Bacterial Community on a Guyot in the Northwest Pacific Ocean Influenced by Physical Dynamics and Environmental Variables

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Abstract Bacterial communities in sediments of the Caiwei Seamount, a typical guyot located in the northwest Pacific Ocean, were investigated. A total of 727,879 16S ribosomal RNA gene sequences were retrieved from eight sediment samples of the top (mean depth = 1,407 m) and the base (mean depth = 5,525 m) of the guyot through pyrosequencing of V6 hypervariable region and clustered into 32,844 operational taxonomic units. Abundant-weighted UniFrac metric partitioned bacterial assemblies into two categories (the top community and the base community) by principal coordinates analysis, consisting with the grouping of sampling stations by environmental variables. Differences in depth and physicochemical properties of the surrounding environment (e.g., concentrations of dissolved oxygen and geochemical elements) between the top and the base of the guyot may cause this partition of bacterial communities, whereas the typical fluid flow around the guyot may potentially contribute to the bacterial dispersal and environmental homogeneity along the same layer, resulting in the similarity of bacterial community structure within the same region (the top or the base). The surface sediment on the top of the guyot harbored the bacterial communities with greater diversity and evenness, represented by Gamma- and Deltaproteobacteria involved in sulfur cycling. At the base of the guyot, Gammaproteobacteria related to sulfur-oxidizing and Chloroferrofunctioning in the decomposition of refractory organic matter dominated, suggesting that the redox condition at the interface of the sediment and the water can influence bacteria-mediated elemental cycling, eventually shaping the physicochemical and geological characteristics of a guyot.

Plain Language Summary Seamounts in northwest Pacific Ocean are most abundant in the world. They have been recognized as important habitats for corals, fish, and etc. The high biodiversity in seamount regions could be a result of efficient food and energy transfer mediated by microorganisms. In this study, we investigated bacterial community composition, structure, and potential metabolic characteristics at different locations of the Caiwei Seamount, a flat-topped seamount (also called as guyot) in northwest Pacific Ocean in order to understand the functions of the seamount ecosystem. Our results showed that the bacterial zonation in the Caiwei Seamount was influenced by both physicochemical variables and physical dynamics. Unique circulation of flow currents in seamount region may enhance the homogeneity of bacterial community at the same depth, while physicochemical variation by depth could be the major factor partitioning bacterial community vertically. The potential ecological functions of bacterial communities are strongly associated with the regional environments. They are actively involved in sulfur and nitrogen cycling, possibly key to energy and substrate productivity.

1. Introduction

Microbial abundance in subseafloor sediment has been estimated to be $2.9 \times 10^{29}$, accounting to total prokaryotic cell abundance in the water column and in soil (Kallmeyer et al., 2012). They play an important role in deep-ocean biogeochemical processes and potentially contribute to high productivity in the deep ocean (McNichol et al., 2018). Microorganisms have been extensively studied in different environments of
Seamounts are the unique environment widely distributed in deep-ocean seafloor (Wessel & Kroenke, 1997). They are the important habitats for marine organisms (Clark et al., 2010). The topographic-induced turbulent mixing at seamounts may potentially cause high primary productivity in the upper water column (Boehlert & Genin, 1987; Polzin et al., 1997), benefiting the fish and benthic communities in seamount areas (Clark et al., 2010; Richer de Forges et al., 2000). Most of seamounts discovered in the world are located in the west Pacific (Kim & Wessel, 2011). Flat-topped seamounts, also called as guyots, are the major types in the west Pacific. The flat top is a result of coral reef growth and erosion as their conical tops reached the sea surface during evolutionary processes (Stanley, 2005). Thus, the top of a guyot is covered by carbonate rock with shallow-water coral and bivalve reefs formed millions of years ago. At the base of a guyot, it is majorly composed of manganese crust or iron-manganese (Fe-Mn) coating precipitating from cold water (Asavin et al., 2008). The varied compositions of sediments at different regions of a guyot provide diverse biological habitats, indicating potential importance of guyots to the deep-sea ecosystem. Currently, there are a few studies on microbial communities in guyot environments, which mostly focus on the communities associated with ferromanganese crust and potentially functioning in metal precipitation (Kato et al., 2018; Nitahara et al., 2011, 2017); however, the patterns of microbial distribution and their relationship with guyot environment on guyots are less understood.

