

Permian-Triassic boundary interval as a model for forcing marine ecosystem collapse by long-term atmospheric oxygen drop

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ABSTRACT

Ecological traits of reefs across the Permian-Triassic boundary interval coincide with a modeled decline of atmospheric oxygen throughout the Permian Period. Selective extinction and recovery patterns within the reef system are observed both at the end of the middle Permian (end-Guadalupian) and at the Permian-Triassic boundary. The end-Guadalupian event selectively affected corals and broke down the cool-water carbonate factory. Sponges, however, were largely unaffected and bloomed in reefs toward the end of the Permian. The end-Permian total destruction of the metazoan reef system only left behind poorly diverse microbial communities. The temporal reef patterns are thus similar to spatial patterns of modern benthic communities approaching oxygen minimum zones. This observation suggests that a decline in oxygen concentrations was at least partly involved in the destruction of reefs, even where there is no direct evidence of oceanic anoxia.

Keywords: reefs, anoxia, mass extinction, recovery, Permian, Triassic.

INTRODUCTION

The Permian mass extinction encompasses the end-Guadalupian (middle Permian) and end-Lopingian (Late Permian) crises (Stanley and Yang, 1994), the latter being the most severe Phanerozoic bioevent, even considering the incompleteness of the fossil record (Peters and Foote, 2002). To explain the mass extinctions around the Permian-Triassic boundary, attention focused during the 1990s on a variety of abrupt kill mechanisms, including ocean hypercapnia (CO₂ poisoning; Knoll et al., 1996), oceanic anoxia (Wignall and Twitchett, 1996), volcanism (Reichow et al., 2002), methane expulsion (Krull and Retalack, 2000), or bolide impact (Becker et al., 2001). More recently, a synergistic scenario of short-term perturbations of the carbon cycle and its far-reaching reorganization with a shift

of the depocenter from the land to the ocean has been proposed (Berner, 2002). Wignall and Twitchett (2002) recognized that the end-Permian anoxia, which developed in shallow- and deep-water environments, lasted considerably longer than comparable Mesozoic oceanic anoxic events, and thus probably controlled the Permian-Triassic boundary crisis. Both mechanisms, the carbon cycle reorganization and the oceanic anoxia, indirectly imply long-term changes of the Earth system as potential controls of the extinction. Despite these new observations, little research has focused on possible links between atmospheric oxygen decline and the fate of marine ecosystems prior to and around the Permian-Triassic boundary. The aim of this paper is (1) to demonstrate possible relationships between atmospheric oxygen drops and oceanic anoxic

events and (2) to evaluate ecosystem proxies that monitor these changes with a high resolution.

PERMIAN-TRIASSIC ATMOSPHERIC OXYGEN FLUCTUATIONS

The contemporary atmospheric oxygen value is 21%; current global geochemical models (Berner and Canfield, 1989; Berner, 1999; Berner et al., 2000) suggest that atmospheric oxygen reached potential maximum concentrations of ~35% during the Pennsylvanian (late Carboniferous) (hyperoxia), gradually dropped to minimum concentrations possibly as low as 15% around the Permian-Triassic boundary, and increased during the Triassic to modeled values of ~18% (Fig. 1). Some uncertainty surrounds these modeling results. An alternative O₂ model proposed by Lenton (2001) involves buffering feedback mechanisms not considered in the former models. The Lenton model suggests that O₂ fluctuations were less pronounced than assumed in the Berner model, but the principal pattern of decreasing oxygen content throughout the Permian and the increase in the Triassic is retained.

The possible links of these secular fluctuations to macroevolutionary processes are underexplored, but the stratigraphic coincidence of reconstructed atmospheric oxygen concentrations and biospheric perturbations suggest that this relationship may be stronger than admitted. Late Paleozoic hyperoxia may have

