

Understanding mechanisms for the end-Permian mass extinction and the protracted Early Triassic aftermath and recovery

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ABSTRACT

Modern study of the end-Permian mass extinction in the marine realm has involved intensive documentation of the fossil content, sedimentology, and chemostratigraphy of individual stratigraphic sections where the mass extinction interval is well preserved. These studies, coupled with innovative modeling of environmental conditions, have produced specific hypotheses for the mechanisms that caused the mass extinction and associated environmental stress. New paleobiological studies on the environmental distribution and ecological importance of brachiopods, benthic molluscs, and bryozoans support the hypothesis that stressful ocean conditions—primarily elevated H₂S levels (euxinia) but also heightened CO₂ concentrations—were the prime causes of the end-Permian mass extinction. These studies also further demonstrate that both the Late Permian interval preceding this mass extinction and the Early Triassic interval that followed were times of similar elevated environmental stress. In the low-diversity Early Triassic biosphere, huge numbers of benthic molluscs, in particular four cosmopolitan genera of bivalves, typically covered the seafloor. That a few marine genera thrived during this time indicates a greater than usual tolerance to some combination of marine anoxia, as well as elevated CO₂ and/or increased H₂S concentrations. Research focusing on experiments with modern organisms similar to those that died, as well as those that thrived, in microcosms where levels of O₂, CO₂, and H₂S can be experimentally manipulated will enable an even more detailed understanding of the nature of this greatest Phanerozoic biotic crisis.

INTRODUCTION

A major drop in global biodiversity defines mass extinctions, as revealed by compilations of taxonomic richness (Sepkoski, 1981). The end-Permian mass extinction (ca. 252 Ma) has long been recognized as the most severe biodiversity crisis in the Phanerozoic (Erwin, 2006), and its associated faunal shift from

the brachiopod-rich Paleozoic Fauna to the mollusc-rich Modern Fauna (Gould and Calloway, 1980; Sepkoski, 1981) represents a fundamental change in the taxonomic structure as well as the ecological architecture of marine animal ecosystems. A range of mechanisms from oceanographic to climatic to extraterrestrial has been proposed to explain the end-Permian mass extinction (e.g., Renne et al., 1995; Knoll et al., 1996; Wignall and Twitchett, 1996; Isozaki, 1997; Krull and Retallack, 2000; Becker et al., 2001; Grice et al., 2005). Similarly, a variety of evidence shows that environmental stress lingered through the Early Triassic, strongly affecting recovery processes (e.g., Schubert and Bottjer, 1992; Woods et al., 1999; Payne et al., 2004; Pruss et al., 2006).

We focus here on paleobiological approaches that incorporate ecological, environmental, and biogeographic analyses during the time leading up to the end-Permian mass extinction as well as the subsequent Early Triassic aftermath and recovery to test the variety of mechanisms hypothesized for this interval of biotic crisis. These new analyses provide the foundation for future experiments in which environmental conditions can be manipulated in microcosms, thus allowing a more comprehensive understanding of the largest biotic crisis of the Phanerozoic.

ANALYTICAL APPROACHES

Recent paleobiological studies have adopted a more quantitative approach to document hierarchical changes, from local to global scales, in the marine biosphere during the Late Permian extinctions and the Early Triassic recovery. The combination of paleoecological analysis, based on counts of fossil assemblages and shell accumulations, with assessment of the changing habitat preferences and geographic distribution of environmentally sensitive animal groups provides a clearer picture of the ecological processes operating at a variety of scales during the Permo-Triassic extinction and recovery interval. These paleoecological analyses build upon results from modern ecology, indicating that (1) abundant species typically play a crucial role in controlling the ecological functioning of their communities (Power et al., 1996), and (2) the correspondence between a taxon's abundance in marine life and death assemblages is relatively faithful (Kidwell, 2001, 2002). As such, fossil accumulations, known as shell beds, provide a rich source of paleoecological data. Shell beds have been used to estimate the identity of ecologically dominant groups in the fossil record (e.g., Clapham et al., 2006) and as proxies for numerical dominance of skeletonized benthic marine invertebrates during important biological transitions, such as the Ordovician Radiation (e.g., Li and Droser, 1999). Both quantitative accounts of

