

Was the Devonian radiation of large predatory fish a consequence of rising atmospheric oxygen concentration?

On the basis of a Mo-based geochemical proxy calibrated to the fossil record of fish, Dahl et al. argued that oxygen levels in the early Paleozoic were 15–50% of present atmospheric levels (PAL) and probably no more than a few percent PAL for the previous 2 billion years (1). It is an interesting result, but the study raised a number of issues.

First, it is difficult to reconcile 15–50% PAL oxygen with the presence of Silurian charcoal, when $\approx 62\%$ PAL oxygen is necessary to sustain wildfire (2).

Second, the correlation between the Devonian radiation of large predatory fish and modeled oxygen rise is not corroborated by contemporaneous molluscan or arthropod records, which exhibit maximum body sizes before the Devonian; or by the collective decreases in maximum body size of chordates, molluscs, and arthropods in the later Paleozoic (figure 2 in ref. 3). Dahl et al. argued that fish are more sensitive to reduced oxygen levels than—for example—bivalves, polychaetes, and crustaceans, but this is to confuse ecologically imposed safety factors with the physiological limits of the fish bodyplan itself. Relatively small benthic organisms are inherently more vulnerable to localized anoxia than pelagic fish and necessarily take on the corresponding adaptations; bottom-dwelling fish are as hypoxia tolerant as most benthic invertebrates (4).

Third, the mass-specific metabolic rate of teleost fish decreases with increasing body size—by an allometric factor of 0.79–0.88 (4). In other words, larger-bodied fish require exponentially less oxygen per unit body mass than smaller ones. It is true, of course, that large fish may require more absolute amounts of oxygen, but this is not an issue for motile organisms with actively pumped circulatory and respiratory systems. Indeed, it is smaller fish with higher mass-specific metabolic rates and more limited motility that are most likely to be challenged by oxygen availability.

Last, the hypoxia tolerance data presented in Dahl et al.'s figure S7 [presumably drawn from the compilations of Gray et al. (2002) and Vaquer-Sunyer and Duarte (2008); see refs. 44 and 43, respectively, of ref. 1] do not support the claim that larger fish require higher oxygen concentrations than smaller ones. Apart from the conspicuous overrepresentation of benthic, estuarine, and/or air-breathing forms in all but the largest size ranks, it is important to appreciate that all of these data come from tank experiments using relatively small-bodied individuals. Because metabolic rates typically decrease exponentially with body size (4), the hypoxia tolerance of 1- to 2-m-long adults will be substantially lower than that depicted in figure S7.

Oxygen-limitation hypotheses offer attractive Earth systems-type explanations for macroevolutionary phenomena but tend to assume that atmospheric oxygen is the only significant control on marine redox chemistry. If, however, there is an important *biological* contribution to ocean structure, then the fundamentally nonuniformitarian nature of Paleozoic and Proterozoic marine ecology must be taken into account. Fish are unquestionably powerful geobiological agents in the modern oceans, both directly and through their coevolutionary impact on zooplankton and phytoplankton dynamics (5). As such, their Devonian radiation is just as likely to have been the cause as the consequence of mid-Paleozoic shifts in oceanic redox.

N. J. Butterfield¹

Department of Earth Sciences, University of Cambridge, Cambridge CB2 3EQ, United Kingdom

1. Dahl TW, et al. (2010) Devonian rise in atmospheric oxygen correlated to the radiations of terrestrial plants and large predatory fish. *Proc Natl Acad Sci USA* 107: 17911–17915.
2. Scott AC, Glasspool IJ (2006) The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. *Proc Natl Acad Sci USA* 103: 10861–10865.
3. Payne JL, et al. (2009) Two-phase increase in the maximum size of life over 3.5 billion years reflects biological innovation and environmental opportunity. *Proc Natl Acad Sci USA* 106:24–27.
4. Nilsson GE, Östlund-Nilsson S (2008) Does size matter for hypoxia tolerance in fish? *Biol Rev Camb Philos Soc* 83:173–189.
5. Butterfield NJ (2009) Oxygen, animals and oceanic ventilation: an alternative view. *Geobiology* 7:1–7.

Author contributions: N.J.B. wrote the paper.

The author declares no conflict of interest.

¹E-mail: njb1005@cam.ac.uk.