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Spatial distribution and environmental/biological co-regulation mechanism of dimethyl sulfur compounds in the eastern Indian Ocean

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Dimethyl sulfur compounds including dimethylsulfoniopropionate (DMSP), dimethyl sulfide (DMS), and dimethyl sulfoxide (DMSO), play a crucial part in global sulfur cycling. The eastern Indian Ocean (EIO), characterized by its remarkable diversity of biomes and climate dynamics, is integral to global climate regulation. However, the regulation mechanism of DMS (P, O) in the EIO remains to be elucidated in detail. This paper presented a field survey aimed at investigating the spatial distribution of DMS (P, O) and their relationships with environmental and biological factors in the EIO. The surface concentrations of DMS, DMSPt, and DMSOt varied from 0.07 to 7.37 nmol/L, 0.14 to 9.17 nmol/L, and 0.15 to 3.32 nmol/L, respectively, and their distributions are attributed to high Chl-a concentration near Sri Lanka and the influence of ocean currents (Wyrтки jets, Bay of Bengal runoff). Higher concentrations of DMS (P) and DMSOt were predominantly observed in water columns shallower than 75m and deeper than 75m deep, respectively. The monthly DMS fluxes in the study area peaked in August. Temperature and Dissolved Silica Index (DSI) were the key environmental determinants for DMS distribution, while nitrate (NO₃⁻) was the primary factor for both DMSPt and DMSOt. In terms of biological factors, *Prochlorococcus* and *Synechococcus* were significant contributors to DMS (P, O) dynamics. *Synechococcus* was the dominant influence on the DMS source and DMSPt sink, whereas *Prochlorococcus* primarily consumed DMSOt. Furthermore, the structural equation modeling (SEM) revealed the relationship between DMS, DMSPt, DMSOt, and the key environmental/biological factors, as well as among them, and together they formed a co-regulatory network in the EIO. This contributes significantly to the advancement of global ecosystem models for DMS (P, O).

KEYWORDS

the eastern Indian Ocean, dimethyl sulfur compounds, co-regulation mechanism, spatial distribution, picophytoplankton

1 Introduction

Dimethyl sulfur compounds (DSCs) are sulfur-containing organic molecules produced by certain phytoplankton species, macroalgae, and angiosperms (Keller et al., 1989; Hatton and Wilson, 2007; Borges and Champenois, 2017). Dimethyl sulfide (DMS) constitutes approximately 40% of sulfur emissions (Wang et al., 2015) and potentially affects climate by forming cloud condensation nuclei (CCN) (Charlson et al., 1987). Nonetheless, the DMS feedback hypothesis continues to be a subject of debate (Quinn and Bates, 2011). Dimethylsulfoniopropionate (DMSP), an amphoteric compound predominantly found in cellular granular form, is the primary DMS precursor and serves various functions, including acting as an antioxidant (Sunda et al., 2002), cryoprotectant (Kirst et al., 1991), osmoregulatory (Vairavamurthy et al., 1985), grazing deterrent (Wolfe et al., 1997), and excess sulfur sinks (Zhang et al., 2019). Similarly, dimethyl sulfoxide (DMSO) shares some functions with DMSP but is notable for its significant membrane permeability (Hatton and Wilson, 2007). Both DMSP and DMSO can be converted to DMS by phytoplankton and bacteria upon release into the water through exudation, cell lysis, grazing, or viral attack (Stefels et al., 2007). Conversely, DMS can be oxidized to DMSO through chemical and photochemical processes (Brimblecombe and Shooter, 1986; Chen et al., 2011; Lidbury et al., 2016). The recent uncovering of the DMSP to DMSO oxidation process is noteworthy (Thume et al., 2018). Given the physiological and ecological significance of DMS (P, O), a comprehensive understanding of the sources and spatial variability of dimethyl sulfur compounds is imperative for global sulfur cycle research.

Over the past three decades, the biogeochemical cycle of dimethyl sulfur compounds has been extensively studied not only in Chinese sea areas but also in open ocean regions. For example, studies in the Yellow Sea and Bohai Sea by Guo et al. (2022) and Yang et al. (2014) revealed higher summer concentrations of DMS and DMSP compared to autumn, attributed to variations in the phytoplankton community, with dinoflagellates and diatoms predominating in summer and autumn, respectively. In the East China Sea, Li et al. (2015) found that the distributions of DMS, DMSP, and DMSO paralleled that of chlorophyll *a* (Chl-*a*), with elevated levels in coastal regions and lower levels in open sea areas, suggesting a significant role of phytoplankton biomass in controlling these sulfur compound concentrations. This conclusion was also supported by a study in the northern South China Sea (Zhai et al., 2020). Additionally, Zhang et al. (2014) noted that DMS (P, O) distributions were mainly influenced by the Yangtze River effluent and various oceanic circulations in the South Yellow Sea and East China Sea. In the Changjiang River Estuary and the coastal East China Sea, phytoplankton biomass and water mass mixing were identified as major factors influencing the distribution of dimethyl sulfur compounds (Jian et al., 2019). And Lee et al. (2010) discovered that the peak concentrations of DMS and DMSP occurred at depths of 40 m and 60–80 m, respectively, aligning with the Chl-*a* maximum depth range in the South Pacific Ocean. Research in the Belgian coastal zone of the North Sea by Speeckaert et al. (2018) linked seasonal variations of these

compounds to phytoplankton succession, with high DMS (P, O) producers, mainly *Phaeocystis globosa*, appearing in spring, and low DMS (P, O) producers, various diatoms species, in early spring and autumn. All these studies indicated that phytoplankton community structure was the main factor affecting DMS (P, O) concentration.

However, it was found that in addition to phytoplankton (mainly dinoflagellates, diatoms, and haptophytes), picophytoplankton, and bacteria also had important effects on DMSP concentration in some studies focusing on open oceans. Studies by Bürgermeister et al. (1990) and Merzouk et al. (2008) in the Atlantic Ocean and Zindler et al. (2013) in the Western Pacific Ocean provided insights into the influence of diatoms and bacterioplankton, respectively, on DMS concentration. Zindler et al. (2013) also emphasized the dominance of nano- and picoplankton in the western Pacific Ocean, highlighting the importance of picophytoplankton in oligotrophic marine sulfur cycling. Both heterotrophic bacteria and picophytoplankton were found to assimilate DMSP (Vila-Costa et al., 2006). In the northwest Atlantic Ocean and the Gulf of Mexico, Malmstrom et al. (2005) demonstrated the significant role of *Synechococcus* in the DMSP flux, with higher per-cell DMSP assimilation in *Synechococcus* than in other prokaryotes, especially under full sunlight conditions (Ruiz-Gonzalez et al., 2012). Some *Synechococcus* species, like *Synechococcus elongatus*, were found to lyse DMSP to produce DMS but did not assimilate DMS (Malmstrom et al., 2005).

Therefore, to accurately evaluate the contributions of marine microorganisms on DMS (P, O) concentration, it is necessary to comprehensively consider the co-regulation mechanism of phytoplankton, and bacteria on DMS (P, O). The Indian Ocean heat content has increased abruptly, due to water and heat exchange with the Pacific Ocean (Lee et al., 2015; Desbruyères et al., 2017). It provides opportunities for sulfur cycling research. Hatton et al. (1999) observed that three weeks after the end of the summer monsoon, the average concentration of dimethyl sulfide compounds in the Arabian Sea's eutrophic region was almost twice those in oligotrophic regions. In the 2001 summer monsoon, Shenoy et al. (2006) measured DMS and DMSP concentrations in the Bay of Bengal from 6° N to 20° N, finding both confined to the upper 40 m of the water column, with diatoms as the primary contributors. Shenoy and Kumar (2007) investigated DMS variability in the Indian Ocean, noting the highest average surface DMS in the Arabian Sea and the highest average flux in the Bay of Bengal. O'Brien et al. (2022) explored DMSPd surface distribution along the 110°E transect, discovering a high concentration of DMSPd in ultra-oligotrophic low-latitude waters, contrasting with nutrient-rich high-latitude waters. Although significant latitudinal variations in DMSP production and cleavage genes were reported, those of DMS and DMSO remain unexplored. It is not difficult to find that previous studies mainly focused on the effects of environmental factors, phytoplankton (mainly dinoflagellates, diatoms, and haptophytes), and latitude on DMS (P, O) in the eastern Indian Ocean (EIO), with the picophytoplankton being neglected. The role of picophytoplankton in the EIO is particularly crucial, with average Chl-*a* concentrations of picophytoplankton accounting for over 49.6% of total Chl-*a* (Wei et al., 2019). Their impact might be overestimated if only bacteria and phytoplankton (mainly dinoflagellates, diatoms, and haptophytes)

contributions to DMS (P, O) are considered. Therefore, a more precise characterization of microorganisms' (phytoplankton, bacteria) contributions to DMS (P, O) concentration in the EIO is essential. This study presents a field survey to ascertain the spatial distribution characteristics of DMS (P, O) in the EIO, assessing their interactions with environmental and biological factors using generalized additive models (GAMs) and structural equation modeling (SEM) to elucidate potential environmental and biological regulatory mechanisms of DMS (P, O). The findings aim to enhance understanding of the biogeochemical cycle of dimethyl sulfur compounds in the EIO.

