.52 Tg S (DOS).

3.3. Spatial Variation in Bacterial Community Structure

This study investigated the differences in bacterial community composition, diversity, and interaction networks between surface and bottom waters in the Bohai and Yellow Seas. At the family level (Figure 2), *Flavobacteriaceae* and S*ynechococcaceae* emerged as the predominant taxa in the surface waters. Conversely, in the bottom layer, a notable decrease in the relative abundances of *Flavobacteriaceae* and *Synechococcaceae* was observed, alongside an increase in the relative abundances of *Pelagibacteraceae* and *Actinobacterial* clade OCS155 (Figure 2). Alpha diversity was significantly higher in bottom waters than in surface waters ($p < 0.001$), as indicated by the Shannon, Simpson, Chao1, and Richness indices (Figure 3a). PCoA analysis further confirmed this spatial separation, showing a clear distinction in bacteria community composition (beta diversity) between the two layers. The first and second principal axes collectively accounted for 36.71% of the explained variance (23.25% and 13.46%, respectively) (Figure 3b). The network analysis revealed that bacterial co-occurrence networks were more complex in the bottom water layer than in the surface layer (Figure 4). The co-occurrence network in bottom waters was larger and more densely connected, with 406 nodes and 5920 edges, compared to the surface network (227 nodes and 1156 edges). Accordingly, the closeness centrality was also significantly higher in the bottom waters ($p < 0.01$; Figure S6 in Supporting Information S1).

3.4. Correlation Between Bacterial Community and Environmental Factors

A Mantel test analyzed the relationship between environmental factors and bacteria community, considering ASVs, family level and bacterial cell abundance (Figure 5). DOC exhibited significant positive correlations with bacterial ASVs diversity, family level community composition, and abundance in both surface and bottom waters (all $p < 0.01$). In surface waters, POC exhibited strong and significant correlations ($p < 0.01$) with bacterial ASVs

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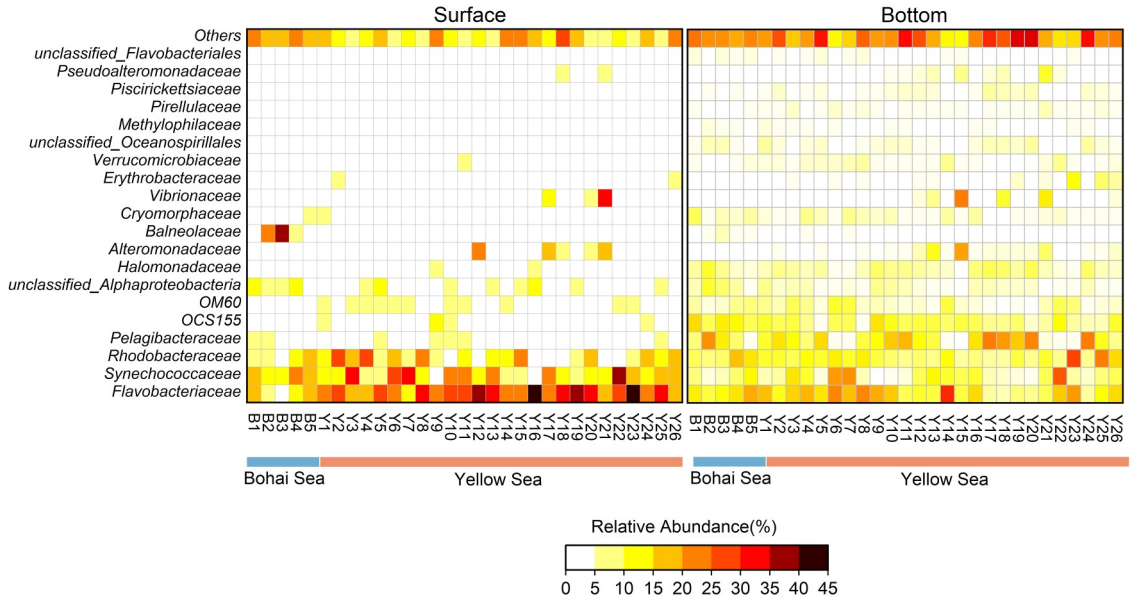


Figure 2. Spatial distribution of bacterial communities in the Bohai and Yellow Seas. The left and right heatmaps display the surface and bottom layers, respectively. The colored bars at the bottom indicate the station locations, with blue for the Bohai Sea and orange for the Yellow Sea. The graph shows the relative abundance of the top 20 taxonomic families, with all other taxa merged into "Others."

and abundance. However, in bottom waters, POC was only significantly correlated with ASVs ($p < 0.01$). Both DOS and POS were significantly correlated (all $p < 0.05$) with bacterial abundance in surface waters. In contrast, in bottom waters, only DOS showed a weak but significant correlation ($p < 0.05$) with both ASVs and abundance. Additionally, in bottom waters, water depth was significantly correlated with ASVs, family level communities, and bacterial abundance ($p < 0.05$), suggesting compositional differences across varying depths.

