

Bacterial biogeography influenced by shelf–basin exchange in the Arctic surface sediment at the Chukchi Borderland

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Summary

It has been known that continental shelves around the Arctic Ocean play a major role in the ventilation of the deep basins as a consequence of shelf–basin exchange. In the present study, we found that bacterial assemblage of the surface sediment was different from that of seawater while seawater harboured local bacterial assemblages in response to the Arctic hydrography. This finding suggests that the Arctic seafloor sediments may have distinctive bacterial biogeography. Moreover, the distribution of bacterial assemblages and physicochemical properties in surface sediments changed gradually from the Arctic continental shelf to deep-sea basin. Based on the results, bacterial biogeography in the Arctic seafloor sediments may be influenced by winnowing and re-deposition of surface sediments through the sediment gravity flow. The present study offers a deeper understanding of shelf convection and its role for the construction of bacterial assemblages in the Arctic Ocean.

Introduction

The Arctic Ocean is not only surrounded by land masses, but is also linked with Pacific and Atlantic Oceans. It

receives a large amount of freshwater from river discharge which is equivalent to 10% of the global run-off (Menard and Smith, 1966; Aagaard and Carmack, 1989). This river discharge leads to unique nutrient loading characteristics affecting productivity at multiple trophic levels. Similarly, seasonal sea-ice dynamics also influence freshwater balance by adding salt to underlying water during sea-ice formation in winter, and releasing freshwater during ice melting periods in the summer season (Macdonald, 2000). In addition, satellite observation since 1979 shows that the Chukchi Borderland is especially vulnerable to sea-ice melting during summer (Stroeve *et al.*, 2012).

The Chukchi Borderland consists of shelf-slope region, deep-sea basin and bathymetric highs over the western Arctic shelf. This region receives the large amount of freshwater from the continents (Serreze *et al.*, 2006; Mauritzen, 2012), and freshwaters are stored in the Arctic upper waters (Giles *et al.*, 2012). The Pacific water flows into this region through the narrow (~85 km) and shallow (~50 m) Bering Strait (Pickart *et al.*, 2010; Hu *et al.*, 2012; Haley and Polyak, 2013), and the Pacific inflow is mostly separated into three distinct branches through Herald Canyon, the Central Channel between Hanna and Herald shoals, and Barrow Canyon (Pickart *et al.*, 2010) (Fig. 1A). In the Chukchi Borderland, the Pacific water (colder and fresher) meets and interacts with the Atlantic water (warmer and saltier). The interaction between the Pacific and Atlantic waters and their fate in the Arctic Ocean are affected by the sea-ice dynamics (Rainville *et al.*, 2011) as well as seafloor topography (Woodgate, 2013). The information about ocean circulation is essential for understanding the climate change and biogeochemical cycles in the Arctic. Indeed, the contribution of bottom-arrested dense water (or brine-enriched bottom water) to intermediate and deep water masses around the shelves has been widely discussed in Arctic oceanography (Aagaard *et al.*, 1981; 1985; Swift *et al.*, 1983; Anderson *et al.*, 1988; Bauch *et al.*, 1995; Backhaus *et al.*, 1997; Haley *et al.*, 2007). Especially, the continental margins around the Chukchi Borderland contribute to cross-slope exchange of salt, nutrient, organic carbon, etc., between the shelf and deep-sea basin (Grebmeier *et al.*, 2009). A variety of mechanisms to

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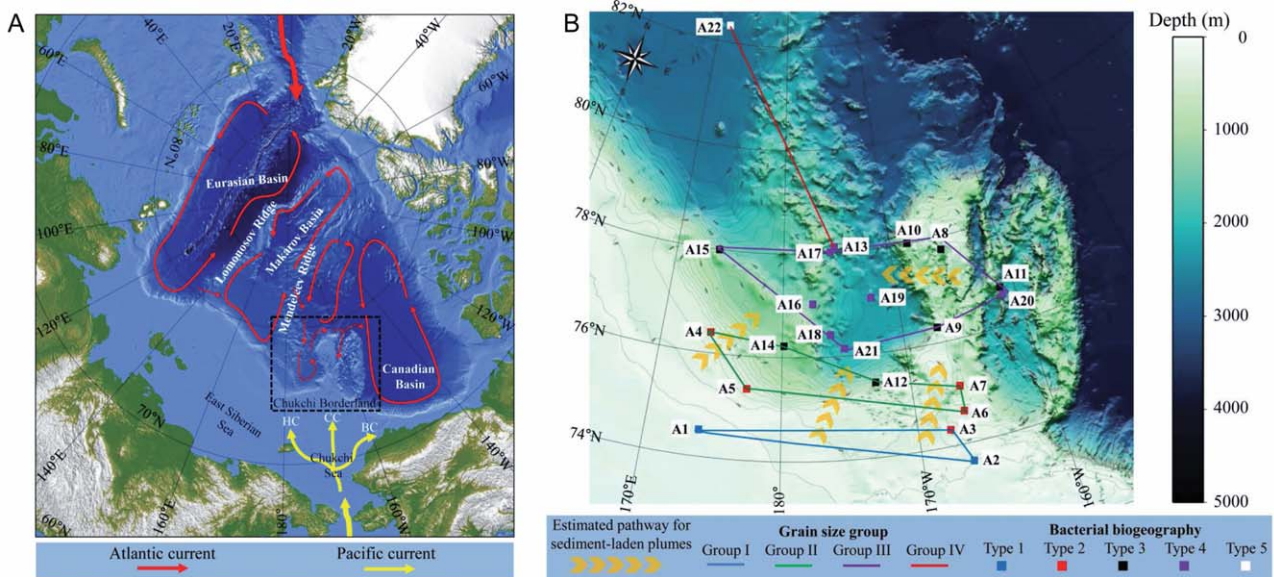


