Deep water Oxygenation in the later Ediacaran oceans (580-538 Ma) and links to emergence and diversification of Ediacaran macrobiota-- A Report submitted as the examined component of the Project Module SXG390

Name: Esther Portela Miranda

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OU Personal Identifier:

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Contents

Abstract

The upper half of the Ediacaran is a key period in evolutionary history. Larger, more complex organisms appeared and diversified, became mobile and built the earliest reefs. This has been linked to increasing oxygen in the oceans. This paper reviews recent literature to examine geochemical evidence for or against deep water oxygenation and how this might have impacted the Avalon, White Sea and Nama assemblages of biota. Understanding the links between ocean chemistry and biota is important for our understanding of evolutionary mechanisms, the impacts of environmental change and search for life on other planets. Indirect oxygenation proxies such as iron speciation, redox sensitive element (RSE) and metal isotopes offer conflicting results. The literature identifies periods of oxygenation pulses termed oceanic oxygenation events (OOEs) but also argues there is a lack of evidence for these. All proxies have associated limitations and uncertainties, and new proxies are being developed with an aim of resolving conflicting data. The timing of developments in the Ediacaran biota can be associated with proposed oxygenation events and there are reasons why increased oxygenation would be beneficial to organisms. However, given there is also evidence against oxygenation, other explanations as to how biota could have survived in low oxygen environments and what triggered their increasing complexity are proposed. The review found a need to resolve conflicts in the data and address gaps in knowledge before links between ocean chemistry and biota can be claimed with more certainty.

(240 words)

Chapter 1 Introduction

1.1 Ediacaran Macrobiota

The Ediacaran Period (635-538 Ma) is divided by the Gaskiers glaciation at 580 Ma (Xiao and Narbonne, 2020). It is a key period in evolutionary history, particularly the upper half (Wei *et al*. 2023), when there is a surge and diversification of macroscopic organisms, which were all benthic (living on or close to the sea floor). These have been placed in three broad fossil groups, called assemblages. The fossil Avalon, White Sea and Nama assemblages represent innovations such as complex multicellularity, mobility and calcification respectively (Xiao and Narbonne, 2020).

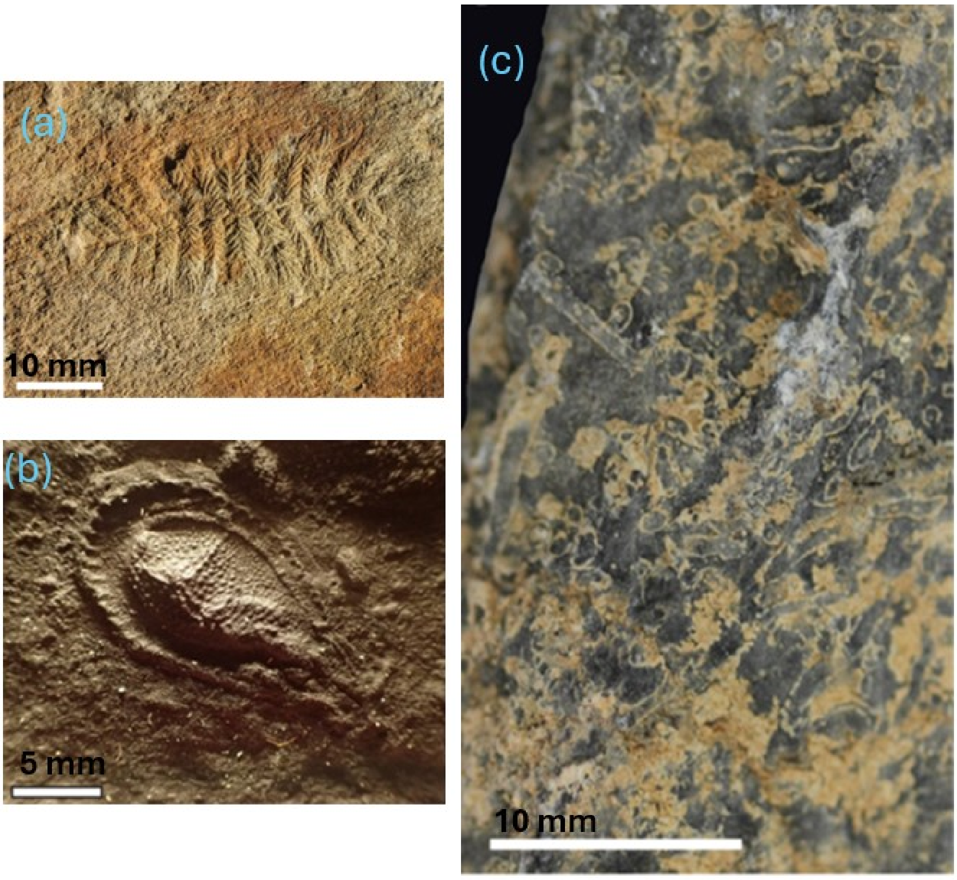

Figure 1: Ediacaran biota. (a) Fractofusus (Avalon), (b) Kimberella (White Sea), (c) Cloudina (Nama). Modified from Dunn and Liu (2017)

