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Distinct Communities of Free-Living and Copepod-Associated Microorganisms along a Salinity Gradient in Godthåbsfjord, West Greenland

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Abstract

Microorganisms such as *Bacteria* and *Archaea* play important roles in the Arctic food web and biogeochemical cycles. Nevertheless, knowledge of microbial community composition in Greenland waters is scarce, and information on microorganisms associated with Arctic zooplankton species is virtually non-existent. We compared free-living microbial communities with those associated with two key copepod species (*Calanus finmarchicus* and *Metridia longa*) along a salinity gradient from the deep waters beyond Fyllas Banke to the inner part of Godthåbsfjord, West Greenland, in summer 2008. Using genetic fingerprinting we found that free-living *Bacteria* (in particular *Alphaproteobacteria*) and *Archaea* varied with environmental factors and formed different communities along the fjord. Microbial communities associated with the two copepod species were clearly different from those in the ambient water. Surprisingly, *Archaea* could not be detected on the copepods. Our results show that zooplankton form ''microbial islands'' in the Arctic pelagic realm with a distinctive community composition and presumably functionality different from the free-living *Bacteria*. Changes in intensity and timing of meltwater runoff due to global warming are expected to affect these microbial assemblages differently, with potentially significantly ramifications for Arctic food webs and biogeochemistry.

Introduction

Microbial diversity is influenced by environmental conditions and in turn influences biogeochemical cycles in aquatic ecosystems. Over the past decades, it has become clear that particle-associated bacteria can far exceed free-living bacteria in concentrations and activities (reviewed by Simon et al., 2002); yet, due to methodological reasons (Grossart, 2010), sampling protocols still often underestimate or totally exclude microbes associated with larger organisms such as zooplankton and fish. Globally, mesozooplankton consume on average 12% of oceanic primary production (Calbet, 2001). Consequently, the diverse and active microbial communities associated with zooplankton can potentially exploit an enormous amount of organic carbon passing through the hosts (reviewed by Tang et al., 2010).

Culture-based studies have shown that zooplankton harbor similar bacterial phylotypes as the ambient water, but in different proportions (Sochard et al., 1979; Delille and Razouls, 1994; Hansen and Bech, 1996), suggesting an active exchange between both habitats, but the different environmental conditions therein favor different microbes. Recent molecular studies showed that free-living and zooplankton-associated bacterial community compositions significantly differ from each other (Grossart et al., 2009) and that the latter can be influenced by the zooplankton's food source (Tang et al., 2009). The zooplankton gut provides an anoxic environment (Tang et al., 2011a) that may support important anaerobic processes such as nitrogen fixation (Proctor, 1997) and methanogenesis (DeAngelis and Lee, 1994). Additionally, migrating zooplankton can transport associated microbes over long distances and across stratified water columns (Grossart et al., 2010). Taken together, these studies suggest that zooplankton are ''microbial islands'' that help maintain microbial diversity, growth, and activity, and serve as important microbial reservoirs and hot spots for increased gene exchange in the pelagic zone (Grossart and Tang, 2010).

Godthåbsfjord (Nuup Kangerla) and other fjords in West Greenland are very productive (Smidt, 1979) and contribute significantly to Greenland's economy (Storr-Paulsen et al., 2004). They are also important feeding grounds for marine mammals (Born et al., 2003; Aquarone, 2004) and wintering habitats for seabirds (Boertmann et al., 2004; Merkel et al., 2006). Greenland fjords are undergoing rapid changes due to global warming and increasing

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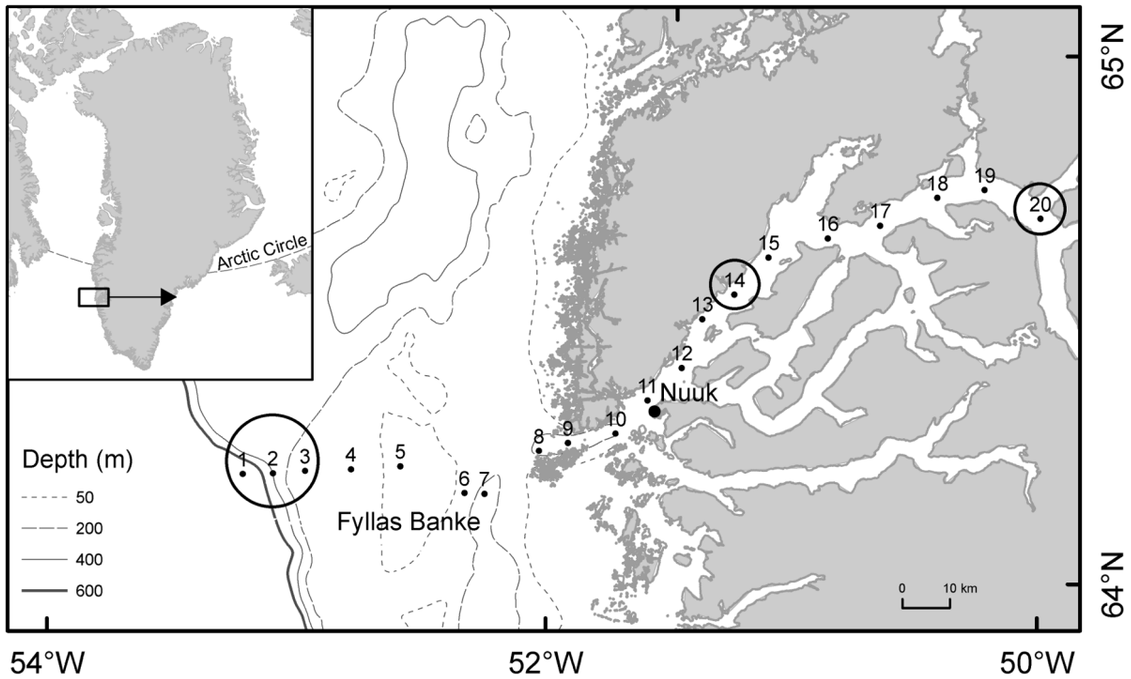

