Ocean Sediments—an Enormous but Underappreciated Microbial Habitat

Modeling proves essential in efforts to understand the estimated $3 \times 10^{29}$ microbial cells that comprise this unusual ecosystem

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Approximately 70% of the Earth’s surface is covered by ocean—on average, under 3,700 m of water. At the seafloor is a blanket of unconsolidated sediment consisting of continental detritus; particulate organic matter; silica- and carbonate-rich, biologically produced hard materials; and void spaces filled with saline fluids of wide-ranging chemistries. Near the continents, especially where relief is high and physical weathering is prominent, the sediment thickness can measure more than 10 km. However, underneath the oligotrophic open ocean gyres, it can be less than 0.1 km, even on seafloor that is tens of millions of years old, and parts of the ocean floor, especially the mid-ocean ridges, young ridge flanks, and ubiquitous seamounts, are naked or covered by only a thin veneer of sediment.

Globally, there are about $3 \times 10^8$ km$^3$ of ocean sediment saturated with $8 \times 10^7$ km$^3$ of porewater that is inhabited by an estimated $3 \times 10^{29}$ microbial cells. Our understanding of these intraterrrestrial microbes and their host environments, especially beyond the near-coastal regimes, remains limited and reliant on the analysis of relatively few samples. When, as in this case, data are sparse and the environment is vast, modeling efforts can facilitate our understanding of the biogeochemical drivers that govern deep life.

Uncertainty whether Microbes Are Active, Dormant, or Dead

In a low-energy environment where metabolic strategies are honed for long-term persistence, it can be difficult to determine if a microbe is dead or alive. An intact cell may be inactive, possibly for thousands of years or longer, even though it is still viable. Assessing the viability of cells typically relies on our ability to culture them. However, environmental microbes are notoriously difficult to culture, with recent estimates claiming that perhaps 0.1–1% can be grown in vitro.

Moreover, dormancy or an extreme form of endospore formation can be observed in some bacteria. Even in million-year-old sediments, the numbers of spores can equal that of vegetative cells, according to Tori Hoehler of NASA Ames and Bo Barker Jørgensen of Aarhus University in Denmark. They assert that, in very stable, low-energy environments such as deep-sea sediments, sporulation appears to be a strategy akin to suicide. Although endospores can survive periods of environmental stress, to flourish, such cells would need to invest considerable energy to germinate and return to vegetative activity. However, energy tends to be in very short supply in these settings.

Archaea and Bacteria Are in Near-Equal Abundance

Life in deep-sea sediments consists mainly of archaea and bacteria, but which domain dominates? The first long sediment cores that were
targeted specifically for microbiology analyses were obtained by the Ocean Drilling Program (ODP) during Leg 201 to the Peru Margin in 2002. Those early excursions plus several dozen more recent ocean sediment studies to quantify the archaea and bacteria yield conflicting results, according to a review by Karen Lloyd of the University of Tennessee.

For example, taxa-specific cell counting techniques (CARD-FISH) and quantitative PCR data point to a preponderance of bacteria over archaea, whereas evidence from analyzing intact polar lipids suggests the opposite. Yet a third assessment, combining FISH, CARD-FISH, metagenomics, and qPCR data, shows that archaeal and bacterial numbers are roughly equal.

Subsequent studies showed that lipid analyses can overestimate archaea but that specific qPCR bias can underestimate them. Meanwhile, some methods accurately determine the ratios of archaea to bacteria, but vastly undercount the total number of cells. Despite these methodological uncertainties, it appears that archaea and bacteria exist in similar abundances in deep-sea sediments. However, culture-dependent and culture-independent techniques are almost exclusively designed for and tested with bacteria, not archaea. This limitation is particularly relevant where archaeal and/or bacterial dark matter—phyla that consist only of uncultured members—makes up a significant fraction of the biomass identified in sedimentary samples.

**Anaerobes Dominate Aerobes in Sediment Ecosystems**

Oxygen levels in most ocean sediments drop below detection limits within a few centimeters of the seafloor. Aerobic respiration of easily degradable organic matter is mostly responsible for this steep decline. However, microbial life in ocean sediments extends to at least 2.5 km below the seafloor, with organic-rich layers extending to such depths near the Shimokita Peninsula of Japan, according to Fumio Inagaki of the Japan Agency for Marine-Earth Science and Technology, Kai-Uwe Hinrichs of the University of Bremen in Germany, and their collaborators.

