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ScienceDirect
Journal of Marine Systems 74 (2008) 774–782
JOURNAL OF MARINE SYSTEMS
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Heterogeneous archaeal communities in the particle-rich environment of an arctic shelf ecosystem

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Received 10 April 2007; received in revised form 11 November 2007; accepted 7 December 2007
Available online 14 December 2007

Abstract

We evaluated the phylogenetic diversity of particle-associated and free-living archaeal assemblages from the Mackenzie River and Beaufort Sea in the western Canadian Arctic. The physico-chemical characteristics of the water separated the sampling sites into three groups: riverine, coastal and marine water, which had strikingly different archaeal communities. The riverine water was characterised by the presence of *Euryarchaeota* mainly belonging to the LDS and RC-V clusters. The coastal water was also dominated by *Euryarchaeota* but they were mostly affiliated to Group II.a. The marine waters contained most exclusively *Crenarchaeota* belonging to the Marine Group I.1a. The results suggest that *Euryarchaeota* in the coastal surface layer are associated with particle-rich waters, while *Crenarchaeota* are more characteristic of Arctic Ocean waters that have been less influenced by riverine inputs. The particle-associated communities were similar to the free-living ones at the riverine and marine sites but differed from each other at the coastal site in terms of the presence or absence of some taxonomic groups in one of the fractions, or differences in the proportion of the phylogenetic groups. However, there was no specific archaeal group that was exclusively restricted to the free-living or particle fraction, and the diversity of the particle-associated archaeal assemblages did not significantly differ from the diversity of the free-living communities.
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Keywords: Archaea; Microbial diversity; Particles; Arctic; Beaufort Sea

1. Introduction

The development of molecular tools has revealed many new marine microorganisms and has cast light on the tremendous microbial diversity in the sea. However, given the sporadic nature of data on microbial diversity in general and of archaeal diversity in particular, there is still little understanding of the distribution of Archaea within and across systems. While only two studies have reported taxonomically significant differences between riverine and marine communities (Crump and Baross, 2000; Galand et al., 2006), others have described the distribution of Archaea in the sea. Several groups of Archaea appear to be cosmopolitan (Massana et al., 2000) and studies at the phylum level (*Euryarchaeota* versus *Crenarchaeota*) indicate changes in community composition with depth (Church et al., 2003; Karner et al., 2001; Kirchman et al., 2007; Massana et al., 1998). *Crenarchaeota* in the cold, deep ocean are thought to be among the most abundant marine microbial cell types (Karner et al., 2001) and recent evidence of their ability

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doi:10.1016/j.jmarsys.2007.12.001

to oxidize ammonia has major implications for global biogeochemical cycling (Konneke et al., 2005; Wuchter et al., 2006). The recognition of the numerical and functional importance of Archaea in the ocean stresses the need to better understand the factors structuring their diversity.

The high proportional abundance of Archaea at some sites and depths in the Arctic Ocean has been correlated with particle-rich waters (Wells and Deming, 2003). Among oceanic regions, the Arctic is strongly influenced by large rivers discharging fresh water and sediments into its coastal seas (Carmack and MacDonald, 2002). While the largest arctic rivers in terms of discharge (Lena, Ob, and Yenesei) originate in Siberia and discharge into the Laptev and Kara seas, the Canadian Mackenzie River discharges the greatest quantity of sediments (Carson et al., 1998), loading the adjacent coastal Beaufort Sea with particles. These particle-rich waters spread to Amundsen Gulf and the western part of the Northwest Passage and contain a high proportion of Archaea within their prokaryotic communities (Wells and Deming, 2003; Wells et al., 2006; Garneau et al., 2006). In a series of ^{3}H-leucine assays of prokaryotic production rates in this region (Vallières et al., 2007), the proportional importance of particle-associated activity increased as a function of particulate organic carbon concentrations and ranged from <20% of total production in outer coastal waters to >95% in Mackenzie River waters.