2 Materials and methods

2.1 Study area and sample collection

The cruise took place from October to November 2020, encompassing field surveys at a total of 19 stations in the EIO, as shown in Figure 1. SA section is situated along the equator, while the SB section is located at the region perpendicular to the equator. By using conductivity-temperature-depth (CTD) sensors (Sea-Bird Electronics Inc., Bellevue, USA) equipped with 1L Niskin bottles, seawater samples in 7 depths (generally in 5, 25, 50, 75, 100, 150,

and 200 m) were collected. Temperature and salinity data were obtained from the seabird CTD sensor. 40 mL seawater for DMS was gathered from CTD slowly into an amber glass via an acid-cleaned Tygon tubing. 25 mL seawater for DMSPt and DMSOt was pretreated with 100 μ L 50% sulfuric acid and 100 μ L 25% hydrochloric acid, respectively, as well as 25 mL seawater filtered by gravitational pressure was collected for DMSPd and DMSOd analysis, and then severally treated with sulfuric acid and hydrochloric acid (Zhai et al., 2018). All DSC samples were sealed and stored in the dark at 4°C and analyzed immediately following their transportation to the lab. The seawater samples of Chl-a and nutrients were filtered through Whatman GF/F glass fiber membranes (25 mm diameter, 0.7 μ m) and immediately stored at -20°C until they were measured. Phytoplankton samples were loaded in 1L polyethylene bottles, fixed with 3% formaldehyde solution, and placed in shade.

2.2 Analytical procedures

Samples of DMS, DMSP, and DMSO were determined using the established method based on ion mobility spectrometry (Peng et al., 2020, 2022). The concentration of DMS was measured via gas stripping, while those of DMSP and DMSO were obtained indirectly by measuring DMS content. The frozen DMSO and DMSP samples were restored to room temperature and then purged with zero air to remove any present DMS. 500 μ L and 200 μ L of KOH (10 mol/L) solution was added to the DMSPt and DMSPd seawater samples, respectively. Then the samples were sealed and placed in the dark at 4°C for 24 h to ensure the DMSP completely converted to detectable DMS (Yang et al., 2016). Subsequently, the concentrations of DMSPt and DMSPd were indirectly obtained by measuring the content of DMS, and the content of DMSPp could be calculated from their difference. The DMSO sample was treated with 200 μ L of 20% TiCl_3 solution, then sealed and placed in a constant temperature water bath at 55°C. After the complete reaction for 1 h, the DMSO in samples could be reduced to DMS and then determined (Kiene and Gerard, 1994). The DMSOp content could be defined as the difference between DMSOt and DMSOd.

According to the method of Hansen and Koroleff (1999), the nutrients in the seawater sample were determined via a Technicon AA3 autoanalyzer (Bran + Luebbe, Norderstedt, Germany). Silicates (DSI) could be determined by using the silicon-molybdenum blue method with a limit of detection (LOD) of 0.02 μ mol/L (Isshiki et al., 1991). The concentrations of nitrate (NO_3^-) and ammonium (NH_4^+) were determined through the cadmium copper column reduction method with a LOD of 0.01 μ mol/L (Wood et al., 1967) and the sodium salicylate method with a LOD of 0.03 μ mol/L (Verdouw et al., 1978), respectively. The concentrations of phosphates (DIP) and nitrite (NO_2^-) were determined using the phosphomolybdenum blue method with a LOD of 0.02 μ mol/L (Taguchi et al., 1985) and the naphthalene ethylenediamine method with a LOD of 0.01 μ mol/L (Wang et al., 2022a), respectively.

The filter membrane of Chl-a was placed into a 10 mL brown glass tube and then extracted with 5 mL acetone with a volume fraction of 90% in the dark at 4°C for 24 h. The content of Chl-a was

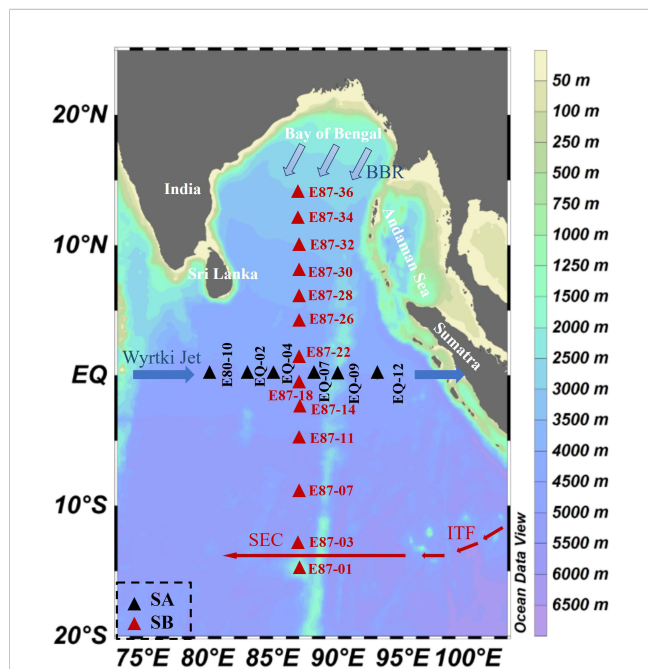


FIGURE 1

Map representing sampling locations and major ocean currents over the eastern Indian Ocean (EIO) from October to November 2020. The current systems include the Bay of Bengal (BBR), Equatorial Jets (Wyrтки jets), South Equatorial Current (SEC), and Indonesian Through Flow (ITF). The red arrow indicates the prevailing circulation throughout the year, and the solid blue arrow indicates the Ejs (Wyrтки jets) occurring in spring and autumn. The thickness of the line indicates the corresponding circulation strength. Black triangles represent the SA section and red triangles represent the SB section (Peng et al., 2015; Wei et al., 2019; Guo et al., 2021; Liu et al., 2022; Ikhsani et al., 2023).

measured by Turner-Designs Trilogy fluorometer (Sunnyvale, CA, USA) (Welschmeyer, 1994). For phytoplankton analysis, 1L samples were concentrated in a 100 mL sedimentation column for 24 to 48 hours. The identification and counting of the phytoplankton cells were conducted by inverted microscope at 400× (or 200×). The methods of Yamaji (1984), Jin et al. (1965), and Sun et al. (2002) were used to determine the species of phytoplankton (Wang et al., 2022b). The abundances of picophytoplankton and bacteria were enumerated via a flow cytometer (FCM, Becton-Dickinson Accuri C6) equipped with a laser emitting at 488 nm (Sgorbati, 2007; Wei et al., 2019).

2.3 Statistical analyses

DMS (P, O) horizontal and vertical distributions were depicted using Ocean data view 4. The aggregated boosted tree (ABT) analysis was applied to quantify the impact of environmental and biological factors on the DMS (P, O) concentrations by the “gbmplus” package with 500 trees for boosting in R. Generalized additive models (GAMs) was adopted to fit relationship between response and explanatory variables by the R package “mgcv”. The structural equation model (SEM) was employed to reveal the causal relationship of DMS (P, O) and key factors. Only when Supplementary Figure S1 was plotted, missing data were imputed using linear interpolation according to the characteristics of the data.

