

Review Article

Heterogeneous and dynamic marine shelf oxygenation and coupled early animal evolution

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It is generally agreed that early diversification of animals and significant rise of atmospheric and oceanic oxygen (O₂) levels occurred in the Ediacaran (635–541 million years ago, Ma) and early Cambrian (ca. 541–509 Ma). The strength and nature of their relationship, however, remain unclear and debated. A recent wave of paleoredox research — with a particular focus on the fossiliferous sections in South China — demonstrates high spatial heterogeneity of oceanic O₂ (redox) conditions and dynamic marine shelf oxygenation in a dominantly anoxic ocean during the Ediacaran and early Cambrian. This pattern shows a general spatiotemporal coupling to early animal evolution. We attribute dynamic shelf oxygenation to a complex interplay among the evolving atmosphere, continents, oceans, and biosphere during a critical period in Earth history. Our review supports the idea of a complex coevolution between increasing O₂ levels and early diversification of animals, although additional work is required to fully delineate the timing and patterns of this coevolution and the mechanistic underpinnings.

Introduction

The Ediacaran (635–541 million years ago, Ma) to early Cambrian (ca. 541–509 Ma) was a key period in the Earth's history, marked by early diversification of animals and a significant rise of atmospheric and oceanic oxygen (O₂) levels [1–4]. Because O₂, as an electron acceptor, releases more energy per electron transfer than any other element used in the metabolisms of complex life [5], rising O₂ levels have long been assumed to have triggered the early appearance and diversification of animals [6–10]. Furthermore, the rise of animals, through feedback mechanisms, may have contributed to the upswing in O₂. For example, animals can increase the sinking rate of organic matter in the water column through grazing and subsequent repackaging of surface-water primary organic matter into larger fecal pellets. Rapid settling minimizes organic decay and thus its corresponding O₂ consumption in the water column, leading to widespread oceanic oxygenation when occurring on a large scale [11,12]. Moreover, enhanced organic burial in sediments favors increased release of photosynthetic O₂ to the atmosphere [13,14].

At the same time, early animals may not have required significant amounts of O₂. Anaerobic mitochondria able to persist in low O₂ environments are well known from the primitive animals [15]. Furthermore, a recent study found that sponges, the simplest and earliest diverging animals in the geologic record [16,17], could have respired in low O₂ environments [18]. Consistent with this assertion, laboratory experiments have shown that sponges can survive in a low O₂ environment down to 0.5% of the present atmospheric level (PAL) [19]. Moreover, data compiled from modern O₂ minimum zones (OMZs) indicate that complex organisms can live in low O₂ waters, although biomass and individual size decrease significantly [20]. Nevertheless, because certain animals, including sponges, have the ability to live under low O₂ conditions, some researchers have decoupled animal diversification from the rise of atmospheric and oceanic O₂ levels during the Ediacaran and early Cambrian (e.g. [21,22]) — but there is more to this story.

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Although some simple animals can tolerate low O_2 (e.g. sessile organisms with high proportions of their cells exposed to seawater), it is generally accepted that more complex animals (e.g. large mobile organisms, including predators) should require more O_2 to meet their energy needs [20,23]. It is therefore necessary that we better understand the patterns and possible relationships between geochemical fingerprints of evolving O_2 contents and paleontological records of early diversification of metazoans and their ecologies. Regrettably, concentrations of oceanic and atmospheric O_2 during the late Ediacaran-to-early Cambrian are not well known, although there is a general consensus that oxygenation generally remained well below modern levels (reviewed in ref. [24]) perhaps until the mid-late Paleozoic [25]. New data, however, suggest a more complex O_2 history during the late Ediacaran and early Cambrian, particularly as expressed in the fossil-bearing stratigraphic sections of South China (e.g. [7–10,26–31]). In this review, we focus on this emerging picture and in the process provide new insights into the possible relationships between increasing O_2 levels and early evolution of animals during the Ediacaran and early Cambrian.

Spatial heterogeneity of oceanic redox and coupled animal ecosystems

Although early studies assumed fully oxygenated Ediacaran–early Cambrian oceans (e.g. [32,33]), a growing body of evidence supports a generally ferruginous deep ocean (low $[O_2]$ and containing free Fe^{2+}) for this period [34,35]. Recent data also point to an ocean that was highly stratified, with a mid-depth euxinic watermass ($[O_2] = 0$ ml/l and containing free H_2S) maintained dynamically on continental shelves between oxic surface waters ($[O_2] > 2$ ml/l) and ferruginous deep waters (Figure 1C) (e.g. [9,36–44]). Such heterogeneity in oceanic redox implies that the local redox conditions must have shaped early animal ecosystems if increasing oceanic O_2 levels indeed played a major role in early animal physiology.

