



## Mass loss of stable hypoxic habitats in the end-Ordovician

Emma Hammarlund (1,2) and Christian J. Bjerrum (2,3)

(1) Translational Cancer Research, Lund University, Scheelevägen 2, 223 81 Lund, Sweden, (2) Nordic Center for Earth Evolution, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark, (3) Department of Geosciences and Natural Resource Management, Section of Geology, University of Copenhagen, DK-1350 Copenhagen, Denmark

Animal diversity was dramatically altered during two extinction pulses in the end-Ordovician, where causes for particularly the first pulse appear contradictory. A range of geological models now support scenarios of both increasing marine anoxia<sup>e.g.1,2</sup> and cooling-driven oxygenation<sup>e.g.3-5</sup>. The scenario of cooling is problematic since, for example, reduced temperatures in a greenhouse world<sup>6</sup> would rather appear a relief of stress than a kill mechanism. The scenario of increasing anoxia is also problematic since, for example, the mid-Ordovician and early Silurian oceans were also prone to develop anoxic water column conditions<sup>2,7</sup> in the low-oxygen Paleozoic world<sup>11</sup>. However, the two scenarios make some sense together when considering that a) the synchronous expansion of the oxic and anoxic niches would reduce the hypoxic niche, and b) that stable hypoxic niches could be argued important for invertebrate animals to manage their tissue renewal and, thus, regeneration<sup>8</sup>. If invertebrate animals indeed require hypoxia – internally or externally – for tissue renewal, the loss of hypoxic habitats could be a significant biotic challenge during both sea-level rise and fall. We evaluate the loss of hypoxic shelf area (0.5-1.5 mg/l) through a combination of models at sea-level fall of 100 m, as possibly associated with the first extinction pulse<sup>9,10</sup>. A mass loss of hypoxic habitats would add to the ongoing gradual modernization of Earth's atmospheric oxygen concentrations<sup>11</sup>. Collectively, these geobiological observations requires us to consider whether the trajectory of animal evolution was defined also by the loss of hypoxic habitats and of the hypoxic Paleozoic world.

1 Hammarlund, E. U. et al. A sulfidic driver for the end-Ordovician mass extinction. *Earth Planet. Sci. Lett.* 331-332C, 128-139, doi:10.1016/j.epsl.2012.02.024 (2012).

2 Zhou, L. et al. Changes in marine productivity and redox conditions during the Late Ordovician Hirnantian glaciation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 420, 223-234 (2015).

3 Lu, X. et al. Marine redox conditions during deposition of Late Ordovician and Early Silurian organic-rich mudrocks in the Siljan ring district, central Sweden. *Chem. Geol.* 457, 75-94 (2017).

4 Pohl, A., Donnadieu, Y., Le Hir, G. & Ferreira, D. The climatic significance of Late Ordovician-early Silurian black shales. *Paleoceanography* 32, 397-423, doi:10.1002/2016PA003064 (2017).

5 Melchin, M. J., Mitchell, C. E., Holmden, C. & Štorch, P. Environmental changes in the Late Ordovician-early Silurian: Review and new insights from black shales and nitrogen isotopes. *GSA Bulletin* 125, 1635-1670, doi:10.1130/b30812.1 (2013).

6 Finnegan, S. et al. The Magnitude and Duration of Late Ordovician-Early Silurian Glaciation. *Science* 331, 903-906, doi:10.1126/science.1200803 (2011).

7 Thompson, C. K. & Kah, L. C. Sulfur isotope evidence for widespread euxinia and a fluctuating oxycline in Early to Middle Ordovician greenhouse oceans. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 313, 189-214, doi:10.1016/j.palaeo.2011.10.020 (2012).

8 Hammarlund, E., Stedingk, K. & Pålman, S. Refined control of cell stemness allowed animal evolution in the oxic realm. *Nature Ecology & Evolution* (2018).

9 Brenchley, P. J., Marshall, J. D., Harper, D. A. T., Buttler, C. J. & Underwood, C. J. A late Ordovician (Hirnantian) karstic surface in a submarine channel, recording glacio-eustatic sea-level changes: Meifod, central Wales. *Geol. J.* 41, 1-22, doi:10.1002/gj.1029 (2006).

10 Ghienne, J.-F. et al. A Cenozoic-style scenario for the end-Ordovician glaciation. *Nature Communications* 5, 4485, doi:10.1038/ncomms5485 (2014).

11 Lenton, T. M. et al. Earliest land plants created modern levels of atmospheric oxygen. *Proc. Natl. Acad. Sci.* 113, 9704-9709, doi:10.1073/pnas.1604787113 (2016).