

Metabarcoding the Arctic Ocean Helps Reveal Its Hidden Microbial Community Composition

Rafet Çağrı Öztürk^{1-3,*} , Yahya Terzi^{1,2,4} , Sheila Rodríguez-Machado² , Ersan Başar⁵ , Ali Muzaffer Feyzioğlu⁶ , Dilek Ustaoglu^{1,3} , Ertuğrul Ağırbaş⁷ , Prosanta Chakrabarty^{2,8} 

¹Department of Fisheries Technology Engineering, Faculty of Marine Sciences, Karadeniz Technical University, Trabzon, 61530, Türkiye

²Museum of Natural Science, Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA

³Aquatic Animal Health and Molecular Genetic Lab, Karadeniz Technical University, 61080 Trabzon, Türkiye.

⁴Institute of Marine Sciences and Technology, Karadeniz Technical University, Trabzon, Türkiye.

⁵Department of Maritime Transportation and Management Engineering, Karadeniz Technical University, Trabzon, Türkiye.

⁶Department of Marine Science and Technology Engineering, Faculty of Marine Sciences, Karadeniz Technical University, Trabzon, Türkiye.

⁷Department of Marine Biology, Faculty of Fisheries, Recep Tayyip Erdoğan University, Rize, Türkiye.

⁸Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA.

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Corresponding Author

E-mail: rafetcagriozturk@gmail.com

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Abstract

The Arctic Ocean supports a unique and dynamic microbial community, yet its composition, structure, and response to environmental shifts remain incompletely understood. In this study, 16S rRNA gene metabarcoding (targeting the V3-V4 and V4-V5 hypervariable regions) was used to assess surface water microbial diversity across 20 stations in the Barents Sea, focusing on latitudinal variations within two contrasting current systems: the West Spitsbergen Current (WSC) and the East Spitsbergen Current (ESC). Our results showed that the microbial community is dominated by three primary families—Pseudoalteromonadaceae, Moraxellaceae, and Flavobacteriaceae (14.20%). Comparative analysis of the V3-V4 and V4-V5 regions reveals that each region captures different aspects of microbial diversity, with V4-V5 detecting a higher number of unique families. Analysis through Nonmetric Multidimensional Scaling (NMDS) reveals distinct community separations between the WSC and ESC, though ANOSIM results indicate no significant within-system differences. Environmental parameters, including pH and temperature, appear closely linked with community composition, reflecting the influence of climatic and oceanographic processes on microbial structure. As global climate change continues to reshape Arctic environments, monitoring microbial diversity is essential to understand and predict shifts in the Arctic Ocean's ecosystem functions.

Introduction

Polar ecosystems are undergoing rapid changes due to the pressure of climate change; the north polar region may be the most susceptible to global warming than other places because of Arctic amplification (the magnified variability of surface air temperatures in that region) transforming the functioning of marine ecosystem (Previdi et al., 2021; Serreze & Barry, 2011). The average water temperature of the Arctic is

increasing faster than the global average for the last couple decades (Koenig et al., 2020; Rantanen et al., 2022). Arctic Sea ice declined nearly 50% since the 1950s and its shrinking at roughly 10% every 10 years (Peng & Meier, 2017). Increasing water temperature decreases sea-ice cover and intensifies hydrological cycles which affects ocean circulation at local and global scales (Grémillet & Descamps, 2023). This raises many questions about the ecological consequences of the diminished polar ice. Recent studies show that the

eastern basin of the Arctic Ocean is in a transitional phase due to perpetually warmer conditions, a process also called "Atlantification" which results in decreased stratification, increased vertical mixing, and changes in primary production (Polyakov et al., 2017; Reigstad et al., 2002).

The Arctic Ocean's upper water column, known as polar surface water, can extend to depths of up to 200 m (Jones, 2001). The surface layer of this column, referred to as the 'polar mixed layer,' reaches up to 50 m in depth and is characterized by low salinity and temperatures that undergoes significant daily and seasonal fluctuations (Talley et al., 2011). Despite being a harsh environment, most of the biological production takes place in the polar surface water layer. Variation in environmental conditions result in seasonal shifts in the composition of microbial communities within the upper water column (Bano & Hollibaugh, 2002; Öztürk et al., 2022, 2024). In addition, hydrographic regime and water circulation also shape spatial microbial community compositions. Despite these challenging environmental conditions, microbial communities thrive and play key roles in photosynthetic carbon assimilation, nutrient recycling, and carbon degradation. Molecular diversity of bacterioplankton in the Arctic Ocean is far from being fully documented and without a general understanding of the microbial organisms that are structuring the function of Arctic ecosystem, it is unlikely we will understand the impacts of future environmental changes.

Advances in genetic techniques, such as metabarcoding and metagenomic have paved the way to address the taxonomic diversity, structure, and composition of microbiota all over the globe (Sunagawa et al., 2015). Recent sampling techniques like metabarcoding, and metagenomic approaches have provided valuable insight into the diversity and functional roles of microbes in the Arctic region. Cao et al. (2020) studied the taxonomic structure of microbiota in Arctic and Antarctic Sea water and compared the overlapping operational taxonomic units (OTUs) between the polar microbiomes and ocean microbiomes in which global ocean microbial diversity was investigated, and dissimilarities highlighted in microbial communities at the surface water between polar and temperate ecosystems. Nearly 19% of the identified OTUs were unique to the Arctic Ocean. Similarly, microbial community composition comparison between the Arctic Ocean (Arctic) and the Southern Ocean (Antarctic) highlighted differences of microbial compositions and 70% of the OTUs were found as unique to the Arctic Ocean (Ghiglione & Murray, 2012). Lee et al. (2019) assessed latitudinal changes in microbial community composition in the western Arctic surface water and found an increasing tendency of the relative abundance of Alphaproteobacteria and Gammaproteobacteria groups, which was attributed to the changes in community composition to physical and biogeochemical characteristics.

