The ocean's veil

Microbial food webs

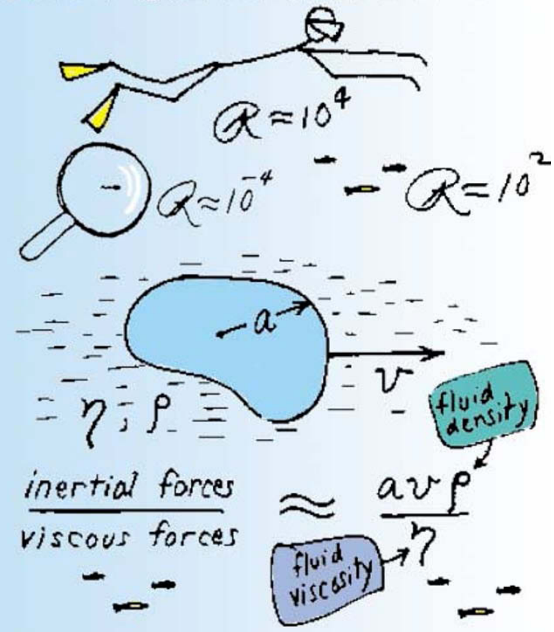
These tightly regulated oceanic communities consume small particles but let larger ones sink into the depths below.

Victor Smetacek

Imagine being whisked in a flight of fantasy into the microbial world of the oceans' sunlit layer, and being able to see the smallest organisms on the planet running its largest ecosystem. At your new, micrometre-sized scale, water is so thick and viscous that attempting to swim through it would be futile. Yet some peculiar-looking bacteria and other strange organisms would be zooming through the honey-thick medium with effortless ease. It is too early to write a guidebook on life in the microbial environment, and such a text would soon be outdated, because surprises continue to pour in.

Just 25 years ago, the physics of this environment were revealed for the first time by E. M. Purcell in a delightful lecture to a gathering of physicists (he called bacteria "animals"). The habitat he sketched, with his collage of equations, is a wonderland so radically different to our sensory experience that intuition seems only to be right for the wrong reasons.

Viscous forces rule micrometre-sized organisms just as the force of gravity rules those at the large end of the size spectrum. We, as large animals, tend to equate 'viscous' with 'slow', but in actuality the microbial realm is full of activity. The medium is continuously and thoroughly mixed by molecular diffusion, supplying dissolved nutrients to cell surfaces with such relentless efficiency that it matters little whether a cell stays put or moves around at a few body lengths per second. To experience a change of surroundings, a bacterial cell has to race against its medium with the speed of a greyhound — about 20 body lengths per second. This is the speed attained by our gut bacteria (*Escherichia coli*), yet some planktonic bacteria can move five times faster.



Wonderland: equations sketched by Purcell in his lecture on the physics of the microbial world.

These motile bacteria are propelled by rigidly rotating flagella, which are driven by reversible rotary motors. Purcell calculated that rotating this propeller costs surprisingly little energy and, in a viscous world, bumping into an object causes no damage. So bacteria can afford to zip around at their maximum speed, restlessly searching for nutritive hotspots such as leaking large organisms or flocks of detritus. But many bacteria are non-motile and thrive on nutrients supplied by molecular diffusion.

Planktonic microbial communities — comprising bacteria, viruses and the smallest protists (eukaryotes less than $5\ \mu\text{m}$ in size) — which inhabit the surface layers of all water bodies, run their food webs in a strikingly similar manner. The bulk of the 'plants' (cyanobacteria and algae) and 'animals' (protozoa) are represented by relatively few genera from several ancient, widely separated lineages, suggesting that extant species within the food web have coevolved. Although the species composition varies, the structure of the food web in terms of the relative proportions and the maximum abundances of the 'plants', 'animals' and bacteria is remarkably conserved, contrasting strikingly with the huge variation in biomass and abundance of planktonic organisms larger than about $10\ \mu\text{m}$.

When resources are plentiful, microbial growth rates increase significantly, but cell numbers do not exceed a threshold value. The remarkably stable bacterial numbers — ranging around a million cells per millilitre — are explained by the heavy predation pressure of a few genera of flagellated protozoa that hunt, capture and ingest bacterial cells individually. If a bacterial population manages to grow through this predator gauntlet, it is decimated by viruses. So the numbers of bacteria, and apparently also of other microbes, are kept within boundaries by the double lock of predators and pathogens. As in an overgrazed pasture, potential resources are underexploited.

Where predation pressure is heavy, avoidance and defence mechanisms will be selected for — planktonic bacteria hide by forming spores, grow large by forming filaments, produce tough cell walls, secrete toxins and can also flee at high speed. Successful escape reactions can be triggered at encounter, during handling and even after ingestion. So not only do motile bacteria race to find hotspots, but they are also difficult to catch. As their wake is obliterated almost instantaneously by diffusion, they cannot be tracked by predators. But much larger particles (the nutritive hotspots) can be tracked, so bacterial populations growing on or inside them are vulnerable to attack. Many bacteria will be eaten; others will escape from the hotspot. Thus, the rate at which bacteria break down large particles will be slowed by the presence of predators.

Apparently, the stability of bacterial numbers is maintained by a set of interacting biophysical 'rules' that balance the growth and loss rates of cells within the microbial size range. As one ascends the food chain, these rules weaken with increasing organism size — the ciliate predators of microbial organisms can increase their populations by orders of magnitude. So microbial production is channelled up a food chain that is tethered at its base. The excess nutrients are taken up by large algae that end up in large zooplankton. In all cases, the end result is large particles that sink from the surface layer faster than they can be broken down by bacteria. This rain of large particles impoverishes the productive layer and provides food for the deeper-living organisms below, with immense consequences for aquatic ecology, ocean biogeochemistry and global climate.

The microbial network that stretches like a veil across the watery face of the planet functions as a self-restrained, semi-permeable membrane that retains small particles but lets bigger ones pass through. A closer look at the rules of the game in the fast lane of the microbial realm would require an *in situ* computerized telemicroscope. Could such an instrument do for microbial ecology what Galileo's telescope did for astronomy? After all, there are orders of magnitude more bacteria in the ocean than there are stars in the Universe. ■

Victor Smetacek is at the Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany.

FURTHER READING

Copley, J. *Nature* **415,** 572–574 (2002).
Purcell, E. M. *Am. J. Phys.* **45,** 3–11 (1977).
Fenchel, T. *Science* **296,** 1068–1071 (2002).
Finlay, B. J. *Science* **296,** 1061–1063 (2002).
Matz, C. *Mechanisms of Grazing Resistance in Aquatic Bacteria.* Thesis, Univ. Kiel (2002).