FIGURE 1. Sampling stations in Godthåbsfjord, West Greenland. Water samples were collected at all stations. At stations 1–3, *Calanus finmarchicus* was sampled; at stations 10, 14, and 20, *Metridia longa* (marked by black circles). At station 1, a sample of *M. longa* was also taken.

meltwater runoff from the Greenland Ice Sheet (Mortensen et al., 2011; Motyka et al., 2011; Hansen et al., 2012; Mortensen et al., 2013), which potentially affect microbial communities directly, or indirectly by altering phytoplankton (Carmack et al., 2004) and zooplankton succession (Rysgaard et al., 1999). The specific hydrographic structure of the region is described by Mortensen et al. (2011). Microbial diversity and related ecological functions in the Greenland Arctic have only been studied sparingly (Borsheim, 2000; Miteva et al., 2004; Frette et al., 2010), and none of those studies has included microorganisms associated with zooplankton.

In the present study, we compared the microbial community in the ambient water with those associated with two key copepod species (*Calanus finmarchicus* and *Metridia longa*) in Godthåbsfjord, West Greenland (Fig. 1) and investigated how these microbial communities varied along the fjord in relation to environmental variables. The two copepod species have different horizontal and depth distributions along the fjord due to their association with different water masses (Arendt et al., 2010; Tang et al., 2011b). Both reside at different depths allowing them to interact with different microbial communities within the water column (Table 1).

Experimental Procedures

SAMPLING

Samples were collected during 23 July to 3 August 2008, on board the R/V *Dana*, from the shelf slope off Fyllas Banke to the inner part of Godthåbsfjord, which is connected to the Greenland Ice Sheet (Fig. 1; see Tang et al., 2011b, and Arendt et al., 2010, for hydrographical features). Vertical profiles of water temperature, salinity, density, and fluorescence were recorded from the surface to ~5 m above the bottom by a CTD (SBE 19plus, SeaCat) equipped with a Seapoint chlorophyll *a* fluorometer and a Biospherical/Licor sensor. Water samples were collected by Niskin bottles from different depths. On board, a 200 mL aliquot of each water sample was filtered onto a 0.2 μm pore polycarbonate membrane filter, and immediately preserved at −80 °C. Copepod samples were collected with a multinet throughout a diel cycle (sunset, midnight, sunrise, and midday). The numerically dominant species selected for further analysis were females of *Calanus finmarchicus* at stations 1, 2, and 3, and *Metridia longa* at stations 1, 10, 14, and 20. Depending on the size of the species, 2–15 individuals

TABLE 1

Median depth (m) of population mass during daytime (D) and nighttime (N) at the sampled stations based on data of Tang et al. (2011).

	Station 1		Station 2		Station 3		Station 10		Station 14		Station 20	
	D	N	D	N	D	N	D	N	D	N	D	N
Calanus finmarchicus (C4-adult)	80	30	55	30	55	6						
Metridia longa (C4-adult)	250	250					80	80	150	40	60	50

were briefly rinsed in 0.2 μm-filtered seawater, then transferred to cryovials, and immediately preserved at −80 °C until further processing.