Fig. 1. Oceanographic status for the research area. Schematic diagram of idealized bottom water circulation in the Arctic Ocean [A: Pacific inflows from the Chukchi Sea towards the western Arctic Ocean via Herald Canyon (HC), Central Channel (CC) and Barrow Canyon (BC)]. Estimated pathway for sediment gravity flow, grain size distribution and bacterial biogeography in sampled area (B).

explain the shelf–basin exchange, such as wind-driven flow, eddy formation, upwelling, and dense shelf water, have been proposed despite limited observational evidences (Huthnance, 1995; Nikolopoulos *et al.*, 2009). The shelf–basin exchange is also referred to as ‘sediment gravity flow’ for the sediment transport through hyperpycnal plumes (Burt and Allison, 2010). The sediment gravity flows are differentiated by sediment support mechanisms such as turbidity current or debris flow, but their motion is similar to the sediment-laden river plumes that flow to the shelf edge and then down the shelf slope through a submarine canyon as a result of its density relative to the ambient current. With this process, sediments can be transported hundreds of kilometres away from sources (Burt and Allison, 2010).

The pathways of the Pacific and Atlantic waters may provide critical clues to understand the Arctic sedimentary environment. In the modern Arctic Ocean, Pacific and Atlantic waters are isolated to each other, but they could partially intermix as a consequence of the shelf–basin exchange (Midttun, 1985; Huthnance, 1995; Backhaus *et al.*, 1997). Furthermore, the sediment gravity flow transporting terrigenous materials to deep-sea basin (Dade and Huppert, 1994; Burt and Allison, 2010) seems to be mediated by the shelf–basin exchange (Huthnance, 1995; Backhaus *et al.*, 1997; Haley and Polyak, 2013). Advection of fine sediments by the sediment gravity flow in coastal and shelf environments has been widely discussed (Wright *et al.*, 2001), and its suspended sediments may play a key role in water mass formation (Backhaus *et al.*, 1997), sedimentation (Stein *et al.*, 1994) and the

distribution of organic matters. To date, however, there has been no consideration of how sediment gravity flows at Arctic shelves influence the microbial ecology of this unique ecosystem.

As the Arctic Ocean is an ideal environment to study microbial biogeography in response to climate-driven oceanic processes, the composition of microbial assemblages and their spatial distribution have been assessed in the Arctic seawaters (Galand *et al.*, 2009; Kirchman *et al.*, 2010; Bowman *et al.*, 2011; Comeau *et al.*, 2011; Winter *et al.*, 2013; Han *et al.*, 2014; 2015; Monier *et al.*, 2015). Recently, the biogeochemical cycle and microbial biogeography in the Arctic shelf have been paid attention to understand the underlying ecological process in response to environmental changes (Hamdan *et al.*, 2012; Canion *et al.*, 2014). These studies have dealt with the questions of water-depth related difference in microbial assemblages, as well as the difference between pelagic and benthic microbial assemblages in the Arctic Ocean, suggesting the Arctic oceanographic processes affect microbial assemblages.

In the present study, we investigated the distribution of bacterial assemblages in the Chukchi Borderland covering surface water to bottom sediments. Although seawater harboured local bacterial assemblages in response to water masse type, there was no linkage of the bacterial assemblages from seawater to the surface sediment. In addition, bacterial populations at the surface sediment appeared to be distributed with respect to the physicochemical properties (total bacterial DNA, biochemical class and grain size) of the surface sediment,

which is likely caused by the gradient of geological distance from the continental shelf to the deep-sea basin. The sediment transport and its fate over the Arctic shelves are likely influenced by the sediment gravity flow, which in turn alters bacterial biogeography in direct response to changes in the physicochemical properties of the surface sediment.

Results

Oceanographic aspect and sediment property at the Chukchi Borderland

Total 22 sediment samples in order of deeper depth from A1 to A22 were collected from the continental shelf, slope and deep-sea basin in the western Arctic (Chukchi Borderland) (Fig. 1B; see depth information in Table S1). Bottom water masses on sampled area were identified by their temperature and salinity profiles (Fig. S1). Cold waters were more saline around the shelf edge (Pacific water; A1 to A2; 57 to 110 m). Warmer and saltier waters (Atlantic water; A3 to A12; 322 to 1079 m) and hypersaline cold water (Arctic deep water; A13 to A22; 1375 to 2710 m) were distributed along deeper depths. Physicochemical properties of the collected sediment, which were listed in order of deeper depth (A1 to A22; Table S1), represent the different sedimentation pattern. That is, the grain size of surface sediment at shallower depths of the shelf edge area (A1 to A3) primarily consisted of coarse particles, which ranged from 50 to 2000 μm in diameter. In contrast, the grain size from the continental slope to the deep-sea basin was ranged from medium to fine-grained particles ($\leq 50 \mu\text{m}$ in diameter). Especially, there was a significant ($P < 0.01$) increase in the distribution of fine sediment particle ($\leq 2 \mu\text{m}$ in diameter) in response to a deeper water depth, which would indicate winnowing of fine particles from coarse sediments in the investigated area. Moreover, the deoxyribonucleic acid (DNA) content [genomic (g)DNA and bacterial DNA] of the surface sediment was remarkably higher in surface sediments at the shallow area (A1 to A3). Similarly, the shelf edge area (A1 and A2) contained relatively high amount of long-chain, aliphatic, aromatic, polysaccharide, phenolic and nitrogen-containing compounds compared with the other areas (A3 to A22).

