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Diversity of Arctic Pelagic Prokaryotes with an emphasis on photoheterotrophic bacteria: a review

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Abstract

The Arctic Ocean is a unique marine environment with respect to seasonality of light, temperature, perennial ice cover and strong stratification. Other important distinctive features are the influence of extensive continental shelves and its interactions with Atlantic and Pacific water masses and freshwater from sea ice melt and rivers. These characteristics have major influence on the biological and biogeochemical processes occurring in this complex natural system. Heterotrophic bacteria are crucial components of marine food webs and have key roles in controlling carbon fluxes in the oceans. Although it was previously thought that these organisms relied on the organic carbon in seawater for all of their energy needs, several recent discoveries now suggest that pelagic bacteria can depart from a strictly heterotrophic lifestyle by obtaining energy through unconventional mechanisms that are linked to the penetration of sunlight into surface waters. These photoheterotrophic mechanisms may play a significant role in the energy budget in the euphotic zone of marine environments. We can suspect that this role could be of greater importance in the Arctic Ocean where environmental changes triggered by climate change could favor the photoheterotrophic lifestyle. Here we review advances in our knowledge of the diversity of marine photoheterotrophic bacteria and discuss their significance in the Arctic Ocean gained in the framework of the Malina cruise.

1 Introduction

The Arctic Ocean is the smallest of the five major oceans with 2.8 % of the Earth's total surface (Pidwirny, 2006); it is almost completely surrounded by lands and can be viewed as the Arctic Mediterranean Sea (Coachman and Aagaard, 1974). However, the Arctic Ocean and its marginal seas (the Chukchi, East Siberian, Laptev, Kara, Barents, White, Greenland, and Beaufort; some oceanographers also include the Bering and Norwegian Seas) are the least known basins and bodies of water of the world's oceans owing to their remoteness, hostile weather, and perennial or seasonal ice cover. The Arctic Ocean has the most extensive shelves of any ocean basin, covering about 50 % of its total area. Relative to other ocean basins, rivers play a disproportionately important role in the Arctic Ocean, which contains only about 1 % of the world's ocean volume yet receives approximately 10 % of the global terrigenous DOC load (Aagaard et al., 1985; Opsahl et al., 1999). The DOC concentrations in coastal Arctic waters are twice higher than those in the Atlantic and Pacific Oceans (Cauwet and Sidorov, 1996) highlighting the tight coupling of the Arctic Ocean with terrestrial catchments (Meon and Amon, 2004). In addition to the discharge of large rivers, the Arctic Ocean is also freshened by inflow of relatively low-salinity Pacific waters through the Bering Strait and net precipitation over the ocean surface (Serreze et al., 2006). Sea ice dynamics also play a pivotal role in the salinity regime, adding salt to the underlying water during ice formation and releasing fresh water during ice melting. As a consequence, estuarine gradients are a defining feature not only near-shore, but throughout this landlocked ocean. Due to this large influx of freshwater, the Arctic Ocean is well stratified with a distinctive surface layer of reduced salinity, the polar mixed layer, and density stratification inhibits vertical mixing with warmer, saline Atlantic waters below 200 m, allowing sea ice to form (Aagaard and Coachman, 1975). Inorganic nutrient concentrations exhibit strong regional gradients from high nutrient regimes (e.g., the Chukchi Sea shelf) to oligotrophic conditions (e.g., in the Beaufort Gyre and the Beaufort Sea).

The climate of the Arctic marine environment is marked by extreme seasonality in solar radiation, ice cover and atmospheric temperature and, to a lesser extent, water temperature (Carmack et al., 2006). The winter season in the Arctic is characterized by little or no sun light, of which only a fraction is able to penetrate the thick sea ice and snow layers to the water column below. This mainly affects photosynthetic organisms like phytoplankton, which require sunlight for carbon fixation. Most pronounced changes occur during the spring and early summer, when melting sea ice, melt ponds and rapidly increasing day length allow greater penetration of light to the water column. Despite their low temperatures, arctic waters support a highly productive ice-free season (Garneau et al., 2008), and bacterial activity has been found to be as high as in lower latitudes (Wheeler et al., 1996). Overall, however, the composition, physiology and function of prokaryotic heterotrophs in the marine Arctic are poorly understood, both in terms of spatial variations as well as temporal dynamics (Amon, 2004).

In this article, we first present an updated overview of the diversity of pelagic prokaryotes and their influences on biochemistry and upper food webs in the Arctic Ocean. Then, we focus on our current knowledge of the photoheterotrophic bacterial populations. In the light of recent studies that have been conducted during the Malina cruise, we also discuss the possible changes that could occur in the diversity of photoheterotrophic bacteria in coastal environments of the Beaufort Sea.

2 Diversity of heterotrophic prokaryotes

Early studies conducted in nearshore areas of the western Beaufort Sea investigated the cultivable fraction of the prokaryotic community (Kaneko et al., 1977; Zobell, 1946). Succession of cultivable bacterial phenotypes was demonstrated according to season and geography and in response to algal blooms. These pioneering studies demonstrated that bacterial isolates tend to differ significantly from those found in other marine environments. This observed potential for high genetic diversity was further confirmed by 16S rRNA gene-based molecular analyses of subsurface arctic prokaryotic communities (Ferrari and Hollibaugh, 1999). Early molecular studies analyzed compositional variability in prokaryotic assemblages in Arctic waters (Bano and Hollibaugh, 2002). 16S rRNA gene clone libraries from the Central Arctic (Bano and Hollibaugh, 2002), Western Arctic (Malmström et al., 2007), Greenland Sea (Pommier et al., 2007; Zaballos et al., 2006), Baffin Bay (Pommier et al., 2007), Laptev Sea (Kellogg and Deming, 2009) and Franklin Bay (Collins et al., 2010) revealed that bacterial communities were composed by polar and cosmopolitan phylotypes. Alphaproteobacterial and gammaproteobacterial sequences often formed the dominant phylotypes in planktonic bacterial assemblages. However, Malmström et al. (2007) reported high numbers of gammaproteobacterial (53 % of the clones) and *Bacteroidetes* (29 % of clones) sequences in a Chukchi Sea sample (Western Arctic). *Gammaproteobacteria* and *Bacteroidetes* were also the dominant groups in surface waters of Baffin Bay and Greenland Sea (Pommier et al., 2007).

