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Proteobacteria Dominance and Neutral Assembly Processes of Bacterial Communities in the Chukchi Sea, Arctic

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Abstract. Bacteria play a vital role in maintaining ecosystem functioning under rapidly changing environmental conditions, however, the characteristics and assembly mechanisms of bacterial communities at regional scales in the marine ecosystem of the Arctic Chukchi Sea remain poorly understood. Using 16S rRNA gene amplicon sequencing, we investigated the composition, diversity, and assembly processes of bacterial communities across three distinct water layers (Surface, Middle, and Bottom) in the Chukchi Sea. The results revealed a significant increase in community richness in the Middle and Bottom layers compared to the Surface layer, with Alphaproteobacteria, Cyanobacteriia, and Bacteroidia as the predominant classes. The bacterial community structures differed significantly across the water layers, and their β-diversity was primarily driven by species turnover. Environmental variables explained approximately 48.2% of the variation in community structure, with water depth, dissolved oxygen (DO) and silicate were identified as driving factors ($p<0.05$). Furthermore, network analysis indicated that the bacterial co-occurrence network in the middle layer exhibited greater complexity and stability. The Neutral community model (which explained 61.9% of community variation) and null model analyses collectively demonstrated that while both deterministic and stochastic processes govern bacterial community assembly in the Chukchi Sea, stochasticity is the dominant force. These findings advance our understanding of depth-stratified bacterial ecology in the Chukchi Sea and provide a crucial foundation for future studies on ecosystem responses to ongoing environmental changes in the Arctic.

Keywords: Bacterial diversity; Co-occurrence network; Stochastic processes; Chukchi Sea.

1 Introduction

The Chukchi Sea, in the Arctic Ocean, has a broad, shallow continental shelf and serves as the primary gateway for Pacific water entering the Arctic, playing a pivotal role in Pacific-Arctic material and energy exchange (Dunton et al., 2005; Shimada et al., 2006; Kwok and Rothrock, 2009; Grebmeier and Maslowski, 2014). This unique position makes it a key focus of Arctic marine research, particularly regarding its hydrographic environment and associated ecological processes (Gradinger, 2009; Hopcroft et al., 2010; Mathiset al., 2007).

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A prominent feature of the Arctic Ocean water column is its distinct vertical stratification, typically divided into three discrete layers with contrasting physicochemical properties (Aagaard et al., 1981; Rudels et al., 1996). The cold, low-salinity surface layer is sustained by sea-ice melt and riverine input, featuring a sharp halocline that acts as a physical barrier to vertical mixing, thereby isolating the surface from underlying layers (Carmack et al., 2015; Challet et al., 2025). Beneath the halocline lies the warm, saline Atlantic water layer, which serves as the primary heat source for the Arctic Ocean and modulates regional thermal dynamics and biogeochemical gradients (Polyakov et al., 2017; Wang et al., 2024). The deepest layer consists of cold, hypersaline abyssal water with stable physicochemical conditions and minimal interannual variability. Importantly, this stratification pattern exhibits significant regional differences: marginal seas like the Chukchi Sea, influenced by seasonal ice melt, Pacific water inflow, and shelf-scale processes, display more dynamic stratification and seasonally variable surface layer thickness compared to the central Arctic Basin (Aagaard and Carmack, 1989; Jackson et al., 2010; Zhang et al., 2024). In the Chukchi Sea, summer open-water conditions reinforce vertical stratification, driven by salinity and temperature gradients from sea-ice melt and residual winter water (Day et al., 2013; Weingartner et al., 2013; Tian et al., 2021). Within this stratified system, Bering Sea inflow sequentially displaces meltwater in the upper layer and cold winter water in the lower layer, with the latter persisting in the benthic environment throughout the summer (Day et al., 2013; Weingartner et al., 2013; Tian et al., 2021). While previous studies have documented vertical zonation in the Beaufort Gyre and unique diversity in deeper Arctic water masses (Puthiya et al., 2021; Cao et al., 2020), research on depth-related variation of bacterial communities across surface, middle, and bottom layers in the Chukchi Sea remains limited. This vertical stratification further establishes a fundamental physical framework that partitions the marine environment into distinct physicochemical realms, directly governing microbial niche differentiation and community assembly across the pan-Arctic region (Galand et al., 2009; Puthiya et al., 2021).

Marine microbial communities underpin essential ecosystem functions (Azam and Malfatti, 2007; Falkowski et al., 2008). As the cornerstone of polar marine ecosystems, they play a decisive role in the Chukchi Sea and the broader Arctic Ocean (Kirchman et al., 2007; Boetius et al., 2015; Cao et al., 2020). By driving biogeochemical cycling, supporting the food web, and regulating pollutant transport, microbial communities profoundly influence carbon and nutrient recycling in the region (Wassmann, 2011; Lovejoy et al., 2015; Vipindas et al., 2025).

Revealing microbial diversity assembly mechanisms is a core issue in microbial ecology (Dini-Andreote et al., 2015). For polar ecosystems like the Chukchi Sea, this is critical for predicting climate change responses, biogeochemical stability, and biodiversity conservation (Pan et al., 2025; Liu et al., 2025). Community assembly is driven by deterministic (niche-based) and stochastic (neutral) processes (Stegen et al., 2013). In the Arctic, stochastic processes (primarily dispersal limitation) together with deterministic homogeneous selection jointly govern community assembly (Pan et al., 2025; Han et al., 2023). By contrast, deterministic heterogeneous selection prevails in the Antarctic Peninsula, whereas undominated stochastic processes dominate in circum-Antarctic areas (Liu et al., 2025; Zhanget al., 2022). Yet targeted research in the Chukchi Sea is scarce. Clarifying the relative contributions of deterministic and stochastic processes here will enhance understanding of polar microbial responses and help predict Arctic coastal ecosystem shifts under global warming.

