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.

Keywords: productivity; redox; anoxia; weathering; South China; India

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84	1. Introduction

85
86 Each major mass extinction event in the geologic record has been followed by an interval
87 of restructuring of marine ecosystems, reflected in changes in clade dominance, ecological
88 niche partitioning, and community organization (e.g., [Erwin, 1998](#)). Increased productivity
89 among primary producers and consumers can generate ecological niches higher in the marine
90 trophic system ([Kirchner and Weil, 2000](#)), allowing a progressive rebuilding of a stable,
91 complex ecosystem structure ([Chen and Benton, 2012](#)). Although lacking a specific
92 quantitative definition, “ecosystem recovery” is generally regarded as the reappearance of
93 marine communities with a high biotic diversity and an integrated and complex structure that
94 is stable at multimillion-year timescales ([Harries and Kauffman, 1990](#)). The progress of
95 post-extinction recovery commonly has been evaluated using metrics related to overall
96 biodiversity and/or species origination rates (e.g., [Jacobsen et al., 2011](#); [Payne et al., 2011](#)).
97 However, “ecosystem recovery” is not simply a return to pre-extinction levels of biodiversity
98 but, rather, the expansion and re-integration of entire marine ecosystems or communities
99 ([Erwin et al., 2008](#); [Chen and Benton, 2012](#)) as reflected by metrics such as alpha diversity
100 (i.e., within-community species richness; [Bambach, 1977](#); [Clapham et al., 2006](#)) and
101 ecological tiering ([Twitchett, 1999](#); [Fraiser, 2011](#)).

102 In the case of the Permian-Triassic (P-Tr) boundary mass extinction, an initial, aborted
103 recovery occurred soon after the end-Permian crisis, during the Induan stage of the Early
104 Triassic ([Baud et al., 2008](#); [Brayard et al., 2009](#); [Stanley, 2009](#)), and a more sustained
105 recovery took place during the late Olenekian stage (Spathian substage) ([Chen et al., 2011](#);
106 [Song et al., 2011](#); [Payne et al., 2011](#)), but full ecosystem recovery probably did not occur until
107 the Middle Triassic ([Erwin and Pan, 1996](#); [Bottjer et al., 2008](#); [Chen and Benton, 2012](#)). The
108 recovery of marine invertebrate ecosystems following the end-Permian crisis was apparently
109 the most protracted of any major mass extinction ([Bottjer et al., 2008](#)), i.e., the “Big Five”
110 Phanerozoic mass extinctions of [Sepkoski \(1984, 1986\)](#). An important unresolved issue is
111 what controlled the long duration of the post-extinction recovery interval during the Early
112 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 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-SZ et al., 2011). 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.,

141 [2013](#)). According to high-precision U-Pb dating in South China sections, the interval between
142 these extinction pulses was 60 ± 48 kyr ([Burgess et al., 2014](#)). The end-Permian mass
143 extinction coincided with eruption of the Siberian Traps Large Igneous Province ([Campbell et](#)
144 [al., 1992](#); [Renne et al., 1995](#); [Reichow et al., 2009](#); [Sobolev et al., 2011](#)) as well as with major
145 environmental changes including global sea-level rise ([Hallam and Wignall, 1999](#)), ocean
146 anoxia ([Wignall and Twitchett, 1996](#); [Isozaki, 1997](#)), global warming ([Joachimski et al., 2012](#);
147 [Sun et al., 2012](#); [Romano et al., 2013](#)), and, possibly, marine acidification ([Payne et al., 2010](#);
148 [Hinojosa et al., 2012](#); [Kershaw et al., 2012](#)).

149

150 *2.2. The Early Triassic marine ecosystem recovery*

151

152 The recovery of marine ecosystems during the Early Triassic was a multi-step process.
153 There were several phases of incomplete or aborted recovery during the Induan, and recovery
154 from the P-Tr boundary mass extinction is generally regarded as not having been completed
155 until the Middle Triassic, ~5 Myr after the end-Permian crisis ([Mundil et al., 2004](#);
156 [Ovtcharova et al., 2006](#); [Lehrmann et al., 2006](#); [Shen-SZ et al., 2011](#)). Both benthic and
157 planktonic cyanobacteria bloomed immediately after the end-Permian mass extinction ([Fig. 2](#);
158 [Lehrmann, 1999](#); [Wang et al., 2005](#); [Xie et al., 2005](#); [Luo et al., 2011](#)). Cyanobacterial
159 microbialites reappeared episodically in different regions throughout the Early Triassic but
160 they largely disappeared by the early Middle Triassic ([Baud et al., 2007](#); [Xie et al., 2010](#)). An
161 Early Triassic “chert gap” ([Beauchamp and Baud, 2002](#)) was caused by the loss of biosilica
162 deposits from radiolarians and siliceous sponges, although occurrences of thin chert beds in
163 the late Griesbachian and Dienerian ([Kakuwa, 1996](#); [Takemura et al., 2007](#); [Sano et al., 2010](#))
164 document a temporary local early recovery of siliceous faunas.

165 Some secondary consumers such as conodonts and ammonoids rebounded rapidly from
166 the end-Permian mass extinction ([Orchard, 2007](#); [Brayard et al., 2009](#); [Stanley, 2009](#)). Their
167 rapid recovery may have been assisted by a microphagous habit ([Fischer and Bottjer, 1995](#)),
168 allowing them to benefit directly from increased biomass among primary producers. These

169 clades subsequently declined during biocrises at the end of Griesbachian, Smithian, and
170 Spathian substages of the Early Triassic, although they tended to rediversify rapidly during
171 the intervening intervals (Fig. 2; Brayard et al., 2009; Stanley, 2009). However, conodonts
172 display a strong Lilliput effect during the Smithian/Spathian boundary crisis (Chen et al.,
173 2013). Compared to conodonts and ammonoids, recovery rates for benthic primary consumers
174 such as foraminifers, gastropods, bivalves, brachiopods and ostracods were more gradual (Fig.
175 2; Payne et al., 2011). Among foraminifers, a sustained diversity increase began in the early
176 Smithian (early Olenekian) (Song et al., 2011) and accelerated during the Anisian (early
177 Middle Triassic) (Payne et al., 2011). Similar recovery patterns are observed also among
178 brachiopods (Chen et al., 2005) and ostracods (Crasquin-Soleau et al., 2007). The sizes of
179 gastropod and bivalve shells were reduced across the P-Tr boundary and during the
180 Griesbachian but returned to pre-extinction dimensions by the Anisian (Fig. 2; Fraiser and
181 Bottjer, 2004; Payne, 2005; Twitchett, 2007). However, the high diversity, low dominance,
182 and ecological complexity of mollusc fauna during the late Griesbachian and early Dienerian
183 at Shanggan, South China (Hautmann et al., 2011) and on the Wasit Block in Oman (Krystyn
184 et al., 2003; Twitchett et al., 2004) may represent an early recovery phase of these faunas.

185 The meso-consumer trace-makers and reef-builders can shed light on the recovery of
186 benthic marine ecosystems. Generally, trace-makers decreased during the end-Permian
187 biocrisis and recovered slowly in the Early Triassic (Fig. 2; Pruss and Bottjer, 2004; Chen et
188 al., 2011). Locally, trace-fossil diversity shows occasional peaks during the Griesbachian to
189 Smithian (Twitchett and Wignall, 1996; Twitchett, 1999; Zonneveld et al., 2010; Chen et al.,
190 2011). However, small trace-fossil burrow size, low tiering levels, and low ichnofabric indices
191 (bioturbation) generally persisted until the end of the Smithian substage, and the early
192 Spathian is marked by a strong increase in trace-fossil diversity and complexity (Pruss and
193 Bottjer, 2004; Chen et al., 2011). Nonetheless, Spathian ichnofaunas are less diverse than
194 those of the Middle Triassic (Knaust, 2007). This pattern may suggest a stepwise recovery of
195 trace-makers during Early to Middle Triassic (Twitchett and Barras, 2004). Furthermore, the
196 recovery of trace-makers may have been diachronous, with a more rapid increase in

197 ichnodiversity at high northern paleolatitudes than in the equatorial region (Twitchett and
198 Barras, 2004; Pruss and Bottjer, 2004). With regard to reef-builders, a new metazoan reef
199 ecosystem formed by various sponges and serpulid worms associated with microbial
200 carbonates and eukaryotic organisms developed in the early Smithian, latest Smithian, and
201 early to middle Spathian on the eastern Panthalassic margin, in Utah and Nevada (Fig. 2;
202 Brayard et al., 2011). These equatorial sponge-microbe reefs are found as early as 1.5 Myr
203 after the P-Tr boundary and represent a temporary recovery at least regionally (Brayard et al.,
204 2011, Chen and Benton, 2012). However, the “reef gap”, as represented by the absence of
205 heavily calcified corals, persisted through the Early Triassic (Payne et al., 2006).

206 As for the top trophic level in the marine ecosystem, predatory fish and reptiles
207 displayed different recovery trajectories. Fishes were rare in the Griesbachian-to-Smithian
208 equatorial ocean (Fig. 2; Fraiser et al., 2005; Tong et al., 2006; Zhao and Lu, 2007; Sun et al.,
209 2012) but more common in the middle to late Spathian (Goto, 1994; Wang et al., 2001;
210 Benton et al., 2013). High-latitude regions had a more abundant and diverse fish fauna in the
211 Early Triassic than the equatorial ocean (Scheaffer et al., 1976; Stemmerik et al., 2001; Mutter
212 and Neuman, 2006; Romano and Brinkmann, 2010; Benton et al., 2013). Globally, fish
213 diversity recovered by the Middle Triassic (Jin, 2006; Zhang et al., 2010; Hu et al., 2011).
214 Marine reptiles first reappeared in the Smithian in high-latitude regions (Cox and Smith, 1973;
215 Callaway and Brinkman, 1989) but later, in the Spathian, in equatorial regions (Li et al., 2002;
216 Zhao et al., 2008). A high level of diversity among marine reptiles was achieved by the
217 Middle to Late Triassic (Zhang et al., 2009).

