

Macroecological drivers of archaea and bacteria in benthic deep-sea ecosystems

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Bacteria and archaea dominate the biomass of benthic deep-sea ecosystems at all latitudes, playing a crucial role in global biogeochemical cycles, but their macroscale patterns and macroecological drivers are still largely unknown. We show the results of the most extensive field study conducted so far to investigate patterns and drivers of the distribution and structure of benthic prokaryote assemblages from 228 samples collected at latitudes comprising 34°N to 79°N, and from ca. 400- to 5570-m depth. We provide evidence that, in deep-sea ecosystems, benthic bacterial and archaeal abundances significantly increase from middle to high latitudes, with patterns more pronounced for archaea, and particularly for Marine Group I Thaumarchaeota. Our results also reveal that different microbial components show varying sensitivities to changes in temperature conditions and food supply. We conclude that climate change will primarily affect deep-sea benthic archaea, with important consequences on global biogeochemical cycles, particularly at high latitudes.

INTRODUCTION

Deep-sea sediments, which are the largest ecosystems on Earth, covering ca. 65% of the surface of the globe and ca. 95% of the ocean sea floor, control global biogeochemical cycles (1, 2). Life in the deep-sea sediments is largely constrained by the limited and episodic food supply from the water column, possibly supplemented by benthic chemoautotrophic production (1, 3). Here, total benthic biomass is dominated by prokaryotes (up to more than 90%), and bacteria and archaea play a pivotal role in C production (either heterotrophic or chemoautotrophic), nutrient cycling, and energy transfer to the higher trophic levels (1, 4). Deep-sea prokaryotes are concentrated in surface sediments, where their abundance per unit of volume can be 10^3 to 10^6 times higher than in the dark portion of the water column and in the subsea-floor biosphere (5, 6). Using a modeling approach, the global prokaryotic biomass (reported as “bacteria”) on the sea floor has been estimated in the order of ca. 35 Mt C (7).

Although regional-scale studies reported the presence of significant depth-related patterns of benthic prokaryotic abundance and biomass (8, 9), meta-analyses conducted at global scale suggest that their abundance and biomass remain rather constant with increasing water depth (7, 10, 11). Because food supply to deep-sea benthos changes with depth, latitude, biogeographic region, and related productivity, the lack of depth-related patterns at global scale suggests that prokaryotes are dependent not only on the quality and quantity (or dilution) of organic matter available in the deep sea (12–18) but also on other factors acting at different spatial scales. In particular, high deep-sea biomasses have been reported in highly productive oceanic regions (for example, the North Atlantic and upwelling and polar regions), whereas the oligotrophic conditions support biomass values of one to two orders of magnitude lower (for example, Central Pacific and the deep Mediterranean Sea) (7, 19). Recent studies based on the metabolic theory provided evidence that the relative influence of chemical and thermal energy on deep-sea organisms varies considerably across levels of biological organization and that thermal energy has a major effect at lower levels of biological organization (20). Moreover, benthic deep-sea prokaryotes can be controlled by viral infections able to abate >80% of biomass production (11). We also know that ar-

chaeal abundance increases beneath 1000-m depth and can equal bacterial abundance in the deeper portion of the water column and in subsurface deep-sea sediments. However, the factors explaining such shifts in the relative importance of archaea and bacteria are still largely unknown (5, 6, 21–23). Overall, our knowledge of the patterns and drivers controlling the distributions of bacteria and archaea in deep-sea sediments is completely insufficient to fully comprehend their ecology and response to multiple stressors, including the effects of global change predicted for the coming decades.

Here, we investigated the macroecology of bacteria and archaea in surface deep-sea sediments by means of an intensive and highly replicated macroscale sampling strategy. Two hundred twenty-eight samples were collected from 58 benthic deep-sea sites, spanning from 34°N to 79°N (Fig. 1) and encompassing different physical-chemical and trophic characteristics (for example, from the Arctic to the North Atlantic to the Mediterranean basin, with temperature deltas >10°C at the same depths), and at depths ranging from ca. 400 to 5570 m.

The present study was designed to provide new insights into the following: (i) the factors driving the distribution of benthic bacteria and archaea and, within the domain Archaea, of Marine Group I (MG-I) Thaumarchaeota and MG-II Euryarchaeota, which represent the dominant archaeal groups in surface deep-sea sediments (24, 25), and (ii) the different sensitivity of bacteria and archaea to changing trophic and thermohaline conditions to forecast their potential responses to global changes.

Our results point out the increasing importance of benthic archaea at high latitudes. Our findings also reveal that bacteria and archaea respond with different sensitivity to temperature shifts and changes in food supply, showing a higher sensitivity of archaea, and particularly of the MG-I Thaumarchaeota, to changes in thermal energy. Our results suggest that global climate change will have important consequences on the structure and distribution of deep-sea prokaryotic assemblages, with profound implications on global biogeochemical cycles.

RESULTS

Environmental setting

Bottom water temperature across the different sampling regions investigated ranged from -0.90° to 14.17°C (varying from -0.90° to -0.51°C

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