Marine Group II Archaea: A Review with a Focus on the Arctic Ocean

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Abstract

Marine Group II (MGII) archaea are among the most abundant planktonic archaea in the global ocean, yet no cultured representative exists, and most of what is known about them comes from 16S rRNA gene surveys and metagenome-assembled genomes (MAGs). Here we review the taxonomy, biogeography, physiology, and metabolism of MGII archaea, now proposed as the order *Candidatus* Poseidoniales, with its two main subgroups MGIIa (*Ca.* Poseidoniaceae) and MGIIb (*Ca.* Thalassoarchaeaceae). MGIIa tend to dominate surface waters and are often described as motile and particle-associated, whereas MGIIb are more common at depth. Both subgroups encode enzymes for degrading high-molecular-weight organic matter, and many surface populations carry proteorhodopsin, suggesting a photoheterotrophic lifestyle. MGII archaea co-occur with heterotrophic bacteria such as SAR11 and SAR86 and respond to phytoplankton blooms, although their seasonal patterns differ among ocean regions. We then summarize what is known about MGII archaea in the Arctic Ocean, where they are widespread but comparatively little studied, covering their distribution across water masses, associations with particles, seasonal dynamics, and the metabolic potential of Arctic MAGs. Finally, we discuss how sea ice loss and increasing stratification may affect MGII archaea and outline priorities for future work in this rapidly changing ocean.

1 Introduction of Marine Group II Archaea

1.1 General Description of Marine Archaea

All organisms on the Earth are categorized into one of three domains: bacteria, eukaryotes, and archaea. Archaea are microbes which have a similar cellular structure and size to bacteria but share other biochemical characteristics more with eukaryotes. Archaea are known as showing strong tolerance against extreme environments and are found in such habitats as volcanos, polar regions, deserts, and deep sea vents, and thus, originally all archaea were thought to be extremophiles residing exclusively in extreme environments. However, after mesophilic (mild temperature-loving) archaea were found from the coastal ocean (DeLong,

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1992) and subsurface seawater (Fuhrman et al., 1992), researchers started to study archaea in temperate environments and now recognize archaea are prevalent in many environments on Earth. Marine archaea are mainly divided into four groups: Marine Group I (MGI) archaea (DeLong, 1992; Fuhrman et al., 1992), Marine Group II (MGII) archaea (DeLong, 1992), Marine Group III (MGIII) archaea (Fuhrman & Davis, 1997), and Marine Group IV (MGIV) archaea (López-García et al., 2001). MGI and MGII archaea are the most abundant archaea in the global oceans (Massana et al., 2000; Rinke et al., 2019). We have obtained much information about the biogeography, physiology, and metabolism of MGI archaea. For example, MGI archaea are known as globally distributed archaea from the poles (Bano et al., 2004; DeLong et al., 1994) to the equator (Church et al., 2010; Santoro et al., 2017) and are abundant below the mesopelagic and bathypelagic layers, reaching around 40 % of total prokaryotes (Karner et al., 2001). Also, pure cultures and metagenome-assembled genomes (MAGs) of MGI archaea have been obtained (Hallam et al., 2006; Könneke et al., 2005), leading to the discovery that MGI archaea are major ammonia-oxidizers in the marine ecosystem.

1.2 General Description of Marine Group II Archaea

Compared with MGI archaea, we only have limited information about MGII archaea. Massana et al. (2000) compared archaeal populations from different oceans and phylogenetically classified MGII archaea OTUs (Operational Taxonomic Units, a proxy for species) into two different subgroups: MGIIa and MGIIb. MGII archaea were formerly categorized in the phylum Euryarchaeota (DeLong, 1992), but Rinke et al. (2019) proposed to assign MGII archaea into a new phylum, Thermoplasmatota. Also, they proposed a new order Candidatus Poseidoniales ord. nov. and categorized MGIIa and MGIIb as new families, Candidatus Poseidoniaceae fam. nov. and Candidatus Thalassoarchaeaceae fam. nov., respectively. In addition, each MGII clade was subdivided into subclades (Table 1). Galand et al. (2010) phylogenetically analyzed archaeal 16S rRNA genes and classified MGIIa into three subclades: K, L, and M, and MGIIb into two subclades: N and O. Other metagenomic studies further divided these subclades (e.g., O1–O5) or added new subclades (I, J, and Q), but the numbers and kinds of subclades vary among studies (Orellana et al., 2019; Pereira et al., 2021; Rinke et al., 2019; Tully, 2019). Further investigation of MGII archaeal phylogeny is required, and MGII archaea likely have more diversity waiting to be discovered. Despite these proposed (not yet accepted) taxonomic revisions, most authors still describe them as MGII, and we continue here with this nomenclature. Unlike MGI archaea, we have not obtained a pure culture of MGII archaea yet, and thus we only have limited physiological information about them. However, Iverson et al. (2012) reconstructed the first MGIIa genome from metagenomic data. Martin-Cuadrado et al. (2015) and Royo-Llonch et al. (2021) also reconstructed MGIIb MAGs, so thanks to those reference genomes, we can study the physiology, metabolism, ecological role, and evolutionary history of MGII archaea in silico.

