

# Bacterial community of sediments from the Australian-Antarctic ridge

Yung Mi Lee · Doshik Hahm · You-Jung Jung ·  
Sung Hyun Park · Jongsik Chun · Soon Gyu Hong

Received: 25 October 2013 / Revised: 3 February 2014 / Accepted: 4 February 2014 / Published online: 27 February 2014  
© Springer-Verlag Berlin Heidelberg 2014

**Abstract** Benthic bacterial communities in the ocean comprise the vast majority of prokaryotes on Earth and play crucial roles in the biogeochemical cycles and remineralization of organic matter. Despite the importance of the benthic bacterial communities in the ecosystem, no previous investigations of the bacterial community of sediments from the Australian-Antarctic ridge (AAR) have been conducted to date. In this study, the composition of the bacterial community in the surface sediments from AAR was revealed by the 454 pyrosequencing method. Bacterial communities inhabiting the sediments of AAR were highly diverse, covering 39 distinct major lineages of bacteria. Among them, Gammaproteobacteria, Planctomycetes, Actinobacteria, Deltaproteobacteria, Acidobacteria,

Alphaproteobacteria, Chloroflexi, Bacteroidetes, Chlorobi, and Gemmatimonadetes were dominant, accounting for 85–88 % of the bacterial community. The 16S rDNA sequences of major OTUs with 1 % or higher relative abundance showed high similarity (96.6–100 %) with uncultured environmental sequences that were primarily recovered from the sediments of various areas of the Arctic, Southern, Atlantic, Indian, and Pacific Oceans. As the first report of the bacterial community of marine sediments in the AAR region, the results presented herein suggest that members of the predominant phyla are well adapted to the environment of marine sediment and that the low variability in the bacterial communities of deep-sea sediments might reflect the similar environmental conditions among various regions of the deep sea.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00300-014-1467-0) contains supplementary material, which is available to authorized users.

Y. M. Lee · Y.-J. Jung · S. G. Hong (✉)  
Division of Polar Life Sciences, Korea Polar Research Institute,  
26 Songdomirae-ro, Yeonsu-gu, Incheon 406-840,  
Republic of Korea  
e-mail: polypore@kopri.re.kr

Y. M. Lee · J. Chun  
School of Biological Sciences, College of Natural Science, Seoul  
National University, 599 Gwanak-ro, Gwanak-gu,  
Seoul 151-747, Republic of Korea

D. Hahm  
Division of Polar Ocean Environment, Korea Polar Research  
Institute, 26 Songdomirae-ro, Yeonsu-gu, Incheon 406-840,  
Republic of Korea

S. H. Park  
Division of Polar Earth-System Sciences, Korea Polar Research  
Institute, 26 Songdomirae-ro, Yeonsu-gu, Incheon 406-840,  
Republic of Korea

**Keywords** Bacterial community · Sediment ·  
Pyrosequencing · Australian-Antarctic ridge

## Introduction

Benthic microbial communities in the ocean play significant roles in the biogeochemical cycles and remineralization of organic materials (Ravenschlag et al. 2001; Li et al. 2009). In addition, it has been reported that the fraction of bacteria in the deep sub-seafloor biosphere may comprise one-tenth to one-third of the Earth's total biomass and approximately 70 % of the global prokaryotic biomass (Whitman et al. 1998; Li et al. 2009). As a result, bacterial communities in benthic environments are an important component of the food web as well as biochemical functioning. Accordingly, understanding the microbial community structures in benthic ecosystems is an important first step in understanding benthic ecosystem processes and

**Table 1** Description of sampling site and SSU rRNA tag characteristics

Sample ID	Location	Depth (m)	Summary or SSU rRNA		Diversity indices			
			Reads	No. of OTUs	Chao1	ACE	Shannon	Simpson
KRR1-RC12-S	59°56.4966'S/153°09.3963'E	2,479	1060	450	1,100	1,758	0.92	0.35
KRR1-RC14-S	60°05.1015'S/152°26.1822'E	2,359	1340	425	1,038	1,571	0.87	0.16

the roles that benthic bacteria play in overall oceanic processes (Li et al. 2009).