Co-occurrence network analysis of environmental factors and bacterial communities at the family level further highlighted distinct layer-specific interaction patterns (Figure 6). In surface waters, the number of connections between major bacterial families and environmental factors was lower than in bottom waters. Notably, the taxa directly and significantly correlated with DOC concentration ($r > 0.5$, $p < 0.05$) were only *Vibrionaceae* and unclassified *Rhodothermi*. Those significantly correlated with POC concentration included *Flavobacteriaceae*, *Alteromonadaceae*, *Vibrionaceae*, and *Moraxellaceae*. None of the major taxa showed a significant correlation

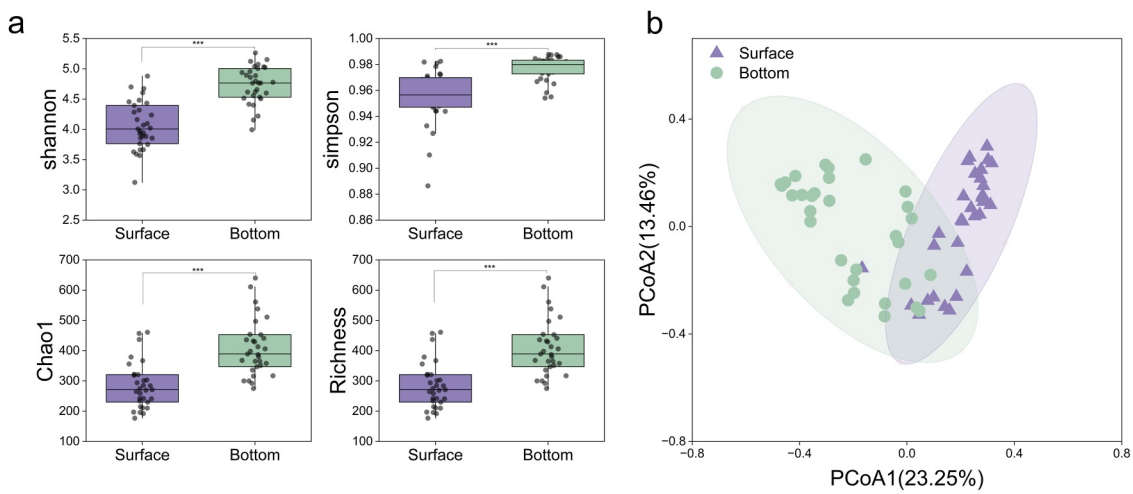


Figure 3. Spatial differences in microbial community diversity. (a) Spatial differences in alpha diversity. (b) Spatial differences in beta diversity (ellipses represent 95% confidence intervals).