218 To summarize, animals that were low in the marine trophic system tended to recover
219 faster than those at higher trophic levels (Fig. 2; cf. Chen and Benton, 2012). Pelagic and
220 nektonic faunas recovered faster than benthos as shown by rapid increases to multiple
221 biodiversity peaks for ammonoids and conodonts during the Early Triassic, versus a slow
222 return to pre-crisis diversity levels by the Middle Triassic for most bottom-dwellers. In
223 Olenekian time, offshore benthos like calcareous algae and *Tubiphytes* recovered faster than
224 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 silicic tuff ages of 251.7 ± 0.4 (Kamo et al., 2003), an Ar-Ar age of 250.3 ± 1.1 Ma for the final stages of extrusive volcanism (Reichow et al., 2009), and younger 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 13600 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 (Johnston, 1980), and rapid climatic changes that may have included both global cooling (Sigurdsson et al., 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

253 then spiked rapidly at the time of this event (Joachimski et al., 2012; Burgess et al., 2014).
254 During the Early Triassic, temperatures reached a maximum in the mid- to late Griesbachian
255 (~36-40°C), cooled slightly during the latest Griesbachian to the early Smithian, and then
256 reached a second peak of extreme warmth in the late Smithian (Fig. 3; Sun et al., 2012,
257 Romano et al., 2013). A pronounced retreat from peak temperatures occurred in the early
258 Spathian, an event resulting in a major turnover and geographic displacement of marine
259 invertebrate faunas (Galfetti et al., 2007a,b; Stanley, 2009). A weak warming episode in the
260 mid-late Spathian was followed by a second large cooling step around the Early-Middle
261 Triassic boundary, yielding distinctly more moderate temperatures during the Anisian
262 although still warmer than in the pre-extinction Late Permian (Sun et al., 2012; Romano et al.,
263 2013).

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

276 Marine productivity can vary greatly during major biocrises (Kump and Arthur, 1999).
277 Several factors during the P-Tr boundary crisis might have led to higher productivity: 1)
278 phosphate liberated from sediments under anoxic conditions can stimulate productivity (Ingall
279 and van Cappellen, 1990), and 2) intensified subaerial weathering can increase the flux of
280 river-borne P to the oceans (Algeo and Twitchett, 2010; Algeo et al., 2011b). Variations in

281 marine productivity can be reconstructed using carbon isotopes or elemental data (Kump and
 282 Arthur, 1999; Algeo et al., 2013; Schoepfer et al., 2014). The ‘biological pump’ removes
 283 ^{12}C -enriched carbon from the ocean-surface layer and transfers it to the ocean thermocline,
 284 producing a vertical gradient in the $\delta^{13}\text{C}$ of dissolved inorganic carbon ($\Delta^{13}\text{C}_{\text{DIC}}$). Changes in
 285 $\Delta^{13}\text{C}_{\text{DIC}}$ can thus provide information about the intensity of the organic carbon sinking flux
 286 and, indirectly, primary productivity (Hilting et al., 2008). A large vertical $\delta^{13}\text{C}_{\text{DIC}}$ gradient in
 287 the Nanpanjiang Basin of South China was interpreted as evidence of elevated marine
 288 productivity during the Early Triassic (Fig. 3; Meyer et al., 2011), although this gradient has
 289 also been attributed to intensified water-column stratification (Song-HY et al., 2013; Luo et
 290 al., 2014). However, an analysis of marine productivity changes based on organic carbon
 291 burial fluxes suggested a productivity crash in Early Triassic seas of the South China craton
 292 (Algeo et al., 2013). The large carbon-isotope excursions of the Early Triassic (Payne et al.,
 293 2004; Tong et al., 2007; Clarkson et al., 2013) were hypothesized to have been due to marine
 294 productivity fluctuations (Algeo et al., 2011b), an inference supported by patterns of
 295 $\delta^{13}\text{C}$ - $\delta^{34}\text{S}$ covariation (Song et al., 2014). The ultimate control on these fluctuations appears to
 296 have been temperature, with warm intervals associated with reduced productivity (Song et al.,
 297 2014).

298 Seawater pH values may have fluctuated during the P-Tr boundary crisis, as shown by
 299 analysis of calcium isotopes (Payne et al., 2010; Hinojosa et al., 2012). Calcium isotopic
 300 fractionation caused by the precipitation of carbonate minerals results in ^{40}Ca -rich marine
 301 sediments and ^{44}Ca -rich in seawater (Skulan et al., 1997; De La Rocha and DePaolo, 2000;
 302 Fantle and DePaolo, 2005; Tang et al., 2008). Abrupt negative excursions of $\delta^{44/40}\text{Ca}$ in both
 303 bulk carbonate and conodont apatite, representing a shift in seawater $\delta^{44/40}\text{Ca}$, occurred
 304 synchronously with the end-Permian biocrisis (Fig. 3; Payne et al., 2010; Hinojosa et al.,
 305 2012). The underlying cause of this change may have been eruption of the Siberian Traps,
 306 which injected a large amount of CO_2 into the atmosphere-ocean system, causing seawater
 307 acidification and increased riverine ^{40}Ca -rich calcium input owing to accelerated terrestrial

308 weathering of carbonates (Payne et al., 2010; Blätter et al., 2011). Ocean acidification during
309 Permian-Triassic transition may lead to the preferential extinction of heavily calcified marine
310 organisms (Knoll et al., 2007; Kiessling and Simpson, 2011; Clapham and Payne, 2011) and
311 could explain the abrupt transition on carbonate platforms from skeletal to microbial and
312 abiotic carbonate factories described by Kershaw et al. (2011).

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

325

326 **3. Study sections**

327

328 Three of the sections chosen for this study are from the South China craton, which was
329 located in the eastern Paleotethys Ocean during the Permian-Triassic transition. The Chaohu
330 section was deposited in a deep ramp setting on the northeastern (paleo-northwestern) margin
331 of this craton, Daxiakou on the mid-ramp of the same margin, and Zuodeng on a shallow
332 carbonate platform within the Nanpanjiang Basin on the southwestern (paleo-southeastern)
333 margin of this craton (Fig. 4A). These sections were widely separated, with a distance of ~650
334 km between Chaohu and Daxiakou, and a distance of ~950 km between the latter and
335 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 Daxiakou, 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 paleomagnetic 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).

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3.2. Daxiakou, Hubei Province, China

383

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

392 depths in the Daxiakou area were ~200-300 m (Song-HY et al., 2013).

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

400

401 3.3. Zuodeng, Guangxi Province, China

402

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

419 Carbonate content at Zuodeng is much higher than for the other study sections, averaging

420 ~95% in upper Changhsingian to Spathian strata with a small decrease to ~80% in the upper
421 Smithian (Fig. 5, Supplementary Table 4). This section consists mainly of thin- to
422 thick-bedded lime mudstone (cf. Wang et al., 2001). The lack of data around the P-Tr
423 boundary is due to this interval being covered at the time of sample collection.

424

425 3.4. Mud, Spiti Valley, India

426

427 The Mud section is located in the Spiti Valley, which is part of the district of Lahul
428 and Spiti, a central area of the western Himalaya in northern India. Lower Triassic strata are
429 well exposed in this area. During the Early Triassic, the study area was located at
430 mid-southern latitudes (~30-35°S) on the northern Gondwanan margin (Fig. 4B; Krystyn et al.,
431 2007). Middle Permian rifting (Stampfli et al., 1991; Garzanti et al., 1996) resulted in the
432 formation of the Neo-Tethys Ocean (Stampfli et al., 1991; Garzanti et al., 1996), and the
433 surface uplift of the rift shoulders resulted in widespread non-deposition, erosion and the
434 unconformities in the stratigraphic record (Stampfli et al., 1991; Garzanti et al., 1996). The
435 study section was deposited in a mid-shelf setting having a gentle slope, as implied by the
436 modest water depths of deposition (~50-70 m) despite the distal location of the section
437 (Krystyn et al., 2007).

438 The base of this section consists of Wuchiapingian to lower Changhsingian strata that are
439 overlain by an unconformity (or highly condensed interval) spanning the upper
440 Changhsingian and lower Griesbachian (Bhargava et al., 2004). The main part of the study
441 section consists of a conformable succession of mid-Griesbachian to lowermost Spathian
442 strata. Ammonoids are common in the upper Griesbachian to lower Smithian interval
443 (Krystyn and Orchard, 1996; Krystyn et al., 2007). Average ammonoid shell size decreases
444 from large in the lower Smithian to small in the middle Smithian (Krystyn et al., 2007),
445 suggesting the development of more hostile environmental conditions at that time. Current
446 bedforms are consistent with a well-oxygenated watermass during the earliest Smithian
447 (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 et al., 2007). 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 $\text{Al}_2\text{O}_3 / (\text{Al}_2\text{O}_3 + \text{K}_2\text{O} + \text{Na}_2\text{O})$ (see Supplementary Information for details). It is a widely used proxy in reconstructing

476 paleoclimate since it is interpreted as a measure of the extent of conversion of feldspars
477 related to the weathering (Young and Nesbitt, 1998; Price and Velbel, 2003). Note that the
478 CIA results for each study section are described in conjunction with weathering fluxes
479 (Section 4.4).

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

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

489 At Zuodeng, Al ranges from <0.1% to 14.3%, with an average value of 0.8% (Fig. 6C). It
490 shows relatively higher values from the late Dienerian to the early Smithian, in the late
491 Smithian, and in the middle Spathian but very low values in other intervals. Fe ranges from
492 <0.1 to 5.0%, with an average value of 0.6%. Fe shows a similar pattern to Al throughout the
493 study section except for the late Griesbachian, where the Al profile shows several peaks that
494 the Fe profile does not.