Investigations of benthic microorganisms have been conducted in the Arctic, Southern, Atlantic, Indian, and Pacific Oceans by culture-based or molecular approaches such as denaturing gradient gel electrophoresis (DGGE), fluorescence in situ hybridization (FISH), terminal restriction fragment length polymorphism (T-RFLP), 16S rRNA gene clone library analysis, and high-throughput sequencing methods (Vetriani et al. 1999; Ravensschlag et al. 2001; Bowman and McCuaig 2003; Luna et al. 2004; Polymenakou et al. 2005; Li et al. 2009; Schauer et al. 2010; Yu et al. 2010). These studies revealed a high diversity in microbial compositions and bacterial communities are correlated with organic carbon contents and inorganic ion concentration (Jørgensen et al. 2013; Ruff et al. 2013). In addition, biogeographical analysis revealed that some phylotypes were common in the Atlantic, Pacific, Antarctic, and Arctic Oceans sediments indicating that some species disperse effectively over a huge distance and therefore are cosmopolitan (Schauer et al. 2010; Zinger et al. 2011).

The Australian-Antarctic ridge (AAR), which is the easternmost portion of the Southeast Indian Ridge, is the largest unexplored expanse of the global mid-ocean ridge system. To the best of our knowledge, no previous studies of the geology, oceanography, or biology of the AAR region have been conducted. Here, we report the bacterial community structure from two sediment samples obtained through an expedition in the AAR region between 150°E and 160°E from March 2 to March 9, 2011.

## Materials and methods

### Sampling

Sediments were entrapped in the metal cups of a rock corer (Bender et al. 1992) when it hits the basement, after which the cups were sealed with vaseline placed in the head of metal cups. Sediment samples were then recovered from two sites 43.2 km apart from each other and 2,400 m deep (Table 1; Fig. 1). The bedrock was mainly composed of basaltic glass and sediment samples were characterized by yellowish beige clay primarily composed of biogenic silica.

Sediment samples were stored at  $-80^{\circ}\text{C}$  until DNA extraction and sequence analysis.

### Bacterial community analysis

Genomic DNA was extracted using a FastDNA SPIN Kit for soil (Q-Biogene, Carlsbad, CA), and the 16S rRNA gene was amplified by PCR using the 27F (Lane 1991) and 518R (Kato et al. 1997) primers with barcodes [primer name: barcode-linker-primer sequence, '27F-P099: TGTC TCAC-AC-AGAGTTTGATCMTGGCTCAG' and '518R-P099: TGTCTCAC-AC-GWATTACCGCGGCKGCTG' for KRR1-RC12-S and '27F-P042: CTCAGAGT-AC-AG AGTTTGATCMTGGCTCAG' and '518R-P042: TGTCT CAC-AC-GWATTACCGCGGCKGCTG' for KRR1-RC 14-S]. Sequencing of the amplicons was carried out by DNalink (Seoul, Korea) using a Roche 454 GS FLX Titanium sequencer. Sequence clustering was performed using TBC (Lee et al. 2012) after trimming and filtering of low quality sequences using the PyroTrimmer software (Oh et al. 2012, <http://pyroTrimmer.kobic.re.kr>). The 3' ends of sequences with low average quality values were trimmed and sequences with ambiguous nucleotides or that were shorter than 300 bp were discarded. Taxonomic affiliation of each cluster was determined by sequence similarity searches against the EzTaxon-e database (Kim et al. 2012). Diversity indices and rarefaction curves were calculated using Mothur (Schloss et al. 2009).

## Results

Processing of raw sequences yielded 1,060 bacterial sequences from KRR1-RC12-S and 1,340 bacterial sequences from KRR1-RC14-S. Bacterial sequences of KRR1-RC12-S and KRR1-RC14-S were clustered into 450 and 425 OTUs, respectively (Table 1). OTU diversity was slightly higher in KRR1-RC12-S than that in KRR1-RC14-S (Table 1). Rarefaction analysis revealed that the plateau levels were not reached in the samples, indicating that further analysis of a larger number of sequences would have revealed additional diversity (Fig. S1).

