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

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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.

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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 reintegration 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 (Spitian 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” Phanerzoic 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 Spitian 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.](image-url)
of marine environmental changes during the Early Triassic as controls on the marine ecosystem recovery, and (4) compare the Early Triassic marine ecosystem recovery with those following other Phanerozoic mass extinctions. Our comparative analysis of recoveries following each of the ‘Big Five’ Phanerozoic mass extinctions is intended to identify general features or patterns of marine ecosystem recovery and their relationships to contemporaneous environmental changes.

2. Background

2.1. The end-Permian biotic crisis

The end-Permian mass extinction was the most severe biocrisis of the Phanerozoic (Fig. 2; Erwin et al., 2002; Irmis and Whiteside, 2011). It killed ~80–96% of marine invertebrate species and ~70% of terrestrial vertebrate species (McKinney, 1995; Benton and Twitchett, 2003). There appear to have been two pulses of marine extinction (Yin et al., 2012; Song-HJ et al., 2013) and environmental disturbance (Xie et al., 2005, 2007), rather than a single event during this biocrisis (Rampino and Adler, 1998; Jin et al., 2000; Shen et al., 2011a). As an example, foram species in South China exhibit a ~57% extinction rate during the latest Permian pulse and a ~31% extinction rate during the earliest Triassic pulse (Song-HJ et al., 2013). According to high-precision U–Pb dating in South China sections, the interval between these extinction pulses was 60 ± 48 kyr (Burgess et al., 2014). The end-Permian mass extinction coincided with eruption of the Siberian Traps Large Igneous Province (Campbell et al., 1992; Renne et al., 1995; Reichow et al., 2009; Sobolev et al., 2011) as well as with major
environmental changes including global sea-level rise (Hallam and Wignall, 1999), ocean anoxia (Wignall and Twitchett, 1996; Isozaki, 1997), global warming (Joachimski et al., 2012; Sun et al., 2012; Romano et al., 2013), and, possibly, marine acidification (Payne et al., 2010; Hinojosa et al., 2012; Kershaw et al., 2012).

2.2. The Early Triassic marine ecosystem recovery

The recovery of marine ecosystems during the Early Triassic was a multi-step process. There were several phases of incomplete or aborted recovery during the Induan, and recovery from the P–Tr boundary mass extinction is generally regarded as not having been completed until the Middle Triassic, ~5 Myr after the end-Permian crisis (Mundil et al., 2010). Both benthic and planktonic cyanobacteria bloomed immediately after the end-Permian mass extinction (Fig. 2; Lehmann, 1999; Wang et al., 2005; Xie et al., 2005; Luo et al., 2011). Cyanobacterial microbialites reappeared episodically in different regions throughout the Early Triassic but they largely disappeared by the early Middle Triassic (Baud et al., 2007; Xie et al., 2010). An Early Triassic “chert gap” (Beauchamp and Baud, 2002) was caused by the loss of biosilica deposits from radiolarians and siliceous sponges, although occurrences of thin chert beds in the late Griesbachian and Dienerian (Kakuwa, 1996; Takemura et al., 2007; Sano et al., 2010) document a temporary local early recovery of siliceous faunas.

Some secondary consumers such as conodonts and ammonoids rebounded rapidly from the end-Permian mass extinction (Orchard, 2007; Brayard et al., 2009; Stanley, 2009). Their rapid recovery may have been assisted by a microphagous habit (Fischer and Bottjer, 1995), allowing them to benefit directly from increased biomass among primary producers. These clades subsequently declined during biocides at the end of Griesbachian, Smithian, and Spathian substages of the Early Triassic, although they tended to rediscover rapidly during the intervening intervals (Fig. 2; Brayard et al., 2009; Stanley, 2009). However, conodonts display a strong Lilliput effect during the Early Triassic, with smaller sizes of gastropod and bivalve shells were reduced across the P–Tr boundary and during the Griesbachian but returned to pre-extinction dimensions by the Anisian (Chen et al., 2013). Compared to conodonts and ammonoids, recovery rates for benthic primary consumers such as foraminifers, gastropods, bivalves, brachiopods and ostracods were more gradual (Fig. 2; Payne et al., 2011). Among foraminifers, a sustained diversity increase began in the early Smithian (early Olenekian) (Song et al., 2011) and accelerated during the Anisian (early Middle Triassic) (Payne et al., 2011). Similar recovery patterns are observed also among brachiopods (Chen et al., 2005a,b) and ostracods (Crassquin-Soleau et al., 2007). The sizes of gastropod and bivalve shells were reduced across the P–Tr boundary and during the Griesbachian but returned to pre-extinction dimensions by the Anisian (Fig. 2; Fraiser and Bottjer, 2004; Payne, 2005; Twitchett, 2007). However, the high diversity, low dominance, and ecological complexity of mollusc fauna during the late Griesbachian and early Dienerian at Shanggan, South China (Hautmann et al., 2011) and on the Wasit Block in Oman (Kristyn et al., 2003; Twitchett et al., 2004) may represent an early recovery phase of these faunas.

The meso-consumer trace-makers and reef-builders can shed light on the recovery of benthic marine ecosystems. Generally, trace-makers decreased during the end-Permian biocrisis and recovered slowly in the Early Triassic (Fig. 2; Pruss and Bottjer, 2004; Chen et al., 2011). Locally, trace-fossil diversity shows occasional peaks during the Griesbachian to Smithian (Twitchett and Wignall, 1996; Twitchett, 1999; Zonneveld et al., 2010; Chen et al., 2011). However, small trace-fossil burrow size, low tiering levels, and low ichnofabrics indices (bioturbation) generally persisted until the end of the Smithian substage, and the early Spathian is marked by a strong increase in trace-fossil diversity and complexity (Pruss and Bottjer, 2004; Chen et al., 2011). Nonetheless, Smithian ichnofaunas are less diverse than those of the Middle Triassic (Knauß, 2007). This pattern may suggest a step-wise recovery of trace-makers during Early to Middle Triassic (Twitchett and Barras, 2004). Furthermore, the recovery of trace-makers may have been diachronous, with a more rapid increase in ichnodiversity at high northern paleolatitudes than in the equatorial region (Pruss and Bottjer, 2004; Twitchett and Barras, 2004). With regard to reef-builders, a new metazoan reef ecosystem formed by various sponges and serpulid worms associated with microbial carbonates and euarkyotic organisms developed in the early Smithian, latest Smithian, and early to middle Spathian on the eastern Panthalassic margin, in Utah and Nevada (Fig. 2; Brayard et al., 2011). These equatorial sponge-microbe reefs are found as early as 1.5 Myr after the P–Tr boundary and represent a temporary recovery at least regionally (Brayard et al., 2011; Chen and Benton, 2012). However, the “reef gap”, as represented by the absence of heavily calcified corals, persisted through the Early Triassic (Payne et al., 2006).

As for the top trophic level in the marine ecosystem, predatory fish and reptiles displayed different recovery trajectories. Fishes were rare in the Griesbianh-to-Smithian equatorial ocean (Fig. 2; Fraiser et al., 2005; Tong et al., 2006; Zhao and Lu, 2007; Sun et al., 2012) but more common in the middle to late Spathian (Goto, 1994; Wang et al., 2001; Benton et al., 2013). High-latitude regions had a more abundant and diverse fish fauna in the Early Triassic than the equatorial ocean (Scheffer et al., 1976; Stemmerik et al., 2001; Mutter and Neuman, 2006; Romano and Brinkmann, 2010; Benton et al., 2013). Globally, fish diversity recovered by the Middle Triassic (Jin, 2006; Zhang et al., 2010; Hu et al., 2011). Marine reptiles first reappeared in the Smithian in high-latitude regions (Cox and Smith, 1973; Callaway and Brinkman, 1989) but later, in the Spathian, in equatorial regions (Li et al., 2002; Zhao et al., 2008). A high level of diversity among marine reptiles was achieved by the Middle to Late Triassic (Zhang et al., 2009).

To summarize, animals that were low in the marine trophic system tended to recover faster than those at higher trophic levels (Fig. 2; cf. Chen and Benton, 2012). Pelagic and nektonic faunas recovered faster than benthos as shown by rapid increases to multiple biodiversity peaks for ammonoids and conodonts during the Early Triassic, versus a slow return to pre-crisis diversity levels by the Middle Triassic for most bottom-dwellers. In Oleneik time, offshore benthos like calcareous algae and Tubiphytes recovered faster than those in nearshore environments in South China (Song et al., 2011). High-latitude biotas recovered faster than equatorial marine biota (Pruss and Bottjer, 2004). These differentiated responses may suggest that the pattern and intensity of environmental changes during the Early Triassic had an important influence on the pathways and tempo of marine ecosystem recovery.

