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Planktonic Marine Archaea

Alyson E. Santoro,[1] R. Alexander Richter,[2] and Christopher L. Dupont[2]

[1]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106, USA; email: asantoro@ucsb.edu

[2]J. Craig Venter Institute, La Jolla, California 92037, USA; email: rrichter@jcvi.org, cdupont@jcvi.org

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Abstract

Archaea are ubiquitous and abundant members of the marine plankton. Once thought of as rare organisms found in exotic extremes of temperature, pressure, or salinity, archaea are now known in nearly every marine environment. Though frequently referred to collectively, the planktonic archaea actually comprise four major phylogenetic groups, each with its own distinct physiology and ecology. Only one group—the marine Thaumarchaeota—has cultivated representatives, making marine archaea an attractive focus point for the latest developments in cultivation-independent molecular methods. Here, we review the ecology, physiology, and biogeochemical impact of the four archaeal groups using recent insights from cultures and large-scale environmental sequencing studies. We highlight key gaps in our knowledge about the ecological roles of marine archaea in carbon flow and food web interactions. We emphasize the incredible uncultivated diversity within each of the four groups, suggesting there is much more to be done.

1. INTRODUCTION

Woese & Fox (1977) first proposed, from a handful of small subunit rRNA sequences, that the methanogenic "bacteria" were actually a lineage as distantly related to other bacteria as they were to eukaryotes. The identification of this lineage, coined the archaeabacteria, showed that a molecular rather than morphological classification best described the evolutionary relationships among organisms and led to the eventual proposal for the domain Archaea, which included methanogens, thermophiles, and halophiles (Woese et al. 1990). From these "extreme" beginnings, the idea that a review in a marine science journal would be devoted to these organisms would have been unthinkable to many, if not most.

Archaea were discovered in the marine plankton within the lifetimes of most marine scientists working today (DeLong 1992, Fuhrman et al. 1992), and we have learned that they are not, in fact, confined to extreme environments, but instead are among the most abundant cells in the ocean (Karner et al. 2001). Though archaea differ fundamentally in their evolutionary history, membrane composition, and regulation of transcription and translation, the more we learn about these seemingly enigmatic organisms, the more we find that their story is not that dissimilar to the famous marine cyanobacteria and heterotrophic bacteria that dominate the surface ocean.

The four groups of planktonic marine archaea—marine group I (MGI) (DeLong 1992, Fuhrman et al. 1992), MGII (DeLong 1992), MGIII (Fuhrman & Davis 1997), and MGIV (López-Garcia et al. 2001b)—were first known only by their 16S rRNA genes (**Table 1**). The cultivation of the first MGI archaeon (*Nitrosopumilus maritimus*) as a chemolithoautotrophic ammonia oxidizer (Könneke et al. 2005), groundbreaking metagenomic studies (Hallam et al. 2006), and the development of marker gene assays (Francis et al. 2005, Wuchter et al. 2006) have led to huge leaps in our ability to interrogate the genomes and physiology of MGI and to track their abundance and diversity in the environment. These findings eventually led to the reclassification of MGI, formerly members of the Crenarchaeota, into their own phylum—the Thaumarchaeota, or "wonder" archaea (Brochier-Armanet et al. 2008, Spang et al. 2010). By comparison, our genomic and physiological knowledge of MGII, MGIII, and MGIV remains meager.

The goal of this review is to focus on recent insights into the ecology of marine planktonic archaea. We review their distribution and abundance in the world's oceans (Section 2) and our still relatively limited knowledge of their physiology (Section 3). We describe how planktonic archaea contribute to marine biogeochemical cycles (Section 4) and review genome evolution and dynamics (Section 5). Finally, we highlight key uncertainties in the role of archaea in the larger marine food web (Section 6) and how they specifically contribute to the flow of energy and materials through marine ecosystems.

By necessity, this article is not a comprehensive review of every study concerning marine archaea in the more than 25 years since their discovery. For more information, we direct readers to two personal histories that place the marine archaea in a narrative context (DeLong 2007, Fuhrman 2011), an excellent review on archaeal physiology (Stahl & de la Torre 2012), and two articles on the continually expanding understanding of archaeal phylogeny and its relationship to the origins of eukaryotes (Adam et al. 2017, Spang et al. 2017).

2. THE DISTRIBUTION AND ABUNDANCE OF THE MAJOR GROUPS OF PLANKTONIC ARCHAEA

The four groups of planktonic archaea differ markedly in both their depth distribution and their overall abundance in the water column (DeLong et al. 2006) (**Figure 1**). Thaumarchaea generally

Table 1 The major groups of planktonic archaea

Original group name	Original reference(s)	Current group name	Updated reference(s)	Basic physiology	Distribution
MGI Crenarchaeota	DeLong 1992, Fuhrman et al. 1992	Group I.1a Thaumarchaeota	Brochier-Armanet et al. 2008	Ammonia-oxidizing chemoautotrophs with potential for mixotrophic uptake of organic carbon	Ubiquitous, particularly abundant below the euphotic zone
MGII Euryarchaeota	DeLong 1992	MGII Euryarchaeota	See MGII.A and MGII.B	See MGII.A and MGII.B	See MGII.A and MGII.B
MGII.A	Massana et al. 2000	MGII.A	Iverson et al. 2012	Motile photoheterotrophs specializing in high-molecular-weight compound degradation, especially proteins	Surface ocean, especially in coastal environments
MGII.B	Massana et al. 2000	Thalassoarchaea	Martin-Cuadrado et al. 2015	Photoheterotrophs (shallow subgroups); heterotrophs (deep subgroups) specializing in high-molecular-weight compound degradation	Throughout the water column, but particularly abundant in the lower euphotic zone and deep chlorophyll maximum layers
MGIII	Fuhrman & Davis 1997	Pontarchaea	Adam et al. 2017, Haro-Moreno et al. 2017	Heterotrophs specializing in high-molecular-weight compound degradation	Originally thought to be confined to the deep sea and marine sediments, now found throughout the water column
MGIV	López-Garcia et al. 2001b	MGIV	None	Unknown (branch basal to the haloarchaea)	Deep sea, brine interfaces

Abbreviation: MG, marine group. Table adapted from Adam et al. (2017).

increase in both absolute and relative abundance with depth and may reach nearly 40% of total cells in the mesopelagic (Karner et al. 2001). MGII archaea, by contrast, are more abundant in shallow waters and decrease in abundance with depth (Massana et al. 1997, Murray et al. 1999). The MGIII and MGIV archaea are rare enough that a definitive abundance pattern cannot be determined, but in general, they are far less abundant than either MGI or MGII and are more frequently detected in the deep mesopelagic and bathypelagic. Here, we briefly review variation in these groups' distribution and abundance in both space and time.

2.1. Marine Group I Thaumarchaea

Thaumarchaea are found from the equator (Church et al. 2010, Santoro et al. 2017) to the poles (Bano et al. 2004, DeLong et al. 1994, Sintes et al. 2013) and from shallow surface waters to the