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

501

502 4.2. Productivity proxies

503

504 We used TOC, phosphorus (P), and excess barium (Ba_{xs}) concentrations to evaluate
505 marine productivity fluxes during the Early Triassic. Ba_{xs} was calculated as the amount of
506 non-detrital barium (see Supplementary Information for details). These are widely used
507 proxies for paleomarine productivity since their accumulation depends on organic matter
508 abundance and preservation (Tribovillard et al., 2006; Calvert and Pedersen, 2007). A method
509 to estimate actual paleomarine productivity values was developed by Schoepfer et al. (2014,
510 [this issue](#)), who established regression equations to evaluate primary and export production as
511 a function of TOC and P mass accumulation rates (MARs) using published data from
512 Cenozoic sediment cores.

513 At Chaohu, TOC ranges from 0.02 to 5.17%, with an average value of 0.28% (Fig. 7A).
514 It shows high values at the P-Tr boundary and in the mid Spathian, and moderately high
515 values from the late Griesbachian to early Dienerian, the late Dienerian to earliest Smithian,
516 and the mid to late Smithian. In contrast, it shows low values in the mid-Griesbachian, early
517 Smithian, and most of the Spathian. P ranges from ~0 to 0.52%, with an average value of
518 0.03%. Ba_{xs} ranges from 0.29 to 2992 ppm, with an average value of 176 ppm. Both P and
519 Ba_{xs} show patterns of variation that are similar to that of TOC, although Ba_{xs} exhibits
520 relatively higher values in the late Griesbachian and mid to late Smithian.

521 At Daxiakou, TOC ranges from 0.06 to 4.65%, with an average value of 0.30% (Fig. 7B).
522 It shows high values at the P-Tr boundary but relatively low values from the Griesbachian to
523 early Smithian. P ranges from ~0 to 2.23%, with an average value of 0.03%. It exhibits a
524 different pattern from TOC, showing relatively high values at the P-Tr boundary and in the
525 late Griesbachian to early Smithian and low values in the mid-Griesbachian and early to
526 mid-Smithian. Ba_{xs} ranges from 1.51 to 895 ppm, with an average value of 78 ppm. It shows a
527 slightly different pattern, with high values at the P-Tr boundary and from the
528 end-Griesbachian to the early Smithian and relatively lower values in the mid-Griesbachian
529 and mid-Dienerian.

530 At Zuodeng, TOC ranges from 0.06 to 1.52%, with an average value of 0.15% (Fig. 7C).
531 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. Ba_{xs} 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. Ba_{xs} 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

560 somewhat higher values in the early Spathian.

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

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

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

573

574 4.4. Weathering fluxes

575

576 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
577 (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
578 fluxes increase sharply at the P-Tr boundary and show peak values during the Griesbachian
579 and Smithian, with a smaller increase in the early Spathian. The CIA ranges from 0.47 to 0.99,
580 with an average of 0.75. High CIA values are found at the P-Tr boundary and in the
581 Griesbachian and Smithian.

582 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
583 (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
584 fluxes increase sharply at the P-Tr boundary and show peak values during the Griesbachian
585 and Smithian. The CIA ranges from 0.50 to 0.96, with an average of 0.80. High CIA values
586 are found at the P-Tr boundary and in the late Griesbachian and Smithian, with significantly
587 lower values in the mid-Griesbachian and Dienerian.

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

594 At Mud, the Al flux ranges from <0.1 to $6.2 \text{ g m}^{-2} \text{ y}^{-1}$, with an average of $1.1 \text{ g m}^{-2} \text{ y}^{-1}$ (Fig.
595 9D). The Fe flux ranges from <0.1 to $3.7 \text{ g m}^{-2} \text{ y}^{-1}$, with an average of $0.8 \text{ g m}^{-2} \text{ y}^{-1}$. Both
596 fluxes are large during the late Griesbachian and late Smithian, and Fe additionally shows a
597 peak around the Dienerian-Smithian boundary. The CIA ranges from 0.40 to 0.98, with an
598 average of 0.72. High CIA values are observed in the late Griesbachian and Smithian.

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

610

611 4.5. Productivity fluxes

612

613 At Chaohu, the TOC flux ranges from 0.01 to $3.9 \text{ g m}^{-2} \text{ y}^{-1}$, with an average of 0.36 g m^{-2}
614 y^{-1} (Fig. 10A). The P flux ranges from 0.1 to $658 \text{ mg m}^{-2} \text{ y}^{-1}$, with an average of 48.5 mg m^{-2}
615 y^{-1} . The Ba_{xs} flux ranges from ~ 0 to $451 \text{ mg m}^{-2} \text{ y}^{-1}$, with an average of $27 \text{ mg m}^{-2} \text{ y}^{-1}$. 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 $2.1 \text{ g m}^{-2} \text{ y}^{-1}$, with an average of $0.32 \text{ g m}^{-2} \text{ y}^{-1}$ (Fig. 10B). The P flux ranges from 0.5 to $6395 \text{ mg m}^{-2} \text{ y}^{-1}$, with an average of $64.6 \text{ mg m}^{-2} \text{ y}^{-1}$. The Ba_{xs} flux ranges from 0 to $350 \text{ mg m}^{-2} \text{ y}^{-1}$, with an average of $10 \text{ mg m}^{-2} \text{ y}^{-1}$. 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 $0.93 \text{ g m}^{-2} \text{ y}^{-1}$, with an average of $0.09 \text{ g m}^{-2} \text{ y}^{-1}$ (Fig. 10C). The P flux ranges from 0.1 to $169.5 \text{ mg m}^{-2} \text{ y}^{-1}$, with an average of $5.7 \text{ mg m}^{-2} \text{ y}^{-1}$. The Ba_{xs} flux ranges from ~ 0 to $61 \text{ mg m}^{-2} \text{ y}^{-1}$, with an average of $2 \text{ mg m}^{-2} \text{ y}^{-1}$. The TOC and Ba_{xs} 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 $1.5 \text{ g m}^{-2} \text{ y}^{-1}$, with an average of $1.1 \text{ g m}^{-2} \text{ y}^{-1}$ (Fig. 10D). The P flux ranges from 1.9 to $183 \text{ mg m}^{-2} \text{ y}^{-1}$, with an average of $20.3 \text{ mg m}^{-2} \text{ y}^{-1}$. The Ba_{xs} flux ranges from ~ 0 to $115 \text{ mg m}^{-2} \text{ y}^{-1}$, with an average of $6 \text{ mg m}^{-2} \text{ y}^{-1}$. 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 Ba_{xs} 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 Ba_{xs} 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 Ba_{xs} 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 3.0 mg m⁻² y⁻¹, with an average of 0.38 mg m⁻² y⁻¹. The V flux ranges from 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 0.24 mg m⁻² y⁻¹ (Fig. 11C). The U flux ranges from 0.01 to 3.7 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, although 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 0.06 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 mid to late Smithian (Fig. 8). With regard to fluxes, the main peaks are in the Griesbachian and Smithian, although modest increases are found also at the P-Tr boundary and in the early Spathian (Fig. 11) and at Mud during the Dienerian. Thus, these intervals were probably associated with more reducing conditions in marine environments than the remainder of the Early Triassic. 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.,

700 [2012; Sun et al., 2012](#)), a major expansion of oceanic anoxia globally ([Brennecke et al., 2011](#)),
701 an abrupt incursion of sulfidic waters into the ocean-surface layer ([Grice et al., 2005; Algeo et](#)
702 [al., 2007, 2008](#)), and large inputs of terrestrial material to shallow-marine areas ([Ward et al.,](#)
703 [2000; Sephton et al., 2005; Xie et al., 2007; Algeo and Twitchett, 2010](#)), all of which are
704 likely to have contributed to the biocrisis. Strong warming led to intensified stratification of
705 the oceanic water-column, as reflected in a large vertical gradient of $\delta^{13}\text{C}_{\text{DIC}}$ ([Song-HY et al.,](#)
706 [2013](#)), and thus to a strongly reduced nutrient supply via upwelling, contributing to a sharp
707 decline in marine productivity. The study sections exhibit only limited evidence for these
708 major environmental changes, however, as the end-Permian and P-Tr boundary are
709 characterized by, at most, a small increase in terrestrial weathering fluxes ([Fig. 9](#)) and a
710 transient shift toward more reducing conditions ([Fig. 11](#); cf. [Grice et al., 2005; Cao et al.,](#)
711 [2009](#)). The muted response of the terrestrial weathering and marine redox proxies in the study
712 sections may be due to their distance from continental sources of siliciclastics and locations in
713 areas with only limited local redox changes. Marine productivity exhibits a more visible
714 change, declining sharply particularly across the South China craton ([Fig. 10](#)), a pattern
715 possibly related to a productivity crash ([Algeo et al., 2013](#)) or to a shift in dominance from
716 eukaryotic algae to bacterioplankton ([Luo et al., 2014](#)).

