**MARINE BIOLOGY**

**Putting the spotlight on organic sulfur**

Diverse dissolved organic sulfur compounds play an active role in ocean biogeochemistry

By Naomi M. Levine

Marine microbes are the engines that drive global biogeochemical cycling in the oceans. They produce and cycle a dissolved organic matter (DOM) reservoir that is roughly as big as the atmospheric carbon dioxide pool (1). Interactions between DOM and marine microbes may also play a key role in the evolving climate through changes in remineralization rates (2). Historically, DOM has been thought of mainly in terms of its carbon, nitrogen, and phosphorus content. On page 456 of this issue, Ksionzek et al. (3) investigate the large pool of dissolved organic sulfur (DOS) compounds in the ocean and show that these compounds also play a key role in ocean biogeochemistry.

Because the sulfate (SO$_4^{2-}$) concentration in the oceans is high, scientists have traditionally assumed that sulfur never limits biological activity. As a result, the biogeochemistry of organosulfur compounds has received less attention than that of the primary limiting nutrients, nitrogen and phosphorus. However, recent work suggests that organosulfur compounds both in the water and the cell may play critical roles in microbial community dynamics (4, 5) and in mediating the interactions between phytoplankton and heterotrophic bacteria (see the figure) (6). These compounds can also provide plasticity for microbes in nutrient limited regions by helping to reduce N and P requirements (7).

Ksionzek et al. now report that DOS accounts for 6700 to 18,600 Tg of sulfur in the ocean and that this pool turns over relatively slowly (less than 0.02% per year). The current knowledge of DOS derives from a small number of compounds that account for only ~25 Tg of sulfur and that turn over rapidly (within hours to days). By quantifying both the size and turnover rates of the DOS pool, the authors highlight an important class of molecules in the ocean and provide evidence for active biogeochemical cycling of DOS through selective remineralization.

Sulfate has an oxidation state of +6, whereas many organic molecules critical for life contain a reduced form of sulfur. For example, thiols, aromatic sulfur, and disulfides contain sulfur in the –2 oxidation state, and sulfonates contain sulfur in the +4 oxidation state. Some of the most ubiquitous heterotrophic bacterial groups in the oceans cannot reduce sulfate and thus depend on external sources of reduced sulfur—namely DOS—to fulfill their sulfur requirements (8, 9). This exploitation of reduced forms of organic sulfur by marine heterotrophs is consistent with the findings of Ksionzek et al.

Using ultrahigh-resolution mass spectrometry, the authors identified 803 different molecular formulas for DOS compounds in Atlantic Ocean samples. About 10% of these compounds only occurred in the surface ocean. The authors also show that the chemical nature of DOS changes as one moves from the surface to the deep ocean: The average S:C ratio of the molecular formula decreases with depth, whereas the molecular size and degree of unsaturation increases with depth. This finding suggests that DOS is preferentially consumed by marine heterotrophs, resulting in both a decrease in the concentration of DOS concentration relative to DOM with depth (see the figure) and a change in the chemical nature of DOS.

Although Ksionzek et al. were able to identify the molecular formulas (C$_x$H$_y$O$_z$N$_s$S$_p$) of many DOS molecules, the identity and function of these organic sulfur compounds remain unknown. Of particular interest are those compounds that are present in the surface ocean but not at depth. Some insight into the potential importance of DOS cycling can be gained from a small number of organosulfur compounds that have been previously studied, in par-
ticular, dimethylsulfide (DMS) and its precursor dimethylsulfiniopropionate (DMSP). These compounds are rapidly cycled by the upper-ocean microbial food web and have low concentrations in the water column (in the nanomole range per liter, compared with micromole per liter for bulk DOS as found by Ksionzek et al.). DMSP is produced by many eukaryotic phytoplankton species and some cyanobacteria (10, 11). Phytoplankton commit up to 10% of net photosynthesis (12, 13) to this single compound, making DMSP a major intracellular metabolite for many phytoplankton groups (6, 14). Interest in DMS and DMSP was initially sparked by their potential role in climate regulation (15), but DMSP may play an important role in several facets of ecosystem dynamics (see the figure).

In the ocean, where the vast majority of organisms are microscopic and the relative distances between them can be large, finding food can be difficult. To overcome this challenge, organisms use chemical signals to locate resources, a process known as chemotaxis. Bacteria also use chemical queues to regulate community behavior (quorum sensing); for example, they may increase the production of antibiotics once a population has reached a certain size. DMSP causes strong chemotactic behavior in heterotrophic bacteria and zooplankton (14) and induces the production of quorum-sensing molecules (15).

Similarly, another organosulfur compound, dihydroxypropane-1-sulfonate (DHPS), is a key participant in an “exchange of goods” (vitamin B12 for organic carbon) between photo- and co-occurring heterotrophs (6).

We are only just beginning to understand the ecological relevance of a handful of the 81 labile (rapidly cycled) DOS compounds identified by Ksionzek et al. in the surface ocean. Some of these organic sulfur compounds may play a critical role in ecosystem dynamics. A necessary next step is to better characterize these DOS compounds (such as their sulfur oxidation state), their turnover rate, and local or regional variations in the composition of DOS. Further work is needed to understand the extent to which microbial dynamics are limited by the availability of reduced sulfur compounds and to elucidate the connection between the small, rapidly cycled, labile DOS pool and the large, non-labile DOS pool. ■

REFERENCES

Warburg meets epigenetics

Glycolysis promotes T cell function by an epigenetic mechanism

By Chirag H. Patel and Jonathan D. Powell

We are all taught in biochemistry class that in the presence of oxygen, cells will use the tricarboxylic acid (TCA) cycle to efficiently generate adenosine 5′-triphosphate (ATP) via oxidative phosphorylation (OXPHOS). However, in 1924, the biochemist Otto Warburg observed that cancer cells do not follow this rule (1, 2). In fact, even in the presence of oxygen, cancer cells will depend on glycolysis (so-called aerobic glycolysis) to inefficiently generate ATP from glucose. More recently, there has been great interest in the observation that effector T cells will also use glycolysis to generate ATP in the presence of oxygen (3, 4). On page 481 of this issue, Peng et al. (5) make an important link between aerobic glycolysis and epigenetic regulation in T helper 1 (Th1) cell differentiation.

It is becoming increasingly clear that metabolic reprogramming (i.e., up-regulating the glycolytic machinery) is a critical component of T cell activation (6). One key glycolytic protein is lactate dehydrogenase (LDHA). LDHA is involved in the conversion of pyruvate to lactate and, more importantly, in the oxidation of nicotinamide adenine dinucleotide (NADH) to regenerate NAD+ and continuously drive glycolysis (7). However, pyruvate that is not converted to lactate is
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