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To address these knowledge gaps, this study analyzed bacterial communities in water samples collected from the Chukchi Sea during the 13th Chinese Arctic Expedition using high-throughput 16S rRNA sequencing. Specifically, the objectives of this study were to:(1) characterize bacterial community structure across the surface, mid-depth, and bottom water layers of the Chukchi Sea; (2) elucidate the diversity and co-occurrence networks of bacterial communities among these three layers; and (3) identify the key environmental factors governing bacterial community distribution and their underlying assembly processes.

2 Material and method

2.1 Study area, field sampling, and chemical analysis

The seawater samples were collected aboard the R/V Xuelong 2 during the summer sea ice melting season of the 13th Arctic Expedition. The investigation was conducted in the Chukchi Sea region (approximately 74°N–78°N, 156°W–168°W). A total of eight sampling stations were established, from which 24 seawater samples were collected. The sampling transect encompassed three geomorphological regimes of the Chukchi Sea–Canada Basin system. Shelf stations (R11, R12, P1_07) were located on the shallow Chukchi shelf, where Pacific water inflow and sea-ice melt dominate hydrographic conditions. Slope stations (R13, P2_05, R16, P2_04) captured the transition from shelf to basin, including the shelf break and upper-to-mid slope. The deepest station (P2_08) was situated in the Canada Basin, where the water column is strongly stratified and influenced by Atlantic water. Water samples were collected using a CTD rosette system from three discrete depths at each station, representing the major water masses of the Arctic Ocean: Surface (S), Middle (M), and Bottom (B) (Fig. 1, Table. S1).

Seawater samples (2 L) were collected from different water layers. Analysis of Environmental Variables Salinity, temperature, dissolved oxygen (DO), and fluorescence profile was measured using the CTD system. For chlorophyll a (Chl a) analysis, 2 L of seawater was filtered through Whatman GF/F glass-fiber filters (0.7 um). Chla was extracted in 90% acetone for 24h in the dark at 4 ° C, and concentrations were determined spectrophotometrically. Nutrients, including ammonia (NH4+), nitrite (NO2−), silicate (SiO32−), and phosphate (PO43−)were measured spectrophotometrically with a San++ continuous flow auto-analyser (Skalar, the Netherlands) after filtering following the procedure described by using a previously described method (Hansen and Koroleff, 1999).

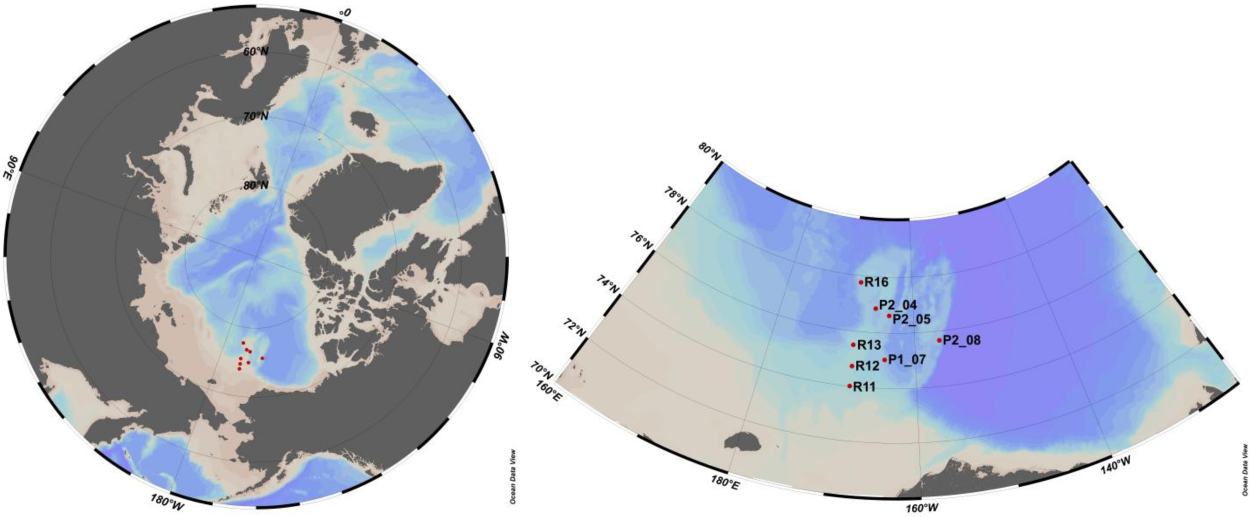

Figure 1: Locations of the eight research stations in the Chukchi Sea

2.2 DNA extraction, qualification, and sequencing analysis

DNA extraction and library preparation for 16S rRNA gene sequencing were performed by Majorbio Bio-Pharm Technology Co., Ltd (Shanghai). The V4-V5 hypervariable regions of prokaryotic 16S rRNA genes were amplified using primers 515F-Y and 926R, with subsequent construction of the amplification libraries. PCR amplification was conducted according to the protocol described by (Zhang et al., 2022). Purified amplicons were pooled in equimolar concentrations and subjected to paired-end sequencing on an Illumina MiSeq platform. Sequence processing was performed using UPARSE (Edgar, 2013), where reads were quality-filtered, dereplicated, and clustered into operational taxonomic units (OTUs) at a 97% similarity cutoff. Taxonomic classification of representative OTU sequences was conducted against the SILVA 138 16S rRNA database (Quast et al., 2013) with a confidence threshold of 70%. A rarefaction curve was generated by plotting alpha diversity indices against the number of randomly sampled sequences per sample (Sanders, 1968; Hurlbert, 1971).