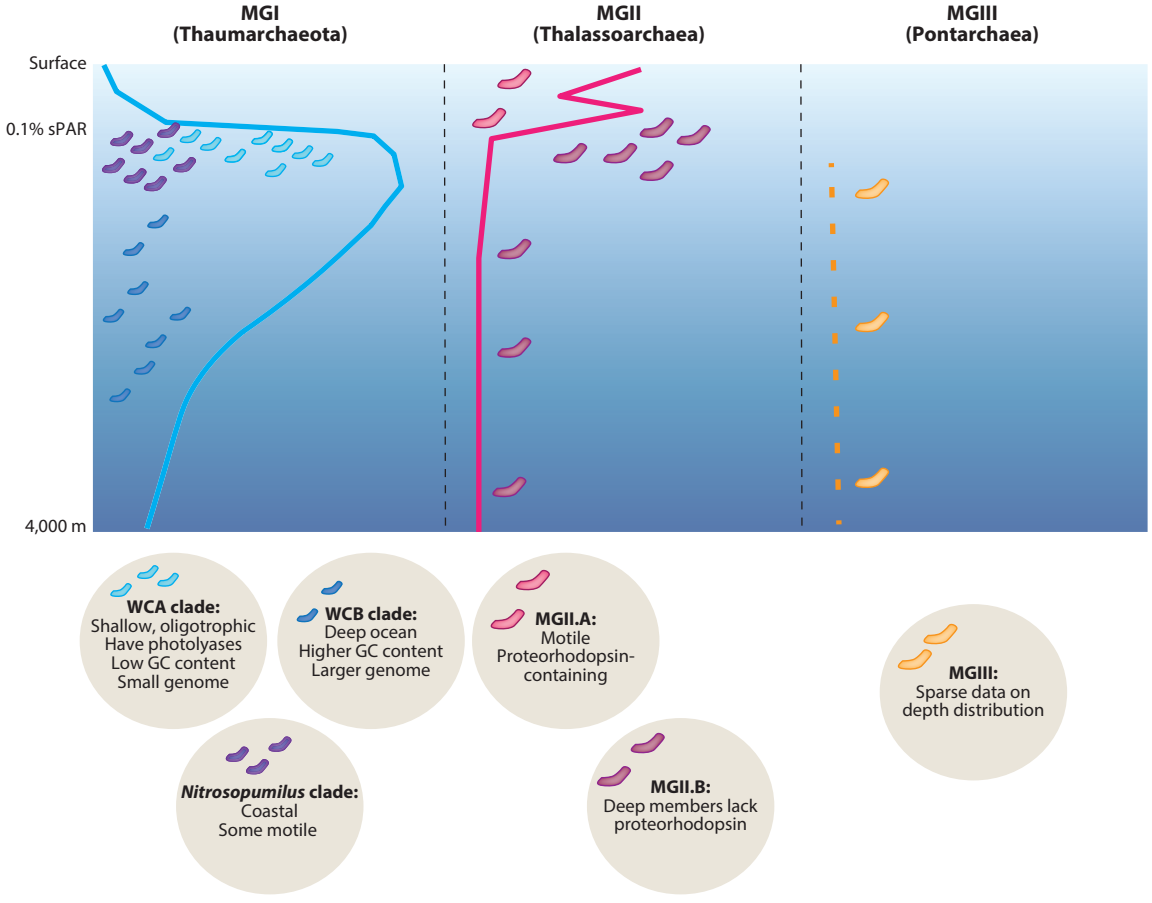


Figure 1

Distribution of the three main groups of planktonic archaea in the marine water column. Both MGI and MGII have distinct clades or ecotypes that preferentially occur in different parts of the water column. Abbreviations: MG, marine group; sPAR, surface photosynthetically active radiation; WCA, water column A; WCB, water column B.

greatest hadal depths (Nunoura et al. 2015). Unlike the MGII–IV archaea, which are uniquely marine, thaumarchaea are found in diverse environments, including soils, sediments, hot springs, and wastewater treatment systems. Within the thaumarchaea, marine representatives are also referred to as the group I.1a Thaumarchaeota (Spang et al. 2010). As discussed below, all cultivated group I.1a thaumarchaea gain energy from the oxidation of ammonia (NH_3), giving them an important role in marine biogeochemistry. This defining metabolism also determines their distribution in the ocean, where their abundance is closely tied to the flux of ammonium (NH_4^+) and the other reduced nitrogen compounds they use for energy.

In the open ocean, thaumarchaea are relatively rare in surface waters; they increase in abundance through the upper mesopelagic and decrease below that depth range (**Figure 1**). This distribution was evident even in the earliest papers that examined the distribution of archaea in the ocean, which found that up to half of 16S rRNA gene clones in the mesopelagic and deep ocean belonged to MGI (Fuhrman & Davis 1997). This pattern continued to be borne out in studies using fluorescence in situ hybridization (FISH) and microscopy (Fuhrman & Ouverney 1998,

Herndl et al. 2005). Quantitative polymerase chain reaction (qPCR) assays for the enumeration of MGI based on both the 16S rRNA gene (Mincer et al. 2007, Wuchter et al. 2006) and the ammonia monooxygenase subunit A gene (*amoA*) (Mosier & Francis 2011) have largely reinforced the initial depth distribution patterns found using microscopy techniques. For example, the peak abundance of MGI 16S rRNA genes was observed in the upper mesopelagic, near the base of the euphotic zone, increasing to 200-m depth in Monterey Bay (Mincer et al. 2007). Similar patterns were found in a transect extending from the California coast to the edge of the North Pacific gyre, where the maximum in MGI abundance in the upper mesopelagic varied with the depth of the euphotic zone (Santoro et al. 2010). This depth distribution—low abundance at the surface, maximal in the upper mesopelagic, and decreasing below that—has been repeatedly observed in wide-ranging locations, such as the Sargasso Sea (Newell et al. 2013), central Pacific (Church et al. 2010), equatorial Pacific (Santoro et al. 2017), and Atlantic (Sintes et al. 2016, Teira et al. 2006a). A potential exception to this pattern is in polar seas, where thaumarchaea reach high abundances at relatively shallow depths (Shiozaki et al. 2016, Sintes et al. 2016).

MGI abundance can vary substantially over time as well, particularly in coastal waters, where they may occasionally form blooms (Hollibaugh et al. 2011). As would be expected in seasonal subtropical and temperate systems, MGI abundance is more variable in surface waters than at depth (Murray et al. 1999, Parada & Fuhrman 2017) and is often correlated with indicators of deep-water upwelling (Mincer et al. 2007, Murray et al. 1999). In the first study to experimentally link MGI with ammonia-oxidizing metabolism in the field, Wuchter et al. (2006) found dynamic seasonal changes in MGI abundance in the North Sea over the course of the year that were correlated with the drawdown of ammonium and a buildup of nitrite and nitrate in surface waters in winter. High abundances of MGI have also been seen during winter in a time-series study in Blanes Bay in the northwestern Mediterranean (Galand et al. 2010). Beman et al. (2010) showed that MGI archaea are highly variable at the San Pedro Ocean Time-Series site.

Based only on *amoA* gene sequences, the open-ocean planktonic thaumarchaea fall into at least two clades, distinct from *N. maritimus*: a shallow-water clade, referred to as the water column A (WCA) or high-ammonia cluster (HAC) clade, which contains "*Candidatus* Nitrosopelagicus brevis" (Santoro et al. 2015), and a deep-water clade, referred to as the water column B (WCB) or low-ammonia cluster (LAC) clade (Francis et al. 2005, Sintes et al. 2013). The WCA clade is generally the dominant group where thaumarchaeal abundance is maximal in the water column (Beman et al. 2008, Shiozaki et al. 2016, Smith et al. 2014a), while the WCB clade is dominant below approximately 300-m depth. A recent reanalysis of the thaumarchaeal *amoA* phylogeny further subdivided the marine thaumarchaea into eight named clades, with the NP-ε-2 clade corresponding to the WCA clade and the NP-α-2.2.2.1 clade approximately, though not exactly, corresponding the WCB clade (Alves et al. 2018). Partitioning of the water column between the WCA and WCB clades can be seen across basin-scale transects (Santoro et al. 2017, Shiozaki et al. 2016, Sintes et al. 2016). Members of the WCB clade are occasionally found in surface waters, particularly in upwelling regions (Damashek et al. 2017, Shiozaki et al. 2016, Smith et al. 2014a), where they appear to be less transcriptionally active (Santoro et al. 2010). Because no cultures yet exist from the deep clade, hypotheses about the physiological underpinnings of this division are difficult to test, but several studies have suggested that the ammonium concentration in the environment determines which clade is present (Sintes et al. 2013, Villanueva et al. 2015). Experimentally testing the hypothesis that the shallow/deep separation is in fact controlled by ammonium will be difficult. It is likely the flux of ammonium through the environment, rather than the concentration, that influences this distinction. Moreover, ammonium fluxes are related to the flux of dissolved organic compounds, which may also be behind the observed niche differentiation.

2.2. Marine Group II Euryarchaea

Like MGI, MGII archaea have been found from polar (Bano et al. 2004, DeLong et al. 1994, Galand et al. 2006) to tropical seas (Schattenhofer et al. 2009). In contrast to MGI, MGII archaea are most abundant in the sunlit waters of the euphotic zone and decrease in abundance with depth (DeLong et al. 2006, Massana et al. 1997, Murray et al. 1999), though they are regularly found below the euphotic zone (Frigaard et al. 2006, Parada & Fuhrman 2017). Some studies have found that MGII archaea are relatively invariant with depth in some locations (Herndl et al. 2005, Teira et al. 2004).

