Deep Ocean Water Research, 26(1), 1–10, 2025

Original

Seasonal variation in bacterial community and environmental properties of deep seawater in Korea

Taehui Yang[1], Se-jin Oh[1], Eun-soek Oh[2], and Heon-joong Kang[2]

Abstract

Until recently, research on marine microbial communities has primarily focused on surface seawater (SSW) and marine sediments. Futhermore, there is limited literature on seasonal variation in mineral components and major nutrients of SSW and Deep seawater (DSW) and their relationship with microbial communities. This study investigated the relationship between microbial communities and environmental factors in seawater from three DSW pumping stations (Goseong: GS, Sokcho: SC, and Ullueungdo: UL) in Korea. The results showed that the microbial diversity of DSW was higher than that of SSW, consistent with previous studies. Additionally, seasonal microbial diversity was lowest in spring and gradually increased until fall across the three region. The number of viable microorganisms in each area was significantly lower in DSW than in SSW. Principle coordination analysis, incorporating microbial communities and environmental factors of each region, indicated that DSW represents a promising source for isolating unclassified bacteria.

***Key Words*:** Deep sea water, Bacterial community, Korea

1. Introduction

Deep sea water (DSW) is defined seawater below 200 m, exists in a perpetually dark environment beyond the reach of sunlight (Yang *et al.*, 2019). This unique habitat exhibits several distinct characteristics:

- **Abundance**: Comprising over 90% of the Earth's seawater volume, DSW represents a vast and largely untapped resource.
- **Low temperature**: With a consistently cold temperature ranges from 2 to 4℃, DSW offers potential for various applications.
- **Nutrient-rich**: Minimal sunlight inhibits photosynthesis, leading to an accumulation of nutrients (e.g., total dissolved nitrogen [TDN], total dissolved phosphorus [TDP], ammonia, nitrate, nitrite) from the decomposition of organic matter. Consequently, DSW exhibits higher nutrient concentrations compared to SSW.
- **Purity**: DSW harbors a significantly lower microbial biomass than SSW, resulting in exceptional biological purity.
- **Stability**: These physical and chemical characteristics remain remarkably consistent year-round.

Although DSW is a global phenomenon, its industrial utilization is currently limited to a few countries, including the United States (Hawaii), Japan, Taiwan, Norway, and South Korea, are currently utilizing DSW for industrial purposes. This restricted use is attributed to several factors. Firstly, direct access to DSW is geographically limited. Secondly, the high initial investment required for infrastructure development, such as intake pipes, pumping systems, and storage tanks, poses a significant financial barrier. Intake pipe installation represents the most substantial cost, necessitating careful site selection to minimize expenses (Hunt *et al.*, 2021).

---

[1] Goseong Deep Sea Water Industry Foundation (Songjiho-ro 42, Goseong-gun, 24747, Korea)

[2] Seoul National University (Gwanak-ro 1, Gwanak-gu, Seoul-si, 08826, Korea)

In East Asia, South Korea, Japan, and Taiwan have actively developed DSW-related industries, establishing intake facilities through government and private sector initiatives. Japan pioneered this development in the 1990s, followed by South Korea in the 2000s. Japan has established a leading role in diverse sectors, including food, aquaculture, and pharmaceuticals (Ju, 2017).

Despite its low biomass, DSW harbors microorganisms uniquely adapted to its extreme conditions. Numerous studies have isolated novel microorganisms from DSW, highlighting the presence of unexplored microbial diversity in these environments (Zhang *et al.*, 2022; Saide *et al.*, 2021; Skropeta and Wei, 2014; Yang *et al.*, 2019). Concurrent advancements in molecular phylogenetic techniques, particularly metagenome sequencing, have revolutionized microbial community analysis. This approach allows for comprehensive and cost-effective acquisition of microbial information from various environments, including seawater, soil, rivers, and even the human body (Roumpeka *et al.*, 2017; Wang *et al.*, 2021; Yang *et al.*, 2021).

While some studies have explored microbial communities in DSW, a comprehensive understanding integrating biological and physicochemical data remains limited. (Campeao *et al.*, 2017; Terahara *et al.*, 2016; Yang *et al.*, 2019).

This study focuses on three DSW intake sites in South Korea: Goseong-gun and Yangyang-gun in Gangwon Province and Ulleung-gun in North Gyeongsang Province. The primary objective is to collect seasonal data on the physical, chemical, and biological properties of DSW and analyze their interrelationships. This analysis will elucidate regional variations in microbial community structures within Korean DSW and examine their relationships with the physicochemical characteristics of DSW. Furthermore, the study aims to identify industrially valuable microorganisms and develop methods for their isolation and cultivation.

2. Material and Method

2.1. Sample collection and *In-situ* measurement

Twentyfour water collections were collected from three DSW sites in Korea, including both DSW and SSW as a comparative counterpart (Table 1 and Fig. 1). Sterile techniques were employed throughout the collection process to prevent cross-contamination, using sterile 2L sampling bottles (2L, New-Kukje Science Co., Ltd.) (Grasshoff *et al.*, 1999).

Immediately following collection, in situ measurements of environmental parameters, including dissolved oxygen (DO, %), salinity (‰), pH, and temperature (℃), were recorded for both DSW and SSW using a portable YSI Pro instrument (YSI, USA). Prior to field deployment, the YSI Pro was calibrated in a controlled labora-

Table 1. Sampling location of DSW and SSW in Korea.