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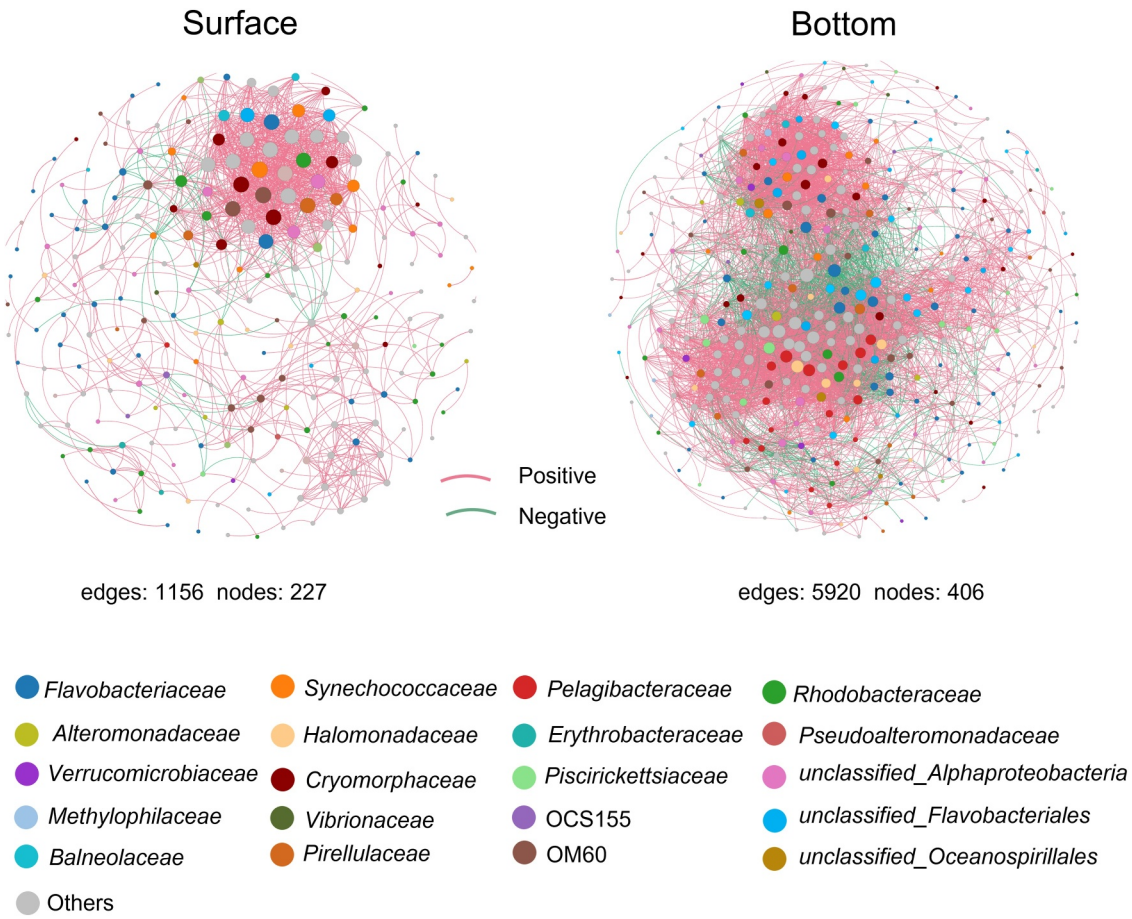


Figure 4. Spatial co-occurrence network differences in bacterial communities. The top 20 taxa in each network are shown, with others grouped as "Others."

with DOS or POS ($p > 0.05$) (Figure 6a). In bottom waters, the associations between major taxa and DOC/POC increased. *Flavobacteriaceae* and OM60 were significantly positively correlated with DOC and POC concentrations ($r > 0.5$, $p < 0.05$), whereas *Alteromonadaceae* was significantly negatively correlated with DOC and POC concentrations ($r < -0.5$, $p < 0.05$). OCS155 showed a significant positive correlation with POC, DOC, and DOS concentrations ($r > 0.5$, $p < 0.05$), while *Nitrospinaceae* was significantly negatively correlated with DOC, POC, and DOS ($r < -0.5$, $p < 0.05$). Additionally, environmental parameters such as chlorophyll *a*, water depth, phosphate, and salinity were significantly correlated with different taxa (Figure 6b). These results reflect the varying metabolic patterns, environmental adaptability, and vertical spatial differences among different taxa, as evidenced by their positive or negative correlations with organic substrates and environmental factors. Correlation analysis is limited to identifying environmental factors significantly linked to bacterial community composition and abundance, whereas elucidating their potential causal relationships requires the use of PLS-PM.

3.5. Assessing the Causal Relationship of Environmental Factors on Bacterial Communities Using PLS-PM

PLS-PM analysis clarified the potential causal relationships among bacterial communities, abundance, and environmental factors across surface and bottom waters, while identifying key controlling factors (Figure 7a). This analysis identified 8 and 9 latent variables explaining variance in bacterial communities and abundance in the surface and bottom layers, respectively. The initial path relationships were specified based on established ecological principles and our specific research hypotheses. This included, for instance, predefined paths from physical factors (e.g., temperature, depth) and biogeochemical parameters (e.g., DOC, DOS) to biological variables (such as bacterial community structure and abundance). The model was then iteratively refined to retain key hypothesized pathways while ensuring satisfactory model fit, as indicated by a GOF value exceeding 0.6. The