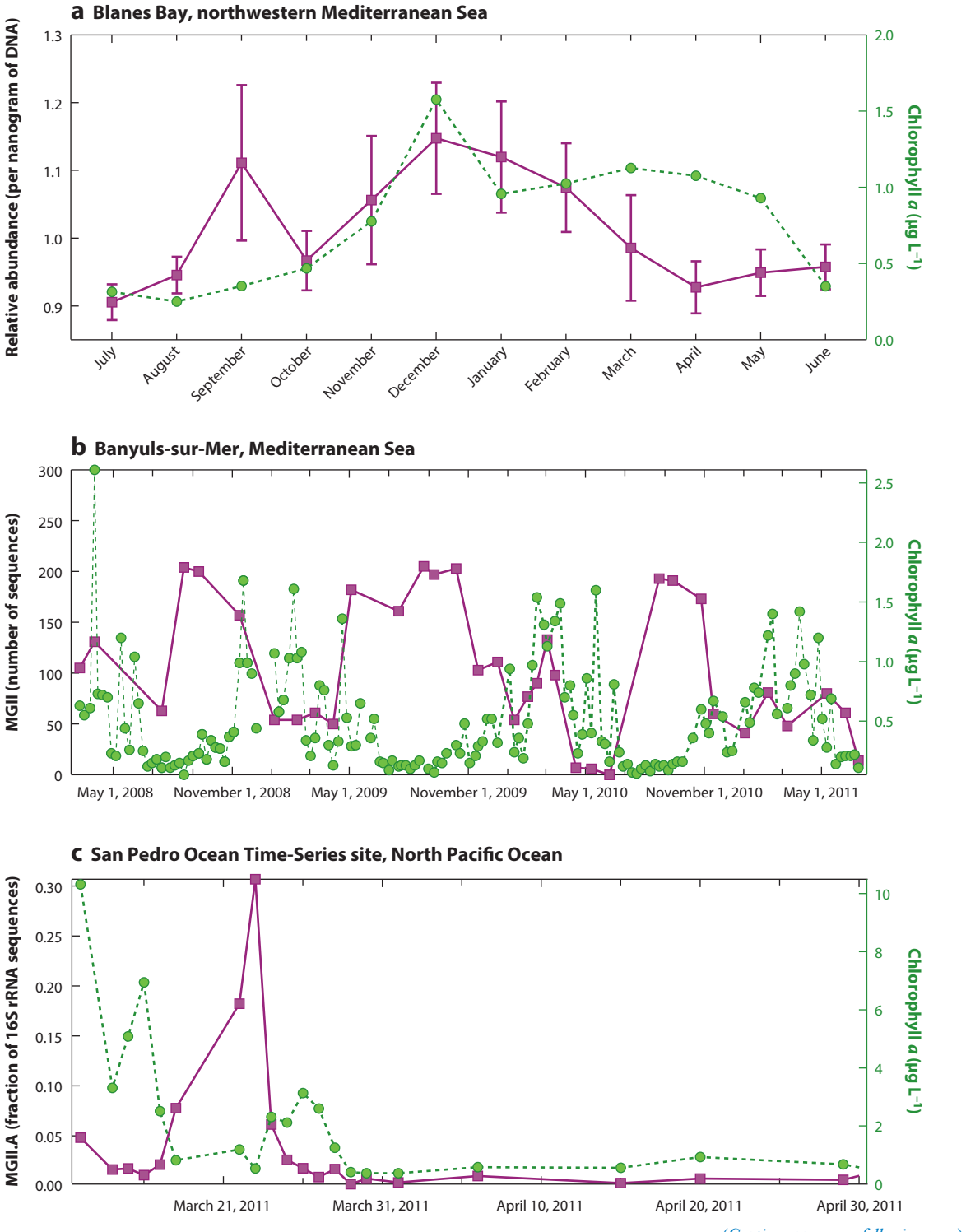
MGII abundance varies greatly over time (**Figure 2**), and these archaea may form transient blooms coincident with or just following phytoplankton blooms (Galand et al. 2010, Mincer et al. 2007), at times reaching more than 30% of the total bacterioplankton (Needham & Fuhrman 2016, Pernthaler et al. 2002). MGII abundance correlates with chlorophyll *a* concentration in some locations (Galand et al. 2010) but not in others (Hugoni et al. 2013), and a coast-to-offshore transect found that MGII archaea were most abundant at the coast (Orsi et al. 2015). MGII archaea are also consistent members of the microbial assemblage within deep chlorophyll maximum layers in oligotrophic regions such as the North Pacific (Orsi et al. 2015) and the eastern Mediterranean Sea (Martin-Cuadrado et al. 2015). A high degree of 16S rRNA diversity exists within MGII (Galand et al. 2010, Hugoni et al. 2013), which may contribute to the observed differences in temporal patterns among differing locations using different quantification techniques.

Correlations between phytoplankton abundance and MGII led to some speculation that they are facultative colonizers of particles. Studies have found that MGII archaea are associated with particulate matter in the Columbia River estuary (Crump & Baross 2000) and with small suspended particles (Kellogg & Deming 2009). Metagenomic and qPCR studies have also found MGII preferentially located in the larger size fractions of size-fractionated libraries (Orsi et al. 2015), while others have found that the degree of particle association varies with depth (Lincoln et al. 2014). It is uncertain whether the appearance of MGII DNA and RNA in the large size fractions is due to true particle association as opposed to aggregation (Martin-Cuadrado et al. 2015) or if some MGII cells are simply large, as studies have observed MGII microscopically in association with detrital material (Orsi et al. 2015) but also as large cells (DeLong et al. 1999).

2.3. Marine Group III and IV Euryarchaea

Although MGIII and MGIV were first identified not long after MGI and MGII (Fuhrman & Davis 1997, López-Garcia et al. 2001b), very little is known about their geographic distribution due to their overall lower abundance in the water column. Until recently (Haro-Moreno et al. 2017), it was thought that MGIII archaea were predominantly deep-sea taxa. In the western Mediterranean, just one MGIII sequence was recovered from a library of 196 archaeal clones from a depth of 450 m (Massana et al. 2000). At the time, the sequences were most closely related to sequences from marine sediments. Since then, representatives of MGIII have been found as members of deep-sea microbial assemblages in multiple locations (Li et al. 2015, Quaiser et al. 2011). Martin-Cuadrado et al. (2008) found MGIII in fosmid libraries from 1,000- and 3,000-m depths in both the Mediterranean and South Atlantic. MGIII archaea were distributed preferentially within anoxic waters of the oxygen minimum zone in the Peru upwelling region (Belmar et al. 2011). A recent study found a distinct clade of MGIII in the euphotic zone of the Mediterranean Sea (Haro-Moreno et al. 2017), suggesting more diversity than was previously recognized within this group.

The first MGIV clone originated from 3,000-m depth in the Antarctic polar front (López-Garcia et al. 2001a). Other MGIV sequences recovered from deep waters of the North Atlantic



(Caption appears on following page)

Figure 2 (*Figure appears on preceding page*)

Variation in the abundance of planktonic MGII archaea across annual, seasonal, and weekly timescales, illustrating their dynamic, blooming nature. (*a*) Average monthly abundance of MGII over 4.5 years at the Blanes Bay Observatory, determined using qPCR for 16S rRNA genes. Data are normalized to the annual average value. (*b*) Number of MGII 16S rRNA gene sequences in pyrosequencing libraries from a microbial observatory in Banyuls-sur-Mer. (*c*) Fractional abundance of MGII.A 16S rRNA gene sequences in amplicon-based tag sequencing libraries from the total bacterioplankton community at the San Pedro Ocean Time-Series site. In panel *a*, the MGII bloom coincides with high phytoplankton abundance (shown as chlorophyll *a*), while in panels *b* and *c*, the MGII bloom follows the phytoplankton blooms. Abbreviations: MG, marine group; qPCR, quantitative polymerase chain reaction. Panels *a–c* adapted from Galand et al. (2010), Hugoni et al. (2013), and Needham & Fuhrman (2016), respectively, with permission.

and Mediterranean (López-Garcia et al. 2001b) branch at the base of the haloarchaea. Beyond these early observations, little is known about this group's distribution.

3. THE PHYSIOLOGY OF PLANKTONIC ARCHAEA

The distribution, abundance, and temporal variability of the major groups of planktonic archaea were early clues to the dramatic differences in their physiology and environmental significance. Murray et al. (1999, p. 129) made a prescient prediction based on a time series of rRNA in the Santa Barbara Channel: "The distribution of the 2 archaeal groups suggested that they responded independently to environmental conditions, are physiologically different, and likely participate in different environmental processes." This turned out to be correct, and not just in the Santa Barbara Channel, as considerable diversity is now apparent within the marine archaea throughout the world's oceans (**Figure 3**).

3.1. The Ammonia-Oxidizing Thaumarchaea

A testament to the enduring importance of cultivation in microbiology, the field of marine thaumarchaeal physiology has been greatly advanced by the availability of pure (Kim et al. 2016, Könneke et al. 2005, Qin et al. 2017b) and enrichment cultures (Ahlgren et al. 2017, Bayer et al. 2015, Berg et al. 2015a, Mosier et al. 2012, Santoro & Casciotti 2011). All cultivated planktonic thaumarchaea grow as chemolithotrophic ammonia oxidizers, oxidizing ammonia for energy and fixing inorganic carbon into biomass. All available genomic, metagenomic (Baker et al. 2012, Konstantinidis et al. 2009, Tully et al. 2012), and single-cell genomic data (Swan et al. 2014) indicate a similar lifestyle, suggesting that ammonia-oxidizing metabolism is a defining feature of this group. Some early reports found mismatches between 16S rRNA gene abundance and the *amoA* gene (Agogue et al. 2008), leading to speculation that not all planktonic thaumarchaea were ammonia oxidizers. Comparisons with metagenomic data, however, suggest potential mismatches in the primer sets used in early *amoA*-based studies that did not capture the deep clades (Konstantinidis et al. 2009). The extent to which all of these *amoA*-containing cells are obligate autotrophs or are able to use organic carbon compounds to supplement their biosynthetic carbon demand is uncertain (see below). Thaumarchaea are able to access reduced nitrogen from urea to support their energy-generating metabolism, and urea utilization has been demonstrated in culture (Bayer et al. 2015, Carini et al. 2018, Qin et al. 2014), single-gene studies (Tolar et al. 2017), and metagenomes (Alonso-Saez et al. 2012, Santoro et al. 2017, Tully et al. 2012). Furthermore, cyanate utilization has been demonstrated in non-marine thaumarchaea (Palatinszky et al. 2015). Whether marine thaumarchaea also utilize other catabolic ammonia-generating pathways (e.g., arginase, guanidase, or cyanase) is an open question.