1.3 Biogeography of MGII Archaea and its Subclades

Surveys of 16S rRNA gene sequences revealed that MGII archaea were abundant in the global oceans from tropical (Schattenhofer et al., 2009) to polar regions (Bano et al., 2004; Galand et al., 2009; Kirchman et al.,

Table 1. Classification of MGII Archaea Subclades

Reference	MGIIa subclades	MGIIb subclades
Galand et al. (2010)	K, L, M	N, O
Orellana et al. (2019)	I, J1–3, K (1, 2, 4), L1–4, M	N1–2, O1–5, P, Q1–2
Rinke et al. (2019)	I, J1–3, K1–2, L1–4, M	N1–2, O1–5, P, Q1–2
Tully (2019)	K, L, M	O (1–5 and WHARN)

Note. Subclades of MGIIa and MGIIb are listed. The number and kinds of subclades differ among the metagenomic studies because each study conducted a different phylogenetic analysis.

2007). Generally, MGIIa are found from surface waters (Frigaard et al., 2006; Galand et al., 2010; Hugoni et al., 2013; Massana et al., 2000; Orellana et al., 2019), while MGIIb can be observed throughout the water column but commonly found from deep waters (Galand et al., 2009; Martin-Cuadrado et al., 2015; Massana et al., 2000; Parada & Fuhrman, 2017; Pereira et al., 2019). Both MGII subgroups can be found throughout the water column, but they usually become abundant at preferred depths. Figure 1 provides a summary of the distribution, physiology (Section 1.4), and metabolic features (Section 1.5) of MGII subgroups.

1.4 Physiology of MGII Archaea

Metagenomic studies revealed that MGIIa have larger genomes (Martin-Cuadrado et al., 2015; Orellana et al., 2019; Pereira et al., 2021; Tully, 2019) and have higher GC content than MGIIb MAGs (Martin-Cuadrado et al., 2015; Orellana et al., 2019). Also, those studies showed that MGIIa and MGIIb have distinct physiological characteristics. Generally, MGIIa are explained as motile and particle-attached archaea (Iverson et al., 2012; Orsi et al., 2015; Rinke et al., 2019; Tully, 2019), while MGIIb are categorized as non-motile (Martin-Cuadrado et al., 2015). However, another metagenomic study suggested that all MGIIa and half of MGIIb MAGs encoded the archaeal flagella gene operon, which may function in cell adhesion, and the highest abundances of the flagellar gene, flaJ, were observed from MGIIb subclade O in the large-sized fraction (3-20 μm), suggesting that along with MGIIa, some MGIIb subclades can be particle-attached (Rinke et al., 2019). Another metagenomic study revealed that free-living and particle-associated MGII archaea have distinct genome contents (Orsi et al., 2015) and correlated with different environmental parameters (Jain et al., 2021; Xie et al., 2018). Also, Salazar et al. (2015) analyzed bathypelagic microbial communities with 16S rRNA gene sequencing and found that deep MGII archaea are potentially free-living, and surface and deep MGII archaea OTUs were phylogenetically distinct. Parada and Fuhrman (2017) reported that the phylogeny of MGII archaea OTUs was more affected by depth stratification than MGI archaea. Those findings suggest that the diversity of MGII archaea clades and subclades supports a variety of physiological traits (e.g., motility and particle association) that allow them to respond to different environmental or biological factors (e.g., temperature, salinity, nutrients, depth, and presence/absence of other microbes).

1.5 Metabolic Features of MGII Archaea

Metabolism of MGII archaea has been studied using metagenomics. For instance, MGII archaeal MAGs encode genes related to degrading high molecular weight compounds such as complex carbohydrates, lipids,