The structure of planktonic archaeal assemblages in arctic waters was investigated only in the early 2000s. Genetic fingerprinting of archaeal communities suggested compositional changes with depth in the Central Arctic (Bano et al., 2004). Contrary to previous studies on antarctic waters, marine group I *Crenarchaea* and marine group II *Euryarchaea* had similar relative proportions in arctic surface samples (Bano et al. ,2004). In the Western Arctic, composition of coastal and river clone libraries differed and suggested the presence of a marine autochtonous community (Galand et al., 2006). *Euryarchaeota* dominated in river and coastal clone libraries while *Crenarchaetoa* prevailed in those from marine waters of the Beaufort Sea (Galand et al., 2008b).

Most recently, massively parallel tag sequencing techniques have improved our knowledge of the prokaryotic diversity in the Arctic Ocean, despite rarefaction analyses still suggested undersampling (Fig. 1). Although a greater abundance of *Gammaproteobacteria* was reported by Kirchman et al. (2010), *Alphaproteobacteria* typically dominate Arctic surface waters, followed by *Gammaproteobacteria* and by *Bacteriodetes*. *Verrucomicrobia* and *Actinobacteria* are also widely recognized as abundant Arctic seawater clades. Low proportions of marine cyanobacterial sequences were generally obtained in marine waters as previously reported (Waleron et al., 2007), although significant contributions were obtained in the attached fraction associated to the Mackenzie plume (Ortega-Retuerta et al., 2013). In the latter study, significant differences between particle-attached and free-living bacterial communities were observed in the open sea, but both fractions showed a similar structure in coastal and river samples. The influence of river inputs on prokaryotic community structure was also demonstrated in previous studies in the Arctic (Galand et al., 2008a; Garneau et al., 2006; Kellogg and Deming, 2009) and in a global comparison of bacterial diversity including Arctic samples (Ghiglione et al., 2012). Pyrosequencing analyses also revealed that sequences belonging to marine group I *Crenarchaeota* form the dominant archaeal group in the Arctic Ocean (Galand et al., 2009).

Fluorescence in situ hybridization (FISH) has also been used to identify archaeal and bacterial phylogenetic groups and to assess their actual cell abundance in natural waters (Alonso-Sáez et al., 2008; Elifantz et al., 2007; Garneau et al., 2006; Kirchman et al., 2007; Wells and Deming, 2003). These studies reported relatively low proportions of *Archaea* in surface waters and confirmed the dominance of *Alphaproteobacteria* (Elifantz et al., 2007; Garneau et al., 2006) or *Bacteroidetes* (Elifantz et al., 2007; Wells and Deming, 2003). With contributions higher that 20 %, SAR11 clade represent the major group (Malmström et al., 2007). Cell abundances of other ubiquitous groups such as SAR86 (*Gammaproteobacteria*) and *Roseobacter* RCA cluster (8 % and 10 %, respectively) were also significant. Seasonal changes in the relative abundance of major bacterial groups were reported and some abundant groups showed relatively high activity at the single-cell level (Alonso-Sáez et al., 2008, 2010; Nikrad et al., 2012).

3 Diversity of photoheterotrophic bacteria

Photoheterotrophic bacteria are microorganisms able to harvest light energy and to utilize dissolved organic compounds as carbon and energy source. Three groups of photoheterotrophic bacteria are currently known in the marine environment. A first group includes the abundant autotrophic cyanobacteria like *Prochlorococcus* and *Synechococcus* capable of facultative heterotrophic growth in nutrient-depleted environments. A second group is formed by aerobic anoxygenic phototrophic (AAP) bacteria. These organisms are obligate aerobes using dissolved organic matter as a source of organic carbon for their metabolism and growth. They harvest light using bacteriochlorophyll *a* (BChl *a*) – based pigments and reaction centers in addition to respiration. The third is composed of diverse bacterial groups that use bacterial rhodopsin as light-driven proton pump.

3.1 Cyanobacteria

Synechococcus spp. and *Prochlorococcus* spp. are prominent constituents of the marine biosphere that account for a significant percentage of the biomass and oceanic primary production (DuRand et al., 2001; Li, 1994; Veldhuis et al., 1997). Although they depend on light for most of their energy production and CO_2 for carbon acquisition, these cyanobacteria have also been shown to take up diverse organic substrates such as amino acids, nucleosides, oligopeptides, urea, sulfur compounds or cyanate (Malmström et al., 2005; Palenik et al., 2003; Zubkov and Tarran, 2005) and use them to produce cellular biomass.

3.1.1 Abundance in the Arctic Ocean

Although cyanobacteria predominate in brackish or freshwater polar environments reaching abundances among the highest reported in natural environment (Powell et al., 2005), their abundance are typically low in marine polar waters (Li, 2009). In both polar oceans, picocyanobacteria follow a general trend of decreasing concentrations and relative abundance with increasing latitudes and strong inverse correlations between cells densities and temperature have been reported (Marchant et al., 1987; Murphy and Haugen, 1985; Rosenbergl, 1993). *Prochlorococcus,* the most abundant photosynthetic organism in the ocean, is widely distributed in subtropical and tropical waters from 40° S to 48° N (Johnson et al., 2006; Partensky et al., 1999b). Due to its temperature sensitivity, its concentrations decline rapidly beyond this band (Marchant et al., 1987). Despite its presence was reported in a sub-Arctic region at latitude 61° N (Buck et al., 1996) and at southern latitudes of the sub-Antarctic (Marchant et al., 1987), *Prochlorococcus* is considered as virtually absent in the polar oceans (Baldwin et al., 2005; Cottrell and Kirchman, 2009; Li, 1994; Lin et al., 2012; Zwirglmaier et al., 2008). *Synechococcus* is more ubiquitous and virtually inhabits all marine and freshwater environments (Partensky et al., 1999a). In the Arctic Ocean, *Synechococcus* has been found in many marine cold environments such as the Chukchi Sea (Cottrell and Kirchman, 2009; Huang et al., 2012), the Beaufort Sea (Cottrell and Kirchman, 2009), off Iceland (Michelou et al., 2007) and near the Greenland and the Barents Sea (Cottrell et al., 2008; Zwirglmaier et al., 2008). Epifluorescence microscopy studies have also reported variable abundances of phycoerythrin-rich cyanobacteria in Resolute Passage (Robineau et al., 1999). The highest cell numbers ($> 10^3$ cells mL^{-1}) were measured between Greenland and Barents Sea during the late summer (Zwirglmaier et al., 2008), in marine waters of lower salinities in Resolute Passage (Robineau et al., 1999) and in Mackenzie river and estuary as well as in coastal sites of Franklin Bay and Admundsen Gulf (Waleron et al., 2007). However, *Synechococcus* abundances measured in the Arctic Ocean are generally lower. In two coastal sites from the Chukchi and Beaufort Seas, densities never exceed more than 100 cells mL^{-1} (Cottrell and Kirchman, 2009) and their concentrations decreased by an order of magnitude in offshore sites near Arctic pack ice (Robineau et al., 1999). Low cyanobacterial abundance (less than 24 cells mL^{-1}) was also measured in the East Greenland Current (Gradinger and Lenz, 1989). Interestingly cyanobacterial abundance did not vary significantly between summer and winter, probably due to heterotrophic activity during the dark period (Cottrell and Kirchman, 2009). During the Malina cruise in summer 2009, *Synechococcus* was completely lacking in Arctic waters of the Chukchi and Beaufort Seas (Balzano et al., 2012) as observed previously (Li, 1998).

