Marine Group II Archaea, potentially important players in the global ocean carbon cycle

Chuanlun L. Zhang1*, Wei Xie1, Ana-Belen Martin-Cuadrado2 and Francisco Rodriguez-Valera2*

1 State Key Laboratory of Marine Geology, Tongji University, Shanghai, China, 2 Department of Producción Vegetaly Microbiología, Universidad Miguel Hernández, Alicante, Spain

Marine Group (MG) I (currently known as Thaumarchaeota) and MG II Archaea were first reported over two decades ago. While significant progress has been made on MG I microbiology and ecology, the progress on MG II has been noticeably slower. The common understanding is that while MG I mainly function as chemolithoautotrophs and occur predominantly in the deep ocean, MG II reside mostly in the photic zone and live heterotrophically. Studies to date have shown that MG II are abundant in the marine aquatic environment and display great seasonal and spatial variation and phylogenetic diversity. They also show unique patterns of organic carbon degradation and their energy requirements may be augmented by light in the photic zone. However, no pure culture of MG II has been obtained and thus their precise ecological role remains elusive.

Keywords: archaea, Marine Group II, heterotrophic metabolism, carbon cycle

INTRODUCTION

In 1992, DeLong and Fuhrman et al. reported the occurrence of archaea in the cold ocean. Two phylogenetic groups were described based on 16S rRNA sequences: Marine Group I (MG I) within the Crenarchaeota and Marine Group II (MG II) within the Euryarchaeota. Before this discovery, archaea were considered to be obligate extremophiles. Subsequent cultivation-independent microbial surveys revealed them to be abundant and widespread in relatively “common” environments like soil or the most extensive habitat on Earth, the oligotrophic ocean.

Over the past 22 years, tremendous progress has been made on characterizing MG I, which have been reclassified as the archaeal phylum Thaumarchaeota (Brochier-Armanet et al., 2008). However, our understanding of MG II remains fragmented and significantly less than MG I. In contrast to MG I, no pure cultures or even enrichments are available for MG II. Breakthroughs have been made, however, in understanding the potential physiology and biochemistry of MG II by metagenomic approaches (Iverson et al., 2012; Deschamps et al., 2014; Martin-Cuadrado et al., 2015; Orsi et al., 2015). This mini-review summarizes our current understanding of this group and provides an outlook for future research on MG II.

ABUNDANCE AND DISTRIBUTION OF MG II AND OTHER EURYARCHAEOTA IN TEMPERATE LATITUDES

Early observations on the distribution of MG II were based on the relative abundance of clones in clone libraries generated from 16S rRNA genes amplified using PCR. In general, MG II contributed...
more to microbial assemblages from surface than deeper waters (Massana et al., 1997) while MG I were found to have more clones in deeper samples, which led to the conclusion that MG II dominate the photic zone and MG I the meso- and bathypelagic waters (Massana et al., 1997, 2000).

The first reliable quantitative analysis of their distribution was provided by fluorescence in situ hybridization (FISH), using either oligo-probes (oligoFISH) or poly-probes (polyFISH). The former tended to give higher estimates of the abundance of all archaea than the sum of MG I and MG II determined by polyFISH (Pernthaler et al., 2002) (Table 1). MG II were estimated to represent around 15% of total archaeal cells in the Atlantic Ocean, with little variation with depth (Teira et al., 2004). In contrast, a time series assessment of planktonic archaea in the Santa Barbara Channel revealed “intermittent” blooms of MG II coinciding with decreases in chlorophyll a (Murray et al., 1999). This was observed that MG II were actually the most common archaeal group in the same region reported the predominance of MG II contributing to the archaeal assemblage at the surface than at depth (Massana et al., 1998).