Taxonomic assignment revealed the presence of 36 and 33 distinct major lineages of bacteria in two sediment

samples (Fig. 2a). Gammaproteobacteria, Planctomycetes, Actinobacteria, Deltaproteobacteria, Acidobacteria, Alphaproteobacteria, Chloroflexi, Bacteroidetes, Chlorobi, and Gemmatimonadetes were the predominant groups, comprising 85–88 % of the bacterial communities (Fig. 2a). Minor bacterial groups included Caldithrix\_p, Cyanobacteria, Elusimicrobia, EU181514\_p, EU245879\_p, EU246057\_p, Fibrobacteres, Firmicutes, GN02, GN04, LD1, Lentisphaerae, Nitrospirae, NKB19, OD1, OP11, OP3, OP8, Betaproteobacteria, DQ499320\_c, Proteobacteria\_uc, SAR406, Thermobaculum\_p, TM6, TM7, Verrucomicrobia, WS3, and WS5. The major order of Gammaproteobacteria was Xanthomonadales, which accounted for 51.3 and 46.3 % of Gammaproteobacteria in KRR1-RC12-S and KRR1-RC14-S, respectively (Fig. 2b). Members of Planctomycetes were primarily assigned to the order Planctomycetales, which accounted for 86.9 and 77.2 % of bacterial communities in KRR1-RC12-S and KRR1-RC14-S, respectively (Fig. 2c). Members of Actinobacteria were mainly assigned to the order EU374107\_o, which comprised 66.4 % of the total bacterial communities in KRR1-RC12-S and 66.0 % of that in KRR1-RC14-S (Fig. 2d).

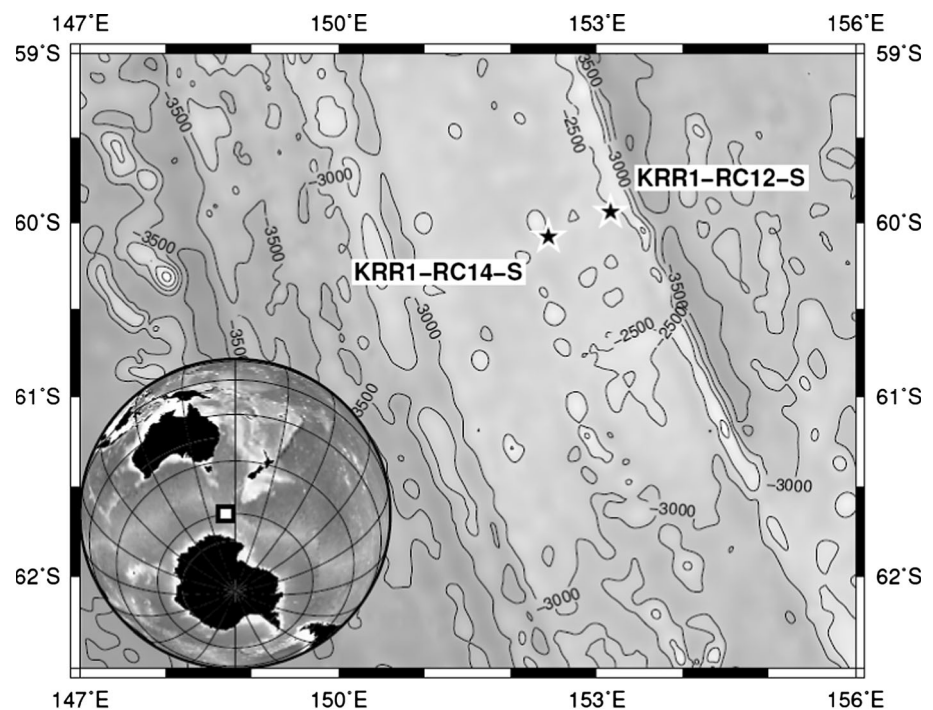
There were 11 and 13 major OTUs with 1 % or higher abundance in KRR1-RC12-S and KRR1-RC14-S (Table 2). An EzTaxon database search ([www.eztaxon.org](http://www.eztaxon.org), Chun et al. 2007) revealed that sequence similarities of the major OTUs to known species ranged between 79.8 and 95.9 %, while they showed high similarity (96.6–100 %) with uncultured environmental sequences in the GenBank database (Table 2). The habitats and geographical origins of the sequences with 97 % or higher sequence similarities to