3 Results

3.1 Horizontal distribution of DMS (P, O)

In the surface layer, concentrations of DMS, DMSPt, and DMSOt varied from 0.07 to 7.37 nmol/L, 0.14 to 9.17 nmol/L, and 0.15 to 3.32 nmol/L, respectively (Figures 2A–C). DMS and DMSPt showed similar distribution patterns, gradually increasing from 14°N to 6°N and then decreasing from 6°N to 14°S (Figures 2A, B). DMSOt, however, was primarily concentrated between 10°N to 5°S (Figure 2C). The highest concentration of DMS (6.56 nmol/L) and DMSPt (7.20 nmol/L) was observed at

station EQ-07, while that of and for DMSOt at EQ-04 (3.06 nmol/L) and E87-18 (3.32 nmol/L) near the equator. This pattern was linked to the Wyrтки jets (WJs) within 2° of the Equator (Wang, 2017), which transported high DMS (P, O) surface seawater from west to east, resulting in higher concentrations from 85°E to 88°E (Wei et al., 2019). Perpendicular to the equator, the highest DMS and DMSPt values were 7.37 nmol/L and 9.71 nmol/L at station E87-28, respectively, correlating with high Chl-a concentrations near Sri Lanka (Figure 2D). These findings align with previous studies indicating a positive correlation between DMS, DMSP concentrations, and Chl-a in coastal regions (Zhang et al., 2014; Li et al., 2015; Zhai et al., 2020).

3.2 Vertical distribution of DMS (P, O)

3.2.1 Overall vertical variation

Figure 3 illustrates the depth-dependent variability of DMS (P, O) concentrations, consistent with findings in the Northern South China Sea (Zhai et al., 2020). Average values of DMS and DMSPt were higher at 5m, 25m, and 50m depths (Figures 3A, B), while the mean value of DMSOt was higher at 75m, 100m, and 150m depths (Figure 3C). Chl-a reached its maximum at 75m (Figure 3D), which did not coincide with the peaks of DMS and DMSPt. A notable shift in DMS (P, O) concentrations occurred at 75m: DMS and DMSPt concentrations decreased sharply beyond this depth, while DMSOt increased. Significant differences in DMS and DMSP concentrations between 75m and 100m depths were identified, and for DMSPt between 50m and 75m, and DMSOt between 5m and 25m depths (Figures 3A–C). Based on these results, four distinct water layers were categorized: 5m (A), 25m, 50m (B), 75m (C), 100m, 150m, 200m (D). Subsequent correlation analysis between DMS (P, O) and environmental/biological factors was conducted for these layers (Supplementary Figure S1, detailed in 3.2.2). DMSPP was the major component of DMSPt from 5m to 75 m, significantly exceeding DMSPD concentrations (Figure 3E). DMSOt concentrations comprised nearly equal proportions of DMSOp and DMSOd, except at 50m and 75m depths where DMSOp was slightly higher (Figure 3F).

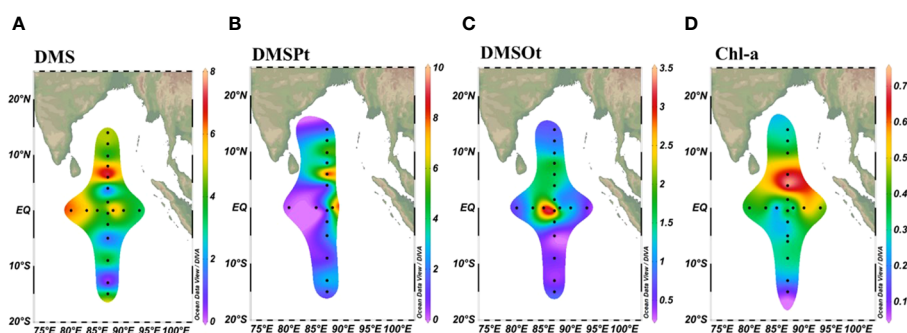


FIGURE 2
Spatial distribution of DMS (A), DMSPt (B), DMSOt (C), and Chl-a (D) at the sea surface (5m) in the IEO.

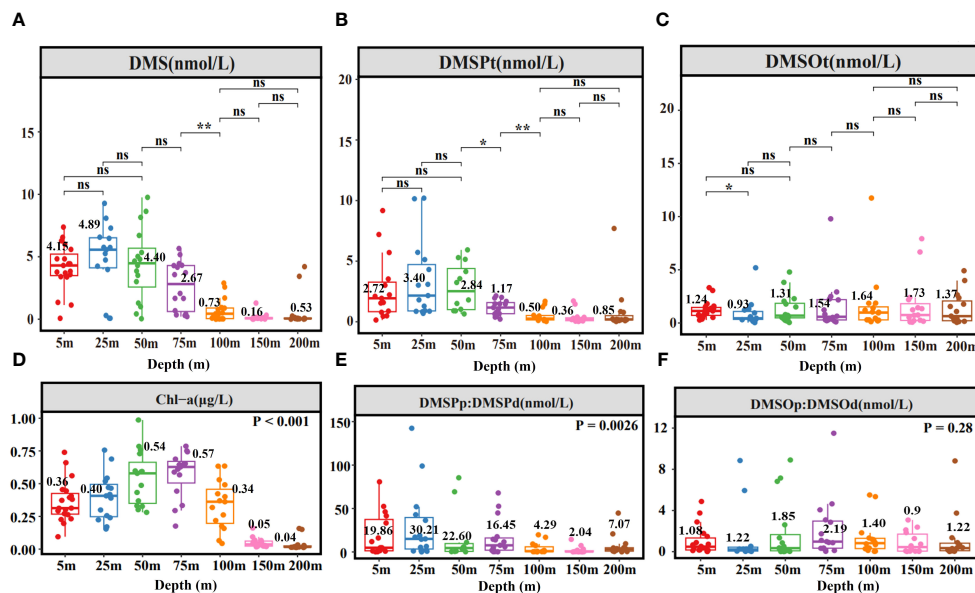


FIGURE 3

Depth box plot of DMS (A), DMSPt (B), DMSOt (C), Chl-a (D), DMSPP: DMSPd (E), DMSOp: DMSOd (F) in EIO. Numbers represent mean values. *, **, ns, indicate significance levels at $p < 0.05$, $p < 0.01$, and $p > 0.05$, respectively.

3.2.2 Section distribution

The SA and SB sections, influenced by the Wyrтки jets, Bay of Bengal runoff (BBR), and South Equatorial Current (SEC), were selected to study the impact of ocean currents on DMS (P, O) distribution. In the SA section, DMS and DMSPt concentrations were confined to depths shallower than 75 m and diminished rapidly beyond 100 m (Figures 4A, B). DMSOt was predominantly observed between 5–100 m depths from 87°E to 95°E and between 100–200m west of 80°E (Figure 4C). Notably, the highest DMS value (9.76 nmol/L) was recorded at 50 m depth at station E80-10, coinciding with a peak in bacterial concentration (Supplementary Figure S2). A significant correlation between DMS and bacteria at 50 m depth (Supplementary Figure S1) highlighted bacteria's role in regulating DMS concentration. The highest DMSPt (10.15 nmol/L) was found at 25 m depth at station EQ-07, and DMSOt (9.79 nmol/L) at 75 m depth at station EQ-09 (Figures 4B, C), likely due to Wyrтки jets, and their distribution of higher concentration was not consistent with that of Chl-a (Figure 4D). In the SB section, DMS and DMSPt concentrations gradually decreased with depth, with peaks (9.27 nmol/L for DMS and 10.20 nmol/L for DMSPt) at 25 m depth at station E87-28 (Figures 4E, F). Significant correlations were noted between DMS, DMSPt, *Prochlorococcus* (*Pro*), and *Synechococcus* (*Syn*) at 25 m depth (Supplementary Figure S1), suggesting their importance in influencing DMS and DMSPt concentrations. DMSOt distribution was more uniform, with concentrations increasing at depths beyond 75m, peaking (11.75 nmol/L) at 100 m depth at station E87-18 (Figure 4G). We observed slight increases in DMS and DMSPt at 200 m depth compared to those at 100m and 150m depths (Figures 4A, E, F). The phenomenon is possibly due to accumulation and sedimentation of suspended organic matter (Speeckaert et al., 2018). DMS (P, O) concentrations were generally higher north of the equator than south, influenced by BBR and SEC. Distinct factors impacted

DMS (P, O) concentrations at different depths: at 25m and 50m, DMS concentration was linked to bacteria, while DMSPt and DMSOt correlated with picophytoplankton and temperature, respectively. From 75m to 200m, DMS was primarily associated with Chl-a, temperature, DIP, and DSI, whereas both DMSPt at 75m and DMSOt at 100–200m were related to *Pro* (Supplementary Figure S1).