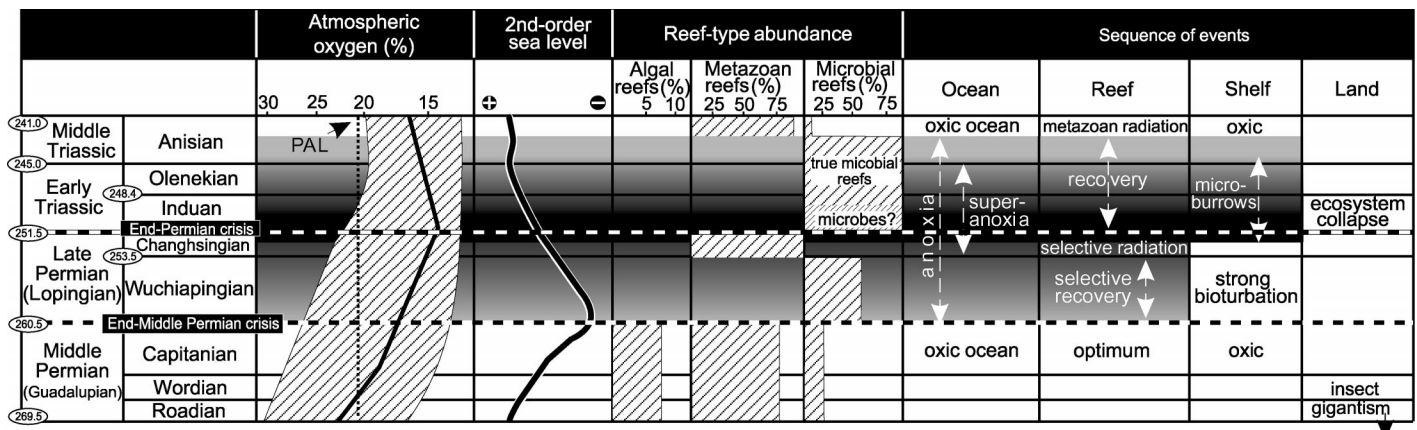


Figure 1. Composite chart showing oxygen (Berner and Canfield, 1989; Berner, 1999), second-order sea level (Weidlich, 2002a; Weidlich and Bernecker, 2003), and ecosystem collapse and recovery patterns on land and in sea (based on Isozaki, 1997; Weidlich, 2002a; Flügel, 2002; Flügel and Kiessling, 2002; Bowring et al., 1999). PAL—present atmospheric level. Darker shading indicates greater intensity of oceanic anoxia. Ages in circles are in Ma.