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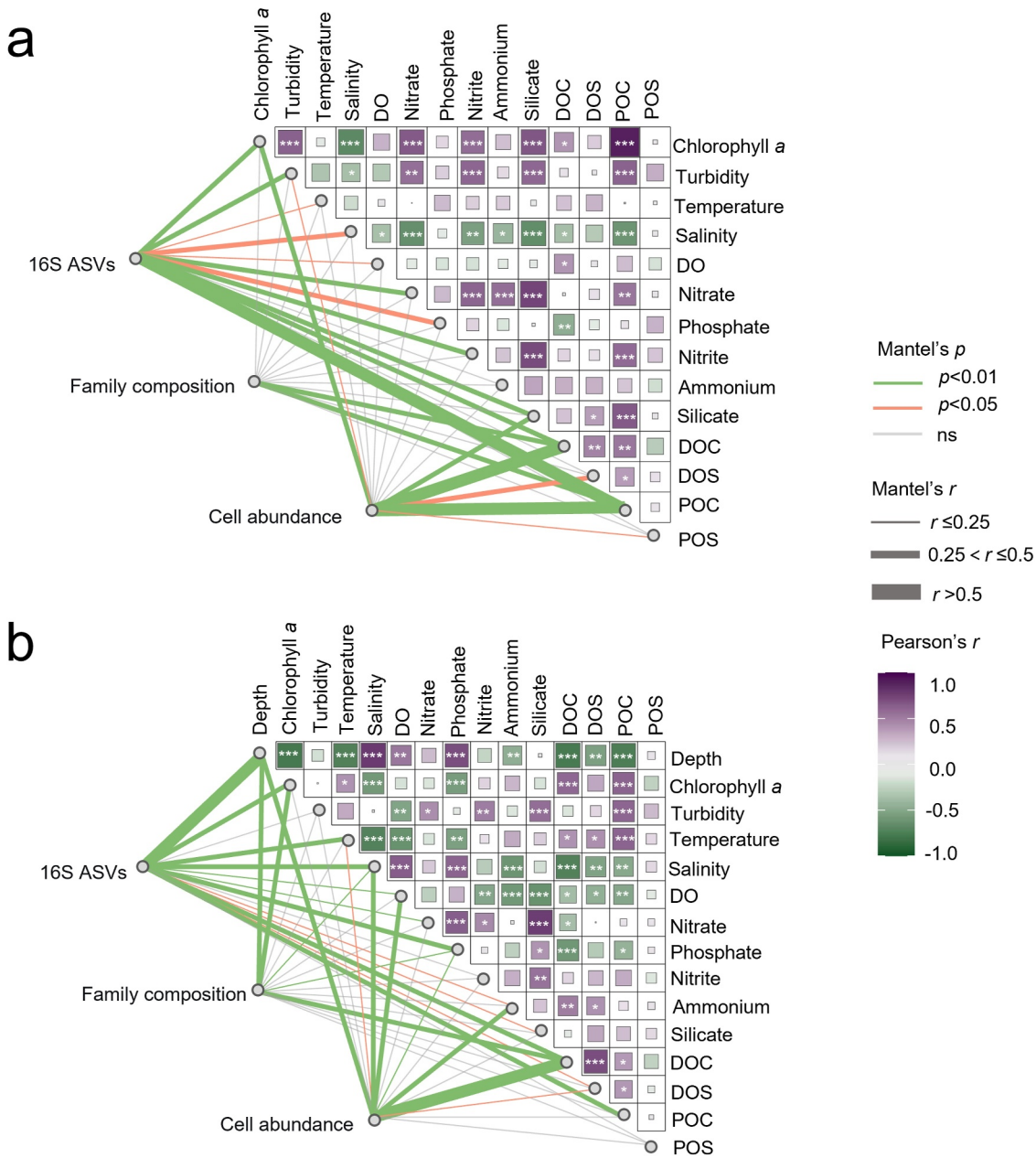


Figure 5. Environmental drivers of bacterial community composition and abundance in the Bohai Sea and Yellow Sea. (a) Surface layer. (b) Bottom layer. The grid on the upper-right represents pairwise comparisons among environmental factors, where the size and color gradient of the color blocks indicate the Pearson correlation coefficient. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. The correlations between bacterial community composition or cell abundance and each environmental factor were analyzed using Mantel tests. The width of the lines represents the Mantel's r value, and the line color indicates the significance tested based on 999 permutations.

final set of path relationships resulting from this refinement process is provided in Table S2 in Supporting Information S1. This data-driven adjustment yielded a statistically valid and parsimonious model, as evidenced by the good fit indices (GOF: 0.722 for surface and 0.702 for bottom waters; Figure 7). The results revealed both shared and distinct factors associated with communities and abundance between the two layers (Table S2 in Supporting Information S1). Environmental factors explained 83% of the community variation in surface waters (Figure 7a), primarily driven by significant negative associations of salinity (path coefficient = −0.59, $p < 0.05$) and DOC (path coefficient = −0.63, $p < 0.05$) with bacterial abundance. Environmental factors collectively explained 87% of the variation in bacterial abundance, with chlorophyll a (path coefficient = 0.44, $p < 0.05$) and DOC (path coefficient = 0.34, $p < 0.05$) significantly promoting bacterial abundance. Conversely, the community