Spatial comparisons between life and local redox records are best undertaken at fossiliferous locations with rock types well suited to geochemical methods for reconstructing paleoredox, such as organic-rich shales. The study of Li et al. [45] focused on the Miaohu Biota (South China) is a typical example. The Miaohu Biota is an Ediacaran assemblage of multicellular eukaryotes with low diversity and simple morphologies dominated by benthic macroscopic algae and only a few putative metazoans [46]. Li et al. [45] studied the paleoredox conditions of the late Ediacaran (~560–551 Ma) black shales containing the Miaohu Biota using well-established iron-based and trace metal geochemical approaches and petrographic analysis [47]. Those data were compared with results from equivalent nonfossil-bearing shales at adjacent sections (<30 km apart). The results indicated that the Miaohu Biota occurred in settings linked to poorly oxygenated (i.e. suboxic) and anoxic but non-euxinic (i.e. ferruginous) bottom waters, in contrast with the persistently euxinic environments suggested for the nonfossiliferous sections. The assignment of the Miaohu Biota to low O_2 settings is consistent with the aforementioned low O_2 tolerance of early animals. We prefer this interpretation over transient oxygenation events in otherwise inhospitable environments because we struggle to imagine how the impacts of those events were confined to Miaohu Biota-bearing black shales but not to the nearby nonfossiliferous euxinic sections. Such low O_2 environments were probably associated with the suboxic to anoxic waters between oxic surface waters and the euxinic intermediate depths of the Ediacaran–early Cambrian shelves and featuring nitrate and Fe–Mn reduction (Figure 1C) [48]. Taken together, these results indicate that the complexities of early animal ecosystems were probably shaped by dynamic local O_2 and H_2S conditions.

A basin-scale test of this relationship was undertaken recently by Jin et al. [9] for the fossiliferous strata of the Cambrian Ages 2 and 3 (~529–514 Ma) on the Yangtze Platform, South China. These authors reconstructed the local redox conditions based on integrated iron and trace metal data from eight correlative sections spanning a range of water depths. This basin-wide dataset revealed a three-layer (oxic surface, euxinic intermediate and ferruginous deep) redox structure on the Yangtze Platform during the earliest Cambrian. It also showed clearly that animal ecosystem complexity was spatially associated with local bottom-water redox conditions, with increasing complexity at more oxygenated shallow settings. Such redox control on the complexity of the early animal ecosystem was similarly observed for the late Ediacaran Nama Biota (Namibia) [49]. The effects of spatially varying O_2 levels on the lifestyles of specific animal types were further tested by Jin et al. [50] through comparison of redox and fossil records from three fossiliferous sections of Cambrian Ages 3 (~521–514 Ma) also on the Yangtze Platform. The authors observed that planktonic and benthic trilobites, as well as sedimentary bioturbation, occurred at settings of inferred oxic bottom waters. In contrast, settings marked by anoxic (including euxinic) bottom waters revealed only planktonic trilobites and an absence of

