

Two-pronged kill mechanism at the end-Triassic mass extinction

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ABSTRACT

High-resolution biomarker and compound-specific isotope distributions coupled with the degradation of calcareous fossil remnants reveal that intensive euxinia and decalcification (acidification) driven by Central Atlantic magmatic province (CAMP) activity formed a two-pronged kill mechanism at the end-Triassic mass extinction. In a newly proposed extinction interval for the basal Blue Lias Formation (Bristol Channel Basin, UK), biomarker distributions reveal an episode of persistent photic zone euxinia (PZE) that extended further upward into the surface waters. In the same interval, shelly taxa almost completely disappear. Beginning in the basal paper shales of the Blue Lias Formation, a Lilliput assemblage is preserved consisting of only rare calcitic oysters (*Liostrea*) and ghost fossils of decalcified aragonitic bivalves. The stressors of PZE and decalcification parsimoniously explain the extinction event and inform possible combined causes of other biotic crises linked to emplacement of large igneous provinces, notably the end-Permian mass extinction, when PZE occurred on a broad and perhaps global scale.

INTRODUCTION

The end-Triassic extinction (ETE; ca. 202 Ma) was one of the largest mass extinction events of the Phanerozoic and temporally correlates with emplacement of the Central Atlantic magmatic province (CAMP; Pálfy et al., 2001). Pulsed CAMP outgassing of CO₂ and SO₂ in large quantities is thought to have triggered the ETE through a cascading series of environmental perturbations, including global carbon cycle changes, rapid warming leading to “hyperthermal” climatic events, and increased continental weathering. In many marine sedimentary basins, such conditions led to stagnation, deoxygenation, and deposition of organic-rich laminated mudstones (e.g., Kasprak et al., 2015). However, the precise mechanism(s) responsible for the extinction event remain elusive.

The Bristol Channel Basin, in the southwestern United Kingdom, although not necessarily globally representative, has become a focal locality for ETE studies employing palynological, paleontological (Warrington et al., 2008, and references therein), and geochemical analyses (Jaraula et al., 2013; Fox et al., 2020). The pronounced negative anomaly in the organic carbon isotope record ($\delta^{13}\text{C}_{\text{org}}$; initial carbon isotope excursion [CIE]; Fig. 1) in the Lilstock Formation at St. Audrie’s Bay (Hesselbo et al., 2002) is routinely used to chemostratigraphically correlate the extinction event and CAMP volcanism among sections on a global scale (e.g., Hesselbo et al., 2002). However, this CIE is stratigraphically offset from the highest occurrence (HO) of key fossil taxa. For example, the HO of foraminiferal, ostracod, and bivalve fauna (Hallam, 1990) is in the overlying basal Blue Lias Formation at the base of finely laminated organic carbon-rich mudstones termed the paper shales (Richardson, 1911). Furthermore, the HO of

conodonts also sits in the lowermost Blue Lias Formation (Swift, 1989). Based on these and other findings, including the HO of the reptile clade Phytosauria in the lowermost Blue Lias Formation (Maisch and Kapitzke, 2010) and a Lilliput assemblage of bivalves at the very base of the paper shales (Fox et al., 2020), recent studies have placed the ETE above the initial CIE in the paper shales, at a separate and slightly younger $\delta^{13}\text{C}_{\text{org}}$ anomaly (Fig. 1; Fox et al., 2020; Wignall and Atkinson, 2020). Despite decades of study establishing extinction of fauna characteristic of the end-Triassic (Fig. 1) and a dearth of calcite- and aragonite-secreting organisms at the extinction horizon, little is known of the killing mechanism(s). To better investigate this critical interval and the cause(s) of the ETE, we undertook high-resolution (i.e., centimeter-scale) biomarker and compound-specific isotope analyses to disentangle ecological community shifts recorded in the fossil record at two sections in the Bristol Channel Basin: St. Audrie’s Bay (51.182833°N, 3.286000°W) and Lilstock (51.200757°N, 3.176389°W).

