



Loss of the sedimentary mixed layer as a result of the end-Permian extinction



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ABSTRACT

The end-Permian mass extinction resulted in the most dramatic degradation of marine bottom communities during the Phanerozoic. One result of this extinction was the long-recognized, extreme reduction in bioturbation of the Early Triassic seafloor. Several lines of evidence (i.e., preferential preservation of epifaunal and very shallow-tier infaunal trace fossils; paucity of mid- and deep-tier trace fossils; absence of mottled bioturbation textures; dominance of cohesive substrates; widespread occurrence of microbially induced sedimentary structures in open-marine environments; ecological composition of Early Triassic communities) show that the reduction in bioturbation was so extreme that the sedimentary mixed layer was eradicated at an interregional scale for the only time since it was established in the early Palaeozoic. The consequences of this for ecosystem function and geochemical cycling must have been profound and yet they have received little consideration. Biogenic mixing of sediments is fundamental to geochemical cycling in extant marine ecosystems, and it also governs ecologically limiting factors such as nutrient fluxes, benthic primary production, and availability of ecospace. The collapse of biogenic sediment mixing during the Early Triassic must have affected geochemical properties of sediments and the seawater, as reflected in the geologic record of the sulphur cycle. Additionally, many of the proxies traditionally used to infer Early Triassic seawater anoxia may rather reflect poor sediment oxygenation arising from the extinction of bioturbators. Because of its impact on seawater and sediment chemistry, the loss of the mixed layer may have been an important, but hitherto little-considered constraint on the recovery from the end-Permian mass extinction.

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1. Introduction

With an estimated loss of as much as 96% of marine species (Raup, 1979) and a drastic decrease in the complexity of ecosystem networks (Erwin, 1994), the end-Permian mass extinction was the most devastating event in the history of metazoan life. The dramatic decline of biological diversity is also reflected in the trace fossil record of this time interval. It is well recognized that trace fossil diversity and rates of bioturbation dropped greatly in the aftermath of the extinction (Wignall and Twitchett, 1996; Twitchett and Barras, 2004) and the possible impact of this reduction in bioturbation on the sulphur cycle has been hypothesized (Canfield and Farquhar, 2009). However, aside from the suggestion that firmground conditions reappeared at or close to the sediment–water interface due to collapse of the mixed layer (Buatois and Mángano, 2011a), the physical and chemical impact of this transient but profound loss of bioturbation has not been considered in depth by palaeontologists

In modern oceans, biogenic sediment mixing is a key controlling factor of oxygen concentration in the sediment, and it influences the biomass of organisms, the rate of organic matter decomposition, chemical cycling and regeneration of nutrients (Lohrer et al., 2004; Solan et al., 2004). The uppermost few centimetres of the sediment-column are water-saturated and completely homogenized due to bioturbation, and thus are referred to as the “mixed layer” (Boudreau, 1998; Teal et al., 2008). The mixed layer is the primary domain of biogenic sediment reworking in the marine realm (Teal et al., 2008) and the main interface of chemical exchange between oceanic water and sediments. It is particularly well developed in sediments deposited at low sedimentation rates, under low energy, in oxygenated bottom-waters (Bromley, 1996). Development of the mixed layer proceeded gradually in tandem with the rise and diversification of bilaterians and progressive ecospace utilization during the early Palaeozoic. The mixed layer has been a characteristic feature of open marine sediments almost continuously since its inception during the Ordovician (Droser et al., 2002). This report uses a systematic literature review on Early Triassic trace fossil data, augmented by the authors' own observations, to document systematically that the sedimentary mixed layer was essentially destroyed during the end-Permian mass extinction.