Metabarcoding studies in the Arctic have so far mostly focused on the Svalbard archipelago. Microbial community compositions in soil (Venkatachalam et al., 2021), glaciers and tidewater (Garcia-Lopez et al., 2019), subglacial water (Sułowicz et al., 2020), coastal sea water (Delpech et al., 2021), sediment (Buongiorno et al., 2019), and air (Cuthbertson et al., 2017) were studied at local scale.

Microbial communities play crucial roles in the biogeochemical cycles in the water column, yet their composition and dynamics remain poorly characterized. Although microbial communities are essential to marine ecosystems, their sensitivity to environmental changes remains inadequately understood. In order to better understand the impact of environmental changes on these microbial communities, a fundamental knowledge about the microbial community compositions is necessary to be established. The aims of this study were to assess latitudinal changes in microbial community composition distribution in the Arctic Ocean and to compare resolution power of V3-V4 and V4-V5 hypervariable regions of 16S rRNA for the microbial diversity estimation.

Material and Method

Sampling

Surface and 10 m depth water were collected during the second Turkish Arctic expedition (TASE-II) in the Barents Sea in July 2022, conducted by R/V PolarXplorer. The samples were obtained using a Niskin bottle from 20 stations (Figure 1). Notably, water sample from 10 meters could not be collected at station S19. Environmental parameters (surface water temperature, dissolved oxygen, oxygen saturation, sigma-t, salinity, and conductivity) were measured. Water samples (1200 ml from each point) were filtered onboard using a vacuum filtration system equipped with 0.22 µm polyethersulfone membrane filters (GVS Filtration Inc.). The filters were then preserved at -20°C during the cruise and transported to the laboratory under cold-chain conditions.

DNA Extraction, PCR Amplification, and Sequencing

DNA extraction from the filters was performed using the DNeasy Power Water Kit (Qiagen, Germany) following the manufacturer's instructions. DNA concentrations quantified by Qubit and DNA quality is assessed by gel electrophoresis.

Microbial diversity was assessed using a 16S rRNA gene-based approach. The preparation of the DNA libraries was based on V3-V4 and V4-V5 hypervariable regions of 16S rRNA gene using the QIAseq 16S/ITS screening panel (Qiagen, Germany), a two-stage PCR workflow. PCR was performed using a QIAseq 16S/ITS PCR set up. The thermal cycling protocol included an initial denaturation at 95°C for 2 minutes, followed by

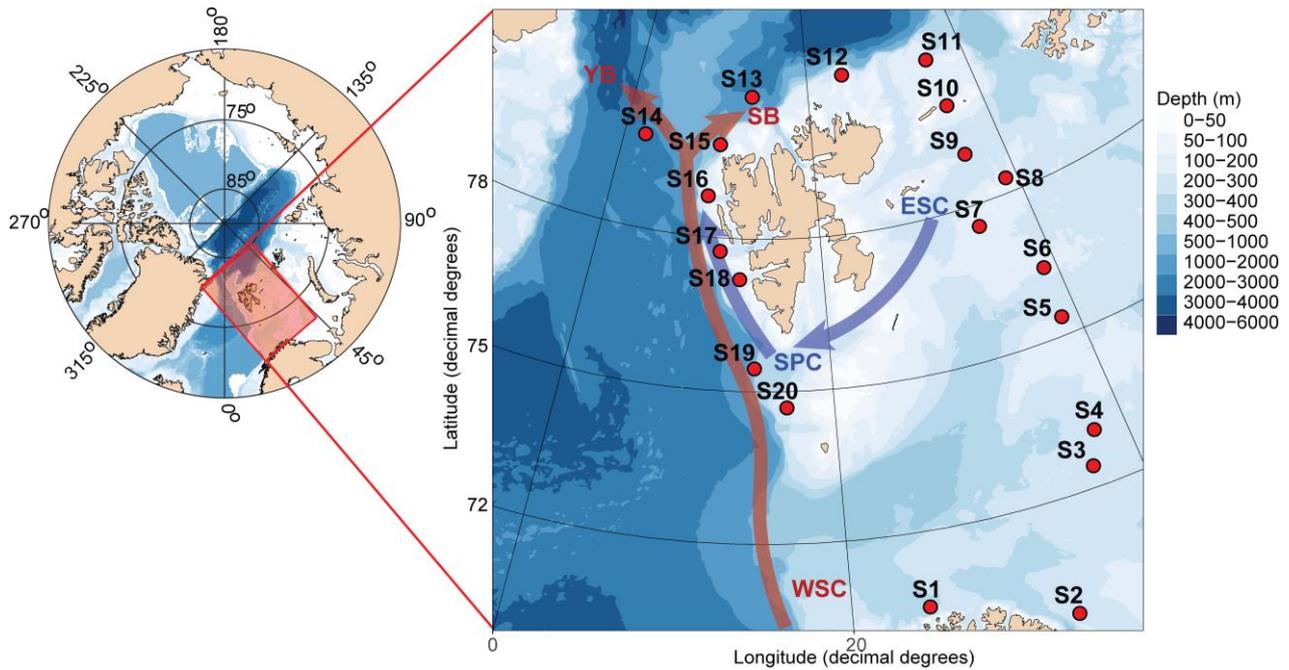


Figure 1. The map illustrates the bathymetry, sampling stations, and the two main current systems. The West Spitsbergen Current (WSC) divides into two branches: the Yermak Branch and the Svalbard Branch. The East Spitsbergen Current (ESC) continues as the Spitsbergen Polar Current (SP).