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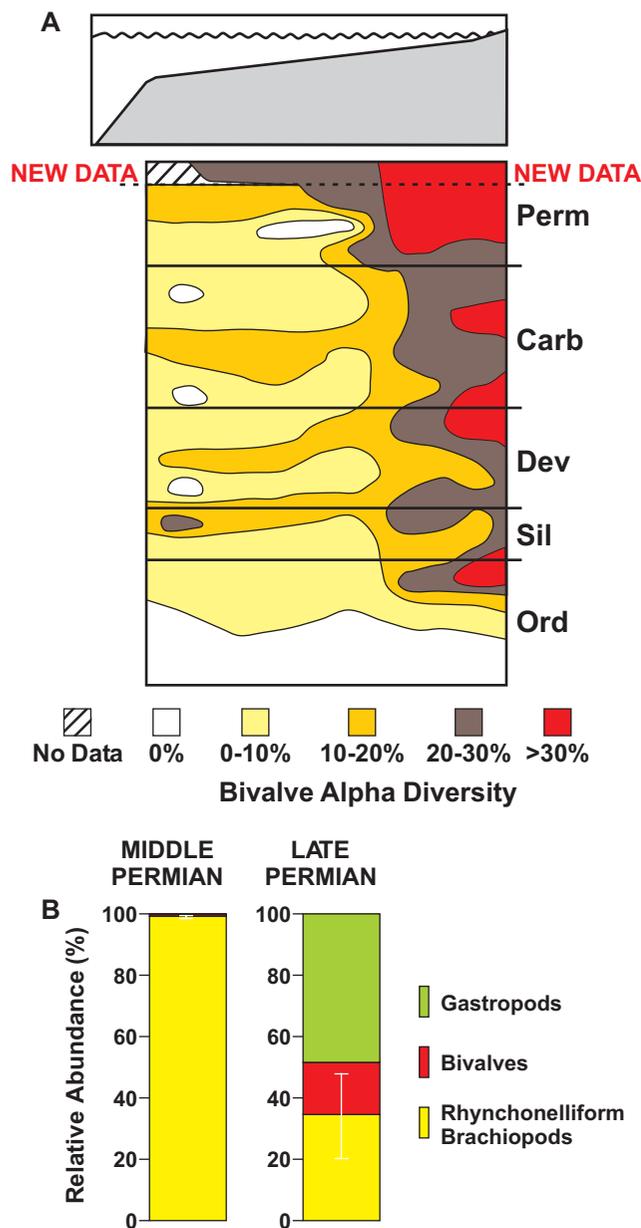


Figure 1. Paleoeological changes in brachiopods and molluscs in the Paleozoic. (A) Time-environment pattern of Paleozoic bivalve alpha diversity, indicating an initial offshore expansion of diverse bivalve assemblages in the Permian; modified from Miller (1988). New Late Permian data (from Clapham and Bottjer, 2007a) show a major offshore increase in bivalve diversity. Hatched pattern in Late Permian slope and basin environments indicates a lack of data. (B) Mean relative abundance of rhynchonelliform brachiopods, bivalves, and gastropods from new Middle and Late Permian offshore samples (from Clapham and Bottjer, 2007a). Error bars indicate 95% confidence intervals.

fossil abundance (Clapham and Bottjer, 2007a, 2007b; Fraiser and Bottjer, 2007b) and semiquantitative assessment of the dominant group in shell accumulations (Fraiser and Bottjer, 2007b) document profound ecological changes in marine animal communities during the Late Permian and Early Triassic.

As part of the ecological assessment of organisms before and after mass extinctions, the paleoenvironmental context of important taxa must also be considered in order to under-

stand how changes in environmental conditions affect different habitats. Assessment of shifts in habitat occupation and environmental variation in diversity also provides a broader perspective on local community changes reconstructed from quantitative counts.

Time-environment (*T-E*) diagrams, which plot the presence or absence, diversity, or abundance of particular taxa against marine environments and geological time, have long been used to understand the evolutionary paleoecology and distribution of these taxa through time (e.g., Jablonski et al., 1983; Sepkoski and Miller, 1985; Bottjer and Jablonski, 1988; Miller, 1988; Powers and Bottjer, 2007) (Figs. 1A and 2A) (for detailed methodology, see Powers and Bottjer, 2007). Once hierarchical biotic changes are addressed at the local community scale through quantitative paleoecological analysis and at the regional scale through documentation of habitat occupation with *T-E* diagrams, the broadest scale of extinction processes is revealed by the changing paleobiogeographic patterns of specific animal groups (e.g., Powers and Pachut, 2008). Plots on paleogeographic maps of occurrences gathered from the primary literature document geographic variations in the severity of the extinction, including the existence of refugia where animals were able to avoid the most severe environmental perturbations and survive to recolonize the globe after conditions became more favorable.