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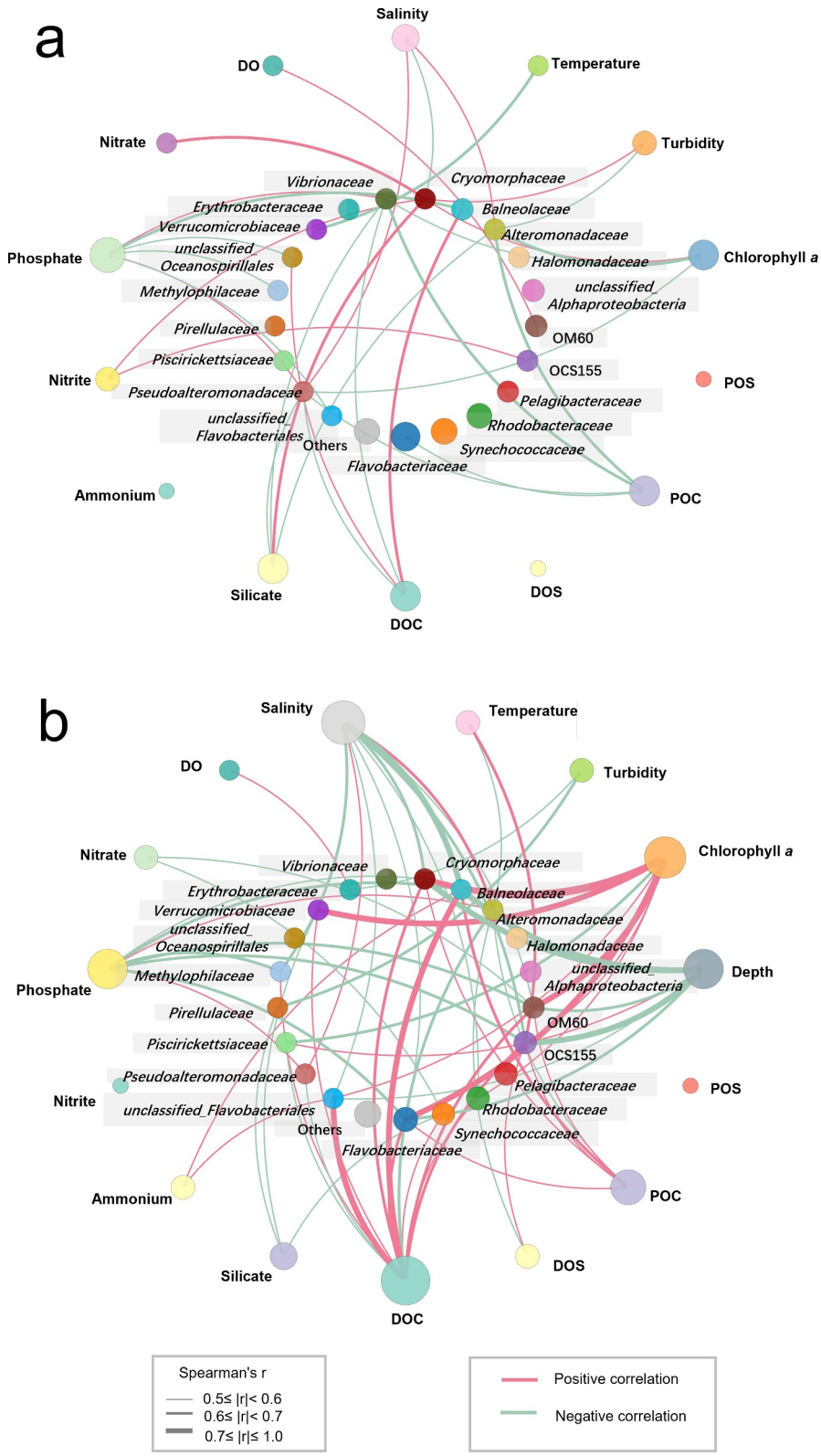


Figure 6. Interaction network between environmental factors and bacterial communities (at the family level). (a) Represents the surface layer, and (b) represents the bottom layer. The outer circle represents various environmental factors, with the size of the circles indicating the number of connections to microorganisms. The inner circle represents the top 20 bacterial taxa in relative abundance, with the size of the circles indicating the magnitude of relative abundance. The thickness of the connecting lines between environmental factors and bacterial communities represents the strength of the correlation. Only edges showing a correlation coefficient $|r| \geq 0.5$ and $p < 0.05$ are displayed. Red connecting lines indicate significant positive correlations, while green connecting lines indicate significant negative correlations.