RESULTS AND DISCUSSION

Acidification and Photic Zone Euxinia Forcing the ETE

Decalcified bivalve taxa exhibiting low diversity (Fox et al., 2020) and a general lack of CaCO₃-secreting organisms (Hallam, 1990) above the Lilliput assemblage in the paper shales give evidence of an acidification event that terminated with the return of calcareous nannoplankton and ammonites later in the sedimentary record (Fig. 1). Termed the biocalcification crisis, this event is placed between the HO of the ammonite

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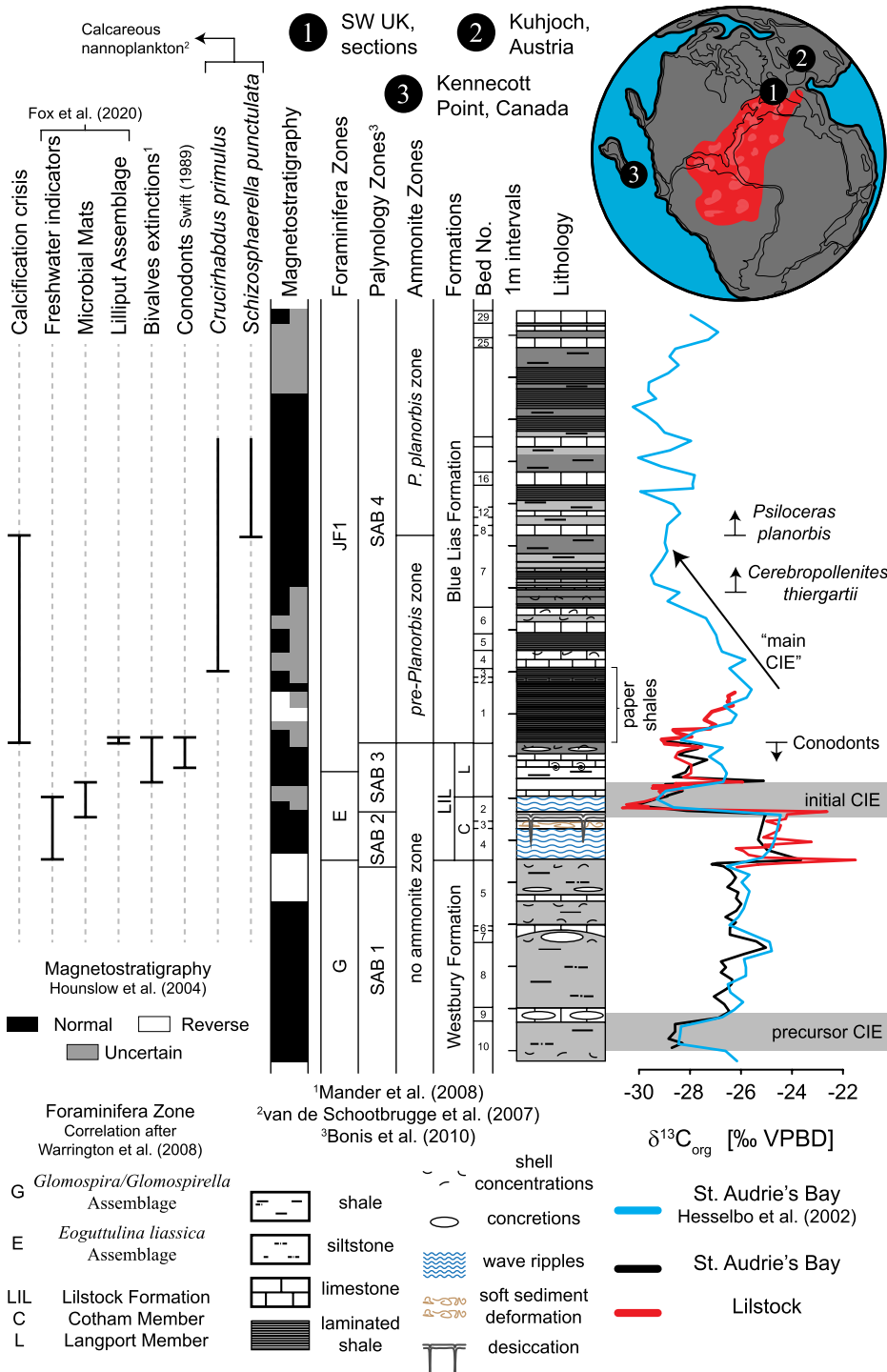


