the true nature of the Si surface (*5*). Despite the success of STM, it was limited to imaging conducting surfaces. In 1988, G. Binnig, a co-inventor of STM, designed an AFM technique that operates at low temperature and in a vacuum, for characterizing the surface of insulators (*6*). Similar to STM, AFM uses a scanning probe tip, but instead of passing a current, it "feels" the surface by sensing the forces that act between probe tip and sample. This enables imaging nonconducting surfaces of insulators, but initially at a far lower resolution than that of STM.

Hütner *et al.* resolved the precise positions of aluminum and oxygen atoms in the α-Al_2O_3 ($\sqrt{31} \times \sqrt{31}$)$R \pm 9°$ surface using a noncontact-mode AFM. They used an AFM tip coated with copper oxide (CuOx) molecules. This terminates the tip with a chemically inert oxygen atom at its apex. The oxygen front atom interacts with many sample surfaces through Pauli repulsion—a repulsive interaction between two atoms as they move closer to each other (*7*). When imaging nonconductive samples such as organic molecules or a semiconductor such as Si with a terminated tip, Pauli repulsion prevails. By contrast, imaging some metal samples such as Copper (Cu) surfaces induces a moderately strong covalent bond between the metal atoms and the oxygen-terminated tip (*8*). On the basis of these previous observations, Hütner *et al.* show that the terminated tip interacts repulsively with oxygen atoms and attractively with aluminum atoms that are on the same surface. This provides sufficient visual contrast to distinguish different atoms in a sample, such as bright spots for oxygen and the dark minima for aluminum atoms (see the figure). This enables determining the positions of different atoms on a complex oxide surface.

Specifically, Hütner *et al.* used frequency-modulation AFM (FM-AFM). It is a way of imaging a surface without physical contact with the probing tip. In FM-AFM, the frequency of an oscillating cantilever changes owing to the force gradient between the tip and a sample. Thus, the frequency shift is a measure of the interaction between the tip and a sample. In its early days, FM-AFM used traditional soft Si cantilevers, oscillating at a large amplitude of about 100 atomic diameters (*9*). This large amplitude technique has been used to resolve the structure of the α-Al_2O_3 ($\sqrt{31} \times \sqrt{31}$)$R \pm 9°$ surface (*10*, *11*), but only roughly. The oscillating sensor only spends a little time close to the sample, which is not optimal for obtaining precise information about the surface structure.

Calculations have shown that for higher resolutions with improved signal-to-noise ratio, the tip should oscillate at a small amplitude closer to the range of chemical bonding forces (*12*). However, traditional silicon cantilevers are too soft to provide stable oscillation in this force field. To overcome this limitation, the qPlus sensor (*12*) was developed with a much larger stiffness of about 1 kN/m, which is ideal for use at small amplitudes. Additionally, the size of the coated probe tip's front atom dictates the resolution limit. For example, an oxygen atom has a diameter 40% that of a metal atom. The carbon monoxide (CO) terminated tip enabled better spatial resolution of the α-Al_2O_3 ($\sqrt{31} \times \sqrt{31}$) $R \pm 9°$ surface. However, the lateral stiffness of the CO termination is rather soft, causing image distortions. Later, a CuOx terminated tip was developed (*13*). That bore a similar small front atom diameter but had a greater lateral stiffness than that of the CO tips. This advance suppressed image distortions while improving spatial resolution.

It is one thing to show proof of principle that the AFM can image insulating surfaces at atomic resolution. It is another to apply this, alongside with state-of-the-art spectroscopy techniques and theoretical models, to answer a long-standing and practical problem. One of the major complications with surface reconstruction is a complete understanding of lower layers, which AFM cannot scan directly. Hütner *et al.* not only pushed AFM to its limit to determine the atomic structure of the α-Al_2O_3 ($\sqrt{31} \times \sqrt{31}$)$R \pm 9°$ surface but also combined photoelectron spectroscopy and density functional theory to elucidate the interface layer underneath the surface. The precisely determined atomic positions from AFM images are important input parameters for building the theoretical model of interface layers that link the surface and the bulk. The proposed model of Hütner *et al.* indeed agrees with spatial data of previous literature (*2*, *10*, *11*) and provides strong evidence for a stoichiometric surface termination. The approach by Hütner *et al.* could be broadly applied to reveal complex surface reconstructions of insulating surfaces. ■

REFERENCES AND NOTES

1. J. I. Hütner *et al.*, *Science* **385**, 1241 (2024).
2. C. C. Chang, *J. Appl. Phys.* **39**, 5570 (1968).
3. A. Zangwill, *Physics at Surfaces* (Cambridge Univ. Press, 1988).
4. G. Binnig *et al.*, *Phys. Rev. Lett.* **50**, 120 (1983).
5. K. Takayanagi *et al.*, *J. Vac. Sci. Technol. A* **3**, 1502 (1985).
6. G. Binnig, *Ultramicroscopy* **42-44**, 7 (1992).
7. L. Gross *et al.*, *Science* **325**, 1110 (2009).
8. F. Huber *et al.*, *Science* **366**, 235 (2019).
9. F. J. Giessibl, *Science* **267**, 68 (1995).
10. C. Barth, M. Reichling, *Nature* **414**, 54 (2001).
11. J. V. Lauritsen *et al.*, *Phys. Rev. Lett.* **103**, 076103 (2009).
12. F. J. Giessibl, *Rev. Sci. Instrum.* **90**, 011101 (2019).
13. H. Mönig *et al.*, *Nat. Nanotechnol.* **13**, 371 (2018).

