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Episodic photic zone euxinia in the northeastern Panthalassic Ocean during the end-Triassic extinction

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ABSTRACT

Severe changes in ocean redox, nutrient cycling, and marine productivity accompanied most Phanerozoic mass extinctions. However, evidence for marine photic zone euxinia (PZE) as a globally important extinction mechanism for the end-Triassic extinction (ETE) is currently lacking. Fossil molecular (biomarker) and nitrogen isotopic records from a sedimentary sequence in western Canada provide the first conclusive evidence of PZE and disrupted biogeochemistry in neritic waters of the Panthalassic Ocean during the end Triassic. Increasing water-column stratification and deoxygenation across the ETE led to PZE in the Early Jurassic, paralleled by a perturbed nitrogen cycle and ecological turnovers among noncalcifying groups, including eukaryotic algae and prokaryotic plankton. If such conditions developed widely in the Panthalassic Ocean, PZE might have been a potent mechanism for the ETE.

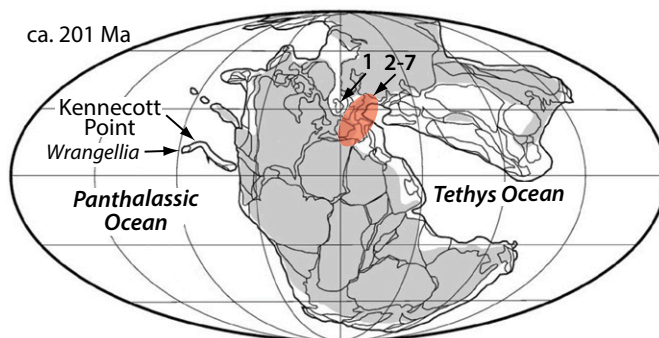
INTRODUCTION

The end-Triassic mass extinction (ETE; ca. 201.4 Ma; Schoene et al., 2010; Blackburn et al., 2013) decimated biodiversity in Earth's marine and terrestrial realms (Hesselbo et al., 2002). The ETE has been linked to one of the most areally extensive large igneous provinces, the Central Atlantic magmatic province (Marzoli et al., 1999; Whiteside et al., 2010), through rapid CO₂-driven global warming, changes in ocean circulation, and ocean acidification and deoxygenation (Kidder and Worsley, 2010; Richoz et al., 2012; Jaraula et al., 2013). Deoxygenation of ocean waters can alter nutrient inventories, thus favoring phytoplankton suited to NH₄⁺ assimilation or nitrogen fixation (Meyer and Kump, 2008; Richoz et al., 2012), and in extreme cases can lead to widespread sulfate reduction and shoaling of toxic H₂S to create photic zone euxinia (PZE), as observed for the end-Permian mass extinction (Grice et al., 2005). However, evidence for such conditions across the ETE is known only from organic-rich shallow-marine sequences deposited in epicontinental seaways of the Tethys and central Atlantic realms (Fig. 1), which were inherently more sensitive to local or regional climatic perturbations and do not provide a reliable picture of global environmental change.

We present an ~3 m.y. record of environmental and ecologic change across the ETE from the Peril and Sandilands Formations exposed on Graham Island, Haida Gwaii (formerly Queen Charlotte Islands), British Columbia, Canada (Ward et al., 2001). This section is ideal to assess changes in ocean redox in neritic waters because sedimentological, paleontological, and paleogeographic data indicate that it was deposited at upper

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	Site	Low O ₂ Deposition	Photic Zone Euxinia	Nutrient Disruption
	Kennecott Point, Canada	Yes	Yes	Yes
1	St. Audrie's & Pinhay Bay, UK	Yes	Yes/Plausible	Yes
2	Frick Swiss Jura, Switzerland	Yes	Yes	Yes
3	Mariental, Germany	Yes	Yes	Yes
4	Mingosheim, Germany	Yes	No	Yes
5	Rosswinkle, Luxembourg	Yes	Yes	Yes
6	Eiberg Basin, Austria	Yes	No	Yes
7	Csövár, Hungary	No	No	Yes