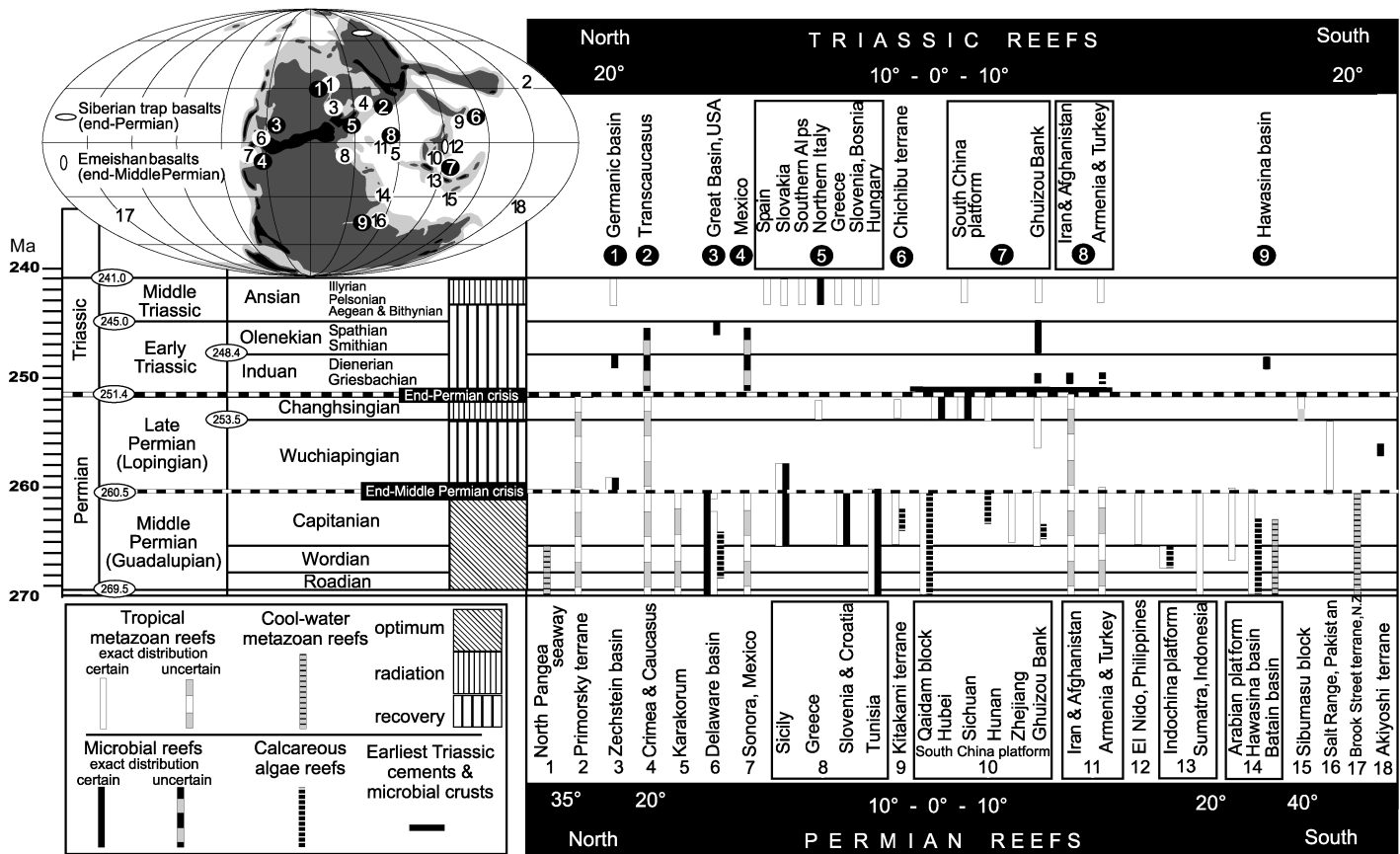


Figure 2. Observed middle Permian–Middle Triassic chronostratigraphy and stratigraphic ranges of reefs plotted against paleolatitude (Weidlich, 2002a; Flügel, 2002; Flügel and Kiessling, 2002). Inset map is Late Permian paleogeographic reconstruction. Black numbers—Permian reefs; white numbers—Triassic reefs.

positively influenced the increase in body size of metazoans, the diversification and ecological radiation of invertebrates, and the exploitation of new habitats (Graham et al., 1995; Dudley, 2000). Modern oxygen minimum zone inhabitants directly respond to oxygen deficiency with opportunistic faunas and dense bacterial populations (Jacobs and Lindberg, 1998; Levin, 2002). We argue that these ecological traits may scale up to macroevolutionary patterns. Our ecosystem data imply that the atmospheric oxygen decline beginning in the Guadalupian was an increasingly limiting long-term factor for reef ecosystems during the 30 m.y. prior to the establishment of the Early Triassic.

PERMIAN-TRIASSIC REEF EVOLUTION

Our analysis of Permian-Triassic reef evolution is founded on the PaleoReef database (for details, see Kiessling et al., 1999; Kiessling, 2001), which summarizes information on 490 Permian-Triassic reefs. The middle Permian (Guadalupian) represents the reef optimum of the late Paleozoic (Weidlich, 2002a, 2002b), as recognized by the highest diversity of reef types, the greatest metazoan diversity,

and an extended reef zone expanding from the equator to a paleolatitude of 35°N and 40°S (Fig. 2). Guadalupian reefs can be differentiated into (1) a tropical reef belt with sponge-microbial reefs, coral reefs, richthofeniid brachiopod reefs, and phylloid algal reefs, and (2) cool-water bryozoan reefs, which are reported from the northern Pangean shelf, the southwestern Tethys Ocean, and the southern Panthalassa Ocean. The end-Guadalupian extinction affected all reef communities, eliminated the cool-water reef communities, caused an apparent loss of 89% in reef carbonate production (e.g., the contribution of reefs to the gross carbonate production on platforms and ramps), and was associated with a reef diversity loss of 55% (alpha diversity). Coral extinctions in the area of the equatorial South China (or Yangtze) platform were profound but selective, with nondisseminated, solitary and dendroid corals doing best during the crisis (Wang and Sugiyama, 2000). Reefal ecosystem response varied geographically: the demise of Tethyan metazoan and microbial reefs was abrupt, whereas reefs of the Delaware Basin were gradually replaced by microbial communities (Fig. 2). This heterogeneous pattern at the end of Guadalupian suggests that the reef demise was gradual rather than abrupt.

After the end-Guadalupian extinction, Late Permian (Lopingian) sponge-microbial and dendroid coral reef locations were restricted to a narrow equatorial reef belt (Fig. 2). Although Lopingian reefs resemble their Guadalupian ancestors in biotic composition, the difference is an obvious shift toward diverse coralline sponge communities as well as impoverished coral and richthofeniid brachiopod faunas. The enigmatic calcimicrobe *Shamovella* (“*Tubiphytes*”) settled more frequently in reefs than in the Guadalupian (Senowbari-Daryan and Flügel, 1993). The restructured Lopingian reef system has a limited fossil record in the Wuchiapingian, but bloomed by the Changhsingian (Fig. 2), with reef-production rates similar to those of the late Guadalupian. Sponge microbial and dendroid coral reefs persisted until the end of the Permian in the South China platform. The rapid and dramatic end-Permian reef collapse led to a >99% loss of carbonate production (Flügel and Kiessling, 2002), a diversity loss of 86% (alpha diversity), and the final extinction of rugose corals, tabulate corals, and richthofeniid brachiopods. Although sponges were strongly affected, their extinction rates were reduced compared with the other reef organisms (Fig. 3). Shortly after the Permian-Triassic boundary (Figs. 1 and 2), carbonate cement crusts and precipi-

