Paleophysiology as Paleobiology in the Age of Earth Systems Science: An Example from the Permo-Triassic Boundary

1. Introduction

a. For obvious reasons, paleontologists have long concentrated on morphology and diversity, the two features of ancient life most clearly recorded in rocks.

b. Over the past two decades, however, Earth Systems science -- and especially Earth systems history -- has shown that the comings and goings of species through time reflect changes in the physical environment as much as they do evolutionary novelty. Particularly in the case of mass extinction, catastrophic environmental change drives major changes in the composition of marine and terrestrial biotas.

c. Physiology provides the proximal interface between organisms and their environment. Thus, to the extent that physiological information can be gleaned from fossils, this might illuminate the causes and consequences of major extinctions. In this paper, we explore the relationships among physiology, evolutionary history, and environmental catastrophe through the example of end-Permian mass extinction.

2. Paleophysiology: what can we know?

a. Not all aspects of an extinct species' biology can be captured in the fossil record (Clark). It is unlikely, for example, that we can know with quantitative accuracy the basal metabolic rate of Ordovician trilobites or the temperature optimum for a Devonian brachiopod.

b. That said, many basic features of physiology can be inferred from fossils -- including some features that are key to understanding evolutionary fate on an environmentally dynamic planet. In part this is because some basic features of physiology relate to features of anatomy and morphology characteristic of higher taxa and, thus, reliably inferred from fossils. Gas exchange in marine invertebrates, for example, is mediated by respiratory elaborations such as gills, features closely related to phylogeny and thus inferable for skeletal fossils whose systematic relationships are known.

c. Other features of physiology can be known in a comparative sense, even if absolute measurements are impossible. For example, we might not know the precise basal metabolic rate of a clam and a brachiopod in Jurassic rocks, but we can have confidence that the metabolic rate of the clam exceeded that of the brachiopod. And we can reason that the clam's metabolic rate scaled with temperature roughly as codified by the Q10 law (double rate for every 10 degree C increase in T).

d. Paleobotanists have been differentially well attuned to paleophysiology, largely because plants are strongly biophysical entities in which important aspects of physiological function relate directly to anatomy and morphology. Thus, leaf form finds use as a proxy for climate (recall that the famous Koeppen diagrams of climate are actually vegetation maps). From preserved anatomy, paleobotanists can estimate water conductance quantitatively; from stomatal distribution they can make at least broad estimates of growth rate in early vascular plants.

e. Marine microplankton have also been the subjects of paleophysiological scrutiny, largely because physiology can influence the chemical abundances in skeletons that provide paleoeocenaographic proxies. To date, much effort has gone into avoiding “vital effects” but it is easy to envision a future in which vital effects, now understood, will provide ever sharper tools for paleoceoanogrphic research.

f. Marine invertebrates are the fossils for which paleophysiology is least developed but most promising. Fossil invertebrates chronicle evolution through more than 5000 million years of Earth history, and the fates of faunas have long been interpreted in the context of changing ocean circulation and chemistry. In particular, mass extinctions have long been recognized as key biological events, yet biology has played second fiddle to geological and geochemical efforts to evaluate these events. What can we learn when fossils bear paleophysiological witness to a great extinction?

3. The end-Permian extinction

a. Generally regarded as the most severe of all mass extinctions.

- -- estimated loss of xx% marine families, xx% genera, and xx% species.
- -- major reorganization of marine ecosystems in aftermath (Bambach et al., 2002).
- -- impact on land as well, although plant and vertebrate records less well preserved.

b. Many hypotheses for extinction -- the important point is that each makes predictions of how diversity would have been effected, and these can be tested against observed patterns of extinction and survival.

3.1. Proposed trigger mechanisms

a. Bolide impact
b. Siberian Trap extrusion
c. Oceanographic mechanisms: methane release, ocean overturn (potentially related to a and b).

3.2 Proposed kill mechanisms:

a. Productivity collapse
b. Asphyxia (anoxia)
c. Hypercapnia

Knoll et al. (1996) claimed that paleophysiological data can constrain kill mechanisms. Nearly a decade later, what is the status of this claim?

4. Physiological Selectivity at the P-Tr boundary

a. Knoll et al. (1996) divided marine fauna into two groups based on predicted vulnerability to hypercapnic stress. This parsing was based a large corpus of experimental data; paleontological interpretation was based on physiological features that can be estimated reliably from preserved fossils.

b. Groups of organisms characterized by low basal metabolic rate, limited circulatory system, little elaboration of respiratory surfaces, and formation of calcium carbonate skeletons under conditions of minimal physiological buffering -- high probability of extinction (81% of genera in Changsingian). Calciate brachiopods, bryozoans, corals, echinoderms, sponges.

c. In contrast, groups of organisms characterized by relatively high basal metabolic rate, more highly elaborated circulatory systems and respiratory surfaces, and formation of calcium carbonate skeletons from physiologically well buffered fluids or without carbonate skeletons -- lower probability of extinction (38% of genera). Mollusks, arthropods, chordates.

d. Knoll et al. also compared six pairings of taxa within clades, and found that in every case the group predicted to be more vulnerable experienced significantly higher extinction rate. Critics noted that the numbers of taxa involved were sometimes low, limiting the statistical power of individual comparisons. Nonetheless, the likelihood that all comparisons would favor the same result by chance is $1/2^6$, or 1/64.

e. Here we separate the four physiological descriptors used to bin Late Permian animals, and evaluate their individual effects.

