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Marine redox and nutrient dynamics linked to the Cambrian radiation of animals

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ABSTRACT

The early Cambrian witnessed an increase in metazoan ecosystem complexity, likely linked to enhanced oxygen and nutrient availability. However, while improved stratigraphic and geochemical records suggest that the Cambrian explosion occurred under highly dynamic redox conditions, mechanistic links to nutrient availability and early Cambrian evolutionary innovations are poorly constrained. Here, we report paleoredox and nutrient data for two drill cores documenting late Cambrian Stage 2 to Stage 3 (~522 to 514 Ma) strata from the Yangtze Block, South China. The development of water column euxinia during Cambrian Stage 2 led to extensive recycling of P, fueling elevated primary production and hence an increase in atmospheric and shallow marine oxygen concentrations. The resulting expansion of oxygenated shelf area promoted sedimentary P retention, and in combination with a diminished supply of P from upwelling, drove a transition to oligotrophic shallow marine conditions during Cambrian Stage 3. Reduced primary production and limited water column oxygen consumption allowed for the stabilization of oxygenated continental shelf habitats that supported a burgeoning biotic complexity.

INTRODUCTION

The early Cambrian (Fortunian–end Stage 3; ca. 538.8–514 Ma) witnessed the abrupt appearance and rapid diversification of most modern animal phyla during the ‘Cambrian Explosion’ (Knoll and Carroll, 1999; Erwin et al., 2011; Wood et al., 2019). A wide range of potential triggers for the Cambrian Explosion have been proposed, including intrinsic developmental and ecological innovations (Erwin et al., 2011), and extrinsic changes (particularly oxygen levels) to environmental habitability (Smith and Harper, 2013; Knoll and Carroll, 1999; Lenton et al., 2014). The first animals likely had low oxygen demands (Mills et al., 2014), however the larger and more metabolically active skeletonizing animals that appeared during the early Cambrian would have required considerably higher oxygen levels (Sperling et al., 2013). Indeed, potential links between pulses of shallow-ocean oxygenation and biodiversity have been recorded on the early Cambrian Siberian platform (He et al., 2019; Zhuravlev et al., 2022) and in South China (Chen et al., 2015; Li et al., 2017).

The availability of the bio-limiting nutrients phosphorus (P) and nitrogen (N) likely also exerted an important control on environmental habitability, with P generally considered to be the ultimate limiting nutrient for primary production on geological timescales (Tyrell, 1999). These nutrients control the degree of regional oxygen production and consumption, as well fueling more complex life (Brocks et al., 2017). Depositional redox conditions also control P recycling, resulting in feedbacks that dictate the evolution of regional marine redox state (Schobben et al., 2020; Bowyer et al., 2023). However, despite their fundamental importance for ecosystem habitability and animal evolution, integrated records of redox and P cycling in the early Cambrian are highly limited (see Creveling et al., 2014).

Here, we report a geochemical study of shelf and slope successions from the Yangtze Block, South China. We utilize Fe speciation, redox sensitive trace element systematics and P phase partitioning to evaluate contemporaneous marine redox conditions and controls on primary productivity. These data allow a detailed assessment of redox and nutrient controls on the major biological events that occurred during the early Cambrian.

GEOLOGIC SETTING AND MATERIALS

We investigate two drill cores from the Yangtze Block, deposited in an open-marine continental shelf (ZK 402) and slope (CY 1) setting (see Supplemental Material[1] for full details of the geologic setting and methods). Both cores preserve a relatively continuous record spanning the latter part of Cambrian Stage 2 through Cambrian Stage 3, offering a prime opportunity to evaluate biogeochemical changes across an interval that captures a major evolutionary event.

RESULTS AND DISCUSSION

Oceanic redox dynamics during the early Cambrian

We employ a combination of Fe speciation and redox-sensitive trace metal (RSTM; Mo, U, V) systematics (see Text S3) to provide a robust framework for interpreting depositional redox conditions (e.g., Tribovillard et al., 2006; Poulton, 2021). In modern and ancient marine sediments, a highly reactive (Fe_{HR}) to total Fe (Fe_T) ratio of >0.38 provides an indication of anoxia, while Fe_{HR}/Fe_T <0.22 suggests oxic conditions, with values between considered equivocal. When anoxia is indicated, the extent of pyritization (Fe_{Py}) of the Fe_{HR} pool is used to differentiate between ferruginous (Fe_{Py}/Fe_{HR} <0.6) or euxinic (Fe_{Py}/Fe_{HR} >0.8) conditions (Poulton, 2021). Generally, RSTMs tend to be less soluble under reducing conditions, leading to authigenic enrichments in the sediment, with Mo in particular requiring the presence of dissolved sulfide (Tribovillard et al., 2006).