MOLECULAR BIOLOGICAL ANALYSES

We used *Bacteria*-specific denaturing gradient gel electrophoresis (DGGE) to look for the overall phylotype diversity. Because DGGE showed only one band for each dominant phylotype (i.e. at least 1% of the community that was targeted by the respective primers), we also used more taxon-specific DGGE to capture the diversity within a particular phylogenetic taxon. Nucleic acids were extracted with phenol-chloroform and zirconium beads (Allgaier and Grossart, 2006). Thereafter, parts of the 16S rRNA gene was amplified for (i) *Archaea* with the primer pair 344f-gc (Raskin et al., 1994) and 915r (Casamayor et al., 2002) in a nested approach after amplification with the primer pair 21f (DeLong, 1992) and 1492r (Lane, 1991), (ii) *Bacteria* with 341f-gc (Muyzer et al., 1993) and 907r (Teske et al., 1996), (iii) *Alphaproteobacteria* with 341f-gc and Alf968r (Neef et al., 1999), and (iv) *Actinobacteria* with HGC236f-gc and HGC664r (Glöckner et al., 2000). DGGE was conducted using an IngenyPhorU system. All gels were loaded with at least three standard samples (both sides and in the middle) to increase comparability between different gels. Gels were run for 20 h at 100 V and stained with SybrGold; the gel pictures were imported into GelComparII and analyzed by using the Dice coefficient based on presence/absence of bands only. Dominant DGGE bands were excised, eluded in 1xTE buffer, reamplified using the same primers as for DGGE but without the GC clamp, cleaned with PEG (Rosenthal et al., 2003), and sequenced commercially (Macrogen, Korea). Analyses of DGGE banding patterns were done in Primer6 using non-metric multi-dimensional scaling (MDS), analysis of similarities (ANOSIM), and Mantel-Test (RELATE function).

Clone libraries were constructed for one water sample and one sample of each copepod species from station 1 using the bacterial primer 27f (Giovannoni, 1991), and the universal primer 1492r (Lane, 1991) for *Bacteria*, and the same primer set as for DGGE for *Archaea*. This station was chosen as it was the only station with both copepod species present. Copepod samples were from 100–200 m depth, whereas the water sample was from 100 m since water samples from 100–200 m depth were almost identical (only one different DGGE band). Cloning was done following the manufacturer's protocol of the pGEM-T easy cloning kit (Qiagen), and clones were then sequenced commercially. All sequences were deposited in the European Bioinformatics Institute (EMBL-EMI) under the accession numbers HE863328–HE863652 and were aligned using the SINA aligner of the SILVA database (http://www.arb-silva.de) and manual corrections in ARB (http://www.arb-home.de). Trees were constructed within ARB; the final tree was constructed using FASTTREE 2.1.4 (Price et al., 2009) and checked for stability by comparing the different approaches.

Results

COMMUNITY COMPOSITION OF FREE-LIVING PROKARYOTES

The water samples showed diverse DGGE banding patterns for *Archaea*, *Bacteria*, *Alphaproteobacteria*, and *Actinobacteria* along the fjord and with depth based on the partial 16S rRNA gene. Among them, detected diversities of *Archaea* and *Actinobacteria* were lowest with an average of 6 and 7 bands, and a maximum of 12 and 11 bands for an individual sample, respectively. *Bacteria*-specific DGGE revealed an average of 15 and a maximum of 21 bands per sample. *Alphaproteobacteria* showed an average of 15 and a maximum of 20 bands per sample. *Bacteria* among samples were phylogenetically similar and had lowest similarities of ~50%; *Alphaproteobacteria* and *Actinobacteria* differed more and had lowest similarities of only 30%. *Archaea* varied the most among samples and had lowest similarities of 18%.

Comparison of DGGE banding patterns with environmental data revealed a tight correlation with station and depth and hence with salinity and density (Table 2). Significant differences were also detected among the three regions (slope, outer sill, main fjord basin) for all primer sets (Table 2). Dependence on stations based on ANOSIM was found for *Bacteria*, *Alphaproteobacteria*, and *Archaea* (Table 3), and it was also evident for *Actinobacteria* based on the Mantel-Test (Table 2). Among the measured environmental variables, salinity (correlating with station), density, and depths had the strongest effects.

COMPARISON BETWEEN FREE-LIVING AND COPEPOD-ASSOCIATED PROKARYOTES

We did not detect any *Archaea* in our copepod samples. Although we yielded a PCR amplification product with the correct

TABLE 2

Results of Mantel-Test (9999 permutations, Primer6 Relate function) for the comparison of DGGE banding pattern (presence/absence of bands using DICE correlation) of the water samples and environmental data. Significances are given in bold.