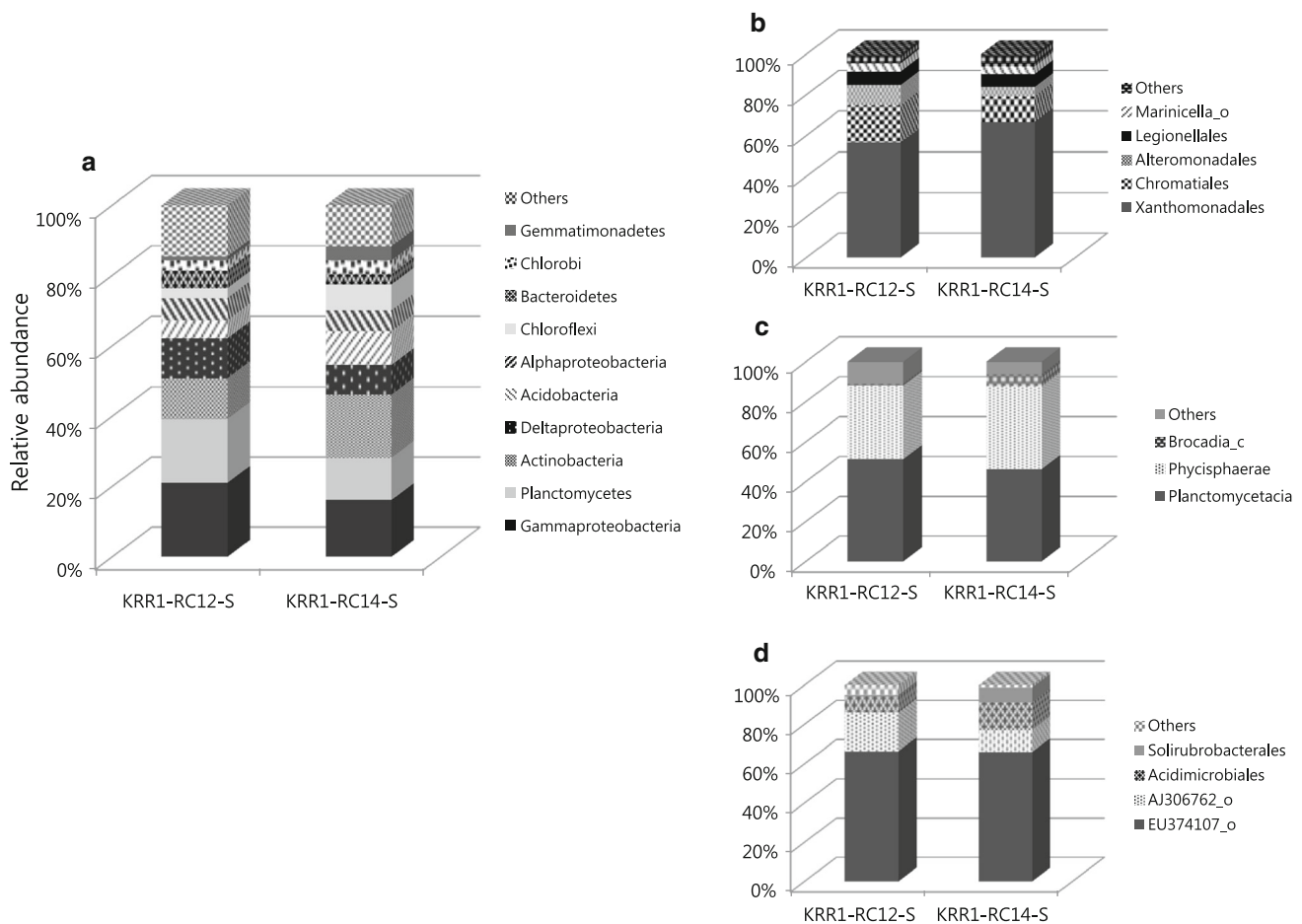
major OTUs were analyzed by a blast search of the GenBank database. The number of sequences that could be grouped with major OTUs ranged from 1 to 207 and included sequences from diverse habitats such as marine sediments, sea floor lava, sea water, deep-sea organisms, fresh water sediments, and soil (Table 2). Among these habitats, marine sediments were the primary source of the major OTUs (Table 2). Most of the major OTUs were widely distributed in the Arctic, Southern, Atlantic, Indian, and Pacific Oceans (Fig. S2a). Some of the major OTUs were recovered from cold-seep or hydrothermal vent environments (Fig. S2b).