Name of facility	Position (latitude)	Position (longitude)	depth(m)	Name of place	Sampling date (yyyy, mm, dd)
Korea research institute of ships & ocean engineering	38.33469	128.52143	620	Goseong prefecture	2023, 02, 13 2023, 05, 16
Songjiho Beach	38.33483	128.35246	0	Goseong prefecture	2023, 08, 16 2023, 11, 07
Global deep seawater Co. Ltd.	38.18467	128.60570	600	Sokcho city	2023, 02, 14 2023, 05, 30
Sokcho Beach	38.18529	128.60760	0	Sokcho city	2023, 08, 11 2023, 11, 08
Ulleung-gun fisheries cooperation	37.49342,	130.91024	160	Ulleungdo prefecture	2023, 02, 24 2023, 05, 17
Naesujeon Mongdol Beach	37.50797,	130.91449	0	Ulleungdo prefecture	2023, 08, 18 2023, 11, 09

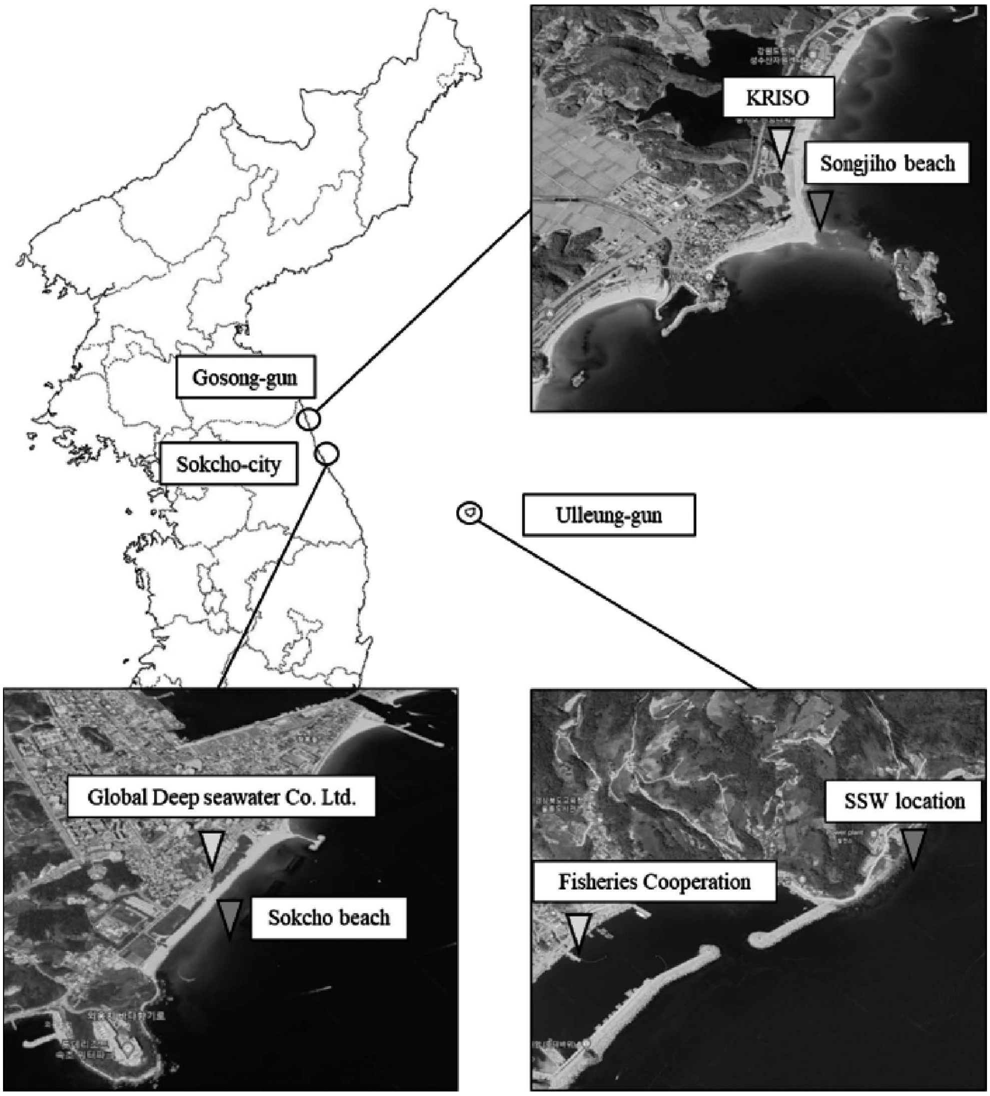

Fig. 1. Sampling location of sea-water. Blue triangle shows deep seawater sampling location, and Red triangle shows surface seawater sampling location of three prefectures.

tory setting using YSI calibration solutions (3169, 3821, 3822, 3823) for each sensor (electrical conductivity and pH).

2.2. Viable cell counts

Viable mesophilic cells were determined by dispensing 1 mL of seawater sample onto a Petrifilm Aerobic Count Plate (AC, 3M) and incubating at 25℃ for 48 hours (n = 3) for confirming the microbial water quality. Resulting colonies (fewer than 100 colonies per plate) were enumerated and expressed as colony-forming units per mL (cfu/mL).

