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# Prokaryotic community structure and key taxa in the Arabian Sea's oxygen minimum zone

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Microbial communities within oxygen minimum zones (OMZs) play crucial roles in the marine biogeochemical cycling. Arabian Sea (AS) has one of the largest OMZs among the global oceans, however, knowledge about the microbial ecology of the AS OMZ remained limited. In the present study, 44 water samples collected from six stations across the AS, spanning from the deep chlorophyll maximum (DCM) layer to 4000m depth were analyzed. High-throughput sequencing of 16S rRNA genes revealed the structural diversity of bacterial and archaeal communities, influenced primarily by depth and dissolved oxygen (DO) levels. Distinct community compositions were observed across different oxygen gradients, with shifts in the relative abundance of key taxa. Notably, *Desulfosarcinaceae*, UBA10353, *Nitrospina*, SUP05, Sva0996\_marine\_group, *Microtrichaceae*, and *Nitrosopumilus* emerged as bioindicator taxa in the AS hypoxic zones. Co-occurrence network analysis identified SAR324, *Alteromonadaceae*, and *Sphingomonadaceae* as keystone taxa. The spatial and depth-wise distribution patterns revealed that *Desulfosarcinaceae* was predominantly found in the hypoxic zones of the Arabian Sea, whereas UBA10353, *Nitrospina*, SUP05, *Microtrichaceae* and SAR324 were ubiquitous across AS, Bay of Bengal (BOB), and Eastern Tropical North Pacific (ETNP) OMZs, with OTU-level niche differentiation observed for the latter two. Functional profiling using FAPROTAX predicted higher metabolic potential for nitrogen and sulfur in the OMZ compared to other layers of the AS. Our findings provide valuable insights into the distribution, structure, and diversity of microbial communities in the AS OMZ, highlighting the ecological roles of key taxa in hypoxic environments. The established sequence database offers a foundation for further research into the complex interactions within these microbial ecosystems.

## KEYWORDS

hypoxic zone, OMZ, bioindicators, keystone taxa, Arabian Sea, microbial diversity

## 1 Introduction

The oceans boast a captivating ecosystem, replete with diverse habitats like cold seeps, hydrothermal vents, and oxygen minimum zones (OMZs) (Li et al., 2021b; Baumgartner et al., 2022; Chen et al., 2022). The microbial community inhabiting each habitat play a pivotal role in governing the oceans' biogeochemical cycles, actively engaging in nearly all oceanic biogeochemical processes. Understanding the ecological roles and functions of marine microbes requires thorough investigation of their biodiversity. Till now, extensive research has been conducted on the microbial diversity of the Indian Ocean. AS is a biologically productive tropical basin in Indian Ocean, located between the Horn of Africa and southern Asia, with the Gulf of Oman in the north and the Red Sea through the Gulf of Aden in the west. The northern border between Pakistan and Iran is a world-class transportation hub. Covering an area of 3.86 million square kilometers, with a maximum depth of 5203m and an average depth of 2734m (Corfield et al., 2010).

Ocean models predict that the dissolved oxygen levels in the global ocean will decline by 1% to 7% by 2100 due to a combination of warming-induced decreases in oxygen solubility and reduced deep-sea ventilation (Long et al., 2016). AS, Eastern Tropical North Pacific (ETNP), Eastern Tropical South Pacific (ETSP), and Bay of Bengal (BOB) form the major OMZs of the world ocean (Ulloa and Pantoja, 2009). There are currently three definitions of ocean hypoxia thresholds: hypoxia ( $< \sim 63 \mu\text{M}$ ), microbial hypoxia ( $< \sim 20 \mu\text{M}$ ) and functional anoxia ( $< \sim 0.05 \mu\text{M}$ ), and hypoxia zone throughout the water column is often detected at depths between 200 meters and 1,000 meters (Paulmier and Diana, 2009; Rixen et al., 2020). The total volume of waters characterized by oxygen concentrations below  $20 \mu\text{M}$  in the global ocean estimated to be  $15 \times 10^{15} \text{ m}^3$ , among of which, the northern Indian Ocean accounts for 21%, equivalent to  $3.13 \times 10^{15} \text{ m}^3$ . As a classic hypoxic zone, Arabian Sea hosts the largest proportion of this oxygen-deficient water body, accounting for approximately  $2.5 \times 10^{15} \text{ m}^3$ , while only a small fraction is found in the Bay of Bengal ( $0.6 \times 10^{15} \text{ m}^3$ ) (Acharya and Panigrahi, 2016). Earlier reports suggested that OMZ regions in the Northern Indian Ocean (AS and BOB combined) made up more than 50% of the global OMZs (Helly and Levin, 2004). The formation of OMZs in the Arabian Sea is linked to inadequate ventilation from the ocean surface to the interiors, along with elevated oxygen consumption due to intense biological productivity. Coinciding with an active denitrification zone, the AS\_OMZ is among the largest anoxic regions in the oceans, sometimes DO drops as low as  $0.1 \mu\text{M}$  (Gilles-Gonzalez, 2001; Stramma et al., 2008). Understanding the vital role of microbial communities in the Arabian Sea is crucial for unraveling the global biogeochemical and climatic processes mediated by these microbes. Generally, most marine microbes are uncultivable, and with the advent of molecular methods and high-throughput sequencing, methodological advances are more conducive to exploring the biodiversity and biogeography of microorganisms in different sea (Kaeberlein et al., 2002; Puspita et al., 2012; Jin et al., 2022).

In OMZ, element cycling is primarily mediated by special microorganisms. Recurrent reports have highlighted the prevalence of *Proteobacteria* as the dominant phylum among the microbial communities across the Indian Ocean. Other taxa at class level including the *Betaproteobacteria*, *Deltaproteobacteria*, *Actinobacteria*, *Nitrospina*, *Planctomycetacia*, and SAR406 were also reported, although their relative abundance varied along the depths and locations sampled in the Indian Ocean OMZ (Bandekar et al., 2018; Fernandes et al., 2020; Jin et al., 2022; Li et al., 2022; Rangamaran et al., 2022). Although *Proteobacteria* predominates in the water column, significant change in the composition of the bacterial community was observed and varied with depth and DO levels in the water and sediment samples in the Arabian Sea (Rangamaran et al., 2022). Previous reports based on clone libraries revealed the vertical partitioning of bacterial communities between the surface and OMZ at the Arabian Sea Time Series (ASTS) location, however no apparent seasonal variation among OMZ bacterial communities (Bandekar et al., 2016, 2018). By comparing the prokaryotic community composition of the ASTS, India's Idea 2 station (I2) in AS and the BoB Time Series in the BOB, higher relative abundance of bacteria involved in anammox was observed in ASTS and I2 stations (Fernandes et al., 2020). In a recent report, distinct microbial community compositions of OZ and OMZ waters were observed in 131 samples collected from the Andaman Sea and eastern BoB epipelagic waters from 2 to 200 m, and important bioindicator taxa across oxygen gradients were identified (Guo et al., 2022). While several studies have documented the microbial community composition within the Arabian Sea, the majority have concentrated on particular locations or water layers (such as epipelagic waters). A comparative analysis with other significant oxygen minimum zones (OMZs) across the world's oceans, including the Bay of Bengal (BOB) and the Eastern Tropical North Pacific (ETNP), remains largely absent. Consequently, a thorough understanding of microbial diversity and distribution in the OMZ regions of the Arabian Sea, particularly transitioning from typical hypoxic to non-hypoxic zones, is yet to be fully elucidated.

With the rapid development of molecular methods, high-throughput sequencing technologies have been widely applied in the exploring of biodiversity of microorganisms using targeted sequencing of conserved regions (e.g., 16S or 18S rRNA gene sequencing) or shotgun metagenomics. There are currently some challenges for interpretation of biological information in targeted sequencing approach, due to the limitation such as the primer bias or short sequence amplification. The high costs associated with deep sequencing in shotgun metagenomics also limits full exploitation. Although the information provided by amplicon sequencing of 16S rRNA genes are not enough to interpret the ecological functions of microbial community, it is still an effective and economic approach to characterize the microbial diversity and structure in large number of samples (Lynch and Neufeld, 2015; de Muinck et al., 2017). The composition of environmental bacterial communities are usually complex, so identifying crucial bioindicator taxa would help to understand the community structure and functional differences in specific habitats. In addition to identifying

bioindicators, keystone taxa with high degree and tight centrality of microbial interaction networks also play an important role in driving the microbial community structure and maintaining the network stability (Banerjee et al., 2018). Therefore, in order to comprehensively understand the performance of prokaryotes community and their ecological significance in the OMZ, it is necessary to integrate the physicochemical properties, community composition, biomarker taxa, and interaction networks.

In this study, we collected a total of 44 water samples from 6 stations across the typical hypoxic zones in northern Arabian Sea, through transition zones, to the non-hypoxic zones in the southern AS, covering depths from the deep chlorophyll maximum (DCM) layer to 4000m near the bottom. This comprehensive sampling spanned regions with different oxygen gradients to explore and compare the spatial and vertical composition of bacterial and archaeal communities. To achieve this, we employed Illumina sequencing of the 16S rRNA genes from the collected samples. Additionally, we downloaded and integrated publicly available 16S rRNA high-throughput sequencing data from the Bay of Bengal and the eastern tropical North Pacific Ocean for a broader analysis. We identified bioindicators and keystone taxa, analyzing their spatial and depth-wise distribution patterns across the Arabian Sea (AS), Bay of Bengal (Bob), and the eastern tropical North Pacific (ETNP). Furthermore, we investigated the major environmental factors influencing the prokaryotic community structure and predicted potential functional profiles. The sequence database established in this study will contribute to a comprehensive understanding of the distribution and structure of microbial communities and their key members within the AS oxygen minimum zone (OMZ).