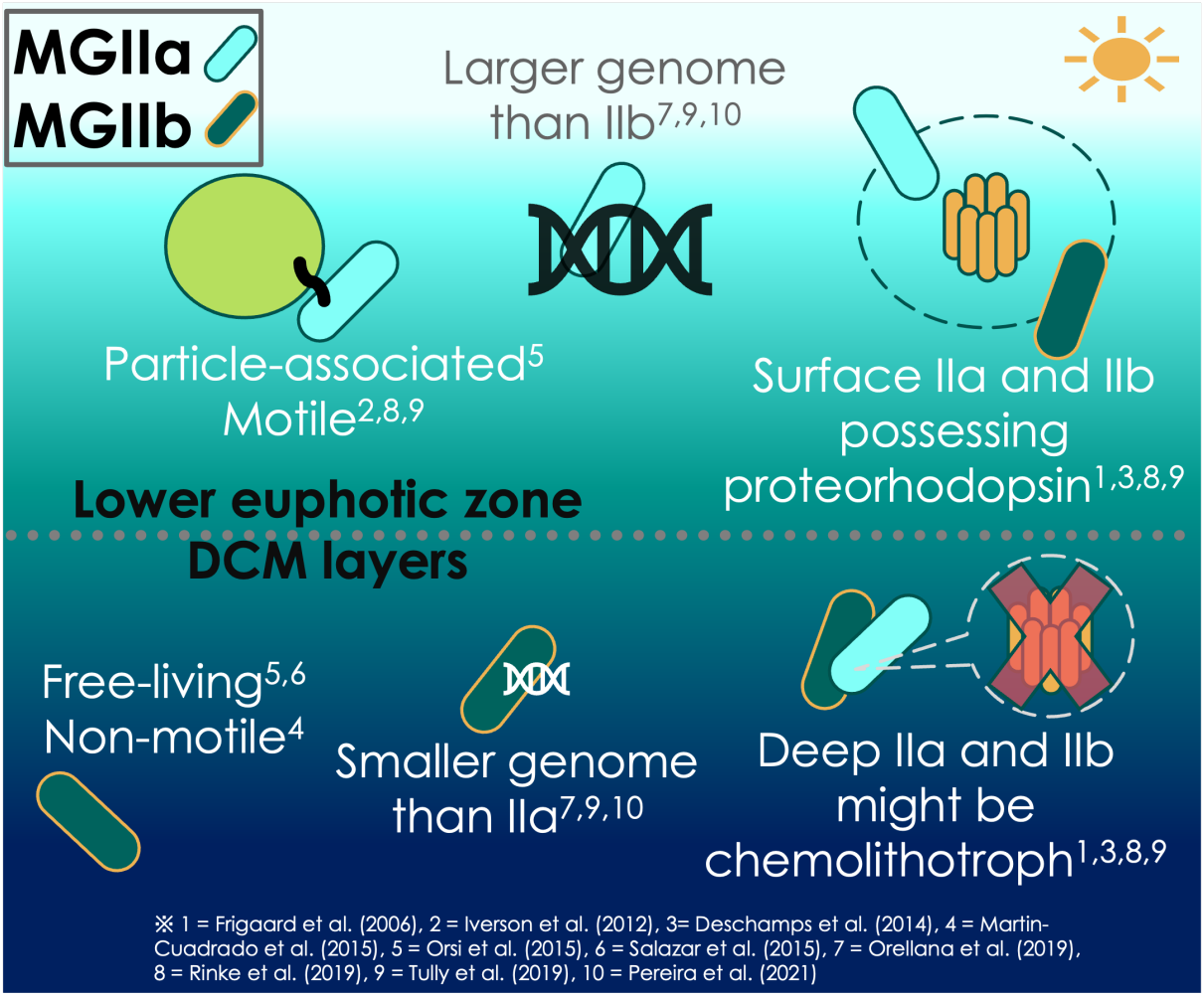


Figure 1. Graphical Summary of the Distribution, Physiology, and Metabolism of MGII Archaea. MGIIa and MGIIb are drawn as light-blue and dark-green rod cells, respectively. Superscripts next to each characteristic represent the references, listed at the bottom.

and protein (Iverson et al., 2012; Li et al., 2015; Martin-Cuadrado et al., 2015; Rinke et al., 2019; Tully, 2019), suggesting that MGII archaea have heterotrophic metabolism and potentially contribute to marine carbon cycles (Zhang et al., 2015). For instance, MGII MAGs encoded carbohydrate-active enzymes (CAZYs), which hydrolyze polysaccharides (Li et al., 2015; Qu et al., 2022; Rinke et al., 2019; Tully, 2019). Also, MGIIa and MGIIb MAGs encoded fatty acid and protein degradation pathways, suggesting that MGII archaea may have a particle-associated, heterotrophic lifestyle (Iverson et al., 2012; Li et al., 2015; Rinke et al., 2019; Tully, 2019). Motility is the main factor that differentiates MGIIa (motile) and MGIIb (non-motile) genomes, but they also adapt to different niches based on their ability to degrade high molecular weight organic matter. For example, MGIIb MAGs showed the potential to degrade agar, which may contribute to degrading the algal cell wall, and xenobiotics (Martin-Cuadrado et al., 2015). Both MGIIa and MGIIb MAGs possessed genes encoding transporters, and enzymes that degrade sugars, amino acids, and peptides (Orellana et al., 2019; Rinke et al., 2019; Tully, 2019). An important metabolic feature of many MGII archaea is that they