12 cycles of denaturation at 95°C for 30 seconds, annealing at 50°C for 30 seconds, and extension at 72°C for 2 minutes, with a final extension step at 72°C for 7 minutes. A secondary PCR was performed to attach the QIAGEN index barcodes. QIAseq magnetic beads were used for amplicon clean-up and DNA concentration was quantified with Qubit. Samples were diluted to 2 nM, pooled, and sequenced on MiSeq using the MiSeq Reagent Kit v3 (Illumina).

Bioinformatics

Bioinformatic data analysis were conducted using the CLC Genomics Workbench (v. 22.0.2) along with the Data QC and OTU Clustering workflow from the Microbial Genomics Pro Suite Module (v. 22.1.2). QIAseq 16S/ITS Demultiplexer tool was used to demultiplex raw reads and to group based on analyzed region. The trim Reads tool of CLC Genomics Workbench was used for adapter and quality trimming. Low read numbers were filtered with the filter samples based on the number of reads tool. OTU clustering for each region (V3-V4 and V4-V5) was performed using the OTU Clustering tool. The reads are aligned to the SILVA 16S v132 reference sequence database, using a 97% similarity threshold, and OTU tables were created for each region.

Data Analysis

Alpha diversity estimates and rarefaction curves were calculated using the Alpha Diversity tool of CLC Genomics Workbench. The relationship between

microbial abundance and latitude was determined using Spearman rank correlation. Alpha diversity indices (Shannon index and Pielou’s evenness index) were calculated using vegan (Oksanen et al., 2020) package of R. Wilcoxon test was used for comparing alpha diversity indices between the current systems since the data did not fall in a normal distribution. Microbial community composition was visualized using nonmetric multidimensional scaling (NMDS). ANOSIM was used comparing microbial community composition between WSC and ESC. Following a significant difference in ANOSIM results SIMPER analysis was performed to identify taxa that contributed to the community difference between depth strata and stations. The data analyses were performed using R (ver. 4.3.1). Environmental variables were incorporated into the weighted Unifrac distance matrix to evaluate their impact on beta diversity. The 'envfit' function in the *vegan* package was used to identify the environmental factors and taxa contributing to the observed differences.

Results

Rarefaction curve analysis, performed at the specified sequencing depth, indicated good coverage of richness across the samples. The species coverage indices (Good’s coverage) were predominantly above 99%, demonstrating sufficient sequencing depth. Classification of OTUs at 97% similarity using the SILVA database identified a total of 225 OTUs at the family level, with 176 determined from surface water samples and 193 from samples taken from 10 meters deep. For

both depths Pseudoalteromonadaceae, Flavobacteriaceae, and Moraxellaceae were the most common families (Figure 2). While more OTUs from Pseudoalteromonadaceae were determined using V3-V4 region, V4-V5 region determined more OTUs from Flavobacteriaceae, and Moraxellaceae. V3-V4 and V4-V5 regions determined 17 and 36 distinct families in surface water respectively while these numbers were 17 and 48 for deep water samples.

The analysis of the V3-V4 hypervariable region revealed 15 distinct taxa at the phylum level, with Proteobacteria (83.95%), Bacteroidetes (14.77%), and Cyanobacteria (1.05%) being the most abundant. At the family level, 176 taxa were identified, with Pseudoalteromonadaceae (47.49%), Moraxellaceae (19.91%), and Flavobacteriaceae (12.56%) representing the dominant families (Figure 3). Similarly, a comprehensive analysis of the V4-V5 hypervariable

region identified 20 phyla. Proteobacteria accounted for 81.77% of the total abundance, followed by Bacteroidetes at 16.54%, and Cyanobacteria at 1.42%. A total of 193 families were identified, with Pseudoalteromonadaceae (46.51%), Moraxellaceae (17.73%), and Flavobacteriaceae (14.01%) being the most abundant (Figure 3). Although in most of the stations the relative abundance was dominated by Pseudoalteromonadaceae, the family was not observed in some of the stations (Figure 3).

An increasing abundance with latitude was determined which was significant for V4-V5 region at surface water ($R^2 = 0.25$, $p < 0.05$) and V3-V4 region at 10 meters ($R^2 = 0.23$, $p < 0.05$). The average Shannon index in surface water (0 m) was 1.32 ± 0.12 and 1.40 ± 0.13 for ESC and WSC respectively. On average, the Shannon index at a depth of 10 meters was 1.13 ± 0.09 for ESC and 0.96 ± 0.07 for WSC. The Shannon index was similar for