## 2 Materials and methods

### 2.1 Sample collection and methodology

Seawater samples were collected from 6 stations located the Arabian Sea of northern Indian Ocean during China DY72 cruise onboard the Research Vessel Shen Hai Yi Hao. These stations (Latitude: 10.132553°N-17.326766°N, Longitude: 63.103385°E-68.303971°E, water depth: 3550m-4458m) was sampled from 17th May 2022 to 28th May 2022 (Spring intermonsoon), spanning the north to the south of Arabian Sea. Stations of CTD03, CTD04 and CTD05 located in the northern AS were defined as the core OMZ in AS. Stations CTD02 and CTD06 located in the middle of AS were defined as OMZ transition zones, while CTD08 in the southern AS as a non-hypoxia zone. For most stations, the sampling depths included deep chlorophyll maximum (DCM), oxygen minimum zone (OMZ), 1000 m, 2000 m, and the bottom. In total, 44 samples from 6 stations were collected from AS. These samples were divided into 4 groups based on DO and depth, including euphotic zones (AS\_UP), OMZ (AS\_OMZ), bathypelagic zone (AS\_DOWN) and CK (CTD08). DO levels below 20  $\mu$ M are defined as the AS\_OMZ group. Although the DO values of CTD03-100 was 22.1188  $\mu$ M, but CTD03-100 was still categorized to AS\_OMZ group. DO level higher than 20  $\mu$ M and depth over or equal to 100m is defined as

the AS\_UP group. Depth below or equal to 1000m is defined as the AS\_DOWN group. The detailed information of sampling sites and depths were provided in Figure 1 and Supplementary Table 1.

Seawater samples were collected using a Conductivity-Temperature-Depth (CTD) rosette system fitted with 24 Niskin bottle sampler (Seabird Electronics, Washington, NY, United States) mounted with an oxygen sensor (Crescentini et al., 2012). Eight liters' seawater were filtered through 0.22  $\mu$ m sterivex filters (Millipore, United States). The filter samples were immediately frozen in liquid nitrogen and stored at  $-80^{\circ}\text{C}$  until DNA extraction. The nutrient parameters including silicate, phosphate, nitrate, nitrite and ammonium were measured using Skalar Autoanalyser (Skalar Analytical, Netherlands) following standard methods.

### 2.2 Total genomic DNA extraction and quality inspection

Genomic DNA was isolated using DNeasy PowerSoil Pro Kit following the manufacturer's protocol (QIAGEN, Germany, [www.qiagen.com/insights](http://www.qiagen.com/insights)). The concentration of the extracted DNA was measured using a Qubit 3.0 Fluorometer (Life Technologies, ThermoFisher Scientific, USA) and the Equalbit 1x dsDNA HS Assay Kit (Vazyme, China, [www.vazyme.com](http://www.vazyme.com)). Before sequencing, the quality and concentration of DNA were determined again by 1.0% agarose gel electrophoresis and NanoDrop<sup>®</sup> ND-2000 spectrophotometer (Thermo Scientific Co., Ltd., USA).

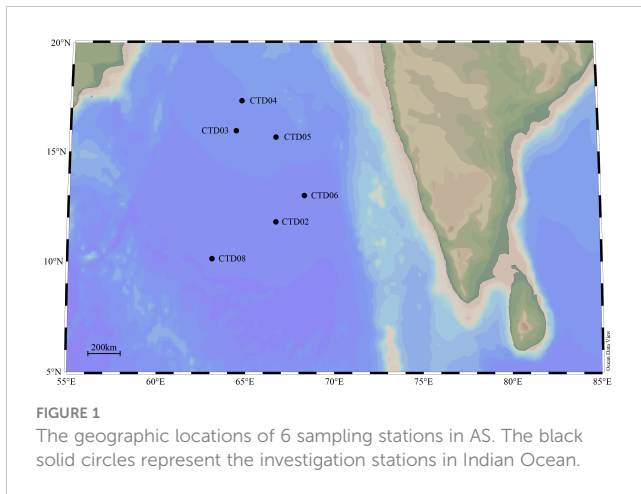
### 2.3 Amplification of 16S rRNA gene

The primer set 338F (5'-ACTCCTACGGGAGGCAGCAG-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') was used to amplify the V3-V4 region of bacterial 16S rRNA gene. The primer set 524F10extF (5'-TGTCAGCCGCCGCGGTAA-3') and Arch958RmodR (5'-YCCGGCGTTGAVTCCAATT-3') was used for the amplify the V4-V5 region of archaeal 16S rRNA gene (Claesson et al., 2009).

PCR reaction was carried out in a 20  $\mu$ L reaction volume containing DNA (10 ng), 0.8  $\mu$ L each of primers (10  $\mu$ M), 4  $\mu$ L 5x FastPfu buffer, 0.4  $\mu$ L FastPfu polymerase, BSA 0.2  $\mu$ L and 250 mM dNTPs (TransGen, China, [www.transgen.com/enzyme/226](http://www.transgen.com/enzyme/226)). PCR cycling conditions maintained were as follows: initial denaturation at 95°C for 3 min, followed by cycle denaturation at 95°C for 30 s, annealing at 55°C for 30 s, extension at 72°C for 45 s for a total of 27 cycles and a final extension for 10 min at 72°C. For archaeal 16S rRNA gene amplification, PCR cycling conditions maintained 35 cycles.

### 2.4 Illumina sequencing and bioinformatic analysis

Purified amplicons were pooled in equimolar amounts and paired-end sequenced on an Illumina MiSeq PE300 platform/



**FIGURE 1**  
The geographic locations of 6 sampling stations in AS. The black solid circles represent the investigation stations in Indian Ocean.

NovaSeq PE250 platform (Illumina, San Diego, USA) according to the standard protocols by Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China).

Raw reads of AS in this study were processed using QIIME 2 pipeline. QIIME 2 was used to do downstream analysis of raw sequence data generated by PE250 (Bokulich et al., 2018; Bolyen et al., 2019). In brief, raw sequence data were demultiplexed using the demux plugin, followed by primer trimming using the cutadapt plugin. Subsequently, sequences underwent quality filtering, denoising, merging, and chimera removal utilizing the DADA2 plugin (Martin, 2011; Callahan et al., 2016). Non-singleton amplicon sequence variants (ASVs) were aligned using MAFFT and then utilized to construct a phylogenetic tree with FastTree2 (Katoh et al., 2002; Price et al., 2009). The bacterial samples were standardized to 12,481 sequences per sample, whereas the archaeal samples were standardized to 7,537 sequences per sample. Alpha diversity metrics, including Sobs (number of species observed), Shannon (microbial diversity in the sample), and Coverage (species coverage), and beta diversity metrics (Jaccard distance) were calculated with Mothur v1.30.1 (Schloss et al., 2009). ASVs were taxonomically classified using the classify-sklearn Naïve Bayes taxonomy classifier against the SILVA Release 138 database, encompassing both bacteria and archaea.

Publicly accessible 16S rRNA gene high-throughput sequencing data were obtained from the National Center for Biotechnology Information (NCBI) for the Bay of Bengal (Bob) and the eastern tropical North Pacific Ocean (ETNP). This dataset encompassed 30 samples from the deep chlorophyll maximum (DCM) and oxygen minimum zone (OMZ) layers of the Bay of Bengal, as well as 66 samples from the DCM, OMZ, and 2000m depth layers of the ETNP (Gu et al., 2022; Li et al., 2022). To enhance our comparative analysis, these datasets were integrated with the 16S rRNA gene sequencing data collected from the Arabian Sea (AS) of this study. Utilizing UPARSE 7.1, the sequences were clustered into operational taxonomic units (OTUs) based on a 97% sequence similarity threshold. For each OTU, the most representative sequence in terms of abundance was chosen, following the methodology established previously (Beman et al., 2021; Gu et al., 2022).

## 2.5 Diversity and statistical analyses

The similarity matrix was used to perform cluster analysis in Primer 6 (PRIMER-E, Plymouth, UK) using a group-average linking method and non-metric multidimensional scaling analysis (NMDS). Screening of environmental parameters using Variance inflation factor (VIF) analysis. Canonical correspondence analysis (CCA) was performed using Past-3 software to assess the influence of environmental parameters on bacterial and archaeal community structure (<https://folk.uio.no/ohammer/past/>).

Previous research showed that Molecular Ecological Network Analysis Pipeline (MENAP) can construct ecological association networks named molecular ecological networks (MENs) through Random Matrix Theory (RMT)-based methods to explore the interactions between bacterial and archaeal communities (<http://ieg2.ou.edu/MENA>) (Deng et al., 2012). In this study, we use the network building process given by the NEMAP creator for analysis and select “Regress Poisson distribution only” to ensure that the type of network belongs to Poisson distribution. The parameters used to construct the network were shown in Supplementary Table 4. In this study, we choose the connectors ( $z_i \leq 2.5$ ,  $P_i > 0.62$ ) as the keystone in community (Deng et al., 2012; Berry and Widder, 2014). We used the Kruskal-Wallis rank sum test, FDR multiple testing correction, and the Tukey-kramer *Post-hoc* test (0.95) to resolve differences between each group of species (Schloss et al., 2009).

