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Interactive comment on “Mass extinctions past and present: a unifying hypothesis” by S. A. Wooldridge

S. A. Wooldridge

Received and published: 19 August 2008

pH ESTIMATES ACROSS THE PHANEROZOIC:

As qualified in the modelling efforts of Caldeira (2007a), many uncertainties exist in the ambitious effort to reconstruct the carbonate chemistry conditions across the Phanerozoic. It is however well understood that the carbonate chemistry of seawater is largely controlled by three constraints: atmospheric $p\text{CO}_2$, ocean carbonate-ion concentration (CO_3^{2-}) and oceanic calcium (Ca^{2+}) concentration. For the modern mode of deep-sea and shallow-water carbon cycling - and for time-scales much longer than the ca. 5-10 kyr adjustment time of the marine carbonate cycle - the ocean as a first approximation is roughly saturated with respect to calcite i.e., precipitation and dissolution of biogenic CaCO_3 maintains the oceans close to thermodynamic equilibrium with calcite. Therefore under such conditions, the assumption of a constant saturation state appears jus-

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tifiable, and indeed this stability has been quantitatively confirmed by the independent modelling efforts of Ridgwell (2005). However, a persuasive argument is forwarded by Ridgwell (2005) that the responsive deep-sea carbonate sink which characterises the modern mode of calcium carbonate recycling only become active in the Mid Mesozoic with the ecological success of calcifying planktic taxa. Prior to this transition, it appears possible that the ocean could attain states of extreme saturation during the Permian and Triassic as well as during the late Precambrian. However, of particular interest here, is the additional finding of Ridgwell (2005) that in contrast to the ocean saturation, the evolution of pH exhibits much less of a change in behaviour given the presence or absence of the deep-sea sedimentary sink. Thus, overall, ocean pH is responding primarily to changes in atmospheric $p\text{CO}_2$ and oceanic $[\text{Ca}^{2+}]$. Uncertainty in the estimates of Phanerozoic pH is therefore currently dominated by uncertainty in atmospheric CO_2 (Ridgwell, 2005).

GRADUAL VS. ABRUPT EXTINCTION PATTERNS:

Given the reviewers (W. Kiessling) considerable expertise in the area of deep time patterns, it is not for me to argue on the quality of the fossil evidence to distinguish between gradual or abrupt extinction patterns. The point to be highlighted is that the urease hypothesis can potentially accommodate both explanations. Abrupt extinction patterns associated with rapid changes in pH would appear to be the most parsimonious outworking of the urease hypothesis. However, a gradual or stepwise extinction pattern could also be envisaged to result from the differential ability of organisms to biologically 'buffer' changes in environmental pH (even via simple migration when possible).

EXTERNAL VS. INTERNAL (CELLULAR) pH:

Cells regulate their internal pH (pH_i) by maintaining a difference compared with the extracellular medium (Roos and Boron, 1981). Consequently, when extracellular pH varies, pH_i also varies, with the difference depending on the intracellular buffering capacity. For most animals, invertebrates and vertebrates, pH_i is set to values 0.5-0.8

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pH units below the extracellular medium (Portner et al. 2004). Of particular relevance for the urease hypothesis, is the fact that this difference corresponds with the dual pH optima ($8.2 - 7.6 = 0.6$) that has been suggested for the urease pH activity profile (Wooldridge 2008; Fig. 2).

Brookbank and Whiteley (1954) suggest that urease may function to mobilise nitrogen from storage compounds in the eggs of marine invertebrates (e.g. sea urchins). Given the suggested pH optima in urease activity @ 7.6, it appears more than coincidental that Payan et al. (1983) found that after fertilisation the intracellular pH in sea urchin eggs is actively maintained at pH 7.64.

Upon consideration of the suggested importance of urease in the initial stages of biomineralisation, whether one believes the initial stages of biomineralisation to take place intracellularly (pH 7.6) or in external microenvironments created between the tissue and skeleton (pH 8.2), then urease enzyme activity is suggested to be optimal when the external environment pH ~ 8.2 . Of course, if the process is indeed external, then biomineralisation may still be favourable even with an external environment pH ~ 7.6 . This may have relevance for infaunal marine invertebrate species they bury themselves in the seafloor sediments (see next).

BENTHIC FORAMINIFERA @ THE KT BOUNDARY:

As highlighted by the reviewer's comments, my suggestion that Culver (2003) shows the extinction pattern of benthic foraminifera to be depth-dependent is indeed incorrect. Whilst a depth-dependent extinction pattern is evident at the KT boundary for many calcifying marine organisms (Caldeira 2007b), benthic foraminifera not only do not demonstrate this depth variation, but they also display surprising low overall extinction rates (Culver 2003). This stands in stark contrast to planktic foraminifera and calcareous nanoplankton that underwent severe extinction (Culver 2003).

Upon further consideration however, the limited extinction of benthic foraminifera at the KT boundary does actually fit with the central tenets of the urease hypothesis. The

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key is to consider that metabolic CO₂ production (respiration) in marine sediments causes the near surface pore water pH to dramatically fall below that of the oceanic seawater value. Indeed, it is commonly observed within reef sediments that the pore water pH (0-5cm) is @ 7.6 (Morse and Mackenzie, 1990; Burdige et al. 2008). Again, this displays an uncanny coherence to the proposed urease activity maximum @ pH 7.6 (Wooldridge 2008; Fig. 2). There is good reason to suggest that this benthic pH may have remained fairly constant across the KT boundary; but potentially, more so at depositional (clastic) locales where organic material continued to maintain sediment respiration rates. On this note, it appears relevant that Kiessling et al. (2007) was able to demonstrate for the TJ boundary that benthic organisms which preferred carbonate environments were more strongly hit than benthic organisms which preferred siliciclastic substrates.

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5, S1448–S1452, 2008

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