PROPOSED MECHANISMS FOR LONG-TERM ENVIRONMENTAL STRESS AND MASS EXTINCTION

Mechanisms for environmental stress during the Permian-Triassic transition, including the end-Permian mass extinction, varied over space and time. Potential sources of environmental stress include a range of gradual and catastrophic processes, such as reduced concentrations of atmospheric O_2 (Huey and Ward, 2005), widespread oceanic anoxia (Wignall and Twitchett, 1996; Isozaki, 1997; Huey and Ward, 2005), euxinia (H_2S poisoning) (Nielsen and Shen, 2004; Grice et al., 2005; Kump et al., 2005), increased oceanic CO_2 concentrations (hypercapnia) (Knoll et al., 1996), massive volcanism and global warming (Renne et al., 1995; Kamo et al., 2003), CH_4 oxidation (Krull and Retallack, 2000; Ryskin, 2003), and an extraterrestrial impact (Becker et al., 2001).

Environmental stress during the Late Permian was likely initiated at the end of the Middle Permian, during the development of deep-water anoxic conditions associated with the Permian-Triassic superanoxia event (Isozaki, 1997). Deep waters were even euxinic in some basins during the early Late Permian, several million years before the end-Permian mass extinction (Nielsen and Shen, 2004). Geochemical and sedimentological data indicate that Late Permian deep-water environmental stress, including euxinia and high CO_2 concentrations, persisted into the Early Triassic (Isozaki, 1997; Woods et al., 1999; Payne et al., 2004; Pruss et al., 2004) and that upward excursion of these deep-water conditions into shallow environments was the ultimate cause of the end-Permian mass extinction, during which 80% of marine species and 49% and 63% of marine and terrestrial families disappeared (Raup and Sepkoski, 1982; Stanley and Yang, 1994; Benton, 1995). These deep-water, and intermittently shallow-water, H_2S -rich conditions were exacerbated by the effects of massive Siberian Trap