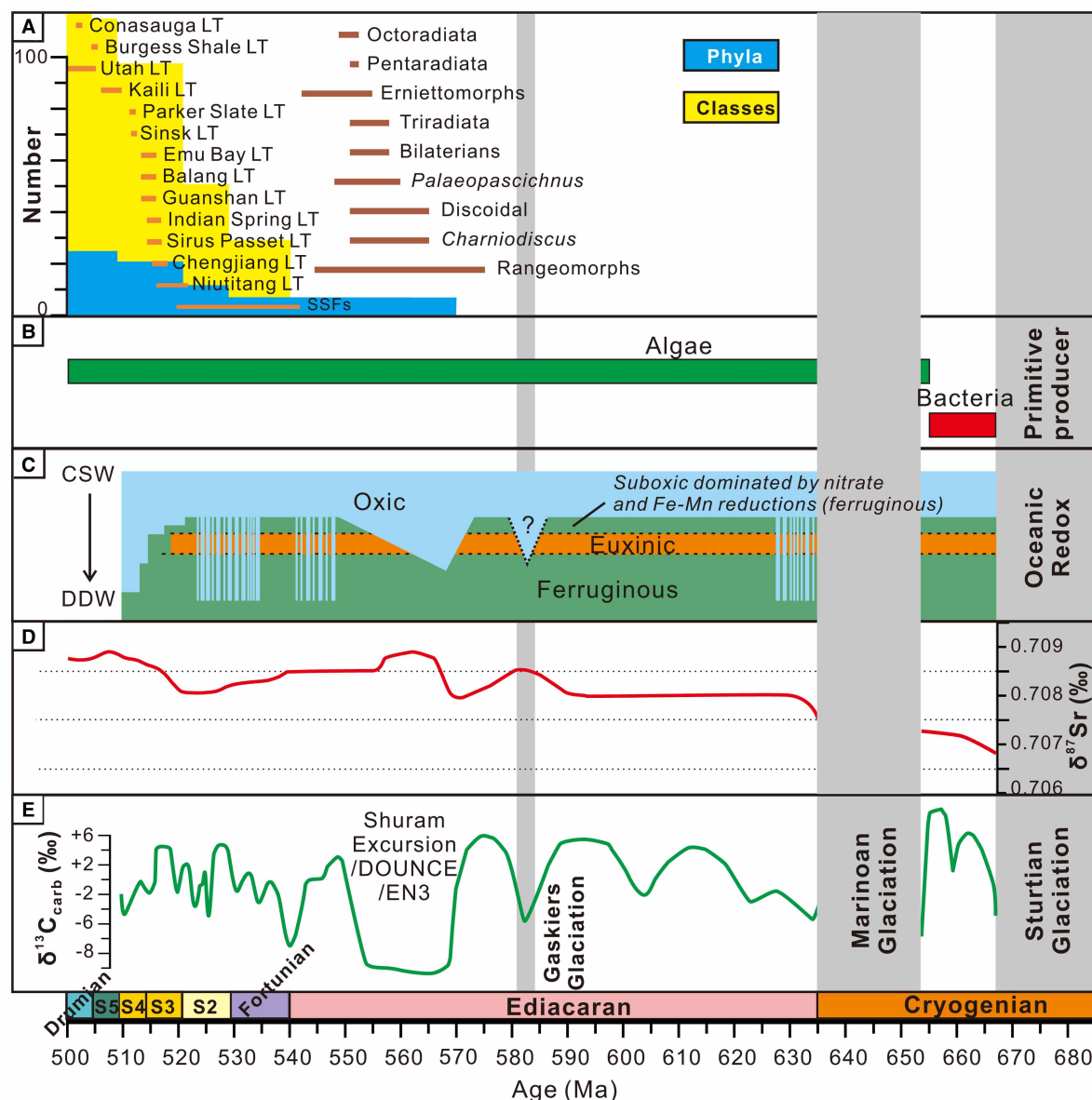


Figure 1. Timeline of biological and environmental changes spanning the late Cryogenian, Ediacaran, and early Cambrian periods.

(A) Important fossil records [3,79] and number of phyla and classes globally [1], **(B)** evolution of the main primitive producer in the ocean [76], **(C)** a new picture of marine redox evolution documented in this review; see the text for details. The dynamic shelf oxygenations are mainly based on insights from refs [9,10,27,28,31,44,49,54,56–60]. **(D)** Strontium and **(E)** carbonate-carbon isotope ($\delta^{13}\text{C}_{\text{carb}}$) chemostratigraphy [80]. Abbreviations: LT, Lagerstätte; SSFs, small shelly fossils; CSW, coastal shallow water; DDW, distal deep water; S2 (to S5) = Stages 2 (to 5).

bioturbation. Taken together, the key inference is that O_2 levels and their dynamics profoundly shaped local ecosystems of early animals in the Ediacaran–early Cambrian oceans.

Other views on the relationship between early animals and O_2 have emerged. Johnston et al. [39] found persistently ferruginous environments for the fossiliferous Ediacaran strata of Wernecke Mountains, north-western Canada, and downplayed the relationship between early metazoan diversification and increasing O_2 levels in the Ediacaran. Ediacaran–early Cambrian metazoans preserved in reducing environments were also documented in rocks from Russia, Newfoundland and South China (e.g. [36,45,51–54]). Very recently, the

early Cambrian Chengjiang Biota, which represents the peak of the Cambrian Explosion, was similarly found to be preserved in local O₂-depleted environments [55]. These observations can be explained by either transportation of the buried animals from more hospitable settings [55], transient oxygenation of the anoxic waters [54,56–60], or tolerance to low O₂ environments for some of the early animals [18,19], although more test studies are needed. Importantly, all these possibilities link early animal ecosystems to at least local O₂ conditions.