encode proteorhodopsin and have a photoheterotrophic lifestyle (Deschamps et al., 2014; Frigaard et al., 2006; Iverson et al., 2012; Martin-Cuadrado et al., 2015; Rinke et al., 2019). Proteorhodopsin is composed of retinal (vitamin A) and opsin protein and functions as a light-driven proton pump, which receives light energy, generating a proton-gradient, which can be used to produce ATP. Metagenomic studies revealed that both MGIIa and MGIIb encode the proteorhodopsin gene (pR) (Frigaard et al., 2006; Hugoni et al., 2013; Iverson et al., 2012; Li et al., 2015; Martin-Cuadrado et al., 2015; Orellana et al., 2019; Rinke et al., 2019; Thrash et al., 2017; Tully, 2019). Also, MAGs from surface and DCM layers in the global ocean, which were reconstructed from TARA Oceans metagenomes, contained proteorhodopsin (Pereira et al., 2019). However, fosmid clones and MAGs of MGII archaea, retrieved below the euphotic zone, did not contain pR, suggesting that MGII archaea in mesopelagic and bathypelagic layers may lack proteorhodopsin and have different metabolic traits from surface MGII archaea (Deschamps et al., 2014; Frigaard et al., 2006; Li et al., 2015; Martin-Cuadrado et al., 2008; Rinke et al., 2019; Thrash et al., 2017; Tully, 2019). In fact, Rinke et al. (2019) reported that genera of Ca. Poseidoniales (J1, J2, and J3) and Ca. Thalassoarchaeaceae (Q1 and Q2), whose MAGs were recovered from deep water down to 5000 m, did not encode pR and had positive correlation with sampling depth. Also, those MAGs were highly abundant where nitrate and phosphate concentration was high, which can explain their great abundance in deep water and suggest that they may have different metabolisms than surface MGII genera. It is also suggested that MGII archaea may have acquired proteorhodopsin from bacteria through horizontal gene transfer (HGT) (Deschamps et al., 2014; Frigaard et al., 2006). However, we don't know what kind of driving force led MGII archaea to obtain proteorhodopsin with HGT in their evolutionary history. To reveal functional and metabolic roles of proteorhodopsin on MGII archaea, further study should be conducted from physiological, metabolic, and evolutionary perspectives.

1.6 Correlations Between MGII Archaea and Other Microbes

To understand the biogeography of MGII archaea, we need to investigate biological factors which influence MGII archaeal distribution. Many studies have found correlations between MGII archaea and heterotrophic bacteria. For example, SAR11 and SAR86 are representative heterotrophic bacteria that correlate with MGII archaea. SAR11 dominate 25 % of the total bacterioplankton and utilize labile substrates like amino acids (Giovannoni, 2017). SAR86, which has been successfully cultured recently (Ramfelt et al., 2024), is known as having proteorhodopsin and potentially the ability to degrade carbon compounds such as lipids and polysaccharides (Dupont et al., 2012). Beman et al. (2011) found that the abundance of MGII archaeal 16S rRNA genes correlated with the abundance of OTUs of SAR11, SAR86, and Bacteroidetes (Beman et al., 2011). Also, Ottesen et al. (2013) conducted metatranscriptomic analysis and observed that transcriptional regulations of MGII archaea were synchronized with those of SAR11 and SAR86, suggesting that they may respond to the same environmental signals (Ottesen et al., 2013). Also, Parada and Fuhrman (2017) monitored interactions between MGII archaea and other microbial communities from surface to deep waters for five years and found that MGII archaea were associated with representative marine heterotrophic bacteria such as SAR11, SAR86, SAR202, SAR406, and SAR324 at different depths. Pereira et al. (2021) reconstructed MAGs from the Northwestern Mediterranean Sea and found that one MAG of MGIIb subclade O co-occurred with SAR86 and Rhodobacteraceae, while another MGIIb MAG was associated with SAR324, suggesting

that different MGII archaea subclades have different associations with heterotrophic bacteria. The reason why MGII archaea have associations with heterotrophic bacteria is unknown, but a possible answer is that MGII archaea and those heterotrophic bacteria listed above are known as proteorhodopsin-possessing microbes. Thus, sharing similar metabolism and ecological niches may lead to the formation of microbial networks between MGII archaea and heterotrophic bacteria. Besides heterotrophic bacteria, correlations between MGII archaea and phytoplankton have been reported. For instance, Orsi et al. (2015) conducted bottle incubations and found that MGII growth was stimulated and had a growth rate on the order of 0.47 d^{-1} by the addition of a picoeukaryotic phytoplankter, *Micromonas pusilla*, a cosmopolitan green alga (Foulon et al., 2008). Interestingly, a zooplankter, *Salpa* sp., was also present inside of the bottle, suggesting that it may have grazed upon *Micromonas pusilla* and released small peptides that stimulated the growth of MGII archaea. Another study found that the abundance of MGII archaea increased after a phytoplankton bloom (Needham & Fuhrman, 2016; Parada & Fuhrman, 2017). Surveys of 16S rRNA gene sequences in the Northwestern Mediterranean Sea revealed that the relative abundance of MGIIb was correlated with the concentration of nutrients and the presence of phytoplankton (Galand et al., 2010; Hugoni et al., 2013). Galand et al. (2010) also reported that sequences from MGIIb became abundant with phytoplankton such as *Prochlorococcus* (one of the most abundant cyanobacteria on Earth; Partensky et al., 1999), *Micromonas*, and diatoms. They found that MGIIb relative abundances started to increase once chlorophyll-a concentration reached the first peak, and then disappeared when the main phytoplankton bloom started, suggesting that they can be outcompeted by other phototrophic microbes. Several metagenomic studies suggested that MGII archaea may have associations with algae to utilize algae-derived carbon (Li et al., 2015; Orsi et al., 2016; Tully, 2019) and this might be the reason why MGII archaea share associations with phytoplankton.

