Natural proportions

Redfield ratios: the uniformity of elemental ratios in the oceans and the life they contain underpins our understanding of marine biogeochemistry.

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An interesting empirical observation in biology is the relationship between the elemental composition of organisms and ecosystems. All organisms are composed primarily of a mixture of six major elements: hydrogen, carbon, nitrogen, oxygen, phosphorus and sulphur. But the proportion of these basic ingredients varies between organisms — and such variations can lead to interesting properties within ecosystems.

For example, in the oceans most of the biomass comprises small drifting organisms (plankton) that are rich in nitrogen. These organisms are essentially functionally similar ensembles of metabolites, often encased in a shell formed from the most readily available ingredients. Much plankton is consumed by other plankton with similar chemical compositions. The result is that on average, the nitrogen:phosphorus (N:P) ratios of plankton in the oceans are remarkably similar throughout the world, averaging approximately 16:1 by atoms. When these organisms or their body parts sink into the ocean interior, their energy-rich bodies are consumed by bacteria which, in aerobic conditions, oxidize the organic matter to form dissolved inorganic nutrients, especially CO_2, NO_3^- and PO_4^{3-}.

In 1934, Alfred Redfield wrote a now classic paper in which he proposed that the N:P ratio of plankton (16:1) causes the ocean to have a remarkably similar ratio of dissolved NO_3^- and PO_4^{3-}. This hypothesis suggested that, devoid of life, the chemical composition of the oceans would be markedly different. The concept of Redfield ratios has been fundamental to understanding of the biogeochemistry of the oceans ever since.

The basic problem with Redfield ratios is that they are empirical. The ratios were originally derived from measurements of the elemental composition of plankton, and the NO_3^- and PO_4^{3-} content of seawater from a few stations in the Atlantic, but were subsequently supported by hundreds of independent measurements. Yet there is no known reason why the average N:P ratio of plankton should be 16:1. Why not 6:1? Or 60:1? If one looks at the elemental composition of individual species of phytoplankton grown under nitrogen or phosphorus limitation, the N:P ratio can vary from around 6:1 to 60:1. Redfield understood this problem, but did not try explain it, except to note that the N:P ratio of inorganic nutrients in the ocean interior was an average, and that small-scale variability around the mean was to be expected. Despite many reports that the elemental composition of organisms in a region of the ocean does not conform to Redfield ratios, or that the elemental composition of marine phytoplankton grown in cultures is not 16:1, Redfield's fundamental concept remains valid. It cannot be rationalized by reductionist arguments, nor refuted by anecdotal observations. The fact that the NO_3^-:PO_4^{3-} ratio in the interior of all major ocean basins is remarkably similar to the N:P ratio of plankton is due to the residence times of these two elements in the ocean (roughly 10^4 years), relative to the ocean's circulation time (roughly 10^3 years). As the residence times exceed the mixing times by an order of magnitude, it should not be surprising that the NO_3^-:PO_4^{3-} ratios in the ocean interior are remarkably constant. The specific elemental composition that is the Redfield ratio is truly an 'emergent' property that reflects the interaction of multiple processes, including the acquisition of the elements by plankton, the formation of new biomass and the remineralization of the biomass by bacteria in the ocean interior, as well as losses of nutrients from the ocean because of burial in the sediments (for example, phosphorus in apatite), or outgassing to the atmosphere (for example, production and loss of N_2, due to denitrification).

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Just drifting along: a phytoplankton bloom.

Can the elemental ratios in the ocean change? In principle the answer is 'yes' — but only on timescales comparable to residence times of the nutrients. But why should they change? They could change as the diversity of organisms in the ocean changes in response to climate or other evolutionary selection mechanisms, or if the bacteria responsible for the remineralization of the organic matter in the oceans shift their preferences in elemental selection. Lakes undergo similar processes as oceans, but their elemental compositions are much more variable. The larger the lake, the less its elemental composition is influenced by the surrounding terrestrial ecosystem, and the more likely it is to track that of the plankton within it.

Although Redfield's concept is 70 years old, it is only just beginning to impact terrestrial ecology. Recent studies on the global patterns of nitrogen and phosphorus in terrestrial plant leaves suggest that these reflect the availability of the two nutrients in soils. But are the nutrients in the soils determined by the N:P ratios in the leaves, or vice versa? The issue of causality — which basically is no longer debated for the oceans — has prompted a search for an analogue for Redfield ratios in terrestrial ecosystems. The search may be a long one, but it will almost certainly result in a better understanding of the global patterns of processes that determine the distribution of the major elements within those ecosystems.

Redfield's concept was an elegant empirical observation that has no simple reductionist explanation, let alone proof. The emergent elemental ratios in the oceans result from scaling the average biochemical composition of organisms in large environments with slow exchanges. As with Newtonian physics, it should not be surprising that the concept fails at very small scales. Nonetheless, it is a powerful organizing principle that illustrates how biological processes at ecosystem levels can alter the distribution of elements on Earth and should be used to help guide us in our understanding of natural biogeochemical patterns and how humans influence them. ■

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FURTHER READING

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