3.3 Sea-to-air fluxes of DMS

The sea-to-air exchange flux of DMS was estimated using the stagnant film model and relevant empirical equations (Saltzman et al., 1993; Nightingale et al., 2000). The fluxes ranged from 3.44 to 329.03 $\mu\text{mol m}^{-2} \text{d}^{-1}$, with an average of 79.76 $\mu\text{mol m}^{-2} \text{d}^{-1}$. The highest fluxes, 329.03 $\mu\text{mol m}^{-2} \text{d}^{-1}$ at station E87-28 and 265.99 $\mu\text{mol m}^{-2} \text{d}^{-1}$ at station E80-10 showed a general weakening trend from west to east and north to south, consistent with the surface DMS distribution (Figures 2A, 5A). DMS, temperature, and wind speed based on data collected between 1987 and 2001 of the eastern Indian Ocean (data retrieved from the DMS Database: <https://saga.pmel.noaa.gov/dms/>) were analyzed to determine if there was a transient change of DMS concentration and sea-to-air flux (Figures 5B, C). DMS concentration with no significant correlation to the sampling site (Figures 5D, E). While the sampling site's impact was less pronounced for fluxes (Figures 5G, H), there was a peak in sea-to-air flux around 15°N–20°N (Figure 5G). Both DMS concentration and fluxes varied seasonally but with different trends, probably due to wind speed (Figures 5F, I). DMS concentration increased monotonically from June to November (Figure 5F). However, the fluxes increased from June to August and decreased from September to November (Figure 5I), which aligns with the previous study indicating DMS emissions elevated during the

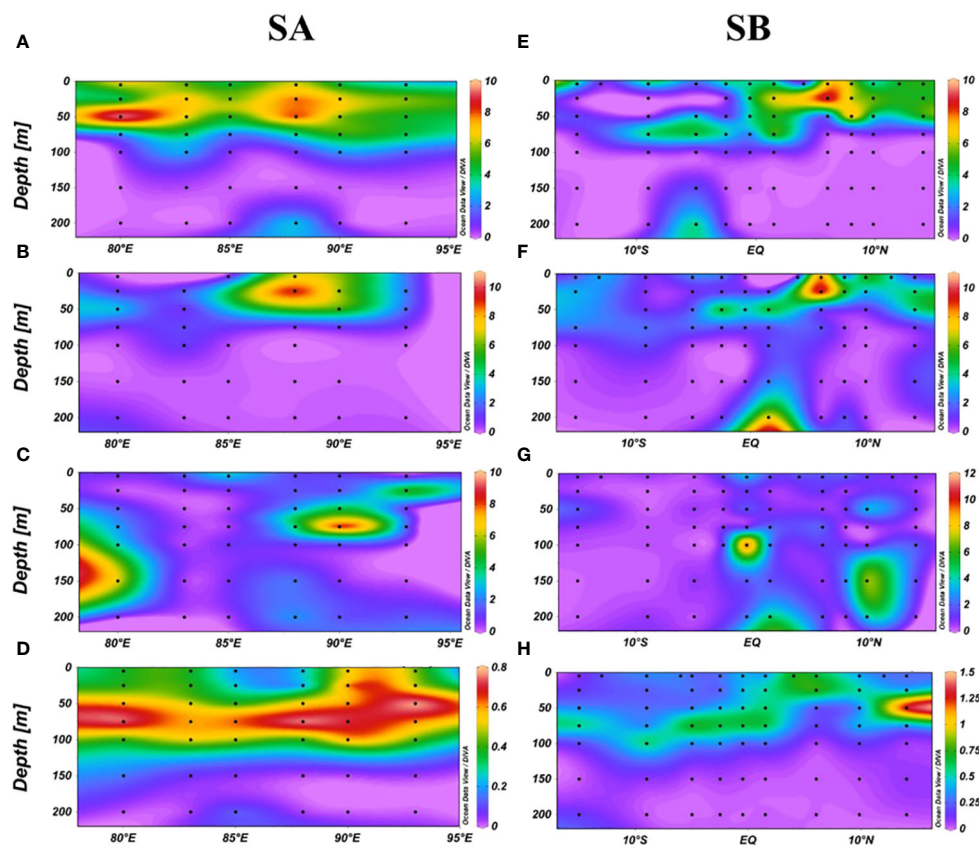


FIGURE 4
Vertical distribution of DMS (A), DMSPt (B), DMSOt (C), Chl-a (D) in the SA section, and DMS (E), DMSPt (F), DMSOt (G), Chl-a (H) in the SB section.

Central Indian Ocean summer (Hulswar et al., 2022). The monthly mean fluxes in these six years (1987, 1998, 1999, 2000, 2001, 2020) were shown in Supplementary Table S1.

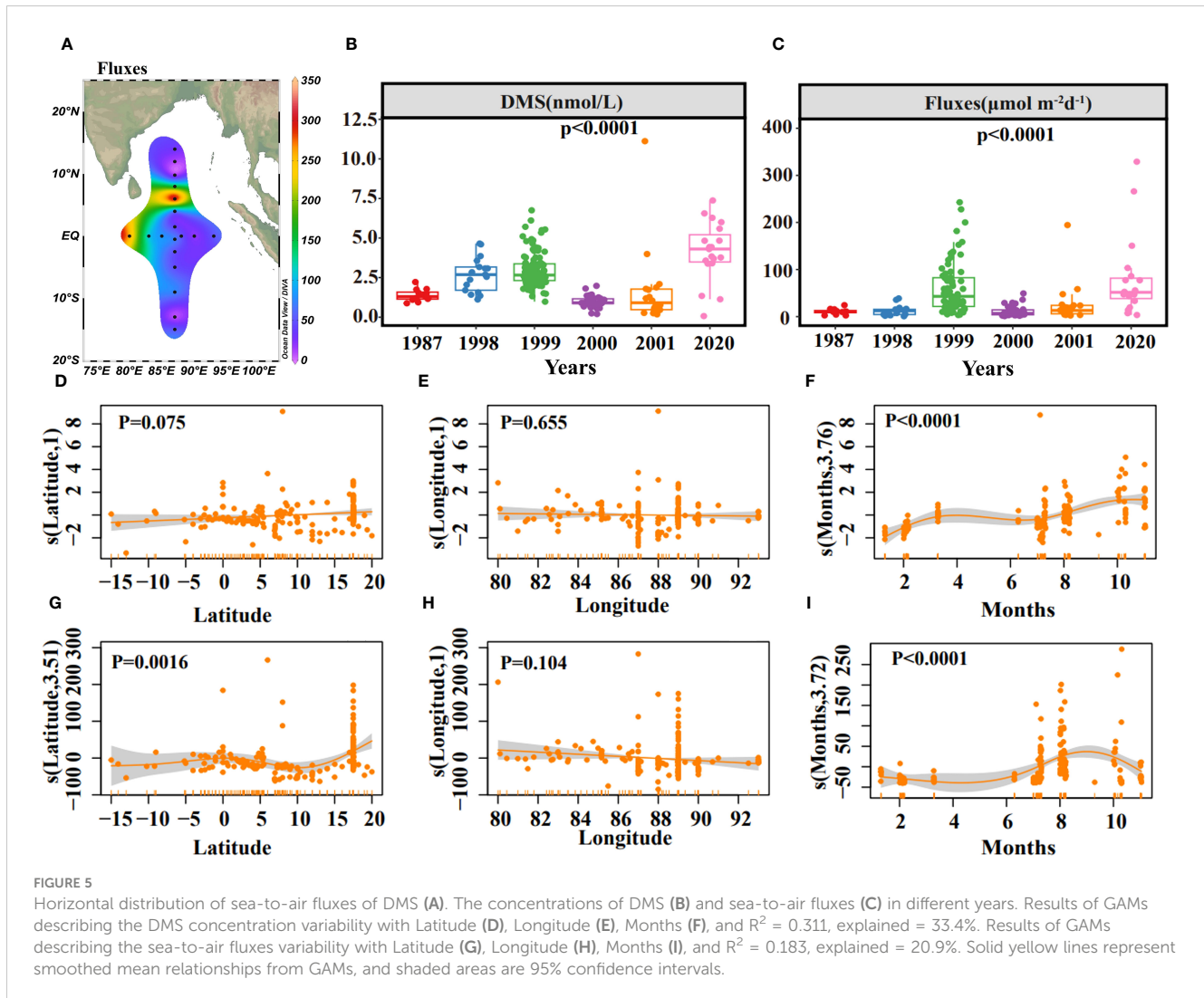
3.4 The relation between DMS (P, O) and environmental/biological factors

Spearman's correlation analysis elucidated the relationship between DMS (P, O) and environmental/biological factors throughout the water column. Temperature showed a significant positive correlation with DMS (P), while NO_3^- , DIP, and DSI were negatively correlated. Chl-a, *Pro*, and *Syn* all correlated positively with DMS (P). However, no factors were significantly correlated with DMSOt (Figure 6A). These results aligned with those for different groups in Supplementary Figure S1. An aggregated boosted tree (ABT) analysis quantified the relative impacts of different parameters on the DMS (P, O), indicating temperature and DSI as the most significant for DMS, and NO_3^- for DMSPt and DMSOt. *Pro* significantly affected the concentrations of DMS, DMSPt, and DMSOt, with latitude also having a notable effect on DMSOt (23.33%). In addition, *Syn* significantly affected DMS contents. Bacteria and Chl-a were important biological factors affecting DMSPt, while

Chl-a and *PEuks* for DMSOt (Figures 6B–D). The top four important parameters of the ABT model would be fitted nonlinearly using generalized additive models (GAMs).