## Discussion

The predominant taxa identified in this study, Gammaproteobacteria, Planctomycetes, Actinobacteria, Deltaproteobacteria, Acidobacteria, Alphaproteobacteria, and Bacteroidetes, have also been shown to be dominant in sediments from other areas such as the Arctic Ocean, Antarctic Ocean, Eastern Mediterranean Sea, and North-eastern Pacific Ocean (Bowman and McCuaig 2003; Li et al. 2009; Polymenakou et al. 2009; Kouridaki et al. 2010; Park et al. 2011). These findings may indicate that members of the predominant taxa are well adapted to the surficial layer of deep-sea sediments regardless of geographical location. Furthermore, the low variability of the bacterial communities of deep-sea sediments across geographical locations might reflect the low environmental variation in the deep sea (Zinger et al. 2011).

**Fig. 1** Map showing the sampling sites (black stars). The water depths are indicated in gray shades and contours. The white square in the globe inset represents the study area located between New Zealand and the Antarctica





**Fig. 2** Relative abundance of phylogenetic groups (a) at the phylum or class level in case for Proteobacteria, (b) at the order level for Gammaproteobacteria, (c) at the order level for Planctomycetes, and (d) at the order level for Actinobacteria. \*Others include *Bacteria\_uc*, *Caldithrix\_p*, *Cyanobacteria*, *Elusimicrobia*, *EU181514\_p*,

*EU245879\_p*, *EU246057\_p*, *Fibrobacteres*, *Firmicutes*, *GN02*, *GN04*, *LD1*, *Lentisphaerae*, *Nitrospirae*, *NKB19*, *OD1*, *OP11*, *OP3*, *OP8*, *Betaproteobacteria*, *DQ499320\_c*, *Proteobacteria\_uc*, *SAR406*, *Thermobaculum\_p*, *TM6*, *TM7*, *Verrucomicrobia*, *WS3*, and *WS5*. Taxa names were defined in the EzTaxon-e database (Kim et al. 2012)

Many phylotypes of Gammaproteobacteria are known to be related to free-living and symbiotic sulfur oxidizers (Bowman et al. 2005). Phylotypes related to Planctomycetes are known to catalyze important transformations in global carbon and nitrogen cycles and autotrophic bacteria that are members of Planctomycetales scavenge nitrite via anaerobic ammonium oxidation (Tal et al. 2006; Musat et al. 2010). Phylotypes related to Actinobacteria may play important roles in the decomposition of recalcitrant organic materials in the sea floor (Jensen et al. 2005). Although there is a limitation to infer the ecological roles of the detected bacterial communities because of a large fraction of extracellular DNA concentrations which is co-extracted with the DNA of living cells (Corinaldesi et al. 2011), based on previously known ecological roles of dominant groups, the benthic bacteria of the AAR likely play crucial roles in biogeochemical cycles in this ecosystem.

Major OTUs with 1 % or higher abundance showed low similarities with known species, while they showed high

similarity with uncultured environmental sequences. The discrepancy in similarity search results between described species and uncultured clonal sequences implies that there has been little effort to culture bacterial species from deep-sea environments or that it is difficult to culture these organisms. Because there is such little information regarding deep-sea benthic microorganisms, we attempted to analyze the major habitats from which major OTUs are recovered. The results revealed that the main habitats of major OTUs were marine sediments from the Arctic, Southern, Atlantic, Indian, and Pacific Oceans. These findings imply that major OTUs recovered from AAR sediments are closely related to bacterial species that are globally distributed in marine sediment. Some major OTUs were recovered from cold-seep or hydrothermal vent environments. The miniature autonomous plume record (MAPR) attached to the rock corer revealed increased temperature and turbidity in this area (*unpublished data*), which implies the existence of hydrothermal vents near the