Significant uncertainties remain in the biochemistry of ammonia oxidation in the thaumarchaea. The overall oxygen stoichiometry (NH_3:O_2 ratio of 1:1.5) appears to be the same as for the

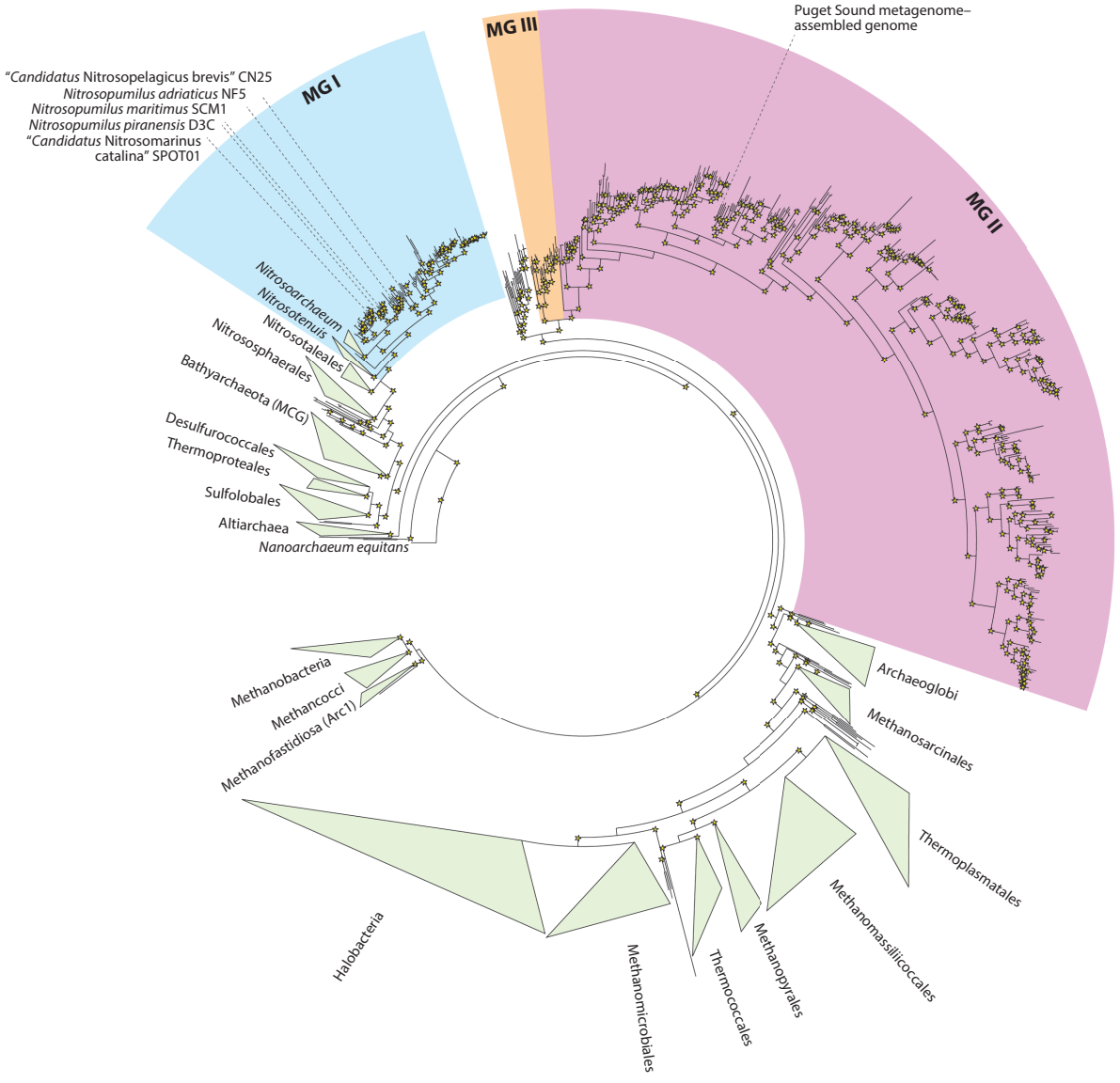


Figure 3

Phylogeny of the marine planktonic archaea. The tree is a maximum-likelihood (RAxML) reconstruction built on a concatenated alignment of 32 proteins from 1,360 archaeal genomes, including metagenome-assembled genomes, single-cell genomes, and cultivated isolates, using ETE 3 (Huerta-Cepas et al. 2016). Phylogenetic markers were selected by hmmsearch (Finn et al. 2011) against AMPHORA2 markers (Wu & Scott 2012). Stars indicate support values >0.95. All data were obtained from the National Center for Biotechnology Information's GenBank database or the Joint Genome Institute's Integrated Microbial Genomes database. Abbreviations: AMPHORA, Automated Phylogenomic Inference Application; ETE, Environment for Tree Exploration; MG, marine group; RAxML, Randomized Axelerated Maximum Likelihood.

ammonia-oxidizing bacteria (Martens-Habbena et al. 2009, Stahl & de la Torre 2012), and, like ammonia-oxidizing bacteria, thaumarchaea incorporate only one oxygen atom from water into nitrite (NO_2^-) during ammonia oxidation (Santoro et al. 2011). Until very recently, ammonia-oxidizing bacteria were thought to employ a two-step oxidation pathway, where ammonia is first oxidized to hydroxylamine (NH_2OH) by ammonia monooxygenase and subsequently to NO_2^- by hydroxylamine oxidoreductase (Arp et al. 2002). No homolog of hydroxylamine oxidoreductase has yet been identified in any thaumarchaeal genome (Hallam et al. 2006, Kerou et al. 2016, Walker et al. 2010), yet thaumarchaea have been shown to produce NH_2OH (Liu et al. 2017, Vajrala et al. 2013), suggesting that it is the product of ammonia monooxygenase in both ammonia-oxidizing bacteria and archaea. Thaumarchaea also produce nitric oxide (NO) as an obligate intermediate (Martens-Habbena et al. 2015), potentially from the activity of the copper-containing nitrite reductase NirK (Kozlowski et al. 2016), which is present in all sequenced mesophilic thaumarchaea (Kerou et al. 2016). NO could then react with NH_2OH to form NO_2^- (Kozlowski et al. 2016), forming a three-step ammonia oxidation pathway. A three-step pathway for bacterial ammonia oxidation was recently proposed, whereby ammonia is oxidized first to NH_2OH, then to NO, and finally to NO_2^- (Caranto & Lancaster 2017), raising the possibility that ammonia oxidation in the archaea is also a three-step process (Carini et al. 2018). Detailed biochemical characterization of the individual enzymes in the archaeal ammonia oxidation pathway will be necessary to resolve these uncertainties.

Several aspects of thaumarchaeal physiology suggest adaptation to a particularly oligotrophic way of life, consistent with the vanishingly low ammonium concentrations in most of the open ocean. The half-saturation constant (K_m) for NH_3/NH_4^+ uptake by *N. maritimus*, isolated from a marine aquarium, is among the lowest measured in culture—133 nM (Martens-Habbena et al. 2009)—and field-based estimates of community substrate affinity in the open ocean, in which thaumarchaea are the dominant ammonia oxidizers, push this value even lower, as low as 27 nM (Peng et al. 2016). Contributing to their adaptation to low nutrient availability, marine thaumarchaea are small, giving them a high surface-area-to-volume ratio. They are small enough to pass through a filter with a 0.45-μm pore size (Könneke et al. 2005, Santoro & Casciotti 2011). Yet, despite their high substrate affinity and economical cell size, thaumarchaea apparently compete poorly with phytoplankton for NH_4^+ in some environments (Smith et al. 2014b, Wan et al. 2018).

The carbon fixation pathway employed by the thaumarchaea—a modified version of the 3-hydroxypropionate/4-hydroxybutyrate cycle—is one of the most efficient microbial carbon fixation pathways in terms of cell biomass generated per ATP (Könneke et al. 2014). The free energy yield of ammonia oxidation ($\Delta G^{0\prime} = -274.7$ kJ mol^{-1}) is relatively low, however, and this biosynthetic efficiency does not translate to fast growth. For example, the reported specific growth rates for thaumarchaea range from 0.17 d^{-1} for "*Ca*. N. brevis" (Santoro & Casciotti 2011) to 0.78 d^{-1} for *N. maritimus* SCM1 (Qin et al. 2014). The active carbon species in the 3-hydroxypropionate/4-hydroxybutyrate cycle is the carbonate ion, not carbon dioxide (Berg et al. 2007), which may be the explanation behind reports of minimal pH dependence of marine ammonia oxidation rates in some studies (Fulweiler et al. 2011). Indeed, cultivated ammonia-oxidizing archaeal isolates show pH optima for growth markedly lower than the pH of seawater (Qin et al. 2014). By contrast, some studies have shown significant negative effects of low pH on marine ammonia oxidation (Beman et al. 2011a).