Marine particles are composed of various types of organic and inorganic matter of both terrestrial and aquatic origin. They are enriched in nutrients compared to the surrounding water and are hot-spots of microbial activity. Microorganisms colonizing particles tend to be more abundant than free-living organisms and heterotrophic production of particle-associated communities tends to be higher than production in free-living communities (Simon et al., 2002; Zimmermann-Timm, 2002). Bacterial particle-associated assemblages often differ from their free-living counterparts in freshwater, estuaries and marine systems (Acinas et al., 1999; Bidle and Fletcher, 1995; Crump et al., 1999; Crump and Baross, 2000; Selje and Simon, 2003). For Archaea, the only existing comparison is from the estuary of the Columbia River where particle-associated archaeal assemblages had higher diversity and different taxonomic composition than their free-living counterparts (Crump and Baross, 2000). We have found no reports to date on the taxonomic identity of particle-associated communities of Archaea from purely marine or riverine waters.

The aim of this study was: (i) to compare particle-associated and free-living communities in a geographical region where the abundance of Archaea has previously been correlated with particle concentrations; (ii) to test the hypothesis that archaeal communities are specific to particular aquatic habitats. We described the archaeal communities by cloning and sequencing the 16S rRNA gene from communities sampled across a region stretching from the Mackenzie River to the Beaufort Sea. The study area included 5 sites with different particle loads and encompassed riverine, coastal and open marine waters.

2. Material and methods

2.1. Sample collection and environmental conditions

The study was carried out during sampling cruises conducted in 2002 and 2004 within the framework of Canadian Arctic Shelf Exchange Study (CASES). Sites R3 in the Mackenzie River (69°15.85′ N, 134°05.93′ W) and S1 in the Lake Mackenzie (69°51.78′ N, 132°38.62′ W) were reached by ship-based helicopter. Samples were collected with a 5-Liter Niskin bottle and salinity and temperature were measured with a SBE-19 conductivity, temperature and depth (CTD) profiler. The marine site 303 (70°47.35′ N, 126°56.02′ W) was collected from the icebreaker CCGS *Amundsen* using a Seabird Carousel rosette system of 12-Liter PVC bottles equipped with a Seabird 911+ CTD with fluorometer, transmissometer, pH, oxygen and Photosynthetically Active Radiation (PAR) probes. The estuarine site Z2 (69° 30.60″ N 133° 13.80″ W) was sampled from a Zodiac with a 5-Liter Go-Flow bottle and a SBE-19 CTD (conductivity–temperature–depth) profiler. The coastal site 65 (70° 08.75″ N 133° 30.69″ W) was sampled from the icebreaker CCGS *Pierre Radisson* with 12-Liter Niskin bottles mounted on a SBE Carousel Rosette system equipped with a SBE911-plus CTD profiler.

Microbial biomass was collected by sequentially filtering 1–4 L of seawater through a 47 mm-diameter, 3 μm pore-size polycarbonate filter to capture the particle-associated microbial fraction followed by a 47 mm-diameter 0.2 μm Durapore filter (Millipore) to collect the free-living fraction. The 3 μm pore size was selected based on initial ^{3}H-thymidine and ^{3}H-leucine assays showing that much of the inshore heterotrophic activity in this system was associated with particles retained by this filter type and porosity (Garneau et al., 2006). Filters were stored in buffer (50 mM tris, 40 mM EDTA and 0.75 M sucrose) and frozen at −80 °C until the nucleic acid was extracted as in Lovejoy et al. (2006).

Data for chlorophyll *a*, particulate inorganic (PIM) and organic (POM) material, dissolved organic matter

(DOC), suspended particulate matter (SPM), prokaryotic abundance and the methods used for the measurements are given in Galand et al. (2006, 2008), and were used here to identify the three different types of water: riverine, coastal and marine. Additional environmental and phylogenetic information for the three microbial domains (Bacteria, Archaea and Eukarya) are given in Galand et al. (2008).