2.3. Preprocessing for Microbial Analysis

To characterize the microbial communities, present in the samples, microorganisms were concentrated from the samples, and the DNA (16S rRNA) was analyzed using molecular genetic methods (Campeao *et al.*, 2017). For DSW, approximately 20 L were filtered, while 2 L of SSW were filtered using a sterilized filtration system (Reusable Filter Holder 500 mL, Nalgene). A sequential filtration process was employed, first using a 3.0 μm membrane filter to remove attached bacteria, followed by a 0.2 μm membrane filter to capture living bacteria (ADVACTEC). The 0.2 μm membrane filters containing the concentrated microorganisms were stored in conical tubes (SPL) at −20℃ until DNA extraction. The total

DNA of the microorganisms, bacterial 16S rRNA PCR, and and subsequent sequencing for metagenome analysis were performed by CJ Bioscience Co., Ltd. for metagenome analysis.

2.4. Microbial community analysis

Metagenome data, encompassing 24 samples (3 regions, 4 seasons, and 2 depths), were analyzed using the EZ Biocloud server (https://www.ezbiocloud.net) to assess alpha and beta diversity and generate metagenome taxonomy profiles. Principal Coordinate Analysis (PCA) and clustering analysis were conducted by CJ Bioscience Co., Ltd. to investigate correlations between environmental factors and microbial community composition.

3. Result and Discussion

3.1. Environmental Factors (Temperature, DO, Salinity, and Viable Cell)

The temperature in DSW ranged from 5℃ to 14℃ across seasons, with a simultaneous rise in the temperatures of both DSW and SSW observed in August and November (Fig. 2a). Regionally, GS (Gangwon Province) had the lowest temperature followed by SC (Yangyang) and UL (Ulleungdo), which were similar to the surface water temperature. Overall, SSW was warmer than DSW, with the lowest temperature recorded in GS DSW.

For comparison, DSW (depth 319 m) in the Taitung region of Taiwan exhibits unstable annual temperature variation ranging from 11℃ to 14℃ (Yiing-Jang *et al.,* 2020). This instability is attributed to Taiwan's susceptibility to seasonal environmental factors, particularly typhoons during summer and autumn.

In 2023, Typhoon Khanun, the year's 6th typhoon of the year, moved northward along Korea's eastern coast from late August to early September. Coastal upwelling caused by the typhoon likely affected the thermocline layer's depth, leading to changes in the region's DSW temperature.

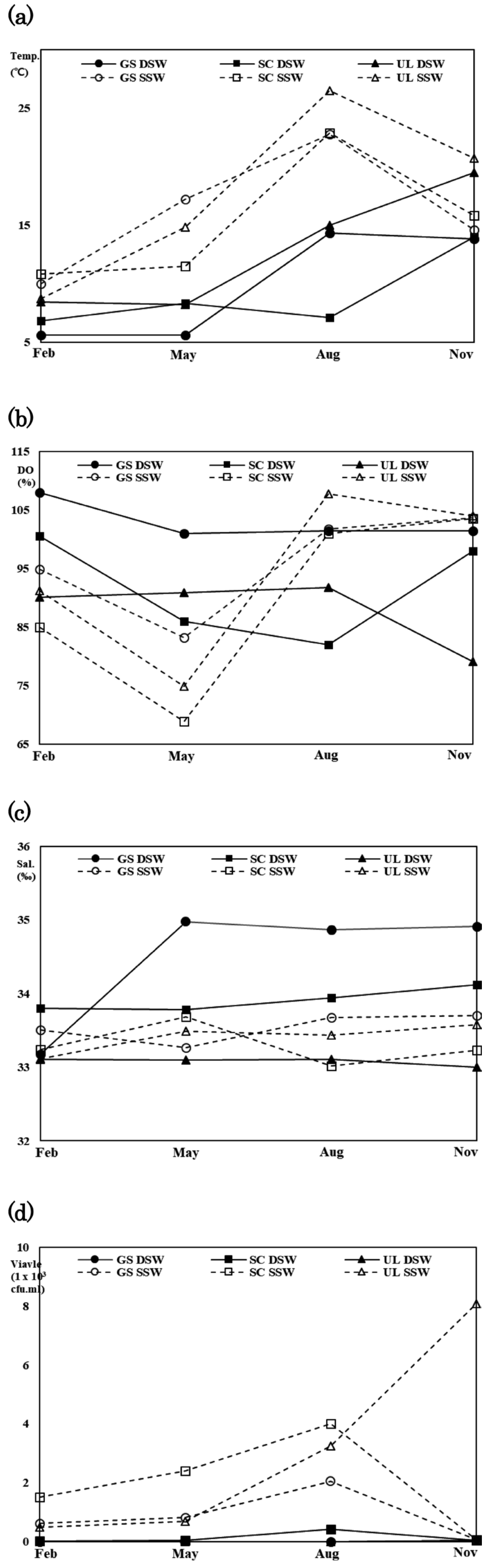

Fig. 2. Variation of environmental factors in each samples through the season. (a) Temperature, (b) DO (%), (c) Salinity, (d) viable cell counts.