**Table 2** Taxonomic information and habitats of similar sequences with major OTUs

OTU name*	Abundance (%)			Class	Scientific name	Similarity (%)	Accession no.	Origins of environmental sequences†									
	KRR1-RC-12-S	KRR1-RC-14-S	RC-14-S					Total‡	Marine sediment	Seafloor lavas/basalt	Sea water	Deep-sea organisms	Sediment (fresh water)	Cold seep	Hydrothermal chimney	Soil	Others§
OTU_01	2.17	6.49		Actinobacteria	Nitriiruptoridae	<i>Enzeya tangerina</i> F10(T)	85.7	AB478418	81	80	1	#	#	#	#	#	#
OTU_02	3.78	3.58		Actinobacteria	Nitriiruptoridae	<i>Enzeya tangerina</i> F10(T)	85.3	AB478418	47	36	#	3	4	2	#	#	2
OTU_03	1.60	1.42		Actinobacteria	Nitriiruptoridae	<i>Enzeya tangerina</i> F10(T)	85.7	AB478418	17	16	1	#	#	#	#	#	#
OTU_04	0.00	2.09		Actinobacteria	Acidimicrobidae	<i>Aciditerrimonas ferritducens</i> IC-180(T)	85.6	AB517669	51	50	#	#	#	#	#	1	#
OTU_05	2.17	0.90		Proteobacteria	Alphaproteobacteria	<i>Pedomicrobium manganicum</i> ACM 3038(T)	95.9	X97691	132	78	22	#	#	5	#	#	14
OTU_06	0.66	1.04		Proteobacteria	Alphaproteobacteria	<i>Dichotomicrobium themohalophilum</i> DSM 5002(T)	94.0	FR733679	207	49	4	#	#	6	1	#	111
OTU_07	1.23	0.15		Proteobacteria	Deltaproteobacteria	<i>Desulfonema magnum</i> DSM 2077(T)	89.1	U45989	1	1	#	#	#	#	#	#	#
OTU_08	1.23	0.00		Proteobacteria	Deltaproteobacteria	<i>Desulfobacterium indolicum</i> DSM 3383(T)	89.0	AJ237607	4	4	#	#	#	#	#	#	#
OTU_09	0.00	3.66		Proteobacteria	Gammaproteobacteria	<i>Natromocella acetinitritica</i> ANL 6-2(T)	93.7	EF103128	83	81	#	#	1	#	#	1	#
OTU_10	0.94	2.09		Proteobacteria	Gammaproteobacteria	<i>Thioalkalivibrio thiocyanodentrificans</i> ARHD1(T)	92.0	AY360060	142	117	13	2	3	1	1	#	5
OTU_11	2.26	0.90		Proteobacteria	Gammaproteobacteria	<i>Thioalkalivibrio nitratireducens</i> ALEN 2(T)	91.2	AY079010	199	167	13	3	7	#	#	#	1
OTU_12	1.89	0.45		Proteobacteria	Gammaproteobacteria	<i>Thioalkalivibrio thiocyanodentrificans</i> ARHD1(T)	89.9	AY360060	22	18	#	3	#	#	#	1	#
OTU_13	1.04	0.67		Proteobacteria	Gammaproteobacteria	<i>Thioalkalivibrio thiocyanodentrificans</i> ARHD1(T)	92.5	AY360060	119	100	10	2	1	3	#	2	#
OTU_14	1.13	0.07		Proteobacteria	Gammaproteobacteria	<i>Thioalbus dentrificans</i> S4(T)	91.9	EU837269	19	18	#	1	#	#	#	#	#
OTU_15	0.00	1.19		Proteobacteria	Deltaproteobacteria	<i>Desulfonataicus anaerophilicus</i> TeSi(T)	80.3	FJ194951	17	15	#	1	#	#	#	#	1

Table 2 continued

OTU name <sup>#</sup>	Abundance (%)			Class	Phylum	Closest known species*	Similarity (%)	Accession no.	Origins of environmental sequences <sup>†</sup>									
	KRRI-12-S	KRRI-RC-14-S	RC-14-S						Total <sup>‡</sup>	Marine sediment	Sea floor lavas/basalt	Sea water	Deep-sea organisms	Sediment (fresh water)	Cold seep	Hydrothermal chimney	Soil	Others <sup>§</sup>
OTU_16	0.00	1.27		Actinobacteria	Actinobacteridae	<i>Kinoseporia mikantensis</i> NBRC 16234(T)	79.8	AB377117	10	6	4	#	#	#	#	#	#	#
OTU_17	2.45	3.13		Chlorobi	Ignavibacteria	<i>Ignavibacterium album</i> Mat9-16(T)	89.2	AB478415	25	25	#	#	#	#	#	#	#	#
OTU_18	0.00	1.72		Chloroflexi	Anaerolineae	<i>Levilinea saccharolytica</i> KIBI-1(T)	86.1	AB109439	51	49	#	#	#	1	#	#	#	#
OTU_19	0.28	1.12		Planctomycetes	Planctomycetia	<i>Blastopirellula marina</i> DSM 3645(T)	85.1	AANZ01000021	19	12	5	1	0	#	#	#	#	1
OTU_20	0.00	1.04		Gemmatimonadetes	Gemmatimonadetes	<i>Gemmatimonas aurantiaca</i> T-27(T)	82.8	AP009153	16	15	#	#	#	1	#	#	#	#