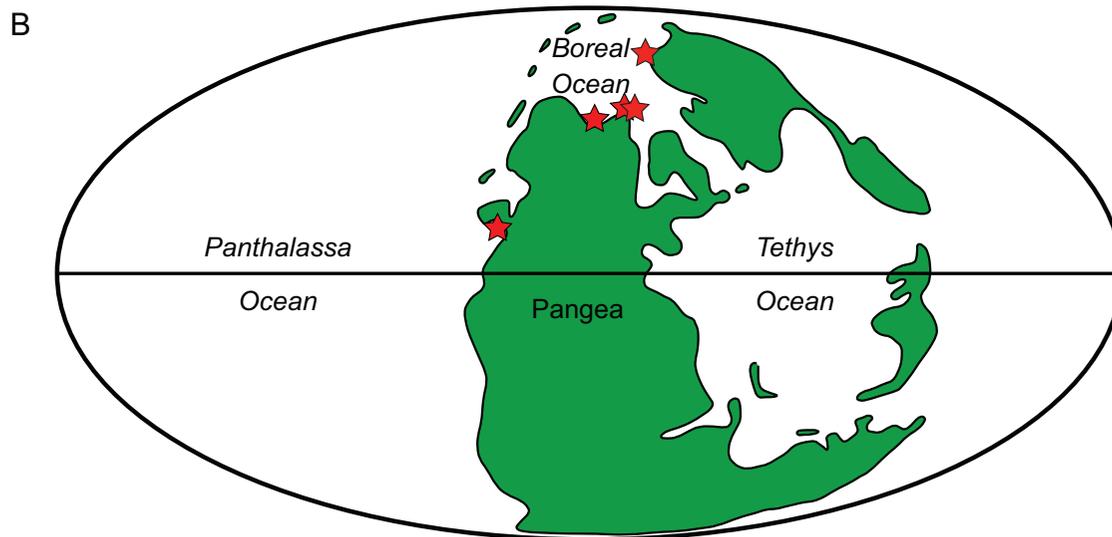
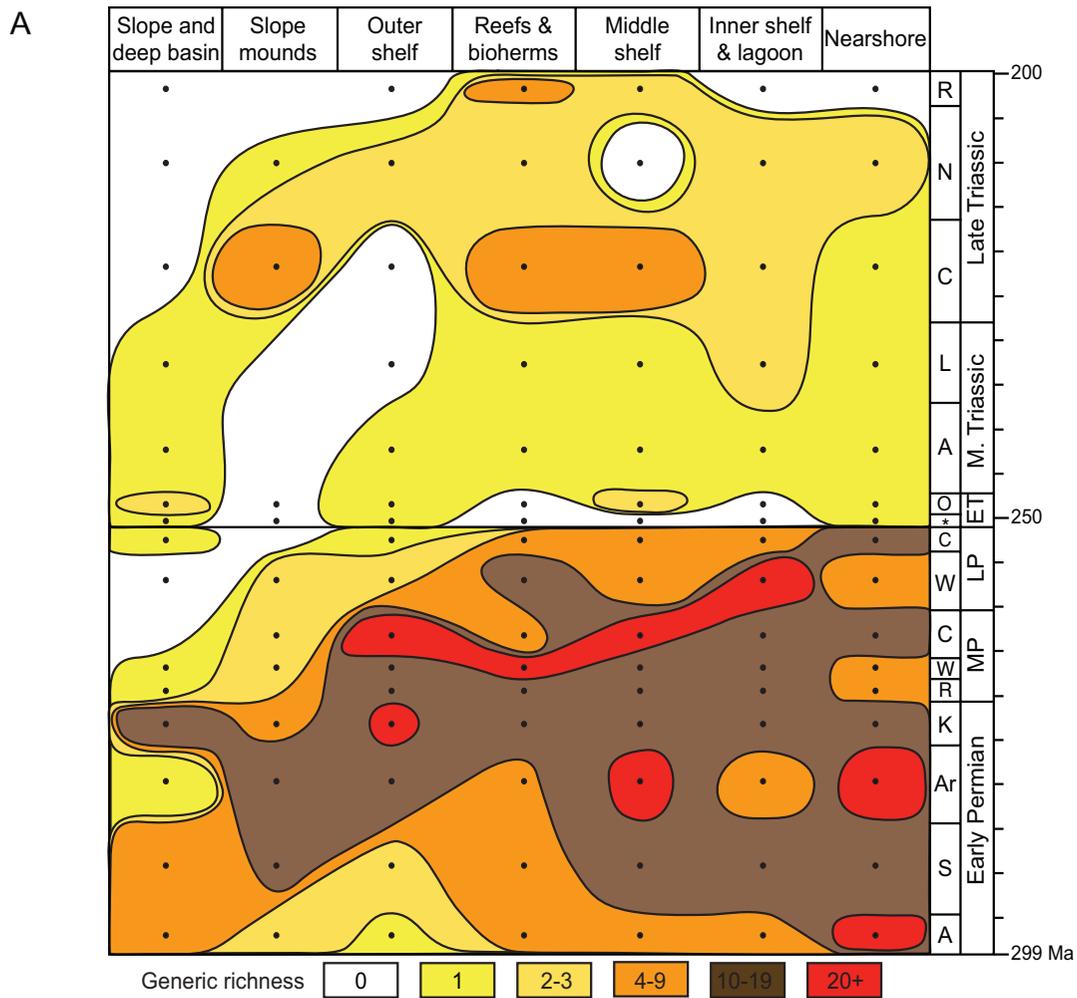


Figure 2. Environmental and geographic distribution of stenolaemate bryozoans. (A) Contoured Permian-Triassic time-environment (*T-E*) diagram of marine bryozoans. Each dot represents a data point, either for assemblage with the greatest bryozoan generic richness in each *T-E* bin, or for absence of bryozoans validated by the taphonomic control group; modified from Powers and Bottjer (2007). Abbreviations from the bottom up: A—Asselian; S—Sakmarian; Ar—Artinskian; K—Kungurian; R—Roadian; W—Wordian; C—Capitanian; W—Wuchiapingian; C—Changhsingian; *—Induan; O—Olenekian; A—Anisian; L—Ladinian; C—Carnian; N—Norian; R—Rhaetian; MP—Middle Permian; LP—Late Permian; ET—Early Triassic. (B) Paleobiogeographic distribution of Early Triassic bryozoans indicated by stars. Modified from Powers and Pachut (2008).

volcanism (Renne et al., 1995; Kamo et al., 2003), which increased atmospheric CO₂ concentrations, enhancing the possibility for hypercapnia and/or ocean acidification and biocalcification crises (Knoll et al., 1996).