The Caiwei Seamount is a deep-sea guyot located in the northeast of the eastern Marianas Basin of the west Pacific Ocean at a latitude and longitude of 15.0°–16.2°N and 145.6°–155.8°E (Figure 1). The depth of the top is between 1,500 and 1,600 m and that of the base is approximately 5,500 m. The Caiwei Seamount is covered by cobalt-rich crusts, the density of which increases with depth. Other mineral resources, such as nickel, copper, iron, and manganese are also rich on the seamount (Wang et al., 2016). The Caiwei Seamount has been extensively surveyed by the China Ocean Mineral Resources R&D Association (COMRA) for mineral resources and megafaunal community (Wang et al., 2016; Xu et al., 2016); however, the microorganisms that are potentially important in food web and energy transfer in seamount ecosystem have not been investigated yet. In this study, bacterial community structure in sediment samples of the Caiwei Seamount were studied for enhancing our understanding in (1) diversity and genetic fingerprinting of guyot bacterial community, (2) interaction between bacterial community structure and guyot environments, and (3) potential roles of bacteria in biogeochemical processes of the Caiwei Seamount that could be extremely important in food and energy transfer, shaping the ecological function of the guyot ecosystem.

2. Materials and Methods

2.1. Sample Collection and environmental Variables

Sediment samples were collected from the Caiwei Seamount located in the west Pacific Seamount Province during the DY27 cruise of the R/V Haiyang Liu Hao in July, 2012. Using multiple corer (surface area = 0.00785 m², height = 0.6 m) as well as box corer (surface area = 0.25 m²) systems, four sediment samples were obtained at the flat top of the seamount (1,362–1,500 m in depth; MAMC01, MAMC02, MAMC03, and MAMC04) and four were collected at the base of the seamount (5,269–5,920 m in depth; MABC02, MAMC06, MABC06, and MAMC08; Figure 1 and Table S1). Box corer samples were immediately subsampled using push corers. The top 5 cm of sediment were collected in all sediment cores and stored at −20°C until analysis in the laboratory for subsequently microbiological and geochemical experiments. Seawaters were also collected from the surface to the depths close to the seafloor near stations MAMC02 and MAMC04 at the top of the seamount (MACTD01 and MACTD04) and stations MABC02, MABC06 and MAMC08 at the base of the seamount (MACTD07, MACTD08, and MACTD06) using 8 L Niskin bottles mounted on a rosette frame equipped with a SBE917 CTD system (Sea-Bird Electronics, Inc.; Figure 1 and Table S1).

Concentrations of dissolved oxygen (DO) in seawaters were measured following the Winkler method (Winkler, 1888). For nutrient measurements, seawater samples were collected into 500-ml high-density
polyethylene bottles and filtered onto cellulose acetate filters (47-mm diameter and 0.45-μm pore size). Concentrations of ammonia, nitrite, and phosphate were determined using a standard colorimetric method (Grasshoff et al., 1999), and nitrate concentrations were measured using a cadmium-reduction method coupled with diazotization (Grasshoff et al., 1999). Elemental analysis of sedimentary concentrations of total organic carbon (TOC) and nitrogen (TON) were performed using an Elementar Vario Micro Cube (Elementar, Germany). Elemental contents of P, S, Si, B, Ca, Na, Al, Fe, K, Mg, Zn, Cu, Mn, Ba, Ni, Cr, Co, Li, Sr, V, and Pb were determined using inductively coupled plasma optical emission spectrometer (ICP-OES, Optima 8000DV, PerkinElmer, USA).

2.2. DNA Extraction, Polymerase Chain Reaction Amplification, and Sequencing

DNA was extracted from the sediment samples (0.5 g of each sample) using the FastDNA® Spin kit for soil (MP Biomedicals, USA). The environmental DNA was then used as polymerase chain reaction (PCR) template, and bacterial 16S rRNA genes were amplified using primers 967F (5′-CAACGCGAAGAACCTTACC-3′) and 1046R (5′-CGACAGCCATGCANCACCT-3′) targeting at the V6 hypervariable region (Sogin et al., 2006). PCR amplification was performed in 50-μl reaction volume containing 5 μl of 10 × reaction buffer, 1.5 μl of 10 mM dNTP, 1 μl of 10 μM each primer, 2 μl of template, and 1 μl of 5 U/μl Pfx50™ DNA polymerase (Invitrogen, USA), supplemented with double-distilled water. Thirty cycles of amplification were carried...
out under the following conditions: denaturation at 94°C for 15 s, annealing at 57°C for 30 s, and elongation at 68°C for 30 s. The quality and quantity of the genomic DNA were determined by 2% agarose gel electrophoresis with DL2000 DNA marker (TaKaRa, China) and by a Qubit® fluorometer (Invitrogen, USA) with Qubit dsDNA BR Assay kit (Invitrogen, USA). The barcoding, sequencing, and quality assurance processes of PCR products were performed at the Beijing Genome Institute (BGI, Shenzhen). The sequencing was performed using Solexa paired-end sequencing technology (HiSeq2000 system, Illumina, USA). The sequencing data have been deposited at NCBI Sequence Read Archive under accession number SRR7888608-SRR7888615.

2.3. Sequence and Statistical Analysis
Sequences analysis was performed by QIIME v1.8.0 software package (Caporaso, Kuczynski, et al., 2010). Sequences were clustered into operational taxonomic units (OTUs) at 97% sequence identity with uclust.