During late Cambrian Stage 2 to early Stage 3 (interval I), the development of persistent euxinia at both sites is suggested by a combination of high Fe_{HR}/Fe_T (>0.7) and high Fe_{Py}/Fe_{HR} ratios (0.69 ± 0.11 for ZK 402 and 0.92 ± 0.04 for CY 1; Fig. 1; Table S1). This interpretation is supported by high enrichment factors (EFs; see Text S2) for the RSTMs and high Mo_{EF}/U_{EF} ratios. During the initial stages of interval II (middle to late Stage 3), a decline in Fe_{HR}/Fe_T ratios, EF values and Mo_{EF}/U_{EF} ratios occurs in both drill cores (Fig. 1). Subsequently, on the shelf (ZK 402), Fe_{HR}/Fe_T ratios and RSTM enrichments remain persistently low. This suggests a transition to dominantly oxic conditions, although occasional minor increases in Fe_{HR}/Fe_T ratios, EF values and Mo_{EF}/U_{EF} ratios may indicate transient, short-lived anoxia. On the slope (CY 1), despite decreasing trends in redox proxy data from intervals I to II, values remain elevated, indicating continued euxinia, perhaps punctuated by episodic ferruginous intervals (lower Mo_{EF}/U_{EF} ratios; Fig. 1).

A compilation of global Fe speciation data (Text S4; Table S2) provides further insight into spatio-temporal variability in marine redox state (Fig. 2A). While the majority of data are from South China, a stratified early Cambrian ocean is apparent, with oxic surface waters overlying ferruginous deeper waters (with occasional euxinia), prior to the latter part of Stage 2 (Fig. 2). Euxinia then became common in outer shelf to slope settings, before extending into shallow shelf settings at the Stage 2-Stage 3 boundary. A clear transition to expanded shelf oxygenation then occurred, while deeper waters remained largely anoxic during Stage 3. The local marine redox state inferred from Fe speciation data is consistent with estimates of global marine redox from U and Mo isotopes (Fig. 2). Carbonates from South China, Siberia and Morocco in the latest Fortunian and Stage 2 document negative $\delta^{238}U$ excursions (Wei et al., 2018; Dahl et al., 2019), suggesting episodic expansions of seafloor anoxia during these intervals. By contrast, consistently higher $\delta^{238}U$ data recorded in carbonates from Siberia and shales from South China in Stage 3 (Dahl et al., 2019; Wei et al., 2020) provide evidence for more widespread oxygenation. Furthermore, modern-like $\delta^{98}Mo$ signatures in Cambrian Stage 3 also suggest a major expansion of oxic seafloor (Chen et al., 2015).

Marine eutrophication and animal diversification

High total organic carbon (TOC) and total P (P_{tot}) concentrations recorded in the lower part of interval I in both drill cores (Fig. 3) potentially indicate high marine primary productivity and nutrient levels. The greenhouse climate of the early Cambrian (Hearing et al., 2018), likely drove enhanced chemical weathering (Peters and Gaines, 2012; Lipp et al., 2021) and hence a high terrigenous nutrient influx. Alternatively, or in addition, high nutrient levels could have occurred via upwelling of nutrient-replete deep ocean waters (e.g., Behrenfeld et al., 2006; Bowyer et al., 2017). Upwelling can be evaluated using Co (ppm)×Mn (wt%) values, whereby upwelling systems are characterized by low sedimentary Co and Mn concentrations due to their depletion in upwelled deep-ocean waters, in addition to recycling of Mn back to the water column under reducing conditions. However, restricted basins are characterized by relatively high Co and Mn concentrations due to relatively high riverine inputs and limited water exchange with the open ocean (Sweere et al., 2016).