The Avalon assemblage is characterized by soft bodied organisms that were anchored to the sea floor and had a frondlike shape like Fractofusus (Figure 1a). Some organisms in the later White Sea assemblage like Kimberella (Figure 1b), have been found associated with trace fossils, animal characteristics of movement and feeding. In the Nama assemblage, there is a decline in species diversity but Cloudina, organisms with carbon carbonate skeletons which constructed reefs appeared. Figure 1c shows a group of these tubular organisms. (Dunn and Liu., 2017).

1.2 Paleoredox Reconstructions

Redox (oxidation-reduction) conditions are reconstructed to investigate links between ocean chemistry and the evolution of the biosphere (Poulton and Canfield, 2011). This in turn can inform investigations of life outside Earth (Lyons *et al*., 2021) and how marine organisms could be impacted by changes to the environment as a result of current climate change.

The terminology used in redox studies is defined in Table 1.

Redox terminology	
Redox term	**Definition**
Anoxic	No oxygen present
Euxinic	Anoxic, with free sulfide present
Ferruginous	Anoxic, no sulfide and high free iron
Suboxic	Extremely low oxygen at the boundary with anoxia
Oxic	Similar to the modern surface ocean

Table 1: Definition of redox terminology (Cole et al., 2020)

It is well established that in the Neoproterozoic there was a shallow layer of oxygenated (from atmospheric diffusion) top water, with euxinic or ferruginous conditions underneath. The appearance and evolution of the Ediacaran biota has been linked to an increase in oxygen of enough magnitude to oxygenate deep waters (subsurface waters from shelf to abyssal plains) (Li *et al*., 2020).

As direct measurements of oxygen levels are not possible to obtain for deep Earth history, redox is reconstructed using indirect proxy methods. Oceanic redox conditions can affect the abundances of certain minerals or elements and isotopic ratios, which can be measured from carbonate sediments and shales or mudstones. Redox conditions can then be inferred from these values. Local proxies provide information about conditions at a specific locality. Global proxies suggest the mean state of the ocean (Sperling *et al*., 2022). Local conditions need to be independently assessed before a global proxy can be applied and interpreted.

1.2.1 Redox Proxies

Iron speciation is the process of obtaining the relative proportion of iron mineral species in ancient sediments. (Yuan *et al*., 2023). Highly reactive iron normalised to total iron in sediments (Fe_{HR}/Fe_T), indicates whether these were deposited under an anoxic or oxic body of water. (Miller *et al*., 2017).

RSE (uranium, molybdenum, vanadium and chromium) are removed from the water column in reducing environments. When a low proportion of the ocean floor is reducing, the concentrations of RSE are high, reflecting higher concentrations in the sediment and indicating an oxygenated water column (Miller *et al*., 2017).

Uranium, molybdenum, thallium and vanadium isotopes are global proxies which can be used to resolve discrepancies derived from iron speciation and RSE studies. These metals have isotopes which occur at different redox states. These isotope ratios (expressed as $\delta^{238}U$, $\delta^{98}Mo$, $\varepsilon^{205}Tl$, $\delta^{51}V$) are recorded in sedimentary rocks and can provide information on oceanic redox conditions at the time of sediment deposition (Neilsen, 2020).

1.3 Objectives

1. Outline how deep oceanic redox conditions are investigated in past environments and how this is relevant for our understanding of evolutionary developments in Ediacaran macrobiota.

2. Evaluate whether proxies for oceanic redox conditions in the mid-late Ediacaran support or not increased deep water oxygenation.

3. Asses proposed links between oceanic oxygenation and impact on the evolution of Ediacaran macrobiota based on temporal correlations between redox conditions and biotic assemblage turnover and evolutionary events.

1.4 Methods

Most literature for the research was obtained through searches using the Open University library catalogue. Google scholar was also used as well as journal references. Sources were evaluated for credibility and relevance.

Chapter 2

Geochemical Evidence for and Against Widespread Oceanic Oxygenation

This section reviews the literature that investigates Ediacaran redox conditions using iron speciation, redox sensitive element (RSE) and isotope proxies.