PERMIAN PRELUDE

Compilations of marine animal diversity show that the shift in global taxonomic richness from diverse rhynchonelliform (“articulate”) brachiopods to diverse molluscs occurred at the Permian-Triassic boundary, coincident with the end-Permian mass extinction event (e.g., Sepkoski, 1981). That concurrence has been used to argue that the mass extinction was the primary cause of this ecological change by eliminating previously dominant brachiopods and allowing molluscs to rise to prominence (e.g., Gould and Calloway, 1980). Pioneering environmental and ecological analysis of the prelude to this transition through the use of *T-E* diagrams (e.g., Miller, 1988) showed the beginnings of an increase in bivalve molluscs across middle shelf environments in the Middle Permian (Fig. 1A), although data were not available from the Late Permian (Clapham and Bottjer, 2007a, 2007b) until recently.

Ecological changes at the local paleocommunity level prior to the end-Permian extinction have been reconstructed from abundance counts of >33,000 fossil individuals from 24 silicified Middle and Late Permian paleocommunities (Clapham and Bottjer, 2007a, 2007b). The counts document a significant ecological shift in fossil abundance in offshore environments, from rhynchonelliform brachiopods to gastropods and bivalves, between the Middle and Late Permian, despite the fact that the relative global taxonomic richness of those groups was essentially unchanged (Fig. 1B). The shift in numerical dominance was also accompanied by major ecological changes as motile gastropods and infaunal bivalves became more prominent members of Late Permian communities.

A compilation of the global onshore-offshore distribution of marine bryozoans within nearly 400 Permian-Triassic assemblages reveals that the pronounced ecological changes in local paleocommunities were symptomatic of a more widespread phenomenon affecting offshore habitats in the Late Permian. The generic richness of bryozoans declined significantly in the Late Permian, with the most severe effects observed in offshore settings from which bryozoans were progressively restricted and finally eliminated significantly before the extinction event (Powers and Bottjer, 2007) (Fig. 2A). Although not based on a similar comprehensive global data set, onshore-offshore trends in the mean abundance of microgastropods and maximum gastropod size can be observed in the Late Permian, with larger gastropods inhabiting shallow settings, while the microgastropod abundance and maximum size in offshore habitats were strikingly similar to the Early Triassic (Clapham and Bottjer, 2007a).

These new data on the environmental distribution and ecological structure of Late Permian assemblages further demonstrate that processes leading to the end-Permian mass extinction commenced around the Middle-Late Permian boundary (Clapham and Bottjer, 2007a, 2007b; Powers and Bottjer, 2007). The preferential drop in abundance of brachiopods and assemblage diversity of bryozoans in Late Permian offshore environments, coincident with the increase in molluscan abundance, indicates that stressful conditions for brachiopods and

bryozoans were encroaching over time from the deep ocean onto shelf environments, and argues against an extraterrestrial cause for the extinction. That this ultimately led to the end-Permian demise of brachiopods and bryozoans, contrasted with an increase in molluscs, indicates that the anoxic, and locally euxinic, nature of this deep ocean water was highly stressful to brachiopods and bryozoans but not to certain benthic molluscs (Clapham and Bottjer, 2007b).

EARLY TRIASSIC AFTERMATH AND RECOVERY

The end-Permian mass extinction marks the beginning of the second phase of the prolonged Permian-Triassic biotic crisis, with biotic recovery beginning only 4–5 m.y. later (Lehrmann et al., 2006), toward the end of the Early Triassic (Spathian). Full recovery, including a return to pre-extinction diversity and ecological complexity, did not occur until some time in the Middle Triassic (Hallam, 1991; Erwin and Pan, 1996). Carbon isotopic data demonstrate large negative and positive excursions throughout the Early Triassic, indicating changes in the carbon cycle not seen since Cambrian and earlier times (e.g., Atudorei, 1999; Payne et al., 2004; Corsetti et al., 2005; Pruss et al., 2006). Quantitative paleoecological analysis at various temporal and spatial scales has revealed short-term and long-term changes within benthic level-bottom shallow marine paleocommunities that were facilitated by protracted Early Triassic deleterious environmental conditions (Figs. 3 and 4).

