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Environmental controls on marine ecosystem recovery following mass extinctions, with an example from the Early Triassic

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ABSTRACT

The recovery of marine ecosystems following a mass extinction event involves an extended interval of increasing biotic diversity and ecosystem complexity. The pace of recovery may be controlled by intrinsic ecosystem or extrinsic environmental factors. Here, we present an analysis of changes in marine conditions following the end-Permian mass extinction with the objective of evaluating the role of environmental factors in the protracted (~5-Myr-long) recovery of marine ecosystems during the Early Triassic. Specifically, our study examines changes in weathering, productivity, and redox proxies in three sections in South China (Chaohu, Daxiakou, and Zuodeng) and one in northern India (Mud). Our results reveal: 1) recurrent environmental perturbations during the Early Triassic; 2) a general pattern of high terrestrial weathering rates and more intensely reducing marine redox conditions during the early Griesbachian, late Griesbachian, mid-Smithian, and (more weakly) the mid-Spathian; 3) increases in marine productivity during the aforementioned intervals except for the early Griesbachian; and 4) stronger and more temporally discrete intervals of environmental change in deepwater sections (Chaohu and Daxiakou) relative to shallow and intermediate sections (Zuodeng and Mud). Our analysis reveals a close relationship between episodes of marine environmental deterioration and a slowing or reversal of ecosystem recovery based on metrics of biodiversity, within-community (alpha) diversity, infaunal burrowing, and ecosystem tiering. We infer that the pattern and pace of marine ecosystem recovery was strongly modulated by recurrent environmental perturbations during the Early Triassic. These perturbations were associated with elevated weathering and productivity fluxes, implying that nutrient and energy flows were key influences on recovery. More regular secular variation in deepwater relative to shallow-water environmental conditions implies that perturbations originated at depth (i.e., within the oceanic thermocline) and influenced the ocean-surface layer irregularly. Finally, we compared patterns of environmental disturbance and ecosystem recovery following the other four "Big Five" Phanerozoic mass extinctions to evaluate whether commonalities exist. In general, the pace of ecosystem recovery depends on the degree of stability of the post-crisis marine environment.

Contents

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1. Introduction

Each major mass extinction event in the geologic record has been followed by an interval of restructuring of marine ecosystems, reflected in changes in clade dominance, ecological niche partitioning, and community organization (e.g., Erwin, 1998). Increased productivity among primary producers and consumers can generate ecological niches higher in the marine trophic system (Kirchner and Weil, 2000), allowing a progressive rebuilding of a stable, complex ecosystem structure (Chen and Benton, 2012). Although lacking a specific quantitative definition, "ecosystem recovery" is generally regarded as the reappearance of marine communities with a high biotic diversity and an integrated and complex structure that is stable at multimillion-year timescales (Harries and Kauffman, 1990). The progress of post-extinction recovery commonly has been evaluated using metrics related to overall biodiversity and/or species origination rates (e.g., Jacobsen et al., 2011; Payne et al., 2011). However, "ecosystem recovery" is not simply a return to pre-extinction levels of biodiversity but, rather, the expansion and re-integration of entire marine ecosystems or communities (Erwin, 2008; Chen and Benton, 2012) as reflected by metrics such as alpha diversity (i.e., within-community species richness; Bambach, 1977; Clapham et al., 2006) and ecological tiering (Twitchett, 1999; Fraiser, 2011).

In the case of the Permian–Triassic (P–Tr) boundary mass extinction, an initial, aborted recovery occurred soon after the end-Permian crisis, during the Induan stage of the Early Triassic (Baud et al., 2008; Brayard et al., 2009; Stanley, 2009), and a more sustained recovery took place during the late Olenekian stage (Spathian substage) (Chen et al., 2011; Payne et al., 2011; Song et al., 2011), but full ecosystem recovery probably did not occur until the Middle Triassic (Erwin and Pan, 1996; Bottjer et al., 2008; Chen and Benton, 2012). The recovery of marine invertebrate ecosystems following the end-Permian crisis was apparently the most protracted of any major mass extinction (Bottjer et al., 2008), i.e., the "Big Five" Phanerozoic mass extinctions of Sepkoski (1984, 1986). An important unresolved issue is what controlled the long duration of the post-extinction recovery interval during the Early Triassic. At least three hypotheses have been advanced, linking the protracted recovery to: (1) the intensity of the mass extinction (Sepkoski, 1984; Solé et al., 2002), (2) the persistence of harsh environmental conditions (Hallam, 1991; Isozaki, 1997; Payne et al., 2004; Erwin, 2007), and (3) episodic occurrence of strong environmental disturbances during the recovery interval (Algeo et al., 2007, 2008; Orchard, 2007; Retallack et al., 2011) (Fig. 1).

Examination of long-term records of Early Triassic marine environmental conditions has the potential to provide information relevant to these hypotheses. In this study, we (1) review existing literature on the recovery of marine ecosystems following the end-Permian mass extinction, (2) analyze changes in marine productivity and redox conditions at four locales in China and India from the latest Permian through the Spathian substage of the Early Triassic, (3) evaluate the importance

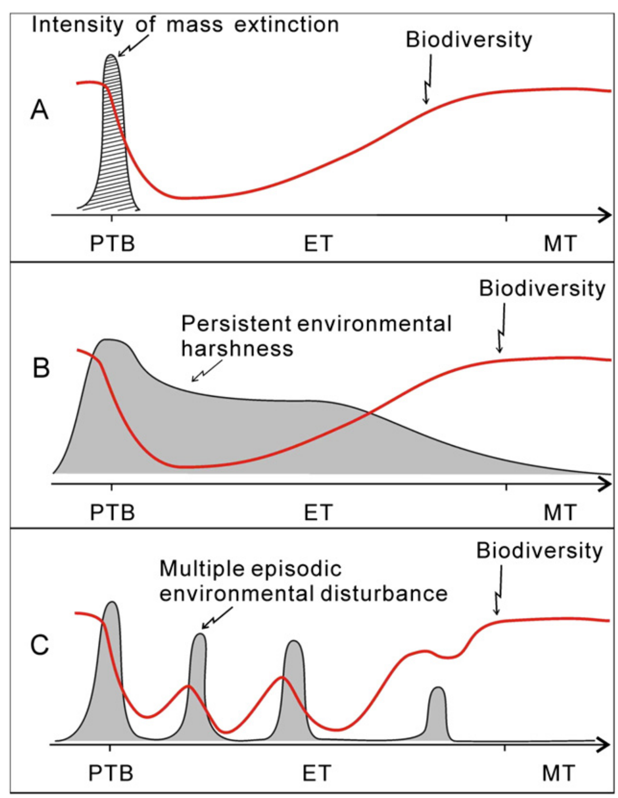

Fig. 1. Three hypotheses to account for the protracted recovery of Early Triassic marine ecosystems, linking it to (A) the intensity of the mass extinction (Solé et al., 2002); (B) the persistence of harsh environmental conditions (Hallam, 1991; Isozaki, 1997; Payne et al., 2004); and (C) the episodic recurrence of major environmental perturbations (Orchard, 2007; Stanley, 2009; Algeo et al., 2011a; Retallack et al., 2011). The heavy solid line represents a general biodiversity trend (cf. Tong et al., 2007b), and the shaded lines represent extinction intensity (A) or environmental stresses (B and C). PTB: Permian–Triassic boundary. ET: Early Triassic. MT: Middle Triassic.