Dissolved oxygen (DO) levels were generally higher in DSW compared to SSW, with DSW showing elevated DO levels in February and May November (Fig. 2b). However, SSW exhibited higher DO than DSW. This seasonal variation is attributed to several factors. During winter, oxygen consumption by biological activity exceeds oxygen production through photosynthesis in SSW (Kolber *et al.*, 2000). Additionally, cold water's physical properties support higher oxygen saturation in DSW. Consequently, SSW typically has lower DO than DSW during winter (Mavropoulou *et al.*, 2020). Conversely, increased biological photosynthesis in surface waters during summer leads to higher DO in SSW in August and November. Salinity remained between 33‰ and 34‰ , showing no significant regional or seasonal variations.

The viable cell count in seawater was significantly lower in DSW than in SSW (Fig. 2d). Regionally, GS DSW had the lowest viable cell count (1.3 to 46 cfu/mL), while Ulleungdo's (UL) surface water recorded the highest (489 to 8,033 cfu/mL). Seasonally, August had the highest average viable cell count (1,634 cfu/mL). Among DSW samples, SC DSW exhibited the highest average viable cell count (132 cfu/mL). Consistent with Imada (2013), DSW typically contains approximately 1,000 times fewer viable cells than SSW. The relatively higher viable cell counts observed in some DSW samples are likely influenced by seasonal factors. It is necessary to had confirm the broad range of temperature and various incubation conditions for counting entire bacteria in DSW and SSW samples. For these reason, this result should discuss for microbial-safe water quality. Nevertheless, it seems that DSW is more appropriate for industrial applications, e.g., drinking water, foods, etc., because of its microbial water quality than SSW (Lee, 2014).

3.2. Metagenome Taxonomy Profiling

Twentyfour analytical samples were uploaded to EzBioCloud for phylogenetic analysis, with taxonomic composition classified by season. At the phylum level (Fig. 3a), *Proteobacteria* and *Bacteroidetes* were dominant across all regions and depths, showing similar patterns in most samples. In February, *Actinobacteria* were notably abundant in DSW, especially in SC DSW (14.7%). In May, *Cyanobacteria* were detected in GS SSW (11.5%), SC SSW (26.1%), and DSW (11.5%). In August, *Verrucomicrobia* were relatively more abundant in GS DSW (14.8%) compared to other regions, while *Chloroflexi* were detected exclusively in UL SSW. In November, *Cyanobacteria* increased in GS SSW (38.91%) and SC SSW (35.22%) compared to their respective DSWs.

At the genus level (Fig. 3b) in February, *Aurantivirga* (24.6%) was the most dominant genus in GS DSW and was present in all regions. *Amphritea* was uniquely distributed in the GS region, while *Sulfitobacter* was found in all regions except SC DSW. Notably, *Sulfitobacter* dominated GS SSW (56.2%), while *Polaribacter* (33.1%) was dominant in UL SSW. The genus *Aurantivirga* is closely associated with deep-sea environments, particularly due to the characteristics of its type species, *Aurantivirga profunda* (Song *et al.*, 2015) which first isolated from deep seawater in the Pacific Oceans, and it is suggest that they are well-adapted to extreme conditions.

In May, *Sulfitobacter*, which had dominated GS SSW in February, dominanted GS DSW (52.3%). While *Sulfitobacter* was widely distributed in GS and UL seawater, its presence in SC was less than 6%, showing regional differences but no significant depth-related variations. *Sulfitobacter* is a genus of marine bacteria belonging to the family *Rhodobacteraceae* within the phylum *proteobacteria*. It is widely distributed in the marine environment and plays a critical role in biogeochemical cycles, particularly sulfur and carbon cycling (Cui *et al.*, 2024). *Synechococcus* dominant both SC SSW (26.1%) and SC DSW (11.5%).

In August, clear regional differences in microbial communities were observed. Dominant genera included: GS DSW (unclassified genus CP017259, 13.8%), GS SSW (*Thioalkalispiraceae*_uc, 30.7%), SC DSW (*Polaribacter*, 20.3%), SC SSW (*Marivivens*, 39.7%), UL DSW (*Pelagi-*