717 During the Griesbachian, the development of a hyper-greenhouse climate resulted in
718 tropical sea-surface temperatures that were persistently $>35^{\circ}\text{C}$ ([Fig. 12; Sun et al., 2012](#)). This
719 warming contributed to expansion of marine anoxia ([Fig. 11](#)) through lowering of the
720 solubility of dissolved oxygen in seawater and increasing the flux of river-borne nutrients to
721 shallow-marine areas via enhanced chemical weathering ([Fig. 9; Algeo and Twitchett, 2010](#)).
722 A consistently positive relationship is seen between redox conditions and marine productivity
723 ([Fig. 12](#)), suggesting that organic carbon sinking fluxes controlled the expansion of oceanic
724 oxygen-minimum zones ([Algeo et al., 2011a](#)). High seawater temperatures and widespread
725 reducing conditions probably operated in tandem to keep benthic biotas under stress and to
726 delay marine ecosystem recovery. As a result, benthic biotas were dominated by opportunistic

727 lineages of eurytopic bivalves, gastropods, and ostracods (Erwin, 1998). Relatively high
728 productivity levels during the Griesbachian (Fig. 10) offered adequate food resources for
729 nekton, resulting in a transient diversification among conodonts and ammonoids (Stanley,
730 2009). High productivity may reflect dominance of bacterioplankton (Xie et al., 2010; Luo et
731 al., 2014), which would have enhanced recycling of nutrients in the ocean-surface layer and
732 reduced the organic carbon sinking flux (D'Hondt et al., 1998) and, thus, account for a
733 decrease in the vertical gradient of $\delta^{13}\text{C}_{\text{DIC}}$ (Song-HY et al., 2013). However, at the end of
734 Griesbachian, extreme warmth (Sun et al., 2012) and more widespread oceanic anoxia (Fig.
735 11) destroyed this surface-ocean ecosystem, resulting in a second-order mass extinction
736 among conodonts and ammonoids (Brayard et al., 2006; Orchard, 2007; Stanley, 2009) and
737 further depressing the benthic ecosystem. Expansion of the oceanic oxygen-minimum zone at
738 this time would have resulted in a contraction of the ecospace available to planktic and nektic
739 organisms (Fig. 13A).

740 The Dienerian was characterized by a warm climate, although one that was slightly
741 cooler ($\sim 32\text{-}35^\circ\text{C}$) than that of the late Griesbachian (Fig. 12; Sun et al., 2012). As a
742 consequence of this relative cooling, terrestrial weathering fluxes were reduced (Fig. 9). In the
743 marine environment, the Dienerian was characterized by lower marine productivity (Fig. 10)
744 and a shift toward more oxidizing (or less reducing) conditions (Fig. 11). This substage was
745 associated with a small negative excursion of $\delta^{13}\text{C}_{\text{carb}}$ (Tong et al., 2007a) and intermediate
746 and relatively stable vertical $\delta^{13}\text{C}_{\text{DIC}}$ gradients (Song-HY et al., 2013), which are consistent
747 with reduced marine productivity as well as a modest weakening of oceanic water-column
748 stratification. With regard to marine biotas, the Dienerian exhibits increasing diversity among
749 conodonts and ammonoids (Stanley, 2009) and other marine fauna (Tong et al., 2007a) and an
750 increase in trace-fossil size (Twitchett, 1999; Chen et al., 2011; Fig. 2). Lower levels of
751 oceanic productivity were probably associated with a greater proportion of eukaryotic
752 plankton relative to bacterioplankton, which favored relatively greater export of organic
753 carbon and nutrients from the ocean-surface layer (cf. D'Hondt et al., 1998). Comparatively

754 cooler climatic conditions and contraction of the oceanic oxygen-minimum zone would have
755 resulted in an expansion of the ecospace available to conodonts and ammonoids in the surface
756 ocean (Fig. 13B). Thus, somewhat less severe environmental conditions in the Dienerian
757 (relative to the Griesbachian) triggered a limited marine ecosystem recovery, although the
758 brief interval since the end-Permian mass extinction (~0.5 Myr) may have insufficient for a
759 complete recovery of marine ecosystems (e.g., [Kirchner and Weil, 2000](#)).

760 The Dienerian-Smithian boundary was characterized by a transient temperature
761 minimum (~30-32°; [Sun et al., 2012](#)) and a large positive excursion (ca. +6‰) of $\delta^{13}\text{C}_{\text{carb}}$
762 globally ([Payne et al., 2004](#); [Tong et al., 2007a](#); Fig. 12). Positive $\delta^{13}\text{C}$ excursions are
763 commonly associated with elevated marine productivity ([Kump and Arthur, 1999](#)). All four
764 study sections show a substantial increase in terrestrial weathering fluxes at this time (Fig. 9),
765 with two (Chaohu and Daxiakou) also showing evidence of increased marine productivity
766 (Fig. 10). This pattern suggests that the increase in marine productivity may have been driven
767 by enhanced riverine nutrient fluxes, possibly with an additional stimulus from upwelling of
768 nutrient-rich deep waters owing to more vigorous thermohaline circulation as a consequence
769 of climatic cooling and a steeper latitudinal temperature gradient. A concurrent shift toward
770 somewhat more reducing conditions (Fig. 11) may have been driven by high O_2 demand
771 associated with an enhanced sinking flux of organic matter. With regard to marine biotas, this
772 interval witnessed the maximum diversification of conodonts and ammonoids during the
773 Early Triassic ([Stanley, 2009](#); Fig. 12), and a limited increase in the diversity of echinoderms,
774 brachiopods, and forams ([Chen et al., 2005](#); [Chen and McNamara, 2006](#); [Song et al., 2011](#)),
775 suggesting improvements in both the ocean-surface and benthic ecosystems. Cooler
776 temperatures and a contraction of oceanic oxygen-minimum zones resulted in an expansion of
777 the ecospace available to marine faunas, and high productivity offered rich food resources for
778 this ecosystem ([Brayard et al., 2006](#); [Orchard, 2007](#); [Stanley, 2009](#)). Enhanced oceanic
779 overturning circulation generally results in improved ventilation of the global ocean (resulting
780 in more ecospace availability), while simultaneously intensifying anoxia in limited areas of
781 active upwelling (owing to greater nutrient fluxes to the ocean surface layer). The

782 Dienerian-Smithian boundary thus represents an episode of significantly ameliorated marine
783 environmental conditions prior to the onset of the Smithian crisis, and it may have laid a
784 foundation for more rapid ecosystem recovery at the beginning of the Spathian, ~0.5 Myr
785 later (e.g., [Erwin, 2008](#); [Chen and Benton, 2012](#)).

786 The Smithian coincided with a major environmental and biotic crisis within the Early
787 Triassic. It was characterized by development of a second hyper-greenhouse, with peak
788 temperatures >38°C ([Sun et al., 2012](#); [Romano et al., 2013](#)), a large negative excursion of
789 $\delta^{13}\text{C}_{\text{carb}}$ ([Payne et al., 2004](#); [Tong et al., 2007](#)), and a maximum vertical gradient in the $\delta^{13}\text{C}$ of
790 DIC ([Song-HY et al., 2013](#); [Fig. 12](#)). The negative shift in $\delta^{13}\text{C}_{\text{carb}}$ is likely to reflect a strong
791 decline in marine productivity, and the large vertical $\delta^{13}\text{C}$ gradient an intensification of
792 oceanic water-column stratification, both in response to extreme warming of the
793 ocean-surface layer. In the study sections, the Smithian exhibits a large increase in terrestrial
794 weathering fluxes ([Fig. 9](#)), reflecting stronger chemical weathering due to warming, and
795 intensified marine anoxia ([Fig. 11](#)), due to a combination of riverine nutrient inputs and
796 stronger water-column stratification. Productivity levels appear to have increased at this time
797 in two of the study sections (Chaohu and Daxiakou; [Fig. 10](#)), although it is possible that these
798 deep-water sections are recording enhanced organic matter preservation as a consequence of
799 OMZ expansion rather than actual increases in surface-water productivity. Warming and other
800 environmental stresses resulted in a major extinction event among conodonts and ammonoids
801 at the end of the Smithian ([Brayard et al., 2006](#); [Orchard, 2007](#); [Stanley, 2009](#); [Fig. 12](#)).
802 Expansion of the oceanic oxygen-minimum zone at this time would have resulted in a
803 contraction of the ecospace available to planktic and nektic organisms ([Fig. 13C](#)).

804 The Spathian marks the onset of a sustained recovery of marine ecosystems that was
805 completed in the Middle Triassic ([Bottjer et al., 2008](#); [Chen and Benton, 2012](#)). It was
806 characterized by a pronounced climatic cooling from the hyper-greenhouse conditions of the
807 preceding ~2 Myr, with tropical sea-surface temperatures falling to ~30-32°C ([Sun et al.,](#)
808 [2012](#); [Romano et al., 2013](#); [Fig. 12](#)). In the study sections, it is marked by large declines in

809 terrestrial weathering fluxes, marine productivity, and the intensity of marine anoxia (Figs.
810 9-11). The decline in productivity can be attributed to a reduced supply of nutrients from
811 riverine sources following climatic cooling and stabilization of terrestrial landscapes (Looy et
812 al., 1999, 2001; Hermann et al., 2011) and from upwelling sources following a flushing out of
813 the deep-ocean nutrient inventory as a result of re-invigorated thermohaline circulation at the
814 Smithian-Spathian boundary (Zhang et al., 2014). Improved ocean ventilation and reduced
815 organic carbon sinking fluxes were responsible for a shift toward less reducing conditions
816 globally (Fig. 12). These environmental changes coincided with a gradual rediversification of
817 pelagic organisms, rapid rediversification among benthic organisms and trace-makers, and
818 higher-level integration of marine trophic systems (Chen et al., 2005; Orchard, 2007; Stanley,
819 2009; Song et al., 2011; Chen et al., 2011; Chen and Benton, 2012). The more sustained
820 ecosystem recovery of the Spathian relative to the Dienerian can be attributed to several
821 factors, including a longer time interval, a cooler climate, less widespread marine anoxia, and
822 generally more stable environmental conditions (Fig. 13D).