	All	Salinity	Temperature	Fluorescence (Chl *a*)	Density	Depth	Station
Bacteria	$R = 0.246$	$R = 0.12$	$R = 0.011$	$R = 0.134$	$R = 0.113$	$R = 0.116$	$R = 0.52$
	$\mathbf{p = 0.0003}$	$\mathbf{p = 0.0142}$	$p = 0.388$	$\mathbf{p = 0.0079}$	$\mathbf{p = 0.0177}$	$\mathbf{p = 0.0107}$	$\mathbf{p = 0.0001}$
Archaea	$R = 0.137$	$R = 0.143$	$R = 0.051$	$R = -0.01$	$R = 0.13$	$R = 0.115$	$R = 0.116$
	$\mathbf{p = 0.0178}$	$\mathbf{p = 0.0198}$	$p = 0.2026$	$p = 0.528$	$\mathbf{p = 0.022}$	$\mathbf{p = 0.0058}$	$\mathbf{p = 0.0254}$
Alphaproteobacteria	$R = 0.211$	$R = 0.282$	$R = 0.113$	$R = 0.087$	$R = 0.276$	$R = 0.175$	$R = 0.427$
	$\mathbf{p = 0.0004}$	$\mathbf{p = 0.0001}$	$\mathbf{p = 0.0288}$	$p = 0.0559$	$\mathbf{p = 0.0001}$	$\mathbf{p = 0.0006}$	$\mathbf{p = 0.0001}$
Actinobacteria	$R = 0.073$	$R = 0.047$	$R = 0.028$	$R = -0.018$	$R = 0.042$	$R = 0.043$	$R = 0.262$
	$p = 0.0884$	$p = 0.1732$	$p = 0.2835$	$p = 0.6163$	$p = 0.1845$	$p = 0.1391$	$\mathbf{p = 0.0001}$

TABLE 3

ANOSIM results (Primer6) of DGGE banding pattern similarity of zooplankton and water samples in relation to each other and in dependence of sampling area. Significances are given in bold.

		Bacteria		*Alphaproteobacteria*		*Archaea*		*Actinobacteria*	
		R	*p*	*R*	*p*	*R*	*p*	*R*	*p*
Zooplankton vs. water	Water vs. Zooplankton (*C. finmarchicus* + *M. longa*)	0.687	**0.001**	0.630	**0.001**	—	—	—	—
	Water vs. *C. finmarchicus* vs. *M. longa*	0.930	**0.001**	0.804	**0.001**	—	—	—	—
	Water vs. *M. longa*	0.953	**0.001**	0.858	**0.001**	—	—	—	—
	Water vs. *C. finmarchicus*	0.905	**0.001**	0.814	**0.001**	—	—	—	—
Sampling stations	Water and zooplankton samples	0.101	**0.029**	0.226	**0.001**	—	—	—	—
	Water	0.488	**0.001**	0.650	**0.001**	0.170	0.024	0.075	0.155
	M. longa	0.046	0.321	0.157	0.169	—	—	—	—
	C. finmarchicus	0.595	**0.001**	0.702	**0.001**	—	—	—	—
Regions	Water and zooplankton samples	0.173	**0.004**	0.154	**0.001**	—	—	—	—
	Water	0.627	**0.001**	0.353	**0.002**	0.314	**0.009**	0.299	**0.002**
	M. longa	0.046	0.333	0.157	0.149	—	—	—	—
	C. finmarchicus	—	—	—	—	—	—	—	—

length, it likely did not belong to 16S rRNA genes because the sequences obtained by clone libraries did not yield any match in BLAST, the SILVA database, or RDP (Ribosomal Database Project), and could not be reasonably aligned by the ARB integrated aligner or SINA aligner of the SILVA homepage. However, it is also possible that *Archaea* in the samples were not detected due to primer biases or interference from other DNA. *Actinobacteria* were only detectable in the ambient water with specific PCR, and the relatively weak PCR products indicated that *Actinobacteria* were less abundant than the other tested phylogenetic taxa.

DGGE with *Bacteria*-specific PCR products on copepod samples resulted in 11–22 bands per sample of *Calanus finmarchicus*, and 6–12 bands per sample of *Metridia longa* with two dominant bands representing chloroplasts. *Alphaproteobacteria* showed a comparable diversity with 9–16 and 7–13 DGGE bands per sample of *C. finmarchicus* and *M. longa,* respectively. Four of these bands were present in almost all copepod samples representing *Rhodobacteraceae* (*Sulfitobacter* sp. and *Thalassiobius* sp.). ANOSIM analyses using DGGE banding patterns of *Bacteria* and *Alphaproteobacteria* revealed a strong correlation with sampling station for *C. finmarchicus*, but not for *M. longa* (Table 3). For the latter, also, no correlation with the sampling region was found. Comparison of DGGE banding patterns of water samples and both copepod species showed significant differences (Table 3 and Fig. 2).

Clone libraries and sequences of DGGE bands revealed 39 different prokaryotic clusters containing sequences from water and/or copepod samples originating from the same water mass (Fig. 3). Four of these clusters contained clones from water plus at least one of the copepod species, whereas all other clusters represented either free-living (22 clusters) or copepod-associated (11 clusters) *Bacteria*. *Archaea* (2 clusters) were exclusively found in the ambient water. Furthermore, *Oceanospirillales* and members of the *SAR11* cluster—well known to be free-living—were exclusively found in water samples in all regions. Our clone libraries from both copepods and ambient water at station 1 indicated substantial differences among sample types even at the class level (Fig. 4). A large fraction of the sequences from *M. longa* belonged to chloroplasts, which may originate from ingested phytoplankton.

