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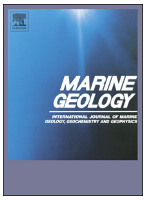

A review of prokaryotic populations and processes in sub-seafloor sediments, including biosphere:geosphere interactions

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ABSTRACT

A general review of the sub-seafloor biosphere is presented. This includes an update and assessment of prokaryotic cell distributions within marine sediments, current deepest 1922 m, and the impact of this on global sub-seafloor biomass estimates. These global estimates appear relatively robust to different calculation approaches and our updated estimate is 5.39×10^{29} cells, taking into consideration new data from very low organic matter South Pacific Gyre sediments. This is higher than other recent estimates, which is justified as several sediments, such as gas hydrate deposits and oil reservoirs, can have elevated cell concentrations. The proposed relationship between elevated cell concentrations and Milankovitch Cycles in sequential diatom rich layers at some sites, demonstrates not only a dynamic deep biosphere, but also that the deep biosphere is an integral part of Earth System Processes over geological time scales. Cell depth distributions vary in different oceanographic provinces and this is also reflected in contrasting biodiversity. Despite this there are some clear common, sub-seafloor prokaryotes, for *Bacteria* these are the phyla *Chloroflexi*, *Gammaproteobacteria*, *Planctomycetes* and the candidate phylum JS1, and for *Archaea* uncultivated lineages within the phylum *Crenarchaeota* (Miscellaneous Crenarchaeotal Group and Marine Benthic Group B), *Euryarchaeota* (SAGMEG, Marine Benthic Group-D/Thermoplasmatales associated groups) and *Thaumarchaeota* (Marine Group I). In addition, spores, viruses and fungi have been detected, but their importance is not yet clear. Consistent with the direct demonstration of active prokaryotic cells, prokaryotes have been enriched and isolated from deep sediments and these reflect a subset of the total diversity, including spore formers that are rarely detected in DNA analyses.

Activities are generally low in deep marine sediments (~10,000 times lower than in near-surface sediments), however, depth integrated activity calculations demonstrate that sub-surface sediments can be responsible for the majority of sediment activity (up to 90%), and hence, are biogeochemically important. Unlike near-surface sediments, competitive metabolisms can occur together and metabolism per cell can be 1000 times lower than in culture, and below the lowest known maintenance energies. Consistent with this, cell turnover times approach geological time-scales (100–1000s of years). Prokaryotic necromass may be an important energy and carbon source, but this is largely produced in near-surface sediments as cell numbers rapidly decrease. However, this and deposited organic matter may be activated at depth as temperatures increase. At thermogenic temperatures methane and other hydrocarbons, plus H_2, acetate and CO_2 may be produced and diffuse upwards to feed the base of the biosphere (e.g. Nankai Trough and Newfoundland Margin). Temperature activation of minerals may also result in oxidation of sulphides and the formation of electron acceptors, plus H_2 from low temperature (~55 °C) serpentenisation and water radiolysis. New mineral surface formation from fracturing, weathering and subduction etc. can also mechanochemically split water producing both substrates (H_2) and oxidants (O_2 and H_2O_2) for prokaryotes. These and other biosphere:geosphere interactions may be important for sustaining a globally significant sub-seafloor biosphere.

1. Introduction

Approximately 70% of the Earth is covered by seawater and most of this area also has sediments, which accumulate over geological time scales and now they contain the largest reservoir of organic carbon (~$15{,}000 \times 10^{18}$ g, Hedges and Keil, 1995). In addition, there are contrasting habitats within these sediments (Fig. 1), ranging from organic rich shelf/margin sediments to Mud Volcanoes and Carbonate Mounds, and organic poor Pacific Ocean Gyre sediments. However, intense degradation of sedimenting organic matter in the water column and near surface sediments, resulting in recalcitrant organic matter in subsurface layers, combined with characteristically low temperatures and elevated pressures led to the consideration that deep marine sediments were too

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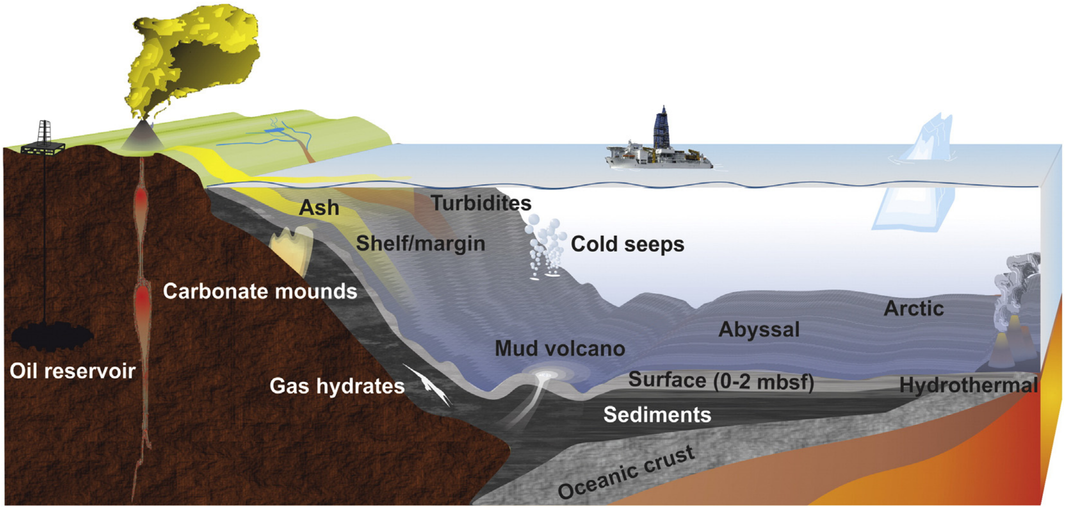