823

824 5.2. Spatial variation in Early Triassic marine environmental conditions

825

826 Although the four study sections generally show similar patterns of secular variation in
827 weathering, productivity, and redox proxies, some differences exist among the sections that
828 are probably controlled by paleogeographic location, water depth, and local bathymetry. First,
829 the deep-ramp sections (Chaohu and Daxiakou) show peak weathering fluxes that are ~3X
830 greater than for the mid-shelf section (Mud) and ~10X greater than for the shallow-platform
831 section (Zuodeng; Fig. 9). These differences reflect relative proximity to sources of detrital
832 siliciclastics and local bathymetry (e.g., the relative isolation of the shallow-platform section
833 from detrital influx). Second, average CIA values are somewhat higher in the peri-equatorial
834 South China sections (~0.75-0.80) relative to the mid-latitude Mud section (0.72), a difference
835 that is attributable to variations in weathering intensity as a function of climate. Third,
836 productivity proxy fluxes show some variation among the study sections (Fig. 10). Fluxes are

837 similar for Chaohu, Daxiakou, and Mud but lower for Zuodeng, suggesting diminished
 838 marine productivity on shallow-platform tops relative to open-marine ramp and shelf settings.
 839 Fourth, redox proxy fluxes differ significantly among the study sections, with Chaohu
 840 exhibiting comparatively large fluxes, Daxiakou and Zuodeng intermediate fluxes, and Mud
 841 small fluxes (Fig. 11). These differences appear to be related to both water depth and
 842 paleogeographic location. Chaohu was the deepest section, with water depths of ~300-500 m
 843 putting it within the ocean thermocline and, thus, subject to influence by an expanding
 844 oxygen-minimum zone. However, the higher redox proxy fluxes for all South China sections
 845 relative to Mud suggest that the eastern Paleo-Tethys Ocean was subject to generally more
 846 strongly reducing conditions than the southern Neo-Tethys Ocean during the Early Triassic
 847 (Fig. 4B). Finally, all types of proxies exhibit a better-defined pattern of secular variation in
 848 the deep-ramp sections (Chaohu and Daxiakou) than elsewhere (Figs. 9-11). We attribute this
 849 relationship to differences in depositional water depth, which was >200 m for the deep-ramp
 850 sections but <100 m for the mid-shelf and shallow-platform sections (Section 3). With
 851 increasing water depths, sections were under greater influence by the oceanic
 852 oxygen-minimum zone, expansion of which occurred over discrete time intervals (Feng and
 853 Algeo, 2014). In contrast, the study sections located within the ocean-surface layer (<100 m)
 854 may have experienced more irregular secular variation in environmental conditions.

856 *5.3. Influences on weathering, productivity, and redox fluxes*

858 Modeling of geochemical proxy fluxes suggests a close relationship of changes in
 859 terrestrial weathering intensity, marine productivity rates, and ocean redox conditions
 860 throughout the Early Triassic (Figs. 9-11). Our interpretation, as presented above, is that this
 861 covariation reflects real relationships among these environmental parameters. Specifically,
 862 higher weathering intensities tend to result in increased riverine nutrient fluxes, leading to
 863 enhanced marine productivity (at least in coastal areas), and thus to intensified marine anoxia
 864 (again, possibly focused in coastal areas) (cf. Algeo et al., 1995, 2011a). These relationships

865 are natural consequences of strong climate warming, as occurred repeatedly during the Early
866 Triassic ([Fig. 12](#); [Joachimski et al., 2012](#); [Sun et al., 2012](#); [Romano et al., 2013](#)). We
867 recognize, however, that the relationships among these environmental parameters may vary in
868 detail and can have alternative linkages. For example, expansion of marine anoxia can
869 potentially lead to enhanced organic carbon burial fluxes in the absence of any change in
870 marine productivity. We also recognize that the patterns exhibited by the four study sections
871 inherently represent local marine environmental conditions ([Fig. 13](#)) that may or may not
872 mirror contemporaneous global oceanographic changes. However, the strong similarities
873 among some of the study sections, particularly those deposited at deeper water depths (i.e.,
874 Chaohu and Daxiakou), suggest that our results have probably captured some aspect of global
875 marine environmental changes during the Early Triassic.

876 An additional important influence on the proxy fluxes is sediment bulk accumulation rate
877 (BAR). These fluxes represent the multiplicative product of raw proxy concentrations and
878 BAR ([Supplementary Information](#)), so an increase in either input variable can lead to higher
879 calculated fluxes. The observation that, for each study section, the concentration profiles ([Figs.](#)
880 [6-8](#)) and flux profiles ([Figs. 9-11](#)) tend to exhibit similar features reflects the influence of raw
881 concentrations on calculated fluxes. However, a degree of auto-correlation among the various
882 proxy fluxes results from the use of a common age-thickness model for each study section
883 and is unavoidable in studies of this type. The analysis of four widely separated sections (note
884 that the three Chinese sections cover >1500 km of the South China craton) helps to
885 compensate for this situation and serves as a test of the validity of results because each study
886 section makes use of an independent, site-specific age-thickness model (e.g., [Section 5.2](#)).
887 Moreover, our use of CIA also provides a check on the degree of procedural auto-correlation
888 of results because CIA is a proxy that is completely independent of BAR. CIA shows
889 unambiguous positive covariation with BAR-based weathering proxies (i.e., Al and Fe) in the
890 Chaohu, Daxiakou, and Mud sections ([Fig. 9](#)), in which CIA exhibits maxima at the PTB or
891 early Griesbachian, the late Griesbachian, the Dienerian-Smithian boundary or early Smithian,
892 and the Smithian-Spathian boundary. The weathering proxies in general do not show a

893 coherent pattern of secular variation in the third study section (Zuodeng), possibly because its
894 paleodepositional setting (i.e., a shallow-marine carbonate platform) was not conducive to
895 recording weathering fluxes.

896

897 *5.4. Recovery patterns following other Phanerozoic mass extinctions*

898

899 The marine ecosystem recovery following the end-Permian mass extinction is regarded
900 as having been longer than those following other major Phanerozoic biocrises ([Bottjer et al.,](#)
901 [2008; Chen and Benton, 2012](#)), although a detailed comparison with other recovery events
902 has been lacking to date. In the following analysis, we examine patterns of marine ecosystem
903 recovery following the other four “Big Five” Phanerozoic mass extinctions and consider their
904 relationship to contemporaneous environmental conditions. This analysis reveals both
905 commonalities and dissimilarities in the ecosystem recoveries following different mass
906 extinction events.

907 The Cretaceous-Paleogene (K-Pg; formerly the Cretaceous-Tertiary, or K-T) boundary
908 mass extinction at 66.0 Ma ([Renne et al., 2013](#)) is the most thoroughly investigated to date. It
909 killed off ~50% of marine genera and ~70% of species ([Jablonski and Chaloner, 1994;](#)
910 [Sepkoski, 1998; Alroy et al., 2008](#)), with high extinction rates among marine reptiles,
911 ammonoids, rudist bivalves, planktonic foraminifera, and calcareous nanofossils ([Pospichal,](#)
912 [1994; Marshall and Ward, 1996; Arenillas et al., 2000; Bown, 2005; Fastovsky and Sheehan,](#)
913 [2005; Fig. 14A](#)). The coincidence in timing between the Chicxulub bolide impact and the
914 K-Pg boundary extinction suggests that the impactor was the major cause of this mass
915 extinction ([Jolley et al., 2010; Renne et al., 2013](#)), although the lethality of the impact may
916 have been enhanced by long-term environmental stresses associated with the Deccan Traps
917 eruptions ([Courtillot et al., 1986; Courtillot et al., 1988; White and Saunders, 2005; Chenet et](#)
918 [al., 2007](#)).

919 Algal primary productivity may have recovered very rapidly, in less than a century
920 following the K-Pg boundary impact ([Fig. 14A, Sepúlveda et al., 2009](#)). However,

921 redevelopment of an integrated marine ecosystem with extended trophic chains took longer
922 and proceeded in two stages: a rapid initial phase and a delayed second phase (Coxall et al.,
923 2006). The initial phase took about 1 Myr (Sepúlveda et al., 2009; Hull et al., 2011; Alegret,
924 2012) and involved recovery of planktonic organisms such as dinoflagellates (Brinkhuis et al.,
925 1998; Hildebrand-Habel and Streng, 2003), planktic foraminifera (Coccioni and Luciani, 2006;
926 Hull et al., 2011), and radiolarians (Hollis et al., 2003), as well as coralline red algae (Aguirre
927 et al., 2007). The delayed second phase of recovery lasted for ~4 Myr following the boundary
928 crisis (Coxall et al., 2006) and culminated in a new diversity peak among planktic
929 foraminifera (Olsson et al., 1999) and re-establishment of reef communities (Baceta et al.,
930 2005).

931 The nutrient status of the early Danian ocean remains controversial, with some studies
932 inferring high nutrient levels (Alegret and Thomas, 2009; Alegret et al., 2012) and others low
933 nutrient levels (Coxall et al., 2006; Fuqua et al., 2008). Warmer conditions (as documented by
934 a $\delta^{18}\text{O}$ shift; Fig. 14A) caused the oceanic oxygen-minimum zone to expand, decreasing the
935 ecospace available to pelagic organisms. These adverse conditions abated 3-4 Myr after the
936 K-Pg boundary crisis, stimulating an increase in pelagic biodiversity and full redevelopment
937 of the marine food web (Coxall et al., 2006; Yamamoto et al., 2010). The post-K-Pg-boundary
938 recovery can be traced through carbon cycle changes in the early Paleocene (Fig. 14A). The
939 vertical (shallow-to-deep) $\delta^{13}\text{C}$ gradient in seawater DIC increased in two steps,
940 corresponding to the two stages of ecosystem recovery (Coxall et al., 2006, Fig. 14A). The
941 first step is marked by an increase in $\Delta^{13}\text{C}_{\text{vert}}$ from 0 to ~1‰ within 1 Myr of the crisis, and
942 the second step by an increase to ~2‰ within 3 million years of the crisis. The latter value is
943 similar to the $\Delta^{13}\text{C}_{\text{vert}}$ observed in modern marine systems and, thus, marks the
944 re-establishment of an efficient biological pump by the late Danian, that is, less intense
945 recycling of organic matter in the ocean-surface layer resulted in more export to the
946 chemocline and deep ocean (D'Hondt et al., 1998; Coxall et al., 2006).