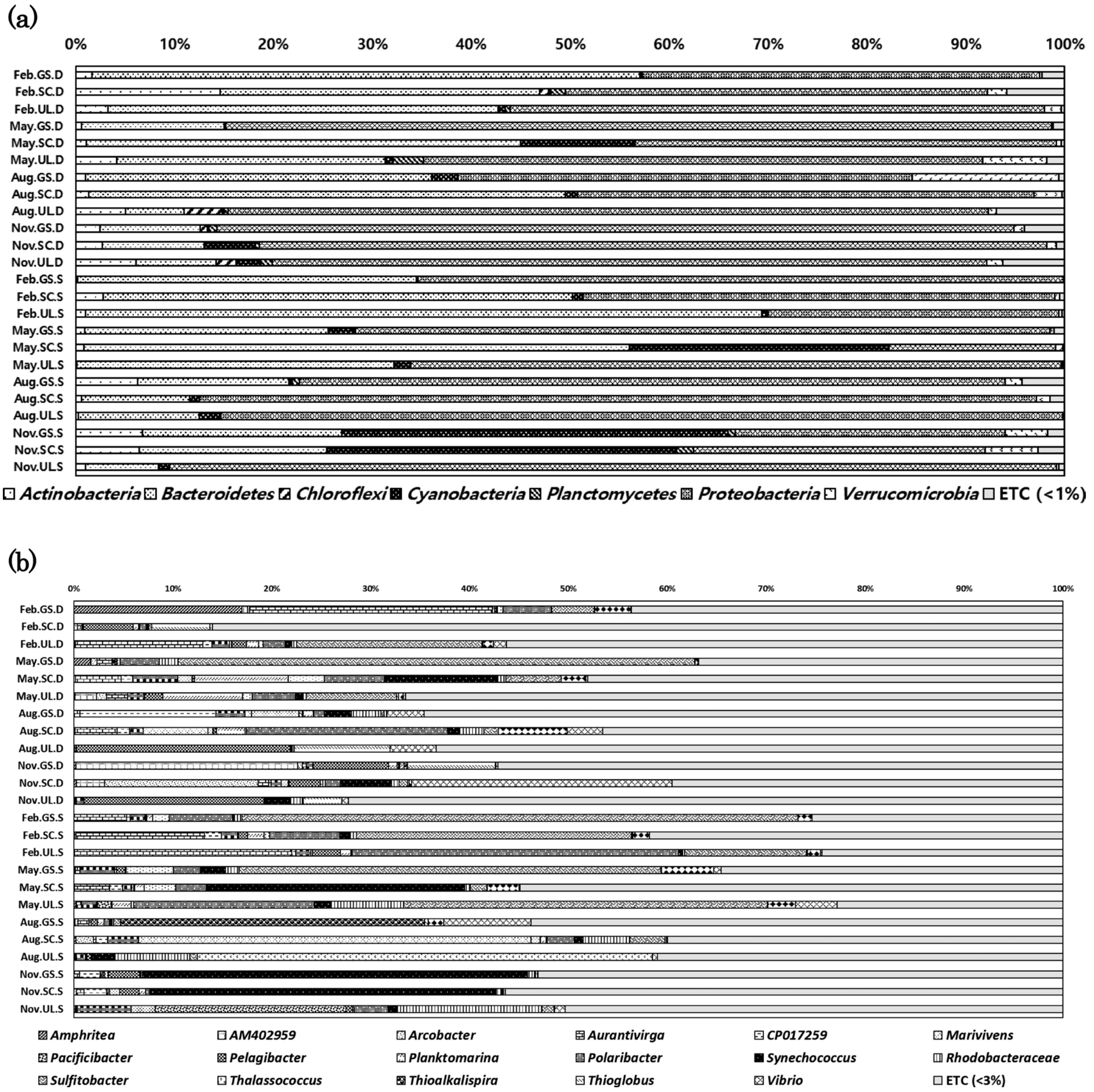

Fig. 3. Bacterial composition of deep sea water and surface sea water in Korea. (a) Phylum rank, (b) Genus rank. Y-axis means bacterial community samples and X-axis means percentage of sample's phyla and genus. Bar covered with patterns meaning different taxa.

bacter, 21.6%), and UL SSW (*Thalassococcus*, 46.0%). These variations are likely influenced by regional environmental factors such as temperature and nutrient availability. *Thioalkalispira* is a bacteria primarily involved in sulfur oxidation processes in marine environments. These bacteria are typically found in saline and alkaline conditions, such as marine sediments and hydrothermal vent areas. They play a crucial role in the sulfur cycle by oxidizing hydrogen sulfide (H_2S) to sulfate (SO_4^{2-}), thereby contributing to nutrient cycling and maintaining the balance of sulfur compounds in marine ecosystems (Sorokin *et al.*, 2012). It seems that Genus *Thioalkalispira* role in the sulfur cycling replaced the *Sulfitobacter* in August GS SSW.

In November, GS DSW was dominated by an unnamed genus (AM402959, 22.4%), while *Vibrio* (26.3%) and *Pelagibacter* (18.1%) were dominant in SC DSW and UL DSW, respectively. *Synechococcus* was dominant in GS DSW (38.9%) and SC DSW (35.1%), while *Pacificibacter* was dominant in UL DSW (19.3%), reflecting geographical influences on microbial communities.

The proportion of unclassified bacteria was 5.6% in DSW and 3.1% SSW. This suggests that DSW contains a higher proportion of unknown microorganisms, making it a promising resource for isolating novel microorganisms (Terahara *et al.*, 2016; Yang *et al.*, 2019).

3.3. Alpha-diversity and beta-diversity analysis (PCA)

Alpha-diversity analysis was assessed using OTUs (Operational Taxonomic Units, Cut-off 1%) and diversity indices (ACE, Chao, Shannon, and Simpson), as shown in Table 2. The target reads per sample ranged from 20,000 to 50,000, with OTU counts varying significantly from 400 to 1,900. However, there is no correlation between the target reads and OTU counts. The ACE and Chao indices displayed consistent patterns, with the highest values recorded in November for UL DSW (ACE: 2,316; Chao: 2,195). Similarly, diversity indices showed their highest values in November for UL DSW (Shannon: 5.81; Simpson: 0.02). Higher Shannon index values indicate greater diversity, whereas for the Simpson index, values closer to 0 represent higher diversity.