2.3 Data processing and analysis

After obtaining the original OTUs table, the standardized analysis was carried out subsequently. All statistical analyses were performed using R 4.2.2. Alpha diversity indices (Shannon and ACE) were calculated using the vegan package (Shannon, 1948; Chao and Lee, 1992), while phylogenetic diversity (PD) was calculated using the phyloseq package following Faith's method (Faith, 1992). Non-metric multidimensional scaling (NMDS) and ANOSIM were performed using vegan (Kruskal, 1964; Clarke, 1993). Beta diversity and its components (turnover and nestedness) were calculated based on the Jaccard dissimilarity index using the adespatial package (Baselga, 2010). Box plots were generated using ggplot2 and ggpubr. For co-occurrence network analysis, a correlation matrix was computed using the psych package, and the network was visualized using Gephi 0.9.2 (Bastian et al., 2009). The neutral community model (Sloan et al., 2006) and C-score null model (Stone and Roberts, 1990) were fitted using the Hmisc, minpack.lm, stats4, and devtools packages in R. Differences between groups were assessed using Spearman ' s rank correlation and one-way ANOVA with Duncan ' s post-hoc test in SPSS 27.0. Spatial mapping was performed using ArcMap 10.8.

3 Results

A total of 1,546,163 high-quality bacterial sequences were retrieved after quality filtering. Sequences were clustered into 4,474 bacterial OTUs at a 97% sequence similarity threshold, which were further assigned to 42 phyla and 613 genera. The rarefaction and Shannon curves of all samples gradually plateaued with increasing sequencing reads (Fig. S1), confirming sufficient sequencing depth to fully capture the bacterial diversity across the water column, with higher community richness and diversity observed in middle and bottom layers relative to surface waters.To elucidate the vertical differentiation of dominant bacterial communities in the Chukchi Sea, we characterized community taxonomic profiles at the class level (Fig. 2). The bacterial assemblages presented distinct stratification along the water column. Surface waters were overwhelmingly dominated by Alphaproteobacteria, Bacteroidia, and Cyanobacteria, with average relative abundances of 26.31%, 24.50% and 21.94%, respectively. Consistent with surface layers, Proteobacterial classes still prevailed in middle and bottom waters, though their total aggregate abundance decreased to 30.53% (Middle) and 32.21% (Bottom). The relative abundances of Bacteroidia and Cyanobacteria were markedly higher in surface water compared with middle (10.47% Bacteroidia, 2.59% Cyanobacteria) and bottom layers (8.74% Bacteroidia, 9.49% Cyanobacteria).

By contrast, the cumulative proportion of minor bacterial classes (average relative abundance < 1%) was substantially elevated in mid and bottom waters. Among all proteobacterial subgroups, Alphaproteobacteria showed the most dramatic shifts in relative abundance across different water depths.

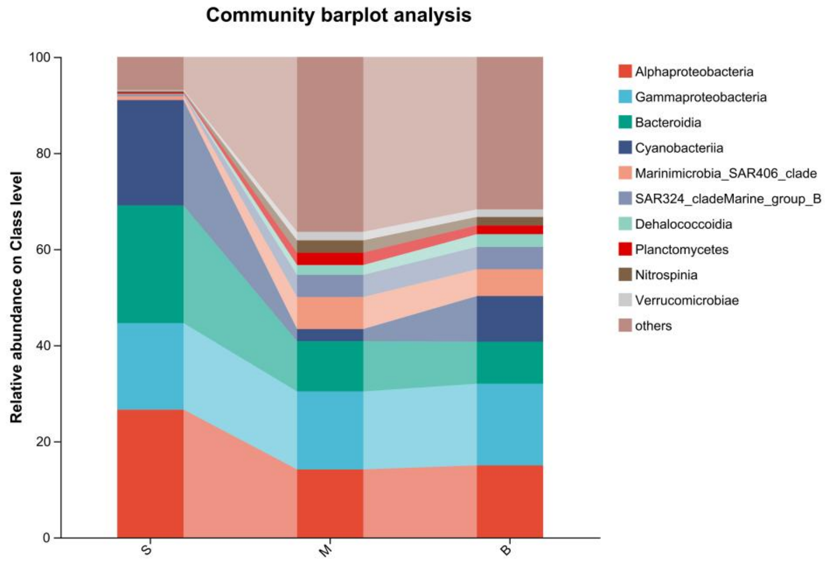

Figure 2: Stacked bar chart showing relative abundances of dominant bacterial classes (average relative abundance > 1%) across three vertical water layers: S (surface layer), M (middle layer), and B (bottom layer). Unannotated taxa and low-abundance lineages were pooled into the "others" category.

For α-diversity (Fig. 3a,b), both species richness and the Shannon index were significantly higher in the Middle water layer (Shannon index: 4.55, Ace index: 1175) and Bottom water layer (Shannon index: 4.51, Ace index: 1152) than in the Surface layer (Shannon index: 3.42, Ace index: 532). A total of 977 shared OTUs were detected across all three water layers (Fig. 3c). Specifically, 419, 973 and 968 unique OTUs were exclusively identified in the Surface, Middle and Bottom layers, respectively. In addition, the total number of OTUs in the Surface layer (1,630 OTUs) was remarkably lower than that in the Middle (2,938 OTUs) and Bottom layers (2,997 OTUs).