Prediction of metabolic pathways based on 16S rRNA amplicon data was performed using FAPROTAX, FAPROTAX is a database that maps prokaryotic taxa to metabolic or other ecologically relevant functions based on representative literature in culture (Deng et al., 2012; Louca et al., 2016).

## 2.6 Nucleotide accession numbers

The raw sequencing reads have been deposited in the NCBI Sequence Read Archive (SRA) database under the accession number PRJNA993832.

## 3 Results

### 3.1 Physico-chemical characteristics

Metabarcoding analysis of 44 water samples from 6 CTD stations in Arabian Sea (AS) was carried out in the present study. Samples were collected from subsurface to deep (bathypelagic) water ranging from 62m to 4000m (Figure 1). All the 44 samples could be divided into 4 groups including AS\_UP, AS\_OMZ and AS\_DOWN, as well as control group (CTD08), which were defined by DO concentrations and depth. The physicochemical parameters of the samples were presented in Supplementary Table 1 and Supplementary Figure 1. In AS, the DO concentrations were almost below the detection threshold in the OMZs ranging from about 150m to 1200m in CTD03, CTD04 and CTD05 stations

(Supplementary Figure 1). For CTD02 and CTD06 stations, the DO values were also below  $20\mu\text{M}$  in the OMZs from about 150m to 1000m. However, as a control group, CTD08 located far from the mainland, and the DO values in this water columns were above  $62\mu\text{M}$ , significantly different from other stations.

### 3.2 Alpha diversity and beta diversity of microbial communities

In this study, a total of 44 bacterial and 43 archaeal sequence data sets were obtained, respectively. About 1.74 million bacterial sequences and 2.14 million archaeal sequences were retrieved from all the samples, resulting in a total of 11174 bacterial and 1628 archaeal ASVs. The alpha diversity of microbial communities in AS was compared among 44 samples (Supplementary Figures 2, 3). The coverage of microbial communities in each group was almost 1.000, and the rarefaction curves were bent toward the saturation plateau, indicating that the sampling sizes were sufficient to reflect the microbial community diversity in the 44 samples (Supplementary Figures 2, 3).

Alpha diversity analysis further showed that bacteria exhibited the highest richness (Kruskal-Wallis rank sum test, Chao1: 123–646), followed by archaea (Kruskal-Wallis rank sum test, Chao1: 6–134). Bacteria still exhibited the highest diversity (Kruskal-Wallis rank sum test, Shannon, 2.550842–5.18124), followed by archaea (Kruskal-Wallis rank sum test, Shannon, 1.524161–3.996356) (Supplementary Figure 3). The bacterial community diversity showed no significant difference among AS\_UP, AS\_OMZ and AS\_DOWN ( $p=0.1408$ ). For archaea, increased species richness ( $p=0.02774$ ) and diversity ( $p=0.001736$ ) were observed in AS\_OMZ, compared to AS\_UP and AS\_DOWN communities (Supplementary Figure 3).

Non-metric multidimensional scaling (NMDS) analysis was also employed to decipher the community differences at ASV level (Taguchi and Oono, 2005). As illustrated by NMDS for bacteria, the microbial community from AS\_UP group was significantly separated from AS\_OMZ group along the Y-axis (Figure 2). The archaeal community was structured by DO and

depth, and clustered according to different groups (Figure 2). The samples from the AS\_UP, AS\_OMZ and AS\_DOWN clustered individually, indicating the compositions of the archaeal communities in these three groups are distinct (Figure 2).

### 3.3 Microbial community composition in the water column of Arabian Sea

The composition of the microbial communities of in AS were compared in 44 water samples of 6 stations. For the 3 groups (AS\_UP, AS\_OMZ and AS\_DOWN), 268 shared ASVs of bacteria were identified belonging to 251 shared genera and in respect of the archaea, 109 shared ASVs belonging to 15 shared genera of 6 phyla were identified in 43 samples (Supplementary Figure 4).

Analysis of the bacterial community composition of the 44 samples revealed that *Proteobacteria*, *Actinobacteriota*, *Bacteroidota*, SAR406, *Firmicutes*, *Chloreflexi*, *Cyanobacteria*, SAR324, *Nitrospinota* were dominant phyla across nearly all samples, although their relative abundance varied among different samples. *Proteobacteria* (accounting for 27.67%–94.94%) was the most dominant phylum across all samples followed by *Actinobacteriota* (0.69%–27.64%), *Bacteroidota* (0.89%–16.69%), *Cyanobacteria* (0.1%–7.48%), and *Marinimicrobia\_SAR406* (0%–23.84%) in AS (Figure 3).

At the class level, *Alphaproteobacteria* (9.23%–52.11%) and *Gammaproteobacteria* (17.12%–80.05%) was the most dominant classes in AS samples, and the relative abundance of *Gammaproteobacteria* were higher than that of *Alphaproteobacteria*. Other predominant class included *Acidimicrobiia* (0.2%–26.5%), *Bacteroidia* (0.4%–16.7%), SAR406 (0%–23.8%), *Actinobacteria* (0%–11.6%), *Bacilli* (0%–23.4%), *Cyanobacteriia* (0%–7.5%), *Dehalococcoidia* (0%–9.3%) and SAR324 (0%–7.0%). The relative abundances of *Acidimicrobiia* and SAR406 were highest in the OMZs, and lowest in deep sea (AS\_DOWN). Besides, *Nitrospina*, *Desulfobacteria* and *Vicinamibacteria* also exhibited highest relative abundance in the OMZ communities. On the contrary, *Cyanobacteriia* was more dominant in group AS\_UP (2.32%–7.45%), but almost undetectable in group AS\_OMZ and AS\_DOWN (Supplementary Figure 5).

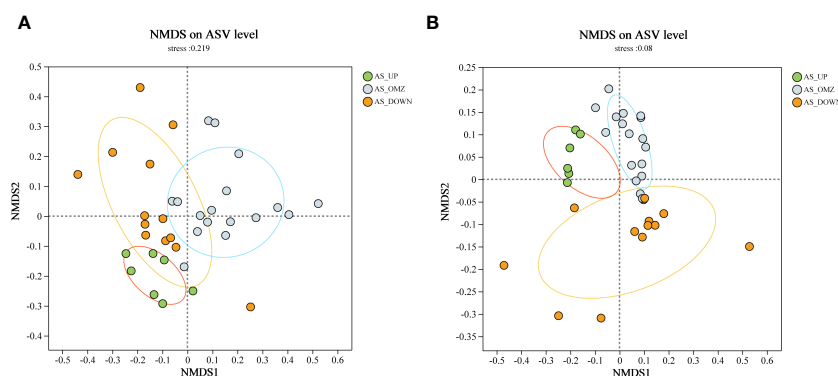


FIGURE 2

NMDS plot based on Bray-Curtis distance among AS\_UP, AS\_OMZ and AS\_DOWN communities. (A) bacterial communities at ASV level (B) archaeal communities at ASV level.

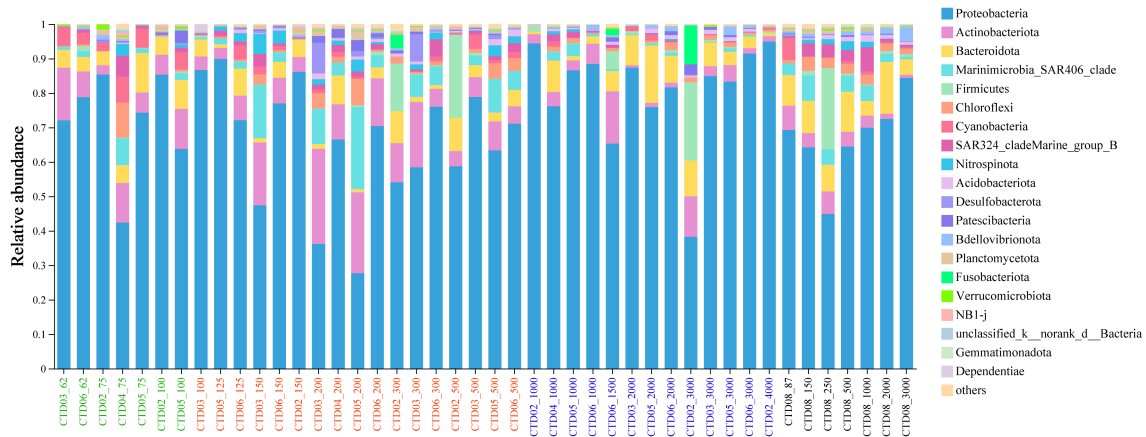


FIGURE 3  
Microbial community composition of AS at phylum level.

