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High temperature and low oxygen perturbations drive contrasting benthic recovery dynamics following the end-Permian mass extinction

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ABSTRACT

The end-Permian mass extinction event was the greatest loss of biodiversity ever experienced on the planet. The event is thought to have been triggered by the initiation of the volcanic eruptions of the Siberian Traps. The five million year recovery interval that followed the extinction event was strongly influenced by the environmental effects of sustained volcanic eruptions including extreme temperature events and persistent global and regional oxygen minimum zones. The effects of these environmental perturbations on the paleoecological recovery of the benthic marine fauna were studied in two depositional units from the Southwestern United States representing two substages during the Early Triassic recovery. The Smithian Sinbad Limestone was influenced by high sea surface temperatures and contains a relatively high diversity fauna that exhibits extremely small body size. Gastropods that lived in this environment were size-limited, a possible result of metabolic stress due to extreme temperatures. These microgastropods were able to become dominate components of the benthic fauna by occupying niche space vacated by other taxa that were excluded by high temperatures. The Spathian Virgin Limestone shows evidence for low oxygen conditions. The resulting low diversity benthic fauna had a more ecologically complex community structure than the Smithian Sinbad Limestone including the occupation of epifaunal tiering space by crinoids. As the prevalence of aerobic facies increased through time, diversity, body size, and the complexity of faunal interactions also increased suggesting that low oxygen conditions were the limiting factor for the benthic recovery in that region. The differences in diversity and community structure between the two units highlight the importance of environmental and temporal differences in driving the recovery patterns of the benthic fauna following the extinction event. High temperature events and low oxygen conditions restricted the benthic fauna in different ways but both contributed to the delay in recovery from the end-Permian mass extinction.

1. Introduction

The end-Permian mass extinction 252 million years ago resulted in the most devastating loss of biodiversity on the planet (McGhee et al., 2012; Payne and Clapham, 2012). Following the initial volcanic events that contributed to the extinction, additional environmental perturbations during the recovery interval continued to inhibit the rapid return of ecological complexity and biodiversity. Using new collections made from the previously studied Smithian Sinbad Limestone and the Spathian Virgin Limestone of the Southwestern United States (Fig. 1) (Blakey, 1974; Dean, 1981; Schubert and Bottjer, 1995; Woods et al., 1999; Fraiser and Bottjer, 2004; Pruss and Bottjer, 2004; Nützel and Schulbert, 2005; Goodspeed and Lucas, 2007; Brayard et al., 2010; Hofmann et al., 2012; Marenco et al., 2012) the paleoenvironmental context of each sample is used to improve interpretations of Early Triassic benthic paleoecology and recovery patterns during successive climatic events (Fig. 2).

The end-Permian mass extinction event coincides with emission of volcanic gases that preceded flood basalt volcanism of the Siberian Traps (Svensen et al., 2009; Sobolev et al., 2011). Associated with this volcanic activity was the release of carbon dioxide and other toxic gases such as sulfur, chlorine, and fluorine due to the heating of evaporite, carbonate, and coal deposits rich in petroleum and organic matter (Svensen et al., 2009; Black et al., 2012). The emissions from the Siberian Traps elevated pCO_2 levels to multiple times pre-industrial values (Saunders and Reichow, 2009; Sobolev et al., 2011). The immediate effects of these eruptions would have included the climatic consequences of coal ash entering the stratosphere and encircling parts of the globe (Grasby et al., 2011; Ogden and Sleep, 2012). Oxygen isotopes preserved in conodont apatite suggest that equatorial sea surface temperatures were over 35 °C (Fig. 2) (Joachimski et al., 2012; Romano et al., 2012; Sun et al., 2012). The quantity of carbon dioxide released over such a short interval would have been capable of generating an ocean acidification event. This is supported by excursions in calcium isotopes and rhenium/osmium isotopes synchronous with carbon isotope swings at the Permian–Triassic boundary (Georgiev et al., 2011; Hinojosa et al., 2012) and the loss of calcium carbonate skeleton building reef fauna