One short-term paleoecological pattern revealed by analysis of Lower Triassic shell beds is the opportunistic proliferation of microgastropods—gastropods with greatest dimension <1 cm—in shallow marine subtidal to middle shelf environments (Fraiser and Bottjer, 2004; Fraiser et al., 2005) (Fig. 4). Microgastropod-dominated shell beds occur globally during the aftermath of the end-Permian mass extinction and represent a non-actualistic phenomenon. Fraiser and Bottjer (2007a) proposed that microgastropods were able to survive the chemically and/or physiologically harsh environmental conditions during the Early Triassic better than most skeletonized benthic marine invertebrates. This phenomenon had begun by the Late Permian in offshore environments, supporting the hypothesis that poisonous deep-waters contributed to changes in paleocommunity structure (Clapham and Bottjer, 2007a).

Quantitative data of fossil marine assemblages found in The Paleobiology Database (www.paleodb.org) show that rhynchonelliform brachiopods, in contrast to benthic molluscs (bivalves and gastropods), declined in abundance throughout the Late Permian and Early Triassic before recovering to abundance levels similar to those of the Late Permian during the Middle and Late Triassic (Fig. 3) (Clapham and Bottjer, 2007b). Field examination of Lower Triassic shell beds from around the world reveals a similar trend: bivalves dominate 70% of Lower Triassic shell beds, and rhynchonelliform brachiopods dominate only a small percentage of the studied shell beds (Fig. 4). Four bivalve genera, *Claraia*, *Eumorphotis*, *Promyalina*, and *Unionites*, are the most widespread and numerically abundant bivalve genera during the Early Triassic (Hallam and Wignall, 1997; Fraiser and Bottjer, 2007b). Of these, *Unionites* is typically the most common in shallow marine environments.

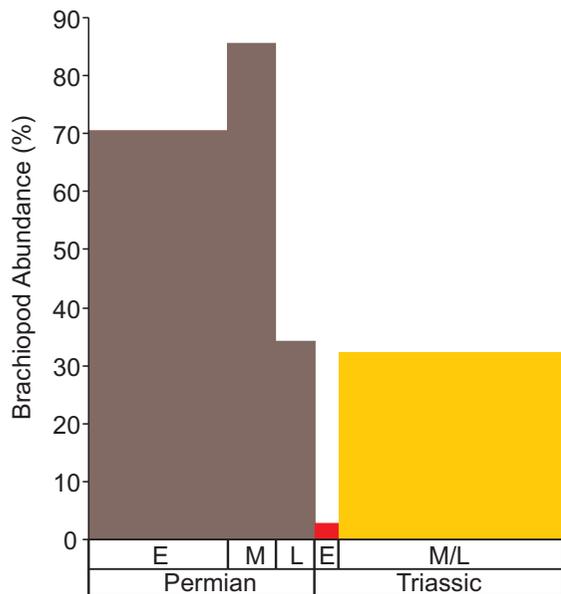
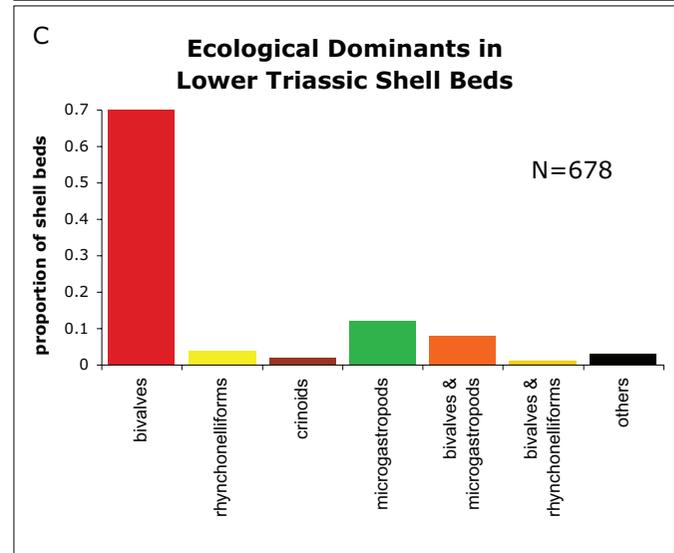
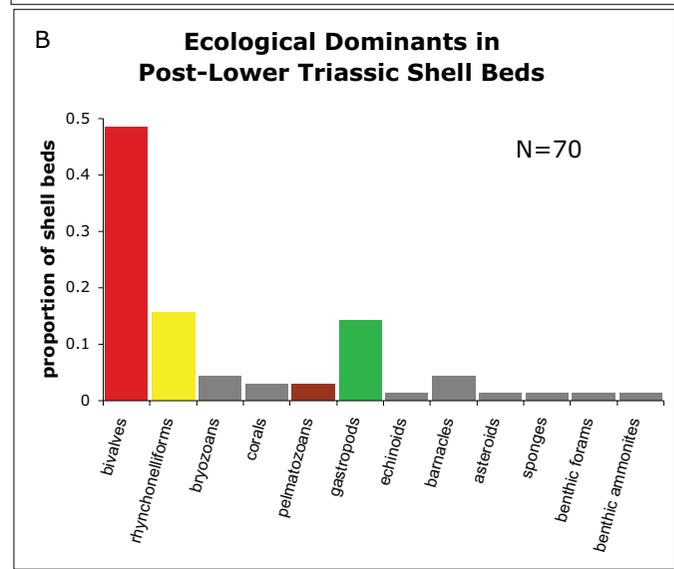
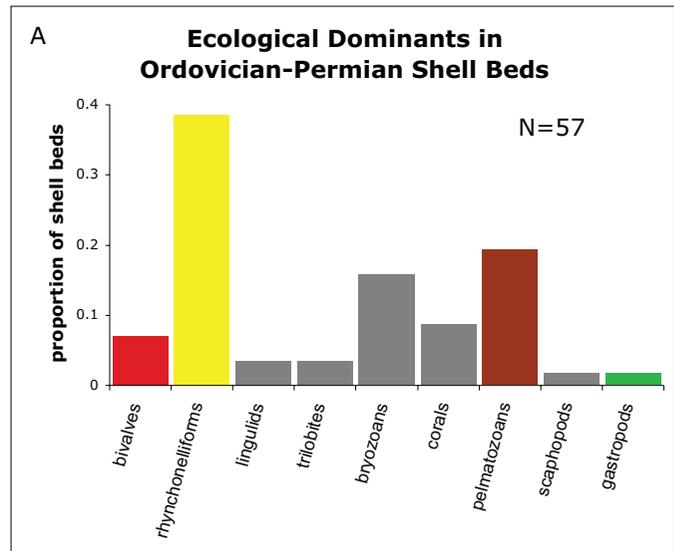