Thus, anaerobic metabolisms dominate in these sediments, especially those in which sulfate reduction is coupled to organic matter oxidation. In fact, geochemical analysis and modeling techniques demonstrate that, globally, sulfate reduction accounts for three-fourths of carbon mineralization—that is, conversion of organic carbon to carbon dioxide in these ecosystems, according to Martin Thullner of the Helmholtz Centre for Environmental Research in Leipzig, Germany, and his collaborators. Their finding is supported by the first transcriptional analysis of sub-seafloor sulfate-reducing bacteria that was conducted by William Orsi from the Ludwig-Maximilians University in Munich, Germany, and his colleagues.

Aerobic respiration follows far behind sulfate reduction, accounting for a mere 15% of organic matter that is degraded in the top 50 cm of sediments. How does this jibe with the claims of Steve D’Hondt of the University of Rhode Island (URI) that perhaps as much as 40% of the ocean floor is covered by sediments that are oxic all the way through the sediment packet, from the sediment-water interface to the underlying basement rock? One plausible answer is that this 40% is restricted to material that is found below oligotrophic, open-ocean gyres, where little sediment accumulates, little organic matter is deposited, and, consequently, limited oxygen is consumed.

In some ocean sediments, oxygen levels first decrease with depth before increasing as the underlying rocky crust is approached. This change in pattern is due to upward diffusion from oxic aqueous solutions that flow through the upper basement. In these oxic-anoxic-oxic sandwiches, aerobes dominate near the sediment-bottom water interface and perhaps again near the sediment-basement interface, but anaerobes call the shots in between.

**Modeling Helps To Describe Sedimentary Ecosystems**

Cell counts and sequencing efforts are helping to describe the numbers, viability, and variety of microorganisms in marine sediment. However, the relative inaccessibility of these environments, the difficulty of cultivating representative microorganisms, and the long timescales associated with some of their lifestyles are major impediments to obtaining a comprehensive understanding of the complex marine sediment ecosystem. Hence, we turn to modeling, using additional datasets and other approaches to connect microorganisms to their appropriate geochemical environments. Energy availability, temperature, and
metabolic reaction rates are three key factors that shape sedimentary microbial ecosystems.

All living things depend on redox reactions to obtain energy. In ocean sediments, many different minerals, aqueous solutes, and organic matter serve as the electron donors and acceptors in such reactions. Moreover, in the absence of light energy, the identities and concentrations of these ingredients, together with temperature and pressure, determine how much energy is available from redox reactions. The calculated Gibbs energies of these reactions reveal which metabolic strategies are thermodynamically possible and which environmental variables, including temperature, pressure, pH, salinity, organic matter content, and oxygen levels, control or at least influence microbial activity.

For example, in oxic sediments with ample organic matter, aerobic respiration typically yields the most energy at 100–120 kJ per mole of electrons transferred, and aerobic heterotrophs typically dominate the microbial communities. However, with increasing temperature or other environmental stressors, the energy required for cellular maintenance increases, so the energy available for growth and other cellular functions becomes a smaller and smaller fraction of the total used by organisms. An additional energetic challenge results from the low energy yields associated with most anaerobic metabolisms in deep-sea sediments, including globally dominant sulfate reduction, which has peak yields of about 20 kJ, but more commonly yields about 10 kJ per mole of electrons transferred, or less.

Energy calculations can be coupled with other modeling approaches to infer rates of microbial processes in marine sediments. For example, to determine such rates for microbes in the extremely low-energy sediment packet below the South Pacific Gyre, we used a continuum model to quantify particulate organic matter degradation rates and combined these with thermodynamic calculations and cell counts to infer microbial power usage. Based on that analysis, the resident cells could be persisting on as little as a few hundred zeptowatts (zW or 10⁻²¹ W). For comparison, sulfate reduction in deep sediments translates to about 100 zW, based on values from Hoehler and Jørgensen, while numbers from Hans Røy of Aarhus University and colleagues

**FIGURE 1**

Global sediment thickness [km]

Thickness (in km) of marine sediments. Note that the top of the scale (dark red) corresponds to ≥8 km, with the thickest sediments >18 km.
for deep sediment aerobes equate to about 5,000 zW. Meanwhile, typical maintenance power measured in the laboratory for aerobic heterotrophs is several orders of magnitude higher, about one picowatt (or 10^9 zW).

