REVIEW

Marine archaea and archaeal viruses under global change
[version 1; referees: 2 approved]

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Abstract
Global change is altering oceanic temperature, salinity, pH, and oxygen concentration, directly and indirectly influencing marine microbial food web structure and function. As microbes represent >90% of the ocean’s biomass and are major drivers of biogeochemical cycles, understanding their responses to such changes is fundamental for predicting the consequences of global change on ecosystem functioning. Recent findings indicate that marine archaea and archaeal viruses are active and relevant components of marine microbial assemblages, far more abundant and diverse than was previously thought. Further research is urgently needed to better understand the impacts of global change on virus–archaea dynamics and how archaea and their viruses can interactively influence the ocean’s feedbacks on global change.
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Recent insights on marine archaea and their respective viruses

Research on archaea has increased exponentially over the last few years, but marine archaea and the viruses able to infect them have received little attention despite their global relevance1–6 (Figure 1). Moreover, most of the current knowledge on archaea and archaeal viruses is based on culturable extremophiles inhabiting peculiar high-temperature, high-salinity, or low-pH environments2–6, while the archaeal taxa most represented in the ocean remain almost completely uncultured10–16, as well as their viruses17. Several new archaeal phyla have been described in the last 15 years thanks to gene surveys, metagenomics studies, and single-cell next-generation sequencing projects16,18–22. While the earliest archaeal phylogenetic trees reported only two phyla (i.e. the Crenarchaeota and Euryarchaeota), the current view of the taxonomic and functional diversity of archaea has greatly expanded. Besides Euryarchaeota, three additional archaeal clades have been recently proposed: the TACK superphylum (including Crenarchaeota, Korarchaeota, Thaumarchaeota, Aigarchaeota, and Batharchaeota), the DPANN superphylum (including archaeal Richmond Mine acidophilic nanorganism [ARMAN], Diapherotrites, Nanohaloarchaea, Parvarchaeota, Aenigmarchaeota, and Nanoarchaeota), and the ASGARD superphylum (including Lokarchaeota, Thorarchaeota, Odinararchaeota, and Heimdallarchaeota)16,23–27. Moreover, findings based on current culture-independent molecular approaches point out that a large fraction of archaeal diversity is still awaiting discovery18.

Marine ecosystems host 3.9×10^30 prokaryotic (i.e. bacterial and archaeal) cells and 4.3×10^31 viruses29. These components represent ~90% of the global microbial abundance and largely contribute to organic matter cycling and biogeochemical processes on a global scale30–32. Most of such microbes live in deep-sea ecosystems (i.e. waters and sediments below 200 m water depth), which cover more than 65% of the Earth’s surface and represent 95% of the biosphere volume31,32. Archaea are ubiquitous and abundant in marine ecosystems. Although bacteria tend to outnumber archaea in the world’s oceans, archaea make an important contribution to microbial biomass in deep waters (with abundances equivalent to those of bacteria at depths of >1000 m) and in surface and subsurface marine sediments33,34. Different archaeal taxa can be numerically dominant in specific environmental conditions. In oxygenated waters and sediments, four major groups of archaea prevail, including marine group (MG)-I Thaumarchaeota and MG-II, MG-III, and MG-IV Euryarchaeota15, while novel archaeal taxa have been recently identified in anoxic ecosystems including marine subsurface sediments16,27. MG-I Thaumarchaeota are among the most abundant microbes in the deep ocean, and they play key roles in global C and N cycles through CO₂ fixation coupled with ammonium/ammonia oxidation, which can generate the greenhouse gas nitrous oxide (N₂O) as a by-product34–36, and can display heterotrophic/phototrophic lifestyles35,36, while the physiology and metabolism of MG-III and MG-IV Euryarchaeota, preferentially inhabiting the ocean interior at relatively low abundances, still remain poorly understood37–39. In subsurface and anoxic sediments, still poorly resolved archaeal groups, such as anaerobic methanotrophic archaea (ANME) and members of the deep sea archaeal group (DSAG) and of the miscellaneous Crenarchaeota group (MCG), can account for a large fraction of prokaryotic standing stocks40–42 and are thought to significantly contribute to biogeochemical cycles and global ecosystem functioning21,26,27,41.