Figure 2. Concentrations of geochemical elements measured in sediment samples collected from the top and the base of the Caiwei Seamount. The differences in concentration between the top and the base are all significant ($p$-values $< 0.05$; $t$ test). The error bar represents standard deviation.
OTUs were aligned to full-length 16S rDNA sequences with PyNAST (Caporaso, Bittinger, et al., 2010) and assigned taxonomy with uclust (Edgar, 2010). Species diversity, richness, and rarefaction curves were conducted with a step size of 500 and 10 repetitions at each step. Beta diversity was analyzed with 90,330 sequences per sample, which is the smallest library.

The weighted UniFrac metric was computed to quantify the relatedness of OTUs retrieved from the top and the base of the seamount, and the results were displayed by the principal coordinate analysis (Lozupone et al., 2006). The similarity percentage (SIMPER, Primer 6) analysis was used to determine the sequences that mostly contributed to community dissimilarity between top and base samples of the seamount (Hamdan et al., 2013). Individual t test run in R (R Development Core Team, 2011) was used to test the statistical significance of spatial differences in geochemical measurements and bacterial abundances between top and base samples of the seamount. Principal component analysis (PCA) and redundancy analysis (RDA) were applied to detect the similarity of environmental conditions among stations and correlations between bacterial distribution and environmental variables, respectively (Canoco 5.1; Ter Braak & Šmilauer, 2012).

3. Results

3.1. Physical and Geochemical Characteristics in Seawaters and Sediments

The hydrochemical characteristics in surrounding seawaters of the top and the base of the seamount were similar (i.e., salinity, pH, and concentrations of ammonia, nitrite, nitrate, and phosphate) except temperature and DO (Table S2). Temperature was higher in seawater overlying the top of the seamount, while DO concentrations were in an opposite trend (Table S2). Concentrations of the major geochemical elements were in a similar range in samples collected from the same region (top or base of the Caiwei Seamount), but significantly different between samples collected from two regions (t test, p < 0.01; Figure 2). The sediments from the base contained higher concentrations of metal elements (i.e., Fe, Mn, Al, and Mg) but lower in Si, Sr, and Ca (Figure 2). TIC and TIN were the major components of TC (99.80 ± 0.38%) and TN (95.40 ± 1.77%) in sediments at the top, respectively, while TOC and TON occupied greater proportions of TC (75.40 ± 3.69%) and TN (92.30 ± 5.92%) at the base, respectively. Samples were well explained by variations in physicochemical parameters of the sediment (Figure 3a) as well as the seawater listed in Table S2 (Figure 3b) by PCA analysis.

3.2. Bacterial Diversity

A total of 727,879 sequences were retrieved from eight samples and clustered into 32,844 OTUs (0.03 cut-off). The number of sequences of each station (90,985 ± 629) was similar, but that of OTUs ranged from 6,000 to 10,859 (Table 1). According to rarefaction analysis and Chao 1 statistic often used to estimate the depth of coverage by sequencing, bacteria communities were under sequenced by 41–64% in samples (Figure 4 and Table 1). The Chao 1 indices were not statistically different between top and base stations (t test, p = 0.71), but two top stations MAMC02 and MAMC03 as well as one base station MAMC06, located at the northern and eastern sides of the seamount, had relatively higher Chao 1 indices in comparison to those in sedimentary samples collected from the southern part of the seamount (MAMC01 and MABC02; Table 1). It indicated that the northern part of the seamount potentially harbored more OTUs than the south. Shannon and Simpson indices were averagely greater in samples from the top of the seamount (t test, p < 0.01; Table 1), suggesting higher bacterial diversity and evenness in sediments from the top of the seamount.

