populations to crash; the vegetation does not necessarily recover when the climate returns to normal interglacial conditions. The pollen records are mirrored by variations in the Antarctic atmospheric methane record (*6*), suggesting a more global vegetation response to these events and subsequent lack of recovery.

The results of Tzedakis *et al.* (*6*) imply that in some areas, the relationship between climate change and vegetation is not reversible. This observation has important implications for future climate change, because it suggests that once an ecological threshold has been crossed, a return to the previous climatic conditions does not guarantee a similar reversal in vegetation (see the figure, bottom panel). This sort of bifurcation has previously been suggested for the relationship between surface ocean salinity and the rate of deep-ocean circulation (*7*), but it may be more prevalent in the climate system than previously thought (*8*).

Why are climatic and ecological thresholds so different? The distribution of different vegetation types, or biomes, is controlled by a number of different climatic factors, such as annual and seasonal temperature, annual and seasonal precipitation, and the atmospheric carbon dioxide concentration (*9*). Jennerjahn *et al.* (*5*) provide an excellent example of a tropical ecological threshold that is primarily controlled by the duration of the dry seasonal and not the total annual rainfall. But it is also important how these climatic factors interact. For example, until recently it was assumed that large parts of the Amazon rainforest could not survive glacial climates. There is, however, growing evidence that the majority of the Amazon rainforest survived the climatic threshold of the last ice age (*10*). Modeling suggests that the colder glacial temperatures counterbalanced the worst effects of the drier conditions and lower atmospheric carbon dioxide concentrations by reducing water and carbon loss (*9*). In the case of the Amazon, the combination of two different climatic thresholds—aridity and cooling—did not produce a significant ecological threshold (see the figure, top panel).

Given the right set of climatic changes, vegetation distributions can vary on time scales of less than 50 years (*4*). However, the reports of Jennerjahn *et al.* (*5*) and Tzedakis *et al.* (*6*) illustrate that unless we understand ecological thresholds and their relationship to climate change, we cannot predict how or when vegetation will change as a result of global warming. Moreover, we do not know whether these changes will be reversible.

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MICROBIOLOGY

Microbial Life Breathes Deep

Edward F. DeLong

The apparent paucity of deep-sea biota led the 19th-century biologist Edward Forbes to question the very existence of life at depths greater than 550 m. Subsequent oceanographic expeditions soon laid Forbes' "azoic theory" to rest, with discoveries of a diverse and abundant marine fauna flourishing in the greatest depths of the oceans. In parallel ways, contemporary microbial surveys are expanding the range of known habitats where microbial life thrives. On page 2216 of this issue, D'Hondt and colleagues (*1*) now report evidence for metabolically diverse and active microbial communities buried deep within marine sediments nearly 0.5 km below the seafloor (see the figure). Using chemical clues hidden deep within marine sediment cores, these investigators infer how subseafloor microbes eat and breathe (*1*). They suggest that certain microbial activities deviate substantially from standard models (*2*) of microbial metabolism in subseafloor sediments.

How important are the microbial communities buried deep within the marine sediments that overlay two-thirds of Earth's surface? Counting microbes under the microscope (which does not distinguish living from dead organisms) reveals that substantial numbers of microbes must exist in deep seafloor sediments (*3*). Quantitative estimates indicate that the vast majority of these sediment-associated microbes (97% or so) reside in the upper 600 m of sediment (*3*, *4*). Microbial cell numbers range from 10^8 cells per gram of sediment just below the seafloor, to about 10^4 cells per gram of sediment 0.5 km deep in the subsurface (*3*). This substantial subsurface microbial biomass raises a number of interesting questions. Do these microbes represent well-preserved remnants of a microbial burial at sea? Alternatively, do these organisms thrive actively in the subsurface and, if so, what do they eat and how do they breathe? Does microbial activity vary with the depth and geochemical gradients found deep within the sediments? D'Hondt *et al.* (*1*) begin to answer these questions with their analyses of deep-sea sediment cores recovered from the equatorial Pacific Ocean off the coast of Peru. Some of their conclusions are rather unexpected.

Comparative analyses of the geochemistry of subseafloor sediment cores is providing new insights into subsurface microbial life. The sediment cores collected by D'Hondt *et al.* were sampled to depths of 420 m. Samples include those from the Peruvian shelf, the Peru Trench, and further offshore from open-ocean sediments. Similar to previous studies (*3*), D'Hondt *et al.* discovered remarkable numbers of microbes in sediment samples, which decreased with increasing sediment depth. These investigators also measured potential respiratory electron acceptors (oxidants), including sulfate and nitrate. The flux of these oxidants can serve as markers of specific microbial activities, because certain microbes use them to respire in the absence of oxygen. The occurrence and distribution of other microbial metabolic by-products—carbon dioxide, ammonia, sulfide, methane, manganese, and iron—also provide metrics of microbial activity. Profiles of these biologically processed compounds paint a picture of how microbial activities may be partitioned in the deep sediment, and serve as indicators of which metabolic pathways are crucial.