Concerning archaeal viruses, a putative provirus has been identified in a recently isolated MG-I thauarchaeon42, and DNA sequences

![Figure 1. Number of publications regarding archaea, subdivided into publications on marine or non-marine archaea (left chart) and publications on archaea or on viruses of archaea (right chart), as searched through the Web of Science database. The following keywords were used in the searches for archaea: archaea or archaebacteria or archaeobacteria. The following keywords were used in the searches for marine archaea: marine archaea or ocean archaea or sea archaea, also using the terms archaebacteria or archaeobacteria. The following keywords were used in the searches for viruses of archaea: archaea virus or archaebacteria virus or archaeobacteria virus. Research on archaea has increased over the past few decades, but relatively little focus has been directed towards marine archaea and archaeal viruses, despite the current compelling evidence of their relevant role at the global level.](image-url)
of putative viruses infecting MG-I Thaumarcheota are abundant in seawater and sediments\textsuperscript{1,4,5,6,8–10}. Increasing evidence suggests that marine viruses infecting members of other dominant archaeal taxa are widespread and likely highly abundant both in the water column (e.g. putative viruses of pelagic MG-II Euryarchaeota\textsuperscript{1,5,6} and in sediments (e.g. putative viruses of anaerobic methane-oxidizing euryarchaeota\textsuperscript{46} and other still-unclassified archaeal viruses\textsuperscript{14}). All of these viruses are still uncultured\textsuperscript{15}, and the virus–archaea interactions occurring in marine ecosystems remain largely unknown\textsuperscript{4,44}.

**Impacts of climate changes on marine archaea**

Since the beginning of the industrial revolution, anthropogenic activities have progressively enhanced terrestrial fluxes of greenhouse gases, increasing atmospheric concentrations of CO\textsubscript{2}, CH\textsubscript{4}, and N\textsubscript{2}O by 40%, 150%, and 20%, respectively\textsuperscript{49,50}. This process has triggered climate changes causing warming, oxygen depletion, and acidification of the oceans as well as altered precipitation regimes, increased ice melting, and shifting patterns (generally, a decrease) of global primary production and carbon export to the ocean interior. All these changes have been reported to influence the biodiversity and functioning of marine ecosystems\textsuperscript{1–5}.

Marine archaea are key actors in the cycling of all the aforementioned greenhouse gases\textsuperscript{26,33,35–38}. Our knowledge on the potential consequences of global climate changes on archaea is very limited and almost entirely based on studies of MG-I Thaumarcheota\textsuperscript{14,15,13,13,13}. Indeed, the recent success in culturing several MG-I Thaumarcheota as pure isolates or in enriched mixed cultures has provided the first insights into their responses to changes in seawater temperature, oxygen concentrations, and pH\textsuperscript{11,13,14,13,38}. The emerging view suggests high functional diversity and metabolic plasticity within the MG-I Thaumarcheota, including members with different sensitivities to seawater warming, acidification, and oxygen depletion\textsuperscript{11,14,33}. Thus, specific MG-I Thaumarcheota more adapted to such conditions could be competitively advantaged in future scenarios of global change\textsuperscript{1,13}.