Generalized additive models (GAMs) confirmed temperature, DSI, *Pro*, and *Syn* as strong predictors of DMS (all $P < 0.05$). DMS concentration increased with rising temperature and decreasing DSI (Figures 7A, B). An increased abundance of *Syn* and *Pro* was beneficial for higher DMS concentrations (Figures 7C, D). The interaction model indicated that DMS concentration increased significantly after 23°C and decreased with rising DSI (Figure 8A). The interplay between *Pro* and *Syn* suggested that maximum DMS contents occurred at their highest abundance, with *Syn* contributing more to DMS concentration than *Pro* (Figure 8B).

For DMSPt, *Pro*, bacteria, Chl-a, and NO_3^- were strong predictors (all $P < 0.05$). DMSPt concentration increased with a rising abundance of *Pro*, bacteria, and Chl-a, but decreased with increasing NO_3^- (Figures 7E–H). Surprisingly, in the interaction of Chl-a and NO_3^- , DMSPt concentration decreased with increasing Chl-a (Figure 8C). The interaction between *Pro* and bacteria showed a unique peak in DMSPt concentration at around 50 bacteria (Figure 8D). The DMSPt concentration first increased and then decreased with rising bacteria abundance, while it continuously increased with *Pro* abundance. The highest DMSPt



was observed when bacteria were around 50 and *Pro* abundance was at its maximum. If both X and Y axes were zero, axis Z still had intercepted, indicating the presence of other vital microorganisms affecting DMSpt in the EIO (Figures 8C, D). Based on the ABT results, we proceeded to explore the effect of *Pro* and *Syn* interaction on DMSpt. *Syn* had a greater impact on DMSpt than *Pro* (Figure 8E), and DMSpt decreased with increasing Chl-a in the interaction of Chl-a and other biological factors (Figures 8F–H).

Latitude, NO_3^- , and *Pro* were significant indicators for DMSOt in GAMs (Figures 7I–K, all $P < 0.05$), while the relationship between DMSOt and Chl-a could not be fitted ($R^2 < 0$, data not shown). DMSOt concentration enhanced as the location approached the northern latitude (Figure 7I) and had a broad peak around $5 \mu\text{mol/L NO}_3^-$ (Figure 7J). The correlation between *Pro* and DMSOt was monotonically negative (Figure 7K). The interaction between NO_3^- and latitude was complex, with a single peak in DMSOt concentration at 5°N and $10 \mu\text{mol/L NO}_3^-$ (Figure 8I). Lower *Pro* abundance near the equator favored increased DMSOt (Figure 8J).

4 Discussion

4.1 DMS (P, O) distribution variations

In surface seawater, the DMS concentrations observed in this study were within the range reported for open sea areas (Table 1), yet the mean value was marginally higher. The mean DMSpt concentration resembled that in the Western Pacific Ocean during the survey period 2009.10.9 to 10.24 but was lower compared to other regions. The mean DMSOt value aligned with those in the Arabian Sea, but was lower than in the Western Mediterranean and Western Pacific Ocean. Notably, even in identical sea areas and seasons, the range and mean value of DMS (P, O) exhibited slight variations due to differences in specific sampling locations and timings, as exemplified by studies in two different periods in the Western Pacific Ocean in Table 1. The temporal and spatial variability of the DMS (P, O) might correlate with distinct microbial community structures in various oceanic regions (Shenoy and Kumar, 2007).

Vertically, DMS and DMSpt concentrations were primarily found in water columns shallower than 75 m, whereas higher

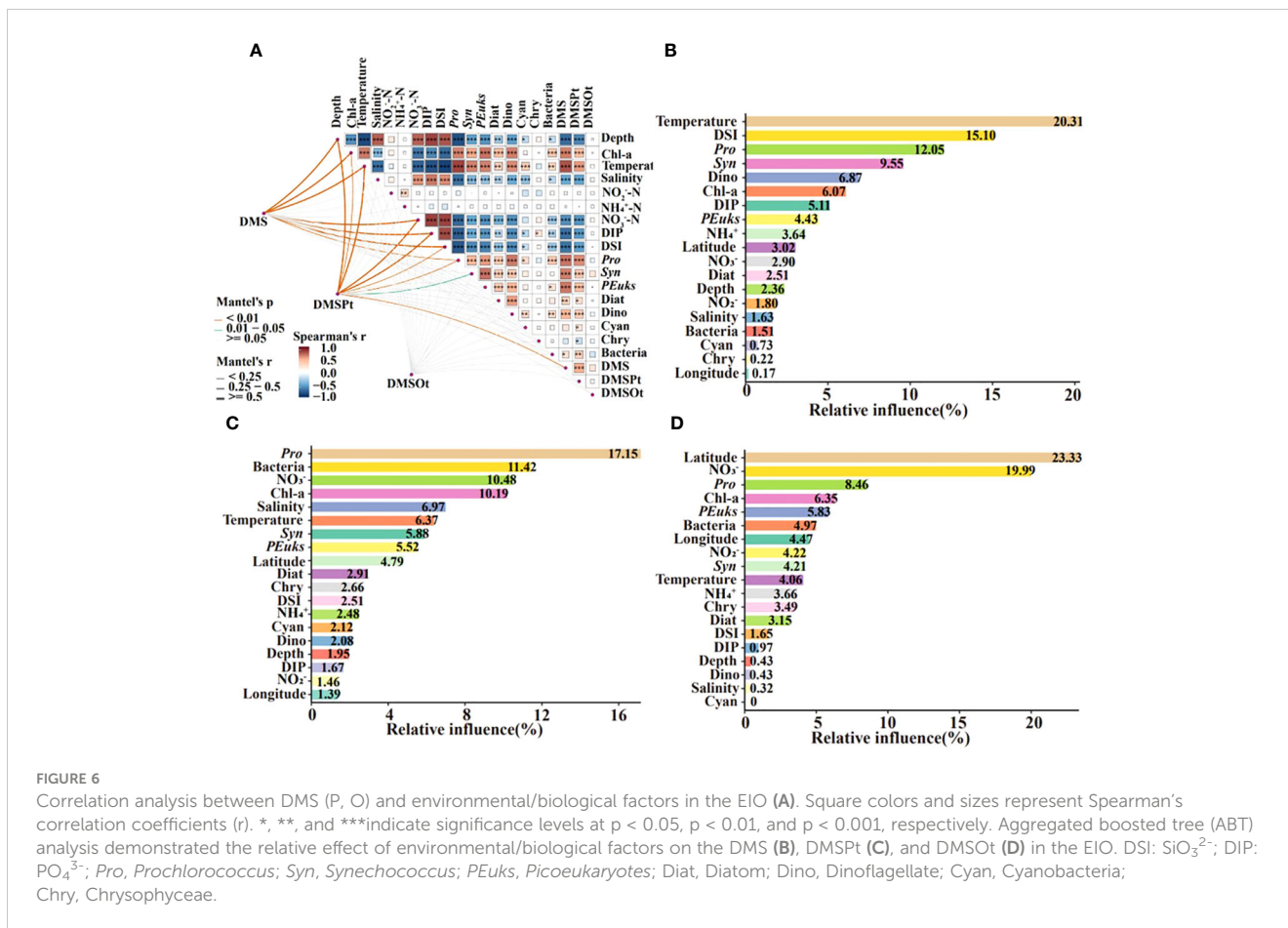


FIGURE 6

Correlation analysis between DMS (P, O) and environmental/biological factors in the EIO (A). Square colors and sizes represent Spearman's correlation coefficients (r). *, **, and *** indicate significance levels at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively. Aggregated boosted tree (ABT) analysis demonstrated the relative effect of environmental/biological factors on the DMS (B), DMSPt (C), and DMSOt (D) in the EIO. DSI: SiO_3^{2-} ; DIP: PO_4^{3-} ; Pro, *Prochlorococcus*; Syn, *Synechococcus*; PEuKs, *Picoeukaryotes*; Diat, Diatom; Dino, Dinoflagellate; Cyan, Cyanobacteria; Chry, Chrysophyceae.