Bacterial assemblages in the seawater and surface sediment

Bacterial sequence data sets of the Arctic seawater (accession number ERP002081 and ERP003637) and surface sediment (ERP007066) were analysed by using an operational taxonomic unit (out) clustering at the 97%

similarity level. In Fig. 2A, the beta-diversity pattern, explained by the principal coordinate analysis (PCoA) plot, clearly demonstrates that there are different bacterial assemblages in seawater and surface sediment at the Chukchi Borderland. Among the seawater samples, the bacterial assemblages were separated into two groups; an upper layer (surface mixed layer and Pacific waters; at 7 to 90 m) and a deeper layer (Atlantic and Arctic deep waters; at 145 to 1800 m) due to water mass characteristics (Fig. 2B). The number of observed OTUs was compared between the seawater and surface sediment samples (Fig. 2C and D and Table S2). The SAR11 clade has been known to be dominant in surface seawater (7 m) of the western Arctic Ocean (Han *et al.*, 2014), as well as other oceans (Morris *et al.*, 2002). However, the relative abundance of one of SAR11 subgroups, SAR11 group I (ARC_sea1 OTU), was distinctly decreased from that of the upper to the deeper layers. Other seawater populations: *Polaribacter*, *Balneatrix*, RCA clade, SAR86 clade, Arctic96BD 19 clade, *Flavobacteriaceae*, NS5 marine group and SAR11 group II showed a similar pattern with SAR11 group I. In contrast, SAR324 clade (ARC_sea2 OTU), one of the most common clades in the deeper layer (Wright *et al.*, 1997; López-García *et al.*, 2001; Pham *et al.*, 2008), was nearly barren in the upper layer. Overall, the relative amounts of abundant shared OTUs in the upper layer decreased in the deeper layer. These phylogenetic results were highly correlated with the taxonomy-supervised analysis for the bacterial biogeography along the stratified water columns at the Chukchi Borderland (Han *et al.*, 2015). However, the most popular *Actinobacterium* (ARC_sf1 OTU) and uncultured seafloor clone (ARC_sf2 OTU) in the surface sediment were absent in the seawater samples.

The beta-diversity pattern of bacterial assemblages in the surface sediment was clustered into five types, Type 1 (A1 and A2), Type 2 (A3, A4, A5, A6 and A7), Type 3 (A8, A9, A10, A11, A12, A14 and A15), Type 4 (A13, A16, A17, A18, A19, A20 and A21) and Type 5 (A22) (Fig. 3A). Among bacterial assemblages in the surface sediment, Type 1 (A1 and A2), which is close to the shelf edge, was separated from the others on Axis1 in the PCoA. The other types from Type 2 to 5, which are arranged along Axis2 in the PCoA, were distributed according to deeper depths (see depth information of sampled area in Table S1). That is, Types 1 to 5 were assigned along geological distance over the continental shelf, and this clustering pattern was similar to that of grain size distribution (Fig. 3B), in which surface sediments were clustered into four groups, Group I (A1, A2 and A3), Group II (A4, A5, A6, A7, A12 and A14), Group III (A8, A9, A10, A11, A15, A16, A17, A18, A19, A20 and A21) and Group IV (A13 and A22).