A comprehensive polyFISH approach was applied to examine the waters off the Antarctic Peninsula for vertical and temporal changes in archaeal cell abundance (Church et al., 2003). The results showed that MG II were low in abundance (<10% of total picoplankton) throughout the water column and did not differ significantly between summer and winter (Church et al., 2003). Based on these results and those of others (DeLong et al., 1998; Massana et al., 1998, 2000; Murray et al., 1999), Church et al. (2003) concluded that MG II were not numerically abundant in the plankton communities of the Southern Ocean. The occurrence of marine MG III and MG IV, two new lineages of Euryarchaeota that are closely related to MG II, has also been observed in deep waters of the Antarctic Polar Front (López-Garcia et al., 2001a,b).

Bano et al. (2004) were the first to report on the occurrence of MG II, MG III, and MG IV in the Arctic Ocean (Table 1). They also made a comparison of archaeal distribution between Arctic and Antarctic waters and observed that some euryarchaeotal ribotypes were unique to each system. Galand et al. (2006) further observed that MG II were actually the most common archaeal group in 16S rRNA gene clone libraries constructed from the coastal Beaufort Sea. They speculated that the greater abundance of MG II in the Arctic Ocean may be related to the higher availability of labile organic matter from land surrounding the Arctic, as demonstrated by the significant impact of terrestrial derived particles on coastal archaea in the Mackenzie River-influenced Beaufort Sea (Galand et al., 2006, 2008; Wells et al., 2006). Euryarchaeotal abundance was very low throughout the year in surface waters of the Western Arctic (Kirchman et al., 2007; Alonso-Sáez et al., 2008) (Table 1), which lacked direct river inputs (Galand et al., 2008).

**DIVERSITY AND PHYLOGENY OF MG II AND OTHER EURYARCHAEOTA**

Early studies using 16S rRNA gene phylogenies showed limited diversity of the MG II group and placed it in close association with Thermoplasma or methanogens (DeLong et al., 1992; Fuhrman et al., 1992; Massana et al., 1997, 2000). Nevertheless, two major clusters within MG II (which became the MG II.a- and MG II.b lineages later on) and a third branch (MG III) within the Euryarchaeota were also identified in these studies (Fuhrman et al., 1992; Massana et al., 2000).

Our knowledge of MG II diversity was enhanced by the application of high throughput sequencing and metagenomic analysis to studies of bacterial community composition, which revealed expansive diversity of MG II in coastal or estuarine waters. For example, Bano et al. (2004) observed that certain MG II sequences were predominately found in the surface water, the mixed-layer, or the halocline in the Arctic Ocean. Similarly, Galand et al. (2009a) observed a higher diversity of MG II in Arctic surface water in comparison to MG III that were more diverse in deeper Arctic water. Liu et al. (2009) observed that MG II had the greatest diversity in surface water, which decreased with depth in the Gulf of Mexico. Lincoln et al. (2014a) reported that MG II contributed a much higher proportion to total archaeal operational taxonomic units (OTUs) at shallower depths in the Pacific Ocean; however, different...
TABLE 1 | Abundance and distribution of Marine Group II in temperate latitudes and polar oceans.