2.3. Environmental change during the Early Triassic recovery

During the recovery interval following the end-Permian mass extinction, major changes in the environment related to volcanism, sea level, and paleoceanographic conditions took place. The eruption of the Siberian Traps large igneous province (LIP), which had begun at ~252 Ma close to the P–Tr boundary, continued strongly for ~1.5 Myr and more weakly for several million years longer (Fig. 3). The eruption history of this LIP is delineated by U–Pb ages for gabbroic intrusive rocks of 252 ± 4 Ma (Kuzmichev and Pease, 2007) and siliceous spong e 251.7 ± 0.4 (Kamo et al., 2003), an Ar Ar ages of 242.2 ± 0.6 Ma for a basalt (Reichow et al., 2009). This range of dates documents activity of the Siberian Traps LIP from 252 Ma to 242 Ma with a main eruptive phase at ~252 to 250 Ma (Reichow et al., 2009). Altogether, the Siberian Traps degassed ~6300 to 7800 Gt sulfur, ~3400 to 8700 Gt chlorine, and ~7100 to 13,600 Gt fluorine (Black et al., 2009). The eruption of the Siberian Traps large igneous province (LIP), which had begun at ~252 Ma close to the P–Tr boundary, continued strongly for ~1.5 Myr and more weakly for several million years longer (Fig. 3). The eruption history of this LIP is delineated by U–Pb ages for gabbroic intrusive rocks of 252 ± 4 Ma (Kuzmichev and Pease, 2007) and siliceous spong e 251.7 ± 0.4 (Kamo et al., 2003), an Ar Ar ages of 242.2 ± 0.6 Ma for a basalt (Reichow et al., 2009). This range of dates documents activity of the Siberian Traps LIP from 252 Ma to 242 Ma with a main eruptive phase at ~252 to 250 Ma (Reichow et al., 2009). Altogether, the Siberian Traps degassed ~6300 to 7800 Gt sulfur, ~3400 to 8700 Gt chlorine, and ~7100 to 13,600 Gt fluorine (Black et al., 2012). The high volatile contents increased the likelihood that volatiles reached the stratosphere and, thus, caused a drastic deterioration of global environments through direct toxicity and acid rainfall (Devine et al., 1984), ozone depletion (Johnson, 1980), and rapid climatic changes that may have included both global cooling (Sigurdsson et al., 1991).
1992; Wignall, 2001; Timmreck et al., 2010) and global warming (Ganino and Arndt, 2009). This interval coincided with a long-term eustatic rise from the Late Permian until the middle Late Triassic, with the most rapid rise during the Early Triassic (Fig. 3; Haq et al., 1987; Haq and Schutter, 2008).

Major changes in tropical sea-surface temperatures accompanied the P–Tr boundary crisis. Temperatures increased gradually from ~60 kyr prior to the mass extinction event and then spiked rapidly at the time of this event (Joachimski et al., 2012; Burgess et al., 2014). During the Early Triassic, temperatures reached a maximum in the mid- to late Griesbachian (~36–40 °C), cooled slightly during the latest Griesbachian to the early Smithian, and then reached a second peak of extreme warmth in the late Smithian (Fig. 3; Sun et al., 2012; Romano et al., 2013). A pronounced retreat from peak temperatures occurred in the early Spathian, an event resulting in a major turnover and geographic displacement of marine invertebrate faunas (Galfetti et al., 2007a,b; Stanley, 2009). A weak warming episode in the mid-late Spathian was followed by a second large cooling step around the Early–Middle Triassic boundary, yielding distinctly more moderate temperatures during the Anisian although still warmer than in the pre-extinction Late Permian (Sun et al., 2012; Romano et al., 2013).

Ocean redox conditions exhibit pronounced geographic and secular variation during the latest Permian and Early Triassic. More reducing conditions developed widely at mid-water depths (i.e., with the oceanic thermocline) during the pre-extinction late Changhsingian (Algeo et al., 2012; Shen et al., 2013; Feng and Algeo, 2014). The end-Permian crisis was marked by a transient expansion of anoxia into shallow-marine settings, especially in the Tethyan Ocean (Fig. 3; Horacek et al., 2007; Grice et al., 2005; Algeo et al., 2007, 2008; Bond and Wignall, 2010; Brennecka et al., 2011; Shen et al., 2011b), although some places (e.g., Oman, Iran).
remained oxic (Krystyn et al., 2003; Richoz et al., 2010). Thereafter, the Early Triassic is characterized by a complex pattern of redox variation (Song et al., 2012; Grasby et al., 2013). The intensity of anoxia appears to have declined during the Spathian, and episodes of marine anoxia seem to have terminated around the Early–Middle Triassic boundary (Hermann et al., 2011; Song et al., 2012).

Marine productivity can vary greatly during major biocrises (Kump and Arthur, 1999). Several factors during the P–Tr boundary crisis might have led to higher productivity: 1) phosphate liberated from sediments under anoxic conditions can stimulate productivity (Ingall and van Cappellen, 1990), and 2) intensified subaerial weathering can increase the flux of river-borne P to the oceans (Algeo and Twitchett, 2010; Algeo et al., 2011b). Variations in marine productivity can be reconstructed using carbon isotopes or elemental data (Kump and Arthur, 1999; Algeo et al., 2013; Schoepfer et al., 2014-this volume). The “biological pump” removes 13C-enriched carbon from the ocean-surface layer and transfers it to the ocean thermocline, producing a vertical gradient in the δ13C of dissolved inorganic carbon (Δ34CDOC). Changes in Δ34CDOC can thus provide information about the intensity of the organic carbon sinking flux and, indirectly, primary productivity (Hilting et al., 2008). A large vertical δ34CDOC gradient in the Nanpanjiang Basin of South China was interpreted as evidence of elevated marine productivity during the Early Triassic (Fig. 3; Meyer et al., 2011), although this gradient has also been attributed to intensified water-column stratification (Song-HY et al., 2013; Luo et al., 2014). However, an analysis of marine productivity changes based on organic carbon burial fluxes suggested a productivity crash in Early Triassic seas of the South China craton (Algeo et al., 2013). The large-carbon-isotope excursions of the Early Triassic (Payne et al., 2004; Tong et al., 2007a; Clarkson et al., 2013) were hypothesized to have been due to marine productivity fluctuations (Algeo et al., 2011b), an inference supported by patterns of δ13C–δ18S covariation (Song et al., 2014). The ultimate control on these fluctuations appears to have been temperature, with warm intervals associated with reduced productivity (Song et al., 2014).

Seawater pH values may have fluctuated during the P–Tr boundary crisis, as shown by analysis of calcium isotopes (Payne et al., 2010; Hinojosa et al., 2012). Calcium isotopic fractionation caused by the precipitation of carbonate minerals results in 40Ca-rich marine sediments and 44Ca-rich in seawater (Skulan et al., 1997; De La Rocha and van Cappellen, 2000; Fantle and DePaolo, 2005; Tang et al., 2008). Abrupt reductions of δ44/40Ca in both bulk carbonate and conodont apatite, representing a shift in seawater δ44/40Ca, occurred synchronously with the end-Permian biocrisis (Fig. 3; Payne et al., 2010; Hinojosa et al., 2012). The underlying cause of this change may have been eruption of the Siberian Traps, which injected a large amount of CO2 into the atmosphere-ocean system, causing seawater acidification and increased riverine 40Ca-rich calcium input owing to accelerated terrestrial weathering of carbonates (Payne et al., 2010; Blätter et al., 2011). Ocean acidification during Permian–Triassic transition may lead to the preferential extinction of heavily calcified marine organisms (Knoll et al., 2007; Clapham and Payne, 2011; Kiessling and Simpson, 2011) and could explain the abrupt transition on carbonate platforms from skeletal to microbial and abiogenic carbonate factories described by Kershaw et al. (2011).

To summarize, eruption of the Siberian Traps during the Late Permian to Early Triassic resulted in a major perturbation of the atmosphere–ocean system. Environmental changes linked to early phases of the eruption appear began slowly during an interval of at least ~60 kyr preceding the main mass extinction, but accelerated sharply at the end of the Permian. Major environmental effects related to continuing eruption of Siberian Traps flood basaltss persisted for ~1.5 to 2.0 million years during the Early Triassic, with some effects continuing until the Early–Middle Triassic boundary, nearly 5 million years after the end of the Permian. The main phase of the eruption, coinciding with the Induan Stage of the Early Triassic, coincided with highly disturbed marine ecosystems, sea-level rise, seawater acidification, and widespread oceanic anoxia. These relationships show that environmental instability coincided with, and probably caused or contributed to, the delayed recovery of marine ecosystems during the Early Triassic.

3. Study sections

Three of the sections chosen for this study are from the South China craton, which was located in the eastern Paleotethys Ocean during the Permian–Triassic transition. The Chaohu section was deposited in a deep ramp setting on the northeastern (paleo-northernwestern) margin of this craton, Daxiangou on the mid-ramp of the same margin, and Zuodeng on a shallow carbonate platform within the Nanpanjiang Basin on the southwestern (paleo-southern) margin of this craton (Fig. 4A). These sections were widely separated, with a distance of ~650 km between Chaohu and Daxiangou, and a distance of ~950 km between the latter and Zuodeng. The fourth study section is Mud, from the Spiti Valley of northern India, which was located in the south-central Neotethys Ocean during the Permian–Triassic transition (Fig. 4B). We collected a total of 794 samples from 167 m of section at Chaohu, 302 samples from 71 m of section at Daxiangou, 351 samples from 109 m of section at Zuodeng, and 135 samples from 26.5 m of section at Mud. Average sample spacing thus ranges from 20 to 31 cm for the four study sections, which equates to an average temporal interval of ~4 to 10 kyr between samples (see Supplementary Table 1 for the geologic timescale used in this study, and the Supplementary Information for age–depth models of the study sections).

3.1. Chaohu, Anhui Province, China

The Chaohu section is located in proximity to Chaohu city in Anhui Province (Fig. 4A). It is a composite section comprising sections at West Majiashan, West Pingdingshan, and South Majiashan, all of which are located within a ~1-km2 area (Tong et al., 2003). These sections contain, respectively, the narrow P–Tr boundary interval, the Griesbachian to Smithian, and the Spathian (Fig. 5), according to conodont biostratigraphic data (Zhao et al., 2007). The top of the South Majiashan section coincides approximately with the Spathian–Anisian (Early–Middle Triassic) boundary (Zhao et al., 2007). During the Early Triassic, the Chaohu area was on the deep lower margin of a ramp about 300 km to the north (paleo-west) of the Cathaysia Oldland (Fig. 4A; Tong et al., 2003). Estimated depositional water depths in the Chaohu area were ~300–500 m (Song-HY et al., 2013). However, relative sea-level elevations began to decrease during the Spathian (Tong et al., 2001, 2007b; Chen et al., 2011) as a consequence of a collision between the North China and South China blocks that culminated in the late Middle Triassic (Li, 2001).