Average diversity indices were higher for DSW (Shannon: 4.28; Simpson: 0.065) than for SSW (Shannon: 3.62; Simpson: 0.12). Seasonally, species diversity indices showed the following trends: in February (Shannon: 3.54, Simpson: 0.12), May (Shannon: 3.64, Simpson was 0.10), August (Shannon: 4.13, Simpson: 0.08), November (Shannon: 4.48, Simpson: 0.068). This indicates that species diversity was lowest in winter (February) and increased steadily through autumn (November).

Beta-diversity analysis using PCA, revealed seasonal clustering patterns among samples.

- February (Fig. 4a): Samples clustered into three groups. UL SSW and SC SSW were grouped together, while UL DSW, SC DSW, and GS SSW formed another cluster. However, GS DSW did not cluster with seawater from other regions. UL SSW correlated strongly with *Bacteroidetes*, while SC SSW was closely associated with *Cyanobacteria*. The microbial communities of UL DSW and SC SSW were linked to *Actinobacteria*, *Proteobacteria*, and *Verrucomicrobia*.
- May (Fig. 4b): SSW from all three regions, along with

Table 2. Alpha-diversity of seawater in Korea

Sample	Target reads	OTUs	ACE	CHAO	Shannon	Simpson
230213GSD	44,584	1,038	1,189.87	1,104.44	3.82	0.09
230214SCD	44,725	1,352	1,554.67	1,465.20	4.68	0.03
230224ULD	51,240	889	1,080.11	1,005.76	3.79	0.07
230516GSD	28,945	642	851.55	772.52	2.86	0.26
230530SCD	39,919	651	814.45	754.10	3.21	0.11
230517ULD	34,507	879	1,088.76	1,014.53	4.70	0.02
230809GSD	43,632	957	1,156.01	1,059.38	4.44	0.03
230811SCD	53,134	1,095	1,287.39	1,201.48	4.25	0.04
230818ULD	41,542	1,058	1,197.74	1,135.85	4.59	0.04
231107GSD	21,601	1,177	1,461.12	1,345.67	4.81	0.03
231108SCD	26,227	1,074	1,433.32	1,307.75	4.41	0.05
231109ULD	23,429	1,974	2,361.07	2,195.80	5.81	0.02
230213GSS	37,309	432	528.77	492.45	2.36	0.31
230214SCS	52,752	1,148	1,430.84	1,323.69	3.62	0.10
230224ULS	45,424	997	1,164.50	1,079.32	2.99	0.17
230516GSS	36,487	717	945.09	916.09	3.86	0.06
230530SCS	33,087	605	794.88	720.94	3.74	0.05
230517ULS	37,905	731	949.39	888.69	3.48	0.12
230809GSS	40,722	1,679	1,888.66	1,772.69	4.27	0.10
231108SCS	20,808	1,344	1,890.00	1,713.86	4.45	0.07
230818ULS	51,103	697	796.43	751.97	2.79	0.23
231107GSS	30,818	1,023	1,482.90	1,336.09	3.96	0.10
230811SCS	51,652	1,576	2,160.84	1,976.15	3.76	0.16
231109ULS	23,649	1,025	1,310.80	1,207.19	4.17	0.05

D: DSW, S: SSW, GS: Goseong, SC: Sokcho, UL: Ulleungdo.

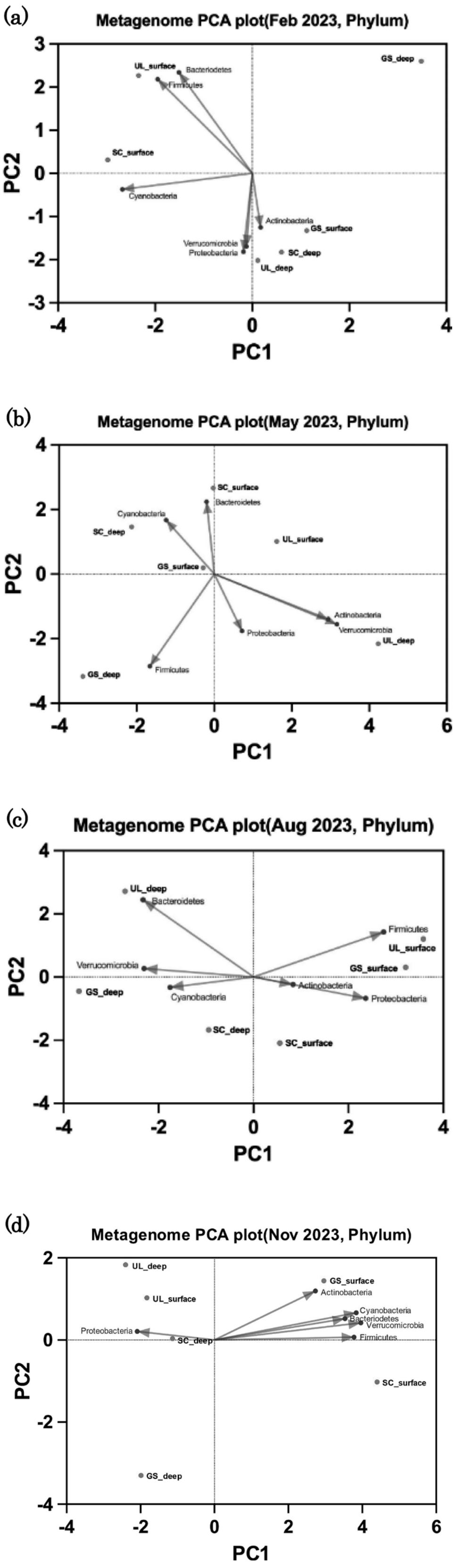

Fig. 4. PCA analysis of seawater samples in Korea. (a) February, (b) May, (c) August, (d) November. The arrow represents environmental factors related to each seawater sample. The dot means seawater samples. The Y-axis and X-axis represent the relative positions that show the distance between each sample.