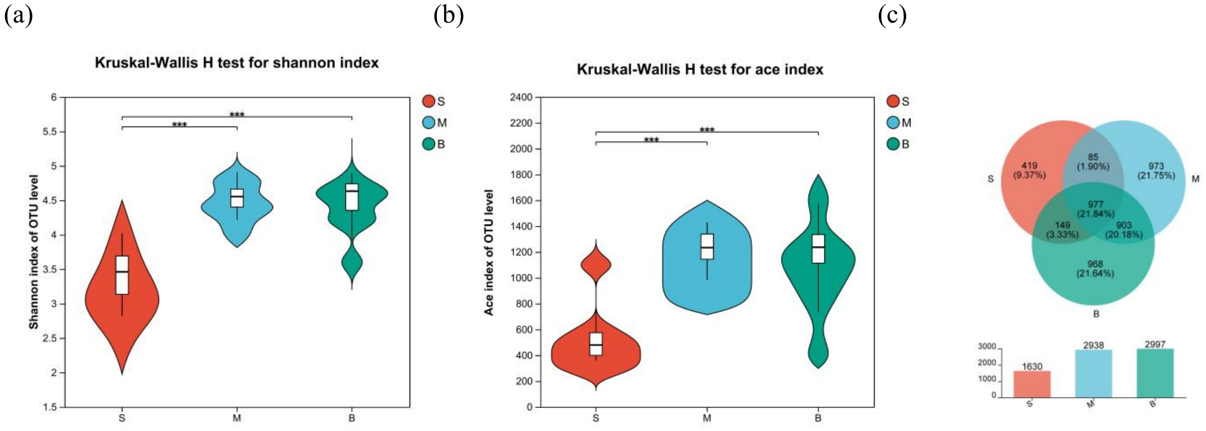

Figure 3: α-diversity and OTU distribution of microbial communities in three vertical seawater layers (S, M, B). (a) Violin plots of Shannon index based on Kruskal–Wallis H test; (b) Violin plots of ACE richness index based on Kruskal–Wallis H test; (c) Venn diagram illustrating shared and unique OTUs across groups; the bar charts below display total OTU counts for each layer. Triple asterisks (***) above pairwise comparison lines indicate highly significant intergroup differences ($p < 0.001$).

For β-diversity patterns, Non-metric Multidimensional Scaling (NMDS) ordination at the OTU level was performed (Fig. 4a). The NMDS analysis yielded a stress value of 0.06 and a coefficient of determination $R^2 = 0.32631$ ($P = 0.001$), which verified the robustness of the ordination and revealed statistically distinct microbial community compositions among the three groups. Samples from group S were clearly separated from groups M and B along the NMDS1 axis, whereas samples of groups M and B partially overlapped with one another. This pattern suggested that the community structure of the surface group (S) differed substantially from the middle (M) and bottom (B) groups, while the middle and bottom layers harbored more similar microbial assemblages. The boxplot analysis (Fig. 4b) further supported this result: the pairwise between-group distance ($R = 0.3715$, $P = 0.001$) was significantly larger than the within-group distance, confirming highly significant community dissimilarities across the three water layers.

To further partition the sources of bacterial community variation identified earlier, the analysis revealed that community dissimilarity among the S, M, and B groups was predominantly driven by species turnover. (Fig. 4c). Consistent with this pattern of high compositional replacement, the ecological niche width, as estimated for the middle and bottom water layers, was significantly broader than that of the surface water (Fig. 4d), suggesting an expansion of habitat or resource use with depth.