Discussion

The Greenland Ice Sheet is the largest ice body on land after the Antarctic Ice Sheet, and global warming continues to threaten its existence (Krabill et al., 2000; Chen et al., 2006; Hanna et al., 2008). Maximum summer melting of the Greenland Ice Sheet has accelerated in recent decades, especially in SW Greenland (Rignot and Kanagaratnam, 2006; Velicogna and Wahr, 2006), which could inject large amounts of freshwater into Arctic fjords (Rysgaard et al., 2003; Willis et al., 2006; Mortensen et al., 2011, 2013). Breaching of ice-dammed lakes would also discharge a huge amount of freshwater from supraglacial lakes into the western Greenland coastal sea (Krawczynski et al., 2009). Indigenous biota must adjust or otherwise succumb to these changes.

Increased freshwater addition to the surface layers (0–20 m depth) enhances the estuarine circulation (Kaartvedt and Svendsen, 1990; Rysgaard et al., 2003), i.e. brings nutrient-rich water up in front of the ice sheet and stimulates primary production at the innermost part of the fjord. However, another and much more important freshwater source to the Godthåbsfjord is the subglacial freshwater discharge (30–60 m depth) recently described by Mortensen et al. (2013). This subglacial discharge strengthens the upwelling in the bottom of the fjord, but in the fjord proper the freshwater intensifies stratification, traps heat in the surface waters, reduces mixing of nutrients to the surface layer after the spring bloom, and favors small phytoplankton growing in the pycnocline. These changes in the primary producers will impact the succession, composition, and production of the zooplankton and the higher trophic levels (Greene et al., 2008). In light of our results, these changes will likely also influence both the free-living and zooplankton-associated microbial community compositions, an aspect lesser studied in Greenland climate change research, but one that poten-