Modeling approaches can also be used to predict under what environmental conditions specific metabolic processes occur and at what rates they proceed. Sandra Arndt at Bristol University in the United Kingdom and colleagues constructed a reaction transport model to identify what, if any, biogeochemical processes are operating in sediments that were investigated as part of ODP Leg 207 on the Demerara Rise in the equatorial Atlantic. They determined that 100 million-year-old black shales, which are hundreds of meters beneath the sediment-water interface, produce methane that is then oxidized anaerobically (AOM) higher up in the sediment column by consortia of sulfate-reducing and methane-oxidizing microorganisms. Further, these AOM rates are much slower than those nearer the sediment-water interface, but in line with metabolic rates of organisms living in the deep biosphere.

To expand such metabolism modeling from site-specific to the global sub-seafloor sediment ecosystem requires large-scale quantitative assessments of particular sediment properties. However, the requisite data on global ocean sediment volume and corresponding pore water volume and temperatures are poorly known. To remedy this, we recently integrated and reevaluated seismic survey, bathymetry, and heat flow data to generate detailed global maps of sediment thickness and temperature. One such map depicts the distribution of the 3×10^9 km^3 of ocean sediment which, if spread out evenly across the ocean floor, would average 720 m in depth (Fig. 1). Viewed in this way, 23.5% of the ocean floor is covered by less than 100 m of sediment, yet more than 10 km of sediment have accumulated in the Bay of Bengal, the Gulf of Mexico, in Arctic regions, and elsewhere.

Another result of recent efforts to combine global datasets with modeling approaches can be seen in Fig. 2. Here, maps depict the three-dimensional distribution of temperature in marine sediments, which influences the types of microbial groups in a given region (thermophiles, mesophiles, or psychrophiles), their levels of metabolic activity, the thermodynamic tendency of reactions to happen, the rates of these reactions, and the diffusion of metabolic reactants and products. The temperature in about 1/4 of global sediment is less than 20°C (Fig. 2A), conditions most preferred by cold-loving psychrophiles. However, about 75% of global sediment is less than 80°C, a temperature range suitable for extensive biological activity, including that of mesophiles and thermophiles (Fig. 2B). Although some archaea and bacteria grow in the laboratory at temperatures higher than 100°C, even to as high as about 120°C, biotic processes in natural environments appear to be nearly inconsequential above about 80°C.

Prospects for Probing Microbial Ecosystems in Sediments and Rocks on and off Earth

In 1955, Richard Morita and Claude ZoBell of the Scripps Institute of Oceanography in San Diego reported the bottom of the open ocean biosphere to be 7.5 meters below the seafloor (mbsf). With access to far more advanced cell-counting techniques, D’Hondt of URI and colleagues more recently analyzed similar sedimentary environments below the Pacific Ocean gyres, extending this limit to at least 75 mbsf. Meanwhile, by integrating available microbial cell counts from marine sediments—those from oligotrophic ocean gyres as well as those from nutrient-rich near-shore settings—Jens Kallmeyer of the Helmholtz Centre in Potsdam, Germany, and his colleagues determined a global total of 3×10^29 microbial cells in marine sediments—a figure that is now widely accepted.

What about the porous basement rocks that lie below these sediments? A modest sampling of rocky outcrops on the seafloor and cores retrieved from targeted ocean drilling into basement rock hint at another intriguing microbial habitat, one that may be even larger and is certainly even less understood than the enormous, little-understood ocean sediments discussed here.

Why limit these investigations to planet Earth? Mars, our second-nearest neighbor planet, was once warm and wet, with a large ocean likely having occupied much of its northern hemisphere about 4 billion years ago. Recent and planned missions to the Red Planet tend to focus on sedimentary features and evidence of past life, but surface oceans and, hence, the water-saturated sediments, are long gone. Perhaps not surprisingly, the oceanographic and planetary science communities are now joining forces to develop mission concepts for exploring other extraterrestrial worlds, ones with present-day
oceans at or near the surface. These relatively near-term extraterrestrial missions include ones to Europa (a moon of Jupiter) and to Enceladus and Titan (two moons of Saturn). Nevertheless, even the most optimistic among us realizes that it will take at least several decades before extraterrestrial ocean sediments on Europa or elsewhere can be investigated directly. Until then, the micro-

**FIGURE 2**

Thicknes (in m) of marine sediments that are (a) <20°C and (b) <80°C. Note that the top of the scales (dark red) correspond to ≥1,400 m and ≥6,000 m, respectively.
bial secrets that are buried in the sediments and rocks below the Arctic, Pacific, Atlantic, Indian, and Southern Oceans on Earth will have to do.

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