Fig. 1. Diagram of some of the major sub-seafloor biosphere habitats.

extreme for life (Morita and Zobell, 1955). Therefore, when in 1994 Parkes et al. proposed the presence of a globally significant prokaryotic deep biosphere in sub-seafloor sediments (Parkes et al., 1994), with an estimated global biomass of 10% of total biosphere carbon, it was rather contentious. The perceived low energy supply coupled with geological time scales resulted in the view that most microorganisms in sub-seafloor sediments must be either inactive or adapted for extraordinarily low metabolic activity (D'Hondt et al., 2002). However, as was originally suggested (Parkes et al., 1994), most cells were subsequently shown to be active (Schippers et al., 2005; Biddle et al., 2006; Schippers et al., 2010; Lloyd et al., 2013a), hence, these subsurface prokaryotes (*Archaea* and *Bacteria*) are indeed able to survive on very limited energy flux (~1000 times lower than required by laboratory cultures, Hoehler and Jorgensen, 2013). These results also suggest that laboratory "live fast die young" microbial cultures are inadequate for understanding the energy requirements and survival of sub-seafloor prokaryotes, and also probably most *Bacteria* and *Archaea* in the natural environment. Hence, we have to re-consider our understanding of some fundamental principles of microbiology, such as minimum cell energy requirements, cell survival, dormancy, minimum metabolic rates, as well as biosphere:geosphere interactions. The first global census of prokaryotic biomass (Whitman et al., 1998), suggested that subsurface prokaryotes (terrestrial and sub-seafloor) might even account for the majority of prokaryotic cells on Earth and with ~70% of total prokaryotic biomass residing in sub-seafloor sediments. This further increased the concern about the energy sources available to support such an enormous biomass and the basis for such estimates, including whether detected intact cells were indeed living or just fossils. In this review we address these questions along with other aspects of the sub-seafloor biosphere. In addition, we summarise recent sub-seafloor biosphere research results, which further reinforce the presence of a surprisingly large prokaryotic habitat in ocean sediments, with some unique biodiversity, and which functions on "geological" time scales.

2. Global biomass estimates of the sub-seafloor biosphere

Additional sites (1738 counts, from our published and unpublished results) including from the Atlantic Ocean and Mediterranean Sea (Fig. 2) have been added to the original data on prokaryotic cell distributions with depth in marine sediments published by Parkes et al. (1994, 299 counts), which was based solely on Pacific Ocean sites. Intact prokaryotic cells were present in all samples analysed, even including deep sourced mud volcano breccia and hydrothermal samples (estimated upper temperature 160 °C, Parkes et al., 2000) and this reinforces the ubiquitous presence of prokaryotes in sub-seafloor sediments (total 2037 cell counts). However, despite the approximate factor of 7 increase in numbers of cell counts, the resulting cell depth regression is little changed (Log cells = 8.05 − 0.68Log depth. R^2 = 0.70, compared to

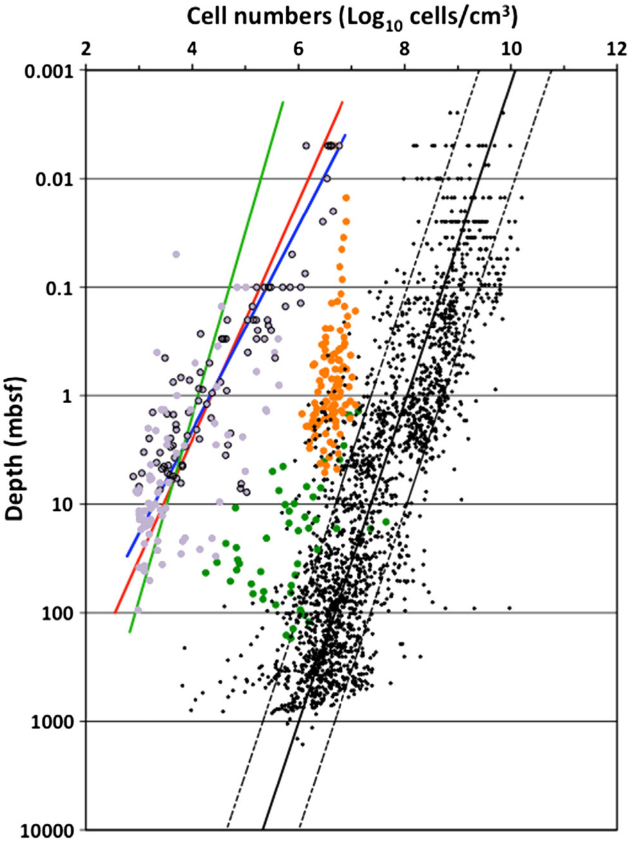

Fig. 2. Depth (metres below sea floor) distribution of prokaryotic cells in sub-surface sediments at 106 locations, including 17 ODP/IODP Legs, black dots. Bold black regression line is Log cells = 8.05 − 0.68 Log depth. (R-sq = 0.70 & n = 2037) and light dashed lines are 95% lower and upper prediction limits. Orange circles are mud volcano breccia samples and green circles are hydrothermal samples. Mauve circles with a black outline are South Pacific Gyre samples, presented by Kallmeyer et al., 2012, with blue regression line through samples, the red regression is for these same samples plus additional data from an IODP Cruise (mauve circles) to the same sites (Expedition 329 Scientists, 2011), and the green regression line is only through the later IODP cruise data. There is no significant difference (F = 0.79; d.f. = 1, 2105) in slope between this IODP cruise data regression (green line) and the regression (black line) through cell-depth distributions in other marine sediments (black dots).

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