2.1 Iron Speciation and Redox Sensitive Elements

Iron speciation data from Newfoundland, an Avalon assemblage fossil bearing region, supports deep water oxygenation commencing at around ~580 Ma and remaining stable for at least 15 million years (Canfield *et al*., (2007; 2008). However, because of a return to anoxic conditions after this and evidence for ferruginous anoxic oceans in other locations, conditions appear to be fluctuating and heterogenous (Canfield *et al.,* 2008). This is demonstrated by the lack of a coeval oxygenation signal in northwestern Canada (Johnston *et al*., 2013), which also contains Avalon assemblage fossils.

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Figure 2.1: Iron geochemical data showing how oxygenation does not increase significantly in the Ediacaran. Modified from Sperling *et al*., (2015)

Iron speciation is limited to offering information about a specific location and time (Canfield *et al*., 2008). To study conditions on a global scale, Sperling *et al*. (2015), apply statistical analysis to a large iron-based dataset. This highly influential work finds no statistically significant oxygenation signal. Time binned (grouped data into time intervals for analysis) iron data, however, would require a large change in global oxygen for a statistically significant signal. Therefore, their study does not rule out a small increase in oxygen.

Despite the strong evidence against oxygenation from Sperling *et al.* (2015), RSE data from South China indicates widespread oxygenation between 560-551 Ma (Kendall *et al.,* 2015) and RSE enrichments at ~635 Ma, ~580 Ma, and ~560 Ma, interpreted as high magnitude oxic pulses (Sahoo *et al.,* 2016). They are the first to record multiple oceanic oxygenation events (OOEs) in a single stratigraphic succession (Figure 2.2) providing evidence for large shifts in redox conditions.

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Figure 2.2: Geochemical profiles of strata from the Wuhe section, South China. OOEs (A, B, C, D) are highlighted and correspond with episodes of RSE enrichments (Mo, V, U, Cr, Re). Figure from Sahoo *et al.* (2016).

Miller *et al*. (2017), test the OOE hypothesis using a high-resolution dataset from northwest Canada and find no RSE enrichments, in contrast with South China sites. Direct comparisons between the two localities are challenging because of the poor temporal constraints, the condensed nature of sediments in South China and differing local redox environments, being ferruginous in Canadian sites, euxinic in South China (Miller *et al*., 2017).

In Western Brazil, Caxito *et al.* (2024) do not find iron speciation or an RSE signal for deep ocean oxygenation conditions from 555-541 Ma. This challenges the proposal for oxygenation between 560-551 (Kendall *et al*., 2015).

2.2 Isotope Proxies

Besides RSE enrichments, Kendall *et al*. (2015) also finds that increased δ^{238}U values indicate a period of widespread oxygenation. Increased δ^{238}U values found in

South China, Siberia and the USA were also found to correlate with negative carbon isotope values, representing the Shuram Excursion (SE) (Zhang *et al*., 2019). The SE is the largest negative carbon isotope anomaly in Earth's history, reflecting a perturbation in the carbon cycle. Mechanisms have been proposed to explain it that would involve the oxidation of a large dissolved organic carbon pool in the oceans, meaning oceans would be substantially oxic at the time (Fike *et. al*., 2006). Zhang *et al*. (2019) suggest that if the SE occurred at around 580 Ma, it would support oxygenation after the Gaskiers glaciation (Canfield *et al*., 2007), while a 560 Ma occurrence would support the findings of Kendall *et al.* (2015). However, recent studies proposed that the SE started later than 580 Ma and ended before 560 Ma (Rooney *et al*., 2020).

The correlation of increased δ^{238}U values with the SE is significant because of the hypothesized link between the SE and oxygenation (Grotzinger *et al*., 2011). But in ferruginous conditions uranium isotopic fractionation may not distinguish between suboxic or oxic conditions and therefore higher δ^{238}U may record a shift from a euxinic to ferruginous ocean instead of widespread oxygenation (Gong et al.,2023).

Molybdenum isotope proxies have yielded inconclusive results. High δ^{98}Mo values found by Kendall *et al*. (2015) are in line with their uranium and RSE data, reflecting oxygenation between 560-551 Ma. But low δ^{98}Mo values from coeval shales in the Czech Republic (Kurtzweil *et al*., 2015) contradict this. Kendall *et al*. (2015) also found negative δ^{98}Mo values which can result from local reduction processes associated with locally enhanced oxygenation (Ostrander *et al*., 2019). These were also found by Ostrander et al. (2019) when they analysed the same samples as Sahoo *et al*. (2016) for δ^{98}Mo. These occurred at the times of proposed OOE's, indicating local processes such as fluctuations in sea level and basin connectivity could be linked to OOEs. But coeval data from a new section in South China identified 3 OOEs with no associated negative δ^{98}Mo values. Here they increase at the time of RSE enrichment suggesting global oxygenation. However, they acknowledge local processes may also affect proxies, with local factors enhancing the signal for a global event (Yuan *et al*., 2023).