The origin of picocyanobacteria in the Arctic marine environment is controversial. Several authors argue for a strong contribution of allochtonous inputs like rivers or transport by advection from surrounding oceans (Gradinger and Lenz, 1989; Vincent et al., 2000; Waleron et al., 2007) while others hypothesize for brackish communities autochtonous to the Arctic Ocean and adapted to cold environments (Cottrell and Kirchman, 2009; Huang et al., 2012).

3.1.2 Diversity in the Arctic Ocean

Marine *Synechococcus* exhibit a high genetic diversity and are divided into three major subclusters, 5.1, 5.2 and 5.3. Among numerous clades unveiled by different gene markers (more than 20 based on 16S–23S internally transcribed spacer), clades I, II, III and IV are dominant on a global scale (Ahlgren and Rocap, 2012; Zwirglmaier et al., 2008). These lineages show different geographic niche exploitation. Clades I and IV dominate in nutrient-rich coastal waters at high latitudes, while clade II is widely distributed in subtropical and tropical oceanic waters (Huang et al., 2012; Zwirglmaier et al., 2008).

Using 16S rRNA-targeted probes specific for *Synechococcus* clades, Zwirglmaier et al. (2008) showed that clades I and IV dominated *Synechococcus* communities in an area between Norwegian, Greenland and Barents Seas, both clades yielding approximately equal hybridization signals. The significance of these clades up to 62° N in the North Atlantic was further confirmed by Huang et al. (2012) (Fig. 2). In the southern Bering Sea (56–60° N) where clade IV was not detected, clade I represented a significant portion of the *Synechococcus* community (Huang et al., 2012). The latter study evidenced a clear shift of *Synechococcus* community structure with increasing latitude and decreasing temperature. Clade I occurred rarely or was not detected in the northern Bering Sea and Chukchi Sea (62–72° N) where the euryhaline clades CB1 and CB5 prevailed. Although these two clades were originally isolated from the Chesapeake Bay, their prevalence in the northern Bering Sea and the Chukchi Sea suggests an autochthonous rather than a riverine or estuarine origin. In the Beaufort Sea that is strongly influenced by the Mackenzie River, only sequences closely related to freshwater and brackish *Synechococcus* were detected (Waleron et al., 2007).

However, regarding their very low abundance in the polar oceans, picocyanobacteria probably play a little role on the pelagic carbon and energy flow in this part of the globe (Díez et al., 2012; Gradinger and Lenz, 1989; Koh et al., 2012).

3.2 Aerobic anoxygenic phototrophic bacteria

Cyanobacteria are not the only bacteria that can use light energy in the upper water column. In the late 1970s, novel aerobic photosynthetic bacteria containing bacteriochlorophyll *a* (BChl *a*) were isolated from seaweeds, sand, bottom sediments, and seawater in the Bay of Tokyo (Harashima et al., 1978; Shiba et al., 1979). In contrast to their anaerobic counterparts, these organisms now called aerobic anoxygenic phototrophic (AAP) bacteria thrive in oxic conditions.

Rediscovered in the early 2000s, AAP bacteria were thought to be abundant and widespread in the euphotic zone of the open ocean and to contribute significantly to photosynthetically driven electron transport (Kolber, 2000, 2001; Rathgeber et al., 2004). Kolber et al. (2000) suggested that AAP bacteria might be abundant in oligotrophic oceanic regions where the capacity to harvest light energy may provide photoheterotrophs a competitive advantage over chemoheterotrophs. Latter studies showed that their abundance and distribution vary greatly among oceanic regimes, suggesting that there is a broad range of potential ecological niches for these microbes (Cottrell et al., 2006; Lehours et al., 2010; Mašín et al., 2006; Sieracki et al., 2006; Yutin et al., 2007). It seems however that AAP bacteria are more abundant in shelf and coastal areas than in the open ocean (Schwalbach and Fuhrman, 2005; Sieracki et al., 2006). AAP bacteria can exceed 10 % of total prokaryotes in estuaries (Cottrell et al., 2010; Waidner and Kirchman, 2007) but typically account for a small percentage (2 to 4 %) in open ocean waters (Cottrell et al., 2006; Jiao et al., 2007) where high abundances were recorded however (Lami et al., 2007). Despite lower AAP bacterial abundances have been reported in oligotrophic pelagic environments, these bacteria constitute a very dynamic part of marine microbial communities and may contribute significantly to the upper ocean carbon cycle (Koblížek et al., 2007).