Throughout their sediment cores, D'Hondt and co-workers found abundant

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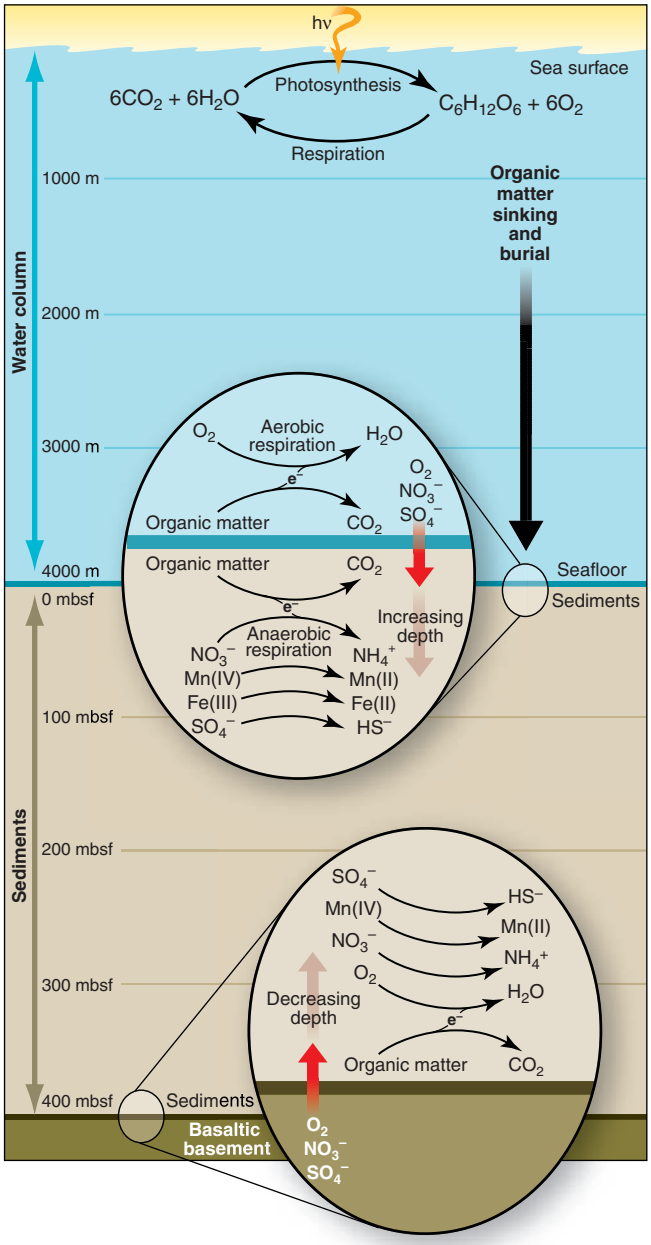

The ups and downs of organic matter. Microbial respiration at the ocean's surface and in the sediments of the subseafloor. At the sea surface, photosynthesis captures light energy in the ocean's photic zone, driving subsequent transformations of energy and organic matter that propagate as far down as 400 m below the seafloor (mbsf). In the aerobic water column, respiratory processes use oxygen to oxidize organic matter to carbon dioxide (CO_2). (**Top inset**) In the upper sediments of the seafloor, oxygen is rapidly depleted and alternative electron acceptors, such as nitrate (NO_3) and sulfate (SO_4), that diffuse downward from the water column are commandeered by certain Archaea and bacteria for respiration. These electron acceptors are used in a predictable sequential series, according to the free energy yielded by their reduction. (**Bottom inset**) D'Hondt *et al.* (*1*) observe that oxygen, NO_3, and SO_4 also diffuse upward from the deep basaltic basement of the sediment, resulting in an "upside down" electron acceptor consumption series. This series somewhat mirrors that seen in near-surface sediments. All of these processes rely ultimately on the oxygen and organic matter produced by photosynthesis in the ocean's photic zone.