947 The Triassic-Jurassic (Tr-J) boundary mass extinction resulted in the demise of ~53% of

948 marine genera (Sepkoski, 1996) and ~80% of species (Sepkoski, 1994). It eliminated
949 conodonts and severely affected brachiopods and gastropods (McRoberts et al., 1997;
950 Tomašových and Siblík, 2007), as well as ammonoids, bivalves, corals and ostracods
951 (McRoberts and Newton, 1995; Kiessling, 2001, 2005; van de Schootbrugge et al., 2007;
952 Mander and Twitchett, 2008; Fig. 14B). Eruption of the Central Atlantic magmatic province
953 (CAMP) and the resulting global warming were the major causes of this mass extinction
954 (Marzoli et al., 1999; McElwain et al., 1999; Hesselbo et al., 2002; van de Schootbrugge et al.,
955 2009; Schoene et al., 2010; Ruhl et al., 2011).

956 Marine ecosystem recovery began rapidly in the Early Jurassic, within 120 k.y. (Ruhl et
957 al., 2010) to 290 k.y. of the extinction event (Bartolini et al., 2012). Recovery was marked by
958 increases in diversity during the earliest Hettangian among pelagic carbonate producers
959 (radiolarians, calcareous nanofossils) (Clémence et al., 2010), molluscs (McRoberts et al.,
960 1997), ammonoids (Hesselbo et al., 2002; Guex et al., 2012), and brachiopods (Tomašových
961 and Siblík, 2007). This initial recovery (Fig. 14B) was followed by a second extinction event
962 among ammonoids during the early Hettangian (Guex et al., 2004, 2012). A second, longer
963 (~2-3-Myr) recovery phase (Fig. 14B) is evidenced by more diverse radiolarian assemblages
964 in the mid to late Hettangian (Longridge et al., 2007), rediversification of ammonoids in the
965 late Hettangian (Guex et al., 2012), and increases in the diverse of gastropod and coral faunas
966 in the early Sinemurian (Seuß et al., 2005).

967 A large (~5‰), rapid negative carbon isotope excursion occurred at the end of Triassic
968 (Korte et al., 2009; Schoene et al., 2010; Bartolini et al., 2012), and was followed a positive
969 excursion (~3‰) in the lower Hettangian (Williford et al., 2007; Korte et al., 2009; Schoene et
970 al., 2010; Bartolini et al., 2012; Fig. 14B), suggesting an extreme carbon cycle disturbance at
971 the T-J boundary. Paleobotanical data provide evidence of a rapid global warming at the T-J
972 boundary (McElwain et al., 1999; Ruhl et al., 2011), and a subsequent cooling resulted from
973 high marine productivity and enhanced organic matter burial (Korte et al., 2009). A long-term
974 negative carbon isotope excursion during the early and middle Hettangian coincided with a
975 greenhouse climate and widespread oceanic anoxia (Ruhl and Kürschner, 2011; Richoz et al.,

976 [2012; Bartolini et al., 2012](#)), hindering the recovery of marine ecosystems until the
977 Hettangian-Sinemurian boundary ([Bartolini et al., 2012; van de Schootbrugge et al., 2013](#)),
978 when the carbon cycle stabilized ([Bartolini et al., 2012; Guex et al., 2012](#)). The initial
979 recovery of pelagic and benthic organisms during the early Hettangian was impeded first by
980 large climate fluctuations and then by a long-term global warming that resulted in marine
981 environmental stresses including warming, seawater acidification, and anoxia ([Richoz et al.,](#)
982 [2012; van de Schootbrugge et al., 2013](#)). These factors contributed to an extinction event
983 among ammonoids in the mid-Hettangian and a protracted recovery among many elements of
984 the marine nekton and benthon during the Hettangian ([Guex et al., 2004, 2012](#)). Falling
985 atmospheric $p\text{CO}_2$ by the late Hettangian resulted in a cooler climate and ameliorated marine
986 environmental conditions, leading to a second stage of recovery among plankton ([Bartolini et](#)
987 [al., 2012](#)) and benthon ([Seuß et al., 2005](#)) during the Sinemurian stage. Thus, the Early
988 Jurassic marine ecosystem recovery tracks contemporaneous environmental changes very
989 well.

990 The Late Devonian mass extinction comprised a series of crises during an interval of ~20
991 Myr, of which the largest were at the Givetian-Frasnian (G-F), Frasnian-Famennian (F-F), and
992 Devonian-Carboniferous (D-C) boundaries ([Walliser, 1996, House, 2002; Morrow et al., 2011;](#)
993 [Fig. 14C](#)). Collectively, these crises killed ~50-60% of marine genera and ~82% of species
994 ([Jablonski, 1991; McGhee, 1996](#)). Many clades of marine invertebrates suffered multiple
995 declines, including brachiopods, trilobites, corals, and stromatoporoids ([Copper, 1986; Stearn,](#)
996 [1987](#)), and most colonial rugose corals went extinct at the F-F boundary ([Fig. 14C, Copper,](#)
997 [2002; Shen and Webb, 2004](#)). The F-F mass extinction evidenced a collapse of the metazoan
998 reef ecosystem after the mid-late Devonian acme of metazoan reefs and a replacement by
999 microbial reefs ([Copper, 2002](#)).

1000 The immediate cause of the Late Devonian crisis appears to have been rapid changes in
1001 seawater temperatures and redox conditions ([Joachimski et al., 2004; Chen et al., 2005](#)). For
1002 example, the F-F cooling event severely affected the tropical-marine ecosystem, especially
1003 reef metazoans and, thus, is the probable cause of this mass extinction ([Copper, 1986, 2002](#)).

1004 However, the ultimate cause of the Late Devonian crisis is likely to have been the spread of
1005 higher land plants and consequent changes in nutrient cycling ([Algeo et al., 1995, 2001](#);
1006 [Algeo and Scheckler, 1998](#)). A progressive expansion of terrestrial floras during the Devonian
1007 resulted in intensified chemical weathering of land areas, releasing more nutrients that
1008 stimulated algal blooms and a consequent expansion of anoxia in epicontinental seas. These
1009 paleobotanical developments resulted in a long-term decline in atmospheric $p\text{CO}_2$ owing to an
1010 increase in both organic carbon burial and silicate weathering, resulting in strong global
1011 climatic cooling ([Algeo et al., 1995](#)). The Late Devonian was a time of transition from the
1012 Middle Paleozoic greenhouse to the Late Paleozoic icehouse ([Fig. 14C](#); [Isaacson et al., 2008](#)).
1013 Each of the Late Devonian crises coincided with a major global cooling event, the episodes at
1014 the F-F and D-C boundaries being particularly pronounced ([Joachimski et al., 2004](#); [Buggisch](#)
1015 [and Joachimski, 2006](#); [Kaiser et al., 2006, 2008](#)). It is not certain whether the spread of higher
1016 land plants was gradual and merely created background conditions for the development of
1017 episodic marine biocrises, or whether it actively triggered each crisis through pulses of
1018 expansion ([Algeo and Scheckler, 2010](#)).

1019 Because of the multi-episode nature of the crisis, there was at least a partial recovery of
1020 marine ecosystems following each extinction event. For example, brachiopods and ostracods
1021 underwent a modest recovery during early Famennian, following the F-F boundary event,
1022 although they remained low in diversity ([Casier and Lethiers, 1998](#); [Baliński, 2002](#); [Sokiran,](#)
1023 [2002, Fig. 14C](#)), and stromatoporoids began to recover during the early and middle
1024 Famennian but went extinct at the D-C boundary ([Metherell and Workman, 1969](#); [Stearn,](#)
1025 [1987](#); [Webb, 1998](#)). A permanent recovery did not begin until after the D-C boundary crisis.
1026 Bryozoans recovered to their pre-extinction level of diversity during the Early Carboniferous
1027 ([Bigey, 1989](#)). Some corals (e.g., *Pseudouralinia*, *Siphonophyllia*) and brachiopods (e.g.,
1028 *Eochoristites*, *Martiniella*) recovered in the middle Tournaisian of the Early Carboniferous
1029 ([Liao, 2002](#)). The extinction of colonial rugose corals at the F-F boundary resulted in
1030 replacement of metazoan reefs by small microbial patch reefs ([Pickett and Wu, 1990](#); [Webb,](#)
1031 [1998](#); [Morrow et al., 2011](#)), with regrowth of large barrier reefs delayed until the Visean ([Dix](#)

1032 and James, 1987; Webb, 1998, 1999; Wahlmann, 2002; Fig. 14C). Loss of large metazoans
 1033 during this crisis permitted the establishment of novel ecologies dominated by microbial
 1034 communities (Wood, 2004). However, the final marine ecosystem recovery required the
 1035 high-trophic-level ecosystem community establishment (e.g., Chen and Benthos, 2012).

1036 The Late Ordovician (Hirnantian) mass extinction (Fig. 14D) eliminated ~24% of
 1037 families and 85% of species of marine invertebrates (Jablonski, 1991; Sepkoski, 1996;
 1038 Brenchley et al., 2001; Sheehan, 2001). It was particularly severe among trilobites,
 1039 brachiopods, molluscs (Sepkoski, 1984; Adrain et al., 2000; Harper and Rong, 2008), and
 1040 graptolites and conodonts (Brenchley et al., 2001; Sheehan, 2001; Fan and Chen, 2007;
 1041 Rasmussen and Harper, 2011a,b). The immediate cause of this extinction was the Hirnantian
 1042 glaciation (Brenchley et al., 1995; Gibbs et al., 1997; Sheehan, 2001; Sutcliffe et al., 2006). A
 1043 second extinction, ~1 Myr later, decimated the cool-adapted ‘Hirnantian fauna’ and was
 1044 caused by a rapid termination of glaciation (Sheehan and Coorough, 1990). The Early Silurian
 1045 (Llandovery epoch) was a transitional interval from the Late Ordovician icehouse to a middle
 1046 Paleozoic greenhouse (Kaljo and Martma, 2000; Brand et al., 2006). Warming conditions, the
 1047 killing factor in the second extinction, prevailed during the Llandovery, although interrupted
 1048 by two brief glaciations during the Aeronian stage (Caputo, 1998; Azmy et al., 1998, 1999;
 1049 Delabroye et al., 2011; Finnegan et al., 2011; Fig. 14D).