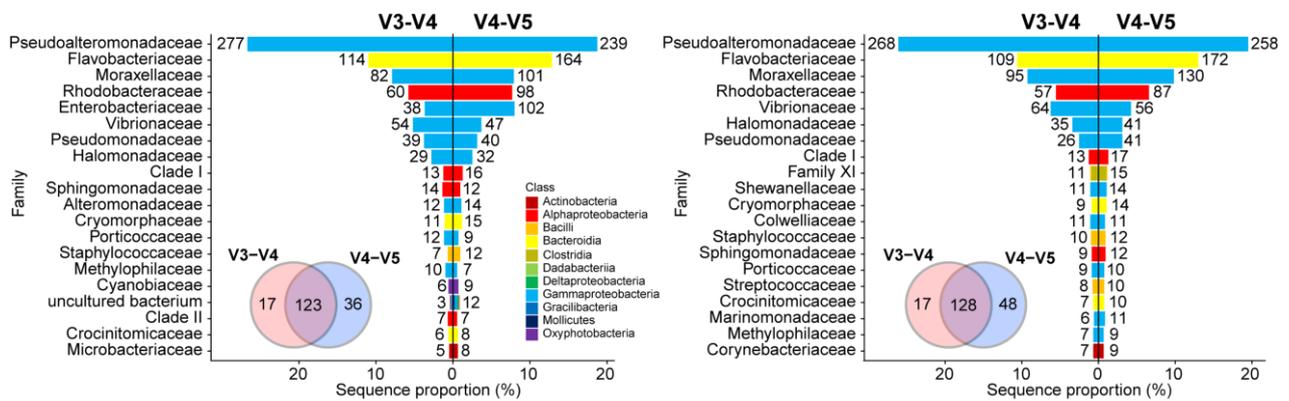


Figure 2. The primary taxonomic families identified in the V3–V4 and V4–V5 datasets from surface (left) and ten meters depth (right). The numbers in each bar shows the count of observed OTUs associated with family. Families representing more than 70% of the dataset were included to the graph. Venn diagrams showing shared and distinct family numbers for V3–V4 and V4–V5 datasets.

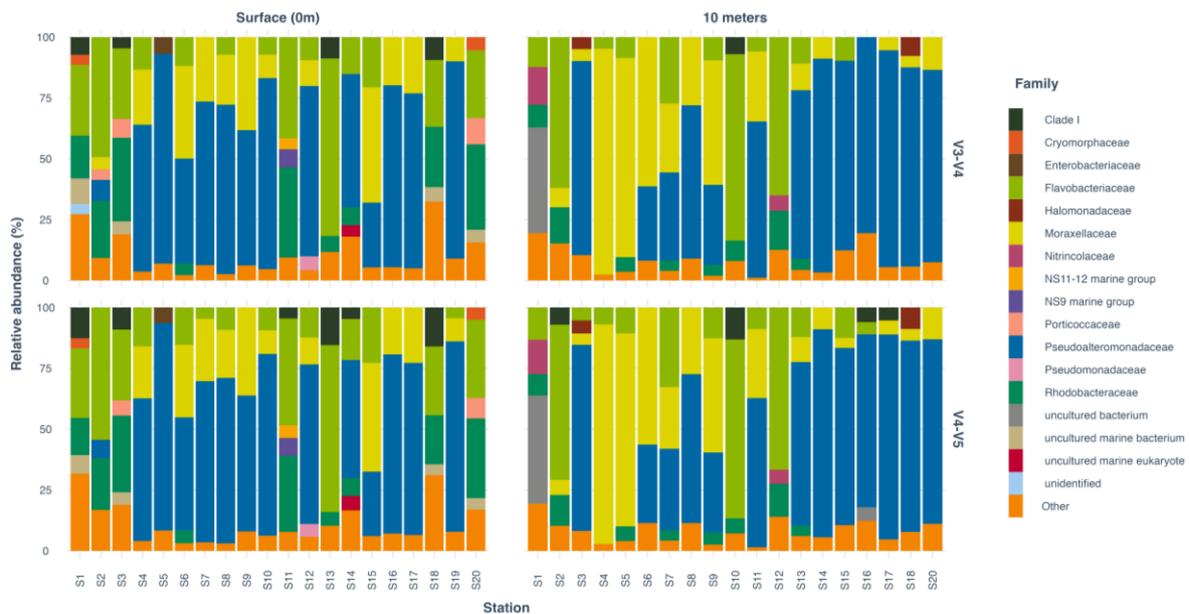


Figure 3. Relative abundances of microbial organisms at family level by depth and hypervariable region.

ESC and WSC in both depths (Wilcoxon test, $p > 0.05$) (Figure 4). Pielou’s evenness index averaged 0.35 ± 0.03 and 0.34 ± 0.03 for ESC and WSC respectively in surface water. In 10 meters depth the Pielou’s evenness index was 0.29 ± 0.02 for ESC and 0.24 ± 0.02 for WSC. Similar to the Shannon index the Pielou’s evenness index was similar in both current systems and depths (Wilcoxon test, $p > 0.05$).

Nonmetric multidimensional scaling (NMDS) revealed some separation in microbial communities between surface and 10 meters depth for both current systems (Figure 5). While there was no significant difference between the current systems in surface waters with respect to microbial communities (ANOSIM, $p > 0.05$), a significant difference was found at 10 meters depth. SIMPER results determined 64.68% overall average of which determined by Pseudoalteromonadaceae (47.43%), Moraxellaceae (23.97%), and Flavobacteriaceae (14.20%). Temperature and pH appeared to be two closely linked environmental parameters with community composition. Yet, only pH was found as a significant factor ($p < 0.05$) influencing the microbial community structure in surface water causing a difference between sampling sites.

Discussion

Compared to the V3-V4 dataset, V4-V5 datasets generally consisted of more OTUs in both depth strata. The number of observed OTUs associated with the members of the families of Pseudoalteromonadaceae, Flavobacteriaceae, Moraxellaceae, Rhodobacteraceae, and Pseudomonadacea showed substantial differences between V3-V4 and V4-V5 dataset. Members of the families of Pseudoalteromonadaceae and Pseudomonadacea generally associated with organic matter degradation (Buchan et al., 2005). Flavobacteriaceae that includes key heterotrophic bacteria genera such as Polaribacter, which were reported to respond to phytoplankton blooms in high and mid-latitudes (Avcı et al., 2020; Fadeev et al., 2018, 2021). Rhodobacteeaceae including the genus Sulfitobacter known to play a role in the assimilation of dimethylsulfoniopropionate produced from decomposition of organic matter and production of dimethyl sulfide, a gas known to have a cooling effect on the climate.