4.1 Binned Late Permian genera into three groups:

-- Calcium carbonate skeleton, massive with respect to supporting tissue, formed from fluids minimally buffered by physiology: calcareous sponges, ciliate brachiopods, bryozoans, corals, echinoderms, calcareous forams
-- Calcium carbonate skeleton, moderate with respect to supporting tissue; formed from relatively well buffered fluids. Mostly mollusks
-- Skeleton made of material other than calcium carbonate: lingulid brachiopods, fish, agglutinated forams, conodonts

g. results 90% of A die; 9% of C; b is intermediate 38%. To a first approximation, then skeletal physiology was destiny during end-Permain catastrophe.

h. Looking further at group b; groups deemd more vulnerable to hypercapnic stress on the basis of features other than skeletal physiology suffered extinctions at twice the rate of less vulnerable groups.

i. Why might this pattern obtain? Brief explanation of physiological basis for pattern IF CO2 INCREASED.

j. Extinctions on land – CO2 increase not likely to be sufficient to cause direct hypercpanic stess in vascular plants and vertebrates (cite data, both on diffusion in iar and stress experiments), but CO2 increase provides a sword with two edges – land biota vulnerable to rapid climatic change associated with infux of CO2 – Retallack's "post-apocalyptic greenhouse". Briefly review data (Rees, Looy, retallakc on Plants; Benton, Ward, Smith on vertebrates; Labandiera on insects).

4.2. Observed pattern of extinction and survival is thus consistent with hypothesis of hypercapnia. Is it equally consistent with other proposed kill mechanisms?

k. Productivity collapse – fails to predict broad pattern of extinction, as groups with higher metabolic needs survive differentially well. Also fails to predict more specific patterns: sea anemones vs. corals, calcified vs. uncalcified algae; epifuanal vs. infuanal bivalves, etc. Vermeij asserts in book that all extinction begin with productivity collapse. While we cannot demonstrate an absence of short term collapse of primary production, observed patterns of extinction strongly indicate that this was not the principal kill mechanism.

i. Anoxia: Anoxia gains support from two lines of evidence and a stratigraphic pattern that links them locally. Hallam, Wignall, Twitchett show that dysoxia to anoxia developed widely in beneath mixed layer of ocean, beginning in basal Triassic. Anoxia is known to be a powerful kill mechanism for animals. And locally, basal Triassic black shales contain few if any of the taxa found in better aerated beds directly beneath them.

-- Brief thoughts of local anoxia and its effects vs. global anoxia.

-- Like productivity collapse, anoxia has problem explaining why groups with greatest oxygen tend survive differentially well. Here, however, other factors come into play: size decrease, loss of skeleton

-- Oxygen depletion also claimed as killer of animals of land. Drop of PO2 of about 25% would wreak havoc among land animals – but would have little or no effect on marine invertebrates; a drop in PO2 sufficient to affect marine animals (ca. 85-90 % drop) would kill all land animals indiscriminantly). Obviously, more complicated scenarios involving ocean circulation are possible, even probable. These depend of global warming, and hence elevated CO2.

-- Not clear why oxygen decline would hurt vascular plants – expect just the opposite, if anything.

-- Summary

5. Paleophysiology in Early Triassic Oceans

a. Early Triassic characterized by a set of linked paleontological and geological phenomena: low diversity, small size, reduced biomass, reduced bioturbation, expansion of microbial mats, oddball precipitates, crazy C-isotopes, no animal reefs, no coal, evidence of anoxia, etc.

b. These phenomena set in motion by P-Tr event. Thus, understanding the Early Triassic may sharpen constraints on the extinction itself.

c. Review of small size and its possible physiological relationships.

d. Review of low biomass its possible physiological relationships, including Q10.

e. Review skeletal selectivity in early Triassic oceans – cnidarians, algae, sponges. Stratigraphic pattern of reemergence of these, as well as brachiopods, bryozoans, etc.

f. All biological and geological phenomena can plausibly be linked to persistent greenhouse conditions over 4-7 Ma. Greenhouse conditions, in turn, likely require increased PCO2. (Note that anoxia, however real and widespread, becomes a dependent phenomenon here.)

g. Thus, conditions set in place at P-Tr boundary converge with paleophysiological inferences of extinction in implicating catastrophic increase in CO2. This doesn’t eliminate anoxia as a potent kill mechanisms locally, nor does it eliminate the effects of H2S, which would be an indiscriminant killer on shelves flooded by anoxic waters. It simply requires that these phenomena be seen as consequences of higher PCO2.

7. Constraints on trigger mechanism?

a. We believe that the physiological and climatic affects of elevated CO2 provide a good fit to what we know about P-Tr organisms and environments. We do not claim that hypotheses favoring anoxia or productivity collapse have been categorically eliminated as principal kill mechanisms. But advocates of such hypotheses must articulate physiologically compelling arguments that favor them.

b. If CO2 increase is correct, what could be its source?

  i. Knoll et al. favored ocean overturn – maybe not so much favored today.

  ii. Bolide?

  iii. Siberian traps – the affects of conduits through carbonate and roasting of peats.

  iv. In general, provide BRIEF comments on this.

c. If CO2 is the culprit, what could explain its persistence through Early Triassic?

6. Summary and Conclusions