DMSOt concentrations occurred at depths deeper than 75 m. Influenced by the west-to-east Wyrтки jets, elevated DMS (P, O) values were primarily observed near the equator between 87°E and 90°E in the SA section. In the SB section, DMS (P, O) distribution was influenced by the BBR and SEC. The greater precipitation than evaporation in the Bay of Bengal resulted in a low salinity layer north of 8°N (Supplementary Figure S2H) (Rao and Jayaraman, 1968; Sengupta et al., 2006), which stimulated phytoplankton production (Figure 4H). Concurrently, the SEC transported high-nutrient and high-Chl-a seawater from east to west south of 5°S (Figure 4H; Supplementary Figures S2I–K), leading to lower DMS (P, O) values (Gao et al., 2021). However, due to missing data from some sampling sites south of the equator, biomass and DMS (P, O) concentrations were likely underestimated (Figures 4E–H).

4.2 Environmental factors in relation to DMS (P, O)

Temperature emerged as the most critical environmental factor affecting DMS concentration, in line with previous studies (Boyd et al., 2013; Guo et al., 2022). The metabolic processes of phytoplankton, including those involving enzymes essential for

DMS production and metabolism, are temperature-dependent (Gao et al., 2017). Notably, the impact of temperature on DMS was modulated by the interaction between temperature and DSI (Figures 7A, 8A). DSI indirectly regulated DMS concentration by influencing the biomass of *Pro* and *Syn*. The significant negative correlation between DSI and these organisms suggested that high DSI concentrations inhibited their growth (Figure 6A), corroborating findings from Wang et al. (2022c). DMSPt content increased with intensifying nitrogen limitation, as illustrated in Figure 7H. Previous research highlighted the role of the transamination reaction in the DMSPt synthesis pathway, allocating nitrogen to new amino acids (Dacey et al., 1987; Hanson et al., 1994; Colmer et al., 1996; Gage et al., 1997; Curran et al., 1998). Therefore, abundant DMSPt could conserve nitrogen in cells under nitrogen-limited conditions (Stefels, 2000), particularly in the oligotrophic waters of the EIO. Meanwhile, NO_3^- was identified as the most influential environmental factor for DMSOt through ABT analysis (Figure 6D) and SEM (Figure 9A). The optimal NO_3^- concentration for DMSOt production was around 5 $\mu\text{mol/L}$, as indicated in Figure 7J, with an interaction effect of NO_3^- and latitude observed at 10 $\mu\text{mol/L}$ (Figure 8I). These results suggest an optimum NO_3^- concentration for DMSOt production; relevant Laboratory evidence is needed to validate the result.

4.3 Biological factors in relation to DMS (P, O)

4.3.1 Biological factors in relation to DMS

Current understanding posits that *Syn* and *Pro* impact to DMS concentration via two pathways: cleaving DMSP to produce DMS or synthesizing DMS directly. While some studies suggested that certain cyanobacteria cleaved DMSP to yield DMS (Malmstrom et al., 2005), the consistently positive correlation between DMSPt and *Syn*, *Pro* in this study indicated that this pathway was not predominant. If *Syn* and *Pro* produced DMS by cleaving DMSP, a negative correlation between DMSPt and these organisms would be expected; however, we observed the opposite (Figure 8E). Additionally, Carrion et al. (2015) discovered that cyanobacteria possess the gene *mddA*, which encodes a methyltransferase that methylates methanethiol (MeSH) to generate DMS. More importantly, *Syn* and *Pro* can uptake MeSH from the ocean, with *Syn* exhibiting a higher assimilation capacity than other prokaryotic communities (Malmstrom et al., 2005),

providing precursors for DMS synthesis. Therefore, the positive correlation between DMS and *Syn* and *Pro* likely arises from their synthetic capability. Given its high MeSH assimilation efficiency and widespread distribution (Supplementary Figure S3), *Syn* is likely a significant DMS source in the EIO.

4.3.2 Biological factors in relation to DMSPt

The monotonically positive correlation between DMSPt and the abundance of *Syn*, *Pro*, as seen in Figure 8E, contradicts Keller et al.'s (Keller et al., 1989) finding that cyanobacteria produce negligible DMSPt. This suggests that the observed correlation is not due to direct synthesis by *Syn* and *Pro*. We propose that *Pro* and *Syn* efficiently uptake and store DMSPt. Previous research indicated that low- or non-DMSP-producing species like diatoms and cyanobacteria absorbed DMSPt, while strong DMSPt producers such as chrysophyceae and dinoflagellate cannot (Vila-Costa et al., 2006). Cyanobacteria, due to their larger size, incorporate more DMSPt per cell than heterotrophic bacterium. However, on a per biovolume basis, heterotrophic bacteria demonstrate the highest DMSPt uptake efficiency, followed closely by

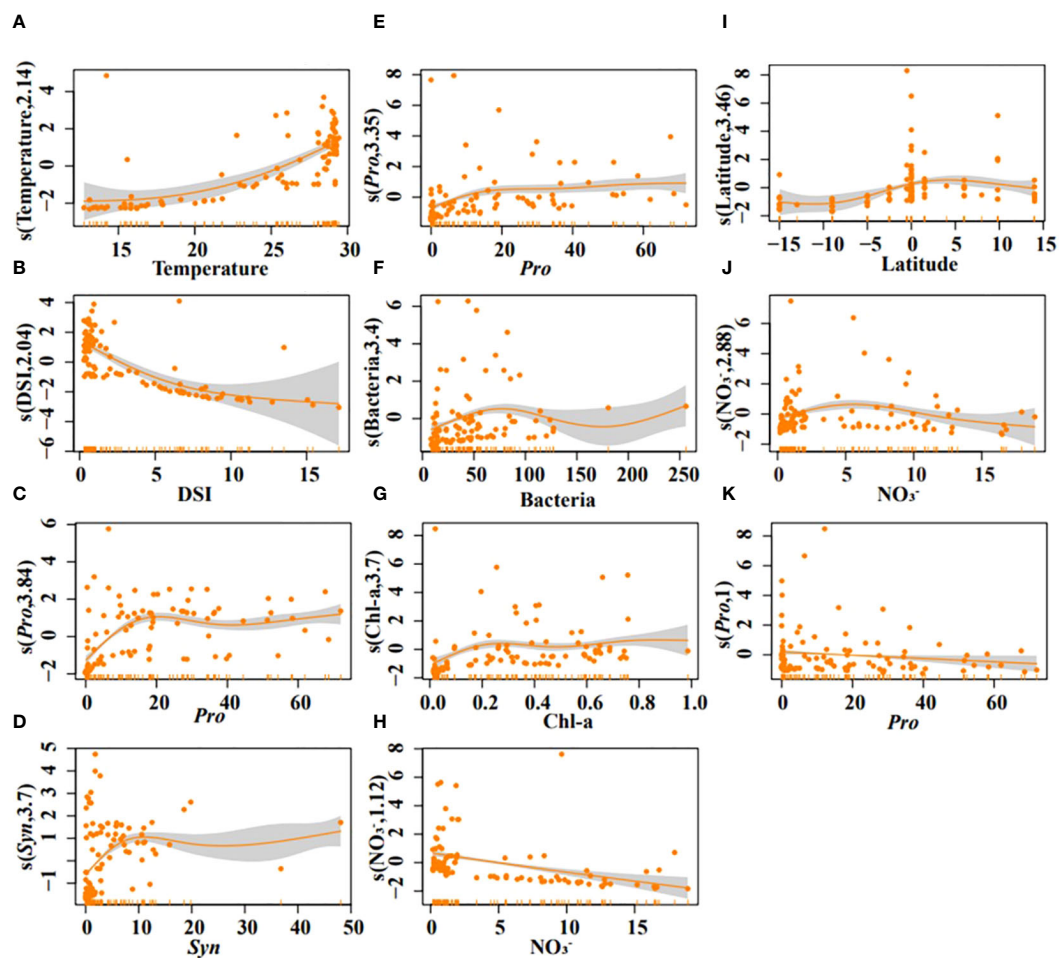


FIGURE 7
Results of GAMs describing the variability of DMS (A–D), DMSPt (E–H), and DMSOt (I–K) with environmental/biological factors in the EIO. Temperature (A), DSI (B), *Pro* (C), and *Syn* (D); *Pro* (E), bacteria (F), Chl-a (G), and NO_3^- (H); Latitude (I), NO_3^- (J), *Pro* (K).