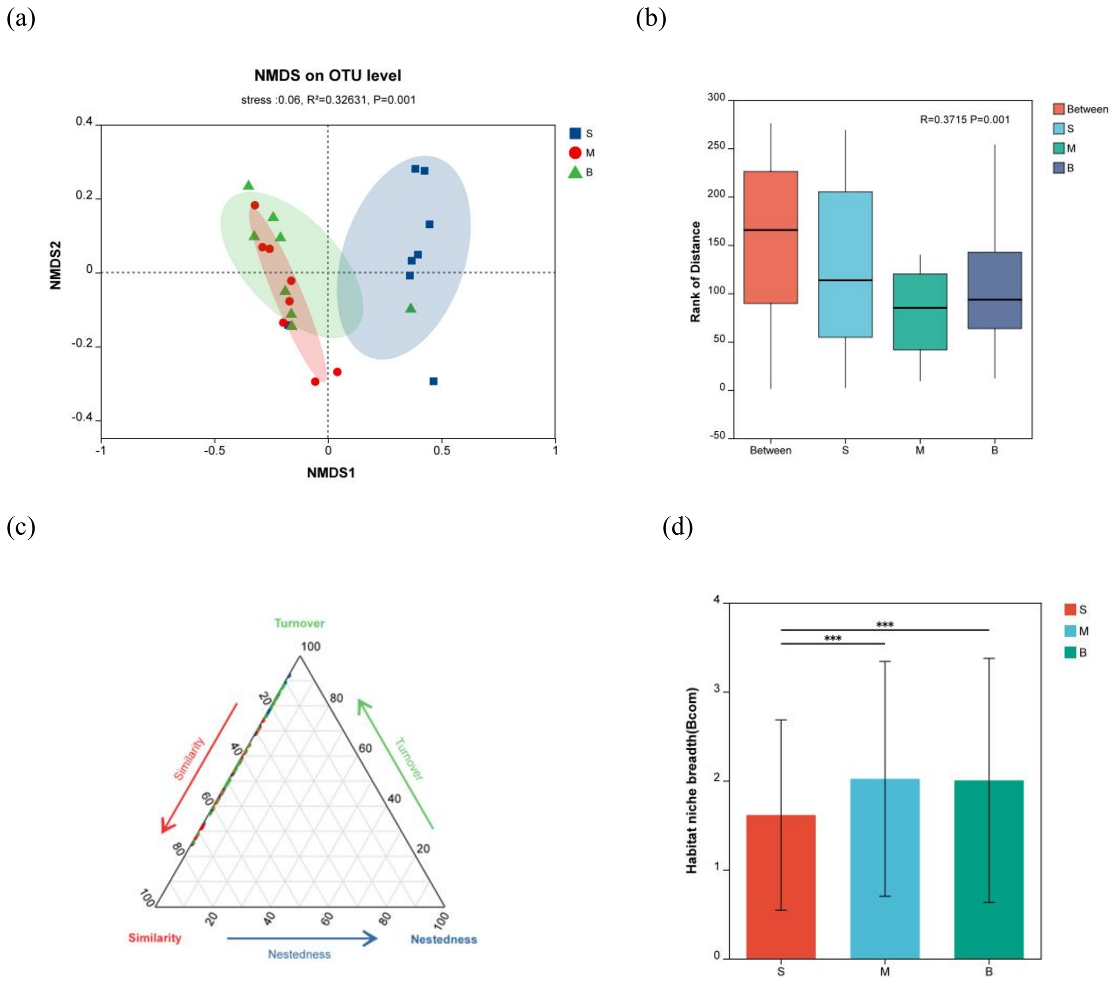

Figure 4: *β*-diversity patterns of bacterial communities across three vertical water layers. (a) Non-metric Multidimensional Scaling (NMDS) ordination based on Bray–Curtis dissimilarity at the OTU level; stress = 0.06, $R^2 = 0.32631$, P = 0.001. Shaded ellipses represent 95% confidence intervals for each group. (b) ANOSIM test of Bray–Curtis distance ranks (R = 0.3715, P = 0.001). "Between" indicates inter-group distances, while S, M and B denote intra-group distances of the three layers. (c) Ternary plot partitioning total *β*-diversity into similarity, species turnover and nestedness components. (d) Comparison of habitat niche breadth (Bcom). Asterisks (***) represent extremely significant intergroup differences ($P < 0.001$).

The environmental variables were shown in Table S1. Redundancy analysis (RDA) demonstrated that the first two axes explained 36.7% and 11.5% of the total variation, respectively, with a cumulative explanation rate of 48.2% (Fig. 5a). Monte Carlo permutation tests further identified water depth, dissolved oxygen (DO), and silicate (SiO_2) as factors significantly correlated with microbial community structure variation (Table S2). Subsequent variation partitioning analysis (VPA)

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showed that these four groups of factors (Depth, DO, SiO2, and other environmental variables) collectively explained 45.8% of the total community variation, leaving a large proportion unexplained (54.2%, Fig. 5b).

(a) (b)

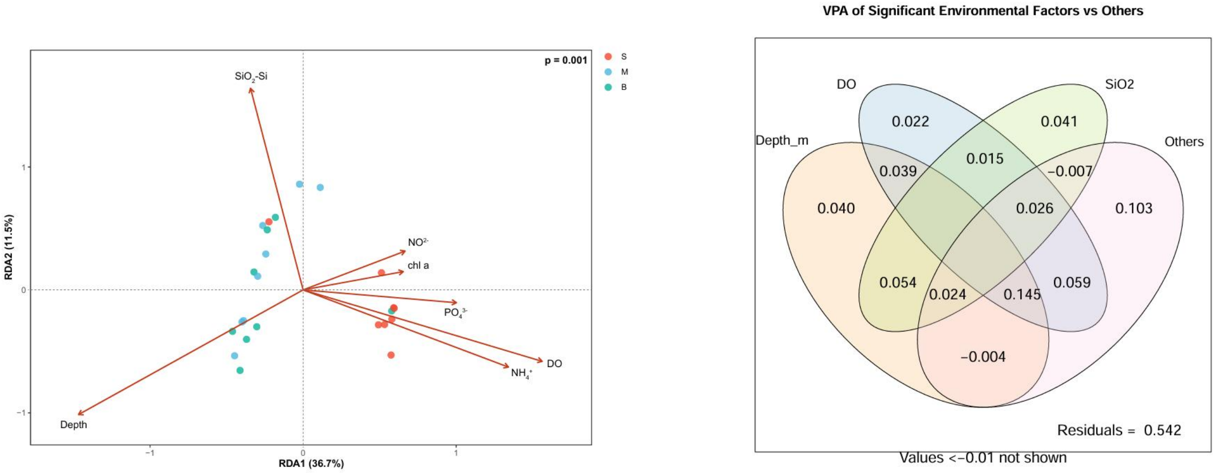

Figure 5: Links between water environmental variables and bacterial community composition based on db-RDA and VPA. (a) db-RDA ordination (Bray-Curtis distance) of bacterial communities. colored points denote different sample groups. (b) VPA Venn diagram showing adjusted R^2 of community variation explained by depth, SiO_2, DO and other environmental factors. Values < −0.01 are omitted. Abbreviations: NO_2^-, nitrite; PO_4^{3-}, phosphate; SiO_2-Si, silicate; NH_4^+, ammonium nitrogen; DO, dissolved oxygen.L: Light;chl a, chlorophyll a.

To assess bacterial interaction patterns and investigate microbial stability, co-occurrence networks were constructed based on Spearman's correlations among the top 100 OTUs by abundance (Fig. 6a), revealing distinct topological organization with depth. All three networks exhibited a prevalence of positive correlations, as reflected by the higher proportion of edges denoting cooperative or co-occurring interactions compared to those indicating negative associations. The Middle layer network displayed the highest complexity, comprising 100 nodes and 1,007 edges. In contrast, the Surface layer network consisted of 100 nodes and 694 edges, while the Bottom layer network contained 98 nodes and 822 edges. Notably, the dominant phyla identified in these networks included Proteobacteria, Actinobacteria, Cyanobacteria, and Bacteroidota, which formed the core structural components across all layers. We analyzed three topological centrality metrics—Degree Centrality, Closeness Centrality, and Betweenness Centrality—to evaluate the importance of specific nodes within the networks (Fig. 6b). The distribution of degree centrality showed that the Middle (M) layer generally maintained higher connectivity compared to the Surface (S) and Bottom (B) layers. Closeness Centrality was notably higher in the Middle (M) layer compared to both S and B layers. For Betweenness Centrality, the Bottom (B) layer exhibited a wider distribution with several outliers reaching higher values (>0.10).