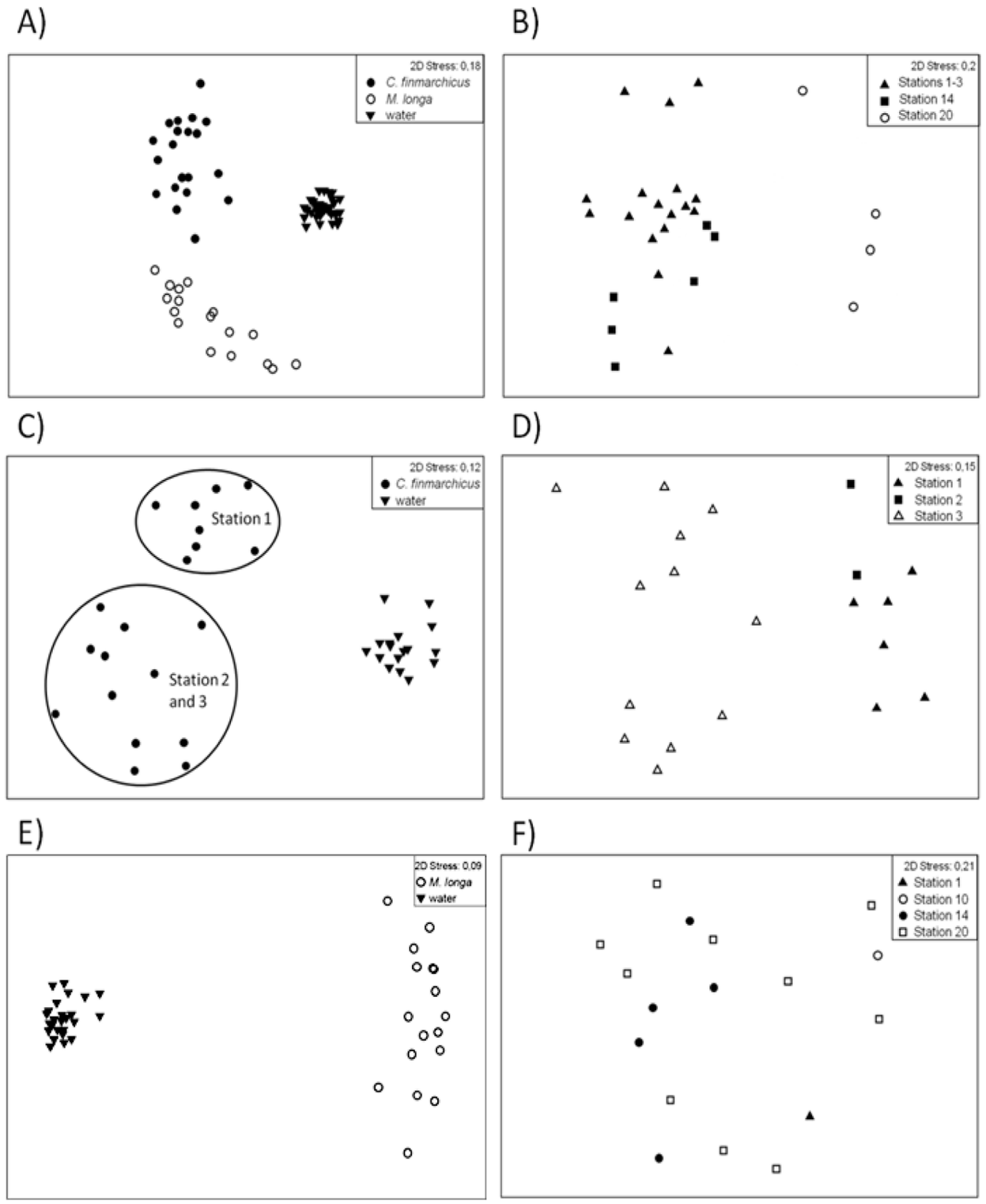

FIGURE 2. Multi-dimensional scaling (MDS) based on the denaturing gradient gel electrophoresis (DGGE) banding patterns with bacterial specific primers: (a) all samples, (b) water samples, (c) water (stations 1–3) and *C. finmarchicus* samples, (d) *C. finmarchicus* samples, (e) water (all stations) and *M. longa* samples, and (f) *M. longa* samples.

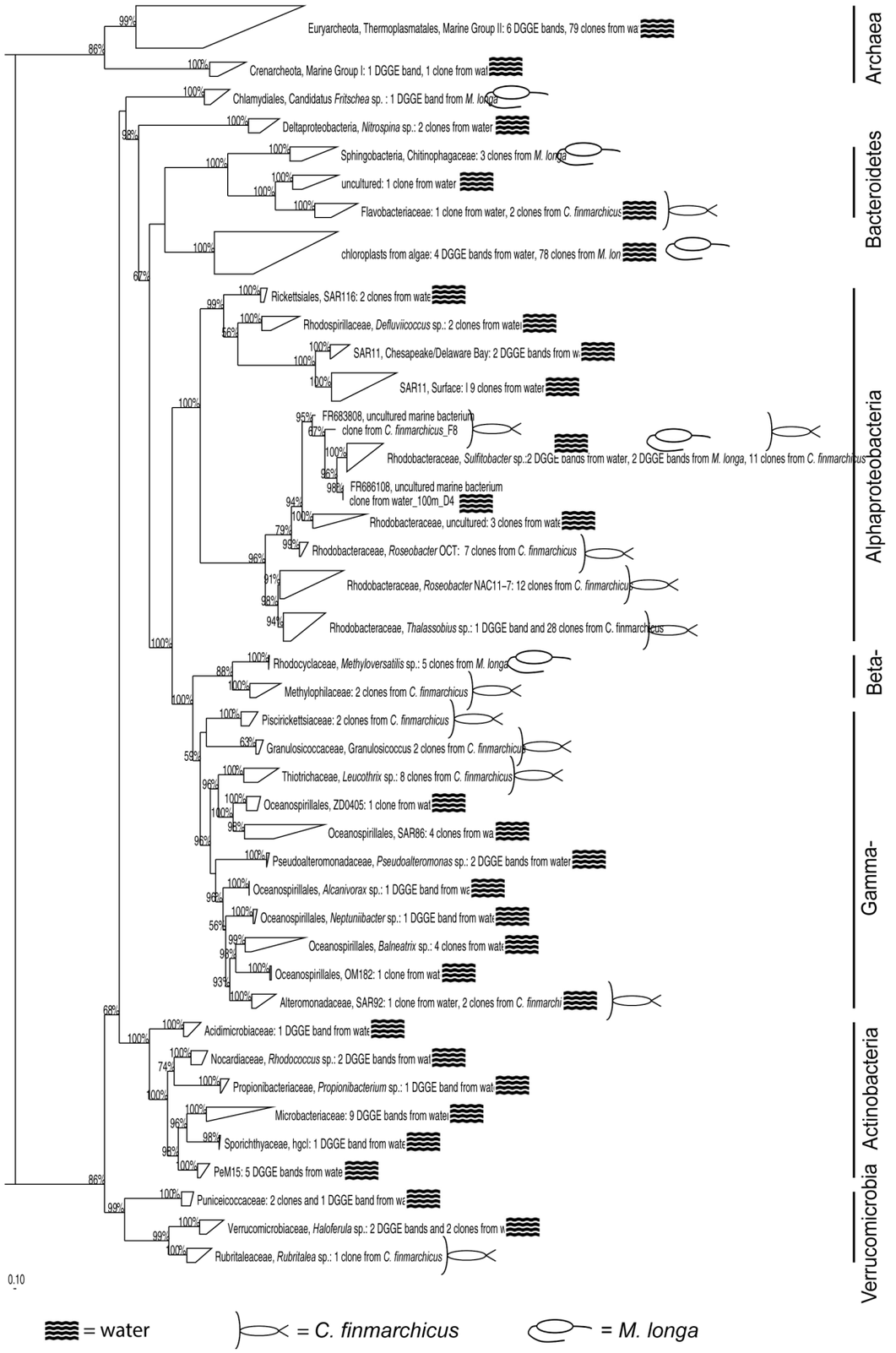

FIGURE 3. Phylogenetic tree of clone libraries and cut-out DGGE bands from water and copepod samples constructed with the ARB software. All *Actinobacteria*-related sequences originated from a selective DGGE on *Actinobacteria*.

