

Hidden hydrogen cycles in the ocean



Characterization of an ancient chemosynthetic process in modern oceans prompts investigation into microbial metabolisms that might be hiding in the dark.

A common adage states that scientists know more about space than the oceans. Notably, more humans have visited the moon than have visited the deepest ocean trenches. The unknowns in the marine environment extend from the topographical to the microscopic. Every millilitre of seawater contains a million microorganisms, and an order of magnitude more viruses, but most of these organisms remain uncharacterized and uncultured. In the narrow band of sunlit surface ocean, cyanobacteria and eukaryotic phytoplankton form the base of the food web, and fix inorganic carbon into organic matter. Heterotrophic microorganisms and viruses consume and control the fate of this fixed carbon as it sinks through the water column. However, vast ocean ecosystems exist beyond the reaches of the sun. What happens without light in the ocean depths remains mysterious. In this issue, two Articles characterize how marine microorganisms in the dark ocean interior capitalize on an abundant and accessible energy source, namely hydrogen (H_2), that has long been overlooked. These findings showcase that a physiological capability thought to be important in the origins of life on Earth had been hiding in plain sight in the modern ocean.

The discovery in 1977 of flourishing biological systems around deep-sea hydrothermal vents challenged the paradigm that sunlight fuelled all ecosystems on Earth. In the pitch dark of the ocean floor, several thousand metres from the sunlight that bathes the surface ocean, chemosynthetic bacteria and archaea were found. These microorganisms use reduced inorganic compounds spewed from hydrothermal vents, instead of using photons, to yield the energy required to fix inorganic carbon into biomass¹. High-energy compounds, such as H_2 , are likely to have been produced by geochemical reactions in the Earth's interior since the initial formation of the oceans. Therefore, the

microbial capacity to use H_2 likely predates the evolution of photosynthesis. Microbial participation in these biogeochemical interactions in the deep ocean might offer clues about the origins of life on Earth². Hydrogen is an accessible and abundant energy source throughout the water column, but the extent to which it might be used by marine microorganisms and might influence present ocean biogeochemistry has not previously been characterized.

In soil microbial communities, the ability to use H_2 for respiration and carbon fixation is widespread, and is thought to be important for survival when other resources are scarce³, even though H_2 is a trace gas that makes up only a minuscule portion of the atmosphere and presents many challenges for catalytic extraction⁴. However, in marine systems, H_2 is relatively abundant: in addition to being enriched due to geochemical reactions in deep-sea environments, H_2 in the surface ocean is supersaturated up to 15-fold relative to atmospheric concentrations. Despite the enrichment of this high-energy molecule, it was assumed that H_2 oxidation was a rare capability in marine microbial communities³. Now, with the rapid proliferation of metagenomic and metatranscriptomic sequencing datasets that span diverse ocean environments, researchers are able to probe metabolic potential and gene expression with unprecedented geospatial coverage. When combined with incubations, culturing experiments and modelling, cross-disciplinary investigations are primed to illuminate hidden dimensions of marine microbial communities.

In this issue of *Nature Microbiology*, Lappan and colleagues reassess the importance of H_2 oxidation in the ocean. The authors combine genomic surveys, biogeochemical modelling and culture-based analyses to show that marine bacterial use of H_2 is more important in the pelagic ocean than previously thought. Genes enabling the use of H_2 were found in 11 marine bacterial phyla. These bacteria are only present at low abundance in pelagic microbial communities. Expression of H_2 -oxidizing gene transcripts in global ocean metatranscriptomes is high, however, with modelled rates indicating that H_2 may be able to exclusively support growth of some microorganisms.

Furthermore, the presence of these genes increases with depth, which might mean that H_2 oxidation is important in ocean regions that are resource scarce, oxygen limited and dark.

A second Article in this issue, by Molari and colleagues, also demonstrates a previously unappreciated facet of marine H_2 oxidation. Using multi-omics, the authors find that a hydrogenotrophic bacterial species named *^USulfurimonas pluma* is ubiquitous in non-buoyant hydrothermal plumes. These plumes originate from hydrothermal fluids that contain increased concentrations of reduced gases including hydrogen sulfide (H_2S) and H_2 , can reach up to hundreds of metres off the seafloor and can drift for thousands of kilometres away from the source. Although *^US. pluma* has a suite of genes for sulfur oxidation, the authors report that genes for H_2 hydrogenases were expressed up to 500 times higher in plume samples.

Together, these Articles show that an ancient metabolic process has been hiding in plain sight across the modern ocean. Although some marine bacteria readily capitalize on the comparatively high concentration and sizable energy yield of H_2 , this capability is still perplexingly rare among marine microorganisms. One answer to this conundrum could lie in the resource investment necessary to make H_2 hydrogenases; these enzymes have a high iron requirement, but this micronutrient is in vanishingly short supply across much of the ocean. Interestingly, Molari and colleagues found high expression of the iron storage protein ferritin in *^US. pluma*, which could hint at a strategy to maximize resource availability for hydrogenase production.

These findings highlight a need to re-evaluate how H_2 oxidation, and other overlooked metabolic processes, might impact marine microbial ecology and interface with planetary biogeochemical cycles. Of particular interest will be research that investigates the intersection of microbial physiology with anthropogenic and climate change impacts, such as the spread of marine oxygen minimum zones, deep-sea mining, altered patterns of ocean circulation caused by rising temperatures, or droughts on land increasing iron-rich dust deposition to the sea surface. Using

cross-disciplinary approaches it will be exciting to learn what other microbial metabolic treasures have remained hidden in the depths of the ocean.

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