1.7 Correlations Between MGII Archaea and Environmental Factors

Physicochemical parameters such as temperature, salinity, and concentration of nutrients significantly influence MGII archaeal distributions, which vary widely with the seasons. Previous studies reported that MGII subclades have specific seasonal preferences in different oceans. For example, 16S rRNA gene sequencing in the Northwestern Mediterranean Sea found that MGIIa sequences were abundant during summer when nutrients are scarce and phytoplankton are less abundant, while MGIIb sequences were abundant during winter when nutrient concentrations and the abundance of phytoplankton are high (Galand et al., 2010; Hugoni et al., 2013). The other metagenomic study, conducted in the southern North Sea, agreed, reporting that MGIIa MAGs dominated 23 % of the microbial community in summer samples, while MGIIb MAGs were abundant in winter samples (Orellana et al., 2019). Orsi et al. (2015) collected samples in the central California current system (CCS) during the summer and found that MGIIa was most abundant in the larger size fraction, dominating the 16S rRNA clone libraries. However, a time-series metagenomic study, conducted in the Northwestern Mediterranean Sea, reported that relative abundances of MGIIa and MGIIb MAGs were high during autumn and winter, and both MGIIa and MGIIb MAGs completely disappeared from surface waters during summer, suggesting that MGIIa and MGIIb may become abundant in response to changes in environmental conditions (Pereira et al., 2021). However, a metatranscriptomic study from Sapelo Island (Georgia, USA) contradicted those studies, reporting that MGII transcripts were mostly from MGIIb

in summer metatranscriptomes, while MGIIa transcripts dominated in autumn and winter (Damashek et al., 2021). Parada and Fuhrman (2017) reported that MGIIa and MGIIb did not show any seasonal patterns in the San Pedro Channel (California, USA). Community analysis with parallel 16S rRNA gene pyrosequencing in the subarctic and the subtropical gyre in the northwestern Pacific Ocean found that MGIIb were found throughout the water column and were especially abundant at 300-2000 m depth, while MGIIa were abundant at surface and 5000 m in the subarctic and the subtropical gyre (Kaneko et al., 2016). Also, MGIIb showed high relative abundance in surface waters during October and April in the subtropical gyre and during October in the subarctic gyre, while MGIIa were highly abundant during July in both subtropical and subarctic gyres. There is still great uncertainty regarding the influence of environmental factors on the distributions of MGII archaea.

2 MGII Archaea in the Arctic Ocean

2.1 Biogeography of MGII Archaea in the Arctic Ocean

MGII archaea have been found frequently from the Arctic Ocean including the central Arctic Ocean (Bano et al., 2004), the Beaufort Sea and the Mackenzie River (Galand et al., 2008), the Chukchi Sea and the Canada Basin (Kirchman et al., 2007), and the western Arctic (Galand et al., 2009). Earlier studies explained MGII archaeal distribution in the Arctic Ocean, but those studies showed different results. For instance, Bano et al. (2004) investigated archaeal assemblages in the central Arctic Ocean with PCR-denaturing gradient gel electrophoresis (DGGE) analysis and found that MGII archaea were more abundant in deep water than in surface water and showed equal relative abundance with MGI archaea. On the other hand, Kirchman et al. (2007) analyzed the abundances of bacteria and archaea in the Chukchi Sea and Canada Basin with FISH and found that Euryarchaea (MGII archaea) were detected in only a few samples from surface to 500 m, making up < 10 % of total DAPI (4',6-diamidino-2-phenylindole) counts, and were mostly outnumbered by crenarchaea (MGI archaea). Alonso-Sáez et al. (2008) analyzed prokaryotic community compositions in Franklin Bay with FISH and showed that DAPI counts of Euryarchaea were less than 6 % through the year, in agreement with Kirchman et al. (2007). These studies showed different results because they collected samples from different seasons and adopted different kinds of methodology. However, thanks to the pioneering study of Galand et al. (2009), which was the first taxonomic description of archaeal communities with parallel tag sequencing, 16S rRNA gene sequencing became the standard method for studying archaeal distributions in the Arctic Ocean and helped us understand the unknown structure of Arctic archaeal communities. Those authors conducted 16S rRNA gene sequencing and analyzed samples from eight different kinds of water masses in different regions in the Arctic Ocean (Baffin Bay, Beaufort Sea, Chukchi Sea, Bering Sea, and Amundsen Gulf). They found that different water masses harbored different archaeal OTUs, and MGI archaea OTUs were abundant in deep water samples, while MGII archaea OTUs were abundant in surface water samples, and 85 % of the Pacific surface water samples in the Beaufort Sea were dominated by a single MGII OTU. Also, MGIIb OTUs were abundant in deep water samples, while MGIIa OTUs were abundant in surface samples, which corresponded with the results from previous research (Frigaard et al., 2006; Galand et al., 2010; Hugoni et al., 2013; Martin-Cuadrado et al., 2015; Massana et al., 2000; Orellana et al., 2019; Parada