At the family level, *Alteromonadaceae* and *Sphingomonadaceae* were the most dominant family in AS followed by *Rhodobacteraceae*, *Saccharospirillaceae*, *Flavobacteriaceae*, *Thalassospiraceae*, *Microtrichaceae*, *Moraxellaceae*, SAR406\_clade, *Marinobacteraceae*, UBA10353 and *Hyphomonadaceae*. *Alteromonadaceae* family dominated in most samples, and exhibited higher relative abundances in AS\_UP and AS\_DOWN than AS\_OMZ. *Sphingomonadaceae* was also widely distributed in different depths in AS and more abundant in deep sea below 1000 meters (Supplementary Figure 6). *Moraxellaceae* appeared to increase in abundance with decreasing DO concentrations in AS\_OMZ and AS\_DOWN, when compared with AS\_UP. *Microtrichaceae* tended to distribute in AS\_UP and AS\_OMZ, and was most abundant in OMZ communities. Besides, other dominant taxa included UBA10353, *Nitrospinaceae*, *Thioglobaceae*, *Desulfosarcinaceae* were also significantly enriched in AS-OMZ communities. However, *Cyanobiaceae*, *Actinomarinaceae*, *Legionellaceae*, NS9\_marine\_group, OCS116 and SAR86\_clade seemed to mainly distributed in AS\_UP, but with low or undetectable abundance in AS\_OMZ and AS\_DOWN (Supplementary Figure 6).

At the genus level, the top 10 abundant genera with high relative abundance included *Alteromonas*, *Acinetobacter*, unclassified\_f: *Alteromonadaceae*, *Thalassospira*, *Oleibacter*, *Sphingobium*, Sva0996\_marine\_group, SAR406\_clade, *Erythrobacter* and *Marinobacter* (Figure 4). *Alteromonas* dominated in most of the samples in AS-UP. *Acinetobacter* and *Thalassospira* were mainly distributed in OMZ and deep layer in AS. Interestingly, *Oleibacter* showed high abundance in two samples (CTD05\_125m, CTD06\_1000m). Sva0996\_marine\_group, belonging to *Acidimicrobiia* class, increased relative abundance in AS OMZ layer (Figure 4). Other predominant genus such as *Sphingobium*, *Erythrobacter* and *Marinobacter* showed no significant differences among the three genus in these groups.

Among the detected archaea, two classes *Nitrososphaeria* and *Thermoplasmata* were found of wide distribution throughout the water column, with the abundance accounting for over 90% in 43 samples. *Nitrososphaeria* have higher relative abundance below the DCM layers, while *Thermoplasmata* was more abundant in the AS\_UP group (Supplementary Figure 7). At the family level, the three most abundant taxa included *Nitrosopumulaceae*, norank\_o\_

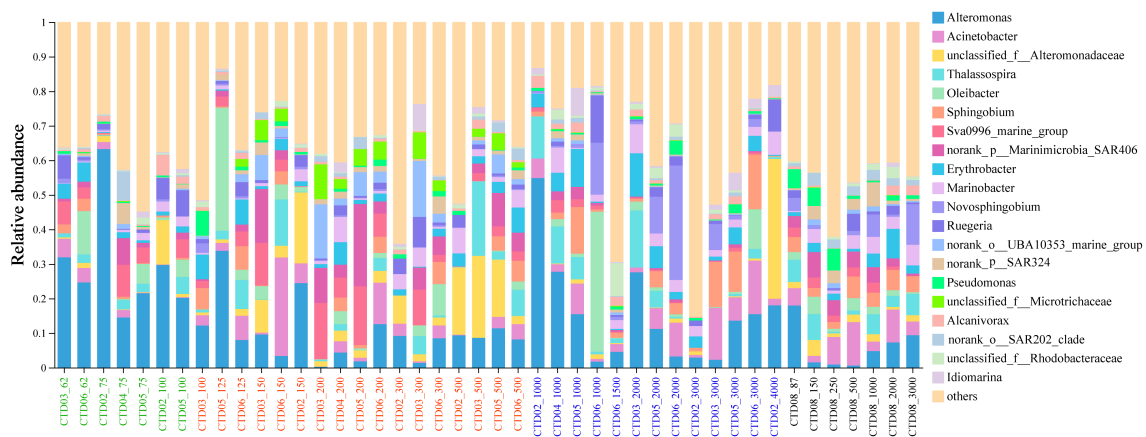


FIGURE 4  
Microbial community composition of AS at genus level.

Marine\_Group\_II and norank\_c\_Thermoplasmata in majority of the communities, except for four samples CTD02-500, CTD02-3000, CTD02-4000, CTD06-1500, which were dominated by *Nitrososphaeraceae* family. At the genus level, *Candidatus\_Nitrosopelagicus*, norank\_o\_Marine\_Group\_II and Marine\_Group\_III dominated in upper water layers above 125m, while *Nitrosopumilus*, norank\_o\_Marine\_Group\_II, Marine\_Group\_III dominated in deeper water layers (from 150m to bottom). As the most abundant and prevalent taxa in the water column in AS, *Nitrosopumilaceae* tended to have different ecotypes, among which *Candidatus\_Nitrosopelagicus* distributed in euphotic zones, while *Nitrosopumilus* genus mainly dominated in meso- and bathypelagic water.

### 3.4 Bioindicator taxa and their distribution patterns in the hypoxic zones of Arabian Sea

Each water layer in AS is distinct with respect to the physical oceanographic features, facilitate or inhibit the growth of specific microorganisms. Research on bioindicator taxa may help understand the connection between microbes and specific habitats. In this study, the microbial community composition was further compared to determine the indicator taxa in the hypoxic zone of Arabian Sea. Kruskal-Wallis H test was used to identify at least 30 bioindicator taxa with significant distribution characteristics that could differentiate AS\_UP, AS\_OMZ and AS\_DOWN communities, as well as hypoxic

and non-hypoxic zones communities at the genus or family level (Figure 5). *Candidatus\_Actinomarina*, *Prochlorococcus\_MIT9313* and unclassified\_f\_Cyanobiaceae were identified as bioindicator taxa in AS\_UP communities, which were exclusively distributed in euphotic zones. *Alteromonas* was also one of the important indicator taxa and its relative abundance was higher in the AS\_UP when compared with AS\_OMZ and AS\_DOWN group. Although low relative abundance, SAR86\_clade, NS2b\_marine\_group, NS5\_marine\_group, NS9\_marine\_group and OCS116\_clade were also determined as indicator taxa in AS\_UP communities, with significantly higher abundance than in AS\_OMZ and AS\_DOWN communities. The indicator taxa of the hypoxia zones in AS included unclassified\_f\_Desulfosarcinaceae, norank\_o\_UBA10353, *Nitrospina*, SUP05\_cluster, Sva0996\_marine\_group and unclassified\_f\_Microtrichaceae, which were significantly enriched and exhibited highest relative abundance in AS\_OMZ communities, when compared with AS\_UP and AS\_DOWN communities. For AS\_DOWN, *Novosphingobium*, *Salinicola*, *Oceanobacter* were the indicator taxa of the deep layers (Figure 5).

The spatial and depth-wise distribution patterns of important bioindicator taxa in the hypoxia zones of AS were further analyzed and compared with other OMZs including Bay of Bengal (Bob) and eastern tropical North Pacific Ocean (ETNP) at ASV or OTU levels (Figure 6; Supplementary Figure 8). As one of the most important taxa, *Desulfosarcinaceae* was almost exclusively predominant in the OMZs in CTD03, CTD04, CTD05 and CTD06 stations of AS. However, it was absent in CTD02 and CTD08 stations, as well as in Bob and ETNP OMZs (Figure 6; Supplementary Figure 8). Only

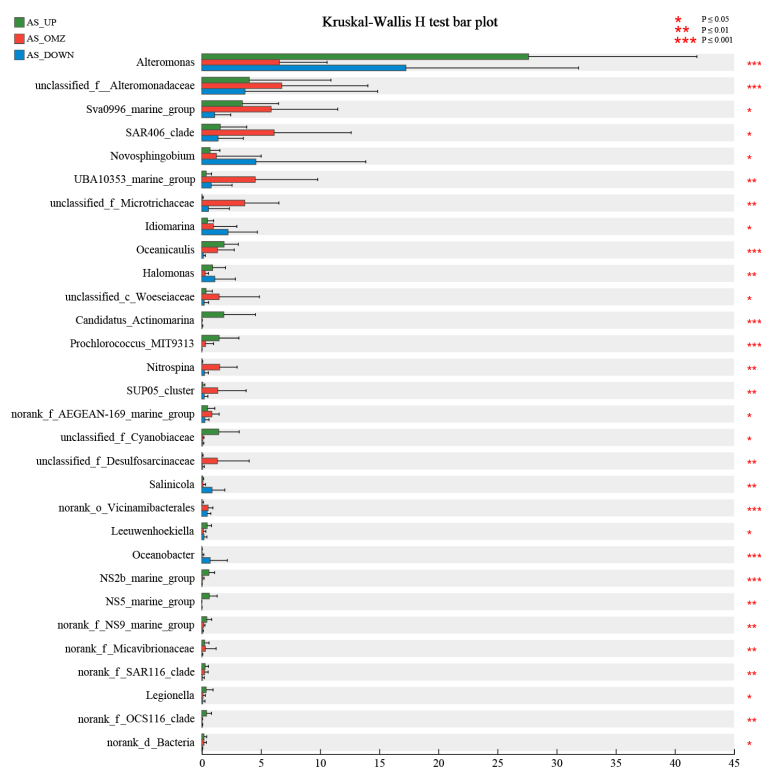


FIGURE 5

The 30 bioindicator taxa that significantly differentiate AS\_UP, AS\_OMZ and AS\_DOWN communities in AS. \*:  $P \leq 0.05$ , \*\*:  $P \leq 0.01$ , \*\*\*:  $P \leq 0.001$ .