Despite new data from South China supporting an OOE hypothesis, the absence of pronounced RSE enrichments from contemporaneous northwestern Canada sediments presents a problem. Thallium isotopes (ε^{205}Tl) have been used to compare these locations because the proxy can be applied to sediments deposited under ferruginous or euxinic conditions (Ostrander *et al.,* 2020). A signal for oxygenation at ~580 Ma was found only in samples from China. Importantly, no increased oxygenation was detected at ~560 Ma, in contrast to other studies (Kendall *et al*., 2015; Sahoo *et al*., 2016; Yuan *et al*., 2023). Compilations of ε^{205}Tl data show near crustal levels of ε^{205}Tl, (indicating low oxygenation) throughout the mid Ediacaran (Figure 2.3), challenging OOE hypotheses. Additionally, oxygenation was not detected in Oman successions deposited during the SE, putting into question the conclusions derived from δ^{238}U studies and mechanisms for the SE. (Ostrander *et al*., 2023).

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Figure 2.3: ε^{205}Tl values from Canada (blue), Oman (orange), and South China (purple) plotted in comparison to crustal inputs and modern seawater. Modified from Ostrander *et al*., (2023).

Fan *et al*., (2021) apply for the first time a δ^{51}V proxy to previously studied south China sections from 567-560 Ma (previously dated 560-551 Ma) and their data supports a widely euxinic ocean. Building on this, Wei *et al*. (2023) carries out further work in South China. In the older samples (560-553 Ma), their δ^{51}V data is in agreement that conditions were euxinic, but they detect modern like oxygenation at 552-551 Ma, with near modern conditions extending into the Cambrian. This is in contrast to most studies describing anoxic conditions in the terminal Ediacaran. Co-variation between δ^{51}V and δ^{98}Mo values may validate vanadium isotope as a redox proxy (Wei *et al*., 2023). Vanadium isotopes, however, have only been studied in modern euxinic settings and how they are affected in ferruginous conditions is unknown.

2.3 Possible Causes for Oxygenation

Shifts in global tectonics and the diversification of algae, which are primary producers, may have altered the marine carbon cycle and triggered global environmental changes, including oxygenation (Lyons *et al.*, 2014). The carbon cycle is affected by several factors that trigger feedback relationships. Biological production will impact atmospheric composition which in turn will exert controls on organic matter production, burial and weathering. Biological productivity is affected by nutrient input (Berner, 2003).

Increased nutrient input may have occurred after the Gaskiers glaciation due to glacial melting. Enhanced continental weathering also increases marine nutrient concentrations (Canfield *et al.*, 2007) and higher sedimentation rates would increase organic matter burial. These processes could have been involved in potential oxygen increases later in the Ediacaran, triggered by tectonic uplift and erosion caused by the formation of Gondwana (Kurtzweil *et al.*, 2015).

In the Ediacaran there were a series of carbon cycle perturbations, including the SE. Carbon isotopes are used to measure carbon burial fluxes. If the carbon cycle was not in a steady state isotopes significantly increase (positive isotope excursion) or decrease (negative carbon isotope excursion) (Grotzinger *et al.*, 2011).

Although the SE has been attributed to diagenetic processes there are multiple lines of evidence suggesting this is a global event which would be difficult to explain via diagenetic mechanisms (Gong *et al.*, 2023). Its large magnitude and duration, however, is also difficult to explain by known processes governing the carbon cycle. Mechanisms that caused the SE may have involved increased oxygenation (Fike *et. al.*, 2006) but this hypothesis does not explain the initial triggers for increased oxygen. The many unresolved questions related to the SE (Grotzinger *et al.*, 2011) make it very difficult to determine its relationship with oxygenation events.

Chapter 3

Links Between Redox Conditions and Biota

Most authors that argue for the existence of OOEs also argue that an increase in oxygenation was probably involved in triggering or at least enabling the development of the Ediacaran biota (Zhang *et al*., 2019; Sahoo *et al*., 2016) due to the concurrent timing with Ediacaran biological events. Given the uncertainties in oceanic oxygenation however, this belief is now questioned. The following section reviews the implications of proposed redox conditions at the timing of each major Ediacaran fossil assemblage.