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A critical analysis suggests that many sedimentary and geochemical signatures, most notably those indicative of anoxia, can readily develop in the absence of sediment mixing. Traditional views emphasize that water column anoxia persisted well into the Early Triassic and was the main inhibitor of re-diversification and ecological restoration (Hallam, 1991; Wignall and Hallam, 1992; Wignall and Twitchett, 1996). This notion remains a leading paradigm (e.g., Chen and Benton, 2012; Pietsch and Bottjer, 2014) but increasingly appears to be at variance with faunal data indicating early recovery of various marine groups (Orchard, 2007; Brayard et al., 2009; Hofmann et al., 2011). Even benthic ecosystems, which are held as classic examples of a delayed recovery (Schubert and Bottjer, 1995), reveal significant restoration signals – not only in putative habitable, oxygenated zones (Twitchett and Barras, 2004; Beatty et al., 2008) but also in regions (e.g., Hautmann et al., 2011; Hofmann et al., 2011, 2013a, 2015) that were proposed to have been widely inhospitable due to anoxia for much of the Griesbachian and beyond (Wignall and Twitchett, 2002). The demise of the mixed layer in marine sediments as a result of the extinction of marine bioturbators may be a key to the understanding of this apparent paradox.

2. Material and methods

The assessment of the history of the mixed layer during the end-Permian extinction and the Early Triassic recovery is based on a literature review (Tables 1 and 2) that incorporates 17 published case studies from the Permian and 13 from the Early Triassic, all focused on the shallow marine record. This environmental setting provides the richest record of trace fossils and represents the zone in which a mixed layer is usually well developed. For each published locality, the studied unit, its location, and its age were tabulated. All original ichnotaxonomic determinations were re-evaluated and adjusted if necessary. Only ichnotaxa illustrated in the original papers were considered, unless the material has been revised for this study. The reported ichnotaxa were classified in terms of their tiering, using the zones established by Bottjer and Ausich (1986) as revised by Mángano and

Buatois (2014). In this scheme, the shallow tier comprises structures produced in the upper 6 cm of the substrate, the mid-tier those produced between 6–12 cm depth in the substrate, and the deep tier those emplaced below 12 cm. The 6-cm boundary reflects approximately the depth above which organisms are challenged by disturbance rather than by maintaining contact with the sediment–water interface and below which these difficulties are reversed in severity (Bush et al., 2007). Below the 12-cm boundary, stresses linked to limited food supply and oxygen content, as well as increased substrate compaction, become extreme limiting factors within the sediment. The very deep zone included in tiering schemes, i.e., deeper than 100 cm, was essentially empty prior to the Mesozoic Marine Revolution and so is not considered in this paper.

Degree of bioturbation was assessed using the bioturbation index (BI) of Taylor and Goldring (1993) as reported in the reviewed papers. In this system, BI = 0 is characterized by no bioturbation (0%). BI = 1 (1–4%) is for sparse bioturbation with few discrete traces. BI = 2 (5–30%) is represented by low bioturbation in sediment that still has preserved sedimentary structures. BI = 3 (31–60%) describes an ichnofabric with discrete trace fossils, moderate bioturbation and still distinguishable bedding boundaries. BI = 4 (61–90%) is represented by intense bioturbation, high trace fossil density, common overlap of trace fossils, and primary sedimentary structures mostly erased. BI = 5 (91–99%) is characterized by sediment with completely disturbed bedding and intense bioturbation. BI = 6 (100%) is for completely bioturbated and reworked sediment, related to repeated overprinting of trace fossils. High variability of bioturbation intensities within individual stratigraphic units reflects sedimentary facies variability, with low-energy fully marine deposits typically displaying intense bioturbation.

The present report also relies on the authors' own observations of Early Triassic trace fossil assemblages, made in the course of several field campaigns. Detailed background information is provided in the published references given for each locality. Localities in western U.S. include measured sections of the Virgin Formation (Hofmann et al., 2013b), Dinwoody Formation (Hofmann et al., 2013a) and the Sinbad Formation and the Thaynes Group (Hofmann et al., 2014). In northwestern

Table 1
Characterization of Early Triassic shallow marine ichnofaunas emphasizing tiering, ichnotaxonomic composition, and bioturbation indices (BI).