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evidence for the "usual suspects"—that is, previously identified biochemical activities of sediment-associated microbes. These processes include carbon oxidation, methane production and consumption, and reduction of sulfate, nitrate, and manganese. The existence of these processes deep within marine sediments may be no big surprise, but their location was in some cases unexpected. Normally, electron acceptors (oxidants such as oxygen, sulfate, and nitrate) diffuse into sediments from the overlying seawater and are then consumed sequentially in a predictable series of metabolic reactions (see the figure). This produces a microbially catalyzed oxidant-depletion profile in which oxygen is reduced first, then nitrate, manganese, iron, sulfate, and finally carbon dioxide. Such profiles are thought to reflect competitive processes that deplete available oxidants, with those yielding the greatest free energy being the first to be consumed (*2*). The profiles of electron acceptors and metabolic by-products in the marine sediment cores typically conform to this predicted series.

There are important ways, however, in which the profiles of electron acceptors in deep sediments observed by D'Hondt *et al*. deviate substantially from the norm. This discovery suggests unsuspected sources of microbial metabolites within subseafloor sediments. In several instances, D'Hondt and colleagues report that oxidants that normally diffuse downward from overlying seawater appear to have entered the sediments from subseafloor sources (see the figure). Several cores provide evidence for sulfates originating from brines below the sediment base, as well as for nitrate and oxygen entering from deep basaltic aquifers underneath the sediment column. This situation produces "upside-down" redox profiles, with atypical sources from beneath sediments providing oxidants such as sulfate and nitrate that enable microbes to respire anaerobically (see the figure). Such microbial respiratory activities may drive cycling of manganese and iron in a sort of "bucket brigade" of cascading respiratory electron shuttles that pass electrons through various sources and sinks. Thus, these new observations imply the presence of a physiologically diverse and active deep-sediment microbiota that operates somewhat differently from model predictions.

The rates of microbial metabolic activities, estimated from the flux of electron acceptors, varied predictably in cores from the different sites. Microbial respiration of sulfate was much greater in sample cores from the continental margin than in those from open-ocean sites. Unexpectedly, respiration rates for subsurface manganese and nitrate were greater at the open-ocean site and were driven entirely by the upward flux of nitrate from the basaltic aquifer beneath the sediments. Also unexpected is the co-occurrence of deep sediment methanogenesis, as well as manganese and iron reduction, within zones of high sulfate. According to the standard hierarchy of energy processing and substrate competition, sulfate-reducing microbes are expected to "win" in zones of high sulfate concentration. The D'Hondt *et al*. work reveals that microorganisms in the deep subsurface (and their energetics) may differ substantially from well-studied model microorganisms in shallow near-surface sediments.

Exactly which microbes are responsible for the subsurface energy cycling revealed by D'Hondt *et al*. remains uncertain. Although viable sediment-associated microbes were recovered by the investigators, the relevance of these microbes to subsurface metabolism is questionable. Many of the recovered bacterial isolates form spores or are close relatives of surface-dwelling bacteria. It seems unlikely that these represent authentic deep subsurface inhabitants. Indeed, microbial survey methods that don't depend on cultivation (*5*) suggest that a quite different suite of indigenous subsurface archaea and bacteria may predominate deep within sediments (*6*–*8*). Such microbes may represent the indigenous, active members of deep-sea microbial communities.

The new observations by D'Hondt *et al*. confirm that subsurface microbes living

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deep in marine sediments ultimately rely on energy sources and oxidants produced from sunlight, rather than subsisting on geochemicals emanating from Earth's interior. Although microbial metabolites seem to wend their way into deep sediments in unexpected and interesting ways, the energy sources and electron sinks produced by photosynthesis still appear to rule the roost, even 0.5 km below the ocean's abyssal plains. Even so, D'Hondt *et al.*'s analyses demonstrate that important, diverse, and qualitatively unique microbial processes occur in the deep, dark environs far below the seafloor.

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PHYSICS

The Electronic Structure of Liquid Lead

Yves Petroff

Crystalline metals have been studied intensively over the past 40 years. Sophisticated theoretical models and experimental tools have resulted in a generally very good understanding of these materials. In contrast, the atomic and electronic structure of liquid metals is poorly understood. In a liquid metal, the atomic structure varies in both time and space, and the only information that can be obtained is averaged. The lack of periodicity makes it also very difficult to determine whether the electrons are bound to individual atoms or delocalized over the entire liquid, because the band structure (which determines the electronic properties) can no longer be measured.