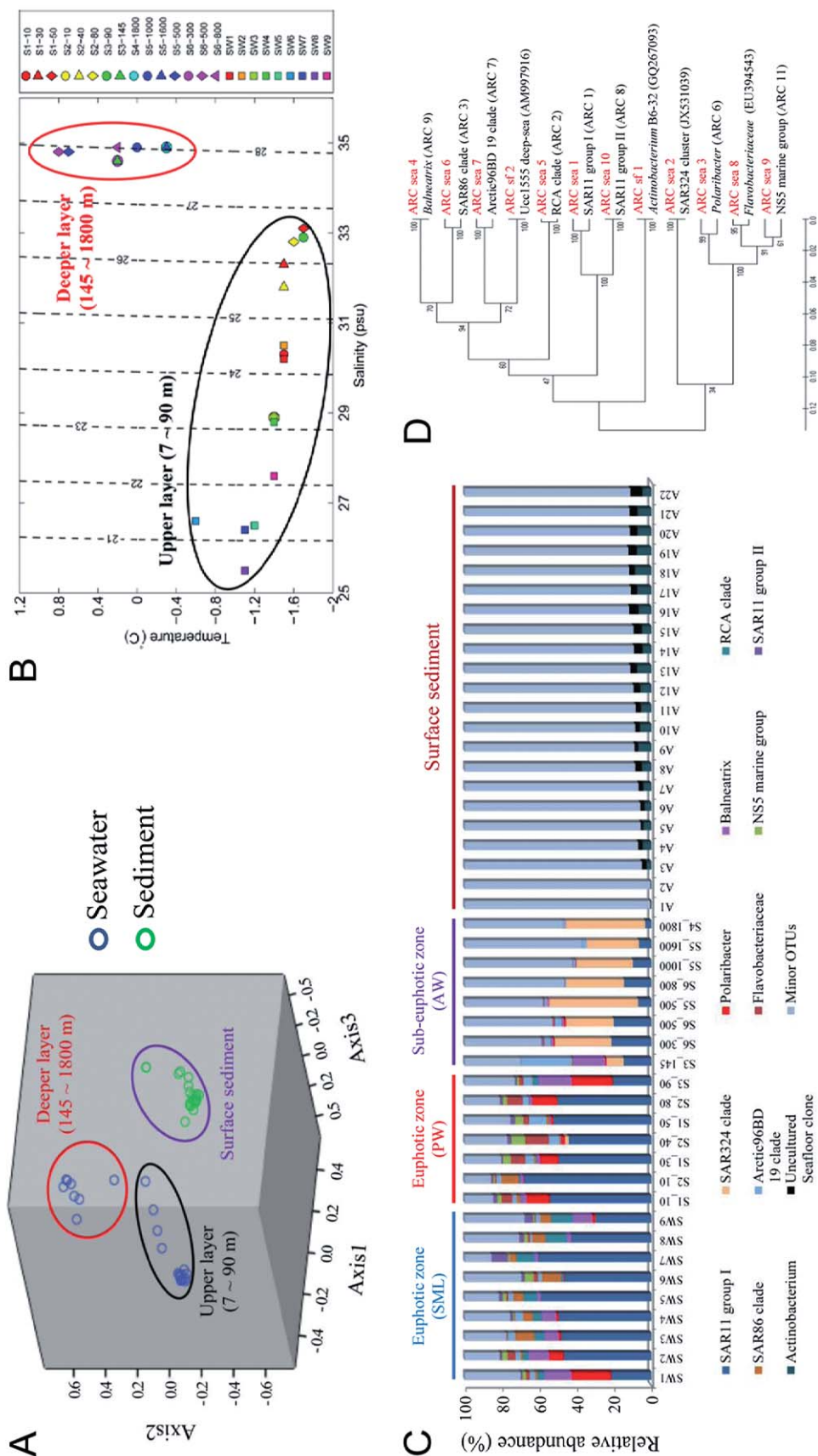


Fig. 2. Discrimination of bacterial assemblages in the Arctic marine samples. Beta diversity between seawater and sediment based on the PCoA analysis (A). Water mass classification of Arctic seawaters by the T-S diagram (B). The black dash line indicates the density (kg m^{-3}). Distribution of the major 12 OTUs (with a frequency over 1% in the sum of sequences) from the seawater to the surface sediment (C) and their phylogeny reconstruction (D) with bacterial clone sequences from Arctic seawater (Han *et al.*, 2014) and GenBank databases (their relative abundance alongside the phylogenetic tree was also described in Table S2). The Unweighted Pair Group Method with Arithmetic Mean (UPGMA) algorithm was used to cluster patterns based on the maximum composite likelihood model. Bootstrap values are indicated at the appropriate nodes (based on 500 bootstrap replicates).