2.2. PCR amplification and cloning

Amplification of archaeal 16S rRNA genes by primers 109F and 934R followed the protocol described in Galand et al. (2006). The primer pair has broad "in silico" and proven actual coverage across a number of archaeal groups compared to other primer pairs currently in use (Banning et al., 2005). PCR products were analyzed by gel electrophoresis, purified with Qiaquick PCR Purification Kit (Qiagen) and cloned with TA cloning kit (Invitrogen) according to the manufacturer's instructions. For each library, positive clones were picked and inoculated into LB media in 96 well-plates. For sites Z2 and 65, clones were screened by RFLP with the restriction enzyme TaqI (Invitrogen) and colonies showing distinct RFLP patterns were sequenced as described earlier (Galand et al., 2006). Several representatives of the most numerous RFLP groups from each sample were sequenced to verify that closely related sequences were represented by the single pattern. The similarity between sequences from the same pattern was always >99%. For sites R3, S1 and 303, clones containing inserts were chosen randomly from each library and sequenced directly, without the fingerprinting step using the vectors' T7p universal primer. Sequences for the free-living clone libraries R3, S1 and 303 were obtained from Galand et al. (2008).

Suspected chimeras were checked by using BLAST with sequence segments separately and then using the Chimera check program at Ribosomal Data Project II (Michigan State University; http://rdp8.cme.msu.edu/cgis/chimera.cgi?su=SSU). Between 1 and 7 chimeras were detected and excluded from each library, with highest numbers for the river. The 16S rRNA sequences are available from the GenBank database under accession numbers EU244220–EU244314.

2.3. Sequence analysis, diversity calculations and statistical analysis

The taxonomic position of the sequences was identified by comparison with sequences available at the GenBank database followed by phylogenetic analysis. Briefly, sequences were compared to the database using the BLAST server at the National Center for Biotechnology Information (NCBI), the approximately 800 bp sequences were aligned using the CLUSTAL W package (Thompson et al., 1994), DNADIST from the program PHYLIP (Felsenstein, 2004) was used to calculate genetic distances with Kimura-2 model with 100 data sets obtained by bootstrapping and a distance tree was estimated with FITCH. The tree was used to select the taxonomical clusters further included in the clustering analysis.

The Shannon–Wiener diversity index and the Chao1 non-parametric richness estimator were calculated with the program DOTUR (Schloss and Handelsman, 2005) through a Jukes–Cantor corrected distance matrix obtained using the DNADIST program from PHYLIP (Felsenstein, 2004). To allow for an unbiased comparison between the results obtained by RFLP screening and the results obtained through direct sequencing, the RFLP screened input file used for computing the distance matrix contained sequences repeated as often as they were present in each RFLP group. The 3% distance level between sequences was used for calculation of diversity estimators. For cluster analysis, a distance matrix was computed from the abundance of taxonomic groups in clone libraries using Bray–Curtis similarity and a dendrogram inferred with the unweighted pair-group average (UPGMA) algorithm as implemented in the program PAST (v 1.63, http://folk.uio.no/ohammer/past/).

The Bray–Curtis similarity matrix was used to generate analysis of similarity (ANOSIM) statistics (Clarke and Green, 1988) to verify the significance of the dendrogram clustering by testing the hypothesis that archaeal communities from a same cluster were more similar in composition to each other than to communities in different clusters. To test for possible differences in diversity between free-living and particle-associated communities, the Shannon indices compiled from abundance data defined at the 3% distance level were compared by a t-test within the program PAST (Hammer and Harper, 2002).