3.1 Avalon Assemblage

Deep ocean oxygenation may have been present for at least 15 million years in the Avalon peninsula region of Newfoundland. This follows the Gaskiers glaciation and is correlated to fossils of the Avalon assemblage in the area. Sustained oxygenation could have allowed the development of these larger and more complex eukaryotes, since their metabolism would have required an ecosystem with greater oxygen (Canfield *et al*., 2007). However, in the Blueflower formation in Northwestern Canada, which also contains Avalon biota, there is no evidence of oxygenation (Johnston *et al*., 2013). The lack of a significant difference with the older non fossiliferous Sheepbed formation is interpreted as an indication that oxygenation was not critical for the appearance of larger biota. However, they suggest that a small change in oxygenation that cannot be detected by their proxies may have represented an important threshold for biota.

Global proxies indicate OOEs just before the appearance of the Avalon assemblage (Yuan *et al*., 2023, Sahoo *et al*., 2016,) at around 580 Ma. After a proposed OE at 635 Ma, diversification rates amongst microorganisms dropped greatly until 580 Ma. For Sahoo *et al*., (2016), this represents the ending a period of reducing conditions unfavourable for biota. If the SE occurred at this time, oxygenation could have been a driver for the emergence the Avalon assemblage (Zhang *et al*., 2019). Ostrander *et al*., (2020) also detect episodic oxygenation in South China samples but not in the Canadian Nadaleen Formation which hosts Avalon assemblage fossils. They believe the event had a short duration and may not have triggered the emergence of the Avalon biota. This is also a view shared by Fan *et al*., (2021), following the lack of evidence for oxygenation between 567-560 Ma. However, Avalon biota diversified between 574 and 564 Ma, which has been linked to the SE, following revised chronology (Yang *et al*., 2021).

If the deep ocean remained anoxic at this time, then an explanation as to how these organisms originated and thrived is needed since they inhabited exclusively deep-water environments. Fan *et al*., (2021) support a hypothesis that temperature was the main factor explaining the presence of Avalon biota in deep sea environments. Cooler deep-sea temperatures would increase tolerance to lower oxygen conditions Fan *et al*., (2021).

3.2 White Sea Assemblage

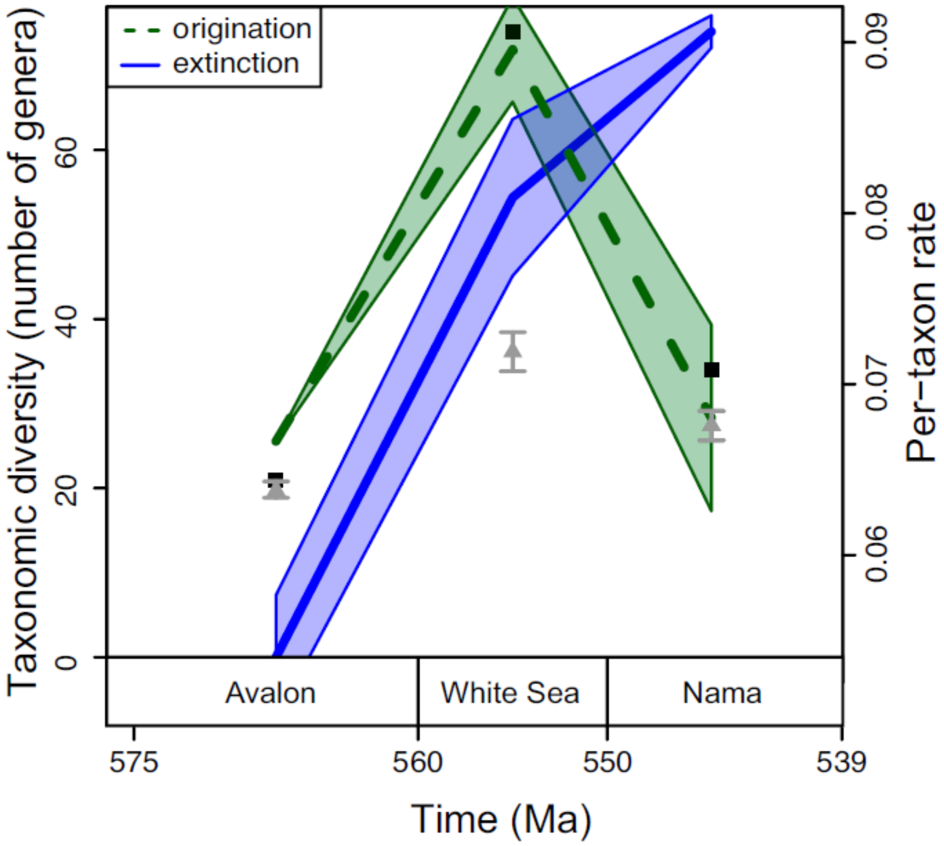

Figure 3: Diversity, origination and extinction rates of biotic assemblages. From Evans *et al*., (2022)