Figure 1. $\delta^{13}\text{C}_{\text{org}}$ records in the southwestern United Kingdom. End-Triassic extinction (ETE) lithology and paleogeographic reconstruction (top) are after Hesselbo et al. (2002), with Central Atlantic magmatic province (CAMP) lateral extent shown in red. Highest occurrence (HO) of conodonts is after Swift (1989). References for other ecological and geophysical data are given in the figure. CIE—carbon isotope excursion; VPDB—Vienna Peedee belemnite.

Choristoceras marshi and lowest occurrence of *Psiloceras spela* in European sections (McRoberts et al., 2012). Correlation between the HO of conodonts in the southwestern UK (Swift, 1989) and the HO of Triassic conodonts at the end of the *C. marshi* zone (Hillebrandt et al., 2013) provides correlative evidence of acidification

at the ETE. In a global context, the biocalcification crisis is evidenced by the major reduction in sedimentary carbonates and biogenic carbonates from secreting organisms, particularly corals, calcareous nannoplankton, benthic foraminifera groups, and some bivalves (Cope, 1991; Hautmann, 2004; van de Schootbrugge

et al., 2007; Lindström et al., 2012; McRoberts et al., 2012; Fox et al., 2020). Likely driven by CAMP-induced rapid outgassing of CO_2 , acidification is a plausible kill mechanism. However, our biomarker and compound-specific isotope investigation revealed that additional ecological stresses may have played important roles in driving extinction.

The paper shales are characterized by low pristane to phytane ratios (Pr/Ph) and high gammacerane index values, supporting anoxia in a well-stratified water column, and increases in C_{40} carotenoids derived from purple sulfur bacteria (okenane) and green-pigmented (chlorobactane) and brown-pigmented (isorenieratane) green sulfur bacteria (Fig. 2). Whereas purple sulfur bacteria (Chromatiaceae) and green-pigmented green sulfur bacteria (Chlorobi) reported below this unit indicate the presence of microbial mats (Fox et al., 2020), coexistence with brown-pigmented Chlorobi and biomarkers for anoxia and stratification indicate photic zone euxinia (PZE), a condition in which toxic H_2S extends upward into the sunlit region of an anoxic water column (e.g., Grice et al., 2005). Due to the higher light-intensity requirements of Chromatiaceae and green-pigmented Chlorobi compared to brown-pigmented Chlorobi (Grice et al., 1998; Brocks and Schaeffer, 2008; Overmann, 2008), the ratio of isorenieratane to okenane and chlorobactane ($\text{iso}/[\text{oke} + \text{chlo}]$) serves as a proxy for the relative depth of the chemocline, where higher values indicate predominance of low-light-adapted photosynthetic bacteria and therefore a deeper chemocline. Thus, the lower paper shales are characterized by a shallower chemocline compared to later in the record, where $\text{iso}/[\text{oke} + \text{chlo}]$ values increase. Below the Blue Lias Formation, $\text{iso}/[\text{oke} + \text{chlo}]$ values are also low. However, this interval is characterized by geochemical and sedimentological evidence for shallowing, freshening, and desiccation, but little evidence for prolonged PZE (Fox et al., 2020, and references therein).