Dynamic shelf oxygenation and coupled animal diversification

Many past efforts have sought to find evidence for global scale ocean oxygenation during the Ediacaran and early Cambrian. While selenium, sulfur, and molybdenum isotope records suggest somewhat progressive oceanic oxygenation since the onset of the Ediacaran at ~635 Ma [8,61–63], other studies suggest multiple episodes of global marine oxygenations — perhaps against a backdrop of still mostly low O₂ conditions in the oceans. For example, Sahoo et al. [7] argued for global marine oxygenation at ~632 Ma based on modern levels of enrichment for redox-sensitive trace elements (RSTEs) and strongly negative sulfur isotope ($\delta^{34}\text{S}$) values in the basal Doushantuo Formation, South China. However, this ~632 Ma oxygenation was recently challenged based on muted enrichments of RSTEs in time-equivalent strata of the Sheepbed Formation, north-west Canada [64]. Other global oxygenation events have been also hypothesized, including one at ~580 Ma based on the global distribution of marine red beds [65] and local patterns of iron speciation [51], at ~560 Ma as expressed in Mo and U abundances and their isotopic signatures [26,29,66], and at ~520 Ma based on global Mo isotope records [8].

Increasing evidence suggests that the Ediacaran-to-early Cambrian interval was dominated by dynamic shelf oxygenation with expanding oxic surface waters (Figure 1C). For example, Sahoo et al. [27] and Gregory et al. [67] argued for multiple oceanic oxygenation events within a framework of predominantly anoxic global Ediacaran–early Cambrian oceans. These putative events are expressed in pulsed enrichments of RSTEs in ~635–520-Ma-old anoxic shales. Additional studies have also suggested transient oxygenation during the Ediacaran and early Cambrian. Shi et al. [10] looked at sulfur cycling during the famous DOUNCE (Doushantuo negative carbon isotope excursion) [also known as the EN3 (Ediacaran negative excursion 3) or the Shuram event] (Figure 1E) recorded in the Ediacaran Doushantuo Formation (South China). The DOUNCE/EN3/Shuram event is marked by a major negative excursion in carbonate carbon isotope data ($\delta^{13}\text{C}_{\text{carb}}$; down to –12‰) and has been attributed to significant atmospheric–oceanic oxygenation between ~580 and 550 Ma [68]. An important finding of the Shi et al. [10] study is that concentrations of surface seawater sulphate increased toward the peak of the DOUNCE in association with a large proximal-to-distal gradient across the South China Basin, providing direct evidence for the oxidation of surface shelf waters during the DOUNCE. These data are consistent with the oxygenation suggested by elevated iodate concentrations in shallow marine carbonates during this period [31]. Most importantly, the shelf oxygenation during the DOUNCE apparently corresponded to global diversification among relatively large, more complex, and more active animals during the late Ediacaran (Figure 1A).

Dynamic shelf oxygenation was also probably expressed on very short timescales. For example, Cheng et al. [58] looked at paleoredox conditions for sponge-bearing black shales of the lower Cambrian Hetang Formation (~535–521 Ma), Lantian, South China, using multiple geochemical proxies. The integrated dataset points to frequent transient deeper-water oxygenation on thousand-year timescales within the early Cambrian anoxic marginal basin, which led to colonization of the seafloor by sponges. Because sponges have been similarly reported from lower Cambrian black shales in Siberia and Greenland, among other locations (summarized in ref. [69]), transient shelf oxygenation may have been a global process. Similar events may have occurred during the early Ediacaran (~632 Ma) and late Ediacaran (~550–541 Ma) and may specifically have contributed to the development of the early Ediacaran Lantian Biota [57,59,60] and the late Ediacaran Nama Biota [49].