3.2.1 Abundance in the Arctic Ocean

The abundance and distribution of AAP bacteria has been poorly studied in high-latitude waters. In the earliest study conducted in arctic marine waters, AAP bacteria were found to constitute 5 to 8 % of the prokaryotic community in coastal waters of the Beaufort and Chukchi Seas (Cottrell and Kirchman, 2009). These authors did not report significant changes in AAP bacterial abundance between summer and winter. During the Malina cruise that crossed the Bering and Chukchi Sea and focused on the southern Beaufort Sea in summer 2009 (http://malina.obs-vlfr.fr), we observed a strong decreasing gradient from the Mackenzie River to the open ocean with a mean AAP bacterial contribution of 7 % in the Mackenzie mouth, 1 % inshore, and 0.1 % offshore (Boeuf, 2013). The highest AAP abundances were found in surface waters of the Mackenzie plume (14 %) and in the benthic nepheloïd layer (BNL) (9 %) (Fig. 3a). These results are in line with those recorded in estuarine systems such as Long Island Sound, Delaware Bay and Chesapeake Bay, where these bacteria can constitute more than 10 % of the prokaryotic community (Cottrell et al., 2010; Schwalbach and Fuhrman, 2005; Sieracki et al., 2006; Waidner and Kirchman, 2008). The low AAP bacterial percentages in shelf and offshore Beaufort Sea samples were similar to those reported in Antarctic waters of the Southern Ocean (Schwalbach and Fuhrman, 2005) and in most oligotrophic temperate and tropical regions (Hojerová et al., 2011; Jiao et al., 2007; Lamy et al., 2011). This is consistent with the trophic status of the Beaufort Sea that is quite oligotrophic in summer (Ortega-Retuerta et al., 2012) with nearly undetectable nitrate levels during the Malina cruise. In contrast to total prokaryote abundance, AAP proportions correlated significantly with ammonium, silicate, total Chl *a*, and the different forms of organic carbon, nitrogen, and phosphorus. This suggests that AAP bacteria may respond to organic supply differently and have higher mineralization capacities than the bacterial community (Boeuf et al., 2013).

3.2.2 Diversity in the Arctic Ocean

Our knowledge on the diversity of AAP bacteria has long been based on cultures (Yurkov and Beatty, 1998). AAP bacteria have been further identified in environmental libraries and in environmental samples using known photosynthetic reaction center genes (Béjà et al., 2002). Wider PCR primers targeting *puf*M gene encoding the M subunit of bacterial photosynthetic reaction centers were then used to expand AAP bacterial diversity in various environments (Yutin et al., 2005). Diverse AAP bacteria were also retrieved in metagenomes from the Atlantic and Pacific Oceans (DeLong et al., 2006; Venter et al., 2004; Waidner and Kirchman, 2005; Yutin et al., 2007). Further studies indicated that AAP communities can be structured differently according to geographical location (Jeanthon et al., 2011; Jiao et al., 2007; Lehours et al., 2010). All these efforts have evidenced the genetic diversity of AAP bacteria with members of the *Alpha*-, *Beta*-, and *Gammaproteobacteria*. Both targeted (Hu et al., 2006; Jiao et al., 2007; Lehours et al., 2010) and nontargeted (Yutin et al., 2007) diversity studies have shown that depending on the location and environment, members of either the *Alpha*- or *Gammaproteobacteria* typically dominate the marine AAP bacterial community. For example, in the Baltic and Mediterranean Seas, most AAP bacteria belonged to *Gammaproteobacteria* (Jeanthon et al., 2011; Mašín et al., 2006), while in the Global Ocean Sampling (GOS) expedition, the *Roseobacter*-like group of *Alphaproteobacteria* dominated the oligotrophic AAP bacterial community (Yutin et al., 2007).

Only a limited number of studies have examined the diversity of AAP bacteria in high-latitude waters. First investigations carried out in the permanently frozen freshwater Lake Fryxell (Antarctica) (Karr et al., 2003) revealed that AAP bacteria living in these habitats were distinct from their marine counterparts. The presence of *puf*M genes in Antarctic seawater and sea ice environment was further demonstrated by Koh et al. (2011). Using the same primer set, both these studies found that *Alphaproteobacteria* dominated the AAP bacterial communities. Seawater clones closely related to *Roseobacter denitrificans* suggest the presence of the ubiquitous RCA cluster in Antarctic waters. In surface waters of the Chukchi and Beaufort Seas, although *puf*M genes belong to phylogroups previously identified in the GOS metagenome (Yutin et al., 2007), most were distinct from those retrieved at lower latitude and in Antarctic waters (Boeuf et al., 2013; Cottrell and Kirchman, 2009; Koh et al., 2011). By examining a couple of coastal sites in summer and winter, Cottrell and Kirchman (2009) revealed the presence of three phylogroups (Fig. 4). Two of them (phylogroup E and F) belonged to the *Rhodobacterales* which is one of the most common alphaproteobacterial order in polar and subpolar oceans (Fu et al., 2010; Ghiglione and Murray, 2012; Niederberger et al., 2010; Prabagaran et al., 2007; Salka et al., 2008; Selje et al., 2004). *Loktanella*-like *puf*M clones (phylotype F) dominated the libraries at both seasons whereas proportions of *Sulfitobacter*-related sequences (phylogroup E) increased in winter. Boeuf et al. (2013) investigated more thoroughly the AAP diversity in the transition zone between offshore and Mackenzie-influenced coastal waters (southern Beaufort Sea) in summer. The presence of *puf*M genes affiliating with *Rhodobacterales* in most of the Beaufort shelf was remarkable (Figs. 3b and 4) and supported by independent isolation of a large number of *Sulfitobacter* and *Loktanella* strains from most of the shelf and offshore stations.

The most striking observation raised by the large coverage of the Beaufort Sea during summer, was the widespread distribution of betaproteobacterial clades in the entire Beaufort shelf (Fig. 4). The most abundant betaproteobacterial clade exhibited a strong river to ocean gradient (Fig. 3b), suggesting that these bacteria grew in the Mackenzie River and then were mixed with Beaufort coastal waters (Boeuf, 2013). These results were in line with the fact that (i) betaproteobacterial *puf*M genes increased in summer coastal libraries (Cottrell and Kirchman, 2009) at higher river flow, (ii) betaproteobacterial AAP bacteria are found in high proportions in estuarine or freshwater habitats (Salka et al., 2011; Waidner and Kirchman, 2008; Yutin et al., 2007), and (iii) *Betaproteobacteria* are commonly found in the Mackenzie River where they are dominant (Galand et al., 2008a; Garneau et al., 2006). AAP bacterial diversity was highest at depths where Pacific Summer Water mixes with the BNL. At these depths, AAP bacteria affiliated to orders *Rhizobiales* and *Sphingomonadales* were common along the Mackenzie shelf but almost absent in surface waters (Figs. 3b and 4).