| Region                        | Water depth (m)* | Biotope       | Type of euryarchaeota | Abundance (FISH or qPCR) | Note                                                                 | References                  |
|-------------------------------|------------------|---------------|-----------------------|--------------------------|----------------------------------------------------------------------|----------------------------|
| **TEMPERATE LATITUDES**       |                  |               |                       |                          |                                                                      |                            |
| Santa Barbara Channel         | <100             | Coastal       | MG II                 | ND                       | First description of MG II as mesophilic, aerobic members of archaea | DeLong, 1992                |
| Santa Barbara Channel         | 533              | Coastal       | MG II                 | 10^5 – 10^6 cells/ml (OligoFISH) | MG II dominate over MG I in surface water                           | Massana et al., 1997       |
| Northeast Pacific             | 500–3000         | Open ocean    | MG II, MG III         | ND                       |                                                                      | Fuhrman and Davis, 1997    |
| Subtropic Atlantic            | 1000             | Open ocean    | MG II                 | ND                       |                                                                      | Fuhrman and Davis, 1997    |
| Monterey Bay, CA              | 450–4424         | Offshore      | MG II                 | 10^4 – 10^5 cells/ml (PoliFISH) | MG II dominate over MG I in surface water                           | DeLong et al., 1999        |
| Santa Barbara Channel         | 300              | Coastal       | MG II                 | ND                       | "Intermittent" blooms of MG II in surface water (<20 m)             | Murray et al., 1999        |
| North Atlantic Ocean          | 2850             | Open ocean    | MG II                 | ND                       | MG II dominate over MG I in surface water                           | Massana et al., 2000       |
| Cantabrian Sea (Atlantic Ocean)| 132              | Slope         | MG II                 | ND                       |                                                                      | Massana et al., 2000       |
| Alboran Sea (Mediterranean Sea)| 941              | Open ocean    | MG II, MG III         | ND                       | MG II dominate over MG I in surface water                           | Massana et al., 2000       |
| Santa Barbara Channel         | 522              | Coastal       | MG II                 | ND                       | MG II dominate over MG I in surface water                           | Massana et al., 2000       |
| North Pacific subtropical gyre| 4750             | Open ocean    | Total Euryarchaeota   | <10% of total DAPI counts ~ 10^3 – 10^4 cells/ml | First seasonal quantification of archaea in the open ocean | Karner et al., 2001         |
| Coastal North Sea (German Bay)| 1                | Coastal       | Total Euryarchaeota   | Euryarchaeota can be >30% of total picoplankton | PolyFISH is better than OligoFISH; observed spring bloom of MGII | Pernthaler et al., 2002     |
| Monterey Bay, CA              | 1097             | Coastal       | Total Euryarchaeota   | Up to 12% of DAPI counts in summer and <1% in winter |                                                                      | Pernthaler et al., 2002     |
| North Atlantic Ocean          | 4000             | Open ocean    | Total Euryarchaeota   | 14–30% of DAPI counts    |                                                                      | Teira et al., 2004         |
| Atlantic Ocean                | 88–3869          | Open ocean    | MG II                 | 10^4 – 10^6 cells/ml     | Improved quantification using CARD-FISH                              | Herndl et al., 2005        |
| North Atlantic Ocean          | 100–4000         | Open ocean    | MG II                 | 16–18% of DAPI counts    | Improved quantification using CARD-FISH                              | Teira et al., 2006         |
| Southern North Sea            | <50              | Coastal       | MG II                 | 2 x 10^4 cells/ml        | Spring and summer blooms                                            | Herfort et al., 2007       |
| Gulf of Mexico                | >600             | Open ocean    | MG II                 | ND                       | MG II dominate the surface-mid-depth waters                          | Lu et al., 2009             |
| South China Sea               | 2418–3839        | Open ocean    | MG II                 | 2–16% of total DAPI counts | MG II dominate the surface water                                    | Zhang et al., 2009         |