3. Results and discussion

3.1. Environmental conditions

The five sampling sites (Table 1) were separated into three physico-chemical groups of aquatic habitats. The first group, riverine water, included station R3 from the Mackenzie River and station S1 from its estuary (Fig. 1). Both had salinities below 1, highest concentrations of

Table 1
Environmental characteristics at stations from the Mackenzie River (R3), Mackenzie estuary (S1 and Z2) and coastal Beaufort Sea (65 and 303)

	Station				
	Riverine		Coastal		Marine
	R3	S1	Z2	65	303
Sampling date	17.06.04	17.06.04	03.10.02	02.10.02	19.06.04
Sample depth (m)	0.5	1.5	1	2	5
Bottom depth (m)	5	9	5	33	260
Temperature (°C)	15.7	1.2	−0.54	−0.44	1.1
Salinity (psu)	0.13	0.97	25.4	26.5	30.86
POM (mg L^{-1})	11.8 (2.8)	11.5 (14.8)	–	–	1.27 (0.18)
PIM (mg L^{-1})	87.2 (6.9)	15.2 (11.1)	–	–	1.74 (1.74)
SPM (mg L^{-1})	99 (9.7)	26.7 (25.9)	17.26	1.75	3.01 (1.92)
DOC (mg C L^{-1})	–	–	2.47	0.88	–
Chl *a* (μg L^{-1})	1.25 (0.25)	1.17 (0.04)	0.51 (0.18)	0.21 (0.12)	0.65 (0.18)
Prokaryotes (10^5 cells mL^{-1})	2.3	10.3	3.9	3.6	4.3

POM: Particulate organic mater; PIM: particulate inorganic mater; SPM: suspended particulate matter; DOC: dissolved organic matter; Chl *a*: chlorophyll *a*. Values in parentheses represent the <3 μm fraction when available.

suspended particulate matter (SPM) and highest chlorophyll *a* values (Table 1). S1 was sampled during spring at a time when the Mackenzie River estuary forms a distinctive feature called Lake Mackenzie (Galand et al., 2008). The lake is formed by the accumulation of riverine water behind a dam of thick sea ice called stamukhi. Throughout the period that the stamukhi retains its integrity (winter to early summer), Lake Mackenzie accumulates freshwater, which explains the riverine conditions at the station S1. The second group, coastal water, included station 65 from the Beaufort shelf and Z2 from the Mackenzie River estuary (Fig. 1). Z2 was sampled in the autumn, a time when the Lake Mackenzie had disappeared and the Mackenzie mouth had reverted to more typical estuarine conditions. Coastal waters were shallow, with higher salinity, lower temperatures and lower suspended particulate matter (SPM) concentrations relative to riverine water (Table 1). The last group represented a marine site, station 303 (Fig. 1). The site had the greatest depth and the water had highest salinity and lowest SPM concentration (Table 1).