The White Sea assemblage has the greatest diversity of the Ediacaran with highest origination rates (Figure 3) and evidence for mobile organisms. This is also a period that has been associated extensively with oceanic oxygenation (Kendall *et al*. 2015, Sahoo *et al*. 2016; Zhang *et al*. 2019; Yuan *et al*., 2023). Mobile organisms would have had greater oxygen requirements (Lyons *et al*., 2021) and deep ocean oxygenation could have reduced the frequency of toxic anoxic water upwelling. Greater stability could have enabled greater diversification and complexity (Kurtzweil *et al*., 2015) The SE has been associated with this assemblage because of a proposed termination at around 551 Ma. However new age models place the SE between 574-567 Ma (Rooney *et al*., 2020). These also challenge the chronology of the South China region therefore, the relationship between the SE, proposed oxygenation events and biological turning points is more uncertain (Gong *et al*., 2023). The SE would more closely correlate with the Avalon assemblage, while the termination of the White Sea assemblage coincides with a separate carbon anomaly that may have followed the SE (Yang *et al*., 2021). Yuan *et al*. (2023) suggest that if oxygenation reached modern levels between 570-560 Ma, the White Sea assemblage could still have been impacted by this interval of oxygenation. The SE may also not be tied to greater oxygenation, because of uncertainties of what caused it and the significance of increased $\delta^{238}U$. Developments in the White Sea assemblage may have instead been driven by primary productivity as it can have effects on ecosystem structure and allow greater abundance and larger size of organisms (Gong *et al*., 2023).

Despite indications for biotic innovations occurring in line with OOEs, there is also abundant evidence against increased oxygenation and Ediacaran assemblages living in low deep-water oxygenation (Ostrander *et al*.,2020; 2023). This does not necessarily mean however that there was no impact on biota deriving from oxygenation changes. Proxies may not detect small changes in oxygen levels that might have been important for biota. In modern ocean areas of low oxygen, a small increase in oxygen can have a great impact on the ecosystem, affecting feeding efficiency, abundance and diversity (Sperling *et al*., 2015). Kurtzweil *et al*., (2015), suggest there could have been greater surface water oxygenation. The deep ocean may not have become more oxygenated because of limited exchange with surface ocean waters. This view is shared by Wei *et al*., (2023), who believe that despite evidence for a euxinic ocean at 560-553 Ma, an increasing oxygen trend determined from $\delta^{51}V$ suggests an increase in extent in oxygenation, which could have particularly affected shallow shelf settings and therefore been important for White Sea assemblage organisms.

3.3 Nama Assemblage

A significant drop in diversity occurred in the transition between the White Sea and Nama assemblages. This has been linked with a drop in oxygen levels following oxygenation during the White Sea assemblage and the termination of the SE (Zhang *et al*., 2019) or with the recently proposed carbon anomaly at 550 Ma (Evans *et al*., 2022). This is supported by the greater survival of organisms with morphologies which had a larger surface area relative to volume. With greater cell contact with seawater, they may have been better adapted to surviving in a low oxygen environment (Evans *et al*., 2022). These organisms are morphologically similar to Avalon type fossils. In late Ediacaran sediments (after 550 Ma) from Khatyspyt Formation in Siberia, these fossils are found associated with both local and global geochemical markers for anoxia. Therefore, these organisms were either tolerant to anoxia or there is not enough resolution in the geochemical data to distinguish oxygenated periods where organisms could have colonised the area (Cherry *et al*., 2022).

However, despite the lower diversity in the Nama assemblage, there was increased complexity and activity of ecosystems engineers (Evans *et al*., 2022). In the Tamego Formation in Brazil (555–541 Ma), there is fossil evidence of Nama Assemblage organisms living in shallow settings while the deep ocean was anoxic, meaning there was no requirement for fully oxygenated conditions for organisms to thrive (Caxito *et al*., 2023). This means calcifying organisms may not have needed widespread oxygenation but there were no bioturbators (organisms that can rework sediments) until fully oxic conditions in the younger Guaicurus Formation (<541), representing the Ediacaran-Cambrian transition.

Between 550 Ma and 540 Ma, most redox studies are in agreement that conditions were anoxic, but a recent vanadium isotope study, suggests otherwise. Wei *et al*., (2023) found indications of widespread oxygenation at 550 Ma and remaining close to modern values into the Cambrian. They therefore assert the role of oxygen in allowing this increased complexity.