Though there is little argument that thaumarchaea in the ocean fix inorganic carbon, the extent to which they are also reliant on organic carbon compounds is not known. Many photoautotrophic organisms are able to facultatively take up organic carbon to support their biosynthetic needs (Muñoz-Marín et al. 2013); thus, it is not unreasonable to expect chemoautotrophs to

employ a similar strategy. *N. maritimus* grows as a strict autotroph, but both its growth rate and its cell yield are enhanced in the presence of α-ketoglutarate (Qin et al. 2014); other isolates appear to require α-keto acids for growth (Qin et al. 2014). By contrast, enrichment cultures and cultures grown in natural seawater often do not show a growth enhancement by organic compounds (Bayer et al. 2015, Santoro et al. 2015), and direct evidence for either assimilation or respiration of organic carbon in cultures is limited (Kim et al. 2016). This has led to the hypothesis that α-keto acids serve an alternative function as scavengers for hydrogen peroxide or other radical oxygen species (Kim et al. 2016), for which thaumarchaea have limited defenses (Hollibaugh 2017). Field data also suggest that wild thaumarchaea are able to take up organic carbon compounds (Ouverney & Fuhrman 2000, Teira et al. 2006b), express transporter proteins for organic compounds (Bergauer et al. 2018), and may gain 20% or more of their cellular carbon from sinking organic matter (Ingalls et al. 2006). As pointed out by Newell et al. (2011), ammonia oxidation rates in the deep mesopelagic are very low, such that the turnover time for deep-ocean thaumarchaea would be on the order of 1,500 days based on ammonia oxidation alone. This suggests that thaumarchaea must be relying on other metabolisms in the mesopelagic to support their abundance there. There are some indications in soil (Weber et al. 2015) and wastewater treatment plants (Mußmann et al. 2011) that heterotrophic, or at least non-ammonia-oxidizing, lineages of thaumarchaea may exist. At present, all cultivated marine thaumarchaea originate from either surface waters or sediments, suggesting the potential for novel metabolism in mesopelagic thaumarchaea. Teasing apart this problem will require a better understanding of the carbon and nitrogen stoichiometry of these organisms, as well as carefully designed stable-isotope-tracing experiments that track the fate of organic carbon into thaumarchaeal biomolecules (Yakimov et al. 2011).

3.2. Heterotrophy in Marine Group II

Metabolic information about MGII dates to some of the earliest metagenomic data from the ocean (Béjà et al. 2000), and an MGII genome was among the first microbial genomes to be completely assembled from metagenomic data (Iverson et al. 2012). Yet, because of the lack of any cultivated representatives, knowledge of the basic physiology of MGII lags significantly behind that of MGI (see the sidebar titled The Origins of Archaeal Lipids in the Marine Water Column). The closest cultivated relative of MGII is *Aciduliprofundum boonei*, a thermophilic, acidophilic, sulfate- and iron-reducing heterotroph isolated from a deep-sea hydrothermal vent. The metabolism and genome of *A. boonei* (Reysenbach & Flores 2008) have been used as benchmarks for interpreting

THE ORIGINS OF ARCHAEAL LIPIDS IN THE MARINE WATER COLUMN

The unique composition of archaeal tetraether membrane lipids makes them distinct biomarkers in both the water column (Ingalls et al. 2006) and sediments (Pearson et al. 2001), where they may record past ocean conditions (Schouten et al. 2002) and indicate shifts in subpopulations of planktonic archaea (Zhu et al. 2016). While tetraether lipids have historically been thought to originate solely from thaumarchaea, these lipids are also present at ocean depths lacking significant populations of thaumarchaea, suggesting they may be produced by other groups of archaea (Lincoln et al. 2014, Turich et al. 2007). This interpretation has been questioned (Schouten et al. 2014), highlighting a critical need for cultures of MGII and MGIII euryarchaea in resolving this issue. Cultures of marine thaumarchaea have provided important insights into how microbial physiology influences the interpretation of archaeal lipids in the environment (Elling et al. 2015, Hurley et al. 2016).

initial MGII metagenome data, including this group's reliance on the transport, hydrolysis, and oxidation of proteins and oligopeptides for energy (Iverson et al. 2012, Thrash et al. 2017), a metabolic capacity that also appears to be common in archaea found in deep-sea sediments (Lloyd et al. 2013). Uptake of phytoplankton-derived proteins by MGII has been confirmed using stable-isotope probing (Orsi et al. 2016), and MGII growth was stimulated in the presence of whole cells of the eukaryotic phytoplankter *Micromonas* (Orsi et al. 2015). The capacity for transport of high-molecular-weight substances is encoded by abundant TonB-dependent transporters, which appear to be particularly enriched in the particle-associated MGII (Orsi et al. 2015), which also contain genes for motility and surface attachment (Iverson et al. 2012). A specialization in high-molecular-weight compounds may explain, in part, the observation that MGII archaea often bloom during or immediately after phytoplankton blooms (Galand et al. 2010, Hugoni et al. 2013, Needham & Fuhrman 2016).

Consistent with their abundance in sunlit surface waters, members of MGII.A and MGII.B contain proton-pumping proteorhodopsin (Frigaard et al. 2006, Iverson et al. 2012), apparently gained in a lateral gene transfer event from bacteria (Deschamps et al. 2014, Frigaard et al. 2006). As is the case for many proteorhodopsin-containing organisms, photoheterotrophy is not obligate and growth in the dark is possible, as demonstrated in dark bottle experiments where MGII archaea had growth rates on the order of 0.5 d^{-1} (Orsi et al. 2015). The TonB-dependent transporters mentioned above rely on the proton motive force for energy, and proton pumping by proteorhodopsin may also serve to facilitate transport of high-molecular-weight compounds. MGII archaea living below the euphotic zone appear to lack proteorhodopsin (Frigaard et al. 2006, Li et al. 2015, Martin-Cuadrado et al. 2008, Thrash et al. 2017).

There is also some evidence that MGII archaea may be facultative anaerobes, containing components of an anaerobic respiratory chain, including a heterodisulfide reductase, a succinate dehydrogenase/fumarate reductase, and a 4Fe–4S cluster protein from the molybdopterin-containing dimethylsulfoxide reductase family, which could be involved in the anaerobic respiration of dimethylsulfoxide (Martin-Cuadrado et al. 2008, Moreira et al. 2004). Evidence of respiratory sulfur metabolism was absent from a set of six MGII metagenome-assembled genomes from the Gulf of Mexico (Thrash et al. 2017). One of these genomes did, however, contain a putative respiratory nitrite reductase gene (*nirK*). In sum, a significant amount of metabolic diversity is already apparent within MGII. If the phylogenetic diversity present in this group is any indication (**Figure 3**), much more physiological and metabolic diversity remains to be discovered.

3.3. The Metabolic Potential of Marine Group III

Very little is known about the metabolic capacity of MGIII. The first genomic data came from three fosmids originating from the Ionian Sea, the Adriatic Sea, and the South Atlantic from depths of 1,000 and 3,000 m (Martin-Cuadrado et al. 2008). These sequences were divergent enough from known sequences that little could be inferred about specific metabolic capacity except for the presence of an ammonium transport system and apparent components of the 3-hydroxypropionate/4-hydroxybutyrate carbon fixation pathway, though these enzymes may also be involved in fatty acid biosynthesis. Like MGII, MGIII archaea appear to be able to utilize high-molecular-weight organic matter. Four MGIII genome bins representing five genomes were assembled from a metagenome from the Guaymas Basin (Li et al. 2015), while parallel metatranscriptomes confirmed high transcriptional expression of genes for predicted extracellular peptidases and chitinase, flagellum-driven motility, glucose transport, and fatty acid transport.

Eight bins assembled from various marine metagenomes were used to identify a new clade of MGIII inhabiting epipelagic waters (Haro-Moreno et al. 2017). This clade appears to have an aerobic photoheterotrophic lifestyle, with a blue-light-tuned proteorhodopsin, superoxide dismutase, alkyl hydroxyperoxidase, an apparent capacity for glycolysis, carbon oxidation via the tricarboxylic acid cycle, and the Embden–Meyerhof–Parnas (EMP) pathway for hexose metabolism. In addition to proteorhodopsin, adaptations to the epipelagic environment include the presence of photolyase genes and phosphonate uptake, which may serve as a phosphorus source in inorganic phosphorus–deficient waters.