Transient oxygenation on the shelf may have given way to persistent shelf oxygenation during Cambrian Ages 3 and 4 (Figure 1C). Li et al. [28] extended the findings of Jin et al. [9] from Cambrian Stages 2 and 3 to the end of Stage 4 (~509 Ma), yielding a clear redox picture of the early Cambrian Yangtze Platform. Mid-depth anoxic waters during Age 2 gradually transitioned to stably oxic waters by Age 4 via a persistent expansion of surface oxic waters from shallow to deep beginning in Age 3 (~521 Ma). It is not known how long stable oxygenation lasted on the shelf, but anoxic shelves returned at least transiently by the ~499-Ma-old

Steptoean Positive Carbon Isotope Excursion (SPICE) [70]. Persistent shelf oxygenation during Ages 3 and 4 was also found to be temporally coincident with metazoan diversification and ecological expansion in South China, including regional replacement of small shelly faunas and sponge-dominated communities (Fortunian and Age 2) by more complex arthropod- and echinoderm-rich biotas (Ages 3 and 4) and a corresponding global increase in diversity of basic metazoan body plans and preservation of complex biota (Figure 1A). Furthermore, gradual expansion of complex arthropod-dominated biotas from shallow shelves to lower-slope facies and invasion of deeper settings by sponges, echinoderms, and trilobites provide strong evidence for O₂-level controls on the evolution of early animals (see Figure 2 in [28]).

Other studies have painted a different picture. Sperling et al. [24] compiled iron proxy data through the interval of interest and argued for a persistence of low marine oxygenation during the Ediacaran and Cambrian. Similarly, a recent study of ratios of Fe³⁺ to total Fe in hydrothermally altered basalts formed in ocean basins suggests that the global deep ocean was not persistently oxygenated until the Devonian [35]. Importantly, however, both sets of results may not be incompatible with episodes of oxygenation, particularly if expressed primarily in shelf surface waters. Unlike the enrichment patterns for RSTEs, iron speciation and the basalt data constrain only local conditions and may be biased toward deeper, anoxic settings. It is possible therefore that those data correctly reveal the backdrop of mostly low O₂, particularly in the deep ocean, but miss the dynamics of transient shelf oxygenation captured in the global perspectives offered by RSTEs. Future research should explore the sensitivity of patterns in RSTEs to the complexities of redox stratification in the ancient oceans and the critical controlling factors, including the roles of euxinia at intermediate water depths and patterns of organic matter production and burial on ocean margins.

Mechanisms for dynamic shelf oxygenation

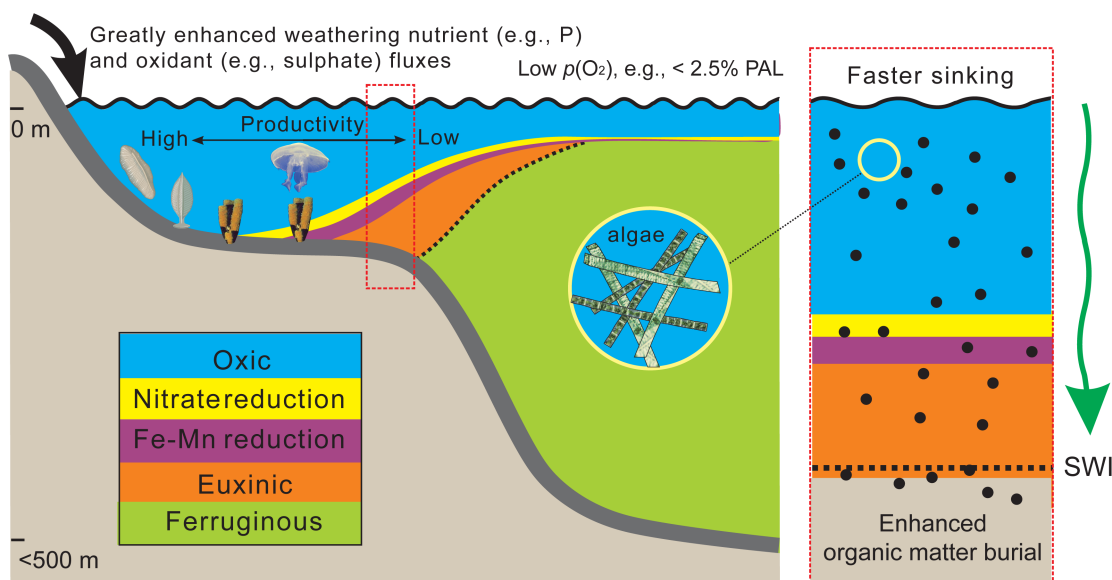
Dynamic shelf oxygenation of Ediacaran and early Cambrian oceans probably reflects the transitional status between the dominantly anoxic conditions of earlier oceans and the oxic conditions that prevailed in later Phanerozoic oceans [2,25,35,71]. Within this framework, for example, records of transient local shelf oxygenation on thousand-year timescales could reflect bottom-hugging turbidites and density flows that transferred O₂ to deeper waters [58] — rather than reflecting a breakdown of fundamental stratification during the Ediacaran and early Cambrian.