three ASVs were assigned to *Desulfosarcinaceae* in AS, which belonging to *Desulfobacterales* of *Desulfobacterota* phylum, with the most abundant ASV890 belonging to one unclassified taxa, and the other two affiliated with SEEP-SRB1. Similar distribution pattern was observed for another important indicator taxa UBA10353, which was phylogenetically closely related to *Arenicellaceae* family of *Gammaproteobacteria*. UBA10353 was also significantly enriched in the OMZ communities in AS. For this taxa, ASV879, ASV678 and ASV666 were the most abundant ASVs, accounting for more than 90%, and were mainly distributed in the hypoxic zone of CTD03, CTD04, CTD05 and CTD06 stations but absent in CTD02 and CTD08. They seemed to increase their relative abundance toward anoxic conditions in AS. Besides, these ASVs (corresponding to OTU11318, OTU11316, OTU11385) were found to be unique to AS OMZ communities when compared with Bob and ETNP OMZs (Figure 6; Supplementary Figure 8). Moreover, *Nitrospina* was also identified as important bioindicator taxa in OMZs, and predominantly distributed in hypoxic zones of AS. ASVs affiliated with *Nitrospina* mainly represented by ASV1121 and ASV632. They were almost exclusively dominated in the OMZ communities of CTD03, CTD04, CTD05 and CTD06 except for CTD02 and CTD08, and also enriched in Bob OMZs and ETNP OMZs (as represented by OTU11457 and OTU5252) (Figure 6; Supplementary Figure 8). Likewise, SUP05 group were also significantly enriched in the OMZs of AS except for CTD02 and CTD08 stations, and were identified as important bioindicator taxa. The dominant ASVs represented by ASV635 and ASV4913 were phylogenetically related to *Thioglobus* genus. This taxa were ubiquitous and abundant not only in AS OMZs but also in Bob and

ETNP OMZs (as represented by OTU4763) (Figure 6; Supplementary Figure 8).

With regard to *Microtrichaceae*, it was predominant not only in the OMZs of AS but also in AS\_UP. ASVs affiliated with *Microtrichaceae* formed at least two phylogenetic clades, one belonging to Sva0996\_marine\_group, and the other belonging to unclassified\_f\_Microtrichaceae (as represented by ASV625), among which the latter tended to dominated in the mesopelagic water (Figure 6; Supplementary Figure 8). Besides, at least two ecotypes of Sva0996\_marine\_group were present in AS, one dominated in euphotic zone (as represented by ASV1180 and ASV1189) and the other prevailed in OMZ zones (as represented by ASV638 and ASV959). Similar distribution pattern was also observed in Bob and ETNP OMZs (Figure 6; Supplementary Figure 8).

### 3.5 Environmental parameters affecting the structure of microbial communities

Prior to Canonical Correspondence Analysis (CCA) to examine the influence of environmental parameters on bacterial and archaeal community structure, Variance Inflation Factor was used to screen the environmental parameters analysis to ensure the accuracy of the CCA analysis (remove Salinity, Silicate, Phosphate and Temperature) (O'Brien, 2007).

The results showed that environmental parameters including DO, depth,  $\text{NO}_3^-$ , and  $\text{NO}_2^-$  exhibited significant influences on bacterial and archaeal communities. DO, depth, and nitrate were the most significant environmental factors. For bacterial communities in AS, the first two ordination axes of CCA

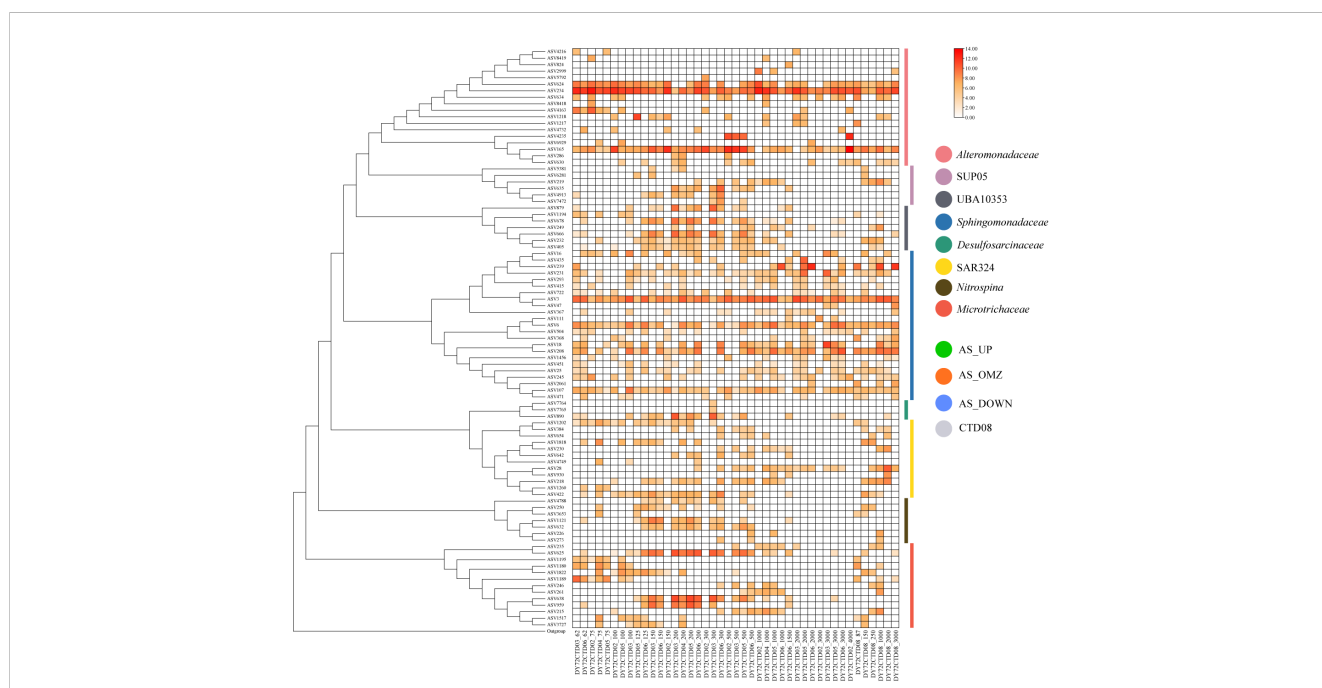


FIGURE 6  
Heatmap displaying the distribution and log-transformed relative abundance of major ASVs.



accounted for 8.44% of the explained total variance in ASV level (Figure 7, Supplementary Table 2). CCA indicated that among the five different parameters, DO seemed to separate the bacterial communities into ‘oxygen content’ and OMZ communities (Figure 7). For archaeal community in AS, the first two ordination axes of CCA accounted for 16.06% and 6.85% of the explained total variance in ASV level. Similar to bacterial, archaeal samples in AS\_OMZ was negatively correlated with DO. The archaeal communities in group AS\_DOWN was strongly influenced by depth. Besides,  $\text{NO}_2^-$  and  $\text{NH}_4^+$  had a small impact on the archaeal community (Figure 7).

Spearman correlation heatmap showed the correlation between the bacteria families and environmental parameters (Supplementary Figure 9, Supplementary Table 3). In AS, there was no significant correlation between *Alteromonadaceae* and any environmental parameters. As another important taxon, *Sphingomonadaceae*, exhibited a significant positive correlation with depth and  $\text{NO}_3^-$  in AS. Interestingly, *Microtrichaceae* were affected by almost all environmental parameters in AS (except for  $\text{NO}_3^-$ ) (Supplementary Figure 9). In AS, there was no significant correlation of *Nitrosopumilaceae* with any environmental parameters. However, Marine Group II was significantly positively correlated with DO (Supplementary Figure 10, Supplementary Table 3).

### 3.6 Co-occurrence patterns of microbial community and functional prediction

Keystone taxa not only maintained the structures and functions of microbial community, but also considerably influence community networks (Berry and Widder, 2014). A co-occurrence network was generated to explore interactions among bacterial and archaeal communities and identify keystone taxa in this study (Supplementary Figure 11, Supplementary Table 4). In the network, each node represents an ASV, with the size of each node proportional to the number of its associations (degree). Connections between nodes represent strong and significant correlations of abundance ( $|r| > 0.7$ ,  $p < 0.01$ ). In this study, we choose the connectors ( $z_i \leq 2.5$ ,  $\text{Pi} > 0.62$ ) as the keystone in community. As a

result, ASV84 (*Marinobacteraceae*), ASV237 (*Pseudomonadaceae*), ASV264 (*Mycobacteriaceae*), ASV28 (SAR324\_clade), ASV182 (*Flavobacteriaceae*), ASV16 (*Sphingomonadaceae*), ASV95 (*Rhizobiaceae*) and ASV234 (*Alteromonadaceae*) were identified as keystone of bacterial ASVs. ASV154 (*Nitrosopumilaceae*) and ASV156 (*f\_norank\_o\_norank\_c\_Thermoplasmata*) were identified as keystone of archaeal ASVs.

Through Functional Annotation of Prokaryotic Taxa (FAPROTAX) analysis, various functional process was predicted. Chemoheterotrophy was the most active metabolic process in different water layers in AS, while Photoautotrophy and Photoheterotrophy processes were very active in the up layer and weakened with the increase of water depth. Strong Nitrate\_reduction was observed in AS. The potential for denitrification, nitrification, aerobic nitrite oxidation, dark sulfide/sulfur compounds oxidation were predicted and more abundant in the OMZs in AS (Supplementary Figure 12, Supplementary Table 5).