The low Co×Mn values in the lower part of interval I are similar to those of modern upwelling systems (<0.4 ppm%; Sweere et al., 2016), suggesting strong upwelling (Text S5). This internal marine nutrient supply was augmented by nutrient recycling from the sediment, which we evaluate via the phase partitioning of P. This approach quantifies four operationally-defined P pools (Thompson et al., 2019), including Fe-bound P (P_{Fe}), authigenic carbonate fluorapatite, biogenic apatite and $CaCO_3$-bound P (P_{auth}), detrital apatite (P_{det}), and organic-bound P (P_{org}). Reactive P (P_{reac}) represents potentially mobile P during transport and early diagenesis, and is calculated as the sum of P_{Fe}, P_{auth} and P_{org}.

P_{org} is preferentially released from organic matter (C_{org}) via anaerobic remineralization, resulting in C_{org}/P_{org} ratios above the Redfield ratio of 106/1 (Ingall et al., 1993). In addition, P_{Fe} may be released during reductive dissolution of Fe (oxyhydr)oxide minerals (Slomp et al., 1996). A proportion of this P may undergo ‘sink switching’ to authigenic phases in the sediment (Slomp et al., 1996). However, P may also be recycled back to the water column, particularly under sulfidic conditions, potentially driving a positive productivity feedback (Van Cappellen and Ingall, 1996).

In samples from interval I, molar C_{org}/P_{org} and C_{org}/P_{reac} ratios are significantly greater than the Redfield ratio of 106/1 (Fig. 3), demonstrating release of P from organic matter (C_{org}/P_{org}) and recycling back to the water column (C_{org}/P_{reac}). This recycling occurs alongside high P_{tot} contents relative to average shale (0.009; Turekian and Wedepohl, 1961), suggesting particularly high levels of bioavailable phosphate in the overlying water column. Expanded euxinia (Fig. 2) would have resulted in a high degree P recycling in continental margin settings, promoting a strong positive productivity feedback following upwelling to the surface ocean (Van Cappellen and Ingall, 1996), and providing a food supply for early mobile animals (Fig. 4). Furthermore, increased TOC burial in shelf and slope environments as a consequence of enhanced primary productivity likely contributed to gradual atmospheric and shallow ocean oxygenation (He et al., 2019). Hence, increased oxygen availability and food supply in the shallow ocean drove the major evolutionary event recorded by the Chengjiang and Qingjiang lagerstätte, which occur coincident with the first appearance of mineralized trilobites in Cambrian Stage 3 (Fig. 2; Sun et al., 2022). The gradual decline in TOC and P in the upper part of interval I may be related to the development of weakly euxinic conditions and weakened upwelling, leading to a decrease in bioavailable P and hence lower TOC burial.

Oligotrophic stabilization of shelf oxygenation

Total P (as P_{tot} and P_{tot}/Al ratios) and TOC remain low throughout interval II in both cores, suggesting reduced levels of productivity and nutrient availability (Fig. 3). Variability in TOC and P may also be influenced by changes in redox conditions, lithology and sedimentation rate. However, the decrease in TOC and P in both cores initially occurs in shale in the upper part of interval I, which was deposited under euxinic conditions. Furthermore, despite the lithological differences between the two cores in interval II (and possible corresponding changes in sedimentation rate), a synchronous decline in TOC and P is observed in both cores, suggesting that productivity was the dominant control on TOC and P variability (Text S6).

Given the generally enhanced continental weathering flux indicated for the early Cambrian (including during intervals I and II; Peters and Gaines, 2012; Lipp et al., 2021), the decline in nutrient levels likely reflects a reduction in sedimentary P recycling and P upwelling from deeper waters. During interval II, P_{tot}/Al ratios remain below average shale in both drill cores (Fig. 3). On the shelf (ZK 402), ferruginous samples in the lower part of interval II have elevated C_{org}/P_{org} and C_{org}/P_{reac} ratios relative to the Redfield ratio, but with values that are considerably lower than those of interval I (Fig. 3). This suggests that the extent of P recycling was considerably diminished, with lower P_{tot}/Al ratios implying a major overall decrease in bioavailable P. Furthermore, while the dominantly oxic samples from the rest of interval II also have high C_{org}/P_{org} ratios, C_{org}/P_{reac} ratios plot below the Redfield ratio. This suggests that the P released during early diagenesis was fixed in the sediment as authigenic phases (supported by an increased proportion of P_{auth}; Fig. 3). This C/P pattern implies very low bioavailable P, consistent with most modern oligotrophic settings, which are characterized by higher C_{org}/P_{org} ratios and lower C_{org}/P_{reac} ratios (Slomp et al., 2013).