(Continued)
| Region                          | Water depth (m)* | Biotope         | Type of euryarchaeota | Abundance (FISH or qPCR) | Note                                                                 | References                      |
|--------------------------------|------------------|-----------------|-----------------------|--------------------------|----------------------------------------------------------------------|--------------------------------|
| Mediterranean Sea              | 20               | Coastal         | MG IIa, MG IIb, MG III| Relative sequence        | First observation of seasonal differentiation within MG II; MG IIa (winter), MG IIb (summer) | Galand et al., 2010             |
| Coastal northwest Mediterranean Sea | 3                | Coastal         | MG IIa, MG IIb | Relative sequence        | Same conclusion as above                                             | Hugoni et al., 2013             |
| Pacific Ocean                  | >500             | Open ocean      | MG III               | Up to $4 \times 10^5$ cells/L | MG II outnumber MG I throughout the water column in large particle (3- to 57-µm) fractions | Lincoln et al., 2014a           |
| POLAR OCEANS                   |                  |                 |                       |                          |                                                                      |                                |
| Coastal Antarctica             | 0                | Coastal         | Total Euryarchaeota  | >60% of total archaea   | Estimated based on the difference between total archaea and MG I     | DeLong et al., 1994             |
| Coastal Antarctica             | 0                | Coastal         | MG II                | ND                       |                                                                      | Murray et al., 1998            |
| Coastal Antarctica             | <10              | Coastal         | MG II                | $10^4$ cells/ml          | MG II is minor fraction of total archaeal plankton (3–40 m) (under sea ice) | DeLong et al., 1998             |
| Antarctica Peninsula           | 500–1000         | Strait          | MG III               | ND                       |                                                                      | Massana et al., 1998           |
| Antarctic polar front           | 3000             | Strait          | MG II, MG III, MG IV | Exclusively euryarchaeotal species |                                                                      | López-García et al., 2001a  |
| Antarctic polar front           | 3000             | Strait          | MG II, MG III, MG IV | ND                       |                                                                      | López-García et al., 2001b |
| West of Antarctic Peninsula    | 200–500          | Shelf           | MG II                | $10^4$ cells/ml          |                                                                      | Church et al., 2003            |
| Antarctic polar front           | 500              | Strait          | MG II                | ND                       |                                                                      | Moreira et al., 2004           |
| Canadian Archipelago            | 7–600            | Archipelago     | Total archaea        | ND                       | Archaea correlate significantly with particle concentrations          | Wells and Deming, 2003        |
| Arctic Ocean/Antarctic         | 55–235           | Nearshore to offshore | MG II, MG III, MG IV | Equal abundance in MG I and MG II | No seasonal variation, but variation occurs with depth                | Bano et al., 2004             |
| Beaufort Shelf/Franklin Bay     | 0–150            | Coastal         | MG II                | ND                       |                                                                      | Wells et al., 2006            |
| Beaufort Shelf                 | 5–33             | Coastal         | MG II                | ND                       |                                                                      | Galand et al., 2006            |
| Western Arctic Ocean            | 0 ≥ 500          | Shelf to basin  | MG III               | <10% of total DAPI counts |                                                                      | Kirchman et al., 2007         |
| Western Arctic Ocean            | 3–100            | Coastal         | MG II                | <5% of total DAPI counts |                                                                      | Alonso-Sáez et al., 2008      |
| Beaufort Shelf                 | 5–260            | Nearshore to offshore | MG II               | ND                       |                                                                      | Galand et al., 2009a          |
| North Water (Arctic)            | 62–180           | Nearshore to offshore | MG II, MG III, MG IV | $10^4$–$10^5$ copies/mL | MG IIa dominates                                                       | Galand et al., 2009b          |
| Arctic Ocean                    | 50–3820          | Offshore        | MG II, MG III, MG IV | Dominance of MG III in deep water |                                                                      | Galand et al., 2008           |

*Bottom water depth or max sampling depth.
§Not determined using either FISH or qPCR.
∫Inferred from difference between MG I abundance based on qPCR and archaeal community composition in metagenomic datasets.
individual OTUs dominated the MG II population at different depths. The predominance of MG II in surface water and MG III in deep water was also observed in the South China Sea (Tseng et al., 2015). Overall, MG I share >94% 16S rRNA gene sequence similarity, whereas MG II only share 85% (Massana et al., 2000; Bano et al., 2004; Herfort et al., 2007), hence, MG II appear to be more phylogenetically diverse than MG I.

GENOMICS AND METAGENOMICS OF MG II AND THEIR PREDICTED PHYSIOLOGY

The distributions and abundances of MG II ribotypes (as well as MG III or MG IV) indicate that planktonic *Euryarchaeota* occupy diverse ecological niches (Murray et al., 1999; Hugoni et al., 2013; Lincoln et al., 2014a). However, little is known about the underlying mechanisms of niche partitioning among these organisms. The differences in distributions of MG IIa and MG IIb during different seasons observed in the Mediterranean Sea were attributed to differential sensitivity to temperature or nutrient and oxygen availability (Hugoni et al., 2013). Overall, our understanding of the ecological and biogeochemical functions of MG II is very fragmentary and incomplete, largely due to the lack of pure cultures and whole genomes that would allow us to better study the physiology and biogeochemistry of these organisms. However, information from metagenomics and reconstructed or partially assembled genomes is providing insights about these microbes.

