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OCEAN SCIENCE

Microbial proteins and oceanic nutrient cycles

Ocean microbes respond to limited nutrients by tuning the abundance of specific proteins

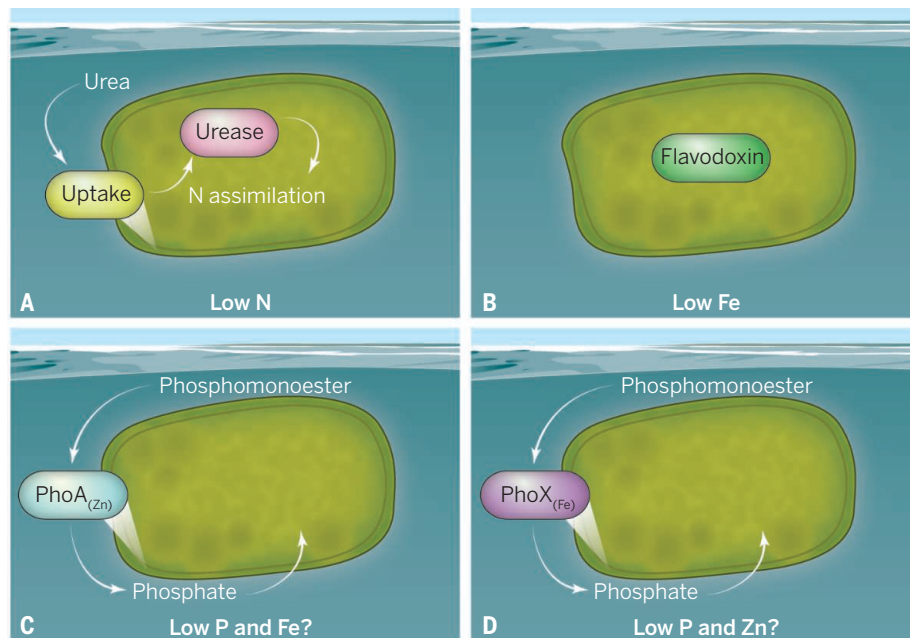
By C. Mark Moore

Marine microbes play a central role in the biogeochemical cycles of carbon and nutrients such as nitrogen, phosphorus, and iron. The processes that control these complex cycles range from subcellular metabolism to the properties and dynamics of whole oceanic regions. Two studies in this issue provide further insight into how fundamental biological processes affect biogeochemical cycles in the oceans. On page 1173, Saito *et al.* (1) show how nutrient availability drives large-scale patterns in the abundances of nutrient-related proteins. The catalytic site in one such protein, reported on page 1170 by Yong *et al.* (2), suggests a potential biochemical linkage between two key nutrient cycles.

Phytoplankton—the tiny single-celled photosynthetic organisms that form the base of the marine food web—are responsible for roughly half of global oxygen production. The sinking and breakdown of the organic material produced by these organisms lowers atmospheric carbon dioxide concentrations and removes essential nutrients from the surface ocean (3). Limited availability of some of these nutrients, particularly nitrogen (N) and iron (Fe), can be a key constraint on the productivity of surface ocean regions (3).

The coupling between carbon and nutrient cycles depends on the activity, composition, and abundance of the macromolecules that make up most biological material (3). Over the past two decades, oceanographers have therefore increasingly turned to molecular biology techniques to interrogate the abundance, activity, and diversity of marine microbes and the biomolecules they contain. For example, changes in lipid composition have been linked to nutrient availability (4).