Figure 3. Relative abundance of rhynchonelliform brachiopods (normalized to include only brachiopods, bivalves, and gastropods) from 181 Permian and Triassic quantitative assemblages, indicating a Middle (M) to Late (L) Permian decline followed by a dramatic reduction in the Early (E) Triassic and then a recovery in the Middle and Late (M/L) Triassic. Modified from Clapham and Bottjer (2007b).

Analysis of shell bed data available in the primary literature places these results into a broader context (Fraiser and Bottjer, 2007b) (Figs. 4A and 4B). Tabulation of Ordovician to Permian and post–Early Triassic shell beds reflects major characteristics of Sepkoski’s evolutionary faunas, with dominance by rhynchonelliform brachiopod shell beds during the Paleozoic (Fig. 4A) and dominance by bivalve shell beds during the post–Lower Triassic (Fig. 4B) (Fraiser and Bottjer, 2007b). Not only was there a short-term increase in bivalves during the Early Triassic, but a long-term, permanent change was also facilitated: It was not until the aftermath of the end-Permian mass extinction that bivalves numerically dominated the majority of nearshore and shelf environments globally (Fraiser and Bottjer, 2007b) (Fig. 4C). Perhaps the ability of bivalves to become the most abundant skeletonized invertebrate in benthic marine environments was due to the large extinction of rhynchonelliform brachiopods during the end-Permian mass extinction, their preferential occupation of nearshore habitats, and physiological characteristics that enabled them to thrive during periods of oceanic and atmospheric stress during the Permian-Triassic transition.



Figure 4. Ecological dominants in post-Cambrian shell beds. (A, B) Ecological dominants in Ordovician to Permian and in post-Lower Triassic shell beds; from Kidwell (1991) and Fraiser and Bottjer (2007b). (C) Ecological dominants in Lower Triassic shell beds; data from Fraiser and Bottjer (2007b). Rhynchonelliform brachiopods numerically dominate Ordovician-Permian shell beds; bivalves numerically dominate Lower Triassic and post-Lower Triassic shell beds. N—total number of shell beds included in each analysis. No data for Lower Triassic shell beds were listed in Kidwell (1991). Data are from nearshore, inner shelf, and middle shelf environments.