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OCEANOGRAPHY

Going deep on marine lipid metabolism

Marine bacteria cooperate to degrade lipids in sinking particulate organic matter

By **Florence Schubotz**

Marine algae account for almost half of global carbon fixation. A substantial proportion of this photosynthetic biomass is exported to the deep ocean through the biological carbon pump (see the figure). As algal biomass sinks through the water column, it is slowly degraded by diverse microorganisms (*1*). Ultimately, only a fraction reaches the seafloor, where it becomes buried over geologic timescales (*2*). Although studies have uncovered the microbial networks associated with sinking particle degradation (*3*), the processes that transform organic material as it descends remain poorly understood. On page 1182 of this issue, Behrendt *et al.* (*4*) report that cooperation between marine bacteria with distinct dietary preferences for lipid components of sinking organic matter can influence the transport efficiency of lipid carbon to the seabed. Understanding how microbial metabolism constrains the biological carbon pump is vital given its role as a regulator for atmospheric carbon dioxide (CO_2) concentrations (*2*).

Landmark ocean surveys have provided molecular details on particulate organic matter (POM) in the equatorial Pacific (*5*), which have since been confirmed across the world's oceans. In surface waters, POM is dominated by amino acids and proteins (~60%), lipids (5 to 30%), and carbohydrates (3 to 18%), with the remainder of organic material uncharacterizable at the molecular level (*6*, *7*). As POM sinks, the uncharacterizable organic material steadily increases to more than 80%, whereas amino acids, lipids, and carbohydrates are degraded, albeit to a differing extent. Lipids compose <3% of the organic carbon that reaches the seafloor and are thus considered part of the labile organic matter pool that is either readily broken down to CO_2 or transformed into dissolved forms.

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Lipids are structurally diverse molecules found in every living organism, with important structural and functional roles (*8*). High-throughput lipidomics now allow the simultaneous analysis of all lipid classes, including intact polar membrane lipids (such as phospholipids, glycolipids, and aminolipids), storage lipids (such as triacylglycerols), pigments (such as chlorophyll and carotenoids), sterols and hopanols, ether lipids, and free fatty acids (*7*, *9*, *10*). However, to characterize the complete lipidome in the deep ocean requires large samples, making it difficult to link it to small-scale microscopic processes occurring on sinking particles.

To overcome this challange, Behrendt *et al.* used nano-lipidomics, a method that bypasses the detection limits of traditional lipid analyses, permitting the lipidome analysis of single aggregates, such as marine snow and fecal pellets (*11*). By combining nano-lipidomics with experiments using organic matter–degrading (heterotrophic) bacteria isolated from marine particles, the authors captured microscale microbial processes occurring during the degradation of a single algal lipid droplet. They visualized these processes using a fluorescence microscopy–based imaging technique that allows for time-resolved and quantitative high-throughput lipidomic analysis. The results show that lipids are not degraded haphazardly but are selectively degraded by specific bacteria. For example, high-energy triacylglycerols were untouched by some heterotrophic isolates. Furthermore, a wide range of delay times in the onset of lipid degradation was observed among the isolates, ranging from several hours to days. The most plausible explanation for this delay is the build-up of chemoattractants (metabolites generated by primary colonizers) to sufficient concentrations to kick-start secondary metabolizers (*12*).