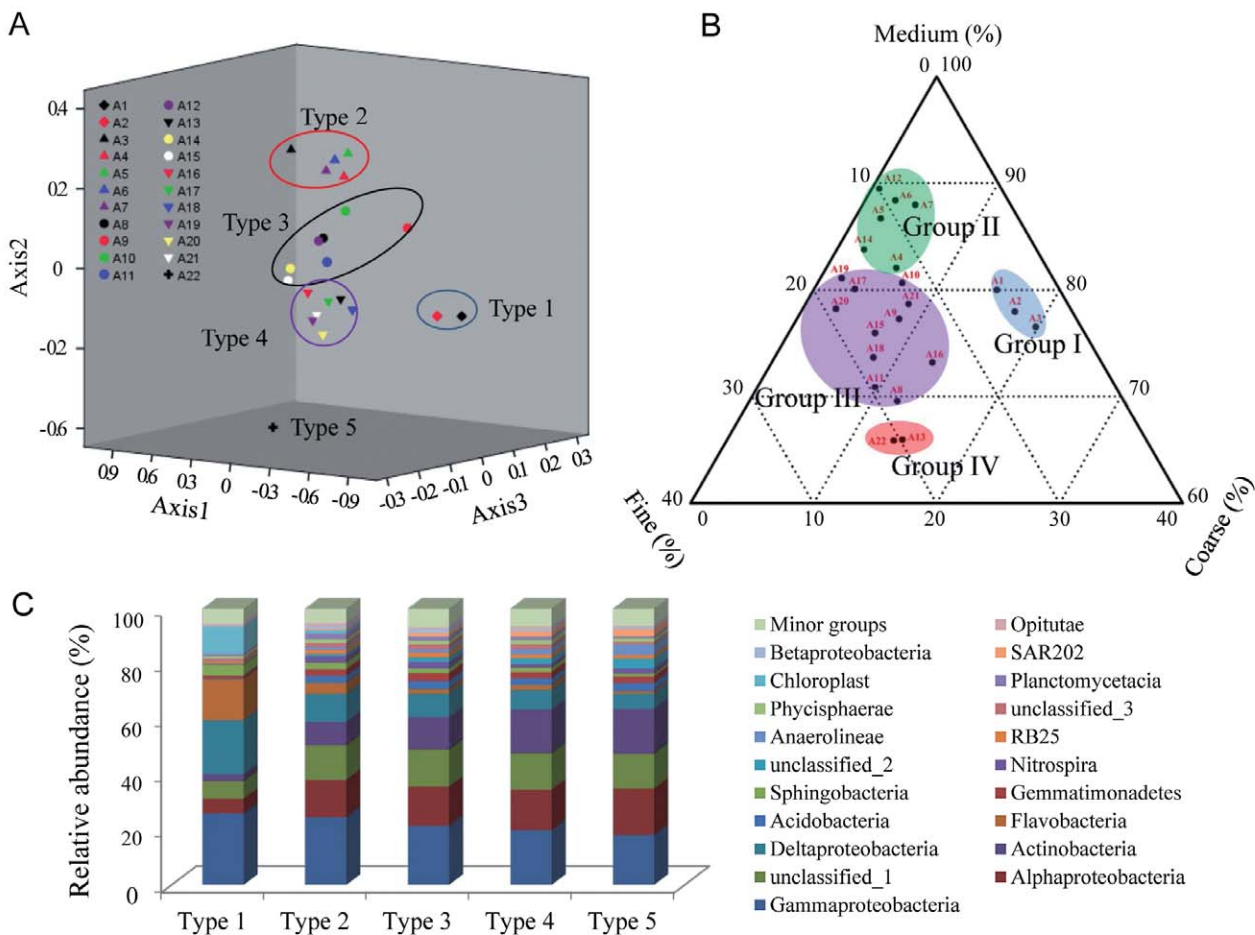


Fig. 3. Discrimination of bacterial assemblages within the sediment samples. Bacterial beta diversity (A) and grain size distribution of surface sediment samples (B) and the composition of bacterial assemblages (class level) in clustered samples (C). Determination if the samples came from different group was tested by using the Kruskal–Wallis and Jonckheere–Terpstra statistical methods (Table S3). Percentages and standard deviation values among groups was shown in Table S3. The distribution of all bacterial populations including minor groups (the sum of rare taxa having a frequency of < 1% in the total sequences) was shown in Table S5.

The patterns of both bacterial beta diversity and grain size in the surface sediment matched well with the geological distance over the continental shelf on the bathymetric map of the Chukchi Borderland (Fig. 1B). These patterns were also consistent with alpha diversity (species richness and evenness; Table 1), in which the indices gradually decreased from the continental slope

(Type 2) to the deep-sea basin (Type 5), except along the shelf edge (Type 1). The pattern of alpha diversity among the clustered sediments was explained by the taxonomic classification (Fig. 3C). We found that 20 majority taxa (class level) of bacterial assemblages in the surface sediment, with a frequency over 1% in the sum of samples, occupied 93.9% of the total surface sediment sequences

Table 1. Alpha diversity of bacterial assemblages in surface sediment.

Type of bacterial biogeography (n = clustered samples)	Species richness		Species evenness	
	Ace	Chao1	Shannon	Inverse Simpson
1 (n = 2)	4212 ± 776*	2273 ± 298	5.5 ± 0.2	72 ± 8.3
2 (n = 5)	5510 ± 334	3221 ± 166	6.3 ± 0.1	182 ± 24.4
3 (n = 7)	5217 ± 576	2953 ± 304	6.0 ± 0.1	116 ± 9.8
4 (n = 7)	4563 ± 589	2564 ± 280	5.8 ± 0.1	83 ± 5.6
5 (n = 1)	3304	2064	5.4	61

*Values are the average ± standard deviation values for each clustered bacterial biogeography type.

($n = 77\ 082$). Of the major taxa, the distribution was similar within clustered types apart from Type 1. For example, sequences of *Gammaproteobacteria* were most predominant in all clusters including Type 1. However, sequences of *Alphaproteobacteria*, *unclassified_1*, and *Actinobacteria* were dominant from Type 2 to Type 5, but relatively not popular in Type 1. In contrast, sequences of *Deltaproteobacteria*, *Flavobacteria* and chloroplast (phytoplankton) were popular in Type 1 but relatively not in others. Nevertheless, the relative abundance of major taxa seems to constantly increase or decrease from Type 1 to Type 5. This trend was estimated by a statistical hypothesis testing.

Statistical hypothesis testing

The variation of the major taxa among the clustered types in the PCoA (Fig. 3A) was statistically estimated by non-parametric analysis of variance (ANOVA) tests (Table S3), in which Kruskal–Wallis method was used to determine if the samples came from different cluster. Among the tested major taxa ($n = 20$), the distribution of 13 taxa was statistically independent in all samples according to clustered types ($P < 0.05$). A *post hoc* comparison test in the non-parametric ANOVA using Jonckheere–Terpstra method shows 12 of the tested taxa were significantly distributed in order of clustered types (Type 1 to 5; $P < 0.05$). That is, the non-parametric ANOVA tests support that the distribution of the major bacterial populations in the surface sediment changed in response to the bathymetry trend of the Chukchi Borderland. This hypothetical linkage between the bathymetric trend and the bacterial populations was further estimated by a linear relationship.