The devastation of the end-Permian mass extinction is also reflected in the onshore-offshore distribution of bryozoans during the Early Triassic, with most environments containing no bryozoans and only one to two genera in others (Powers and Bottjer, 2007) (Fig. 2A). Bryozoan assemblage generic diversity remained low across all marine settings until the Late Triassic, when they recolonized most marine environments (Fig. 2A). The paleobiogeographic range of bryozoans in the Early Triassic mirrors their sporadic environmental distribution, with bryozoan localities restricted to high-latitude settings along northwest Pangea in eastern Panthalassa (Fig. 2B), and contrasts sharply with their Permian cosmopolitan distribution and widespread environmental range, particularly within the Tethyan Sea (Powers and Bottjer, 2009). This suggests that the Boreal realm may have acted as a geographic refugium during the Early Triassic (Powers and Pachut, 2008) (Fig. 2B). The Middle and Late Triassic environmental recovery of bryozoans (Fig. 2A) is also reflected by a much broader geographic distribution than in the Early Triassic (Powers and Pachut, 2008).

These new faunal analyses show that some combination of the euxinic marine conditions that first appeared at the Middle-Late Permian boundary with new CO₂ stress from Siberian volcanism continued through the Early Triassic (Isozaki, 1997; Payne and Kump, 2007). These environmental conditions adversely affected rhynchonelliform brachiopods and bryozoans but did not adversely affect a select group of benthic molluscs, which proliferated wildly during this time.

DISCUSSION

These results are consistent with a protracted oceanographic crisis during the Late Permian and Early Triassic. Unlike the mass extinction at the end of the Cretaceous, where taxonomic selectivity studies of brachiopods and bivalves indicate a crash in primary productivity associated with bolide impact (e.g., Rhodes and Thayer, 1991; Knoll et al., 2007), this Late Permian-Early Triassic crisis was likely caused by some combination of euxinia and/or high CO₂ in the oceans. Questions about the precise kill mechanisms and physiological reasons for survivorship and opportunism can now be addressed by revisiting pioneering experimental approaches (e.g., Thayer, 1985), taking advantage of research programs that have been initiated to understand the modern crisis of greenhouse gas-linked environmental change (e.g., Hoegh-Guldberg et al., 2007; Knoll et al., 2007).

For example, exposure of modern scleractinian corals to elevated CO₂ in microcosms resulted in skeleton dissolution and survival of the corals as soft polyps (Fine and Tchernov, 2007). As previously discussed, increased CO₂ concentrations in seawater, with corresponding ocean acidification, are also conditions that occurred during the end-Permian mass extinction and the Early Triassic (Fraiser and Bottjer, 2007a). One of the most pronounced biotic changes during the end-Permian mass extinction was the disappearance of Paleozoic tabulate and rugose corals and coral reefs from the geological record and the emergence of scleractinian corals and reefs after the recovery interval in the Middle Triassic (e.g., Stanley and Fautin, 2001; Stanley, 2003, 2007). The microcosm experiments confirm that rather than becoming extinct, corals may have existed as soft-bodied, anemone-like forms through the Early

Triassic, only reappearing in the fossil record after ocean acidification subsided in the Middle Triassic so that they could once again form mineralized skeletons (Stanley, 2007).

These remarkable results with microcosm experiments demonstrate that future work should focus on studies of other modern organisms similar to those that died, as well as those that thrived, where levels of O₂, CO₂, and H₂S can be experimentally manipulated. For example, the shallow infaunal burrower *Unionites* is the most abundant of the dominant Early Triassic bivalves (Fraiser and Bottjer, 2007b). At other times, members of this extinct genus inhabited stressed environments (e.g., Posenato, 2008), and if a suitable stand-in for Early Triassic *Unionites*, with similar skeletal and physiological properties, could be found in the modern fauna, it might be possible to determine whether its resilience in the face of reduced O₂ or increased CO₂ or H₂S concentrations would have allowed it to dominate shallow benthic environments. Continued use of such innovative new approaches places even more detailed understanding of the nature of this greatest Phanerozoic biotic crisis within reach.

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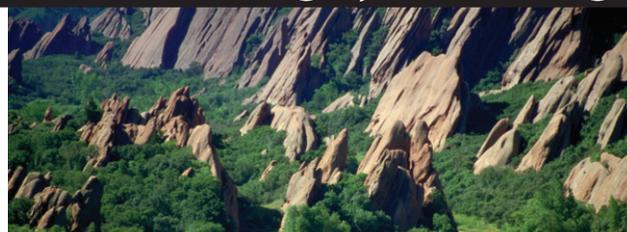
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