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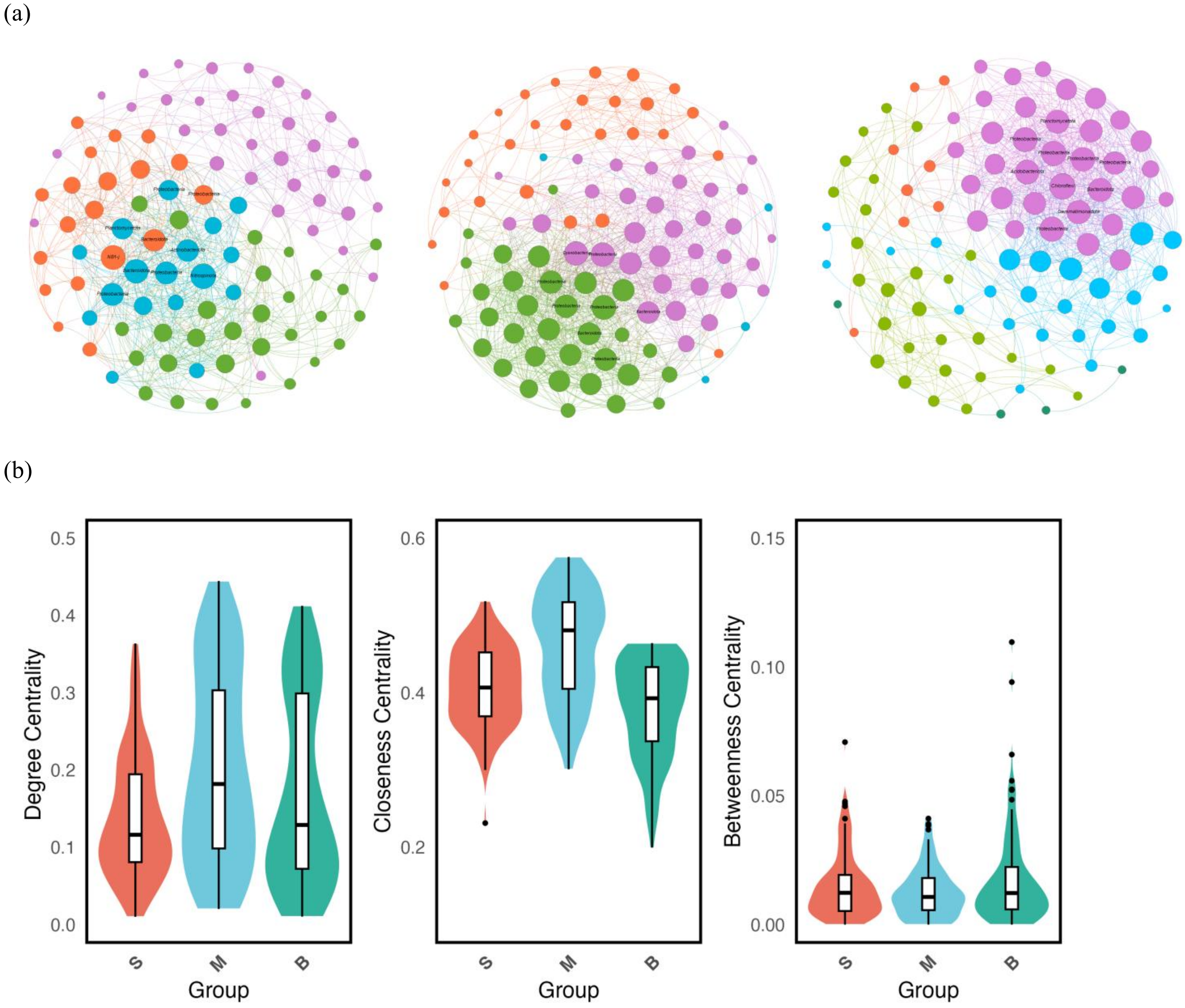

Figure 6: Bacterial co-occurrence networks and topological characteristics across three seawater layers (S, M, B). (a)Co-occurrence network visualizations for three water layers. Nodes represent bacterial OTUs, and edges denote significant correlations ($P<0.05$, ｜Spearman's ρ｜>0.5). Node colours represent distinct network modules partitioned by Gephi, and node size scales with degree centrality (larger nodes have more interconnections). Network properties: S (100 nodes, 694 links), M (100 nodes, 1007 links), B (98 nodes, 822 links). (b) Violin-box plots illustrating the distribution of three core topological metrics (degree, closeness, and betweenness centrality) among S, M and B layers.

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Neutral community model (NCM) and ecological process quantification revealed that microbial community assembly in the Chukchi Sea was predominantly governed by stochastic processes, particularly dispersal limitation (DL) and drift (DR), which collectively accounted for over 90% of the relative importance (Fig. 7a). The NCM explained 61.91% of the variation in species occurrence frequency (R^2=0.6191) with a low migration rate (m=0.0729), confirming significant dispersal limitation in this region (Fig. 7b). In contrast, deterministic processes such as homogeneous and heterogeneous selection contributed minimally, aligning with the broader pattern of stochastic dominance in Arctic microbial communities.

(a) (b)