This section has been subject to detailed analysis of conodont and ammonoid biostratigraphy (Zhao et al., 2007), sequence stratigraphy (Tong, 1997; Li et al., 2007), carbon isotopes (Tong et al., 2007a), and palaeomagnetic polarity (Tong et al., 2003), permitting development of a high-resolution geochronological framework for this study. The West Pingdingshan section is a candidate for the Global Stratotype Section and Point (GSSP) of the Induan–Olenekian boundary (Tong et al., 2003). Conodonts are found in abundance in the upper Griesbachian through Dienerian-Smithian boundary, the middle Smithian, and lower Spathian but are rarer in other stratigraphic intervals (Tong et al., 2003; Zhao et al., 2007). Foraminifers are found in the Induan stage (Song et al., 2011), ammonoids are particularly abundant around the Smithian–Spathian boundary, and some marine vertebrate fossils are found in the Olenekian (Tong et al., 2003).

The carbonate fraction of the sediment shows an increase upsection at Chaohu, from ~30% around the P–Tr boundary to ~40–70% in the Griesbachian and Dienerian, ~75% in the Smithian (except for a local decline to ~20% in the mid-Smithian), and ~87% in the Spathian (Fig. 5, Supplementary Table 2). Chert, which is probably mainly of biogenic origin, decreases upsection, from ~28% around the P–Tr boundary to ~5%
in the Spathian. Clay-mineral content shows a similar upsection decrease, from ~50% around the P–Tr boundary to ~8% in the Spathian. These mineralogic changes are reflected in an upsection shift in lithology from cherty mudrock with minor limestone interbeds around the P–Tr boundary to thin-bedded marls with mudrock interbeds in the Griesbachian and Dienerian, dominant mudrock with marlstone interbeds in the Smithian, and thick-bedded limestone with marlstone interbeds in the Spathian (Fig. 5; Tong et al., 2003, 2007a; Guo et al., 2008).

3.2. Daxiakou, Hubei Province, China

The Daxiakou section is located in Xingshan county, Yichang city, in the Yangtze Gorge area of Hubei Province (Fig. 4A). During the Early Triassic, it was located in a deep-ramp setting on the northern margin of the South China Block (Tong and Yin, 2002; Zhao et al., 2005), ~850 km from the Kangdian Oldland (Fig. 4A). Conodont biostratigraphy shows that the section spans the early Changhsingian through mid-Smithian interval (Zhao et al., 2005). Fossils of ammonoids, conodonts, and bivalves, among others are found in particular abundance in upper Dienerian to lowermost Smithian strata (Li et al., 2009), implying relatively high primary productivity at that time (Tong, 1997). Estimated depositional water depths in the Daxiakou area were ~200–300 m (Song-HY et al., 2013).

The carbonate component is high (~80%) throughout the section except for the P–Tr boundary interval and in Dienerian to lower Smithian strata (Fig. 5, Supplementary Table 3). In the P–Tr transition, average carbonate, chert, and clay-mineral contents are ~30%, ~20%, and 50%, respectively, and strata consist of thin-bedded, dark-gray to black cherty shales (cf. Wu et al., 2012). In the Dienerian to lower Smithian, average carbonate, chert, and clay-mineral contents are ~60%, ~10%, and ~30%, respectively, and strata consist of marlstones with mudrock intercalations.

3.3. Zuodeng, Guangxi Province, China

The Zuodeng section is located in Zuodeng county, Tiandong city, in Guangxi Province. During the Early Triassic, this section was located on a carbonate platform (the Debao Platform) within the Nanpanjiang Basin (Fig. 4A), a deep-marine embayment on the southwestern (paleo-southeastern) margin of the South China Block that existed from the Late Paleozoic to the Late Triassic (Enos et al., 1997). The Debao Platform was one of many isolated, shallow carbonate platforms within this basin, the largest being the Great Bank of Guizhou (Lehmann et al., 2007). The Nanpanjiang Basin was adjacent to a subduction-zone volcanic arc along the South China–Indochina plate margin (Cai and Zhang, 2009), where volcanism was more intense than on the northern margin of the South China Block (e.g., Xie et al., 2010). This section ranges from the upper Changhsingian through the lower Spathian, as shown by conodont biostratigraphy (Yang et al., 1986; Tong et al., 2007a). Abundant gastropods and ostracods are found in the upper Griesbachian (Wang et al., 2001) and prolific ammonoids, conodonts, and fishes in the lowermost Smithian (Yang et al., 1986). Estimated depositional water depths in the Zuodeng area were ~30–50 m based on the energy subtidal feature of the Lower Triassic limestones for the Debao isolated platform (next to the Pingguo isolated platform, Lehmann et al., 2007).

Carbonate content at Zuodeng is much higher than for the other study sections, averaging ~95% in upper Changhsingian to Spathian strata with a small decrease to ~80% in the upper Smithian (Fig. 5, Supplementary Table 4). This section consists mainly of thin- to thick-bedded limestone (cf. Wang et al., 2001). The lack of data around the P–Tr boundary is due to this interval being covered at the time of sample collection.

3.4. Mud, Spiti Valley, India

The Mud section is located in the Spiti Valley, which is part of the district of Lahul and Spiti, a central area of the western Himalaya in northern India. Lower Triassic strata are well exposed in this area. During the Early Triassic, the study area was located at mid-southern latitudes (~30–35°S) on the northern Gondwana margin (Fig. 4B; Krystyn et al., 2007). Middle Permian rifting (Stampfli et al., 1991; Garzanti et al., 1996) resulted in the formation of the Neo-Tethys Ocean (Stampfli et al., 1991; Garzanti et al., 1996), and the surface uplift of the rift shoulders resulted in widespread non-deposition, erosion and the unconformities in the stratigraphic record (Stampfli et al., 1991; Garzanti et al., 1996). The study section was deposited in a mid-shelf setting having a gentle slope, as implied by the modest water depths of deposition (~50–70 m) despite the distal location of the section (Krystyn et al., 2007).

The base of this section consists of Wuchiapingian to lower Changhsingian strata that are overlain by an unconformity (or highly condensed interval) spanning the upper Changhsingian and lower Griesbachian (Bhargava et al., 2004). The main part of the study section consists of a conformable succession of mid-Griesbachian to lowermost Spathian strata. Ammonoids are common in the upper Griesbachian to
lower Smithian interval (Krystyn and Orchard, 1996; Krystyn et al., 2007). Average ammonoid shell size decreases from large in the lower Smithian to small in the middle Smithian (Krystyn et al., 2007), suggesting the development of more hostile environmental conditions at that time. Current bedforms are consistent with a well-oxygenated watermass during the earliest Smithian (Krystyn et al., 2007). The Mud section is a candidate GSSP for the Induan–Olenekian boundary, which was formerly placed at the Bed 12/13 contact (Krystyn et al., 2007) but has been revised downward to approximately the Bed 9/10 contact (Brühwiler et al., 2010).

The Wuchiapingian to lower Changhsingian strata are composed of siliceous shale, with a ~25% chert fraction (Fig. 5, Supplementary Table 5). A sharp change in lithology occurs at the P–Tr unconformity, with Lower Triassic strata consisting dominantly of carbonates. However, low carbonate content is found in limited intervals of the Dienerian and lower Spathian, which consist mainly of marlstones (cf. Krystyn...
For most of Lower Triassic strata, it consists of thin-bedded argillaceous limestone with shale intercalation (e.g., Krystyn et al., 2007) and the average carbonate, shale and chert are ~78%, ~16% and ~6%, respectively (Fig. 5).

4. Results

We report raw values for geochemical proxies for terrestrial chemical weathering, marine productivity, and marine redox conditions in Sections 4.1 to 4.3. We then used an age-thickness model for each study section (see Supplementary Information for details) in order to calculate fluxes for the same proxies (Sections 4.4 to 4.6). All raw chemostratigraphic data and calculated flux values for the four study sections are given in Supplementary Tables 2 to 5.

4.1. Weathering proxies

We used Al and Fe concentrations as well as the chemical index of alteration (CIA) to evaluate terrestrial weathering changes during the Early Triassic. In predominantly carbonate successions such as those of the present study, increases in Al and Fe (which are present mainly in clay minerals) can be due to climatically controlled fluctuations in subaerial weathering rates (cf. Sageman et al., 1997). CIA was calculated as Al2O3 / (A12O3 + K2O + Na2O) (see Supplementary Information for details). It is a widely used proxy in reconstructing paleoclimate since it is interpreted as a measure of the extent of conversion of feldspars related to the weathering (Young and Nesbitt, 1998; Price and Velbel, 2003).

Note that the CIA results for each study section are described in conjunction with weathering fluxes (Section 4.4).

At Chaohu, Al ranges from ~0.1 to 15.0%, with an average value of 4.6% (Fig. 6A). It shows generally high values from the P–Tr boundary to the Smithian, followed by generally lower values in the Spathian. Fe ranges from ~0.1 to 14.9%, with an average value of 2.7%. Fe shows a similar pattern to Al throughout the study section.

At Daxiakou, Al ranges from ~0.1 to 18.1%, with an average value of 2.3% (Fig. 6B). It shows lower values in the early Griesbachian and the early Spathian and higher values from the late Griesbachian through the Dienerian with a short interlude of relatively low values in the early Dienerian. Fe ranges from ~0.1 to 9.0%, with an average value of 1.5%. Fe shows a similar pattern to Al within the Induan stage.

At Zuodeng, Al ranges from ~0.1% to 14.3%, with an average value of 0.8% (Fig. 6C). It shows relatively higher values from the late Dienerian to the early Smithian, in the late Smithian, and in the middle Spathian but very low values in other intervals. Fe ranges from ~0.1 to 5.0%, with an average value of 0.6%. Fe shows a similar pattern to Al throughout the study section except for the late Griesbachian, where the Al profile shows several peaks that the Fe profile does not.

