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Bacterial communities along stratified water columns at the Chukchi Borderland in the western Arctic Ocean

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ABSTRACT

An expedition of the IBRV *ARAON* took place in the Arctic Ocean during the summer of 2010. To investigate the hydrographic features and bacterial variations in water columns, we categorized 16 water samples collected from distinct water masses at the Chukchi Borderland in the western Arctic Ocean. Bacterial diversity, relative abundance, and community composition were determined based on a pyrosequencing approach, and their relationship with water mass properties was considered. *Alphaproteobacteria* (43.2%), *Gammaproteobacteria* (16.7%), *Flavobacteria* (13.7%), and *Deltaproteobacteria* (12.0%) were the most common bacteria found in all samples, and the relative abundance of these predominant taxa represent the population dynamics of bacterial communities in different water masses (from the euphotic to the sub-euphotic zone) in the Arctic Ocean. Furthermore, the relative abundance of *Alphaproteobacteria* and its subgroup, SAR11 group I, were significantly related to depth change in water columns, suggesting that environmental heterogeneity caused by changes in depth may play an important role in bacterial population dynamics. In this study, bacterial communities in the Arctic Ocean exhibit biogeographic patterns according to the type of water mass. The halocline layer between the Pacific winter water and Atlantic water exhibits a variation in the composition of bacterial communities, which may be influenced by mixing of Pacific winter water and Atlantic water.

1. Introduction

Marine microbial ecology is currently an important research topic owing to the role of microbes in the marine ecosystem (DeLong et al., 2006; Field et al., 1997; Fuhrman and Davis, 1997; Fuhrman et al., 2008; Giovannoni et al., 1996; Giovannoni and Stingl, 2005; Hansman et al., 2009; Hewson et al., 2006; Karner et al., 2001; Pham et al., 2008; Pommier et al., 2007; Teira et al., 2006). Studies on marine bacterial ecology in the Arctic have been much less frequent than those in temperate oceans because of the difficulty in accessing Arctic areas. Recently, however, several reports on the distribution, structure, and abundance of bacterial communities have described interactions with oceanographic traits in the Arctic Ocean (Bowman et al., 2012; Comeau et al., 2011; Han et al., 2014; Kirchman et al., 2010; Winter et al., 2013; Zeng et al., 2013).

The Arctic Ocean is hydrographically complex and considered a double estuary with inflows of Pacific (through the Bering Strait) and Atlantic (through the Fram Strait) water (Carmack, 2007; Yamamoto-Kawai et al., 2008). A northward Pacific-origin current enters into the Chukchi Sea and mixes with the northern Atlantic water. The mixed water masses exhibit distinctive characteristics in terms of temperature, salinity, density, dissolved oxygen (DO), and nutrient characteristics that depend on the seafloor topography. These properties are useful to study ocean characteristics, and they directly distinguish water mass structure and its distribution. In most oceans including the Arctic, temperature–salinity (*T–S*) diagrams segregate the water mass into fine scales, but other important properties can also be used to characterize water masses that are not obvious in *T–S* diagrams (Emery, 2001).

From an ecological standpoint, an ecosystem consists of discrete areas that are defined as patches (Pickett, 1985). Each patch has a local community that represents a given environment. We hypothesized that this ecological concept could aid in understanding bacterial distribution across stratified water columns in the Arctic Ocean. Galand et al. (2009) have reported that Arctic water masses harbor distinct bacterial communities, suggesting that the water mass could be a key factor in microbial biogeography because the environmental heterogeneity in terms of water mass properties may favor a specific bacterial community.

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We tested this hypothesis by collecting water samples along a transect line at the Chukchi Borderland in the western Arctic Ocean from the continental shelf of Chukchi Sea to the Northwind Ridge near the Chukchi Plateau. Our study was designed to encompass a bacterial biogeographic change along water columns that ranged from euphotic to deep sub-euphotic zones, defined by photosynthetically active radiation (PAR), a measure of sunlight. We then conducted pyrosequencing, targeting the V1–V3 region of the bacterial 16S rRNA gene to shed light on bacterial communities in water samples collected. The major aim of the current study was to understand bacterial diversity of water columns in the Arctic Ocean. This study also considered the possibility of water mass identification by using biological properties such as composition and abundance of the bacterial community.

2. Materials and methods

2.1. Sample collection and sequencing

The IBRV *ARAON* expedition to the Pacific sector of the Arctic Ocean took place in July 2010, during which 16 seawater samples were obtained from water columns. The samples were collected using a conductivity–temperature–depth (CTD) rosette system (Sea-Bird, SBE-911plus) and immediately passed through 3-μm-pore membrane filters (ADVANTEC, Japan) to separate eukaryotes, followed by filtration using 0.2-μm-pore membrane filters (ADVANTEC) to capture prokaryotic bacteria. The samples were then stored in a deep-freezer (−80 °C) aboard the IBRV *ARAON* and transported to our laboratory on ice. DNA extraction, amplification of the prokaryotic 16S rRNA gene (V1 to V3), and pyrosequencing using a 454 GS FLX Titanium Sequencing System were performed as described previously (Han et al., 2014). All the pyrosequencing reads obtained were submitted to the Sequence Read Archive (SRA) under accession number ERP003637. Temperature, salinity, DO, fluorescence, PAR, and light transmission at all of the sampled depths were characterized using a variety of sensors contained in the CTD rosette system.

