Cryptic Links in the Ocean

Andreas Teske

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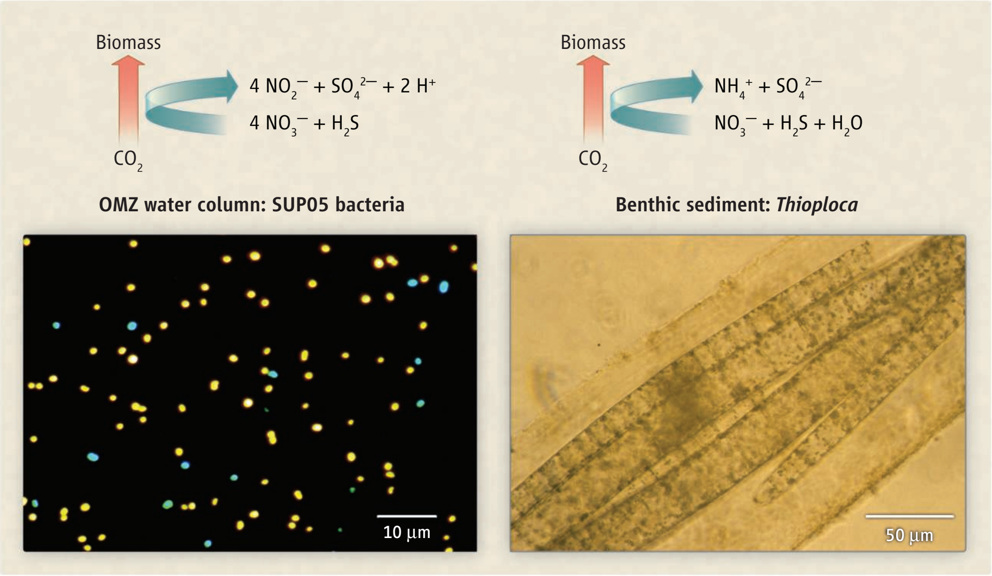
OCEANS

Cryptic Links in the Ocean

Analysis of the bacterial communities in oxygen-depleted water columns reveals a new strategy how microbes link the nitrogen and sulfur cycles in the ocean.

Andreas Teske

Oxygen depletion in the ocean water column, in stratified basins such as the Santa Barbara and Cariaco basins, and in enclosed anoxic oceans such as the Black Sea provide vivid examples of a type of marine habitat where multicellular life gradually disappears with depth as oxygen is consumed by respiration and not replenished. Only bacteria and archaea with anaerobic metabolisms persist, controlling the microbial cycling of nitrogen, sulfur, metals, and carbon. Genuine fondness for these environments and their anaerobic microbial inhabitants, although possibly an acquired taste, is widespread among marine microbiologists and geochemists who are tracing the path of key elements and the role of microbes in the ocean's biogeochemical economy. On page 1375 of this issue, Canfield *et al*. (*1*) analyze the microbial cycling of nitrogen and sulfur in the oxygen minimum zone offshore of northern Chile. They show that our working hypotheses on microbial interactions and processes of stratified marine water columns have overlooked a critical component: the contribution of the "cryptic" microbial sulfur cycle.



Ocean biochemistry. Simplified scheme of sulfur and nitrogen cycle linkages for pelagic SUP05 bacteria, contrasted with benthic filaments of *Thioploca*. Lower left, epifluorescence in situ hybridization image of SUP05 cells, appearing in yellow, from the Suiyo Seamount hydrothermal plume; lower right, bright-field image of sheathed benthic *Thioploca* filaments from shelf sediments underlying oxygen-depleted water near Concepción, Chile.