At Mud, Al ranges from ~0.1 to 11.4%, with an average value of 3.5% (Fig. 6D). It shows high values from the end of the Griesbachian to earliest Smithian and at the end of the Smithian but low values during most of the Smithian. Fe ranges from 0.4 to 20.7%, with an average value of 2.8%. Fe shows high values from the late Griesbachian to earliest Dienerian and in the early Smithian but low values during most of the Dienerian and Smithian. The Fe and Al profiles show rather different patterns in this section.

4.2. Productivity proxies

We used TOC, phosphorus (P), and excess barium (Baex) concentrations to evaluate marine productivity fluxes during the Early Triassic. Baex was calculated as the amount of non-detrital barium (see Supplementary Information for details). These are widely used proxies for paleoceanic productivity since their accumulation depends on organic matter abundance and preservation (Tribovillard et al., 2006; Calvert and Pedersen, 2007). A method to estimate actual paleoceanic productivity values was developed by Schoepfer et al. (2014-this volume), who estimated regression equations to evaluate primary and export production as a function of TOC and P mass accumulation rates (MARs) using published data from Cenozoic sediment cores.

To evaluate TOC, we used Relationships 3 and 7 (Fig. 7A). At Chaohu, TOC ranges from 0.02 to 5.17%, with an average value of 0.28%. It shows high values at the P–Tr boundary and in the mid-Spathian, and moderately high values from the late Griesbachian to early Dienerian, the late Dienerian to earliest Smithian, and the mid to late Smithian. In contrast, it shows low values in the mid-Griesbachian, early Smithian, and most of the Spathian. P ranges from ~0 to 0.52%, with an average value of 0.03%. Baex ranges from 0.29 to 2992 ppm, with an average value of 176 ppm. Both P and Baex show patterns of variation that are similar to that of TOC, although Baex exhibits relatively higher values in the late Griesbachian and mid to late Smithian.

At Daxiakou, TOC ranges from 0.06 to 4.65%, with an average value of 0.30% (Fig. 7B). It shows high values at the P–Tr boundary but relatively low values from the Griesbachian to early Smithian. P ranges from ~0 to 2.23%, with an average value of 0.03%. It exhibits a different pattern from TOC, showing relatively high values at the P–Tr boundary and in the late Griesbachian to early Smithian and low values in the mid-Griesbachian and early to mid-Spathian. Baex ranges from 1.51 to 895 ppm, with an average value of 78 ppm. It shows a slightly different pattern, with high values at the P–Tr boundary and from the end-Griesbachian to the early Smithian and relatively lower values in the mid-Griesbachian and mid-Dienerian.

At Zuodeng, TOC ranges from 0.06 to 1.52%, with an average value of 0.15% (Fig. 7C). It shows generally low values for the entire Early Triassic, although with a small increase during the late Griesbachian–early Dienerian and the early Smithian. P ranges from ~0 to 0.30%, with an average value of 0.01%. It exhibits a different pattern from TOC, with generally high values during the late Smithian and Spathian (punctuated by peaks in the end-Smithian and mid-Spathian) and low values from the Griesbachian to mid-Smithian. Baex ranges from 0.39 to 920 ppm, with an average value of 40 ppm. It shows low values (<30 ppm) through most of the Early Triassic but two peaks in the mid-Dienerian and mid-Spathian.

At Mud, TOC ranges from 0.07 to 2.71%, with an average value of 0.49% (Fig. 7D). It shows high values in the Dienerian and low values in the late Griesbachian, Smithian, and early Spathian. P ranges from 0.01 to 0.85%, with an average value of 0.07%. It shows a gradual upsection decrease. Baex ranges from 0.1 ppm to 1723 ppm, with an average value of 166 ppm. It shows high values in the Dienerian and late Griesbachian, and low values in the Smithian and early Spathian.

4.3. Redox proxies

We used Mo, U, and V concentrations to evaluate ocean redox changes during the Early Triassic. Redox-sensitive trace elements typically become enriched in marine sediments under reducing conditions (Algeo and Maynard, 2004; Algeo and Lyons, 2006; Tribovillard et al., 2006; Algeo and Tribovillard, 2009). Reducing conditions, characterized by low O2 and/or high H2S concentrations in bottomwaters, are produced by some combination of decreased ventilation, commonly due to sluggish watermass circulation, and high respiratory oxygen demand, commonly due to a high sinking flux of organic matter (Pedersen and Calvert, 1990).

At Chaohu, Mo ranges from ~0 to 149 ppm, with an average of 3.4 ppm (Fig. 8A). U ranges from ~0 to 52 ppm, with an average of 3.5 ppm. V ranges from ~1 to 2892 ppm, with an average of 110 ppm. For all three proxies, high values are observed at the P–Tr boundary and in the late Griesbachian, Dienerian, and late Smithian. In addition, the V profile exhibits enrichment in the mid-Smithian, and both the Mo and V profiles show a short episode of somewhat higher values in the early Smithian.

At Daxiakou, Mo ranges from ~0 to 604 ppm, with an average of 7.3 ppm (Fig. 8B). U ranges from ~0 to 39 ppm, with an average of...
2.9 ppm. V ranges from <1 to 1326 ppm, with an average of 53 ppm. For all three proxies, high values are observed at the P–Tr boundary and in the Dienerian, and V shows an additional peak in the late Griesbachian that is not seen in the Mo and U profiles.

At Zuodeng, Mo ranges from ~0 to 102 ppm, with an average of 3.8 ppm (Fig. 8C). U ranges from ~0 to 68 ppm, with an average of 6.8 ppm. V ranges from ~0 to 162 ppm, with an average of 14.0 ppm. For all three proxies, high values are observed in the late
Dienerian and Smithian, with additional enrichment of V in the early Spathian.

At Mud, Mo ranges from 1 to 24 ppm, with an average of 2.4 ppm (Fig. 8D). U ranges from 0.3 to 7.3 ppm, with an average of 2.0 ppm. V ranges from 10 to 528 ppm, with an average of 132 ppm. For all three proxies, high values are observed in the Dienerian.

4.4. Weathering fluxes

At Chaohu, the Al flux ranges from <0.1 to 36 g m⁻² y⁻¹, with an average of 6.4 g m⁻² y⁻¹ (Fig. 9A). The Fe flux ranges from <0.1 to 25 g m⁻² y⁻¹, with an average of 3.9 g m⁻² y⁻¹. Both fluxes increase sharply at the P–Tr boundary and show peak values during the Griesbachian and Smithian, with a smaller increase in the early Spathian. The CIA ranges from 0.47 to 0.99, with an average of 0.75. High CIA values are found at the P–Tr boundary and in the Spathian.

At Daxiakou, the Al flux ranges from <0.1 to 33 g m⁻² y⁻¹, with an average of 3.8 g m⁻² y⁻¹ (Fig. 9B). The Fe flux ranges from <0.1 to 18 g m⁻² y⁻¹, with an average of 2.7 g m⁻² y⁻¹. Both fluxes increase sharply at the P–Tr boundary and show peak values during the Griesbachian and Smithian. The CIA ranges from 0.50 to 0.96, with an average of 0.80. High CIA values are found at the P–Tr boundary and in the late Griesbachian and Smithian, with significantly lower values in the mid-Griesbachian and Dienerian.

At Zuodeng, the Al flux ranges from <0.1 to 11.7 g m⁻² y⁻¹, with an average of 0.46 g m⁻² y⁻¹ (Fig. 9C). The Fe flux ranges from <0.1 to 3.7 g m⁻² y⁻¹, with an average of 0.37 g m⁻² y⁻¹. The Fe flux is relatively larger during the late Griesbachian, whereas the Al flux is greater during the late Dienerian; both fluxes exhibit higher values during the Smithian and early Spathian. The CIA ranges from 0.39 to 0.99, with an average of 0.81. Relatively higher CIA values are observed in the Griesbachian and Smithian.

At Mud, the Al flux ranges from <0.1 to 6.2 g m⁻² y⁻¹, with an average of 1.1 g m⁻² y⁻¹ (Fig. 9D). The Fe flux ranges from <0.1 to 11.7 g m⁻² y⁻¹, with an average of 0.46 g m⁻² y⁻¹. Both fluxes increase sharply at the P–Tr boundary and show peak values during the Griesbachian and Smithian. The CIA ranges from 0.47 to 0.99, with an average of 0.75. High CIA values are found at the P–Tr boundary and in the Spathian.
3.7 g m\(^{-2}\) y\(^{-1}\), with an average of 0.8 g m\(^{-2}\) y\(^{-1}\). Both fluxes are large during the late Griesbachian and late Smithian, and Fe additionally shows a peak around the Dienerian–Smithian boundary. The CIA ranges from 0.40 to 0.98, with an average of 0.72. High CIA values are observed in the late Griesbachian and Smithian.

Summarizing patterns of variation in the weathering proxies, high Al and Fe concentrations are observed mainly at the P–Tr boundary and in the late Griesbachian, Dienerian, and mid to late Smithian (Fig. 6). With regard to fluxes, the main peaks in the Al and Fe profiles are at the P–Tr boundary and in the late Griesbachian and mid to late Smithian (Fig. 9). Thus, these intervals were probably associated with enhanced inputs of terrestrial detrital material to the marine study areas. The similar trends of these geochemical proxies despite differences in lithology among the four study sections suggest that lithologic variation did not exert a strong influence on these proxies. CIA values show essentially the same patterns of secular variation as the Al and Fe fluxes. This is a significant observation because CIA is independent of secular variation in bulk–sediment fluxes and, thus, serves to confirm patterns of secular variation in the other weathering proxies.

4.5. Productivity fluxes

At Chaohu, the TOC flux ranges from 0.01 to 3.9 g m\(^{-2}\) y\(^{-1}\), with an average of 0.36 g m\(^{-2}\) y\(^{-1}\) (Fig. 10A). The P flux ranges from 0.1 to 658 mg m\(^{-2}\) y\(^{-1}\), with an average of 48.5 mg m\(^{-2}\) y\(^{-1}\). The Bax flux ranges from ~0 to 451 mg m\(^{-2}\) y\(^{-1}\), with an average of 27 mg m\(^{-2}\) y\(^{-1}\). All three proxies show a similar pattern of secular variation, with peak fluxes in the mid to late Griesbachian and the Smithian, and smaller increases around the P–Tr boundary and in the early Spathian.