Proposed mechanisms for transient shelf oxygenation between ~580 and ~550 Ma carry extra weight because they have implications for the contemporaneous DOUNCE/EN3/Shuram event (Figure 1E) and associated diversification of the Ediacaran Biota (Figure 1A) [10]. Because the DOUNCE/EN3/Shuram event was accompanied globally by increased ⁸⁷Sr/⁸⁶Sr ratios (Figure 1D) and coastal concentrations of seawater sulphate [10], we can surmise that elevated continental weathering contributed — perhaps via global tectonic activity associated with microcontinent collisions that stitched together Gondwana during the middle Ediacaran [72]. Two factors, in particular, may have contributed (Figure 2A). First, if mid-Ediacaran atmospheric O₂ levels were low (e.g. <2.5% of the PAL), local marine primary productivity (i.e. photosynthetic O₂ release) would have controlled the dissolved O₂ concentrations of the surface oceans [73]. Under such conditions, elevated continental weathering would deliver high fluxes of nutrients (e.g. P) and oxidants (e.g. sulphate) to coastal oceans. The former would stimulate shelf oxygenation via increased productivity [72]. Second, recent studies suggest a fundamental shift in the P cycle at ~800–635 Ma [74,75], which may have triggered a rise in algal contributions to marine ecosystems (Figure 1B) [76]. Algae produce relatively large organic particulates, favoring rapid sinking rates, enhanced burial, and O₂ accumulation. It is also likely that sponges contributed to the oxygenation by filtering out reduced carbon from the water column that would otherwise serve as an O₂ sink [12]. We can imagine, therefore, that eukaryotic diversification, including the emergence of animals stimulated by an independent rise in O₂, could have contributed to a further increase through positive feedbacks.

Persistent shelf oxygenation between ~521 and ~510 Ma was probably related to higher atmospheric O₂ levels (perhaps >10–25% PAL) as required for complex Cambrian ecosystems (Figure 1A) [23,77]. Greater organic burial (e.g. [78]) linked to faster sinking of organic particulates may have driven the increases. An additional and related consequence would have been an enhanced biological pump in early Cambrian oceans [12].

Under higher atmospheric O₂ levels, dissolved O₂ concentrations in the surface ocean are controlled principally by the atmosphere, as suggested by the biogeochemical modeling of Reinhard et al. [73]. Furthermore, rapid evolution of predatory animals after 521 Ma may have played a role. Predation can result in packaging of low-trophic level organic matter into larger fecal pellets and thus accelerated organic sinking, thus minimizing O₂ consumption via decay in the water column (Figure 2B) [11]. Another positive feedback relates to the

A ca. 580–550 Ma (Significant transient shelf oxygenation)



B ca. 521–509 Ma (Persistent shelf oxygenation)