3.3. Phylogenetic Composition

Of total obtained bacterial sequences, Proteobacteria dominated the bacterial communities in all sediment samples (top: 57.4 ± 1.1%, base: 54.3 ± 2.7%) followed by Acidobacteria (top: 11.5 ± 0.6%, base: 7.7 ± 0.4%) and Gemmatimonadetes (top: 7.2 ± 0.5%, base: 9.4 ± 0.4%) in top and base sediments, respectively. The phylum Chloroflexi also occupied a greater proportion in base sediments (9.1 ± 1.7%) than in the top (2.9 ± 0.4%; t test, p = 0.001; Figure 5 and Table 2). The rest of phylotypes were scattering over a broad taxonomic distribution including Planctomycetes, Nitrospirae, Actinobacteria, the division NC10, and Bacteroidetes (>1% at least at one location). All these dominating bacterial groups occupied approximately 96.7% and 94.8% of total
retrieved bacterial sequences from the top and base sediments, respectively (Figure 5). Other phyla, which are more than 0.1% but less than 1% of total retrieved bacterial sequences, are listed in Table S3. Gammaproteobacteria were the dominant taxa within the phylum of Proteobacteria in all samples (top: 26.0 ± 1.2%, base: 28.9 ± 1.5%; t test, p = 0.04) and were mostly represented by the order Thiotrichales constituting 11.3 ± 0.5% and 19.2 ± 1.2% of total sequences in top and base sediments, respectively (t test, p < 0.001; Table 2). More than 98% of the sequences of Thiotrichales were classified into the Piscirickettsiaceae family, which includes several genera of S-oxidizing chemolithoautotrophs (Barco et al., 2017; Zhang et al., 2017). The order Chromatiales, also called the purple sulfur bacteria capable of photosynthesis using sulfide, thiosulfate, H$_2$, or NO$_2$ etc. as the electron donor under anaerobic or microaerophilic conditions (Hunter et al., 2009), was the secondly most abundant group of Gammaproteobacteria and represented 6.5 ± 0.8% and 3.1 ± 0.3% of the retrieved sequences at the top and the base, respectively (t test, p < 0.001; Table 2). Deltaproteobacteria, Alphaproteobacteria, and Betaproteobacteria in the phylum Proteobacteria were also relatively abundant (>1% of total sequences), but only Deltaproteobacteria showed a greater proportion on the top (16.44 ± 1.10%; t test, p < 0.001) and were mostly related to the candidate division NB1-j and the order Syntrophobacteriales (Table 2). Deltaproteobacteria are usually related to sulfate reduction in anoxic environments (López-García et al., 2003; Ye et al., 2016). The order Rhodospirillales, almost 100% composed of the family Rhodospirillaceae, occurred abundantly at both locations, amounting to more than half abundance of Alphaproteobacteria (Table 2). Rhodospirillaceae has also been reported to function as a sulfur-oxidizer (Zhang et al., 2017). The proportion of Betaproteobacteria was relatively minor compared to Gammabacteria, Deltabacteria, and Alphaproteobacteria, of which the order Burkholderiales were the major members in sediments from top stations (>1%; Table 2). Although numbers of Nitrosomonadales in the class Betaproteobacteria were in a small proportion (<1%), the family Nitrosomonadaceae recognized as major ammonia oxidizers was found to be one of important identified family members at the base (Purkhold et al., 2003; 0.99 ± 0.07%; t test, p < 0.001). The nitrite-oxidizing Nitrospiraceae in the order Nitrospirales represented almost all generated Nitrospira sequences and became a major group in sediments from the top (1.67 ± 0.23%; t test, p < 0.001). With the cutoff of 0.1, only 2.6% and 2.3% of total sequences on average were grouped to known genera on the top and the base, respectively.
3.4. Bacterial Community Structure

The abundance-weighted UniFrac analysis using the principal coordinate analysis separated samples into two distinct communities with the bacterial groups from the same region (top or base) clustering together on the axis of PC1 (76.7%; Figure 6). Proportions of OTUs shared by top and base stations (26.6 ± 4.4%) of the seamount were lower than those of unique OTUs they owned, while samples collected at the same region tend to share more OTUs (top 45.6 ± 8.1%, base 40.3 ± 3.7%; Table 3). Permutational multivariate analysis of variance analysis showed that bacterial community composition was significantly different between top and base regions at OTU level ($p = 0.036$, $r^2 = 0.739$).

SIMPER analysis revealed that major bacterial groups (% of total reads > 1%) had different contributions to the dissimilarity of the bacterial community structure between top and base stations if considering their abundances and compositions (Table S4). Three OTUs belonging to the family Piscirickettsiaceae of the order Thiotrichales (denovo28753, denovo16605, and denovo4356) and one OTU classified into the order Chromatiales in Gammaproteobacteria (denovo16603) contributed to a total of 11.4% of the dissimilarity, in which the former had greater abundances in samples from the base while the latter had a higher number of sequences in samples from the top sediments (Table S4). Two OTUs belong to the family Rhodospirillaceae in the order Rhodospirillales of Alphaproteobacteria (denovo20286 and denovo17655), one OTU identified to the family Syntrophobacteraceae in the order Syntrophobacterales and NB1-j in Deltaproteobacteria (denovo12887), and two OTUs from Acidobacteria (denovo2989 and denovo6417) added the total contribution up to ~20% of the dissimilarity subsequently (Table S4).