Light-harvesting capability of MG II was first deduced from genomic fragments containing proteorhodopsins (Frigaard et al., 2006). So far only MG II from the photic zone are found to contain the proteorhodopsin gene, which occurs in about 10% of the euryarchael population (Frigaard et al., 2006). It has been suggested that proteorhodopsins could support a photoheterotrophic lifestyle by generating a light-driven chemiosmotic potential (Frigaard et al., 2006; Iverson et al., 2012). Summer peaks of abundance and activity of MG II.a in surface water of the Mediterranean Sea were attributed to the enhanced preyophototy in response to greater irradiance (Hugoni et al., 2013).

Despite the identification of proteorhodopsins in MG II genomes, Deschamps et al. (2014) did not find any genes encoding proteorhodopsin homologs in a MG II/III-*Euryarchaeota* dataset of nine metagenomes from deep-Mediterranean waters. Similarly, Baker et al. (2013) failed to detect any proteorhodopsin genes in the deep Guaymas metatranscriptome. These results support an earlier conclusion that deep-sea dwelling MG II *Euryarchaeota* are different from proteorhodopsin-containing MG II living in the ocean photic zone (Frigaard et al., 2006). Deschamps et al. (2014) also noted that the deep sea MG II *Euryarchaeota* have abundant genes targeting amino acid, carbohydrate and lipid transport and metabolism, which are typical of heterotrophic prokaryotes. Orsi et al. (2015) found that the rhodopsins of MG II in metagenomes from large cell size fractions (>0.8 µm) are phylogenetically distinct from rhodopsin genes found in metagenomes obtained with smaller size fractions, suggesting a possible difference in photoheterotrophy between the free-living and the particle-associated MG II groups.

Iverson et al. (2012) obtained the first nearly complete genome of a MG II, belonging to subgroup II.a, from metagenomic assemblies obtained from surface seawater in the Puget Sound. The genome suggested that MG IIa was a particle-associated microbe and the cells were predicted to be motile, photo-heterotrophic and capable of degrading polymers such as proteins and lipids. This validated the prediction of Béjà et al. (2000) that surface MG II were capable of proteolysis. The deep water genomic fragments (Moreira et al., 2004; Martin-Cuadrado et al., 2008; Deschamps et al., 2014) do not seem to have this metabolic feature. More recently, Orsi et al. (2015) quantified the abundance and distribution of MG II 16S rRNA genes in size-fractionated seawater samples from the euphotic zone of the central California Current System and showed that MG II abundance was highest in the particulate fraction, indicating that some MG II euryarchaeotes were physically associated with particles. These authors also found that the genome content of particle-attached MG II suggested an increased capacity for surface adhesion, transcriptional regulation and catabolism of high molecular weight substrates.

Another genome of MG II was assembled from the Mediterranean deep chlorophyll maximum (DCM), which belonged to subgroup II.b (Martin-Cuadrado et al., 2015). The authors used FISH to detect these cells in DCM samples and proposed the Class *Thalassoarchaeae* (archaea from the sea) to name members of the MG II.b. They also confirmed by recruitment of genomic fragments from the Mediterranean Sea and Puget Sound that *Thalassoarchaeae* are inhabitants of the oligotrophic photic zone while MG IIa are adapted to more coastal or even estuarine (brackish) habitats, which indicate that subgroups of MG II may represent different ecotypes. Two recent metatranscriptomic studies (Baker et al., 2013; Ottesen et al., 2013) found that MG II transcripts were present at levels similar to numerically dominant groups like *Peleagibacter* or SAR86. Actually, metatranscriptomic data show in general much greater contribution of MG II than their expected numbers from metagenomics would predict, suggesting that MG II populations may be very dynamic and capable of responding rapidly to changing conditions.