Changes in the number of OTUs in V3-V4 and V4-V5 datasets indicates that on OTU level, the diversity of

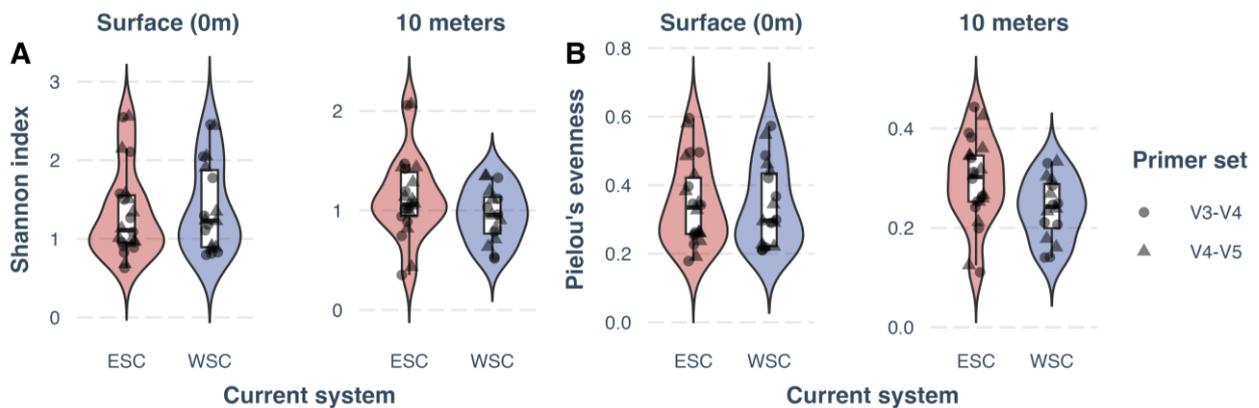


Figure 4. Distribution of alpha diversity indices namely, Shannon index (A) and Pielou’s evenness index (B) in surface water and 10-meter depth from West Spitsbergen Current (WSC) and East Spitsbergen Current (ESC) systems.

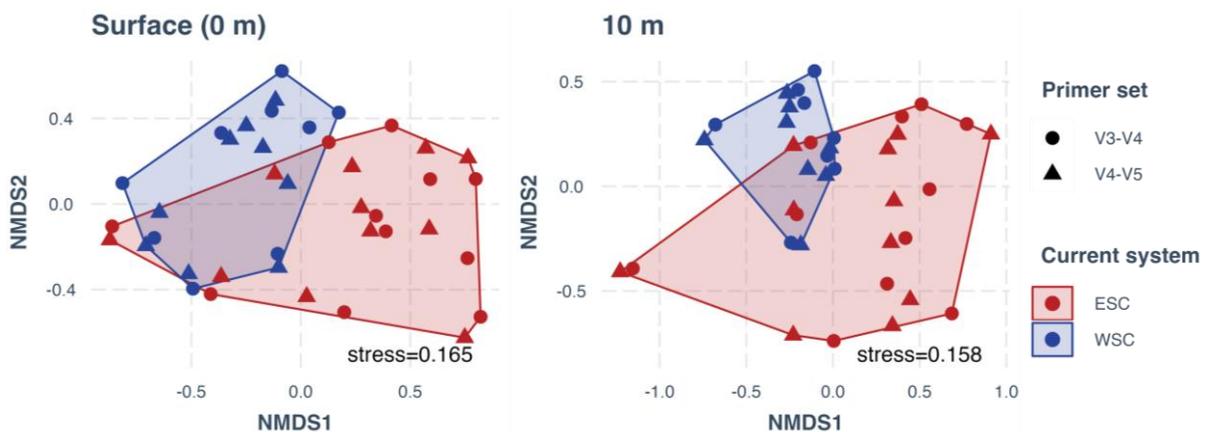


Figure 5. Nonmetric multidimensional scaling (NMDS) plots comparing microbial communities in surface water (left) and 10 meters depth (right) from West Spitsbergen Current (WSC) and East Spitsbergen Current (ESC) systems.

different microbial groups are captured differently by different primer sets that target different hypervariable regions of 16S rRNA gene regions (Kerrigan et al., 2019; Yang et al., 2016). The number of OTU differences between V3-V4 and V4-V5 datasets were consistent with those of previous studies in polar regions (Fadeev et al., 2021; Varliero et al., 2024). Similar differences were also observed while comparing number of OTUs between different hypervariable regions of different genes (Jackson et al., 2021; Willis et al., 2019). Despite the differences observed on OTU level between datasets, the overall taxonomic composition was consistent. For both depth strata, Gammaproteobacteria (mainly the families of Pseudoalteromonadaceae and Pseudomonadaceae), Bacteroida (mainly the family Flavobacteriaceae), Alphaproteobacteria (mainly the family Rhodobacteraceae) dominated the seawater. Overall, bacterial community composition found in this study was consistent with reports of previous studies (Fadeev et al., 2018, 2021; Feyzioğlu et al., 2023; Galand et al., 2009; Han et al., 2015; Kirchman et al., 2010; Malmstrom et al., 2007; Rapp et al., 2018; Wilson et al., 2017).