3.5. Correlations Between Bacterial Community and Environmental Variables

The RDA analysis showed that the bacterial groups were well divided into two clusters (top and base) by environmental factors on the axis of RDA 1, which explained 79.2% of variations. The axis of RDA 2 increased the explained variation to 90.7% (Figure 7). BPC015 and Sva0725 in Acidobacteria, CL500-15 in Planctomycetes, Chromatiales in Gammaproteobacteria, Syntrophobacterales and NB1-j in Deltaproteobacteria, and Nitrospirales in Nitrospira were intensely associated with TIC (%) and concentrations of Ca and Si (mg/g). Similarly, the bacterial groups with higher weights at the base of the seamount, including Thiotrichales in Gammaproteobacteria, Sva0853 in Deltaproteobacteria, Rhodobacterales in Alphaproteobacteria, B110 in Acidobacteria, CCM11a in Planctomycetes, Acidimicrobiales in Actinobacteria, and SAR202 in Chloroflexi, were clustered with depth and the environmental factors that were greater at the base (e.g., TOC, TON, Fe, Mn, S, and P; Figure 7). Other metal or ions (e.g., Cu, Zn, Mg, and Na) were strongly correlated with the selected factors, thus were not included in the analysis. Variabilities in Pseudomonadales in Gammaproteobacteria, Burkholderiales in Betaproteobacteria, and Rhodospirillales in Alphaproteobacteria among stations were not significantly explained by environmental variables, the proportions of which were consistent in samples collected from the top and the base of the seamount.
4. Discussions

4.1. Factors Influencing Patterns of Bacterial Community Composition and Structure

Increasing studies have shown that microbial community composition and structure can be relatively consistent in similar marine environments even though the distance was thousands of kilometers away or heterogeneous in environments with different characteristics but only in a few tens of kilometers (Agogué et al., 2011; Hewson et al., 2007; Inagaki et al., 2006; Walsh et al., 2015). In this study, PCA analysis showed that sampling stations were highly divided into two categories (top and base) by environmental variables collected from surrounding waters and sediments (Figure 3), indicating environmental homogeneity at the top or the base but great varieties between two regions. Consistently, bacterial community structure showed similar pattern (Figures 5 and 6), supporting a tight association between bacterial community and environmental variation.

Besides the effect of physiochemical characteristics, patterns of bacterial community composition and structure in sediments could also be influenced by fast bacteria dispersal near seafloor, which transit through
water along the route of the fluid flow, contributing to the similarity of bacterial community composition and structure within the same region (Hamdan et al., 2013; Schauer et al., 2010). In an idealized model, the incoming flow over the seamount is separated, creating a circulation around the seamount and forming eddies or wakes at the lee side in a stratified ocean (Chapman & Haidvogel, 1992). The dynamics is even more complex when the incoming flow is oscillating (i.e., tidal current). The interaction between internal wave and bathymetry will potentially cause the reflection of internal waves or the generation of the internal tide (Gilbert & Garrett, 1989), accompanied by strong turbulent mixing. Measurements of turbulent kinetic energy near a shallow seamount show 100 to 10,000 times larger than regions far away from seamount areas (Lueck & Mudge, 1997). Nevertheless, majority of the flow near seamounts tends to follow the isobath despite of localized enhanced turbulent mixing regions. At the region of the Caiwei Seamount, the