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itself was significantly negatively associated with bacterial abundance (path coefficient = −0.53, $p < 0.01$). In bottom waters, environmental factors explained 87% of the variation in the community and 79% of the variation in bacterial abundance (Figure 7b). The PLS-PM indicated a significant negative path from dissolved oxygen to the bacterial community (path coefficient = −0.46, $p < 0.05$) and a significant positive path from DOC to bacterial abundance (path coefficient = 0.97, $p < 0.01$). However, the model indicated that no significant direct path was found from DOS to either community structure or bacterial abundance in either water layer (all $p > 0.05$). DOC was the only variable showing a significant direct path to DOS, with a path coefficient of 0.53 ($p < 0.05$) in surface waters and 0.86 ($p < 0.01$) in bottom waters.

4. Discussion

4.1. Differences in Organic Sulfur Concentration and Stoichiometry Between the Bohai-Yellow Seas and the Open Ocean

In this study of the Bohai and Yellow Seas as typical shelf marginal seas, POS/DOS concentrations and molar C:S ratios (Figure 1 and Table 1) were comparable to previously observed ranges in the Yangtze River Estuary and adjacent East China Sea (Dong et al., 2024). The DOS concentrations were higher than those in the surface open ocean (0.31 ± 0.09 μmol S/L) (Ksionzek et al., 2016), with molar C:S ratios (46 ± 12) substantially lower than that characteristic of open ocean (C:S = 230:1) (Raven, 2025). Phillips and Ksionzek et al. reported closely matching molar C:S ratios for surface dissolved organic matter in the open ocean, at 213 ± 32 (0–150 m) (Phillips et al., 2022) and 221 ± 31 (0–105 m) (Ksionzek et al., 2016), respectively. For POS, very few data sets are available for the open ocean, with only limited reports from the Southern California Bight and the marginal seas of the Northwest Pacific. The molar C:S of POS in the Bohai and Yellow Seas (Table 1) was lower than that of sinking particles (average C:S = 119:1, range = 35:1–246:1) and suspended particles (average C:S = 224:1, range = 145:1–284:1) in the Southern California Bight (Matrai & Eppley, 1989), but close to that previously reported for the marginal seas of the Northwest Pacific adjacent to the study area (average C:S = 48:1, range = 15:1–200:1) (Chen et al., 1996). These results indicate that the concentration of organic sulfur in the Bohai and Yellow Seas is higher than those previously reported for the open ocean.

Both POS and DOS concentrations in the Bohai and Yellow Seas showed significant negative correlations with the molar C:S ratio ($p < 0.0001$), whereas only POC exhibited a significant relationship with the molar C:S ratio ($p < 0.0001$) (Figure S7 in Supporting Information S1). These results suggest that organic sulfur concentration is a key regulator of organic matter carbon-sulfur stoichiometry in this coastal system. Previous studies indicate that organic sulfur is a more labile and reactive component than organic carbon and tends to be preferentially removed during oceanic current transport (Longnecker et al., 2020). Therefore, we propose that during the horizontal export of organic matter from the Bohai and Yellow Seas to the open ocean and the concurrent mixing of water masses, organic sulfur is likely removed more rapidly than organic carbon. This differential removal could explain the observed pattern of higher organic sulfur concentrations and lower C:S ratios in coastal waters, in contrast to lower organic sulfur concentrations and higher C:S ratios in the open ocean.

4.2. Potential Controlling Factors of Organic Sulfur in the Bohai and Yellow Seas

Chlorophyll *a* commonly serves as a proxy for phytoplankton (Boyer et al., 2009). DOS had been demonstrated to originate primarily from primary production in the ocean (Phillips et al., 2022). Additionally, a positive correlation between POS and chlorophyll *a* has been observed in the Southern California Bight, suggesting that POS in this region derives from phytoplankton (Matrai & Eppley, 1989). However, the results of this study show that neither DOS nor POS concentrations significantly correlate with chlorophyll *a* levels in either the Bohai or Yellow Seas (Figures 5 and 7), consistent with total organic sulfur in the Atlantic Ocean (Longnecker et al., 2020). This indicates significant regional variations in organic sulfur, and the distribution of organic sulfur in the Bohai and Yellow Seas may be influenced by more complex conditions.

