Kump et al. (2005) have suggested that the emission of H$_2$S to the atmosphere from a Late Permian to Early Triassic euxinic (anoxic deep waters) ocean helped to bring about the massive extinction of organisms. Berner (1989; 2005) has suggested that the rate of burial of terrestrially derived organic matter during this period decreased considerably. We demonstrate here how decreased terrestrial organic burial should have led to positive feedback and reinforcement of H$_2$S release, due to both a drop in atmospheric O$_2$ and a rise in atmospheric CO$_2$.

Positive feedback is best illustrated in terms of a systems analysis diagram (Fig. 1). To start, consider the eruption of the Siberian plateau basalts (e.g., Benton and Twitchett, 2003; Grard et al., 2005). These authors suggest that this eruption should have led to an increase in atmospheric CO$_2$ and global warming, including warming of the ocean, via the atmospheric greenhouse effect (Fig. 1, arrows a and b). A coupled ocean-atmosphere general circulation model (Kiehl and Shields, 2005) has shown that high CO$_2$ and ocean warming at this time likely led to decreased circulation and the development of a stratified anoxic ocean (arrow c). Stratification then should have brought about increased oceanic areas of bacterial sulfate reduction, a process that takes place only at depth in the absence of dissolved oxygen (arrow d). Hydrogen sulfide is produced by bacterial sulfate reduction. If the zone of H$_2$S production gets close enough to the ocean surface, the H$_2$S may escape into the atmosphere and kill organisms (Kump et al., 2005). Thus, as sulfate reduction increased, occasional emissions of H$_2$S into the air led to increased die-offs of land plants (arrows e and f).

Protracted lethal H$_2$S episodes should have led to a decrease in the standing crop of land plants, resulting in less production and less burial over time of organic debris derived from plants (arrow g). During the Permian, land plants were a major contributor to global organic matter deposition and burial (Berner, 2005). For every mole of organic matter buried, one mole of CO$_2$ is removed from the atmosphere via the overall reaction:

$$\text{CO}_2 + \text{H}_2\text{O} \rightarrow \text{CH}_2\text{O} + \text{O}_2$$

therefore, decreased organic burial should have led to an increase in atmospheric CO$_2$ (arrow h). (The production of dead debris following short-term sporadic lethal episodes would exert only a long-term effect on CO$_2$.) Because this cycle began with an increase in CO$_2$ and ends with a further increase in CO$_2$, the whole cycle is reinforced and should have led to further poisoning of plants by H$_2$S.

There is another positive feedback cycle shown by the succession of arrows e-f-g-h and e-f-g-i-j-k. More sulfate reduction led to increased H$_2$S emission to the atmosphere, increased die-off of plants, and less terrestrially derived organic burial. Less organic burial should have led to less O$_2$ production (Eq. 1) and a reduction of atmospheric O$_2$ (Berner, 2005) (arrow i). Less atmospheric O$_2$, upon gas exchange between the atmosphere and ocean, would then have led to reduced oceanic O$_2$ and the enhancement of sulfate reduction (arrows j and k). Thus, increased sulfate reduction, by way of the poisoning of plants and lowering of atmospheric O$_2$, led to a further increase in sulfate reduction.

In summary, the two cycles (b-c-d-e-f-g-h and e-f-g-i-j-k) both lead to positive feedback and reinforcement. An odd number of bullseyes leads to negative feedback and stabilization. Cycles b-c-d-e-f-g-h and e-f-g-i-j-k both lead to positive reinforcement.

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We welcome the comment by Berner and Ward on our 2005 paper, and appreciate the double meaning of “positive reinforcement” in its title, reflecting the absence of criticism of our work. The feedbacks they describe are likely components of the end-Permian biosphere upheaval, and the positive sign of the feedback loops are likely correct. However, the strength and response time of individual couplings among system components in their diagram are uncertain, but these are amenable to evaluation through numerical modeling. Perhaps the long biotic recovery time and persistence of extreme oceanic conditions through the early Triassic (e.g., Woods et al., 1999; Payne et al., 2004) was at least in part a consequence of the stiffing effects of these self-enforcing feedback loops.

One subtle issue is the cause of oceanic anoxia. Berner and Ward link ocean warming and anoxia through the vigor of ocean circulation, but we, among others, have shown that the more important factor is warming of deep-water source regions, because of the inverse solubility of $O_2$ in seawater as a function of temperature (Hotinski et al., 2001). Reductions in meridional overturning rate, in and of themselves, have less effect on deep-water oxygen concentrations because the reduction in $O_2$ supply is matched by a reduction in $O_2$ demand: reduced upwelling limits the export of organic material from the surface ocean and thus the rate of consumption in the deep sea (Broecker and Peng, 1982). Moreover, stagnation of circulation is not synonymous with ocean stratification; the modern ocean is vigorously circulating but strongly stratified in nutrient concentrations and modestly stratified in $O_2$ concentration. The biological pump is a worthy competitor to the thermohaline circulation of the ocean.

A number of important issues remain to be resolved before the hypothesis of $H_2S$ as the proximal kill mechanism for the end-Permian mass extinction will be widely accepted, including 1) whether phosphate concentrations can build up to the necessarily very high concentrations needed to sustain such deep anoxia (the ocean would have to be highly supersaturated with respect to various apatite phases; however, Framvaren Fjord and the Black Sea currently demonstrate high levels of supersaturation); 2) whether during the transition from oxic to anoxic conditions, denitrification would rob the ocean of all nutrient nitrogen (however, recent analysis indicates that nitrogen fixation may well be able to keep pace with denitrification, given a much lower Fe requirement than previously thought; Arrigo, 2005); and 3) whether $H_2S$ has a selective lethality (relatively little is known about $H_2S$ toxicity, especially among important groups such as insects, which suffered their only mass extinction in geologic history during the Late Permian; Erwin, 2006). Moreover, fundamental uncertainty exists concerning the nature of the pre-Mesozoic biological pump: in the absence of planktonic calcifiers that produce the bulk of the ballast for settling biogenic particles in the ocean today, would there be an effective transfer of organic matter to the deep sea that could keep pace with increased upwelling of nutrients from below? All of these issues are prime for research, and we look forward to the results of ongoing and future investigations.

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