## 4 Discussion

The OMZs in the ocean have been expanding and intensifying in recent decades. Microbial communities play a crucial role in the formation and function of OMZ, mediating the global biogeochemical and climatic process (Rixen et al., 2020). The present study aimed at elucidating the microbial composition and diversity across different oxygen gradient in the water column of the Arabian Sea, and determination of key bioindicator taxa in the hypoxia zones through 16S rRNA gene high-throughput sequencing.

### 4.1 Differences in physicochemical parameters and their effect on the prokaryotic community

It is reported that the formation and maintenance of AS OMZ was due to intense seasonal surface blooms, coupled with a land-locked northern boundary and limited northern ventilation (Vallivattathillam et al., 2023). Using switchable trace oxygen

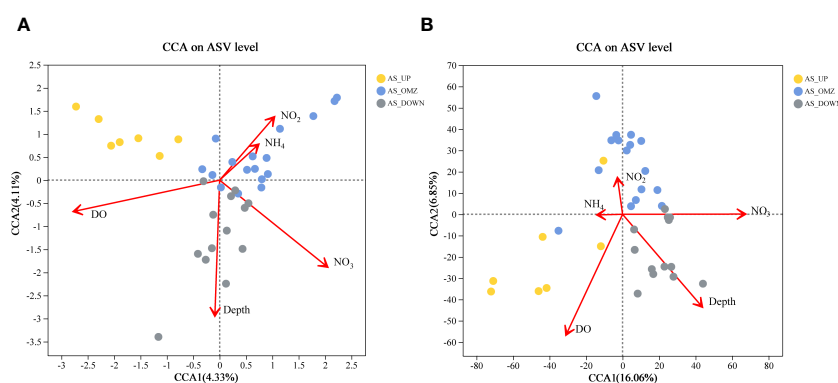


FIGURE 7

Canonical Correspondence Analysis ordination diagram of bacterial and archaeal communities. (A) bacterial at ASV level in AS (B) archaeal at ASV level in AS.

(STOX) amperometric microsensors, researchers have identified essentially oxygen-free waters in the nitrite-rich regions of the Arabian Sea, particularly in the Omani Shelf (Jensen et al., 2011). In this study, the variation observed in DO levels along the depth of water column among the sampled locations (except for CTD08) are consistent with results previously described in Arabian Sea OMZs, where the DCM and near bottom depths are well-oxygenated, and the DO values in OMZs are below the defined threshold ( $<20 \mu\text{M}$ ) (Beal et al., 2013). The thickest OMZs in this study were observed in stations CTD03, CTD04 and CTD05 located in the northern Arabian Sea, ranging from about 100m to 1500m. They were recognized as the core OMZ zone here, with the DO values almost undetectable from about 150m to 1200m. In the OMZ transition zone, for CTD02 and CTD06 stations, their DO values were also below  $20 \mu\text{M}$  in the OMZs from about 150m to 1000m. In contrast, high DO values (above  $62 \mu\text{M}$ ) were observed in the water column of CTD08 station located in the southern AS far from the mainland, which might be due to the relatively limited impact of terrestrial organic matter input, indirectly leading to less intense microbial oxygen consumption activity in OMZ (Fernandez-Alamo and Färber-Lorda, 2006). Hence, CTD08 station was considered as non-hypoxic zone, and used as a control group in this study. In AS, no significant difference of the salinity was observed in the horizontal direction of the water column. However, the salinity gradually decreases with increasing water depth, consistent with previous research (Supplementary Figure 1) (Al-Said et al., 2018; Bandekar et al., 2018). The nitrate concentrations were low in DCM layer in this study across the sampled locations, however, they were higher in the OMZs and deep layers. The low surface nitrate concentrations might be due to high primary productivity in AS (Kumar et al., 2001). Nitrite accumulation was observed not only in the surface layers (DCM) but also in the mid and deeper depths in most locations, which might drive nitrification process. High nitrite concentration accompanied with low DO such as at 300m of CTD03 station, was profit for biological processes denitrification, and implied intense denitrification process (Ulloa et al., 2012).

The structure of microbial communities is often influenced by variable ocean environmental conditions with geographical isolation and environmental parameters (Yan et al., 2018). Variations in environmental conditions and competition across the oxygen gradient might account for the difference observed between surface and OMZ bacterial communities (Long et al., 2021). The analysis of relationships between environmental factors with microbial community revealed that dissolved oxygen (DO), depth, nitrate ( $\text{NO}_3^-$ ), and nitrite ( $\text{NO}_2^-$ ) were the significant environment factors in this study, which might co-shape microbial communities. DO has been detected as a crucial factor to significantly structure and differentiate the microbial community composition in the oxygenated upper waters and hypoxic OMZs in AS. Similarly, DO was also considered as the important driver responsible for the changes in microbial communities in the hypoxic zone in Gulf of Mexico and the eastern tropical North Pacific Ocean (ETNP) (Beman et al., 2013). Other environmental parameters including depth and nitrate exerted significant impacts on the structure of bacterial and archaeal communities in AS.

## 4.2 Bacterial community composition and important taxa – key members in OMZ

The alpha diversity index results revealed the highest archaeal richness and diversity in the AS\_OMZ and AS\_UP communities compared to the AS\_DOWN community (Supplementary Figure 3). While the AS\_OMZ appeared to have greater bacterial diversity, no significant difference in richness was found between it and the AS\_DOWN. This is consistent with previous findings in the epipelagic waters of the Andaman and the eastern Bay of Bengal (Supplementary Figure 3) (Guo et al., 2022). NMDS analysis revealed that bacterial community of AS\_OMZ was significantly different from AS\_UP group, while AS\_DOWN community seemed to overlap with AS\_OMZ and AS\_UP. Though AS\_DOWN samples were geographically adjacent to the AS\_OMZ, the DO levels were closer to AS\_UP layers, which might lead to mixed characteristics in bacterial community composition between AS\_UP and AS\_DOWN. For archaea, the beta diversity analysis showed a clear difference between samples from AS\_UP, AS\_OMZ and AS\_DOWN, confirming dissimilar archaeal community structure in the different depths.

Bacterial community in all samples in this study was found to be dominated by *Proteobacteria*, *Actinobacteria*, *Bacterioda*, SAR406\_clade, *Firmicutes*, *Chloreflexi*, *Cyanobacteria*, SAR324 and *Nitrospinota*, similar to others found in various pelagic OMZ (Sun et al., 2021; Gu et al., 2022). *Gammaproteobacteria* and *Alphaproteobacteria* dominated through the water column in AS. The dominance of these phylotypes has been well documented in a variety of pelagic marine zones including the ETSP-OMZ, Northwest Mediterranean Sea, Tropical Western Pacific Ocean and Southern AS (Fuchs et al., 2005; Stevens and Ulloa, 2008; Crespo et al., 2013; Ganesh et al., 2013; Sun et al., 2021). The *Bacteroidetes* was known to be associated with phytoplankton and abundant at surface waters (Fandino et al., 2001). However, *Bacterioda* abundance did not significantly decrease with depth in the OMZ of AS in this study.

*Alteromonadaceae* was one of the most dominant representative of *Gammaproteobacteria* in AS, and exhibited high relative abundances in the whole water column in AS. However, *Alteromonadaceae* was previously reported to dominate in the deeper water in ETSP (Stevens and Ulloa, 2008). In this study, ASVs affiliated with the family *Alteromonadaceae* were primarily phylogenetically related to *Alteromonas macleodii* and *Alteromonas lipolytica*, with both species being widely distributed throughout the water column in AS. No obvious niche partition was observed for *Alteromonas* in this study. OTU2530 affiliated with *Alteromonas macleodii* predominated not only in the UP, OMZ and DOWN of AS, but also in the water column of Bob and ETNP (Figure 4), irrespective of water depth. Previous reports in OMZ suggest that *Alteromonas* participate in complex carbon metabolism pathways and co-exist with other key microbial players in the carbon cycle, such as *Marinobacter* and *Prochlorococcus* (Gao et al., 2017; Koch et al., 2020; Frühe et al., 2021; Henríquez-Castillo et al., 2022). *Alteromonas macleodii* has been intensively studied and well-known to niche specialization. The surface ecotype of *Alteromonas macleodii* was found to be globally abundant and

recognized for its capability to degrade sugars and amino acids and colonize particulate organic matter with much slower sinking rates. In contrast, the deep ecotype displayed a higher potential of degrading recalcitrant compounds and colonizing relatively large particles that sink rapidly to meso and bathy pelagic depths (Ivars-Martinez et al., 2008). Ecologically they are often associated to nutrient-rich environments such as particulate material, marine snow, or marine animals, accompanied with complex metabolic potential which strongly supports the ability to survive in various environments. Although *Alteromonadaceae* constituted a minor proportion of the metagenomic data, they significantly contributed to gene transcription across various marine environments, from mesotrophic coastal California waters to the oligotrophic subtropical North Pacific, highlighting their crucial role in sustaining ecosystem functions (Sherwood et al., 2015). The dominance of *Alteromonas* may partly attributed to the abundance of sinking particulate matter in the northern AS (P Vijayan et al., 2023).