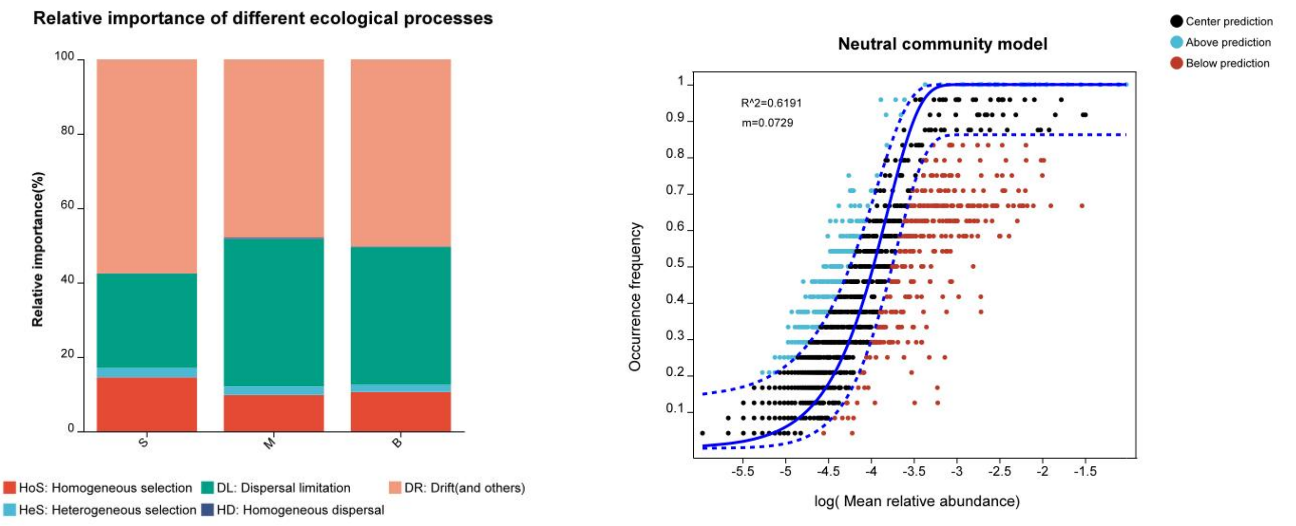

Figure 7: Microbial community assembly processes assessed via null model and neutral community model (NCM) across three seawater layers (S, M, B). (a) Stacked bar chart showing the relative contribution of five assembly processes: homogeneous selection (HoS), heterogeneous selection (HeS), dispersal limitation (DL), homogenizing dispersal (HD), and drift (DR). Deterministic processes include HoS and HeS; stochastic processes consist of DL, HD and DR. (b) Neutral community model fit. Black dots represent OTUs falling within the neutral prediction confidence interval; blue dots indicate taxa above neutral prediction, and red dots represent taxa below neutral prediction.

4 Discussion

4.1 Vertical Patterns of Bacterial Community Composition, Diversity in the Chukchi Sea

We investigated the vertical distribution patterns of bacterial community composition, diversity, and assembly across Surface (S), middle (M), and bottom (B) water layers in the Chukchi Sea. The community composition exhibited classic vertical stratification characteristics of Arctic microbial communities (Galand et al., 2010; Han et al., 2014; McFarlin et al., 2017). Proteobacteria were dominant across all layers; Alphaproteobacteria were more abundant in the surface layer and closely associated with primary production, while Gammaproteobacteria increased with depth and tended to be balanced in the middle and bottom layers, reflecting their stronger adaptability to deeper water environments and organic matter input from sea-ice melting (Fadeev et al., 2021a; Vipindas et al., 2023).

The Marinimicrobia_SAR406_clade, a typical deep-water-adapted taxon, exhibits significantly higher relative abundance in the middle and bottom layers than in the surface layer. This distribution pattern is consistent with global marine and Arctic deep-water research results (Galand et al., 2010), and further confirms that the SAR406 clade prefers mesopelagic and bathypelagic habitats. As barophilic and psychrophilic bacteria, their enrichment in the middle and bottom layers is closely related to their ecological functions in material cycling, especially in the degradation of refractory dissolved organic matter, which plays an important role in maintaining the stability of the deep-sea ecosystem and regulating carbon sequestration processes (Vipindas et al., 2023). Other auxiliary taxa also show vertical distribution differences that are consistent with ecological niche differentiation. For example, Bacteroidia is relatively abundant in the surface layer but less abundant in the middle and bottom layers, a pattern supported by previous studies which documented the enrichment of Bacteroidia in the surface mixed layer of the western Arctic Ocean during the sea-ice melting period (Han et al., 2014). Bacteroidia shows a slight enrichment trend in the middle and bottom layers, which is consistent with previous findings that Bacteroidia is involved in biogeochemical cycling in Arctic deep waters (Galand et al., 2010). This vertical differentiation pattern, in which surface taxa are mainly associated with primary production and middle-bottom taxa are mainly associated with biogeochemical cycling of nutrients, essentially reflects the habitat filtering effect of vertical environmental gradients (such as water column stratification and nutrient distribution) during the sea-ice melting period (Stedmon et al., 2011).

In terms of diversity, Alpha-diversity increased with depth, indicating that deeper water acts as a microbial diversity reservoir in this polar system (Kraemer et al., 2024). β-diversity also progressively rose with depth, which may be attributed to enhanced water column stratification and heterogeneous organic matter inputs that promote niche differentiation among bacterial communities (Galand et al., 2008; McFarlin et al., 2017).

In summary, the vertical variation characteristics of bacterial communities observed in this study not only replicate the classic niche differentiation pattern of microbial communities in the Arctic Ocean but also further confirm the key role of vertical environmental gradients in shaping the composition of bacterial taxa during the sea-ice melting period. These results provide an important structural basis for further exploring the functional contributions of key bacterial taxa (such as SAR406 clade and core classes of Proteobacteria) in the biogeochemical cycle of the Arctic Ocean(Buongiorno et al., 2019).

4.2 Stochastic Processes Dominate Community Assembly Despite Vertical Niche Differentiation

The bacterial communities in different water layers showed similar composition at the class level, with Alphaproteobacteria, Gammaproteobacteria, and Bacteroidia consistently dominating the assemblages, indicating no fundamental shift in the overall community structure. However, ternary plot analysis revealed that community variation across water layers was primarily driven by species turnover, indicating obvious vertical niche differentiation and implying strong environmental filtering.