Figure 1. End-Triassic paleogeographic reconstruction (ca. 201 Ma; Scotese, 2004) showing the approximate locations of the Kennecott Point strata and other correlative end-Triassic extinction (ETE, red shading) strata that span the late Rhaetian to late Hettangian. Gray shading indicates submerged land. Further discussion about other records can be found in the GSA Data Repository (see footnote 1).

bathyal to outer neritic conditions on the flanks of the Wrangellia terrane (Fig. 1), an oceanic flood basalt plateau (Longridge et al., 2007). Our results demonstrate the occurrence of PZE and ecologic turnovers across the ETE within open ocean waters on the northeastern margin of the Panthalassic Ocean, the largest ocean basin of the Mesozoic world, and support the notion that ocean deoxygenation, euxinia, and the disruption of nutrient cycling might have been widespread extinction agents.

A 3 m.y. RECORD OF ENVIRONMENTAL AND ECOLOGICAL CHANGE

We analyzed shales and siltstones deposited in an outer shelf to upper slope setting (Haggart et al., 2001) representative of open ocean conditions. Using gas chromatography–metastable reaction monitoring–mass spectrometry (GC–MRM–MS), a high-sensitivity MS technique that affords a high signal-to-noise ratio and elevated selectivity of targeted

lipid classes (see the GSA Data Repository¹), we studied the distribution of bacterial C_{27–35} triterpanes and algal C_{26–30} steranes, as well as isorenieratane and C_{18–22} aryl isoprenoids indicative of green sulfur bacteria that thrive under PZE. Changes in oxygenation were assessed using redox-sensitive biomarker ratios and N isotopes. Aliphatic and aromatic hydrocarbons were analyzed in full scan by GC-MS and by GC-MRM-MS using predetermined precursor-product reactions (Table DR1 in the Data Repository). Total ion chromatograms of aliphatic hydrocarbons indicate a “hump” of unresolved complex mixtures of varying intensity, implying a varying degree of biodegradation. Nonetheless, easily biodegradable short-chain n-alkanes and acyclic isoprenoids such as pristane and phytane are abundant through most of the section, indicating that biodegradation overall is rather moderate, and most important, that the more stable biomarkers such as cyclic C_{27–29} steranes and C_{27–35} hopanes are unlikely to have been affected by biodegradation.

The gammacerane index (a in Fig. 2), an indicator of water-column stratification (Sinninghe Damsté et al., 1995), displays elevated although variable values across the record, suggesting recurring episodes of water stratification and possible oxygen deficiency in the water column. Proxies for water-sediment interface redox (Peters et al., 2005), the homohopane (HHI; b in Fig. 2) and 28,30-dinorhopane (DNH; c in Fig. 2) indices, indicate reduced bottom-water oxygen across the duration of ecological stress estimated as ~600 k.y. based on correlation to the Newark Basin presented in Whiteside et al. (2010) and into the Early Jurassic relative to Late Triassic background values, with a temporary return to oxic conditions immediately after the ETE, as observed elsewhere (e.g., van de Schootbrugge et al., 2013; Richoz et al., 2012). Notably, biomarker concentrations indicative of PZE became established following the development of reducing conditions in bottom waters (e, d in Fig. 2). Together, these results demonstrate a marked shift in water-column redox state through the ETE, likely associated with the intensification and vertical expansion of an intermediate-water oxygen minimum zone (OMZ). Increasing deoxygenation would have led to a shallowing of the chemocline and the occurrence of sulfidic waters up to the photic zone. Our results provide the first conclusive evidence for the occurrence of PZE in the northeastern Panthalassic Ocean.