SC DSW, clustered together. In contrast, DSW from the other regions displayed distinct patterns. UL DSW was closely associated with *Actinobacteria* and *Verrucomicrobia*, whereas microbial communities in other regions correlated with *Cyanobacteria* and *Bacteroidetes*.

- August (Fig. 4c): UL SSW and GS SSW clustered together, while GS DSW and UL DSW formed separate clusters. UL DSW correlated strongly with *Bacteroidetes*, while GS DSW was linked to *Verrucomicrobia*. SSW microbial communities were primarily associated with *Firmicutes* and *Proteobacteria*.
- November (Fig. 4d): UL SSW and DSW, along with SC DSW, clustered together, while the microbial communities of other regions exhibited distinct PCA distribution patterns. The microbial community of GS SSW showed a strong correlation with *Actinobacteria*.

The PCA analysis across the four seasons suggests that GS DSW consistently exhibited distinct clustering patterns, indicating that it is a unique type of seawater, clearly differentiated from seawater in other regions.

3.4. Microbial community variations by environmental parameter change

Following changes in environmental parameters, the microbial community structure in each sample exhibited seasonal variations. The most dominant microorganism, *Synechococcus* sp. (Phylum: *Cyanobacteria*), was prevalent in all regions throughout the year, except for a few specific locations. It predominantly dominated GS and SC SSW in May and November (Fig. 5a). *Synechococcus*, a representative marine cyanobacterium, is known to differentiate into resting cells under nitrogen-limited conditions, similar to other cyanobacteria (Sauer *et al.*, 2001; Stal, 2009; Roth-Rosenberg *et al.*, 2020).

Although nutrient analyses (e.g., NO_2^-, NO_3^-, NH_4^+, and PO_4^{3-}) were not conducted, it is presumed that unfavorable growth conditions for *Synechococcus* in August, including light availability, nutrient depletion, and physical factors, may have limited its proliferation. Various studies have reported that vertical mixing along the east coast, caused by typhoons during summer, can alter surface water movement in SSW and impact environmental factors in DSW (Byun and Cho, 2022).

In early August 2023, Typhoon Khanun struck the Korean Peninsula, generating southerly winds along the east coast's sea surface. This likely triggered upwelling from deeper layers due to the Ekman transport effect (Price *et al.*, 1987). This upwelling likely introduced sediments from the seafloor, potentially influencing the microbial communities in both DSW and SSW.

4. Conclusion

The microbial community and environmental factors of DSW along Korea's eastern coast reflect both regional characteristics and seasonal environmental influences. Among the DSW regions, UL DSW was the least affected by environmental changes, maintaining distinct characteristics compared to other seawater regions throughout the year. Notably, despite the geographical proximity of GS and SC, their microbial communities were distinctly different. This suggests that while geographic features partially influence microbial community structures, other factors may play a significant role.

Compare to another country, especially Japan, bacterial communities and physical properties of DSW are similar in overall (physical properties and dominant bacteria phyla), but different in detail (dominant bacteria genera in regions). As same as difference of microbial communities in Korean DSW, it seems that their differences occurred from geographical disparity.

However, this study is limited to a one-year, four-season analysis, long-term monitoring of microbial communities and environmental factors is necessary to confirm the recurrence and consistency of these phenomena. Additionally, Korean DSW exhibited a higher proportion of unclassified genera compared to SSW, with microbial communities within DSW showing significant diversity and differences. These findings highlight DSW's high potential value as a resource for discovering novel microorganisms. Continued efforts to explore and develop useful microorganisms from Korean DSW as a biological resource are essential.

Acknowledgement

This study was supported by the 2023 Goseong-gun Gangwon-do, the Korea Research Institute of Ships & Ocean Engineering (KRISO), Global Deep-Sea Water Co., Ltd., and Ulleung-gun Gyeongsangbuk-do as part of the Deep-Sea Water Bio Bank Development Project (Project No.: GDIF-202301).

References

Byun, S. S. and C. B. Cho (2022) Coastal upwelling observed off the East coast of Korea and variability of passive sound detection environment. J. Acoust. Soc. Kr., 41, 601–609.

Campeao, M. E., L. Reis, L. Leomil, L. de Oliveira, K. Otsuki, P. Gardinali, O. Pelz, R. Valle, F. L. Thompson and C. C. Thompson (2017) The deep-sea microbial community from the Amazonian basin associated with oil degradation. Front. Microbiol., 8, 1019.

Cui, H., S. Fan, W. Ding and W. Zhang (2024) Genomic Analysis of novel *Sulfitobacter* bacterial strains isolated from marine biofilms. Mar. Drugs 22, 289, doi: 10.3390/md22070289.

Grasshoff, K., K. Kremling and M. Ehrhardt (1999) Methods of Seawater Analysis, Wiley-VCH, Weinheim, Germany, 632.