Some ecological studies argue that organisms in the Nama assemblage were generalists, capable of surviving redox fluctuations at the terminal Ediacaran (Evans *et al*., 2022). However, a study by Eden *et al*., (2022) claims the opposite. They found that they were more specialist organisms, inhabiting specific environments. This reflects greater ecosystem complexity and an ecological development from the White Sea assemblage instead of a recovery from an extinction event. (Eden *et al*., 2022). This drop in diversity at around 550 Ma then, may be explained by mechanisms other than a transition from oxygenated to anoxic conditions. These indicate evolutionary dynamics that have been found in later Cambrian biota. (Eden *et al*., 2022). For Eden *et al*., (2022) the Nama represent a continuous development of complex ecosystem that carries on in the Cambrian while for Evans *et al*, (2022), challenging redox conditions led to preferential survival of low oxygen adapted organisms that could have survived into the Cambrian.

Chapter 4

Discussion

A review of the literature suggests that whether deep ocean oxygenation occurred during the later Ediacaran or not remains unresolved due to large gaps in knowledge and contradictions in the data. It is widely suggested though, that if widespread oxygenation did occur, anoxic conditions returned afterwards (Canfield *et al*., 2008; Sahoo *et al*., 2016).

Large shifts in redox conditions are supported by the finding of OOEs, however, evidence for these is problematic for various reasons. Local iron speciation studies find both oxic and anoxic conditions (Canfield *et al*., 2008; Johnston *et al*., 2013). Large scale statistical analysis of iron speciation data supports anoxia. But this method cannot detect small scale redox changes (Sperling *et al*., 2015).

There are discrepancies between global proxy results too. RSE and δ^{98}Mo results differ according to location. Local factors might be the reason, particularly for data from South China sites, where much data supporting OOEs comes from. Dating and stratigraphy are also uncertain for this locality. δ^{98}Mo data can only be obtained from sediments deposited in strongly euxinic local conditions and limits comparisons between sites with different redox conditions (Miller *et al*., 2017).

While iron speciation, RSE and δ^{98}Mo data differs between locations, Uranium isotope δ^{238}U values increase in multiple locations in the mid Ediacaran (Kendall *et al*.,2015, Zhang *et al*., 2019, Gong *et al*.,2023), providing the strongest evidence for oxygenation. These usually correlate with carbon isotope values and are linked to the SE. Since mechanisms of the SE are thought to involve large scale oceanic oxygenation (Fike *et al*., 2006), it reinforces the validity of the δ^{238}U data as an indicator of oxygenation. However, processes involved in the SE are still heavily debated, and there are alternative hypotheses that don't involve oxygenation (Grotzinger *et al*., 2011). Additionally, if the proxy cannot differentiate between globally suboxic and oxic conditions when the local environment is ferruginous, increases in δ^{238}U may not reflect large magnitude oxygenation (Gong *et al*., 2023).

Thallium isotope studies are in agreement against significant oxygenation for the mid Ediacaran (Ostrander *et al*., 2020; 2023). Vanadium isotope data supports these findings for at least part of the mid Ediacaran (Fan *et al*., 2021) but reveals signs of oxygenation in the later Ediacaran (Wei *et al*., 2023). This contradicts most studies, which suggest anoxic conditions at this time.

ε^{205}Tl and δ^{51}V proxies are still relatively new but may be key for resolving knowledge gaps. This is because the ε^{205}Tl proxy can be applied in both euxinic and ferruginous paleoenvironments, and the δ^{51}V proxy does not require fully anoxic local conditions. It can also offer higher temporal resolution which can be better applied to track coeval changes in biota (Ostrander *et al*., 2019; Wei e*t al*., 2023). However, δ^{51}V proxy has not been tested in modern ferruginous environments and is difficult to apply (Neilsen, 2020) and ε^{205}Tl can only be used in basins that were well connected to the global ocean (Ostrander *et al*., 2019).

Literature relates increasing oceanic oxygenation with the appearance of larger, more mobile and complex organisms, because they would have higher oxygen demands (Kurtzweil *et al*., 2015, Sahoo *et al*., 2016). Deep water oxygenation would also reduce toxic upwelling from euxinic conditions for organisms living in shallow settings, creating a more stable environment (Kurtzweil *et al*., 2015).

If widespread oxygenation did not occur, alternative explanations for biological innovations could be environmental drivers like temperature, nutrient availability (Kurtzweil *et al*., 2015) and primary productivity (Gong *et al*., 2023). Biota may have been adapted to lower oxygen environments (Fan *et al*.,2021; Evans *et al*., 2022). A small increase in oxygen could have meant surpassing an important threshold (Johnston *et al*., 2013; Sperling *et al*., 2015). This might have involved only surface waters but would have an impact on organisms living in shallow shelf settings (Wei *et al*., 2023, Caxito *et al*., 2023).