*Sphingomonadaceae*, *Thalassospiraceae* and *Rhodobacteraceae* of *Alphaproteobacteria* were also significantly contributing to microbial communities, which were mainly represented by genera of *Sphingomonas*, *Thalassospira* and *Ruegeria*, respectively. *Sphingomonadaceae* are prevalent in various environments and metabolically versatile, which could utilize a wide range of organic compounds as well as many types of refractory contaminants, such as Bisphenol A (BPA) and aromatic hydrocarbon compounds (Kertesz and Kawasaki, 2010; Göker et al., 2017; Oh and Choi, 2019). Previous reports in OMZ suggest that high abundance of *Sphingomonadaceae* may be driven by high concentrations of phosphate and ammonia (Liu et al., 2015). *Rhodobacteraceae* is considered as one of the most abundant groups of bacteria in marine ecosystem, comprising photoheterotrophic and chemoheterotrophic species. The diverse metabolic capabilities of *Rhodobacteraceae*, including the utilization of organic compounds, sulfur oxidation, carbon monoxide oxidation, and dimethylsulfoniopropionate (DMSP) degradation, enable them to thrive in a wide range of environments (Brinkhoff et al., 2008; Elifantz et al., 2013; Pujalte et al., 2014). In addition, the ability of *Rhodobacteriaceae* (*Sagittula* genus) from the OMZ region to fix  $N_2$  has been demonstrated (Martínez-Pérez et al., 2018).

Several important taxa were determined as indicator taxa of the OMZs in AS in this study including unclassified\_f\_*Desulfosarcinaceae*, UBA10353, SUP05\_cluster, *Nitrospina*, Sva0996\_marine\_group, unclassified\_f\_*Microtrichaceae*. Among these, relatively high abundances of UBA10353, SUP05, *Nitrospina* have also been detected in other OMZs, including Gulf of Alaska, ETSP and ETNP (Beman and Carolan, 2013; Muck et al., 2019; Sun et al., 2019). *Desulfosarcinaceae*, belonging to *Desulfobacterales* of the class *Desulfobacteria*, was determined as an abundant member and key indicator taxa in hypoxic zones of AS. The spatial and depth-wise distribution patterns indicated that *Desulfosarcinaceae* was unique to AS communities, which almost exclusively inhabited in the OMZs of AS (CTD03, CTD04, CTD05, CTD06), however absent in CTD02 and CTD08 stations as well as in Bob and ETNP OMZs communities (Figure 6; Supplementary Figure 8). ASVs (OTUs) affiliated with *Desulfosarcinaceae* were closely related with SEEP-SRB1. It was

reported that the family *Desulfosarcinaceae* including genera such as *Desulfosarcina*, *Desulfatitalea*, SEEP-SRB1, and Sva0081 sediment group, were sulfate-reducing bacteria (SRB). Members of this group have been identified as strict anaerobes, exhibiting both respiratory and fermentative metabolic pathways. They have been found in anoxic brackish water environments as well as marine habitats, including water-flooded oil fields (Galushko and Rozanova, 1991; Watanabe et al., 2017). Previous evidences also suggested that *Desulfobacterales* were important  $H_2$ -scavengers in marine sediments as well as in microbial mat community, and also played important roles in nitrogen cycling of mangrove ecosystem (Burow et al., 2014; Dyksma et al., 2017; Nie et al., 2021). Metabolic pathway prediction based on publicly available genomes of *Desulfosarcinaceae* also indicated the genetic potential of chemolithotrophy via Wood–Ljungdahl pathway as well as nitrogen fixation in this study. The dominant presence of *Desulfosarcinaceae* suggested the crucial roles involved in the carbon, nitrogen, sulfur and hydrogen cycles in OMZs of AS. The ecological functions and *in situ* activities of *Desulfosarcinaceae* in the hypoxic zone of AS will be further explored based on metagenomics and metatranscriptomes data.

UBA10353 was another abundant taxa and predominated in the OMZ core in AS, which was phylogenetically closely related to *Arenicellales* order of *Gammaproteobacteria* (Martínez-Pérez et al., 2022). A similar distribution pattern of this group has also been found in OMZs, including the deeper layers of the western Mediterranean Sea, the OMZ core of Tropical Mexican Pacific, the OMZ and OLZ of the Andaman Sea and eastern BoB epipelagic waters (Pajares et al., 2020; Martínez-Pérez et al., 2022). The spatial distribution patterns analysis based on AS, Bob and ETNP data showed that the dominant taxa of UBA10353 shifted between different sea areas (Figure 6; Supplementary Figure 8). For example, OTU11318, OTU11316 and OTU11385 seemed to be exclusively distributed in the hypoxic zone of AS except for CTD02 and CTD08, and they were absent in Bob and ETNP OMZ communities. OTU5267, OTU2157 and OTU4614 dominated in the OMZ and deep communities of ETNP, but showed low relative abundance in AS and Bob OMZ communities. UBA10353 was speculated to have the potential of mixotrophy lifestyle encoding the genes for the Calvin-Benson-Bassham cycle and heterotrophic metabolism (Martínez-Pérez et al., 2022). However, knowledge about the ecology, genetics, and functions of UBA10353 are still limited.

*Nitrospina* and SUP05 groups were also significantly enriched in the OMZs of AS in this study and were identified as important bioindicator taxa. In this study, the dominant taxa of *Nitrospina*, as represented by OTU11457 and OTU5252, were enriched not only in the AS OMZ, but also in Bob OMZ and ETNP OMZ communities (Figure 6; Supplementary Figure 8). Surprisingly, this taxa was also detected in the communities from ETNP 2000m. *Nitrospina* bacteria were recognized as aerobic nitrite oxidizers, playing a crucial role in nitrification processes in the BSI (Red Sea) and in the OMZ (ETSP) habitats (Ngugi et al., 2016). The differences observed by previous studies between novel *Nitrospina* OMZ MAGs from cultured representatives and all MAGs from non-OMZ environments suggest niche differentiation of *Nitrospina* in the ocean (Sun et al., 2019). Similar distribution pattern was also observed for SUP05

group. In AS, BOB and ENTP OMZs, SUP05 was mainly dominated by OTU4763, and showed no obvious ecotype differentiation between different sea areas (Figure 6; Supplementary Figure 8). SUP05 are known chemolithoautotrophs and have the potential for carbon fixation and sulfur oxidation (Mattes et al., 2020). Members of these groups are globally distributed in OMZs, such as in OMZs of the Arabian Sea, ETSP, ETNP, and BoB, which might contribute to the carbon, nitrogen and sulfur cycles in the OMZ (Bryant et al., 2012; Ulloa et al., 2012; Bandekar et al., 2018). *Microtrichaceae* were abundant not only in the OMZs of AS but also in the upper water column (AS\_UP). Similar distribution pattern was also observed in Bob and ETNP (Figure 6; Supplementary Figure 8). Most of the ASVs affiliated with *Microtrichaceae* formed at least two clades, one belonged to Sva0996\_marine\_group, which was reported that proliferated on the fouling-release surface, one belonged to unclassified\_f\_Microtrichaceae. Besides, Sva0996\_marine\_group exhibited the potential for niche partitioning, one ecotype seemed to colonize in the OMZs and the other preferred to inhabit in the euphotic zones in AS (Papadatou et al., 2021; Guo et al., 2022). In this study, the surface ecotype was represented by ASV1195 and ASV1180, and the deep ecotype was represented by ASV625, ASV638 and ASV959 (Figure 6; Supplementary Figure 8). *Microtrichaceae* has been enriched in the oxygen limited zones communities in Mexican Pacific upwelling, which have been reported to be involved in nitrification-anammox systems and demonstrate the capability to hydrolyze and metabolize complex organic matter (Wang et al., 2020; Li et al., 2021a; Guo et al., 2022; Pajares et al., 2023).

The SAR324 group is known to inhabit a wide range of environments and is particularly abundant in OMZs and deeper depths, including deep-sea hydrothermal vents (Malfertheiner et al., 2022). Although the relative abundance of SAR324 did not significantly differ in the water column of AS in this study, a distinct depth distribution pattern was observed. Specifically, ASV1818 was detected above 200m, ASV1202 and ASV384 were found specifically above the OMZ, ASV422 was exclusively present within the OMZ, and ASV28 was identified from the OMZ to deeper depths (Figure 6; Supplementary Figure 8). However, higher relative abundance of SAR324 were detected in ETNP compared with AS and Bob. In addition, the niche specialization of SAR324 in ETNP were more obvious. For example, OTU2233 dominated in the surface waters, while OTU2280 prevailed in the OMZ and deep layers. SAR324\_clade, newly proposed as its own candidate phylum, is globally relevant in the ocean aphotic zone and prevail throughout the water column from surface waters to the abyss, with abundance maxima correlating with low-oxygen concentrations (Wright et al., 1997; DeLong et al., 2006; Wright et al., 2012; Dick et al., 2013; Hawley et al., 2014; Thrash et al., 2017; Aldunate et al., 2018; Rajpathak et al., 2018; Malfertheiner et al., 2022). SAR324 possesses versatile and extensive metabolic repertoire, encompassing both heterotrophic and autotrophic pathways, and exhibited distinct depth and temporal distributions that clearly differentiated ecotypes (Boeuf et al., 2021; Malfertheiner et al., 2022). SAR324\_clade was identified as keystone taxa that maintained the structures and functions of microbial community in AS, similar to that in Andaman Sea and eastern BoB (Guo et al., 2022).