To estimate the linkage, the bathymetric trend was considered from maximum depths of sampled locations (A1 to A22), and the 20 major taxa were considered to be the representative populations of the surface sediment assemblages for statistical analyses. Table S4 shows that the relative abundance of 11 major taxa (68.7% of the surface sediment sequences) was significantly correlated ($P < 0.05$) with water-depth change. Six of them (*Alphaproteobacteria*, *Actinobacteria*, *unclassified_2* taxon, *Anaerolineae*, *Phycisphaerae* and *SAR202*) showed positive correlations (Table S4); their relative abundance increased with deeper water depth. In contrast, the relative abundances of the other five taxa such as *Gammaproteobacteria*, *Deltaproteobacteria*, *Flavobacteria*, *Sphingobacteria* and chloroplast (phytoplankton) showed negative correlations (Table S4); their relative abundance decreased with the deeper water depth. Causality for these correlations between the 11 major taxa and the geological distance (depth) was determined by a linear regression analysis (Fig. S2).

Discussion

Comparison of bacterial assemblages

Bacterial assemblages were compared between seawater and surface sediment. The bacterial assemblage of seawater is matched with water mass identification. For example, the surface mixed layer water is strongly affected by sea-ice melting and river discharge during summer. The inflow of Pacific water is great beneath the surface mixed layer, and deep waters (Atlantic and Arctic deep waters) flow below Pacific water. These stratified waters have been classified by the water mass characteristics of temperature and salinity (Coachman and Barnes, 1961; Shimada *et al.*, 2001; Steele *et al.*, 2004; Carmack *et al.*, 2008) and clearly affected a biogeography of bacterial assemblage (Galand *et al.*, 2009; Han *et al.*, 2015). More specially, the gradual decrease of SAR 11 group I from the upper euphotic to deeper sub-euphotic layers may suggest that the population dynamics of SAR11 group I is in large part due to the sinking of dense water in the brine ejection process that occurs during the sea-ice formation (Han *et al.*, 2014; 2015). However, there was no shared OTU between the seawater and surface sediment samples in the tested level (97% similarity), and the assemblage differentiation between seawater and sediment was similar as shown in the Alaska Beaufort Shelf (Hamdan *et al.*, 2012), suggesting that the bacterial assemblages of the surface sediment is not directly originating from seawater at the Chukchi Borderland.

Potential mechanisms for sediment transport mediating bacterial dispersal to seafloor

The Arctic sedimentation is not in steady state, but rather dynamic in response to infrequent oceanographic events (O'Brien *et al.*, 2011). Recent sedimentation processes in the Arctic Ocean would be responsible for sediment gravity flows, sea-ice drift and transport in suspension influenced by distinct current systems such as cyclonic eddies, wind-induced upwelling and downwelling, and shelf beak jets (Wahsner *et al.*, 1999; O'Brien *et al.*, 2011). Such oceanographic events could be cooperated to transport the sediment from the shelf to deep-sea basin in the Arctic. In the present study, the distribution of bottom waters on the Chukchi Borderland was well matched with the Arctic water mass types (Pacific, Atlantic, and Arctic Deep waters) according to the bathymetric trend, which may contribute to the shelf–basin exchange (Shapiro *et al.*, 2003; Ivanov *et al.*, 2004; Grebmeier *et al.*, 2009; Ivanov, 2011). This pattern is supported by grain size distribution, biochemical class, total bacterial DNA content and bacterial diversity in the surface sediment. Moreover, the sedimentation rate was higher in the shelf (201 m depth, 0.022 cm per year) than deep-sea

basin (2135 m depth, ~ 0.001 cm per year) at the Chukchi Borderland in the modern climate condition (Stein *et al.*, 2010), implying hemipelagic deposits. Such sedimentation from the Arctic shelf to the deep-sea basin in the sampled area was likely influenced by the sediment gravity flow in the current environment (Stein *et al.*, 1994).

In coastal and shelf environments, a sediment transport mediated by river plumes has been widely observed (Ogston *et al.*, 2000; Traykovski *et al.*, 2000; Wright *et al.*, 2001). During the sediment transport by river plumes across the continental shelves, the sediments are freshly delivered by settlement from the plumes, and further mixed with ambient seawaters before moving downslope under the gravity influence (Wright *et al.*, 2001). Similarly, the Pacific inflow may drive a sediment-laden plume originated from river outflows in shallow depths towards the Chukchi Borderland. Then, the hyperpycnal (negatively buoyant) plume exerts the sediment transport across the continental shelves in large part, and then the sediment in the inner shelf can be delivered with flux convergence resulted from high wave and bottom currents (Wright and Friedrichs, 2006). Backhaus and colleagues (1997) also suggested the role of the hyperpycnal plume to entrain fine-grained particles which covers the surface layer in the continental slope. In the modern Arctic Ocean, large polynya has seasonally occurred in the area from the Bering Strait to the shelf edge of the Chukchi Borderland (Nguyen *et al.*, 2012; Stroeve *et al.*, 2012), and the dense shelf water caused by polynya descends inside the canyons such as Central, Herald and Barrow Canyons (Nguyen *et al.*, 2012). Considering the fate of the dense shelf water (Ohshima *et al.*, 2013), the sediment may reach the deep-sea basin by flowing down the canyons. Thus, the hyperpycnal plume during ice melting season and/or brine-enriched bottom water during sea-ice formation may play a key role in transporting sediments across the continental shelf at the Chukchi Borderland as a consequence of the shelf–basin exchange mediated by the sediment gravity flow. In polar seas, however, it has been believed that shelf ice significantly contributes to the formation of the brine-enriched shelf water, which can sufficiently sink to deep-sea basins. Although this paradigm was shifted by the evidence from Antarctic Bottom Water, which is directly linked to the brine rejection from seasonal sea-ice formation (polynyas) (Ohshima *et al.*, 2013), the same argument for the Arctic Ocean has been under discussion because of limited direct observations (Bauch *et al.*, 2011; 2012; Mackensen and Nam, 2014).