### Table 2

| Taxonomy                          | Top Mean ± SD | Base Mean ± SD | p-value  |
|-----------------------------------|---------------|---------------|----------|
| Gammaproteobacteria               | 26.0 ± 1.18   | 28.9 ± 1.48   | 0.041    |
| Thiotrichales                     | 11.3 ± 0.50   | 19.2 ± 1.23   | 0.000    |
| Chromatiales                      | 6.52 ± 0.81   | 3.07 ± 0.27   | 0.000    |
| Pseudomonadales                   | 1.28 ± 0.98   | 1.00 ± 0.47   | 0.676    |
| Deltaproteobacteria               | 16.4 ± 1.06   | 10.4 ± 0.96   | 0.000    |
| NB1-j                             | 7.64 ± 0.45   | 3.89 ± 0.10   | 0.000    |
| Syntrophobacterales               | 6.33 ± 1.09   | 3.13 ± 0.73   | 0.005    |
| Sva0853                           | 0.47 ± 0.07   | 1.50 ± 0.21   | 0.000    |
| Alphaproteobacteria               | 12.4 ± 1.70   | 13.7 ± 2.6    | 0.493    |
| Rhodospirillales                  | 6.24 ± 1.62   | 8.28 ± 2.25   | 0.250    |
| Rhodobacterales                   | 0.85 ± 0.08   | 1.46 ± 0.36   | 0.028    |
| Betaproteobacteria                | 2.14 ± 0.88   | 1.21 ± 0.08   | 0.122    |
| Burkholderiales                   | 1.14 ± 0.97   | 0.18 ± 0.07   | 0.139    |
| Acidobacteria                     | 11.5 ± 0.58   | 7.66 ± 0.41   | 0.000    |
| Acidobacteria-6                   | 2.65 ± 0.08   | 1.12 ± 0.11   | 0.000    |
| BFC015                            | 1.66 ± 0.13   | 0.66 ± 0.07   | 0.000    |
| RB25                             | 2.34 ± 0.20   | 0.83 ± 0.06   | 0.000    |
| Sva0725                           | 2.26 ± 0.44   | 0.37 ± 0.10   | 0.000    |
| BPC102                           | 1.42 ± 0.19   | 2.26 ± 0.45   | 0.025    |
| B110                             | 1.42 ± 0.19   | 2.26 ± 0.45   | 0.024    |
| Solibacteres                      | 1.03 ± 0.27   | 0.23 ± 0.07   | 0.003    |
| Gemmatimonadetes                  | 7.22 ± 0.49   | 9.44 ± 0.44   | 0.001    |
| Gemm-2                            | 4.09 ± 0.39   | 3.71 ± 0.27   | 0.213    |
| Gemm-1                            | 1.95 ± 0.08   | 4.60 ± 0.47   | 0.000    |
| Chloroflexi                       | 2.92 ± 0.36   | 9.12 ± 1.72   | 0.001    |
| SAR202                            | 2.06 ± 0.26   | 4.63 ± 1.20   | 0.011    |
| S085                             | 0.26 ± 0.05   | 3.87 ± 1.12   | 0.001    |
| Planctomycetes                    | 3.37 ± 0.37   | 3.16 ± 0.19   | 0.399    |
| OM-190                            | 1.62 ± 0.21   | 0.71 ± 0.15   | 0.001    |
| CL500-15                          | 1.06 ± 0.13   | 0.51 ± 0.13   | 0.002    |
| Physicisphaerae                   | 0.69 ± 0.16   | 2.01 ± 0.15   | 0.000    |
| CCM11a                            | 0.42 ± 0.09   | 1.11 ± 0.08   | 0.000    |
| Nitrospirae                       | 1.69 ± 0.22   | 0.59 ± 0.09   | 0.000    |
| Nitrosiwa                         | 1.69 ± 0.22   | 0.59 ± 0.09   | 0.000    |
| Nitrospirales                     | 1.69 ± 0.22   | 0.59 ± 0.09   | 0.000    |
| Actinobacteria                    | 1.40 ± 0.33   | 1.83 ± 0.31   | 0.146    |
| Acidimicrobia                     | 1.05 ± 0.32   | 1.55 ± 0.30   | 0.095    |
| Acidimicrobiales                  | 1.05 ± 0.32   | 1.55 ± 0.30   | 0.095    |
| NC10                              | 1.27 ± 0.29   | 0.13 ± 0.03   | 0.001    |
| wb1-A12                           | 1.27 ± 0.29   | 0.13 ± 0.03   | 0.001    |
| Bacteroidetes                     | 1.00 ± 0.31   | 1.64 ± 0.18   | 0.023    |

Note. The mean was calculated by averaging data from four stations on the top and the base, respectively. The p-values were calculated by t test. Higher values are in bold.

Abbreviation: SD, standard deviation.
northeast trade winds drive the westward surface current all year round from surface to 4,000 m. According to the data collected with current meter (Seaguard RCM) and ADCP (WHLR75kHz) deployed at nine sites surrounding the seamount, a huge anticyclonic eddy cycling around the seamount was detected (Figure 8). The anticyclonic eddy was averagely stronger at the depth of approximately 1,000 m, right

Figure 6. Weighted UniFrac distances for sediment operational taxonomic units data retrieved from the top (blue dot) and the base (red square) of the Caiwei Seamount. The results are displayed by the principal coordinate analysis (Lozupone et al., 2006).

Table 3

| Station   | Top      | Base      | Top      | Base      |
|-----------|----------|-----------|----------|-----------|
| MAMC01    | 6,168 (100) | 3,544 (100) | 3,326 (36) | 3,305 (44) |
| MAMC02    | 3,544 (58) | 10,895 (100) | 4,250 (46) | 3,943 (53) |
| MAMC03    | 3,326 (54) | 4,250 (39) | 9,222 (100) | 3,978 (53) |
| MAMC04    | 3,305 (54) | 3,943 (36) | 3,978 (43) | 7,499 (100) |
| Base      | MABC02   | 1,829 (30) | 2,292 (21) | 2,095 (23) | 2,002 (27) | 6,000 (100) | 2,852 (36) | 2,549 (38) | 2,737 (37) |
| MAMC06    | 1,803 (29) | 2,465 (23) | 2,148 (23) | 1,967 (26) | 2,852 (48) | 7,999 (100) | 2,818 (42) | 3,125 (43) |
| MABC06    | 1,560 (25) | 2,017 (19) | 1,838 (20) | 1,709 (23) | 2,549 (43) | 2,818 (35) | 6,688 (100) | 2,728 (37) |
| MAMC08    | 1,810 (29) | 2,401 (22) | 2,153 (23) | 1,969 (26) | 2,737 (46) | 3,125 (39) | 2,728 (41) | 7,345 (100) |

Note. Numbers in the brackets are the percentages (%) of shared OTUs in total numbers of OTUs in samples of the stations on the top row. The gray-shaded areas are the comparisons between the same sample, used for differentiating from those between different samples. Abbreviation: OTUs, operational taxonomic units.
above the top layer of the seamount, driving the clockwise current transport on the top of the seamount (average current velocity: 7.7–10.1 cm/s; Figure 8). It may potentially enhance the bacterial transit and sinking. Similarly, at the base of the seamount, although the seamount seems acting as a barrier among stations, the clockwise flow cycled around the seamount (average current velocity: 2.8–5.0 cm/s; Figure 8), still being able to drive bacterial dispersal and potentially contributing to the similarity of

Figure 7. Correlations between bacterial groups and environmental factors in samples collected from sediments of the top and the base of the Caiwei Seamount by redundancy analysis (RDA).