Where okenane and chlorobactane abundances are highest, the $\delta^{13}\text{C}_{29}$ *n*-alkane record mirrors the minor negative $\delta^{13}\text{C}_{\text{org}}$ excursion, possibly related to the CAMP (Fig. 3). The $\delta^{13}\text{C}$ values of regular isoprenoids (pristane and phytane) and *n*-alkanes (C_{17-19}) also show negative excursions, although they are more variable (Fig. 3). Significant decreases in okenane and chlorobactane abundances later (higher) in the paper shales (Fig. 2) are possibly related to lower light availability due to a deepening of the chemocline and/or due to increased algal productivity in the euphotic zone (Grice et al., 1998; Brocks and Schaeffer, 2008; Overmann, 2008). Here, $\delta^{13}\text{C}$ values of pristane, phytane, and C_{17-19} *n*-alkanes show a positive isotope excursion, and, based on their isotopic differences, carbon fixation shifted to increased autotrophic

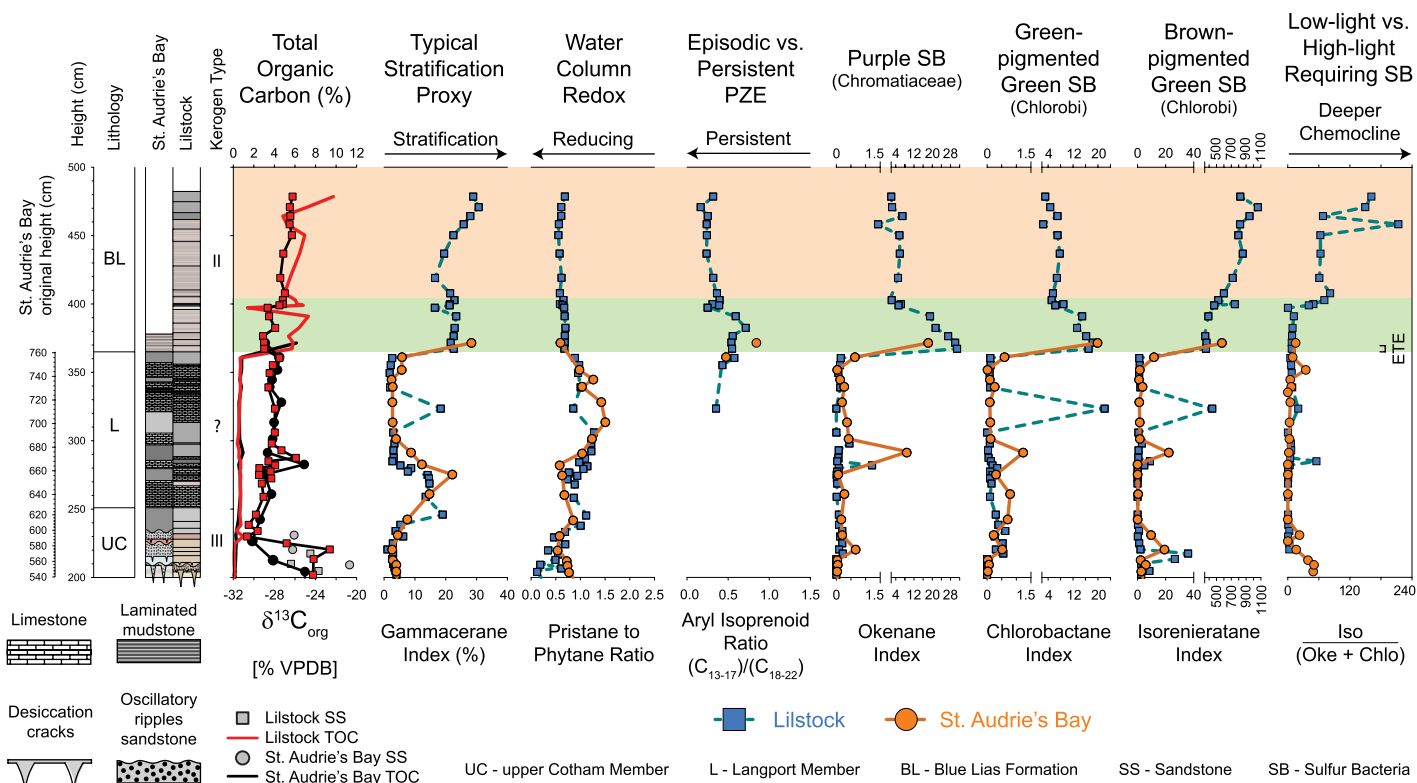


Figure 2. Biomarker-inferred redox and photic zone euxinia (PZE) conditions at St. Audrie's Bay (circles, solid lines) and Lilstock (squares, dashed lined) in the Bristol Channel Basin, UK, relative to $\delta^{13}\text{C}_{\text{org}}$ and total organic carbon (TOC). Two depositional environments are indicated by green (shallow redoxcline) and pink (deeper chemocline) bars. Biomarkers are below, and ecological indicators are above, each profile. Pristane to phytane ratios and gammacerane, okenane (Oke), chlorobactane (Chlo), and isorenieratane (Iso) indices up to the base of the Blue Lias Formation were reported by Fox et al. (2020). Details are provided in the Supplemental Material (see footnote 1). VPDB—Vienna Pee Dee belemnite; ETE—End-Triassic extinction.

production (Fig. 3; Grice et al., 2005). Elevated isorenieratane abundances in this interval show PZE continued but was limited to the lower region of the photic zone, and low Pr/Ph and aryl isoprenoid ratios throughout the paper shales demonstrate persistent PZE (Fig. 2; see the Supplemental Material¹; Schwark and Frimmel, 2004).

These results suggest the paper shales formed in two different sequential depositional environments, which were related to chemocline depth and carbon isotope chemistry. First, at the extinction horizon in the basal Blue Lias Formation, high abundances of Chromatiaceae and green-pigmented Chlorobi biomarkers and low iso/(oke + chlo) values support a shallow chemocline with PZE extending throughout much of the photic zone. Biomarker $\delta^{13}\text{C}$ values of marine organisms show a negative excursion and are variable compared to isotopic shifts in higher land plants. In modern-day ecosystems,