In the slope setting (CY 1), C_{org}/P_{org} ratios are elevated and C_{org}/P_{reac} ratios scatter close to the Redfield ratio during interval II, with higher values for euxinic samples and lower values for ferruginous samples (Fig. 3 and Fig. S4). These is consistent with a dynamic P response to the prevailing water column redox conditions, with intermittently enhanced P recycling back to the water column under euxinic conditions, although the lower P_{tot} contents relative to interval I (Fig. 3) suggest that water column P concentrations were likely greatly diminished overall. In addition, elevated Co×Mn values suggest that this limited flux of regenerated P was likely not efficiently transported to the photic zone, due to much lower rates of upwelling, thereby resulting in the development of oligotrophic conditions on the shelf (Fig. 4). This would have reduced primary productivity in surface waters, thus decreasing the amount of dissolved O_2 consumed during the oxidation of sinking organic matter, and thereby stabilizing oxic conditions in shelf environments.

Our data demonstrate that variability in ocean circulation and sedimentary P recycling played a critical role in marine redox and nutrient dynamics during the early Cambrian. Prevailing euxinia along continental margins and active ocean circulation during late Cambrian Stage 2 to early Stage 3 resulted in intensified sedimentary P recycling in deep waters and enhanced nutrient supply to the surface ocean (Fig. 4). Increased primary production would have led to higher atmospheric and shallow marine oxygen levels, and hence an expansion of oxic waters. The enhanced oxygen availability and food supply likely facilitated the early Cambrian bioradiation that occurred at this time. The expanded oxic seafloor area and diminished ocean circulation that occurred during middle to late Cambrian Stage 3 then promoted the retention of sedimentary P in shelf areas, and along with reduced upwelling, resulted in a decrease in shallow marine nutrient levels. Under the ensuing oligotrophic conditions, stable oxygenated continental shelves developed, thereby creating habitats that supported a burgeoning diversity in animal life.

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Data Availability

All data that support the findings of this study are provided in Supplementary Tables S1 and S2.

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FIGURE CAPTIONS

Fig. 1. Stratigraphic plots of Fe speciation, RSTM EFs and Mo_{EF}/U_{EF} ratios for drill cores ZK402 and CY 1. Fm, Formation; Ed, Ediacaran; Fo, Fortunian; DY, Dengying; LCP, Liuchapo.

Fig. 2. Marine redox conditions and biodiversity patterns during the early Cambrian. A. Compilation of Fe speciation data for platform, shelf, slope and basin environments from 541 Ma to 514 Ma. Blue and orange lines represent the LOESS curves. B. Global diversity of phyla and classes (Erwin et al., 2011) and major Cambrian lagerstätten (Sun et al., 2022). C. Schematic evolution of local marine redox conditions based on iron speciation data. D. Schematic evolution of global marine redox conditions based on Mo and U isotope records (Chen et al., 2015; Dahl et al., 2019; Wei et al., 2020).

Fig. 3. Stratigraphic distribution of TOC, $\delta^{13}C_{org}$, P_{tot}, P_{tot}/Al, C_{org}/P_{org}, C_{org}/P_{reac}, Co×Mn and P phase partitioning.

Fig. 4. Summary of marine redox and nutrient cycling during the early Cambrian. A.

Persistently euxinic conditions on the shelf and slope promoted P regeneration into the water column. Recycled P was transported to the photic zone by active upwelling, resulting in a positive productivity feedback that led to increased C_{org} burial, and ultimately atmospheric and shallow marine oxygenation. B. P was effectively fixed in shelf sediments. Continued euxinia in slope environments may have resulted in intermittent P recycling to the water column, but P in deep waters was not effectively transported to the photic zone due to decreased upwelling, which limited primary production and O_2 consumption.

[1] Supplemental Material. Detailed geological setting, methods, supplemental notes, Figures S1–S4 and Tables S1–S2. Please visit https://doi.org/10.1130/XXXX to access the supplemental material, and contact editing@geosociety.org with any questions.