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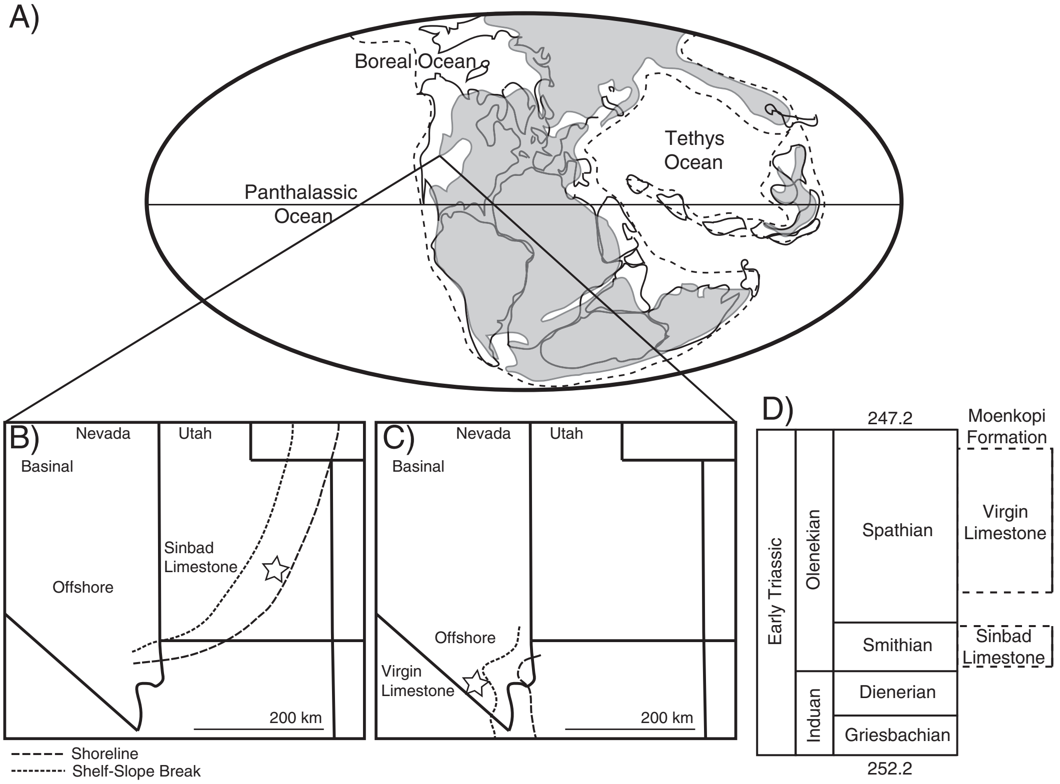

Fig. 1. Three maps depict the paleogeographic context and regional study sites for the Sinbad Limestone and Virgin Limestone and a time scale shows their position in Early Triassic time. A. A paleogeographic map of the Early Triassic depicts the global context for the Southwest United States localities (modified from Scotese, 2010). B. Map shows the study sites for the Sinbad Limestone in the San Rafael Swell (38°59′51.0″N, 110°40′53.2″W). Two dashed lines represent the shoreline and the shelf slope break. The Smithian Stage Sinbad Limestone of the Moenkopi Formation represents deposition under an epicontinental sea, therefore the onshore environment was wide (Blakey, 1974; Dean, 1981; Goodspeed and Lucas, 2007). (Map modified from Goodspeed and Lucas, 2007). C. The Virgin Limestone at Lost Cabin Springs in the Spring Mountains (base of section 36°05′00.0″N, 115°39′13.3″W) (Marenco et al., 2012). The relatively deep Spathian Stage Virgin Limestone of the Moenkopi Formation and the more narrow shelf contrast with the broad shoreface regions of the Smithian Sinbad Limestone. (Modified from Marzolf, 1993 and Woods, 2009). D. Time scale for the Early Triassic and stratigraphy of the Moenkopi Formation in Utah and Nevada (Mundil et al., 2004; Lehrmann et al., 2006; Shen et al., 2011).

and other invertebrates (Clapham and Payne, 2011; Kiessling and Simpson, 2011).