Figure 8. The time-averaged observed bottom current vector of the Caiwei Seamount by nine bottom mounted mooring stations (15 m above the bottom). An anticyclonic circulation around the seamount was detected.
bacterial community composition and structure along the circulation of the seamount. Overall, it is concluded that the bacterial community composition and structure in a guyot may be coinfluenced by physico-chemical variables and unique physical dynamics.

4.2. Interaction Between Bacterial Community and Environmental Gradients

Although the richness of bacterial communities was similar in two regions, the significant difference in diversity and evenness indicated the compositional and physiological heterogeneity between the top and the base of the seamount (Dang & Lovell, 2016; Kato et al., 2018). Based on the assigned taxonomy of the bacterial community by 16S rRNA genes in this study, the potential physiological and metabolic features of bacteria were found relating to environmental gradients in the Caiwei Seamount.

The abundance and metabolic features of bacteria in marine sediments are related to the organic contents and oxidation-reduction potentials (Zobell, 1955). Usually, oxygen in the sediment is depleted rapidly from the surface. Zonation of microbial community and activity rely on the type and the availability of electron donors and acceptors, which have been intensely studied in dark environments (Orcutt et al., 2011). In the Caiwei Seamount, oxygen and nutrient concentrations were measured through the water column of the guyot (Figure S1). The oxygen concentration was found lowest at ~1,000 m, above the top of the seamount (Figures S1a, S1c, and S1e). The cooccurrence of the phosphate peak and lowest pH at the same depth suggests a rapid degradation of organic matter by microbes (Figure S1). Consequently, the reduced gradient of oxygen in seawater near the top inhibits the diffusion of oxygen from the sediment surface to the deeper depth and a relatively reduced environment is formed in a shallower depth of the sediment. Other electron acceptors, such as NO$_3^-$, Fe$^{3+}$, Mn$^{4+}$, and SO$_4^{2-}$, may be subsequently reduced and play more important roles in the acquisition of carbon and energy by microorganisms (Reimers et al., 2013). Moreover, a greater proportion of Deltaproteobacteria related to sulfate reduction (e.g., NB1-j) and syntrophic sulfate reduction (Syntrophobacteales) were detected at the same layer, an indicator of low or depleted oxygen in the sediment (Baumgartner et al., 2006; Orcutt et al., 2011).

In comparison, at the base of the Caiwei Seamount, DO concentrations in surrounding seawater were almost 2 times greater than those measured near the top of the seamount (Table S2), possibly a result of slow decomposition of recalcitrant organic matter accumulated on the base after a long sinking process (Kallmeyer et al., 2012). The elevated oxygen gradients enhanced the diffusion of oxygen to the deeper depth of the sediment and affected the microniches in the sediments (D’Hondt et al., 2009). Oxidized forms of Fe and Mn were much more abundant at the base (Figure 2), which can be formed by abiotic kinetics under aerobic conditions or by microbial oxidation of reduced iron and manganese compounds (Emerson & Moyer, 2002; Orcutt et al., 2011; Schippers & Jørgensen, 2002). However, in the sediment collected from the top 5-cm layer, bacteria reported that were mostly affiliated to iron oxidation in marine environments were not detected, such as *Mariprofundus ferrooxydans* in Zetaproteobacteria (Emerson et al., 2007) and *Leptothrix* spp. in Betaproteobacteria (Hedrich et al., 2011). This could be the bias of sampling depth. Decreased proportion of sulfate-reducing Deltaproteobacteria and increased S-oxidizing Gammaproteobacteria both reflected the reduction of the redox potentials as a result of increased oxygen. The presence of the phylum *Chloroflexi* related to the decomposition of the refractory organic compounds is an evidence of greater proportions of recalcitrant organic matter (Landry et al., 2017), reducing decomposition rate and oxygen consumption. Substrates for S-oxidizing bacteria at the base of the seamount may be a variety of sources, such as elemental S (S$_0$), organosulfur, pyrite (FeS$_2$), and Chalcopryte (CuS). The SAR202 cluster belonging to this phylum has been recently found metabolizing several organosulfur compounds, being a sulfite-oxidizer and important in sulfur turnover in the dark ocean (Mehrshad et al., 2017). Due to the accumulation of complex and refractory organic matter that may reduce the efficiency of energy acquisition by bacteria in base sediments of the seamount, and considering similar bacterial richness between the top and the base of the seamount, there must be energy sources to compensate. Nitahara et al. (2011) has reported that chemolithotrophs are the major energy sources for sustaining the microbial ecosystem on the Mn crust, where both degradation of organic compounds by anaerobes and fermenters would be limited. S-oxidizing bacteria have been recognized as one group of major primary producers in benthic environments, supporting heterotrophic bacteria and benthic organisms (Ye et al., 2016). Moreover, OTUs classified as ammonia-oxidizing chemolithoautotrophic bacterium *Nitrosospira* in the Betaproteobacteria were also detected within sediment samples from the base of the seamount. Although ammonia-oxidizing
Thaumarchaeota were not analyzed in this study, they have been reported as the major group of chemoheterotrophs in sediments of similar guyot environment in northwest Pacific Ocean (Kato et al., 2018; Nitahara et al., 2011, 2017). Therefore, the domination of sulfur-oxidizing bacteria and ammonia-oxidizing microbes at the base of the seamount may play vital roles in food and energy supply.