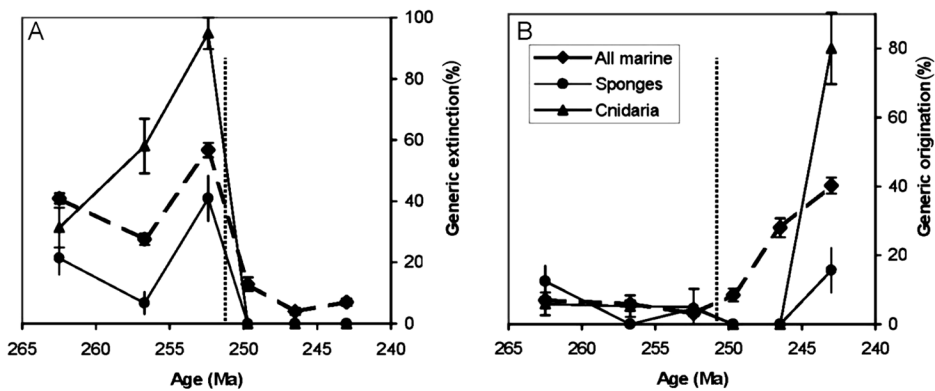


Figure 3. Extinction (A) and origination (B) metrics for important reef builders and all marine invertebrates around two Permian mass extinctions. Well-defined genus ranges from Sepkoski (2002) were binned into geologic stages, and singletons were excluded. Error bars represent one standard deviation in each direction. Permian-Triassic boundary is marked by dotted line.

tates of uncertain microbial affinity were laid down at different stratigraphic levels in a narrow equatorial belt (see Flügel, 2002, for review). After the reef collapse, probably during the late Griesbachian, the first true microbial buildups grew in an area comparable to the latest Permian reef domain (e.g., Kershaw et al., 1999; Lehrmann et al., 2003). In the next step, microbial communities occupied an extended equatorial belt and later invaded deeper-marine environments. Scleractinian coral and sponge reefs started to colonize the shelves not before the Anisian (Middle Triassic) in an extended equatorial zone (Figs. 1 and 2). Biodiversity values comparable to the Guadalupian reef optimum were achieved during the Late Triassic (Flügel, 2002).

POSSIBLE LINKS TO ATMOSPHERIC OXYGEN DECLINE

During the Guadalupian, cool-water bryozoan reefs flourished in regions that were oxygenated, as indicated by bioturbated sediments. The presence of massive (colonial) corals and reef-building brachiopods in the tropics indicates well-oxygenated low-latitude oceans, because metabolic oxygen requirements of benthic animals significantly rise with an increase in water temperature (Jacobs and Lindberg, 1998). The Guadalupian reef optimum coincided with high modeled atmospheric oxygen concentrations (20%–25%). The end-Guadalupian reef demise may have been linked to a regional perturbation of the carbon cycle (implied by the depletion of ^{13}C mentioned by Jin et al., 1998) and an oxygen decline below a critical threshold favoring local dysoxic or anoxic oceanic conditions (Fig. 1). With the exception of sponges, extinction rates of metazoan reef builders are in the range of all marine organisms and coincide with the gradual atmospheric oxygen drop (Fig. 3).

Although no sedimentary record of anoxia is evident in latest Permian reefs, sponges and

opportunistic dendroid corals resemble modern oxygen minimum zone communities (Levin, 2002) in that the body size of reef builders is reduced and framework communities are dominated by sponges. Similar to modern sponges (Wilkinson, 1983), latest Permian sponges may have survived oxygen limitation by excess oxygen production of symbiotic cyanobacteria. Another possibly advantageous sponge adaptation is their reproduction strategy, which enables their gemmules to survive under anoxic conditions for a longer time than other organisms (Reiswig and Miller, 1998). The carbonate cement crusts (Woods et al., 1999), enigmatic microbial crust (Kershaw et al., 1999), and calcimicrobial framestones (Lehrmann et al., 2003) immediately after the Permian-Triassic boundary reflect an extraordinary oceanic event, probably related to the collapse of oxygen-dependent carbonate-secreting metazoans during the diachronous onset of the oceanic anoxic event. Anoxia affected the reef ecosystem for ~ 7 m.y. after the Permian-Triassic boundary and impeded the return to late Paleozoic reef-builder diversities until the end of the Triassic, when atmospheric oxygen had increased to $\sim 18\%$.