The assembly of bacterial communities in the Arctic during sea-ice melting was governed by a combination of deterministic and stochastic processes, with stochastic processes playing a dominant role (Jain et al., 2021; Le Moigne et al., 2020; Keuschnig et al., 2023). This finding aligns with previous studies in Arctic environments. In a high Arctic fjord,

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stochastic processes—particularly dispersal limitation—play a crucial role in structuring both particle-associated and free-living bacterial communities, with distinct depth-related assembly patterns (Jain et al., 2021). Similarly, stochastic assembly processes dominate within Siberian thermokarst ponds of identical geomorphological origin, reflecting the high biogeochemical variability of these Arctic freshwater systems (Le Moigne et al., 2020). Furthermore, while environmental selection plays a significant role in Arctic snowpack microbial communities, certain taxonomic signals fit the neutral assembly model, indicating that deterministic and stochastic processes co-govern microbial community structure (Keuschnig et al., 2023). To further disentangle the contributions of deterministic versus stochastic processes, we applied the neutral community model (NCM) and null model analyses. The NCM showed that the majority of taxa fell within the 95% confidence interval, with a high model fit (R2), indicating that species abundance distributions were largely consistent with neutral expectations. Null model analyses further quantified the relative importance of ecological processes, revealing that stochastic processes—primarily dispersal limitation and ecological drift—outweighed deterministic processes in shaping community structure (Han et al., 2023; Galand et al., 2010). These results align with the dynamic hydrological conditions of the Arctic, characterized by frequent water mass exchange, high water mobility, and weak environmental filtering under extreme conditions, all of which promote random dispersal and taxon drift (Galand et al., 2010; Fadeev et al., 2021b).

Consistently, variation partitioning based on environmental and spatial variables showed that measured environmental factors explained less than half (45.8%) of the community variation, leaving 54.2% of the variation unexplained. This low explanatory power provides indirect but compelling evidence that deterministic processes (e.g., environmental filtering) play a limited role overall, which is in line with the stochastic-dominated conclusion derived from neutral and null models. The unexplained fraction likely represents contributions from unmeasured stochastic processes, such as dispersal limitation and drift, as well as potential biotic interactions (e.g., competition, mutualism) or unmeasured environmental variables (e.g., light, particulate organic matter).

Taken together, although deterministic processes — evident from vertical niche differentiation — contribute to community variation across layers, stochastic processes collectively dominate the assembly of bacterial communities in this Arctic ecosystem. The interplay between these two types of processes ultimately shapes the microbial community structure during the critical period of sea-ice melting. Our findings provide insights into the mechanisms underlying microbial community assembly in polar marine environments and highlight the necessity of integrating both deterministic and stochastic frameworks in future studies.

4.3 Depth-Dependent Network Topology and Ecological Stability

The co-occurrence network analysis revealed distinct topological architectures across water layers, reflecting depth-dependent variations in microbial community stability and functional organization. The Middle (M) layer exhibited the most complex network structure, characterized by the highest edge density (1,007 edges) and degree and closeness centrality. This dense interconnectivity suggests a highly stable and resilient community, consistent with the "stability-complexity" hypothesis (May, 1973; Zhou et al., 2010), where increased link density enhances robustness against environmental perturbations. In ecological networks, positive correlations represent cooperative or facilitative interactions, while negative correlations denote competition or antagonism (Faust and Raes, 2012). The predominance of positive correlations across all water-layer networks indicates that cooperative relationships, such as metabolic cross-feeding and syntrophy, outweigh competitive exclusion among bacterial communities. The middle (M) layer had the highest connectivity and most centralized network structure, with two major modules dominated by Proteobacteria and Cyanobacteria/Bacteroidota, respectively; their intensive inter-module connections support tight coupling between heterotrophic and phototrophic guilds, consistent with strong niche partitioning driven by vertical stratification (Sunagawa et al., 2015). The surface (S) layer showed a more decentralized network, likely reflecting stochastic assembly under strong abiotic filtering (e.g., UV radiation and temperature fluctuations) (Fuhrman et al., 2015). The bottom (B) layer exhibited a "bottleneck" architecture with high-betweenness taxa acting as keystone connectors, a pattern typical of resource-limited environments near the sediment interface, where Proteobacteria, Acidobacteriota, and Chloroflexi dominate and drive organic matter degradation (Banerjee et al., 2018; Orsi, 2018). Overall, these network patterns clearly demonstrate that increasing water depth and associated vertical environmental gradients shape both community composition and biotic interaction structure on the Arctic (Vipindas et al., 2023).

5 Conclusion

In conclusion, a distinct vertical stratification pattern of bacterial communities and increasing alpha diversity (richness and diversity indices) from surface to bottom have been demonstrated in the Chukchi Sea. Proteobacteria, Bacteroidota, and Cyanobacteria were identified as the dominant phyla, with core classes within Proteobacteria exhibiting clear depth-related variations. Species turnover was shown to be the primary driver of β-diversity. Water depth, dissolved oxygen and silicate were identified as important factors driving the variation ofcommunity structures ($P < 0.05$). Stochastic processes were demonstrated to play a dominant role in governing bacterial community assembly, although deterministic processes also contributed. Our study provides a better understanding of the diversity patterns, vertical distribution characteristics, and ecological assembly mechanisms of bacterial communities in a key Arctic shelf sea ecosystem.

Code and data availability

The raw sequence data reported in this paper have been deposited in the Genome Sequence Archive (Genomics, Proteomics & Bioinformatics 2025) in National Genomics Data Center (Nucleic Acids Res 2025), China National Center for Bioinformation / Beijing Institute of Genomics, Chinese Academy of Sciences (GSA: CRA044522) that are publicly accessible at https://ngdc.cncb.ac.cn/gsa.

Author contributions

LZ, CZ, and WL designed and conceptual-ized the study. LZ analysed data and wrote the manuscript. WL and HD reviewed and edited this manuscript. RG participated in the creation of the picture. HL and YY performed molecularbiology analysis. CZ collected the samples.

Competing interests

The contact author has declared that none of the authors has any competing interests.

Disclaimer

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