pH changes impact carbon leakage, mechanisms of carbon concentration, and activity of carbonic anhydrase in dehydrating HCO_3^- , all of which affect carbon isotope fractionation in phytoplankton (Wang et al., 2016). These effects of acidification on phytoplankton, in conjunction with intense PZE and its associated precipitation of bio-essential elements (Takahashi et al., 2014), possibly account for the marine $\delta^{13}\text{C}$ variations at the extinction horizon. The second depositional environment was characterized by a decline in Chromatiaceae and green-pigmented Chlorobi and increases in brown-pigmented Chlorobi and iso/(oke + chlo), consistent with contraction of sulfidic conditions. The coinciding shift to autotrophic production and positive $\delta^{13}\text{C}$ excursions in biomarkers of marine organisms agree with a ^{13}C -enriched euphotic zone due to increased carbon fixation and reduced light availability to Chromatiaceae and Chlorobi. Elevated abundances in brown-pigmented Chlorobi biomarkers support continued PZE but restricted to lower-light levels of the water column.

The invocation of H_2S toxicity as a driver for the ETE is supported by increases in isorenieratane and aryl isoprenoids (Richoz et al., 2012; Jaraula et al., 2013; Kasprak et al., 2015), and pyrite framboid diameter analysis (Atkinson and Wignall, 2019). However, for the first

time, we report that PZE was not only persistent, but, due to increased abundances of biomarkers derived from sulfur bacteria that require elevated light intensities and H_2S , PZE extended into shallower depths of the photic zone than previously thought. The presence of these organisms supports increased stress to epipelagic nektonic and planktonic communities. Furthermore, increased precipitation of bio-essential elements associated with periods of PZE have suppressive effects on marine life and its recovery during extinction events (Takahashi et al., 2014). Given that PZE biomarkers are observed in European and Canadian sections, which represent a range of depositional settings including open ocean (Richoz et al., 2012; Jaraula et al., 2013; Kasprak et al., 2015), PZE at the ETE may have had global extent, although perhaps not everywhere simultaneously. Effects of euxinia on calcifying organisms are poorly understood, but short-term intervals have resulted in planktonic foraminifera extinction (Oba et al., 2011). In conjunction with acidification, PZE may thus explain the near lack of fauna during the ETE biocalcification crisis. Additionally, anoxia is shown to be an important stressor on modern coral analogues experimentally (Altieri et al., 2017), and that ocean anoxic events frequently result in a species richness decline in calcareous

¹Supplemental Material. Details of the methodology, biomarker data, Rock-Eval pyrolysis, episodic versus persistent PZE, and full ecological changes relative to biomarker distributions. Please visit <https://doi.org/10.1130/GEOLOGY.S.17139236> to access the supplemental material, and contact editing@geosociety.org with any questions.