Such changes in ocean redox state must have influenced the cycling of N, a feature that we are able to monitor through $\delta^{15}\text{N}$ isotopic signatures of sedimentary organic matter. The $\delta^{15}\text{N}$ values for most of the Rhaetian preceding the ETE (+2‰ to +4‰) are representative of sediments underlying surface waters with rather limited bioavailable nitrogen and low isotopic fractionation (Brandes and Devol, 2002). A drop in $\delta^{15}\text{N}$ values (–1‰ to +2‰) just before and during the ETE indicates a distinct change in nutrient inventories, leading to enhanced N₂ fixation from diazotrophic cyanobacteria (Kuypers et al., 2004), and/or phytoplankton utilization of ¹⁵N-depleted NH₄⁺ from upwelled OMZ waters (Higgins et al., 2012). Both scenarios imply an altered N cycle resulting from decreased oxygen availability, either by a low N/P ratio favoring diazotrophic phytoplankton, or NH₄⁺ replacing nitrate as the predominant form of recycled N. This shift in nutrient cycling coincides with our evidence for oxygen-deficient bottom waters (HHI, DNH indices), but precedes any major increase in indicators for the occurrence of PZE (Chlorobi markers; d, e in Fig. 2). The instability of geochemical signals in this interval (~10 m of strata) may represent a transitional interval of increasingly reducing conditions that favored microbial metabolisms other than sulfate reduction, with episodic changes in the vertical position of the chemocline and nutrient cycling.

The development of reducing conditions in open waters off the margin of Wrangellia through chemocline shallowing is possibly analogous to modern environments off the Peru-Chile and Benguela (Angola) margins, where oxygen-deficient, nutrient-rich upwelled waters influence surface waters far offshore (Paulmier and Ruiz-Pino, 2008). However, in the case of the ETE, conditions must have occurred with at least periodic accumulation of free H₂S in surface waters. In such a situation, euxinic bottom waters develop through enhanced sulfate reduction at the water-sediment interface and expand to surface waters through further sulfate reduction in an anoxic water column, possibly driven by phosphate release and eutrophication (Meyer and Kump, 2008). PZE and nitrogen limitation would be sustained as long as carbon export was able to maintain elevated rates of microbial denitrification and sulfate reduction, both of which suppress eukaryotic primary production and trigger an environmental cascade of extinction and/or inhibited origination of new organisms. The develop-