Syn, *Pro*, and *PEu*ks (Vila-Costa et al., 2006; Ruiz-Gonzalez et al., 2012). Spielmeier et al. (2011) used isotopically labeled DMSP ($[^{13}\text{C}_2\text{D}_6]$ DMSP) to study its fate in phytoplankton, finding that diatoms, which do not produce DMSP, exhibited intense uptake signals without converting the absorbed DMSP to other substances. This supports the notion that absorbed DMSP is stored rather than metabolized. Petrou and Nielsen (2018) also observed that *Thalassiosira weissflogii*, a non-DMSP-producing diatom, completely retained ingested DMSP within the cell for at least 6 hours, indicating a significant DMSP sink in non-producing species. DMSP uptake, an energy-expending process, is presumably more efficient in incorporating reduced sulfur from DMSP directly than from sulfate (Kiene et al., 2000). In this study, *Pro* was the dominant prokaryotic phytoplankton numerically, followed by *Syn* (Supplementary Figure S3). However, *Syn* exhibited a notably higher DMSP absorption capacity than *Pro* (Ruiz-Gonzalez et al., 2012), making it an important DMSP sink in the EIO.

The positive correlation of DMSP with Chl-a in Figure 7G was consistent with previous findings (Zhang et al., 2014; Zhai et al., 2020), yet a negative synergy of Chl-a with other factors was presented in Figures 8F–H. Despite Chl-a's positive effect on DMSP, the consumption of DMSP by chlorophyll-rich phyto- and picoplankton appeared more significant under the influence of Chl-a and other biological factors. Given bacteria's capacity to synthesize and metabolize DMSP (Stefels et al., 2007; Curson et al., 2017), DMSP contents fluctuated with bacteria abundance, as shown in Figures 7F, 8D. At lower bacterial abundance levels, an initial promoting effect on DMSP was observed, followed by an inhibitory effect as bacteria abundance increased. When bacterial abundance exceeded 200, DMSP was again stimulated to increase (Figure 8D). This fluctuation suggests that bacteria communities modulate their response (production or degradation) to DMSP based on their abundance, though the underlying regulatory mechanism remains unexplored.

4.3.3 Biological factors in relation to DMSOt

A negative correlation between *Pro* and DMSOt was observed in Figures 7K, 8J, yet relationships of DMSOt and other biological factors could not be fitted by GAMs ($R^2 < 0$, data not shown). Combined with SEM results (discussed in 4.4), *Pro* emerged as the most important factor for DMSOt consumption.

4.4 The contributions of the key factors to DMS (P, O)

The SEM not only elucidated the causal relationships among different microorganisms and DMS (P, O), but also clarified the interconversion process among DMS, DMSPt, and DMSOt (Figure 9A). The total effects of phytoplankton (-0.141) and bacteria (-0.196) on DMS were negative, whereas those of picophytoplankton (0.429), DMSPt (0.32), and DMSOt (0.19) were positive. These findings suggest that DMS is mainly produced by picophytoplankton, DMSPt cleavage, and DMSOt reduction, yet is predominantly consumed by phytoplankton and bacteria in the EIO. The direct effect of picophytoplankton (0.55) on DMSPt was positive, while the indirect effect was negative (-0.033), consistent with observations that most picophytoplankton take up DMSPt for intracellular storage, and certain species cleave DMSP. The overall effects of bacteria and phytoplankton on DMSPt were positive (0.05) and negative (-0.11), respectively, indicating that bacteria contribute to the DMSPt source, whereas phytoplankton primarily depletes it. The overall effect of picophytoplankton on DMSOt was negative (-0.206), exceeding that of bacteria (-0.15). In addition, the indirect positive effect of phytoplankton on DMSOt (0.0088) suggests that phytoplankton are biological producers of DMSOt. Moreover, the total positive effect (0.1288) of DMSPt on DMSOt demonstrates that DMSPt oxidation is a significant source

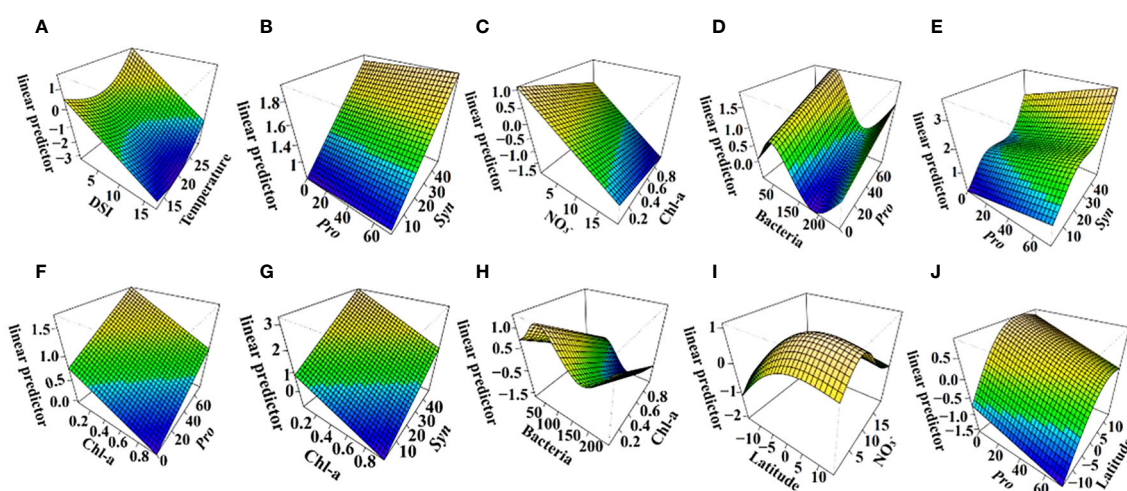


FIGURE 8

Linear predictor of DMS (A, B), DMSPt (C–H), and DMSOt (I, J) with interaction of environmental/biological factors based on GAMs in the EIO. $R^2 = 0.638$, explained = 68.3% (A, B); $R^2 = 0.421$, explained = 46.4% (C–H); $R^2 = 0.12$, explained = 23.7% (I, J).

TABLE 1 The concentrations of DMS, DMSPt, and DMSOt in surface seawater in areas of the open sea.

Investigation time	Investigation area	DMS (nmol/L)	DMSPt (nmol/L)	DMSOt (nmol/L)	Reference
2020.10-11	EIO	0.07-7.37	0.14-9.17	0.15-3.32	This study
	Average	4.15±1.87	2.72	1.24	
1993.6	Western Mediterranean	0-19.3	–	0.07-61.9	Simo et al. (1997)
	Average	2.9±4.3	–	16.6±13.7	
1994.8.27-10.4	Arabian Sea	0.6-5.3	7.5-35.6	1.5-13.2	Hatton et al. (1999)
	Average	2.1	18.5	4.3	
2001.6.6-8.2	Bay of Bengal	0.2-11.1	0.7-22.7	–	Shenoy et al. (2006)
	Average	1.7±2.5	8.8	–	
2009.10.9-10.24	Western Pacific Ocean	–	–	–	Zindler et al. (2013)
	Average	0.9	3.6	15.9	
2015.11.8-2016.1.11	Western Pacific Ocean	0.93-2.16	3.55-10.77	3.86-12.01	Xu et al. (2021)
	Average	1.32	7.53	8.02	
1997-2004	Atlantic	0.27-2.44	3.05-26.43	–	Bell et al. (2010)
	Average	1.09	8.81	–	
2015.7.10-8.20	Canadian Arctic	0.2-12	<1-160	–	Jarníková et al. (2018)
	Average	2.7±1.5	30±29	–	
2016 winter	Antarctic Peninsula (Ryder Bay)	0.1-7.1	–	–	Webb et al. (2019)
	Average	0.7	–	–	
2018.5.11-30	North Atlantic Ocean (Icelandic Sea)	–	6.8-117.2	–	Lee et al. (2023)
	Average	–	44.9±34.3	–	
2019.5.12-31	North Atlantic Ocean (Icelandic Sea)	–	17.1-248.7	–	
	Average	–	95±52.3	–	

of DMSOt in the EIO. (The calculation procedure of direct effect, indirect effect, and total effect was shown in [Supplementary Table S2](#)).