2.2. Sequence analyses

In total, 60,259 sequencing reads were obtained from the 16 samples after a filtering process (ChunLab, Republic of Korea, http://www.chunlab.com) was conducted. In brief, sequencing reads from the different samples were separated with unique barcodes. Then, the barcode, linker, and PCR primer sequences were removed from the original sequencing reads. The resulting sequencing reads were processed further for quality trimming and chimera removal. The checked sequences were taxonomically assigned using the EzTaxon-e Database (http://eztaxon-e.ezbiocloud.net) (Kim et al., 2012). The operational taxonomy units (OTUs) were defined with the MOTHUR program version 1.29 (Schloss et al., 2009) and used for the subsequent alpha diversity analysis.

In the alpha diversity analysis, the species richness was estimated based on the ACE (Abundance-base Coverage Estimator) and Chao1 indices, and species evenness was calculated with the Shannon and Simpson indices (Shaw et al., 2008). Principal coordinates analysis (PCoA) was used to visualize data similarities in beta diversity using the Fast UniFrac software (Hamady et al., 2009).

2.3. Statistical analyses

Principal Component Analysis (PCA) was performed to search a single axis, accounting for variation of water mass properties by using the Canoco 5 program (ter Braak and Šmilauer, 2012). Further statistical analyses were performed to investigate the relationship between the bacterial populations and water mass properties. The sequences were normalized before the statistical analyses. In brief, the relative abundance of each population was calculated, and the minor populations with a lower relative abundance of less than 1% in each sample were excluded from further analyses. To verify the link between the water mass properties and the major bacterial populations along the water columns, we performed a nonparametric correlation analysis using the Spearman's rho test. To identify tendencies toward a relationship between the major populations and the water mass properties, we first considered the effect of the property on the population abundance. All the water mass properties were inputted together to form a stepwise linear regression model, and the data were checked for normality (normal p–p plot), autoregression (Durbin–Watson), and outliers (standardized residual) with regression diagnostics. All the statistical analyses were performed using the SPSS program (version 16.0, SPSS Institute, Cary, NC, USA).

Table 1
Water mass properties and geological information in samples.

Station	Sample	Water mass[Ψ]	Date [mon/day/yr]	Latitude [N°]	Longitude [E°]	Depth [m]	Temp. [°C]	Salinity [psu]	DO [mg/l]	Fluor. [mg/m^3]	PAR [W/m^3]	Sigma-t [kg/m^3]	X-miss [%]
S1	S1_10	PWW	7/20/2010	73.13	−168.95	10	−1.5	30.3	16.4	0.5	256.1	24.4	98.642
	S1_30	PWW	7/20/2010	73.13	−168.95	30	−1.5	32.3	15.7	1.6	22.6	26.0	92.092
	S1_50	PWW	7/20/2010	73.13	−168.95	50	−1.7	33.1	11.1	1.2	0.2	26.7	91.673
S2	S2_10	SMLW	7/21/2010	73.51	−166.99	10	−1.4	28.9	13.4	0.5	118.1	23.2	98.687
	S2_40	PWW	7/21/2010	73.51	−166.99	40	−1.5	31.8	12.6	1.3	4.7	25.6	95.690
	S2_80	PWW	7/21/2010	73.51	−166.99	80	−1.6	32.8	9.5	0.6	0	26.4	97.267
S3	S3_90	IW1	7/23/2010	73.75	−167.03	90	−1.7	32.9	11.0	0.6	0	26.4	98.139
	S3_145	IW2	7/23/2010	73.75	−167.03	145	0.2	34.6	8.3	0.6	0	27.8	86.162
S4	S4_1800	AW	7/25/2010	75.00	−160.00	1800	−0.3	34.9	9.1	0.5	0	28.1	99.977
S5	S5_500	AW	7/26/2010	75.03	−159.47	500	0.7	34.8	9.4	0.3	0	27.9	99.953
	S5_1000	AW	7/26/2010	75.03	−159.47	1000	0	34.9	9.5	0.3	0	28.0	99.904
	S5_1600	AW	7/26/2010	75.03	−159.47	1600	−0.3	34.9	9.2	0.3	0	28.1	99.966
S6	S6_50	PSW	7/31/2010	75.98	−156.44	50	0	30.2	12.1	0.5	12.1	24.2	98.903
	S6_300	AW	7/31/2010	75.98	−156.44	300	0.2	34.6	8.7	0.2	0	27.8	99.948
	S6_500	AW	7/31/2010	75.98	−156.44	500	0.8	34.8	9.4	0.1	0	27.9	99.965
	S6_800	AW	7/31/2010	75.98	−156.44	800	0.2	34.9	9.6	0.1	0	28.0	99.991

[Ψ] SMLW: Surface mixed layer water; PSW: Pacific summer water; PWW: Pacific winter water; IW1: Intermediate water (boundary depth of PWW); IW2: Intermediate water (boundary depth of AW); AW: Atlantic water.