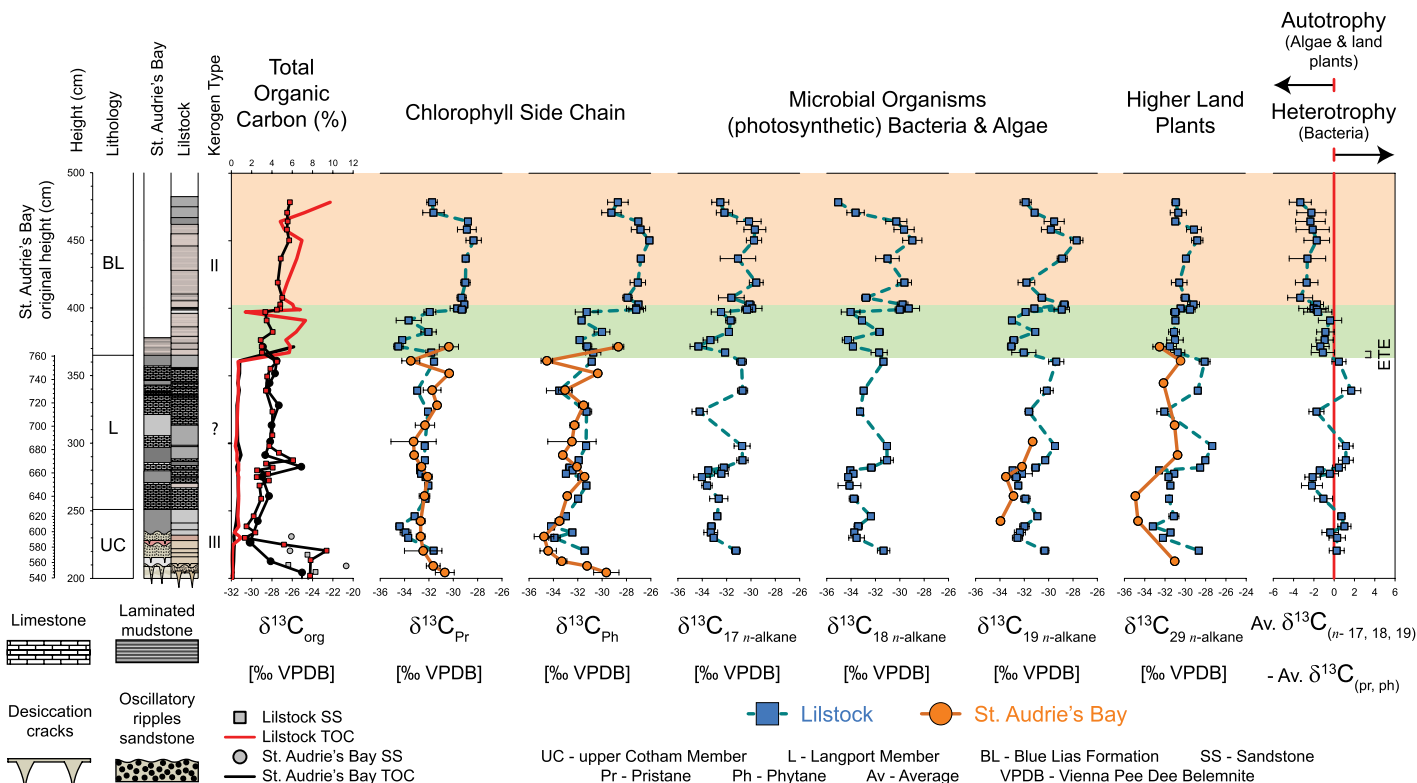


Figure 3. Compound-specific carbon isotope analysis at St. Audrie's Bay (circles, solid lines) and Lilstock (squares, dashed lines) in the Bristol Channel Basin, UK. Two depositional environments are indicated by green (variable but negative excursions in regular isoprenoids and *n*-alkanes) and pink (positive excursions and shift to more autotrophy) bars. Biomarkers are below, and ecological indicators are above, each profile. $\delta^{13}\text{C}$ of biomarkers to the base of the Blue Lias Formation were reported by Fox et al. (2020). Details are provided in the Supplemental Material (see footnote 1). ETE—End-Triassic extinction; TOC—total organic carbon.