Proteins are also useful biomarkers of nutrient stress (5). Surveys of oceanic microbial populations have revealed many diverse nutrient transport proteins in low-nutrient systems (6). Saito *et al.* now use quantitative proteomic mass spectrometry to determine changes in the absolute abundance of multiple proteins over oceanic scales spanning thousands of kilometers. Sampling across



How proteins respond to nutrient limitations. The availability of limiting nutrients varies throughout the oceans. Saito *et al.* (1) show that urease proteins associated with uptake and assimilation of urea, an organic N source, are abundant in low-N regions (A); in contrast, the flavodoxin protein, which can replace an Fe binding equivalent, is abundant in a low-Fe region (B). In low-P regions, uptake of P from phosphomonoesters can be facilitated by alkaline phosphatase enzymes such as PhoA and PhoX. Yong *et al.* (2) show that a member of the PhoX family (II) binds Fe, in contrast to the Zn-binding PhoA. Selection between these enzymes, or the organisms containing them, might thus be expected in low-P environments depending on the relative availability of Zn (C) or Fe (D).

a transition between mainly N-limited and mainly Fe-limited regions, the authors focus on proteins associated with the abundant open-ocean phytoplankton *Prochlorococcus* (7). They observe coherent changes in the abundances of multiple-nutrient stress-related proteins, demonstrating *in situ* microbial responses to varying nutrient limitation regimes (see the figure, panels A and B).

“Over the past two decades, oceanographers have therefore increasingly turned to molecular biology techniques to interrogate the abundance, activity, and diversity of marine microbes and the biomolecules they contain.”

They are able to detect these large-scale patterns of multiple nutrient limitations without the need for complex time-consuming incubation experiments (3).

Understanding of protein abundance and function is particularly important because these macromolecules catalyze and mediate the reactions that drive biogeochemical cycles (8). Proteins can also be a large sink for cellular nutrients, including N and trace metals (3). Saito *et al.* show that in the boundary region sampled between the low-N and low-Fe regions, essential cellular N resources are simultaneously allocated to different proteins related to N and Fe stress, at least at the community level. These results argue against a simple interpretation where only one nutrient becomes limiting at a time, instead suggesting a degree of colimitation (3, 9).

Many catalytic proteins require transition metals, including Fe, Mn, Co, Ni, and Zn (10). Requirements for such proteins are a key driver of the potential for these nutrients to become (co)limiting in the oceans (9). A new example of this potential

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is provided by Yong *et al.* Under conditions of low phosphorus (P) availability, marine microbes extract inorganic phosphate from organic phosphomonoester substrates using alkaline phosphatase enzymes (11). The best-studied of these enzymes, PhoA, binds Zn, leading to suggestions that P and Zn may be colimiting in certain environments (9, 11). However, the alternative PhoX family of phosphomonoesterases does not require Zn and appears to be more widely distributed in marine systems (11).

Yong *et al.* show that a member of the PhoX family binds 2 Fe and 3 Ca atoms in a catalytic cofactor that has several distinctive characteristics. From the biogeochemical perspective, the presence of Fe in the PhoX active site suggests a direct biochemical linkage between the Fe and P cycles, which could lead to these elements becoming colimiting. The relative availability of Zn or Fe in low P environments might thus drive selection between PhoA and PhoX or between the organisms capable of producing these enzymes (11) (see the figure, panels C and D). Techniques of the type used by Saito *et al.* could be used to determine whether distributions of PhoA and PhoX correspond to patterns of P, Zn, and Fe availability in the oceans.

The two studies (1, 2) substantially advance our understanding of some of the microbial proteins that influence global nutrient cycles. Wider application of the techniques used by the authors holds great promise for further discoveries. Many metal-binding proteins remain largely uncharacterized (10, 12). Proteomic identification and quantification techniques (1, 6) could also be combined with biogeochemical rate measurements to decipher how microbial proteins operate to maintain elemental cycles (8). Given the dual role of proteins as biogeochemical catalysts and as a major sink for nutrients, fuller characterization (2), alongside quantification of abundance (1) and activity, could provide a fundamental mechanistic underpinning of the coupled nutrient cycles. ■