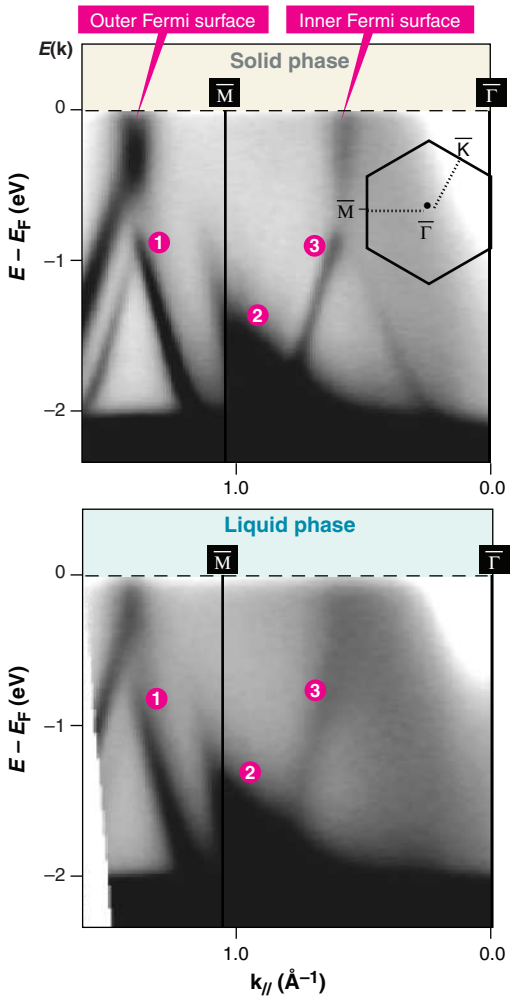
On page 2221 of this issue, Baumberger *et al.* (*1*) report the first direct measurements of the band structure of liquid lead at the lead/copper interface. They use angular resolved photoemission to show that the Fermi surface (which separates the occupied electronic states from the empty ones) persists in the liquid phase and that the localization of the electronic wave function depends strongly on the symmetry of the two $p_{x,y}$ bands of lead.

Four years ago, Reichart *et al.* (*2*) introduced a trick to enable them to study the atomic structure of liquid lead. It has been predicted (*3*, *4*) that in monatomic three-dimensional liquids such as lead, atoms should cluster to form icosahedrons. Reichart *et al.* argued that at the interface of liquid lead with a silicon (001) surface, the potential of the silicon surface cannot cause any long-range ordering in the lead, but that it can break the icosahedrons into pentagonal halves, which can be captured at the silicon surface in a preferred orientation. They therefore measured the scattering of totally reflected (evanescent) x-rays, which are sensitive only to the liquid structure at the interface, from a liquid lead layer supported on Si(001). They detected a five-fold local symmetry and obtained experimental evidence for the predicted icosahedral fragments.

Baumberger *et al.* (*1*) now study the electronic properties of a liquid lead film on a copper surface. They perform angular resolved photoemission spectroscopy to obtain the band structure $E(\mathbf{k})$ of liquid lead. To do so, they investigate a lead monolayer supported on a copper (111) surface as the temperature is raised through the melting transition (at 568 K) of the film. Lead films on Cu(111) grow layer by layer with a defined orientation (they form "epitaxial films") (*5*). Because of the proximity of the Cu(111) substrate, information about the momentum of the electronic states of the liquid phase can be retrieved.

Before discussing the results, we have to introduce a few definitions. A three-dimensional crystal can be described with three noncoplanar vectors, which define a unit cell. Associated with each crystal lattice is the reciprocal lattice, which is also defined by three vectors. A very simple relationship exists between the vectors of the direct space and the reciprocal (or momentum) space. The Brillouin zone is a subsection of the reciprocal lattice that includes all the important symmetry points. For three-dimensional crystals, the Brillouin zone is a polyhedron.

The results are summarized in the figure, which shows the experimentally observed band structure of the lead monolayer along the symmetry direction $\bar{\Gamma}\bar{M}$ for the solid (top panel) and for the liquid (bottom panel). The authors observed an inner and an outer Fermi surface (see the figure). These two Fermi surfaces persist in the liquid phase. Around the $\bar{M}$ point, three bands are observed in both phases. Bands **1** and **3** are due to the $p_{x,y}$ states of lead, and band **2** results from the *sp* band of copper. The



From solid to liquid. Experimental band structure $E(\mathbf{k})$ along the $\bar{\Gamma}\bar{M}$ direction for a lead monolayer on a copper (111) surface, obtained by angular-resolved photoemission. (**Top**) Solid layer at room temperature. Small hexagon: two-dimensional Brillouin zone of the lead layer. E_F is the Fermi energy, and $k_{//}$ is the momentum of the photoelectron. (**Bottom**) Same for the liquid layer at 585 K.

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