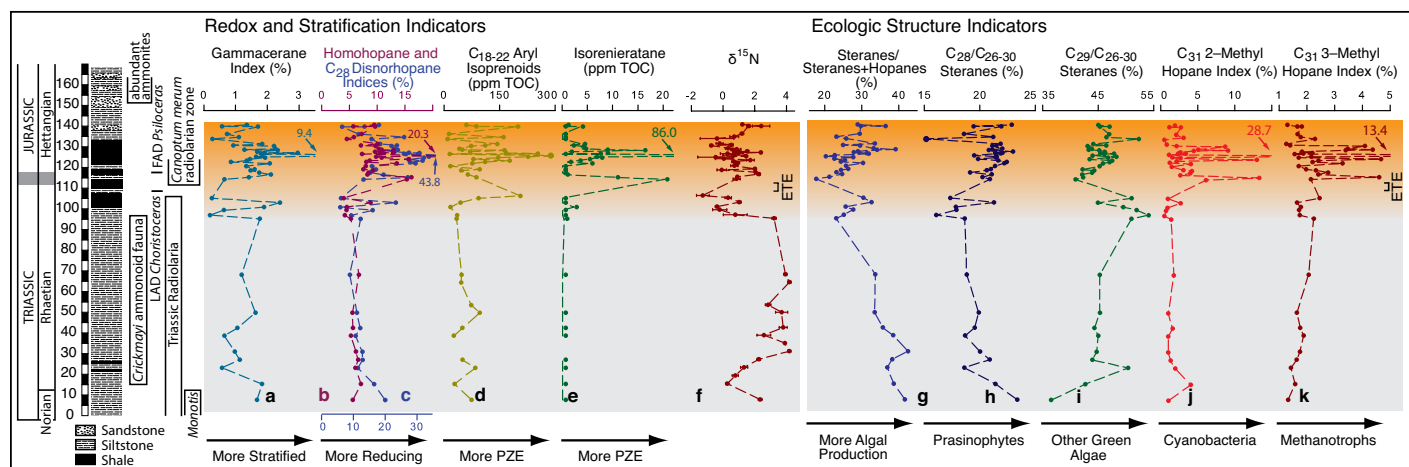


Figure 2. Biomarker and isotopic data indicative of ocean redox state (plots a–f), and planktonic ecology (plots g–k). An interpretation of each ratio is indicated by an arrow at the base of the plot. End-Triassic extinction (ETE) brackets (on right) show the estimated range of the extinction horizon. See the GSA Data Repository (see footnote 1) for sources for lithostratigraphy, biostratigraphy, and ETE placement. Colored arrows and numbers in plots a, b, c, e, j, and k mark an outlier sample (see the Data Repository). Gradient in background color indicates the environmental transition from Late Triassic to Early Jurassic. The Rhaetian-Hettangian (Triassic-Jurassic) boundary is shown as a gray bar that encompasses the uncertainty between the base of the *Canoptum merum* radiolarian zone and the base of the FAD of *Psiloceras*. PZE—photic zone euxinia; FAD—first appearance datum; LAD—last appearance datum; TOC—total organic carbon.

¹GSA Data Repository item 2015114, methods, notes, references, and supplementary tables and figures, is available online at www.geosociety.org/pubs/ft2015.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

ment of PZE in an upper bathyal and outer neritic environment, however, suggests that other factors also contributed to oxygen depletion and its maintenance over time (see discussion following).

The fact that PZE persisted for ~600 k.y. into the Jurassic in multiple ocean basins implies a substantial global reorganization of marine biogeochemistry. The development of PZE via intensified sulfate reduction must have been associated with variations in carbon fixation and export, as well as with elevated biological oxygen demand. Variations in carbon fixation and export have been proposed to explain isotopic anomalies in both carbonate and bulk organic carbon (Ward et al., 2001, 2004; Williford et al., 2007) and sulfur (Williford et al., 2009) at this location. To test this hypothesis, we used lipid biomarkers to reconstruct variations in planktonic ecology, including microbial processes associated with reducing conditions and altered nutrient budgets.

LIPID BIOMARKERS AS INDICATORS OF PLANKTONIC ECOLOGY

The composition of the plankton communities was assessed by analyzing the relative contributions of algal steranes (C_{26-30}) and bacterial hopanes (C_{27-35}) (steranes/steranes + hopanes, S/S + H ratio; g in Fig. 2), of C_{28} sterol and C_{29} sterol-producing algae (C_{28}/C_{26-30} , C_{29}/C_{26-30} ratios; g, h in Fig. 2), and of cyanobacteria and methanotrophic bacteria (2- and 3-methylhopane indices, respectively; 2-MeHI and 3-MeHI; i, j in Fig. 2). These results demonstrate that changes in ecologic structure across the ETE are synchronous with redox shifts. A progressive decline in eukaryotic plankton contribution (decreasing S/S + H values) began in the early Rhaetian and reached minimum values at the ETE and earliest Jurassic, with no evident recovery within the span of our record (g in Fig. 2). Previous studies have documented substantial shifts in algal groups through the ETE, including a reduction of calcifying organisms and an increased prasinophyte presence (van de Schootbrugge et al., 2007, 2013). We document an inverse trend for the relative contribution of C_{28} steranes, produced by chlorophyll-a and chlorophyll-c containing phytoplankton, as well as by prasinophytes and C_{29} steranes, produced by Chlorophyta (Peters et al., 2005; Kodner et al., 2008). Because both fossil and geochemical records suggest that the major radiation of chlorophyll-a- and chlorophyll-c-producing algae occurred later in the Mesozoic and in the Cenozoic (Peters et al., 2005), we propose that at least part of the increased relative contribution of C_{28} steranes derive from prasinophytes. This inference is consistent with our paleoredox reconstruction and N isotope data, because prasinophytes thrive in the presence of reduced N species associated with expanded OMZs (Prauss, 2007). Shifts in the distribution of eukaryotic plankton were accompanied by an increased contribution of hopane-producing cyanobacteria (2-MeHI) and methanotrophic bacteria (3-MeHI) following the ETE (i, j in Fig. 2). Elevated 2-MeHI coupled with $\delta^{15}N$ values ~0‰ or lower suggest a contribution from N_2 -fixing cyanobacteria, likely favored by the presence of sub-Redfield N/P ratios (Kuypers et al., 2004) resulting from phosphate released from sediments (Mort et al., 2007), and N loss through denitrification and annamox (anaerobic ammonium oxidation) (Kuypers et al., 2004). Elevated 3-MeHI values are consistent with increased methanotrophy coupled with intense methanogenesis in sulfide-rich waters and sediments, as observed in modern euxinic settings (Blumenberg et al., 2007). Expanded euxinia and reduced availability of fixed N would create conditions hostile to most primary producers, thus favoring prasinophytes and bacterioplankton (Fig. 3).