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PHYSICS

Particle physics in a superconductor

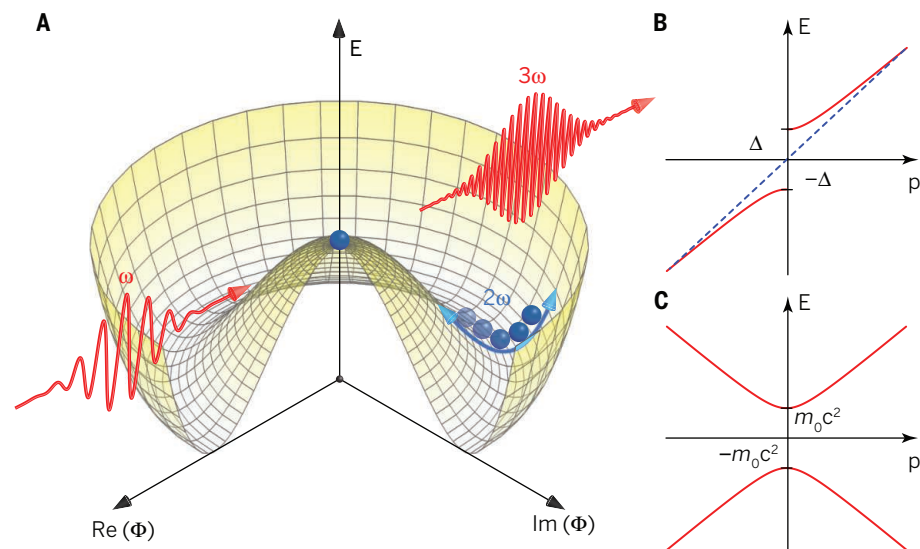
A superconducting condensate can display analogous behavior to the Higgs field

By Alexej Pashkin and Alfred Leitenstorfer

The recent discovery of the Higgs boson has created a lot of excitement among scientists. Celebrated as one of the most fundamental results in experimental physics (1), the observation of this particle confirms the existence of the associated Higgs field that plays a pivotal role in the Standard Model of particle physics. Because of the Higgs boson's large mass (about 125 GeV), it could be detected only in the world's largest and most powerful accelerator—the Large Hadron Collider at CERN, Geneva. Although it sounds strange, the theoretical proposal of the Higgs mechanism was actually inspired by ideas from condensed matter physics, which typically works at much lower energies (a few electron volts or less). In 1958, Anderson discussed the appearance of a coherent excited state in superconducting condensates with spontaneously broken symmetry (2). Later, this approach was advanced by

Nambu (3). The existence of superconducting condensates has been firmly established. In contrast, unambiguous experimental evidence for the coherent excited state (called the Higgs mode) had been missing. On page 1145 of this issue, Matsunaga *et al.* (4) report direct observation of the Higgs mode in the conventional superconductor niobium nitride (NbN) excited by intense electric field transients.

Conventional superconductivity appears in metals when the phases of electronic wave functions lock to each other, forming a macroscopic quantum state that conducts current without energy dissipation. It can be described by a complex order parameter $\Phi(\mathbf{k}) = |\Phi(k)|\exp(i\phi)$, which acquires a nonzero value only in the superconducting state. A result of this description is that a superconducting phase transition must lead to a spontaneous breaking of symmetry. Consequently, the energy of the system shows a minimum at a certain value of the radial amplitude $|\Phi(k)|$, which is, how-



The Higgs amplitude mode. (A) Energy of a system as a function of the complex order parameter Φ in a state with spontaneously broken symmetry. The Higgs mode corresponds to the amplitude oscillations of Φ shown by the blue arrow. The excitation by a light pulse at half the resonance frequency starts a coherent oscillation of the order parameter. The induced superconducting current is nonlinear and leads to emission of the third harmonic of the excitation wave. (B) Energy of quasi-particles as a function of their momentum near the Fermi energy of a normal metal (dashed blue line) and a superconductor with energy gap 2Δ (solid red line). (C) Energy of a relativistic particle-antiparticle system with rest mass m_0 as a function of its momentum.