Environmental conditions did not improve following the extinction event. Rather, repeated perturbations within the carbon and oxygen isotope records indicate recurrent volcanic eruptions extended throughout the Early Triassic, which lasted for five million years following the extinction event (Fig. 2) (Payne et al., 2004; Sun et al., 2012). The largest negative carbon isotope excursion, occurring across the Smithian to Spathian boundary within the Olenekian, is correlated with the most negative oxygen isotope values suggesting that a large eruptive pulse drove extensive warming, producing equatorial sea surface temperatures over 35 °C (Sun et al., 2012). Extreme warming from increased atmospheric CO_2 resulted in gentle thermal gradients between the equator and poles that likely promoted sluggish ocean circulation and subsequent anoxic conditions (Wignall and Twitchett, 2002; Algeo et al., 2011a, 2011b; Grasby et al., 2013). Extensive equatorial oxygen minimum zones in the Panthalassic Ocean are indicated by dysaerobic and anaerobic facies in sections in Panthalassa as well as models of the Early Triassic ocean system (Wignall and Twitchett, 2002; Algeo et al., 2010; Winguth and Winguth, 2012). In addition to enduring expansive oxygen minimum zones, transient regional low oxygen events have been documented within each of the three major Early Triassic ocean basins, including the Panthalassic Ocean, Tethys Ocean, and Boreal Ocean (Twitchett, 1999; Woods et al., 1999; Mata and Bottjer, 2011; Beatty et al., 2008; Grasby et al., 2013). These low oxygen events were devastating for the benthic fauna and resulted in low diversity and low abundance of recovering taxa (Beatty et al., 2008; Grasby et al., 2013).

The effects of prolonged environmental stress on the recovery of the benthic fauna were ecologically profound. The Early Triassic benthos is often dominated taxonomically by a low diversity bivalve “disaster fauna” assemblage and limited additional taxa (Hallam and Wignall, 1997). Five particular genera: *Claraia*, *Eumorphotis*, *Leptochondria*, *Promyalina*, and *Unionites* are considered the most numerically abundant bivalves in the Early Triassic and all but *Claraia* remain important throughout the Early Triassic (Hallam and Wignall, 1997). The inarticulate brachiopod *Lingula* and a few additional bivalve species were also opportunistic taxa becoming abundant in the wake of the extinction (Rodland and Bottjer, 2001; Benton, 2003; Zonneveld et al., 2007; Chen and Benton 2012). In addition to the low diversity and low evenness that typify the Early Triassic benthos, the prevalence of extremely small body sizes, termed the “Lilliput Effect” (sensu Urbanek, 1993) is another ubiquitous phenomenon. Many classes of molluscs, foraminifera, and echinoderms show extremely small body size following the extinction event (Fraiser and Bottjer, 2004; Twitchett, 2007; Payne et al., 2011) although this is not ubiquitously the case (Chen and McNamara, 2006; McGowan et al., 2009; Brayard et al., 2010). This phenomenon is especially pervasive in the Smithian Sinbad Limestone of the Southwestern United States and the Lower Triassic Werfen Formation of the Italian Dolomites where “microgastropods,” under 10 mm in height, dominate the entire assemblages (Twitchett, 1999; Fraiser and Bottjer, 2004; Nützel and Schulbert, 2005; Twitchett, 2007). Their small size reflects the suite of environmental conditions that limited their growth, including high temperature and resultant metabolic changes, decreased oxygen solubility, and potentially limited nutrient availability (Irie and Fischer, 2009; Melatunan et al., 2013).