Shallow tier	Mid tier	Deep tier	BI	References
<i>Conichnus</i> isp., <i>Cruziana</i> isp., <i>Diplichnites</i> isp., <i>Halimedes</i> isp., <i>Helicodromites</i> isp., <i>Palaeophycus tubularis</i> , <i>Planolites montanus</i> , <i>Protovirgularia</i> isp., <i>Rhizocorallium</i> isp., <i>Rusophycus</i> isp.	<i>Diplocraterion</i> isp., <i>Rosselia socialis</i> , <i>Spongiomorpha</i> isp., <i>Thalassinoides</i> isp.		0–3	Zonneveld et al. (2010a,b)
<i>Cruziana problematica</i> , <i>Diplichnites</i> isp., <i>Phycodes</i> isp., <i>Planolites montanus</i> , <i>Rusophycus</i> isp., <i>Spongiomorpha seilacheri</i> , <i>Spongiomorpha</i> isp., <i>Thalassinoides suevicus</i> , <i>Spongiomorpha</i> isp.	<i>Diplocraterion</i> isp.		0–4	MacNaughton and Zonneveld (2010)
<i>Arenicolites</i> isp., <i>Diplocraterion</i> isp., <i>Planolites</i> isp., <i>Skolithos</i> isp.			0–2 (BI 0 dominant)	Beatty et al. (2008)
<i>Asteriacites</i> isp., <i>Arenicolites</i> isp., <i>Planolites</i> isp., <i>Diplichnites</i> isp., <i>Rhizocorallium</i> isp.		<i>Diplocraterion</i> isp.	1–4	Knaust (2010b) Fraiser and Bottjer (2009)
<i>Curvolithus?</i> isp., <i>Helminthopsis</i> cf. <i>abeli</i> , <i>Lockeia</i> isp., <i>Palaeophycus tubularis</i> , <i>Planolites montanus</i> , <i>Rhizocorallium</i> isp., <i>Spongiomorpha</i> isp., <i>Thalassinoides</i> cf. <i>suevicus</i>			0–3 (BI 2 dominant)	Twitchett and Wignall (1996), Hofmann et al. (2011)
<i>Balanoglossites</i> isp., <i>Gastrochaenolites</i> isp., <i>Planolites</i> isp.			0–6 (BI 1 dominant)	Knaust (2010b)
	<i>Diplocraterion parallelum</i>		0–1 (BI 0 dominant)	Chen et al. (2011)
	<i>Lingulichnus</i> isp.		0–1	Šimo and Olšovský (2007) Zonneveld et al. (2007)
<i>Arenicolites</i> isp.			0–4 (BI 0 dominant)	Chen et al. (2011)
<i>Arenicolites</i> isp., <i>Lockeia</i> isp., <i>Palaeophycus striatus</i> , <i>Spongiomorpha</i> isp., <i>Taenidium serpentinum</i> , <i>Thalassinoides</i> isp., <i>Treptichnus apsorium</i> , <i>Treptichnus bifurcus</i>			0–3 (BI 0 dominant)	Chen et al. (2012), Luo and Chen (2014)
<i>Rhizocorallium</i> isp., <i>Palaeophycus</i> isp., <i>Planolites</i> isp., <i>Thalassinoides</i> isp., <i>Gyrochorte</i> isp.		<i>Arenicolites</i> isp., <i>Skolithos</i> isp.	0–4 (BI 0 dominant)	Fraiser and Bottjer (2009)
<i>Archaeonassa fossulata</i> , <i>Arenicolites</i> isp., <i>Diplocraterion</i> isp., <i>Furculosus carpathicus</i> , <i>Gyrochorte</i> isp., <i>Helminthoidichnites tenuis</i> , <i>Palaeophycus</i> isp., <i>Planolites beverleyensis</i> , <i>Planolites</i> isp., <i>Rhizocorallium</i> isp., <i>Thalassinoides</i> isp., <i>Treptichnus apsorium</i> , <i>Treptichnus bifurcus</i>			0–4 (BI 0 dominant)	Chen et al. (2011)
<i>Rhizocorallium</i> isp., <i>Laevicyclus</i> isp., <i>Arenicolites</i> , <i>Gyrochorte</i> isp., <i>Planolites</i> isp., <i>Asteriacites</i> isp., <i>Thalassinoides</i> isp.			0–4	Pruss and Bottjer (2004)

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