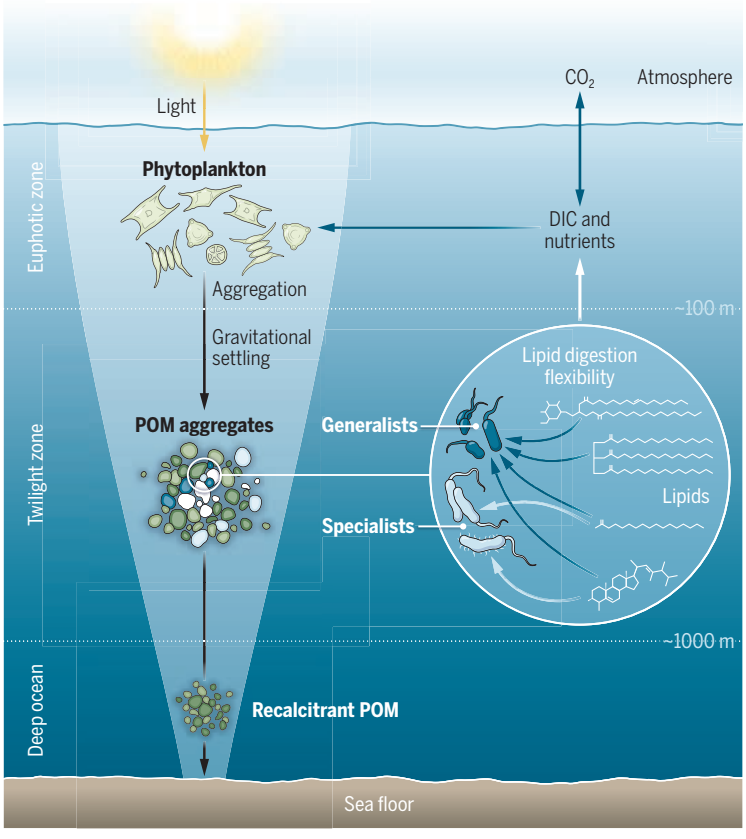
By linking changes in lipid composition to the presence of lipid degradation genes in the isolates, Behrendt *et al.* found the observed dietary selectiveness not to owe to taxonomic relatedness but to differences in the enzymatic repertoire. Even related bacterial species can have very distinct dietary preferences and cooperate with other microorganisms in synergistic or antagonistic ways. To explore the dynamics of multispecies communities during lipid degradation, the authors constructed synthetic communities composed of isolates with distinct dietary preferences. Some bacteria formed syntrophic relationships that accelerated lipid degradation, whereas others inactivated each other. Disentangling the role of complex associations by studying more environmentally realistic microbial compositions will be a task for future POM degradation studies.

To address how microbial interactions in the lab translate to processes in the ocean, Behrendt *et al.* incorporated their findings into a particle export model. The model distinguishes itself from other approaches by separating the degradable lipid phase from the nondegradable mineral ballast phase of the sinking particle. It also incorporates their experimentally determined degradation rates and delay times. The model suggests that the transfer efficiency of lipid molecules in small particles (50 μm diameter) is low, depending on the degradation rate and not the delay time because particle sinking time is long. For larger, fast sinking particles (500 μm diameter), delay time has a greater effect on transfer efficiencies. Given that less than 10% of lipids get exported to the deep sea, this implies that lipid-containing particles are small and contain synergistic bacterial communities optimized in lipid degradation.

It remains to be shown how these findings transcribe to the microbial regulation of organic carbon export to the deep sea (*13*). Behrendt *et al.* demonstrate that lipidomics can be combined at the microscale with other -omics approaches to link the genetic repertoire of organisms to the degradation of individual organic compounds. Capturing the intricacies of POM degradation and carbon export will require combining -omics studies on whole communities with the quantitative analysis of organic matter turnover, including lipids, carbohydrates, and proteins. Mass spectrometry imaging on whole particles may be invaluable for monitoring changes in organic matter composition on small spatial and temporal scales to cover the full range of molecular complexity (*14*). Using these approaches to generate a unified formulation of POM composition and reactivity is fundamentally important to understand the contemporary and future global carbon cycle. ■

Microbial interactions modulate ocean carbon export

The export efficiency of photosynthetically produced carbon from the surface to the deep ocean is determined by the interplay of environmental, ecological, and compositional factors. In the mid-mesopelagic (twilight) zone of the ocean, sinking particulate organic matter (POM) is primarily degraded by bacteria, releasing nutrients and dissolved inorganic carbon (DIC). Using new lipidomic assays, Behrendt *et al.* show that POM lipid degradation efficiency depends on dietary preference and synergistic or antagonistic bacterial interactions to control transfer of organic carbon to the ocean floor.



REFERENCES AND NOTES

1. M. H. Iversen, *Annu. Rev. Mar. Sci.* **15**, 357 (2023).
2. D. A. Siegel *et al.*, *Annu. Rev. Mar. Sci.* **15**, 329 (2023).
3. G. J. Herndl *et al.*, *Annu. Rev. Mar. Sci.* **15**, 461 (2023).
4. L. Behrendt *et al.*, *Science* **385**, eaab2661 (2024).
5. S. G. Wakeham *et al.*, *Geochim. Cosmochim. Acta* **61**, 5363 (1997).
6. J. J. Kharbush *et al.*, *Front. Mar. Sci.* **7**, 518 (2020).
7. B. R. Edwards, *Annu. Rev. Mar. Sci.* **15**, 485 (2023).
8. Y.-M. Zhang, C. O. Rock, *Nat. Rev. Microbiol.* **6**, 222 (2008).
9. J. R. Collins *et al.*, *Anal. Chem.* **88**, 7154 (2016).
10. S. Ding *et al.*, *Front. Microbiol.* **12**, 659315 (2021).
11. J. E. Hunter *et al.*, *Environ. Sci. Technol.* **55**, 15456 (2021).
12. M. S. Datta *et al.*, *Nat. Commun.* **7**, 11965 (2016).
13. F. Azam, F. Malfatti, *Nat. Rev. Microbiol.* **5**, 782 (2007).
14. W. Liu *et al.*, *Front. Earth Sci.* **10**, 931157 (2022).

10.1126/science.ads0919