



Bacterial Vesicles in the Ocean
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occurred 4000 years ago), human intensification (modeled as population growth), and climate change. Ecological extinction was declared when populations dwindled to fewer than 500 individuals.

Such simulation studies will conceal regional and local responses to various parameters, as well as subtle interplay at fine spatial and temporal scales. But the main findings were clear-cut. Human intensification featured in 80% of the successful simulations, compared to the inclusion of climate change (44%) and dingo invasion (16%). Prowse *et al.* then analyzed a subset of these simulations using boosted regression trees (11) to assess the importance of different model parameters on the probability of successfully predicting the extinction of mainland thylacines and devils. This analysis confirmed humans as the main driver of the mainland extinctions. Human intensification was the most influential factor, followed by the initial human density and the rate of

human predation on kangaroos (see the second figure). Climate change became important when the latter two parameters were at their lowest values, but dingoes had a negligible effect. Predictive success was affected more by human attack rates on kangaroos than on thylacines and devils; thus, human hunting of these native carnivores had less influence than did human predation on their common prey.

Vindication of the dingo for the extirpation of the thylacine and devil on mainland Australia puts people—and perhaps climate change—squarely in the frame. Humans are also implicated in the demise of the Australian megafauna (3–6). However, searching for prehistoric synergies among extinction drivers is made more difficult by the declines in quantity and quality of evidence further back in time, hampering efforts to resolve the causes of megafaunal extinction from dated fossils, artefacts, and proxy records of climatic and ecological change. Prowse

et al.'s scenario-testing approach (2) offers a new lens through which to study the range of dynamic interactions and impacts responsible for this earlier mass extinction.

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ECOLOGY

Bacterial Vesicles in the Ocean

David Scanlan

Marine microbes play a key role in global nutrient cycling (1). Phytoplankton account for less than 1% of the photosynthetic biomass on Earth, yet contribute almost half of the world's primary production (2). In open oceans between ~45°N and ~40°S, cyanobacteria of the genus *Prochlorococcus* dominate the phytoplankton (3). *Prochlorococcus* is the smallest free-living phototroph; its genome is subject to miniaturization (4), and distinct ecotypes are adapted to the strong gradients of light and nutrients in the surface ocean (5). On page 183 of this issue, Biller *et al.* (6) identify a further striking feature of *Prochlorococcus*: the production of extracellular vesicles that may play a role in carbon cycling, gene transfer, and viral defense.

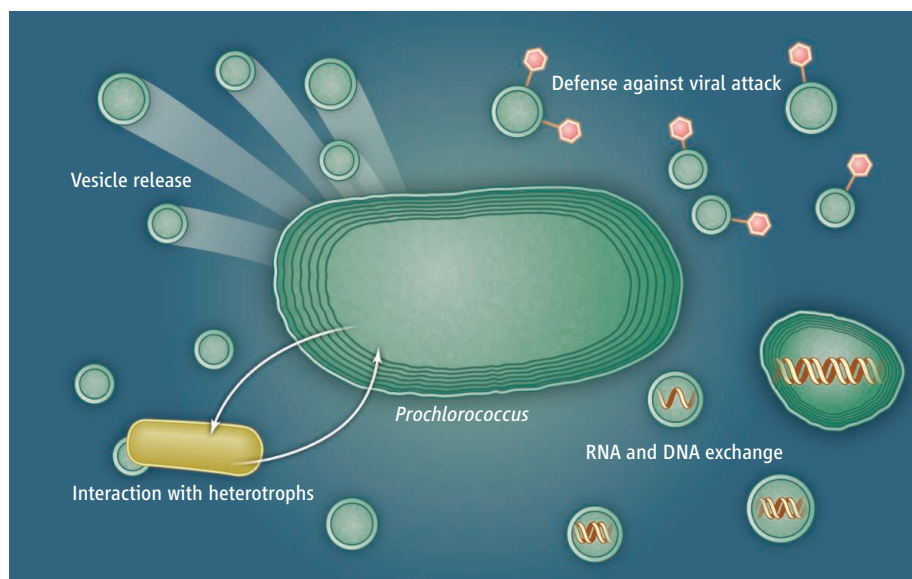
Biological production of extracellular vesicles is widespread, with vesicles produced by species across all three branches of the tree of life (7). In Gram-negative bacteria, vesicles are produced when small regions of the outer membrane bulge away from the cell before pinching off and being released (8). Biller *et al.* carefully purified 70 to 100 nm-

sized membrane-bound extracellular vesicles from exponentially growing *Prochlorococcus* cells. The vesicles contain not only periplasmic and outer-membrane proteins but also proteins characteristic of inner membrane

Vesicles released by phytoplankton may play key roles in carbon cycling, viral defense, and gene transfer.

and cytoplasmic compartments, although their relative abundance is unknown. They also contain DNA and RNA.