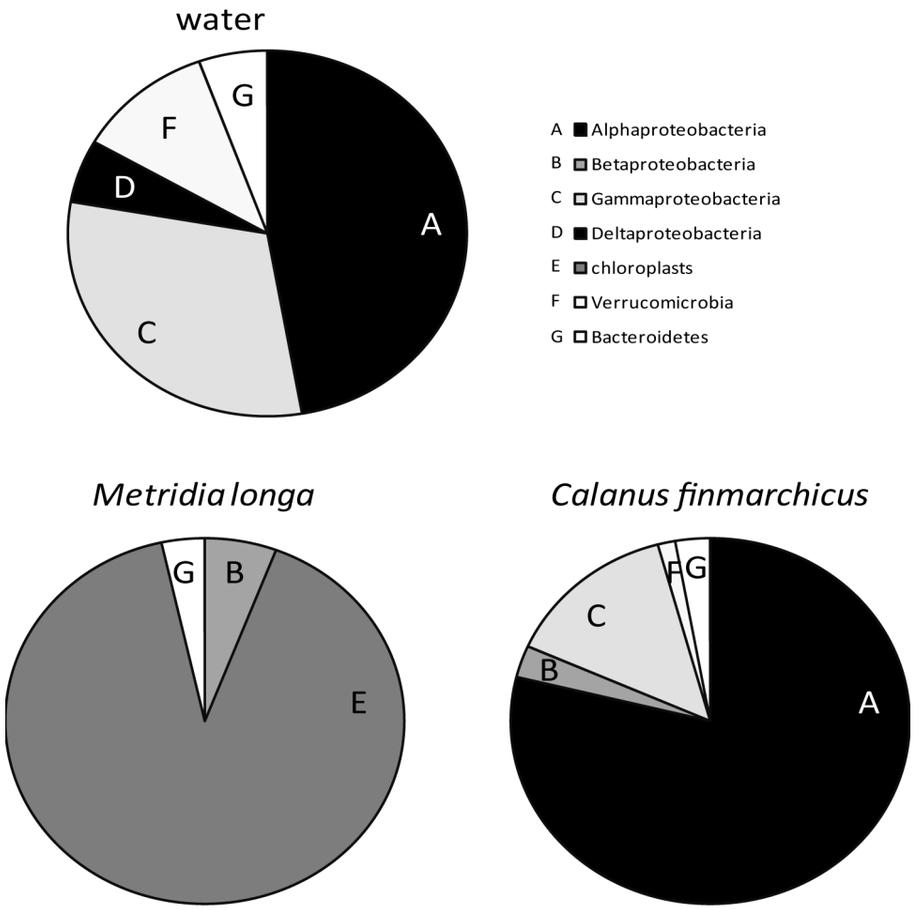

FIGURE 4. Distribution of obtained clones from two copepod species and their ambient water.

tially has significant ramifications for the region's productivity and biogeochemistry.

COMMUNITY COMPOSITION OF FREE-LIVING PROKARYOTES

Previous studies of the bacterial community composition in the Central Arctic Basin reported between 12 and 30 DGGE bands (Ferrari and Hollibaugh, 1999) of which *Bacteria* were mainly composed of *SAR11*, other *Alphaproteobacteria*, *Gammaproteobacteria*, *CFBs*, and *Verrucomicrobia* (Bano and Hollibaugh, 2002). In addition, other studies found mainly *Alphaproteobacteria* and *Bacteroidetes* in pack ice and polar waters (Brinkmeyer et al., 2003; Garneau et al., 2006; Alonso-Saez et al., 2008). We found similar bacterial community composition in our study site (Godthåbsfjord) with the addition of *Nitrospina* spp. (*Deltaproteobacteria*) and *Actinobacteria*, the latter only detectable by specific PCR with no respective sequences in DGGE fingerprinting and clone libraries. We also found members of the *Oceanospirillales* cluster such as *Neptuniibacter* sp. and the *Verrucomicrobia Haloferula* sp., which have not been reported for Arctic marine waters before.

The reported abundance of *Archaea* in Arctic waters varies between 1.3% (Garneau et al., 2006) and 16% (Alonso-Saez et al., 2008). These *Archaea* are mostly composed of the *Marine Groups I*, *II*, and *IV*, with *Group I* being the most dominant (Bano et al., 2004). In our study, we found *Marine Group II* (*Euryarcheota*) and only one DGGE band from *Marine Group I* (*Crenarcheota*), which could be due to biases in our primer system (Gantner et al., 2011) or sampling time as they were also found in low abundances in the prior summer (Alonso-Saez et al., 2008).