Although *Gammaproteobacteria* represent one third of the bacterial community in arctic marine waters (Kirchman et al., 2010), no gammaproteobacterial AAPs were found at coastal sites of Chukchi and Beaufort Seas (Cottrell and Kirchman, 2009) (Fig. 4). We confirmed this trend during the Malina cruise since only a few *puf*M clones belonging to the gammaproteobacterial phylogroup K were recovered in North Pacific Ocean samples but none were obtained above 62° N. Similarly, no clones of this phylogroup were found in Antarctic sea ice and seawater (Koh et al., 2011). This seems to indicate that polar waters are exceptions to its widespread distribution (Jeanthon et al., 2011; Lehours et al., 2010; Yutin et al., 2007).

3.3 Proteorhodopsin-containing bacteria

An additional type of phototrophy has also been recently found in marine surface waters. Proteorhodopsins (PR) are retinal-binding integral membrane proteins discovered *via* environmental genomic surveys in the early 2000s (Béjà et al., 2000, 2001; de la Torre et al., 2003; Venter et al., 2004). PR are homologues of bacteriorhodopsins discovered in the halophilic archeon *Halobacterium salinarum* four decades ago (Oesterhelt and Stoeckenius, 1971). Their designation was based on the discovery of metagenomic fragments that linked the first discovered of these PR genes to a small subunit ribosomal RNA (SSU rRNA) gene defining the uncultured SAR86 group II, a gammaproteobacterial group widespread in marine plankton (Béjà et al., 2000; Suzuki et al., 2001).

Subsequent PCR-based gene surveys, screenings of BAC and fosmid libraries, metagenomic and genome analyses have identified a wide variety of PR genes (Béjà et al., 2001; de la Torre et al., 2003; Man et al., 2003). PRs were found in diverse bacterial groups, including the ubiquitous SAR11 groups (Giovannoni et al., 2005; Giovannoni and Stingl, 2005), the abundant coastal clade SAR 92 (Stingl et al., 2007), as well as in strain HTCC 2255 (*Rhodobacterales*), marine *Flavobacteria* (Gómez-Consarnau et al., 2007; González et al., 2008; Riedel et al., 2010; Yoshizawa et al., 2012) and planktonic *Archaea* (Frigaard et al., 2006). Phylogenies of PR amino acid sequences are not consistent with those of 16S rRNA, suggesting that PR genes have acquired by lateral gene transfer (Frigaard et al., 2006; Sabehi et al., 2004). Proteorhodopsins were so far detected in coastal and open ocean environments, but also in freshwater, estuarine and brackish ecosystems (Atamna-Ismaeel et al., 2008; Rusch et al., 2007).

3.3.1 Diversity in the Arctic Ocean

Only very few molecular surveys have reported PR bacteria in marine polar waters. Antarctic PR sequences have been detected in coastal surface waters near Anvers island, Western Antarctic Peninsula (Béjà et al., 2000; Williams et al., 2012) and in sea ice and brine samples of the Ross Sea (Koh et al., 2010). Sequences analyses revealed that Antarctic PRs showed similarity to previously reported PR sequences, although most of the sequences were generally distinct. Cottrell and Kirchman (2009) reported the first study on PR bacterial diversity in Arctic waters. Although limited to a couple of coastal sites, this study revealed a diverse collection of PR genes, only a few of them belonging to previously identified groups. Clones libraries were mainly composed of alpha- and gammaproteobacterial PR types and their composition changed between summer and winter (Fig. 5). During the Malina cruise in the Beaufort Sea, we surveyed the PR diversity in different water masses using the same primer set and compared the composition of DNA and cDNA libraries (Fig. 5). An alphaproteobacterial group entirely composed of arctic sequences that we called “Arctic” dominated in most surface libraries confirming earlier results of Cottrell and Kirchman (2009). Contributions of SAR11 sequences were higher in cDNA than in DNA libraries, suggesting that this clade is highly active in arctic waters (Boeuf, 2013). With the exception of Mackenzie plume samples, high proportions of gammaproteobacterial PR mostly composed of SAR92-like and IMCC2047-like sequences were found in DNA libraries. Only a few clones aligned with the SAR86 clade of PR genes, which was reported to comprise the majority of Antarctic pelagic PR sequences (Béjà et al., 2001). Additionally, coastal surface and Mackenzie plume libraries contained significant amounts of *Flavobacteria* sequences. Contrasting to AAP community composition, only a limited number of few betaproteobacterial PR sequences were obtained along the Mackenzie plume although primer sets targeting freshwater clades were specifically tested. Our study revealed that Beaufort Sea PR sequences did not match closely with Antarctic ones, supporting the fact that PR genes from the Northern and Southern Hemispheres are not similar.

3.3.2 Abundance in the Arctic Ocean

Unlike *Cyanobacteria* and AAP bacteria, abundance of PR prokaryotes cannot be estimated using direct methods such as flow cytometry or epifluorescence microscopy.

Quantitative PCR (qPCR) is the technique that has been mostly used to examine the distribution of PR genes (Campbell et al., 2008; Riedel et al., 2010; Suzuki et al., 2001) and to measure their expression in natural waters (Lami et al., 2009). Alternatively, the abundance of PR genes has been evaluated from the frequency of clones carrying PR genes in environmental DNA libraries (Rusch et al., 2007; Sabehi et al., 2005; Venter et al., 2004).

PR bacteria have been estimated to contribute for up to 65 % (mean of 50 %) of the bacterial community in the Sargasso Sea, from 7 to 57 % (mean of 23 %) in the North Atlantic Ocean, about 13 % in the Mediterranean Sea and 35 % in the North Sea (Campbell et al., 2008; Riedel et al., 2010; Rusch et al., 2007; Sabehi et al., 2005; Venter et al., 2004). Alphaproteobacterial groups represent generally the highest fraction among PR bacteria. Among them, the ubiquitous SAR11-like cluster is the sole to contribute to 10 % of the overall community and almost 18 % in the Sargasso and Mediterranean Seas (Boeuf, 2013; Campbell et al., 2008).