CREDIT: (LOWER LEFT) A. MARUYAMA/AIST, JAPAN

Why cryptic? In principle, microbial processes should reveal themselves by the reaction partners that are produced and consumed. For example, the dominant anaerobic respiration pathway in the marine environment, sulfate reduction—the use of the seawater anion sulfate for respiration by specialized groups of bacteria and archaea—generates the end product sulfide. The gradual disappearance of sulfate, concomitant with sulfide production, would be a reliable indicator for microbial sulfate reduction. Yet studies of marine sediments have already shown that these microbial processes are easily camouflaged; sulfide accumulation is often held in check by specialized sulfide-oxidizing bacteria, as long as suitable oxidants are available. For example, the continental shelf of Chile and Peru harbors extensive microbial mats of filamentous bacteria, the sulfide-oxidizing, nitrate-reducing *Thioploca* species (*2*, *3*). In conjunction with a highly active microbial iron cycle in the upper sediments, the *Thioploca* mats reoxidize sulfide so efficiently that the amount of sulfide actually remains near the detection limit within the mat, despite an extremely high sulfate reduction rate in the immediately surrounding sediment (*4*). The water column of northern Chile contains an oxygen minimum zone (OMZ) in which sulfate reduction accounts for a surprisingly large proportion of total carbon remineralization. However, the resulting sulfide is reoxidized so efficiently that it does not accumulate, effectively camouflaging sulfate-reducing activity in the water column. In both habitats, sediment and water column, cryptic sulfur cycling does not mean that the process is environmentally irrelevant. On the contrary, preventing the buildup of free sulfide by instant reoxidation is essential to counter sulfide toxicity.

Canfield *et al*. link cryptic, nitrate-driven sulfur cycling to characteristic sulfur-oxidizing microbial communities of the Chilean OMZ. Previously, this bacterial community had been identified by 16*S* rRNA gene sequencing (*5*); Canfield *et al*. reexamined the OMZ bacteria by high-throughput sequence sampling of all detectable microbial genomes in the water column. The dominant sulfur-oxidizing bacterial lineage was identified as the SUP05 cluster within the γ-proteobacteria, a cosmopolitan cluster of yet-uncultured bacteria that is consistently associated with anaerobic marine water columns (*6*). The acronym SUP refers to the original discovery of these bacteria in the hydrothermal plume of Suiyo Seamount, a submarine volcano near Japan (*7*). SUP05 bacteria from this location appear as micrometer-sized coccoid to slightly oval individual free-swimming cells, unattached to particles (see the figure). The Chilean results link the SUP05 lineage with cryptic sulfur cycling and answer the question of why SUP05 sulfide oxidizers are also found in anaerobic, but apparently sulfide-free, waters.

The results also imply that cryptic sulfur cycling and its microbial catalysts are more widespread than currently documented. For example, the SUP05 cluster constituted the most frequently recovered bacterial group in hydrothermal vent plumes at the Mid-Cayman Rise, the deepest currently known hydrothermal vents at 5000 m depth (*8*).

How resilient is this microbial ecosystem

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in the Chilean OMZ? In sediments with a high input of easily degradable biomass that fuel sulfate reduction, microbial sulfide production can overwhelm the nitrate pool and lead to sulfide poisoning of life in the seabed; sulfide-blackened dead *Thioploca* mats (nicknamed "*Thioploca nigra*") are a frequent occurrence on the Chilean shelf sediments (*9*). In the OMZ water column, the chemistry balance is tilted toward sulfide limitation. Comparison of the redox stoichiometries of the pelagic SUP05 group and benthic *Thioploca* lends plausibility to this scenario. Benthic *Thioploca* reduce nitrate to ammonia in order to oxidize sulfide as effectively as possible in a 1:1 ratio of nitrate and sulfide (*10*). The SUP05 populations favor a more parsimonious mode of sulfide oxidation by the reduction of nitrate to nitrite, with a sulfide/nitrate stoichiometry of 1:4 (see the figure). The dominant OMZ bacteria may have additional, as yet unexplored, mechanisms of coping with sulfide limitation.

As a caveat, such scenarios oversimplify the very complex nitrogen cycle; they neglect the highly active microbial cycling of ammonia in the oxycline (*11*). They also do not take into account anaerobic ammonia-oxidizing bacteria in the water column, which combine nitrite and ammonia to nitrogen gas (*5*). To trace the dynamics of sulfide oxidation and nitrate reduction processes and their microbial populations, Canfield *et al.* call for systematic seasonal studies.