& Fuhrman, 2017; Pereira et al., 2019). Other studies observed that MGII archaea became abundant with specific conditions and the specific sites in the Arctic Ocean. For example, Amano-Sato et al. (2013) analyzed archaeal community compositions in different water masses on the Pacific side of the Arctic Ocean (Chukchi Sea, Bering Sea, East Siberian Sea, and Canada Basin) using CARD (catalyzed reporter deposition)-FISH and found that relative abundances of Thaumarchaeota were generally more abundant than Euryarchaeota, though at one sampling station in the Chukchi Sea, Euryarchaeota dominated 15 % of total prokaryotic cell counts and showed positive correlations with temperature and ammonium concentration. This result suggested that MGII archaea may outnumber MGI archaea at hot spots with favorable environmental conditions for them. Similarly, community analysis of microbial populations in different size fractions, which was conducted in Kongsfjorden (Svalbard, Norway), reported that MGII archaea Amplicon Sequence Variants (ASVs, a proxy for species or strain) were the most abundant archaea in surface water from different size fractions, followed by MGI ASVs (Jain et al., 2021), and this is one example showing that MGII archaea can be more abundant than MGI archaea in the Arctic Ocean.

2.2 Correlations Between MGII Archaea and Other Microbes in the Arctic Ocean

Several studies reported that MGII archaea in the Arctic Ocean interacted with other microbes in their communities. For instance, Royo-Llonch et al. (2021) reported that during spring and summer, MAGs which showed heterotrophic metabolism and are potentially chemolithoautotrophic or mixotrophic were highly expressed, and MAGs of Chloroflexi (SAR202) and Arctic MGIIb were the most active in the mesopelagic layer. Also, community analysis in the Barents Sea (Thiele et al., 2023) revealed that the relative abundance of MGII archaea was higher in sub-surface waters (>50 m) than in surface waters, and other heterotrophic bacteria such as SAR202, SAR324, and SAR406 showed the same pattern as MGII archaea, which corresponded with studies in other oceans (Ottesen et al., 2013; Parada & Fuhrman, 2017). Those authors also found that the relative abundance of SAR86 in surface waters was constant through the seasons, while ASVs abundant in summer included other members of the Gammaproteobacteria. This result implies that MGII archaea were not abundant in surface waters during summer because other bacteria that have similar ecological roles may outcompete MGII archaea in the Barents Sea. In fact, according to Ottesen et al. (2013), the overall abundance of MGII archaeal transcripts negatively correlated with that of SAR86 in the central California coast, suggesting that MGII archaea may have a similar niche with other heterotrophic bacteria such as SAR86 and may lose in competition against them (Ottesen et al., 2013). These findings suggest that MGII archaea may also interact with other heterotrophic bacteria elsewhere in the Arctic Ocean, including the Bering and Chukchi Seas.

2.3 Correlations Between MGII Archaea and Environmental Factors in the Arctic Ocean

Like MGII archaea in other oceans, MGII subclades in the Arctic Ocean show different seasonal preferences. For example, in a pan-Arctic metagenomic survey (Royo-Llonch et al., 2021), a MAG of MGIIa subclade L1 was the only MGII archaea MAG detected in surface layers through the Arctic Ocean and was abundant in Baffin Bay and Davis Strait during autumn, and in the Pacific Arctic during summer. In the sub-chlorophyll

maximum layer, a MGIIa subclade L1 MAG was highly expressed in the Atlantic Arctic during spring. Two MAGs of MGIIb subclade O2 were abundant in Baffin Bay and Davis Strait during autumn in the mesopelagic layer. In addition, a MAG of unclassified MGIIb was highly expressed in the mesopelagic layer of the Atlantic Arctic during spring, and the Kara and the Laptev Seas during summer, while MGIIa MAGs were abundant in autumn (Royo-Llonch et al., 2021). In the Barents Sea, Thiele et al. (2023) found that the relative abundance of MGII archaea ASVs was about 1 % during spring and winter at all sampling stations, but their abundance was quite low (<0.1 %) during summer when a late phytoplankton bloom occurred. Furthermore, MGII archaea, SAR202, SAR324, and SAR406 ASVs had positive correlations with phosphate, nitrate, and silicate concentration in surface water, while other bacteria which were abundant in summer surface waters such as SAR92, OM60, *Polaribacter*, *Ulvibacter*, and Flavobacteriaceae showed negative correlations with those inorganic nutrients and were positively correlated with other parameters such as season, temperature, chlorophyll-a concentration, cell abundance, and nitrite concentration. This implies that phytoplankton-derived organic matter may have been depleted by other heterotrophic bacteria, leading to a lower abundance of MGII archaea. However, cluster analysis of archaeal 16S rRNA genes with DGGE analysis (Bano et al., 2004) revealed that MGII archaeal sequences were abundant in summer and autumn, though archaeal phylogeny was mostly influenced by depth stratification, not by seasonal differences. Therefore, further investigations should be conducted to understand the seasonal preferences of MGII archaea.