At Daxiakou, the TOC flux ranges from ~0.01 to 2.1 g m\(^{-2}\) y\(^{-1}\), with an average of 0.32 g m\(^{-2}\) y\(^{-1}\) (Fig. 10B). The P flux ranges from 0.5 to 6395 mg m\(^{-2}\) y\(^{-1}\), with an average of 64.6 mg m\(^{-2}\) y\(^{-1}\). The Bax flux

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ranges from 0 to 350 mg m\(^{-2}\) y\(^{-1}\), with an average of 10 mg m\(^{-2}\) y\(^{-1}\).

All three proxies show a similar pattern of secular variation, with peak fluxes in the Griesbachian and Smithian.

At Zuodeng, the TOC flux ranges from 0.03 to 0.93 g m\(^{-2}\) y\(^{-1}\), with an average of 0.09 g m\(^{-2}\) y\(^{-1}\) (Fig. 10C). The P flux ranges from 0.1 to 169.5 mg m\(^{-2}\) y\(^{-1}\), with an average of 5.7 mg m\(^{-2}\) y\(^{-1}\). The Baxs flux ranges from ~0 to 61 mg m\(^{-2}\) y\(^{-1}\), with an average of 2 mg m\(^{-2}\) y\(^{-1}\). The TOC and Baxs profiles show similar patterns of secular variation characterized by peak values in the late Griesbachian to early Dienerian, with low values through the remainder of the section. In contrast, the P profile shows peak values in the late Smithian to early Spathian, with low values through the remainder of the section.

At Mud, the TOC flux ranges from 0.01 to 1.5 g m\(^{-2}\) y\(^{-1}\), with an average of 1.1 g m\(^{-2}\) y\(^{-1}\) (Fig. 10D). The P flux ranges from 1.9 to 183 mg m\(^{-2}\) y\(^{-1}\), with an average of 20.3 mg m\(^{-2}\) y\(^{-1}\). The Baxs flux ranges from ~0 to 115 mg m\(^{-2}\) y\(^{-1}\), with an average of 6 mg m\(^{-2}\) y\(^{-1}\). Patterns of secular variation differ among the three productivity-proxy fluxes. The P flux profile most closely matches secular variation in the South China sections, with high values in the late Griesbachian and Smithian, and low values in the Dienerian. In contrast, the TOC flux profile for Mud peaks in the Dienerian and shows low values in the Griesbachian and Smithian, and the Baxs flux profile peaks in the mid to late Smithian and shows low values through the remainder of the section.

Summarizing patterns of variation in the productivity proxies, high TOC, P and Baxs concentrations are found mainly at the P–Tr boundary and in the late Griesbachian, Dienerian, and mid to late Smithian, with a smaller peak in the early Spathian (Fig. 7). With regard to fluxes, the main peaks in the TOC, P and Baxs profiles are in the late Griesbachian and mid to late Smithian (Fig. 10). Thus, these intervals were probably associated with elevated rates of marine productivity relative to the remainder of the Early Triassic. In contrast to the weathering proxies, the productivity proxies exhibit low values around the P–Tr boundary, suggesting a decline in marine productivity during the end-Permian crisis interval.

### 4.6. Redox fluxes

At Chaohu, the Mo flux ranges from 0.01 to 11 mg m\(^{-2}\) y\(^{-1}\), with an average of 0.29 mg m\(^{-2}\) y\(^{-1}\) (Fig. 11A). The U flux ranges from 0.01 to 350 mg m\(^{-2}\) y\(^{-1}\), with an average of 10 mg m\(^{-2}\) y\(^{-1}\).
3.0 mg m$^{-2}$ y$^{-1}$, with an average of 0.38 mg m$^{-2}$ y$^{-1}$. The V flux ranges from the 0.1 to 174 mg m$^{-2}$ y$^{-1}$, with an average of 11 mg m$^{-2}$ y$^{-1}$. All three proxies show similar patterns of secular variation, with peak fluxes in the Griesbachian and Smithian. The Mo and U profiles also show a peak around the P–Tr boundary, and the Mo and V profiles show another peak in the early Spathian.

At Daxiakou, the Mo flux ranges from 0.01 to 2.1 mg m$^{-2}$ y$^{-1}$, with an average of 0.19 mg m$^{-2}$ y$^{-1}$ (Fig. 11B). The U flux ranges from 0.01 to 2.6 mg m$^{-2}$ y$^{-1}$, with an average of 0.27 mg m$^{-2}$ y$^{-1}$. The V flux ranges from 0.01 to 73 mg m$^{-2}$ y$^{-1}$, with an average of 5.9 mg m$^{-2}$ y$^{-1}$. All three proxies show similar patterns of secular variation, with peak fluxes in the Griesbachian and Smithian. The Mo and U profiles also show a peak around the P–Tr boundary.

At Zuodeng, the Mo flux ranges from 0.01 to 7.4 mg m$^{-2}$ y$^{-1}$, with an average of 0.41 mg m$^{-2}$ y$^{-1}$ (Fig. 11C). The U flux ranges from 0.01 to 4.9 mg m$^{-2}$ y$^{-1}$, with an average of 0.41 mg m$^{-2}$ y$^{-1}$. The V flux ranges from 0.01 to 6.4 mg m$^{-2}$ y$^{-1}$, with an average of 0.83 mg m$^{-2}$ y$^{-1}$. The three proxies show similar patterns of secular variation, with minor differences. Peak values are in the late Dienerian and Smithian for the Mo flux profile, in the mid-Griesbachian, late Dienerian, and Smithian for the U flux profile, and in the Griesbachian, early Dienerian, late Dienerian, and Smithian for the V flux profile.

At Mud, the Mo flux ranges from 0.01 to 0.35 mg m$^{-2}$ y$^{-1}$, with an average of 0.07 mg m$^{-2}$ y$^{-1}$ (Fig. 11D). The U flux ranges from 0.01 to 0.41 mg m$^{-2}$ y$^{-1}$, with an average of 0.07 mg m$^{-2}$ y$^{-1}$. The V flux ranges from 0.49 to 20 mg m$^{-2}$ y$^{-1}$, with an average of 3.5 mg m$^{-2}$ y$^{-1}$. The three proxies show similar patterns of secular variation, with peak values in the late Smithian. The Mo and V profiles exhibit a second, but somewhat smaller, peak in the Dienerian.

Summarizing patterns of variation in the redox proxies, high Mo, U and V concentrations are found mainly at the P–Tr boundary and in the late Griesbachian, Dienerian, and Smithian for the Mo flux profile, and in the Griesbachian, early Dienerian, late Dienerian, and Smithian for the V flux profile.

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Secular variation in the redox proxies broadly mirrors that seen for the weathering and productivity proxies, suggesting close connections between all three environmental parameters.

5. Discussion

5.1. Relationship of weathering, productivity, and redox variation to Early Triassic global events

The results above document major secular changes in weathering, productivity, and redox fluxes during the Early Triassic. In the following discussion, we consider relationships of these environmental proxies to coeval global events, in order to explore potential controls on the protracted recovery of Early Triassic marine ecosystems. Our analysis begins with the end-Permian mass extinction and proceeds through the Spathian, thus covering the full Early Triassic recovery interval.

The end-Permian crisis is generally regarded as having been triggered by the onset of massive eruptions of the Siberian Traps Large Igneous Province (Renne et al., 1995; Korte et al., 2010). It was marked by a general collapse of marine ecosystems, as reflected in biodiversity, trace fossil, and ecological tiering data (Erwin et al., 2002; Erwin, 2005; Fig. 12). This event was accompanied by an extreme climatic warming of >10 °C (Joachimski et al., 2012; Sun et al., 2012), a major expansion of oceanic anoxia globally (Brennecka et al., 2011), an abrupt incursion of sulfidic waters into the ocean-surface layer (Grice et al., 2005; Algeo et al., 2007, 2008), and large inputs of terrestrial material to shallow-marine areas (Ward et al., 2000; Sephton et al., 2005; Xie et al., 2007; Algeo and Twitchett, 2010), all of which are likely to have contributed to the biocrisis. Strong warming led to intensified stratification of the oceanic water-column, as reflected in a large vertical gradient of δ13C\text{DIC} (Song-HY et al., 2013), and thus to a strongly reduced nutrient supply via upwelling, contributing to a sharp decline in marine productivity. The study sections exhibit only limited evidence for these major environmental changes, however, as the end-Permian and P–Tr boundary are characterized by, at most, a small increase in terrestrial weathering fluxes (Fig. 9) and a transient shift toward more reducing conditions (Fig. 11; cf. Grice et al., 2005; Cao et al., 2009). The muted response of the terrestrial weathering and marine redox proxies in the study sections may be due to their distance from continental sources of siliciclastics and locations in areas with only limited local redox changes. Marine productivity exhibits a more visible change, declining sharply particularly across the South China craton (Fig. 10), a pattern...
possibly related to a productivity crash (Algeo et al., 2013) or to a shift in dominance from eukaryotic algae to bacterio-plankton (Luo et al., 2014).

