## Atmospheric oxygen and biological evolution in the aftermath of the GOE

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Geobiological build-up of atmospheric oxygen was essential for the establishment of the modern Earth-system, including the evolution of aerobic metabolism and crown-group eukaryotes. Geochemical proxies record the first substantial appearance of free oxygen during the early Proterozoic Great Oxygenation Event (GOE), but its subsequent history is difficult to track. The conspicuously delayed appearance of macroscopic organisms in the fossil record has been used to argue that oxygen levels remained substantially below levels required to sustain animal metabolism for the remainder of the Proterozoic. In this view, it is geologically constructed 'permissive environments' that provided the first-order control on the Ediacaran/Cambrian radiations of macroscopic life.

The 'oxygen limitation hypothesis' has been supported by evidence of oceanic stratification and deep-water anoxia/euxinia through much of the Proterozoic; it is worth noting, however, that such conditions are also found in Palaeozoic and Mesozoic oceanic anoxic events (OAEs), which are demonstrably unrelated to atmospheric oxygen levels. I will argue here that Phanerozoic OAEs offer a compelling analogue for the Meso-Neoproterozoic oceans, that the first-order control on oceanic structure is biological, and that the evolution of metazoans was the cause rather than the consequence of oceanic ventilation in the early Palaeozoic.

Animals are powerful geobiological agents, and in the modern oceans represent both a majority of standing biomass and a key component of the biological pump (via the production of faecal pellets and marine snow). Even more importantly, the evolution of relatively large and/or biomineralized phytoplankton – those prone to aggregation and vertical transport – is most readily explained by the top-down selective pressure of mesozooplankton, an evolutionary innovation that first appeared in the early Cambrian. Semi-natural experiments in modern lakes reveal powerful positive feedback effects by suspension-feeding metazoans on ecosystem structure, typically resulting in hysteresis between two alternative stable states: on the one hand a stratified turbid water-column dominated cyanobacterial picoplankton, and on the other well mixed clear water conditions dominated by eukaryotic nano- and microplankton. These same alternative states describe the overall expression of the Proterozoic vs Phanerozoic oceans (except for the transitory return to stratified cyanobacterial oceans during OAEs). Thus, the geochemical features being marshaled in support of persistently low levels of atmospheric oxygen through the Proterozoic appear to be the default condition of aquatic ecosystems in the absence of top-down control by suspension-feeding animals. By extension, the pronounced biogeochemical perturbations of the late Neoproterozoic and early Palaeozoic are more likely to represent a metazoan-induced ventilation of the deep sea than a sudden rise in atmospheric oxygen. The patterns of atmospheric oxygenation following the GOE have yet to be resolved.

## References

Butterfield, N. J., 2009, Oxygen, animals and oceanic ventilation – an alternative view. Geobiology 7:1–7.