1050 Marine ecosystems began to recover following the end-Ordovician extinctions, although
 1051 climate fluctuations during the Aeronian stage complicated the recovery pattern. Microbialite
 1052 resurgence in the immediate aftermath of the Late Ordovician extinction coincided with an
 1053 interval of low-diversity megafaunal communities (Sheehan and Harris, 2004).

1054 Diversification of brachiopods and trilobites proceeded during the Rhuddanian, the first stage
 1055 of the Early Silurian (Krug and Patzkowsky, 2004; Owen et al., 2008; Huang et al., 2012),
 1056 representing the initial recovery of marine faunas (Fig. 14D). Crinoids and coral began to
 1057 diversify from the Rhuddanian in the Early Silurian (Kaljo, 1996; Ausich and Deline, 2012).

1058 Climate fluctuations during the Llandovery resulted in a delay in the recovery of marine
 1059 ecosystems (Copper, 2001; Gouldey et al., 2010). Full recovery of reef ecosystems took place

1060 by the mid-Aeronian stage, ~4 Myr after the end-Ordovician crisis ([Copper, 2001](#)).

1061

1062 *5.5. Evaluation of hypotheses regarding controls on marine ecosystem recovery*

1063

1064 Three hypotheses have been advanced for the apparent delay in recovery of marine
1065 ecosystems following the end-Permian mass extinction, linking the duration of the recovery
1066 interval to: (1) the intensity of the mass extinction ([Sepkoski, 1984](#); [Solé et al., 2002](#)), (2) the
1067 persistence of harsh environmental conditions ([Hallam, 1991](#); [Isozaki, 1997](#); [Payne et al.,](#)
1068 [2004](#); [Erwin, 2007](#)), and (3) episodic occurrence of strong environmental disturbances during
1069 the recovery interval ([Algeo et al., 2007, 2008](#); [Orchard, 2007](#); [Retallack et al., 2011](#); [Fig. 1](#)).
1070 Our analysis above of four Lower Triassic sections (Chaoahu, Daxiakou, Zuodeng, and Mud)
1071 demonstrates unambiguously that there were large fluctuations in marine environmental
1072 conditions during the Early Triassic, and these disturbances were linked to transient
1073 biodiversity crises among coeval marine faunas and relapses in marine ecosystem complexity
1074 and integration. We conclude that episodic environmental disturbances were integral to the
1075 pattern and pace of marine ecosystem recovery during the Early Triassic.

1076 Is it possible to draw general inferences about controls on marine ecosystem recovery
1077 following mass extinctions? With regard to duration, there is considerable variation among
1078 the recovery intervals following the “Big Five” Phanerozoic mass extinctions. If defined on
1079 the basis of (1) re-attainment of biodiversity equal to or exceeding pre-crisis levels, and (2)
1080 re-development of stable, well-integrated trophic systems, then the duration of the recovery
1081 interval was ~4 Myr for the end-Ordovician crisis, ~10 Myr for the F-F crisis, ~5 Myr for the
1082 end-Permian crisis, ~2.5 Myr for the end-Triassic crisis, and ~3 Myr for the end-Cretaceous
1083 crisis ([Fig. 14](#)). These durations are closely linked to the interval of disturbed environmental
1084 conditions that followed each extinction event. The shortest recovery interval, ~2.5 Myr after
1085 the end-Triassic crisis, was associated with rapid cooling with minimal climate fluctuations
1086 during the earliest Jurassic ([Korte et al., 2009](#)), suggesting that amelioration of marine
1087 environmental conditions proceeded quickly following the CAMP eruptions ([Marzoli et al.,](#)

1088 [1999; McElwain et al., 1999; Hesselbo et al., 2002; Schoene et al., 2010; Ruhl et al., 2011](#)).
1089 The ~3-Myr-long interval of recovery following the end-Cretaceous crisis was also associated
1090 with comparatively stable environmental conditions during the early Paleogene ([Coxall et al.,](#)
1091 [2006](#)). In contrast, the longest recovery interval, ~10 Myr after the F-F crisis, was interrupted
1092 by two glaciation episodes ([Joachimski et al., 2004; Kaiser et al., 2006, 2008; Isaacson et al.,](#)
1093 [2008](#)) during which environmental conditions deteriorated and marine ecosystem recovery
1094 was halted or reversed ([Chen et al., 2005](#)). The second-longest recovery interval, ~5 Myr after
1095 the end-Permian crisis, was also associated with repeated environmental disturbances ([Algeo](#)
1096 [et al., 2007, 2008; Retallack et al., 2011](#)). Thus, unsettled environmental conditions following
1097 the main extinction crisis appear to be a strong control on the pattern and pace of marine
1098 ecosystem recovery.

1099 Various types of environmental perturbations can contribute to destabilization of
1100 recovering marine ecosystems. First, temperature is clearly important, as most marine
1101 creatures are adapted to live within a relatively narrow temperature range ([Brenchley and](#)
1102 [Harper, 1998](#)). Extreme temperatures were a major factor in delayed ecosystem recovery
1103 during the Early Triassic ([Sun et al., 2012; Romano et al., 2013](#)), and strong climate
1104 fluctuations were important during other recovery intervals, e.g., the Late Devonian
1105 ([Joachimski et al., 2004; Buggisch and Joachimski, 2006; Isaacson et al., 2008](#)) and the Early
1106 Silurian ([Finney et al., 1999; Gouldey et al., 2010; Finnegan et al., 2011](#)). Second, nutrient
1107 inventories and patterns of nutrient cycling can be important. Changes related to shifts from
1108 eukaryotic to microbial primary production following the end-Cretaceous ([D'Hondt et al.,](#)
1109 [1998](#)) and end-Permian mass extinctions ([Grice et al., 2005; Xie et al., 2010](#)) probably
1110 influenced rebuilding of marine trophic systems (e.g., [Chen and Benton, 2012](#)). Third, ocean
1111 redox conditions, which are linked to temperature and nutrient cycling, influence the
1112 availability of ecospace for metazoans (e.g., [Fig. 13](#)). Development of reducing conditions
1113 leads to hypercapnia and hypoxemia, which are lethal to most marine invertebrates ([Pörtner,](#)
1114 [2001](#)). Fourth, ocean acidification, which is commonly linked to elevated atmospheric $p\text{CO}_2$,
1115 impedes the growth of calcifying organisms. A possible transient increase in seawater acidity

1116 during the Early Triassic (Payne et al., 2010; Hinojosa et al., 2012) and early Paleocene
1117 (Alegret et al., 2012) are thought to have influenced the rate of recovery of some faunal
1118 components of marine ecosystems.

1119 Other potential influences on rates of marine ecosystem recovery, i.e., persistently harsh
1120 environmental conditions (Hallam, 1991; Isozaki, 1997; Payne et al., 2004; Erwin, 2007) or
1121 magnitude of the extinction event (Sepkoski, 1984; Solé et al., 2002), may play a role as well.
1122 Although environmental conditions exhibit a tendency to fluctuate strongly following a
1123 biocrisis rather than remaining persistently harsh, at least some crises were followed by
1124 protracted intervals of generally inhospitable conditions. The best-documented example is the
1125 Early Triassic, during which tropical sea-surface temperatures remained persistently high
1126 ($>32^{\circ}\text{C}$) for at least 2 Myr following the end-Permian crisis (Sun et al., 2012; Romano et al.,
1127 2013). The Late Devonian may provide another example, owing to the persistence of strongly
1128 oxygen-depleted conditions in shallow-marine seas for intervals of millions of years
1129 following the G-F and F-F crises (Algeo et al., 1995). In both cases, conditions fluctuated
1130 during these extended intervals of environmental deterioration, yielding no distinct dividing
1131 line between persistently harsh conditions and recurrent environmental disturbances. With
1132 regard to the influence of magnitude of the extinction event, there appears to be no strong
1133 correlation with the duration of the recovery interval (e.g., Kirchner and Weil, 2000; Erwin,
1134 2001). There are intrinsic limits to how quickly ecosystems are capable of recovery that
1135 depend on rates of biotic evolution and, thus, re-occupation of vacated ecological niches
1136 (Sepkoski, 1998; Kirchner and Weil, 2000). However, it appears that such rates are at least an
1137 order-of-magnitude faster than the durations of even the shorter marine ecosystem recoveries
1138 (Hairston et al., 2008).

1139

1140 6. Conclusions

1141 The overriding control on the pattern and pace of marine ecosystem recovery following a
1142 mass extinction event is environmental stability or lack thereof. An analysis of environmental
1143 variation following the end-Permian mass extinction demonstrates that the protracted (~5-Myr)

1144 interval of recovery of Early Triassic marine ecosystems was due to recurrent environmental
1145 perturbations. These perturbations were associated with high terrestrial weathering fluxes,
1146 elevated marine productivity, and more intensely reducing oceanic redox conditions, and they
1147 appear to have been triggered by episodes of strong climatic warming, possibly linked to
1148 stages of increased magmatism in the Siberian Traps Large Igneous Province. The main
1149 perturbations following the end-Permian extinction occurred during the early Griesbachian,
1150 late Griesbachian, mid-Smithian, and (more weakly) the mid-Spathian. These episodes were
1151 stronger and more temporally discrete in deepwater sections (Chaohu and Daxiakou) relative
1152 to shallow and intermediate sections (Zuodeng and Mud), probably because warming and
1153 attendant effects were felt most strongly in the oceanic thermocline region. The observed
1154 relationships between weathering and productivity fluxes imply that nutrient and energy flows
1155 were key influences on the pattern and pace of marine ecosystem recovery. Comparison with
1156 recovery patterns following the other four “Big Five” Phanerozoic mass extinctions suggests
1157 that marine ecosystem recovery in general depends on the stability of the post-crisis marine
1158 environment. Persistent environmental stresses may also play a role in the pace of ecosystem
1159 recovery, but there is no clear correlation to the magnitude of mass extinction event.