During the Griesbachian, the development of a hyper-greenhouse climate resulted in tropical sea-surface temperatures that were persistently >35 °C (Fig. 12; Sun et al., 2012). This warming contributed to expansion of marine anoxia (Fig. 11) through lowering of the solubility of dissolved oxygen in seawater and increasing the flux of river-borne nutrients to shallow-marine areas via enhanced chemical weathering (Fig. 9; Algeo and Twitchett, 2010). A consistently positive relationship is seen between redox conditions and marine productivity (Fig. 12), suggesting that organic carbon sinking fluxes controlled the expansion of oceanic oxygen-minimum zones (Algeo et al., 2011a). High seawater temperatures and widespread reducing conditions probably operated in tandem to keep benthic biotas under stress and to delay marine ecosystem recovery. As a result, benthic biotas were dominated by opportunistic lineages of eurytopic bivalves, gastropods, and ostracods (Erwin, 1998). Relatively high productivity levels during the Griesbachian (Fig. 10) offered adequate food resources for nektont, resulting in a transient diversification among conodonts and ammonoids (Stanley, 2009). High productivity may reflect dominance of bacterioplankton (Xie et al., 2010; Luo et al., 2014), which would have enhanced recycling of nutrients in the ocean-surface layer and reduced the organic carbon sinking flux (D’Hondt et al., 1998) and, thus, account for a decrease in the vertical gradient of δ13C_carb (Song-HY et al., 2013). However, at the end of Griesbachian, extreme warmth (Sun et al., 2012) and more widespread oceanic anoxia (Fig. 11) destroyed this surface-ocean ecosystem, resulting in a second-order mass extinction among conodonts and ammonoids (Brayard et al., 2006; Orchard, 2007; Stanley, 2009) and further depressing the benthic ecosystem. Expansion of the oceanic oxygen-minimum zone at this time would have resulted in a contraction of the ecospace available to planktic and nektic organisms (Fig. 13A).

The Dienerian was characterized by a warm climate, although one that was slightly cooler (~32–35 °C) than that of the late Griesbachian (Fig. 12; Sun et al., 2012). As a consequence of this relative cooling, terrestrial weathering fluxes were reduced (Fig. 9). In the marine environment, the Dienerian was characterized by lower marine productivity (Fig. 10) and a shift toward more oxidizing (or less reducing) conditions (Fig. 11). This substage was associated with a small negative excursion of δ13C_carb (Tong et al., 2007a) and intermediate and relatively stable vertical δ13C_carb gradients (Song et al., 2013a,b), which are consistent with reduced marine productivity as well as a modest weakening of oceanic water-column stratification. With regard to marine biotas, the Dienerian exhibits increasing diversity among conodonts and ammonoids (Stanley, 2009) and other marine fauna (Yang et al., 1986; Wang et al., 2001; Tong et al., 2003; Krystyn et al., 2007; Zhao et al., 2007; Li et al., 2009; Song et al., 2011); trace fossil burrow size, ichnodiversity, and tiering (Chen et al., 2011); and alpha diversity (Hofmann et al., 2013, 2014).
enhanced riverine nutrient fluxes, possibly with an additional stimulus from upwelling of nutrient-rich deep waters owing to more vigorous thermohaline circulation as a consequence of climatic cooling and a steeper latitudinal temperature gradient. A concurrent shift toward somewhat more reducing conditions (Fig. 11) may have been driven by high O₂ demand associated with an enhanced sinking flux of organic matter. With regard to marine biotas, this interval witnessed the maximum diversification of conodonts and ammonoids during the
Early Triassic (Stanley, 2009; Fig. 12), and a limited increase in the diversity of echinoderms, brachiopods, and forams (Chen et al., 2005a; Chen and McNamara, 2006; Song et al., 2011), suggesting improvements in both the ocean-surface and benthic ecosystems. Cooler temperatures and a contraction of oceanic oxygen-minimum zones resulted in an expansion of the ecospace available to marine faunas, and high productivity offered rich food resources for this ecosystem (Brayard et al., 2006; Orchard, 2007; Stanley, 2009). Enhanced oceanic overturning circulation generally results in improved ventilation of the global ocean (resulting in more ecospace availability), while simultaneously intensifying anoxia in limited areas of active upwelling (owing to greater nutrient fluxes to the ocean surface layer). The Dienerian–Spathian boundary thus represents an episode of significantly ameliorated marine environmental conditions prior to the onset of the Smithian crisis, and it may have laid a foundation for more rapid ecosystem recovery at the beginning of the Spathian, −0.5 Myr later (e.g., Erwin, 2008; Chen and Benton, 2012).

The Smithian coincided with a major environmental and biotic crisis within the Early Triassic. It was characterized by development of a secondary hyper-greenhouse, with peak temperatures >38 °C (Sun et al., 2012; Romano et al., 2013), a large negative excursion of δ13Ccarb (Payne et al., 2004; Tong et al., 2007a,b), and a maximum vertical gradient in the δ13C of DIC (Song et al., 2013a,b; Fig. 12). The negative shift in δ13Ccarb is likely to reflect a strong decline in marine productivity, and the large vertical δ13C gradient an intensification of oceanic water-column stratification, both in response to extreme warming of the ocean-surface layer. In the study sections, the Smithian exhibits a large increase in terrestrial weathering fluxes (Fig. 9), reflecting stronger chemical weathering due to warming and intensified marine anoxia (Fig. 11), due to a combination of riverine nutrient inputs and stronger water-column stratification. Productivity levels appear to have increased at this time in two of the study sections (Chaohu and Daxiakou; Fig. 10), although it is possible that these deep-water sections are recording enhanced organic matter preservation as a consequence of OMZ expansion rather than actual increases in surface-water productivity. Warming and other environmental stresses resulted in a major extinction event among conodonts and ammonoids at the end of the Smithian (Brayard et al., 2006; Orchard, 2007; Stanley, 2009; Fig. 12). Expansion of the oceanic oxygen-minimum zone at this time would have resulted in a contraction of the ecospace available to planktonic and nektonic organisms (Fig. 13C).

The Spathian marks the onset of a sustained recovery of marine ecosystems that was completed in the Middle Triassic (Bottjer et al., 2008; Chen and Benton, 2012). It was characterized by a pronounced climatic cooling from the hyper-greenhouse conditions of the preceding −2 Myr, with tropical sea-surface temperatures falling to ~30–32 °C (Sun et al., 2012; Romano et al., 2013; Fig. 12). In the study sections, it is marked by large declines in terrestrial weathering fluxes, marine productivity, and the intensity of marine anoxia (Figs. 9–11). The decline in productivity can be attributed to a reduced supply of nutrients from riverine sources following climatic cooling and stabilization of terrestrial landscapes (Looy et al., 1999, 2001; Hermann et al., 2011) and from upwelling sources following a flushing out of the deep-ocean nutrient inventory as a result of re-invigorated thermohaline circulation at the Smithian–Spathian boundary (Zhang et al., 2014). Improved ocean ventilation and reduced organic carbon sinking fluxes were responsible for a shift toward less reducing conditions globally (Fig. 12). These environmental changes coincided with a gradual rediversification of pelagic organisms, rapid rediversification among benthic organisms and trace-makers, and higher-level integration of marine trophic systems (Chen et al., 2005a,b; Orchard, 2007; Stanley, 2009; Chen et al., 2011; Song et al., 2011; Chen and Benton, 2012). The more sustained ecosystem recovery of the Spathian relative to the Dienerian can be attributed to several factors, including a longer time interval, a cooler climate, less widespread marine anoxia, and generally more stable environmental conditions (Fig. 13D).

5.2. Spatial variation in Early Triassic marine environmental conditions

Although the four study sections generally show similar patterns of secular variation in weathering, productivity, and redox proxies, some differences exist among the sections that are probably controlled by palaeogeographic location, water depth, and local bathymetry. First, the deep-ramp sections (Chaohu and Daxiakou) show peak weathering fluxes that are ~3× greater than for the mid-shelf section (Mud) and ~10× greater than for the shallow-platform section (Zuodeng; Fig. 9). These differences reflect relative proximity to sources of detrital siliciclastics and local bathymetry (e.g., the relative isolation of the shallow-platform section from detrital influx). Second, average CIA values are somewhat higher in the peri-equatorial South China sections (~0.75–0.80) relative to the mid-latitude Mud section (0.72), a difference that is attributable to variations in weathering intensity as a function of climate. Third, productivity proxy fluxes show some variation among the study sections (Fig. 10). Fluxes are similar for Chaohu, Daxiakou, and Mud but lower for Zuodeng, suggesting diminished marine productivity on shallow-platform tops relative to open-marine ramp and shelf settings. Fourth, redox proxy fluxes differ significantly among the study sections, with Chaohu exhibiting comparatively large fluxes, Daxiakou and Zuodeng intermediate fluxes, and Mud small fluxes (Fig. 11). These differences appear to be related to both water depth and palaeogeographic location. Chaohu was the deepest section, with water depths of ~300–500 m putting it within the ocean thermocline and, thus, subject to influence by an expanding oxygen-minimum zone. However, the higher redox proxy fluxes for all South China sections relative to Mud suggest that the eastern Paleo-Tethys Ocean was subject to generally more strongly reducing conditions than the southern Neo-Tethys Ocean during the Early Triassic (Fig. 4B). Finally, all types of proxies exhibit a better-defined pattern of secular variation in the deep-ramp sections (Chaohu and Daxiakou) than elsewhere (Figs. 9–11). We attribute this relationship to differences in depositional water depth, which was >200 m for the deep-ramp sections but <100 m for the mid-shelf and shallow-platform sections (Section 3). With increasing water depths, sections were under greater influence by the oceanic oxygen-minimum zone, expansion of which occurred over discrete time intervals (Feng and Algeo, 2014). In contrast, the study sections located within the ocean-surface layer (<100 m) may have experienced more irregular secular variation in environmental conditions.