Cluster analysis of the OTUs from the water samples revealed that bacterial communities were largely similar between the two current systems in surface waters but exhibited significant differences at a depth of 10 meters. Changes of bacterial abundance with latitude at both depth strata supports the idea that latitude significantly influence the distribution of bacterial communities in the Arctic (Han et al., 2014, 2015; Lee et al., 2019; Ortega-Retuerta et al., 2013; Yergeau et al., 2017). Previous study by Lee et al. (Lee et al., 2019) find link between environmental parameters (temperature, salinity, chl-a) and latitudinal change in bacterial distribution in Arctic region. In this study, only pH appeared to be a significant factor linked with bacterial distribution in surface water ($p < 0.05$).

Conclusion

Microbial community composition in two main current systems: The West Spitsbergen Current (WSC) and The East Spitsbergen Current (ESC) in surface waters of Arctic Ocean was investigated using two different hypervariable region of 16S rRNA during summer 2022. Results indicated that microbial community abundance were increased at surface waters with latitude and microbial diversity captured by V4-V5 hypervariable region was higher compared to that of V3-V4. The microbial community compositions were found as similar in both current systems. Since only pH was found significant in influencing microbial structure, exploring other factors such as seasonal ice coverage and nutrient availability might provide a more holistic context.

Ethical Statement

Not applicable.

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Author Contribution

Rafet Çağrı Öztürk: Conceptualization, Formal analysis, Investigation, Writing-Original Draft, Supervision; **Yahya Terzi:** Conceptualization, Formal analysis, Investigation, Writing-Original Draft, Visualization; **Sheila Rodriguez-Machado:** Investigation, Writing-Review & Editing; **Ersan Başar:** Investigation; **Ali Muzaffer Feyzioğlu:** Investigation; **Dilek Ustaoglu:** Investigation; **Ertuğrul Ağırbaş:** Investigation; **Prosanta Chakrabarty:** Project administration, Funding acquisition, Writing-Review & Editing.

Conflict of Interest

The authors declare that they have no known competing financial or non-financial, professional, or personal conflicts that could have appeared to influence the work reported in this paper.

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References

- Avcı, B., Krüger, K., Fuchs, B. M., Teeling, H. & Amann, R. I. (2020). Polysaccharide niche partitioning of distinct *Polaribacter* clades during North Sea spring algal blooms. *The ISME Journal*, 14(6), 1369–1383. <https://doi.org/10.1038/s41396-020-0601-y>
- Bano, N. & Hollibaugh, J. T. (2002). Phylogenetic composition of bacterioplankton assemblages from the Arctic Ocean. *Applied and Environmental Microbiology*, 68, 505–518. <https://doi.org/10.1128/AEM.68.2.505-518.2002>
- Buchan, A., Gonzalez, J. M. & Moran, M. A. (2005). Overview of the marine Roseobacter lineage. *Applied and Environmental Microbiology*, 71, 5665–5677. <https://doi.org/10.1128/AEM.71.10.5665-5677.2005>
- Buongiorno, J., Herbert, L. C., Wehrmann, L. M., Michaud, A. B., Laufer, K., Røy, H., Jørgensen, B. B., Szynekiewicz, A.,