\* Closest known species with each major OTU were retrieved by EzTaxon database search (Chun et al. 2007)

# OTUs with 1 % or higher abundance in KRRI-RC-12-S and KRRI-RC-14-S were selected

‡ Sequences with 97 % or higher sequence similarities with respective major OTUs were retrieved by blast search in GenBank database and their habitat information was parsed from the database information

† Total means the number of sequences with 97 % or higher sequence similarity with each major OTU by blast search in GenBank database

§ Others include lake water, ice, biofilm, gold mine, skin, or nitrogen removal reactor

sampling sites. These observations suggest that some of the major OTUs are related to chemosynthesis-based ecosystems in deep-sea environments.

As the first report of the bacterial community of marine sediments in the AAR region, this study revealed that the bacterial communities inhabiting the sediments of AAR were highly diverse and that many bacteria found in this region were similar to those recovered from marine sediments in other geographical areas. Additionally, bacterial OTUs that have been found in hydrothermal vents or cold-seep sites were recovered and hydrothermal signals were detected, implying that some of the major OTUs could have originated from chemosynthesis-based ecosystems. Future studies on the function and physiology of the majority of marine sediment prokaryotes should be conducted to tie the bacterial communities of live or intact cells to their ecological roles.

**Acknowledgments** We thank the crew of the R/V ARAON for their assistance during sampling and Je-Keun Rhee (Seoul National University) for help preparing the figures. This work was supported by the Korea Polar Research Institute (Grant PPI2040).