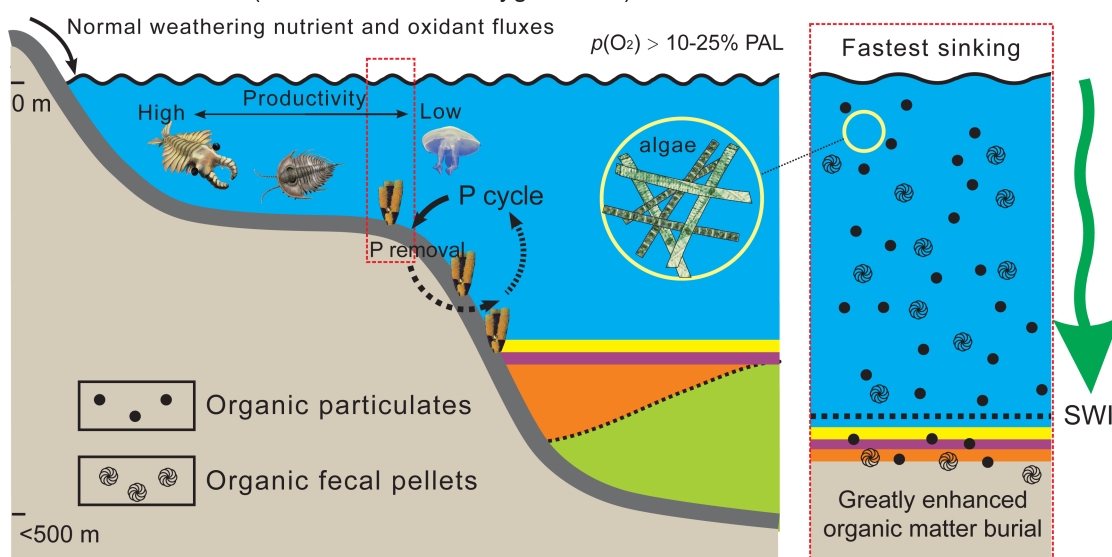


Figure 2. Schematic representations of possible mechanisms for dynamic shelf oxygenation during the Ediacaran–early Cambrian oceans.

(A) Mechanisms for transient shelf oxygenation during ~580–550 Ma. Greatly enhanced weathering nutrient and oxidant fluxes under low atmospheric O_2 levels and faster sinking of bigger organic particles due to the rise of algae and filter-feeding animals together probably contributed to this significant shelf oxygenation. The $p(O_2)$ of <2.5% PAL is a modeling threshold value under which the distribution of surface ocean O_2 is controlled principally by local productivity [73]. (B) Mechanisms for persistent shelf oxygenation during ~521–509 Ma. Persistently increasing atmospheric O_2 levels and the fastest sinking of large fecal pellets due to the rise of predatory animals together probably contributed to this persistent shelf oxygenation. The $p(O_2)$ of >10–25% PAL is a minimum value required by the more complex Cambrian animals [23,77]. See the main text for detailed explanations. Abbreviations: SWI, sediment–water interface. Note: redox zones are not in scale exactly.

P cycle in shelf areas: persistent oxygenation of bottom waters on shelves would increase P removal into sediments, in turn decreasing local productivity and O₂ demand and contributing to local water column oxygenation (Figure 2B) [12].

Conclusions and future work

A recent wave of marine redox studies, particularly those focused on fossil-bearing stratigraphic sections in South China, has revealed a complex spatiotemporal landscape of marine oxygenation within the context of coeval animal evolution during the Ediacaran (635–541 Ma) and early Cambrian (541–510 Ma). This work exposes patterns of high spatial redox heterogeneity and dynamic shelf oxygenation, despite the long persistence of a dominantly anoxic deep ocean — along with spatiotemporal coupling of animal evolution. Early transient events of shelf oxygenation probably gave way to a persistent oxygenation during early Cambrian Ages 3 and 4, which we can attribute to substantially elevated atmospheric O₂ levels and positive feedbacks stemming from the appearance of widespread predatory animals. Taken together, our review presents the details of an admittedly end-member view — specifically, a complex coevolution between increasing O₂ levels and early diversification of animals during a critical period in Earth history. Beyond local controls, we assert that patterns of animal innovation and perhaps extinction were deeply affected by changing environments on a global scale, while acknowledging that animals, through positive feedbacks, may have furthered the process of biospheric oxygenation.

Despite the long-standing debate about animals and O₂, we can all agree that much remains to be done and that future work should focus, at high spatiotemporal resolution, on the best possible records of evolving shallow marine oxygenation and coeval patterns of animal diversification and ecosystem structure and dynamics with better dating and stratigraphic correlation.

Summary

- A recent wave of marine redox studies revealed high spatial redox heterogeneity and dynamic shelf oxygenation along with spatiotemporal coupling of animal evolution in Ediacaran and early Cambrian.
- Dynamic shelf oxygenation can be attributed to a complex interplay among the evolving atmosphere, continents, oceans, and biosphere during the Ediacaran and early Cambrian.
- Our review supports the idea of a complex coevolution between increasing O₂ levels and early diversification of animals, although additional work is required to fully delineate this coupling and the mechanistic underpinnings.

Abbreviations

DOUNCE, Doushantuo negative carbon isotope excursion; EN3, Ediacaran negative excursion 3; Ma, million years ago; O₂, oxygen; PAL, present atmospheric level; RSTEs, redox-sensitive trace elements.

Author Contribution

C.L. designed and led the writing of this review. C.L., M.C., M.Z., and T.W.L. wrote the paper.

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Competing Interests

The Authors declare that there are no competing interests associated with the manuscript.

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