The organic matter in the Bohai Sea and the Yellow Sea is influenced by the inputs of the Yellow River and the Yangtze River, respectively (Fan et al., 2018; Guo et al., 2022). Recent studies suggest that the contribution of terrestrial inputs to coastal organic matter has been underestimated (Yi et al., 2025). As a component of the bulk organic matter pool, organic sulfur may therefore be regulated by terrestrial inputs. The Bohai and Yellow Seas are characterized by complex hydrodynamics (Liu et al., 2020; Zhou et al., 2015) and relatively shallow water depths (Zhou et al., 2021). Sediment resuspension releases organic matter into the water column

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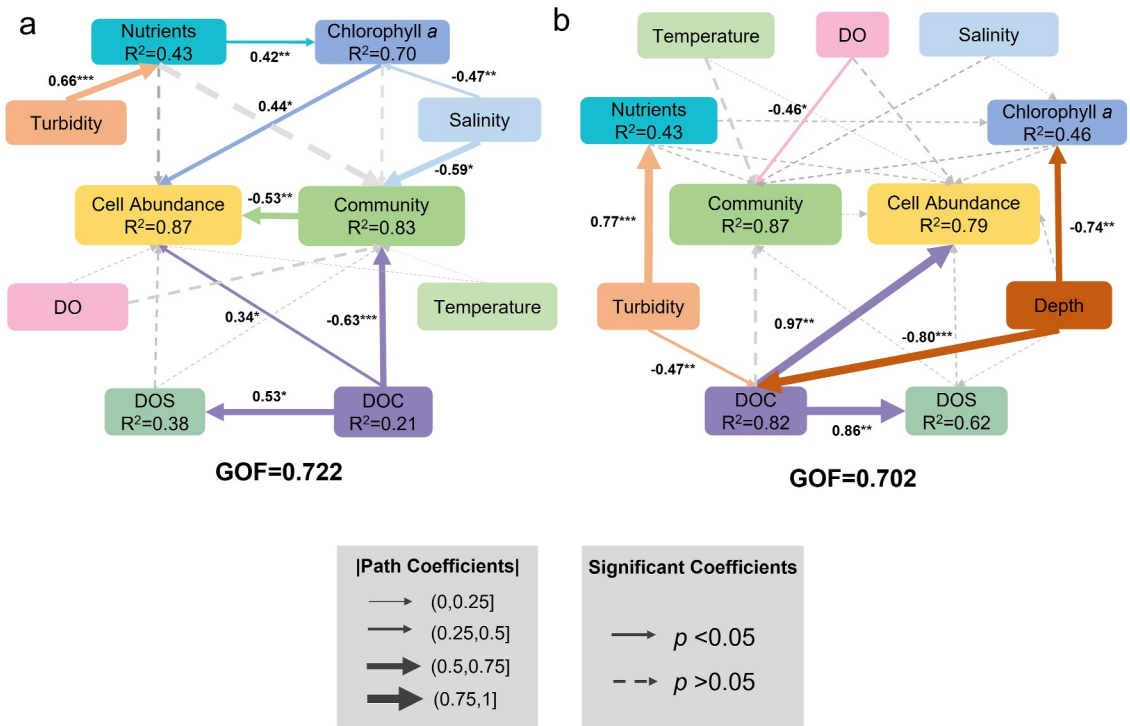


Figure 7. PLS-PM of bacterial communities and main environmental factors. The arrows indicate causal relationships, and the numbers represent the path coefficients of the independent variables to dependent variables. Non-significant path relationships were simplified in the display. Arrow width corresponds to the strength of the path coefficients, with solid arrows representing significant paths and dashed arrows representing non-significant paths. (a) Represents the surface layer, and (b) represents the bottom layer. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

(Qiao et al., 2016), and the particulate and dissolved organic carbon-to-sulfur ratios in the Bohai and Yellow Seas are close to those reported for sulphurized sediments in coastal environments (Phillips et al., 2022; Raven, 2025; Raven et al., 2016). This may imply that organic sulfur in the Bohai and Yellow Seas could also originate from sediment efflux. However, considering that C:S ratios can only provide preliminary insights into the sources of coastal organic sulfur, future studies should further integrate sulfur isotopes and molecular signatures to more accurately identify the origins of organic sulfur in coastal areas. Additionally, Organic sulfur exhibited higher degradation rate constants than organic carbon in the ocean (Ksionzek et al., 2016), indicating greater lability and reactivity (Ksionzek et al., 2016; Longnecker et al., 2020; Phillips et al., 2022). Intense UV radiation represents another important factor influencing surface ocean organic sulfur distribution. Mass spectrometry data revealed higher loss of sulfur-containing organic molecules under UV irradiation (D'Andrilli et al., 2015). These factors may collectively explain the observed decoupling between organic sulfur and chlorophyll *a* in the Bohai and Yellow Seas, thereby highlighting the complexity of the factors controlling organic sulfur distributions in this region.