4. THE ACTIVITY AND BIOGEOCHEMICAL IMPACT OF PLANKTONIC ARCHAEA

4.1. Thaumarchaeal Impacts on Nitrogen, Carbon, and Trace Metal Cycling

Thaumarchaeal metabolism is directly coupled to the biogeochemical cycles of carbon and nitrogen in the ocean through its role in carbon fixation and ammonia oxidation to nitrite, the first step of nitrification. The abundance of thaumarchaeal *amoA* genes is often correlated with ammonia oxidation rates (Beman et al. 2008, Peng et al. 2016, Shiozaki et al. 2016, Smith et al. 2014a), and it is now clear that the predominant ammonia oxidizers in the oceanic water column are the thaumarchaea. Ammonia-oxidizing archaea outnumber ammonia-oxidizing bacteria in nearly every study that has quantified both groups of organisms in the marine water column (Beman et al. 2008, Santoro et al. 2010, Wuchter et al. 2006); DNA sequences originating from ammonia-oxidizing bacteria are rare in open-ocean metagenomes.

Ammonia oxidation has been linked to production of the greenhouse gas nitrous oxide (N_2O) in cultures of ammonia-oxidizing archaea (Löscher et al. 2012, Qin et al. 2017b, Santoro et al. 2011), through analysis of geochemical tracer distributions in the ocean (Nevison et al. 2003), and through direct isotope-labeling experiments (Ji et al. 2015, Yoshida et al. 1989). As mentioned above, ammonia-oxidizing archaea also produce nitric oxide (NO) (Kozlowski et al. 2016, Martens-Habbena et al. 2015), a short-lived gas that reacts to form nitrite (NO_2^-) in oxygenated, aqueous solution (Hughes 2008). In the presence of a strong nucleophile such as Fe^{2+} or NH_2OH, a known intermediate of thaumarchaeal metabolism (Liu et al. 2017, Vajrala et al. 2013), NO may be reduced to N_2O. The extent to which NO is involved in N_2O formation during archaeal ammonia oxidation is not clear, but it appears that N_2O is produced by multiple pathways both in cultures (Kozlowski et al. 2016, Santoro et al. 2011, Stieglmeier et al. 2014) and in the field (Trimmer et al. 2016). Outstanding questions in this area include controls on the yield of N_2O from archaeal ammonia oxidation (i.e., how much N_2O is made for every mole of NH_3 oxidized), whether N_2O is formed inside archaeal cells through either enzymatically or nonenzymatically catalyzed reactions, and whether N_2O can form abiotically from NO outside cells in the conditions found in water column.

Autotrophic (or mixotrophic) growth in the mesopelagic and deep ocean is fueled by the delivery of reduced substrates (ammonium and urea) from above. The distribution of ammonia oxidation rates follows a power law function with depth, similar to the particulate organic carbon attenuation curve (Newell et al. 2011, Smith et al. 2016, Ward 2008). Following from this, the abundance of thaumarchaea in the mesopelagic should be related to the organic matter flux from the euphotic zone: Oceanic regions of high organic matter export should have a higher abundance of thaumarchaea than areas of low export. This is, in fact, exactly what is observed (**Figure 4**). Though there are limited data sets of thaumarchaeal abundance that span regions of high and low export flux, a high abundance of thaumarchaea has been observed in the equatorial upwelling

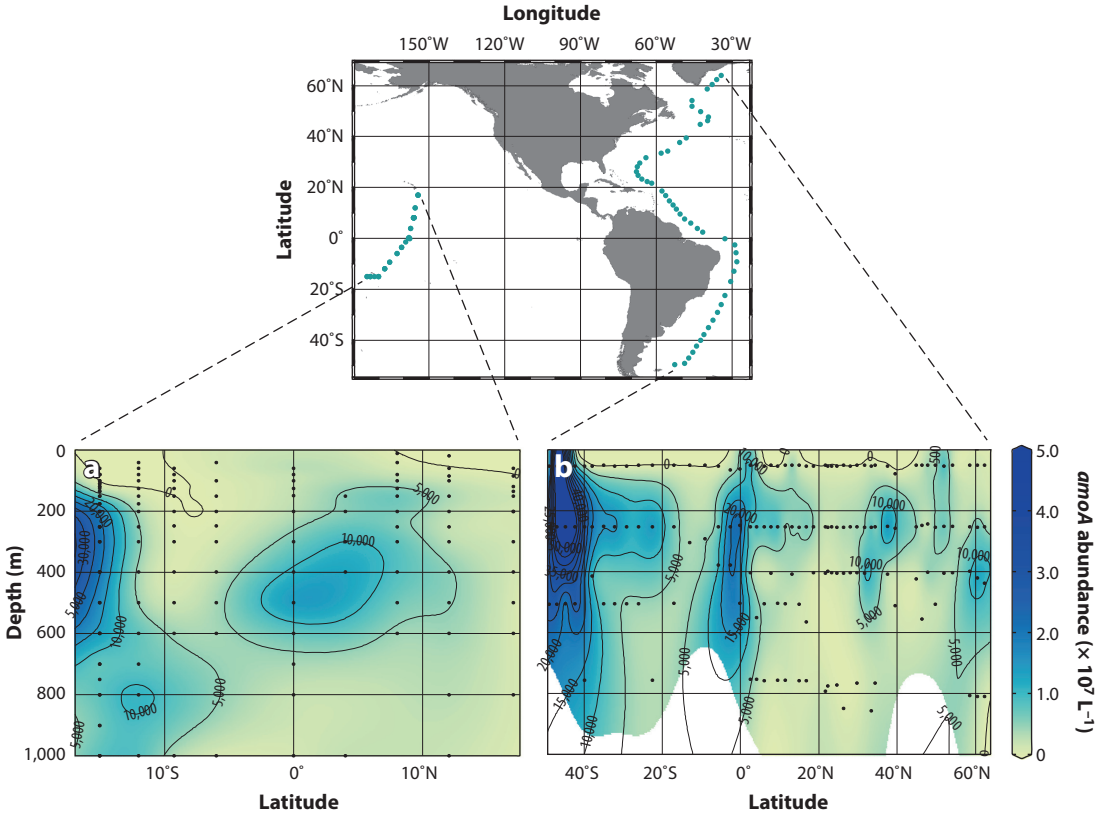


Figure 4

Abundance of thaumarchaeal *amoA* genes determined using qPCR in (*a*) the Pacific and (*b*) the Atlantic, showing relatively high abundances of thaumarchaea below the equatorial upwelling in both basins. Abbreviation: qPCR, quantitative polymerase chain reaction. Data taken from Santoro et al. (2017) and Sintes et al. (2016).

regions of both the Atlantic (Schattenhofer et al. 2009, Sintes et al. 2016) and the Pacific (Church et al. 2010, Santoro et al. 2017), although thaumarchaea make up a smaller fraction of total cells in the meso- and bathypelagic at the equator (Varela et al. 2008).

As autotrophs, thaumarchaea also play a role in the marine carbon cycle. Radiocarbon analyses of archaeal lipids in sediments first suggested that MGI archaea were autotrophs (Pearson et al. 2001). Lipid radiocarbon was later used to infer a predominantly autotrophic lifestyle for MGI in the water column, as more than 80% of their lipid carbon came from the inorganic pool (Ingalls et al. 2006). The origins of the other 20% of archaeal carbon, however, are still uncertain (see Section 3.1). In support of these findings, experimental evidence for active autotrophic inorganic carbon assimilation in marine thaumarchaea is widespread (Herndl et al. 2005, Yakimov et al. 2011). Incubation experiments using added radiocarbon tracer have estimated the total magnitude of carbon fixation by deep archaea at 6.55×10^{13} mol C y^{-1} (Herndl et al. 2005). Marine thaumarchaea may have additional links to the carbon cycle through production of the greenhouse gas methane (CH_4). Some thaumarchaea contain the genes to synthesize methylphosphonate (Metcalf et al. 2012), a precursor of methane production in the ocean. The ammonia monooxygenase enzyme has homology to particulate methane monooxygenase, suggesting that

it could be inhibited by methane or, perhaps more intriguingly, participate in marine methane oxidation.

Thaumarchaea are particularly important to biogeochemical cycling in oxygen minimum zones. The microbial processes that return fixed nitrogen to the atmosphere—denitrification and anaerobic ammonium oxidation (anammox)—rely on the provision of oxidized nitrogen compounds by nitrification. Nitrate (NO_3^-) produced by nitrification is the substrate for the first step of denitrification, while nitrite (NO_2^-) produced as a result of ammonia oxidation also serves as a substrate for the nitrogen-loss process of anammox (Lam et al. 2007). Thaumarchaeal genes and transcripts are abundant at oxyclines (Beman et al. 2008, Berg et al. 2015b, Labrenz et al. 2010, Newell et al. 2011, Peng et al. 2016) but have also been detected within the anoxic core of an oxygen-deficient zone (Stewart et al. 2012). Given that N_2O yields from ammonia oxidation increase dramatically with decreasing oxygen concentration (Ji et al. 2015, Qin et al. 2017b), the activity of thaumarchaea in oxygen minimum zones has the potential to significantly increase marine N_2O storage as oxygen concentrations in the ocean decline (Martinez-Rey et al. 2015).