Additionally, sediments in the Arctic Ocean have lower biogenic components than other oceans due to sea-ice cover, and primarily consist of terrigenous matters (Stein, 2008). For instance, total bacterial DNA content and the proportion of chloroplast (phytoplankton) in the surface sediment remarkably decreased from the shelf edge (A1

and A2), suggesting that these samples are likely to be at the edge of nutrient availability entering the Arctic seafloor as settling organic matter (Stein, 2008). This result can be interpreted as a 'marine snow' event of organic matter formed in a euphotic zone or coastal margins that enters oceans (Gray and Elliott, 2009). The lower bacterial DNA of the surface sediments in the deep-sea basin may result from the small number of particle-attached bacteria or lack of nutrients, as suggested by the lower sedimentation rate in the deep-sea basin. Furthermore, considering an important role of methane as a carbon and energy source to microorganism in the subsurface area at the Chukchi shelves (Savvichev *et al.*, 2007), we need to reconsider its influence on the bacterial biogeography and biomass of the surface sediment in a further study.

Seafloor bacterial biogeography

Generally, it has been recognized that the distribution of microbiota can be patchy in an environment and is spatially similar to nearby sites (Bell *et al.*, 1993). That is, the bacterial assemblages are associated with biotic factors that characterize certain habitat types. In the present study, bacterial assemblages of the surface sediment were entirely separated from those of seawater, probably due to the habitat specificity. On the other hand, the dispersal that has been applied in ecological community models (Peay *et al.*, 2010), refers to the movement of individuals (immigration or emigration) between habitats. In the present study, the unique local bacterial assemblages of the surface sediment seem to be largely affected by an abiotic interaction alongside geological distance from the continental shelf to the deep-sea basin (here in dispersal limitation). Indeed, most benthic bacteria are readily aggregated into the sediment particles, and thus sediment transport through winnowing and redeposition processes may influence dispersal of bacterial populations in the surface sediments. Furthermore, statistical results showed that the relative abundance of major bacterial populations in surface sediment uniformly changes from the continental shelf to the deep-sea basin in accordance with bathymetric trends at the Chukchi Borderland. Our findings suggest that the dispersal limitation of bacterial assemblages may be linked with oceanographic events to drive winnowing and redeposition of sediments at the Chukchi Borderland. Taken together, a hypothetical process for sediment transport mediated by sediment gravity flow was illustrated in Fig. 4 that summarizes winnowing and re-deposition of the plume-borne sediment (Backhaus *et al.*, 1997; Burt and Allison, 2010) and dispersal limitation in bacterial assemblage of the surface sediment at the Chukchi Borderland. In the schematic illustration, the sediment gravity flow descends towards the deep-sea basin by following a topographic depression on the continental

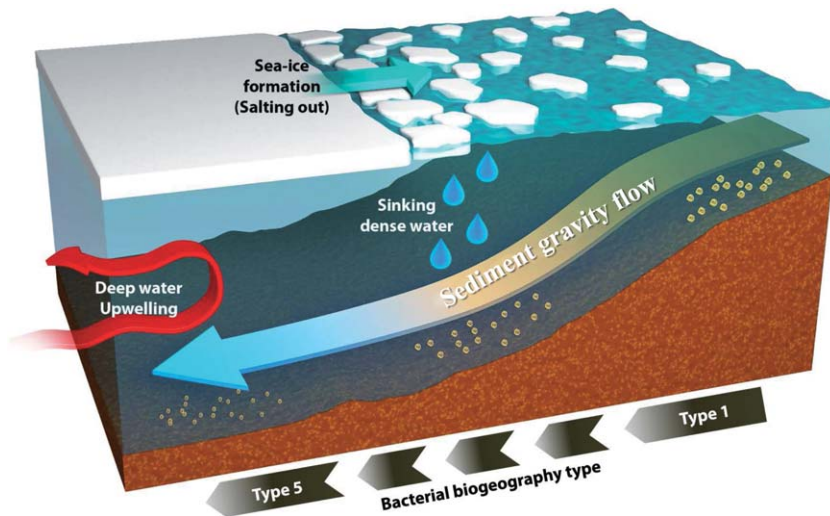


Fig. 4. Proposed schematic process for sediment transport by the sediment gravity flow. Deposition of plume-borne sediments could be mediated by the sediment gravity flow, which could drop down coarser sediments near the shelf edge, and the fine-grained sediments are likely to be transported into the continental margin. This sediment transport can be linked with bacterial biogeography type (Type 1 to 5) on the surface sediment at the Chukchi Borderland.