Hunt, J. D., N. D. A. B. Weber, B. Zakeri, A. T. Diaby, P. Byrne, W. Leal Filho and P. S. Schneider (2021) Deep seawater cooling and desalination: Combining seawater air conditioning and desalination. SCS, 74, 103257.

Imada, C. (2013) Treasure hunting for useful microorganisms in the marine environment. In "Marine Microbiology: Bioactive Compounds and Biotechnological Applications." (ed. By S. K. Kim), Wiley-VCH, Weinheim, 21–31.

Ju, H. H. (2017) International case studies for deep sea water industry - Focusing on the Taiwan case, 2016. JKAIS, 17, 537–47 (in Korean).

Kolber, Z. S., C. L. Van Dover, R. A. Niederman and P. G. Falkowski (2000) Bacterial photosynthesis in surface waters of the open ocean. Nat., 407, 177–179.

Lee, C. L. (2015) The advantages of deep ocean water for the development of functional fermentation food. Appl. Microbiol. Biotechnol., 99, 2523–2531.

Mavropoulou, A. M., V. Vervatis and S. Sofianos (2020) Dissolved oxygen variability in the Mediterranean Sea. J. Mar. Syst., 208, 103348.

Price, J. F., R. A. Weller and R. R. Schudlich (1987) Wind-driven ocean currents and Ekman transport. Sci., 238, 1534–1538.

Roumpeka, D. D., R. J. Wallace, F. Escalettes, I. Fotheringham and M. Watson (2017) A review of bioinformatics tools for bio-prospecting from metagenomic sequence data. Front. Genet., 8, 23.

Roth-Rosenberg D., D. Aharonovich, T. Luzzatto-Knaan, A. Vogts, L. Zoccarato, F. Eigemann, N. Nago, H. Grossart, M. Voss and D. Sher (2020) *Prochlorococcus* cells rely on microbial interactions rather than on chlorotic resting stages to survive long-term nutrient starvation. mBio 11:10.1128/mbio.01846–20

Sauer, J., U. Schreiber, R. Schmid, U. Völker and K. Forchhammer (2001) Nitrogen starvation-induced chlorosis in *Synechococcus* PCC 7942. Low-level photosynthesis as a mechanism of long-term survival. Plant Physiol., 126, 233–243.

Saide, A., C. Lauritano and A. Ianora (2021) A treasure of bioactive compounds from the deep sea. Biomed., 9, 1556.

Skropeta, D. and L. Wei (2014) Recent advances in deep-sea natural products. Nat. Prod. Rep., 31, 999–1025.

Song, J., A. Choi, M. Im, Y. Joung, S. Yoshizawa, J.-C. Cho and K. Kogure (2015). *Aurantivirga profunda* gen. nov., sp. nov., isolated from deep-seawater, a novel member of the family *Flavobacteriaceae*. IJSEM, 65, 4850–4855

Sorokin, D. Y., M. S. Muntyan, A. N. Panteleeva and G. Muyzer, 2012. *Thioalkalivibrio sulfidiphilus* sp. nov., a haloalkaliphilic, sulfur-oxidizing *gammaproteobacterium* from alkaline habitats. IJSEM, 62, 1884–1889.

Stal, L.J. (2009) Is the distribution of nitrogen - fixing cyanobacteria in the oceans related to temperature?. Environ. Microbiol., 11, 1632–1645.

Terahara, T., K. Yamada, J. Nakayama, Y. Igarashi, T. Kobayashi and C. Imada (2016) Bacterial community structures of deep-sea water investigated by molecular biological techniques. Gene, 576, 696–700.

Wang, S., Z. Yan, B. Hänfling, X. Zheng, P. Wang, J. Fan and J. Li (2021) Methodology of fish eDNA and its applications in ecology and environment. Sci. Total Environ., 755, 142622.

Yang, C., D. Chowdhury, Z. Zhang, W. K. Cheung, A. Lu, Z. Bian and L. Zhang (2021) A review of computational tools for generating metagenome-assembled genomes from metagenomic sequencing data. Comput. Struct. Biotechnol. J., 19, 6301–6314.

Yiing-Jang, Y., W. Chan-Chuan, H. Ping-Yi, W. Cheng-Yun, K. S. Chu and P. Su-Cheng (2020) Verification of the internal tide off Zhiben coast, Taitung, southeast Taiwan. TAO: Terrestrial, AOSL, 31, 77–83.

Yang, T., K. Yamada, J. Nakayama and Y. Igarashi (2019) Bacterial community structure analysis of deep-sea water and surface seawater in Japan by pyrosequencing. Deep Ocean Wat. Res., 19, 137–146.

Yang, T., K. Yamada, T. Zhou, E. Harunari, Y. Igarashi, T. Terahara, T. Kobayashi and C. Imada (2019) Akazamicin, a cytotoxic aromatic polyketide from marine-derived Nonomuraea sp. J. Antibiot., 72, 202–209.

Zhang, Z., Y. In, K. Fukaya, T. Yang, E. Harunari, D. Urabe, C. Imada, N. Oku and Y. Igarashi (2022) Kumemicinones A–G, cytotoxic angucyclinones from a deep sea-derived *actinomycete* of the genus *Actinomadura*. J. Nat. Prod., 85, 1098–1108.

(Received: December 11, 2024; Accepted: February 7, 2025)