Global warming is expected to have a stronger impact on marine ecosystems at high latitudes\textsuperscript{35,59}, where pelagic and benthic MG-I Thaumarcheota are particularly abundant and highly metabolically active\textsuperscript{1,4,5,6,6,6,6}. While primary production is expected to decrease at tropical and mid-latitudes, an increase is expected at high latitudes\textsuperscript{51,63–64}. If confirmed, these shifts will alter the quantity and quality of food supply to the seafloor\textsuperscript{65}, with downstream consequences on organic matter remineralization and supply of ammonia needed for sustaining the metabolism of nitrifying MG-I Thaumarcheota. On one hand, such changes could have a differential impact on MG-I Thaumarcheota at different latitudes\textsuperscript{49}. On the other hand, inter-strain hallmarks of different members within MG-I Thaumarcheota, including chemotaxis, motility, and versatility in organic substrate utilization, might be factors able to influence their relative distribution under future scenarios of global change\textsuperscript{13}. Current evidence suggests that the shifts in food supply caused by global change\textsuperscript{14,65} could influence also the distribution and abundance of MG-II Euryarchaeota, which are believed to be heterotrophs\textsuperscript{11,3,36} and whose abundance in benthic deep-sea ecosystems can be controlled by the availability of organic matter\textsuperscript{14}. Nonetheless, the lack of available culturable strains for this and other newly discovered archaeal taxa\textsuperscript{15,16} limits our ability to predict their metabolic/physiological response to global changes.

Recent studies have provided the first insights into the possible effects of temperature changes on archaeal assemblages. While manipulative experiments have suggested no significant effects of temperature shifts from 8 to 20°C on the rates of ammonia oxidation by archaea\textsuperscript{45}, temperature itself has been shown to be a significant macroecological driver of the global patterns of distribution of MG-I Thaumarcheota in benthic deep-sea ecosystems\textsuperscript{45}. In polar ecosystems, the enhanced ice melting due to global warming has the potential to influence the composition and relative abundance of marine archaea by releasing ice-associated microbes\textsuperscript{67,68} and favoring specific MG-I Thaumarcheota pre-adapted to grow at lower salinity\textsuperscript{11}. Moreover, as nitrification in Thaumarcheota is dependent upon oxygen levels and is inhibited by anoxic conditions\textsuperscript{11}, the expansion of oxygen-depleted marine zones induced by warming and eutrophication can contribute to influence on the composition and functioning of archaeal assemblages\textsuperscript{69–71}. However, the impacts of such changes, including the relative feedbacks of different archaeal taxa and the consequences on carbon and nutrient cycling, remain virtually unexplored\textsuperscript{11}.

**Virus–archaea interactions in the oceans under global change**

Daily virus-induced mortalities of marine prokaryotes are in the range of 0.1–40% of the standing stock\textsuperscript{72–73}, implying that every year approximately 10\textsuperscript{10} to 10\textsuperscript{12} prokaryotic cells are infected and killed by viruses in marine ecosystems\textsuperscript{72}. However, the extent to which viruses specifically impact archaea in the oceans is largely unknown, and this represents a significant gap for a better comprehension of the functioning of the world’s oceans.

The relative contribution of archaea to the prokaryotic stock has been reported to increase with increasing water column depth and along the vertical profile of the sediment\textsuperscript{53,59}. Also, viruses are suggested to play more relevant roles delving deeper in the ocean interior and in the subsurface, where the virus-to-prokaryote abundance ratios and the representation of virus-related DNA sequences in metagenomes is typically higher\textsuperscript{74–79}. Recent studies provide evidence of a high virus-induced mortality on archaea (mainly on MG-I Thaumarcheota) in benthic deep-sea ecosystems, resulting in the release of ~0.3 to 0.5 gigatons of carbon per year globally\textsuperscript{1}. MG-I Thaumarcheota use CO\textsubscript{2} to produce biomass, while viruses kill them, releasing their labile cellular content, thus enhancing organic matter remineralization and respiration processes of uninfected heterotrophic microbial components\textsuperscript{1}. In turn, the stimulation of heterotrophic processes can enhance nitrogen regeneration processes, supplying 30 to 60% of the ammonia required to sustain archaeal chemosynthetic C production in deep-sea sediments\textsuperscript{1}. Understanding the factors able to influence this complex network of microbial CO\textsubscript{2}-consuming and CO\textsubscript{2}-producing processes will provide insights into the ability of the oceans to act as source or sink for this important greenhouse gas.

Since viral replication is linked with host metabolic state, impacts of global changes on the physiology and metabolism of archaea will likely influence also virus–archaea dynamics\textsuperscript{80}. At the same
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Version 1

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