COPEPOD-ASSOCIATED PROKARYOTES

Many of the sequences were found only on one of the two copepod species, suggesting host-specific affiliation of *Bacteria* with the caveat that the large amount of chloroplast sequences may have disguised bacterial community composition associated with *M. longa*. A DGGE band related to Candidatus *Fritschea* sp. of the *Chlamydiales* (Fig. 3) was found in all except one sample of *M. longa*, but in none of the *C. finmarchicus* samples. This bacterial species is known to be an insect endosymbiont (Everett et al., 2005) or pathogen (Corsaro and Greub, 2006). Likewise, a potentially chitinolytic bacterium related to *Chitinophagaceae* was only detected in *M. longa*, consistent with the more omnivorous nature of *M. longa* that includes other copepods in its diet, in contrast to *C. finmarchicus*, which primarily feeds on phytoplankton (Sargent and Falk-Petersen, 1988).

In contrast to *M. longa,* many sequences of *Roseobacter* sp. were detected on *C. finmarchicus.* This group is also known to be associated with *Calanus* spp. of the North Sea (Møller et al., 2007) and *Acartia tonsa* of the Chesapeake Bay (Tang et al., 2009). *Roseobacter*-affiliated sequences obtained in our study belonged to two different clades (Fig. 3): (i) the *clade OCT* was previously

found in sea ice, sediment, coastal water, and deep-sea sediment, and (ii) the *clade NAC11-7* was detected in coastal waters, on phytoplankton, and in a sample of a brittle star (Buchan et al., 2005), as well as on copepods in the North Sea (Gerdts et al., 2013). Thus, the *clade OCT* seems to be adapted to cold environments whereas the other clade seems to be generally associated with other organisms. Some sequences we found associated with copepods were also detected in four copepod species in the North Sea including *Flavobacteriaceae*, *Sulfitobacter* spp., and *Sphingobacteria* (Gerdts et al., 2013). These results suggest that the respective bacteria are adapted to a life interacting with copepods over a broad geographic range. Many of the sequences such as *Flavobacteriaceae* (Tian et al., 2009), *Methylophilaceae* (Galand et al., 2008), *Thiotrichaceae* (Tian et al., 2009), and *Piscirickettsiaceae* (Tian et al., 2009) have also been described for polar regions. Interestingly, the group *Methylophilaceae* was mainly found in rivers (Liu et al., 2012; Murkherjee et al., 2013) suggesting that these bacteria originated from meltwater.

While our analysis on the 16S rRNA gene level provides important information on the genetic diversity of the bacterial communities, information on the functionality of these bacterial communities is still lacking. Nevertheless, the distinctions in bacterial community composition among the two copepod species and the ambient water suggest that these different bacterial communities may drive different biogeochemical processes in the water column. For example, the *Chitinophagacea* in *M. longa* may aid prey digestion by breaking down chitin. In addition, bacteria on the carapaces of the copepods may protect the hosts against pathogens and foulers (reviewed in Wahl et al., 2012). The anaerobic gut of copepods may support methanogenesis (DeAngelis and Lee, 1994) that is otherwise not favored in the oxic water column. Further investigation into the functional genotypes of these bacteria will be valuable.

MICROBIAL ISLANDS IN A CHANGING OCEAN

Bacteria and zooplankton are mostly seen as separate functional groups in an ecosystem only weakly and indirectly linked via nutrient cycling and trophic interactions (Azam and Malfatti, 2007). However, in reality *Bacteria* and zooplankton can be tightly linked with each other (Grossart and Tang, 2010; Tang et al., 2010) such that zooplankton can directly affect bacterial behavior, growth, and biogeochemical activities (Dattagupta et al., 2009). In our study, we found distinct differences between dominant free-living and zooplankton-associated microbes, supporting the notion that zooplankton can be viewed as islands supporting distinctive communities in the microbial ocean.

Free-living bacteria and zooplankton-associated bacteria may respond to environmental changes differently. For example, a previous study has shown that zooplankton bodies effectively protect attached bacteria from environmental stresses that decimate free-living bacteria and the zooplankton (Tang et al., 2011c). Alteration of salinity by increased ice melting and other environmental changes due to global warming and human activities is expected to influence biodiversity and carbon dynamics within Greenland fjords (Rysgaard and Glud, 2007; Post et al., 2009). However, these predictions have not yet considered possible changes to microbial islands associated with particles and higher organisms. Based on our results, changes in salinity and stratification due to meltwater runoff would strongly influence the free-living microbial community composition, especially *Bacteria*, *Archaea*, and *Alphaproteobacteria*. In Godthåbsfjord, changes in water temperature and meltwater intrusions are also expected to alter the zooplankton community compositions (Tang et al., 2011b; Møller et al., 2012), which could lead to the emergence of different zooplankton-associated bacterial communities. We suggest that climate change research in Greenland and other Arctic regions take into consideration the potential changes and responses of these microbial islands.

Acknowledgments

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