4.3. Limited Associations of Organic Sulfur With Bacterial Community and Abundance in the Bohai and Yellow Seas

Although marine bacteria can rapidly assimilate phytoplankton-derived organic sulfur within minutes to days (Kiene et al., 2000; Landa et al., 2019), the path model showed no significant direct relationship between DOS and bacterial community composition or abundance (Figure 7), even in more diverse bottom waters (Figures 3b and 4b). This may be attributable to the particularly low concentration of bioavailable organic sulfur. Although the concentrations of both DOS and POS in the Bohai and Yellow Seas are at the micromolar level, the low C:S ratios, as previously discussed, indicate that the organic sulfur in these seas is likely influenced by the release of sulphurized sediments. Sulphurized-organic sulfur typically exhibits high stability and is difficult for heterotrophic bacteria to utilize (Raven et al., 2021). The concentration of bioavailable organic sulfur is likely quite low. For example, DMSP is considered one of the most abundant representatives of algal-derived organic sulfur (Li et al., 2024), yet its concentration in the Bohai and Yellow Seas is only at the nanomolar level

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(mean concentrations of DMSP in dissolved and particulate states were 7.7 (1.3–22.4) and 37 (5–98) nmol/L in summer, respectively) (Zhang et al., 2023). Furthermore, our previous research in the Bohai and Yellow Seas has shown that sulfonates, another major class of algal-derived organic sulfur (including representative compounds such as Sulfoquinovosyldiacylglycerol (SQDG), SQ, Sulfoquinovosylglycerol (SQGro), and 2,3-dihydroxypropane-1-sulfonate (DHPS)), are also present at only nanomolar levels in particles (mean concentrations: SQDG 52.3, range 3.8–103.5; SQ 14.0, range 2.5–28.4; DHPS 1.7, range 0.02–4.2; SQGro 0.68, range 0.06–2.27 nmol/L) (Ma et al., 2025). This study only examined the correlation between free-living bacterial taxa and DOS, previous research indicates that free-living bacterial communities are generally more sensitive and dynamic in response to fluctuations in organic matter composition compared to the typically more stable particle-attached bacterial communities (Liu et al., 2024). This pattern suggests that if the more responsive free-living community shows no significant relationship with DOS, then the more resilient particle-attached community is even less likely to be structured by POS. Combined with the generally low concentrations of major dissolved and particulate algal-derived organic sulfur substrates, organic sulfur likely plays a limited role in shaping the composition of both particle-attached and free-living bacterial communities. And only a few bacterial lineages (such as *Roseobacter* clade) can specifically metabolize these phytoplankton-derived organic sulfur substrates (Chen et al., 2021; Liu et al., 2023; Wang et al., 2017). In contrast, the bacterial community dynamics remain predominantly governed by the availability and composition of bulk organic substrates, particularly polysaccharides, proteins, and lipids (Behrendt et al., 2024; Teeling et al., 2012). In addition, most bacteria can satisfy their cellular sulfur demands by converting assimilated sulfate into sulfur-containing amino acids and lipids (Moran & Durham, 2019), rather than relying entirely on environmental organic sulfur. Together, these factors result in environmental organic sulfur playing a limited role in shaping the composition and abundance of bacterial communities in the Bohai and Yellow Seas.

5. Conclusions

Our investigation of organic sulfur in the Bohai and Yellow Seas revealed higher concentrations of organic sulfur and lower molar C:S ratios in this coastal system relative to those reported for open ocean environments in previous studies. PLS-PM analysis showed that DOS was not significantly directly associated with the composition or abundance of bacterial communities in the Bohai and Yellow Seas. This is likely due to its low concentration in the bioavailable organic sulfur pool and its selective utilization by specific bacterial taxa. Building on this work, the application of high-resolution mass spectrometry for molecular speciation, combined with sulfur isotope source tracing, will be critical in future research to unravel the composition and origins of organic sulfur in coastal systems.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The raw 16S rRNA sequencing data had been deposited in the National Omics Data Encyclopedia (NODE, https://www.biosino.org/node/) database under the accession number OEX00032468. The data for DOS, POS, other environmental parameters, and the relative abundance of bacterial communities in this study can be found at https://figshare.com/s/4a75ca9b27b76d22bc4f.

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