Some sites containing Avalon assembly fossils were locally oxic (Canfield *et al*., 2007) while others were not (Johnston *et al*., 2013). Globally, an OOE is proposed shortly before the appearance of the Avalon assemblage (Yuan *et al*., 2023; Sahoo et al., 2016,) which could potentially be explained by environmental changes after the Gaskiers glaciation (Canfield *et al*., 2007). In a low oxygen scenario, the existence of Avalon biota could be explained by morphological adaptations to lower oxygen conditions (Evans *et al*., 2022) with low deep ocean temperatures increasing low oxygen tolerance (Fan *et al*.,2021).

Oxygenation, the SE and the White Sea assemblage are commonly linked by the literature. It was the most diverse assemblage (Figure 3), with oxygen demanding mobile organisms. Concurrent oxygenation is widely supported (Kendall *et al*., 2015; Sahoo *et al*., 2016; Zhang *et al*., 2019; Yuan *et al*., 2023). But new proxy data also suggests anoxia (Ostrander et al., 2020; 2023). New chronostratigraphic models for the SE and strata in South China adds to the uncertainties derived from the interpretation of oxygenation proxies and the mechanisms of the SE (Gong *et al*., 2023). Since the White Sea biota lived in shallow environments, oxygenation of surface waters instead of widespread oxygenation might have key (Kurtzweil *et al*., 2015; Wei *et al*., 2023).

The date of ~551-550 Ma is associated with a significant loss of diversity and high extinction rates and the turnover from the White Sea to the Nama assemblage (Figure 3). This could have been caused by a transition from oxygenated to anoxic conditions. The magnitude of extinction and preferential survival of organisms with low oxygen adapted morphologies suggests this is the case (Evans *et al*., 2022). Evidence from geochemical proxies is strong against any significant oxygenation with no OOEs identified at this time and no local oxygenation at fossil bearing sites. The appearance of bioturbation is associated with later oxygenation at the Ediacaran-Cambrian transition (Cherry *et al*., 2022; Caxito *et al*., 2024). However, new $\delta^{51}V$ data proposes near modern oxygenation at around 550 Ma. Challenges are offered by ecological studies too, which argue that a catastrophic extinction event did not occur, and that the Nama assemblage represents a specialisation of organisms and greater ecosystem complexity (Eden *et al.*, 2022), a hypothesis that would align well with at least a partially oxygenated ocean at this time.

Chapter 5

Conclusions and Future Work

Literature supports either anoxic or fluctuating redox conditions in the mid-late Ediacaran. Distinguishing between these two scenarios is complicated by limitations and uncertainties of redox proxies. Iron speciation data compilations and thallium isotope studies mostly support no increased oxygenation while uranium isotope studies do, particularly during the Shuram Excursion. Redox Sensitive Element and molybdenum isotope studies support different scenarios depending on the locality.

Conflicting evidence may derive from proxy limitations which include not enough sensitivity to detect small scale changes, confounding local effects and a lack of understanding of their behaviour in ferruginous conditions. $\varepsilon^{205}Tl$ and $\delta^{51}V$ are key new proxies that may resolve some gaps in knowledge. There are also uncertainties about local processes operating in studied localities and chronostratigraphy. This is particularly relevant for data from South China, which is a key Ediacaran site.

If oxygenation events occurred, they were probably triggered by changes in the carbon cycle related to increased weathering from tectonic changes or post glacial processes. Relevant carbon anomalies like the SE are not fully understood.

There is evidence both for and against oxygenation at the time of all Ediacaran assemblages. Higher oxygen could have allowed larger more complex organisms and environmental stability but other environmental variables like temperature and nutrient input could also have triggered changes. Organisms could have developed low oxygen adaptations or benefited from increased oxygen in surface water only.

Some future work that could be done to address gaps and contradictions in knowledge could be gaining a better understanding of the behaviour of $\delta^{238}U$ and $\delta^{51}V$ under ferruginous conditions and the impact of local effects on data, particularly in relation to RSE and δ98Mo proxies. There could also be further development and application of the $\delta^{51}V$ proxy.

Continued work to determine the chronology, stratigraphic relationships and operating local processes in South China would benefit both paleoredox reconstructions and investigations relating to Ediacaran biota. Determining the triggers, mechanisms and chronology of the SE would resolve some relevant unknowns. Of importance would also be investigating whether increased surface water oxygenation instead of widespread oxygenation could have triggered key biotic changes and further ecological and biological studies to determine the needs of Ediacaran biota and reconstruct their environments.

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