A diagram summarizing the key metabolic functions of the MG II as derived from metagenomics is displayed in Figure 1. In general, MG II metabolic genes include those encoding functions associated with glycolysis, the tricarboxylic acid cycle, and phosphorylation complexes indicative of aerobic respiration. However, the identification of some of the genes of the assimilatory sulfate reduction pathway in the *Thalassoarchaeae* genomic fragments (Martin-Cuadrado et al., 2008, 2015) suggests capacity for anaerobic respiration within low-oxygen microenvironments such as organic particles, which is supported by Orsi et al. (2015). In addition, a complete non-oxidative pentose phosphate pathway was identified in both available genomes of MG II, but some of the enzymes of the irreversible oxidative branch were not found in MG II.b, probably due to the incompleteness of this genome. Several transporters were
identified, but the nature of the substrates could not be identified in most of the cases. An agarase-like gene is present in the MG II.b (Figure 1); however, it is unknown whether this group of archaea can use agar as carbon source. Transporters for branched-chain amino acids and di/oligopeptides were very abundant, supporting the model that protein degradation may be important to the metabolism of these microbes. Also, sequences encoding several drug-efflux pumps were abundant in both clades, which was suggested to indicate a defensive lifestyle, typical of organisms exposed to natural toxins, i.e., from blooms of cyanobacteria producing marine biotoxins (Martin-Cuadrado et al., 2015).

Last but not least, the biogeochemical function of MG II is receiving increasing attention. The TEX$_{86}$ paleo sea surface temperature proxy was originally based on the premise that archaeal lipids used in formulating the proxy are solely produced by *Thaumarchaeota* living in the surface ocean (Schouten et al., 2002). However, evidence increasingly demonstrates that temperature is not the only variable affecting the tetraether lipid distribution in the ocean (see reviews by Pearson and Ingalls, 2013; Schouten et al., 2013). In particular, the biological source of tetraether lipids in the ocean requires further consideration. Recently, Lincoln et al. (2014a) and Wang et al. (2015) provide evidence supporting an earlier speculation (Turich et al., 2007) that MG II may be significant contributors to tetraether lipids in coastal and open oceans. This is, however, still a highly debated topic (Lincoln et al., 2014b; Schouten et al., 2014) and a critical step and potentially growing area of research is verifying tetraether production by MG II under controlled laboratory conditions, using either enrichment or, hopefully, pure cultures.

**SUMMARY AND FUTURE RESEARCH DIRECTIONS IN MARINE ARCHAEA**

Archaea are now recognized as equally important as bacteria in the global ocean carbon cycle. Advances in MG I (*Thaumarchaeota*) research over the past two decades have been tremendous, particularly in our understanding of the ecological and biogeochemical functions of these organisms. In comparison, our understanding of MG II, despite their
widespread occurrence in the ocean, is still rudimentary. Recently, the concept of the microbial carbon pump (Jiao et al., 2010) further highlighted the importance of microorganisms (including both archaea and bacteria) in long-term storage of dissolved organic carbon, which is the largest pool of organic carbon in the ocean. While a number of issues hinder advancing our understanding of the microbial processes mediating ocean biogeochemistry, the lack of information on archaea is particularly severe (Kujawinski, 2011). Archaea have several unique features that distinguish them from bacteria, including membrane lipids that are more resistant to degradation than bacterial lipids and capability in surviving harsh environments in which carbon metabolism by other organisms may be inhibited. Future research on marine archaea, including both MG I and MG II, may focus on the following topics in order of importance and ease of accomplishment for the fields of microbial ecology and biogeochemistry:

1. Increasing genomic coverage of MG II lineages using metagenomics and single-cell genomics.

2. Enriching and isolating MG II followed by physiological and biochemical studies.

3. Validating the lipid composition of MG II and re-evaluating the sources of GDGTs in the open ocean.

4. Distinguishing relative contributions of archaea and bacteria in the production and transformation of recalcitrant dissolved organic carbon in the ocean.

5. Elucidating the evolutionary and/or horizontal gene transfer pathways of MG II in contrast to or in concert with MG I.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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