In the polar marine waters, PR bacteria were detected throughout the annual cycle (Cottrell and Kirchman, 2009; Williams et al., 2012) but their abundance has not been extensively assessed. Cottrell and Kirchman (2009) compared the seasonal abundance of two clades retrieved from two coastal sites of the Chukchi and Beaufort Seas. Their abundance was not found to differ significantly between summer and winter. Using the set of PR sequences previously amplified from the Beaufort Sea (Boeuf, 2013), we designed qPCR primers to target among the most abundant groups in the libraries. By adding together their abundance estimates, these groups accounted between 0.9 % and 44.7 % (mean of 15.3 %) of the total bacterial community (Fig. 6a) (Boeuf, 2013). The ubiquitous SAR11-like PR clade dominated in the Beaufort Sea and was preferentially distributed offshore and above the DCM layer where mean contributions exceeded 10 % of the total bacterial community (Fig. 6b). This contribution is close to the percentage of SAR11 16S rRNA gene determined from pyrosequencing data obtained from the western Arctic Ocean (Kirchman et al., 2010). Consistent with clone library data, the "Arctic" clade, second most abundant PR clade in the libraries, was preferentially distributed in surface waters. It represented up to 24 % of the offshore bacterial community. The alphaproteobacterial HOT2C01 cluster was found in high proportions in Sargasso Sea (26 %) while decreasing to 8 % in the North Atlantic (Campbell et al., 2008). In the Beaufort Sea, this cluster was mostly present in coastal areas but its contribution was low (2 %) (Boeuf, 2013). Surprisingly, although proportions of PR *Gammaproteobacteria* were high in most clone libraries where they overdominated at depth (Fig. 5), they represented a minor fraction of the total bacterial community in all samples (mean < 1 %). These results indicate that relative frequencies of PR genes in clone libraries do not reflect their real abundance in natural communities. Our quantitative data indicate that PR genes are abundant in the Beaufort Sea, suggesting the high contribution of PR phototrophy in Arctic waters. Alphaproteobacterial PR genes dominate and their distribution in coastal and offshore waters suggests that factors other than light control their abundance.

4 Potential impact of global change

The Arctic Ocean is a key player in global climate regulation as well as a particularly sensitive system that has already undergone serious perturbations due to climate warming (Camill, 2005; Peterson et al., 2002). The total volume and extent of the sea ice are reducing (Walsh, 2008) leading to an increase of river runoff (Peterson et al., 2002) and a decrease in the surface layer salinity of the Arctic Ocean (ACIA, 2005). An additional consequence is the accelerating permafrost melting (Nelson, 2003) and coastal erosion (Rachold et al., 2000). The increasing delivery of organic carbon is suspected to enhance the mineralization process carried out by heterotrophic bacteria in the estuarine and coastal Arctic Ocean (Meon and Amon, 2004) and thus release a large amount of CO_2 in atmosphere (Kling et al., 1991). Excluding the potential shift of surrounding Oceans connections, currents and icecap drifting (Hopcroft et al., 2008) that may profoundly affect bacterial communities at both regional and global scales, global warming could impact bacterioplankton by modifying its local environment (physical aspect) and its nutrient sources and interactions in the food web (biotic aspect). The lengthening of the open-water period is likely to stimulate primary production via increased light availability, which in turn would enhance bacteria production (Arrigo et al., 2008; Zhang et al., 2010). These models all assume that more open water will lead to increased mixing and entrainment of nutrients into the upper water column. Alternatively, the freshening of the Arctic could lead to stronger salinity stratification and fewer nutrients being entrained into the euphotic zone.

In the Beaufort Sea, distributions of AAP and PR bacteria and their relationships with environmental parameters show strong differences. The most abundant AAP bacterial clade is strongly influenced by nutrient-rich river inputs. The freshening of the arctic coastal regions could therefore favor the survival of halotolerant freshwater AAP bacteria and expansion of their habitat (Boeuf, 2013). The impact of the phototrophic lifestyle on energy requirements and carbon metabolism of these bacteria is unknown. Examination of their distribution in other arctic coastal regions and their contribution to biogeochemical cycling is needed.

The decrease in ice thickness and the shift from perennial ice pack to seasonal ice (Perovich, 2011) could favor under-ice massive phytoplankton blooms in the Arctic (Arrigo et al., 2012). Such structural shifts of Arctic marine ecosystems could in turn be favorable to AAP bacteria of the *Roseobacter* clade (González et al., 2000; Suzuki et al., 2001) and PR groups (*Flavobacteriaceae*, alphaproteobacterial “arctic” clade, and gammaproteobacterial SAR92 clade) that exhibit a strong responsiveness to phytoplankton blooms. A long-term consequence of further increasing stratification will be reduction of the vertical flux of nutrients to the euphotic zone and decreasing productivity. Low-nutrient conditions in the upper Beaufort Sea could therefore be particularly favorable to bacterial groups adapted to oligotrophic conditions (SAR11 and other alphaproteobacterial PR groups) whose photoheterotrophic capabilities provide a competitive advantage (Gómez-Consarnau et al., 2010; Steindler et al., 2011).

The current knowledge suggests that microbial processes in the Arctic Ocean are particularly sensitive to environmental changes and have potentially large impacts on carbon flows and other ecosystem functions. How photoheterotrophic microbes adjust to these changes will probably have impacts on the marine ecosystem of the Arctic Ocean. Understanding how they interact and influence higher food webs as well as biogeochemical cycling in this system is necessary. Future research should examine communities present in less explored central Arctic regions and include thorough analyses of seasonal influences on microbial processes.

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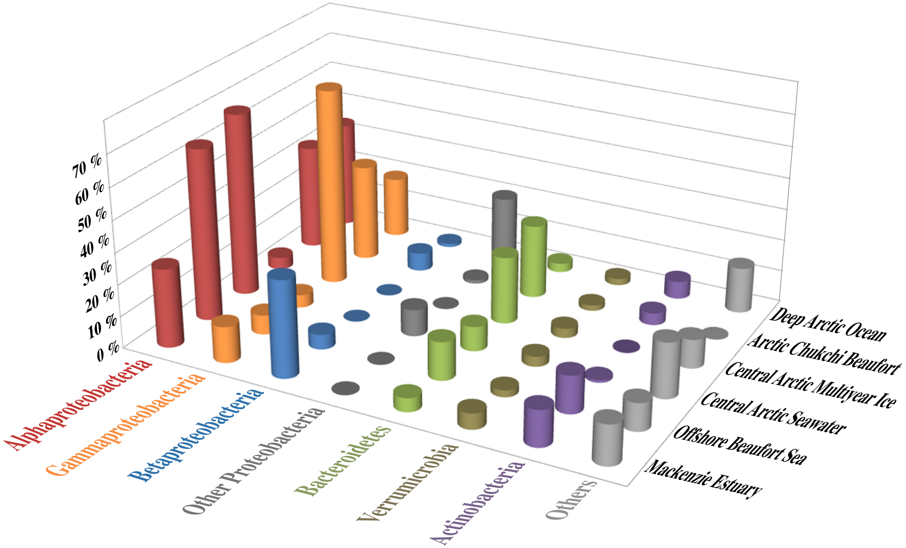

Fig. 1. Relative abundance of major phyla identified in pyrosequencing studies of the Deep Arctic Ocean (Galand et al., 2010); the Arctic Chukchi Beaufort (Kirchman et al., 2010), the Central Arctic Multi-year Ice and the Central Arctic seawater (Bowman et al., 2012), the offshore Beaufort Sea and the Mackenzie estuary (Ortega-Retuerta et al., 2013).