1160

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1162

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1167

1168 **References**

1169

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2092 **FIGURE CAPTIONS**

2093

2094 **Figure 1.** Three hypotheses to account for the protracted recovery of Early Triassic marine
2095 ecosystems, linking it to (A) the intensity of the mass extinction (Solé et al., 2002); (B) the
2096 persistence of harsh environmental conditions (Hallam, 1991; Isozaki, 1997; Payne et al.,
2097 2004); and (C) the episodic recurrence of major environmental perturbations (Orchard, 2007;
2098 Stanley, 2009; Algeo et al., 2011a; Retallack et al., 2011). The heavy solid line represents a
2099 general biodiversity trend (cf. Tong et al., 2007b), and the shaded lines represent extinction
2100 intensity (A) or environmental stresses (B and C). PTB: Permian-Triassic boundary. ET: Early
2101 Triassic. MT: Middle Triassic.

2102

2103 **Figure 2.** General patterns of biodiversity and ecological change during the
2104 Permian-Triassic transition and Early Triassic. Gr. = Griesbachian; Dien. = Dienerian; Sm. =
2105 Smithian; SWI = sediment-water interface. For the tiering column, positive and negative
2106 values are elevations in centimeters relative to the sediment-water interface (SWI).
2107 Biodiversity data: conodont (Orchard, 2007; Stanley, 2009), ammonoid (Stanley, 2009; Yuri
2108 and Abnavi, 2013), radiolarian (Racki and Cordey, 2000), foraminifera (Song et al., 2011;
2109 Payne et al., 2011a), brachiopod (Chen et al., 2005; Yuri and Abnavi, 2013), and echinoderm
2110 (Chen and McNamara, 2006). Trace fossils: diameter (Twitchett, 1999; Chen et al., 2011) and
2111 ichnodiversity (Chen et al., 2011). Lilliput effect: maximum gastropod size (Payne, 2005) and
2112 mean foraminifer size (Payne et al., 2011b; Rego et al., 2012). Tiering data (Twitchett, 1999)
2113 and alpha diversity data (Hofmann et al., 2013, 2014). Recovery stages 1 and 2 are defined in
2114 this study. The timescale is a modified version of that of Algeo et al. (2013) (see
2115 Supplementary Table 1).

2116

2117 **Figure 3.** Volcanic and oceanic environmental changes during the Permian-Triassic
2118 transition and Early Triassic. Abbreviations as in Figure 2. Timing of Siberian Traps eruptions

is interpretative. Data sources: $\delta^{13}\text{C}_{\text{carb}}$ (Payne et al., 2004), sea-level elevations (Haq et al., 1987; Haq and Schutter, 2008), vertical $\Delta^{13}\text{C}$ of DIC (Song-HY et al., 2013), bioapatite $\delta^{18}\text{O}$ (Sun et al., 2012; Romano et al., 2013), $\delta^{34}\text{S}_{\text{sulf}}$ (Song et al., 2014), $\delta^{44/40}\text{Ca}$ (Payne et al., 2010; Hinojosa et al., 2012), and ocean redox (Kakuwa, 2008; Wignall et al., 2010; Song et al., 2012; Grasby et al., 2013).

Figure 4. Permian-Triassic paleogeography of (A) South China (modified from Tong et al., 2007a), and (B) the world (modified from Algeo et al., 2013). Am = Amuria; Kz = Kazakhstan; NC = North China; SC = South China; Tm = Tarim.

Figure 5. Stratigraphic variation in lithology of the four study sections. Lithologies calculated per Eqs. 1-3 in Supplementary Information. The timescale at left is plotted relative to thickness in the Chaohu section and is non-linear; note the different thickness scales for the four sections.

Figure 6. Chemostratigraphic profiles of weathering proxies (Al and Fe) for the four study sections. Vertical scales are identical to those in Figure 5.

Figure 7. Chemostratigraphic profiles of productivity proxies (TOC, P, and Ba_{xs}) for the four study sections. Vertical scales are identical to those in Figure 5.

Figure 8. Chemostratigraphic profiles of redox proxies (Mo, U, and V) for the four study sections. Vertical scales are identical to those in Figure 5.

Figure 9. Profiles of weathering fluxes and CIA (chemical index of alteration) for the four study sections.

2146 **Figure 10.** Profiles of productivity proxy fluxes for the four study sections.

2147

2148 **Figure 11.** Profiles of redox proxy fluxes for the four study sections.

2149

2150 **Figure 12.** Generalized patterns of marine environmental, biodiversity, and ecosystem
2151 change in the four study sections during the Early Triassic. The weathering, productivity, and
2152 redox profiles are based on Figures 9-11. Data sources: sea-surface temperatures (SST) ([Sun
2153 et al., 2012](#)); $\delta^{13}\text{C}_{\text{carb}}$ and generic diversity ([Tong et al., 2007a](#)); fossil abundance ([Yang et al.,
2154 1986](#); [Wang et al., 2001](#); [Tong et al., 2003](#); [Zhao et al., 2007](#); [Krystyn et al., 2007](#); [Li et al.,
2155 2009](#); [Song et al., 2011](#)); trace fossil burrow size, ichnodiversity, and tiering ([Chen et al.,
2156 2011](#)); and alpha diversity ([Hofmann et al., 2013, 2014](#)).

2157

2158 **Figure 13.** Integrated model showing relationships between environmental change,
2159 shallow-marine ecospace, and marine ecosystem recovery during the Early Triassic. The
2160 Griesbachian (A) and Smithian (C) are generally characterized by stronger volcanism,
2161 enhanced weathering and riverine nutrient fluxes, an expanded OMZ, more intense
2162 water-column stratification, weaker upwelling, and limited ecospace. In contrast, the
2163 Dienerian (B) and Spathian (D) are generally characterized by weaker volcanism, decreased
2164 weathering and riverine nutrient fluxes, a contracted OMZ, less intense water-column
2165 stratification, stronger upwelling, and expanded ecospace.

2166

2167 **Figure 14.** Patterns of environmental change and marine ecosystem recoveries following
2168 other major mass extinctions: (A) Cretaceous-Paleogene (K-Pg) boundary, (B)
2169 Triassic-Jurassic (Tr-J) boundary, (C) Late Devonian, and (D) Ordovician-Silurian (O-S)
2170 boundary. Data sources: (A) volcanism ([Renne et al., 2013](#); [Keller, 2003](#)), impacts ([Keller,
2171 2003](#)), $\delta^{13}\text{C}_{\text{carb}}$ ([D'Hondt et al., 1998](#); [Coxall et al., 2006](#)), $\delta^{18}\text{O}$ ([D'Hondt and Zachos, 1993](#);
2172 [Norris, 1996](#); [Birch et al., 2012](#)), planktic foraminifera diversity ([Keller, 2003](#); [Coxall et al.,
2173 2006](#); [Gallala et al., 2009](#)), nanoplankton diversity ([Hull et al., 2011](#)), algal productivity

2174 ([Sepúlveda et al., 2009](#); n.b., S/(S+H) = sterane/(sterane+hopane) ratio), nektonic carnivore
 2175 alpha diversity ([Sessa et al., 2012](#)), ecological tiering at the sediment-water interface ([Sessa et](#)
 2176 [al., 2012](#)); (B) CAMP volcanism ([Olsen et al., 2002](#); [Deenen et al., 2010](#); [Blackburn et al.,](#)
 2177 [2013](#); [Guex et al., 2012](#); [Deenen et al., 2010](#); [Ruhl et al., 2010](#)), $\delta^{13}\text{C}_{\text{org}}$ ([Ruhl et al., 2011](#);
 2178 [Bartolini et al., 2012](#); [Williford et al., 2007](#)), $\delta^{18}\text{O}$ ([Korte et al., 2009](#)), warm and cool
 2179 intervals ([Schoene et al., 2010](#)), sea-level elevations ([Haq et al., 1987](#)), diversity of bivalves,
 2180 ammonites, brachiopods, and reefs ([Hallam, 1996](#)); (C) sea-level elevations ([Johnson et al.,](#)
 2181 [1985](#); [Algeo et al., 2007](#); [Isaacson et al., 2008](#)), $\delta^{13}\text{C}_{\text{carb}}$ ([Buggisch and Joachimski, 2006](#)),
 2182 climatic oscillations ([Isaacson et al., 2008](#)), tropical sea surface temperatures (SSTs)
 2183 ([Joachimski et al., 2004](#)), R-CO_{2(atm)} ([Berner, 1994](#); n.b., RCO₂ = ratio of atmospheric CO₂ in
 2184 past to “modern” value of ~300 ppmv), stromatoporoid diversity ([Stearn, 1987](#); [Webb, 1998](#);
 2185 [Morrow et al., 2011](#)), reef-building coral diversity ([Webb, 1998](#)); and (D) sea-level elevations
 2186 ([Johnson et al., 1991](#); [Couto et al., 2013](#)); $\delta^{13}\text{C}_{\text{carb}}$ ([Finney et al., 1999](#); [Cramer et al., 2011](#);
 2187 [Kaljo and Martma, 2000](#); [Gouldey et al., 2010](#); [Delabroye et al., 2011](#)), $^{87}\text{Sr}/^{86}\text{Sr}$ ([Azmy et al.,](#)
 2188 [1999](#); [Gouldey et al., 2010](#)), tropical SSTs ([Finnegan et al., 2011](#)), glaciations ([Caputo, 1998](#);
 2189 [Azmy et al., 1998](#); [Delabroye et al., 2011](#)), crinoid diversity ([Ausich and Deline, 2012](#)),
 2190 graptolite diversity ([Fan and Chen, 2007](#)), coral diversity ([Kaljo, 1996](#)), brachiopod recovery
 2191 stage ([Rong and Harper, 1999](#)).
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