5.3. Influences on weathering, productivity, and redox fluxes

Modeling of geochemical proxy fluxes suggests a close relationship of changes in terrestrial weathering intensity, marine productivity rates, and ocean redox conditions throughout the Early Triassic (Figs. 9–11). Our interpretation, as presented above, is that this covariation reflects real relationships among these environmental parameters. Specifically, higher weathering intensities tend to result in increased riverine nutrient fluxes, leading to enhanced marine productivity (at least in coastal areas), and thus to intensified marine anoxia (again, possibly focused in coastal areas) (cf. Algeo et al., 1995, 2011a). These relationships are natural consequences of strong climate warming, as occurred repeatedly during the Early Triassic (Fig. 12; Joachimski et al., 2012; Sun et al., 2012; Romano et al., 2013). We recognize, however, that the relationships among these environmental parameters may vary in detail and can have alternative linkages. For example, expansion of marine anoxia can potentially lead to enhanced organic carbon burial fluxes in the absence of any change in marine productivity. We also recognize that the patterns exhibited by the four study sections inherently represent local marine environmental conditions (Fig. 13) that may or may not mirror contemporaneous global oceanographic changes. However, the strong similarities among some of the study sections, particularly those deposited at deeper water depths (i.e., Chaohu and Daxiakou), suggest that our results have

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probably captured some aspect of global marine environmental changes during the Early Triassic.

An additional important influence on the proxy fluxes is sediment bulk accumulation rate (BAR). These fluxes represent the multiplicative product of raw proxy concentrations and BAR (Supplementary Information), so an increase in either input variable can lead to higher calculated fluxes. The observation that, for each study section, the concentration profiles (Figs. 6–8) and flux profiles (Figs. 9–11) tend to exhibit similar features reflects the influence of raw concentrations on calculated fluxes. However, a degree of auto-correlation among the various proxy fluxes results from the use of a common age-thickness model for each study section and is unavoidable in studies of this type. The analysis of four widely separated sections (note that the three Chinese sections cover ~1500 km of the South China craton) helps to compensate for this situation and serves as a test of the validity of results because each study section makes use of an independent, site-specific age-thickness model (e.g., Section 5.2). Moreover, our use of CIA also provides a check on the degree of procedural auto-correlation of results because CIA is a proxy that is completely independent of BAR. CIA shows unambiguous positive covariation with BAR-based weathering proxies (i.e., Al and Fe) in the Chaohu, Daxiakou, and Mud sections (Fig. 9), in which CIA exhibits maxima at the PTB or early Griesbianch, the late Griesbianch, the Dienerian–Smithian boundary or early Smithian, and the Smithian–Spathian boundary. The weathering proxies in general do not show a coherent pattern of secular variation in the third study section (Zuoqiong), possibly because its paleodepositional setting (i.e., a shallow-marine carbonate platform) was not conducive to recording weathering fluxes.

5.4. Recovery patterns following other Phanerozoic mass extinctions

The marine ecosystem recovery following the end-Permian mass extinction is regarded as having been longer than those following other major Phanerozoic biocises (Bottrj et al., 2008; Chen and Benton, 2012), although a detailed comparison with other recovery events has been lacking to date. In the following analysis, we examine patterns of marine ecosystem recovery following the other four “Big Five” Phanerozoic mass extinctions and consider their relationship to contemporaneous environmental conditions. This analysis reveals both commonalities and dissimilarities in the ecosystem recoveries following different mass extinction events.

The Cretaceous–Paleogene (K–Pg; formerly the Cretaceous–Tertiary, or K–T) boundary mass extinction at 66.0 Ma (Renne et al., 2013) is the most thoroughly investigated to date. It killed off ~50% of marine genera (Sepkoski, 1996) and ~80% of species (Sepkoski, 1994). It eliminated conodonts and severely affected brachiopods and gastropods (McRoberts et al., 1997; Tomášových and Siblík, 2007), as well as ammonoids, bivalves, corals and ostracods (McRoberts and Newton, 1995; Kiessling, 2001, 2005; van de Schootbrugge et al., 2007; Mander and Twitchett, 2008; Fig. 14B). Eruption of the Central Atlantic magmatic province (CAMP) and the resulting global warming were the major causes of this mass extinction (Marzoli et al., 1999; McElwain et al., 1999; Hesselbo et al., 2002; van de Schootbrugge et al., 2009; Schoene et al., 2010; Ruhl et al., 2011).

Marine ecosystem recovery began rapidly in the Early Jurassic, with in 120 k.y. (Ruhl et al., 2010) to 290 k.y. of the extinction event (Bartolini et al., 2012). Recovery was marked by increases in diversity during the earliest Hettangian among pelagic carbonate producers (radiolarians, calcareous nanofossils) (Clémence et al., 2010), molluscs (McRoberts et al., 1997), ammonoids (Hesselbo et al., 2002; Guex et al., 2012), and brachiopods (Tomášových and Siblík, 2007). This initial recovery (Fig. 14B) was followed by a second extinction event among ammonoids during the early Hettangian ( Guex et al., 2004, 2012). A second, longer (~2–3 Myr) recovery phase (Fig. 14B) is evidenced by more diverse radiolarian assemblages in the mid to late Hettangian (Longridge et al., 2007), rediversification of ammonoids in the late Hettangian (Guex et al., 2012), and increases in the diversity of gastropod and coral faunas in the early Sinemurian (Seuß et al., 2005).

A large (~5‰), rapid negative carbon isotope excursion occurred at the end of Triassic (Korte et al., 2009; Schoene et al., 2010; Bartolini et al., 2012), and was followed a positive excursion (~3‰) in the lower Hettangian ( Williford et al., 2007; Korte et al., 2009; Schoene et al., 2010; Bartolini et al., 2012; Fig. 14B), suggesting an extreme carbon cycle disturbance at the T–J boundary. Paleobotanical data provide evidence of a rapid global warming at the T–J boundary (McElwain et al., 1999; Ruhl et al., 2011), and a subsequent cooling resulted from high marine productivity and enhanced organic matter burial (Korte et al., 2009). A long-term negative carbon isotope excursion during the early and middle Hettangian coincided with a greenhouse climate and widespread oceanic anoxia (Ruhl and Küsters, 2011; Bartolini et al., 2012; Richoz et al., 2012), hindering the recovery of marine ecosystems until the Hettangian–Sinemurian boundary (Bartolini et al., 2012; van de Schootbrugge et al., 2013), when the carbon cycle stabilized (Bartolini et al., 2012; Guex et al., 2012). The initial recovery of pelagic and benthic
organisms during the early Hettangian was impeded first by large climate fluctuations and then by a long-term global warming that resulted in marine environmental stresses including warming, seawater acidification, and anoxia (Richoz et al., 2012; van de Schootbrugge et al., 2013). These factors contributed to an extinction event among ammonoids in the mid-Hettangian and a protracted recovery among many elements of the marine nektion and benthion during the Hettangian (Gux et al., 2004, 2012). Falling atmospheric pCO2 by the late Hettangian resulted in a cooler climate and ameliorated marine environmental conditions, leading to a second stage of recovery among plankton (Bartolini et al., 2012) and benthion (Seub et al., 2005) during the Sinemurian stage. Thus, the Early Jurassic marine ecosystem recovery tracks contemporaneous environmental changes very well.

The Late Devonian mass extinction comprised a series of crises during an interval of ~20 Myr, of which the largest were at the Givetian–Frasnian (G–F), Frasnian–Famennian (F–D), and Devonian–Carboniferous (D–C) boundaries (Walliser, 1996; House, 2002; Morrow et al., 2011; Fig. 14C). Collectively, these crises killed ~50–60% of marine genera and ~82% of species (Jablonski, 1991; McGhee, 1996). Many clades of marine invertebrates suffered multiple declines, including brachiopods, trilobites, corals, and stromatoporoids (Copper, 1986; Stearn, 1987), and most colonial rugose corals went extinct at the F–F boundary (Fig. 14C, Copper, 2002; Shen and Webb, 2004). The F–F mass extinction evidenced a collapse of the metazoan reef ecosystem after the mid-late Devonian acme of metazoan reefs and a replacement by microbial reefs (Copper, 2002).

The immediate cause of the Late Devonian crisis appears to have been rapid changes in seawater temperatures and redox conditions (Joachimski et al., 2004; Chen et al., 2005a, 2005b). For example, the F–F cooling event severely affected the tropical-marine ecosystem, especially reef metazoans and, thus, is the probable cause of this mass extinction (Copper, 1986, 2002). However, the ultimate cause of the Late Devonian crisis is likely to have been the spread of higher land plants and consequent changes in nutrient cycling (Algeo et al., 1995, 2001; Algeo and Scheckler, 1998). A progressive expansion of terrestrial floras during the Devonian resulted in intensified chemical weathering of land areas, releasing more nutrients that stimulated algal blooms and a consequent expansion of anoxia in epicontinental seas. These paleobotanical developments resulted in a long-term decline in atmospheric pCO2 owing to an increase in both organic carbon burial and silicate weathering, resulting in strong global climatic cooling (Algeo et al., 1995). The Late Devonian was a time of transition from the Middle Paleozoic greenhouse to the Late Paleozoic icehouse (Fig. 14C; Isaacson et al., 2008). Each of the Late Devonian crises coincided with a major cooling event, the episodes at the F–F and D–C boundaries being particularly pronounced (Joachimski et al., 2004; Buggisch and Joachimski, 2006; Kaiser et al., 2006, 2008). It is not certain whether the spread of higher land plants was gradual and merely created background conditions for the development of episodic marine biocrises, or whether it actively triggered each crisis through pulses of expansion (Algeo and Scheckler, 2010).

Because of the multi-episode nature of the crisis, there was at least a partial recovery of marine ecosystems following each extinction event. For example, brachiopods and ostracods underwent a modest recovery during early Famennian, following the F–F boundary event, although they remained low in diversity (Casier and Lethiers, 1998; Balinski, 2002; Sokirak, 2002, Fig. 14C), and stromatoporoids began to recover during the early and middle Famennian but went extinct at the D–C boundary (Metherell and Workman, 1969; Stearn, 1987; Webb, 1998). A permanent recovery did not begin until after the D–C boundary crisis. Bryozoans recovered to their pre-extinction level of diversity during the Early Carboniferous (Bigey, 1989). Some corals (e.g., Pseudouralia, Siphonophylia) and brachiopods (e.g., Eochoristites, Martinella) recovered in the middle Tournaisian of the Early Carboniferous (Liao, 2002). The extinction of colonial rugose corals at the F–F boundary resulted in replacement of metazoan reefs by small microbial patch reefs (Pickett and Wu, 1990; Webb, 1998; Morrow et al., 2011), with regrowth of large barrier reefs delayed until the Viséan (Dix and James, 1987; Webb, 1998, 1999; Wahlmann, 2002; Fig. 14C). Loss of large metazoans during this crisis permitted the establishment of novel ecologies dominated by microbial communities (Wood, 2004). However, the final marine ecosystem recovery required the high-trophic-level ecosystem community establishment (e.g., Chen and Benton, 2012).