Analysis of the *N. maritimus* SCM1 genome (Walker et al. 2010) identified an unusual abundance of genes encoding blue copper proteins in the thaumarchaea, where they appear to be integral components of the respiratory chain. Coupled with the putative copper requirements for ammonia monooxygenase and NirK, this high copper requirement suggests that another important biogeochemical impact of planktonic thaumarchaea is on trace metal cycling and that ammonia oxidation in the ocean may occasionally be copper limited. *N. maritimus* becomes copper limited at free copper concentrations that are much lower ($10^{-12.7}$ M) than are found in most of the mesopelagic (Amin et al. 2013) but apparently does not produce copper-binding ligands to access copper at lower concentrations (Amin et al. 2013). Addition of exogenous metal chelator, however, inhibited ammonia oxidation rates in the equatorial Pacific (Santoro et al. 2017). Copper is strongly complexed at depths where thaumarchaea are abundant (Jacquot et al. 2013), suggesting that as-yet-uncultivated ammonia-oxidizing archaea may have different abilities to access this key trace metal.

4.2. Organic Matter Cycling by Marine Groups II and III

The relative paucity of experimental data for MGII and MGIII metabolism leaves their biogeochemical impact speculative and reliant almost solely on inferences derived from metagenomic, metatranscriptomic, and metaproteomic data. MGII and MGIII appear to be heterotrophic, with a specialization in high-molecular-weight compounds; thus, their primary biogeochemical impact is on the carbon cycle (reviewed in Zhang et al. 2015). In the euphotic zone, MGII archaea appear to occupy a similar niche to other photoheterotrophic marine microbes, such as the SAR86 clade, where they are likely involved in the uptake and degradation of phytoplankton-derived organic matter (Ottesen et al. 2013). Deep-sea MGII and MGIII archaea also appear to be involved in the degradation of high-molecular-weight compounds such as proteins and lipids and high-molecular-weight carbohydrates such as glucan, agar, and chitin (Li et al. 2015, Martin-Cuadrado et al. 2015), as well as more labile carbon and nitrogen sources, like amino acids (Baker et al. 2013), indicating that they affect the deep-ocean dissolved organic carbon pool. Further supporting this, MGII transporter proteins for peptide and amino acid uptake were recently detected in a deep-ocean metaproteome (Bergauer et al. 2018). MGII archaea may also play a role in the marine sulfur cycle through their potential utilization of dimethylsulfoxide or disulfide as an electron acceptor (Martin-Cuadrado et al. 2008).

Experiments have shown that MGII archaea take up both leucine and bicarbonate in the mesopelagic and deep ocean (Herndl et al. 2005). The growth of MGII archaea was stimulated by

the addition of whole cells of a eukaryotic phytoplankter (Orsi et al. 2015), which, interestingly, was enhanced in the presence of zooplankton grazers. In the deep ocean, MGII archaea assimilate phytoplankton-derived exopolymeric substances, accounting for more than 50% of exopolymeric substance uptake in the meso- and bathypelagic of the northwestern Mediterranean (Boutrif et al. 2011), confirming their inferred role in the turnover of high-molecular-weight compounds in the deep ocean. Additional information concerning the rates of growth, carbon turnover, and nitrogen uptake from these groups is critically lacking.

5. GENOME DYNAMICS IN THE PLANKTONIC ARCHAEA

The first substantial, though incomplete, genome assembly of a marine archaeon was generated from the host-associated thaumarchaeon *Cenarchaeum symbiosum* (Hallam et al. 2006). Since then, four genomes from cultivated planktonic marine thaumarchaea and four genomes from thaumarchaea from benthic environments have been completely or nearly completely sequenced. Together, two of these, the *N. maritimus* and "*Ca*. N. brevis" genomes, recruit only a small fraction of available metagenomic data at 90% nucleotide identity but recruit a much higher fraction at 50% nucleotide identity (Santoro et al. 2015). In some locations, however—such as Station ALOHA and the Bermuda Atlantic Time-Series Study station—"*Ca*. N. brevis" can reach high local abundances (Ahlgren et al. 2017). This overall low-identity recruitment leads to the conclusion that there is substantial phylogenetic diversity in the environment that has yet to be cultivated, a conclusion also reached in a comprehensive analysis of thaumarchaeal *amoA* genes (Alves et al. 2018). Further supporting this idea, Swan et al. (2014) identified 796 proteins found only in single-cell genomes, most of which could not be assigned to any Clusters of Orthologous Groups (COG) category. A phylogenetic inference based on core proteins of dozens of recently acquired thaumarchaea genomes, including those from single-cell genomics and metagenomic assembly, shows that this is indeed the case (**Figure 3**). At least five clades of marine Thaumarchaeota in this phylogenetic inference lack a cultivated representative. The disparity between cultivated representatives and environmental genome diversity is even greater in MGII, where there appear to be at least two entire uncultivated phyla (**Figure 3**).

Nearly every physicochemical parameter in the ocean relevant to microbial life varies with depth. As a result, depth is frequently observed as a main driver of community structure and niche differentiation in marine microbes (DeLong et al. 2006); the marine archaea are no exception (Biller et al. 2012, Sintes et al. 2015). As both MGI and MGII archaea can be found throughout the water column, they are attractive systems for studying the effects of these environmental gradients on gene content and genome architecture. Metagenomics and single-cell genomics have been useful in this regard, particularly as cultivated representatives of the deep clades for both lineages are lacking. Mende et al. (2017) recently showed that the thaumarchaea transition from small-genome, low-GC-content organisms in the surface waters of the open ocean to larger, higher-GC-content organisms at depth, which may be part of a strategy to minimize cellular nitrogen requirements. The epipelagic thaumarchaea, closely related to "*Ca*. N. brevis," appear to contain photolyase (Luo et al. 2014, Santoro et al. 2015, Swan et al. 2014), as do some members of the *Nitrosopumilus* clade (Bayer et al. 2015). The shallow clade apparently lacks genes for methylphosphonate biosynthesis that are present in *N. maritimus* (Metcalf et al. 2012). Members of both the shallow and deep clades appear to be able to use urea (Santoro et al. 2017, Swan et al. 2014). Differences between shallow and deep MGII are also emerging, with members of MGII.A apparently confined to surface waters, while the other clades of MGII are distributed deeper in the water column (**Figure 1**).

Like the genomes of many abundant planktonic microbes, the "*Ca*. N. brevis" genome has evidence of streamlining (Giovannoni et al. 2014, Santoro et al. 2015). It has the lowest number of paralogs of any archaeal genome (4 per megabase), contains minimal intergenic noncoding DNA, and has exceptionally low GC content, all of which might be potential adaptations to nutrient-poor oligotrophic environments (Giovannoni et al. 2014). At 1.23 Mb, the "*Ca*. N. brevis" genome may represent the minimal genome for a chemoautotroph, but as a scaffold, it still allows for small genetic changes that alter phenotype in major ways. A recently characterized, nearly identical (99.9% nucleotide identity) strain of "*Ca*. N. brevis" acquired the ability to grow on urea simply by acquiring urease and a urea transporter (Carini et al. 2018).

Coupled genomic and metagenomic analysis has verified that genomic islands—regions of the genome poorly represented at a population scale—are present in the genomes of both *N. maritimus* and "*Ca*. N. brevis" (Santoro et al. 2015, Tully et al. 2012, Walker et al. 2010) as well as in single-cell genomes (Swan et al. 2014). These regions, frequently flanked by integrases and transposases (Ahlgren et al. 2017), are often associated with modifications to the cell surface, potentially as a defense against grazing predation or phage. Occasionally they contain genes useful for adaptation for a specific environment; one *N. maritimus* island contains a putative Pst high-affinity phosphate uptake system. This same Pst system was also present in the metagenome from the Sargasso Sea, where phosphate concentrations are frequently at the nanomolar level, but not in "*Ca*. N. brevis" genomes (originating from the Pacific) or the coastal Gulf of Maine thaumarchaea (Tully et al. 2012). Islands related to cell surface proteins have also been found in MGIII (Haro-Moreno et al. 2017). Such island regions may be evidence of horizontal gene transfer (López-García et al. 2015), though the prevalence and type of horizontal gene transfer deserve reexamination using the expanded genomic resources now available (**Figure 3**). A DNA phosphorothiolation and associated restriction system identified in the genome of "*Candidatus* Nitrosomarinus catalina" SPOT01 suggest a potential mechanism to protect against such foreign DNA transfer in thaumarchaea (Ahlgren et al. 2017).

Thaumarchaeal transcripts are among the most abundant transcripts that can be definitively identified in marine metatranscriptomes; thus, metatranscriptomics has played a major role in our understanding of this group. Thaumarchaea are generally among the most abundant organisms in terms of transcripts from any pelagic environment outside of the surface ocean (Baker et al. 2013, Stewart et al. 2012), with substantial genome coverage, and thus are easy to compare with culture-based experiments (Carini et al. 2018, Qin et al. 2017a). This suggests that even relatively shallow metatranscriptomes could be used for studying the diversity and genome-scale transcriptional regulation of thaumarchaea in situ. Culture studies also suggest, however, that subtle changes in non-highly-expressed genes correlate with changes in growth or nutrient status (Carini et al. 2018).