- Faiia, A., Yeager, K. M., Schindler, K. & Lloyd, K. G. (2019). Complex Microbial Communities Drive Iron and Sulfur Cycling in Arctic Fjord Sediments. *Applied and Environmental Microbiology*, 85(14).
<https://doi.org/10.1128/AEM.00949-19>
- Cao, S., Zhang, W., Ding, W., Wang, M., Fan, S., Yang, B., Mcminn, A., Wang, M., Xie, B., Qin, Q.-L., Chen, X.-L., He, J. & Zhang, Y.-Z. (2020). Structure and function of the Arctic and Antarctic marine microbiota as revealed by metagenomics. *Microbiome*, 8(1), 47.
<https://doi.org/10.1186/s40168-020-00826-9>
- Cuthbertson, L., Amores-Arrocha, H., Malard, L., Els, N., Sattler, B. & Pearce, D. (2017). Characterisation of Arctic Bacterial Communities in the Air above Svalbard. *Biology*, 6(2), 29.
<https://doi.org/10.3390/biology6020029>
- Delpech, L.-M., Vonnahme, T. R., McGovern, M., Gradinger, R., Præbel, K. & Poste, A. E. (2021). Terrestrial Inputs Shape Coastal Bacterial and Archaeal Communities in a High Arctic Fjord (Isfjorden, Svalbard). *Frontiers in Microbiology*, 12.
<https://doi.org/10.3389/fmicb.2021.614634>
- Fadeev, E., Cardozo-Mino, M. G., Rapp, J. Z., Bienhold, C., Salter, I., Salman-Carvalho, V., Molari, M., Tegetmeyer, H. E., Buttigieg, P. L. & Boetius, A. (2021). Comparison of Two 16S rRNA Primers (V3–V4 and V4–V5) for Studies of Arctic Microbial Communities. *Frontiers in Microbiology*, 12. <https://doi.org/10.3389/fmicb.2021.637526>
- Fadeev, E., Salter, I., Schourup-Kristensen, V., Nöthig, E.-M., Metfies, K., Engel, A., Piontek, J., Boetius, A. & Bienhold, C. (2018). Microbial Communities in the East and West Fram Strait During Sea Ice Melting Season. *Frontiers in Marine Science*, 5.
<https://doi.org/10.3389/fmars.2018.00429>
- Feyzioglu, A. M., Terzi, Y., Öztürk, R. Ç., Başar, E., Yıldız, İ. & Ağırbaş, E. (2023). Flow cytometric investigation and comparison of *Synechococcus* spp. pico-, nano- and microplankton in the Arctic and Antarctic polar regions during the summer period of 2019. *Marine Biology Research*, 19(10), 574–581.
<https://doi.org/10.1080/17451000.2023.2299995>
- Galand, P. E., Casamayor, E. O., Kirchman, D. L. & Lovejoy, C. (2009). Ecology of the rare microbial biosphere of the Arctic Ocean. *Proceedings of the National Academy of Sciences*, 106(52), 22427–22432.
<https://doi.org/10.1073/pnas.0908284106>
- Garcia-Lopez, E., Rodriguez-Lorente, I., Alcazar, P. & Cid, C. (2019). Microbial Communities in Coastal Glaciers and Tidewater Tongues of Svalbard Archipelago, Norway. *Frontiers in Marine Science*, 5.
<https://doi.org/10.3389/fmars.2018.00512>
- Ghiglione, J. F. & Murray, A. E. (2012). Pronounced summer to winter differences and higher wintertime richness in coastal Antarctic marine bacterioplankton. *Environmental Microbiology*, 14(3), 617–629.
<https://doi.org/10.1111/j.1462-2920.2011.02601.x>
- Grémillet, D. & Descamps, S. (2023). Ecological impacts of climate change on Arctic marine megafauna. *Trends in Ecology & Evolution*, 38(8), 773–783.
<https://doi.org/10.1016/j.tree.2023.04.002>
- Han, D., Ha, H. K., Hwang, C. Y., Lee, B. Y., Hur, H.-G. & Lee, Y. K. (2015). Bacterial communities along stratified water columns at the Chukchi Borderland in the western Arctic Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 120, 52–60.
<https://doi.org/10.1016/j.dsr2.2015.01.018>
- Han, D., Kang, I., Ha, H. K., Kim, H. C., Kim, O.-S., Lee, B. Y., Cho, J.-C., Hur, H.-G. & Lee, Y. K. (2014). Bacterial Communities of Surface Mixed Layer in the Pacific Sector of the Western Arctic Ocean during Sea-Ice Melting. *PLoS ONE*, 9(1), e86887.
<https://doi.org/10.1371/journal.pone.0086887>
- Jackson, E. E., Hawes, I. & Jungblut, A. D. (2021). 16S rRNA gene and 18S rRNA gene diversity in microbial mat communities in meltwater ponds on the McMurdo Ice Shelf, Antarctica. *Polar Biology*, 44(4), 823–836.
<https://doi.org/10.1007/s00300-021-02843-2>
- Jones, E. P. (2001). Circulation in the Arctic Ocean. *Polar Research*, 20(2), 139–146.
<https://doi.org/10.1111/j.1751-8369.2001.tb00049.x>
- Kerrigan, Z., Kirkpatrick, J. B. & D'Hondt, S. (2019). Influence of 16S rRNA Hypervariable Region on Estimates of Bacterial Diversity and Community Composition in Seawater and Marine Sediment. *Frontiers in Microbiology*, 10.
<https://doi.org/10.3389/fmicb.2019.01640>
- Kirchman, D. L., Cottrell, M. T. & Lovejoy, C. (2010). The structure of bacterial communities in the western Arctic Ocean as revealed by pyrosequencing of 16S rRNA genes. *Environmental Microbiology*, 12(5), 1132–1143.
<https://doi.org/10.1111/j.1462-2920.2010.02154.x>
- Koenig, T., Key, J. & Vihma, T. (2020). Climate Change in the Arctic. In A. Kokhanovsky & C. Tomasi (Eds.), *Physics and Chemistry of the Arctic Atmosphere* (pp. 673–705). Springer.
- Lee, J., Kang, S.-H., Yang, E. J., Macdonald, A. M., Joo, H. M., Park, J., Kim, K., Lee, G. S., Kim, J.-H., Yoon, J.-E., Kim, S.-S., Lim, J.-H. & Kim, I.-N. (2019). Latitudinal Distributions and Controls of Bacterial Community Composition during the Summer of 2017 in Western Arctic Surface Waters (from the Bering Strait to the Chukchi Borderland). *Scientific Reports*, 9(1), 16822.
<https://doi.org/10.1038/s41598-019-53427-4>
- Malmstrom, R., Straza, T., Cottrell, M. & Kirchman, D. (2007). Diversity, abundance, and biomass production of bacterial groups in the western Arctic Ocean. *Aquatic Microbial Ecology*, 47, 45–55.
<https://doi.org/10.3354/ame047045>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E. & Wagner, H. (2020). *vegan: Community Ecology Package*.
- Ortega-Retuerta, E., Joux, F., Jeffrey, W. H. & Ghiglione, J. F. (2013). Spatial variability of particle-attached and free-living bacterial diversity in surface waters from the Mackenzie River to the Beaufort Sea (Canadian Arctic). *Biogeosciences*, 10(4), 2747–2759.
<https://doi.org/10.5194/bg-10-2747-2013>
- Öztürk, R. Ç., Feyzioglu, A. M. & Altinok, I. (2022). Prokaryotic community and diversity in coastal surface waters along the Western Antarctic Peninsula. *Polar Science*, 31, 100764. <https://doi.org/10.1016/j.polar.2021.100764>
- Öztürk, R. Ç., Feyzioglu, A. M., Capkin, E., Yıldız, İ. & Altinok, I. (2024). Effects of environmental parameters on spatial and temporal distribution of marine microbial communities in the southern Black Sea. *Marine Environmental Research*, 195, 106344.
<https://doi.org/10.1016/j.marenvres.2024.106344>
- Peng, G. & Meier, W. N. (2017). Temporal and regional variability of Arctic sea-ice coverage from satellite data. *Annals of Glaciology*, 59, 191200.