## References

- Bender J, Langmuir C, Reynolds J, Ryan B, Kastens K (1992) Rock coring: a new development in petrological sampling of the oceanic ridge crest. *RIDGE Events* 3:19–21
- Bowman JP, McCuaig RD (2003) Biodiversity, community structural shifts, and biogeography of prokaryotes within Antarctic continental shelf sediment. *Appl Environ Microbiol* 69:2463–2483
- Bowman JP, McCammon SA, Dann AL (2005) Biogeographic and quantitative analyses of abundant uncultivated  $\gamma$ -proteobacterial clades from marine sediment. *Microb Ecol* 49:451–460
- Chun J, Lee JH, Jung Y, Kim M, Kim S, Kim BK (2007) EzTaxon: a web-based tool for the identification of prokaryotes based on 16S ribosomal RNA gene sequences. *Int J Syst Evol Microbiol* 57:2259–2261
- Corinaldesi C, Barucca M, Luna GM, Dell’Anno A (2011) Preservation, origin and genetic imprint of extracellular DNA in permanently anoxic deep-sea sediments. *Mol Ecol* 20:642–654
- Jensen PR, Gontang E, Mafnas C, Mincer TJ, Fenical W (2005) Culturable marine actinomycete diversity from tropical Pacific Ocean sediments. *Environ Microbiol* 7:1039–1048
- Jørgensen SL, Thorseth IH, Pedersen RB, Baumberger T, Schleper C (2013) Quantitative and phylogenetic study of the Deep Sea Archaeal Group in sediments of the arctic mid-ocean spreading ridge. *Front Microbiol* 4:299
- Kato C, Li L, Tamaoka J, Horikoshi K (1997) Molecular analyses of the sediment of the 11,000-m deep Mariana Trench. *Extremophiles* 1:117–123
- Kim OS, Cho YJ, Lee K, Yoon SH, Kim M, Na H (2012) Introducing EzTaxon-e: a prokaryotic 16S rRNA gene sequence database with phylotypes that represent uncultured species. *Int J Syst Evol Microbiol* 62:716–721
- Kouridaki I, Polymenakou PN, Tselepidis A, Mandalakis M, Kenneth L, Smith J (2010) Phylogenetic diversity of sediment bacteria from the deep Northeastern Pacific Ocean: a comparison with the deep Eastern Mediterranean Sea. *Int Microbiol* 13:143–150
- Lane (1991) 16S/23S rRNA sequencing. In: Stackebrandt E, Goodfellow M (eds) *Nucleic acid techniques in bacterial systematics*. Wiley, New York, pp 115–175
- Lee JH, Yi H, Jeon YS, Won S, Chun J (2012) TBC: a clustering algorithm based on prokaryotic taxonomy. *J Microbiol* 50:181–185
- Li H, Yu Y, Luo W, Zeng Y, Chen B (2009) Bacterial diversity in surface sediments from the Pacific Arctic Ocean. *Extremophiles* 13:233–246
- Luna GM, Dell’Anno A, Giuliano L, Danovaro R (2004) Bacterial diversity in deep Mediterranean sediments: relationship with the active bacterial fraction and substrate availability. *Environ Microbiol* 6:745–753
- Musat F, Wilkes H, Behrends A, Woebken D, Widdel F (2010) Microbial nitrate-dependent cyclohexane degradation coupled with anaerobic ammonium oxidation. *ISME J* 4:1290–1301
- Oh J, Kim BK, Cho WS, Hong SG, Kim KM (2012) PyroTrim: a software with GUI for pre-processing 454 amplicon sequences. *J Microbiol* 50:766–769
- Park SJ, Park BJ, Jung MY, Kim SJ, Chae JC, Roh Y, Forwick M, Yoon HI, Rhee SK (2011) Influence of deglaciation on microbial communities in marine sediments off the coast of Svalbard, Arctic Circle. *Microb Ecol* 62:537–548
- Polymenakou PN, Bertilsson S, Tselepidis A, Stephanou EG (2005) Links between geographic location, environmental factors, and microbial community composition in sediments of the eastern Mediterranean Sea. *Microb Ecol* 49:367–378
- Polymenakou PN, Lampadariou N, Mandalakis M, Tselepidis A (2009) Phylogenetic diversity of sediment bacteria from the southern Cretan margin, Eastern Mediterranean Sea. *Syst Appl Microbiol* 32:17–26
- Ravenschlag K, Sahn K, Amann R (2001) Quantitative molecular analysis of the microbial community in marine Arctic sediments (Svalbard). *Appl Environ Microbiol* 67:387–395
- Ruff SE, Arnds J, Knittel K, Amann R, Wegener G, Ramette A, Boetius A (2013) Microbial communities of deep-sea methane seeps at Hikurangi Continental Margin (New Zealand). *PLoS One* 8:e72627
- Schauer R, Bienhold C, Ramette A, Harder J (2010) Bacterial diversity and biogeography in deep-sea surface sediments of the South Atlantic Ocean. *ISME J* 4:159–170
- Schloss PD, Westcott SL, Ryabin T, Hall JR, Hartmann M, Hollister EB, Lesniewski RA, Oakley BB, Parks DH, Robinson CJ, Sahl JW, Stres B, Thallinger GG, Van Horn DJ, Weber CF (2009) Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Environ Microbiol* 75:7537–7541
- Tal Y, Watts JEM, Schreier HJ (2006) Anaerobic ammonium-oxidizing (Anammox) bacteria and associated activity in fixed-film biofilters of a marine recirculating aquaculture system. *Appl Environ Microbiol* 72:2896–2904
- Vetriani C, Jannasch HW, MacGregor BJ, Stahl DA, Reysenbach AL (1999) Population structure and phylogenetic characterization of marine benthic archaea in deep-sea sediments. *Appl Environ Microbiol* 65:4375–4384
- Whitman WB, Coleman DC, Wiebe WJ (1998) Prokaryotes: the unseen majority. *Proc Natl Acad Sci USA* 95:6578–6583
- Yu Y, Li H, Zeng Y, Chen B (2010) Phylogenetic diversity of culturable bacteria from Antarctic sandy intertidal sediments. *Polar Biol* 33:869–875
- Zinger L, Amaral-Zettler LA, Fuhrman JA, Horner-Devine MC, Huse SM, Mark Welch DB, Martiny TBH, Sogin M, Boetius A, Ramette A (2011) Global patterns of bacterial beta-diversity in seafloor and seawater ecosystems. *PLoS One* 9:1–11