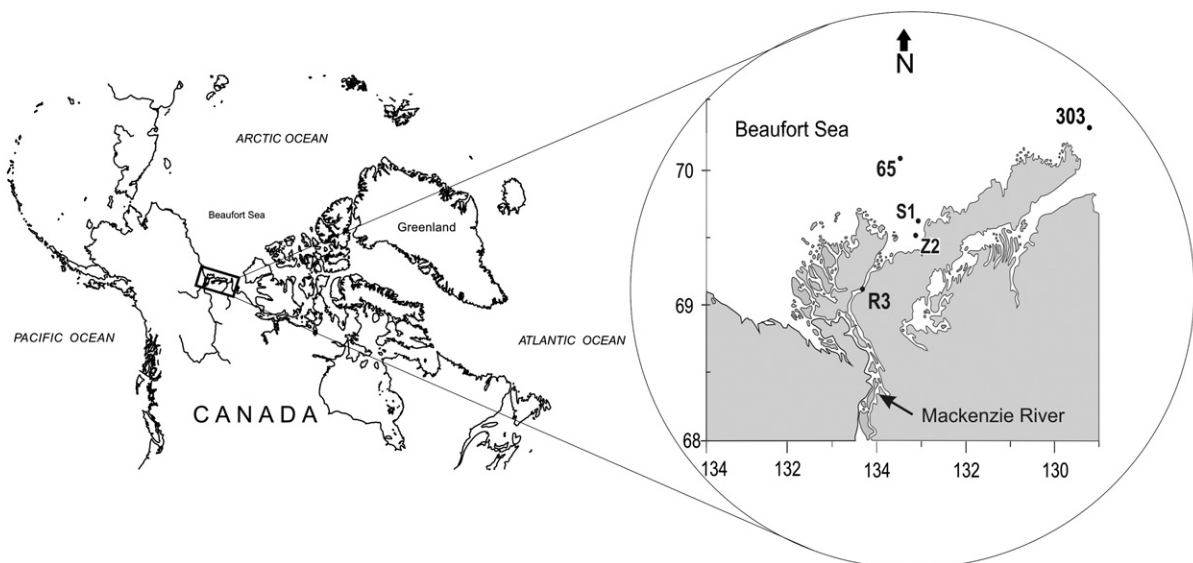

Fig. 1. Location of the sampling sites in the Mackenzie River and Beaufort Sea, Canadian Arctic.

3.2. Free-living versus particle-associated archaeal communities

Analyses of archaeal clone libraries from the three water mass types revealed that there were only minor differences between free-living and particle-associated communities at some sites but clear differences at other sites. These differences included the presence or absence of some taxonomic groups in one of the fractions, and differences in the proportion of the phylogenetic groups. The most noticeable difference was at site S1 where Group II.a represented more than 30% of the particle-associated clones but was totally absent from the free-living library (Fig. 3). Group II.a is a classically marine group suggesting a marine origin for the sequences detected at the site S1. It remains unknown why the Group II.a was only detected in the particle fraction when it was present in both fractions of the adjacent coastal sites (Fig. 3). There were also some clear differences in composition at station 65 marked by the presence of the RC-V cluster and a high proportion of Marine Group I.1a.B in the free-living fraction and not in the particle-associated one (Fig. 3). At site Z2, the difference between fractions was due to variations in the proportion of the phylogenetic groups present rather than the presence or absence of some groups (Fig. 3). Despite the differences in community composition between fractions at those three sites, groups that were detected in the particle fraction at one site were in the free-living fraction at another site; thus we could not identify any phylogenetic groups that were typical of one specific fraction. Additionally, there were no significant differences in diversity between free-living and particle-associated Archaea.

Crump and Baross (2000) compared archaeal communities in the temperate Columbia River and despite a small number of clones, they found differences between fractions in the estuary. Several studies have also compared fractionated bacterial communities and most have reported differences between fractions in rivers, estuaries and marine systems (Acinas et al., 1999; Bidle and Fletcher, 1995; Crump et al., 1999; Crump and Baross, 2000; Selje and Simon, 2003). Our results indicate that as for Bacteria, free-living and particle-associated Archaea can also show differences in community structure. Some Archaea have been identified as endobionts of protists (Lange et al., 2005), and it is possible that some of the archaeal sequences detected in the >3 µm fraction might originate from this source.

There were very small differences between fractions at some of the sites. The smallest differences between free-living and attached fractions were for the riverine site R3 and the marine site 303 (Fig. 3). At site R3 in the Mackenzie River, the same phylogenetic groups were present in similar proportions in both fractions and in the Beaufort Sea site 303, both fractions were dominated by the same phylogenetic group (Fig. 3). Similarly, Hollibaugh et al. (2000) found that there were no differences in bacterial communities between fractions in the San Francisco Bay. The authors suggested that finer additional fractionation of the particles may have revealed different communities. The same might hold for Archaea in the Mackenzie River and Beaufort Sea where differences may exist between communities but not at our separation threshold of 3 µm.