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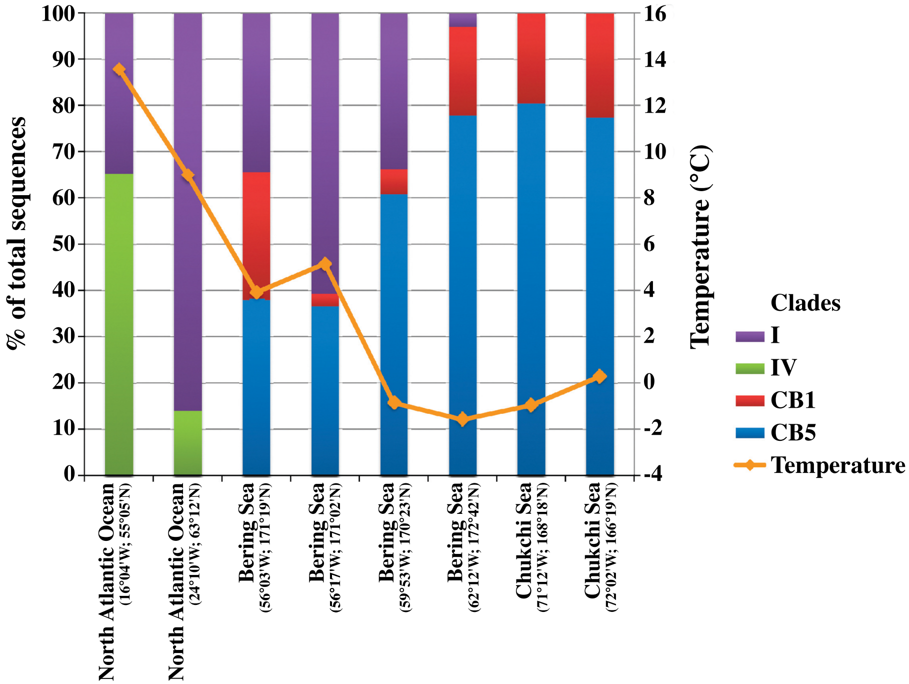

Fig. 2. *Synechococcus* community composition calculated from environmental sequences recovered in high-latitude regions. Reprinted by permission from Macmillan Publishers Ltd: The ISME Journal (Huang et al., 2012).

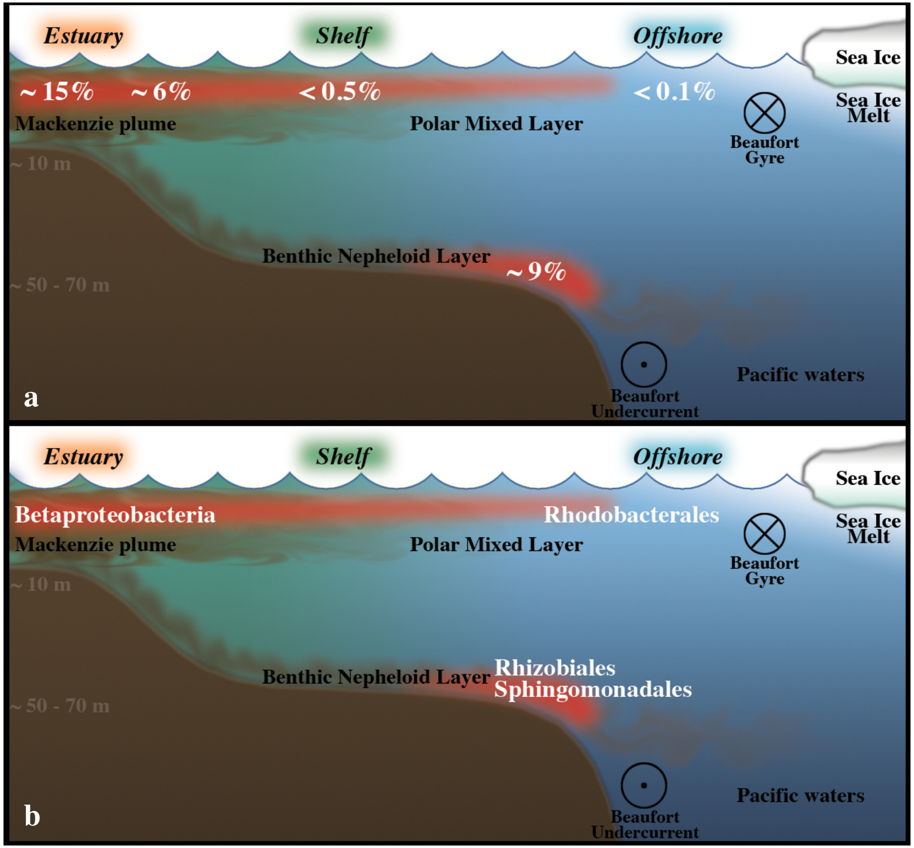

Fig. 3. Schematic diagram representing the changes in abundance **(a)** and diversity **(b)** of major AAP bacterial clades along an onshore-offshore transect of the Beaufort Sea. AAP proportions were calculating by dividing AAP bacterial numbers (enumerated by infrared epifluorescence microscopy) by the total prokaryotic numbers (DAPI counts).