The SEM results are consistent with GAM's conclusions and provide insights into the possible sources and sinks of DMS (P, O) in the EIO ([Figure 9B](#)). DMS primarily originates from picophytoplankton production, followed by DMSPt cleavage, and DMSOt reduction. Phytoplankton and bacteria act as DMS sinks. For DMSPt, aside from bacteria, macroalgae, angiosperms, and some corals are also important sources ([Shaw et al., 2022](#)). Picophytoplankton serves as a significant DMSPt sink through assimilative storage, while the relatively low proportion of phytoplankton ([Supplementary Figure S3](#)) consumes DMSPt as a carbon and sulfur source ([Simo, 2001](#)). The primary sources of DMSOt are dominated by DMSPt oxidation, with picophytoplankton and bacteria as the main consumers.

4.5 DMS efflux into the atmosphere

The sea-to-air fluxes of DMS in various sea areas are compiled in [Supplementary Table S3](#) in [Supplementary Material](#). The DMS fluxes of 79.76 $\mu\text{mol m}^{-2} \text{d}^{-1}$ in this study exceeded those in other seas, attributed to higher wind speeds ranging from 2.4 to 14.5 m/s, averaging 8.58 m/s in our survey areas. Although our wind speeds were lower than those reported by [Zhai et al. \(2020\)](#), the lower DMS concentration led to lower sea-to-air flux in the Northern South China Sea. The monthly mean fluxes changing in this investigation area were different from those of global monthly mean fluxes but were similar to those of the Northern Hemisphere reported by [Wang et al. \(2020\)](#), which increased from February to August and decreased from September to November, with a peak in August ([Supplementary Table S1](#)). This is mainly because of the higher fluxes in this study area located in the Northern Hemisphere ([Figure 5G](#)). The survey regions cover $6.29 \times 10^6 \text{ km}^2$, accounting for 8.91% of the total EIO and 1.65% of the global

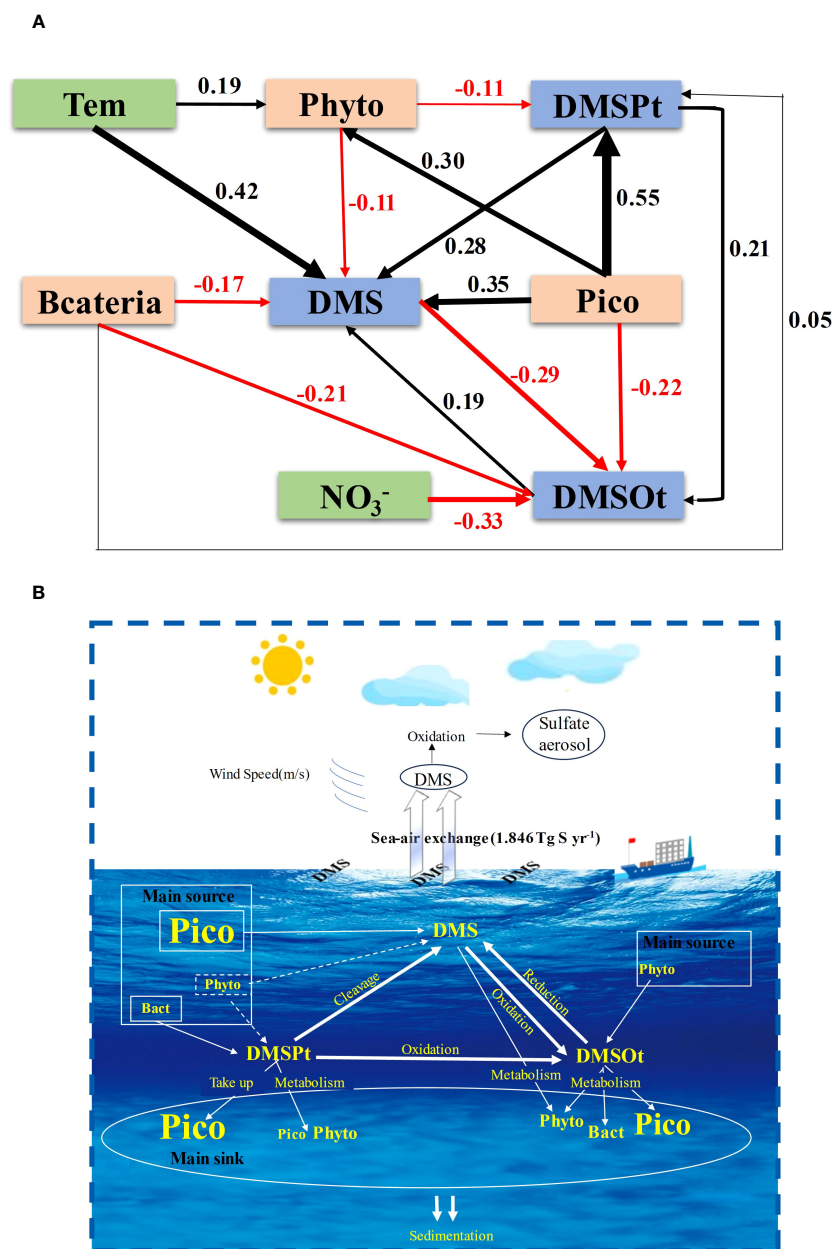


FIGURE 9
 The structural equation model (SEM) examined the contributions of the key environmental/biological factors to DMS (P, O) in the EIO (A). (Chi-square = 1.402, P = 0.966, GFI = 0.996, RMSEA < 0.05). A schematic diagram of the main source and main sink for DMS (P, O) in the EIO (B). The dashed line indicated the underlying process but not the result. Pico (picophytoplankton) included *Syn*, *Pro*, and *PEuks*; Phyto (phytoplankton) included diatom, dinoflagellate, cyanobacteria, and chrysophyceae.

ocean area, respectively. Missing data, including fluxes of April, May, and December were imputed using spline interpolation, and the monthly mean fluxes over the 12 months were summed to obtain the annual fluxes (1.846 Tg S yr⁻¹) (Supplementary Table S1). If this annual flux is used to evaluate the contribution of DMS emissions in this study area to global DMS emissions, it accounted for 9.17% of the global DMS annual fluxes based on reported by Wang et al. (2020) (20.12 Tg S yr⁻¹) and occupied 6.81% based on reported by Hulswar et al. (2022) (27.1 Tg S yr⁻¹). DMS is a known major source of cloud

condensation nuclei (CCN), and increased atmospheric DMS can enhance CCN formation, potentially amplifying the albedo effect and mitigating the greenhouse effect (Charlson et al., 1987). The emission flux in the Indian Ocean thus has an important impact on global climate change. Although the survey area and months are limited and cannot represent the monthly flux variation of the whole eastern Indian Ocean, we hope that the results of this study will provide data support for further assessment of monthly climatology of DMS fluxes for the entire Indian Ocean.

5 Conclusion

This study elucidated the spatial distribution and environmental/biological co-regulation mechanism of dimethyl sulfur compounds in the EIO during 2020. Elevated concentrations of DMS, DMSPt, and DMSOt were predominantly observed at stations E87-28, E87-18, and EQ-07, areas characterized by coastal influences and oceanic currents. Vertically, peak concentrations of DMS and DMSPt were identified at depths of 25 m and 50m, respectively, whereas the maximum for DMSOt varied, being observed at 75 m in the SA section and 150 m in the SB section. Critical environmental determinants for DMS (P, O) were identified as temperature, DSI, and NO_3^- , with picophytoplankton emerging as the most influential biological factor. *Syn* was pinpointed as not only the primary source of DMS but also the main sink of DMSPt, while *Pro* was found to be the principal consumer of DMSOt. Overall, the interplay of DMS (P, O), biological elements, and environmental factors collectively governs the occurrence and distribution of dimethyl sulfur compounds in the EIO. Furthermore, the monthly DMS fluxes increased from June to August and decreased from September to November in this study. These insights are significant for advancing our understanding of the biogeochemical cycling of dimethyl sulfur compounds in the EIO and offer a crucial scientific foundation for broader global sulfur cycle research. Looking ahead, a comprehensive understanding of the genes related to DMS (P) synthesis and metabolism in the EIO remains a key objective for future research.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#). Further inquiries can be directed to the corresponding author.

Author contributions

LP: Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. CF: Visualization, Writing – original draft, Writing – review & editing. YG: Data curation, Writing – review & editing. CD: Data curation, Writing – review & editing. XW: Data curation, Writing – review & editing. GZ: Data curation, Writing – review & editing. JS: Conceptualization, Methodology, Project administration, Resources, Supervision, Visualization, Writing – review & editing.

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Conflict of interest

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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.2024.1395292/full#supplementary-material>

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