3.3. Distribution of Archaea from the Mackenzie River to the Beaufort Sea

The archaeal clone libraries grouped significantly (ANOSIM, $p<0.05$) into three distinct clusters according to the site they originated from. Consistent with our hypothesis, the results indicate a clear habitat-dependent pattern in the phylogenetic composition of the communities (Fig. 2). The first cluster included R3 and S1 demonstrating that the two riverine sites had similar archaeal communities (Fig. 2). The riverine assemblages were dominated by *Euryarchaeota* mainly from the uncultured RC-V and LDS clusters (Fig. 3). These clusters were originally detected in flooded soils (Grosskopf et al., 1998) and lake sediments (Glissman

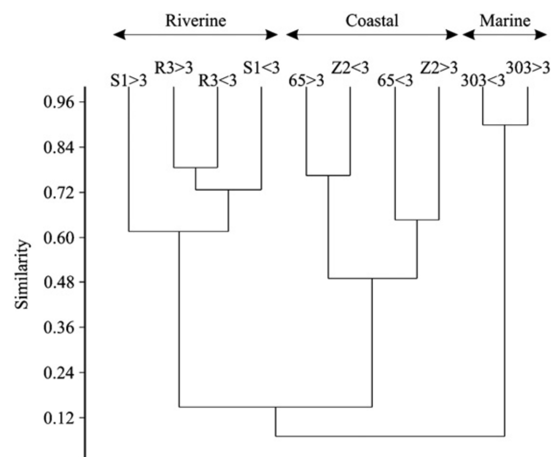

Fig. 2. Dendrogram representing the similarity between the phylogenetic composition of free-living (<3) and particle-associated (>3) archaeal clone libraries from riverine (R3 and S1), coastal (Z2 and 65) and marine (303) water sampled from the Mackenzie River through the Beaufort Sea. The dendrogram was inferred using the unweighted pair-group average (UPGMA) algorithm for the taxonomic group defined in Fig. 3 and based on a distance matrix computed with Bray–Curtis similarity.

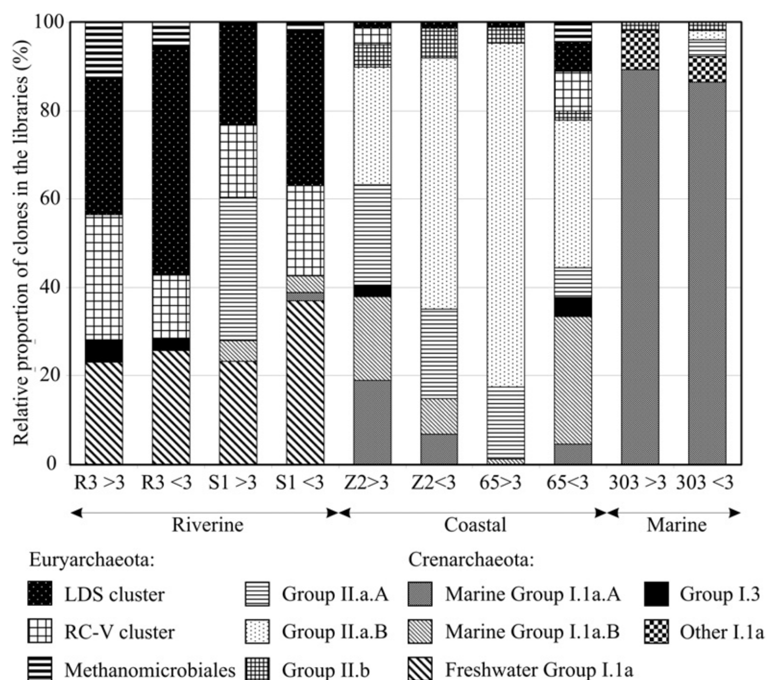

Fig. 3. Community structure of free-living (<3) and particle-associated (>3) Archaea in clone libraries from riverine (R3 and S1), coastal (Z2 and 65) and marine (303) water sampled from the Mackenzie River and the Beaufort Sea. Communities are represented by the relative abundances of clones in the different phylogenetic clusters. The group named Other I.1a includes all crenarchaeotal sequences that were not affiliated to Marine Group I.1a. A, I.1.B or Freshwater Group I.1a.

et al., 2004), and we have previously noted that they were predominant Mackenzie River clone libraries (Galand et al., 2006, 2008) suggesting that they may be a consistent component of riverine archaeal communities. The composition of the S1 community differed slightly from R3 with the additional presence of the Group II.a of probable marine origin. S1 was situated in the freshwater Lake Mackenzie (see materials and methods for definition), and exchanges taking place between the lake and the adjacent Beaufort Sea through and below the porous ice dam probably brought the Group II.a to site S1. Crenarchaeotal sequences were also present in both fractions of the riverine libraries and belonged mainly to the newly defined Freshwater Group I.1a, a freshwater sub-cluster of the Marine Group I.1a (Galand et al., 2008).