4.3. Comparison of Bacterial Community on Guyots to Other Seafloor Environments

The bacterial community composition in sediments of the Caiwei Seamount is similar to that in abyssal environment enriched with polymetallic nodules and other guyots that have been explored in Pacific Ocean (Kato et al., 2018; Liao et al., 2011; Lindh et al., 2017; Nitahara et al., 2011, 2017; Shulse et al., 2016), but had key difference from active seamount environments (López-García et al., 2003; Moyer et al., 1995; Scott et al., 2017; Teske et al., 2002). The family Piscirickettsiaceae and the order Chromatiales in Gammaproteobacteria, the family Rhodospirillales in Alphaproteobacteria, Chloroflexi and Deltaproteobacteria found in the Caiwei Seamount are also the common groups in deep-sea surface sediment as well as at seafloor with polymetallic nodule, even with similar relative abundances in the samples (Shulse et al., 2016). Although we did not sequence archaean 16S rRNA in this study, as removing sequence contamination from total bacterial sequences, we found that about 75% of detected archaean sequences were identified to be Thaumarchaeota (data not shown), similar to results from the seafloor and seamount in Pacific Ocean (Kato et al., 2018; Nitahara et al., 2011, 2017; Zinke et al., 2018). It is believed that Thaumarchaeota could be the key group in the Caiwei Seamount and play an important role in guyot ecosystem. It needs to be investigated in future studies.

Two ubiquitous groups Zetaproteobacteria and Epsilonproteobacteria in hydrothermal vents were not retrieved from any sequence pool of the Caiwei Seamount in this study. Iron-oxidizing bacteria Zetaproteobacteria have been mostly described as “gradient organisms” because they tend to colonize at the interface between aerobic and anoxic zones (Hedrich et al., 2011). Thus, the nondetection of Zetaproteobacteria in the Caiwei Seamount could be due to lower surrounding temperature and chemical gradient at the interface between sediment and water column (Scott et al., 2017). The presence of Epsilonproteobacteria usually related to the oxidation of hydrogen sulfide in deep-sea sediments where vents surround and the hydrogen sulfide is abundantly supplied (López-García et al., 2003). In sediment environments of the Caiwei Seamount, the redox potentials may not be low to the level with rapid and plenty supply of hydrogen sulfide by sulfate-reducers as the sources to support the growth of Epsilonproteobacteria. Different from hydrothermal system, bacterial communities in the Caiwei Seamount are dominated by the sulfur-cycle associated groups commonly existing on the surface of oligotrophic oceanic sediments.

5. Conclusions

Currently, there are only a few studies on microbial community in seamounts located in the northwest Pacific Ocean, but most focused on communities in niches associated with Fe-Mn crusts. In this study, we investigated bacterial community compositions and structures from locations featured by different environmental characteristics in order to understand the diversity of microniches, microorganisms, and metabolic potentials in a guyot ecosystem. Our results indicate that the bacterial community structures and compositions are similar in sediments from the same region (top or base of the seamount) but different between two regions, highly associated with the depth and environmental variables, such as DO concentrations, elemental densities, and availabilities of organic matter. The homogeneity of microniches and bacterial communities at the same depth of the Caiwei Seamount suggests a key effect of physical dynamics on guyot environment and biological community, while heterogeneous patterns vertically emphasize the important of physicochemical characteristics on the formation of bacterial niches. Bacterial metabolic potentials inferred from bacterial community compositions also suggest a strong interaction between microbial modification and environmental impact.

More than 90% of OTUs were not assigned to genus level, indicating that a large proportion of unknown species, diversity, and hidden functions in guyot ecosystem need to be explored in future. As we are working on isolating new species through culture methods, we will apply metagenomic analysis on guyot samples to reveal unknown genetic diversity and functions, increasing sequencing resolution to identify key species as well as their spatio-temporal variations in guyot ecosystem.
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