- Polyakov, I. V., Pnyushkov, A. V., Alkire, M. B., Ashik, I. M., Baumann, T. M., Carmack, E. C., Goszczko, I., Guthrie, J., Ivanov, V. V., Kanzow, T., Krishfield, R., Kwok, R., Sundfjord, A., Morison, J., Rember, R. & Yulin, A. (2017). Greater role for Atlantic inflows on sea-ice loss in the Eurasian Basin of the Arctic Ocean. *Science*, 356(6335), 285–291. <https://doi.org/10.1126/science.aai8204>
- Prevdi, M., Smith, K. L. & Polvani, L. M. (2021). Arctic amplification of climate change: a review of underlying mechanisms. *Environmental Research Letters*, 16(9), 093003. <https://doi.org/10.1088/1748-9326/ac1c29>
- Rantanen, M., Karpechko, A. Yu., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T. & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, 3(1), 168. <https://doi.org/10.1038/s43247-022-00498-3>
- Rapp, J. Z., Fernández-Méndez, M., Bienhold, C. & Boetius, A. (2018). Effects of Ice-Algal Aggregate Export on the Connectivity of Bacterial Communities in the Central Arctic Ocean. *Frontiers in Microbiology*, 9. <https://doi.org/10.3389/fmicb.2018.01035>
- Reigstad, M., Wassmann, P., Wexels Riser, C., Øygarden, S. & Rey, F. (2002). Variations in hydrography, nutrients and chlorophyll a in the marginal ice-zone and the central Barents Sea. *Journal of Marine Systems*, 38(1–2), 9–29. [https://doi.org/10.1016/S0924-7963\(02\)00167-7](https://doi.org/10.1016/S0924-7963(02)00167-7)
- Serreze, M. C. & Barry, R. G. (2011). Processes and impacts of Arctic amplification: A research synthesis. *Global and Planetary Change*, 77(1–2), 85–96. <https://doi.org/10.1016/j.gloplacha.2011.03.004>
- Sułowicz, S., Bondarczuk, K., Ignatiuk, D., Jania, J. A. & Piotrowska-Seget, Z. (2020). Microbial communities from subglacial water of naled ice bodies in the forefield of Werenskioldbreen, Svalbard. *Science of The Total Environment*, 723, 138025. <https://doi.org/10.1016/j.scitotenv.2020.138025>
- Sunagawa, S., Coelho, L. P., Chaffron, S., Kultima, J. R., Labadie, K., Salazar, G., Djahanschiri, B., Zeller, G., Mende, D. R., Alberti, A., Cornejo-Castillo, F. M., Costea, P. I., Cruaud, C., D'Ovidio, F., Engelen, S., Ferrera, I., Gasol, J. M., Guidi, L., Hildebrand, F., ... Bork, P. (2015). Structure and function of the global ocean microbiome. *Science*, 348(6237), 1261359–1261368. <https://doi.org/10.1126/science.1261359>
- Talley, L. D., Pickard, G. L., Emery, W. J. & Swift, J. H. (2011). Arctic Ocean and Nordic Seas. In *Descriptive Physical Oceanography* (pp. 401–436). Elsevier. <https://doi.org/10.1016/B978-0-7506-4552-2.10012-5>
- Varliero, G., Lebre, P. H., Adams, B., Chown, S. L., Convey, P., Dennis, P. G., Fan, D., Ferrari, B., Frey, B., Hogg, I. D., Hopkins, D. W., Kong, W., Makhalanyane, T., Matcher, G., Newsham, K. K., Stevens, M. I., Weigh, K. V. & Cowan, D. A. (2024). Biogeographic survey of soil bacterial communities across Antarctica. *Microbiome*, 12(1), 9. <https://doi.org/10.1186/s40168-023-01719-3>
- Venkatachalam, S., Kannan, V. M., Saritha, V. N., Loganathachetti, D. S., Mohan, M. & Krishnan, K. P. (2021). Bacterial diversity and community structure along the glacier foreland of Midtre Lovénbreen, Svalbard, Arctic. *Ecological Indicators*, 126, 107704. <https://doi.org/10.1016/j.ecolind.2021.107704>
- Willis, C., Desai, D. & LaRoche, J. (2019). Influence of 16S rRNA variable region on perceived diversity of marine microbial communities of the Northern North Atlantic. *FEMS Microbiology Letters*, 366(13). <https://doi.org/10.1093/femsle/fnz152>
- Wilson, B., Müller, O., Nordmann, E.-L., Seuthe, L., Bratbak, G. & Øvreås, L. (2017). Changes in Marine Prokaryote Composition with Season and Depth Over an Arctic Polar Year. *Frontiers in Marine Science*, 4. <https://doi.org/10.3389/fmars.2017.00095>
- Yang, B., Wang, Y. & Qian, P.-Y. (2016). Sensitivity and correlation of hypervariable regions in 16S rRNA genes in phylogenetic analysis. *BMC Bioinformatics*, 17(1), 135. <https://doi.org/10.1186/s12859-016-0992-y>
- Yergeau, E., Michel, C., Tremblay, J., Niemi, A., King, T. L., Wyglinski, J., Lee, K. & Greer, C. W. (2017). Metagenomic survey of the taxonomic and functional microbial communities of seawater and sea ice from the Canadian Arctic. *Scientific Reports*, 7(1), 42242. <https://doi.org/10.1038/srep42242>