DISCUSSION

Global Permian-Triassic reef patterns are consistent with modeled atmospheric change and indicate that a gradual oxygen decline within the Permian made reef communities vulnerable to abrupt environmental perturbations. Reef builders lacking adaptations to increasingly dysoxic conditions were selectively affected by the first event ~ 9 m.y. before the global spread of dysoxic or anoxic conditions. The Emeishan flood basalts in China (Fig. 2), and probably basalts in India, are either contemporaneous with the end-Guadalupian mass extinction (Zhou et al., 2002) or slightly post-date the crisis (Ali et al., 2002). They may be responsible for the prolonged (7 m.y.) recov-

ery phase and for global warming, thereby preventing the cool-water and phylloid algal reefs from recovery.

Paleontological, geochemical, and sedimentological data confirm our findings (Fig. 1). Finely laminated pelagic sedimentary rocks (Isozaki, 1997) track contemporaneous deep-sea oxygen deficiency from the end of the middle Permian to the Early Triassic (anoxia and superanoxia, Fig. 1). As indicated by decreasing bioturbation size and intensity, rising second-order sea level (second-order sequences are long lasting and have an approximate duration of 5–20 m.y.; see Weidlich and Bernecker, 2003) may have facilitated the spread of anoxia on the newly flooded shelves and increased the devastating character of the extinction (Fig. 1). High- and low-latitude shelf sections in many areas also show that anoxic conditions preceded the end-Permian crisis and lasted until the Early Triassic (Wignall and Twitchett, 2002) or even until the Middle Triassic (Isozaki, 1997). New sedimentological data that point to a diachronous onset of oceanic anoxia (Wignall and Newton, 2003) reflect local oceanographic changes and do not challenge the global pattern.

Tracers of atmospheric oxygen decline are scarce in terrestrial ecosystems (Fig. 1); however, the characteristic end-Permian fungal spike (e.g., Visscher et al., 1996) may point to fouling of plant organic matter owing to reduced insect grazing because (1) insects are extremely important in the consumption of dead plant material (Wilson, 1987) and (2) they were presumably severely affected by the atmospheric oxygen drop owing to the inherent limitations of their tracheal system.

CONCLUSIONS

Although uncertainties exist regarding modeled atmospheric oxygen concentrations and the physiology of ancient reef builders, we conclude that the coincidence of modeled atmospheric oxygen concentration and selective reef collapse across the Permian-Triassic boundary interval were ecologically linked. Two novel aspects result from our finding: (1) Decreasing atmospheric oxygen is monitored in the distributional pattern and biological composition of reefs prior to sedimentary tracers on oceanic anoxia and (2) oceanic anoxic events may directly result from declining atmospheric oxygen, a situation that differs significantly from Quaternary oceanographic patterns. Conventionally, anoxic events are regarded to result from short-term ocean stagnation, as documented by Pleistocene millennial-scale changes of the thermohaline circulation patterns in the North Atlantic (Rahmstorf, 2002), a model that does not apply to the Permian-Triassic boundary crisis. The invalidity of this assumption was dem-

onstrated by using general circulation models (Hotinski et al., 2001). Although our findings agree with rapid extinction scenarios at the end of the Permian (Bowring et al., 1999), the early response of the reef ecosystem in the Guadalupian supports the view that atmospheric oxygen decrease preconditioned marine ecosystems to extinction.

Oceanic anoxic events are repeated phenomena of Earth history, especially during the Mesozoic. However, the oceanic anoxic events of the Permian-Triassic boundary interval had the most devastating character. The Early Cretaceous oceanic anoxic events gave rise to a number of reef crises, but never caused a mass extinction (Wilson and Norris, 2001), unlike the described Permian-Triassic boundary pattern. We speculate that during a phase of high atmospheric oxygen, reef ecosystems were more stable and were not affected globally by oceanic anoxic events.

Independent lines of evidence support our hypothesis of atmospheric oxygen as a direct long-term control factor on Permian oceanic anoxic events and consequently on the evolution of marine benthic communities. We urge more research on the potential effects of atmospheric changes on marine communities.

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