*Cyanobacteria*, *Candidatus\_Actinomarina*, SAR86\_clade, NS2b\_marine\_group, NS5\_marine\_group, NS9\_marine\_group and OCS116\_clade were also determined as bioindicator taxa in AS\_UP communities, with significantly higher abundance than in AS\_OMZ and AS\_DOWN communities. The most abundant ASVs of *Cyanobacteria* in this study were affiliated with *Prochlorococcus\_MIT9313* and unclassified\_f\_Cyanobiaceae in AS. *Prochlorococcus* is primarily abundant in warm oligotrophic waters, particularly in the subtropical gyres of the Indian and western Pacific Ocean (Flombaum et al., 2013). As indicator taxa of AS\_UP, *Candidatus\_Actinomarina* was reported as a subclass of exclusively marine *Actinobacteria* with small cells and genomes (Ghai et al., 2013). SAR86 is an abundant and ubiquitous heterotroph in the surface ocean. In previous researches, at least 5 subgroups of SAR86 were identified based on pan-genome analysis, each of which exhibits distinct geographic distribution patterns correlated with specific environmental parameters (Sabeji et al., 2004; Levin and Angert, 2015; Hoarfrost et al., 2019; López-Pérez et al., 2020).

### 4.3 Archaeal community composition with depth distribution patterns

Archaea are now recognized to be as crucial as bacteria in driving the biogeochemical cycles within the global ocean (Herrndl et al., 2005; Knittel et al., 2005; Leininger et al., 2006; Lipp et al., 2008). The occurrence of archaeal groups in the Eastern Tropical South Pacific OMZ, as well as in northern Chile and other oxygen-deficient ecosystems, indicates the active involvement of archaea within these OMZ environments (Woebken et al., 2007; Quinones et al., 2009; Belmar et al., 2011; Stewart et al., 2012). In contrast to the bacterial domain, less was known about archaeal community structure and diversity in the OMZ of AS, although previous studies had reported on ammonia-oxidizing archaea in AS (Pitcher et al., 2011; Peng et al., 2013).

In this study, depth-dependent distribution patterns were observed within the archaeal community. *Crenarchaeota* and *Thermoplasmata* dominated throughout the water column in AS. Not only abundant in the euphotic zone, the relative abundance of *Crenarchaeota* tended to increase with depth and also dominated the OMZ and bathypelagic archaeal communities, similar to previous results observed in other marine environment such as in Gulf of Alaska and the Atlantic Ocean (Shiozaki et al., 2016; Sintes et al., 2016; Muck et al., 2019; Abdulaziz et al., 2020). ASVs of *Crenarchaeota* were mostly phylogenetically affiliated with *Candidatus\_Nitrosopelagicus* and *Nitrosopumilus* of *Nitrosopumilaceae* family, among which *Candidatus\_Nitrosopelagicus* almost exclusively inhabited in the euphotic zones in AS, while *Nitrosopumilus* prevailed in the OMZs and deeper layers (Rinke et al., 2013; Sow et al., 2022).

*Thermoplasmata* (formerly Marine\_Group\_II) predominated not only in the water column in AS of this study, but also in ETSP, Atlantic Ocean (Pereira et al., 2019). Marine Group II exhibited higher relative abundance in the euphotic zone than the deeper water samples in AS, which was consistent with the common understanding that MGII reside mostly in the surface ocean, Marine Group II showed unique patterns of organic carbon degradation and their energy

requirements may be augmented by light in the photic zone (Zhang et al., 2015). Besides, Marine Group II was also abundant in deep-sea waters in this study of AS. Although Marine Group II exhibited high relative abundance throughout the water column of AS, the taxonomic composition of Marine Group II differed in the surface and deep water samples. It has been previously found that Marine Group II lived heterotrophically and displayed great seasonal and spatial variation and phylogenetic diversity (Zhang et al., 2015). Marine Group III (MGIII) were initially described by Fuhrman and Davis from deep marine plankton samples and generally regarded as low-abundance members of deep mesopelagic and bathypelagic communities (Fuhrman and Davis, 1997; Haro-Moreno et al., 2017). Only a few studies report the presence of MG-III in the photic zone. In this study, MG-III was found throughout the water column in AS, not only in the OMZ and bathypelagic layers, but also in the euphotic zones. However, their physiology and ecological roles in oceanic environments remain poorly understood. *Crenarchaeota* and *Thermoplasmata* exhibit specific dominant taxa in different water layers, indicating niche differentiation, metabolic or functional diversity of closely related taxa at the genus or ASV levels, these findings are in line with earlier research results (Rinke et al., 2018; Sow et al., 2022).

#### 4.4 Function prediction from FAPROTAX

FAPROTAX has been extensively utilized for the microbial functional annotation of the biogeochemical process (Louca et al., 2016). The microbial functional prediction based on the taxonomic information of the 16S rDNA gene revealed a significant variation of carbon, nitrogen and sulfur metabolism potential across different oxygen gradients in the Arabian Sea. Photoautotrophy and photoheterotrophy processes were more active in the up layer and weakened with the increase of water depth. The potential for denitrification, nitrification, aerobic nitrite oxidation, nitrogen respiration, nitrate respiration, dark sulfide/sulfur compounds oxidation were more abundant in the OMZs in AS. However, functions including hydrocarbon degradation and aromatic compound degradation seemed to exhibit higher predicted abundances in deeper layers. Similar results were previously observed in the Andaman Sea and eastern BoB (Guo et al., 2022). Nitrogen cycling are intensively active in anoxic water such as OMZs, wherein denitrification and anammox have been recognized as the major process associated with nitrogen loss in the Arabian Sea (Ward et al., 2009; Jensen et al., 2011). Despite oxygen concentrations within the samples from the OMZ of this study being below 20 $\mu$ M, the predicted abundance of denitrification genes was notably lower than that of nitrification genes. This suggests that nitrification might be a predominant nitrogen cycling process in the OMZ of the AS. High abundance of ammonia oxidation genes abundance could be attributed to the significant presence of *Nitrosopumilaceae*, while aerobic nitrite oxidation genes in AS OMZ samples could well be associated with the abundant presence of *Nitrospina*. Sulfur cycling are also important for biogeochemical process in OMZs (Wright et al., 2012; Long et al., 2021). Sulfur metabolism functions such as dark sulfide/sulfur compounds oxidation were predicted to be more active in the OMZ of AS than in the oxygenic water samples. Sulfur

cycle associated bacterial taxa might contributed by SUP05, SAR324, SAR406, *Desulfovibrionales* and so on in the OMZ of AS, which also potentially coupled nitrogen and carbon cycling (Bertagnolli et al., 2017; Callbeck et al., 2018; Boeuf et al., 2021). Although potential microbial populations involved in carbon, nitrogen and sulfur metabolism were predicted here, however, their actual activities *in situ* were unclear. Functional profiling of AS samples should be interpreted with caution, as they rely on predictive models derived from 16S rRNA sequence data. Further investigation based on metagenome and metatranscriptome data is required to understand the ecological roles of the dominant microbes present in the OMZ regions of AS.

## 5 Conclusion

In conclusion, this study has shed light on the complex prokaryotic community structures within the Arabian Sea's oxygen minimum zones (OMZs). Our comprehensive analysis of 44 water samples across various depths and oxygen gradients in the Arabian Sea has revealed a significant correlation between microbial community composition and environmental parameters, particularly dissolved oxygen (DO) and depth. Bacterial communities demonstrated greater richness and diversity compared to archaeal communities throughout the water column in the Arabian Sea. The composition of these microbial communities shifted markedly across the different oxygen gradients and depths. Notably, key bioindicator taxa such as *Desulfosarcinaceae*, UBA10353, *Nitrospina*, SUP05, Sva0996\_marine\_group, and *Microtrichaceae* were prominent in the core of the OMZ. Additionally, SAR324, *Alteromonadaceae*, and *Sphingomonadaceae* were recognized for their pivotal roles as keystone taxa. These taxa exhibited distinct spatial and depth-wise distribution patterns across AS, BoB and ETNP. Notably, *Desulfosarcinaceae* displayed an exclusive distribution within the hypoxic zones of the Arabian Sea, suggesting a specialized adaptation to anoxic niches. In contrast, UBA10353, *Nitrospina*, SUP05, *Microtrichaceae*, and SAR324 exhibited a cosmopolitan distribution, indicating their ubiquity and potential adaptability across different OMZs. The functional profiling of microbial communities, as predicted by FAPROTAX, indicated an enhanced potential for denitrification, nitrification, and sulfur oxidation in the OMZ. However, the actual *in situ* activities of these microbes remain to be elucidated through future metagenomic and metatranscriptomic studies. Collectively, our findings significantly contribute to the understanding of the distribution, structure, and diversity of microbial communities in the Arabian Sea's OMZ. This knowledge is crucial for predicting the ecological roles and responses of these communities to changing oceanographic conditions and informs further research into the complex microbial ecology and function within OMZs.

## 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 in the article/Supplementary Material.

## Author contributions

DL: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. LW: Writing – original draft, Writing – review & editing, Formal analysis, Data curation, Funding acquisition. FJ: Data curation, Writing – review & editing. XZ: Resources, Investigation, Writing – review & editing. QX: Resources, Investigation, Writing – review & editing. XLZ: Resources, Investigation, Writing – review & editing. QZ: Supervision, Writing – review & editing. ZS: Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential 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.2024.1380819/full#supplementary-material>

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