The authors show that vesicles are produced not only by *Prochlorococcus*, but also



Multipurpose vesicles. Biller *et al.* show that *Prochlorococcus* produce vesicles that may play functional roles in defending against viral attack, interactions between heterotrophs and *Prochlorococcus*, and horizontal gene transfer. This is a schematic presentation and is not to scale.

by a marine *Synechococcus* strain, the sister group to *Prochlorococcus*, potentially extending vesicle production to organisms that are ubiquitous in oceans across the world. Indeed, Biller *et al.* were able to purify structures containing protein and various lipids indicative of vesicles from natural seawater collected at coastal and oligotrophic sites off the American east coast. Thus, vesicles are produced in the open ocean and not only by pathogens and biofilm-inhabiting microbes living at high cell density.

In the cultures and natural samples analyzed by Biller *et al.*, the vesicles are as abundant as the organisms themselves (and in some cases up to 10 times more so). They are also relatively stable, with numbers remaining constant for more than 2 weeks. This has important consequences for the nature and origin of dissolved organic carbon (DOC) in the ocean. DOC in turn supports microbial growth and hence plays a key role in the global carbon cycle through the microbial loop.

Why would an organism like *Prochlorococcus*, which is clearly well adapted to the nutrient-poor open ocean, shed vesicles containing large amounts of carbon, nitrogen, and phosphorus that have been hard work to win? The authors speculate on several different avenues (see the figure), all of which are ripe for future research. First, the labile carbon released in such vesicles may stimulate heterotrophic growth. Some marine heterotrophs are known to positively stimulate the growth of *Prochlorococcus*. Indeed, all currently sequenced *Prochlorococcus* strains lack the enzymes for catalase or catalase-

peroxidase, making the organism highly susceptible to oxidative damage. Heterotrophic “helper” bacteria can compensate for this loss (9), an idea that has been called the Black Queen hypothesis, where gene loss in free-living organisms like *Prochlorococcus* may leave them dependent on co-occurring microbes for lost metabolic functions (10).

Second, the extracellular vesicles may transfer DNA fragments between organisms, thereby facilitating horizontal gene transfer. This idea is not new (9), but the fact that vesicles from both cultured bacteria and natural marine communities contain DNA hints at a potentially widespread mechanism for moving DNA (and RNA) between cells.

Perhaps the most evocative of the functions put forward by Biller *et al.* is the idea that the vesicles might prevent phage attack by acting as decoys. Viruses, including marine cyanophages, which specifically infect cyanobacteria, are very abundant in marine systems (11, 12). The extracellular vesicles reported by Biller *et al.* are enriched in outer membrane components, suggesting that they harbor phage receptors that can act to directly bind viral particles. Indeed, the authors show that purified vesicles bind phage particles; many of these vesicle-attached phage particles possess an altered morphology suggestive of DNA injection into the vesicles. However, it remains to be shown whether, and if so how, these vesicles affect phage-host infection dynamics at concentrations found in the ocean.

Extracellular vesicle release by the most abundant marine phototroph, and likely many

other marine microbes, provides a crucial bridge between microbes and the biotic and abiotic world. The environmental variables that affect production and stability of the vesicles will be important to decipher. High local concentrations of compounds within vesicles, possibly including toxins that deter grazers as well as viral predators, suggest that much remains to be learned about the function of such biologically derived colloids. Given that some eukaryotes are also known to produce extracellular vesicles, it will be interesting to find out whether eukaryotic phytoplankton produce similar structures. If such vesicles are produced by bloom-forming species, this could have further profound implications for carbon release and carbon cycling in marine systems.

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PHYSICS

Enabling Optical Analog Computing with Metamaterials

Ari Sihvola

Progress in the development of calculating machines has led to modern computers that represent and treat data digitally. In principle, the physical platform on which computation is done is irrelevant: A digital computer can be realized with vacuum tubes, discrete transistors, integrated circuits, pneumatic valves, or optical logic gates. However, digital optical computing is

not the only way in which computing can be done with light. On page 160 of this issue, Silva *et al.* (1) show theoretically that the direct manipulation of light waves can offer extraordinary possibilities toward analog computing. Instead of representing quantities by discrete bits, the input and output data are expressed as continuous electric fields of light. The necessary mathematical operations are realized through the interaction of the wave with metamaterials, microstructured composites that respond in ways that cannot be realized in isotropic materials (2).

The manipulation of light with structured materials could allow mathematical operations to be performed with compact optics.

Furthermore, the wavelength-scale dimensions of such computing machines make them extremely compact.

Digital computing is exact in the sense that algebraic operations are deterministic; an abacus is a simple example of a computer that keeps track of discrete numbers. On the other hand, the operation of a slide rule comes with finite precision and accuracy because this analog computing process is inherently connected with the mechanical movement of matter. Hence, advances in material technology were essential to progress in the

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