and benthic communities (e.g., Watkins et al., 2005; Mattioli et al., 2008). Consequently, we argue that the development of persistent and intense PZE in conjunction with acidification leads to major ecological stress, and that these conditions together were important for driving the ETE. These features are the most compelling evidence of CAMP-induced environmental perturbations throughout the latest Rhaetian, and they plausibly relate the negative $\delta^{13}\text{C}$ anomaly in the lower Blue Lias Formation to CAMP activity.

Organic-rich laminated lithologies are often host to Lagerstätten assemblages that preserve articulated fossils. Lack of bioturbation and preservation of microlaminations in lacustrine and marine settings indicate deposition below the wave base and persistent water-column stratification and bottom water anoxia (Olsen, 1990). Although the facies of the paper shales conform to this model, the absence of fish or any articulated fossils (Hallam, 1990; confirmed by our field observations) is consistent with acidification and PZE driving extinction, although this may also have been related to basin restriction. This lack of fossil content, in addition to the microlaminations, is anomalous compared to superficially similar orbitally paced units above the paper shales that do have

abundant fossils. From field observations, the paper shales immediately succeeding the Lilliput assemblage are nearly devoid of shelly taxa, with the exception of decalcified bivalves, supporting acidification. However, Mander et al. (2008) reported shelly taxa specimens (*Modiolus* sp., *Liostrea* sp., and *L. hisingeri*) in the uppermost layers, and Atkinson and Wignall (2019) reported *Liostrea* sp. in the lower paper shales, and references therein). Major increases in foraminifera species richness and preserved foraminiferal test linings occur above this interval (Bonis et al., 2010; Clémence and Hart, 2013), signaling diminishing effects of acidification (Fig. 4). Biomarker and pyrite framboid analyses in shale/dark marl lithologies support cyclical euxinic conditions into the *P. planorbis* zone (Jaraula et al., 2013; Atkinson and Wignall, 2019), suggesting stable conditions with increased continental weathering during shale/dark marl deposition and storm events/mixing during limestone and light marl formation

(Weedon et al., 2017). Above the lowest occurrence of *P. planorbis*, bivalve assemblages increase in diversity but not in abundance (Mander et al., 2008), suggesting localized effects of acidification and PZE inhibited the return of pre-extinction ecological conditions.

CONCLUSIONS

The fully marine expression of the ETE in the southwestern UK is in the basal Blue Lias Formation, during an acidification event with persistent and intense PZE and its associated redox conditions. This combination of ecological stressors explains many observations within the lower Blue Lias Formation, including the lack of well-preserved vertebrate fossils, near absence of shelly taxa in the paper shales, and subsequent increases in species richness upward toward the termination of the biocalcification crisis. Furthermore, acidic and euxinic conditions are the most compelling evidence of CAMP-induced environmental perturbations thought to drive the ETE throughout the latest Rhaetian. In future studies, high-resolution sampling for biomarkers and their $\delta^{13}\text{C}$ values, in conjunction with ecological community shifts, will be critical to properly evaluate the global extent and significance of combined ecological stressors in the ETE and similar extinctions.

