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The importance of oxygen for the disparate recovery patterns of the benthic macrofauna in the Early Triassic

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ABSTRACT

The end-Permian mass extinction, 252 million years ago, decimated life on Earth including the benthic marine invertebrate macrofauna. A return to pre-extinction levels of diversity and complex ecological systems took approximately 5 million years. This review provides the most up to date synthesis of the progression of the benthic marine invertebrate macrofaunal recovery. We found the rates and patterns of the benthic recovery to vary both across the globe and between different investigators. The continuation of deleterious environmental conditions including low oxygen concentrations and high temperatures likely played a large role in the delayed recovery. Ocean basins, such as Neo-Tethys, show evidence for continued oxygenation past the extinction event which extended the lifespan and diversity of specific benthic communities. Shortly after the extinction boundary, shoreface environments with moderate wave energy were sites of water column oxygenation that supported a more rapid return to diverse and ecologically complex benthic communities. We find that the location and longevity of oxygenated environments is an overarching mechanism that partially explains varied global recovery patterns. Synergistic perturbations including an acidification event at the Permian–Triassic boundary and high temperature events contributed to lasting environmental perturbations. In an effort to standardize future results and discussion of the benthic recovery, we support the use of a modified recovery rubric proposed here.

1. Introduction

The end-Permian mass extinction 252 million years ago was the most devastating crisis effecting life on Earth, resulting in the loss of approximately 95% of species on the planet (Erwin, 2006). The recovery from this event is commonly thought to have lasted up to five million years, including the entire Early Triassic, and is often considered to be a step like process (Hallam, 1991; Schubert and Bottjer, 1995; Galfetti et al., 2007; Tong et al., 2007; Chen et al., 2010; Pietsch and Bottjer, 2010; Chen and Benton, 2012). Study of the Early Triassic recovery interval provides an extensive geohistorical data set on the relationship between biotic and environmental recovery with application to the modern anthropogenic biological crises. To that purpose, the research community focuses on the chemical, geological, environmental, and biological conditions that existed during the recovery event. These studies by various interest groups span the globe and have produced a plethora of contrasting results about the rates and processes that dictated the benthic marine invertebrate recovery. This review will use the habitable zone (Beatty et al., 2008), an established relationship between oxygen and depositional energy gradients, and a revised ecological recovery rubric (Twitchett et al., 2004; Twitchett, 2006) to assess the benthic marine invertebrate recovery. The purpose of this analysis is to provide an overarching perspective on the Early Triassic literature and to develop evaluative tools for an improved study of disparate localities representing the recovery interval.

The hypothesized extinction mechanisms are the environmental changes resulting from the eruption of the Siberian Traps flood basalts. Before the main body of the eruption, the extinction may have been initiated by gaseous CO_2, SO_2, HF, and HCl released from the plume head and pipes (Saunders and Reichow, 2009; Svensen et al., 2009; Sobolev et al., 2011). The basalts intruded through evaporite beds, coal, and peat deposits leading to greater carbon and volatile release (Svensen et al., 2004, 2009). This was followed by the eruption which covered 7 million square kilometers (Courtillot and Renne, 2003). The release of volatile gasses is thought to be responsible for global warming, ocean stratification, and subsequent changes in ocean circulation that led to the development of oxygen minimum zones and widespread anoxia (Wignall and Twitchett, 1996; Hotinski et al., 2001; Winguth and Maier-Reimer, 2005; Chen and Benton, 2012; Joachimski et al., 2012; Sun et al., 2012). Increased atmospheric carbon is also associated with the development of ocean acidification at the extinction boundary and hypercapnic stress throughout the recovery interval (Caldeira and Wickett, 2003; Payne and Kump, 2007; Kiessling and Simpson, 2011; Chen and Benton, 2012; Hinojosa et al., 2012).

Compounding stressful marine conditions including increased temperatures, anoxia, euxinia, and hypercapnia were likely sustained beyond the extinction boundary into the Early Triassic by repeated eruptions of the Siberian Traps flood basalts (Payne et al., 2004; Knoll et al., 2007; Joachimski et al., 2012; Sun et al., 2012). Evidence for

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Table 1
The sedimentological, biological, and chemical indicators of ancient oxygen levels used in this review. Summarized from Wignall and Twitchett (1996, 2002) and references therein.

Sedimentological	
Fine laminations	Anoxic/low oxygen conditions reduce bioturbation, can also result from high sedimentation rate
High organic carbon content/black shales	Anoxic/low oxygen conditions reduce organic remineralization. High carbon content can also result from changes in productivity and sedimentation
Biological	
Low diversity, horizontal bioturbation or shallow bioturbation depth, small body size (Savrda and Bottjer, 1986)	Anoxic/low oxygen conditions reduce bioturbation depth and result in smaller trace maker body size.
“Paper pectens” such as *Claraia*	Thin shelled bivalve taxa resistant to dysoxic conditions (Wignall, 1994)
Chemical	
Depleted thorium/uranium	Th/U < 3 suggests enrichment of authigenic uranium (Langmuir, 1978; Myers and Wignall, 1987)
Pyrite (framboids)	Pyrite deposition and framboids are diagnostic of euxinic conditions (Wilkin et al., 1996)

continued eruptions comes from carbon isotope excursions documented at each of the major stage boundaries (Payne et al., 2004; Payne and Kump, 2007). Support for continued deleterious conditions comes from the geochemistry of the Early Triassic rock record. High temperatures at low latitudes are calculated from oxygen isotope data from South China sections (Joachimski et al., 2012; Sun et al., 2012). The oxygen isotope excursions and inferred warming events are correlated with carbon isotope excursions suggesting that additional carbon excursions throughout the Early Triassic would have been matched by temperature swings.