6. ARCHAEA IN PLANKTONIC MARINE FOOD WEBS

While planktonic archaea certainly play a role in marine food webs, specific information about their consumers, commensals, and viruses (reviewed in Danovaro et al. 2017) is lacking. Top-down controls are known to exhibit significant effects on marine microbial abundance and community structure (Pernthaler 2005). Yet it has also been hypothesized that small size may help avoid grazing predation (Massana et al. 2009), and the marine thaumarchaea are among the smallest cells in the ocean.

Few studies have attempted to specifically quantify the impact of predation and viral lysis on archaea in the ocean or the dark ocean in general (reviewed in Medina et al. 2017), the predominant habitat of archaea. Grazing rates are high at redox interfaces in the water column, where thaumarchaea are known to be active and abundant, and indeed thaumarchaea have been detected within

the food vacuoles of ciliates and dinoflagellates grazing there (Anderson et al. 2012). As they have eluded cultivation for so long, marine archaea are likely extremely sensitive to the shipboard bottle experiments typically used to measure grazing rates. New technologies for conducting grazing experiments at in situ temperature, pressure, and oxygen concentration (Pachiadaki et al. 2016) will likely be necessary to accurately measure the grazing of archaea, or any other microbe, in the dark ocean.

In the absence of grazing and lysis rates, metagenome-mining approaches targeting archaeal phage discovery are beginning to yield exciting results (Vik et al. 2017). A provirus identified in a terrestrial thaumarchaeon (Krupovic et al. 2011) was used to assign a putative thaumarchaeal host to the most abundant viral fosmid in the Saanich Inlet (Chow et al. 2015), and putative genes of phage origin were found in thaumarchaeal single-cell genomes (Chow et al. 2015, Labonte et al. 2015) and the genome of "*Ca*. N. catalina" (Ahlgren et al. 2017). Viruses are capable of transmitting auxiliary metabolic genes among their hosts, and intriguingly, a thaumarchaeal *amoC* gene was identified in the *Tara* Oceans viral metagenome (Roux et al. 2016). A suite of three more recent studies greatly expanded what was known about archaeal viruses in the ocean, particularly with respect to viruses of MGII and MGIII. Philosof et al. (2017) identified a new and widespread class of double-stranded DNA viruses, the magroviruses, which putatively infect MGII and were detected primarily in the viral fraction. These tailed phages contain nearly all elements of the archaeal replication machinery. Six novel archaeal virus clusters were recovered from the eastern tropical North Pacific (Vik et al. 2017). While this study was not able to definitely assign hosts, there were a higher abundance and diversity of presumptive archaeal phages in surface waters—depths enriched in MGII. Fifty-eight partial phage genomes representing four clades of MGII viruses were assembled from the *Tara* Oceans data set and Osaka Bay, Japan (Nishimura et al. 2017) and partially overlapped with the magrovirus genomes, which also contained archaeal replication machinery.

An increasing number of network (Steele et al. 2011) and co-occurrence (Beman et al. 2011b) studies are beginning to elucidate interactions between planktonic archaea and other members of the microbial community. Several studies have found a covariation of thaumarchaea and nitrite-oxidizing bacteria of the genus *Nitrospina* that carry out the second step of nitrification in both space (Mincer et al. 2007, Santoro et al. 2010) and time (Beman et al. 2011b, Parada & Fuhrman 2017) at a ratio (~6:1) that may be defined by the relative energy yields of these two processes (**Figure 5**). MGII archaea have both negative (Steele et al. 2011) and positive correlations with some phytoplankton groups, although an obligate association with any one group of phytoplankton has not been shown (Needham & Fuhrman 2016, Parada & Fuhrman 2017). A network analysis of the *Tara* Oceans data set found limited interactions of archaea with bacteria and eukaryotes when compared with other pairwise comparisons but co-occurrence of MGII with several phytoplankton taxa (Lima-Mendez et al. 2015).

The biochemical and ecological bases for apparent interactions between archaea and other plankton are almost completely unknown, but there have been some exciting recent developments. For example, thaumarchaea produce cobalamin, the precursor to vitamin B_{12}, which they may share with other organisms in the water column that require cobalamin but are unable to produce it (Heal et al. 2017). Conversely, MGII.A archaea apparently lack the ability to synthesize cobalamin and biotin and may also require reduced sulfur sources, which they would need to acquire from other members of the planktonic community (Iverson et al. 2012). Teasing apart these interactions will require an integrated effort of laboratory-based physiological studies, field observations, and stable-isotope-labeling approaches targeting the extracellular organic matter produced and consumed by planktonic archaea—more than enough for another 25 years of study.

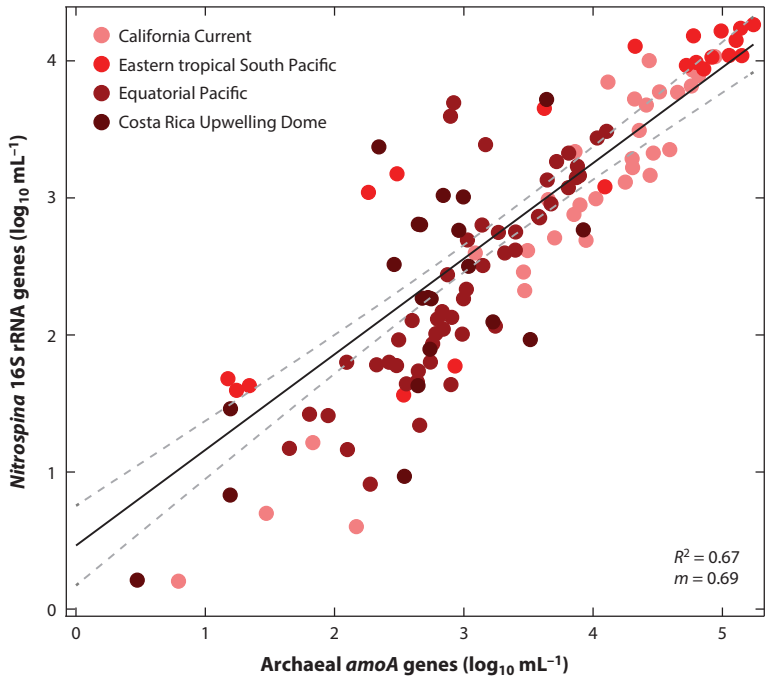


Figure 5

Covariation of ammonia-oxidizing thaumarchaea and the nitrite-oxidizing bacterial genus *Nitrospina* throughout the Pacific. Data taken from Buchwald et al. (2015), Santoro et al. (2010, 2017), and A.E. Santoro (unpublished data).

SUMMARY POINTS

1. The planktonic archaea comprise at least two phyla and a growing number of class-level designations. Though it is convenient to refer to them collectively, they are in reality four distinct groups with diverse geographical distributions, physiologies, and ecologies.
2. The thaumarchaea, formerly known as the marine group I (MGI) archaea, are a widespread group of chemolithotrophic organisms that are found in nearly every marine environment. They contribute significantly to nitrogen and carbon cycling through their role in ammonia oxidation, the first step of nitrification. They are most abundant in the mesopelagic, where their abundance is closely tied to the flux of sinking organic matter.
3. The MGII archaea are a diverse group of uncultivated heterotrophic and photoheterotrophic organisms that are found throughout the water column and specialize in the breakdown of high-molecular-weight compounds. In the euphotic zone, an apparent reliance on phytoplankton-derived organic matter leads to dramatic variations in MGII abundance over annual, seasonal, and daily timescales. Extensive, uncharacterized metabolic diversity likely exists within this group.
4. The MGIII archaea are heterotrophic organisms that are found throughout the water column but primarily in the deep sea. Detailed information on their physiology and biogeochemical impact is still lacking.

5. Because they exist throughout the water column, both the thaumarchaea and MGII archaea are useful systems for understanding how the physical and chemical environment influences genome content and evolution in marine microbes.

FUTURE ISSUES

1. A better understanding of the physiological diversity in uncultivated marine thaumarchaea is needed, including the capacity for mixotrophy and the use of alternate sources of reduced nitrogen for energy. This would be greatly aided by cultures from the deep clades of marine thaumarchaea.
2. Thorough comparative (meta)genomics and phylogenomics studies will be required to understand the metabolic differences between the different subclades of MGII and whether they actually constitute new phyla themselves.
3. Stable-isotope-probing studies combined with targeted heterologous expression experiments, where proteins from uncultivated organisms are expressed in laboratory strains, will help to resolve the specificity of organic matter compound uptake and utilization by MGII and MGIII.
4. Despite growing repositories of qualitative information on the geochemical significance of the marine archaea, quantitative data on growth rates, carbon turnover, and carbon fixation by these cells is still needed.
5. Progress in understanding the role of MGII and MGIII in marine food webs is hindered by the lack of cultured isolates. Cultivating MGII, however, will continue to be challenging because they are sympatric with other abundant photoheterotrophic marine bacteria that have also proved resistant to cultivation, such as SAR86.
6. Better food web studies are necessary to understand top-down controls on archaeal abundance and the sharing economy between archaea and other microbes.

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