2.4 Physiology of MGII Archaea in the Arctic Ocean

MGII archaea in the Arctic Ocean have been found in association with particles. Wells and Deming (2003) conducted fluorescent in situ hybridization (FISH) in the Canadian Archipelago and reported that the abundance of archaea increased toward the nepheloid layer and showed strong positive correlation with particles, and in the nepheloid layer, they positively correlated with PON. Also, Wells et al. (2006) found that archaea positively correlated with particles and PON and were abundant in suspended particles and detritus-rich water in the Beaufort shelf and Franklin Bay, suggesting that archaea in the Beaufort shelf might have allochthonous and riverine origin. However, two studies (Galand et al., 2006; Galand et al., 2008) compared 16S rRNA clone libraries from the Mackenzie River and the coastal Beaufort Sea and found that archaeal compositions were distinct among riverine, coastal, and marine water samples, suggesting that archaeal assemblages in this region have autochthonous origin. Also, MGII were the predominant archaea in coastal water samples, which are strongly influenced by river input, and associated with particles (Galand et al., 2006; Galand et al., 2008), and were not only restricted to large/small-sized fractions, suggesting that MGII archaea may occupy different niches according to their physiology and metabolism, and thus, have diverse metabolic traits in the Arctic riverine, coastal, and marine systems (Galand et al., 2008). Another community analysis in the high arctic fjord, Kongsfjorden (Svalbard, Norway), found that MGII archaea ASVs and OTUs were the most dominant in free-living and particle-attached fractions in surface waters, and MGIIa OTUs/ASVs dominated 22 % of total sequences in the particle-attached fraction, while MGIIb OTUs/ASVs were abundant (6.6 %) in the free-living fraction (Jain et al., 2021). These authors also reported that several OTUs/ASVs which were assigned as MGII archaea showed equal abundance in both free-living and particle-attached fractions, suggesting that they are not phylogenetically distinct and may switch their

lifestyle (free-living to particle-attached or vice-versa) between MGII archaeal communities. Overall, the physiology of MGII in the Arctic Ocean remains unknown and thus, further study is necessary to understand environmental or biological factors that influence the MGII physiology.

2.5 Metabolic Characteristics of MGII Archaea in the Arctic Ocean

Royo-Llonch et al. (2021) conducted a comprehensive metagenomic and metatranscriptomic survey through the Arctic Ocean (Pacific Arctic, Atlantic Arctic, Arctic Archipelago, Baffin Bay and Davis Strait, Kara-Laptev and North Atlantic) and reconstructed 530 MAGs, including 526 microbial species. These authors reconstructed five MGII archaea MAGs: two MGIIa MAGs (subclades K1 and L1) and three MGIIb MAGs (two of subclade O2 and one unclassified) and found that all MGII MAGs encoded sbm genes (Predicted dinucleotide-binding enzyme and Methylmalonyl-CoA mutase, N-terminal domain/subunit) which are related to carbon fixation, and all MAGs except for MGIIa subclade K1 MAG encoded the coxS gene (aerobic carbon-monoxide dehydrogenase small subunit), which is involved in carbon monoxide oxidation. Interestingly, the unclassified MGIIb MAG encoded the nirA gene (ferredoxin-nitrite reductase), which is involved in assimilatory nitrite reduction, suggesting that this MGIIb lineage may be able to use nitrite as a nitrogen source. The diversity and distribution of pR genes in the Arctic Ocean have been surveyed. Boeuf et al. (2016) studied the abundance and distribution of pR genes and found that proteorhodopsin-containing taxa dominated 45 % of the total bacterioplankton throughout the photic zone in the southern Beaufort Sea and Mackenzie River during summer, and pR gene abundance and distribution had more correlation with low nutrient concentration than light. Also, those pR genes were mostly affiliated to Gammaproteobacteria, Alphaproteobacteria, and Bacteroidota. Especially, pR genes of SAR11 made up 63 % of the proteorhodopsin-containing community. Another study showed that Gammaproteobacteria-like pR sequences were always dominant in the Amundsen Gulf during winter (Nguyen et al., 2015). Also, pR gene abundance showed seasonality, as flavobacterial pR genes, which were the second most dominant pR genes in early winter, were replaced with alphaproteobacterial pR genes in late winter, suggesting that this transition follows carbon dynamics. Compared with proteorhodopsin-containing bacteria in the Arctic Ocean, proteorhodopsin-containing archaea are less studied. Especially, MGII archaea are well-known to interact with heterotrophic bacteria such as SAR11 or SAR86, which are representative proteorhodopsin-containing bacteria, and thus investigating proteorhodopsin-containing MGII archaea in the Arctic Ocean can help us understand the ecological and biogeochemical roles of photoheterotrophy in the Arctic Ocean.