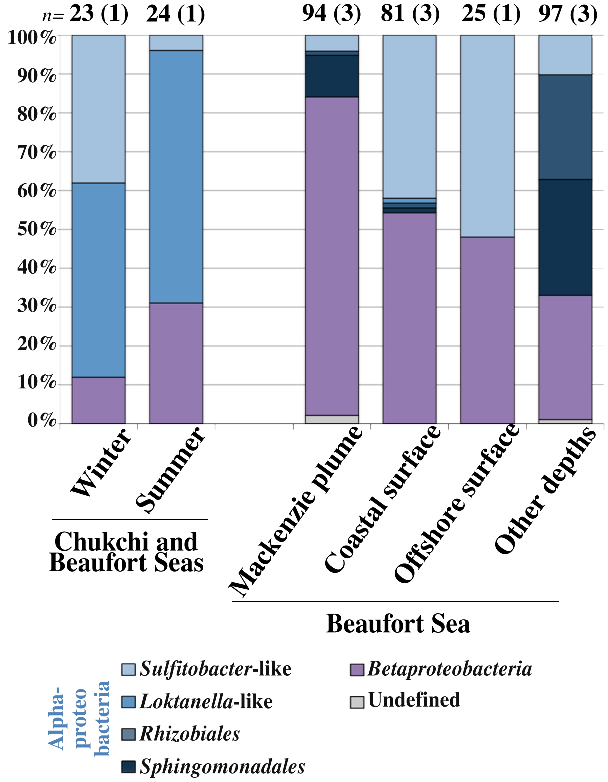

Fig. 4. Relative abundance of *puf*M genes in clone libraries obtained from Arctic Ocean samples. Clones were retrieved from coastal samples of the Chukchi and Beaufort Seas in summer and winter (Cottrell and Kirchman, 2009) and from the Mackenzie plume, coastal and offshore surface waters and other depths (Boeuf et al., 2013). The numbers of clones and libraries analyzed are indicated in bold and between brackets, respectively.

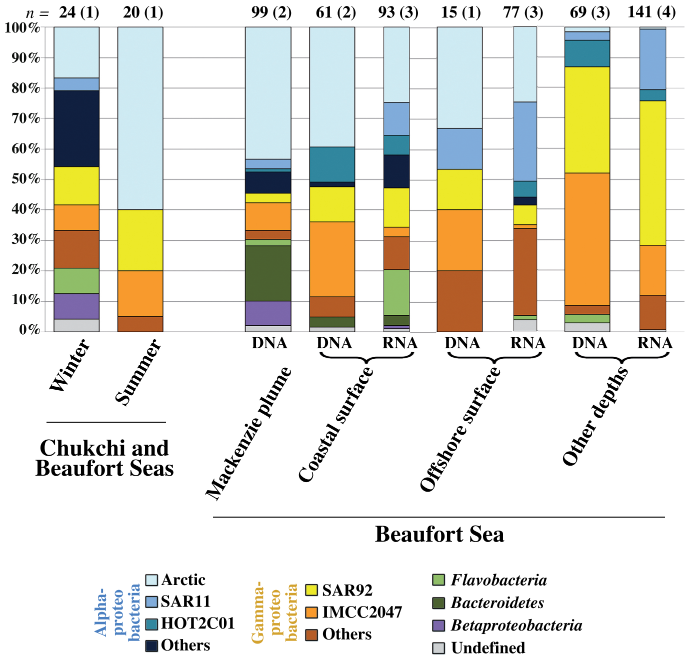

Fig. 5. Relative abundance of PR genes in clone libraries obtained from Arctic Ocean samples. Clones were retrieved from coastal samples of the Chukchi and Beaufort Seas in summer and winter (Cottrell and Kirchman, 2009) and from the Mackenzie plume, coastal and offshore surface waters and other depths (Boeuf, 2013). The numbers of clones and libraries analyzed are indicated in bold and between brackets, respectively.

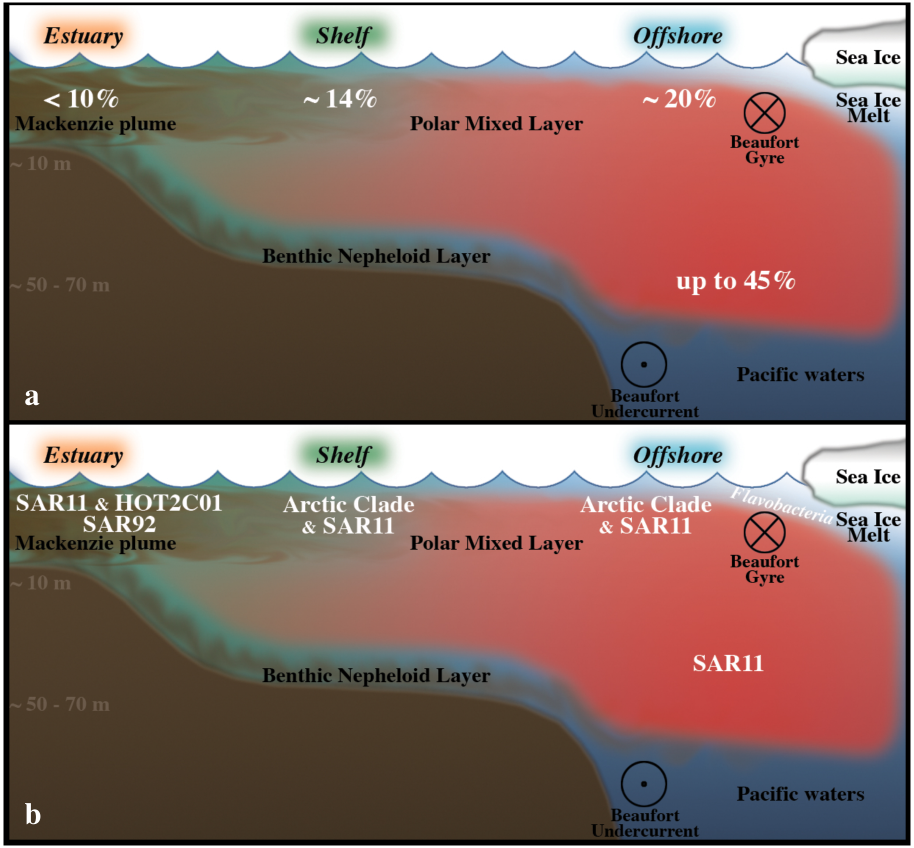

Fig. 6. Schematic diagram representing the changes in abundance **(a)** and diversity **(b)** of major PR bacterial clades along an onshore-offshore transect of the Beaufort Sea. Total PR abundance **(a)** was calculating by summing the relative proportions of the eight most abundant clades in the clone libraries (Fig. 5).