The second cluster grouped together the two coastal sites Z2 and 65 (Fig. 2). These differed greatly from the freshwater clusters, consistent with the conclusion that the river is not an allochthonous source of the coastal Archaea (Galand et al., 2006). The latter hypothesis had been advanced on the basis of correlations between Archaea and particles (Wells et al., 2006), and although it is no longer supportable for Archaea, allochthony may explain the widespread presence of freshwater picocyanobacteria in this coastal region (Waleron et al., 2007). The libraries at both Z2 and 65 were dominated by euryarchaeotal sequences but these were different from the riverine *Euryarchaeota* (Fig. 3). The coastal libraries contained mostly sequences belonging to the marine Group II.a and among *Crenarchaeota*, the most abundant sequences belonged to Marine Group I.1a.B (Fig. 3). High abundances of *Euryarchaeota* have been reported earlier from surface waters of temperate oceans but rarely for polar environments, which are usually dominated by *Crenarchaeota* (Massana et al., 2000; Bano et al., 2004; Kirchman et al., 2007). The coastal and the riverine clone libraries had the highest diversity (Table 2; Fig. 4) suggesting that Archaea are more diverse in riverine or river influenced waters than in more marine waters. Such a result has been reported earlier for a coastal lagoon which had higher archaeal diversity than its adjacent sea (LaMontagne and Holden, 2003) and for the Columbia River estuary (Crump and Baross, 2000).

The marine libraries (303) formed the third cluster and in contrast to the coastal libraries, the marine libraries contained almost exclusively sequences affiliated to the crenarchaeotal marine Group I.1a (Fig. 3). The archaeal community at the marine station resembled

Table 2
Diversity of free-living (<3) and particle-associated (>3) archaeal communities in the Mackenzie River (R3), the Mackenzie estuary (S1 and Z2) and the coastal Beaufort Sea (65 and 303)

	Riverine				Coastal				Marine	
	R3<3	R3>3	S1<3	S1>3	Z2<3	Z2>3	65<3	65>3	303<3	303>3
No. of OTUs	21.5	30	29	23	7	9.5	12.5	5.5	4	2.7
Shannon index	2.8	3.2	2.7	2.7	1.3	1.3	1.8	0.5	0.3	0.1
Chao1 (±95% CI)	35.5±25	90±50.7	64.5±41.5	70±38.6	7.5±7	24.5±12.8	18±18.5	7±5.6	4.5±4	3.4±2.5
No. of clones	36	40	56	42	75	79	46	86	52	57

Number of OTUs and diversity indices were estimated for a 97% distance threshold between sequences.

earlier descriptions of arctic surface communities for which *Crenarchaeota* were dominant in both the central Arctic Ocean (Bano et al., 2004) and the Western Arctic Ocean (Kirchman et al., 2007). More variability has been observed in Antarctic waters where surface Archaea communities may follow seasonal patterns with a dominance of *Crenarchaeota* during winter (Church et al., 2003; Massana et al., 2000) and a prevalence of *Euryarchaeota* during summer (Church et al., 2003) and early spring (Massana et al., 1998). Arctic winter data is needed to test whether the communities exhibit similar seasonality. Members of marine *Crenarchaeota* have recently been identified as ammonia oxidisers (Konneke et al., 2005) and data suggest a major role for Archaea in oceanic nitrification (Wuchter et al., 2006). The high number of Crenarchaeota detected in Arctic waters could indicate a potential for Archaea in providing new nutrients to Arctic waters, known to be depleted in nitrate (Yamamoto-Kawai et al., 2006).