3 Future Challenges and Perspectives of Studying Marine Group II Archaea in the Arctic Ocean

3.1 Importance of Studying Marine Microbial Ecology in the Arctic Ocean

As the Arctic Ocean is more vulnerable to climate change than other oceans, we need to understand how climate change can alter the Arctic microbial community composition. However, only a few studies reported that MGII archaea composition can be changed by sea ice melting. Comeau et al. (2011) compared microbial

community compositions in the subsurface chlorophyll maximum layer in the Beaufort Sea before and after the sea ice minimum in 2007 and observed that the microbial composition of eukaryotes, bacteria, and archaea significantly changed: for eukaryotes, stramenopile OTUs significantly decreased after 2007, and ciliate OTUs dominated eukaryotic communities instead; for bacteria, Bacteroidetes OTUs considerably decreased, while the relative abundance of alphaproteobacterial and gammaproteobacterial OTUs was relatively constant; for archaea, MGI archaea OTUs made up 60 % of total archaeal sequences, but decreased after 2007, while the relative abundance of MGII archaea OTUs was not changed before and after sea ice minima. Kraemer et al. (2024) also conducted community comparative analysis in the Canada Basin from 2004 to 2012, including two sea ice minima (2007 and 2012) and found relative abundance of most ASVs decreased over time after sea ice minima, and those ASVs were mostly dominated by Proteobacteria and Bacteroidota. On the other hand, those authors reported that relative abundances of euryarchaeal and thaumarchaeal ASVs increased after the sea ice minima. Neither study identified why MGII archaea maintained or increased their relative abundance through the sea ice minima. One possible factor is that warming and ocean acidification synergistically increase the growth of the Arctic picoeukaryote *Micromonas pusilla* (Hoppe et al., 2018). As *Micromonas pusilla* can stimulate the growth of MGII archaea (Orsi et al., 2015), the high abundance of *Micromonas pusilla* might be related to the stable or increasing euryarchaeal abundance after the sea ice minima. To answer this question, we need to know which microbes increase/decrease before/after sea ice melting and whether they have association with MGII archaea in microbial communities. Additionally, ocean stratification, which is formed by global warming, may also influence MGII archaeal distribution and abundance in the Arctic Ocean. For instance, Tremblay et al. (2008) observed that due to ocean stratification, nitrate and nitrite concentrations significantly decreased in the upper mixed layer, suggesting that primary production in the euphotic zone can be affected if stratification is bolstered in the Beaufort region. Also, Li et al. (2009) observed the increase of small algae at the upper 150 m of the Canada Basin, which suggested that due to ocean stratification, nutrient influx decreased and led to a reduction in cell size. The decline of primary production and the high abundance of microbes with small-sized cells can influence marine biogeochemical cycles and food webs and may influence the abundance of MGII archaea, which associate with phytoplankton and can degrade complex compounds. Therefore, investigating the effect of climate change on microbial communities is essential to understand MGII archaea in the Arctic Ocean.

3.2 Possible Future Work About Marine Group II Archaea in the Arctic Ocean

MGII archaea are one of the most representative marine archaea and are ubiquitously detected in surface waters across the global oceans, yet their ecology in the Arctic Ocean remains poorly characterized. Because MGII archaea have not been cultured yet, their metabolic properties have not been experimentally resolved, leaving the functional role that these archaea play within the Arctic marine ecosystems largely unknown. Nevertheless, the recent discovery of novel subgroup MGIIc (Liu et al., 2023) and their past evolutionary adaptation process to brackish environment (Fan et al., 2024) have begun to expand our understanding of this group, signaling a new phase of MGII archaea research. Therefore, investigating MGII archaea, that is a flagship lineage of marine archaea with respect to its distribution, diversity, and putative metabolic functions in the distinctive environment of the Arctic Ocean, also helps us understand the ecological role of marine

archaea in this region.

Moreover, expanding metagenomic analyses would allow the metabolic repertoires of surface- and deep-water subgroups and subclades to be compared directly, giving us the opportunity to find the Arctic-specific metabolism of MGII archaea. Contrasting the genomic potential of shallow, photoheterotrophic populations with that of their deeper counterparts could reveal how these archaea have adapted to the Arctic marine environment and clarify the ecological roles they play across the water column. It would also be interesting to look at how MGII archaea respond to phytoplankton blooms in highly productive inflow regions such as the Bering and Chukchi Seas, where blooms are especially strong. Following how their abundance and activity change in different bloom stages would show how closely they are linked to primary production. Finally, physical conditions in the Arctic Ocean vary greatly from place to place and season to season, with a strong seasonal light cycle, the presence or absence of sea ice, inflowing Atlantic and Pacific waters, and large inputs of freshwater and land-derived organic matter from rivers. This makes it a good place to study what environmental factors shape MGII archaea. Looking at how the proportions of MGIIa and MGIIb, and their subclades change with water mass, depth, season, and the timing of spring phytoplankton blooms would give us a high-resolution picture of where these archaea live and what role they play in the Arctic Ocean.

Author contributions

R.S. reviewed the literature and wrote the manuscript. R.E.C. supervised the study.

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Competing interests

The authors declare no competing interests.

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