DISCUSSION

Our results are consistent with environmental changes stemming from variations in ocean circulation and ventilation, such as predicted for greenhouse climates (Kidder and Worsley, 2010). The expansion of OMZs during hothouse conditions may be aided by density stratification due to intense evaporation over epicontinental basins and/or a reduced latitudinal thermal gradient, suppressing high-latitude deep-water forma-

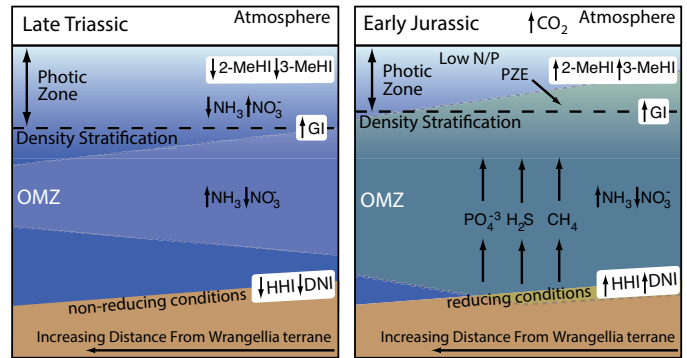


Figure 3. Schematic representation of the dominant biogeochemical modes for the Late Triassic (left) and Early Jurassic (right). Arrows next to chemical species indicate relative concentration changes under different redox potentials, and arrows in white boxes indicate the expected changes in biomarker distributions. The change in oxygen minimum zone (OMZ) shading from light blue to green indicates the high levels of H_2S in the Jurassic. PZE—photic zone euxinia; GI—gammacerane index; HHI—homohopane index; DNI— C_{28} 28,30 dinorhopanes; 2-MeHI, 3-MeHI—2- and 3-methylhopane indices, respectively (see text).

tion, thermohaline circulation, and ocean ventilation (Kidder and Worsley, 2010). Massive pulses of atmospheric CO_2 (to ~4400 ppm) from phases of Central Atlantic magmatic province volcanism (Schaller et al., 2011) are now more precisely dated to the ETE (Blackburn et al., 2013), and are synchronous with marine extinctions (e.g., Whiteside et al., 2010), fossil flora suggestive of increased CO_2 and extreme warming (McElwain et al., 1999), and enhanced wildfire activity (Belcher et al., 2010). The rise in pCO_2 was also coincident with a major disruption in biocalcification (van de Schootbrugge et al., 2007), possibly caused by ocean acidification, such as during the late Permian. The presence of an expanded OMZ and PZE across the ETE would have enhanced the effects of ocean acidification on calcifying organisms through organic-matter respiration and CO_2 release, as observed in modern oxygen-depleted environments (Cai et al., 2011), and the changes in nutrient inventories driven by oxygen deficiency and euxinia would have affected both calcifying and noncalcifying planktonic organisms.

CONCLUSIONS

We provide the first direct evidence of a stressed marine system in the Panthalassic Ocean during the ETE due to PZE, indicating that PZE was not restricted to epicontinental seas (Richoz et al., 2012). These results also reconcile previous studies suggesting a prolonged disruption in the carbon and sulfur isotope systems due to major shifts in redox conditions and marine productivity, ending with the return of ammonoid fossils in the mid-Hettangian (Ward et al., 2001, 2004; Williford et al., 2007, 2009). Our results contribute to a growing body of evidence suggesting that large-scale reorganizations of the ocean system resulting in episodes of oxygen-depleted and euxinic waters are a common feature of mass extinction events associated with greenhouse climates, and may constitute an extinction mechanism. These results are relevant for understanding the consequences of projected trends in atmospheric CO_2 levels, global warming, and ocean acidification and deoxygenation, which could lead to a state shift in Earth's biosphere, and mass extinction (Barnosky et al., 2012).

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