slope or reach density equilibrium at an intermediate depth, which causes lateral intrusion into ambient water masses. Energy and turbulence of the sediment gravity flow would eventually become less at the continental margin, at which time a sediment-laden plume would allow sediments to settle. Lastly, the circulation of Arctic deep water in the basin may influence the transport of the suspended sediment after the intruding plume touches the bottom at the continental margin. In this sediment transport, a consequence of sediment loss would allow the plume to become less dense than ambient water masses, and increasing buoyancy would initiate upward motion of the plume. Indeed, the upwelling of deep waters has been observed in the western Arctic Ocean (Aagaard and Roach, 1990; Woodgate *et al.*, 2005; Mathis *et al.*, 2012). The fate of the sediment gravity flow may be linked with the upwelling of deep waters in the Arctic shelves. Our hypothesis suggests that winnowing and re-deposition processes mediated by the sediment gravity flow influence the bacterial biogeography on the Arctic seafloor.

Conclusion

The integrated process for sediment transport mediated by the sediment gravity flow may drive dispersal limitation (gradual decrease or increase in the relative abundance) of bacterial assemblages on the surface sediment. Thus, bacterial biogeography caused by dispersal limitation of bacterial assemblages may explain Arctic oceanographic events, in parallel with the traditional ocean observation, such as that revealed by the T-S diagram and grain size analysis.

Experimental procedures

Sediment cores ($n=22$) and oceanographic data were obtained from the icebreaking research vessel (IBRV) *ARAON* Arctic cruises. A bathymetric chart and the profiles of

temperature and salinity in bottom waters were constructed to illustrate the oceanographic status of seafloor around the research area. Samples of surface sediment consisted of the top section (2 cm slices) of box or multiple sediment cores. Physicochemical properties of surface sediment were estimated by the distribution of total bacterial DNA, biochemical class and grain size. The content of total bacterial DNA was measured by using a real-time, quantitative polymerase chain reaction in gDNA extracted from the sediments (each 0.25 g dry weight). Biochemical class in sediment samples was determined by using pyrolysis gas chromatography/mass spectrometry to show difference between the sediment samples (White and Beyer, 1999; Guo *et al.*, 2004). For analysis of particle size distribution, sediments (17–20 g dry weight per sample) were sieved through a 2 mm sieve, and measured using a laser diffraction system (Mastersizer 3000, Malvern Instruments, Malvern, UK). Particles were defined as: coarse (50–2000 μm), medium (2–50 μm) and fine (0–2 μm) dia size. A pyrosequencing approach (454 GS FLX Titanium Sequencing System) was used to analyse bacterial diversity (alpha and beta diversity) and assemblage composition in the surface sediment as well as both seawater and surface sediment. Prokaryotic 16S rRNA gene sequences were amplified from the extracted genomic DNA using primers targeting the V1 to V3 hyper-variable regions. Analysis of pyrosequencing data was done using the MOTHUR program (Schloss *et al.*, 2009). Statistical analyses were done using the SPSS program. The relative abundance of bacterial assemblages according to bathymetric trend was evaluated by using a non-parametric ANOVA (Kruskal–Wallis and Jonckheere–Terpstra methods), Spearman's rho and linear regression analysis. Details concerning the above analytical methods are described in the supplementary information.

Acknowledgements

This study was supported by the Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education, Science and Technology (2012R1A1A2043811), the Polar Academic Program (PD12010 and PD15010) of KOPRI, and the Basic

Research Projects in High-tech Industrial Technology through a grant provided by GIST in 2015. S. I. N. is supported by Basic Research Program (PE15062) of KOPRI. All authors thank Dr. G. T. Lee in the National Instrumentation Center for Environmental Management (NICEM) for the grain size analysis using laser diffraction. We also thank the crew members and scientists of the *ARAON* who assisted with sample collections at sea.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Fig. S1. Temperature and salinity profiles of bottom waters overlying surface sediment at the Chukchi Borderland. Conductivity-Temperature-Depth (CTD) data were visualized by the OCEAN DATA VIEW software.

Fig. S2. Relative abundance of major bacterial populations ($n = 11$) in association with depth change. The correlation coefficients were already described, and the bacterial populations in this figure were not shown over the P -value 0.05 in Table S4. The regression coefficient (R^2) and linear slope were calculated by a linear regression analysis in SPSS. The X-axis scale (rank of depth) assigns 1 to the smallest rank of depth.

Table S1. Sampling details and analytical properties of surface sediment. The grain size of sediments was classified into three types; coarse (50–2,000 μm), medium (2–50 μm) and fine particles (0–2 μm). The distribution of sediment grain sizes was projected on a triangular diagram (Fig. 3B).

Table S2. Distribution of major OTUs ($n = 12$) from surface mixed layer to surface sediment. Taxonomic identification of OTUs was described in phylogenetic lineage in Fig. 2D. Minor OTUs denote the sum of rare OTU having a frequency of < 1% in the total sequences.

Table S3. The percentage and standard deviation values of major bacterial populations (class level) in clustered samples and non-parametric ANOVA test. Minor groups denote the sum of rare taxa having a frequency of < 1% in the total sequences.

Table S4. Non-parametric correlation between bacterial populations and depth.

Table S5. The percentage of all bacterial taxa in the surface sediment (class level).