Coastal communities dominated by *Euryarchaeota* Group II.a contrasted sharply with the marine assemblages. Coastal waters were more influenced by the discharge of the Mackenzie River with lower salinity and higher particle loads and an abundance of euryarchaeotal sequences suggesting that *Euryarchaeota* in Arctic surface water is associated with specific physico-chemical characteristics. Using fluorescence in situ hybridization techniques, Kirchman et al. (2007) reported very low abundance of *Euryarchaeota* in surface waters of the Western Arctic, a region with very little direct river inputs. In contrast *Crenarchaeota* have been reported from upper mixed layer waters with little river influence such as in the central Arctic Ocean (Bano et al., 2004), and the Western Arctic (Kirchman et al., 2007), suggesting that these waters have more in common with meso- and bathypelagic waters, where *Crenarchaeota* are most often reported (Teira et al., 2006).

4. Conclusions

The Arctic Ocean is strongly influenced by the surrounding large rivers that supply significant amounts of particles to adjacent seas. Particle-rich waters of the Arctic harbour diverse and abundant communities of

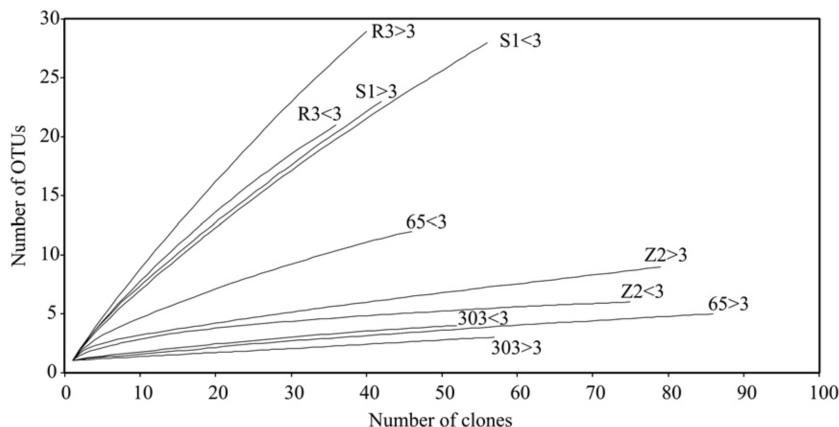

Fig. 4. Rarefaction curves calculated for the archaeal clone libraries from the free-living (<3) and particle-associated (>3) fractions of riverine (R3 and S1), coastal (Z2 and 65) and marine (303) water sampled from the Mackenzie River through the Beaufort Sea. Rarefaction is calculated with DOTUR at the 3% distance level.

Archaea (Garneau et al., 2006; Wells et al., 2006), which could play an important role in processing terrigenous inputs. Our study shows that there are clear differences in community composition of the Beaufort Sea region, not only between the river and the sea but also between coastal and offshore systems. The three sites with their particle-associated microenvironments likely provide qualitatively distinct inorganic and organic substrates for Archaea, leading to the distinct communities within these environments. The two different groups of *Euryarchaeota* detected in riverine and coastal waters may be more adapted to particle-rich waters, while the *Crenarchaeota* found in the marine system could be less involved in processing particulate matter and more adapted to oceanic conditions, including such as autochthonous organic carbon and oligotrophy. In addition, we found substantial archaeal diversity in these communities, implying that even extreme arctic environments are habitats for taxonomically diverse microbiota.

Acknowledgements

Financial support for this study was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Canada Research Chair program, Fonds québécois de recherche sur la nature et les technologies (FQRNT) and Indian and Northern Affairs Canada. We thank the officers and crew of the CCGS *Amundsen* and *Pierre Radisson,* and C. Martineau, S. Roy, R. Terrado, M.-J. Martineau and M. Rautio for field assistance and analysis. We also thank two anonymous reviewers for their insightful comments. This work was conducted within the Canadian Arctic Shelf Exchange Study (CASES).

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