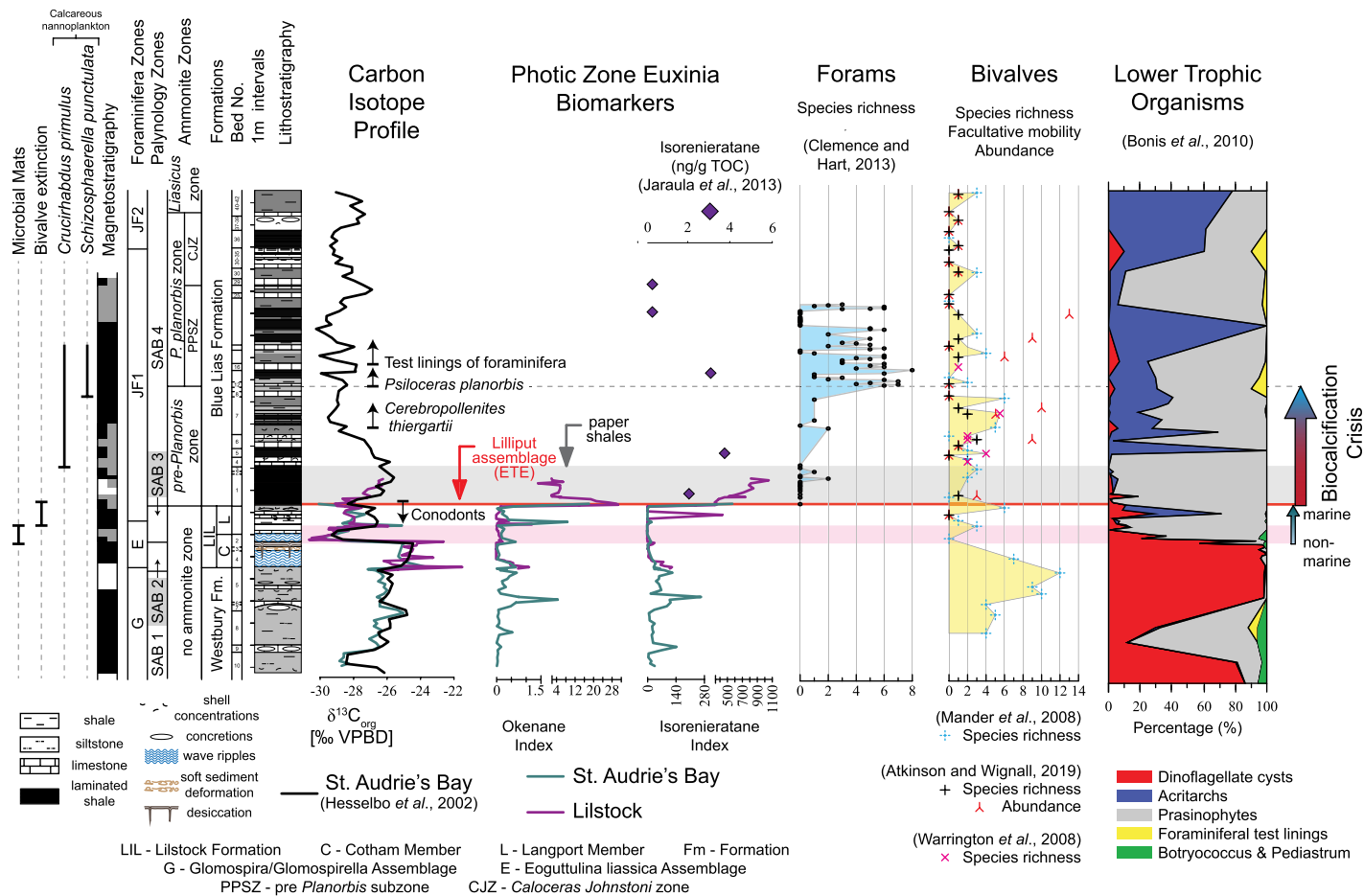


Figure 4. Ecological shifts relative to anoxia (paper shales), biocalcification crisis, and photic zone euxinia (PZE) in the Bristol Channel Basin, UK. Note: Bivalve species richness increases after intense PZE, and foraminifera species richness increases with the return of *Psiloceras planorbis*. Details are provided in the Supplemental Material (see footnote 1). ETE—End-Triassic extinction; TOC—total organic carbon; VPDB—Vienna Pee Dee belemnite.

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