The Late Ordovician (Hirnantian) mass extinction (Fig. 14D) eliminated ~24% of families and 85% of species of marine invertebrates (Jablonski, 1991; Sepkoski, 1996; Brenchley et al., 2001; Sheehan, 2001). It was particularly severe among trilobites, brachiopods, molluscs (Sepkoski, 1984; Adrain et al., 2000; Harper and Rong, 2008), and graptolites and conodonts (Brenchley et al., 2001; Sheehan, 2001; Fan and Chen, 2007; Rasmussen and Harper, 2011a,b). The immediate cause of this extinction was the Hirnantian glaciation (Brenchley et al., 1995; Gibbs et al., 1997; Sheehan, 2001; Sutcliffe et al., 2006). A second extinction, ~1 Myr later, (demoted the cooled-`Hirnantian fauna’ and was caused by a rapid termination of glacialiation (Sheehan and Corrohour, 1990). The Early Silurian (Llandovery epoch) was a transitional interval from the Late Ordovician icehouse to a middle Paleozoic greenhouse (Kaljo and Martin, 2000; Brand et al., 2006). Warming conditions, the killing factor in the second extinction, prevailed during the Llandovery, although interrupted by two brief glaciations during the Aeronian stage (Caputo, 1998; Azmy et al., 1998, 1999; Delabroye et al., 2011; Finnegan et al., 2011; Fig. 14D).

Marine ecosystems began to recover following the end-Ordovician extinctions, although climate fluctuations during the Aeronian stage complicated the recovery pattern. Microbialite resurgence in the immediate aftermath of the Late Ordovician extinction coincided with an interval of low-diversity megafaunal communities (Sheehan and Harris, 2004). Diversification of brachiopods and trilobites proceeded during the Rhuddanian, the first stage of the Early Silurian (Krug and Patzkowsky, 2004; Owen et al., 2008; Huang et al., 2012), representing the initial recovery of marine faunas (Fig. 14D). Crinoids and coral began to diversify from the Rhuddanian in the Early Silurian (Kaljo, 1996; Austin and Deline, 2012). Climate fluctuations during the Llandovery resulted in a delay in the recovery of marine ecosystems (Copper, 2001; Goudey et al., 2010). Full recovery of reef ecosystems took place by the mid-Aeronian stage, ~4 Myr after the end-Ordovician crisis (Copper, 2001).
5.5. Evaluation of hypotheses regarding controls on marine ecosystem recovery

Three hypotheses have been advanced for the apparent delay in recovery of marine ecosystems following the end-Permian mass extinction, linking the duration of the recovery interval 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). Our analysis above of four Lower Triassic sections (Chaohu, Daxiakou, Zuodeng, and Mud) demonstrates unambiguously that there were large fluctuations in marine environmental conditions during the Early Triassic, and these disturbances were linked to transient biodiversity crises among coeval marine faunas and relapses in marine ecosystem complexity and integration. We conclude that episodic environmental disturbances were integral to the pattern and pace of marine ecosystem recovery during the Early Triassic.

Is it possible to draw general inferences about controls on marine ecosystem recovery following mass extinctions? With regard to duration, there is considerable variation among the recovery intervals following the “Big Five” Phanerozoic mass extinctions. If defined on the basis of (1) re-attainment of biodiversity equal to or exceeding pre-crisis levels, and (2) re-development of stable, well-integrated trophic systems, then the duration of the recovery interval was ~4 Myr for the end-Ordovician crisis, ~10 Myr for the F–F crisis, ~5 Myr for the end-Permian crisis, and ~3 Myr for the end-Cretaceous crisis (Fig. 14). These durations are closely linked to the interval of disturbed environmental conditions that followed each extinction event. The shortest recovery interval, ~2.5 Myr after the end-Triassic crisis, was associated with rapid cooling with minimal climate fluctuations during the earliest Jurassic (Korte et al., 2009), suggesting that amelioration of marine environmental conditions proceeded quickly following the CAMP eruptions (Marzoli et al., 1999; McElwain et al., 1999; Hesselson et al., 2002; Schoene et al., 2010; Ruhl et al., 2011). The ~3–Myr-long interval of recovery following the end-Cretaceous crisis was also associated with comparatively stable environmental conditions during the early Paleogene (Coxall et al., 2006). In contrast, the longest recovery interval, ~10 Myr after the F–F crisis, was interrupted by two glaciation episodes (Joachimski et al., 2004; Kaiser et al., 2006, 2008; Isaacson et al., 2008) during which environmental conditions deteriorated and marine ecosystem recovery was halted or reversed (Chen et al., 2005a,b). The second-longest recovery interval, ~5 Myr after the end-Permian crisis, was also associated with repeated environmental disturbances (Algeo et al., 2007, 2008; Retallack et al., 2011). Thus, unsettled environmental conditions following the main extinction crisis appear to be a strong control on the pattern and pace of marine ecosystem recovery.

Various types of environmental perturbations can contribute to destabilization of recovering marine ecosystems. First, temperature is clearly important, as most marine creatures are adapted to live within a relatively narrow temperature range (Brenchley and Harper, 1998). Extreme temperatures were a major factor in delayed ecosystem recovery during the Early Triassic (Sun et al., 2012; Romano et al., 2013), and strong climate fluctuations were important during other recovery intervals, e.g., the Late Devonian (Joachimski et al., 2004; Buggisch and Joachimski, 2006; Isaacson et al., 2008) and the Early Silurian (Finney et al., 1999; Gouldrey et al., 2010; Finnegan et al., 2011, 2012). Second, nutrient inventories and patterns of nutrient cycling can be important. Changes related to shifts from eukaryotic to microbial primary production following the end-Cretaceous (D’Hondt et al., 1998) and end-Permian mass extinctions (Gric et al., 2005; Xie et al., 2010) probably influenced rebuilding of marine trophic systems (e.g., Chen and Benton, 2012). Third, ocean redox conditions, which are linked to temperature and nutrient cycling, influence the availability of ecospace for metazoa (e.g., Fig. 13). Development of reducing conditions leads to hypercapnia and hypoxemia, which are lethal to most marine invertebrates (Pörtner, 2001). Fourth, ocean acidification, which is commonly linked to elevated atmospheric pCO₂, impedes the growth of calcifying organisms. A possible transient increase in seawater acidity during the Early Triassic (Payne et al., 2010; Hinojosa et al., 2012) and early Paleocene (Alegret et al., 2012) are thought to have influenced the rate of recovery of some faunal components of marine ecosystems.

Other potential influences on rates of marine ecosystem recovery, i.e., persistently harsh environmental conditions (Hallam, 1991; Isozaki, 1997; Payne et al., 2004; Erwin, 2007) or magnitude of the extinction event (Sepkoski, 1984; Solé et al., 2002), may play a role as well. Although environmental conditions exhibit a tendency to fluctuate strongly following a biocrisis rather than remaining persistently harsh, at least some crises were followed by protracted intervals of generally inhospitable conditions. The best-documented example is the Early Triassic, during which tropical sea-surface temperatures remained persistently high (>32 °C) for at least 2 Myr following the end-Permian crisis (Sun et al., 2012; Romano et al., 2013). The Late Devonian may provide another example, owing to the persistence of strongly oxygen-depleted conditions in shallow-marine seas for intervals of millions of years following the G–F and F–F crises (Algeo et al., 1995). In both cases, conditions fluctuated during these extended intervals of environmental deterioration, yielding no distinct dividing line between persistently harsh conditions and recurrent environmental disturbances. With regard to the influence of magnitude of the extinction event, there appears to be no strong correlation with the duration of the recovery interval (e.g., Kirchner and Weil, 2000; Erwin, 2001). There are intrinsic limits to how quickly ecosystems are capable of recovery that depend on rates of biotic evolution and, thus, re-occupation of vacated ecological niches (Sepkoski, 1998; Kirchner and Weil, 2000). However, it appears that such rates are at least an order-of-magnitude faster than the durations of even the shorter marine ecosystem recoveries (Hairstone et al., 2008).

6. Conclusions

The overriding control on the pattern and pace of marine ecosystem recovery following a mass extinction event is environmental stability or lack thereof. An analysis of environmental variation following the end-Permian mass extinction demonstrates that the protracted (~5-Myr) interval of recovery of Early Triassic marine ecosystems was due to recurrent environmental perturbations. These perturbations were associated with high terrestrial weathering fluxes, elevated marine productivity, and more intensely reducing oceanic redox conditions, and they appear to have been triggered by episodes of strong climatic warming, possibly linked to stages of increased magmatism in the Siberian Traps Large Igneous Province. The main perturbations following the end-Permian extinction occurred during the early Griesbachian, late Griesbachian, mid-Smithian, and (more weakly) the mid-Spathian. These episodes were stronger and more temporally discrete in deepwater sections (Chaohu and Daxiakou) relative to shallow and intermediate sections (Zuodeng and Mud), probably because warming and attendant effects were felt most strongly in the oceanic thermocline region. The observed relationships between weathering and productivity fluxes imply that nutrient and energy flows were key influences on the pattern and pace of marine ecosystem recovery. Comparison with recovery patterns following the other four “Big Five” Phanerozoic mass extinctions suggests that marine ecosystem recovery in general depends on the stability of the post-crisis marine environment. Persistent environmental stresses may also play a role in the pace of ecosystem recovery, but there is no clear correlation to the magnitude of mass extinction event.


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