The Chilean OMZ and continental shelf provide two examples for microbial sulfur and nitrogen cycling ecosystems that thrive in a highly dynamic balance and persist through annual or interannual oscillations in redox regime and water column stratification (*12*, *13*). With ocean temperatures and anthropogenic water column anoxia on the rise, nitrate-dependent microbial controls on sulfide concentrations will become increasingly relevant; in the near future, we will certainly hear more about these resilient microbial engines of the changing world oceans.

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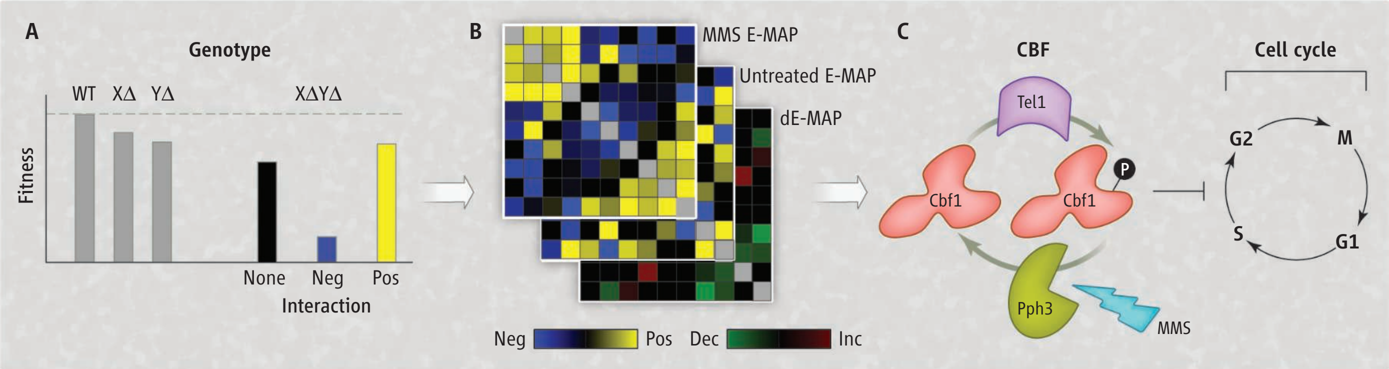
GENETICS

The DNA Damage Road Map

Comparing maps of gene interactions offers insight into how yeast cells repair DNA damage.

Nir Friedman[1,2] **and Maya Schuldiner**[3]

If you were on your way to a new country, you would pack a map to help you find the major cities, roads, and interesting places to explore. Recently, researchers have created similar maps to help them start unraveling the complex architecture of a cell. These maps are created by measuring genetic interactions, specifically the effect that a mutation in one gene has on the phenotype of a mutation in a second gene (see the figure). Using novel genetic tools for studying budding yeast (*1*) and automated technology, investigators can now systematically and rapidly measure these genetic interactions (epistasis) for all pairs in gene subsets of interest (about 400 to 800 genes). The resulting E-MAPs (epistasis miniarray profiles) (*2*) have helped chart interactions for a diverse array of cellular processes, including the early secretory pathway, chromosome function, signaling pathways, and RNA processing (*3*, *4*). These E-MAPs, however, have all have been collected from cells grown under the same condition: in a rich growth medium. But just as a snowstorm can block some roads and force changes in traffic, changing environmental conditions can cause cells to rewire their genetic networks, necessitating the drawing of a new map. On page 1385 of this issue, Bandyo-



Compare and contrast. (**A**) E-MAPs are created by measuring the effect of gene mutations on a phenotype of interest such as fitness. By comparing wild-type (WT) strains to single mutations (XΔ, YΔ) and their combinations (XΔYΔ), investigators can identify mutation pairs that have no effect (black bar, right), a negative effect that is greater than expected (blue bar), or a positive effect that is less than expected (yellow bar). (**B**) By comparing E-MAPs of yeast cells grown under treated (MMS) and untreated conditions, researchers created a dE-MAP illustrating the change in interactions (increased or decreased) between the two conditions. (**C**) The dE-MAP highlighted the role of Tel1 and Pph3 in regulating Cbf1 activity in cell cycle checkpoints (right).

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