Low oxygen conditions also persisted in both the Tethyan and Panthalassic Oceans for much of the Induan and were sustained in Panthalassa through the Olenekian (Wignall and Twitchett, 2002; Woods, 2009). Evidence for extensive anoxic and low oxygen conditions spanning the Early Triassic include fine laminations and high organic carbon content as well as low diversity, shallow bioturbation (Table 1). Microbially dominated anachronistic facies suggest that the Early Triassic seafloor more closely resembled the low oxygen Precambrian before metazoan grazers were ecologically important (Pruss et al., 2006; Baud et al., 2007; Kershaw et al., 2012). Recent research suggests that in some areas, especially Neo-Tethys, the lack of abiotic carbonate fans and the presence of metazoans within the microbialites support a more regional control on microbialite development over widespread low oxygen perturbations (Kershaw et al., 2011, 2012). Euxinia is represented by biomarkers such as isorenieratane from sulfur reducing bacteria as well as changes in stable isotope ratios representing burial of isotopically depleted sulfur as pyrite (Raiswell and Berner, 1985; Grice et al., 2005). The effects of hypercapnia (CO_2 poisoning) are evidenced by the well-buffered, high-metabolic physiology of the fauna that were selected to survive the extinction event (Knoll et al., 2007). Recent reviews have co-opted the effects of hypercapnia into the role of ocean acidification in extinction and recovery intervals (Kiessling and Simpson, 2011; Payne and Clapham, 2012). A mechanism to explain the Early Triassic recovery should be able to incorporate most, if not all, of the aforementioned synergistic environmental perturbations.

This paper will present evidence in support of the relationship between depositional energy gradients, increased oxygenation, and therefore improved environmental conditions for the benthic invertebrate recovery. The habitable zone is a region of the Early Triassic shoreface that showed the greatest bioturbation intensity and trace fossil generic diversity (Fig. 1) (Beatty et al., 2008). The habitable zone is located above storm wave base where moderate wave activity persists. These higher energy environments are thought to be able to ameliorate dysoxic and anoxic conditions by mixing in atmospheric oxygen at a faster rate and to greater depths than diffusion processes alone (Wallace and Wirick, 1992; Beatty et al., 2008). The habitable zone is bounded on the shoreward side by the high wave stress regions of the swash and upper shoreface where biodiversity and trace preservation are reduced (Beatty et al., 2008; Zonneveld et al., 2010).

The habitable zone is an Early Triassic phenomenon resulting from unique environmental conditions. The Middle Triassic (Ladinian), the Cenozoic, and the Modern are not limited by deep water anoxia. Therefore, the greatest bioturbation diversity and intensity can be found in the proximal offshore, offshore transition, and lower shoreface environments (Fig. 1) (Zonneveld et al., 2010). In Griesbachian and Dienerian aged sections from British Columbia and Alberta, Canada the highest diversity and intensity of bioturbation is found in the lower shoreface and offshore transition while the proximal offshore is depauperate. The addition of oxygen through wave aeration into the habitable zone environment supported benthic re-diversification (Beatty et al., 2008). Anoxic conditions in the proximal offshore and basinal environments, below storm wave base, cannot be reached by wave mixed oxygen. These regions experienced reduced diversity and colonization in the Early Triassic relative to well oxygenated and highly colonized offshore environments in the modern (Bambach, 1977; Beatty et al., 2008; Zonneveld et al., 2010). During the Early Triassic, anoxic offshore water masses encroached on shelf settings in upwelling regions or during times of transgression making broad shelves and ramps the best for forming and sustaining a wide habitable zone (Fig. 2) (Woods, 2009; Zonneveld et al., 2010).

Wallace and Wirick (1992) have shown that modern storm events have the ability to inject lasting oxygen into deep marine settings. Their results show that high amplitude storm waves were correlated with rapid increases in oxygen saturation (up to 109%) at sensors placed at 19 m and 34 m depth. The proposed mechanism is the injection of pressurized air bubbles to depth by storm waves. The process of oxygen depletion was slow and lasted 5 to 15 days in cold water climates (0 °C at 19 m) and was likely the result of diffusion and respiration.

These findings are in support of the development of wave oxygenated habitable zones in the Early Triassic. In addition, cool water temperatures are an important control on oxygen saturation so we may expect that cooler, high-latitude settings were preferential for lasting oxygenation in the habitable zone (Beatty et al., 2008; Zonneveld et al., 2010).

The habitable zone was used as a lens by which to interpret recovery patterns for many other Early Triassic shelf ecosystems. We investigated the development of similar wave energy gradients in siliciclastic and carbonate shelf systems across the globe using sedimentological descriptions available from the literature. The efficacy of various environments including isolated platforms, shelves, and epicontinental seas in buffering the benthic invertebrate recovery is one focus of this paper. Benthic recovery was first documented and interpreted within individual stratigraphic sections and then various shoreface localities with habitable zone development were compared. Carbonate platform environments generally do not have the high energy shoreface environments necessary for the development of a habitable zone. However, the platform margin may have provided a moderate energy, oxygenated setting for benthic recovery. The role of local depositional environments may help to explain the observed patterns of differential recovery rates across the Early Triassic globe.

In addition to wave aeration general ocean basin characteristics might have also influenced the rate and pattern of recovery. In the