A watery arms race

Victor Smetacek

Imagine yourself in a light forest looking upwards, seeing in your mind's eye only the chlorophyll-bearing cells of the canopy floating in mid-air, free from the attachment of leaves, twigs, branches and trunks. Now forget the forest and the trees, and see only blurred clouds of tiny green cells obscuring the blue sky beyond. You are looking at a phytoplankton bloom of a density typical of lakes and coastal oceans. Forests and algal blooms fix about the same amount of carbon — a few grams per square metre per day — because both are based on essentially the same photosynthetic machinery, fuelled by chlorophyll *a* in chloroplasts, the descendants of free-living cyanobacteria that have since evolved into plant organelles by endosymbiosis.

Chloroplasts provide their host cells with food in return for resources and protection. The land was colonized by one type of chloroplast/host cell, and the evolution of its various life-supporting systems is, from a human perspective, a straightforward success story: from algal slime to tropical rainforest. Indeed, the sole function of land plants, as considered in the thought experiment above, is to provide the chloroplasts with water and nutrients and give them access to light.

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Safe: diversity in plankton has its roots in defence.

Competition for resources and resource space has shaped the evolution of form and function in terrestrial vegetation. Can one apply the same evolutionary criteria to the other main plant life-form on our planet — the free-floating plankton of the pelagic realm? The phytoplankton bloom is suspended in a soup of resources, circulated by the wind within the sunlit surface layer. Its chloroplasts are provisioned by this viscous medium and do not require life-supporting hosts. Moreover, a striking feature of pelagic systems is the recurrent pattern of annual species succession. This is different from succession in land plants because the various stages, dominated by characteristic phytoplankton species, last for only a few weeks. There may be competition between species at the same stage for light and nutrients, but hardly at all between species of different stages. Apparently, space-holding plankton has not evolved.

So what other forces shape plankton cells, and are they the same as those that drive succession? Photosynthesis in plankton is spread across about ten different divisions, as separate from one another as land plants are from animals. Many of the lineages have species that function as algae ('plants') or as ingestors of particles ('animals'); many species do both. Generally, species with chloroplasts look no different to their relatives without them — cell shape does not reflect the mode of nutrition. Properties of the host cell, including shape, must do more than improve the photosynthetic efficiency of chloroplasts. Indeed, the enormous diversity of lineages and shapes present in unicellular plankton has defied explanation.

Although adoption by a host must have imposed many changes on the chloroplast, one main function of host cells is to protect chloroplasts against attack. The many mechanical and chemical defence systems evolved by land plants have elicited an equally heterogeneous arsenal of attack systems among their enemies, ranging from viruses to fungi, insects to elephants. Defence systems need to be deployed at the level of the leaf and are therefore not reflected in gross morphology, but they can be expensive. Hence there are fast-growing and slow-growing plants, all fuelled by chloroplasts, but differing in the degree of investment in defence.

The range of defence systems in plankton is only now coming to light. The size range of phytoplankton spans three orders of magnitude, but that of its predators spans five orders, from micron-scale flagellates to shrimp-sized krill. Pathogens (viruses and bacteria) pose a further challenge. Most predators and pathogens feed or infect selectively. Smaller predators hunt individual cells, whereas larger ones use feeding currents, mucous nets or elaborate filters to collect them *en masse*. Captured cells are pierced, ingested, engulfed or crushed, but have evolved specific defence measures. They can escape by swimming or by mechanical protection; mineral or tough organic cell walls ward off piercers or crushers. In adapting to deterring predators, cells have increased in size, formed large chains and colonies, or grown spines. Noxious chemicals also provide defence.

Plankton

"Planktonic evolution is ruled by protection and not competition. The many shapes of plankton reflect defence responses to specific attack systems."

Obviously, none of these defence mechanisms conferred by host cells provides universal protection to chloroplasts. Most phytoplankton cells are eventually eaten or succumb to pathogens. Rapid fluctuation in population size favours survival fitness, more cycles and hence more adaptation to attack. If the carbon fixed by planktonic chloroplasts is invested mainly in this biological 'arms race', then planktonic evolution is ruled by protection and not by competition. The many different shapes and life cycles reflect responses to specific attack systems.

Suppose that competition for light rather than protection were the driving force in shaping pelagic ecosystems. Faced with a single, optimal solution, algae could well have evolved more efficient photosynthetic machinery. Improved energy use would favour production of hydrocarbons as both a buoyancy aid and a reserve substance. The ocean surface would then be covered with oily scum that would, as well as changing the planetary heat budget, severely reduce evaporation and hence rainfall on the continents, where life as we know it could not then have evolved. Luckily for us, this did not happen, and we have our blue, white and brown planet with its smudges of green, instead of dark green (or even black) oceans and bare, brown continents. ■

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FURTHER READING

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